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Review

Behavioral biology of marine mammal deterrents: A review and prospectus

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ABSTRACT

Marine mammal depredation of fisheries is a concern from a scientific, management, and conservation perspective. This conflict has prompted the development of non-lethal deterrents, a management technique that uses aversive stimuli to elicit avoidance. Animals are expected to be sensitive to cues of danger to avoid sources of mortality. Deterrents capitalize on behavioral mechanisms such as threat detection, assessment and learning. A deterrent must create enough risk, or cost, that it overcomes the heightened foraging benefits of depredation. Theoretically, effective deterrence relies on altering the relative costs and benefits to the individual depredator by creating a perceived risk associated with human resources. Here we discuss the underlying behavioral basis of how deterrents generate avoidance. We review deterrents applied to marine mammals to mitigate conflict with fisheries and suggest that fear conditioning could be useful in this context. This is discussed in the context of some potential management concerns of application of non-lethal deterrents in the wild.

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1. Introduction

The recovery of certain animal populations, combined with the expansion of human populations and the fragmentation of habitats, has caused substantial overlap between humans and wildlife. This spatial and temporal overlap creates direct conflicts over human resources and products, including livestock, crops, fish, and garbage. Human wildlife conflict (HWC), defined broadly, refers to wildlife behaviors that negatively influence human goals or vice versa (Madden, 2004). HWC occurs when wildlife kill domesticated animals, or eat garbage or crops. It is well documented in terrestrial ecosystems and seen when carnivores prey upon livestock and elephant/primate forage in crops (Naughton-Treves, 1998; O'Connell-Rodwell et al., 2000; Treves and Karanth, 2003).

In marine ecosystems, HWC is globally distributed and taxonomically widespread because of commercial fishing (Northridge, 1991). Numerous mammals, including pinnipeds, false killer whales (*Pseudorca crassidens*), killer whales (*Orcinus orca*), sperm whales (*Physeter macrocephalus*), and bottlenose dolphins (*Tursiops truncatus*) have been reported to steal fish from fishing lines, nets, fish ladders or aquaculture pens (Yano and Dahlheim, 1995; Gillman et al., 2006; Sigler et al., 2008; Read, 2008; Forney et al., 2011). This behavior is referred to as depredation.

The alteration of wildlife habitat whereby fishing lines or aquaculture pens are introduced to animals' environments has shifted the costs and benefits of natural mammal foraging by creating novel concentrations of prey. To the individual depredator, exploiting fishing resources represents a more efficient feeding strategy than natural foraging. There are lower costs in terms of energy, time, and travel for locating/acquiring prey. For example, when depredating demersal, long-line fishing vessels, sperm whales do not have to dive to forage at their typical depth and fishing lines also offer a high concentration of debilitated prey (Mathias et al., 2009). However, depredation incurs (potentially lethal) costs from entanglement with, or ingestion of fishing gear. In addition to creating novel concentrations of prey, human activities may reduce foraging resources previously available to natural predators, via direct take (and in some cases overfishing) or via a number of indirect paths altering the trophic web. Because animals seek to maximize foraging efficiency by reducing time, energy, or distance travelled while foraging (Krebs and Davies, 1987), the low cost of depredating from fishing lines/aquaculture pens or higher costs of searching for food in a disturbed habitat offer heightened motivation for learning to associate foraging resources with humans/human habitat.

Marine mammal depredations of fisheries resources are a concern from both scientific, management, and conservation perspectives because there are direct socio-economic impacts upon fisheries, a potential for reducedfishstocincreased marine mammal mortality, and potential (and realized) retaliatory actions by fisherman. This conflict has stimulated to the development of non-lethal deterrents designed to ward off wildlife (Pemberton and Shaughnessy, 1993; Read, 2008).

Deterrents, defined broadly are management techniques that use aversive stimuli to prevent animals from utilizing human resources (Ramp et al., 2011). A deterrent stimulus is defined as an aversive, harmful, fearful, or noxious stimulus that elicits defensive responses in animals (Gotz and Janik, 2010). A deterrent must create enough risk (real or perceived) so that the costs of using a resource are greater than the foraging benefits of depredation (Fig. 1).

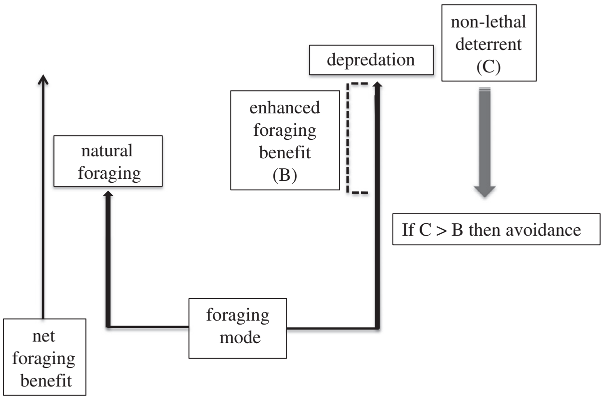

Fig. 1. How deterrents work. When the costs created by a non-lethal deterrent (C) exceed the benefits of depredation (B), animals should resume 'natural' foraging.

