Review paper

Reducing bycatch in gillnets: A sensory ecology perspective

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ABSTRACT

Sensory capacities and perceptual challenges faced by gillnet bycatch taxa result from fundamental physiological limits on vision and constraints arising within underwater environments. To reduce bycatch in birds, sea turtles, pinnipeds and blue-water fishes, individuals must be alerted to the presence of nets using visual cues. Cetaceans will benefit but they also require warning with cues detected through echolocation. Characteristics of a visual warning stimulus must accommodate the restricted visual capacities of bycatch species and the need to maintain vision in a dark adapted state when foraging. These requirements can be provided by a single type of visual warning stimulus: panels containing a pattern of low spatial frequency and high internal contrast. These are likely to be detectable across a range of underwater light environments by all bycatch prone taxa, but are unlikely to reduce the catch of target fish species. Such panels should also be readily detectable by cetaceans using echolocation. Use of sound signals to warn about the presence of gillnets is not recommended because of the poor sound localisation abilities of bycatch taxa, cetaceans excepted. These warning panels should be effective as a mitigation measure for all bycatch species, relatively easy to deploy and of low cost.

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1. Introduction: the problem of gillnet bycatch

Bycatch of seabirds in gillnet fisheries is a worldwide problem that is estimated to result in the deaths of at least 400,000 birds annually (Lewison et al., 2014; Zydelis et al., 2013). This rate of bycatch is thought to be unsustainable for some species, and there is evidence that in some localities gillnet bycatch has resulted in severe reductions in the numbers of breeding birds (Osterblom et al., 2002; Regular et al., 2013). Bycatch is also a well-established issue for other animals groups including sea turtles (Chelonioidea), pinnipeds, cetaceans and blue water fish (Tunas *Thunnus spp.* and billfish *Istiophoridae* and *Xiphiidae*) (Fritsches and Warrant, 2006; Lewison et al., 2014; Myers and Worm, 2003; Reeves et al., 2013; Wallace et al., 2013). It is recognised that there is an urgent need to reduce this bycatch, but at the same time, in order to obtain support and adoption by the fishing industry, it is desirable not to reduce the efficiency of gillnet fishing. Spatial and temporal closures of fisheries have a role to play in managing the impact of gillnets (Regular et al., 2013), but these may be difficult to establish and enforce. Thus, technological solutions to gillnet bycatch, of which there are currently few, are sought as important additions to the suite of prospective management measures. Ideally a technological solution is sought that will be effective for all bycatch species and is easy to deploy.

This review is a contribution towards the achievement of that aim. It provides an analysis of the sensory ecology of bycatch-gillnet interactions. The aim is to understand the factors which predispose animals to become entangled in gillnets as bycatch and to suggest how this understanding can be used to reduce bycatch.

Sensory ecology has been variously defined but can be summarised as, "The investigation of the information that under-lies an animal's interactions with its environment" or "How organisms acquire and respond to information" (Dusenbery, 1992; Stevens, 2013). A sensory ecology approach has provided insights into the bases of many broad classes of interactions between animals and their environments, especially with respect to foraging (Martin, 2012), and to investigate some of the key general problems which birds face in human modified environments. This includes understanding the sensory and cognitive bases of fatal interactions between flying birds and large human artefacts that are conspicuous to humans, such as wind turbines, power lines and oil platforms, and which can cause high levels of bird mortality (Martin et al., 2012; Martin and Shaw, 2010; Shaw et al., 2010).

A sensory ecology approach has been discussed with the aim of reducing the bycatch of sea turtles in longline and gillnet fisheries (Swimmer and Brill, 2006; Southwood et al., 2008) and some solutions stemming from this work have recently been tested (Wang et al., 2013, 2010).

As a framework for investigating collisions or net entanglement, sensory ecology employs the premise that such problems are not simply explained as the result of animals "making mistakes", i.e. a hazard is detected but there is a cognitive failure to interpret the danger of the hazard. A sensory ecology framework, when applied to net entanglement, assumes that under many circumstances bycatch prone species can and do detect nets, but there are limits to their ability to detect them and it is when those limits are breached that animals may get caught. To describe these as "mistakes" is simply to admit that from a human perspective we do not know what is going on. Sensory ecology tries to understand the limits of sensory performance and employ this to reduce the situations when these limits are met. This is an approach pioneered by research into why motorists make "mistakes" and have accidents e.g. Clarke et al. (1995). The results of such work are widely seen today in that roads are heavily signed with standardised signals; lines, chevrons, lights, cats eyes, etc. For many circumstances the information that these signals provide is redundant and unnecessary for safe driving. However, when visibility is reduced, for example, due to lower light levels, rain, and fog, the perceptual limit of driving may be reached. Under these circumstance these gross signals become crucial for accident avoidance.

A similar approach is employed here to the reduction of net entanglement leading to bycatch. However, since bycatch species have a different suite of sensory abilities and extract different kinds of information from the world compared with humans, it is not possible to make simple assumptions based upon human experience and data and apply these to bycatch species and situations. What follows is an attempt to understand those limits and how they apply in the particular circumstances of underwater environments. This information is then used to propose signals which will have applicability in reducing bycatch across a wide range of species and situations.

2. Methods

Sources were selected starting with the personal reference collection of the authors and then searching from the information held on key references in the ISI (Web of Science) database using the Citation Network tools. Further information was gained through personal correspondence with various authors. Gathered sources were used for: 1. collation and analysis of available data on species which are prone to bycatch in gillnets, 2. analysis of the sensory information used to guide the foraging of these species and analysis of their known sensory capacities, with emphasis upon vision, 3. review of the fundamental mechanisms and constraints upon vision in vertebrates, 4. collation and analysis of the perceptual (mainly visual) challenges posed by the tasks of foraging in marine waters. Finally, analyses of these sensory capacities and perceptual challenges were used to determine a mitigation method for gillnet bycatch which will have general applicability and utility in the reduction of gillnet bycatch across a wide range of taxa.

3. Gillnet bycatch species

Species which have been recorded as subject to gillnet bycatch (including driftnets) are numerous and they are drawn from a range of taxa including birds, sea turtles, pinnipeds, cetaceans and blue water fish (Lewison et al., 2014). Bycatch prone bird species come from a range of orders and families (Zydelis et al., 2013). They include species which differ markedly in their foraging ecology, suggesting that the problem of gillnet bycatch may derive from rather broad and general sensory ecology factors rather than specific factors which predispose only certain species. For this reason birds are the main focus of this review, since they exemplify the same sensory ecology issues as befall other gillnet bycatch prone taxa. Importantly, the visual capacities of birds and ecological factors which limit their vision are relatively well understood and probably represent the situation in most vertebrate eyes at low light levels.

A recent review of gillnet bycatch marine mammal species (Reeves et al., 2013) has also shown that a broad spread of species are affected, suggesting that the problems posed for bycatch mammal species are also very general, rather than species-specific. Thus, among marine mammals it has been shown that at least 75% of odontocete species, 64% of mysticetes, 66% of pinnipeds, and all sirenians and marine mustelids have been recorded as subject to gillnet bycatch over the past 20-plus years. However, the numbers of individuals involved is less clear. Cetacean bycatch information is relatively sparse although it has been possible to identify species and populations at high risk. The scale of pinniped and sirenian bycatch remains poorly documented, especially at the population level. However, marine mammal bycatch is regarded as a critical issue in the prevention of marine mammal diversity and abundance loss (Reeves et al., 2013). With the exception of cetaceans and pinnipeds, all bycatch species rely primarily upon visual information to guide their foraging or to gain access to foraging substrates. Cetaceans may rely primarily upon echolocation in foraging although vision may also be used (Au and Nachtigall, 1997; Kastelein et al., 1999; Philips et al., 2003). Pinnipeds may use cues derived from their tactile senses as well as vision (Dehnhardt et al., 1997, 2001, 2003).

Zydelis et al. (2013) presented evidence that a total of 148 seabird species are "susceptible" to gillnet bycatch. Susceptible birds are defined in broad terms as "those seabirds which predominantly forage by diving for fish or benthic fauna". They are drawn from 10 avian orders and 15 families (Table 1). Such a broad definition of susceptibility is clearly justified since of the 148 species judged to be susceptible, birds from 81 of those species have been recorded as caught in gillnets. In addition there are a further 23 surface foraging bird species which were not considered susceptible but have nevertheless been recovered dead as a result of gillnet bycatch.

The majority of birds that are caught as bycatch are from just eight species and these are defined as "high impact" species (Zydelis et al., 2013) (Table 2). These are also drawn from a relatively broad taxonomic base which includes four orders and four families and embrace birds which employ quite different foraging ecologies within the marine environment.

This breadth in the taxonomic range of susceptible and high impact bird species suggests that the causes of gillnet bycatch are unlikely to be a product of a well-defined aspect of foraging behaviour or of specialisation of the sensory capacities which mediate them. Thus, beyond the observation that diving beneath the water surface can make almost any bird, pinniped, cetacean or sea turtle vulnerable to bycatch, there is unlikely to be a narrow suite of behaviours and sensory capacities that predispose these animals to gillnet bycatch. Therefore solutions that seek a general reduction in gillnet bycatch will need to take into account broad principles rather than be able to focus upon manipulation of specific behaviours or interventions that apply to just a narrow range of species characteristics. This is not to say that species and location specific solutions to gillnet by catch are not viable, see for example Melvin et al. (1999), but the attempt here is to identify generic problems and generic solutions.

3.1. Seabird gillnet bycatch species

Among birds, high impact bycatch species (Table 2) exhibit three main combinations of diet and foraging behaviours:

1. Surface diving to take sessile prey (molluscs) which are removed from underwater substrates at depths down to 50 m (Anatidae) (Cramp and Simmons, 1977).
2. Surface diving to take evasive mobile prey (fish) from the water column at a range of depths down to 150 m (Sphensicidae, Alcidae), e.g. Hedd et al. (2009) and Williams (1995) mainly in open waters.

Table 1
Gillnet bycatch "susceptible" bird taxa. Names and taxonomy follow {Gill and Donsker (2014) 738/id}.

ANSERIFORMES
Anatidae, Ducks, Geese and Swans

GAVIIFORMES
Gaviidae, Loons

SPHENISCIFORMES
Spheniscidae, Penguins

PROCELLARIIFORMES
Diomedeidae, Albatrosses
Procellariidae, Petrels and Shearwaters
Hydrobatidae, Storm Petrels
Pelecanoididae, Diving Petrels

PODICIPEDIFORMES
Podicipedidae, Grebes

PHAETHONTIFORMES
Phaethontidae, Tropicbirds

PELECANIFORMES
Pelecanidae, Pelicans
Sulidae, Gannets and Boobies
Phalacrocoracidae, Cormorants and Shags

SULIFORMES
Fregatidae, Frigatebirds

CHARADRIIFORMES
Alcidae, Auks
Laridae, Gulls, Terns and Skimmers

ANSERIFORMES
Anatidae, Ducks, Geese and Swans

Table 2
Gill net bycatch "high impact" species. Names and taxonomy follow Gill and Donsker (2014).

