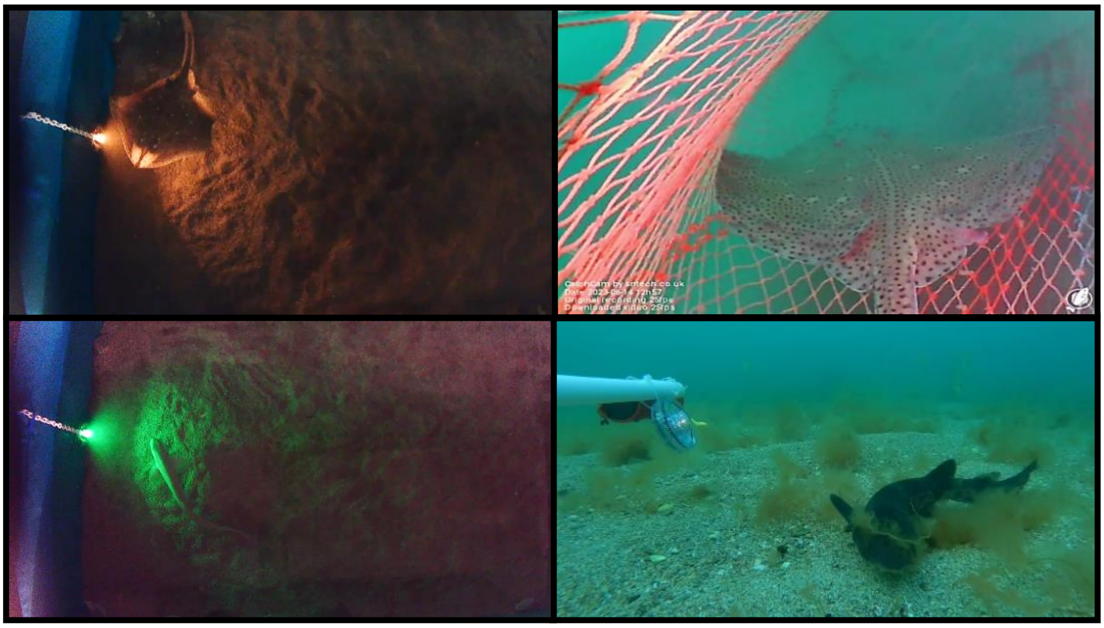
The Application of Sensory Ecology to Reduce Fisheries Bycatch



Submitted by Jasmine Alice Somerville to the University of Exeter as a thesis for the degree of Doctor of Philosophy in Biological Sciences, February 2024.

I certify that all material in this thesis which is not my own work has been identified and that any material that has previously been submitted and approved for the award of a degree by this or any other University has been acknowledged.

JSomerville

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Thesis Abstract

The way in which animals use their sensory systems to perceive their environment can be described under the discipline of sensory ecology. A growing area from this discipline is its application to tackle wildlife conservation issues. One such example is in fishing, where sensory-driven technologies have been applied to reduce the unintended capture of non-target species (bycatch) in nets. Specifically, artificial light (which has historically been used for attracting species) is being increasingly trialled to repel bycatch from gear. However, with past light deployments, there has been little consideration of how species might view different light colours, as well as how underwater conditions might affect light visibility. As bycatch-reduction with light has sometimes been unsuccessful in certain fishing contexts, I adopted a sensory ecology approach to optimise light-use in fishing. By using a vision model, I predict which light colours might be most visible to target and bycatch species when considering their vision, the ambient light at depth, and LED (light-emitting diode) emission spectra. I then explore whether the model output could be linked to behaviour towards light in fish within captive and wild contexts. Although I found that a UK shark species (*Scyliorhinus canicula*) had increased interactions with more visually stimulating light colours in captivity, light was generally less effective as a behavioural stimulant for marine species in both a non-invasive ocean setting and a trawling scenario. My thesis results suggest that other sensory factors might be more influential on behaviour in wild contexts, and that LEDs can be less contrasting to the background with increased ambient light levels, which might reduce their effectiveness. However, where light-use is already successful in fishing, the sensory ecology approach could be applied to further increase the likelihood of a bycatch species' receptiveness to light, by considering their vision within a fishing context.

Acknowledgements

Firstly, a huge thank you to my parents. My mum instilled in me the importance of giving your best in whatever job you do, and has been a source of inspiration to me in terms of her work ethic and her ability to go above and beyond when completing any task. Thank you for also being a support in my personal life (which never seems to be smooth sailing, sorry about that). A massive thank you to my dad, who has always been passionate about wildlife and nature, and is one of the reasons why I pursued the field of conservation and ecology. Some of my earliest memories are of my dad wading in ponds with me and my sister to look for tadpoles, and pointing out birds in the garden or sky, which has since been my form of relaxation (apart from I prefer to wade in the sea now). Thank you for also always having time for me if I've ever needed to chat about a problem (which is probably quite frequently).

Similarly, I want to thank my grandparents, who also immersed me in the natural world whilst growing up. They introduced me to drawing, which was based on the wildlife that we found in their garden. Although years of painting has probably trashed numerous work surfaces of theirs, art has given me some much needed time away from research, and has also contributed to my PhD work. My grandparents' advice and optimism for life in general is also a source of inspiration to me, and I hope to always share their attitude for life and their dedication to family.

Thank you to my sister and brother-in-law - the countless photos and videos of their cats on the family WhatsApp group has kept me thoroughly entertained during my PhD. Their wedding was also a personal highlight during my PhD – a very fond memory during stressful work times! I also know that my sister is always at the end of a phone if I ever need her, and that she will always provide brilliant (and brutally honest) advice for me, which I will always be grateful for.

Thank you to my aunty Alma, who has given up so much time over the years to help me with applications and general life advice. I remember she suggested that I apply for a degree in Zoology, as I loved science and animals. Now, here I am! So thank you for starting this career path for me.

As well as family, I want to thank my best friends (Grace, Molly, Ruth, Annie, Kris, Toby, Matt, Lewis, Pending, Will) who I started my university journey with 10

years ago. I have my fondest memories with these friends, and seeing them regularly over the years has kept me sane and provided some much needed time away from my PhD thesis. I honestly wouldn't have completed my PhD without you all, and I am so lucky that all of you would pick up the phone to me if I ever needed support (which again, is probably frequently).

Thank you to my PhD friends, especially Laura, Menno and Ryan – these guys have provided some much needed laughs over the years, and it's been lovely to share the PhD journey (and struggle) with them. With this, a massive thank you to everyone in the Sensory Ecology lab as well – whether its providing cake at lab meetings or drinks at Xmas meet-ups, the support from the group has always been amazing.

My home friends – which include my school, college and work friends. I am so grateful to still maintain regular contact with them, and that they are still a source of support for me. Even though we don't meet up frequently, I know that when we do, it's like picking up from where we last left things.

I also want to say a special thank you to Rosy, Yas, Jas, Joshy, Rose and Day. Each of them have really helped with my mental wellbeing in recent times. Whether it's providing laughs, nights in or out, or company after my knee surgery, they've definitely helped to ease the stress of final year PhD life. Joshy in particular – he has continually provided some questionable (but edible) pasta-based meals and numerous cups of tea in the last few weeks. Thank you for keeping me sane after my surgery.

And finally, a massive thank you to my supervisors Martin and Jon, for giving me the opportunity to conduct research with this PhD position. Martin's general PhD advice, optimism and draft comments have really helped me cross the finish line in the last few months. And my PhD funders – SafetyNet Technologies – they have immersed me in the start-up culture, have considered me as one of the team, and have helped me see how to run a business transparently. Particularly Grace, Dan, Pete and Tom – all of their advice and support over the years has helped massively with my confidence! Finally, a massive thank you to Rachel and the RV Sepia team at the MBA, as well as Emily Sulivan, Alix Harvey and Kevin the engineer, who provided me with some amazing training and experiences during my time with them at the MBA.

I owe my PhD to all of the incredible people that have inspired me along the way - thank you for helping me cross the finish line!

COVID 19 statement

During the first year of my PhD (2019-2020), I had research funds to seek collaborations with external research insititutes, as I needed large tanks and a research vessel to carry out my intended research, which my university campus did not have. However, with the outbreak of COVID and subsequent lockdowns, it was a challenge to acquire external facilities for **Chapter 3**, where it was often the case that the facilities' would need to prioritise their own researchers' work first, which had also been impacted by COVID. For these reasons, there was a five month delay with starting my intended laboratory work. Although I was thankfully granted a funded PhD extension, the shift in the timeline meant that my planned laboratory work did not coincide seasonally with species that I needed from the wild, which were being collected by the external facility (the Marine Biological Association). Therefore, my work ended up being conducted over a longer period of time whilst waiting for the appropriate sample sizes. This also meant I had to change the desired species that I was testing – originally, I had set out to test only skates and flatfish, but whilst waiting for a sufficient sample size for these species, I collected data with catsharks, as it was unknown whether the other species would end up being sufficient in terms of numbers. The delays and the additional time needed for data collection had knock-on effects for other chapters, particularly for conducting my own fieldwork in **Chapter 4**.

I had also planned to conduct sea trials with ILVO (Flanders Research Institute for Agriculture, Fisheries and Food) in Belgium, to test different light colours in a fishing context. However, trials were delayed due to COVID, and subsequent issues with the vessel once field trials had started meant that the work had to be stopped. There was unfortunately no time to re-do trials to collect data, and so I could not include this in my PhD.

Author's declaration

My PhD was part funded by the University of Exeter (the Sensory Ecology and Evolution Research Group), and SafetyNet Technologies, who are a start-up company that began manufacturing LEDs to fit on fishing gears around ten years ago, to reduce bycatch with lights. As the team were mainly engineers at the time, they wanted to further understand the effect of lights on species, which is why the PhD position came about. SafetyNet Technologies have not had any influence on my methodology, results or the interpretation of my results – their sole input has been to provide funds and equipment for me to trial.

All illustrations and figures were created by me, apart from product images of the LEDs and camera, which were provided by SafetyNet Technologies with their permission. Oscar Millar, who was a master's student that I supervised, provided me with a diagram of fieldwork equipment for **Chapter 4**, which he gave me permission to use in my thesis.

Chapter 2:

This chapter was published in *Fish and Fisheries* on 26th March 2024. https://doi.org/10.1111/faf.12827. My supervisors, Martin Stevens and Jon Blount, provided me with advice and methodology for the quantum-catch model. I subsequently found model components (species sensitivity and ocean irradiance data) within the literature. Sara Mynott - who was previously part of the Sensory Ecology and Evolution Research Group - provided R code for figure plotting, initial radiance measurements with SafetyNet Technologies' LED product, and some species sensitivity data, as Sara conducted work with SafetyNet Technologies before my PhD started. I subsequently wrote a quantum-catch R script for the model calculations.

Chapter 3 & 5:

I provided funds to the Marine Biological Association in Plymouth for the hire of their aquaria and research vessel *MBA Sepia*, so that I could conduct laboratory and field trials. I designed and analysed these experiments.

Chapter 4:

Master's students Francesca Della Valle, Jade Roberts and Oscar Millar collected data for this chapter, where data was used for their masters' projects, and collectively for my PhD chapter. I assisted with some of the fieldwork for each student, and I analysed and interpreted the data from all students for this chapter. In spring and summer of 2023, I was set to conduct further data collection but due to a knee ligament injury in spring 2023, I was physically unable to carry out any further work.

Contents

Thesis Abstract..2
Acknowledgements..3
COVID 19 statement..5
Author's declaration..6
Contents..8
List of Figures..11
List of Tables..12
List of Appendix Tables..12
List of Appendix Figures..12
Chapter 1: General Introduction..13
  Sensory ecology..13
  Bycatch..13
  Bycatch-reduction with light..14
  Historical light-use in fishing..15
  Behaviour towards light..16
  Vision..17
  Light transmission underwater..19
  Vision modelling..22
  Research aims..22
  Chapter aims..24
Chapter 2: The use of vision modelling to design bycatch reduction devices using light..27
  Abstract..27
  Table of contents..28
  Key words..29
  Introduction..29
  Materials and methods..32
    LEDs..32
    Ocean backgrounds..33

Vision modelling 34
Results 36
Case studies 36
Case study 1 - Eastern Bering Alaska Pollock Fishery 36
Case study 2 - Scottish Nephrops Mixed Demersal Fishery 38
Case study 3 - Portuguese Trammel Net Mixed Fishery 41
Case study 4 - Brazilian Longline Tuna Fishery 43
Discussion 44
Acknowledgements 48
Data availability statement 49
Conflict of Interest 49
Chapter 3: Behavioural responses of elasmobranchs and flatfish towards artificial light and use of visual modelling for application in bycatch-reduction. 50
Abstract 50
Introduction 51
Materials and methods 55
Quantum-catch model 56
Behavioural trials 58
Statistical analysis 59
Results 61
Quantum-catch output 61
Behaviour 62
Catsharks 62
Skates 64
Plaice 68
Discussion 72
Chapter 4: The use of BRUVs to assess the natural behaviour of marine species towards artificial light for future consideration in fishing trials 77
Abstract 77
Introduction 78
Materials and methods 81

Vision modelling 81
BRUVs 84
BRUV drops 84
Observer bias 84
BRUV design 85
Statistical analysis 87
Results 88
Vision modelling 88
BRUVs 89
Observations 89
MaxN 93
Discussion 96
Chapter 5: No evidence that artificial light deters a UK shark species from capture in an experimental trawling scenario 101
Abstract 101
Introduction 102
Materials and methods 105
Vision modelling 108
Ethics 109
Statistical analysis 109
Results 110
Catshark abundance 110
Catshark escape ability 111
Vision modelling 112
Discussion 113
Chapter 6: General Discussion 118
Summary of results 118
Model evaluation 120
Behaviour evaluation 123
Captive scenario 124

Wild context 125
Fishing scenario 125
Alternative sensory stimulants 126
Future sensory ecology application 128
Practical implications 130
Model adoption 131
Concluding remarks 131
Appendices 133
Appendix Tables 133
Appendix Figures 150
References 155

List of Figures

Figure 1 18
Figure 2 21
Figure 3 23
Figure 4 26
Figure 5 33
Figure 6 34
Figure 7 38
Figure 8 40
Figure 9 42
Figure 10 44
Figure 11 57
Figure 12 61
Figure 13 64
Figure 14 67
Figure 15 71
Figure 16 83
Figure 17 86
Figure 18 87
Figure 19 89
Figure 20 91
Figure 21 92

Figure 22 94
Figure 23 95
Figure 24 107
Figure 25 110
Figure 26 112
Figure 27 113
Figure 28 115
Figure 29 122
Figure 30 128

List of Tables

Table 1 63
Table 2 66
Table 3 68
Table 4 70
Table 5 72
Table 6 90
Table 7 93
Table 8 111

List of Appendix Tables

Appendix Table 1.......... 133
Appendix Table 2.......... 133
Appendix Table 3.......... 138
Appendix Table 4.......... 149

List of Appendix Figures

Appendix Figure 1.......... 150
Appendix Figure 2.......... 151
Appendix Figure 3.......... 152
Appendix Figure 4.......... 153
Appendix Figure 5.......... 154

Chapter 1: General Introduction

Sensory ecology

From how a kestrel spots its prey from metres above, to how a beetle might navigate a forest floor, the use of animal sensory systems are vital for an individual's survival within the environment. The discipline dedicated to understanding how animals perceive and respond to their environment with their senses is known as sensory ecology (Stevens, 2013). Sensory ecology specifically explores how sensory systems have adapted to detect and respond to stimuli such as sound, chemicals, light, magnetism, and movement (Elmer et al., 2021; Stevens, 2013; von der Emde, 2001; Wiltschko and Wiltschko, 2005). The knowledge of how animals process and respond to these cues allows for a better understanding of how particular niches are occupied, and how animals may ultimately evolve, adapt and survive within their habitats (Stevens, 2013).

In more recent times, sensory ecology has been applied to solve wildlife conservation and management issues, which often stem from anthropogenic disturbances or impacts (Elmer et al., 2021). Some examples in terrestrial systems include the improvement of animal welfare in horse jumping, where researchers used the knowledge of horse vision to increase the visibility of the poles to horses, to reduce their chance of injuries (Paul and Stevens, 2020). Another example includes the use of sound to reduce bird strike, where frequencies that are detectable by Eurasian starlings (*Sturnus vulgaris*) are used to avert them from airfields (Swaddle et al., 2016). Sensory ecology approaches have also been applied to invasive species management, where a study sterilised feral female goats in the Galapagos Islands, as well as chemically inducing them to produce pheromones to attract male goats (Cruz et al., 2009). This increased mating, but led to no offspring, and thus the population was eradicated overtime (Cruz et al., 2009). As such, the understanding of animal systems and senses to tackle management and conservation issues is a growing area (Elmer et al., 2021), where unique sensory systems can allow for unique technological innovation.

Bycatch

In the marine world, a major conservation issue is bycatch in fishing, which is the incidental capture of non-target species in fishing gear (Lewison et al., 2004; Pardo et al., 2017). Some bycatch species can be retained and sold, but if they are not commercially viable, they are returned to sea as discards (Reeves et al., 2013). This can occur when species are not of legal size, have exceeded a total allowable catch limit (TAC), or have a conservation status of protected, endangered or threatened (Pérez Roda et al., 2019). The capture process can lead to injury and mortalities in some bycatch species, and has resulted in population declines over time for others (Lewison et al., 2004; Pardo et al., 2017; Peckham et al., 2007). As bycatch is thought to be greatly underreported in some fisheries, the real impact to populations is unknown (Veiga et al., 2016). However, based on global fisheries data from 2010-2014, estimates have suggested that of all catch that is legally landed, 10.8% is likely to be discarded. This equates to 9.1 million tonnes annually (Pérez Roda et al., 2019).

Given the above, bycatch-reducing devices (BRDs) are being trialled to tap into the sensory systems of bycatch species (Martin and Crawford, 2015) to deter them from nets (Brewer et al., 1998). Senses that have been successfully exploited so far include auditory, vision, and electrosensory (Doherty et al., 2022; Nguyen and Winger, 2019a; Omeyer et al., 2020). With sound, devices called pingers have been used, which exploit the high frequency sounds that cetaceans are able to hear, and has successfully deterred them from nets in several trials (Mangel et al., 2013; Omeyer et al., 2020). Similarly, electrical pulses have been used to deter elasmobranchs from hooks in a device known as SharkGuard, which is thought to momentarily overstimulate their unique electrosensory system (Doherty et al., 2022). With vision, artificial lights have been added to gears; for example, in turtles, the knowledge of their sensitivity to UV wavelengths led to UV light deployment on a static gear, which reduced turtle bycatch by nearly 40% while maintaining target capture rates (Wang et al., 2013).

Bycatch-reduction with light

Proposed mechanisms for how bycatch can be reduced with lights are by increasing the visibility of nets in fishing scenarios, or by repelling certain species away from nets (Hannah et al., 2015; Melli et al., 2018). This has been achieved by various light colours in both active (trawling) and passive (static gears) contexts (Nguyen and Winger, 2019a). With passive fishing gears, green light has consistently been used, as bycatch has been reduced across locations and species when using this colour. For example, alongside the UV light study (Wang et al., 2013), turtle bycatch has been reduced with green lights (Bielli et al., 2020;

Ortiz et al., 2016), which has also been the case for cetaceans (Bielli et al., 2020), seabirds (Bielli et al., 2020; Mangel et al., 2018) and elasmobranchs (Senko et al., 2022). In trawling scenarios, white light on an escape panel (specifically designed for undersized fish to exit nets) has reduced bycatch of small fish like whiting (*Merlangius merlangus*) and haddock (*Melanogrammus aeglefinus*) (Southworth et al., 2020), as well as blue light for Chinook salmon (*Oncorhynchus tshawytscha*) (Lomeli and Wakefield, 2019). With green lights on the footrope of a trawl (the bottom part of the trawl mouth), eulachon (*Thaleichthys pacificus*) bycatch was reduced (Hannah et al., 2015), and with green lights on the headrope, Pacific halibut (*Hippoglossus stenolepis*) bycatch was reduced (Lomeli et al., 2018).

In some studies, lights have not had the desired effect of reducing bycatch in both passive and active fishing scenarios. In a trawling setting, researchers added white light to the headrope of a net and found an increase in target catch of Deepwater rose shrimp (*Parapenaeus longirostris*), as well as an increase in the bycatch of undersized horse mackerel (*Trachurus trachurus*) and European hake (*Merluccius merluccius)* (Geraci et al., 2021). Additionally, although Lomeli et al., (2018) found that Pacific halibut bycatch could be reduced with green light, the catch of Dover sole (*Microstomus pacificus*) was also reduced, which would not be a desired outcome for fishers targeting this species (Lomeli et al., 2018). With gillnets, a recent study also found that plunge diving birds such as guillemots (*Uria aalge*) were attracted to green lights on the nets, where there was an increase in their capture rates (Sigurdsson, 2023). This was similar in another study with seabirds, where flashing white lights increased the capture of Long-tailed ducks in gillnets (Field et al., 2019). From these trial results, it seems that behaviour towards light can be hard to predict across species and in certain fishing contexts, as responses to light can be variable.