The goal of a deterrent is to create aversive stimulus that excludes wildlife from human resources and/or habitats (Mason et al., 2001). Animal threat detection and response mechanisms evolved to identify environmental cues of danger and then to activate appropriate defense responses and avoidance (Lang et al., 2000; Frid and Dill, 2002; Eilam et al., 2011). From a functional (i.e., evolutionary) perspective, there is often a survival advantage for the early and rapid detection of threatening stimuli (Öhman, 1997; Blumstein 2010a,b). In many circumstances, the costs of failing to respond to threatening stimulus far outweigh costs of a false positive response (over-reaction to innocuous stimuli (Bouskila and Blumstein, 1992; Sih, 1992; Mineka and Ohman, 2002). Animals are therefore expected to be sensitive to cues of danger (predation, conspecific aggression, or dangerous environmental features) because death leads to an abrupt reduction in future direct fitness (Endler, 1986; Blanchard, 2008). The capacity to detect threatening stimuli therefore, has been under intense selection, resulting in evolution of specialized mechanisms of threat assessment, learning, and behavioral response (Blanchard, 2008; Eilam et al., 2011). Deterrent stimuli capitalize upon the mechanisms of threat detection and avoidance (Frid and Dill, 2002; Parsons and Blumstein, 2010; Biedenweg et al., 2011).

Below we discuss the underlying behavioral basis of how deterrents generate avoidance and review deterrents applied to marine mammals to mitigate conflict with fisheries. Schematically, Fig. 2 breaks down animal response to deterrent stimuli into mechanisms of aversion, decision-making and learning. Table 1 provides relevant definitions of behavioral principles that will be referred to throughout this review. What follows is a discussion of these underlying behavioral mechanisms.

2. Avoidance mechanisms

Defensive behaviors describe the responses of individuals to threatening stimuli (Blanchard, 2008). In nature, defensive responses to risky situations or stimuli, such as a predatory encounters, can broadly be divided into two categories; immediate defensive responses to a direct encounter (flight), or avoidance behaviors that decrease the probability of encountering danger based upon indirect cues (Lima and Dill, 1990; Brodie and Formanowicz, 1991). The two categories are underpinned by two distinct mechanisms, fear and anxiety (Blanchard et al., 1993; Blanchard, 2008). Fear and anxiety are reliant upon two separate neurochemical pathways (McNaughton and Corr, 2004). Fear is defined as a short-term fight or flight response involving heightened physiological arousal that reduces impact of impending threat (Grillon, 2008). By contrast, anxiety is sustained and precipitated by potential, ambiguous, or contextual threats (Blanchard, 2008; Grillon, 2008; Eilam et al., 2011).

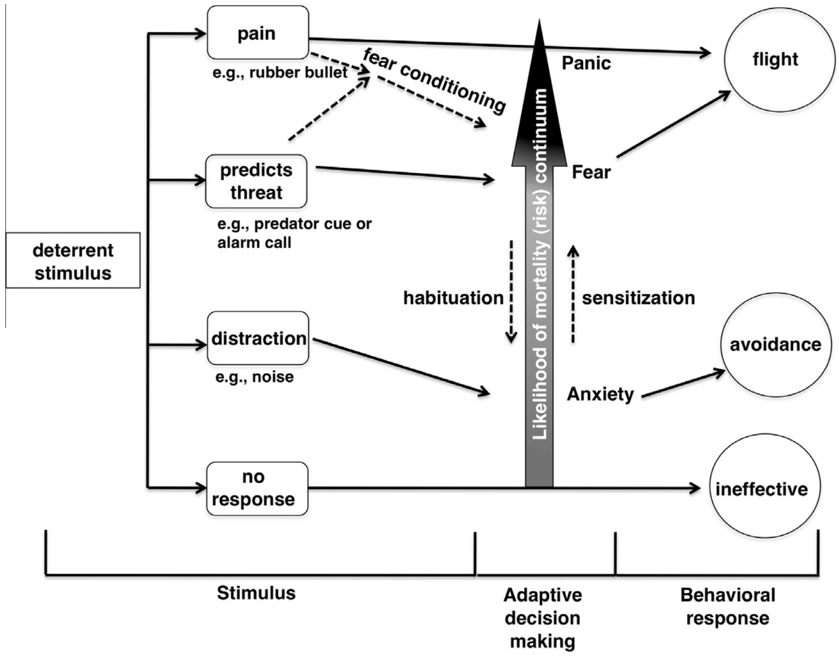

Fig. 2. A mechanistic framework of the behavioral biology of deterrents. The stimulus component involves the mechanisms by which deterrents elicit aversion: pain, threat (direct or predicted), or distraction. Upon detection, the deterrent stimulus is assessed in terms of mortality risk, which ultimately guides the behavioral response. Learning mechanisms are illustrated (with the dotted lines) and either act by decreasing (habituation) or increasing (sensitization) a deterrent's perceived risk.

Table 1
Relevant behavioral principles for wildlife deterrence.

