OPEN ACCESS

REVIEW

Sound, chemical, and light detection in sea turtles and pelagic fishes: sensory-based approaches to bycatch reduction in longline fisheries

Amanda Southwood[1],*, Kerstin Fritsches[2], Richard Brill[3], Yonat Swimmer[4]

[1]Department of Biology and Marine Biology, University of North Carolina Wilmington, 601 S. College Rd., Wilmington, North Carolina 28403, USA

[2]School of Biomedical Sciences, University of Queensland, Brisbane, Queensland 4072, Australia

[3]NOAA-NMFS Cooperative Marine Education and Research Program, Virginia Institute of Marine Science, PO Box 1346, Gloucester Point, Virginia 23062, USA

[4]NOAA Fisheries, Pacific Islands Fisheries Science Center, 2570 Dole St., Honolulu, Hawaii 96822, USA

ABSTRACT: Mortality due to capture in longline fisheries has been implicated as a significant factor contributing to population declines for several species of threatened or endangered sea turtles. Identification of methods to reduce or prevent sea turtle bycatch is a high priority for fisheries managers and a necessary component of conservation efforts. One approach to reducing sea turtle interactions with longline fisheries is to take into account the behavior of sea turtles and the factors that lead them to interact with fishing gear. An understanding of the sensory cues that attract sea turtles to longline gear could help guide efforts to develop gear and bait that is less attractive, non-detectable, or even repellent to sea turtles. This paper presents a review of morphological, physiological, and behavioral studies conducted to assess the auditory, chemosensory, and visual capabilities of sea turtles, as well as the large pelagic fishes that are targeted by longline fisheries. We discuss the potential for exploiting differences in the sensory biology of these evolutionarily distinct groups to refine longline fishing techniques and reduce incidental bycatch of sea turtles without impacting the catch rates of targeted fish species. Based on the current evidence, differences in visual capabilities of sea turtles and pelagic fishes provide a promising avenue for development of a sensory-based deterrent.

KEY WORDS: Endangered species · Conservation · Chemoreception · Hearing · Vision

INTRODUCTION

Pelagic longline fishing involves spacing hundreds to thousands of vertical branch lines with baited hooks along a monofilament main line that is suspended in the water column by a series of floats. Shallow-set longlines (<100 m depth) target swordfish *Xiphias gladius*, mahi mahi *Coryphaena hippurus*, and surface-feeding tuna species (e.g. yellowfin tuna *Thunnus albacares*), while deep-set longlines (>100 m depth) target bigeye tuna *T. obesus* and bluefin tuna *T. thyn-*

nus. Unintended capture of non-target species, or bycatch, in longline gear includes elasmobranchs, teleosts, marine mammals, birds, and sea turtles (Harrington et al. 2005).

Bycatch of sea turtles in longline gear has been implicated as a significant source of mortality for endangered leatherback turtles *Dermochelys coriacea* and loggerhead turtles *Caretta caretta* in both the Pacific and Atlantic Oceans, and threatened olive ridley turtles *Lepidochelys olivacea* in the Pacific Ocean (Balazs & Pooley 1994, Spotila et al. 2000, Lewison et

al. 2004). As a result, United States (US) regulatory agencies have enacted numerous temporal and gear-based mitigation measures to reduce or prevent capture of sea turtles by the US longline fleets. Swordfish fleets operating in the Pacific and Atlantic Oceans have been subject to large scale time-area closures so that interactions might be avoided (NMFS 1999, 2000, 2001). However, the US fleet comprises <5% of the total longline effort in the Pacific Ocean (Lewison et al. 2004), and <10% of the total longline effort in the Atlantic Ocean (Witzell et al. 2001). Fishing fleets from other nations continue to operate in areas deemed by the US government to be high-risk for sea turtle interactions. Given that fishery closures are not a mitigation method that other fishing nations are likely to adopt, the usefulness of this approach for reducing sea turtle bycatch is limited.

Recent experiments have shown that simple alterations in gear configurations and bait can result in large-scale reductions in sea turtle bycatch, and there is a growing interest in identifying economical and practical fishing techniques that minimize bycatch without impacting target species catch rates. For example, Watson et al. (2005) found that the use of 18/0 circle hooks in a North Atlantic swordfish fishery significantly reduced both the number of sea turtle interactions and the incidence of hook ingestion. Similar results were obtained when 18/0 circle hooks were incorporated into the Hawaiian swordfish fleet (Gilman et al. 2007). There are, however, some limitations to using this purely mechanical approach. The size of sea turtles interacting with longline gear may vary between fisheries, and circle hook design may not be equally effective at preventing capture for all size classes of sea turtles (Read 2007). There is also evidence that circle hooks reduce catch rates of target species in some fisheries (Largarcha et al. 2005 as cited in Read 2007), although in the majority of cases target species catch rates are unaffected. Most managers and conservationists agree that circle hooks show great promise for reducing bycatch and minimizing hooking severity under many conditions, and efforts to further refine this mitigation measure are ongoing. Nevertheless, continued research into alternative gear and bait modifications is necessary to mitigate bycatch for fisheries in which circle hooks are not effective or in which fishers are unwilling to adopt circle hooks as a mitigation tool. Fisheries managers recognize the need to have a broad array of bycatch reduction strategies based on mechanical, behavioral, and physiological approaches so that management measures can be customized for various regional fisheries.

Consideration of sea turtle behavior and the nature of interactions between sea turtles and fishing gear may lead to innovative solutions to the bycatch problem. The factors that attract sea turtles and target fish species to longline gear and bait are not well understood, but multiple sensory cues are probably involved. Sea turtles and pelagic fishes are evolutionarily distinct groups of animals with differences in sensory biology that may influence the ways in which they interact with fishing gear. Identification of differences in sensory capabilities of sea turtles and pelagic fishes, as well as potential sensory attractants or repellents for these animals, could guide efforts to refine fishing techniques to more specifically target desired species and to reduce capture of sea turtles. We present a review of morphological, physiological and behavioral studies conducted to assess the auditory, chemosensory, and visual capabilities of sea turtles and large pelagic fishes. Our review of fish sensory capabilities focuses on teleost species, as they are the primary targets of the majority of longline fisheries. We also include notes on hearing, olfaction, and vision in pelagic sharks, as they are specifically targeted by some fisheries and a bycatch species of concern in other fisheries. We discuss the potential for exploiting differences in the sensory biology of sea turtles and pelagic fishes to develop economically viable gear modifications to reduce sea turtle bycatch, and comment on the advantages and disadvantages of this approach.

HEARING

Pelagic fishes

The use of sound for intra- and inter-specific communication, predator detection, prey location, and orientation are well documented for fish (Myrberg et al. 1976, Mann et al. 2001, Tolimieri et al. 2002, Bass & McKibben 2003, Popper 2003a). To date, all fish species that have been tested have shown the capacity to detect and respond to sounds in their environment. Hearing capabilities of the pelagic fishes targeted by longline fisheries have been studied less than in other species, primarily due to the logistic difficulties of maintaining these large animals in captivity and conducting controlled experiments with them. Nevertheless, morphological studies and a limited amount of physiological and behavioral data provide important insight as to their hearing capacity.

The general morphology of the ear has been described for bluefin tuna (Song et al. 2006) and skipjack tuna *Katsuwonus pelamis* (Popper 1981). As with other fishes, there is no external opening to the ear and the canals and arrangements of bones in the ear are typical of teleosts (Popper 2003b). Ultrastructural examinations of the sensory epithelia in these tunas

suggest that they are hearing generalists, as they lack specializations in either hair cell orientation or concentration to enhance hearing (Popper 1981, Song et al. 2006).

Behavioral and physiological studies provide evidence that tunas are hearing generalists that detect low frequency sounds <1000 Hz. Iversen (1967, 1969) was first to describe behavioral responses of scrombrid fish to underwater sounds, and demonstrated that yellowfin tuna and kawakawa *Euthynnus affinis* detect sounds within the range of 50 to 1100 Hz with highest sensitivity at 300 to 500 Hz. Studies employing the auditory brainstem response (ABR) technique have demonstrated that yellowfin tuna respond to auditory stimuli within the frequency range of 200 to 700 Hz, and are most sensitive to sounds between 200 and 400 Hz (Table 1, Fig. 1) (Moein Bartol & Ketten 2006, R. W. Brill unpubl. data).