Historical light-use in fishing

Before its use in bycatch-reduction, light was used to attract target catch, where records from thousands of years ago show that fishermen would start bonfires on the beach to attract fish to shallow waters (Nguyen and Winger, 2019a). This slowly developed to torch use, where fishermen would wade into the shallows and catch fish with torches and spears (Solomon and Ahmed, 2016). In the early

1900s, oil and acetylene fires were used to catch tuna (*Thunnus*. spp) in Hawaii (Arimoto et al., 2010).

As technologies developed, incandescent and metal halide lamps were taken aboard boats, which were placed above the water surface during night-time fishing (Solomon and Ahmed, 2016). However, the lamps were heavy and increased fuel costs for boats, leading to the adoption of more energy-efficient lights in the form of light-emitting diodes (LEDs) (Nguyen and Winger, 2019a). Other advantages of LEDs are that they can be battery-powered and waterproof, and are therefore able to be deployed on nets to affect catch behaviour underwater (Nguyen and Winger, 2019a).

Light is still used to attract catch to nets or hooks in some fisheries; for example, in squid jigging, lights are placed above boats at night in the Pacific Ocean surrounding Japan to attract squid to hooks (Solomon and Ahmed, 2016). Additionally, lights are used in pots and traps to attract crustaceans, which has been adopted in the Alaska snow crab (*Chionoecetes opilio*) fishery (Nguyen and Winger, 2019b) and UK scallop (*Pecten maximus*) fisheries (Enever et al., 2022).

Behaviour towards light

Whether light is used to attract or repel species from nets, the underlying mechanism is light-mediated movement. Across some marine species (and terrestrial species), the natural movement towards or away from light is known as phototaxis (Jékely, 2009). For example, phytoplankton (which are primary sources of energy in aquatic food systems) are dependant on light for photosynthesis (Winder and Sommer, 2012). Therefore, phytoplankton-feeders such as krill will undergo light-mediated migration to source their prey (Hobbs et al., 2021). The movement of plankton species has knock-on aggregation effects for larger marine predators, which rely on zooplankton like krill for food (Hill et al., 2006). Hence, light is an important cue for food across many trophic levels (Utne-Palm et al., 2018).

Light is also a key mediator of circadian rhythm in many species, where the presence or absence of light can dictate the activity levels of animals (Sigholt et al., 1995). In turtles, natural light can visually guide nestlings to the sea after they hatch on beaches (Kamrowski et al., 2012). Light can also be a visual aid for cuttlefish, where they can view particular planes of light that are undetectable to the human eye (polarised vision) to enable them to avoid predators in turbid waters (Schroer and Hölker, 2016). For many coral species, certain phases of the lunar cycle are a cue for mass spawning events (Davies et al., 2023).

As natural light is important for marine ecosystems, extensive work has been conducted to assess the impacts of artificial light at night (ALAN) on marine species (Marangoni et al., 2022). This form of pollution is often from urbanised coastal areas, where studies have shown that a range of marine species are negatively impacted (Kamrowski et al., 2012; Marangoni et al., 2022; Zapata et al., 2019). For example, artificial lights can disorientate turtle nestlings away from the sea (Kamrowski et al., 2015), and alter migratory flight paths for birds (Rodríguez et al., 2022), which can increase energy expenditure and predation risk for both species (Marangoni et al., 2022).

As artificial light (above and below water) can alter the behaviour of a range marine species, and in some cases, have undesirable effects, there is a need to further understand behavioural responses in a fishing context, when using light as a bycatch-reduction device.

Vision

One way to understand behavioural responses to light is to consider how animals may view light, as light-mediated reactions of species are likely to be influenced by visual adaptations (Baden et al., 2020; Cronin et al., 2014). As such, previous fishing with light studies have considered spectral sensitivity when choosing light colours (Utne-Palm et al., 2018), as this is a measure of how sensitive an animal's eye is to wavelengths of light (Lythgoe and Partridge, 1989). Spectral sensitivity can differ between species (Figure 1) and is measured via the photoreceptor cells in the eye, which absorb incoming light (Cronin et al., 2014). Specific photoreceptor types include rods or cones (or rhabdom in invertebrates; Cronin, 1986), where rods process light in dim environments and cones detect light in brightly lit habitats (Lythgoe and Partridge 1989). Species with more than one cone type can often perceive different colours (Lythgoe and Partridge 1989), as different cones can contain chemical pigments that only absorb particular wavelengths of light, which are; short-wavelength (SW), medium-wavelength (MW), long-wavelength (LW) and in some cases, ultraviolet (UV) sensitive cone cells (Lythgoe and Partridge, 1989). As well as photoreceptor cells, light intake can be controlled by ocular media (such as the lens), which can either allow or block shorter wavebands from reaching the retina (Thorpe et al., 1993).

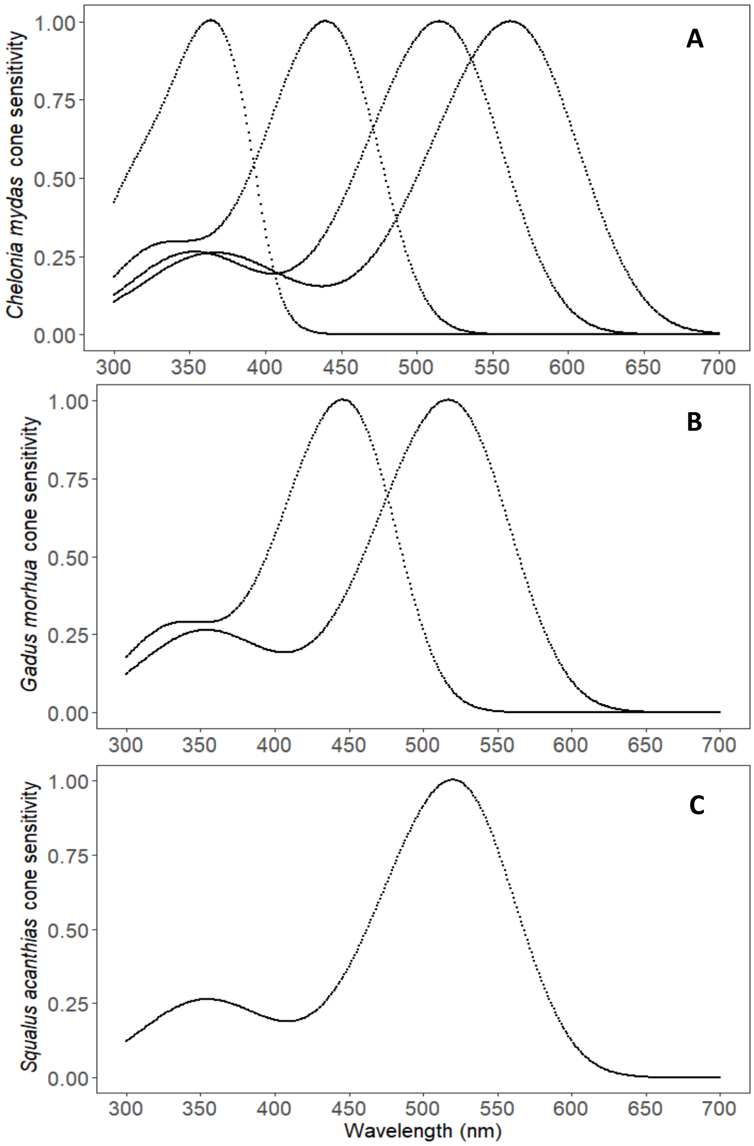


Figure 1:

The cone sensitivities of three different marine species across 300-700 nm (the visible light spectrum). A) Green turtle (*Chelonia mydas*) sensitivity which includes a UV sensitivity. The peaks are: 365, 440, 515 and 563 nm (Schuyler et al., 2014). This species is therefore tetrachromatic. **B)** Cod (*Gadus morhua*) sensitivity, with 446 and 517 nm peaks (Bowmaker, 1990) and is therefore dichromatic. **C)** Spurdog (*Squalus acanthias*) sensitivity, with a single cone peak of 520 nm (Kalinoski et al., 2014) and is therefore monochromatic.

Ways in which sensitivity to light can be measured in species is through behavioural or physiological assessments (DeVoe et al., 1997). For physiological measurements, the main two methods are electroretinograms (ERGs) or microspectrophotometry (MSP) (DeVoe et al., 1997; Rocha et al., 2016), where the former is determined by measuring the electrical responses of photoreceptor cells to monochromatic flashes (DeVoe et al., 1997), and the latter measures the ability of photoreceptor cells to absorb and reflect different wavelengths (Arrese et al., 2002). Behavioural discrimination studies can also provide information about spectral sensitivity, through colour-choice experiments with prior animal training (Risner et al., 2006), and behavioural tests are ultimately essential to determine if and how animals respond to light.

In addition to spectral sensitivity, temporal vision can be important when considering responses to flashing light, which was considered in a previously mentioned study with seabirds (Field et al., 2019). Temporal vision can be determined via critical flicker fusion frequency (cFFF), which is the point at which flashing light becomes continuous (Donner, 2021), and can also be measured by behavioural discrimination studies, or ERGs (Donner, 2021). In teleost fish, cFFF values can be highly variable and can range from 30 to 60 Hz (McComb et al., 2010), whereas in humans, cFFF is more likely to fall between 35 to 40 Hz (Muth et al., 2023).

The variability in vision adaptations across marine animals are likely to be dependent on their ecology and habitat (Lythgoe, 1988). For example, some species such as skate (*Raja.* spp), can have a completely rod-dominated retina, which may be explained by their nocturnal nature (Hart and Collin, 2015), and other species such as swordfishes have a high cFFF (40 Hz; Fritsches et al., 2005), which may be due to their need to capture fast-moving prey (Healy et al., 2013).

Light transmission underwater

In addition to visual adaptations, the ocean environment can play a key role in how light might be perceived by species (Arimoto et al., 2010). At greater depths, red light attenuates first, as longer wavelengths of light have lower energy compared to shorter wavelengths of light, and so blue light can transmit to greater depths (Kirk, 1977). Water bodies can also vary in how much light is absorbed and transmitted, which is dependent on the presence of plankton, as well as organic particle decay (Lythgoe, 1988). As such, water bodies vary in colour. Specifically, freshwater is more likely to be green-brown due to dissolved organic decay from nearby land, oceanic waters are more likely to be blue due to very little nutrients or particles, and coastal waters are more likely to be blue-green from plankton (Jerlov, 1968; Lythgoe and Partridge, 1989; Lythgoe, 1988). Water bodies have subsequently been classified into types based on their colour and particle properties (Jerlov, 1968). For example, oceanic and coastal water types from most clear to most turbid have been classified by Jerlov, (1968) as type I, IA, IB, II, III for oceanic waters, and type 1C, 3C, 5C, 7C, 9C for coastal waters, which can also be applied to various depths (Figure 2) (Jerlov, 1968; Williamson and Hollins, 2023). It has also been shown that variable light transmission in water bodies can effect behaviour; for example, increased turbidity (the presence of suspended particles) can reduce foraging success, reaction distances and sexual signalling efficacy for some species due to the reduction in water transparency (Li et al., 2013; Sundin et al., 2016; Utne-Palm, 1999). Hence, background light availability can impact visibility and behaviour.

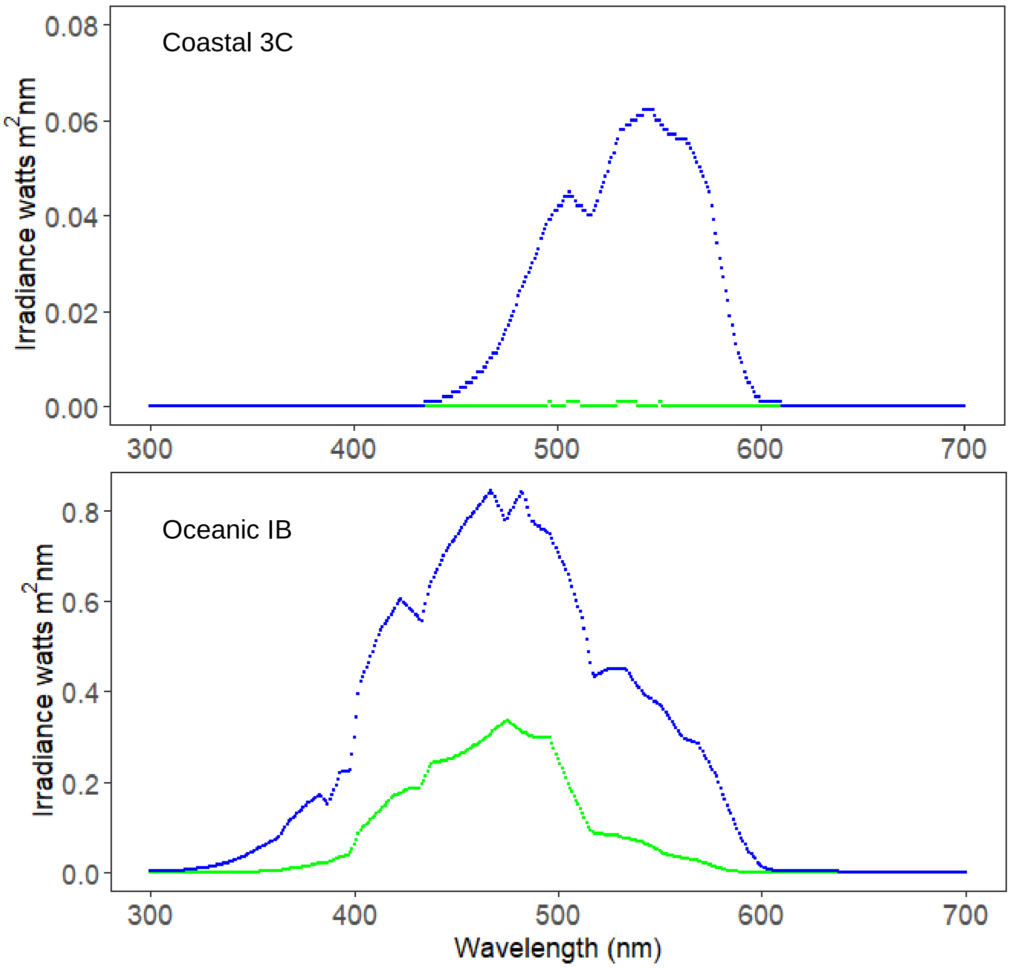


Figure 2:

Example of water types quantified by Jerlov, (1968). The graphs showcase spectral irradiance measurements (ambient light spectra under certain conditions; Endler, 1993) across the visible light spectrum (300-700 nm) for different water types and depths. The top graph represents the coastal water type 3C, which is the fourth most turbid water type out of a possible five coastal water types (Jerlov, 1968). The bottom graph represents oceanic water type IB, which is the third most turbid water type out of six oceanic water types. In both graphs, the blue dots represent spectral irradiance at 20 m depth, whereas the green dots represent irradiance at 50 m depth. For water type IB, there is more ambient light at both 50 m and 20 m depth compared to the coastal waters, which is likely due to coastal waters having more plankton than oceanic waters (Lythgoe, 1988). Hence, more light is absorbed in water type 3C. Additionally, the spectral peaks for both oceanic IB depths are shifted towards the blue part of the spectrum (between 400-500 nm) whereas the peaks are more green-shifted for coastal type 3C. As there are less suspended particles in oceanic water types, shorter-wavebands of light can be transmitted to further depths as they have more energy, giving oceanic waters an appearance of blue (Lythgoe, 1988). The data from this graph was extracted from Sticklus et al., (2018) using an online graph extractor programme called Graphreader (Larson, 2022).

Vision modelling

One way to predict how animals might view light across different habitats is through vision models, including so-called quantum-catch models (Endler, 1991). Quantum-catch outputs will give the predicted number of light units (photons) that are absorbed by photoreceptor cells within an animal's eye when they are viewing a given object (Endler, 1991). Specifically, the model considers animal photoreceptor sensitivity and their ocular media transmittance, as well as the ambient light conditions and the reflectance of the object (Cronin et al., 2014; Renoult et al., 2017). In terrestrial systems, these types of model have been used to understand how avian plumage may have evolved across habitats (Stoddard and Prum, 2008), how spiders might camouflage in their environment (Théry and Casas, 2002) and how sexually selected traits are viewed (Amy et al., 2008). In the marine environment, quantum-catch models have been used to consider whether the visual adaptations of fish can be linked to the certain habitats and depths that they occupy (Singarajah and Hárosi, 1992; Hárosi, 1996; Wilkins et al., 2016). However, to my knowledge, these models have not yet been applied to bycatch-reduction with light.

Research aims

As fishing with light studies have only considered the spectral sensitivity of species when considering vision, and reactions to artificial lights can be variable, my thesis aims to apply a sensory ecology approach to bycatch-reduction with light. Specifically, I aim to quantify how target and bycatch species view LED colours in different fishing conditions and depths through the use of a quantum-catch model. This is so that an optimum light colour can be chosen in order to maximise the visibility of lights to bycatch species. However, the model outputs need to be calibrated with behavioural data in order to confirm any predictions about the visibility of light colours to species (Olsson et al., 2018). Therefore, I will also aim to see if visibility can be linked to behaviour towards light, which I will assess in different aquatic contexts (captive versus wild), with the ultimate aim to optimise light-use and further reduce bycatch in fishing.

The LED device used to test these aims is a product called *Pisces*, which is produced by my PhD funders (*SafetyNet Technologies*). *Pisces* is plastic-encased circular LED and has the possibility of six different colour modes, where I additionally had a custom amber LED made to cover the span of the visible light spectrum (Figure 3). Each colour mode also has four different brightness settings (Appendix Table 1) and the possibility of four different flash rates: 2 Hz, 4 Hz, and 32 Hz, or continuous light (0 Hz). The LED settings can be changed by a remote control and LEDs can be wirelessly recharged when the batteries are low. *Pisces* is also neutrally buoyant in water and can be deployed to depths of up to 250 m.

Figure 3:

LED device *Pisces* and remote made by SafetyNet Technologies. The colour modes and corresponding peak wavelengths are as follows, from left to right, top to bottom: royal blue 447 nm; red 627 nm; amber, 592 nm; blue 471 nm; white 456 nm; cyan 499 nm; green, 518 nm, where amber was custom made for my thesis in order to have another longer wavelength colour mode to test in addition to red. The dimensions of *Pisces* are 127.5 mm diameter and 41 mm thickness, with a weight of 325 g in air and 80 g in seawater. The remote control switches the LED on and off, which can be also be controlled by the water activation function, where LEDs will only turn on once submerged. These images were taken by SafetyNet Technologies, who have given me permission to use in my thesis.

Chapter aims

Chapter 2 aims to apply the model to bycatch issues around the world, by considering both target and bycatch species' perceptions of LED colours in particular fishing scenarios. As the model is intended to be applied to as many commercial species as possible, I utilised photoreceptor sensitivity and ocular media measurements of commercially relevant species from the literature (see Appendix Table 2), as well as ocean classification data from the literature, which was based on depths where species are fished. From this, I considered how lights could be deployed in future fishing trials. My research questions were:

1) Do bycatch and target species view light colour modes differently?
2) Does ocean type and depth affect the visibility of lights?
3) How can the vision model be applied to fishing with light trials to help reduce bycatch?

For **Chapter 3**, a controlled aquarium setting was used to test whether a link existed between the model output and the behaviour of target (plaice, *Pleuronectes platessa*), and bycatch species (skates, small-eyed, *Raja microocellata*; blonde, *R. brachyuran* and spotted *R. montagui*) and catsharks (*Scyliorhinus canicula*). This was to observe any light-mediated behaviours, and to more easily quantify responses in a controlled setting (Ciriaco et al., 2003; Marchesan et al., 2005; Yochum et al., 2022). I used different light colours as well as flashing light (4 Hz), and quantified behaviour from video observations. My main research questions were:

1) What behavioural responses does each species have towards light in general?
2) Given ambient tank conditions, does the most visible light colour to species (inferred from the model) invoke stronger behavioural responses?
3) Do behavioural responses to flashing light differ to continuous light?

Chapter 4 aimed to test the vision model and behaviour link in a non-invasive wild context, using baited underwater remote video cameras (BRUVs; Sherman et al., 2018). This was to observe the natural behaviour of UK marine species towards light, without the added risk of capture and stress like in a fishing context. It was also a relatively inexpensive way to observe behaviour in the wild, by utilising the nearby coast to the university. Specifically, I compared the abundances of species (to the family level) between light and no-light BRUVS, where BRUVs with lights were either green, red or white. Two models of visions were created, which predicted how two common coastal families might view different colour modes in shallow water contexts. *Pisces* were deployed on BRUVs, and flash modes (4 Hz and 32 Hz) were additionally tested. My main research questions were:

1) Does light increase species' abundances (to the family level) to BRUVs?
2) Do abundances differ between flashing and continuous light?
3) Given ambient water conditions, does the most visible light colour (inferred from the model) lead to greater abundances of species to the family level?