Behavioral principle	Definition
Fear	A short-term fight or flight response to direct threat involving heightened physiological arousal (Grillon, 2008)
Anxiety	Response to potential/ambiguous danger or treat (Marks, 1987)
Habituation	Non-associative learning involving a reduction of behavioral response to repeated exposure to stimuli that is not due to sensory fatigue (Groves and Thompson, 1970)
Sensitization	Non-associative learning exemplified by a heightened sensory responsiveness after exposure to aversive stimuli (Plappert et al., 1999)
Dual process theory of habituation	An observed behavior after repeated exposure to a stimulus represents the sum of the two underlying learning processes of habituation and sensitization (Groves and Thompson, 1970)
Fear conditioning	Associative learning process after pairing of aversive stimulus (unconditioned stimulus, US, e.g., a shock) to an innocuous stimulus (conditioned stimulus, e.g., a neutral tone—(Fanselow, 1984; Grillon, 2008))
Extinction	Decrease in learned responsiveness because the CS is no longer reinforced with the unconditioned stimulus (Domjan and Burkhard, 1986)

The distinction between proximate mechanisms of fear and anxiety are well recognized by those who study laboratory animals, but there is no reason to believe these distinctions are a laboratory artifact. Fear is seen when an individual responds to a direct threat (e.g., an attacking predator), whereas anxiety is induced with potential or contextual threat such as response to olfactory cues that signal possible predator presence (Blanchard et al., 1993; Blanchard, 2008). These two mechanisms of behavior are unique, and believed to be governed by distinct neural mechanisms (Charney and Deutch, 1996; Grillon, 2002, 2008; Davis, 2006). Behaviorally, anxiety is associated with increased risk assessment (vigilance), avoidance of anxiety-associated stimuli or areas, and increased sensory sensitivity that is designed to better evaluate the true threat, whereas fear involves immediate flight responses (Blanchard et al., 1993; Eilam et al., 2011).

Non-lethal deterrent stimuli elicit fear or anxiety to create behavioral avoidance of human resources. Ultimately, the pathway to avoidance behaviors (Fig. 2) depends on the characteristics of the aversive stimulus as well mechanisms of threat analysis and learning.

3. Decision making is often adaptive

After detecting a threatening stimulus, individuals analyze the characteristics of the stimulus as well as the environmental context to assess the level of risk to generate an adaptive behavioral response (Blanchard et al., 1990; Lima and Dill, 1990). The process of risk assessment can be described as a continuum with stimuli that pose no risk at the bottom and stimuli that signal imminent danger at the top (Fig. 2). Fanselow and Lester (1988) describe this as the "predatory imminence continuum" and show that a given behavioral response depends upon where an individual perceives its own location on the continuum. For example, when exposed to scent cues that predict predator presence, anxiety is elicited in laboratory rats and behavioral responses involve avoidance strategies that reduce the likelihood of encounter. Conversely, direct encounters with a real threat (an approaching experimenter) elicit flight (Blanchard et al., 1990). We extend Fanselow and Lester's (1988) predatory imminence continuum concept for non-lethal deterrents to include aversive stimuli other than predators (Fig. 2). Ultimately, where an individual perceives its location on the likelihood of mortality (risk) continuum guides the individual's behavioral response (Fanselow and Lester, 1988).

4. What are the characteristics of threatening or aversive stimuli?

Stimuli that are recognized as threatening or aversive can disrupt behavior and create long-term avoidance (Frid and Dill, 2002; Rianne, 2007; Rau and Fanselow, 2009). Defensive behaviors are observed in response to a variety of different stimuli such as pain, predator cues, or dangerous contexts (Blanchard et al., 1990). In addition to incorporating relevant sensory modalities of threat detection, generating avoidance depends upon the characteristics of the stimulus that elicits aversion (Talling et al., 1998). Deterrent stimuli are either inherently aversive or are learnt through conditioning. Thus, responses to deterrents fall naturally into (1) simple exposure to painful stimuli (2) stimuli that are predictive of threat, (3) or stimuli that are aversive through distraction. We classify non-lethal deterrent stimuli by these mechanisms (Fig. 2): pain (e.g., rubber bullets); stimuli that are predictive of threat (e.g., predator sound or alarm calls); or disruption (e.g., noise – Bomford and Obrien, 1990). These mechanisms evoke varying levels of risk and thus elicit varying responses and they can be viewed somewhat continuously along a continuum of mortality risk (Fig. 2), which we will discuss below.

4.1. Painful stimuli

Pain in animals is defined as a harmful sensory event from damage or potential injury (Zimmermann, 1986). From a functional perspective, pain is adaptive because it signals danger and elicits immediate escape behaviors (Patrick, 1991). Thus, a painful stimulus signals imminent risk (predator attack) and falls on the upper end of the perceived level of risk continuum (Fig. 2). Pain provokes fear responses and flight behaviors designed to immediately remove the individual from the situation. For example, high intensity shocks on laboratory rodents are shown to induce species-specific defense involving a burst of motor responses (Fanselow and Lester, 1988). These captive experiments emphasize that painful stimuli elicit fear associated defense responses characteristic of predator attack in lab rats (*Rattus norvegicus*).

Physical characteristics of painful stimuli include intensity, loudness, suddenness, or duration (Boissy, 1995). Painful stimuli are often tactile but can span other modalities. For example, harsh acoustic stimuli can be painful (Bomford and Obrien, 1990). Psychophysical investigations are useful in understanding the characteristics of acoustic stimuli that induce aversion in animals (Gotz and Janik, 2010). Novel acoustic stimuli may be inherently threatening (Gray, 1987), but the structure of the sound in an acoustic deterrent should incorporate species-specific psychophysical characteristics that contribute to aversion. Zwicker and Fastl (1999) developed a model that identified increased sharpness, increased loudness, increased roughness and decreased tonality as the four contributors to perceived unpleasantness of sound in humans. Gotz and Janik (2010) tested this model and demonstrated that the same characteristics contribute to aversion of sound in captive grey seals.

