

REVIEW

Behavioural drivers of the ecological roles and importance of marine mammals

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ABSTRACT: Marine mammals feed at a variety of trophic levels, occur from freshwater to open-ocean ecosystems and are found across virtually all latitudes. Due to their high historical, and sometimes present-day, abundances, capability for large-scale movements and high metabolic rates, they have the potential to affect the structure and function of ecosystems through a variety of mechanisms over both ecological and evolutionary time. Usually, the effects of marine mammals on ecosystems are explicitly or implicitly considered to occur through their ability to remove prey through direct predation. Recent empirical studies and a rich theoretical framework, however, demonstrate that marine mammals can affect ecosystems through more diverse pathways, including those that are driven by marine mammal behaviour. Thus, non-consumptive effects of and on marine mammals may be critical in shaping their ecological importance. Non-consumptive effects may include risk effects, whereby predators induce costly changes to prey behaviour that impact prey population sizes or the magnitude and spatiotemporal patterns of prey impacts on communities (e.g. behaviour-mediated trophic cascades). Changes in the abundance of large apex predators (both marine mammals and sharks) and the introduction of perceived and real risks (human disturbance) may also affect behaviours of marine mammals and their prey that cascade to the wider ecosystem; the conditions under which such cascading effects might be most important, however, remain poorly understood. Other behaviour-driven ecological roles of marine mammals may include foraging tactics that facilitate the foraging of other species (especially seabirds), translocating nutrients and linking the dynamics of spatially distinct food webs.

KEY WORDS: Marine mammals · Risk effects · Behaviourally mediated indirect interactions · BMII · Nutrient transport · Behavioural facilitation

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INTRODUCTION

Understanding the ecological roles and importance of marine megafauna is becoming increasingly crucial in light of both historical and ongoing anthropogenic changes to both their populations and those of their prey and predators (e.g. Lewison et al. 2004, Estes 2006, Read et al. 2006, Heithaus et al. 2008,

2010, Ferretti et al. 2010, Roman et al. 2014). Among megafaunal taxa, marine mammals (cetaceans, pinnipeds, sirenians, marine otters *Lontra felina*, sea otters *Enhydra lutris* and polar bears *Ursus maritimus*) are of particular interest for several reasons. First, they have the potential to consume considerable portions of primary production in a system owing to their large body sizes, potentially high

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abundances and high metabolic rates (Katona & Whitehead 1988, Bowen 1997, Roman et al. 2014). Second, with ca. 128 species ranging in size from 14–45 kg sea otters to 150–170 t blue whales *Balaenoptera musculus*, marine mammals fill a broad range of ecological niches including herbivores (sirenians), benthic invertivores (grey whales *Eschrichtius robustus*, walrus *Odobenus rosmarus*), batch-feeders on plankton and small schooling fish (balaenopterid whales) and both intermediate (most pinnipeds and cetaceans) and truly apex carnivores (e.g. mammal-eating killer whales *Orcinus orca* and polar bears). Third, marine mammals occur in all oceans from polar to tropical regions, and from coastal to oceanic waters extending from the surface to depths exceeding 2500 m for some deep-diving species such as Cuvier's beaked whales *Ziphius cavirostris* (Schorr et al. 2014). Some species even inhabit freshwater riverine systems and lakes (Leatherwood et al. 1983). Because of their tolerance for a broad range of conditions and the high movement capacity of some species such as humpback whales *Megaptera novaeangliae* (Dawbin 1966), sperm whales *Physeter macrocephalus* (Whitehead 2003) and killer whales (Durban & Pitman 2012), marine mammals have the potential to exert their effects on a diversity of ecosystems, in a variety of contexts and across broad spatial scales (Roman et al. 2014). Fourth, marine mammal populations are undergoing both declines and recoveries in many locations around the world (Magera et al. 2013), necessitating a functional understanding of their ecological roles and importance to predict the consequences of these changes.

To date, most ecological studies of marine mammals have focused on describing their diets and foraging behaviour (e.g. Bowen et al. 2002, Sargeant et al. 2005) and on how their distributions, abundances and behaviours are affected by both abiotic (physiographic and dynamic oceanographic variables; e.g. Forney 2000, Mannocci et al. 2014, and see Gregr et al. 2013 for a review) and biotic factors (e.g. prey availability or, more often, proxies of prey abundance and predation risk; Thompson et al. 1991, Heithaus & Dill 2002, Wirsing et al. 2008). Recently, considerable attention also has been focused on understanding how anthropogenic disturbance affects abundance and behaviour of marine mammals (Bejder et al. 2006, Lusseau & Bejder 2007, Holt et al. 2011, Pirotta et al. 2015), and the potential for global climate change to induce distribution shifts (e.g. MacLeod 2009). Although there are notable exceptions, the ecological roles marine mammals play in communities, and especially the potential for changes in their

abundance to affect the distribution and abundance of their prey and the structure and function of wider ecosystems, require further investigation (but see Bowen 1997, Estes et al. 1998, Gerber et al. 2009, Morissette et al. 2010, 2012, Roman et al. 2014).

