

RESEARCH REVIEW

Human activities change marine ecosystems by altering predation risk

ELIZABETH M. P. MADIN¹, LAWRENCE M. DILL², APRIL D. RIDLON³, MICHAEL R. HEITHAUS⁴ and ROBERT R. WARNER³

¹*Department of Biological Sciences, Macquarie University, Sydney, NSW 2109, Australia,* ²*Evolutionary and Behavioural Ecology Research Group, Department of Biological Sciences, Simon Fraser University, 8888 University Drive, Burnaby, BC V5A 1S6, Canada,* ³*Department of Ecology, Evolution and Marine Biology, University of California, Santa Barbara, CA 93106, USA,* ⁴*Department of Biological Sciences, Florida International University, 3000 NE 151st Street, North Miami, FL 33181, USA*

Abstract

In ocean ecosystems, many of the changes in predation risk – both increases and decreases – are human-induced. These changes are occurring at scales ranging from global to local and across variable temporal scales. Indirect, risk-based effects of human activity are known to be important in structuring some terrestrial ecosystems, but these impacts have largely been neglected in oceans. Here, we synthesize existing literature and data to explore multiple lines of evidence that collectively suggest diverse human activities are changing marine ecosystems, including carbon storage capacity, in myriad ways by altering predation risk. We provide novel, compelling evidence that at least one key human activity, overfishing, can lead to distinct, cascading risk effects in natural ecosystems whose magnitude exceeds that of presumed lethal effects and may account for previously unexplained findings. We further discuss the conservation implications of human-caused indirect risk effects. Finally, we provide a predictive framework for when human alterations of risk in oceans should lead to cascading effects and outline a prospectus for future research. Given the speed and extent with which human activities are altering marine risk landscapes, it is crucial that conservation and management policy considers the indirect effects of these activities in order to increase the likelihood of success and avoid unfortunate surprises.

Keywords: behaviour, fishing, human impacts, indirect effects, marine ecosystem, nonconsumptive effects, nonlethal effects, predation risk, Predator–prey interactions, risk effects, trophic cascades

Received 21 December 2014; revised version received 28 August 2015 and accepted 29 August 2015

Introduction

Humans are altering marine systems in diverse ways and over unprecedented spatial and temporal scales, resulting in many unexpected outcomes. For example, predator harvest has been occurring for millennia, resulting in both direct (Jackson *et al.*, 2001) and indirect consequences (Heithaus *et al.*, 2008; Babcock *et al.*, 2010). The extent of human influence on marine communities is accelerating (Steneck *et al.*, 2004) as the global influence of humanity continues to stretch into the farthest reaches of the world's oceans. Recent insights suggest what some of the consequences of this ever-expanding footprint might be, revealing a wide range of previously undocumented repercussions of changing marine predator abundances (e.g. Heithaus *et al.*, 2008). Scientists now have a firm grasp on many of the direct effects of predator harvest in natural

marine ecosystems (e.g. reduced predator abundance and biomass). Relatively less understood are what the indirect, cascading consequences on marine ecosystems may be, although evidence of this is growing (Heithaus *et al.*, 2008; Babcock *et al.*, 2010; Estes *et al.*, 2011). Importantly, much of what is known in this area relates to lethal effects. In contrast, risk effects (e.g. influences of predator presence on prey behaviour, reproduction, and other trait-mediated responses; see Box 1) due to changing predator populations are not as well studied, despite many advances in the past decade from the experimental literature (reviewed by Long & Hay, 2012). Here we review the more subtle, but potentially more pervasive, indirect effects of human activities that alter predation risk in natural marine ecosystems.

Risk effects, or the outcome of behavioural responses of prey to their predators (Box 1), have long been recognized (Lima & Dill, 1990), but the potential magnitude of their ecosystem-level effects remained largely underappreciated until recently (Schmitz *et al.*, 2004). Risk effects affect a diverse array of organisms across a

Correspondence: Elizabeth M. P. Madin, tel. +61 4 3012 1426, fax +61 2 9850 8245, e-mail: dr.elizabeth.madin@gmail.com

Box 1 Terminology

Two important sets of distinctions about types of interactions among organisms must be made to establish context here: *direct* vs. *indirect* interactions and *risk* effects vs. *lethal* effects. Definitions, synonyms and examples are given below. We partially follow the terminology used in Creel & Christianson (2008).

Predation risk

The probability of an individual being killed by a predator during a given time period. Mathematically, predation risk can be represented as the product of the probability of encountering a predator, the probability of failing to escape a predator (conditional probability of prey death) and the amount of time spent vulnerable to encountering a predator (Lima & Dill, 1990).

Direct interaction

The influence of one individual or species (the *donor* or *initiator*) on another (the *recipient* or *receiver*) when not mediated or transmitted through a third individual or species. For example, a predator captures prey or prey changes behaviour to avoid a predator.

Indirect interaction

The influence of one individual or species (the *donor* or *initiator*) on another (the *recipient* or *receiver*) that is mediated or transmitted by a third individual or species (the *transmitter*). For example, a predator consumes prey, leading to an increase in the prey's food resource. This interaction type consists of a sequence of at least two direct interaction steps.

Lethal effects

The consequence of predator–prey interactions that occur as a direct result of a successful predatory attack. For example, a change in prey density solely as a result of prey being consumed by predators is a direct lethal effect, whereas a consequent increase in the prey's food resource is an indirect lethal effect. Although 'density effect' is commonly used in the literature for what we refer to as a 'lethal effect,' it should be avoided in this context because density changes are the result of lethal effects, risk effects *and their interaction* (Abrams, 2007; Heithaus *et al.*, 2008). We acknowledge that, in some cases, risk effects (defined below) can potentially also result in death (i.e. be lethal; Abrams, 2007). *Synonyms*: consumptive effects, numerical effects, density effects, direct predation effects.

Risk effects

The result of predator–prey interactions that occur via changes in a trait or behaviour of a prey. *Direct risk effects* occur when predation risk affects prey behaviour, and *indirect risk effects* result from a three (or more)-level interaction involving a risk-induced trait or behavioural response. For example, a change in a prey's behaviour (e.g. decreased feeding rate) or physical trait (e.g. antipredator defence that reduces foraging efficiency) as a result of predation risk is a direct risk effect of a predator, whereas a consequent increase in the prey's food resource is an indirect risk effect of the predator. Direct and indirect risk effects can be the result of behaviourally or trait-mediated interactions (BMIs/TMIs) and behaviourally or trait-mediated indirect interactions (BMII/TMII), respectively. *Synonyms*: nonconsumptive effects, behavioural/trait effects, nonlethal effects.

Note that both direct and indirect interactions can be mediated by either lethal or risk effects. In instances where risk effects have led to true community-level trophic cascades (i.e. involving more than just three strongly-interacting species), we refer to an indirect risk effect as a 'risk-induced trophic cascade' to reflect the commonly used term for this effect.

Importantly, by changing characteristics of predatory species (e.g. density, size structure, geographic range, etc.), humans can initiate both direct and indirect interactions as well as cause lethal and risk effects (i.e. as the *donor* or *initiator*). Here we consider the effects of any interactions involving a third organism or species (a *receiver*)

Box 1 (continued)

to be an indirect effect of human activity. For example, humans (the *initiator*) harvest predators, reducing predator (the *transmitter*) density and thus predation risk for prey (the *recipient*), potentially resulting in a risk effect of altered prey behaviour. A further indirect risk effect may also result, for example a change in the prey's food abundance (an additional *recipient*). In this regard, both the human activity and the changes in predator density have generated indirect risk effects (i.e. on prey behaviour and the prey's food resource, respectively).

wide range of ecosystem types (see reviews by Lima & Dill, 1990; Lima, 1998; Dill *et al.*, 2003; Werner & Peacor, 2003; Schmitz *et al.*, 2004; Heithaus *et al.*, 2008; Peckarsky *et al.*, 2008). Generally speaking, predators can scare more prey and from a much greater distance than they can kill. Likewise, prey can respond to changes in risk from one moment to the next, going back and forth in their responses, whereas prey cannot return from death. The widespread and rapid effects of predation risk suggest that they have substantial capacity to shape animal behaviour and subsequently the ecosystem components with which these animals interact. Experimental evidence suggests that while lethal effects tend to attenuate through food webs, risk effects tend to amplify, generating a relatively stronger signal on prey resources than on prey themselves (Preisser *et al.*, 2005). Despite many important advances in the past decade (reviewed by Long & Hay, 2012), risk effects still remain less comprehensively documented in marine vs. other systems, particularly in the field. This likely reflects relatively lower sampling effort in marine systems due to the inherent logistical challenges of working in oceans (Dill *et al.*, 2003). However, evidence from experimental systems suggests that the greatest risk effects are likely found in marine relative to terrestrial and freshwater systems (Preisser *et al.*, 2005). Importantly, the high phyletic diversity and large proportion of consumers that are generalists in marine vs. terrestrial systems render marine systems particularly favourable for the transmission of risk effects (Long & Hay, 2012). Mounting evidence is revealing diverse direct risk effects in natural marine systems (Heithaus *et al.*, 2012). It is likely that continued study of these effects will reveal a greater number and diversity of risk effects – both direct and indirect – than have thus far been catalogued.

With this review and prospectus, we aim to present available evidence and make informed predictions about 1) how human activities indirectly alter predation risk for prey animals, 2) how predation risk affects marine animal behaviour, and 3) the ecological, evolutionary and conservation implications of these behavioural responses. We examine existing evidence for human-induced indirect risk effects, whereby human activities affect predation risk, sub-

sequently causing changes in the traits or abundance of prey and other interacting species (Box 1). Towards this end, we draw on marine, freshwater and terrestrial literature. We also present new, synthetic evidence to this effect from natural marine ecosystems. Our ultimate goal is to 'connect the dots' of current knowledge regarding how humans can indirectly affect animal behaviour, potentially altering ecological and evolutionary processes, via risk effects in natural marine ecosystems. Lastly, we present a predictive framework for how and when human alterations of risk in oceans are most likely to lead to cascading indirect effects and a roadmap for future research.