Studies of acoustic attraction in ocean-dwelling shark species support the general conclusion that sharks, like pelagic teleosts, are low frequency specialists (Myrberg 2001). Silky sharks *Carcharinus falciformis* and oceanic white-tip sharks *Carcharinus longimanis* are attracted to low frequency sound within the range of 25 to 1000 Hz, with attractiveness increasing as sound frequency decreases (Myrberg et al. 1972, 1976). Irregularly

pulsed sounds, such as might be generated by struggling prey, are more attractive than regularly pulsed sounds (Myrberg et al. 1976). Sudden transmission of high intensity sound at close range prompts an immediate and rapid withdrawal in both silky sharks and oceanic white-tip sharks (Myrberg et al. 1978). However, both species rapidly habituate to such signals.
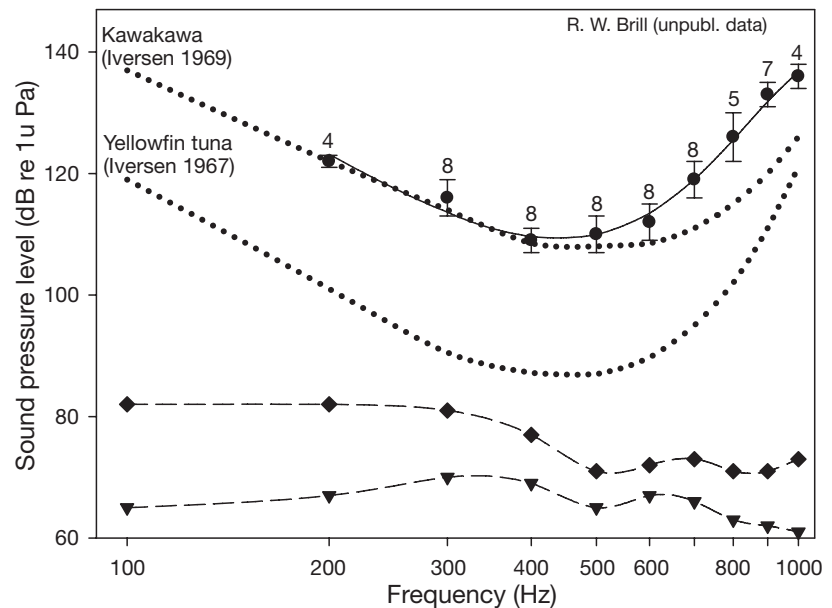

Fig. 1. *Thunnus albacares* and *Euthynnus affinus.* Hearing curve for yellowfin tuna recorded using the auditory brainstem response (ABR) technique (solid line; R. W. Brill unpubl. data). Numbers above the data points are the number of yellowfin tuna from which data were obtained. The hearing curves from Iversen (1967, 1969) obtained using behavioral means have been added for comparison (dotted lines). The dashed lines at the bottom of the graph show noise levels aboard the ship (◆) and in the laboratory (▲) where the hearing experiments were conducted (R. W. Brill unpubl. data). Error bars: SE

Table 1. Hearing capabilities of pelagic fishes and sea turtles as measured using behavioral and electrophysiological techniques. ABR: auditory brainstem response

Species	Range (Hz)	Highest sensitivity (Hz)	Technique	Source
Fishes				
Thunnus albacares	50–1100	300–500	Behavioral responses	Iversen (1967)
	200–700	200–400	ABR	Moein Bartol & Ketten (2006) K. A. Brill (unpubl. data)
Euthynnus affinus				
	100–1100	500	Behavioral responses	Iversen (1969)
Turtles				
Chelonia mydas				
	100–1000	300–400	Cochlear potentials (air)	Ridgway et al. (1969)
	100–800	600–700 (juvenile) 200–400 (sub-adult)	ABR (underwater)	Moein Bartol & Ketten (2006)
Caretta caretta				
	250–1000	250	ABR (air)	Moein Bartol et al. (1999)

Sea turtles

Although the ecological role of hearing has not been well studied for sea turtles, hearing capacity has been inferred from morphological and electrophysiological studies. The morphology of the ear in sea turtles is similar to that found in terrestrial and semi-aquatic turtles (Wever 1978), with the exception of a layer of fat that lies directly beneath the tympanum (Moein Bartol & Musick 2003). Lenhardt et al. (1985) speculated that sound conduction would be optimized in water, based on the ratio of the area of tympanic membrane to the area of the oval window in the middle ear; however, sea turtles show behavioral and physiological responses to sounds delivered in both air and water.

Results from electrophysiological studies of hearing capabilities of sea turtles show that they hear low frequency sounds within the range of 100 to 1000 Hz with greatest sensitivity at 200 to 400 Hz (Table 1). Ridgway et al. (1969) recorded cochlear potentials of green turtles *Chelonia mydas* exposed to sounds delivered from a loudspeaker in air and mechanical vibrations delivered directly onto the tympanum in air. Green turtles responded to aerial sounds with the range of 100 to 1000 Hz and vibrations within the range of 100 to 700 Hz, with greatest sensitivity at 300 to 400 Hz for both experimental protocols. ABRs of juvenile loggerhead turtles exposed to vibrations delivered to the tympanum in air show responses to low frequency stimuli within the range of 250 to 1000 Hz, with highest sensitivity at 250 Hz (Moein Bartol et al. 1999). More recently, ABRs have been recorded in green sea turtles exposed to underwater sound stimuli (Moein Bartol & Ketten 2006). Under these experimental conditions, green turtles displayed a measurable ABR to sound stimuli within the range of 100 to 800 Hz, with greatest sensitivity between 600 and 700 Hz for juvenile turtles and 200 to 400 Hz for sub-adult turtles.

Deterrent potential

The idea of using an auditory deterrent to prevent sea turtles from entering a particular coastal area or interacting with machinery or anthropogenic operations is not new. O'Hara & Wilcox (1990) assessed the feasibility of using seismic air guns discharged underwater to prevent loggerhead turtles from entering a water intake canal for a nuclear power plant in Florida. Turtles would not breach a 30 m perimeter around the source of the noise, but to achieve this result the sound output had to exceed 200 dB re 1 uPa @ 1m in the 250 to 1000 Hz range. This very high level of sound intensity is likely to affect the behavior of other animals that detect sounds within the low frequency range and potentially cause hearing damage to organisms at close range (Popper 2003a). Moein et al. (1994, as cited in Moein Bartol & Musick 2003) also investigated the effects on sea turtle behavior of loud sounds generated from seismic air guns (175 to 179 dB re 1 uPa @ 1m, 100 to 1000 Hz) fired underwater. The purpose of the study by Moein et al. (1994) was to assess the feasibility of using auditory deterrents to clear sea turtles from the paths of hopper dredges. Juvenile loggerhead turtles held in in-water net enclosures (18 × 61 × 3.6 m) were repeatedly exposed to air gun blasts and monitored for behavioral responses. The investigators found that although loggerhead turtles initially avoided the region where the noise source was located, over a short period of repeated exposure the avoidance response rapidly waned (Moein et al. 1994). This decrease in the behavioral avoidance response could be due to habituation or to hearing impairment caused by repeated exposure to high intensity sounds.

Habituation to acoustic signals is an important issue with respect to the feasibility and long-term effectiveness of an acoustic deterrent. High frequency acoustic pingers have been used with some success to prevent marine mammals from interacting with gillnets, but the use of this approach has generated concern that cetaceans may become habituated to the pingers (Cox et al. 2001) or come to associate pingers with a potential source of food (Cox et al. 2003). Additionally, there is evidence that acoustic pingers deter fish species that are capable of detecting the high frequency sounds they emit (Nestler et al. 1992, Dawson et al. 1998). Both sea turtles and longline target species are hearing generalists that detect sounds within a similar range, so any sound generated to prevent sea turtles from interacting with gear would also be detected by, and potentially have a deterrent effect on, target species.

General criticisms aimed at auditory deterrents for marine mammals are also applicable to the use of auditory signals to prevent sea turtles from interacting with longline fisheries. Scientists, managers, and conservationists all agree that we should avoid increasing anthropogenic sound levels in the ocean unless it is absolutely necessary to do so. Considering the problems and difficulties associated with the use of auditory deterrents and the low likelihood that an acoustic signal could selectively deter sea turtles from interacting with longline gear without affecting target species catch rates, we conclude that efforts to identify an effective sensory deterrent are best directed elsewhere.

CHEMORECEPTION

Pelagic fishes

The term 'chemoreception' refers to an organism's ability to sense chemical cues in its environment by taste (gustation) or smell (olfaction). Numerous studies

have shown that fish use chemical cues to detect and locate prey, to navigate during short- and long-distance migrations, and for intraspecific communication related to reproduction and predator avoidance (Weldon 1990, Hara 1993, Zimmer & Butman 2000, Atema et al. 2002, Doving & Stabell 2003, Wisenden 2003 and references therein). The detailed structure of olfactory and gustatory organs is well described for many teleosts and elasmobranchs (Kleerekoper 1978, Hara 1993, Hansen & Zielinski 2005), but very few data exist on the morphology of these sensory structures in tunas and billfish. The olfactory organ of the skipjack tuna is similar in structure to that of other teleost fish (Gooding 1963). Further studies are necessary to describe the gross morphology and sensory structures for other species of tunas and billfish.

Results from behavioral studies show that chemical cues play a role in food detection and search behavior in tuna. Captive yellowfin tuna have strong behavioral responses to the introduction of prey rinses and amino acid extracts into their holding tank (Atema et al. 1980). Presence of prey odors induces an increase in swimming speed, tight circling in the region where odor was encountered, breakdown of coordinated schooling behavior, and appearance of 'feeding bars' (dark stripes that appear on tuna while feeding). Although prey odors cause an increase in searching behavior, tunas seldom locate the odor source. These results suggest that chemical cues are important for initiating search behavior in tunas, but other sensory cues, mainly vision, are probably critical for actually locating prey once a search has been initiated (Atema et al. 1980).