Species' ecological roles in communities are typically defined in terms of feeding relationships despite the fact that a species' role also includes a variety of non-feeding interactions including facilitation and habitat modification (Paine 1980, Kéfi et al. 2012). Yet, especially from the standpoint of conservation and management, a more encompassing view is critical to predicting how changes in the abundance of particular species will affect populations of their food sources, competitors and, ultimately, the structure and function of ecosystems (Heithaus et al. 2008). Many marine mammals are upper trophic level consumers. Thus, as a group, they are often referred to in the literature and popular press as 'top' or 'apex' predators. Those that are apex predators can affect prey populations and ecosystems 'from the top down' by consuming and/or altering the traits of other species (Heithaus et al. 2008, Wirsing et al. 2008). Yet, most marine mammals are also prey (Stirling 1984, Estes et al. 1998, Reidman 1990, Heithaus 2001, Heithaus & Dill 2002, Weller 2009, Ford et al. 2011). Their predators include a wide range of species, including other marine mammals (primarily killer whales, polar bears and several pinnipeds), sharks (primarily *Lamnidae* spp., *Hexanchidae* spp. and *Carcharhinidae* spp.), crocodiles (*Crocodylus* spp.), a diversity of terrestrial carnivores and a few bird species (Reeves et al. 1992, Heithaus 2001, Weller 2009). In their role as mesopredators (or mesoconsumers), marine mammals could be important in affecting populations or behaviours of their predators 'from the bottom up' as well as in transmitting the effects of larger predators to lower trophic levels (a top-down effect).

Not all roles of marine mammals will involve predator–prey interactions. For example, cetaceans and possibly some pinnipeds may facilitate the foraging of other species, like seabirds but also humans, by making previously unavailable prey accessible or preventing the escape of these species to deeper waters (Evans 1982, Pitman & Ballance 1992, Bräger 1998, Dill et al. 2003, Anderson & Lovvorn 2008). Also, marine mammals might facilitate 'bottom-up' stimulation of primary production by promoting nutrient cycling and serve as mobile vectors for the transport of nutrients across microhabitats and ecosystem boundaries (Kanwisher & Ridgway 1983, Katona & Whitehead 1988, Preen 1995, Smetacek & Nicol 2005, Lavery et al. 2010, Smith et al. 2013, Roman et al. 2014).

To distinguish a species' role from its ecological importance, we here refer to a species' ecological importance as the consequences of a substantial change in a species' abundance that will in turn affect communities and ecosystems while its role includes its trophic position and interactions regardless of how critical it is to the wider functioning of ecosystems (Heithaus et al. 2010). Existing studies of the ecological importance of marine mammals derive primarily from bioenergetic models that can be used to estimate food requirements and potential biomass removal rates of prey (e.g. Furness 1984, Winship et al. 2002, Smout et al. 2014) and ecosystem models that predict the broader ecosystem consequences of marine mammal removals (Libralato et al. 2006, Gerber et al. 2009). These models can quantify the magnitude of trophic overlap between marine mammals and fisheries and, consequently, have been the basis for management of both marine mammal populations and anthropogenic harvest. Although these models do include some behavioural dynamics, the means by which behaviour—both of marine mammals and their prey—shapes the ecological roles and importance of marine mammals remain understudied and underappreciated.

Myriad behavioural decisions can affect a species' role and importance. Patterns of habitat use and movements, grouping, food selection, and specific foraging tactics can all shape the spatiotemporal pattern and strength of a species' ecological interactions. Of particular importance to elucidating the links between marine mammal behaviour and ecological dynamics, therefore, is understanding the factors that drive behaviour. Such an appreciation is especially critical for predicting how changing ecological conditions, both biotic and abiotic, will ultimately affect ecological dynamics through behavioural shifts in marine mammals. While there have been numerous studies of factors influencing marine mammal behaviour, often underappreciated is the possibility that marine mammal behaviour may be shaped by predation risk (e.g. Norris & Dohl 1980, Corkeron & Connor 1999, Heithaus 2001, Heithaus & Dill 2002, Ford & Reeves 2008, and see Wirsing et al. 2008 for a review). Because of the central role predation risk can play in a wide array of behavioural decisions (see Lima & Dill 1990), we first update our understanding of risk effects on and by marine mammals. Then, we more broadly review how these, and other behaviours, of marine mammals may affect their ecological roles and importance. Our goal is to provide a framework for future studies on behaviour-mediated effects of marine mammals on aquatic ecosystems.

RISK EFFECTS

Interaction webs include bottom-up and top-down processes, both direct and indirect. Recently, Estes et al. (2011) argued that strong top-down effects of large predators are likely the rule rather than the exception based on the broad-scale community rearrangements that accompany the loss or reintroduction of top predators. There remains, however, debate about the generality of top-down control and the degree to which top-down effects are transmitted by direct predation or non-consumptive pathways (often referred to as 'risk effects;' see Heithaus et al. 2008, Peckarsky et al. 2008, Kauffman et al. 2010, Winnie 2012, Middleton et al. 2013).

Most animals have a diverse suite of behaviours to reduce the probability of being killed by a predator (see Lima & Dill 1990, Brown & Kotler 2004 for reviews). A number of studies have highlighted that investment in these anti-predator behaviours can be substantial, even when predator-inflicted mortality is rare (Lima & Dill 1990, Creel & Christianson 2008, Heithaus et al. 2008, Creel 2011). Such behaviours may include shifts in activity and habitat use, changes in group size, modification of foraging rates or prey selection and increased vigilance (Lima & Dill 1990, Heithaus et al. 2007a, Wirsing et al. 2007a,b, 2010). Behavioural reactions to predator presence or attack range from immediate responses to threats to changes in habitat and resource use at ecological or evolutionary time scales (e.g. Lima & Dill 1990, Brown & Kotler 2004). The specific nature of behavioural responses to risk, however, depends on multiple factors and how they influence probabilities in the steps of a predator-prey interaction. For example, prey escape tactics, physical features of habitat (e.g. depth, visibility) and predator hunting mode can singly, or through all possible interactions, affect the nature and magnitude of 'risk effects' (Heithaus et al. 2009, Wirsing et al. 2010).