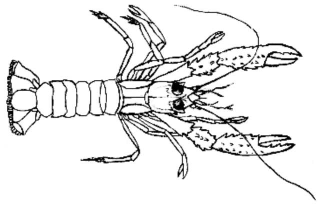
Finally, knowledge from previous chapters was applied to an experimental trawling scenario in **Chapter 5,** to see if an optimal light colour could be used to reduce the bycatch of catsharks with light, which to my knowledge, had not yet been trialled. I used a vision model for catsharks in conjunction with behavioural responses from laboratory experiments to infer the colour of LEDs on the net. I conducted alternate trawls (lights on versus lights off) in collaboration with the Marine Biological Association in Plymouth using their research vessel *MBA Sepia*. I also deployed a trawl video camera, produced by my PhD funders (*CatchCam*; Figure 4), to observe the behaviour of fish in the trawl, and to assess if catsharks were likely able to see and respond to lights. My main questions were:

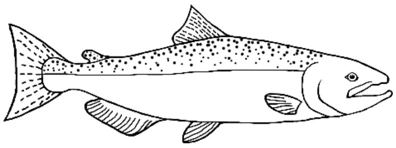
1) Can catshark capture be reduced by the use of an optimal light colour in an otter trawl?
2) Is light position sufficient for maximising behavioural responses to light?

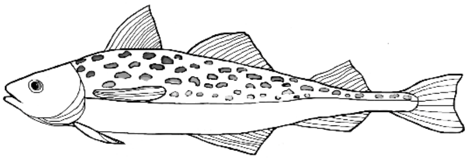
Figure 4:

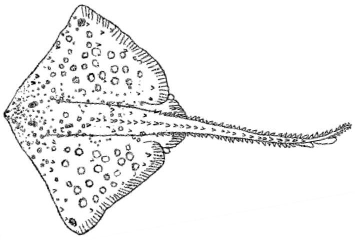
The camera (*CatchCam*) and equipment used for experimental trawls in Chapter 5. The camera is a cylindrical unit which is wirelessly charged. It also emits WiFi so that footage can be reviewed on deck with a digital tablet, after fishing. The camera comes with an LED lamp (which emits white or red light), where both units can be placed in the green trawl attachment. This image was taken by SafetyNet Technologies, who have given permission for use in my thesis.

Overall, my thesis aims to optimise a BRD in the form of artificial light, where I use a sensory ecology approach to consider how species view and respond to artificial light stimuli in their environment. From this, I aimed to further assess whether the vision model and behavioural responses can be applied to reduce bycatch in a fishing with light trial.









Chapter 2: The use of vision modelling to design bycatch reduction devices using light

***Jasmine Somerville[a], Jon Blount[a] & Martin Stevens[a]**

[a]Faculty of Environment, Science and Economy, Department of Ecology and Conservation, University of Exeter, Penryn Campus, Penryn, TR10 9FE

*Corresponding author JS: jas275@exeter.ac.uk

Author contribution

JS: Conceptualisation, investigation, writing-original draft, methodology, formal analysis. JB & MS: Supervision, writing-review and editing, conceptualisation, visualisation, methodology.

Abstract

Artificial light can be used to deter unwanted non-target catch (bycatch) from fishing gear, which is thought to be achieved by repelling bycatch, or highlighting escape routes on nets. To select for responses in bycatch species, light should 1) cause the bycatch species to avoid capture, and 2) not invoke the same

reaction in target species. One way to maximise the chance of a bycatch species responding to light is to ensure the light colour used is more visible to bycatch species. Some studies have considered the visual sensitivity of certain species to address this. In particular, the wavebands of light that a species is sensitive to. However, using this measurement alone is incomplete as it does not consider other factors that affect visibility, such as the ambient light spectrum, and wavelength-dependant light attenuation in different water types and depths. To account for these variables, and to more accurately predict how both target and bycatch species view light colours in a fishing context, we used a model of the vision of commercially relevant species in fisheries across the world. From this, we show whether a light colour is more visible to a bycatch species compared to a target species in a particular depth and water type, and how modelling can be used to make informed assessments of the selection of relevant light colours in fishing. We also discuss limitations of using vision models alone, and the need for corresponding behaviour and/or fishing trials with lights.

Table of contents

Abstract
  Key words
  Introduction
  Materials and methods
    LEDs
    Ocean backgrounds
    Vision modelling
  Results
  Case studies
    Case study 1 - Eastern Bering Alaska Pollock Fishery
    Case study 2 - Scottish Nephrops Mixed Demersal Fishery
    Case study 3 - Portuguese Trammel Net Mixed Fishery
    Case study 4 - Brazilian Longline Tuna Fishery
  Discussion
  Acknowledgements

Data availability statement

Conflict of Interest

Key words

Bycatch-mitigation, artificial light, visual ecology, vision model, bycatch-reduction

Introduction

Historically, light in fishing has been used to attract catch to nets, where records indicate that fishermen first used fire to attract fish to shallow waters (Arimoto et al., 2010). This exploits the natural behaviours of some marine organisms towards light within their environment (Melli et al., 2018), where natural sources of light can be an important cue for many biological and behavioural processes (Marangoni et al., 2022). For example, the mass movement of fish and plankton through the water column can be determined by light, which is known as diel vertical migration (Berge et al., 2020). Light is also important in aiding visual cues for crucial behaviours such as mating and hunting (Maggi et al., 2020), as well as influencing spawning events in some marine taxa (Davies et al., 2023). As such, light is an essential part of the life cycles of marine species (Marangoni et al., 2022).

Research is now focusing on light use for manipulating the behaviour of bycatch species (non-target catch; Lewison et al., 2004) to enable them to avoid capture in nets, particularly for unwanted bycatch species that do not have commercial use (Nguyen and Winger, 2019a). Laboratory experiments have shown that species can have varied responses to light colour modes; for example, in one study, European seabass (*Dicentrarchus labrax*) were repelled by green and blue light, whereas the common grey mullet (*Mugil cephalus*) were attracted to shorter-wavelength light (Ciriaco et al., 2003; Marchesan et al., 2005). Additionally, Chinook salmon (*Oncorhynchus tshawytscha*) showed an increased aversion to white light compared to blue light (Yochum et al., 2022), and Atlantic horse mackerel (*Trachurus trachurus,* Carangidae) have shown attraction to blue light (Sardo et al., 2020).

When applying lights to fishing gears, bycatch-reduction has been demonstrated with turtles, whitefish (haddock *Melanogrammus aeglefinus,* Gadidae and whiting *Merlangius merlangus,* Gadidae) and elasmobranchs (Bielli et al., 2020; Senko et al., 2022; Southworth et al., 2020; Wang et al., 2013). For example, in a gillnet fishery where turtles were regularly bycaught, researchers used UV LEDs (light-emitting diodes) to reduce green turtle (*Chelonia mydas,* Cheloniidae) bycatch (Wang *et al.*, 2013). This was based on the knowledge that turtles had UV vision, whereas the target catch did not (Wang et al., 2013). Subsequently, there was a 39.7% reduction in green turtle bycatch whilst the target catch was unaffected, which was likely due to the increased visibility of the net to turtles (Wang et al., 2013). Other successful examples have occurred in trawl scenarios, where white LEDs added to an escape panel increased the reduction of undersized whiting bycatch, which was thought to be achieved by increasing the visibility of exit routes on the net (Southworth et al., 2020).

However, light may not be effective in all fisheries. For example, researchers found that when adding white and green light to the headrope of a trawl in an experimental trawling scenario, the catch rate of both target (deep water rose shrimp; *Parapenaeus longirostris,* Penaeidae) and undersized bycatch species *(*horse mackerel and European hake Merluccius merluccius*,* Gadidae) increased in the Mediterranean Sea (Geraci et al., 2021). In another study, researchers found no effect of light in separating bycatch fish from shellfish when placing green LEDs in upper and lower compartments of a trawl in the North Sea (Melli et al., 2018). Therefore, for bycatch-reduction with light to be successful, the target and bycatch species need to be simultaneously achieving desired behavioural responses towards light in a given fishing context. For example, target species need to be unaffected by/attracted to light, and bycatch species need to be attracted to an escape route on the net or, more easily able to see the net to avoid it.

To exploit these differences, researchers have previously concentrated on the spectral sensitivity of target and bycatch species (Utne-Palm et al., 2018), where spectral sensitivity is the wavebands of light that a species is sensitive to (van der Kooi et al., 2021). Specifically, marine vertebrates and invertebrates process light through specialised photoreceptor cells within the retinas of the eyes (Arimoto et al 2010). For vertebrates, photoreceptor types include rods and cones, where rods process light in dim environments, and cones detect certain wavelengths of light in brightly lit habitats (Lythgoe and Partridge 1989). Species with more than one cone type often, though not necessarily, have the ability to discriminate between parts of the light spectrum, or colour vision (Lythgoe and Partridge 1989). Marine invertebrates possess either rhabdom or ciliary cells, which tend to have a smaller spectral range than cones (Cronin, 1986). In oceans and seas, as a general guide, visual adaptations are tuned to the light environment, such as different depths; for example, deep sea species are less likely to have colour vision due to the limited ambient light, and tend to have vision shifted towards shorter and medium wavelength ‘blue-green’ light due to a lack of longer-wavelength cone cells since longer wave light is absent in deeper water (Warrant and Locket, 2004). By contrast, shallow living species are more exposed to sunlight and may therefore possess colour vision capabilities utilising several cone types with greater sensitivity to a wider range of wavelengths (Lythgoe and Partridge, 1989).

As well as photoreceptors, ocular media (e.g. the lens and other structures) within the eyes can act as filtering mechanisms by controlling light intake, and are also often linked to ecology (Thorpe et al., 1993). For example, the lens can either allow or block UV from entering the retina (Thorpe et al., 1993). In coral reef fish species, researchers found that 49.8% of fish possessed ocular media that absorbed and blocked UV light (Siebeck and Marshall, 2001), where this mechanism has likely evolved to reduce damage from the increased levels of UV light in coral reefs (Siebeck and Marshall, 2001).

When considering how marine species might view light in a fishing context, the emitted light spectra from LEDs (or any light emitting device) also needs to be quantified. Specifically, radiant light needs to be quantified, which is either a combination of reflectance and irradiance (ambient light spectra under certain conditions), or light directly produced by an object such as an LED (Endler, 1993). Additionally, background light will play a role in how an LED is viewed by marine species, which can change at different depths due to light attenuation (Lythgoe, 1988). For example, in a shallow ocean setting where ambient light availability is high, LEDs may contrast less against the background and therefore be less visible. By contrast, at greater depths with little ambient light, LEDs will have a greater contrast to the background. Additionally, oceanic, coastal and freshwater environments differentially absorb and transmit light, due to sediment and suspended particle types, which can affect the background colour of the water body (Jerlov, 1968; Lythgoe and Partridge, 1989). Therefore, an LED's contrast to the background may change depending on water type and/or depth.

A model that exists in order to quantify how animals might view an object against a background is a quantum-catch model (Lagorio, 2012). These models predict how many light units (photons) are absorbed by an animal's photoreceptor(s) cells, based on the animal's photoreceptor types and sensitivity, and the radiant light arriving from an object in an environment (Endler, 1991). In the marine environment, quantum-catch models have been used to determine whether fish visual adaptations can be linked to their habitats (Hárosi, 1996; Wilkins et al., 2016). As of yet, they have not been applied to fishing with light.

As vision alone does not consider how light attenuates in an ocean environment, or how contrasting an LED is against a given ocean background, we aimed to quantify how different coloured lights might be viewed in ocean contexts to target and bycatch species, by using a quantum-catch model. From this, we discuss how LEDs could potentially be trialled as a bycatch-reduction device (BRD; Brewer et al., 1998) in four example fisheries.

Materials and methods

LEDs

For LED radiance, we used a product called *Pisces* (SafetyNet Technologies) which is a circular waterproof LED that is specifically designed to fit on fishing gear at depths of up to 250m. *Pisces* has the possibility of different colour modes (Figure 5), where we included seven different options in our model. LED radiances were measured in dark conditions from a distance of 50 cm in air, using spectroradiometer JETI specbos 1211-2, to produce spectral curves across the visible light spectrum (300-700nm) for each LED colour mode.

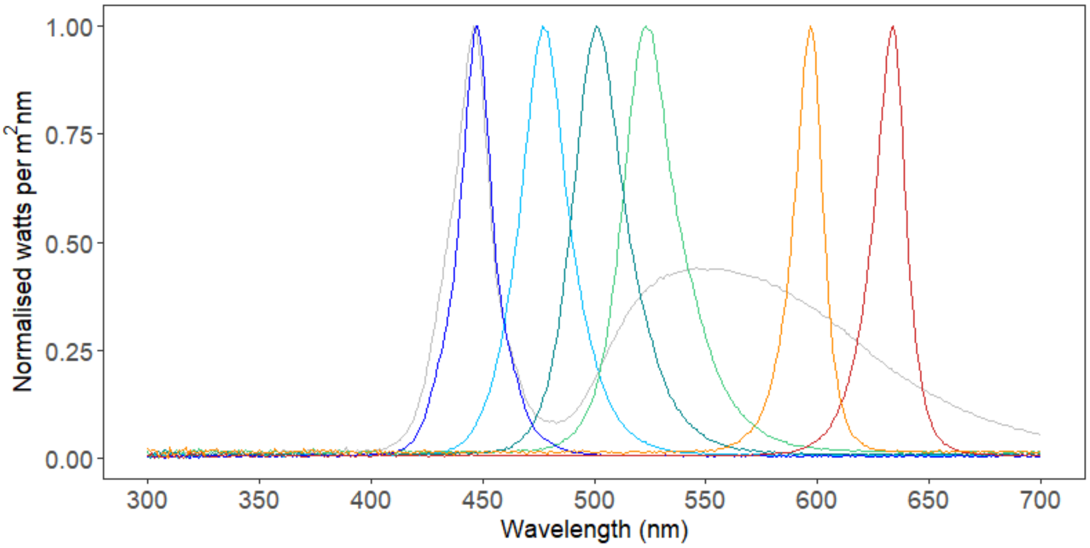


Figure 5:

Light emission spectra for seven different colour modes of SafetyNet Technologies' LED Pisces. The peak wavelength are as follows: White, 456nm; Royal blue, 447nm; Blue, 471nm; Cyan, 499nm; Green, 518nm; Amber, 592nm; Red, 627nm.

Ocean backgrounds

Water bodies have previously been categorised into several broad types by Jerlov (1968), which were based on their background irradiances. Water types were either coastal or open ocean, each with differing levels of turbidity and thus background colour (Jerlov, 1968). Jerlov (1968) quantified irradiances of global water bodies from direct measurements, by using a photometer with different optical filters to measure light availability at various depths (Williamson and Hollins, 2022). The classifications have since expanded to consider additional water parameters and greater depths for more accurate under water irradiance values (Williamson and Hollins, 2022).

To account for different background conditions in the model, we used the irradiances of two different ocean types at several depths, to ascertain how LEDs might be viewed against them. We used data extracted from Sticklus et al., (2018) using Graphreader, which is a free online graph extractor programme (Larson, 2022), where data was replotted (Figure 6) using the statistical programme R (R Core Team, 2021) and R package "ggplot2" (Wickham, 2016). The data is based on Jerlov's (1968) quantifications of a clear ocean (JIB) and a slightly more turbid ocean (JIII), with the additional consideration of absorption and scattering properties of each water type (Sticklus et al., 2018). The data was derived from measurements made in clear sky conditions, with the sun at zenith angle at 30° (Sticklus et al., 2018).

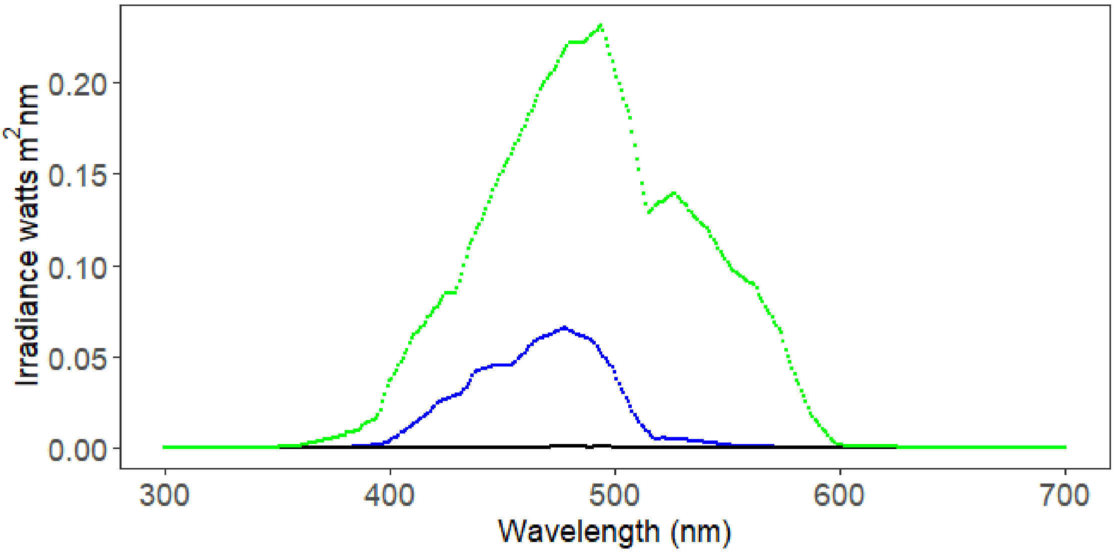


Figure 6:

Ocean irradiance data, based on Jerlov's (1968) ocean type classifications across the visible light spectrum. The green dots represent ocean type III at 20 m depth, which has the highest irradiance values. The blue dots represent the clearest ocean type IB at 100 m depth, which shows that some ambient light is still available at this depth. By contrast, the black dots represent ocean type III at 100 m, which is the most turbid ocean type and hence there is less ambient light due to absorption by suspended particles.

Vision modelling

To assess how target and bycatch species view different light colours in ocean contexts, we quantified the potential visibility of LEDs using the following equation:

$$Qc = \int_{300}^{700} I(\lambda)Ac(\lambda)\, d(\lambda)$$

where Qc is the summed photoreceptor quantum-catch for the background, or each LED colour mode. Qc is calculated from the normalised product of photoreceptor sensitivity type *c* of an animal $Ac(\lambda)$ (derived from the product of ocular media transmission and photoreceptor sensitivity at every 1 nm interval) and the normalised irradiance of each ocean background or LED colour mode radiance $I(\lambda)$, integrated in 1 nm intervals across the spectrum $d(\lambda)$(300-700 nm). Thorpe et al., (1993) lens transmission categories or direct lens measurements from the literature (Nelson et al., 2003) were used for ocular media. Photoreceptor sensitivity curves were generated from inputting peak photoreceptor sensitivities into the Govardovskii et al., (2000) visual pigment template model. This widely used pigment model is a mathematical equation that generates standardised photoreceptor sensitivity curves from peak sensitivity values of a photoreceptor (λmax) where the full spectral sensitivity curve has not been directly measured.

To understand how visible each LED colour mode is against the ocean background (background contrast), we defined the model output as “visual stimulation”, which was calculated using the following equation (Crothers and Cummings, 2013),

$$\text{Visual stimulation} = \frac{\left(\frac{\sum Qc(light\ colour)}{\sum Qc(ocean\ background)}\right)}{n(c)}$$

where the output is the ratio of the predicted total number of photons reaching the eye of the animal, combined across all receptor types, for the specific LED Qc against the ocean background spectrum Qc, and divided by the number of photoreceptor types $n(c)$ that an animal possesses. Therefore, the model produces a measure that predicts how stimulated the visual system of a species is when viewing an LED colour mode of *Pisces* in a particular ocean context from irradiance data (Figure 5&6). However, the model does not tell us how a species will react to the light (e.g. if they will be attracted or repelled). For full quantum-catch modelling methodology, see Endler and Miekle, (2005) and Stevens et al., (2009) and Data Availability Statement.

Photoreceptor sensitivity and ocular media information was based on available information from the literature (see Data availability statement – *Bycatch and* *target species vision data.xlsx*). Ocular media transmission curves were also extracted from the literature using Graphreader (Larson, 2022). Where ocular media information was unavailable in the literature, closely related species were used instead. For invertebrates, photoreceptor sensitivity curves were used due to lack of ommatidium (ocular media in invertebrates) information in the literature. For three out of eight species used in the model, ocular media and/or photoreceptor sensitivity information was obtained from juvenile species (see specific case studies below, and Data availability statement).

Results

Here we have applied the model to four example bycatch issues around the world, where light could be considered as a potential BRD. Model outputs show the visual stimulation values of species, and whether the bycatch or target species is more stimulated by light colours. We discuss how to consider the appropriate light colour modes to trial in fishing with light from the model outputs.

Case studies

Case study 1 - Eastern Bering Alaska Pollock Fishery

Target: Alaska pollock (*Gadus chalcogrammus,* Gadidae)
Bycatch: Chinook salmon (*Oncorhynchus tshawytscha,* Salmonidae)
Waters: Bering Sea, North Pacific
Depth: 100 m and greater (Fissel et al., 2013)
Gear type: Pelagic trawl nets (Ianelli and Stram, 2015)

Chinook salmon are taken as bycatch in the Alaska pollock fishery (Ianelli and Stram, 2015). From the year 2000, there were marked declines in salmon runs in western Alaska, compared to runs from the previous 20 years (Witherell et al., 2002). As 40% of global whitefish are produced from the Eastern Bering Pollock fishery (Fissel et al., 2013), there has since been pressure to greatly reduce salmon bycatch.