4.2. Stimuli that predict threat

In nature, animals are expected to be sensitive to stimuli or environments that are correlated with threat or danger. Historically, they include stimuli that are from salient predators or other threats or stimuli that arise from conspecific aggression (Gray, 1987). Stimuli that indicate a threat (sight or sound of attacking predator), elicit defensive responses (Gray, 1987). Animals may innately recognize threatening predator cues, or may have evolved predispositions to learn from specific cues preferentially (Griffin and Evans, 2003). Examples include fearful responses to foxes (*Vulpes vulpes*), but not goats (*Capra hircus*), by tammar wallabies (*Macropus eugenii*) (Griffin et al., 2001), fearful responses to cat odor in rats (Dielenberg and McGregor, 2001), or fearful responses to snakes by primates (including humans) (Öhman and Mineka, 2003). Killer whales have been observed preying on all species of marine mammals except manatees and river dolphin species (Jefferson et al., 1991), and can elicit fearful responses in marine mammals (Cummings and Thompson, 1971; Baird and Stacey, 1989; Deecke et al., 2002).

4.2.1. Conditioned stimuli

Conditioned stimuli arise when animals learn to associate a previously neutral stimulus with an aversive event and subsequently exhibit conditioned fear. Threatening encounters cause an immediate type of associative learning that enables animals to acquire predictive information from a threatening cue or context (Fanselow and Ponnusamy, 2008). There is a clear adaptive benefit of learning from threatening situations because cues or context provide information how to respond and detect future dangerous events. This learning process, called *fear conditioning*, is a Pavlovian form of associative learning.

Pavlovian fear conditioning has been extensively studied in laboratory animals. Experimentally, individuals are exposed to an aversive stimulus, (unconditioned stimulus, US, typically a shock) which is paired to an innocuous stimulus (conditioned stimulus or CS, e.g., a neutral tone (Grillon, 2002; Fanselow and Ponnusamy, 2008). The unconditional stimulus facilitates conditioning of fear reactions to the conditional stimulus. Conditioning occurs quickly in just one or several pairings in part because the aversive stimulus facilitates rapid fear learning. Following conditioning, the individual will subsequently show fear and anxiety when exposed to the neutral stimulus (CS) or environmental context because of associative learning (Grillon, 2002). *Fear conditioning* has been extensively studied in rats, which exhibit long lasting fear responses, over weeks or months, to neutral stimuli associated with shocks (Gale et al., 2004; Rianne, 2007).

The physical characteristics of threatening stimuli such as the modality, movement, suddenness and proximity also influence the magnitude of a fear response (Gray, 1987). The direction of approach and whether it looms or fills the visual field all are examples of movement features of stimuli that may modify flight distance (Gray, 1987; Ellison et al., 2012). Additionally, sudden stimuli can elicit startle responses that potentiate flight (Gray, 1987; Yeomans et al., 2002; Gotz and Janik, 2011).

4.3. Masking, disruptive or distracting stimuli

A stimulus that prevents or distracts animals from biologically important tasks, like assessing predation risk or communication can be perceived as aversive and may elicit avoidance. For instance, the *distracted prey hypothesis* predicts that stimuli (in any modality) can distract and divert attention away from risk assessment (Chan et al., 2010). Animals are expected to exhibit anxiety and avoidance of distracting stimuli because of their impact on proper risk assessment. In odontocetes, a masking stimulus may reduce effectiveness of echolocation and thus prevent the individual from locating the fishing resource (Mooney et al., 2009). Marine mammals avoid anthropogenic acoustic stimuli from a variety of sources including ship noise or geophysical surveys (Nowacek et al., 2007), suggesting that a deterrent signal can capitalize on mechanisms of distraction.

5. Learning and motivation influence the response to deterrent stimuli through time

The capacity to learn from threatening encounters is functional because it guides how an animal can adaptively respond to an immediate threat and anticipate/avoid future danger. For example, by learning the cues that predict a predator attack, a prey species is able to modify its behavior and through avoidance, it reduces the probability of death (Domjan, 2005). From this functional learning perspective, learning about deterrent stimuli influences the adaptive decision making process and can modify an individual's behavioral response to deterrent stimuli through time. Each learning mechanism can produce increases or decreases in (defensive) responsiveness (Fig. 2). Incorporating the learning mechanisms involved in animal response to threat is necessary for long-term deterrence.

Failure to recognize a predator may have substantial fitness costs (Lima and Dill, 1990). Conversely, anxiety or stress from over-generalized threat recognition may be costly in terms of energy or time allocated to unnecessary defenses. Animals may habituate to repeated exposures of potentially threatening stimuli with recurring exposure (Groves and Thompson, 1970). *Habituation* involves single stimulus learning involving a reduction of behavioral response to repeated exposure to stimuli that is not due to sensory fatigue. Habituation to deterrent stimuli in cases of human wildlife conflict represents a major limitation toward long-term deterrent success (Shivik, 2006), thus, detailed knowledge of how habituation occurs is necessary if we are to reduce the likelihood of its occurrence (Blumstein and Fernández-Juricic, 2010).