In general, risk effects can result in lost foraging or reproductive opportunities and reduced energy intake and growth rates that could impair reproduction (e.g. Lima & Dill 1990, Brown & Kotler 2004, Creel & Christianson 2008). The presence of predators may induce stress that can negatively impact reproduction without influencing foraging (Creel 2011, Mukherjee et al. 2014). Because risk effects are often experienced by large proportions of populations, relative to direct predation, in some cases, risk effects of predators may equal or exceed the impacts of direct predation on prey populations (Werner & Peacor 2003, Schmitz et al. 2004, Preisser et al. 2005,

Heithaus et al. 2008, Creel 2011). Importantly, however, consumptive and non-consumptive effects cannot be completely separated and often the interaction of these 2 effects has a larger impact than either mechanism in isolation (e.g. Werner & Peacor 2003, Heithaus et al. 2008). For example, effective anti-predator behaviour may result in lost body condition due to lower foraging rates that, in turn, induces compromised individuals to take greater risks that may result in their falling victim to predators (Sinclair & Arcese 1995, Heithaus et al. 2008).

Risk effects on marine mammals (marine mammals as prey)

Anti-predator behaviour has been documented in numerous marine mammal taxa (see also Ford & Ellis 1999, Wirsing et al. 2008, Heithaus & Dill 2009). Although most documented anti-predator behaviour involves acute responses to predator presence, a growing number of studies focused on behaviours that reduce risk over longer temporal scales, such as habitat shifts or changes in group size. Short-term responses to risk include flight, changes in grouping, or in some cases attacking or mobbing of predators (Heithaus & Dill 2009). For example, beaked whales exposed to playbacks of killer whale vocalizations moved directionally away from the sound source suggesting avoidance (Allen et al. 2014). Bottlenose dolphins *Tursiops cf. aduncus* approached by a ca. 3 m long white shark *Carcharodon carcharias* exhibited a more extreme response, leaping away from the shark for a prolonged period (Connor & Heithaus 1996). Similarly, in the north-eastern Pacific, immediate risk from killer whales induces groups of harbour porpoises *Phocoena phocoena* and Dall's porpoises *Phocoenoides dalli* to coalesce while making high-speed directional escape manoeuvres towards shallow waters (Jefferson et al. 1991, Ford & Ellis 1999). During attacks from predators, some large baleen whales shift habitats. During their northbound migration from calving to feeding grounds, grey whales travel close to shallow waters along the shoreline when attacked by killer whales (Barrett-Lennard et al. 2011). It appears that the behavioural responses of mysticetes to direct predatory attacks generally take the form of either physical defence (fight) or escape (flight, Ford & Reeves 2008). The former tactic is adopted by species with robust bodies and slow swimming speeds (e.g. grey whales, right whales *Eubalaena* spp., humpback whales), while the latter is used by fast-swimming species with

streamlined body shapes (rorqual whales other than humpback whales). In sperm whales, antipredator behaviours include rosette formation (or a 'marguerite', with heads together and tails out) to deter killer whales (Pitman et al. 2001, Whitehead 2003).

Over longer time periods, habitat shifts and group formation appear to be the most common tactics for reducing risk. For example, group living — especially in delphinids (Norris & Dohl 1980, Heithaus 2001) but also for pinnipeds (Nordstrom 2002) hauling-out on shore where terrestrial predators are common — is likely a response to predation risk. Among harbour seals *Phoca vitulina*, larger haul-out groups are more likely to detect predators (Da Silva & Terhune 1988). In delphinids, group sizes generally increase with distance from shore (which may be a proxy for predation danger, Gygax 2002) and also tend to be lowest in species that experience minimal predation risk (e.g. river dolphins; Gomez-Salazar et al. 2012). There are, however, many drivers of group size beyond predation risk, including foraging and social considerations (Baird & Dill 1996, Connor et al. 1998). Many odontocetes exhibit fission–fusion dynamics that allow individuals to move among group sizes based on their current activities, with resting groups usually being larger than foraging groups in the same habitats (e.g. Heithaus & Dill 2002). Risk may also structure the nature of fission–fusion dynamics within species. For example, spinner dolphins *Stenella longirostris* around the main Hawaiian Islands apparently exhibit fission–fusion dynamics because individuals moving between groups have ready access to nearshore resting habitats that are relatively safe from sharks. In Midway Atoll (far-western Hawaii), on the other hand, the prevalence of open water where shark risk is high putatively leaves dolphins travelling alone with few options for resting and, as a result, promotes considerably higher group stability (Karczmarski et al. 2005). Interestingly, predation risk can also drive sympatric marine mammals to form temporary mixed-species aggregations, or associations of individuals of different species involved in similar activities. Associations between spinner and pantropical spotted dolphins *S. attenuata* in the eastern tropical Pacific and the western Indian Oceans (Perrin et al. 1973, Ballance & Pitman 1998) appear to provide protection against predators, including large sharks and other delphinids (Norris & Dohl 1980, Scott & Cattanach 1998, Kiszka et al. 2011). For example, around the Mozambique Channel island of Mayotte (SW Indian Ocean), spinner dolphins use deeper waters off the barrier reef where pantropical spotted dolphins are most

abundant, and associate with spotted dolphins when transiting between resting or socializing areas (Kiszka et al. 2011). Mixed-species groups also form for other reasons, including foraging and social benefits (Stensland et al. 2003 for a review), and further work on such dynamics in odontocetes is needed to determine their relative importance.