Chinook salmon have three cone cell sensitivities of 434 nm, 510 nm and 565 nm, and a rod cell sensitivity of 508 nm, meaning they are trichromatic (Flamarique, 2005). By contrast, Alaska pollock have a peak sensitivity of 498 nm

(Beatty, 1969). Salmon are therefore likely to be more sensitive to longer-wavelengths than pollock, which have medium-wavelength sensitivity (Figure 7A).

For the visual model output, in both clear and turbid ocean conditions in the typical fishing depths of 100 m, salmon is more visually stimulated by light than pollock for all colour modes apart from blue and cyan in clean oceans (Figure 7B). In general, both species are more visually stimulated in more turbid oceans, as there is less ambient light and therefore, the LEDs are more contrasted against the background. Both species are least stimulated by red light, and most visually stimulated by white light. However, white light provides the biggest difference in visual stimulation values between both species, with salmon being much more stimulated. We would therefore recommend trialling white light. It may also be worthwhile avoiding blue and cyan light, as both fish are similarly stimulated by these colours, which could lead to similar behaviour, although this would need to be tested.

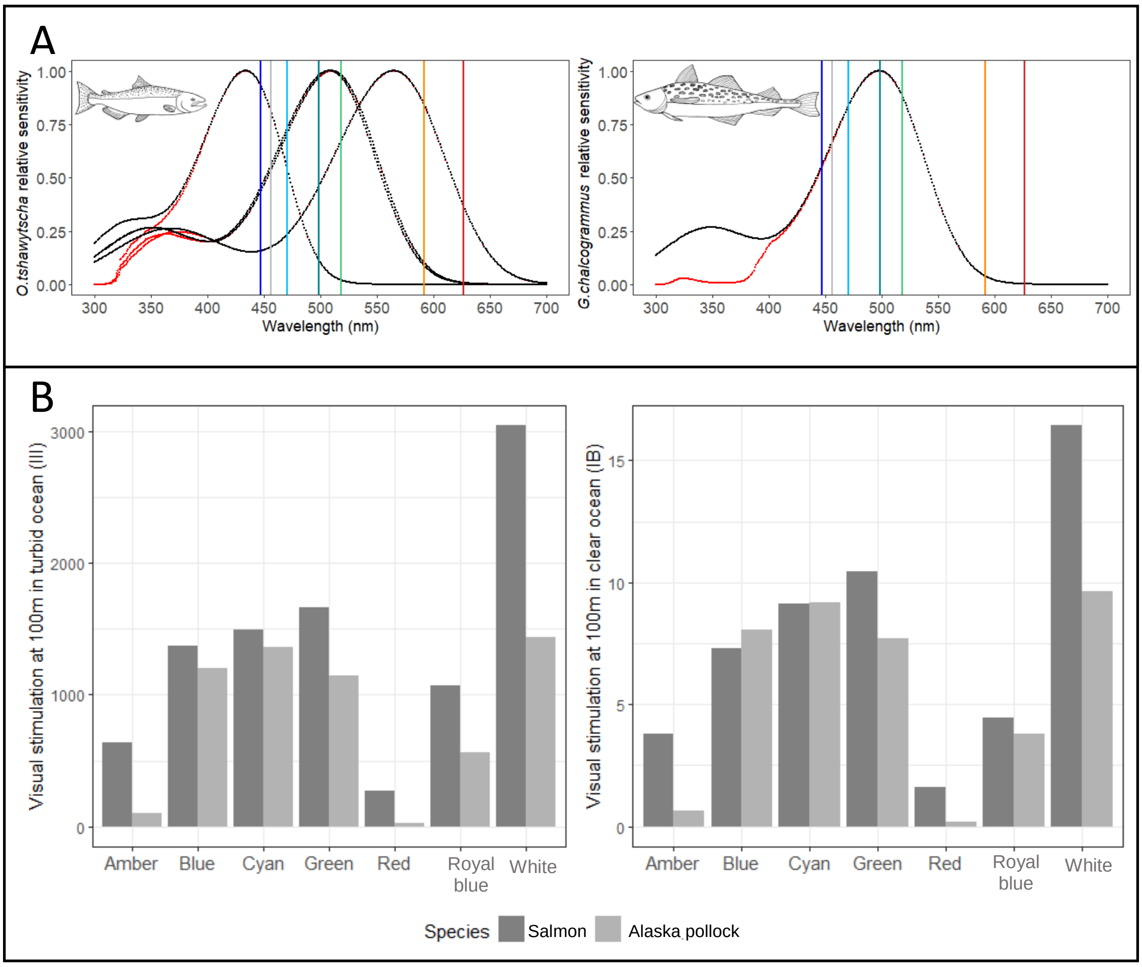


Figure 7:

A) Photoreceptor sensitivities for Alaska pollock (left) and Chinook salmon (right). The black curves represent the photoreceptor sensitivities of each species, and the red curves represent the inclusion of ocular media sensitivity, where both indicate reduced sensitivity to shorter-wavelengths of light. The vertical lines represent the peak wavelength (nm) of each colour mode of the Pisces LED. **B)** The visual model output for each LED colour mode against two different ocean backgrounds. The x axis is each LED colour mode, and the y axis is a prediction of how visually stimulated a species would be when viewing that colour mode in a particular ocean condition.

Case study 2 - Scottish Nephrops Mixed Demersal Fishery

Target: Nephrops (*Nephrops norvegicus,* Nephropidae)

Bycatch: Undersized cod (*Gadus morhua,* Gadidae)

Waters: North Sea, Atlantic Ocean

Depth: 100 m (Cosgrove et al., 2019)

Gear type: Single and/or Multi-rig trawls (Cosgrove et al., 2019)

Nephrops are a shellfish which had the highest value across all landed species from EU demersal trawls in 2010, with a value of €322M (Cosgrove et al., 2019). Nephrops mixed fisheries can also legally land whitefish like haddock, cod and whiting. However, size selectivity on gears can be an issue, where undersized whitefish below minimum conservation reference size (MCRS) (European Parliament, 2019) are often bycaught (Catchpole and Revill, 2008; Cosgrove et al., 2019). As such, escape panels on nets have been used to allow undersized fish such as cod to escape (Catchpole and Revill, 2008; Palder et al., 2023).

In terms of vision, Nephrops have rhabdom with a peak sensitivity of 515 nm (Johnson et al., 2002). To our knowledge, juvenile cod photoreceptors have not yet been anatomically measured. However, a genomic analysis revealed that cod of all life stages express SWS2 and RH2 cone opsins, which are visual pigment types that indicate a sensitivity to blue and green parts of the visible light spectrum respectively (Valen et al., 2014). This is in line with the two cone cell sensitivities of 446 nm and 517 nm which were measured in adult cod (Bowmaker, 1990). The genomic study also found that larval and juvenile cod are likely to express three medium-wavelength cone opsin subtypes (RH2 types), whereas adults possess one. This suggests that juveniles are more sensitive to medium-wavelength light, which is likely due to them frequenting greater depths than adults, where there is less light available (Valen et al., 2014). When comparing cod vision to Nephrops, cod are likely to have an additional shorter-wavelength sensitivity.

For the model output, at 100 m depth in turbid ocean (III), cod is more visually stimulated by royal blue, and slightly more stimulated by white and blue light compared to Nephrops (Figure 8B). In clear ocean at the same depth, Nephrops becomes more stimulated by all colour modes apart from royal blue. In particular, white becomes more visible to Nephrops compared to cod, with the reverse effect in turbid waters. However, visual stimulation decreases for both species in clearer conditions, due to more ambient light availability. Therefore, for fishing gears that catch Nephrops and also use an escape panel to reduce the capture of MCRS cod, we recommend using white light to reduce undersized cod bycatch, as although it is also highly stimulating for Nephrops (and more stimulating to them in clear conditions) the selectivity panel should not allow for Nephrops' escape. If the gear type cannot guarantee Nephrops' containment, then royal blue light could be trialled, as there is a greater difference in visual stimulation values between both species, which is consistent across both turbid and clear waters.

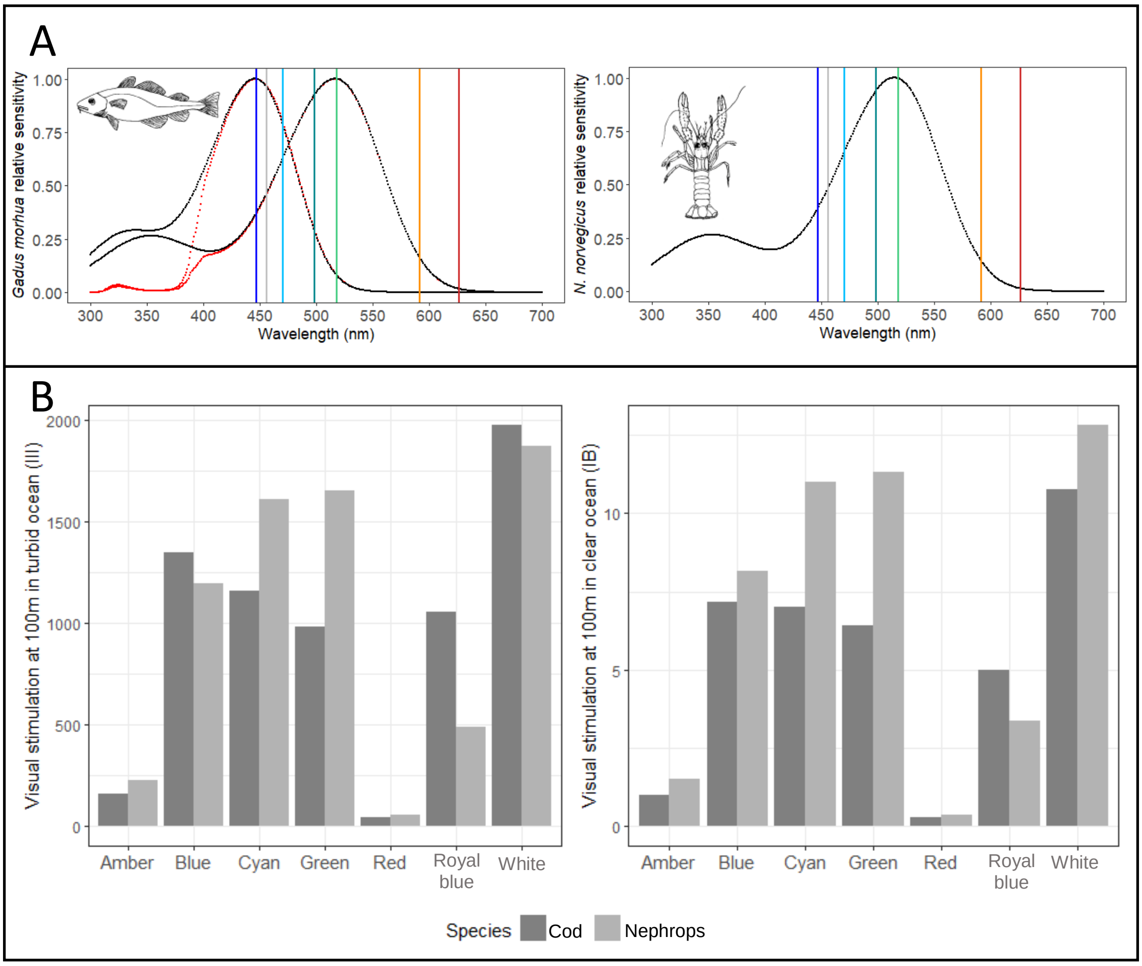


Figure 8:

A) Photoreceptor sensitivities for Nephrops (left) and cod (right). The black lines represent the photoreceptor sensitivities of each species, and the red curve represents the inclusion of ocular media sensitivity for cod, which indicates a reduced sensitivity to shorter-wavelengths of light. The vertical lines represent the peak wavelength (nm) of each colour mode of *Pisces*. **B)** The visual model output for each LED colour mode against two different ocean backgrounds. The x axis is each LED colour mode, and the y axis is a prediction of how visually stimulated a species would be when viewing that colour mode in a particular ocean condition.

Case study 3 - Portuguese Trammel Net Mixed Fishery

Target: Common sole (*Solea solea,* Soleidae)

Bycatch: Thornback ray (*Raja clavata,* Rajidae)

Waters: Atlantic Ocean

Depth: 10 -100 m (Baeta et al., 2010),

Gear type: Trammel net

The trammel net mixed fisheries in Portugal are mainly artisanal, where the main target species are flatfish such as common sole (Baeta *et al.*, 2010). Other target species can include cuttlefish (*Sepia officinalis*, Sepiidae) (Batista et al., 2009). A prominent bycatch issue within this fishery are elasmobranchs such as skate species, which can be caught in nets between 10-100 m depths across seasons (Baeta et al., 2010). Although some individuals can be retained for commercial use, closed seasons have been implemented for skates, as well as a ban on the capture of undersized individuals (Silva et al., 2021). We chose to use thornback ray to represent skate in this case study, which is based on its prominence in the fishery (Baeta et al., 2010) and the availability of vision data in the literature. We modelled vision within depths of 20 m and 50 m to represent this fishery.

In terms of vision, common sole have two medium-wavelength sensitivity peaks of 523 nm and 536 nm, a shorter peak of 472 nm and a longer-wavelength peak of 559 nm, as well as a rod cell sensitivity of 511 nm (Frau et al., 2020), which was based on measurements of juvenile sole. Thornback ray on the other hand, have one rod sensitivity peak of 496 nm (Govardovskiĭ and Lychakov, 1977) (Figure 9A). It is worth noting that the size of the skate used for this photoreceptor measurement is unknown. Therefore, it is unknown whether possible differences in vision exist between juveniles and adults, although *Raja* species are thought to have mainly rod-dominated retina with a sensitivity to medium-wavelength light (Ripps and Dowling, 1990).

For the model output, at 50 m depth, sole is slightly more visually stimulated by all colour modes apart from royal blue and blue in both ocean types. At 20 m depth, the pattern is the same except that thornback ray is slightly more stimulated by cyan in both ocean types. For both species, visual stimulation values are higher at 50 m depth due to less ambient light, and white and red are the most and least visually stimulating colour modes respectively, for all ocean types and depths. For the colour modes where thornback ray have higher visual stimulation values, blue or royal blue may be the best options to trial as there is a greater difference to the comparable outputs for sole, but only slightly. LEDs may be more effective to trial at 50 m depth or greater due to generally higher stimulation values.

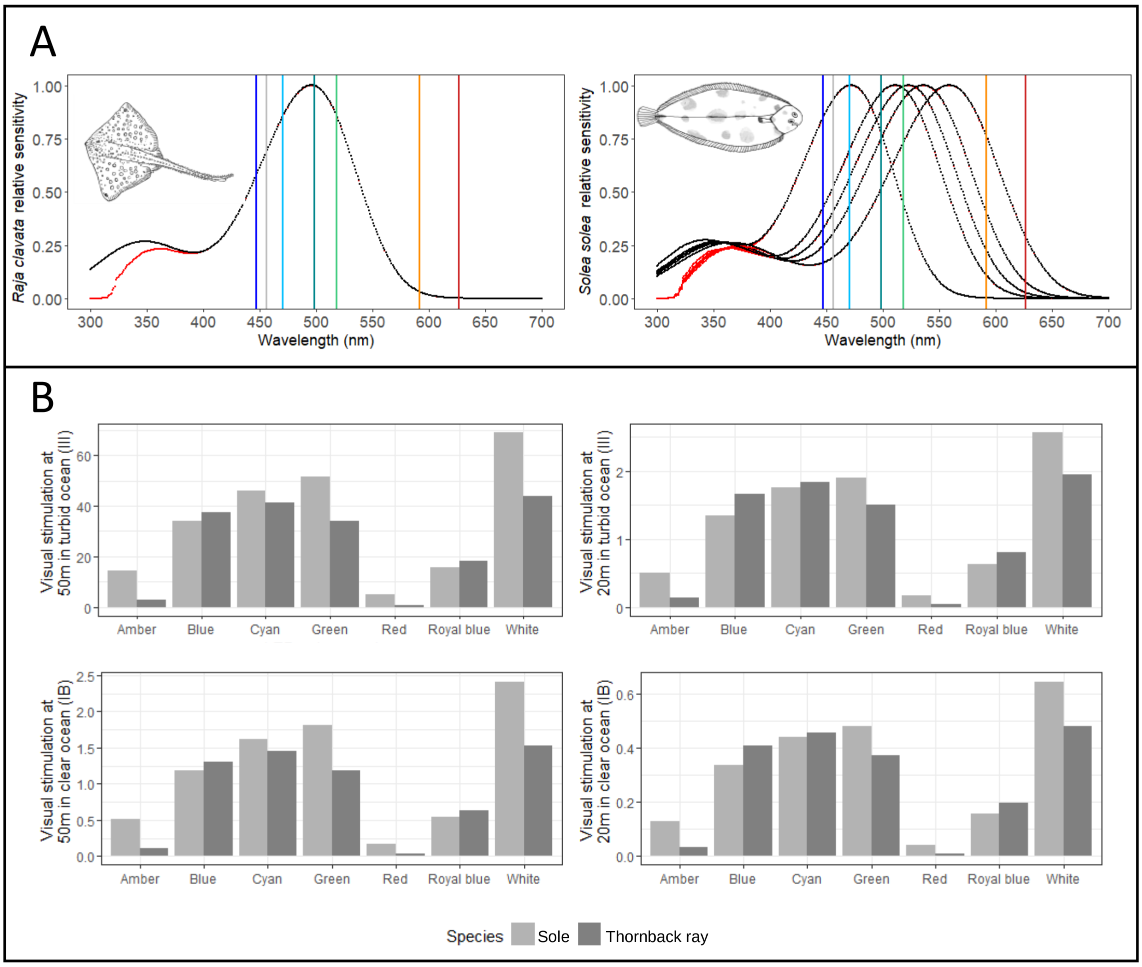


Figure 9:

A) Photoreceptor sensitivities for thornback ray (left) and common sole (right). The black lines represent the photoreceptor sensitivities of each species, and the red curve represents the inclusion of ocular media sensitivity, which indicates a reduced sensitivity to shorter-wavelengths of light for both species. The vertical lines represent the peak wavelength (nm) of each colour mode of *Pisces*. **B)** The visual model output for each LED colour mode against two different ocean types, where the top row is 50 m and 20 m depth in turbid ocean, and the bottom row is 50 m and 20 m depth in clear ocean.

Case study 4 - Brazilian Longline Tuna Fishery

Target: Yellowfin tuna (*Thunnus albacares*)

Bycatch: Scalloped hammerhead shark (*Sphyrna lewini*)

Waters: Atlantic Ocean

Depth: 100 m (Bezerra et al., 2016)

Gear type: Longline

Longline fisheries are one of the main contributors to shark bycatch globally, where longlines can target tuna and swordfish (Bezerra et al., 2016). Of the shark bycatch, hammerheads (*Sphyrna* spp.) are classified as endangered under the International Union for the Conservation of Nature (IUCN; Bezerra, Travassos and Hazin, 2016).

In terms of vision, yellowfin tuna have peak cone sensitivities of 426 nm and 485 nm, with a rod sensitivity of 482 nm (Loew et al., 2002). Scalloped hammerheads (measured from a juvenile) have a cone sensitivity peak of 530 nm (McComb et al., 2010), suggesting that hammerheads are more adapted to viewing medium-wavelength light, compared to the shorter-wavelength sensitivity of tuna (Figure 10A).

For the model output, at 100 m depth, the hammerhead is more stimulated by six out of seven colour modes for both ocean types, but tuna is more stimulated by royal blue. This suggests that medium to long-wavelength modes are more suited to hammerheads in both ocean types. The biggest difference between hammerheads and tuna is the green light, which could therefore be the best option to trial on longlines.