	Main diet component	Foraging behaviour	Main sense for location of prey
ANSERIFORMES			
Anatidae, Ducks, Geese and Swans			
Greater Scaup *Aythya marila*	Sessile molluscs	Surface diving in coastal and open waters to mid-depth range <50 m	Tactile cues from bill
Long tailed duck *Clangula hyemalis*	Sessile molluscs	" " "	Tactile cues from bill
GAVIIFORMES			
Gaviidae, Loons			
Red-Throated Loon (Diver) *Gavia stellata*	Evasive fish	Surface diving in coastal waters to mid-depth range <10 m	Vision
SPHENISCIFORMES			
Spheniscidae, Penguins			
Humboldt Penguin *Spheniscus magellanicus*	Evasive fish	Surface diving in open waters to depth ≤150 m	Vision
Yellow-eyed penguin *Megadyptes antipodes*	Evasive fish	" " "	Vision
Little penguin *Eudyptula minor*	Evasive fish	" " "	Vision
CHARADRIIFORMES			
Alcidae, Auks			
Common Murre (Guillemot) *Uria aalge*	Evasive fish	Surface diving in open waters to depth ≤150 m	Vision + tactile + random encounters?
Thick-billed Murre (Guillemot) *U. lomvia*	Evasive fish	" " "	Vision + tactile + random encounters?

3. Surface diving to predominantly shallow depths (<10 m) (Gaviidae) (Carboneras, 1992; Cramp and Simmons, 1977) typically in coastal waters.

Among the fuller list of susceptible species (Table 1) all of the above diets and foraging behaviours are found with the addition of three further foraging techniques:

1. Taking evasive prey (fish) and slow moving prey (crustaceans and molluscs e.g. squid) following plunge dives to shallow depth (Pelecanidae, Sulidae, Diomedeidae, Procellariidae, Hydrobatidae, Phaethontidae, Pelecanoididae).
2. Taking evasive prey at shallow to mid-depths from surface dives with the prey often disturbed from substrates or hiding places (Phalacrocoracidae, Podicipedidae). This foraging may take place both in relatively clear and in turbid coastal waters.
3. Taking small generally non-evasive prey from or close below the water surface (Laridae). These food items may be detected by sight from above the water surface (terns and gulls) but the Skimmers take prey by surface trawling guided by tactile, rather than visual cues (Martin et al., 2007a).

4. The role of vision in birds

The evolution of eyes 500 million years ago changed forever the information that underlies animals' interactions with their environments including other animals (Parker, 2003). It also established the primacy of vision as the source of information used to guide animal behaviour. This primary reliance upon vision as a source of information is particularly the case in birds. While this is easily asserted from the evidence of casual observations, it is also well supported by evidence that relatively large portions of the brains in most species of birds are devoted to the analysis of information from vision, and that the "intelligent" behaviours of birds are based primarily upon visual information (Emery, 2006; Karten and Hodos, 1967; Reiner et al., 2005; The Avian Brain Nomenclature Consortium, 2005). However, it should be noted that although vision is a primary sense for gaining information in vertebrates, other senses can also provide a rich array of information about the environment. For example, it has long been recognised that echolocation provides cetaceans with a rich source of information that can match that provided by vision (Kellogg, 1958).

Only in a handful of extant bird species is vision not the primary sense used to guide foraging and the detection of food and predators were, and still remain, the principal drivers of the evolution of vision in birds (Martin, 2012). Controlling locomotion is an important role for vision in birds, but it may not have been the prime driver.

4.1. The role of vision in seabird gillnet bycatch species

It is highly probable that all of the species listed in Tables 1 and 2 that take prey from the water column, or close to the seabed, use vision to detect prey and to direct their prey catching behaviour. Only among the ducks is there evidence that a sense other than vision is used for prey detection and procurement. While there is no direct evidence for tactile prey detection in either Great Scaup or Long-Tailed Ducks, by analogy with Blue Ducks *Hymenolaimus malacorhynchos* (Martin et al., 2007a) this seems likely.

It cannot be concluded that even the visually guided foragers are capable of detecting prey at a relatively long distance. Even at high light levels prey may be detected and pursued at close range only, especially in turbid waters. Evidence for this comes from research among the Phalacrocoracidae. In these species, there is evidence that their prey is often hidden, highly cryptic or of low contrast in turbid waters. Foraging birds force hidden prey to make an escape response which is detected and taken at close range, aided by rapid neck extension in a similar fashion to prey capture in herons (Ardeidae) (Watanuki et al., 2007, 2008; White et al., 2007). There is also evidence that grebes (Podicipedidae) may disturb fish which are driven towards the surface where they are detected in silhouette from below (Piersma et al., 1988) and this technique may be used by other taxa.

Therefore, with the exception of the Skimmers (Martin et al., 2007b) and the ducks, all gillnet susceptible birds (Table 1) are highly likely to be visually guided foragers, but it should not be assumed that their spatial resolution is high and that they detect and pursue prey items from a distance.

It should also be noted that while many of these species forage during day time, many (including all those in the high impact category (Table 2)) may also forage regularly during twilight or night time, see for example Camphuysen (1998); Cramp and Simmons (1977); Gremillet et al. (2005); Nilsson (1969); Piersma et al. (1988); Regular et al. (2010); Regular et al. (2011); Systad and Bustnes (2001) and Wanless et al. (1999). Furthermore, even when foraging in day time, some taxa (especially Sphensicidae and Alcidae) may typically forage at depths at which ambient light levels are attenuated to equal those commonly experienced at the water surface under twilight and moonlit night time conditions (crepuscular and nocturnal light levels) (Hedd et al., 2009; Martin, 1990, 1999; Regular et al., 2010, 2011; Wilson et al., 1993) (see Section 6 for discussion of the perceptual challenges posed by amphibious vision and the marine environment).

Because of the way that foraging auks and penguins dive to depths that follow the diel vertical migrations of their preferred prey species (Regular et al., 2010, 2011; Wilson et al., 1993), they may in fact always be foraging at low light levels, diving to depths during the day at which ambient light levels equate to those of twilight or lower, or foraging at night nearer the surface. Thus from the sensory perspective, these birds may be regarded as twilight or nocturnal foragers (Martin, 1999). This is an interesting observation with respect to understanding how these birds respond to changes in abundance of prey within daily cycles, but it also has important implications for their visual capacities; in particular the assumptions that can be made about both the sensitivity and spatial resolution of their vision when foraging (Martin, 2012). These in turn have important implications for understanding why these species are commonly subject to gillnet bycatch.

5. Sensory capacities of seabird bycatch species

Little is known specifically about the sensory capacities of any of the bird species listed in Tables 1 and 2. The most pertinent information on vision underwater in birds is that on the underwater acuity and visual fields of Great Cormorants *Phalocrocorax carbo*. The relationships between vision and the foraging technique of cormorants and other Phalacrocoracidae have been discussed in some detail (Martin et al., 2008; White et al., 2007, 2008) and these provide insights which probably have wide applicability to aquatic foraging birds. There is also data on the eye structure, visual fields and retinal photopigments (which provide an insight into the capacity for colour vision and spectral sensitivity) in Humboldt Penguins *Spheniscus humboldti* (Bowmaker and Martin, 1985; Martin and Young, 1984) and on the visual fields, eye structure and foraging at depth in King Penguins *Aptenodytes patagonicus* (Martin, 1999). There is also data on visual fields in a number of Procellariiform species and in Black Skimmers *Rhynchops niger* (Martin, 1998; Martin et al., 2007b; Martin and Brooke, 1991; Martin and Prince, 2001) and these have been discussed with reference to the relationships between visual fields and these species' particular foraging techniques. There is also recent, but unpublished, data on the visual fields of two species of auks Alcidae, Common Guillemot (Murre) *Uria aalge* and Atlantic Puffin *Fratercula arctica* (Martin, unpublished).

In addition to these species-focused studies, a number of studies have explored (in general terms) the limits of visual performance of vertebrates with respect to colour vision, the breadth of the visible spectrum (based upon knowledge of retinal photoreceptor pigments), visual fields, spatial resolution and sensitivity (Martin and Osorio, 2008).

For these studies to be of value in the discussion of the factors which contribute to bycatch they need to be combined with knowledge of the general nature of the perceptual challenges that the underwater environment poses. This is especially important for these birds since they are amphibious; functioning primarily in air but foraging underwater. It is well documented that the perceptual challenges faced underwater are significantly different from those in air (Lythgoe, 1979; Lythgoe and Partridge, 1989), but it is particularly challenging to be able to function guided by visual cues in both air and water.

6. Perceptual challenges of amphibious vision

Aerial and aquatic environments pose quite different sets of perceptual challenges for vision. It is not straight forward to determine the extent to which either sets of challenges have shaped or honed the visual system characteristics of amphibious animals or whether natural selection has favoured compromise solutions to the different challenges faced. The challenges faced by a visual system that can function under water and in air can be considered under three headings: optical, irradial and spectral.

6.1. Optical challenges of seeing in both air and water

The eyes of all vertebrates employ the same optical structure. They are referred to as simple eyes (in comparison with the often repetitive structures that make up the eyes of the majority of invertebrates) or camera eyes (a description of the key functional aspect of their structure; the projection of an image of the world onto a surface where it is analysed) (Land and Nilsson, 2012; Martin, 1983).

The simple eye optical system is comprised of two main elements; a cornea and a lens. Together they produce an image of the world upon the retina, which is the structure where image analysis begins. The cornea is a relatively simple curved surface at the front of the eye. In eyes that operate primarily in air, the cornea's optical function is essentially to provide a curved boundary between air and the fluid filled chamber of the eye (which at a good approximation is a boundary between air and water). The difficulty that a simple eye faces upon entering water is that the refractive power of the curved cornea is abolished. This is because it no longer acts as a lens; it no longer is a boundary between media of different refractive index. The consequences of this loss of refractive power have been investigated in some detail (Sivak, 1976, 1978; Levy and Sivak, 1980; Sivak et al., 1999; Katzir and Howland, 2003).

The image is no longer focused on the retina but is focused behind it, resulting in a blurred (defocused) image: the brightness of the image is reduced because the effective size of the entrance pupil becomes smaller, and the limits of the visual field of each eye (the extent of the external world that is imaged on the retina) will decrease. The extent of these changes upon immersion are a function of the refractive power of the cornea in air. The more powerful (more highly curved) the cornea the greater will be these changes upon immersion.

Amphibious vision also poses a challenge for species (such as pinnipeds, cetaceans and sea turtles) which primarily operate below the water surface but which may occasionally use vision in air. In these species there may be a gain in refractive power when the eye leaves water and so the animal can effectively become short sighted and visual fields may become broader and the image brighter.

6.2. Light levels and spectral challenges of foraging within water

In addition to the decrease in image brightness due the optical effects of immersion, entering water also results in an immediate decrease in the levels of ambient light compared with above the surface. Natural light falling on the water surface (irradiance from the sun, skylight, moon, stars) is reduced initially because of the reflection of light from the surface i.e. not all light passes through into the water. We appreciate this readily by the high brightness of light reflected back from any

water surface. In addition to this initial loss of light by reflection, water absorbs and scatters light such that at the depths at which the "high impact" auks, ducks and penguins forage (Table 2), the attenuation of light is significant. This effect is seen in the clearest of natural waters (Tyler and Smith, 1970) with the result that at a depth of 200 m, even in these waters, irradiance is decreased about 100-fold.

Scattering of light within the water column also results in significant changes to the distribution of light. At the surface, light appears to come from directly above and the direction of the sun can be clearly determined. However, with increasing depth, the distribution of light becomes less clearly delineated as coming from above and by about 40 m, the position of the sun above the surface may not be discernible.

In addition to these reductions in irradiance there is also a very marked differential spectral absorption of light with increasing depth. Again, this is a property of the clearest natural waters, such that by 200 m the available light becomes noticeably blue to the human eye. This indicates that there has been selective absorption of light at longer wavelengths in the visible spectrum, and also at shorter (violet) wavelengths.