Sharks have well-developed olfactory organs, and are renowned for their ability to detect and track small concentrations of prey chemicals in their environment (Kleerekoper 1978). Studies with coastal shark species (nurse sharks *Ginglymostoma cirratum* and lemon sharks *Negaprion brevirostris*) have demonstrated that the presence of prey or prey extracts induces rheotactic and klinotactic search behavior (Kleerekoper 1978, Hodgson & Mathewson 1978, Hueter et al. 2004), although successful localization and acquisition of prey items appears to require additional sensory cues. The limited data available for pelagic species of sharks indicate that chemical cues may trigger search behavior and a downstream approach to the general location of prey (Strong et al. 1992).

Although the data on chemoreception in large pelagic fishes are limited, it is reasonable to assume that chemical odors associated with bait contribute to the strike/no strike decision. Mejuto et al. (2005) conducted field experiments using longline gear with different bait types, and found that swordfish catch rates using artificial bait filled with pieces of mackerel were significantly greater than catch rates using artificial

bait that contained no mackerel. The 2 bait types were visually identical, and these results suggest that the final decision to strike baited hooks may be strongly influenced by chemical cues. Therefore, alterations to the chemical signature of longline bait may have a significant effect on catch rates of target species.

Sea turtles

In tetrapods, chemoreception is accomplished by olfaction, vomerolfaction (i.e. chemical detection using the vomeronasal organ), or gustation. Morphological data lends support to the idea that turtles use vomerolfaction, rather than olfaction, to detect chemical cues in the aquatic medium. A comparison of sensory epithelia from turtles that utilize a variety of habitats reveals that the vomeronasal epithelium is more widely distributed in the nasal cavity of highly aquatic turtles than in terrestrial species (Parsons 1971), and dye experiments with the freshwater Reeve's turtle *Geoclemys reevesii* showed that the vomeronasal epithelium is routinely exposed to water, whereas sections of the nasal cavity lined with olfactory epithelia are kept dry (Shoji et al. 1994). In loggerhead sea turtles, the vomeronasal epithelium is widely distributed and olfactory epithelium is restricted to the dorsal portion of the nasal cavity (Saito et al. 2000).

The chemosensory abilities of sea turtles have been an object of study for many years, as there is a great interest in the role that chemical cues play in navigation, migration, and natal homing for these species (Carr 1967). It is clear that sea turtles are capable of detecting and responding to chemical cues in their aquatic environment. Manton et al. (1972) used an operant conditioning technique involving a food reward to test the chemosensory abilities of juvenile green turtles and found that they could detect a variety of chemicals underwater. Anosmia induced in green turtles by injecting $ZnSO_4$ intranasally resulted in a loss of ability to detect chemicals, suggesting that the primary receptors used for aquatic chemoreception in sea turtles are in the olfactory and vomeronasal epithelia, rather than in the gustatory receptors in the mouth.

One of the earliest studies to focus on the ecological relevance of chemoreception in sea turtles was directed at assessing the role that chemical cues might play in allowing hatchling sea turtles to imprint on their natal beach and subsequently migrate back to this beach as breeding adults. Owens et al. (1982) demonstrated that loggerhead turtles exposed to morpholine (5×10^{-5} M) in an artificial nest cavity and in seawater holding tanks after hatching preferentially oriented toward morpholine in a circular choice tank. Similar experiments with green turtle hatchlings

showed that they preferentially orient towards chemical cues encountered early in life (Grassman & Owens 1987). Sea turtles use magnetic orientation to navigate the oceans during long-distance migrations (Lohmann et al. 1999, 2004), but artificial imprinting experiments show that waterborne chemical cues may also play an important role in natal homing (Owens et al. 1982, Grassman & Owens 1987).

The aspect of chemoreception most relevant to interactions with longline fisheries is the role of chemical cues in food detection, recognition, and location in sea turtles. This is a particularly important issue for species of sea turtles that ingest longline bait, such as pelagic-stage loggerhead turtles and olive ridley turtles. Leatherback turtles are dietary specialists that feed primarily on gelatinous prey, and the majority of leatherback interactions with longline gear are the result of foul-hooking in the flippers or carapace rather than attempts to ingest squid or mackerel bait. Laboratory trials show that loggerhead turtles are able to detect chemicals emanating from bait and associate those chemicals with a food source (Grassman & Owens 1982, Southwood et al. 2007). Hatchling loggerhead turtles displayed strong feeding responses to fish odors, an ability to distinguish between several different food types based on chemical cues, and a readiness to adapt to new diets (Grassman & Owens 1982). Leatherback hatchlings also displayed strong behavioral responses when presented with food homogenate (Constantino & Salmon 2003), although the relevance of chemical cues in attracting this species to longline gear is debatable.

Although chemical cues elicit feeding behavior in loggerhead, green, and leatherback turtles (Manton et al. 1972, Grassman & Owens 1982, Constantino & Salmon 2003, Southwood et al. 2007), the majority of experimental evidence suggests that visual cues are of primary importance in locating prey. Constantino & Salmon (2003) found that when visual and chemical cues associated with jellyfish prey were simultaneously presented to leatherback post-hatchlings, they ignored the current created by chemical delivery and oriented towards the visual stimuli instead. When tested separately, visual stimuli evoked a more robust feeding response than did chemical stimuli (Constantino & Salmon 2003). Likewise, captive-reared juvenile loggerhead turtles demonstrated limited ability to track and locate a food source in the absence of visual cues, even when strong behavioral responses were elicited by the presence of food chemicals (Southwood et al. 2007).

As with pelagic fishes, chemical cues play a role in sea turtles' bite/no bite decision once a food item has been visually located. Piovano et al. (2004) demonstrated that loggerhead turtles showed an ability to distinguish between fishing lures based on odor. Loggerhead turtles presented with either odorless squid-shaped plastic lures or identical lures concealing a small piece of fish bit the lures containing the fish with significantly greater frequency. These studies highlight the importance of an integrated approach towards sensory deterrents, as both visual and chemical cues are likely to attract sea turtles to longline gear and contribute to potentially harmful interactions.

Deterrent potential

The use of chemical additives to make longline bait less attractive or to make it more difficult for sea turtles to locate is appealing from both an economic and enforcement perspective. Chemical modifications would be relatively easy to implement in longline fisheries, as bait could be chemically treated prior to packaging and distribution. Dockside surveillance to ensure that only treated baits were permitted on longline vessels would be sufficient to support enforcement of this mitigation measure, as opposed to costly at-sea observer programs.

Unfortunately, an effective chemical deterrent has yet to be identified for sea turtles in spite of significant efforts in this area. Sea turtles will willingly consume squid bait that has been treated with naturally occurring defensive compounds (squid and sea hare ink), alkaloids (capsaicans derived from habenero chili peppers), and pungent substances (Table 2) (Swimmer et al. 2007). Interestingly, parallel trials with yellowfin tuna and skipjack tuna showed that these target fish species were also willing to consume squid bait that had been treated with the same variety of chemicals (Swimmer et al. 2007).

Terrestrial reptiles and amphibians display avoidance and defensive behavior when presented with skin extracts and rinses from predators (Dial 1990, Weldon 1990). Shark predation on sea turtles has been documented in nearshore environments (Balazs 1980, Fergusson et al. 2000, Heithaus 2001, Heithaus et al. 2002a,b), but the degree of juvenile and adult sea turtle mortality due to natural predation in the pelagic environment where longline fisheries are operating is unknown. Predator avoidance in sea turtles is thought to be based primarily on visual cues, but chemical cues may alert sea turtles to the presence of a predator as well. Captive-reared loggerhead turtles were not deterred from eating squid bait treated with skin secretions from live wild-caught tiger sharks (Southwood et al. 2007); however, association of a predator's scent with a threat may be learned rather than innate. If this is the case, behavioral responses to shark-derived chemicals may be more pronounced in wild-caught sea turtles than in captive-reared sea turtles, and further studies in this area are warranted. The effects of shark-derived compounds on behavior of

Table 2. Feeding responses of green sea turtles presented with squid bait treated with various compounds in attempts to identify a chemical deterrent to feeding (modified from Swimmer et al. 2007). Yellowfin tuna and skipjack tuna readily ate bait that was treated with each compound listed, as did green sea turtles

Chemical additive	Turtles that ate treated bait (%)
Natural defense compounds	
Aplysia ink	85.7 (n = 7)
Loligo spp. ink	100 (n = 8)
Pungent and bitter compounds	
Quinine hydrochloride	100 (n = 3)
Citric acid	100 (n = 4)
Lactic acid	100 (n = 6)
Urea	100 (n = 5)
Habenero chili extract	100 (n = 5)
Wasabi oil	100 (n = 6)
Garlic	100 (n = 5)
Cilantro	100 (n = 5)

tunas and other target fish species, including elasmobranchs, also need to be investigated. Identification of compounds that would selectively deter sea turtles without altering the behavior and catch rates of targeted fishes is a major hurdle in pursuing chemical deterrents as a means of reducing sea turtle bycatch.