At the evolutionary scale, killer whale predation risk may have been the primary selective factor favouring the use of communication and echolocation sounds by a range of small cetacean species, including phocoenids, delphinids and kogiids, that killer whales hear poorly or not at all (Morisaka & Connor 2007). Predation risk also appears to have helped to shape migratory routes and seasonal movements of some marine mammals, including large whales. For instance, humpback whales embark on what are the longest known mammal migrations from low-latitude breeding to high-latitude feeding grounds (Dawbin 1966, Whitehead & Moore 1982); in so doing, they undoubtedly pay substantial energetic costs (Stone et al. 1990). Corkeron & Connor (1999) suggested that elevated predation risk from killer whales at high latitudes may have contributed to the evolution of whale migrations where they annually abandon productive foraging grounds to reproduce at safer latitudes. Risk effects are also likely to drive daily movements of some marine mammals. In the tropics, spinner dolphins enter atolls, sheltered bays and lagoons through reef channels in the morning for resting and socializing, and leave in the afternoon to feed offshore overnight (Norris & Dohl 1980, Gannier & Petiau 2006), primarily on mesopelagic prey such as myctophids (Perrin et al. 1973, Dolar et al. 2003). This daily movement pattern is likely to have been driven by predation risk by large sharks in the oceanic environment (Norris & Dohl 1980, Heithaus 2001). Similarly, when at risk from killer whales, dusky dolphins *Lagenorhynchus obscurus* off Kaikoura, New Zealand, exhibit diel movements between relatively safe inshore resting areas and more dangerous offshore feeding areas (Srinivasan & Markowitz 2009).

Predation risk may influence diving behaviour of numerous species, which could, in turn, influence energetics, prey selection and habitat use (Heithaus & Frid 2003, Frid et al. 2007a), thereby modifying the ecological roles of marine mammals diving under the risk of predation. Although rarely considered for marine mammals, predation risk-sensitive diving could be one explanation for discrepancies between observed diving behaviour and that predicted by optimal diving models based solely on energetic cur-

rencies (Frid et al. 2007a). While the specific changes in diving behaviour made in response to predation risk may vary with factors including the type of predator and the relationship between diving time and energy intake rate (Heithaus & Frid 2003), several studies suggest that marine mammals do account for risk when making diving decisions. Northern elephant seals *Mirounga angustirostris* appear to modify their diving behaviour when they depart from and arrive at haul-out sites under risk from white sharks, spending a greater amount of time swimming along the bottom (Le Boeuf & Crocker 1996). In Prince William Sound, Alaska, diving harbour seals underutilise relatively rich fish resources in deep strata by reducing the number of dives to, and time spent per dive at, depths used by Pacific sleeper sharks *Somniosus pacificus* (Frid et al. 2007a,b). Similarly, juvenile Steller sea lions *Eumetopias jubatus* in western Alaska underutilise either predictable or profitable prey species such as wall-eye pollock *Theragra chalcogramma* and Pacific herring *Clupea pallasii* depending on the relative predation risk posed by mammal-eating killer whales, Pacific sleeper sharks and/or larger conspecifics (Frid et al. 2009). In the context of Steller sea lion decline in western Alaska, such information is critical to better predict how these predators can respond both to natural and anthropogenic drivers (e.g. prey depletion due to fisheries) of habitat and resource selection, respectively. Shifts in diving patterns in response to predation risk, however, may be hard to detect without explicitly studying spatio-temporal patterns in predation risk. For example, dugongs *Dugong dugon* in the seagrass ecosystem of Shark Bay, Western Australia, modify their surfacing patterns in response to changing predation risk, but only when engaged in specific, risky, foraging tactics (Wirsing et al. 2011).

Numerous marine mammals have been documented making spatial shifts to reduce the risk of predation. In Shark Bay, both Indo-Pacific bottlenose dolphins *T. aduncus* and dugongs exposed to the threat of tiger shark *Galeocerdo cuvier* predation risk sacrifice food that is abundant over shallow seagrass banks (fish and seagrass, respectively) and instead spend a disproportionate amount of time foraging in the relative safety of deeper waters, which are less productive (Heithaus & Dill 2002, Wirsing et al. 2007a,b). For dolphins, habitat use is also activity-specific. Resting dolphins are found almost exclusively in safer deeper waters (Heithaus & Dill 2002). In this system, risk induces habitat shifts at multiple spatial scales. In both species, indi-

viduals that continue to forage in shallow habitats during periods of high risk avoid foraging over the interior of seagrass meadows (ca. 80% of the total seagrass area) relative to safer bank edges (Heithaus & Dill 2006, Wirsing et al. 2007a, see Heithaus et al. 2012 for a review). Around Seal Island (South Africa), Cape fur seal *Arctocephalus pusillus pusillus* adults avoid habitats where the risk of great white shark predation is elevated following sunrise (De Vos & O’Riain 2010). Behavioural tactics adopted by adult fur seals seem to account for the variance in risk from great white sharks, whereas sharks seem to be influenced by behavioural decisions made by juveniles, which adopt the riskiest movement tactics (swimming alone or in small groups around dawn), highlighting the need for accounting for subgroups within a population when modelling predator–prey interactions (Laroche et al. 2008). Recent evidence also indicates that refugia play an important role in shaping interactions between great white sharks and Cape fur seals, suggesting that seals adjust their anti-predator response as a function of landscape features. Indeed, during periods of high shark abundance, seals tend to reduce their use of open waters and increase their presence in more complex habitats, including kelp forests and shallow reefs (Weisel et al. 2015).