Thus, the space light becomes increasingly narrow in its spectral distribution which is centred in the blue part of the human visible spectrum at wavelengths between 420 and 430 nm. The space light also becomes increasingly darker due to the irradiance loss (Fig. 3, from Tyler and Smith, 1970). These light conditions in themselves pose a significant perceptual challenge for any animals which forage below the water surface. They are particularly challenging for amphibious species since they inevitably face quite different light environments above and below the water surface and, because they tend to dive rapidly, they typically will experience rapid changes in the perceptual challenges that they face.

The effects thus described are a property of pure water which rarely occurs naturally. Such waters tend not to be foraging environments because pure water is inevitably nutrient poor and would not support organisms to be foraged for. In most water bodies, and certainly in most foraging waters, the light environment is more complex due to the presence of suspended matter (living organisms, products of decay, dissolved and suspended minerals) which serve to scatter light and add other selective filtering affects. The effects of these are that light will be attenuated at depths of 100–200 m by much more than 100-fold, and the spectrum of light may have its peak shifted slightly to longer wavelengths, between 420 and 500 nm (Blue–green part of the visible spectrum) with very little, or no light, at shorter wavelengths and none at wavelengths beyond about 550 nm (Lythgoe, 1979).

There is extensive data on the light environment of naturally occurring fresh water types and these can be highly variable in colour due to dissolved materials and the presence of simple organisms (Lythgoe, 1979). A comprehensive description and classification of natural marine water types was produced by Jerlov (1976). He showed that on a global scale, natural water types vary significantly in spectral absorption, especially between pelagic and coastal situations. The result is that the light environments at different depths, and at the same depth in different locations, vary markedly in both irradiance and spectral distribution.

6.3. The decrease in light levels at depth: "nocturnal" foraging

When foraging at depth during daytime a penguin, or an auk, may regularly experience light levels equivalent to those experienced at the surface during twilight or under moonlight (Martin, 1999; Regular et al., 2010, 2011). Such light levels are up to 5 orders of magnitude below those experienced at the surface at the start of the dive. Thus a diving bird may routinely experience the same sensory challenges that are faced by animals that are classed as terrestrial nocturnal foragers, such as owls (Strigidae).

The perceptual challenges of nocturnal foraging in terrestrial species have led to the evolution of a wide range of adaptations of vision, the recruitment of non-visual senses in the location of prey, and the evolution of specific behavioural strategies (Martin, 1990; Warrant, 2008). An additional challenge is that amphibious foragers (such as auks and penguins) which dive during the day, regularly go to depths of 150 m (in order to follow the diel vertical migrations of their prey) (Regular et al., 2010, 2011; Wilson et al., 1993), and dive very rapidly in order to maximise foraging time at depth (Kooyman et al., 1992). Thus these birds also experience a very rapid (1–2 min) transition between day and night time light levels compared to the 20–30 min transition between the low day time and night time light levels that occur in terrestrial habitats during sunrise and sunset transitions (Martin, 1999; Warrant, 2008).

This rapid change (and its reverse upon surfacing) would seem to present particular challenges for maintaining the retina in the appropriately adapted state, especially the dark adapted state that is necessary for the optimal extraction of information from the image produced on the retina at low light levels. In King Penguins, this seems to be achieved by the evolution of an extremely dynamic pupil that is capable of stopping down to a pinhole aperture which protects the retina from high light levels, and also opens to a very wide aperture at low light levels (Martin, 1999). The dynamic range of pupil size in this penguin is about 300-fold. This compares with the 16-fold range of pupil area in pigeons and humans (Marshall et al., 1973; Woodhouse and Campbell, 1975). It is also important to note that in order to achieve maximum sensitivity while at the bottom of the dive it is necessary to keep the retina in a permanently dark adapted state; dives are too short to allow the slow dark adaptation of the retina to occur during a dive (full dark adaptation of a vertebrate retina takes about 40 min with most of the sensitivity gain achieved within 20 min) (Warrant, 2008).

Since these deeper diving birds (auks and penguins) follow the diel vertical migration of their prey, they are either foraging relatively near the surface at night or at depth during the day. The consequence is that whenever these birds are foraging they are doing so at low (crepuscular–nocturnal) light levels.

7. Fundamental limits on vision

The crucial property of all eye types is that they are capable not only of registering general changes in the light levels of the environment, but are also able to determine the position of a light source relative to the animal (Land and Nilsson, 2012). That is, they have the capacity of "spatial vision". Since the first eyes evolved, their subsequent evolution has been in essence a series of refinements of spatial vision. These have resulted in the increasingly accurate and precise determination of the positions of objects within a wide field of view about the animal, and over an increasingly wider range of light levels. It should be noted that colour vision, which is often thought of as something rather different, something that is additional to "simple" spatial vision (simple because it can be achieved in what appears to be a simpler world of black and white), is in fact an elaboration of spatial vision. Colour vision allows the extraction of finer spatial detail by using differences in the wavelengths of light, not just differences in the intensity of the light which is reflected or emitted from different sources and surfaces in the environment.

7.1. Trade-off between sensitivity and spatial resolution

There is an important and fundamental trade-off in vision between the capacities of sensitivity and the ability to resolve spatial detail. This has been discussed in detail by Land and Nilsson (2012) who show that high resolution is not possible at low light levels in any vision system. More pertinent for this discussion is the argument that an eye which has evolved to detect ever lower levels of light inevitably loses its ability to resolve spatial detail at those low light levels, and vice-versa. That is, an eye which is highly sensitive to low light levels is unable to employ the same mechanisms to detect fine detail at high light levels. This is, in fact, a property of any vision system including man-made ones such as photographic and video cameras (Land and Nilsson, 2012). For example, the most sensitive night vision cameras cannot achieve the spatial resolution of those which operate at high day time light levels, and vice-versa.

The importance of this is that while it may be possible at low light levels for an imaging system to contain information about the presence of an object in a scene, the mechanism to extract that information cannot detect the presence of that object with a high degree of certainty. In fact, as a general rule the more sensitive the analysing system becomes, the greater the uncertainty. This is something that we can experience directly ourselves. If we allow our eyes to become fully adapted to the dark and we then try to detect the presence of objects in a dimly lit scene, we cannot see fine detail. This is a direct result of the inevitable trade-off between sensitivity and resolution; it is not just something peculiar to human eyes. But we can also experience how our uncertainty about seeing objects and surfaces fluctuates at low light levels. Even if we stare fixedly at any one part of the dimly lit scene, the amount of detail (and the interpretation that our brain can put upon it) changes, sometimes quite dramatically, all as a result of there being few photons to detect and the uncertainty of their detection.

The important point to note is that this is not just a flaw in the functioning of our eyes and brain, but a genuine demonstration of the limits of vision, how at low light levels it is not possible to achieve high resolution because of the very nature of light itself and the very real problems of extracting information when light is scarce. Of course, human eyes are not the most sensitive within the animal kingdom and natural selection has driven the eyes of some species to trap more photons and achieve brighter images (Martin et al., 2004; Martin, 2012; Warrant, 2008), but inevitably these eyes will also reach a limit on the details that they can detect and at low light levels they too will be subject to the same uncertainties of image sampling.

The clearest manifestations of these properties of vision are measures which show how acuity (resolution) decreases with light level. Such decreases in resolution have been demonstrated in a number of species; exemplified by data from humans, owls, and pigeons (Fig. 1) and Great Cormorants (Fig. 2). Fig. 1 shows that even in an owl, in which absolute sensitivity is close to the theoretical maximum for vertebrate eyes (Martin, 1986), resolution falls continuously with decreasing light levels. Fig. 2 shows that resolution also falls with decreasing light levels in an aquatic foraging bird.

In nocturnally active animals, eyes are typically large and this can be interpreted as an adaptation to trap a high number of photons from the scene in order to produce a relatively bright image on the retina (Land and Nilsson, 2012). An absolutely large entrance aperture (pupil) is especially important for the detection of point sources of light within a scene. Eyes of large size are found in nocturnally active birds including owls (Strigidae) and Oilbirds (Steatornithidae) which fly and forage regularly at low (crepuscular and nocturnal) light levels in terrestrial environments. Although these species probably have eyes that are among the most sensitive found in birds (Martin, 1986; Martin et al., 2004) their vision is not sufficient to guide all foraging; other senses, hearing (owls) and olfaction (oilbirds), are employed in the location of prey. This suggests that although vision in these species is close to the theoretical limit of sensitivity, resolution at low light levels is not sufficient to guide all aspects of their behaviour.

All of the above arguments suggest that the trade-off between sensitivity and resolution that apply to all imaging systems, and which is well understood theoretically, have real consequences for the evolution of vision in vertebrates, especially for those that forage at low light levels.

7.2. Contrast and spatial resolution

Acuity is the simplest measure of the ability of an eye to detect detail in a scene. It provides a measure of the finest detail that can be detected when the contrast in the scene is high, i.e. a black object which reflects or emits little light, positioned
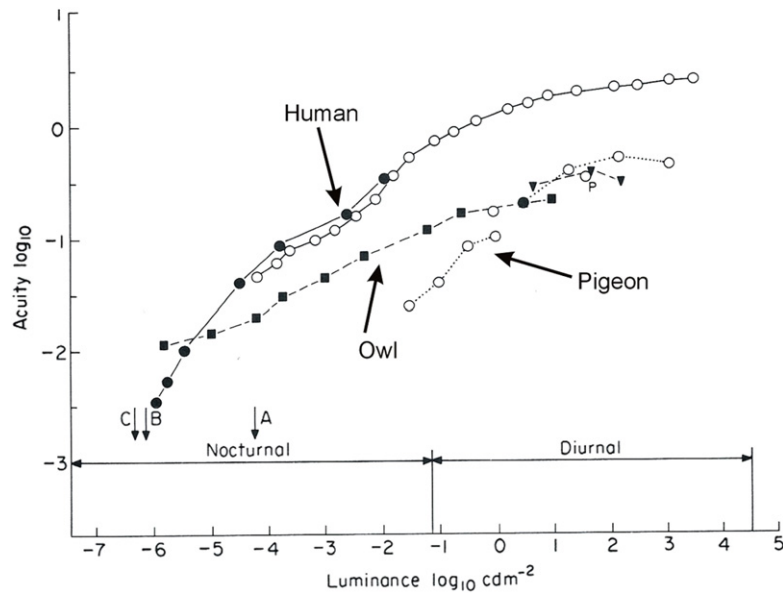
Fig. 1. Minimum separable visual acuity (expressed as Log_{10} of the reciprocal of the minimum separable angle) as a function of luminance in human, pigeon and two owls species. The natural occurring nocturnal and diurnal luminance ranges are indicated. A, B, and C indicate the absolute visual thresholds for Pigeon, Human and Owl respectively.
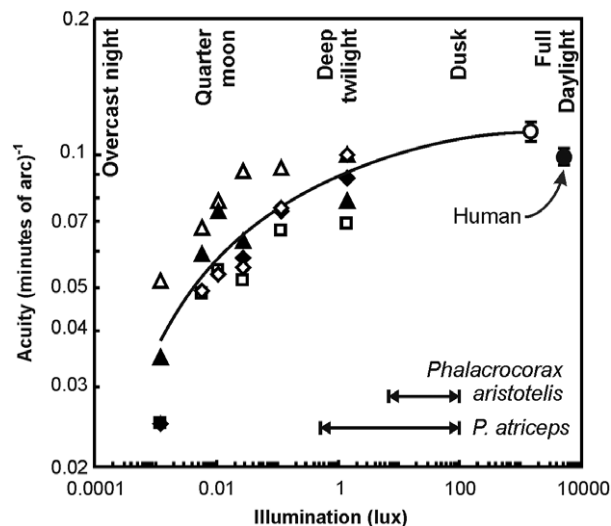*Source:* Figure modified from Martin (1986).