Human activities alter predation risk for prey animals

Because of the ubiquitous nature of human alterations to marine ecosystems at scales from local to global, anthropogenic modification of predation risk may occur through diverse mechanisms (Fig. 1; Table S1). Humans can influence predation risk by altering predator numbers or behaviour and by affecting these predators' prey's ability to respond to risk. Conversely, humans can act as real or perceived predators themselves by directly targeting predatory and nonpredatory species or influencing their behaviour. We primarily focus in his review on the role of humans as real predators, while recognizing the importance of their role as perceived predators. Understanding the different ways that predation risk can be modified is critical to building a predictive framework that can inform management decisions.

One the most obvious and widespread activities affecting predation risk in the ocean is predator harvest. Through alteration of predator numbers, distribution, size structure and behaviour, humans have necessarily and unwittingly caused dramatic spatial and temporal changes in predation risk in oceans the world over (Heithaus *et al.*, 2008; Estes *et al.*, 2011). Overharvesting of predators is largely responsible for the defaunation of the world's oceans (McCauley *et al.*, 2015), which is disproportionately focused on large consumers (predatory and nonpredatory) on both land (Dirzo *et al.*, 2014)

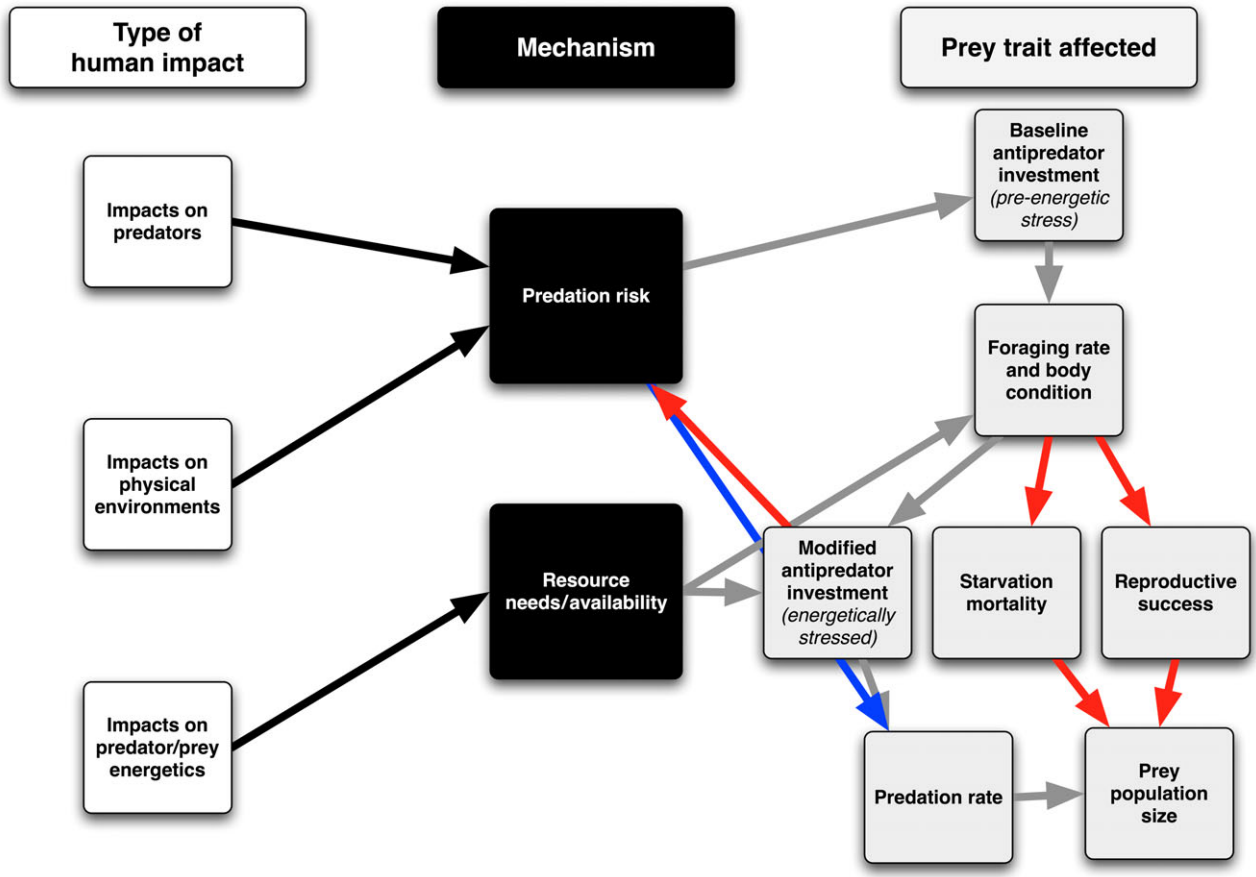


Fig. 1 Conceptual diagram of mechanisms and pathways by which human activities alter risk and lethal effects of predator–prey interactions in any marine/aquatic ecosystem type. White boxes are types of human impacts that affect predation risk and resource needs/availability for prey of marine predators. Black boxes indicate risk effect mechanisms that are altered by human activities. Grey boxes indicate prey traits that are ultimately affected by human activities and/or their outcomes, whether via changes in predation risk or changes in resource needs or availability. Red lines indicate pathways driven purely by risk effects. Grey lines indicate pathways driven by interacting risk and lethal effects. Blue line indicates the only pathway driven purely by lethal effects. Here we do not consider direct effects of humans on prey (other than those mediated by energetic changes that also affect predators) to elucidate the diversity of pathways through which humans can initiate indirect risk effects. Adapted from Heithaus *et al.* (2012). See Table S1 for examples of specific human activities in each category and their resulting direction of change in net predation risk for prey.

and in the sea (Estes *et al.*, 2011). In marine systems, apex predators and secondary consumers (both carnivores) represent 70% of the known recent global and regional marine extinctions (Byrnes *et al.*, 2007). In addition to global and local extinctions of predators, functional extinctions – whereby a species or population no longer plays a significant ecological role and/or is no longer viable – are globally widespread and significant in number (e.g. Myers & Worm, 2003). A key factor that is currently poorly studied is the relationship between predator abundance and the strength of risk effects. An understanding of this relationship is necessary to understand the densities at which predators will continue to induce risk effects that can be ecologically important.

Predator introductions, both accidental and deliberate (Molnar *et al.*, 2008), and human-induced changes in geographic ranges (Sorte *et al.*, 2010) have reshaped predation risk in myriad systems. Non-native predators, including larval or egg predators, can modify the types and levels of risk for prey and can induce behavioural responses in their prey (Beck H, Feary D, Fowler A, Madin EMP, Booth D, unpublished data).

In response to historical declines in predator populations, there has been increasing effort in rebuilding or re-establishing depleted predator populations through conservation tools such as marine reserves. Recovery of predators should elevate predation risk (as seen in terrestrial systems with grey wolf reintroductions; Ripple & Beschta, 2007). Patterns of predation risk

established through these predator rebuilding efforts, however, may not reflect those present historically because of differential recovery within predator guilds. Indeed, responses to management interventions are likely to vary across life-history characteristics or behavioural patterns (e.g. range sizes). For example, wide-ranging, large-bodied shark species, which tend to be true apex predators in coral reef ecosystems (Heupel *et al.*, 2014), may be less likely to rebound than large mesopredatory sharks with more restricted ranges due to variation in apex predators' exposure to fisheries outside reserves and their slower life-history characteristics (Heupel *et al.*, 2014).

Predator harvest also changes the nature of predator assemblages. For example, removal of top predators can lead to changes in the distribution and abundance of smaller mesopredators, in turn affecting predation risk for smaller prey species. These changes can come about both through numerical effects (i.e. changes in mesopredator abundance) and through behavioural effects (Stallings, 2008; Ritchie & Johnson, 2009). In this way, human harvest of top predators reduces risk for top predators' prey (i.e. mesopredators) but increases risk for mesopredators' prey. Therefore, specific consideration of trophic position of a predator (e.g. whether a 'top' predator is actually a large mesopredator) and food web topology will be critical to predicting the nature of anthropogenic changes to risk effects.

Predator harvest may also profoundly alter size structures of predator assemblages, often by preferentially removing the largest predators. Size-selective fishing can lead to dramatic changes in biomass of prey species even in the absence of net changes in predator biomass (Shackell *et al.*, 2010). In addition to reducing net predation risk for prey populations, this may lead to disproportionate risk reductions for larger prey individuals because the only predators capable of consuming them are removed. Interestingly, model predictions suggest that marine fish may also experience a significant shrinkage in body size due to warmer oceans with reduced oxygen under projected future climate change scenarios (Cheung *et al.*, 2012). Because both predatory and nonpredatory species are predicted to undergo this shrinkage, it remains unclear to what extent net predation risk will change as a result. Exploration of individual pair- and group-wise interactions among co-occurring predators and prey would likely lend greater insight.

In addition to changes in predator abundances, human activity can lead to changes in predator behaviour. For example, direct human presence can temporarily reduce predator numbers by essentially 'scaring' predators away, regardless of whether or not the humans pose a genuine threat (Frid & Dill, 2002).

Human disturbance stimuli for both predators and their prey can be considered analogous to predation risk when considered in an evolutionary context and should affect behaviours such as vigilance, fleeing, habitat selection, mating displays and parental investment (Frid & Dill, 2002), and many examples of these effects have been observed on terrestrial animals. Boat and aircraft noise, in particular, have been shown to affect habitat selection and flight behaviours in marine predators (Frid & Dill, 2002).

Human activity frequently modifies habitat for predators and prey, both at local scales (e.g. habitat loss and/or fragmentation; Ripple *et al.*, 2014) and global scales (e.g. warming and/or acidifying waters due to climate change). On local to regional scales, changes in the available habitat in which both predators and prey can live can alter the abundance and composition of predators and can similarly change the amount of available shelter for prey. For example, destructive fishing practices, such as trawling and blast fishing, and activities such as island 'reclamation' (Peh, 2015) can reduce the amount and change the distribution of available shelter habitat for both predators and prey. Conversely, habitat restoration efforts (e.g. artificial coral reefs), fisheries enhancement efforts (e.g. fish aggregating devices, or FADs) and construction of other structures in the marine environment (e.g. oil rigs, jetties, breakwaters) may provide additional size-specific shelter for prey and therefore reduce their net risk of predation. On regional to global scales, climate change-induced range contractions or expansions of habitat-forming species (e.g. mangroves, corals) could lead to local-scale changes in predator and prey abundances by the provision or removal of habitat (Sorte *et al.*, 2010). These alterations may result in novel communities with new predator-prey combinations being created and old ones being disassembled (Ripple *et al.*, 2014), both with obvious implications for predation risk landscapes.