A difficulty with using a purely chemical approach to sea turtle bycatch reduction is that the majority of evidence suggests that visual cues are of primary importance for foraging success in sea turtles and that chemical cues play a secondary role. Therefore, a visual deterrent, rather than a chemical deterrent, could be more effective at preventing sea turtle interactions with longline gear. We must bear in mind, however, that even if an effective visual deterrent is identified and implemented in longline fisheries, bait scents in the vicinity of fishing operations may alert turtles to the presence of food and induce a heightened state of awareness and searching behavior. The effectiveness of a visual deterrent will depend largely on whether or not the turtle's aversion response overrides the feeding response, which is fueled in part by chemical cues. Studies investigating the efficacy of various methods for repelling birds show that a combination of both visual and chemical deterrents is more effective than either on its own (Mason & Clark 1996), and this may also be the most appropriate approach for deterring sea turtles from interacting with longline gear.

VISION

Pelagic fishes

Longline fisheries generally target large pelagic fishes that inhabit the clear waters of the open ocean.

The excellent horizontal and vertical visibility in the pelagic habitat has led to the evolution of highly visual predators with well-developed eyes for prey and predator detection. Much of what is known about pelagic fish vision is derived from anatomical studies of the eye and its nervous tissue, the retina (Tamura et al. 1972, Kawamura et al. 1981, Fritsches et al. 2003b). Photoreceptors within the retina translate light information into neural signals, which are then processed and transmitted to the brain via the retinal ganglion cell layer. Two types of photoreceptor cells, rods and cones, are present in the retina of fishes. Rod photoreceptors maximize sensitivity in dim light, whereas cone photoreceptors function optimally in bright light. The presence of different types of visual pigments in the photoreceptors suggests the ability for color perception at different spectral wavelengths. Variations in the general morphology of eye and distribution of pigments and photoreceptors in the retina have important implications for differences in visual capabilities such as color discrimination and spatial resolution in fishes exploiting habitats at different depths.

Telemetry and tracking studies of large pelagic fish species have shown strong vertical niche partitioning. Striped marlin *Tetrapturus audax*, yellowfin tuna, and mahi mahi typically hunt in the brightly lit surface layers (<100 m) during the daytime hours, whereas swordfish and bigeye tuna prefer to hunt in the dim light at deeper depths (Carey & Robison 1981, Palko et al. 1982, Brill et al. 1993, 1999, Gunn & Block 2001, Musyl et al. 2003). Daytime hunting depth is a strong determinant for the visual capabilities of pelagic fish species, as the surface layers of the ocean provide high light intensities and a larger spectral range, whereas light intensity is drastically reduced and the spectral range is narrowed to near-monochromatic blue with increasing depth.

Water acts as a spectral filter, such that long wavelengths in the red spectrum of visible light are filtered more rapidly than shorter wavelengths. As depth increases, colors perceived as green, blue, and violet progressively dominate and, ultimately, the spectrum of down-welling sunlight narrows to a band of blue light centered at 470 nm (Tyler & Smith 1970). Given the spectral distribution in the open ocean, it is no surprise that the spectral range of pelagic teleosts and elasmobranchs is generally centered at 500 nm and does not extend very far into longer wavelengths in the red part of the spectrum.

Pelagic fishes that hunt close to the surface have a greater capacity for color discrimination than those that hunt in deeper waters (Munz & McFarland 1973, Loew et al. 2002, Fritsches et al. 2003a). For example, the peak sensitivities for the bright-light cone photoreceptors of the surface-feeding striped marlin are

located at spectral wavelengths that appear violet-blue (436 nm), blue (488 nm), and green (531 nm) to a human observer (Fig. 2) (Fritsches et al. 2003a). Adult yellowfin tuna, which also feed in the surface layer, show optimal sensitivity to light in the violet-blue (426 nm) and blue (483 nm) range (Loew et al. 2002). Swordfish and bigeye tuna preferentially hunt in deeper water during the daylight hours, and their photoreceptor anatomy and visual pigments suggest a heightened sensitivity solely to the dominant blue wavelength (Fig. 2) (K. A. Fritsches pers. obs.).

Short wavelength ultraviolet (UV) light (<400 nm) penetrates deep into the ocean; however, none of the tuna or billfish species studied to date appear to extend their visual range into the UV spectrum as their lenses effectively block UV light (Fritsches et al. 2000). Several shark species also have lenses that contain pigments to filter UV light (Hueter et al. 2004). Ultraviolet light is rapidly scattered in the water column, creating a veiling effect (Lythgoe 1979). Blocking light in the UV range could, therefore, be a strategy to increase long-distance sight for improved prey detection.

In addition to the reduction in spectral range with depth, there is also a dramatic decrease in light intensity. With depth, light intensity drops rapidly and reaches star-light levels at 600 to 700 m (Clarke & Denton 1962). Many pelagic fishes have very large eyes, which increases the optical ability to collect photons in the dim depth, improving the sensitivity of the eye. On the other hand, the ability to detect fine detail (spatial resolution), which requires high light intensities, is relatively poor in these species. The blue marlin, for instance, has a spatial resolving power of 8.5 cycles per degree for an average lens diameter of 19 mm in adult fish (Fritsches et al. 2003b). Similar values of spatial resolution have been found in behavioral training experiments with tuna (Nakamura 1968). In comparison, the blue tuskfish *Choerodon albigena*, a coral reef

fish inhabiting a brightly lit habitat, shows a spatial resolution of 15 cycles per degree for a lens diameter of <5 mm (Collin & Pettigrew 1989).

Temporal resolution, or the ability to detect motion, is also affected by light intensity. Visual systems are generally capable of adjusting temporal resolution in response to varying light intensities, akin to changing a camera's shutter speed in response to changing background light. Even so, comparative studies in crustaceans (Frank 1999) and fish (Bullock et al. 1991) have shown that the highest temporal resolution achieved varies considerably between species and is strongly linked to the prevailing brightness of the organism's environment and feeding strategy. Temporal resolution may be assessed by measuring flicker fusion frequency (FFF), e.g. the frequency of a flickering light source at which a visual system ceases to be able to discriminate between each flicker. Flicker fusion frequency varies significantly between fishes that utilize shallow vs. deep water habitats. Swordfish generally hunt in dim light and exhibit a maximal FFF of 40 Hz (Fritsches et al. 2005), whereas yellowfin tuna, a species adapted to hunting in bright light, exhibit a maximal FFF of up to 80 Hz (K. A. Fritsches unpubl. data). The faster FFF of the yellowfin tuna would allow this species to detect fast moving prey in bright light with less risk of motion blur than would be experienced by the swordfish.

Sea turtles

Sea turtles evolved from terrestrial species (Pritchard 1997), and some of their visual capabilities may be attributable to their ancestry as well as their habitat. Most sea turtles spend the majority of their time in the brightly lit surface layers (Lutcavage & Musick 1997) and have well-developed visual systems, especially with regards to their spectral range. Liebman & Granda (1971) identified 3 visual pigments in the cones of the green turtle, with peak sensitivities at 440 nm (blue), 502 nm (green), and 562 nm (yellow) (Fig. 2). Unlike pelagic fishes, sea turtle cone photoreceptors also contain different types of colored oil droplets which act as filters that shift the sensitivity of cones towards longer wavelength (red) part of the spectrum (Liebman & Granda 1975). In green turtles the specific pairing of visual pigments with various types of oil droplets suggests at least 4 spectrally different cone photoreceptors (Mäthger et al. 2007), including one which is sensitive to long wavelengths with a peak around
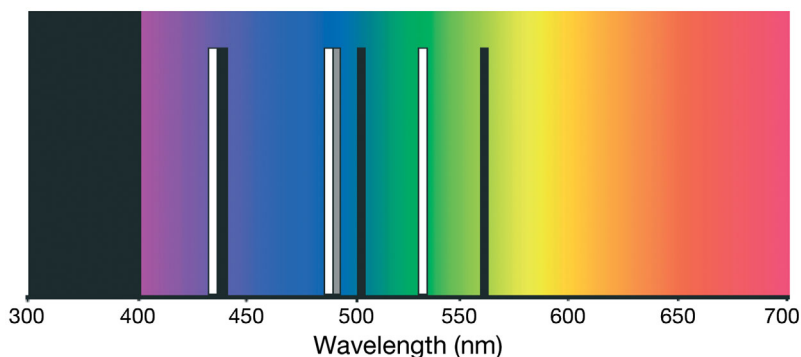

Fig. 2. Comparison of the known peak spectral sensitivities of the striped marlin (white bars; Fritsches et al. 2003), the swordfish (grey bar; K. A. Fritsches unpubl. data) and the green turtle (black bars; Liebman & Granda 1971). The background indicates the colors at the different wavelengths as perceived by the human eye

580 to 600 nm (Granda & O'Shea 1972, Levenson et al. 2004). The presence of oil droplets broadens the spectral range of color perception for both green and loggerhead turtles (Vorobyev 2003, Levenson et al. 2004), and provides them with a greater capacity for color discrimination than pelagic fishes. In contrast, the only existing data for leatherback turtles, which routinely descend to greater depths, shows a limited spectral range with peak sensitivity at approximately 500 nm (Eckert et al. 2006). It should be noted, however, that the leatherback data were collected at night, whereas data for cheloniid species of sea turtles were collected during the day. Differences in spectral sensitivity observed between these species could possibly reflect circadian effects rather than differences in diving and foraging ecology. Further studies are needed to investigate these possibilities.