Fig. 2. Minimum separable visual acuity as a function of illumination in Great Cormorants underwater. Illumination levels equivalent to those received at the earth's surface from natural sources between full daylight and an overcast night are also shown. The horizontal bars indicate the range of mean illumination encountered during the bottom phase of dives for European shags *Phalacrocorax aristotelis* and blue-eyed shags *P. atriceps*. Underwater acuity for young humans is indicated.
Source: Figure modified from White et al. (2007).

against white (highly reflecting throughout the visible spectrum) backgrounds of different brightness. The best stimuli to be used for such tests are gratings (equally spaced black and white stripes). This is what has been measured in Figs. 1–3. However, high contrast stimuli rarely occur in nature and thus acuity measures the theoretical "best" spatial performance of an eye. Typically natural targets reflect some light and backgrounds are rarely white, thus the usual task is in effect to detect grey targets against grey backgrounds.

A straight forward measure of acuity (high contrast stimuli) and how spatial resolution is affected by lower degrees of contrast, was conducted underwater in Great Cormorants and this showed that spatial resolution fell significantly with decreasing contrast (Fig. 3) (White et al., 2007). It was possible to use this data to model how targets (fishes of various sizes and of different contrasts with the background) viewed from different distances, would appear to the birds (Fig. 4).

These models showed not only that the acuity of cormorants was relatively poor underwater (slightly better than humans underwater without a face mask) but that target contrast had a profound effect on the ability of the birds to detect a
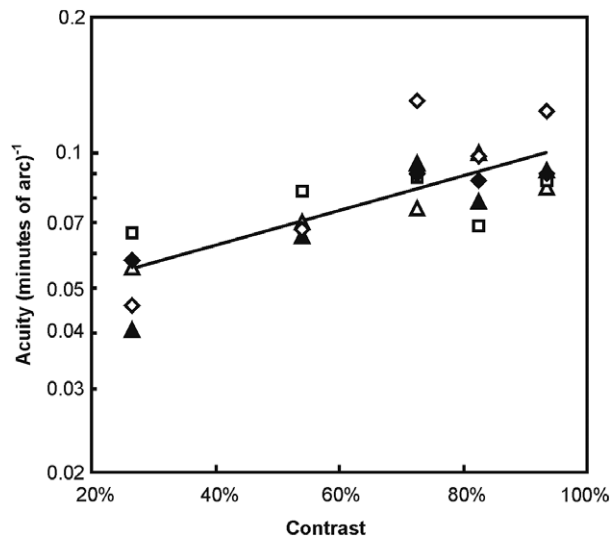
Fig. 3. Effect of contrast on visual acuity of five Great Cormorants. Symbols represent individual birds. The line is a significant function of acuity with contrast.
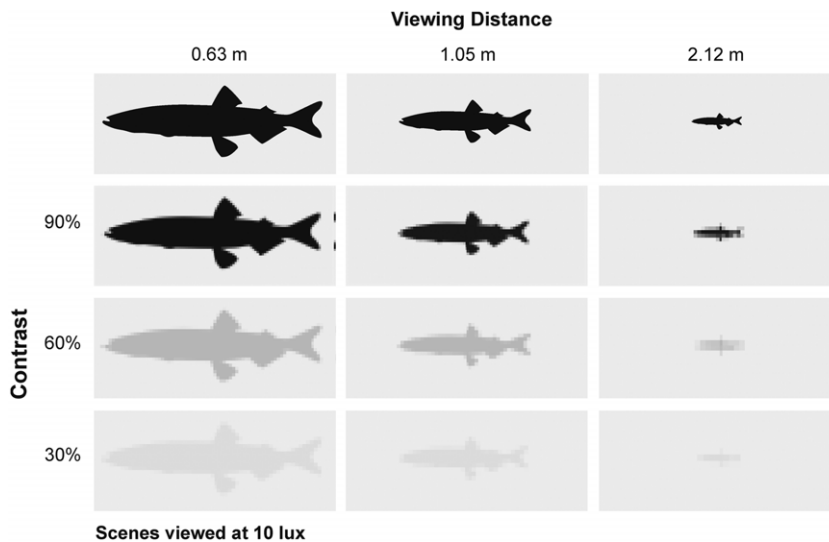*Source:* From White et al. (2007).

Fig. 4. Prey detectability model for a Great Cormorant based upon the data of Figs. 2 and 3 demonstrating the effects of contrast and viewing distance. The model is based upon a Great Cormorant foraging on a capelin *Mallotus villosus* (10 cm total length) type of fish at an ambient illumination of 10 lux, which has a contrast of 90%, 60% and 30% viewed from a distance of 0.63, 1.05 or 2.12 m.
Source: From White et al. (2007).

target. These are the only measures of spatial resolution underwater in any bird. They demonstrate that the vision of these underwater predators is nowhere near equal to that of aerial predators. The results also suggested that because of the relatively poor ability of these birds to detect spatial detail, their foraging requires the use of particular behavioural techniques both to detect and capture their prey (White et al., 2007).

Another approach to investigating the effect of contrast on spatial resolution has been to measure "contrast sensitivity functions" (Ghim and Hodos, 2006). These use display screens to vary the contrast of patterns of striped stimuli. They in effect ask the observer "what is the minimum amount of contrast that you can detect" and this is determined as a function of the width of the stripes. From this it is possible to determine how wide stripes have to be for the smallest contrast to be visible? Studies have shown that birds have surprisingly low contrast sensitivity for achromatic gratings (shades of grey), compared to other vertebrates (Ghim and Hodos, 2006; Harmening et al., 2009; Lind et al., 2012; Lind and Kelber, 2011). Furthermore, in all species tested to date (including humans) contrast sensitivity is highest for relatively large stimuli, and contrast sensitivity declines as stripe widths both increase and decrease away from the widths where contrast sensitivity is highest. All studies have shown that contrast sensitivity in birds is lower than in humans. Most importantly these studies demonstrate that when stimuli are of low contrast the optimal size at which they are most likely to be detected is relatively

large; both very broad and very narrow striped patterns require high contrast to be detected. This has important implications for the kinds of stimuli that a bird might be able to detect in turbid waters where contrast is inevitably reduced.

8. Colour vision and sensitivity in the spectrum in birds

As noted above, colour vision allows the extraction of finer spatial detail by using differences in the wavelengths of light, not just differences in the intensity of light, which are reflected or emitted from different sources and surfaces in the environment.

The colour vision abilities of different species will have evolved primarily for enhancing the spatial information that colour vision can reveal about the presence and properties of certain types of objects that are key in the life of an animal, for example objects used in display behaviours (Endler et al., 2014), particular plumage patterns (Bennett et al., 1997), or particular types of fruits (Burkhardt, 1982). Simply seeing more differences between colours is unlikely to have been the driver of natural selection; it is the spatial information about objects that will have driven selection in the direction of detecting fine differences within the spectrum.

The ability to detect colour has not been determined in any of the taxa listed in Tables 1 and 2. However, it is possible to say something about the possible colour vision, or at least the breadth of the spectrum visible to these birds, from general knowledge of the visual pigments found in the photoreceptors of birds. Among seabirds detailed knowledge of visual pigments are available only for Wedge-tailed Shearwaters *Puffinus pacificus* (Hart, 2004; Hart and Hunt, 2007) and Humboldt Penguins *Spheniscus humboldti* (Bowmaker and Martin, 1985).

Analysis of the image produced by the eye's optical system is initiated by the millions of photoreceptors which are found in all retinas. The photoreceptors are of two functional types – rods and cones – and are classified primarily by the visual pigments which they contain. It is these pigments which trap photons from the image and initiate a cascade of chemical changes that trigger a signal into the nervous system. In the human eye, as well as the rod receptors, there are three types of cone receptors classified according to the position in the spectrum of the peak sensitivity of the photopigments that they contain. It is these cone receptors that provide the basis for colour vision. In birds in general there are rod receptors which contain a specific visual pigment and four types of cone photopigments, whose sensitivities may cover a broader part of the spectrum than that detectable by human eyes (Martin and Osorio, 2008). The important functional difference between rods and cones is that rods function primarily at low light levels (twilight and below), while cones function at higher light levels (the higher levels experienced in twilight and day time). There is a range of light levels at which both types of receptors function but it is important to recognise that during twilight and night time, spatial resolution is purely a property of the rods, and because they are of one type only, colour vision is not possible.

Spectrophotometric measurements of the sensitivity maxima (λ_{max}) of the photopigments found in bird retinas indicate that these fall into five classes (4 in the cone receptors and 1 in the rod receptors). Four of these photopigment classes show a high degree of similarity across a wide range of species and it has been concluded that there is little evidence of adaptive radiation of visual pigments among birds i.e. pigments, and hence sensitivity within the spectrum, do not show particularly fine tuning or subtle difference between species. It has been shown, for example, that the visual pigments found in the eyes of a species of pelagic sea bird (Wedge-tailed Shearwaters *Puffinus pacificus* Procellariiformes Hart, 2004) are very similar to those found in a phylogenetically distant species which is terrestrial and lives in open forest habitats (Indian Peafowl *Pavo cristatus* Galliformes Hart, 2002; Hart and Hunt, 2007).

Of the 4 cone pigment types, one of them, referred to as Short Wave Sensitive (SWS type 1) is differentiated into two types and these types are found in different species. One type has a maximum sensitivity at about 365 nm (λ_{max} at 365 nm) and is referred to as ultraviolet sensitive (UVS), while the other (λ_{max} at 410 nm) is referred to as violet sensitive (VS) (Wilkie et al., 2000). It is the UVS pigment which gives certain (but by no means all) bird species visual sensitivity into the ultraviolet (UV) part of the spectrum (Cuthill et al., 2000). Because of the phylogenetic distribution of UV sensitive photopigments it is thought to have evolved independently on at least four occasions. Thus UV sensitivity is found in most Oscine Passerines (Passeriformes), but excluding the Corvidae, and also in gulls (Laridae Charadriiformes), Ostriches (Struthioniformes), and Parrots (Psittaciformes). UV sensitive pigments have not been found in any amphibious bird species.

To date only Humboldt Penguins have provided a likely exception to the general uniformity of avian photopigments. This species has been reported to have cone pigments that are slightly shifted to have their maxima at shorter wavelengths than other birds but like other diving birds, they lack the UV sensitive pigment (Bowmaker and Martin, 1985).

In addition to the five types of photopigments, the retinas of birds have three morphologically distinct types of photoreceptors: rods, single cones and double cones (Cserhati et al., 1989). Double cones are widespread in vertebrates (Bowmaker and Loew, 2008; Walls, 1942), but absent from all mammals. The function of double cones is thought to be in the provision of a luminance signal; they do not contribute to colour vision (Martin and Osorio, 2008).

Each cone has a specific type of oil droplet in the proximal part of the outer-segment (Bowmaker, 1977; Cserhati et al., 1989; Hart, 2001). These droplets typically contain non-photosensitive pigments based upon carotenoids which act as filters. This filtering of light by the pigmented oil droplets has the effect of sharpening the spectral tuning of the receptors (Hart and Vorobyev, 2005). Such spectral sharpening does not occur in the double cones and the oil droplets in these receptors appear to be clear but they do block UV light from reaching the photopigment.