The energetic requirements and body condition of both predator and prey will play a fundamental role in their foraging and risk-taking behaviours, respectively (Werner & Peacor, 2006). In line with earlier theoretical findings (Lima & Bednekoff, 1999; Luttbeg *et al.*, 2003), field evidence for state-dependent risk-taking exists for both marine prey (Heithaus *et al.*, 2007) and predators (Mukherjee & Heithaus, 2013). In the former, green sea turtles select microhabitats in a condition-dependent manner (Heithaus *et al.*, 2007), suggesting that human-induced or natural changes to the prey's energetic requirements (e.g. via temperature-mediated changes in metabolic rate) or food nutritional quality (e.g. via changes in nutrient input) will have measureable effects on their risk-taking. Likewise, terrestrial predators have been observed and marine predators are

predicted to take risks when foraging in a condition-dependent manner (Mukherjee & Heithaus, 2013). In most cases, foragers are willing to take greater risks as their body condition declines, although some exceptions in terrestrial predators have been noted (Mukherjee & Heithaus, 2013). State-dependent risk-taking is therefore a critical factor in mediating the strength and nature of risk effects (Heithaus *et al.*, 2008), and human activities that may affect predator or prey body condition must be considered when making predictions about risk effects.

Any changes to the available food sources for predators will likely alter their foraging patterns in order to take advantage of food subsidies or compensate for decreased resources. Many human activities change predator abundances either deliberately or unintentionally. Trawling, dredging and aquaculture (e.g. Veale *et al.*, 2000) can attract large numbers of predators, in some cases increasing abundances by up to 200% and persisting for up to three days after the event (Veale *et al.*, 2000). Human activities that provide supplementary food for predators (e.g. ecotourism provisioning (Brunnschweiler & Barnett, 2013); fishing vessel discards (Bodey *et al.*, 2014)) can lead to substantial changes in predator behaviour, abundance and/or local assemblage composition that likely affect real and perceived risk by their potential prey. These changes may have considerable impacts on the spatial scale, temporal pattern and overall magnitude of risk effects for predators' prey.

Some human activities may alter the ability of prey to perceive predation risk and therefore will affect prey vulnerability to predation. Chemical suppression of prey risk perception, for example via pollutants (McIntyre *et al.*, 2012) or ocean acidification (Munday *et al.*, 2014), renders prey more susceptible as they cannot accurately assess risk cues. Human-induced changes in water visibility may alter both real and perceived risk (Wirsing *et al.*, 2014) resulting in increased investment in antipredator behaviour. Importantly, however, if human activities prevent appropriate prey responses to predation risk, predator effects might shift towards lethal mechanisms.

Risk alters diverse prey behaviours

The effects of risk on prey behaviour in marine and other systems have been reviewed elsewhere (Lima & Dill, 1990; Lima, 1998; Dill *et al.*, 2003; Werner & Peacor, 2003; Schmitz *et al.*, 2004; Heithaus *et al.*, 2008; Peckarsky *et al.*, 2008). Diverse studies show that predation risk can alter prey's use of space and temporal patterns of activity, including habitat selection (e.g. Grabowski *et al.*, 2008), time budget (e.g. Heithaus

et al., 2012 and references therein) and movement/ambit (e.g. Lönnstedt *et al.*, 2013); feeding patterns, including feeding rate (e.g. Metcalfe *et al.*, 1987) and diet breadth and quality (e.g. Lehtiniemi & Lindén, 2006); reproduction (e.g., Magnhagen, 1990); social grouping (e.g. Parsons & Eggleston, 2006); and inducible defences (e.g. Leonard *et al.*, 1999).

Existing evidence of indirect risk effects caused by human activity

Coupling our knowledge of the many ways that human activities affect risk with our knowledge of how risk affects prey behaviour leads to the logical conclusion that human activities indirectly affect diverse prey behaviours in the ocean by altering predator abundances and behaviour or other factors that influence predation risk described above. Because many prey behavioural responses to risk can have cascading consequences in communities, it is therefore likely that humans are inducing myriad indirect risk effects (i.e. behaviour-mediated trophic cascades) in marine communities, even when there are no obvious changes in prey population sizes (Heithaus *et al.*, 2008, 2014; Burkholder *et al.*, 2013).

Only two documented examples exist in the literature that we are aware of that explicitly link human activities to risk-induced trophic cascades (Byrnes *et al.*, 2006; Madin *et al.*, 2010a), whereby human-induced changes in the level of risk faced by prey have led to behavioural alterations and subsequent indirect effects on prey resources (in both cases, benthic macroalgae) in natural systems. In the first case, Byrnes *et al.* (2006) used a long-term monitoring data set from within and outside of no-take marine reserves plus a mesocosm behavioural experiment to show that reduced predator diversity, a presumed consequence of human fishing, caused a risk-induced trophic cascade. In a study from a remote coral reef archipelago, Madin *et al.* (2010a) linked observations of predator abundance, herbivore behaviour and algal distribution in natural systems with field-based manipulations of risk and a mechanistic model. They found that different intensities of human population size (and hence presumably fishing pressure) over the archipelago resulted in differences in predation risk and indirectly led to changes in macroalgal distribution by altering herbivore foraging behaviour.

Four additional studies with less direct links to human activities have also demonstrated indirect risk effects. In a Caribbean coral reef system subject to human fishing, Stallings (2008) showed experimentally that reductions in mesopredator activity due to risk-based avoidance of larger predators increased the

Box 2 Shark Bay seagrass ecosystem case study

A long-term study of a relatively pristine seagrass community in Shark Bay, Western Australia, has documented the effects of tiger sharks (*Galeocerdo cuvier*) on the behaviour of their prey and the wider consequences of these risk effects. The subtropical bay experiences seasonal variation in water temperatures and tiger shark abundance. Importantly, tiger shark abundance varies considerably among years for a particular season (e.g. abundances may be low or high during winter), providing a 'natural experiment' (see Heithaus *et al.*, 2012 for a review). Bottlenose dolphins (*Tursiops cf. aduncus*), dugongs (*Dugong dugon*), green sea turtles (*Chelonia mydas*) and pied cormorants (*Phalacrocorax varius*) modify their behaviour in response to variation in risk from tiger sharks. Most dolphins, dugongs and cormorants move to deep water where food and sharks are less abundant, thereby trading food for safety (Heithaus *et al.*, 2012). For those individuals that do remain in shallow habitats, dolphins and dugongs shift to the edges of the seagrass banks, where the sharks are abundant but where they can quickly flee to deeper water if attacked (Heithaus & Dill, 2006; Wirsing *et al.*, 2007a; respectively). Green turtles in good body condition forage on the bank edges as well, but those in poor body condition forage in the more risky bank interiors, where the seagrass is more nutritious (Heithaus *et al.*, 2007). Because they are capable of taking to the air if attacked, cormorants foraging in shallow waters during high-risk times shift to the middle of banks where encounter rates with tiger sharks are lower (Heithaus *et al.*, 2009). Dugongs make other behavioural adjustments when sharks are abundant, including cropping less nutritious seagrass leaves rather than excavating profitable rhizomes, because the latter creates sediment plumes that likely increase the risk of both detection and attack (Wirsing *et al.*, 2007b). These behavioural adjustments to manage risk will reduce food intake, with potential consequences for survival and reproduction (i.e. a direct risk effect resulting from a BMI). They also appear to have wider consequences for the ecosystem. For example, shifts of grazing turtles and dugongs appear to drive the spatial pattern of seagrass abundance and community composition (Burkholder *et al.*, 2013). Experiments show that intense herbivory by turtles and dugongs in safe microhabitats results in lower seagrass biomass that is made up primarily of fast-growing species. In contrast, herbivory by these large grazers plays less of a role in dangerous habitats, where high biomasses of a slow-growing habitat-forming seagrass develop. These spatial patterns of seagrass biomass affect the abundance and composition of teleost communities (Heithaus *et al.*, 2012). Therefore, BMIs between sharks and seagrasses (or other taxa) could be positive or negative depending on their spatial location relative to the sharks. Given that tiger sharks, like other sharks, are in decline worldwide due to overfishing (Ferretti *et al.*, 2010), these studies show the potential for human activities like fishing to cause changes in marine communities through changes in behaviour of the prey of their target (or bycatch) species.

settlement success of small fishes. Trussell *et al.* (2006) demonstrated indirect effects on habitat in a temperate rocky intertidal system in the presence of a human-introduced predator. Snails reduced consumption on barnacles (a habitat-forming species) in risky areas and increased it in safe areas. Bertness *et al.* (2014) experimentally excluded recreationally fished fish and crab predators and found that altered foraging behaviour of an herbivorous crab led to dramatic reductions in marsh grass. This suggests that the salt marsh die-offs observed along coastlines of the Western Atlantic Ocean in recent decades may be in part a consequence of indirect risk effects initiated by fishing (Bertness *et al.*, 2014). Additionally, seasonal declines in the abundance of tiger sharks in the seagrass ecosystem described in Box 2 simulate, in a sense, the net effect of shark declines due to human harvest that are occurring rapidly elsewhere in the world (Ferretti *et al.*, 2010). Findings emerging from this latter system provide a window into the kinds of behavioural responses and

potential cascades that are likely occurring elsewhere but remain undocumented. For example, the loss of large sharks may have led to increased herbivory on seagrasses by increasing populations of green turtles; some of this effect likely is attributable to relaxed predation risk (Heithaus *et al.*, 2014).

