

Predicting ecological consequences of marine top predator declines

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Recent studies document unprecedented declines in marine top predators that can initiate trophic cascades. Predicting the wider ecological consequences of these declines requires understanding how predators influence communities by inflicting mortality on prey and inducing behavioral modifications (risk effects). Both mechanisms are important in marine communities, and a sole focus on the effects of predator-inflicted mortality might severely underestimate the importance of predators. We outline direct and indirect consequences of marine predator declines and propose an integrated predictive framework that includes risk effects, which appear to be strongest for long-lived prey species and when resources are abundant. We conclude that marine predators should be managed for the maintenance of both density- and risk-driven ecological processes, and not demographic persistence alone.

Declines in marine top predators

Predators that occupy high trophic levels in marine habitats, including marine mammals, large teleosts and sharks, have been declining worldwide at a rapid pace [1–4]. Recent estimates suggest that populations of large sharks have declined regionally by 90% or more [3,5]. The status of large tuna, billfish and groundfish [2] and reef-associated predators in human-impacted areas [6] is equally dire. Although the magnitude of some declines is debated, few researchers doubt the generality of sweeping changes to the abundance of upper trophic levels in the oceans. Clearly, accurate prediction of the ecological consequences of these and potential future declines is critical for fisheries and ocean ecosystem management. Ecosystem models currently are the most common method for exploring the wider effects of declining upper trophic levels. These models, however, are driven by detailed system-specific data that might limit the generality of predictions and also preclude parameterization in data-poor situations (Box 1).

Given these concerns, is it possible to make generalized predictions about the likely responses of marine communities to the loss of top predators? Addressing this question requires a functional understanding of how top predators affect the dynamics of marine communities. Recent studies from diverse systems show that predators influence prey populations and communities by inflicting mortality on prey (direct predation) and inducing costly antipredator behavior by their prey (risk effects [7]). Studies in marine

systems involving upper trophic level predators, however, have largely failed to consider risk effects. Here we review studies of community rearrangements following marine top predator declines and of how marine predators influence their communities through direct predation and risk effects. Through this synthesis, we build the case that a framework integrating both direct predation and risk effects can achieve improved predictions on the ecological consequences of marine predator declines.

Marine communities change when top predators decline

Predicting the ecological consequences of reductions in top predators is, in essence, an inquiry into the importance of top-down processes. From groundbreaking work on rocky intertidal shores [8] to the documentation of the keystone role of sea otters in kelp forests [9] and studies of the indirect effects of bird predation [10], among many other examples, there is little doubt that predators have a fundamental influence on the structure and function of marine communities. Hence, widespread declines of large

Glossary

Behaviorally mediated indirect interaction: occurs when changes in the abundance of one species results in a change in the behavior of a second species (a risk effect) that in turn influences a third species.

Density-mediated indirect interaction: occurs when changes in the abundance of one species affect the density of another species through direct predation, which in turn changes densities of a third species.

Direct predation effect: effects of predator-inflicted mortality on prey populations.

Keystone species: a species that has an impact on community structure disproportionate to its abundance.

Megagrazers: large-bodied marine grazers (e.g. green turtles, dugongs and manatees).

Mesoconsumer: predators or herbivores in mid-trophic levels. These species are at risk of predation from top predators, and therefore transmit effects of top predators to lower trophic levels.

Predatory release: when reductions in the density of top predators causes a numerical increase of their prey.

Resource species: in the context of this review, a species that is eaten by mesoconsumers. Depending on the mesoconsumer, resource species are consumers at lower trophic levels (e.g. small teleosts) or primary producers (e.g. seagrasses).

Risk effect: changes in prey species (e.g. distribution, energy state, reproductive output) resulting from behavioral responses to the risk of predation.

State-dependent behavior: behavioral responses to extrinsic factors (e.g. background level of predation risk) that are assumed to maximize fitness in the context of the physiological (e.g. fat stores), environmental (e.g. resource availability) or other states of the organisms that influence residual reproductive value.

Trophic cascade: changes in the relative abundances of multiple species in an ecological community as a result of changes in abundance of one species. Trophic cascades ensue from both direct predation and risk effects of predators.

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Box 1. Modeling the ecosystem effects of top predators

Mass-balance models of ecosystems, such as Ecopath and Ecosim, have been used to assess the ecological consequences of declines in top marine predators (e.g. [58–60]). They focus on the flow of biomass among trophic groups, as determined by trophic efficiency, biomass and diet composition of functional groups. A recent comparative analysis of 34 Ecosim models, covering both coastal and open ocean systems, suggests that large sharks (primarily in the tropics and subtropics) and marine mammals (in temperate and subpolar areas) are the most commonly identified keystone species groups, each with a top rank in 18% of cases [60].