Generally, simple parameters such as intensity, modality, and frequency of exposure influence single-stimulus learning in animals (Groves and Thompson, 1970). Additionally, response decrement can be generalized to stimuli within the same modality that are similar to the original stimulus. These parameters have practical significance for managers deciding which stimuli as well as the schedule at which depredators are exposed. All else equal, the more frequent exposure results in more pronounced habituation (Groves and Thompson, 1970; Rankin et al., 2009). Correspondingly, less intense stimuli result in a response decrement whereas greater intensities may show no habituation (Groves and Thompson, 1970; Rankin et al., 2009). Painful stimuli signal imminent threat (Fig. 2) and are the least likely to be habituated to. Rapid habituation is expected in response to continuous playback of less intense signals (predator sounds) versus sudden and intense stimuli.

Habituation, however, is not ubiquitous and repeated stimulation could lead to sensitization (Groves and Thompson, 1970; Rankin et al., 2009). *Sensitization* refers to a form of non-associative learning exemplified by a heightened sensory responsiveness after exposure to aversive stimuli (Plappert et al., 1999). Thus, in contrast to habituation, sensitization involves heightened risk after repeated exposure. According to the dual process theory of habituation, an observed behavior after repeated exposure to a stimulus represents the sum of the two underlying learning processes of habituation and sensitization (Groves and Thompson, 1970). Deterrents should incorporate some sensitizing mechanism to delay or prevent habituation (Gotz and Janik, 2011).

Habituation and sensitization are the behavioral outcome of the interaction between two underlying neurobiological pathways (Groves and Thompson, 1970; Domjan and Burkhard, 1986). Sensitization is underpinned by the state system. The state system is made up of the components of nervous system that determine overall responsiveness and arousal (Domjan and Burkhard, 1986). Stimuli that are particularly intense, emotionally salient, or startling may activate the state system (Groves and Thompson, 1970). Increased responsiveness is expected to occur if the individual is exposed to the startling stimuli repeatedly while still sensitized from the previous exposure. Gotz and Janik (2011) exposed individual gray seals to harsh, startle-reflex eliciting acoustic stimuli. After just several exposures, the individuals showed heightened flight reflexes whereas individuals exposed to non-startle stimuli habituated. This suggests that sensitizing the startle reflex arc results in increased flight/avoidance responses, which can be used to create effective deterrents (V. Janik pers. Comm.).

Motivation is the behavioral mechanism underlying an individual's assessment of costs/benefits of a given foraging situation. In the case of depredation, the foraging benefits are high, and costs are low, (Fig. 2) resulting in motivation to exploit fisheries. Thus, if a deterrent stimulus repels animals away from a resource, motivation to forage may drive them back to depredation. Learning modifies assessment of the cost/benefit ratio and changes behavior via motivational change, ultimately shaping the frequency of exposure to deterrent stimuli. Habituation occurs after repeated exposure to a stimulus and is rapid when there is short amount of time between exposures to stimuli (Staddon and Higa, 1996). Since the motivation to depredate increases the rate at which an individual is exposed to deterrent stimuli, it accelerates habituation.

6. Review of marine mammal deterrents

A deterrent should exploit animal sensory mechanisms of threat detection to raise the real or perceived costs or risks involved in depredation (Shivik et al., 2003; Biedenweg et al., 2011). There has been a significant effort to develop, implement, and test numerous deterrents that exploit marine mammal sensory modalities, including tactile harassment, chemosensory deterrents that either induces fear or disgust, and acoustic deterrence. Here, we review the basic modalities of deterrents tested in cases of marine mammal depredation. The purpose of this review is to summarize cases of deterrent application, identify knowledge gaps and highlight management concerns of application of non-lethal deterrents. Finally, we propose deterrent strategies that may be useful to manage marine mammal depredation.

6.1. Marine mammal sensory modality background

Generally, mammals use visual, acoustic, and chemosensory modalities to detect threatening stimuli (Apfelbach et al., 2005). The physical characteristics of the aquatic medium (e.g., increased sound transmission and light attenuation) have translated into a reliance on sound for marine mammal detection of predators, communication, and navigation (Schusterman, 1981). Overall, marine mammals exhibit aural sensitivity, visual acuity in the limited portion of water that transmits light, and decreased olfaction (Watkins and Wartzok, 1985; Wartzok and Ketten, 1999). This suggests that acoustic, visual, chemosensory (taste), and tactical are the relevant sensory modalities for marine mammal deterrents. Additionally, deterrent stimuli should incorporate the sensory sensitivity of a given modality (Gilsdorf et al., 2003).

6.2. Chemosensory deterrents

From first principles, the lack of olfactory capacity in marine mammals suggests that deterrents that use of predator scents should be unsuccessful. Chemosensory deterrent mechanisms have focused on taste as a mechanism for inducing aversion. Conditioned taste aversion methods in human/wildlife conflict have produced mixed results in terrestrial systems (Shivik, 2006). While further testing in cases of marine mammal/fishery conflict is necessary, CTA methods had limited effectiveness when tested on sea lions predating salmon from Ballard locks dam in Seattle. Steelhead (*Salmo gairdneri*) laced with an emetic, lithium chloride, were tethered and fed to sea lions to elicit aversion. The animals were observed to have fled the area and believed to have become ill (Gearin et al., 1986). However, the same individuals returned an hour later to continue foraging in the area (Gearin et al., 1986). Further information is needed as to whether marine mammals would generalize their aversion from fishing resources into the wild, but we believe that these strategies are unlikely to be successful.