Terrestrial predators also induce habitat shifts in marine mammals, especially pinnipeds. For example, experimental approaches demonstrated that haul-out behaviour of Pacific harbour seals *P. v. richardsi* is shaped by terrestrial predator exposure (potentially wolves *Canis lupus*, coyotes *Canis latrans* or black bears *Ursus americanus*), with seals preferring isolated haul-out sites that allow for predator avoidance (Nordstrom 2002).

In other, non-marine mammal taxa, predation risk can have large effects on diet selection, specific foraging tactics and even the sequences and durations of different behaviours (Lima & Dill 1990, Brown & Kotler 2004). These issues have been less studied in marine mammals, but have already been documented. For example, dugongs in Shark Bay, Western Australia, modify their time budgets and switch from primarily excavation foraging to cropping seagrass leaves as predation risk from tiger sharks increases (Wirsing et al. 2007c) as well as changing their behavioural sequences between periods of high and low risk (Wirsing & Heithaus 2012). Also, the diving behaviour of seals and sea lions in Alaska suggests that they shift their diets in response to predation risk (Frid et al. 2007a,b, 2009; see above).

Risk effects initiated by marine mammals

As predators, marine mammals can initiate risk effects by inducing shifts in the movements, behaviour and foraging decisions of their prey. In Antarctica, Adélie penguins *Pygoscelis adeliae* and emperor penguins *Aptenodytes forsteri* avoid foraging at night due to predation risk by leopard seals, and food-safety trade-offs could explain penguin movement patterns and the location of penguin foraging grounds in the Southern Ocean (Ainley & Ballard 2012). Similarly, predation risk from New Zealand fur seals *Arctocephalus forsteri* affects the foraging rates of the magpie morwong *Cheilodactylus nigripes*, resulting in lower fish grazing intensity on algae (Connell 2002). In the Canadian Arctic, the distribution of ringed seal pup *Pusa hispida* subnivean lairs is strongly influenced by polar bear predation risk, which is higher in active ice areas. During periods of low natality, lairs tend to be mainly distributed closer to shore, where predation risk is lower (Pilfold et al. 2014). However, during periods of high natality, ringed seals are unable to pup in safer near-shore habitats and are forced to pup farther offshore on active ice areas, where there is greater predation pressure from polar bears (Pilfold et al. 2014). Mammal-eating killer whales likely induce risk effects in the diverse array of species that they consume, including a wide range of marine mammal species (see Jefferson et al. 1991 for a review). These risk effects may be substantial. Models suggest that dusky dolphins making habitat shifts in response to killer whale predation risk could suffer up to a 38% loss of foraging time (Srinivasan et al. 2010). In Alaska, sea otter populations’ shoreward distribution shifts during a period of declining populations and increasing predation risk from killer whales (Peckarsky et al. 2008, see below).

‘Non-predatory’ risk effects

While ‘risk effects’ generally have been defined as occurring relative to the risk of mortality inflicted by predators, other forms of risk can drive behavioural decisions that may impact a species’ ecological role and importance. For example, the literature on ‘risk-sensitive foraging’ often refers to how animals manage the risk of starvation. Other forms of risk may involve that associated with harassment by con- or heterospecifics that may be fatal or result in injury or reduced foraging. For example, off the British Isles and the coast of California, harbour porpoises are

killed, but not eaten, by larger co-occurring common bottlenose dolphins (Ross & Wilson 1996, Cotter et al. 2012). This phenomenon is spatially variable and does not occur in all areas where these 2 species live in sympatry (Ross & Wilson 1996, Patterson et al. 1998). In areas where bottlenose dolphins regularly kill harbour porpoises, porpoises tend to carry fewer energy reserves than expected, suggesting that foraging-risk trade-offs may also occur for species that neither compete for prey nor engage in predator-prey interactions (MacLeod et al. 2007). Modelling exercises suggest that bottlenose dolphin risk effects on harbour porpoises increase starvation mortality at the population level (MacLeod et al. 2014). Within a diverse delphinid community around the tropical island of Mayotte (Mozambique Channel, SW Indian Ocean), spinner dolphins appear to avoid harassment from Indo-Pacific bottlenose dolphins that inhabit the inner waters of the large coral lagoon around the island (Kiszka et al. 2010, 2011). As a result, spinner dolphins rest and socialize along the forereef, rather than conducting these activities inside the lagoon where other spinner dolphin populations, not faced with high densities of bottlenose dolphins in sheltered waters, do (e.g. Norris et al. 1994, Gannier & Petiau 2006). This could result in increased predation risk for spinner dolphins that must avoid bottlenose dolphins. Growing evidence suggests that inter-specific harassment in social contexts (e.g. Herzing & Johnson 1997, Wedekin et al. 2004, Cusick & Herzing 2014) may be underestimated for odontocetes.