Although these models have proven very useful for the development of hypotheses [61], their assumptions that all energy is cycled within a system and that each species' diet is inflexible are not always supported [62,63]. Also, the detailed diet data required for parameterization are often lacking for marine top predators. Mass-balance models also have limited capacity to incorporate risk effects; they might, for instance, predict that observed declines in tuna and cetaceans should benefit pelagic seabird populations because of increased prey availability. In fact, the opposite is true – shared prey become available to birds when subsurface predators drive fish into surface waters [64].

Behavioral optimization theory could enhance the predictive power of current ecosystem models. These models quantify behavioral effects of predators as the fraction of resources that prey give up to optimize safety and foraging needs [20]. Thus, they can predict effects of predators on resource species mediated by both behavioral responses (e.g. habitat shifts) of, and direct predation on, mesoconsumers [65,66]. For example, recent work combining empirical data and theoretical modeling suggests that Pacific sleeper sharks exert strong risk effects on harbor seals in Prince William Sound, Alaska [34]. Most seals appeared to underutilize walleye pollock, which are found contiguously in deep strata where sharks are abundant, and to instead forage primarily in safer, shallower strata where Pacific herring are highly dispersed and therefore likely less profitable than walleye pollock despite their higher energy density [34]. Removal of sharks (see Figure 2) is predicted to indirectly increase seal predation on herring and decrease predation on pollock [66]. The strength of this behaviorally mediated indirect effect, however, might depend on overall resource supply and the energy state of seals [16] (Box 3).

predators across the world's oceans are expected to strongly influence smaller-bodied mesoconsumers and the species that are eaten by mesoconsumers (resource species). For example, research surveys on the US eastern seaboard conducted from 1970 to 2005 indicate rapid declines in the abundance of 11 species of large sharks and concurrent increases for 12 of 14 small elasmobranch mesoconsumers [5]. All large sharks in this system are known predators of small elasmobranchs, which suggests a causal link between these contrasting population trajectories [5]. Similarly, long-line surveys in the tropical Pacific documented up to 10-fold declines in catch rates of 12 large pelagic predators (tunas, billfishes and sharks) from 1950 to 2000 coincided with 10- to 100-fold increases in catches of pelagic stingrays (*Dasyatis violacea*) and other small-bodied mesoconsumers over the same timeframe [11]. These studies suggest that mesoconsumer communities can respond strongly to top predator declines, and that these effects play out over large spatial and temporal scales.

Although the consequences of top predator removal can vary across communities [12,13], an increasing number of studies are detecting large-scale cascading effects. For example, in the northwest Atlantic Ocean (Figure 1), catch rates of cownose rays *Rhinoptera bonasus* have increased

at 9% per year as large sharks have declined. Enclosure experiments show that exploding ray populations (now estimated to exceed 40 million individuals) can quickly eliminate bay scallop populations *Argopecten irradians* and might be responsible for regional declines in this important resource species [5]. This demonstrates that declines in top predators can impact several trophic levels and affect other fisheries. Similarly, the regional collapse of Canadian cod *Gadus morhua* stocks in the early 1990s led to large increases in small pelagic fishes (such as herring) and macroinvertebrates (such as shrimp and crab), which might have contributed to cascading shifts in copepod and even phytoplankton communities [14,15]. Cascading effects are also reported from reef habitats, where overfishing of large teleosts coincided with increases in coral-eating starfish and reductions in reef-building corals and coralline algae [16]. Finally, diet switching by killer whales from pinnipeds to sea otters in the Aleutian Islands appears to have reduced the sea otter populations, thereby releasing urchins from otter predation and ultimately causing the demise of kelp forests as a consequence of urchin overgrazing – a dramatic reversal of the trophic cascade that had previously maintained kelp forests in that region [17]. But what mechanisms drive mesoconsumer release and wider community rearrangement?

The importance of risk effects

Researchers of marine systems involving large-bodied predators often implicitly assume that trophic cascades occur via direct predation (so-called lethal effects) on mesoconsumers. Using this framework, the effects of predation could be fully quantified based on the diets, metabolic rates and abundances of predators and data on prey population dynamics [18]. Declines in top predator abundance should release mesoconsumers from predation and indirectly increase the mortality rate of resource species [5,19]. The loss of top predators is thus predicted to cause numerical increases in mesoconsumers and declines in resource species.

Beyond direct mortality, however, predators also strongly affect prey behaviors, such as foraging [20,21]. A large number of studies show that organisms can reduce predation risk through behavioral mechanisms [20,21]. For example, the planet's largest migration of biomass – the nightly upward movement of mesopelagic animals into surface waters and then back to deep strata – is driven by avoidance of visually orienting predators in productive surface waters during daylight [22]. Such risk effects [7] of predators might either initiate or enhance trophic cascades through behaviorally mediated indirect interactions [23–25] (Box 2).