Clearly the retinas of birds are more complex at the level of the receptors than those of mammals, including humans. Thus, whereas humans have three types of cone receptors plus the rod receptors, it seems that most, if not all, birds have

four types of cones plus rods and that some, but not all, birds may see into the UV, and all will see into the violet part of the spectrum. However, these differences in sensitivity and colour vision apply only at high (day time) light levels when vision is mediated by the cone receptors. At lower (twilight and night time) light levels only the rod receptors are functional. Since these rod receptors have very similar characteristics across all birds and mammals, vision at low light levels, with respect to sensitivity in the spectrum and the absence of colour vision, will be the same across all bird species and it will be similar to that of all mammals, including humans.

8.1. Colour vision and sensitivity in the spectrum in gillnet bycatch birds

This information about visual pigments in birds has wide generality and can be used to make valid statements as regards the vision within the spectrum of those seabirds considered susceptible to gillnet bycatch:

1. When active at high (daytime) light levels they are likely to have colour vision capacities that are similar to that of a wide range of other bird species. This implies the ability to make fine colour discriminations throughout the visible spectrum between ≈400 nm (violet) to ≈650 nm (red).
2. Their visible spectrum does not extend into the ultraviolet (UV) ≈315–380 nm as it does in the oscine passerines, parrots, ostriches and gulls. These latter are the only bird taxa in which vision has been shown to extend into this spectral region.
3. When active at low light levels their vision will be very similar to that found in all other bird species and will have peak sensitivity at ≈500 nm (in the blue–green part of the spectrum); it will not extend into the UV.

A caveat to these generalisations is that the available data for Humboldt Penguins indicates that colour vision could be less acute than in terrestrial bird species (but may still be comparable to that of humans). This is because these penguins seem to have only three cone photopigments compared with the four typical of other birds (Bowmaker and Martin, 1985). However, this cannot be interpreted as a characteristic of all pelagic seabirds since Wedge-tailed Shearwaters have a visual pigment compliment, much like that of the majority of birds species. Humboldt penguins also have lower sensitivity at the long wave (red–orange) part of the spectrum compared with other birds, again including the shearwater. The Humboldt penguin does have a visual pigment which covers the dark blue/violet end of the spectrum 400–420 nm. Thus it might be possible to conceive that this penguin is slightly blue shifted in its daylight vision and this may reflect a general absence of objects reflecting in the orange to red end part of the spectrum in its natural environment (Bowmaker and Martin, 1985). However, the generality of this may be very limited since a number of species of penguins and other seabirds have red reflecting structures on their bills and plumage, and in their mouths, which are thought to have an intraspecific communication function.

The lack of sensitivity to UV among seabirds could be correlated with the lack of short wavelength light at foraging depths in the sea (Section 6.2), but given that nearly half of all birds species probably lack UV sensitivity, this interpretation may be invalid. It is also noteworthy that the peak sensitivity of the rod visual pigments in all birds do not match the position of the peak in the spectral distribution of ambient light (blue 400–450 nm) that occurs with increasing depth in clear oceanic waters. However, there is nothing exceptional about seabirds in this; rod photopigments with very similar peak sensitivities are found in all birds (and other taxa including humans), and this may reflect an optimal solution to detecting photons at low natural light levels (twilight, starlight and moonlight) in terrestrial habitats when ambient light has a broad spectral distribution (Lythgoe, 1979).

9. The distribution of photoreceptors within bird retinas

As described above there is clear evidence that photoreceptor types and visual pigment types show little variation across bird species. However, the distributions and relative numbers of photoreceptor types within the retinas of each eye, and how their inputs are grouped by the ganglion cells before being relayed into the nervous system, can vary markedly (Meyer, 1977). Furthermore, the absolute numbers and packing density of photoreceptors are also known to vary markedly across species. The result is that maximum resolving power (acuity), and hence the detail that a given species can detect within a scene (or its converse, the maximum distance at which a given object can be detected), differ markedly between species and also within an animal's field of view (Land and Nilsson, 2012).

Differences in resolution between species are not trivial. For example, maximum resolution is thought to occur in large raptors and Wedge-tailed Eagles *Aquila audax* have been shown to have an acuity of 0.1 min of arc (Reymond, 1985). In comparison the maximum resolution of a cormorant underwater is fifty times lower at 10 min of arc (human maximum acuity ≈0.4 min of arc) (White et al., 2007). However, the very high density of photoreceptors in the eyes of eagles (as in human eyes) occur in only a very small portion of the entire retina, typically they are located centrally or slightly laterally, midway between the centre and the retina edge. That the portion of the retina with highest acuity occurs centrally within the retina is not without particular significance in birds. This is because unlike humans, in which the eyes project forwards, the eyes of all birds are placed laterally in the skull with the result that the areas of highest acuity does not project forward in the direction of travel (Lisney et al., 2013; Martin, 2009). In birds, areas of highest acuity project not into the forward field of view but considerably lateral, up to 45° laterally from the forward direction, i.e. there is an area of high acuity that projects laterally in each eye, and hence highest acuity is not in the direction of travel. It has been argued that this is an important factor to consider when designing measures to reduce the incidence of collisions of flying birds with human artefacts such as wind turbines and power lines, because flying birds do not look forward in the direction of travel with their region of

highest acuity (Martin and Shaw, 2010). Therefore any gillnet mitigation measures must take account of the lower acuity for forward as compared with lateral viewing.

One particularly intriguing pattern of photoreceptor distribution within retinas is known to occur in some seabirds. This is where the region of highest photoreceptor density, and hence elevated acuity, occurs in a linear strip which projects approximately horizontally across the field of view (Hayes and Brooke, 1990; Meyer, 1977; Tyrell et al., 2013). It is thought that this occurs particularly in birds of open habitats where the horizon is a prominent feature and an elongated region of higher acuity projecting laterally to each side of the birds may be associated with stabilising the eyes/head to the horizon or is the region within which conspecific birds or predators are most likely to occur within the field of view (Hughes, 1977; Tyrell et al., 2013). Such linear areas have been recorded in some species of procellariiform birds (Fernandez-Juricic et al., 2011; Meyer, 1977).

10. Visual fields and the topography of vision

A further major source of variation in the information that is available between bird species arises because of differences in the visual field of each eye, and the way that the two fields are combined. The total visual field determines the space around the animal from which information can be retrieved at any instant. Marked differences in the extent of the region of binocular overlap, its position relative to the bill and in the extent of the blind area above and behind the head, have been recorded (Martin, 2007, 2014). It has been argued that these differences are closely associated with the perceptual challenges which arise from differences in foraging ecology. In particular the requirement to visually control bill position to secure food items and how this is traded-off against the need to detect predators, and in some species the need to avoid imaging the sun, are all important determinants of visual field characteristics. Surprisingly, visual fields do not appear to be directly associated with the perceptual challenges associated with the control of locomotion; this seems to be achieved within the constraints imposed by other factors (Martin, 2012, 2014). Differences in visual fields can be finely tuned and are known to occur between species within the same genus which differ in their foraging techniques (Guillemain et al., 2002), as well as within families (Martin and Portugal, 2011).

These kinds of variation and their association with different foraging tasks are well described in seabirds. For example, marked differences in visual fields have been recorded among procellariiforms, penguins, cormorants and auks (Martin, 2014).

11. Unique world views and their limits

When combined, the different configurations of visual fields and the different distributions of photoreceptors in the retina produce marked differences in "visual topography" between species. Each species probably has a unique "world view" with respect to the overall sector of the world from which it can extract information at any one instant, while within that field of view there will be differences in the distribution of spatial resolution and of colour vision. It has been shown that these differences in world view may be correlated with significant differences in the foraging ecology and foraging behaviour of birds of the same genus (Guillemain et al., 2002), family (Martin and Portugal, 2011) or order (Martin and Prince, 2001). Thus generalisations across species groups, such as those listed in Tables 1 and 2 should be made with caution. However, the fundamental ideas of what may limit vision in different situations (Section 7), the characteristics of photoreceptor pigments in birds (Sections 8 and 9), and the limits of variation in visual topography (Section 10), allow cautious generalisations on the limits of visual ecology in different environments. These permit the development of general guidelines on what might be the limit of visual performance of taxa which are prone to gillnet bycatch and thus allow recommendation of mitigation measures which should be applicable to most, if not all, of the vulnerable species.

12. The sensory world of bycatch species: synthesis

High impact gillnet bycatch bird species include ducks, divers (loons), penguins and auks (Table 2). All dive to depth when foraging and, with the exception of the divers, may regularly reach depths of 50–100 m where they take evasive prey or sessile molluscs. At these depths, even during day time, light levels within the clearest waters are low; within the twilight–night time range. Some of these birds, notably the penguins and auks, also regularly forage during the night.

As in all vertebrates, including cetaceans, sea turtles and pinnipeds, at these low light levels vision will be mediated almost exclusively by the rods system and therefore colour vision cannot be employed. Because of the fundamental limitations on spatial resolution with decreasing light levels, and the low contrast of target objects against the ambient background light, spatial resolution when foraging is highly likely to be very low in all bycatch prone taxa. Foraging birds and pinnipeds may detect and capture even the largest fish in their diet at close range only. A specialised short range foraging technique employing short distance lunges, rather than medium or long distance pursuit, is likely to be the capture technique that is employed as light levels decrease. The only evidence on spatial resolution underwater in birds (Cormorants) has been shown their acuity to be very low compared with terrestrial bird species. It has even been argued that at high (daytime) light levels in moderately turbid waters these birds are still only capable of detecting typical prey items (fish up to 10 cm length) at very short range ($<$1 m) (White et al., 2007) and this is likely to apply also to pinnipeds (Hanke and Dehnhardt, 2013).

The vision of pinnipeds appears to be monochromatic and acuity is low (Hanke et al., 2008). There seems to be an emphasis upon sensitivity that has been traded-off against resolution and this correlates well with these animals' activity at low light levels at depth and during the night. In fact, visual acuity for high contrast stimuli in pinnipeds is very similar at higher light levels to that of Great Cormorants and blue water fish. Thus the acuity of Harbour Seals *Phoca vitulina* (Weiffen et al., 2006) lies between 5.5 and 12.7 min of arc while that of cormorants ≈10 min of arc, tuna ≈5.6–7.5 min of arc (Fritsches and Warrant, 2006). Weiffen et al. (2006) also investigated the effect of water turbidity on acuity in seals and showed that acuity declined very rapidly with increased turbidity but it was also shown that seals will forage in water that is so turbid that vision can yield very little information. Presumably under such conditions, these animals will have emphasised reliance upon tactile cues.

It has been argued that Guillemots (Murres) may, in fact, achieve sufficient food capture rates using random searching once fish prey is at a sufficient, but relatively low, density (Regular et al., 2010, 2011). It has also been argued that deep diving penguins may detect prey items using the light emitted by photophores on the body surface of prey fish, rather than through the detection of the overall outline of the fish (Martin, 1999).

An important difference between pinnipeds and the other species susceptible to gillnet bycatch is that they possess a sophisticated tactile sense derived from vibrissae on the head, particularly around the mouth, which can be used for detailed and subtle tactile discriminations between of objects and to detect disturbances within water (Dehnhardt et al., 1997, 2001, 2003). However, this too functions only at close range, there has to be either direct physical contact between an object and vibrissae or the object has to be close for the water disturbance caused by its movements to be detected (Dehnhardt et al., 2003). Gillnets are unlikely to cause any appreciable disturbance to surrounding water and so they are likely to be detected only at short range through vision or tactile cues. However, water disturbance caused by the movements of struggling fish caught in gillnets could be detected more remotely.