BEHAVIOURAL DRIVERS OF MARINE MAMMAL ECOLOGICAL ROLES AND IMPORTANCE

Initiation and transmission of indirect effects of predation risk

Indirect effects of predation risk occur when changes in behaviour of one species/population/age class (transmitter) are made in response to the presence of another group or species (initiator) that results in changes in the behaviour, population sizes or biomass of a third (receiver) group. Such 3-step indirect effects have been termed behaviourally mediated indirect interactions, or 'BMII's' (Dill et al. 2003). Risk-related BMII's involving marine mammals have been documented in a number of ecosystems. For example, tiger sharks in Shark Bay appear to transmit a BMII between dugongs and Indo-Pacific bottlenose dolphins that is analogous to apparent competition. When present, tiger sharks prefer shal-

low habitats (Heithaus et al. 2002) where dugong densities are highest, resulting in dolphins and other potential tiger shark prey reducing their use of these productive but dangerous habitats (Heithaus & Dill 2002, Dill et al. 2003, Heithaus et al. 2012). White sharks transmit BMII between juvenile Cape fur seals, which attract sharks but do not respond to their presence, and adult fur seals that depart and return to an island colony in South Africa in response to elevated shark attack risk during daylight hours (Laroche et al. 2008). The implications of this intra-specific BMII, however, for population dynamics of fur seals are unknown. In the North Pacific, changes in foraging depths of harbour seals and Steller sea lions may transmit a BMII from sleeper sharks to fish populations, but further work is needed to understand the links between different seal and sea lion diving patterns and population sizes of several taxa of fish prey (Frid et al. 2007a,b, 2009). Similarly, while further empirical work is needed, fur seal-induced reductions in fish grazing rates (Connell 2002) could impact the biomass or community composition of macroalgae, and leopard seal-driven changes to penguin foraging (Ainley & Ballard 2012) could affect the spatiotemporal patterns of penguin impacts to their prey.

BMII's are generally concerned with changes in the behaviour and abundance of a small number of species within a community module and can be considered a class of 'species cascades'. A larger question, then, is whether marine mammal behaviour results in changes in the wider community or ecosystem in a behaviour-mediated trophic cascade (BMTC). There remains debate about the prevalence of BMTC's in natural communities. For example, both the existence and generality of the classic example of wolves inducing elk *Cervus elaphus* to shift their foraging, resulting in widespread changes to vegetation and the wider community (Ripple & Beschta 2004) have recently been challenged (Kauffman et al. 2010, Winnie 2012). Studies from the relatively pristine seagrass ecosystem in Shark Bay suggest that predation-sensitive foraging by dugongs and dolphins does play a role in a BMTC initiated by tiger sharks (Burkholder et al. 2013), whereby seagrass sheltered from turtle—and especially dugong—herbivory by risk from sharks forms dense meadows that provide habitat for fishes and invertebrates (Heithaus et al. 2012). Conversely, safer habitats where dugong and turtle grazing is concentrated are characterized by heavily grazed seagrass communities with low biomass and reduced habitat value to other species like fishes and invertebrates (Burkholder et al. 2013). A BMTC

involving killer whales and sea otters may operate in concert with a cascade that operates through consumptive effects of killer whales. While classically considered to be driven exclusively by increasing consumption of sea otters by killer whales (Estes et al. 1998), it now appears that the killer whale–otter–kelp–wider community cascade in the eastern North Pacific may be amplified by a BMTC (Peckarsky et al. 2008) whereby increasing predation risk induced otters to shift into safer shallower waters. This change apparently resulted in sea urchins dispersing away from urchins damaged or discarded by foraging otters, thereby reducing sea urchin densities and allowing the formation and maintenance of dense kelp patches and associated communities (Watson 1993, Peckarsky et al. 2008). Given the potential top-down impacts of marine mammals on their prey (e.g. Bowen 1997, Libralato et al. 2006, Roman et al. 2014), further work on links between marine mammal behavioural decisions and community and ecosystem dynamics is important for gaining a functional understanding of these many marine systems.

Behavioural facilitation

Although marine mammals may share prey, and appear to compete, with other marine taxa, their presence may actually enhance foraging success and population sizes of these species. For example, cetaceans and seabirds forage in close proximity in many regions but especially in temperate and other productive waters. In most cases, seabirds appear to benefit from these associations (Grebmeier & Harrison 1992, Bräger 1998, Anderson & Lovvorn 2008). Although less common, in some circumstances, other marine mammals and teleosts benefit from cetacean foraging (see below). Schools of pelagic fish such as herrings (*Clupea* spp.) and sardines (*Sardinops* spp.) form tight aggregations near the surface in response to subsurface predators including cetaceans and pinnipeds. As a result, they are more accessible to seabirds in a BMII between marine mammals and seabirds (e.g. Evans 1982, Dill et al. 2003). Long-finned pilot whales *Globicephala melas*, common minke whales *Balaenoptera acutorostrata* and other large balaenopterid whales such as fin whales *B. physalus* have been documented driving deep-dwelling prey species, usually inaccessible to seabirds (e.g. Procellariformes), to the surface (Evans 1982). Grey whales act similarly, bringing benthic prey (particularly ampeliscid amphipods *Ampelisca*

and *Byblis*) to the surface where they are consumed by surface-feeding seabirds such as northern fulmars *Fulmarus glacialis*, black-legged kittiwakes *Rissa tridactyla* and red phalaropes *Phalaropus fulicaria* (Grebmeier & Harrison 1992). Recently, it has been suggested that rising populations of eastern Pacific grey whales, and greater whale feeding activity in benthic habitats, may increase foraging profitability for bottom-feeding birds such as diving ducks, especially the surf scoter *Melanitta perspicillata*, during spring (Anderson & Lovvorn 2008). In the eastern tropical Pacific, Parkinson's petrels *Procellaria parkinsoni* appear to associate with rare deep-diving delphinids (*Peponocephala electra* and *Pseudorca crassidens*) for the purpose of scavenging on large prey scraps (Pitman & Ballance 1992). The foraging activity of marine mammals such as cetaceans can also benefit epipelagic seabirds by drawing them to the surface in tight aggregations, enabling energetic cost reduction associated with diving and landing (Sakamoto et al. 2009). In continental shelf waters of the NW Atlantic, the abundance of common terns *Sterna hirundo* and roseate terns *Sterna dougallii* is closely linked to higher tuna and dolphin densities, suggesting that these subsurface predators facilitate tern foraging (Goyert et al. 2014). In some regions such as off KwaZulu-Natal (SE Africa), during the winter migration of sardines *Sardinops sagax* ('sardine run'), cetaceans such as common dolphins *Delphinus delphis* and Bryde's whales *B. edeni* may facilitate epipelagic predators, including Cape fur seals and several shark species (e.g. *Carcharhinus brachyurus*, *C. brevipinna* and *C. obscurus*; Dudley & Cliff 2010, O'Donoghue et al. 2010). In this context, common dolphins may compact sardine schools that are easier for other predators to forage on, thereby enhancing their net energy intake rates. The overall importance of competitor facilitation initiated by cetaceans to other consumer populations is poorly understood, but some seabird species (e.g. Parkinson's petrels) may be highly dependent on cetaceans for foraging (e.g. Pitman & Ballance 1992).