Risk-induced cascades might be important when mesoconsumers are resource limited and must forgo foraging opportunities to manage predation risk. By lowering their foraging rates or shifting to safer but less profitable resources, mesoconsumers can incur a loss of reproductive output or recruitment [26,27] and alter the mortality rate of the resources they consume. Unlike indirect effects of predator-inflicted mortality, whereby lower densities of mesoconsumers increase the density of resource species, risk

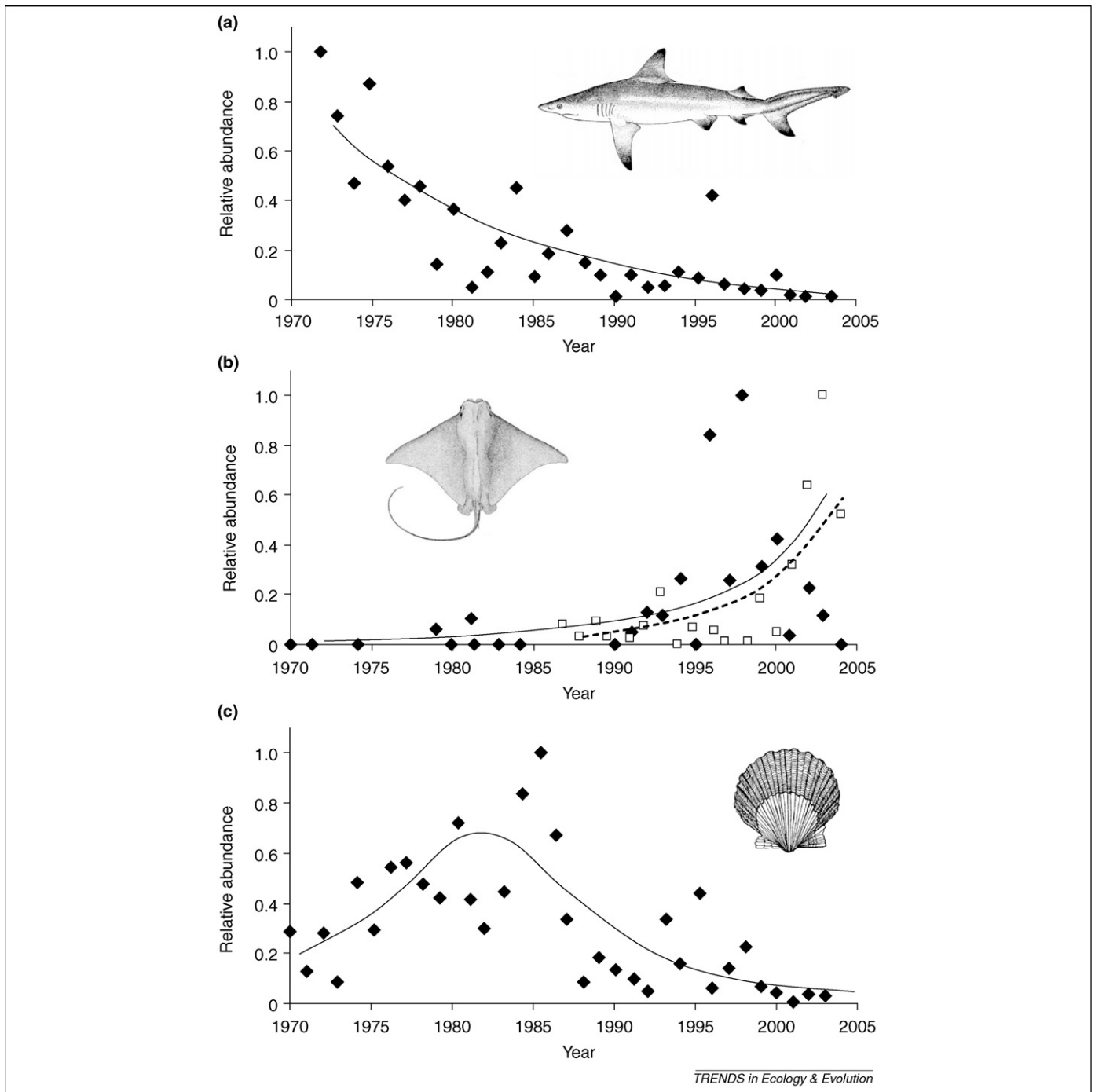


Figure 1. The removal of marine predators can result in cascading effects through communities. As (a) catch rates of large sharks, such as blacktip sharks (*Carcharhinus limbatus*), declined during research surveys along the east coast of the United States, (b) cownose rays began to increase, leading to eventual declines in (c) catches of North Carolina bay scallops (*Argopecten irradians*). Population densities are expressed as proportions of the observed time series maximum. Trend lines are best fits from generalized linear (a,b) or additive models (c). In (b), filled symbols and line denote Delaware Bay surveys, and open symbols and dashed line are Pamlico Sound, NC, surveys. Field experiments confirmed that scallop declines resulted from increased ray predation [5]. Note that the effect of top predator removal on rays and scallops would include both density effects (ray population increases) and possible risk effects such as increased foraging by rays gaining access to previously dangerous habitats. Redrawn from data in [5].