A combination of insights from case studies and first principles provides further insights into where and when human-initiated, risk-induced trophic cascades are likely to occur. Both of the two key case studies, and all except one of the other case studies, are linked in some way to human removal of predators, demonstrating that fishing can cause both species-level indirect risk effects and community-level risk-induced trophic cascades. The study of Trussell *et al.* (2006) provides an interesting counterpoint, suggesting that human predator introductions or relocations, as opposed to harvest, can also likely initiate indirect risk effects. Importantly, these studies focus on only two of the many mechanisms by

which human activity can alter risk. We predict that further enquiry into the indirect risk effects resulting from other mechanisms will reveal similarly diverse ecological repercussions.

Indirect effects of human activity may be dominated by risk effects

It has proven difficult to detail how human-induced changes to risk might cascade through natural ecosystems compared to lethal effects alone. This is largely due to the inseparable nature of these effects, which also interact (e.g. Werner & Peacor, 2003; Abrams, 2007). Indeed, in manipulative experiments, the interactive effect of risk effects and lethal effects may dominate. Adding to difficulties in quantifying effect sizes in natural environments is a lack of undisturbed natural ecosystems where risk effects likely are intact. The coral reefs of the Line Islands archipelago and the seagrass ecosystem of Shark Bay, Australia, provide rare counterpoints.

Palmyra Atoll in the Line Islands remains uninhabited and legally protected from fishing, whereby adja-

cent Kiritimati and Tabuaeran Atolls have increasingly dense human populations that survive largely on seafood for survival. The direct impact of human fishing on predatory fish biomass (i.e. significantly lower predator densities at fished vs. unfished reefs) and hence risk for prey species in this system has previously been documented (Stevenson *et al.*, 2006; Sandin *et al.*, 2008; Madin *et al.*, 2010b).

This human impact gradient has separately been used to explore the cascading effects of fishing operating through presumed lethal (Sandin *et al.*, 2008) and risk (Madin *et al.*, 2010a,b, 2012) effects. Synthesizing data from these independent studies (Fig. 2) provides the first field evidence of the relative magnitudes of risk vs. lethal indirect effects as a consequence of human activity. Prey (e.g. herbivorous and planktivorous fishes) respond strongly in terms of behaviour, but relatively little in terms of biomass, to loss of predators due to fishing (Fig. 2). Trophic cascade theory based solely on lethal effects would predict that prey (e.g. herbivores and planktivores) would exhibit greater biomass in the fished, predator-poor reefs of Kiritimati and Tabuaeran, but this pattern was not observed and

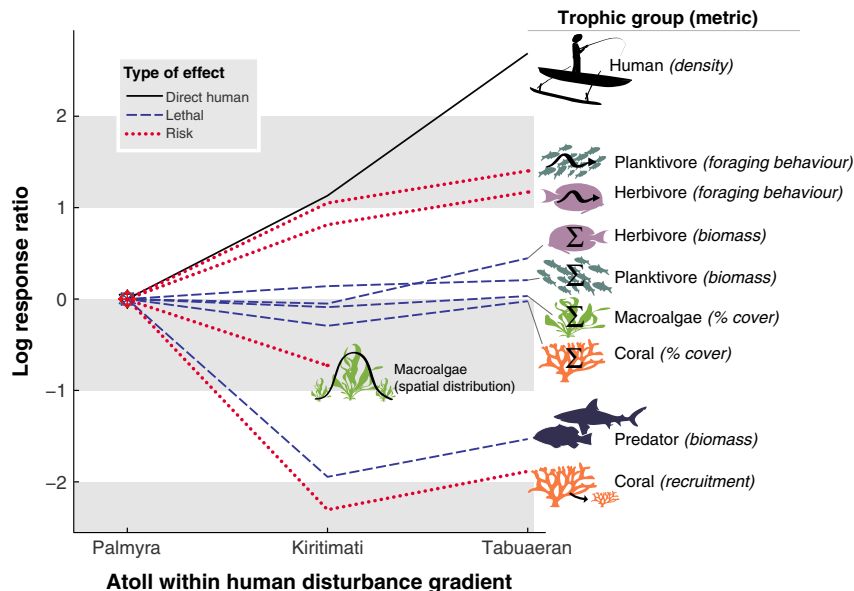


Fig. 2 Field evidence of presumed lethal (darker, blue lines) and risk (lighter, red lines) effects of human fishing on various trophic groups from coral reef ecosystems along a gradient of human fishing pressure in the northern Line Islands archipelago (USA; Republic of Kiribati). Points are log response ratios of values for each trophic group and metric at fished atolls (Kiritimati; Tabuaeran) relative to an unfished baseline (Palmyra), or $\ln(\text{value}_{\text{fished}}/\text{value}_{\text{baseline}})$. This index measures both the sign and the strength of responses within individual metrics (listed in the figure key) to predator removal. Positive values indicate that the metric's value is greater in predator-poor, fished atolls, whereas negative values indicate the metric's value is lower on these reefs than on the unfished, baseline reefs of Palmyra. Herbivore and planktivore foraging behaviour value is excursion size (Madin *et al.*, 2010b); macroalgal spatial distribution value is average patch size ('patchiness'; Madin *et al.*, 2010a only collected at Palmyra and Kiritimati). Although human fishing has resulted in very large reductions in predatory fish biomass across this archipelago, in other systems, similarly significant risk effects have been generated by very small changes in predator biomass (Heithaus *et al.*, 2008). Synthesized from data in Madin *et al.* (2010a,b; black 'human density' line; red lines other than 'coral recruitment') and Sandin *et al.* (2008; blue lines red 'coral recruitment' line). See Fig. 3 for corresponding conceptual diagram.

no evidence was found in support of a trophic cascade in this system driven by changes in density (Sandin *et al.*, 2008). The relative lack of difference in planktivore biomass across the archipelago (Fig. 2, blue line) could conceivably be the result of increased competition for food at the fished atolls. However, this is unlikely given that these islands receive greater oceanic nutrient input than unfished Palmyra, which should enhance fish populations via food subsidies at the fished reefs (Sandin *et al.*, 2008). The relatively small herbivore biomass increase over the gradient (Fig. 2, blue line) may be a consequence of solely lethal effects (e.g. decreased overall mortality and/or change in size structure due to size-selective mortality resulting from fewer predators), or it may be partially due to risk effects (e.g. change in size structure or overall biomass due to increased feeding opportunities, resulting from reduced predation risk). Conversely, the lack of substantial increases in herbivore density may be an indication that either herbivore populations showed little biomass response to predator decline or that human fishing on herbivores themselves replaced natural predation by piscivores and thus keeps herbivore biomass from increasing when predator declines. However, given that most fishing in these islands is focused on predatory species (Sandin *et al.*, 2008), the latter is not a likely explanation for this lack of pattern.

In contrast, the behavioural changes observed (red lines) can likely be attributed solely to risk effects on prey behaviour (Fig. 3). First, the behavioural responses presented in Fig. 3 were tested under conditions of both short-term ('acute') risk and long-term ('chronic') risk, with analogous results (Madin *et al.*, 2010b). Additionally, the effect of perceived predation risk was isolated from other potentially confounding factors using nonlethal, model predators, with corresponding results (Madin *et al.*, 2010a,b), again demonstrating that in situ risk alone was sufficient to alter prey foraging behaviour. Furthermore, alternative explanations are insufficient to explain the observed behavioural patterns. For example, the increasing productivity gradient that occurs from north to south over the archipelago (Sandin *et al.*, 2008) should provide more abundant food resources for herbivores and planktivores at the southerly, fished atolls, in turn resulting in smaller – not larger – foraging excursions in these fished atolls relative to the more northerly, unfished Palmyra. Likewise, other alternative explanations such as habitat complexity, prey body size (a proxy for vulnerability), and competition for food resources and/or space have been explored and found not to be responsible for the observed behavioural patterns (Madin *et al.*, 2010b). Thus, comparison of the relatively larger response

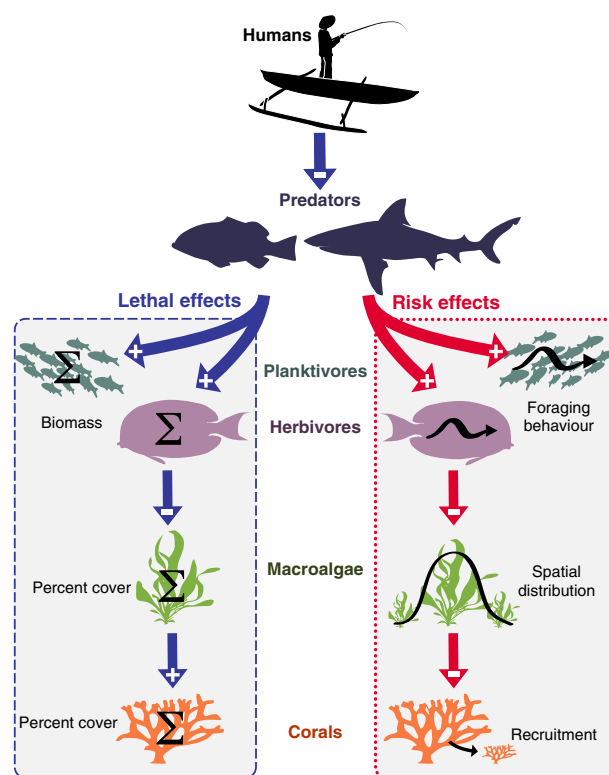


Fig. 3 Conceptual diagram of proposed mechanisms and pathways by which human activities could potentially affect coral reef ecosystems in the northern Line Islands. In the Republic of Kiribati atolls in this system, artisanal fishing pressure (which makes up the vast majority of the total annual catch; Sandin *et al.*, 2008) relies heavily on predatory fishes (both apex and meso), although some herbivores and other trophic groups are harvested. Signs within arrows (+ or -) indicate the *a priori* expected direction of change at each trophic level resulting from the predicted change at the trophic level immediately above. All proposed risk effects (right hand box) have been observed. Some presumed lethal effects (left hand box) have been observed while others have not (Fig. 2). We present here a simplified version of the outcomes that can result from purely risk and purely lethal effects. However, risk effects can also induce biomass reductions in prey species and lethal and risk effects often interact. Corresponding data in Fig. 2.

ratios of prey behaviour (red lines) vs. prey biomass (blue lines) to changes in predator biomass (Fig. 2) demonstrates that risk effects are greater in relative magnitude than any effects of direct predation that may be occurring in this system as a result of human fishing. Indeed, because any changes in prey biomass should be the result of the sum of lethal effects alone, risk effects alone (e.g. behavioural changes that result in density declines; Creel & Christianson, 2008) and the interaction of lethal and risk effects, it is unlikely that lethal effects are strong in this system. In contrast, changes in predation risk are the only plausible explanation for the observed behavioural changes.