'Bottom-up' effects

Although the most obvious roles of predators in ecosystems involve predator–prey interactions, they may also be important in mediating the movement of nutrients within or between depth strata, habitats or ecosystems (Kanwisher & Ridgway 1983, Katona & Whitehead 1988, Polis et al. 1997, Schmitz et al. 2010), thereby facilitating ecosystem production and

population sizes of lower trophic levels (see Roman et al. 2014 for a recent review). Marine mammals may move nutrients from marine to freshwater habitats, from deep-sea to epipelagic water layers and from marine to terrestrial environments (Kanwisher & Ridgway 1983, Katona & Whitehead 1988, Polis et al. 1997, Roman et al. 2014). Several authors have identified faeces and carcasses (Kanwisher & Ridgway 1983, Smith et al. 2013), as well as regurgitation (Krajewski & Sazima 2010), as potentially important sources of marine mammal-derived nutrients. For example, West Indian and African manatees *Trichechus senegalensis* use a range of habitats and may move widely to stay within particular thermal or salinity ranges, and therefore constitute biological links between marine and freshwater ecosystems as they may translocate marine nutrients via excretion (Aragones et al. 2012). Experimental faecal treatments on diatoms (*Fragilariopsis cylindrus* and *F. curta*) demonstrate that pygmy blue whales *B. m. brevicauda* stimulate the growth and photosynthetic performance of marine phytoplankton (Smith et al. 2013). Therefore, these cetaceans contribute to enhanced primary productivity and nitrogen production on their foraging grounds through the release of faecal plumes. Similarly, in the Gulf of Maine, whales and seals may be responsible for enriching the euphotic zone with 2.3×10^4 t N yr⁻¹, which is more than river inputs in this region (Roman & McCarthy 2010). In the Southern Ocean, sperm whales that prey on deep-sea mesopelagic prey defecate iron-rich faeces in the photic zone (50 t yr⁻¹), and stimulate primary production and carbon export from the depths (4×10^5 t yr⁻¹, Lavery et al. 2010) that may stimulate production and, ultimately, enhance fish populations (Lavery et al. 2014).

Not all nutrient transport by whales is from the depths to surface waters. Large whale carcasses falling to the sea floor represent massive pulses of organic matter that appear to be critical to sustaining some deep-sea communities and may represent an important vector for the dispersal of deep-sea chemosynthetic communities over large areas (Smith et al. 1989, Smith & Baco 2003). Whale carcasses may also be important in transporting marine or oceanic energy and nutrients to nearshore and terrestrial habitats. For example, California condors *Gymnogyps californianus* appear to have relied on whale carcasses for considerable portions of their diets historically, and bears make use of stranded marine mammals (Smith 2006). Mass stranding events could be responsible for the movements of considerable amounts of marine-derived nutrients from the open-

sea to inshore and beach areas, especially in regions where these events regularly occur.

The spatiotemporal distribution and abundance of whale falls and carcasses in nearshore and coastal habitats should be closely linked to behavioural processes, including migratory decisions of whales and foraging locations and food selection by killer whales. Indeed, grey whale carcasses are only partially consumed by killer whales, leaving large food sources for other species. Similarly, social cohesion appears to be a factor contributing to mass strandings (i.e. strandings of 3 or more individuals) by several odontocetes (e.g. sperm whales, pilot whales and false killer whales; Cordes 1982).

Pinnipeds may be important vectors for moving nutrients from marine habitats to beaches and nearshore waters through their excretion, and the spatiotemporal pattern of these nutrient inputs will be modified by haul-out behaviour. Hawaiian monk seals *Monachus schauinslandi*, for example, mediate nutrient transport from coral reefs to sandy beaches when hauling out (e.g. Goodman-Lowe 1998, Parrish et al. 2005), and other pinnipeds, polar bears and marine and sea otters almost certainly link marine and terrestrial habitats (e.g. Krajewski & Sazima 2010). While still unexplored, pinniped faecal material likely fertilizes primary producers in nearshore waters, especially where they haul out on rocky outcrops.

Diurnal movements of marine mammals within and across habitats could transport substantial biomass and nutrients. For example, around tropical islands, spinner dolphins feed overnight in offshore waters on mesopelagic prey (e.g. squids, myctophid fishes, prawns) and rest in protected coastal and reef systems during the day (Norris & Dohl 1980). Through excretion (including defecation and regurgitation), they may provide resources for planktivorous reef fishes and transport nutrients from mesopelagic layers to coastal and coral reef systems (Martins Silva et al. 2007). Unfortunately, the relative ecological importance of marine mammal-derived inputs remains unexplored in general (but see Roman et al. 2014).