Pre-exposure to the food before conditioning delays or prevents taste aversion learning. Additionally, as a generalist forager, sea lions may learn that this particular fish species is not good to eat (the taste and smell of a prey item serves as the CS), rather than the animal learning where not to forage.

6.3. Acoustic deterrents

Marine mammals may avoid anthropogenic sounds (Kastelein et al., 2008; Morton and Symonds, 2002; Nowacek et al., 2007) and thus sounds have been used to manage marine mammal/fishery conflict. Acoustic deterrent devices (ADDs) are one of the most widespread non-lethal deterrent methods implemented for marine mammal/fishery conflict (Fjalling et al., 2006; Graham et al., 2009; Jacobs and Terhune, 2002; Jefferson and Curry, 1996; Sepulveda and Oliva, 2005; Shaughnessy et al., 1981). They are primarily used to protect stationary resources such as aquaculture pens or salmon spawning sites.

The basic goal of an ADD (also termed acoustic harassment device AHD) is to create a sound that is painful or distracting enough that it creates aversion and makes the animal flee or prevent it from visiting the area altogether (Jefferson and Curry, 1996). Their use is expected to be effective because marine mammals are particularly sensitive to high intensity sound because of specialized hearing adaptations for underwater sound (Wartzok and Ketten, 1999). Marine mammal species have variable hearing thresholds, as well as variable responsiveness to novelty. This information is essential to properly design an ADD because different hearing sensitivities across species will result in differential behavioral responses (Götz, 2008).

Despite short-term successes in creating aversion, ADDs have not been useful in the long-term because animals seemingly habituate to them or continue depredating (Anderson and Hawkins, 1978; Mate and Harvey, 1987). The low cost prey resources offered by fishing lines or aquaculture pens likely accelerate sea lion habituation to ADDs. After repeated exposure to the ADD, habituation essentially makes the sound a salient neutral stimulus that the animal can learn to associate with fishery resources. This so-called 'dinner bell effect' is observed when the depredators learn to associate the deterrent sound with food resources (Jefferson and Curry, 1996; Mate and Harvey, 1987).

Acoustic deterrent device usage remains controversial because of the risk of harming pinniped hearing and disturbing non-target wildlife (Gordon and Northridge, 2002; Morton and Symonds, 2002). The high source pressure levels of most ADDs on the market can potentially influence hearing by causing temporary threshold shifts (TTS) or even risk permanent hearing damage (Gordon and Northridge, 2002). ADDs aimed at deterring pinnipeds often produce mid-to high frequency high intensity noise that is within the sensitive hearing range of odontocetes. Consequently, ADD usage can cause habitat exclusion in odontocete species such as killer whales and harbour porpoises (*Phocoena phocoena*) (Morton and Symonds, 2002; Olesiuk et al., 2002; Brandt et al., 2013). A successful deterrent should be sufficiently aversive so that it creates avoidance but does not cause hearing damage or excludes or interferes with non-target species.

6.3.1. Pingers

Pingers are a specific type of ADD that uses lower acoustic output (<150 dB (re: 1 μPa)) sounds to prevent bycatch (Götz, 2008). Bycatch represents another form of marine mammal fishery conflict in which marine mammals, commonly small odontocetes like porpoises, fail to detect fishing nets and ultimately become trapped. This incidental mortality is a significant conservation problem, resulting in several hundred thousand animals lost per year and threatening several species with extinction (Jefferson and Curry, 1994, 1996; Read and Wade, 2000; Reeves et al., 2003; Read, 2008). This prompted the development of pingers, devices that give off high frequency but lower intensity acoustic stimuli, with the goal of either alerting the marine mammals to the presence of the net or creating aversion to the net (Dawson et al., 1998). Controlled field experiments have demonstrated that pingers significantly reduce harbour porpoise and common dolphin bycatch (Barlow and Cameron, 2003; Kraus et al., 1997: Carretta and Barlow, 2011) and effectively eliminated beaked whale bycatch in gillnets (Carretta et al., 2008).

The success of pingers and the ineffectiveness of ADDs illustrate the importance of motivation in aversion. In species that actively depredate from gillnets such as bottlenose dolphins and sea lions, pingers fail to induce avoidance (Carretta and Barlow, 2011; Gazo et al., 2008). It is not fully understood how porpoises become entangled in gillnets, but it is likely that porpoises are feeding in the vicinity and are unable to locate the net. Because porpoises appear to not be depredating, there is no heightened benefit to associate/habituate to the pinger, which is evidenced by long-term pinger success. The difference in the effectiveness of pingers is not only related to the benefits of depredation, but probably also with the sensitivity of different species to sound. For instance, the 100% reduction of bycatch in beaked whales suggests enhanced vulnerability of these whales to acoustic pollution (Carretta et al., 2008).