Thus the picture emerges that all of these high impact and vulnerable bird species and pinnipeds, must regularly, possibly habitually, take their fish prey, not through pursuit diving but through either random searching, or following very short range encounters (probably less than 1 m). Furthermore, the fish themselves may not be so evasive as generally imagined since at depth water temperatures may be low and the fishes' escape responses may be sluggish compared with the more rapid escape responses that are possible in warmer surface waters (Hedd et al., 2009). Clearly the idea that these birds and perhaps pinnipeds are pursuit-dive foragers is misleading in that they probably detect and capture prey at only very short range. Their behaviour is not analogous to that of terrestrial predators which can detect prey at long range and hunt down individual quarry. In birds this latter behaviour does require relatively high spatial resolution, probably involving the employment of colour vision to enhance spatial resolution. However, the kind of foraging undertaken by the gillnet capture prone species is quite different. It does not require high visual resolution. Furthermore, because of the fundamental limits on resolution at low light levels and the decrease of visual resolution with decreasing contrast, coupled with the problems of having an amphibious eye (Section 6.1), spatial resolution in these animals underwater must be low. Although visually guided, their foraging techniques must be able to function in the absence of high spatial resolution. Amphibious foraging birds and pinnipeds are likely to have vision which maximises sensitivity when submerged, rather than spatial resolution. Therefore foraging techniques which can function with low spatial information and without colour vision are inevitable. The taking of sessile molluscs at depth by Scaups and Long-tailed Ducks (Table 2) also occurs at depths where light attenuation is significant and results in twilight light levels during day time. The prey items are not evasive and they are probably detected primarily by the use of tactile cues from the bill.

This analysis of the fundamental visual constraints on seeing at low light levels (Sections 6 and 7), the nature of the prey items and the technique for their detection leads to the conclusion that visual acuity in all of these birds and in pinnipeds is very low, probably no better than that demonstrated in Great Cormorants (White et al., 2007). These birds and pinnipeds regularly take prey successfully in highly turbid waters at low light levels. It is also important to note that the acuity of cormorants was measured in free moving birds that were able to use their direction of best viewing to solve the acuity task posed to them. This probably means that they used lateral viewing of the stimuli, not frontal viewing which is likely to be considerably lower than lateral viewing (Martin, 2009). Recognition of such differences in acuity in frontal and lateral fields was an important part in the recommendation that mitigation measures to reduce the incidence of birds flying into obstacles in the terrestrial environment (e.g. wind turbines) need to employ stimuli that require lower resolution than that predicted by the highest measured acuity (Martin and Shaw, 2010).

In this section of the review little has been said about the sensory world of cetaceans in relation to the detection of gillnets. This is because the sensory systems of non-cetacean bycatch prone species operate primarily at short range and with low resolution, and it is these sensory limitations which appear to be the prime cause of their vulnerability to bycatch. Cetaceans have vision, although as in the other groups their acuity is relatively low (Wartzok and Ketten, 1999). Their vision will also be subject to the same general limitations of sensitivity and resolution with decreasing light levels as described above (Section 7). However, cetaceans are also able to employ echolocation to detect objects at a greater distance independently of ambient light conditions (Au and Nachtigall, 1997; Kastelein et al., 1999; Philips et al., 2003). It is not clear to what extent cetaceans actually rely upon visual, as opposed to acoustic, information for the control of much of their behavioural repertoire; it is possible that much of their behaviour can be conducted visually blind, controlled by acoustic cues alone (Kastelein et al., 1999).

There is good evidence that echolocation is the primary sense employed by cetaceans under many conditions, especially by taxa such as porpoises Phocoenidae and dolphins Delphinidae, particularly in turbid inshore waters (Au and Nachtigall,

1997; Philips et al., 2003). However, it does seem clear that acoustic information is often not sufficient to detect gillnets. Furthermore, there is some evidence that improving the echo from gillnets by treating them with substances that increase their density, such as Barium Sulphate, might improve net detectability by cetaceans, but significant differences in effectiveness of such treatment have been reported (Au and Jones, 1991; Bordino et al., 2013; Cox and Read, 2004; Koschinski et al., 2006; Mooney et al., 2007; Trippel et al., 2003). Such treatments are unlikely to have any influence on the net detectability by non-echolocating species. Thus cetaceans may pose a particular and different set of sensory ecology challenges with respect to gillnet bycatch than those faced by birds, sea turtles, blue water fish and pinnipeds which tend to rely upon vision as their primary source of spatial information when submerged, particularly when foraging.

13. A sensory solution to gillnet by catch

In light of the above analysis, there is little problem in understanding why birds and other non-target vertebrates get caught in gillnets. Their underwater acuity is too low to detect the fine net filaments at anything other than very close range. For example, under daytime light levels, a cormorant could in theory detect a 1 mm black filament that contrasted with a white back ground at 300 mm. However, because of the reduced contrast an actual filament against a natural background would not be detected until much closer. Furthermore, in an analogous way to why flying birds may fly into apparently "obvious" artefacts (wind turbines and power lines, fences), birds are probably not keeping a look out directly ahead (Martin et al., 2012), indeed their attention is probably focused upon what lies laterally to both sides of them, since it is in these directions that prey items are more likely to be detected (because of the higher acuity associated with the lateral direction of the best optics of their eyes).

It is worth noting here that such an arrangement is far from detrimental, because it provides a foraging bird with two areas of highest spatial resolution in their visual field either side of the head, rather than the single forward direction of highest resolution which humans are familiar with. That lateral viewing in the pursuit of prey is of fundamental importance is also exemplified by Peregrine Falcons *Falco peregrinus* which fix an individual item of prey within a lateral field of vision and pursue it along a curved flight path rather than fly straight to it. This enables the item to be kept in the region of highest acuity until close to contact (Tucker et al., 2000; Tucker, 2000). Thus the forward vision of the falcon is not tuned to detecting the finest detail in the scene but this does not pose general problems because small hazardous objects lying ahead do not occur in natural situations, it is only when humans place unpredictable artefacts in the airspace that lower acuity in the frontal field poses a problem. In a similar fashion, it seems likely that birds swimming underwater will be guided by visual cues of lower resolution than that used for the detection of prey items. There is evidence that Manx Shearwaters *Puffinus puffinus* have a region of particularly low acuity which projects directly forwards and whose function may be concerned primarily with the control of forward locomotion using cues derived from optic flow fields (Hayes et al., 1991; Hayes and Brooke, 1990).

The overall conclusion is that gillnet capture prone species are being caught because they simply do not see the nets. Their vision has evolved primarily for high sensitivity rather than resolution and they forage under a wide range of low light levels when their vision must be achromatic. Furthermore, their forward vision is likely to have even lower spatial resolution than vision laterally.

The simple, but perhaps not surprising, conclusion to be drawn is that for gillnet bycatch to be reduced, the actual nets need to be made more visible to non-target vertebrates. The complete abolition of gillnet bycatch is probably not achievable, but mitigation measures which reduce bycatch by a significant degree may be possible by working within the broad parameters set by vertebrate vision over a wide range of low light levels. The obvious tension is that nets will need to continue to be invisible to target fish species to maintain fishing efficiency.

It may seem attractive to use light sources to draw attention to the nets and/or to make them more visible. However, this would not seem advisable because of its effects on the adaptation of the retina to ambient light levels. When foraging either at night or at depth vertebrate retinas will have a high degree of dark adaptation (Section 7). Exposure to a light source within the twilight–daylight luminance range within a broad spectral range (400–600 nm) will produce a rapid reversal in adaptation of the retina. This will result in impairment in the retina's ability to resolve detail, and this impairment will last for a period considerably longer than the brief exposure to the light. This is because of the relatively long time necessary for the eye to readapt to the ambient light level (Warrant, 2008). An eye which is not properly adapted to the ambient light regime has lower resolving power than one that is well adapted. Therefore exposure to a light is likely to decrease the probability that parts of the net not immediately illuminated will be less visible.

There is also a practical reason for not using light sources to draw attention to nets. Introducing lights of any types (lower power LEDs, chemical light sticks) in the vicinity of nets will be both time consuming involving an additional technical task at the time of net deployment, and will work only while power sources last. However, these difficulties have been overcome successfully in a test situation (Wang et al., 2010, 2013).

13.1. Warning vulnerable species about the presence of gillnets

To warn vulnerable species about the presence of gillnets a measure is required which:

1. Can alert the species to the presence of the net over a wide range of light levels.
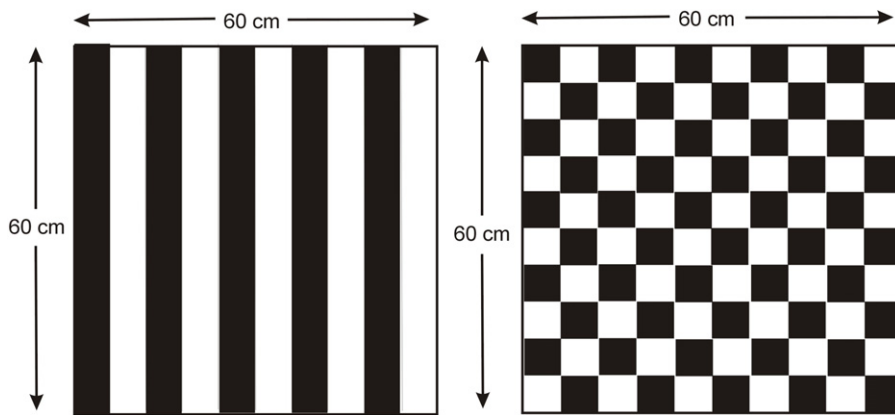2. Does not disrupt the dark adapted state of the animal's retinas.

Fig. 5. Examples of a grating and chequerboard patterns of high contrast recommended for use as stimulus warning panels. The overall dimensions are indicated, the dimension of individual elements, stripes widths and sides of squares, are 6 cm.

3. Has a high probability of being detectable by all animals that are subject to gillnet bycatch.
4. Is relatively simple to deploy and is robust under sea conditions.
5. Does not reduce the catch of target fish by a significant percentage.

To achieve these aims, it is proposed that it would be sufficient to introduce relatively small additions, "warning panels" to the surface of gillnets. The approach proposed is analogous to that of adding objects to power wires and fences which can reduce collision incidences for flying birds. The most important requirement is that the warning panels should be conspicuous over a wide range of naturally occurring low light levels and also be effective under a range of contrast conditions. To achieve this, the warning stimuli need to be both relatively large and/or have high internal contrast (Kleyheeg-Hartman et al., in press; Martin, 2011; Martin and Shaw, 2010; Summers and Dugan, 2001).

The ultimate solution would be to distract birds away from the vicinity of obstructions so that there is no obstacle–bird interaction. In terrestrial habitats this may be possible because obstacles are fixed structures and their surrounding habitat features can be manipulated (Martin and Shaw, 2010). However, this is not an option with gillnets which are deployed in new situations on a daily basis. The aim therefore is to deploy stimuli at the net which alert birds to its presence rather than distract birds away from it. Analogous to power line markers is that these warning panels are repeated frequently along the line of the net (Kleyheeg-Hartman et al., in press).