Risk effects on herbivores in this system appear to be transmitted to primary producers and, potentially, to corals. Variation in macroalgal patchiness (i.e. spatial distribution, a presumed consequence of risk-averse foraging patterns; see Madin *et al.*, 2010a) differs substantially between unfished, predator-rich Palmyra and heavily fished, predator-depauperate Kiritimati. These effects cannot be explained by bottom-up forces, because there is no *a priori* expectation of altered small-scale spatial distribution of macroalgae due to higher overall productivity. The lack of a response in algal per cent cover is consistent with this conclusion. If herbivore density remains relatively stable over the fishing pressure gradient (Fig. 2) and per capita grazing pressure does not change, behavioural changes in the total area used by herbivores for grazing should change the relative intensities of grazing pressure on different areas of the benthos, but would not necessarily change net grazing pressure averaged over all areas. Given these predicted changes in the distribution, but not total amount, of grazing pressure and thus benthic algae, it is plausible that the changes in coral recruitment observed over the archipelago are a consequence of the observed differences in algal spatial heterogene-

ity. However, we cannot rule out that other factors, such as larval connectivity, site geomorphology, previous disturbance events and abiotic conditions, may partially or completely responsible for the patterns of coral recruitment seen in this system.

The Shark Bay ecosystem provides additional, experimental support for the role of risk effects in causing clear top-down effects on the benthic community. Herbivore biomass in this system does not appear to change significantly due to direct predation over space or time, yet herbivore behaviour varies significantly across microhabitats and times with different levels of predation risk (Box 2). These findings, coupled with experimental evidence of the role of risk-averse herbivore foraging behaviours in structuring the dominant primary producer assemblage (Burkholder *et al.*, 2013), point to risk effects as the predominant top-down mechanism of seagrass community regulation and spatiotemporal patterns of large vertebrate abundance in this system.

The results described above, both from our synthesis of two disparate field studies conducted over the same Line Islands gradient of human impact and from the Shark Bay ecosystem with natural predator fluctua-

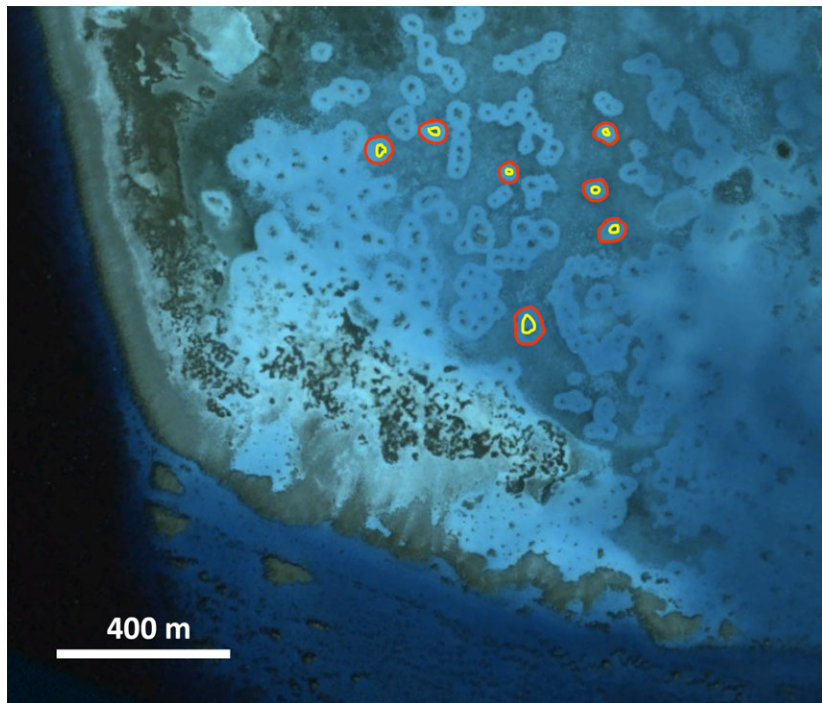


Fig. 4 Patterns of macroalgal (or seagrass) spatial distribution observed over landscape scales that are a likely consequence of risk effects on herbivores. A satellite image shows a shallow coral reef consisting in part of many small patch reefs (yellow circles) surrounded by 'grazing halos' (red circles). These highlighted examples represent only a few of the many grazing halos shown in the image. On patch reefs isolated from one another by sand or other open substrate, herbivores are known to concentrate their grazing in halos around their reef refugia, the likely result of antipredator behaviour to reduce their risk of predation, creating seaweed-free zones (i.e. grazing halos). Grazing halos therefore represent a likely consequence of a cascading, indirect risk effect – and one that may potentially be altered by human activities. Image location: Red Sea. Image copyright 2014 CNES/Astrium, ORION-ME and Google.

tions, demonstrate that, in an absolute sense, predator loss can lead to consistently greater risk effects than lethal effects in natural ecosystems. For this reason, risk effects may be expected to be more generally responsive to perturbations of predator populations (e.g. due to overfishing) than would be lethal effects alone. Theory, however, predicts that reduced resources for mesoconsumer populations could shift this balance towards greater impacts through lethal effects of predators due to condition-dependent risk-taking (e.g. Heithaus *et al.*, 2008).

Risk-based interaction pathways such as this could potentially be used to test the generality of human-induced risk effects in different ecosystems globally, while simultaneously elucidating fishing's indirect risk effects on marine landscapes. In structurally heterogeneous marine habitats, risk effects may lead to large, landscape-scale effects on benthic community structure. For example, on individual coral reefs separated from one another by unsheltered, presumably 'risky' areas, antipredator behaviours by fish and invertebrate herbivores have been suggested as the cause of large-scale patterns of heavily grazed vegetation, called 'grazing halos', surrounding coral patch reefs (Fig. 4; Randall, 1965; Ogden *et al.*, 1973; Armitage & Fourqurean, 2006; Madin *et al.*, 2011). Although risk has not previously been experimentally identified as the ultimate causative factor, one study of seagrass species coexistence within Caribbean grazing halos provides evidence that risk-sensitive foraging drives this pattern. This study showed that faster growing, presumably more palatable seagrass species are more readily consumed at a given distance (i.e. riskiness) from reef shelter than are less palatable species (Armitage & Fourqurean, 2006). All else being equal, herbivores are expected to trade off energy for reduced risk by avoiding riskier areas unless large foraging rewards (e.g. more palatable seagrass) are possible. The approach of Armitage & Fourqurean (2006), analogous to titrating risk for herbivores via 'giving up densities' (GUDs; Brown, 1988), suggests that herbivores vulnerable to predation risk will venture into risky areas to consume highly palatable resources but will not spend time there to consume less palatable resources. This result supports the long-held notion that risk is largely responsible for the formation and maintenance of grazing halos.

Synthesis and prospectus

It is now widely recognized that human activities have widespread effects on predation risk and that risk affects animal behaviour in many ways. Despite the strong suggestion from the collective body of evidence that human alteration of risk should lead to widespread

and diverse indirect effects, very few ocean-based studies have explicitly documented these linkages. We have presented synthetic evidence that indirect effects of human activity in natural ocean ecosystems can be dominated by risk effects. Based on this and the limited number of other examples from natural marine (and other) systems, we can begin to formulate predictions for where and when human alterations of risk may lead to cascading, indirect effects in oceans.

What lessons can be learned from other systems?

Large-scale commercial hunting for predators occurs, and continues to expand, in oceans (McCauley *et al.*, 2015). On land, such large-scale hunting has occurred historically, leading to the extirpation and extinction of numerous large carnivores (and herbivores) (Estes *et al.*, 2011). Today, due to dramatic population declines, efforts to re-establish carnivore (e.g. grey wolf (*Canis lupus*)) populations have led to measureable indirect risk effects, including changes in prey group size (Creel & Winnie, 2005), nutrition (Hernández & Laundré, 2005), reproductive physiology and demography (Creel *et al.*, 2007), and habitat selection (Creel & Winnie, 2005). Some evidence exists that wolf reintroduction has also indirectly led to changes in the distribution, density and height of vegetation that serves as the elk's food source (e.g. Ripple & Beschta, 2007; but see, e.g. Kauffman *et al.*, 2010; Winnie, 2012). These land-based patterns offer valuable insight into what can be expected in the ocean. The existing evidence from experimental marine systems (e.g. Bertness *et al.*, 2014) suggests that similar responses in marine animals' behaviour, physiology and resources may be expected. Indeed, analogous effects of predation risk on marine vegetation have been observed (Madin *et al.*, 2010a; Burkholder *et al.*, 2013), and this type of effect is predicted to scale up to landscape scales comparable to those seen on land (Figs 2 and 4; Madin *et al.*, 2011).