effects might mediate predator effects on resource species without influencing equilibrium population densities of mesoconsumers. This can occur when predation risk alters the intensity and spatiotemporal pattern of mesoconsumer exploitation of resource species without suppressing mesoconsumer populations (i.e. they are not limited by bottom-up forces). Thus, the numerical responses of mesoconsumers and resource species to top predator declines are the sum of direct predation (density-mediated) and risk (behaviorally

mediated) effects [28]. The relative importance of either mechanism varies from case to case, but a growing body of evidence suggests that behaviorally mediated indirect effects can be surprisingly strong [24,25,29–31]. For example, more than 90% of the indirect effect of toadfish (*Opsanus tau*) on juvenile oyster (*Crassostrea virginica*) survival is a result of mud crab (*Panopeus herbstii*) avoidance of toadfish (risk effects) rather than to direct predation on crabs [31].

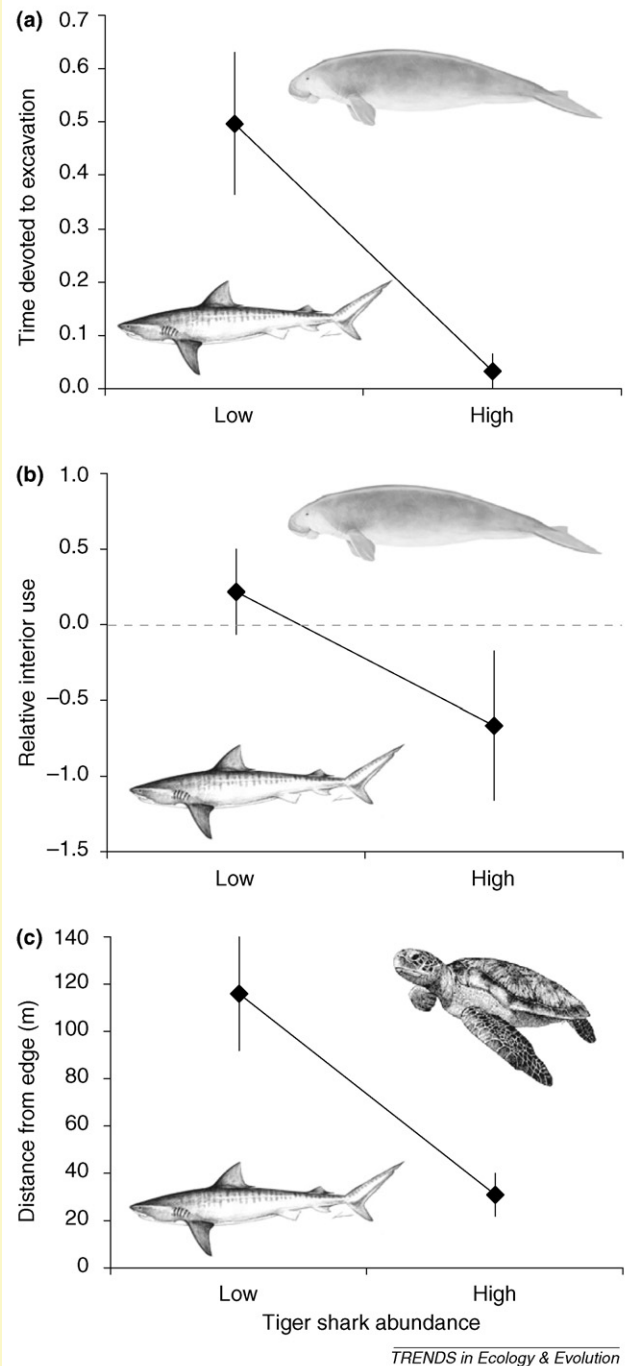
Box 2. Empirical assessments of risk effects

Predators can affect prey populations and community dynamics through direct predation (often called “lethal effects”) and by inducing costly antipredator responses such as shifts away from productive habitats and reduced foraging rates (risk effects [29]). Assessments of lethal effects have dominated the literature, but growing evidence suggests that the consequences of risk effects for prey populations and communities might be of equal or greater magnitude (e.g. [23–25,29]). The surprising strength of risk effects owes in part to their spatial scope; whereas lethal effects are localized within areas of overlap between predators and prey, risk effects can be transmitted widely by prey individuals that switch habitats to avoid danger [30]. Moreover, unlike lethal effects, risk effects are not attenuated by compensatory reproduction by survivors and typically are experienced simultaneously by many prey individuals for prolonged periods [67].