13.2. Warning panels

Acuity (highest visual resolution for high contrast stimuli) in cormorants is ≈10 min of arc at light levels within the higher end of the twilight range. In all vision systems acuity decreases with light levels and with reduced contrast (Section 7, Figs. 1–3), so the best (highest) acuity of cormorants provides a starting point for the design of a stimulus that will be detectable under a range of natural light conditions that birds will experience during foraging. Thus a good guide as to the visual size of an object that would be detectable under a range of naturally occurring conditions would be to assume that the stimulus would need to be at least 10 times above threshold, i.e. it should subtend 100 min of arc. (It is noteworthy that EU eye sight test for car driving requires vision that is able to detect a stimulus that is at least six time larger than the highest acuity of humans threshold (British Standard BS AU 145d; DVLA INF188/1) i.e. safe driving during daylight depends upon stimuli that are at least six time larger than the spatial threshold; driving at night is guided by lights, and night driving without the benefit of lights is hardly possible under modern road conditions.)

A stimulus that can be detected at a particular level of acuity can be translated into the size of an object (of high contrast) that can be just detected at a given viewing distance (this is the basis of the car driving eyesight tests). Thus, in order that a high contrast grating (equally spaced black and white stripes) stimulus panel meeting the 100 min of arc threshold is visible at a viewing distance of 2 m, the stripes should have a width of 60 mm. Alternatively a chequerboard pattern could be used in which individual squares were of 60 mm side. (To be visible at 4 m across a wide range of lower light levels the stripes or chequerboard patterns would need to be 120 mm in width.) To be effective as a grating the whole stimulus should ideally contain at least 10 stripes (or 100 chequerboard squares), and so would need to be 60 cm × 60 cm in overall size (Fig. 5).

Panels like those shown in Fig. 5 would appear to the human eye in daylight as highly conspicuous. However, it should be borne in mind that 60 mm is nevertheless relatively small compared with many of the fish prey that penguins, cormorants, auks and divers regularly take. Therefore, this pattern provides a stimulus which contains the basic spatial element of the smaller kinds of prey that these birds take. However, it would be predicted that elements of the panel (individual stripes or squares) could be detected at a distance of only 2 m over a wide range of lower naturally occurring light levels (twilight to starlight) and low stimulus contrast conditions.

Note there is no advantage in including any element of spectral information (colour) into such a stimulus panel. At the low light levels at which these animals predominantly forage their visual systems are not capable of colour vision. Vision would be mediated only by the rod receptors that contain the RH2 photopigment which has a sensitivity peak at about 500 nm. Furthermore, although this pigment has a detectable spectrum of approximately 400–600 nm (Section 8), at depth there would be very little light at the longer wavelengths (Section 6.2).

Clearly such chequerboard or grating warning panels (printed onto suitable material able to withstand sea conditions) would be detectable by the birds at a distance greater than 2 m under higher light levels condition. For example, at high daylight light levels and in clear water it would be predicted that cormorants would be able to detect the elements of the pattern at a distance of 20 m. Thus this stimulus should be visible to bycatch prone animals from between this distance under ideal viewing conditions (high light levels and low turbidity) and 2 m under low natural light levels and high turbidity.

However, there is no guarantee that the birds will detect or attend to warning panels from these longer distances since at least some species appear to be prepared to forage more or less in the absence of any detailed visual information. All that can be done therefore is to provide a stimulus that is likely to be detectable under a range of light levels and from a minimum distance at which a diving bird is likely to be able to respond to its presence. Two metres has been chosen as the minimum detection distance as it would seem to be a possible limit at which a foraging bird might detect a prey item in it lateral field of view and then be able to change swim direction to take the prey in its bill. Clearly data on the actual prey catching techniques of a range of the more vulnerable bycatch species (e.g. the birds of Table 2, pinnipeds and cetaceans) could refine further this distance. However, given the range of light levels over which the stimulus needs to be detected, 2 m would provide a reasoned starting point from which to begin experimentation. Greater or smaller ideal detection distances would imply a change to the dimensions of the pattern and stimulus panel size, but would not change the nature of the stimulus.

Such a warning panel is designed to be detected by a bycatch prone species which encounter it at random while diving under natural foraging conditions and therefore it should be effective when placed at the actual net surface. Once the stimulus panel is detected an animal is likely to move away from it to avoid collision. Although conceivably the animal could approach to investigate the pattern, this seems unlikely among birds. This is because most of them are likely to be encountering nets when either diving rapidly to foraging depth or are regaining the surface after a foraging bout when they are unlikely to delay their travel; a stimulus panel encountered on the way back to the surface is likely to be simply detected and avoided. However, pinnipeds, cetaceans and turtles are likely to be moving more slowly at these depths and may exhibit curiosity towards the stimulus panel. This will depend upon their degree of neophobia–neophilia and should be investigated.

The question arises as to how frequently animals will need to encounter such stimuli in order to avoid a large area of net. The assumption has been made that such panels should be visible under a range of viewing conditions at a distance of 2 m and this will be achieved as a bird swims past a panel (using lateral visual field viewing) or approaches it at an acute angle. It would seem reasonable to suggest therefore that the panels should be placed against or within the plane of the net in a regular grid with centres at 4 m. Thus a net 76 m × 4 m would contain 19 panels. As each panel is a 60 cm edge square, this would reduce the total catch area of the net by 2.28%. It would be possible in trials to determine whether fish catch is depressed in proportion to the area of the net taken up by the warning stimulus panels.

The requirement for the stimulus panels is that they are high contrast (black and white), double sided (i.e. effective from whichever side of the net that they are approached), and inserted within or against the gillnet surface so that they are deployed with the net, requiring no special preparation at the time of net setting. We recommend a black pattern printed onto a white flexible panel but the choice of material will require expert advice from materials scientist (see Section 13.2.4 for consideration of acoustic reflectance properties of the panels). The panels may require some perforations within the black sectors, for example 2 cm dia holes, to reduce the possibility of drifting in currents. Whatever the materials used the panels are likely to deteriorate with usage but they could be readily replaceable. Furthermore, while their internal contrast may decrease over time due to wear the overall panel could still have some influence on the animal's behaviour although its efficiency is likely to be reduced.

13.2.1. Detectability of warning panels to fish

Warning panels in the net or placed on its surface will inevitably be areas which will not be available for catching fish. However, a fish that encountered a panel is likely to seek a way around it and would then be caught. Thus the ≈2.5% reduction of net surface area would not necessarily lead to a reduction of catch. It is possible however, that a fish detecting the panels will try to avoid it and move away from the net. It is important therefore to consider at what distance a fish might detect the panel and be able to evade capture. This is of course highly dependent on the fish species: some fish are the quarry and the aim is to catch them, but others, particularly the larger blue-water species (e.g. tuna Scombridae and marlin Istiophoridae), should not become gillnet bycatch (Fritsches and Warrant, 2006) although in some situations such species are the catch target. Thus, a stimulus panel that would be detectable to the non-target fish (and to sea turtles and mammals), while at the same time not disrupting the behaviour of quarry fish species, is the ideal.

As in birds, fish retinas contain both rod and cone receptors, but unlike birds the number of different cone receptor types differ markedly across species. Some species have rods and a single cone type and others a rod and four distinct spectral classes of cones (Bowmaker, 1995; Bowmaker and Loew, 2008). The rods however, have a single photopigment of the RH1 types which are found across all vertebrates.

Most variation in fish vision occurs in fresh water species or shallow water coral reef fishes, there is less variation among oceanic fish species. Among the Rays and Sharks (Chondrichthyes), the Skates (Rajidae) have pure rod retinas while some

Rays (Batoidea) have trichromatic colour vision with three spectral classes of single cones. Among the teleost fish, photoreceptors compliments can range from pure rod retinas in deep sea (bathypelagic spp.) species to four cone types capable of making subtle colour discriminations within the spectrum between violet and red (440–600 nm) in shallow freshwater species. However, fish which live in highly turbid or stained water seem not to possess short wavelength (<440 nm) sensitivity and some have only one class of cones and are therefore considered cone monochromats. This probably reflects the absence of light at the short wave end of the spectrum in these turbid and stained habitats.

Epipelagic teleosts species (species that live in the illuminated zone at the surface of the sea, down to about 200 m) tend to be trichromatic or they may be dichromatic, lacking sensitivity at the red or violet ends of the spectrum, presumably also reflecting the absence of light at these wavelengths at depth beyond 100 m in their natural waters (Bowmaker and Loew, 2008; Lythgoe, 1979).

Presented with this diversity it is clearly not possible to provide many generalisations about the sensitivity of fish in the spectrum, or the presence of colour vision. However, as in birds at low light levels (twilight and below), all fish will be dependent upon rod vision with sensitivity centred on approximately 500 nm. The only exception to this may be some bathypelagic species that have sensitivity in the red part of the spectrum which allows the detection of light emitted from photophores (Douglas and Partridge, 1997; Partridge et al., 1992).

Clearly the use of a high contrast (black and white) pattern will not be especially conspicuous to any one particular fish taxon, but as in the birds and pinnipeds it would be detectable to all species and over a wide range of light levels. The distance at which fish will detect the stimulus pattern is likely to be no greater, and will probably be less, than the distance at which birds will detect the same pattern. In fact it is probably only the large eyed blue water fish which will be capable of detecting this stimulus pattern at a greater distance than birds under the same viewing conditions.

As described in Section 7 the decrease in resolution with luminance and contrast is a property of all vision systems. At low light levels the acuity of most fish is likely to be considerably lower than in birds underwater. Detailed measures of spatial resolution are not available for many fish species (Bowmaker and Loew, 2008). Acuity depends upon eye size and since in fish eye size typically increases with age it will change within broad limits over the life time of the animal. The highest recorded acuity (i.e. best performance) among fish are in Tuna *Thunnus spp.* (Nakamura, 1968), with acuity of 5.6 and 7.5 min of arc in Skipjack Tuna *Katsuwonus pelamis* and Mackerel Tuna *Euthynnus affinis* respectively (despite being made 45 years ago, these acuity estimates remain the highest in any fish measured to date). This compares with underwater acuity of 10 min in Great Cormorants. These blue water fish have very large eyes compared to most fish species and it seems likely that the great majority of fish will have lower acuity than these two representative blue water fishes. Thus, using Nakamura's estimates of acuity, tuna would be able to detect the warning stimulus pattern under ideal viewing conditions (high light levels and low turbidity) at about 26–30 m but this would reduce to just over 2 m at lower light levels and/or higher turbidity. It seems likely, therefore, that blue water fish will be able to detect the warning panels as readily as the bycatch bird species. But for smaller fish species the detectability distance of the stimulus panels will be considerably less under comparable viewing conditions. Thus it can be concluded that under many naturally occurring conditions individual panels will not be detectable at distance by quarry fish species and because the panels themselves will be well spaced the catch of fish is not likely to be disproportionately more than by the surface area taken up by the panels (≈2.5%), and could be less. However, for larger fish species such as tuna the panels will be detectable and therefore could warn these fish of the presence of the net. This may be problematic for gillnet (driftnet) fisheries that target tunas, but deployment of the panels in active fisheries (and comparison with standard nets) is the only way to determine the response of target and non-target species and the resulting impact on catch and bycatch levels.

13.2.2. Detectability of warning panels to sea turtles

Sea turtles are subject to gillnet bycatch. Although most investigations have concentrated on the mitigation of sea turtle bycatch in longline fisheries (Lewison et al., 2014; Southwood et al., 2008; Swimmer and Brill, 2006; Wallace et al., 2013) there has been recent work on possible mitigation for gillnet bycatch (Wang et al., 2010).