Most of the land-based examples above result from predator recovery or recolonization, whereas changes in risk in marine systems more frequently result from predator declines. This raises the question of what can be expected when risk is allowed to return to more natural levels in oceans, for example from effective species recovery plans and the establishment of numerous and large marine reserves. The answer may depend on the duration of previous human-induced changes in risk levels (i.e. whether they have occurred over ecological or evolutionary timescales). It may be that the longer the timescale of the change, the longer it may take for risk-induced responses to return to prehuman disturbance levels, a notion supported by comparison of Atlantic vs. Pacific coastal predator green crab

Table 1 Factors and characteristics expected to affect the likelihood of human impacts leading to cascading risk effects. Direction of influence refers to the likelihood of promoting (+) or diminishing (–) risk effect propagation through an ecosystem when considered in isolation. However, many other possible pathways and feedbacks exist and will affect these interactions, potentially creating feedbacks that could either accentuate or dampen the propagation of risk effects through ecosystems

Factor or characteristic	Rationale	Direction of influence	Evidence	Relevance to other systems
Turbidity/visibility	Higher turbidity/lower visibility means prey have diminished ability to assess risk, leading to more cautious behaviour under risky conditions	+	Terrestrial gerbils (Embar <i>et al.</i> , 2011) Strong risk effects seen in highly turbid Shark Bay system (Box 2)	Terrestrial: analogous to 'sightlines' Freshwater: directly relevant
Water chemistry	As seawater pH drops, prey and predators' abilities to detect one another and habitat complexity both decrease	–	Marine prey (Munday <i>et al.</i> , 2014) Marine predators (Allan <i>et al.</i> , 2013; Munday <i>et al.</i> , 2013; Dixson <i>et al.</i> , 2014) Freshwater prey (Leduc <i>et al.</i> , 2013) Marine benthic resources (shelter) (Madin <i>et al.</i> , 2008)	Terrestrial: potentially relevant to particulates and other air pollutants Freshwater: directly relevant
Shelter availability	Abundant shelter allows prey to mediate risk by hiding from predators (promoting risk effects and dampening lethal effects), whereas lack of shelter diminishes this ability (promoting lethal effects and dampening risk effects)	+	Marine prey and their food resources (Grabowski, 2004; Trussell <i>et al.</i> , 2006) Freshwater prey (Finstad <i>et al.</i> , 2007)	Terrestrial: directly relevant Freshwater: directly relevant
Predator and prey diet breadth	Generalist predators should induce behavioural responses in multiple prey species; generalist prey should affect multiple resource species	Generalist: + Specialist: –	Terrestrial prey (Schmitz, 1998) Strong risk effects from generalist predator in Shark Bay system (Box 2)	Terrestrial: directly relevant, despite lower proportion of generalist consumers than marine systems Freshwater: directly relevant
Prey (consumer) mobility and feeding rate	Mobile prey can respond behaviourally to risk over short timescales, decreasing likelihood of mortality and increasing likelihood of transmitting risk effects; mobile prey consumers capable of consuming large quantities of resource are particularly likely to transmit risk effects	Mobile and voracious: + Sedentary with limited food intake: –	Hypothesized, but not explicitly tested	Terrestrial: directly relevant Freshwater: directly relevant

Table 1 (continued)

Factor or characteristic	Rationale	Direction of influence	Evidence	Relevance to other systems
Predator and prey interaction strength	Ecosystem engineers and keystone species should disproportionately transmit both risk and lethal effects	+	Marine prey (Grabowski, 2004) 'Keystone in timidator' concept (Peckarsky <i>et al.</i> , 2008)	Terrestrial: directly relevant Freshwater: directly relevant
Ambient noise level	As ambient noise increases, prey and predators' abilities to detect one another via auditory cues decrease	-	Review of multiple taxa and systems (Weissburg <i>et al.</i> , 2014)	Terrestrial: highly directly relevant (given greater reliance on auditory predator/prey cues in terrestrial vs. marine systems) Freshwater: directly relevant

invasions that have occurred over different timescales (Long & Hay, 2012). Likewise, limited evidence suggests that behaviours that have been affected over ecological timescales may change in concert with increases in risk levels due to marine reserves (Madin *et al.*, 2012).

When does it matter most?

Understanding when and where human modifications to risk effects are most likely to ripple through marine communities (Table 1) is important. In general, the degree to which human activities lead to cascading risk effects is predicted to vary with the body condition of prey species (Heithaus *et al.*, 2008). When prey are in good condition, indirect risk effects should predominate, but when consumer body condition is poor, enhanced risk-taking should lead to pathways involving lethal effects. For this reason, species interactions – whether involving risk, direct predation or their interaction – will be modified by bottom-up factors, and these must be considered when making predictions about ecosystem responses to human activities.

Using this understanding of contingency in risk effects allows derivation of *a priori* predictions about likely impacts of changes to predator numbers – or other modifications of predation risk – due to human activities. For example, theory predicts that predator declines in resource-limited systems (as many terrestrial systems are; Burkepile, 2013) will lead to measurable but dampened effects on mesoconsumer and resource densities relative to habitats with more abundant prey resources (Heithaus *et al.*, 2008). Release from lethal effects is likely to play a relatively larger role in these systems (Wirsing *et al.*, 2014). Moreover, these effects are predicted to be of opposite signs in formerly risky vs. formerly safe microhabitats (Heithaus *et al.*, 2008). A critical question that remains, however,

in systems where risk effects are expected to be more important than consumptive effects is the relationship between remaining predator abundance (and size structure) and the strength of risk release.

What are the conservation implications of understanding risk effects?

To be effective, marine conservation and management policy must explicitly take risk effects and their cascading consequences into account for four key reasons (Dill *et al.*, 2003; Heithaus *et al.*, 2008, 2012). First, considering risk effects could enable early detection of human impacts because they may occur earlier and/or be a more reliable indicator of human impacts than purely lethal effects. For example, grazing halos (Fig. 4) on coral reefs might be expected to become less defined and/or larger as predator populations decline or size structures change (Madin *et al.*, 2011). Secondly, ignoring risk effects may lead to unanticipated effects on populations and communities that humans value. For example, changes in predation risk may affect where coral larvae can settle and grow by affecting coral–algal competition for reef substrate. In this case, humans could indirectly affect the very architecture of coral reefs. Third, changes in predator abundances can alter the ability of marine ecosystems to sequester atmospheric carbon (Wilmers *et al.*, 2012), and it has been hypothesized that this effect may also occur due to changes in the level of predation risk that herbivores face (Atwood *et al.*, 2015). Lastly, behavioural responses to anthropogenic changes in general may allow species to adjust – in both adaptive and maladaptive ways – to anthropogenic changes to marine environments (Wong & Candolin, 2014). Considering risk effects will allow us to anticipate and incorporate these impacts into conservation planning, ultimately increasing its likelihood of success.

What comes next?

Important areas for further investigation of cascading risk effects in marine ecosystems remain. For example, evidence clearly demonstrates that nonhuman variation in predation risk can shape marine communities (reviewed by Dill *et al.*, 2003; Heithaus *et al.*, 2008; Long & Hay, 2012; Benedetti-Cecchi & Trussell, 2014). Terrestrial studies provide strong evidence that risk can alter ecosystem properties, such as plant C:N content and decomposition rates (Hawlena *et al.*, 2012), and preliminary evidence suggests that the former may also occur in oceans (Burkholder *et al.*, 2013). The implications of changing patterns of risk (as opposed to predator abundance; Wilmers *et al.*, 2012) for oceanic carbon sequestration likewise remain undocumented. With greater research effort, it seems likely that pathways such as these stemming from human activity may ultimately be revealed.

More large-scale, long-term studies in natural marine ecosystems (e.g. Box 2) are needed to establish whether results derived from mesocosms or on land scale up and translate, respectively. For example, it is unclear whether animals needing to survive in the wild can invest as heavily in antipredator behaviour as their experimental laboratory counterparts (e.g. Lima & Bednekoff, 1999; Preisser *et al.*, 2005). Limited evidence suggests that relatively low predator densities can still induce reasonably large risk effects in nature (e.g. Box 2); whether this is a general phenomenon is unknown. Effective marine reserves, and especially networks of reserves, will likely become increasingly valuable as a research tool, whereby the impacts of changes in predator biomasses over space and time can be compared (e.g. Byrnes *et al.*, 2006; Madin *et al.*, 2010a; Januchowski-Hartley *et al.*, 2011).

How will climate change affect the likelihood of risk effects propagating through ocean ecosystems? Evidence shows that ocean acidification (i.e. elevated CO₂, leading to decreased ocean pH) may fundamentally affect some prey's risk detection, antipredator behaviour and survival abilities over both shorter (e.g. Munday *et al.*, 2014 and references therein) and longer term (Munday *et al.*, 2014) exposure. Predators' ability to capture prey can likewise be hampered (Allan *et al.*, 2013). The strength and nature of risk effects may also be affected by changing ocean temperatures, which can result in spatial and/or temporal biochemical and physiological asymmetries within species pairs (reviewed by Kordas *et al.*, 2011). In general, climate change is expected to lead to proximate ecological changes (such as individual-level behavioural responses) that ultimately lead to emergent responses in species distributions, productivity, diversity and

microevolution across populations and ecosystems (Harley *et al.*, 2006). What remains unknown is how pervasive these phenomena might be across taxa, if and how they scale up over space and time and, importantly, what other mechanisms of risk transmission might be affected by warmer, more acidic oceans.

It is critical to consider if and how human-altered risk may be shaping evolution in the oceans, for example through eco-evolutionary feedbacks in which interactions between ecological and evolutionary processes occur in contemporary time (Palkovacs, 2011). For example, predator invasion success depends on and affects evolutionary processes (e.g. Sih *et al.*, 2010). Likewise, marine predator harvest changes predator abundance and size structure, likely shaping selective forces on their prey from those favouring antipredator survival traits to those favouring competitive ability (Palkovacs, 2011).

The widespread historical removal of predators in many marine systems globally (Jackson *et al.*, 2001; Estes *et al.*, 2011) suggests that more predator *addition* experiments should be conducted – as well as the more common *exclusion* experiments – to understand how risk effects may have functioned in the past, prior to large-scale predator removal. Basing understanding of risk effects in marine systems from what can be observed in degraded marine systems today may lead to erroneous conclusions about their prevalence and strength (*sensu* the 'shifting baseline syndrome; Pauly, 1995).

Re-examining existing ecological data with explicit consideration of risk effects may prove useful for interpreting previous findings (Peckarsky *et al.*, 2008). For example, risk effects may explain patterns of coral recruitment that have so far been poorly understood (e.g. Sandin *et al.*, 2008; Figs 2–3).

Conclusions

The evidence presented here makes the compelling case that society must consider – in both research and policy – how humans affect marine systems by changing predation risk. Our review and synthesis of existing data has generated both novel conclusions and forward-looking predictions about how human-altered risk effects can cascade through marine ecosystems, even in the absence of apparent lethal effects. This suggests that our understanding of how human activities are shaping ocean ecosystems must consider the linkages between human activities and risk effects. It has been suggested that consideration of risk effects may even help to reconcile such fundamental ecological conundrums as top-down vs. bottom-up forcing (Laundré *et al.*, 2014).