Interestingly, sea turtles also have the capacity to detect light in the UV range, as their lenses and other optical media transmit light to 320 nm, and indirect evidence suggests that the retina might also contain UV cones (Fig. 3) (Mäthger et al. 2007). Although UV radiation is harmful for the retina (Zigman 1971), a number of marine animals do utilize this part of the visual spectrum for intra-specific communication, detection of prey, and navigation (Marshall & Vorobyev 2003). At the present time it is unclear as to how sea turtles might use UV vision; studies investigating this aspect of sea turtle vision are, thus, warranted.

Sea turtles have surprisingly small eyes and possess very small pupils and lenses in relation to their body size (Northmore & Granda 1991), making the optics of their eyes relatively insensitive to dim light (Mäthger et al. 2007). Even the leatherback turtle, which is

known to dive regularly to depths that exceed 500 m (Eckert et al. 1989), has no specific adaptations to significantly increase the sensitivity of its optical design (Brudenall et al. 2008). There are, however, a number of physiological strategies to improve sensitivity to dim light at the retinal level that have not yet been investigated in sea turtles (Warrant 1999). Detection of dim light seems to be a crucial orientation cue in the early life stages of sea turtles, as light sources affect the movements of newly emerged hatchlings and are thought to guide movements from the nest to the sea (Lohmann et al. 1997, Moein Bartol & Musick 2003).

Juvenile loggerhead turtles have a spatial resolving power of 4 to 8 cycles per degree (Bartol et al. 2002), which is similar to that observed for pelagic fish (Table 3). There is also some overlap in the temporal resolving abilities of sea turtles and pelagic fishes (Table 3). Levenson et al. (2004) reported maximal FFF at approximately 40 Hz in intact loggerhead and green turtle adults, and recordings from isolated green turtle eyes revealed FFF of up to 57Hz (K. A. Fritsches unpubl. data). Recordings from adult and hatchling leatherback sea turtles indicate much slower FFF in this species, reaching maximal FFF below 15 Hz (Eckert et al. 2006). The very large difference in temporal resolution between the leatherback turtle and green and loggerhead turtles represents an important divergence in visual capabilities (Eckert et al. 2006), although some of the observed variations in the FFF values between sea turtle species may be attributable to differences in recording techniques.

Deterrent potential

Sea turtles and pelagic fishes are highly visual predators, and visual cues most likely play an important role in attracting both groups of animals to long-line fishing gear. The use of blue and green chemiluminescent lightsticks is a common practice in many longline fisheries, as lightsticks attract target fish species and increase catch per unit effort (CPUE). Given that sea turtles can detect light in the blue−green spectral range, lightsticks may have the unfortunate side effect of attracting sea turtles to longline gear as well. Laboratory experiments have shown that juvenile loggerhead turtles significantly orient towards chemiluminescent blue (peak 440 nm), green (peak 510 nm), and yellow (peak 550 nm) lightsticks, as well as flashing orange (peak 600 nm) light-emitting diode (LED) lightsticks (Wang et al. 2007).

Modifications to lightsticks that exploit differences in visual capabilities or behavior of sea turtles and pelagic fish could be effective at reducing catch rates of sea turtles. Alterations of the spectral output of light-
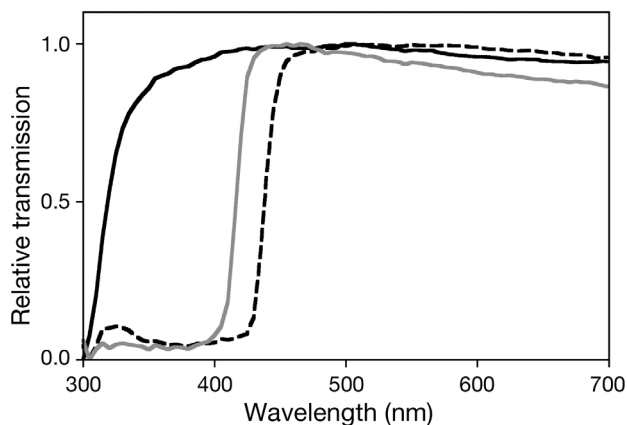

Fig. 3. Spectral transmission data of the lens of the green turtle (black line; Mäthger et al. 2007), the black marlin (grey line; Fritsches et al. 2000) and the mahi mahi (dashed black line; Fritsches et al. 2000). The lenses of the pelagic fishes act as a UV block, while the lens of the green turtle transmits light to the retina far into the UV waveband

Table 3. Spatial and temporal resolution for sea turtles and pelagic fishes. Spatial resolving power is given as the number of cycles (1 black and 1 white bar of a grating) that can be resolved within 1° of visual angle. Temporal resolution is presented as maximal Flicker Fusion Frequency (FFF), the frequency of a flickering light source at which a visual system ceases to be able to discriminate between each flicker. na: not available

Species	Spatial resolving power (cycles degree^{-1})	Temporal resolving power (FFF in Hz)
Fishes		
Thunnus albacares	16–18 (Fritsches & Warrant 2006)	80 (K. A. Fritsches et al. unpubl. data)
Xiphias gladius	7–10 (Fritsches & Warrant 2006)	40 (Fritsches et al. 2005)
Turtles		
Chelonia mydas	na	40–57 (Levenson et al. 2004, K. A. Fritsches et al. unpubl. data)
Caretta caretta	4–8 (Bartol et al. 2002)	40 (Levenson et al. 2004)
Dermochelys coriacea	na	4–12 (Eckert et al. 2006)

sticks provides a promising means of deterring turtles from interacting with longline gear. Hatchling loggerhead turtles from Florida nesting beaches display an aversion to light within the spectral range of 560 to 600 nm (Witherington & Bjorndal 1991), and these wavelengths are not visible to the majority of pelagic fishes targeted by longlines. Although experiments with captive-reared juvenile loggerheads showed an attraction to yellow and orange lightsticks, the spectral emissions of these lightsticks were not in the range repellent to hatchlings (Wang et al. 2007). Whether the loggerhead's aversion to light of 560 to 600 nm wavelength carries over into adulthood is not known, but if it does, lightstick emissions within this narrow spectral band could be effective at repelling loggerhead turtles from longline gear. Unfortunately, this approach is not likely to deter leatherback turtles from interacting with gear, as all current evidence indicates that this species does not detect light at these wavelengths (Eckert et al. 2006).

Another option for lightstick modification is to make simple changes in physical design such that light is emitted predominately downwards rather than in all directions (Lohmann & Wang 2007). This could be accomplished by shading the upper portion of the lightstick. Downward-directed lights would presumably be more difficult to detect from above. Given that loggerhead turtles typically utilize the top 50 m of the water column, this modification may render lights undetectable to loggerheads but still visible to deepwater target species such as swordfish and bigeye

tuna. The efficacy of this approach for preventing detection of lightsticks by leatherback turtles is debatable, given this species' propensity for deep dives.

One of the major differences in visual capabilities of sea turtles and pelagic fish is in their ability (or lack of) to detect UV light. Electrophysiological data suggest that both loggerhead and leatherback turtles detect UV light (Crognale & Eckert 2007, Salmon & Wyneken 2007), and behavioral experiments have shown that hatchling loggerhead turtles are attracted to light in the UV range (Witherington & Bjorndal 1991, Fritsches & Warrant 2006). Ultraviolet light 'decoys' could potentially be used to attract sea turtles to a site distant from longline gear, thus removing turtles from harm's way. The major pitfall of this strategy is that repeated exposure to UV light may damage the human eye (Zigman 1971). Any UV light sources to be used for fisheries applications would have to be very carefully designed in order to prevent damage to the operator.

The innate avoidance behavior induced in sea turtles by visual detection of a predator is another avenue worth exploring for potential deterrents. Captive-reared loggerhead turtles showed a strong avoidance response when they encountered a shark replica in their large (30 × 7 m) seawater holding pen (Higgins 2006). In preliminary field trials, Wang & Swimmer (2007) found a tendency for sea turtle bycatch in gillnets to decrease when shark-shaped objects were attached to nets, and suggested exploiting the predator avoidance response in sea turtles to develop floats or banners that would deter them from interacting with longline gear. A particularly interesting approach would be to construct shark-shaped banners using clear UV-absorbent plastic. When viewed from below, the banner would be invisible to fish but would appear as a black silhouette to sea turtles that can detect UV light. If effective, this approach could be simple and cost-effective, and therefore stand a good chance of being adopted by fishers.