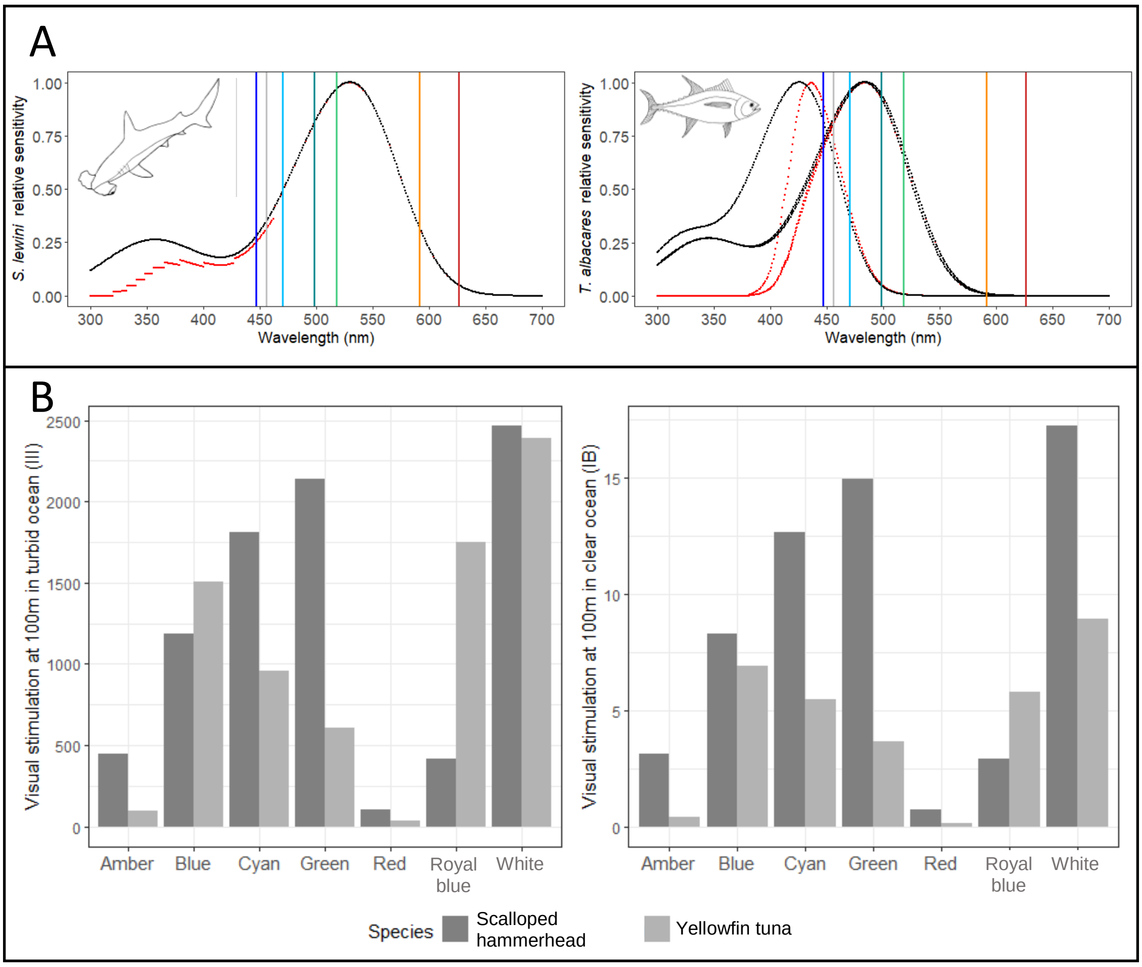


Figure 10:

A) Photoreceptor sensitivities for scalloped hammerhead (left) and yellowfin tuna (right). The black lines represent the photoreceptor sensitivities of each species, and the red curve represents the inclusion of ocular media sensitivity, which indicates a reduced sensitivity to shorter-wavelengths of light for both species, with quite a pronounced shift for tuna. Note that the tuna ocular media information was based on juvenile lens transmission (Thorpe et al., 1993). The vertical lines represent the peak wavelength (nm) of each colour mode of *Pisces*. **B)** The visual model output for each LED colour mode against two different ocean backgrounds.

Discussion

We used a vision model in the form of a quantum-catch model, to explore how commercially relevant species might view LEDs in different fishing conditions, to help assess the visibility of light as a BRD. The model predicts that target and bycatch species are differentially stimulated by light colour modes across different fishing contexts, and that values can change across depth and water type.

In terms of general trends, white light was the most visually stimulating colour mode for all target and bycatch species, which is likely due to the broader spectrum that white light covers compared to the other monochromatic LEDs. As such, white light is likely to excite a broader range of photoreceptors, but may not be the best choice for selective fishing for some gears, since it would be most visible to both target and bycatch species. By contrast, red light was the least visually stimulating for all species. As red light attenuates with depth, red becomes less of a prominent colour in deep oceans (Johnsen, 2012; Marshall, 2017). Hence, many marine species do not possess longer-wavelength photoreceptor cells (Marshall, 2017). Instead, shorter-wavelength photoreceptors are more prominent, as blue light can transmit to greater depths (Johnsen, 2012; Marshall, 2017). This reflected in the model outputs, where longer-wavelength colour modes tend to be less visually stimulating.

Visual stimulation values were also lower in shallow and clear ocean conditions, which is likely due to higher background light levels. The irradiance data used in this model are derived from Jerlov’s (1968) quantifications, which were measured when the sun was directly overhead at a fixed time point (Sticklus et al., 2018). However, the irradiance in the sea during fishing will fluctuate as cloud cover and sun position changes. Therefore, having darker ambient light conditions compared to the measurements we used are likely to only increase visual stimulation values for all colour modes, where the LEDs become more greatly contrasted to the background. Future models could look at considering real time irradiance data, to get a more accurate model output.

The model also assumes that animals are a fixed distance from the LEDs, which is based on the distance that the light was measured with the spectroradiometer (50 cm in a dark room). The LED colours were also measured in air, which does not take horizontal water attenuation into account. However, previous models have found that attenuation can occur after 3-4 m for red colours, and 15-20 m for blue (Zhou et al., 2022). In most fishing scenarios, animals are also likely to be very close to LEDs on nets, and so it was assumed that all light from the LEDs reached the eyes of species within 50 cm. However, further models could explore horizontal attenuation, especially for predicting when marine species are able to first notice an LED on fishing gear in different water conditions, which may be more applicable to passive gear types where fish aren’t contained in a moving net.

In terms of vision, developmental changes can occur from juvenile to adult fish (Carleton et al., 2020). For example, in flounders, juveniles have visual pigments with shorter-wavelength sensitivity, which is lost in the adults and then replaced with longer-wavelength sensitivity (Savelli et al., 2018). This is likely due to a movement towards deeper waters and away from shallow nursery grounds as juveniles develop into adults (Savelli et al., 2018; Siebeck and Marshall, 2007), although this is not the case for cod as previously mentioned (Valen et al., 2014). With regards to tuna, hammerhead and sole, juvenile fish vision information was used, which was based on the availability of visual adaptations in the literature. Therefore, the model output for these species may not be as accurate if fisheries are looking to effect adult bycatch species with light. This also applies to the case studies where we used adult vision data when juvenile information was lacking, or where the size of species was unknown.

For our case study examples, we only looked at one target and bycatch species respectively. However, it is often the case that fisheries target and/or want to avoid multiple species, such as in Case studies 2 and 3 (Batista et al., 2009; Catchpole and Revill, 2008; Palder et al., 2023). The model can still be applied to multiple species, but it may be harder to ascertain an optimal light colour that can select between multiple species. Therefore, we only considered the main target and bycatch species for ease of application.

From our results, hypotheses should be explored around the model output and behavioural responses. For example, research could explore whether light colour modes that are more visible to species can cause greater behavioural responses, which could be easily observed and quantified in a controlled tank setting (Sardo et al., 2020; Yochum et al., 2022). However, these behaviours may not be comparable to a fishing context, as other sensory stimuli during fishing could affect and override any responses to light that were exhibited in a laboratory such as vessel noise, turbidity and stress (De Robertis and Handegard, 2013; Heard et al., 2014; Utne-Palm, 1999).

Additionally, the behaviour of marine species can vary in passive versus active gears (Diaz Pauli et al., 2015; Wilson et al., 2011). For example, in trawls, if a bycatch species is already in the net, an escape response could be induced by adding light to an escape panel (Lomeli and Wakefield, 2019; Southworth et al., 2020). This could be applied to Case study 2 with undersized cod, but would not work for species that are too large to fit through escape panels. An alternative method could be to add light to the headrope or footrope of a trawl, which has previously been shown to reduce bycatch (Hannah et al., 2015; Lomeli et al., 2018). However, whether the bycatch species are swimming out of the nets after capture, or avoid initial capture in the trawl is unknown. Although some studies have previously deployed cameras to assess the general behaviour of species within trawl scenarios (Abangan et al., 2023; Fakıoğlu et al., 2022), direct observations with cameras can be difficult to obtain due to low light availability and harsh conditions during trawling (Rose et al., 2005). For fishing with light trials, a video camera has previously been deployed in a trawl, where footage showed Chinook salmon exiting a net via an illuminated escape panel (Lomeli and Wakefield, 2019, 2012). With camera hardware improvements, as well as the development of A.I. (Artificial Intelligence) behavioural analyses of fish in nets (Abangan et al., 2023), the deployment of cameras are likely to be more widespread in future trials. This will be valuable for assessing behavioural responses to light in fishing, and for understanding optimal light placement in trawls.

For passive gear types such as gill nets, the bycatch species would need to exhibit an avoidance response towards lights on the net, before being caught. Light would therefore need to function by increasing the visibility of the net, or acting as a deterrent itself. However, caution may be needed, as like previously mentioned, light can be an attractant to marine species (Nguyen and Winger, 2019a). In Case studies 3 and 4, where both examples have passive gear types, previous knowledge of light-mediated behaviour may be useful here in order to determine whether elasmobranchs are attracted to light. However, several studies have found that elasmobranch bycatch is reduced when static gears are illuminated, which suggests a net-avoidance response (Bielli et al., 2020; Senko et al., 2022).

If there is no prior light-mediated behaviour available for species, an alternative method may be to investigate the physiology and ecology of the target and bycatch species, where differences have previously been exploited to improve catch selectivity with BRDs (Glass, 2000; Yu et al., 2023). For example, gridded escape panels on nets have been successful in reducing flatfish bycatch whilst maintaining roundfish catch, due to the body shape of flatfish (Yu et al., 2023). Additionally, differences in swim speeds of target and bycatch species can be utilised when positioning BRDs on nets, to allow for bycatch escapement or avoidance (Breen et al., 2004; Broadhurst and Millar, 2023; He, 1993; Ryer, 2008).

By contrast, if target and bycatch species have a similar physiology and ecology, light could invoke similar reactions. For example, in Case study 3, both flatfish and skate are bottom-dwelling, sedentary species, and often bury for camouflage when threatened (Gilman, 2019; Hammerschlag et al., 2017; Spinner et al., 2016). Hence, if both species perceive light as a threat and bury in sediment, this could lead to a loss of target catch (flatfish) within a passive fishing scenario, whereas in a bottom-trawling scenario, it may lead to an increase in bycatch (skate) if the gear makes contact with the seabed.

With the use of the model, our study's main aim was to quantify the vision of both target and bycatch species when viewing different coloured LEDs underwater. From this, we propose further behavioural testing and fishing trials based on the model predictions, to optimise bycatch-reduction and target catch-maintenance with lights. In all circumstances, once vision, behaviour and fishing gears have being considered, it may still be the case that light is not a useful bycatch reducing tool for certain fisheries, and other bycatch-reduction methods should be considered.

Acknowledgements

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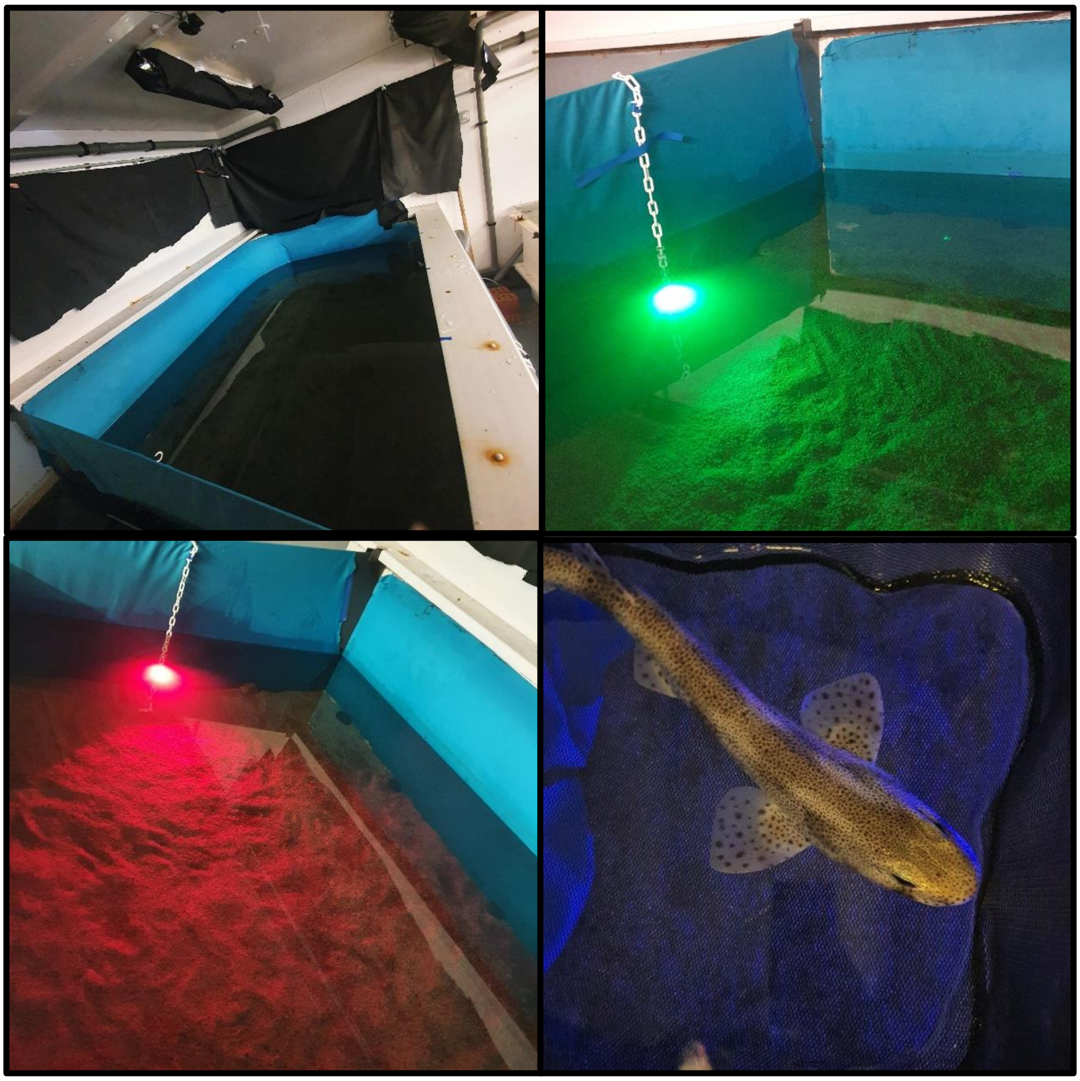
Data availability statement

Data for model components can be accessed here: https://github.com/j-somerville/Light-Vision-Model

Conflict of Interest

The work was funded by the University of Exeter and SafetyNet Technologies as part of the first author’s PhD. SafetyNet Technologies manufacture the LED product (*Pisces*) used in this research.



Chapter 3: Behavioural responses of elasmobranchs and flatfish towards artificial light and use of visual modelling for application in bycatch-reduction.

Abstract

Artificial lights are increasingly being trialled on fishing gear to deter bycatch from nets. One way to maximise their success is for lighting to be tuned such that bycatch species are more affected by it than target species. However, few studies have aimed to quantify how both target and bycatch species view and respond to light. Here, I used models of vision to predict the responses of target (plaice *Pleuronectes platessa*) and bycatch species (small-spotted catshark *Scyliorhinus canicula* and skate *Raja microocellata, R. brachyuran* and *R. montagui*) to light types, and tested these predictions through behavioural responses of fish towards LEDs within a tank setting. I found that, as predicted by vision models,

behavioural responses were linked to the likely visibility of the light emission spectra to species. Specifically, catsharks had more interactions with LEDs that should be more visually stimulating to their vision (white, blue, and green) than other lights. By contrast, skates and plaice were less responsive to light, but those that did respond were more sedentary in the presence of more visually stimulating colour modes (blue and green). The results show how potential responses of target and bycatch fish to artificial lighting could be inferred from visual models, and how differences in target and bycatch species' behaviour towards light exist, such as catsharks showing more interest in lights. This approach may help fisheries to select an optimal light colour for bycatch-reduction trials with light, though further research is needed in order to assess behaviour in a fishing context.

Introduction

Light-mediated behaviour in animals is known as phototaxis, where some species naturally orientate themselves towards or away from light sources (Jékely, 2009). The knowledge of this behaviour has subsequently been utilised in fishing to attract catch to nets, which is thought to have stemmed from fires on the beach thousands of years ago (Arimoto et al., 2010). Now, battery-powered lights are used on nets in modern day fishing (Nguyen and Winger, 2019a), where more recent work has aimed to try and repel bycatch (non-target catch) with light. Research in controlled laboratory settings have found that different species can exhibit varying degrees of attraction or aversion to light, which can also be influenced by the light colour mode (Ciriaco et al., 2003; Marchesan et al., 2005; Utne-Palm et al., 2018; Yochum et al., 2022). For example, European seabass (*Dicentrarchus labrax*) were most repelled by green and blue light after exposure to six different coloured light filters, whereas the common grey mullet (*Mugil cephalus*) showed attraction to shorter-wavelength light (Ciriaco et al., 2003; Marchesan et al., 2005). Additionally, chinook salmon have shown an aversion to light, where white light was less effective in inducing responses (Yochum et al., 2022).

Research on bycatch-reduction with light in the field has subsequently shown successes across a range of taxa and gear types (Bielli et al., 2020; Lomeli et al., 2018; Ortiz et al., 2016; Wang et al., 2007). For example, in trawl scenarios, lights have reduced the bycatch of small pelagic fish through illuminating an escape panel (Southworth et al., 2020), or the headrope of a net (Lomeli et al., 2018). In static gears, lights have reduced the bycatch of elasmobranchs (Senko et al., 2022), turtles (Bielli et al., 2020; Ortiz et al., 2016; Wang et al., 2013) and cetaceans (Bielli et al., 2020) and are thought to highlight the presence of the net. However, in some trials, light has been ineffective at reducing bycatch (Melli et al., 2018), or has led to an increase in bycatch (Geraci et al., 2021). Although these studies show that light differentially effects behaviour across species, the reasons as to why or how behaviour can change are less understood.

Responses to light among species are likely to be influenced by characteristics of vision (Baden et al., 2020; Cronin et al., 2014). In particular, spectral sensitivity is thought to be important, being a measure of how sensitive an animal's eye is to wavelengths of light (Lythgoe and Partridge, 1989). Spectral sensitivity differs among (and sometimes within) species, and can be measured via the photoreceptor cells in the eye, which absorb incoming light (Cronin et al., 2014). In vertebrates, two photoreceptor types exist: cones cells, which are responsible for light absorption in relatively bright conditions, and rod cells, which work in darker environments and encode a scene using brightness and contrast (Lythgoe and Partridge, 1989). Different types of cone cells absorb certain wavelengths of light due to the specific type of chemical structure that they contain, known as a visual pigment (Lythgoe and Partridge, 1989). As such, the main cone types are: short-wavelength (SW), medium-wavelength (MW), long-wavelength (LW) and in some cases, ultraviolet (UV) sensitive cone cells (Lythgoe and Partridge, 1989). Light intake can additionally be controlled by filtering mechanisms within the eyes known as ocular media, which can either allow or block shorter wavebands from reaching the retina (Thorpe et al., 1993).

Depending on their ecology and habitat, marine animals can have various combinations and occurrences of cone cells (Lythgoe, 1988). For example, shark species examined thus far have one cone cell type (Hart and Collin, 2015), whereas some flatfish have three (Hammond, 1968). Alternatively, some species such as skate (*Raja.* Spp), can have a completely rod-dominated retina, which may be explained by their nocturnal nature (Hart and Collin, 2015). In principle, an increased number of cone cell types can allow greater wavelength discrimination and colour vision capabilities, if appropriate comparisons between the cell types are made (Purves et al., 2001).

Although photoreceptor sensitivity, and colour vision in general, is likely to have a key role in behaviour towards light (Marshall et al., 2015) only a few studies have explicitly tested this link in bycatch-reduction with light. One such example was demonstrated with green turtles (*Chelonia mydas*) and gillnets (Wang et al., 2013). The study used the knowledge of turtles possessing UV cone cells to add UV lights to the net, and achieved a 39% reduction in turtle bycatch whilst target catch of sardines was maintained (Wang et al., 2013). As the target catch were unlikely to see UV wavelengths, it was thought that turtles were more able to avoid the net (Wang et al., 2013).

Alternative visual components to light wavelengths that have been explored in bycatch-reduction with light studies include critical flicker fusion frequency (cFFF), which is the point at which flashing light becomes continuous for an animal (Landgren et al., 2014). This threshold differs across species (Jordan et al., 2013); for example, scotopic cFFF in elasmobranchs can range from 16 to 25 Hz (McComb et al., 2010), whereas in teleost fish, the range is from 30 to 60 Hz (Horodysky et al., 2010). In a study that considered cFFF for shark deterrents, researchers found that flashing light may be aversive when used at a bait station, as less sharks approached and consumed the bait, suggesting a potential for future applications as a BRD (bycatch-reduction device) (Ryan et al., 2017).

One way to predict how animals might actually see light is through vision modelling (Hárosi, 1996). For example, a quantum-catch model will give the predicted number of light units (photons) that reach an animal's eye when considering ambient light conditions, photoreceptor sensitivity and ocular media transmission of a given animal (Cronin et al., 2014; Renoult et al., 2017). In the marine environment, quantum-catch models have been used to determine how a fish might view a visual scene at different depths, and hence whether their visual adaptations can be linked to their ecology and habitat (Singarajah and Hárosi, 1992; Hárosi, 1996; Wilkins et al., 2016). However, they have not been applied to bycatch-reduction with light thus far.