Initially, the importance of risk effects was suggested by mesocosm experiments that manipulated predation pressure and risk (see [7]). Recently, substantial risk effects have been documented in natural systems dominated by large vertebrates. For example, reduced rates of recruitment in elk (*Cervus elaphus*) following the reintroduction of wolves (*Canis lupus*) to Yellowstone National Park stem largely from risk effects [26]. Furthermore, wolf reintroduction shifted the spatial pattern of elk herbivory, increasing plant growth rates in riparian areas that elk avoid to minimize risk of predation [57].

Risk effects in marine habitats have been quantified as the amount of resources mesoconsumers will give up to reduce predation risk. Studies in Shark Bay, Australia assessed how tiger sharks influence distributions of large herbivores and mesoconsumers inside two replicated habitats, shallow banks (dangerous) and deep waters (safer), and two microhabitats, seagrass bank interiors (dangerous) and bank edges (safer) [35–40]. To determine risk effects, prey densities within zones are divided by food supply (i.e. seagrass or fish biomass) which would yield equivalent relative densities across zones if expectations of an ideal free distribution were met. Mesoconsumers generally match this prediction when sharks are absent. When sharks are seasonally abundant, deviations from matching food distributions can be used to index the amount of food being exchanged for safety [20]. Using this approach, prey species were found to distribute themselves in a predation-sensitive manner at multiple spatial scales. Risk effects explain these shifts significantly better than correlations with water temperature or other factors (Figure 1) [36–40].

Figure 1. Risk effects of tiger sharks on megagrazers in Shark Bay, Australia. Shifts in (a) foraging tactics and (b) microhabitat use by dugongs optimize trade-offs between risk from tiger sharks and resource intake [37,41]. (c) Green turtles in good body condition (assumed to indicate a good energy state) shift to safe microhabitats with nutrient-poor seagrass when sharks are common [40]. Error bars represent \pm SE. Relative use of microhabitats in (b) is calculated by dividing densities of dugongs in each habitat by the relative abundance of seagrass available in that habitat (Box 2).



Risk effects of marine top predators

The influence of marine top predators such as tuna, sharks and marine mammals on the behavior of mesoconsumers has not yet been evaluated comprehensively [32], and few studies measure the indirect community effects that might arise from these interactions. However, those studies that have done so suggest that risk effects likely are common and might be transmitted to lower trophic levels. For example, the presence of New Zealand fur seals *Arctocephalus forsteri* causes a temperate reef fish (morwong *Chelilodactylus nigripes*) to reduce foraging effort, leading to reduced grazing on turf algae [33]. Because morwong

cannot reduce predation risk by switching habitats [33], risk effects lead to reduced growth rates, amplifying the effects of direct predation on morwong. This should increase the cascading indirect effect of fur seals on algae. Similarly, harbor seals *Phoca vitulina* in Alaska appear to underutilize walleye pollock *Theragra chalcogramma* in deep strata because of risk from Pacific sleeper sharks *Somniosus pacificus* [34] and, theoretically, sharks might indirectly increase seal predation on near-surface fish [16] (Box 1).

More detailed studies of risk effects in marine habitats have focused on seasonally abundant tiger sharks *Galeo-*

cerdo cuvier in Shark Bay, Australia (Box 2). Dolphins *Tursiops aduncus*, dugongs *Dugong dugon* and cormorants *Phalacrocorax varius* forage primarily in productive shallow seagrass habitats when sharks are scarce, but switch to less productive, but safer, deep habitats when sharks are abundant [35–37]. Individual mesoconsumers that continue to forage over shallow habitats modify their behavior by avoiding the riskier interiors of banks and foraging along bank edges where escape routes are present [38–40]. By responding behaviorally to predation risk, prey species incur an energetic cost and do not fully use resource species, which could limit growth and reproductive output [26,27]. Thus, even without direct predation, the risk effects of tiger sharks might limit population size of their prey and likely trigger trophic cascades. Tiger sharks indirectly reduce grazing on seagrasses in dangerous areas while intensifying it in safer habitats [39–41], which is manifested in spatial patterns of seagrass nutrient content [40].