Alterations in the visual appearance of bait have also been explored as a means of reducing sea turtle bycatch. Dying squid bait blue is an effective means of reducing rates of seabird bycatch in longline fisheries (Brothers et al. 1999), and bait dying can easily be implemented in fishing operations. Laboratory studies showed that loggerhead turtles and Kemp's ridley turtles *Lepidochelys kempii* displayed a clear

preference for untreated squid bait versus squid bait that had been dyed blue (Swimmer et al. 2005). Unfortunately, use of blue-dyed bait in field trials did not result in a reduction in sea turtle catch rates (Swimmer et al. 2005). Results from this study emphasize the importance of carefully controlled field trials to assess the efficacy of a potential bycatch reduction measure.

In summary, morphological, physiological, and behavioral studies have identified important differences in the visual capabilities of pelagic fishes and sea turtles, particularly with regard to spectral sensitivity and capacity for UV vision. Management agencies and the fishing industry have expressed a strong interest in exploring ways to exploit these differences to make longline gear more species-specific, and preliminary field trials to assess the potential for using visual deterrents to reduce catch rates of sea turtles are underway (Wang & Swimmer 2007). Controlled laboratory and field studies to assess the behavioral responses of sea turtles and pelagic fishes to visual attractants and repellents are needed in order to identify the most promising avenues for gear modification.

CONCLUSIONS

As with other bycatch reduction methods, the efficacy of sensory-based deterrents may be strongly influenced by numerous factors and techniques that prove useful in reducing sea turtle bycatch in one fishery may not work as well in another. Factors to consider when evaluating the feasibility of incorporating a sensory-based deterrent in a longline fishery would include the oceanographic region where fishing occurs, time of day when gear is set, the target species, age and size class of sea turtles interacting with fishing gear, and diurnal and seasonal variations in sensory capacities. Additionally, we must evaluate the impact that introduction of a sensory stimulus into the pelagic environment might have on other species capable of detecting that stimulus.

Gear modifications to reduce sea turtle bycatch in longline fisheries must be economically viable and relatively easy to implement if they are to be readily adopted by the fishing industry. Identification of differences in sensory capacities of pelagic fishes and sea turtles has stimulated much thought and discussion on innovative yet simple gear modifications to more selectively target fish species. The next step is to conduct rigorous field trials to investigate the effectiveness of sensory-based gear modifications for reducing sea turtle interactions while maintaining catch rates of target species.

LITERATURE CITED

Atema J, Holland K, Ikehara W (1980) Olfactory responses of yellowfin tuna (*Thunnus albacares*) to prey odors: chemical search image. J Chem Ecol 6:457–465

Atema J, Kingsford MJ, Gerlach G (2002) Larval reef fish could use odour for detection, retention and orientation to reefs. Mar Ecol Prog Ser 241:151–160

Balazs GH (1980) Synopsis of biological data on the green turtle in the Hawaiian Islands. NOAA Tech Memo NOAA-TM-NMFS-SWFC-7

Balazs GH, Pooley SG (1994) Research plan to assess marine turtle hooking mortality: results of an expert workshop held in Honolulu, Hawaii November 16–18, 1993. NOAA (Natl Ocean Atmos Adm) Tech Memo NOAA-TM-NMFS-SWFSC-201

Bartol S, Musick JA, Ochs AL (2002) Visual acuity thresholds of juvenile loggerhead sea turtles (*Caretta caretta*): an electrophysiological approach. J Comp Physiol A Sens Neural Behav Physiol 187:953–960

Bass AH, McKibben JR (2003) Neural mechanisms and behaviors for acoustic communication in teleost fish. Prog Neurobiol 69:1–26

Brill RW, Holts DB, Chang RKC, Sullivan D, Dewar H, Carey FG (1993) Vertical and horizontal movements of striped marlin (*Tetrapturus audax*) near the Hawaiian Islands, determined by ultrasonic telemetry, with simultaneous measurement of ocean currents. Mar Biol 117:567–574

Brill RW, Block BA, Boggs CH, Bigelow KA, Freund EV, Marcinek DJ (1999) Horizontal movements and depth distribution of large adult yellowfin tuna (*Thunnus albacares*) near the Hawaiian Islands recorded using ultrasonic telemetry: implications for the physiological ecology of pelagic fishes. Mar Biol 133:395–408

Brothers NP, Cooper J, Lokkeborg S (1999) The incidental catch of seabirds in longline fisheries: worldwide review and technical guidelines for mitigation. FAO Fish Circ 937:1–100

Brudenall D, Schwab IR, Fritsches KA (2008) Ocular morphology of the leatherback sea turtle (*Dermochelys coriacea*). Vet Ophthalmol

Bullock TH, Hofmann MH, New JG, Nahm FK (1991) Dynamic properties of visual evoked potentials in the tectum of cartilaginous fish and bony fish, with neuroethological implications. J Exp Zool Suppl 5:142–155

Carey FG, Robison BH (1981) Daily patterns in the activities of swordfish, *Xiphias gladius*, observed by acoustic telemetry. Fish Bull 79:277–292

Carr A (1967) So excellent a fish. Natural History Press, New York

Clarke GL, Denton EJ (1962) Light and animal life. In: Hill MN (ed) The sea, Vol 1. Interscience, London, p 456–468

Collin SP, Pettigrew JD (1989) Quantitative comparison of the limits on visual spatial resolution set by the ganglion cell layer in twelve species of reef teleosts. Brain Behav Evol 34:184–192

Constantino MA, Salmon M (2003) Role of chemical and visual cues in food recognition by leatherback posthatchlings (*Dermochelys coriacea*). Zoology 106:173–181

Cox TM, Read AJ, Solow A, Tregenza N (2001) Will harbour porpoises (*Phocoena phocoena*) habituate to pingers? J Cetacean Res Manag 3:81–86

Cox TM, Read AJ, Swanner D, Urian K, Waples D (2004) Behavioral responses of bottlenose dolphins, *Tursiops truncatus*, to gillnets and acoustic alarms. Biol Conserv 115:203–212

Crognale M, Eckert S (2007) Spectral and temporal sensitivity of adult and hatchling leatherback sea turtles. In: Swimmer Y, Wang JH (eds) 2006 Sea turtle and pelagic fish sensory workshop, Sept 12–13, 2006. NOAA (Natl Ocean Atmos Adm) Tech Memo NMFS-PIFSC-12, p 9–12

Dawson SM, Read A, Slooten E (1998) Pingers, porpoises and power: uncertainties with using pingers to reduce bycatch of small cetaceans. Biol Conserv 84:141–146

Dial BE (1990) Predator-prey signals: chemosensory identification of snake predators by eublepharid lizards and its ecological consequences. In: MacDonald DW, Muller-Schwarze D, Natynczuk SE (eds) Chemical signals in vertebrates, Vol 5. Oxford University Press, New York, p 555–565

Doving KB, Stabell OB (2003) Trails in open waters: sensory cues in salmon migration. In: Collins SP, Marshall NJ (eds) Sensory processing in aquatic environments. Springer, New York, p 39–52

Eckert SA, Eckert KL, Ponganis P, Kooyman GL (1989) Diving and foraging behavior of leatherback sea turtles (*Dermochelys coriacea*). Can J Zool 67:2834–2840

Eckert S, Levenson D, Crognale M (2006) The sensory biology of sea turtles: what can they see and how can this help them avoid fishing gear? In: Swimmer Y, Brill R (eds) Sea turtle and pelagic fish sensory biology: developing techniques to reduce sea turtle bycatch in longline fisheries. NOAA (Natl Ocean Atmos Adm) Tech Mem NMFS-PIFSC-7

Fergusson IK, Compagno LJV, Marks MA (2000) Predation by white sharks *Carcharodon carcharias* (Chondrichthyes: Lamnidae) upon chelonians, with new records from the Mediterranean Sea and a first record of the ocean sunfish *Mola mola* (Osteichthyes: Molidae) as stomach contents. Environ Biol Fishes 58:447–453

Frank TM (1999) Comparative study of temporal resolution in the visual systems of mesopelagic crustaceans. Biol Bull 196:137–144

Fritsches KA, Warrant E (2006) Differences in the visual capabilities of sea turtles and blue water fishes: implication for bycatch reduction. In: Swimmer Y, Brill R (eds) Sea turtle and pelagic fish sensory biology: developing techniques to reduce sea turtle bycatch in longline fisheries. NOAA (Natl Ocean Atmos Adm) Tech Mem NMFS-PIFSC-7

Fritsches KA, Partridge J, Pettigrew JD, Marshall NJ (2000) Colour vision in billfish. Philos Trans R Soc Lond B Biol Sci 355:1253–1256

Fritsches KA, Litherland L, Thomas N, Shand J (2003a) Cone visual pigments and retinal mosaics in the striped marlin. J Fish Biol 63:1347–1351

Fritsches KA, Marshall NJ, Warrant EJ (2003b) Retinal specializations in the blue marlin: eyes designed for sensitivity to low light levels. Mar Freshw Res 54:333–341