Aspects of vision in sea turtles have been summarised by Southwood et al. (2008) and Fritsches and Warrant (2006) and this shows that sea turtles probably have a trichromatic colour vision system mediated by cones and a standard rod system. Like birds, turtles have coloured oildroplets which act as spectral filters within individual cone receptors and serve to sharpen the spectral sensitivity of individual receptors. This presence of coloured oildroplets strongly suggest the presence of colour vision and this correlates with the tendency of most species of sea turtles e.g. Green *Chelonia mydas* and Logger Head *Caretta caretta* Sea Turtles, to spend their time in the brightly lit surface layers of the ocean. However, Leatherback Sea Turtles *Dermochelys coriacea*, which regularly go to greater depths where light levels decrease and the spectrum narrows, have a narrower spectral range and probably reduced colour vision. There is a suggestion that sea turtles may have vision which extends into the UV part of the spectrum but the evidence is indirect and UV sensitive retinal photopigments have not been identified. Thus (Fritsches and Warrant, 2006) concluded that the visible spectrum of Green Sea Turtles extends from about 400–650 nm and not into the UV.

Data on visual acuity in adult sea turtles is lacking. However, given that there are cone systems, acuity is not likely to be below that of cormorants at high light levels and it will be subject to the same pattern of decrease with light levels and increased turbidity as found in all other vision systems. It is safe to conclude therefore that the warning panels are likely to be no less conspicuous to the larger sea turtles as they would be to diving birds and blue water fishes. However, the response to such a stimulus is not predictable. Because of their large size, warning panels are unlikely to be confused by turtles at

relatively close range with an item of food, which could act as an attraction. It would be hoped that panels would be detected and either ignored or possibly avoided. However, unlike birds, sea turtles would be moving relatively slowly through water and would not necessarily pass by them rapidly while diving to or from the surface. Therefore it would be important to investigate the behaviour of turtles in the presence of these warning panels to determine the animals' response.

13.2.3. Detectability of warning panels to pinnipeds

The senses of pinnipeds have been subject to considerable investigation which has been reviewed recently (Hanke and Dehnhardt, 2013). An important difference between pinnipeds and the other species susceptible to gillnet bycatch is that they possess a sophisticated tactile sense derived from vibrissae on the head, particularly around the mouth, which can be used for detailed tactile discriminations between objects and to detect disturbances within water (Dehnhardt et al., 1997, 2001, 2003). It is thought that these animals can rely upon this sensory information for their orientation and foraging in the absence of light. Thus pinnipeds encountering nets in darkness may have little problem in detecting their presence but may have trouble understanding the nature of the net structure and may investigate it in some detail, thus leading to entanglement. The vision of pinnipeds appears to be monochromatic (Hanke et al., 2008) and acuity is low. Again there seems to be an emphasis upon sensitivity that has been traded-off against resolution and this correlates well with these animals' activity at low light levels at depth and during the night. In fact, visual acuity for high contrast stimuli is very comparable at higher light levels to that of Great Cormorants and blue water fish. Thus the acuity of Harbour Seals *Phoca vitulina* (Weiffen et al., 2006) lies between 5.5 and 12.7 min of arc while that of cormorants ≈10 min of arc, tuna ≈5.6–7.5 min of arc. Weiffen et al. (2006) also investigated the effect of water turbidity on acuity and showed that acuity declined very rapidly with increased turbidity and it was also shown that seals will forage in water that is so turbid that vision can yield very little information. Presumably under such conditions, these animals will have emphasised reliance upon tactile cues. Thus, the stimulus panels are likely to be detectable to pinnipeds at similar distances and light levels as predicted for bycatch prone bird species. However, as discussed for sea turtles, such panels may trigger curiosity rather than aversion or indifference and their response to panels would need investigation under field conditions. This is particularly important to investigate for pinnipeds, as they are known predators of fish captured in gillnets.

13.2.4. Detectability of warning panels to cetaceans

Cetaceans are distinguished from the other bycatch-prone species by their ability to use echolocation with high spatial resolution under conditions of low visibility (Au and Simmons, 2007). Thus they are able to detect prey in the absence of visual cues and would also be able to detect the panels. Panels would present a relatively large acoustically reflective surface which should make the panels acoustically conspicuous. The degree of acoustical reflectance will depend upon the material used for the panels and this may be an additional factor in the choice of material for the panels. Clearly there is likely to be a trade-off between a panel which is flexible and easily deployed and one that will have high acoustic reflective properties, and selection of the best material will require advice from people who know about the range of materials that could provide the required properties. However, if arranged as described on the surface of a net panels should serve to alert the animals to the presence of an obstacle even in the absence of visual cues. As with the pinnipeds it is possible that such panels could actually attract animals to the net as they investigate them and so their response to such panels under field conditions would need to be investigated. However, as with all of the other taxa subject to bycatch, the panels should be conspicuous and alert the animals to the presence of a gillnet which would otherwise be undetectable under many natural conditions.

14. The use of auditory cues to warn of gillnets

The emphasis in all of the above discussion has been upon vision and making bycatch prone species aware of the presence of gillnets through a visual signal. This is logical for birds given their high reliance upon visual information for most tasks including foraging (Section 4). However, sound does play a significant role in the behaviour of birds in terrestrial habitats.

Hearing in birds has been studied in a number of species but not in any of the groups subject to bycatch (Fay, 1992; Gridi-Papp and Narins, 2008). Sensitivity to sound as defined by an audiogram (plots of threshold sound levels as a function of sound frequency) seems to show that most birds are sensitive to sound frequencies between ≈0.1 and 18 kHz, which is similar to that of young humans (Fay, 1992). Birds do not have sensitivity that extends to the high frequencies that is found in many species of mammals. Sensitivity in birds is highest between 1 and 7 kHz, which is a similar frequency range to that of human hearing, and the actual threshold to sound pressure levels is also the same as in humans, although owls show sensitivity elevated by about 10 dB in this region.

The difficulty of using sound as an underwater signal for the presence of a net is that nothing is known about how accurately such sounds could be located by the birds. Certainly in air, the accuracy of auditory localisation is very low in most bird species (Klump et al., 1986; Knudsen, 1980; Popper and Fay, 2005). Sources can be localised in the horizontal plane by most birds to within about 18°–30°, but localisation vertically is lower. Humans can locate sound both vertically and horizontally to within 1° in the region of highest localisation acuity (Popper and Fay, 2005). It is only in owls that sound localisation comparable to that of humans occurs, due to the presence of elaborate outer ear structures (Knudsen, 1980; Norberg, 1968, 1978).

Poor sound localisation in birds arises, in part, because of the small dimensions of the head, but this poor localisation is accommodated for by the bird's ability to move rapidly in the general direction of sound sources and thus "home in" on a sound source of interest. Underwater, sound propagation is less attenuated than in air. Thus, while a sound source could in

theory be attached to a net, the ability of birds to know where that sound is coming from is uncertain. The response of a bird underwater to the sound is also uncertain and would require further investigation to determine whether the birds would be attracted to or would avoid such a source. However, there is evidence that Common Guillemots may be deterred from approaching gillnets by the deployment of active sound emitters "pingers" (Melvin et al., 1999) and this may arise from a generalised neophobia in these birds. Thus the use of sound sources attached to nets may have limited general applicability and so are not recommended until more is known of birds' ability to locate underwater sources.

It is also not clear what the response of sea turtles or larger fish would be to a sound source; they may be indifferent to it. Pinnipeds do use auditory signals. (Hanke and Dehnhardt, 2013) and it is not clear how they would respond to a particular sound source; attraction, avoidance or indifference are all possible responses, also the animals could learn that a sound source was a signal that entangled fish are nearby. Active sound sources have been used as gillnet bycatch mitigation measures with cetaceans and significant reductions in the bycatch of harbour porpoises *Phocoena phocoena* and some dolphin species are reported. It is suggested that this arises from the species neophobic response to such sounds (Dawson et al., 2013).

15. Conclusion

The problem of bycatch in gillnets has been considered here from the perspective of sensory ecology. Sensory ecology attempts to understand the information that is available to an animal when carrying out tasks in particular environments. Consideration of the general importance of vision in birds has led to the conclusion that vision is probably the exclusive source of information available to most diving birds when foraging. Only in a small number of species of ducks is the use of tactile information, gained from receptors in the bill, likely to be used in the location of food items. However, as in all other underwater diving bird species, these ducks will be using vision for guidance to reach and return from foraging surfaces.

The marine underwater environment presents quite specific perceptual challenges for the extraction of visual information from the environment. These challenges arise with respect to light levels, the spectral distribution of light, and turbidity. Consideration of these factors and the fundamental constraints on vision in vertebrates strongly suggest that much, if not all foraging in these bird species is guided by monochromatic vision of low spatial resolution. Vision that is based upon the rod system of retinal photoreceptors requires the eyes to be dark adapted in order to achieve optimal levels of information gain.

It is also highly likely that highest spatial resolution lies lateral to either side of the birds' heads rather than directly ahead in the direction of travel. It is also likely that specialised foraging techniques are necessary to take prey using a rather restricted set of visual information compared with the much richer set of information available to birds foraging in terrestrial environments. It is also likely that some underwater foraging species may do so more or less in the absence of visual information, relying upon random encounters with prey in the water column.

Detailed information on the visual acuity and foraging behaviour of Great Cor morants supports the idea that only very limited visual information is available to birds when foraging. This leads to the conclusion that gillnets cannot be seen by diving birds until at very close range under most foraging conditions.

All of the above considerations regarding the general limitations upon vertebrate visual systems and the nature of the visual challenges of marine environments will apply to other bycatch prone taxa. However, pinnipeds and cetaceans respectively may also have tactile and acoustic information to guide their behaviour underwater but only in the cetaceans can this information be gathered about objects remote from them. The recommendation is that stimulus panels, attached to the plane of the nets, are used to alert/warn bycatch prone species to the presence of the nets. Based upon the known underwater acuity of diving birds and the wide range of light level and turbidity conditions in which they are known to forage, a design for a simple warning panel is proposed. This employs a high contrast (black and white) repeated pattern (grating or chequerboard) at a relatively large size. The panels need to be repeated throughout the net surface but the size and frequency would reduce the net catching area by no more than 2.5%. The panels should be double sided and could be printed on flexible material, attached to the plane of the net and deployed with the net.

It is argued that the use of such panels may not necessarily lead to any decrease in the catch of target fish. It is also argued that such warning panels will be similarly detectable by other bycatch species; blue water fish, sea turtles, cetacean and pinnipeds and should also serve to alert them to the presence of the net. Cetaceans because of their echolocation may detect these panels when no visual information is possible because of low light levels or high turbidity, and the acoustic reflectivity of the panels could be enhanced to aid detection using echolocation.

The use of sound and lights to alert or deter animals from gillnets is not generally recommended. Lights are likely to disrupt the dark adaptation of the animals' vision and lead to a temporary decrease in their sensitivity and spatial resolution and probably increase the chance of being caught in the net. Sounds probably cannot be located underwater accurately by birds and their response to sound underwater is unknown. However, certain sounds do seem to have a deterrent effect in some cetaceans.

Thus the recommended mitigation of simple stimulus panels carrying a high contrast monochromatic pattern is:

1. Based upon what is known of the restricted visual information that is available to animals underwater over the wide range of environmental conditions which they encounter when foraging,
2. Likely to be relatively simple and cheap to construct and deploy.

The recommended spatial characteristics of the panels and their frequency on a net surface could be altered systematically and the most effective sizes for different taxa determined in field trials. However, it would be best to search for a stimulus size that is effective across all bycatch prone taxa.

Role of the funding source

GRM was contracted by BirdLife International through their UK partner Royal Society for the Protection of Birds, to conduct a review of the sensory ecology of gillnet bycatch with a view to proposing mitigation measures. No detailed requirements were made for the review. The work was undertaken by RC as part of his salaried work for his employer. This work was made possible by funding from the David and Lucile Packard Foundation.

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