Identifying key interactions and species

Considering risk effects raises interesting questions that are relevant to understanding the ecological consequences of removing marine top predators. First, what factors influence the relative importance of risk effects and those of direct predation? Second, which top predators are most likely to have disproportionate effects on their communities (through both mechanisms) relative to their abundance (i.e. are keystone species, *sensu* [42])? Small-scale experiments and field studies in terrestrial ecosystems suggest that the relative importance of risk effects and of individual predator species can be context dependent [43,44] and might depend on the energy state (e.g. fat stores) of mesoconsumers, life-history characteristics of predators and mesoconsumers, community diversity and habitat heterogeneity.

Mesoconsumer energy state, which is influenced by bottom-up forces, will affect the relative importance of direct predation and risk effects (Figure 2; Box 3). Risk effects and behaviorally mediated indirect interactions are expected to be strongest when mesoconsumers are in good energy state and able to afford the cost of antipredator behavior (i.e. reduced access to resources). By contrast, direct predation and density-mediated indirect interactions should play a greater role in communities when resources are scarce and mesoconsumers are energetically stressed (Box 3).

Life-history characteristics of mesoconsumers also can influence the relative importance of risk effects. Long-lived species such as small elasmobranchs, marine mammals and sea turtles are predicted to invest more heavily in antipredator behavior than shorter-lived ones [45], leading to more pronounced risk effects. Importantly, for such species, strong risk effects can occur even when direct predation events are rare (Box 2). Thus, the absence (or scarcity) of direct predation events for long-lived mesoconsumers does not equate to an absence of a strong predator effect on those species [7], and their communities. The above does not mean, however, that risk effects will be unimportant for short-lived species. Many studies show that antipredator behavior occurs across species with



Figure 2. Pacific sleeper shark caught as bycatch (along with 11 other individuals of the same species) in a trawl net targeting walleye pollock during a research survey in Shelikoff Strait, Gulf of Alaska. Pollock are important prey of some mesoconsumers, such as seals, that are under prey of Pacific sleeper sharks. Groundfish fisheries might directly alter resources of top predator abundance, and indirectly the foraging behavior of mesoconsumers and exploitation rates of resource species [34] (see Box 3). Photo by Elliott Lee Hazen.

vastly different life histories and in very different habitats [40,46], so risk effects should be inherent to the ecological role of marine top predators.

Factors relating to life-history characteristics of both predators and prey also influence the effects of individual predator species on their communities. A meta-analysis of 114 experimental studies suggested that trophic cascades are strongest where they involve large, mobile vertebrate predators with high metabolic rates, particularly in marine environments [13]. With respect to prey species characteristics, strong cascades were often associated with (benthic) invertebrate herbivores of low metabolic rates [13]. Communities that included large-bodied marine predators and marine vertebrate herbivores, such as sea turtles, were not included in that analysis. Marine megagrazers, however, are known to strongly influence benthic communities [47–50] and respond strongly to their predators behaviorally [46] (Box 2). Thus, their predators might be important in structuring marine plant communities through behaviorally mediated indirect interactions [46] (Box 2).

The meta-analysis discussed above suggested that community diversity did not consistently affect the strength of trophic cascades in experimental studies [13]. Nevertheless, we might expect food webs with low functional predator diversity (i.e. predators have unique diets, hunting modes or patterns of habitat use) to feature relatively strong interactions between individual predator and prey species, and diverse food webs to be characterized by more diffuse interactions, trophic redundancy (i.e. species with similar diets and hunting modes) and resilience to declines in top predator populations. Indeed, interference between multiple predator species and intraguild predation often results in lower rates of consumption of a particular prey type than when a single predator species is present [44]. For example, the strength of top-down effects by large groundfish appears to decline along gradients of species

Box 3. State-dependent behavior and the strength of risk effects

Data on resource availability and the energy state (e.g. fat stores) of mesoconsumers can strengthen predictions of the consequences of declines in marine top predators in part because mesoconsumer energy state will influence the relative strength of risk effects and direct predation on mesoconsumers as well as their transmission to lower trophic levels.

Because individuals in a poor energy state must avoid imminent starvation or the net loss of reproductive output, they have limited scope for predator avoidance. As a result, they will experience higher predation rates, and density-mediated indirect interactions will dominate top predator effects. By contrast, when mesoconsumers are in a good energy state, which is facilitated by abundant resources, they can increase investment in predator avoidance. The result will be lower foraging rates on resource species and the creation of spatial refuges for resource species in habitats with high predation risk. Here, behaviorally mediated indirect interactions are expected to dominate top predator effects [66,68]. Green turtles at risk from tiger sharks behave according to these predictions [40], reducing grazing pressure on seagrasses far from bank edges (dangerous habitats) and intensely along edges (safer habitats).