Risk effects are rarely considered in ecosystem management and conservation planning (Creel & Christianson, 2008), but explicitly considering how humans affect risk and how these effects propagate through ecosystems may avoid many unfortunate 'surprises'. There are many examples throughout history of intentional predator introductions gone terribly wrong. With greater knowledge of indirect risk effects, such as unintended, often devastating consequences could likely have been prevented. Humans are unwittingly repeating history today over very large spatial scales with both direct introductions and climate-induced changes to marine predator ranges. Conversely, we are removing predators from marine ecosystems at unprecedented rates. In both cases, we are doing so with very little knowledge of the potential consequences of these actions. Considering these consequences is imperative.

Acknowledgements

We thank Donald Kramer for helpful discussion and Geoff Trussell and three anonymous reviewers for extremely valuable comments on an earlier version of the manuscript. EMPM was generously supported by the World Wildlife Fund's Kathryn S. Fuller Science for Nature Fund, an Australian Research Council DECRA Fellowship, and a US National Science Foundation International Postdoctoral Fellowship. LMD's work has been funded by NSERC Canada and the PADI Foundation. ADR was funded by a National Science Foundation Graduate Research Fellowship. MRH's work has been supported by the National Science Foundation. RRW gratefully acknowledges support as a Fulbright Senior Specialist, a programme administered by the Bureau of Educational and Cultural Affairs, United States Department of State with the cooperation of the Institute of International Education. Support was also provided by the Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO), which is supported by the Gordon and Betty Moore Foundation and the David and Lucile Packard Foundation. Symbols used in Figs 2 and 3 are courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols). Figs 2 and 3 were much improved by the artistic talents of Nicolle Fuller (www.sayostudio.com). This is PISCO contribution number 452 and Shark Bay Ecosystem Research Project contribution number 80.

Author contribution

EM led the study; EM and RW conceived the idea; EM, RW and AR wrote the first draft of the manuscript; MH designed Fig. 1; all authors contributed substantially to manuscript direction and revisions.

References

Abrams P (2007) Defining and measuring the impact of dynamic traits on interspecific interactions. *Ecology*, **88**, 2555–2562.

- Allan BJM, Domenici P, McCormick MI, Watson S-A, Munday PL (2013) Elevated CO₂ affects predator-prey interactions through altered performance. *PLoS ONE*, **8**, e58520.
- Armitage AR, Fourqurean JW (2006) The short-term influence of herbivory near patch reefs varies between seagrass species. *Journal of Experimental Marine Biology and Ecology*, **339**, 65–74.
- Atwood TB, Connolly RM, Ritchie EG *et al.* (2015) Predators help protect carbon stocks in blue carbon ecosystems. *Nature Climate Change*.
- Babcock RC, Shears NT, Alcalá AC *et al.* (2010) Decadal trends in marine reserves reveal differential rates of change in direct and indirect effects. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 18256–18261.
- Benedetti-Cecchi L, Trussell GC (2014) Intertidal Rocky Shores. In: *Marine Community Ecology and Conservation* (eds Bertness MD, Bruno JF, Silliman BR, Stachowicz JJ), pp. 203–225. Sinauer Associates, Sunderland, MA.
- Bertness MD, Brisson CP, Coverdale TC, Bevil MC, Crotty SM, Suglia ER (2014) Experimental predator removal causes rapid salt marsh die-off. *Ecology Letters*, **17**, 830–835.
- Bodey TW, Jessopp MJ, Votier SC *et al.* (2014) Seabird movement reveals the ecological footprint of fishing vessels. *Current Biology*, **24**, R514–R515.
- Brown JS (1988) Patch use as an indicator of habitat preference, predation risk, and competition. *Behavioral Ecology and Sociobiology*, **22**, 37–47.
- Brunnschweiler JM, Barnett A (2013) Opportunistic visitors: long-term behavioural response of bull sharks to food provisioning in Fiji. *PLoS ONE*, **8**, e58522.
- Burkepile DE (2013) Comparing aquatic and terrestrial grazing ecosystems: is the grass really greener? *Oikos*, **122**, 306–312.
- Burkholder DA, Heithaus MR, Fourqurean JW, Wirsing A, Dill LM (2013) Patterns of top-down control in a seagrass ecosystem: could a roving apex predator induce a behaviour-mediated trophic cascade? *The Journal of Animal Ecology*, **82**, 1192–1202.
- Byrnes J, Stachowicz JJ, Hultgren KM, Hughes RA, Olyarnik SV, Thornber CS (2006) Predator diversity strengthens trophic cascades in kelp forests by modifying herbivore behaviour. *Ecology Letters*, **9**, 61–71.
- Byrnes JE, Reynolds PL, Stachowicz JJ (2007) Invasions and extinctions reshape coastal marine food webs. *PLoS ONE*, **2**, e295.
- Cheung WWL, Sarmiento JL, Dunne J *et al.* (2012) Shrinking of fishes exacerbates impacts of global ocean changes on marine ecosystems. *Nature Climate Change*, **3**, 254–258.
- Creel S, Christianson D (2008) Relationships between direct predation and risk effects. *Trends in Ecology & Evolution*, **23**, 194–201.
- Creel S, Winnie JA (2005) Responses of elk herd size to fine-scale spatial and temporal variation in the risk of predation by wolves. *Animal Behaviour*, **69**, 1181–1189.
- Creel S, Christianson D, Liley S, Winnie JA (2007) Predation risk affects reproductive physiology and demography of elk. *Science*, **315**, 960.
- Dill LM, Heithaus MR, Walters CJ (2003) Behaviorally mediated indirect interactions in marine communities and their conservation implications. *Ecology*, **84**, 1151–1157.
- Dirzo R, Young HS, Galetti M, Ceballos G, Isaac NJB, Collen B (2014) Defaunation in the Anthropocene. *Science*, **345**, 401–406.
- Dixon DL, Jennings AR, Atema J, Munday PL (2015) Odor tracking in sharks is reduced under future ocean acidification conditions. *Global Change Biology*, **21**, 1454–1462.
- Estes JA, Terborgh J, Brashares JS *et al.* (2011) Trophic downgrading of planet Earth. *Science*, **333**, 301–306.
- Embar K, Kotler BP, Mukherjee S (2011) Risk management in optimal foragers: the effect of sightlines and predator type on patch use, time allocation, and vigilance in gerbils. *Oikos*, **120**, 1657–1666.
- Ferretti F, Worm B, Britten GL, Heithaus MR, Lotze HK (2010) Patterns and ecosystem consequences of shark declines in the ocean. *Ecology Letters*, **13**, 1055–1071.
- Finstad AG, Einum S, Forseth T, Ugedal O (2007) Shelter availability affects behaviour, size-dependent and mean growth of juvenile Atlantic salmon. *Freshwater Biology*, **52**, 1710–1718.
- Frid A, Dill LM (2002) Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology*, **6**, 11.
- Grabowski JH (2004) Habitat complexity disrupts predator-prey interactions but not the trophic cascade on oyster reefs. *Ecology*, **85**, 995–1004.
- Grabowski JH, Hughes AR, Kimbro DL (2008) Habitat complexity influences cascading effects of multiple predators. *Ecology*, **89**, 3413–3422.
- Harley CDG, Hughes AR, Hultgren KM *et al.* (2006) The impacts of climate change in coastal marine systems. *Ecology Letters*, **9**, 228–241.
- Hawlena D, Strickland MS, Bradford MA, Schmitz OJ (2012) Fear of predation slows plant-litter decomposition. *Science*, **336**, 1434–1438.