Species that are commonly caught as bycatch are elasmobranchs (sharks, rays and skates), which are globally threatened by overfishing and incidental bycatch due to their low reproductive outputs and slow growth (Dulvy et al., 2014). In the UK, commercially relevant elasmobranchs include skate, which can be obtained from targeted and mixed fisheries (Enever et al., 2009) and are mainly captured from trawls and gillnets (Silva et al., 2012). However, since 1999, various management plans have existed in order to avoid stock depletions, which have included implementing a Total Allowable Catch (TAC) and a minimum landing size for certain fisheries (Silva et al., 2012), where landing size is inferred from minimum conservation reference size (MCRS; 45 cm wing span; Angling Trust, 2022)

Another UK elasmobranch species that is highly susceptible to being caught in active and static fishing gear is the small-spotted catshark (*Scyliorhinus canicula*) (Papadopoulo et al., 2023). Although they are labelled ‘Least Concern’ on the IUCN (International Union for Conservation of Nature) Red List (Ellis et al., 2005), a recent study conducted in Welsh waters found that catsharks were the dominant bycaught species in baited crab pots (Moore et al., 2023). Catsharks were also the dominant bycatch species in scallop dredge fisheries around the Isle of Man (Craven et al., 2013). Within fisheries that target sharks in Europe, catsharks have also been categorised as overexploited (Papadopoulo et al., 2023).

In terms of target catch, flatfish such as plaice (*Pleuronectes platessa*) are a popular fish amongst UK consumers (Kemp et al., 2023), where in 2010, the landed first-sale of plaice from UK ports had a value of £4.6million (Bertelli and Unsworth, 2014). Plaice are mainly caught by demersal trawls (Rogers et al., 1998), where their stocks are also managed by TACs and an MCRS (27 cm; Angling Trust, 2022) like skate (Lehuta and Vermard, 2023).

To my knowledge, behavioural responses towards light have not yet been tested in these species. In terms of vision, skate and catsharks have rod-dominated retina (Gačić et al., 2006; Govardovskiĭ and Lychakov, 1977) which means they rely on brightness and contrast to discriminate a visual scene (Lythgoe and Partridge, 1989), whereby plaice have enhanced colour vision, with three cone cell types plus rod cells (Hammond, 1968). Both skate and plaice are burying species, where this behaviour enables them to catch passing prey, or to hide from predators (Spinner et al., 2016; Youn et al., 2019). By contrast, catsharks are more active, and are an opportunistic scavenger (Papadopoulo et al., 2023).

As quantum-catch models are yet to be applied to fishing with light, even though they should be a valuable tool to predict target and bycatch species responses to light, and work on turtles indicates that responses should link to visual ecology, I aimed to test whether vision is linked to behaviour towards light in UK target and bycatch species. Specifically, I tested: 1) whether the behaviour of target and bycatch species towards different light colours could be explained by a quantum-catch model, and 2) whether behaviour differed between target and bycatch species across different light modalities. I chose to test this in a controlled tank setting to see if a link between vision and behaviour exists, for future consideration in bycatch-reduction with light trials. The target representative was plaice, and bycatch species were the small-spotted catshark and skate (small-eyed, *R. microocellata*; blonde, *R. brachyuran*; spotted, *R. montagui*).

My predictions were that the most visible light colour – inferred from the model output – would cause the greatest behavioural responses in fish, through increased activity and active periods in the presence of more visually stimulating LEDs. I also tested the effect of flashing light, where like a previous study (Ryan et al., 2017), I predicted more aversive responses in species compared to continuous light. I chose a flash rate of 4 Hz, as this was well within cFFF range in both flatfish and elasmobranch species that have previously been evaluated (flounder *Paralichthys dentatus* 42 Hz, Horodysky *et al.*, 2010; spurdog *Squalus acanthias* 19 Hz, Kalinoski *et al.*, 2014)

Materials and methods

Fish were obtained from short hauls via a 15 m otter trawl by the research vessel *MBA Sepia*, at approximate depths of 20 m in Plymouth Sound (UK) during May 2021. Fish used in experiments were 27 skate, which were below MCRS apart from 3 individuals, which were 2 spotted (47.7 and 48.9 cm) and 1 blonde (53 cm) skate. The other 22 skates were 12 blonde (size 15.9 –28.6 cm), 10 spotted (13.5 – 38.4 cm) and 2 small-eyed (41.7 – 42.7 cm). For catsharks, 38 were captured and used (40.3 – 73.1 cm), as well as 14 plaice above MCRS (28.5 – 49.9 cm). All animals were in healthy conditions when captured. Animals were housed in seawater tanks at the Marine Biological Association (MBA) and were acclimatised for two to six weeks to a daily 12 hour light and dark cycle. Feeding regime consisted of twice daily frozen crustaceans or mackerel. Animals were released by *MBA Sepia* after experiments were completed in August 2021. All animals were captured, housed and released under the establishment license at the MBA. Experiments were deemed observational and therefore did not fall under regulated procedures in the Animals (Scientific Procedures) Act 1986, and were approved by external and internal ethical reviews (eCORN003524).

Quantum-catch model

To assess whether the quantum-catch model could predict behaviour towards different light colours, I first quantified the potential visibility of the stimuli using the following model components (Figure 11), which were the photoreceptor sensitivity of plaice (Hammond, 1968), skate (Govardovskiĭ and Lychakov, 1977), and catsharks (Gačić et al., 2006) and their ocular media transmittance (Thorpe et al., 1993); the background reflectance of a blue fabric, which was used as a backdrop in the tank to broadly simulate blue coastal conditions, and the spectrum of light emitted from the six LED colour modes of SafetyNet Technologies' LED device *Pisces*. This can be represented as the following,

$$Qc = \int_{300}^{700} I(\lambda) Ac(\lambda)\, d(\lambda)$$

where Qc is the summed photoreceptor quantum catch for the background, or each LED colour mode. Qc is calculated from the normalised product of photoreceptor sensitivity type *c* of plaice, catsharks, or skate $Ac(\lambda)$ (derived from the product of ocular media transmission and photoreceptor sensitivity at every 1 nm interval) and the normalised background reflectance, or the radiance of each LED colour mode $I(\lambda)$, integrated over 1 nm intervals across the visible light spectrum $d(\lambda)$(300-700 nm).

To understand how visible each LED colour mode was to fish in relation to the tank background (background contrast), visual stimulation was calculated using the following equation (Crothers and Cummings, 2013),

$$\text{Visual stimulation} = \frac{\left(\frac{\sum Qc(light\ colour)}{\sum Qc(tank\ background)}\right)}{n(c)}$$

where the output is the predicted total number of photons reaching the eye of the fish, combined across all receptor types, when considering the ratio of the Qc of an LED against the Qc of the tank background, and divided by the number of photoreceptor types $n(c)$ that a fish possesses. Therefore, the model output is the level of visual stimulation towards a light colour mode in tank conditions. For full quantum-catch modelling methodology, see Endler and Miekle (2005); Stevens et al., (2009); Renoult et al., (2017) and Figure 11.

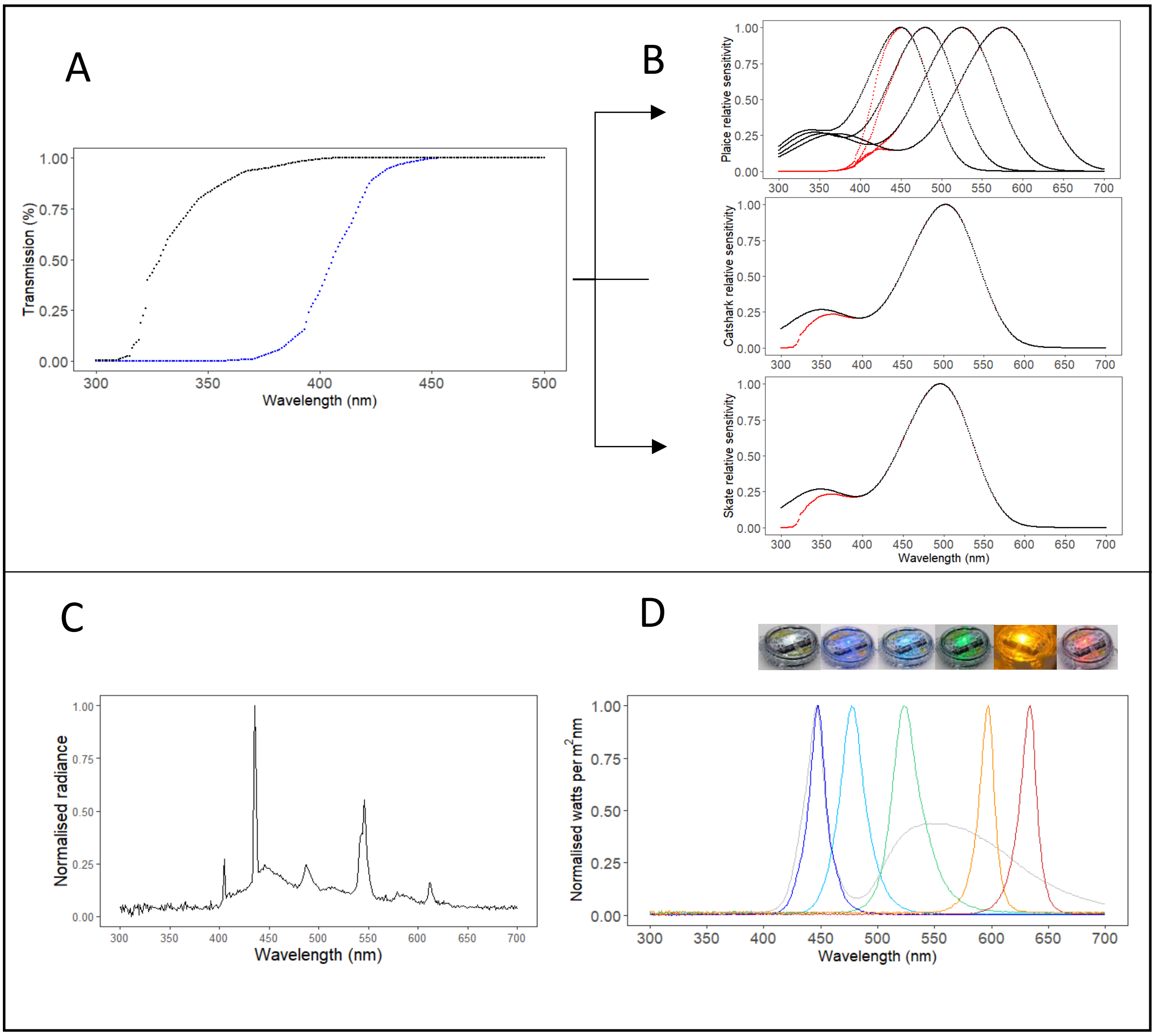


Figure 11:

Components of the quantum-catch model. A) Ocular media transmission of plaice, skate and catsharks, extracted from Thorpe et al., (1993) and re-plotted. Catsharks and skate have a 'type A' ocular media lens transmission, represented by the black data points. Catsharks have a λ50 value of between 316-340 nm, where a median value of 328 nm was used (Thorpe et al., 1993). Skate also had a λ50 value of 328 nm, which was based on the small-eyed skate (*Raja microocellata*) lens transmission, with a λ50 value of 328 nm (Thorpe et al., 1993). Plaice were classified with 'type D' transmission, with a λ50 value of 399-408 nm, where a median value of 404 nm was used (Thorpe et al., 1993), which is represented by the blue data points. **B)** Photoreceptor sensitivity graphs. The top graph of **B)** represents plaice (*Pleuronectes platessa*) cone and rod cell sensitivity (median values: SW λmax 450 nm; MW λmax 480 nm; LW λmax 575 nm; rod λmax 525 nm), which was obtained from Hammond, (1968). The middle graph represents catshark (*Scyliorhinus canicula*) rod cell sensitivity, λmax 502.8 nm, which was obtained from Gačić et al., (2007). The bottom graph represents skate, where thornback ray (*Raja clavata*) was used to represent all skate species used in this experiment due to availability in the literature, where the λmax was 496 nm from Govardovskiĭ and Lychakov, (1977). The graphs were replotted using the Govardovskii et al., (2000) visual pigment template to obtain 1 nm intervals, which is represented by the black data points. The red points are the result of multiplying the raw sensitivity curve by the ocular media sensitivity of each species at 1 nm intervals from 300-700 nm, which represents $Ac(\lambda)$ of the quantum-catch equation. The ocular media of all species reduces the sensitivity of photoreceptors to shorter wavelengths of light. This is likely to be a protective function of the lens in reducing absorption of UV light (Siebeck and Marshall, 2001). **C)** The radiance of the blue polyester tank background, measured in above-water ambient conditions similar to tank conditions, which was measured from 50 cm distance. **D)** The radiances of the normalised energy output of each LED colour mode, measured from a distance of 50 cm. The peak wavelength were as follows: White, 456 nm; Royal blue, 447 nm; Blue, 471 nm; Green, 518 nm; Amber, 592 nm; Red, 627 nm. Graph A data points were extracted using Graphreader (Larson, 2022) and were redrawn in R package ggplot2 (R Core Team, 2021). The spectral emission of the lights and background were measured using the JETI specbos 1211-2 in above-water dark conditions. See https://github.com/j-somerville/Visual-model-behaviour-lights for code and model components.

Behavioural trials

To test the link between the quantum-catch model and behaviour, individual fish were placed in an experimental 2.5 m by 1.7 m tank, which had a blue polyester background and a sand bottom, to simulate natural ocean conditions. Fish had two minutes of acclimatisation time before trials started, as this was the time taken for individuals to resume a normal swimming speed from observations. Individuals were subjected to five minutes of no light and light respectively, for each light colour mode (n=6). Ambient light conditions was one dimmed light above the tank, so behaviour could still be observed in lights off conditions. Two LEDs were placed at opposite ends of the tank for each trial and were defined as either the “control” or “experimental” light. The control light was switched off for the entire 10 minute trial, whereas the experimental light was turned on during the five minutes of light exposure. Therefore, the tank was split into two sections – the “experimental” and “control” side (Appendix Figure 1). The side in which the light was switched on was alternated for each colour mode, to avoid a tank-side bias. Light colour order was randomised for each trial, and the total trial time for each fish was one hour. The brightness of each light colour mode was centred between 48-68 mw m^2 (Appendix Table 1) for all trials. Each trial was repeated with either flashing or continuous light, where this order was also randomised, and took place with two days in-between to reduce fish becoming habituated to the light treatments.

Fish trials were recorded via two webcams (NULAXY 1080p C900) above the tank and analysed using the video programme CowLog (Pastell, 2016), where consistent behaviours were measured. As it was unknown whether fish would be attracted or repelled by light, two assumptions were made. If repelled, I would expect fish to be more active in the control side of tank when the light was turned on. Conversely, if attracted to light, I would expect more time spent in the experimental part of the tank, or more activity around the experimental light.

From video footage, differences in fish behaviour necessitated different response measures. I measured “light interaction” behaviour for catsharks, which was defined as “nudging” the control or experimental LED with their snout. For plaice and skate, I measured “stationary time”, which was the total time spent stationary in either control or experimental sides of the tank, which was recorded after an individual was immobile for at least 15 seconds, and stopped when the fish moved again.

Statistical analysis

To determine whether light colours affected behaviour, general linear mixed models (GLMMs) were used in the statistical programme R (R Core Team, 2021). For catsharks, as light interactions were right-skewed and count data, I used a Poisson distribution. For plaice and skates, stationary totals were continuous but left-skewed. Two models were each used for skates and plaice; the first model compared stationary behaviour in trials where fish were active for at least part of a “lights on” or “lights off” trial, and did not include individuals that were stationary or active for an entire trial (10 minutes), in order to assess whether there was an effect of turning lights on across colour modes. For the second analysis, I re-ran the GLMMs but additionally included individuals that were stationary or active for entire trials (in both lights on and lights off conditions), to further assess whether fish were more likely to be active or stationary for certain colours during each 1 hour trial. As such, the second model fits were poorer compared to the first, due to an increase in stationary totals and a greater left skew. Individuals were removed from all analyses if they did not move for the entire 2 hour trials, which were individuals that stayed stationary across all 6 colour modes and each light type (continuous and flashing).

For all models, each individual skate, catshark and plaice were treated as a random effect. Light side was also a random effect (the side in which light was turned on in the tank). For skates, each species was a random effect due to a small sample size of small-eyed skate (n=2) compared to spotted and blonde skates. Fixed effects for all models included light colour (n=6) and light mode (lights off intercept), and light type (continuous and flashing). Light type order and light order were used to determine whether fish became habituated to light. Control and experimental tank sides were included to determine whether fish were attracted or repelled by light. For skates, I included wing length (cm) to assess whether there were differences in behaviour across different sized skates, as only 3 skates were above MCRS. The model codes were as follows:

1) glmer(behaviour count ~ Light colour + light type+ light order+ light type order + (1|light side) + control_experimental + (1|catshark), family=”poisson”),
2) glmer(stationary time) ~ Light colour + light type+ light order+ light type order + (1|light side) + control_experimental + (1|plaice).
3) glmer(stationary time) ~ Light colour + light type+ light order+ light type order + (1|light side) + control_experimental + wing_length + (1|species)+ (1|skates).

For the second analysis with skates, an optimiser (REML = FALSE, control = lmerControl(optimizer ="Nelder_Mead") was additionally used to enable convergence.

Results

Quantum-catch output

Based on species' vision, the ambient light environment and the LED spectra, the vision model output differed for each LED colour (Figure 12).

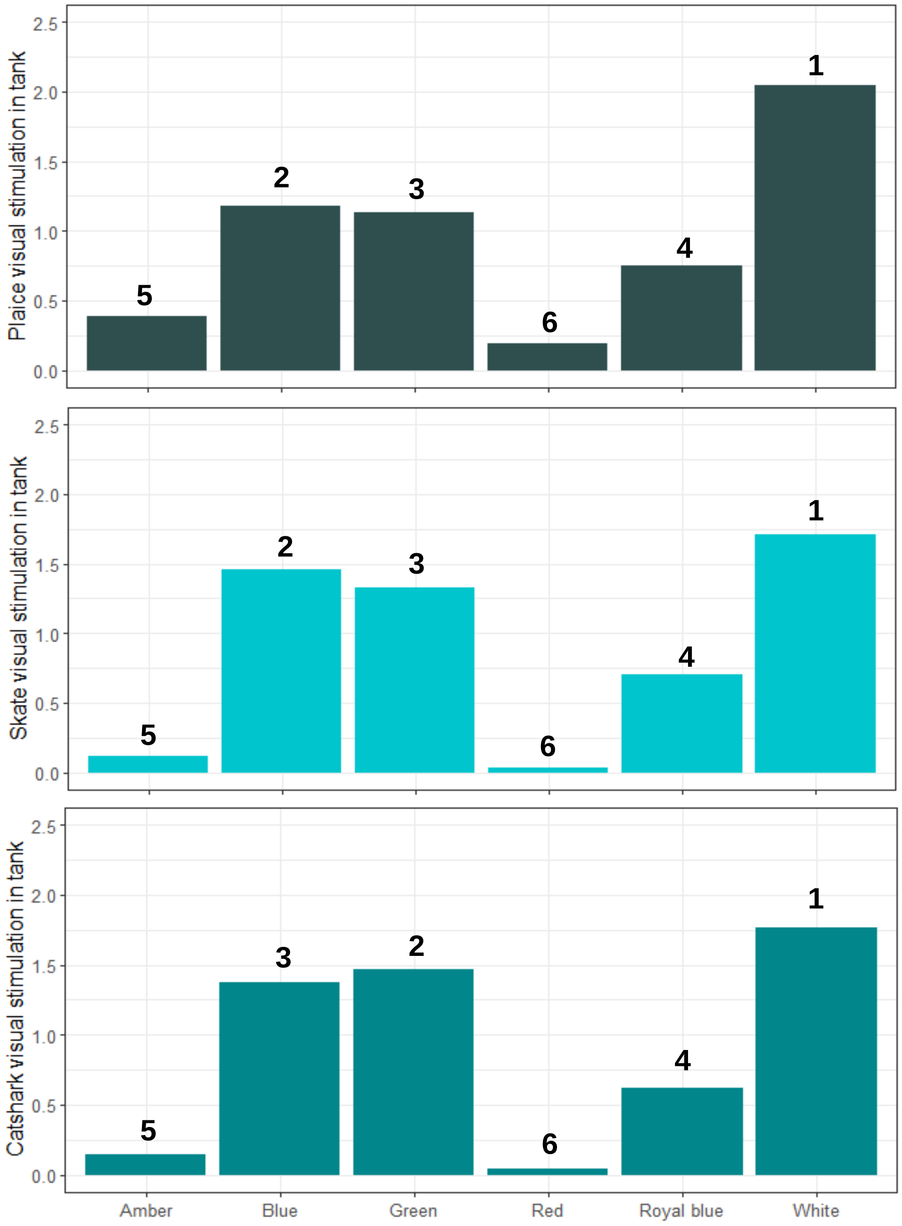


Figure 12:

Visual model output. The numbers 1-6 represent the visual stimulation order from highest to lowest. The y axis represents the visual stimulation values across all photoreceptors for each light colour mode against the tank background, from top to bottom, for plaice, skates and catsharks. All fish are more visually stimulated by white light in the tank conditions. This is likely because white light covers a broader range of the visible light spectrum, meaning photoreceptor cells can absorb more light. Plaice are more stimulated by white and red light compared to skate and catsharks, which is probably due to the increased number of photoreceptor types that they possess, giving greater capacity to absorb a broader range of light. All species are least visually stimulated by red light. Skate and plaice are similar in terms of visual stimulation rankings, whereas catsharks differ by their blue and green light rankings.