A conceptual model of mesoconsumers faced with the decision to forage in habitats that are risky but highly profitable versus those that are in safer but less profitable habitats illustrates how resource availability and mesoconsumer energy state influence the indirect effects of predators on lower trophic levels (Figure 1). Resource scarcity often results in decreased energy state of mesoconsumers, which leads to increased risk taking and hence higher predation rates (Figure 1a–c) [40,69]. Thus, when top predators are abundant and resources are scarce, density-mediated mechanisms (direct predation) dominate over behaviorally mediated effects, and mesoconsumers forage in both safe and dangerous habitats. By contrast, when resources are abundant, mesoconsumers choose safer habitats, and reduce foraging in dangerous habitats even if they are more profitable energetically (Figure 1d–f) [46]. Under these conditions, direct predation on mesoconsumers would be relatively rare and behaviorally mediated effects would dominate. Declines in top predators under both scenarios lead, indirectly, to increases of resources in previously safe (but unprofitable) habitats and declines in (profitable) resources that were once shielded by risk effects of predators [34,70].

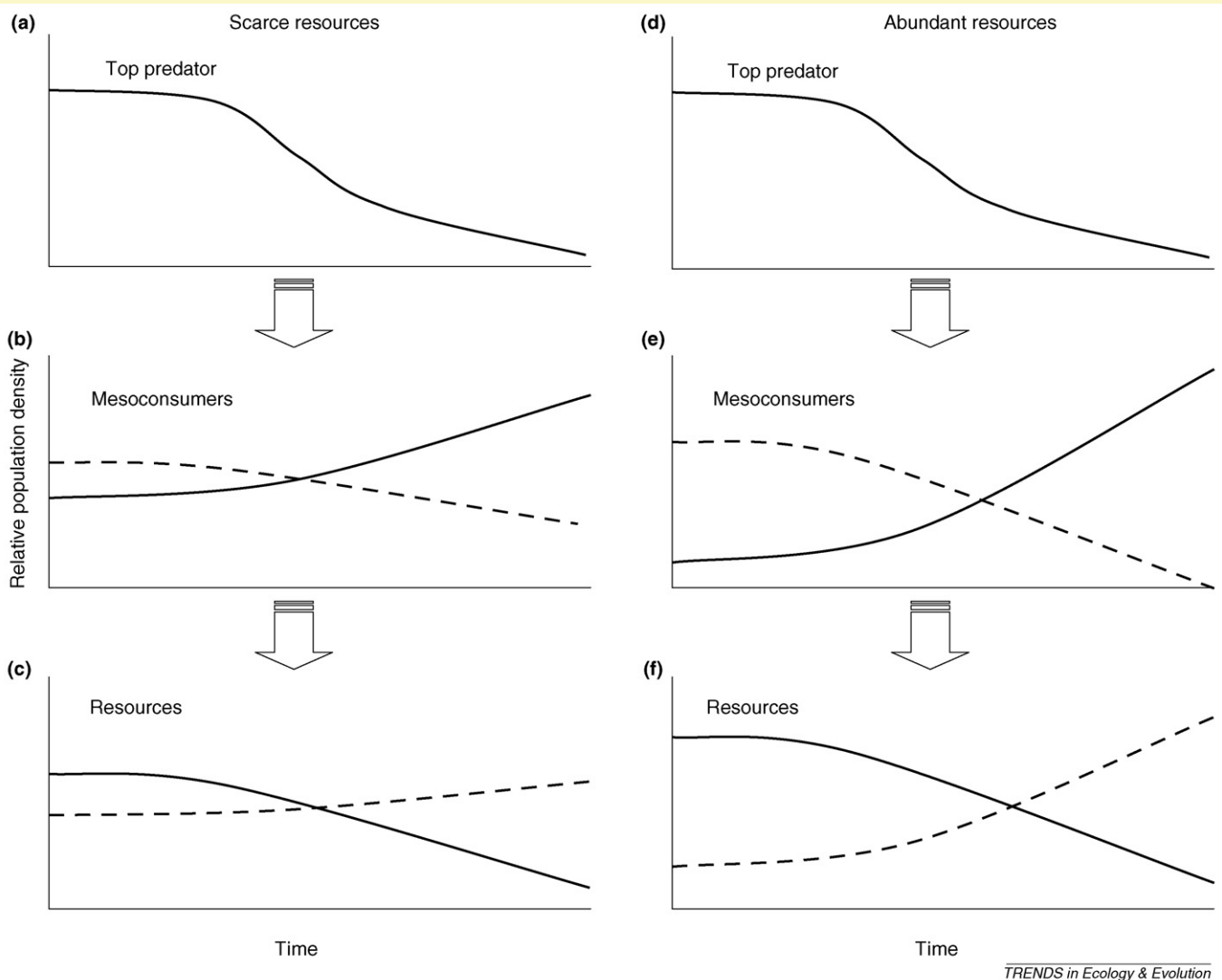


Figure 1. Conceptual model outlining density and risk effects of predator declines when mesoconsumers can choose between spatially distinct resources that differ in expected profitability and exposure to predators. Here we assume that resources are more profitable in dangerous habitats, which is consistent with many studies [21]. Shown are the overall population density of predators (a,d) and the densities of mesoconsumers (b,e) and resource species (c,f) in dangerous habitats (filled lines) and safe habitats (dashed lines) (c,f) under two contrasting scenarios. In (a–c), overall resource levels are low and mesoconsumers are assumed to be in a poor energy state, whereas in (d,e), overall resource levels are higher and mesoconsumers are assumed to be in a better energy state. Block arrows indicate causal links between trophic levels.