- Heithaus MR, Dill LM (2006) Does tiger shark predation risk influence foraging habitat use by bottlenose dolphins at multiple spatial scales? *Oikos*, **114**, 257–264.
- Heithaus MR, Frid A, Wirsing AJ *et al.* (2007) State-dependent risk-taking by green sea turtles mediates top-down effects of tiger shark intimidation in a marine ecosystem. *The Journal of Animal Ecology*, **76**, 837–844.
- Heithaus MR, Frid A, Wirsing AJ, Worm B (2008) Predicting ecological consequences of marine top predator declines. *Trends in Ecology & Evolution*, **23**, 202–210.
- Heithaus MR, Wirsing AJ, Burkholder D, Thomson J, Dill LM (2009) Towards a predictive framework for predator risk effects: the interaction of landscape features and prey escape tactics. *The Journal of Animal Ecology*, **78**, 556–562.
- Heithaus MR, Wirsing AJ, Dill LM (2012) The ecological importance of intact top-predator populations: a synthesis of 15 years of research in a seagrass ecosystem. *Marine and Freshwater Research*, **63**, 1039–1050.
- Heithaus MR, Alcoverro T, Arthur R *et al.* (2014) Seagrasses in the age of sea turtle conservation and shark overfishing. *Frontiers in Marine Science*, **1**, 1–6.
- Hernández L, Laundré JW (2005) Foraging in the “landscape of fear” and its implications for habitat use and diet quality of elk *Cervus elaphus* and bison *Bison bison*. *Wildlife Biology*, **11**, 215–220.
- Heupel MR, Knip DM, Simpfendorfer CA, Dulvy NK (2014) Sizing up the ecological role of sharks as predators. *Marine Ecology Progress Series*, **495**, 291–298.
- Jackson JBC, Kirby MX, Berger WH *et al.* (2001) Historical overfishing and the recent collapse of coastal ecosystems. *Science*, **293**, 629–637.
- Januchowski-Hartley FA, Graham NAJ, Feary DA, Morove T, Cinner JE (2011) Fear of fishers: human predation explains behavioral changes in coral reef fishes. (ed Clifton J). *PLoS ONE*, **6**, e22761.
- Kauffman M, Brodie J, Jules E (2010) Are wolves saving Yellowstone’s aspen? A landscape-level test of a behaviorally mediated trophic cascade. *Ecology*, **91**, 2742–2755.
- Kordas RL, Harley CDG, O’Connor MI (2011) Community ecology in a warming world: the influence of temperature on interspecific interactions in marine systems. *Journal of Experimental Marine Biology and Ecology*, **400**, 218–226.
- Laundré JW, Hernández L, Lopex Medina P *et al.* (2014) The landscape of fear: the missing link to understand top-down and bottom-up controls of prey abundance? *Ecology*, **95**, 1141–1152.
- Leduc AOHC, Munday PL, Brown GE, Ferrari MCO (2013) Effects of acidification on olfactory-mediated behaviour in freshwater and marine ecosystems: a synthesis. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, **368**, 1–14.
- Lehtiniemi M, Lindén E (2006) *Cercopagis pengoi* and *Mysis* spp. alter their feeding rate and prey selection under predation risk of herring (*Clupea harengus* membras). *Marine Biology*, **149**, 845–854.
- Leonard GH, Bertness MD, Yund PO (1999) Crab predation, waterborne cues, and inducible defenses in the blue mussel, *Mytilus edulis*. *Ecology*, **80**, 1–14.
- Lima SL (1998) Nonlethal effects in the ecology of predator-prey interactions. *BioScience*, **48**, 25–34.
- Lima SL, Bednekoff PA (1999) Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. *The American Naturalist*, **153**, 649–659.
- Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, **68**, 619–640.
- Long JD, Hay ME (2012) The impact of trait-mediated indirect interactions in marine communities. In: *Trait-Mediated Indirect Interactions: Ecological and Evolutionary Perspectives* (eds Ohgushi T, Schmitz OJ, Holt RD), pp. 47–68. Cambridge University Press, Cambridge.
- Lönngstedt OM, McCormick MI, Chivers DP (2013) Predator-induced changes in the growth of eyes and false eyespots. *Scientific Reports*, **3**, 2259.
- Luttbegg B, Rowe L, Mangel M (2003) Prey state and experimental design affect relative size of trait- and density-mediated indirect effects. *Ecology*, **84**, 1140–1150.
- Madin JS, Donnell MJO, Connolly SR (2008) Climate-mediated mechanical changes to coral assemblages. *Biology Letters*, **1**, 4.
- Madin EMP, Gaines SD, Madin JS, Warner RR (2010a) Fishing indirectly structures macroalgal assemblages by altering herbivore behavior. *The American Naturalist*, **176**, 785–801.
- Madin EMP, Gaines SD, Warner RR (2010b) Field evidence for pervasive indirect effects of fishing on prey foraging behavior. *Ecology*, **91**, 3563–3571.
- Madin EMP, Madin JS, Booth DJ (2011) Landscape of fear visible from space. *Scientific Reports*, **1**, 14.
- Madin EMP, Gaines SD, Madin JS, Link A-K, Lubchenco PJ, Selden RL, Warner RR (2012) Do behavioral foraging responses of prey to predators function similarly in restored and pristine foodwebs? *PLoS ONE*, **7**, e32390.
- Magnhagen C (1990) Reproduction under predation risk in the sand goby, *Pomatoschistus minutus*, and the black goby, *Gobius niger*: the effect of age and longevity. *Behavioral Ecology and Sociobiology*, **26**, 331–335.
- McCaulley DJ, Pinsky ML, Palumbi SR, Estes JA, Joyce FH, Warner RR (2015) Marine defaunation: animal loss in the global ocean. *Science*, **347**, 1255641–1–1255641–7.
- McIntyre JK, Baldwin DH, Beauchamp DA, Scholz NL (2012) Low-level copper exposures increase visibility and vulnerability of juvenile coho salmon to cutthroat trout predators.
- Metcalfe NB, Huntingford FA, Thorpe JE (1987) The influence of predation risk on the feeding motivation and foraging strategy of juvenile Atlantic salmon. *Animal Behaviour*, **35**, 901–911.
- Molnar JL, Gamboa RL, Revenga C, Spalding MD (2008) Assessing the global threat of invasive species to marine biodiversity. *Frontiers in Ecology and the Environment*, **6**, 485–492.
- Mukherjee S, Heithaus MR (2013) Dangerous prey and daring predators: a review. *Biological Reviews of the Cambridge Philosophical Society*, **88**, 550–563.
- Munday PL, Pratchett MS, Dixon DL, Donelson JM, Endo GGK, Reynolds AD, Knuckey R (2013) Elevated CO₂ affects the behavior of an ecologically and economically important coral reef fish. *Marine Biology*, **160**, 2137–2144.
- Munday PL, Cheal AJ, Dixon DL, Rummer JL, Fabricius KE (2014) Behavioural impairment in reef fishes caused by ocean acidification at CO₂ seeps. *Nature Climate Change*, **4**, 487–492.
- Myers RA, Worm B (2003) Rapid worldwide depletion of predatory fish communities. *Nature*, **423**, 280–283.
- Ogden J, Brown R, Salesky N (1973) Grazing by the echinoid *Diadema antillarum* philippi: Formation of Halos around West Indian Patch Reefs. *Science*, **182**, 715–717.
- Palkovacs EP (2011) The overfishing debate: an eco-evolutionary perspective. *Trends in Ecology & Evolution*, **26**, 616–617.
- Parsons DM, Eggleston DB (2006) Human and natural predators combine to alter behavior and reduce survival of Caribbean spiny lobster. *Journal of Experimental Marine Biology and Ecology*, **334**, 196–205.
- Pauly D (1995) Anecdotes and the shifting baseline syndrome of fisheries. *Trends in Ecology & Evolution*, **10**, 430.
- Peckarsky BL, Abrams PA, Bolnick DI *et al.* (2008) Revisiting the classics: considering nonconsumptive effects in textbook examples of predator-prey interactions. *Ecology*, **89**, 2416–2425.
- Peh KS-H (2015) South China Sea conflict could harm marine environment. *Frontiers in Ecology and the Environment*, **13**, 299–300.
- Preisser E, Bolnick D, Benard M (2005) Scared to death? The effects of intimidation and consumption in predator-prey interactions. *Ecology*, **86**, 501–509.
- Randall JE (1965) Grazing effect on sea grasses by herbivorous reef fishes in the West Indies. *Ecology*, **46**, 255–260.
- Ripple WJ, Beschta RL (2007) Restoring Yellowstone’s aspen with wolves. *Biological Conservation*, **138**, 514–519.
- Ripple WJ, Estes JA, Beschta RL *et al.* (2014) Status and ecological effects of the world’s largest carnivores. *Science*, **343**, 1241484.
- Ritchie EG, Johnson CN (2009) Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters*, **12**, 982–998.
- Sandin SA, Smith JE, Demartini EE *et al.* (2008) Baselines and degradation of coral reefs in the northern Line Islands. *PLoS ONE*, **3**, e1548.
- Schmitz O (1998) Direct and indirect effects of predation and predation risk in old-field interaction webs. *The American Naturalist*, **151**, 327–342.
- Schmitz OJ, Krivan V, Ovadia O (2004) Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecology Letters*, **7**, 153–163.
- Shackell NL, Frank KT, Fisher JAD, Petrie B, Leggett WC (2010) Decline in top predator body size and changing climate alter trophic structure in an oceanic ecosystem. *Proceedings of the Royal Society B: Biological Sciences*, **277**, 1353–1360.
- Sih A, Bolnick DI, Luttbegg B *et al.* (2010) Predator-prey naïveté, antipredator behavior, and the ecology of predator invasions. *Oikos*, **119**, 610–621.
- Sorte CJB, Williams SL, Carlton JT (2010) Marine range shifts and species introductions: comparative spread rates and community impacts. *Global Ecology and Biogeography*, **19**, 303–316.
- Stallings CD (2008) Indirect effects of an exploited predator on recruitment of coral-reef fishes. *Ecology*, **89**, 2090–2095.
- Steneck RS, Vavrinc J, Leland AV (2004) Accelerating trophic-level dysfunction in kelp forest ecosystems of the Western North Atlantic. *Ecosystems*, **7**, 323–332.
- Stevenson C, Katz LS, Micheli F *et al.* (2006) High apex predator biomass on remote Pacific islands. *Coral Reefs*, **26**, 47–51.
- Trussell GC, Ewanchuk PJ, Matassa CM (2006) Habitat effects on the relative importance of trait- and density-mediated indirect interactions. *Ecology Letters*, **9**, 1245–1252.

- Veale L, Hill A, Brand A (2000) An in situ study of predator aggregations on scallop (*Pecten maximus* (L.)) dredge discards using a static time-lapse camera system. *Journal of Experimental Marine Biology and Ecology*, **255**, 111–129.
- Weissburg M, Smee D, Ferner M (2014) The sensory ecology of nonconsumptive predator effects. *The American Naturalist*, **184**, 141–157.
- Werner EE, Peacor SD (2003) A review of trait-mediated indirect interactions in ecological communities. *Ecology*, **84**, 1083–1100.
- Werner E, Peacor S (2006) Lethal and nonlethal predator effects on an herbivore guild mediated by system productivity. *Ecology*, **87**, 347–361.
- Wilmers CC, Estes JA, Edwards M, Laidre KL, Konar B (2012) Do trophic cascades affect the storage and flux of atmospheric carbon? An analysis of sea otters and kelp forests. *Frontiers in Ecology and the Environment*, **10**, 409–415.
- Winnie JA (2012) Predation risk, elk, and aspen: tests of a behaviorally mediated trophic cascade in the Greater Yellowstone Ecosystem. *Ecology*, **93**, 2600–2614.
- Wirsing AJ, Heithaus MR, Dill LM (2007a) Fear factor: do dugongs (*Dugong dugon*) trade food for safety from tiger sharks (*Galeocerdo cuvier*)? *Oecologia*, **153**, 1031–1040.
- Wirsing AJ, Heithaus MR, Dill LM (2007b) Can you dig it? Use of excavation, a risky foraging tactic, by dugongs is sensitive to predation danger. *Animal Behaviour*, **74**, 1085–1091.
- Wirsing AJ, Heithaus MR, Frid A (2014) Cross-fertilizing aquatic and terrestrial research to understand predator risk effects. *WIREs Water*, **1**, 439–448.
- Wong BBM, Candolin U (2014) Behavioral responses to changing environments. *Behavioural Ecology*, **26**, 665–673.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1 Examples of human activities (or outcomes of human activities) that affect predation risk and resource needs/availability and resulting direction of change in net predation risk for prey.