Behaviour

Catsharks

A total of 793 light interaction behaviours were recorded across 252 light trials, where individual catsharks were subjected to 6 continuous light trials and 6 flashing light trials (456 total trials). Out of 38 catsharks, 2 catsharks did not showcase light interaction behaviour.

When light conditions were on, there was a significant increase in the number of light interactions in the experimental side of the tank for all colour modes apart from red, where no significant difference was found between lights off and on conditions (Table 1, Figure 13). Light type did not significantly affect behaviour. Fewer catsharks interacted with red light when the experimental light was turned on, where they exhibited the lowest total and average interaction counts, followed by amber (Figure 13). The random effects show that there was individual variance (see Appendix Figure 2) in response to light, and the side in which the light was on also accounted for a small amount of variance.

Table 1:

GLMM results for light interaction behaviour in catsharks. Significant effects are in bold.

Explanatory variable	**Fixed effects**	**Estimate + STd. error**	**z value**	**P value**
Light interaction (intercept lights off)	Intercept	0.033 ± 0.137	0.244	0.8071
	Amber	0.326 ± 0.142	2.299	**0.0215 ***
	Blue	0.519 ± 0.123	4.230	**2.34e-05 *****
	Green	0.649 ± 0.122	5.300	**1.16e-07 *****
	Red	0.121 ± 0.166	0.728	0.4665
	Royal blue	0.534 ± 0.117	4.546	**5.46e-06 *****
	White	0.594 ± 0.120	4.937	**7.95e-07 *****
Light type (intercept continuous)	Flashing	-0.020 ± 0.072	-1.372	0.1701
Light order (intercept 1)	2	-0.020 ± 0.116	-0.172	0.8636
	3	0.007 ± 0.120	0.059	0.9527
	4	0.056 ± 0.123	0.455	0.6488
	5	0.040 ± 0.130	0.305	0.7602
	6	-0.182 ± 0.144	-1.269	0.2046
Light type order (intercept 1)	2	-0.003 ± 0.073	-0.038	0.9698
Tank side (intercept experimental)	**Control_experimental**	0.410 ± 0.088	4.644	**3.42e-06 *****

Random effect	SD	Variance
Catshark (36)	0.185	0.034
Light side (2)	1.09e-04	1.19e-08

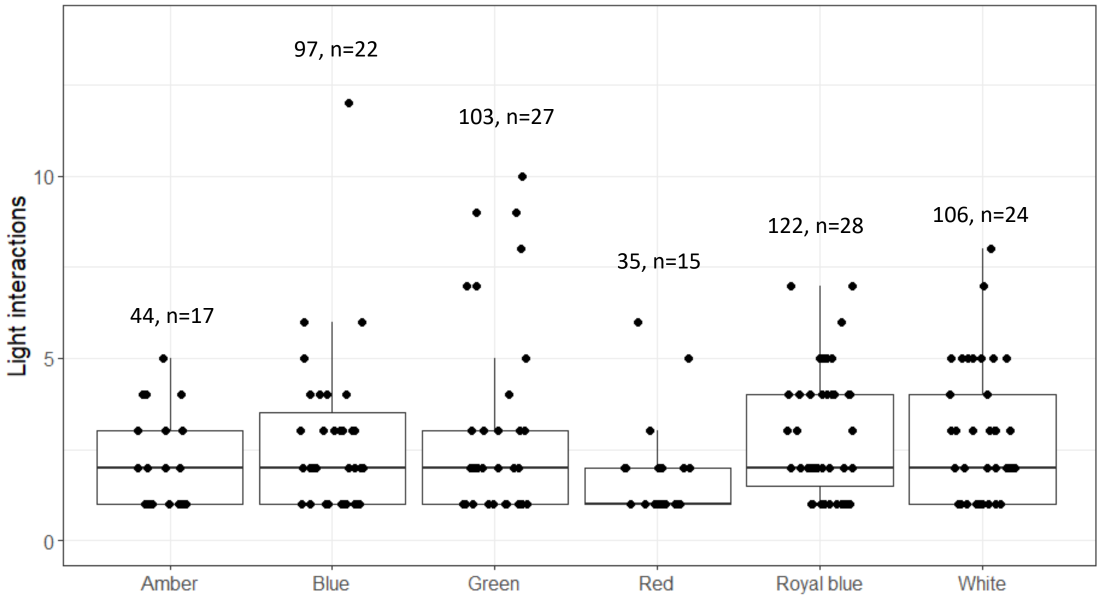


Figure 13:

Light interaction counts for catsharks. Each data point represents an individual catshark and the corresponding number of light interactions with the experimental light when it was turned on. Mean light interactions ± SD were as follows: Amber, 2.20 ± 1.28; blue, 2.77 ± 2.16; green, 2.94 ± 2.71; red, 1.85 ± 1.39; royal blue 2.84 ± 1.70, white, 2.86 ± 1.84. Total light interactions followed by the number of catsharks that interacted with the LED colour are shown above each plot.

Skates

Individual skate were tested in 6 continuous and 6 flashing light trials (324 total trials). The first analysis compared stationary behaviour in trials where skates were active for at least part of a “lights on” or “lights off” trial. This included 110 trials, where 244 stationary totals (s) were recorded in lights on and off conditions, from 22 out of 27 skate (2 small-eyed, 13 blonde, 7 spotted) in the control (n=120) or experimental (n=104) parts of the tank, in flashing and continuous light conditions. Skate that were active for a full 5 minutes (n=10) in either lights off or on conditions had stationary totals of 0 seconds (s) (n=20), and were labelled as being in “both” parts of the tank, as they swam in both experimental and control sides. For 60 trials, 5 spotted skates did not move for each of their 6 trials for both flashing and continuous trials (2 hr light exposure) and so were removed from all analyses.

For this first analysis, stationary totals were longer when lights were turned on for colour modes white (n=13 skates), royal blue (n=13 skates), green (n=12 skates) and blue (n=15 skates), compared to lights off conditions (Table 2; Figure 14), where they spent more time active. There was no preference for the control or experimental side of the tank, but significantly less active skates swimming in both sides of the tank, and no effect of flashing light. There was no trend in behaviour across skates of different wing lengths. After the fifth light colour mode exposure, time spent stationary was significantly longer for skate. The random effects show that there was high variation between species for time spent stationary (Table 2; Figure 14).

For the second analysis, which included additional skates that were active (9 skates across 37 trials) or stationary (20 skate across 117 trials) for the entire 10 minutes in lights on and off conditions for certain colour trials, 552 stationary totals were analysed across 264 trials. The effect of increased stationary behaviour in the presence of white light was lost, but remained the same for green, blue and royal blue lights, but with smaller estimates and p values (Table 3). Time spent stationary also increased after the 3rd, 4th, 5th, and 6th light exposure. After the second set of light trials (with either flashing or continuous light), there was a decrease in stationary behaviour, which may be a stress response from increased exposure to nets (Table 3). The random effects show that variation in total time spent stationary is explained by individual differences between skates (Table 3). See Appendix Figure 3 for individual variation.

Table 2:

First analysis for skate stationary behaviour. This GLMM analysis only includes skates that were active for at least part of a 10 minute trial, to compare the effect of lights off and on across different light modes. Significant effects are in bold.

Explanatory variable	**Fixed effects**	**Estimate + STd. error**	**df**	**t value**	**P value**
Light interaction (intercept lights off)	Intercept	102.4 ± 30.83	15.51	3.321	0.00448**
	Amber	26.17 ± 20.48	225.0	1.278	0.20251
	Blue	70.71 ± 21.44	225.4	3.299	**0.00113***
	Green	78.13 ± 23.92	225.9	3.266	**0.00126***
	Red	20.77 ± 22.47	225.2	0.925	0.35618
	Royal blue	116.9 ± 23.68	225.3	4.936	**1.55e-06*****
	White	58.49 ± 21.56	224.5	2.713	**0.00719***
Light type (intercept continuous)	Flashing	19.95 ± 12.22	227.0	1.633	0.10381
Size (cm)	Wing length	0.225 ± 0.668	49.22	0.337	0.73785
Tank side (intercept control)	Experimental	-12.75 ± 12.43	226.2	-1.026	0.30607
	Both	-192.0 ± 23.25	225.1	-8.257	**1.27e-14*****
Light order (intercept 1)	2	-12.84 ± 17.47	226.3	-0.735	0.46315
	3	-8.057 ± 17.96	225.7	-0.449	0.65407
	4	28.96 ± 21.77	226.5	1.330	0.18474
	5	57.57 ± 19.75	225.1	2.915	**0.00391***
	6	31.55 ± 22.95	225.5	1.375	0.17059
Light type order (intercept 1)	2	7.268 ± 12.48	226.8	0.582	0.56089

Random effect	SD	Variance
Skate (22)	0	0
Species (3)	18.96	395.5
Light side (2)	0	0

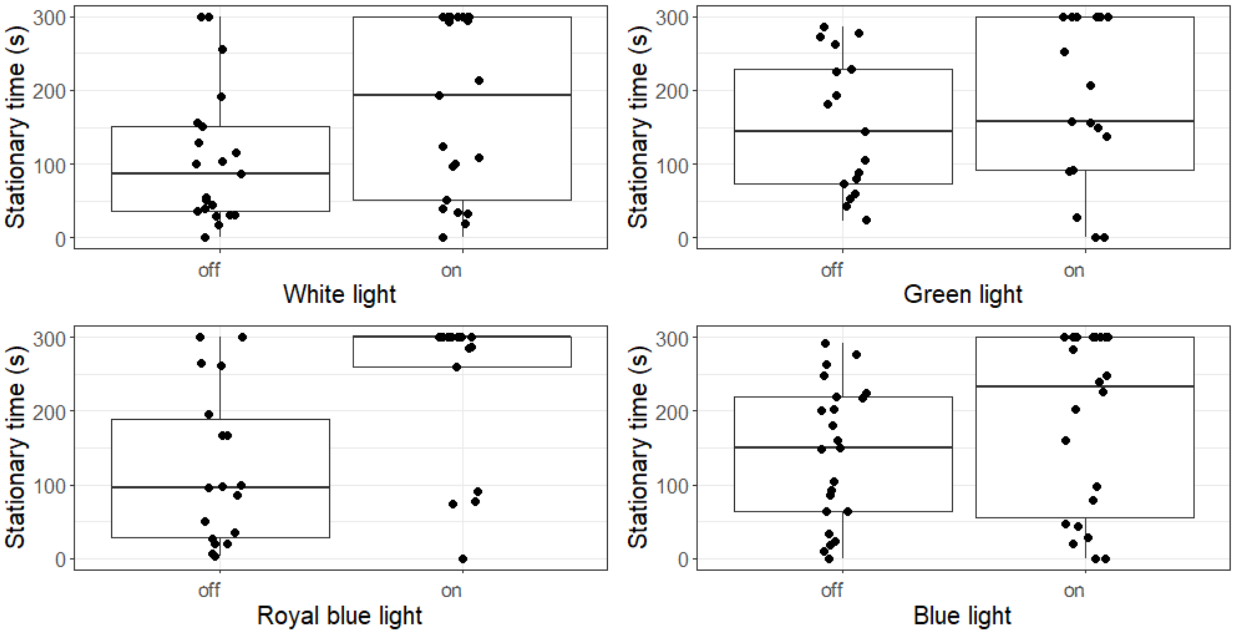


Figure 14:

Total time spent stationary in lights on and off conditions for skate. Each data point represents the time spent stationary for an individual skate in either experimental or control sides of the tank, in flashing or continuous light trials. The mean total time spent stationary ± SD (s) in lights off and conditions were as follows: white light: off, 105.83 ± 91.057 on, 176.11 ± 119.80, green light: off 152.71 ± 93.057, on 180.54 ± 111.80, royal blue light off 122.05 ± 104.41, on 239.816 ± 104.27, and blue light off 142.63 ± 93.279 on 185.29 ± 120.10.

Table 3:

Second analysis for skate stationary behaviour. This GLMM analysis additionally includes skates that were stationary or active for entire 10 minute trial periods, for particular colour modes, as well as skates that were stationary and/or active for only part of a 10 minute trial. Significant effects are in bold.

Explanatory variable	**Fixed effects**	**Estimate + STd. error**	**df**	**t value**	**P value**
Light interaction (intercept lights off)	Intercept	187.3 ± 23.00	39.59	8.146	5.42e-10
	Amber	6.952 ± 12.53	530.5	0.555	0.5792
	Blue	32.45 ± 12.57	528.9	2.582	**0.0101***
	Green	32.00 ± 12.66	531.2	2.528	**0.0117***
	Red	18.03 ± 12.48	529.6	1.445	0.1490
	Royal blue	51.73 ± 12.54	529.6	4.126	**4.29e-05*****
	White	16.87 ± 12.48	530.0	1.352	0.1769
Light type (intercept continuous)	Flashing	2.815 ± 6.741	530.1	-0.783	0.6764
Size (cm)	Wing length	-0.477 ± 0.609	21.87	-1.026	0.4422
Tank side (intercept control)	Experimental	2.236 ± 7.357	531.6	0.304	0.7613
	Both	-207.5 ± 11.88	410.3	-17.47	**< 2e-16*****
Light order (intercept 1)	2	14.86 ± 11.41	535.6	1.302	0.1935
	3	35.01 ± 11.86	537.4	2.952	**0.0033****
	4	80.33 ± 11.68	534.9	6.879	**1.69e-11*****
	5	80.32 ± 11.80	536.1	6.805	**2.70e-11*****
	6	84.99 ± 11.73	535.3	7.247	**1.49e-12*****
Light type order (intercept 1)	**2**	-14.58 ± 6.797	532.9	-2.145	**0.00324***

Random effect	SD	Variance
Skate (22)	25.87	669.4
Species (3)	0	0
Light side (2)	0	0

Plaice

A total of 14 plaice were individually exposed to 6 continuous and 6 flashing light trials (168 total trials). The first analysis compared stationary behaviour in trials where plaice were active for at least part of a “lights on” or “lights off” trial. This included 73 stationary totals across 30 different light trials, which were recorded from 5 plaice in experimental (n=35) and control (n=33) sides of the tank, across lights off and on conditions and in flashing and continuous light. Plaice that were active for a full 5 minutes (n=2) in either lights off or on conditions had stationary totals of 0 s (n=5), and were labelled as being in “both” parts of the tank as they swam in both experimental and control sides. Trials where plaice did not move for the entire time (n=6 light colour modes) for both continuous and flashing experiments (2 hr) were removed from analysis, which included 9 out of the 14 plaice (108 trials out of 168 total trials), meaning that for the majority of trials, plaice showed no response to a change in light conditions.

In the first analysis, stationary totals were shorter when lights were turned on for the red colour mode (n= 3 plaice), compared to off conditions. By contrast, time spent stationary was significantly longer in lights on conditions for the royal blue colour mode (n= 3 plaice). There was no difference in control or experimental parts of the tank, but significantly less active plaice swimming in both sides of the tank, and no effect of flashing light. Plaice were less stationary after exposure to the third light colour (Table 3; Figure 15). The random effects show the side in which the light was turned on accounted for variation in plaice stationary behaviour.

For the second analysis, which included additional plaice that were active (2 plaice across 2 trials) and stationary (4 plaice across 28 trials) for the entire 10 minutes in lights on and off conditions for certain colour trials, 133 stationary totals were analysed across 60 trials. The effect of increased stationary behaviour in the presence of royal blue light was lost, but increased activeness in the presence of red light remained the same, with a lower estimate and p value. General stationary behaviour also increased after the 4th and 5th light exposure. After the second set of light trials (with either flashing or continuous light), there was also an increase in stationary behaviour (Table 5). See Appendix Figure 4 for individual variation.

Table 4:

First analysis for stationary time totals for plaice. This GLMM analysis only includes plaice that were active for at least part of a 10 minute trial, to compare the effect of lights off and on across different light modes. Significant effects are in bold.

Explanatory variable	**Fixed effects**	**Estimate + STd. error**	**df**	**t value**	**P value**
Light interaction (intercept lights off)	Intercept	140.4 ± 36.52	2.422	3.846	0.04492
	Amber	3.136 ± 41.65	56.00	0.075	0.94024
	Blue	-60.51 ± 31.42	56.42	-1.926	0.05915
	Green	-19.02 ± 32.47	56.38	-0.586	0.56036
	Red	-86.89 ± 29.08	56.55	-2.988	**0.00415****
	Royal blue	105.5 ± 44.59	56.04	2.366	**0.02144***
	White	-75.42 ± 57.45	56.35	-1.313	0.19456
Light type (intercept continuous)	Flashing	-8.520 ± 18.83	56.12	-0.452	0.65273
Light order (intercept 1)	2	-58.64 ± 29.36	56.94	-1.997	0.05061
	3	-101.5 ± 36.41	56.99	-2.787	**0.00722****
	4	31.84 ± 33.68	55.59	0.945	0.34852
	5	-14.89 ± 39.97	56.57	-0.372	0.71092
	6	13.47 ± 30.32	56.37	0.444	0.65862
Light type order	2	32.97 ± 21.33	56.03	1.545	0.12788
Light side (intercept control)	Experimental	7.649 ± 19.11	56.73	0.400	0.69079
	Both	-87.41 ± 38.64	56.43	-2.262	**0.02755***
Random effect	SD	Variance			
Plaice (5)	0	0			
Light side	36.79	1353			

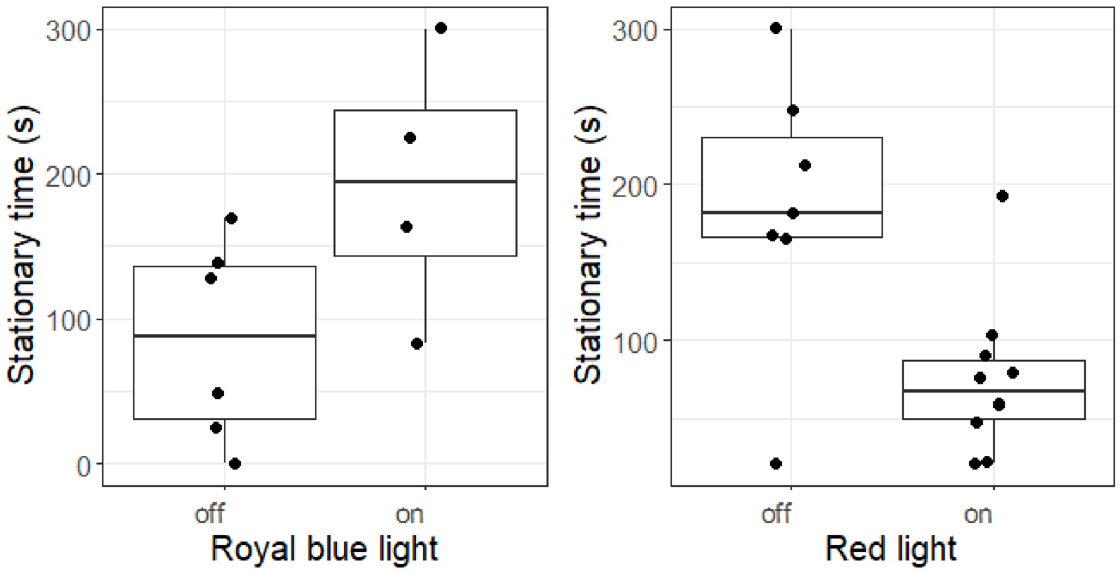


Figure 15:

Total time spent stationary in lights on and off conditions for plaice. Each data point represents the time spent stationary for an individual plaice in either experimental or control sides of the tank, in flashing or continuous light trials. The mean total time spent stationary ± SD (s) for lights off and on were: royal blue, off 84.794 ± 69.100, on 192.659 ± 92.103 and red, off 185.03 ± 87.022, on 74.868 ± 49.242.

Table 5:

Second analysis for stationary time totals for plaice. This GLMM analysis additionally includes plaice that were stationary or active for entire 10 minute trial periods, for particular colour modes, as well as plaice that were stationary and/or active for only part of a 10 minute trial. Significant effects are in bold.