INDIVIDUAL BEHAVIOURAL VARIATION

Variation in the behaviour of marine mammals has been widely documented at multiple levels, including among populations, among age/sex classes of a population, among individuals within an age/sex class and within individuals (e.g. Heithaus & Dill 2009), and all of these sources of variation can modify

the ecological roles and importance of populations or subsets of populations. Because most of these patterns of variation have been considered in detail within the literature, here we focus our discussion on variation within age/sex classes.

In general, there is growing appreciation that individuals within animal populations, sizes and sex classes are often characterized by consistent behavioural differences ('individual specialization' Bolnick et al. 2003, Araùjo et al. 2011). These differences can lead to individuals from the same age/sex class and habitat playing different roles in ecosystems (Bolnick et al. 2003) and even to eventual speciation (e.g. Baird et al. 1992). Individual specialization is well known in marine mammals, but, in many cases, the duration of such specialization is not well known. Sea otters off the California coast exhibit consistent individual differences in prey selection that appear to be maintained by intra-specific competition (Tinker et al. 2008). At Sable Island (eastern Canada), 3 main movement types, differentiated by variation in home range size, travel speed and move length, have been observed in adult grey seals *Halichoerus grypus* (Austin et al. 2004) that would result in individual variation in the spatiotemporal pattern of their potential impacts to ecosystems. Similar inter-individual differences in habitat use are found in harbour seals in north-eastern Scotland (Tollit et al. 1998). Indo-Pacific bottlenose dolphins in Shark Bay show marked and apparently life-long individual variation in the use of certain foraging tactics (Sargeant et al. 2007), with some tactics (e.g. 'sponging', where dolphins carry sponges as a tool to protect their beak from abrasion when foraging on the seafloor) being restricted to small subsets of the population and passed along matrilineal lines (Sargeant et al. 2005). This culturally transmitted tool use allows some individuals to access otherwise unavailable resources (Krützen et al. 2014). Minke whales also have been found to manifest individual differences in foraging, with individuals using the same tactic for periods of up to 5 yr (Hoelzel et al. 1989).

COULD HUMAN IMPACTS AFFECT THE ECOLOGICAL ROLES OF MARINE MAMMALS THROUGH BEHAVIOURAL MODIFICATIONS?

Many anthropogenic factors, including vessel traffic and noise pollution from tourism, commercial shipping, military testing and windfarming, may affect the behaviour, habitat use and activity budgets of marine mammals (e.g. Bejder et al. 2006, Williams

et al. 2006, Bailey et al. 2010). For example, behavioural responses to vessel traffic can lead to increased swimming speed and dive duration (Nowacek et al. 2001), modification of activity budgets (Constantine et al. 2004, Stockin et al. 2008, Pirodda et al. 2015) and changes in habitat use and relative abundance (Bejder et al. 2006). Furthermore, disturbance by vessels and aircraft can disrupt the haul-out behaviour of pinnipeds and reduce the time spent resting (e.g. Salter 1979, Schneider & Payne 1983, Henry & Hammill 2001). The 'Risk Disturbance Hypothesis' suggests that animals should respond to human disturbance (e.g. boat traffic) in a way that is comparable to responses to natural predators (Frid & Dill 2002, Heithaus et al. 2007a). As generally long-lived species, marine mammals would be expected to invest heavily in anti-predator behaviour (or anti-disturbance behaviour in this case; e.g. Frid & Dill 2002) with the potential for behavioural changes to translate to population-level consequences through decreased access to resources and diminished body condition (e.g. Williams et al. 2006, Thompson et al. 2010). By implication, the myriad ecological roles of marine mammals are likely to be modified by behavioural changes made in response to people. For example, the BMTC that dugongs mediate between tiger sharks and seagrass communities (Burkholder et al. 2013) would be predicted to be replicated if boats caused dugongs to abandon particular foraging sites (e.g. Heithaus et al. 2007b).

CONCLUSION

To date, the ecological roles and importance of marine mammals have been viewed primarily through the lens of their consumptive interactions with prey. Here, we broaden our understanding of marine mammal ecology to include the manifold ways that behaviour is critical in shaping their effects in marine ecosystems and beyond. In particular, we emphasize the growing literature on risk effects, whereby predators induce costly changes to prey behaviour that can alter both prey population sizes and the magnitude and spatiotemporal patterns of prey impacts on communities. By implication, changes in the abundance of marine mammals, as well as the introduction of other perturbations that can be perceived as predation risk (e.g. noise pollution, vessel disturbance), may affect behaviours of marine mammal prey that cascade to the wider ecosystem. Furthermore, we emphasize that rather than being true apex predators, most marine mam-

mals are in fact mesopredators that can experience risk effects, and we highlight the conditions under which the cascading risk effects of marine mammals might be most influential as an exciting new frontier for research involving these species. We also examine other behaviour-driven ecological roles of marine mammals including foraging tactics facilitating the foraging of other species and nutrient transport that links the dynamics of spatially distinct food webs. Although evidence is growing, these other behavioural mechanisms remain underappreciated and should serve as the basis for further inquiry. Finally, we highlight intra-specific behavioural variation as an area that needs more attention. Thus far, most studies of the ecological roles and importance of marine mammals have explicitly or implicitly focused on behavioural averages. Yet, there is growing recognition that consistent inter-individual variation in behaviour is not only widespread but also means that individuals in particular populations may often interact very differently with their environment.

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Woods Hole, Massachusetts, USA*

*Submitted: May 16, 2014; Accepted: December 29, 2014
Proofs received from author(s): February 25, 2015*