Fritsches KA, Brill RW, Warrant EJ (2005) Warm eyes provide superior vision in swordfishes. Curr Biol 15:55–58

Gilman E, Kobayashi D, Swenarton T, Brothers N, Dalzell P, Kinan-Kelly I (2007) Reducing sea turtle interactions in the Hawaii-based longline swordfish fishery. Biol Conserv 139:19–28

Gooding RM (1963) The olfactory organ of the skipjack *Katsuwonus pelamis.* FAO Fish Rep 6:1621–1631

Granda AM, O'Shea P (1972) Spectral sensitivity of the green turtle (*Chelonia mydas mydas*) determined by electrical responses to heterochromatic light. Brain Behav Evol 5: 143–154

Grassman MA, Owens DW (1982) Development and extinction of food preferences in the loggerhead sea turtle, *Caretta caretta.* Copeia 1982:965–969

Grassman M, Owens DW (1987) Chemosensory imprinting in juvenile green sea turtles, *Chelonia mydas.* Anim Behav 35:929–931

Gunn J, Block BA (2001). Advances in acoustic, archival, and satellite tagging of tunas. In: Block BA, Stevens ED (eds) Tuna. Physiology, ecology and evolution. Academic Press, San Diego, CA p 167–224

Hansen A, Zielinski BS (2005) Diversity in the olfactory epithelium of bony fishes: development, lamellar arrangement, sensory neuron cell types and transduction components. J Neurocytol 34:183–208

Hara TJ (1993) Chemoreception. In: Evans DH (ed) The physiology of fishes. CRC Press, Boca Raton, FL, p 191–218

Harrington JM, Myers RA, Rosenberg AA (2005) Wasted fishery resource: discarded by-catch in the USA. Fish Fish 6:350–361

Heithaus MR (2001) The biology of tiger sharks, *Galeocerdo cuvier*, in Shark Bay, Western Australia: sex ratio, size distribution, diet, and seasonal changes in catch rates. Environ Biol Fishes 61:25–36

Heithaus M, Frid A, Dill LM (2002a) Shark-inflicted injury frequencies, escape ability, and habitat use of green and loggerhead turtles. Mar Biol 140:229–236

Heithaus M, Dill LM, Marshall GJ, Buhleier B (2002b) Habitat use and foraging behavior of tiger sharks (*Galeocerdo cuvier*) in a seagrass ecosystem. Mar Biol 140:237–248

Higgins B (2006) Shark decoy experiments. In: Swimmer Y, Brill R (eds) Sea turtle and pelagic fish sensory biology: developing techniques to reduce sea turtle bycatch in longline fisheries. NOAA (Natl Ocean Atmos Adm) Tech Mem NMFS-PIFSC-7, p 77–86

Hodgson ES, Mathewson RF (1978) Electrophysiological studies of chemoreception in elasmobranchs. In: Hodgson ES, Mathewson RF (eds) Sensory biology of sharks, skates, and rays. US Office of Naval Research, Arlington, VA, p 227–267

Hueter RE, Mann DA, Maruska KP, Sisneros JA, Demski LS (2004) Sensory biology of elasmobranchs. In: Carrier JC, Musick JA, Heithaus MR (eds) Biology of sharks and their relatives. CRC Press, Boca Raton, FL, p 325–368

Iversen RTB (1967) Response of the yellowfin tuna (*Thunnus albacares*) to underwater sound. In: Tavolga WN (ed) Marine bioacoustics. II. Pergamon Press, Oxford, p 105–121

Iversen RTB (1969) Auditory thresholds of the scrombrid fish *Euthynnus affinis*, with comments on the use of sound in tuna fishing. FAO conference on fish behavior in relation to fishing techniques and tactics. FAO Fish Rep 62: 849–859

Kawamura G, Nishimura W, Ueda S, Nishi T (1981) Vision in tunas and marlins. Mem Kagoshima Univ Res Center S Pac 1:3–47

Kleerekoper H (1978) Chemoreception and its interaction with flow and light perception in the locomotion and orientation of some elasmobranchs. In: Hodgson ES, Mathewson RF (eds) Sensory biology of sharks, skates, and rays. US Office of Naval Research, Arlington, VA, p 269–329

Largarcha E, Parrales M, Rendon L, Velasquez V, Orozco M, Hall M (2005) Working with the Ecuadorian fishing

community to reduce the mortality of sea turtles in long-lines: the first year March 2004–March 2005. Western Pacific Regional Fishery Management Council, Honolulu, HI

Lenhardt ML, Klinger RC, Musick JA (1985) Marine turtle middle-ear anatomy. J Aud Res 25:66

Levenson D, Eckert S, Crognale M, Deegan JI, Jacobs G (2004) Photopic spectral sensitvity of green and loggerhead sea turtles. Copeia 2004:908–911

Lewison RL, Freeman SA, Crowder LB (2004) Quantifying the effects of fisheries on threatened species: the impact of pelagic longlines on loggerhead and leatherback sea turtles. Ecol Lett 7:221–231

Liebman PA, Granda AM (1971) Microspectrophotometric measurements of visual pigments in two species of turtle, *Pseudemys scripta* and *Chelonia mydas.* Vision Res 11: 105–114

Liebman PA, Granda AM (1975) Super dense carotenoid spectra resolved in single cone oil droplets. Nature 253: 370–372

Loew ER, McFarland WN, Margulies D (2002) Developmental changes in the visual pigments of the yellowfin tuna, *Thunnus albacares.* Mar Freshw Behav Physiol 35: 235–246

Lohmann KJ, Wang JH (2007) Behavioral responses of sea turtles to prototype experimental lightsticks. In: Swimmer Y, Wang, JH (eds) 2006 Sea turtle and pelagic fish sensory workshop, Sept 12–13, 2006. NOAA (Natl Ocean Atmos Adm) Tech Memo NMFS-PIFSC-12, p 15–17

Lohmann KMF, Witherington BE, Lohmann CMF, Salmon M (1997) Orientation, navigation, and natal beach homing in sea turtles. In: Lutz PL, Musick JA (eds) The biology of sea turtles, Vol 1. CRC Press, Boca Raton, FL, p 107–136

Lohmann KJ, Hester JT, Lohmann CMF (1999) Long-distance navigation in sea turtles. Ethol Ecol Evol 11:1–23

Lohmann KJ, Lohmann CMF, Ehrhart LM, Bagley DA, Swing T (2004) Geomagnetic map used in sea turtle navigation. Nature 428:909–910

Lutcavage ME, Lutz PL (1997) Diving physiology. In: Lutz PL, Musick JA (eds) The biology of sea turtles, Vol 1. CRC Press, Boca Raton, FL, p 277–296

Lythgoe JN (1979) The ecology of vision. Oxford University Press, Oxford

Mann DA, Higgs DM, Tavolga WM, Souza MJ, Popper AN (2001) Ultrasound detection by clupeiform fishes. J Acoust Soc Am 109:3048–3054

Manton M, Karr A, Ehrenfeld DW (1972) Chemoreception in the migratory sea turtle, *Chelonia mydas.* Biol Bull 143: 184–195

Marshall NJ, Vorobyev M (2003) The design of color signals and color vision in fishes. In: Collin SP, Marshall, NJ (eds) Sensory processing in aquatic environments. Springer-Verlag, New York, p 194–222

Mason JR, Clark L (1996) Grazing repellency of methyl anthranilate to snow geese is enhanced by a visual cue. Crop Prot 15:97–100

Mäthger LM, Litherland L, Fritsches KA (2007) An anatomical study of the visual capabilities of the green turtle, *Chelonia mydas.* Copeia 2007:169–179

Mejuto J, Auton U, Quintans M (2005) Visual acuity and olfactory sensitivity in the swordfish (*Xiphias gladius*) for the detection of prey during field experiments using the surface longline gear with different bait types. ICCAT Coll Vol Sci Pap 58:1501–1510

Moein SE, Musick JA, Keinath JA, Barnard DE, Lenhardt M, George R (1994) Evaluation of seismic sources for repelling sea turtles from hopper dredges. Report from Virginia Institute of Marine Science, Gloucester Point, VA, to US Army Corps of Engineers

Moein Bartol S, Ketten DR (2006) Turtle and tuna hearing. In: Swimmer Y, Brill R (eds) Sea turtle and pelagic fish sensory biology: Developing techniques to reduce sea turtle bycatch in longline fisheries. NOAA (Natl Ocean Atmos Adm) Tech Mem NMFS-PIFSC-7, p 98–105

Moein Bartol S, Musick JA (2003) Sensory biology of sea turtles. In: Lutz PL, Musick JA, Wyneken J (eds) The biology of sea turtles, Vol 2. CRC Press, Boca Raton, FL, p 79–102

Moein Bartol S, Musick JA, Lenhardt ML (1999) Auditory evoked potentials of the loggerhead sea turtle (*Caretta caretta*). Copeia 1999:836–840

Munz FW, McFarland WN (1973) The significance of spectral position in the rhodopsins of tropical marine fishes. Vision Res 13:1829–1874