6.4. Tactile deterrents

Tactile deterrent methods vary, but typically involve physically creating pain or discomfort in depredators to induce aversion. Examples of tactile harassment methods include shooting rubber bullets, blunt-tipped arrows, or rubber buckshot at depredators (Scordino, 2010). The goal of tactile harassment methods is to elicit flight behaviors by creating pain. Illustrative examples of the long-term tactile harassment involve the depredation of spawning salmon in Bonneville dam in the Northwest United States. During tactile hazing individuals exhibit an immediate flight response, but frequently return and learn to either surface infrequently or avoid the shooter (Scordino, 2010).

The creation of a pulsed, low voltage DC electric field aimed to deter pinnipeds predating salmon is a novel tactile harassment technique, analogous to the use of electric fencing to control livestock in terrestrial ecosystems. In both captive setting and wild settings, seals exhibited avoidance to an electrical gradient, but the seals returned to the net once the electric field was turned off (Forrest et al., 2009). Overall, it appears that the electric field deterrent can generate a highly localized and temporary aversion because food motivation drives the animals to return (Shivik et al., 2003). Additional effects on non-pinniped species, especially fish requires further investigation.

The benefit of tactile harassment methods is that painful stimuli create immediate flight responses and are difficult to habituate to. Additionally, pain causes instantaneous and long-term learning (Fig. 2). Fear conditioning enables the animal to derive learned associations and subsequently exhibit fear responses to the stimuli or contexts that predict the tactile deterrent. The goal of tactile deterrents should explicitly be to promote fear conditioning rather than to continuously produce aversive stimuli (e.g., a constant electric fence or permanent presence of shooters).

6.5. Visual deterrents

There is evidence that pinnipeds and dolphins possess sophisticated visual systems (Schusterman, 1981; Kuczaj et al., 2008) and there are observations of pinnipeds using vision to detect predators (Baird and Stacey, 1989). However, visual deterrents have

Table 2
Summary of some management concerns for non-lethal deterrents.

Management concerns for deterrents	Factors that reduce success (costs)	Factors that enhance success (benefits)
Animal welfare	– Stimuli cause permanent damage – Stimuli deter animals completely from habitats of biological importance	– Use perceived aversive signals over intensity – Implement conditioning procedure to reduce exposure to painful stimuli
Applicability	– Cost prohibitive for fishermen – Depredation widespread geographically – Risk to human safety	– Localized depredation – Depredation only exhibited by rogue individuals
Effectiveness	– Behavior prevalent in population – Alternate food sources unavailable – Habituation	– Alternate food sources available – Sensitization – Target rogue individuals or individuals most likely to innovate (e.g., adult males or juveniles)
	– Animals have too much previous experience	– Prevent or limit association with fishery resources
Impacts on non-target wildlife	– Unknown sensory mechanisms – Sensory sensitivity overlap with other marine mammals or fish – Pollution produced by deterrents (e.g., rubber bullets)	– Optimize signal for target animal sensory sensitivity – Multi-modal and varying stimuli deterrent strategy

not been extensively tested in cases of marine mammal/fishery conflict. Fiberglass models of killer whales placed around aquaculture pens (Sepulveda and Oliva, 2005) had a limited effect in deterring depredating pinnipeds. Novel or intense light stimuli elicit aversive responses in sea turtles interacting with gill nets (Wang et al., 2010), but this strategy has not yet been tested on marine mammals.

7. Conclusions

7.1. Implications of deterrents

There are often conflicts between wildlife management and wildlife conservation (e.g., Blumstein 2010a,b; McMahon et al., 2012). Aversive stimuli can elicit fear or anxiety resulting in long term avoidance of an area or a resource (Frid and Dill, 2002; Morton and Symonds, 2002). Based on our review, we suggest that deterrents must incorporate first principles of animal behavior and learning for long-term success. We suggest that there are at least four potential management concerns (Table 2) that require consideration before implementing non-lethal deterrents: impacts on non-target wildlife; animal welfare; applicability; and overall effectiveness.

Because deterrent stimuli are potentially aversive to other taxa, successful application of deterrents must weigh the potential cost to other species with the overall management benefit. Marine mammals are equipped with species-specific sensory mechanisms and sensitivity to assess and detect threats. We, and others (e.g., Gilsdorf et al., 2003; Southwood et al., 2008; Gotz and Janik, 2010; Biedenweg et al., 2011; Ramp et al., 2011), have suggested that non-lethal deterrents should tailor signals toward the particular species' sensory mechanisms and sensitivities. Acoustic pollution has negative impacts (for review see Kight and Swaddle, 2011), especially for marine fauna (Rolland et al., 2012). Different deterrents will have different effects on marine fauna. Acoustic devices differ in their frequency range and acoustic output (emitted level and duty cycle) and the receivers (marine mammal species targeted or not by the deterrents) vary in their acoustic sensitivity and behavioral reactions to sound. The active space of acoustic stimuli will vary based upon the signal characteristics, as well as the receivers' hearing thresholds and responsiveness (i.e., seal scaring devices may deter porpoises 7.5 km away (Brandt et al., 2013)). The differences in sensory abilities, responsiveness to novelty (neophobia), and the learning capacity of other non-target species potentially exposed to deterrent stimuli should be taken into account before and during application to mitigate non-target wildlife impacts.