diversity in the northwest Atlantic [12]. Although this mechanism has not been clearly demonstrated in large-scale marine communities, experimental studies show that increased predation by remaining predator species can compensate the loss of individual predators [44,51]. A decline in predator diversity, however, sometimes will have positive effects on mesoconsumers [44]. For example, in kelp forests the loss of predator diversity, even without changes in predator abundance, increased herbivory through behavioral mechanisms [52]. Thus, strong predator effects, including trophic cascades, might occur in low- and high-diversity systems, but the relative effect of individual predator species removal might decline with increasing diversity and depend on the hunting modes of predators that are removed [12,13,44].

Finally, variation in habitat structure can influence the ecological impacts of top predator declines [53] and the relative strength of risk effects. Classic studies in freshwater systems show that microhabitat differences influence the strength of top-down effects through the habitat-specific ability of prey to respond behaviorally to predators [54]. Similar mechanisms are now known to operate in marine ecosystems. For example, in the above-mentioned toadfish-crab-oyster cascade, the addition of refuges for crabs does not alter the indirect effect of toadfish on oysters because increased hiding by crabs offsets lower predation rates [31]. In other words, greater habitat complexity increased the relative importance of behaviorally mediated indirect effects of toadfish on crabs and oysters. Risk effects can be particularly strong when mesoconsumers can switch among habitats that vary in predation risk (Box 2). In such situations, the loss of top predators could reduce or eliminate spatial refuges for resource species previously sheltered by risk effects of those predators. In combination with increases in mesoconsumer densities, loss of spatial refugia might greatly impact resource species populations.

Toward a predictive framework

Recent studies suggest that marine top predators can exert considerable effects on their prey that can cascade through marine communities. These overall effects might not be caused solely by direct predation; rather, risk effects can contribute a large component of overall predator effects. In most cases, therefore, predictions about how communities will respond to marine predator declines should be improved by an understanding of risk effects and behaviorally mediated indirect interactions. Particularly in the case of vertebrate predators and long-lived prey species, a sole focus on direct predation might greatly underestimate the community effects of predator loss. The management implications of these notions are not trivial. Consider, for instance, that terrestrial studies have argued that imperiled populations of large carnivores should be managed not for demographic persistence alone, but for the maintenance of risk-driven ecological processes [55] and at population densities above thresholds for meaningful interactions [56]. These ideas, we argue, are equally relevant to marine systems, and we encourage discussion on how they might be applied to targets for conservation of marine top predator populations.

A predictive framework for marine community ecology that integrates risk effects and direct predation effects can build on what is already known from other systems. Although some patterns can be context dependent, risk effects of top predators and behaviorally mediated indirect interactions can be quite similar across vastly different ecosystems. For example, the risk effects of tiger sharks described earlier resemble those of wolves on elk and trees in Yellowstone National Park [57], cougars (*Puma concolor*) on mule deer (*Odocoileus hemionus*) and riparian vegetation [28], spiders on grasshoppers and old-field vegetation [46], crabs on snails and barnacles [29], and river fishes on invertebrate predators, chironomids and algae [54]. Using this body of work, together with initial results from marine systems, we suggest that general predictions on the effect of top predator declines might be generated from basic life-history information about interacting species, even if detailed system-specific data are not available [44,46]. Future studies are needed, however, to further elucidate risk effects in marine systems and the factors influencing their relative strength and probability of being transmitted through communities.

As previous authors have cautioned [47,49], inferences about the general strength of top-down effects in undisturbed communities are hindered by the fact that overexploitation is already widespread. Developing a predictive framework that is relevant to conservation therefore requires more studies of ecosystems that have retained or restored top predators. Experimental approaches, including predator enclosures, and observations along gradients of predator density, would provide important insight into the mechanisms that influence marine communities and their direct and indirect responses to predator depletion. Finally, most studies of top marine predators have ignored the dynamics of their prey populations and assumed that prey are behaviorally inert. This lack of empirical studies on mesoconsumers might lead to many faulty assumptions about community dynamics. Thus, more detailed studies of mesoconsumers are a high priority for building a general framework for understanding the consequences of declines in marine top predators.

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