Musyl MK, Brill RW, Boggs CH, Curran DS, Kazama TK, Seki MP (2003) Vertical movements of bigeye tuna (*Thunnus obesus*) associated with islands, buoys, and seamounts of the Hawaiian Archipelago from archival tagging data. Fish Oceanogr 12:152–169

Myrberg AA Jr (2001) The acoustical biology of elasmobranchs. Environ Biol Fishes 60:31–45

Myrberg AA Jr, Ha SJ, Walewski S, Banbury JC (1972) Effectiveness of acoustic signals in attracting epipelagic sharks to an underwater sound source. Bull Mar Sci 22: 926–949

Myrberg AA Jr, Gordon CR, Klimley AP (1976) Attraction of free ranging sharks by low frequency sound, with comments on its biological significance. In: Schuijf A, Hawkins AD (eds) Sound reception in fish. Elsevier, Amsterdam, p 205–228

Myrberg AA Jr, Gordon CR, Klimley AP (1978) Rapid withdrawal from a sound source by open-ocean sharks. J Acoust Soc Am 64:1289–1297

Nakamura EL (1968) Visual acuity of two tunas, *Katsuwonus pelamis* and *Euthynnus affinis.* Copeia 1968:41–49

Nestler JM, Plosky GR, Pickens J, Menezes J, Schilt C (1992) Responses of blueback herring to high frequency sound and implications for reducing entrainment at hydropower dams. N Am J Fish Manag 12:667–683

NMFS (National Marine Fisheries Service) (1999) Western Pacific pelagic fisheries; Hawaii-based pelagic longline area Closure. Fed Reg 64:72290–72291

NMFS (2000) Atlantic highly migratory species; pelagic longline fishery; sea turtle protection measures. Fed Reg 65: 60889–60892

NMFS (2001) Atlantic highly migratory species; pelagic longline fishery; sea turtle protection measures. Fed Reg 66: 36711–36714

Northmore DP, Granda AM (1991) Ocular dimensions and schematic eyes of freshwater and sea turtles. Vis Neurosci 7:627–635

O'Hara J, Wilcox JR (1990) Avoidance responses of loggerhead turtles, *Caretta caretta*, to low frequency sounds. Copeia 1990:564–567

Owens DW, Grassman MA, Hendrickson JR (1982) The imprinting hypothesis and sea turtle reproduction. Herpetologica 38:124–135

Palko B, Beardsley G, Richard W (1982) Synopsis of the biological data on dolphin-fishes, *Coryphaena hippurus* Linnaeus and *Coryphaena equiselis* Linnaeus. In: NOAA (Natl Ocean Atmos Adm) Tech Rep, NMFS Circular 443:28

Parsons TS (1971) Nasal anatomy of trionychid turtles. J Morphol 135:323–334

Piovano S, Balletto E, DiMarco S, Dominici A, Giacoma C, Zannetti A (2004) Loggerhead turtle (*Caretta caretta*) by-catches on longlines: the importance of olfactory stimuli. Ital J Zool (Suppl. 2):213–216

Popper AN (1981) Comparative scanning electron micro-scopic investigations of the sensory epithelia in the teleost sacculus and lagena. J Comp Neurol 200:357–374

Popper AN (2003a) Effects of anthropogenic sounds on fishes. Fisheries 28:24–31

Popper AN (2003b) Sound detection mechanisms and capa-bilities of teleost fishes. In: Collins SP, Marshall NJ (eds) Sensory processing in aquatic environments. Springer-Verlag, New York, p 3–38

Pritchard PCH (1997) Evolution, phylogeny, and current sta-tus. In: Lutz PL, Musick JA (eds) The biology of sea turtles, Vol 1. CRC Press, Boca Raton, FL, p 1–28

Read AJ (2007) Do circle hooks reduce the mortality of sea turtles in pelagic longlines? A review of recent experi-ments. Biol Conserv 135:155–169

Ridgway SH, Wever EG, McCormick JG, Palin J, Anderson JH (1969) Hearing in the giant sea turtle, *Chelonia mydas.* Proc Natl Acad Sci USA 64:884–890

Saito K, Shoji T, Uchida I, Ueda H (2000) Structure of the olfactory and vomeronasal epithelia in the loggerhead turtle *Caretta caretta.* Fish Sci 66:409–411

Salmon M, Wyneken J (2007) Visual physiology and orienta-tion of juvenile leatherbacks and loggerheads. In: Swim-mer Y, Wang, JH (eds) 2006 Sea turtle and pelagic fish sensory workshop, Sept 12–13, 2006. NOAA (Natl Ocean Atmos Adm) Tech Memo NMFS-PIFSC-12, p 5–8

Shoji T, Abe Y, Furihata E, Kurihara K (1994) High sensitivity of the turtle olfactory system to nonvolatile substances: comparison of response properties with those in gustatory systems. Brain Res 666:68–76

Song J, Mathieu A, Soper RF, Popper AN (2006) Structure of the inner ear of bluefin tuna *Thunnus thynnus.* J Fish Biol 68:1767–1781

Southwood AL, Higgins B, Brill R, Swimmer Y (2007) Chemoreception in loggerhead sea turtles: an assessment of the feasibility of using chemical deterrents to prevent sea turtle interactions with longline fishing gear. NOAA (Natl Ocean Atmos Adm) Tech Memo NMFS-PIFSC-10

Spotila JR, Reina RD, Steyermark AC, Plotkin PT, Paladino FV (2000) Pacific leatherback turtles face extinction. Nature 405:529–530

Strong WR Jr, Murphy RC, Bruce BD, Nelson DR (1992) Movements and associated observations of bait-attracted white sharks, *Carcharodon carcharias*: a preliminary report. Aust J Mar Freshw Res 43:13–20

Swimmer Y, Arauz R, Higgins B, McNaughton L, McCracken M, Ballestero J, Brill R (2005) Food color and marine turtle feeding behavior: Can blue bait reduce turtle bycatch in commercial fisheries? Mar Ecol Prog Ser 295:273–278

Swimmer Y, McNaughton L, Southwood A, Brill R (2007) Tests of repellent bait to reduce turtle bycatch in

longline fisheries. Bycatch Commun Network Newsl 5: 18–20

Tamura T, Hanyu I, Niwa H (1972) Spectral sensitivity and color vision in skipjack tuna and related species. Bull Jap Soc Sci Fish Oceanogr 38:799–802

Tolimieri N, Haine O, Montgomery JC, Jeffs A (2002) Ambi-ent sound as a navigational cue for larval reef fish. Bio-acoustics 12:214–217

Tyler JE, Smith RC (1970) Measurements of spectral irradi-ance underwater. Gordon and Breach Science Publishers, New York

Vorobyev M (2003) Coloured oil droplets enhance colour dis-crimination. Proc Royal Soc Lond Ser B Biol Sci 270: 1255–1261

Wang JH, Swimmer Y (2007) Preliminary field trials in Baja California, Mexico with lightsticks and shark shapes. In: Swimmer Y, Wang, JH (eds) 2006 Sea turtle and pelagic fish sensory workshop, Sept 12–13, 2006. NOAA (Natl Ocean Atmos Adm) Tech Memo NMFS-PIFSC-12, p 18–19

Wang JH, Boles LC, Higgins B, Lohmann KJ (2007) Behav-ioral responses of sea turtles to lightsticks used in longline fisheries. Anim Conserv 10:176–182

Warrant EJ (1999) Seeing better at night: life style, eye design and the optimum strategy of spatial and temporal summa-tion. Vision Res 39:1611–1630

Watson JW, Epperly SP, Shah AK, Foster DG (2005) Fishing methods to reduce sea turtle mortality associated with pelagic longlines. Can J Fish Aquat Sci 62:965–981

Weldon PJ (1990) Responses by vertebrates to chemicals from predators. In: MacDonald DW, Muller-Schwarze D, Natynczuk SE (eds) Chemical signals in vertebrates, Vol 5. Oxford University Press, New York, p 500–521

Wever EG (1978) The reptile ear: its structure and function. Princeton University Press, Princeton, NJ

Wisenden BD (2003) Chemically mediated strategies to counter predation. In: Collins SP, Marshall NJ (eds) Sen-sory processing in aquatic environments. Springer, New York, p 236–251

Witherington BE, Bjorndal KA (1991) Influences of wave-length and intensity on hatchling sea turtle phototaxis: implications for sea-finding behaviour. Copeia 1991: 1060–1069

Witzell WN, Epperly SP, Csuzdi LA (2001) Description of the Atlantic Ocean and Mediterranean Sea pelagic longline fisheries. In: Stock assessments of loggerhead and leatherback sea turtles and an assessment of the impact of the pelagic longline fishery on the loggerhead and leatherback sea turtles of the Western North Atlantic. NOAA (Natl Ocean Atmos Adm) Tech Mem NMFS-SEFSC-455, p 108–112

Zigman S (1971) Eye lens colour: formation and function. Science 171:807–809

Zimmer RK, Butman CA (2000) Chemical signaling processes in the marine environment. Biol Bull 198:168–187