Deterrents are not only used to mitigate interactions of marine mammals with human activities (aquaculture or stealing fish from human fisheries), but also to deter marine mammals from natural habitats and natural prey in order to prevent competition with other top-predators: humans. This raises ethical concerns over the appropriate application of deterrents and how widespread their usage should be. Using deterrents for cases of natural foraging may be justified if there is clear documentation of negative impacts and the availability of alternative habitat/resources. Also, the target species should not be declining or endangered. Whether it is acceptable to use deterrents to elicit aversion from fishing gear versus using them to deter marine mammals from feeding in natural habitats over natural prey to avoid competition with humans for the same resource is an open question.

The degree of discomfort animals experience from deterrents raises animal welfare concerns. Exposure hinges upon whether alternative resources/habitat are available. If not, the individuals will have no choice but to continue to forage and be exposed to the deterrents. Deterrent stimuli should never cause permanent damage. The intensity and duration of deterrent stimuli (especially acoustic) are relevant parameters than can be modified to prevent damage.

We believe that deterrents will enhance success and minimize non-target impacts when used in situations where depredation has a narrow spatial extent and can be targeted to nuisance animals. Acoustic deterrents, by their very nature are applied over a relatively broad area and may include marine protected areas or large-scale aquaculture facilities. There is no register of the number of devices in use or lost at sea (some pingers can be active for a year upon being lost) and collecting these data should be a priority because this information can help mitigate the use of such devices. In Scotland, for example, ADD use may contribute to large-scale acoustic pollution (Gordon and Northridge, 2002). In the Rogue River in Southern Oregon, targeted hazing of individual sea lions with cracker shells, rubber bullets and seal bombs successfully reduced depredation of commercial and recreational salmon fishers in the river (Scordino, 2010). This is a sharp contrast with less successful deterrent efforts on sea lions that swim toward salmon ladders in Northern Oregon and Washington. The degree to which the behavior has spread through the population and the geographic extent that requires deterrence may contribute to their effectiveness.

7.2. Enhancing conservation success through fear conditioning–learning matters

Avoidance of possible or potential threat reduces the likelihood of attack whereas fight/flight behaviors are defenses from impending attack. These are distinct functional and behavioral pathways that animals evolved to avoid danger (McNaughton and Corr, 2004). Each is governed by unique proximate mechanisms (anxiety and fear). The capacity of painful or aversive stimuli to induce fear (flight) responses has made them common for managers (Shivik et al., 2003). Fear, however, is short term, and is terminated following the direct escape from threat (Eilam et al., 2011). In other words, once the animal has fled and is out of the immediate vicinity of the stimulus, fear subsides, and motivation will drive the depredator to return. In contrast, anxiety is sustained and can create chronic avoidance as seen in animal models of post-traumatic stress syndrome (Siegmund and Wotjak, 2006). The goal of deterrent stimuli should not be the continual use of stimuli that elicit short-term flight responses, but rather the promotion of anxiety that results in avoidance of potential danger. Thus, first principles strongly suggest that a Pavlovian fear conditioning paradigm will enable depredators to learn the cues/contexts that precede the dangerous/painful stimuli, ultimately resulting in anxiety and avoidance of the anxiety-producing situation.

A Pavlovian fear-conditioning paradigm for deterrents is an ethologically inspired deterrent. Fear conditioning, by facilitating learning of the cues that precede threat, enables individuals to use behavioral responses to move down the risk continuum (Fanselow and Lester, 1988) from fear (flight) to anxiety (avoidance). The application of fear conditioning for deterrents should be species specific, tailoring the stimuli used as US and CS to a species' sensory sensitivities, as well as include combinations of stimuli that belong together. For marine mammals, sound is a salient stimulus that can be used as a CS and a US if sufficiently startling (Gotz and Janik, 2011). Painful or startling stimuli are difficult to habituate to, especially if a once conditioned individual avoids exposure through avoidance. *Extinction*, the decrease in responsiveness to a previously acquired conditioned stimulus with repeated non-reinforced exposure, could be delayed with partial reinforcement. The reinforcement schedule (i.e., when to expose individuals to the CS and US pairing) can be tailored to suit particular situations. If there are many animals depredating (sea lions depredating purse seine nets) and a large turnover of individuals, learning will vary across individuals. This situation will likely require regular reinforcement to ensure new individual conditioning. Alternatively, if a small number of animals feed and repeatedly return it is likely that less regular, but nonetheless periodic, reinforcement schedules will suffice to prevent extinction. Managers should tailor reinforcement schedules to appropriate contexts and some effort must go into identifying the number and diversity of potential depredators.

Given management and conservation concerns, we recommend a cautious approach to deterrents. There are difficulties in designing US and CS and there is the real possibility of impacting non-target organisms or displacing target animals from essential habitat. There is much to learn to optimize deterrent application and to mitigate marine mammal conflict with fisheries. We emphasize that the value of using threatening or painful stimuli is that if effectively conditioned, it can create long-term learned avoidance that does not require using the painful stimulus in the future. Once the animals learn the association (and animals may learn these associations with only a few trials), they will never experience the painful stimuli as long as they avoid the protected resource. We view this, ultimately, as a welfare-friendly solution to human-wildlife conflict.

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