Explanatory variable	Fixed effects	Estimate + STd. error	df	t value	P value
Light interaction (intercept lights off)	Intercept	151.7 ± 32.34	13.04	4.692	0.000418
	Amber	21.23 ± 27.97	113.1	0.759	0.449454
	Blue	-41.03 ± 27.77	113.0	-1.478	0.142245
	Green	-15.96 ± 27.59	113.1	-0.578	0.564110
	Red	-65.10 ± 26.08	113.1	-2.496	**0.013991***
	Royal blue	22.40 ± 29.07	113.0	0.771	0.442452
	White	13.55 ± 30.42	113.1	0.445	0.656905
Light type (intercept continuous)	Flashing	-9.104 ± 15.09	113.1	-0.604	0.547366
Light order (intercept 1)	2	-43.41 ± 26.39	113.0	-1.645	0.102744
	3	44.96 ± 26.52	113.0	1.696	0.092729
	4	70.05 ± 25.75	113.2	2.721	**0.007545****
	5	82.59 ± 26.38	113.3	3.131	**0.002214****
	6	48.11 ± 25.72	113.4	1.871	0.063926
Light type order	**2**	58.69 ± 15.59	113.1	3.764	**0.000267*****
Light side (intercept control)	Experimental	-5.253 ± 15.45	113.4	-0.340	0.734467
	Both	-136.3 ± 33.40	114.6	-4.081	**8.32e-05*****
Random effect	SD	Variance			
Plaice (5)	50.84	2585			
Light side	0	0			

Discussion

The aim of this study was to 1) determine if a visual model (Figure 12) could be used to predict behavioural responses of fish to light, and 2) assess whether behaviour differed in target and bycatch species across different light wavelengths. These aims were chosen to assess whether an optimal colour could be chosen for future bycatch-reduction trials with light. I found evidence to support the first aim, where reactions of each species differed between higher and lower visual model outputs. For aim two, I found some differences in behaviour between target and bycatch species, where catsharks (bycatch) showed a possible “attraction” towards light colours with higher visual stimulation values, and skate (bycatch) and plaice (target) were less responsive to light in general. However, the skates and plaice that were active for at least part of a 10 minute trial were more sedentary in the presence of more visually stimulating colour modes.

For all species, I predicted that white light would cause the greatest behavioural responses, as white had the highest visual stimulation value from the model. For catsharks, average interaction counts with the experimental LED were highest towards white, royal blue, blue and green light (Figure 13). Royal blue light had the greatest total interaction count and a higher number of catsharks showcasing light interaction behaviour, whereas the highest average interaction counts were with green light, although green light had the highest variance (Figure 13). The small behavioural differences between these colour modes could be because the rod cells of the catsharks were similarly stimulated by white, blue, and green colour modes, despite the visual model output. Known as a visual stimulation threshold, this can exist in humans and other vertebrates, where once a light - capture threshold is met, rod cells stop contributing to vision (Kelber, 2018). Red and amber potentially did not reach this threshold, which is reflected through fewer light interactions, and fewer catsharks responding.

The type of behaviour that catsharks exhibited towards light was nudging the experimental LED when it was turned on. Research has found that sharks can nudge objects as an investigatory type of behaviour (McNeil et al., 2016; Sperone et al., 2012) and so the light interactions may not be an attraction to light as such. The behaviour could be related to their electrosensory system, where sharks can have the ability to detect bioelectric potential from surroundings, using electroreceptors in their skin (Kalmijn, 1971). One such behavioural response to electrical fields or currents can be orientation towards the source (Kalmijn, 1971). As LEDs can radiate electric fields (Bozyigit and Wood, 2013), it may be that the catsharks’ were behaviourally stimulated by this. However, the result cannot simply be due to an electrosensory response, since I found differences in the responses of sharks to lights of different spectral emissions.

For skate and plaice, results did not follow predictions as closely, as the majority were not active during trials. As such, two analyses were conducted for both species; one with individuals that were active for at least part of a 10 minute trial, to assess whether light invoked a change in behaviour, and a second analysis that included inactive fish for entire colour trials, to assess the overall effect of light. For individuals that were active for part of a trial, I observed increased stationary behaviour in the presence of more visually stimulating light colours, compared to no-light conditions. This may be explained by the nocturnal ecology of both skates and plaice, where they are more active in darkness or dim light (Hammerschlag et al., 2017; Hunter et al., 2004). In the wild, skate and plaice will often remain sedentary to hide from predators or to capture prey, where they can camouflage and bury in substrate (Spinner et al., 2016; Youn et al., 2019). It could be that plaice and skates were showcasing more caution when more stimulating light colours were switched on, leading to increased time spent stationary.

I also expected increased behaviours in the presence of white light, as it had the highest visual stimulation output. Although white light had an effect on behaviour in skates, where skates were more stationary when white light was turned on, this effect was lost in the second analysis with more inactive skates. Hence, the majority of skates were not bothered by white light, which was also true for plaice. This could be due to the brightness of the white LED, as it had the lowest brightness settings, whereas royal blue had the highest (Appendix Table 1). As the model only accounts for light emission spectra, the brightness of each LED was not considered. To account for this, I tried to standardise the brightness of each LED but was limited to the intensity settings of *Pisces*, which were either normal, medium, or high. This increased brightness of royal blue may have excited photoreceptors more in skates and plaice, where they possibly showed more caution through inactivity, compared to white. This may be the case for catsharks as well, where they had greatest interactions with royal blue. However, it is also important to note that after including plaice that were inactive for entire 10 minute trials for particular colour modes in the second analysis, the effect of royal blue was lost, which suggests that the majority of plaice were also not effected by royal blue light.

For plaice, individuals were more active in the presence of red light in both analyses conducted. As red light attenuates with depth in ocean settings (Jerlov, 1968), red is often not seen at depth; hence, this colour mode may have been more novel to plaice and invoked activeness. However, it is important to note that the sample size of plaice was low and the majority were not responsive at all to light; therefore, it is harder to ascertain whether a link between the model and behaviour exists for them. It could also be the case that other behavioural changes might indicate a better link with vision. For example, the camouflaging colours and burying behaviour of plaice could be measured in the future, in response to different light colours.

For the second aim of comparing target and bycatch behaviour, I found differences between the species tested. In general, the bycatch species (skate and catsharks) were more active than plaice were for at least some parts of the trial (lights off conditions for skates, lights on conditions for catsharks). Although this could largely be due to reasons already discussed, vision may also contribute. As rods have a greater sensitivity to light in darker conditions compared to cones (Lythgoe and Partridge, 1989), it may be that skates and catsharks were more visually stimulated by light compared to plaice, where potential differences in the detection ability of cones and rods is not accounted for in the model. However, the greatest differences in behaviour were seen between sedentary (skates and plaice) and active species (catsharks), which suggests that species' ecology could influence responses to light.

Variation in behaviour also occured between the three skate species tested. For example, skates that were removed from analyses due to being completely inactive for every colour trial were spotted skates. However, some of this variation across species (Table 3) may also be attributed to the unbalanced sample sizes of skate species, where only two small-eyed skates were tested compared to 13 blonde and 12 spotted skates respectively, which was due to the availability of samples collected from the research vessel.

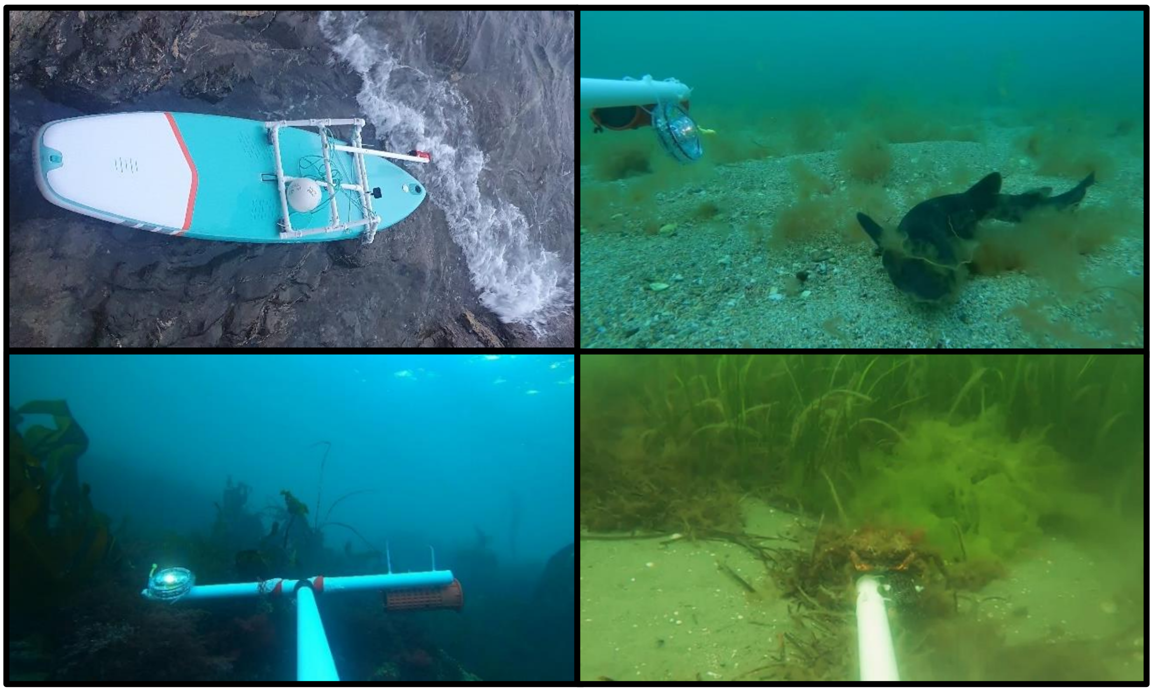
As well as variation between species, I also observed individual variation in responses to light; for example, one catshark nudged a light 12 times (Appendix Figure 2), whereas some only nudged the light once. For skates and plaice, the time spent active also varied between individuals (Appendix Figures 3&5). Further studies could therefore look at repeatability tests to see whether individuals act similarly towards light over time in the same lighting conditions.

However, I found some evidence for habituation to light over time, where plaice and skates became more sedentary after being in the tank for several light exposures. In the second analysis for skates, during the second set of light trials, there was an increase in active skates, which could be a stress response to the increased exposure to nets when moving skates in-between tanks, rather than habituation. However, the implications of individual variation and habituation to light should be further explored in a fishing context, to assess the consequences on the effectiveness of light.

In a fishing context, many other factors need to be considered before trialling lights. Firstly, whether light is the optimum sensory stimulant, as I found that lights were less effective for sedentary species. As previously mentioned, species within this study are effected by both active and passive gear. In an active fishing setting, stress would likely be much higher for fish during the capture process (Heard et al., 2014), and other sensory stimulants, such as the noise of vessels, may be more prevalent than vision (De Robertis and Handegard, 2013).

In terms of catsharks, UK escape panels are not big enough for adult fish to escape, and so lights on trawl headlines may be an option to trial at sea. In a passive scenario, caution may be required when using lights for catsharks, as it could attract them to the net and increase their bycatch. However, the ambient light conditions between fishing and laboratory contexts will be different; for example, increased turbidity in the sea could decrease the visibility of lights (Utne-Palm, 1999). Therefore, ocean irradiance will need to be factored into future models if applied to a fishing context.

By considering the vision and ecology of bycatch and target species, this study has aimed to provide more information for future testing of lights in a fishing context, in order to reduce bycatch. The knowledge of a link between the model and behaviour - particularly for an active shark species – may help researchers to select a light colour that is most likely to induce behavioural responses in fish. However, future work in the field is needed to test the feasibility of light for invoking appropriate behavioural responses in a fishing context.



Chapter 4: The use of BRUVs to assess the natural behaviour of marine species towards artificial light for future consideration in fishing trials

Abstract

Artificial light in fishing can be used to attract catch to nets, or to repel non-target species (bycatch) from gears, depending on the species and the fishing context. For use in bycatch-reduction, light trials have had varied success rates. As demonstrated in **Chapter 3**, quantifying species vision within the underwater environment using vision modelling may help to predict behavioural responses towards light in a controlled laboratory setting. To test if this could be demonstrated in the real world, I explored possible links between the model and behaviour in common species within shallow coastal waters (<10m), using baited remote underwater video cameras (BRUVs) with coloured and flashing lights. For behaviour, I measured abundance through maxN (the maximum number of a species within a single video frame) and observations of species to the family level across different light modalities. I found that abundances 1) marginally increased in lights on versus off BRUVs, 2) did not increase in the presence of more visually stimulating light colours, which were inferred from the vision model, and 3) did not differ between flashing and continuous light. However, these

results varied between families, and were dependant on BRUV location and year of deployment. Although this shows that light could potentially influence the abundance of species, specific light colours and frequencies did not affect behaviour, suggesting that light may be a milder behavioural stimulant in shallow waters compared to previous laboratory settings. As models of vision predict higher visual stimulation values at greater depths, further studies should test if behavioural responses to light will subsequently be more prevalent at depth. It may be the case that background light is an important factor to consider when applying results to future fishing with light trials, to maximise the visibility of LEDs to species.

Introduction

The use of light in fishing to attract catch is thought to have started centuries ago, where bonfires on the beach were used to attract fish to the shallows (Nguyen and Winger, 2019a). In present times, technology has moved towards the use of waterproof and battery-powered lights such as light-emitting diodes (LEDs) (Nguyen and Winger, 2019a). LEDs for attraction purposes are prominent in squid jigging, where vessels fish at night with LEDs above the water surface (Chen et al., 2008). For light application underwater, LEDs have been used to increase catch in pots; for example, in the snow crab (*Chionoecetes opilio*) fishery in Alaska (Nguyen and Winger, 2019b). More recently, researchers discovered that scallops can also be attracted to LEDs in pots underwater in the English channel (Enever et al., 2022).

As the capture of non-target species (bycatch) is a major conservation issue in fishing (Alverson et al., 1994; Anderson et al., 2011; Lewison et al., 2004), research has also focused on whether lights on nets can be used to reduce bycatch (Nguyen and Winger, 2019a). In these circumstances, lights would need to function by increasing the visibility of the surroundings to enable bycatch to see nets and avoid them, or would highlight escape routes on nets (Hannah et al., 2015; Southworth et al., 2020). For example, in trawl scenarios, lights have reduced the bycatch of whiting (*Merlangius merlangus*) through illuminating a size-specific escape panel (Southworth et al., 2020). Other study designs have illuminated the headrope of a trawl, which reduced eulachon (*Thaleichthys pacificus*) bycatch (Hannah et al., 2015) and in static gears, lights have reduced the bycatch of turtles and cetaceans (Bielli et al., 2020), as well as elasmobranchs

(Senko et al., 2022). However, in some trials, light has had no effect on bycatch (Melli et al., 2018), and in other cases, has led to an increase in both target and bycatch species of fish (Geraci et al., 2021), or increased bird bycatch (Sigurdsson, 2023). Without cameras or observations of behaviour in a fishing context, it is difficult to predict how species will respond to light.

To better understand how lights can be selective in behavioural responses between species, controlled tank studies with cameras have explored different light wavelengths (Ciriaco et al., 2003; Marchesan et al., 2005; Ryan et al., 2017; Yochum et al., 2022). For example, studies have found that European seabass (*Dicentrarchus labrax*) were most repelled by green and blue light, whereas the common grey mullet (*Mugil cephalus*) showed an opposite response of attraction to shorter-wavelength light (Ciriaco et al., 2003; Marchesan et al., 2005). In a study with Chinook salmon (*Oncorhynchus tshawytscha*), researchers found that fish can be repelled by light; however, white light was a less effective colour for inducing responses (Yochum et al., 2022).

Due to the variety of responses in fish behaviour towards light, in a previous chapter (**Chapter 3**), I explored whether behavioural responses towards different light colours could be predicted from vision modelling. Specifically, I used a quantum-catch model, which predicts the number of light units (photons) that reach an animal’s eye when viewing an object, by considering ambient light conditions and the vision of a given animal (Cronin et al., 2014; Renoult et al., 2017). Using elasmobranch and flatfish vision within a dark tank setting, I quantified the most visually stimulating light colour modes to fish against the tank background, as well as recording behavioural responses towards light. I found that more visually stimulating colour modes (white, blue and green) induced greater interactions with an LED in a tank for the small-spotted catshark (*Scyliorhinus canicula*), compared to red and amber lights, which were less visually stimulating. However, for sedentary species (skates *Raja sp.* and plaice *Pleuronectes platessa*), I found that fish were less responsive to light in general, although some links to the model were shown.

In addition to light colours, I also explored flash rate within this laboratory setting, as previous studies have found that flashing light can be aversive to fish (Ryan et al., 2017). Flashing light perception is based on critical flicker fusion frequency (cFFF), which is the point at which flashing light becomes continuous for an animal (Landgren et al., 2014), and so a flash rate that is above a species' cFFF will be perceived as continuous light. In the laboratory setting, I found no effect of flash rate on catsharks, plaice and skates. This may have been because a flash rate of 4 Hz was used, which was well below the elasmobranch range of 16 to 25 Hz (McComb et al., 2010) and the teleost range of 30 to 60 Hz (Horodysky et al., 2010) and so was likely to have been too slow to be aversive. A low flash rate was used due to the *Pisces* flash rate settings, where the next highest setting (32 Hz) would have exceeded the cFFF of elasmobranchs. As only one type of flash frequency was explored, a more comprehensive test of behaviour towards flashing light is likely needed.

Although captive tank conditions are optimal for controlling light conditions, they are less comparable to a wild context (Yochum et al., 2022), where light can be variably transmitted in water depending on turbidity (Utne-Palm, 1999), depth and water type (Lythgoe, 1988). Variable light conditions have been shown to effect behaviour in previous laboratory studies, where fish were less effective at catching prey in cloudy water (Utne-Palm, 1999). Additionally, researchers have found that responses to light may differ between wild and captive conditions (Ryan et al., 2017). In one study, researchers recorded the time that sharks spent at a bait station in the presence of different stimuli for testing potential shark deterring devices, including flashing light. In captive conditions, lights caused a reduction in bait uptake for Port Jackson (*Heterodontus portusjacksoni*) and epaulette (*Hemiscyllium ocellatum)* sharks. Interestingly in wild conditions, strobing light on its own did not have the same deterrence effect for white sharks (*Carcharodon carcharias*), but in combination with sound stimuli, did achieve aversion (Ryan et al., 2017). Although this result could be due to differences in responses to light between species, it does highlight a potential for a reduced effect of light as a stimuli in wild contexts.

In wild contexts, a type of bait station that is commonly used to observe marine life is known as a BRUV (baited remote underwater video) (Stobart et al., 2007). BRUVs can either be stereo (two cameras) or mono (one camera), where both types can record fish assemblages and behaviours across marine habitats, but the former can additionally allow for length measurements of individuals (Hall et al., 2021). A common abundance measurement of species in BRUVs, alongside general observations of species, is maxN, which is the maximum number of a species within in a single frame (Stobart et al., 2007). MaxN is designed to eliminate double counting if individuals exit and re-enter the video frame, which reduces the chance of overestimating species abundance (Whitmarsh et al., 2017). As this method of observation is non-invasive, BRUVs can be a useful way of monitoring marine environments over time (Stobart et al., 2007).

As previous studies have found that different light wavelengths can change fish behaviour, and that light may not be as effective in wild contexts, I aimed to explore this further by using BRUVs with and without light to observe behaviour. Specifically, by using the vision model from **Chapter 3**, I explored to the family level, whether: 1) light in general could attract fish, in line with previous findings in passive contexts (Nguyen and Winger, 2019a), 2) whether a vision model could be linked to behaviour in shallow waters (<10m), and 3) whether flashing light could be aversive, based on previous findings that it can be to sharks (Ryan et al., 2017). I expected higher maxNs and observations in lights on conditions, compared to lights off, with increased observations and maxN values in the presence of light colour modes that were the most visually stimulating to common species in the shallow water context, as predicted by the model. For flashing light, I predicted that the highest flash rate (32 Hz) would be the most aversive, followed by 4 Hz. Therefore, I predicted that there would be less species present in flashing light conditions compared to continuous light.

Materials and methods

Vision modelling

To assess whether a quantum-catch model could predict behaviour towards different light colour modes, I first quantified the potential visibility of the stimuli to species belonging to two common families found in a shallow water context (5 m depth), and to also showcase different vision adaptations. These species were the small spotted catshark *Scyliorhinus canicula* (which was also used in vision models across PhD chapters, to compare outputs in different water contexts), and cod *Gadus morhua,* as many observations of pollock (*Pollachius pollachius*) were documented across video footage. However, as pollock photoreceptor information was unavailable in the literature, cod photoreceoptor information was used as both species are within the same family. The following model components were used:

the photoreceptor sensitivities of cod *Gadus morhua* (Bowmaker, 1990) to represent Gadidae family and catsharks *Scyliorhinus canicula* (Gačić et al., 2006) to represent the Scyliorhinidae family, and their ocular media transmittance (Thorpe et al., 1993); the irradiance of shallow coastal waters at 5 m depth (Sticklus et al., 2018) and the spectrum of light emitted from three LED colour modes (white, green and red) of SafetyNet Technologies' LED light device *Pisces*. This can be represented as the following (Figure 16),

$$Qc = \int_{300}^{700} I(\lambda) Ac(\lambda)\, d(\lambda)$$

where Qc is the summed photoreceptor quantum catch for the background, or each LED colour mode. Qc is calculated from the normalised product of photoreceptor sensitivity type *c* of each fish $Ac(\lambda)$ (derived from the product of ocular media transmission and photoreceptor sensitivity at every 1 nm interval) and the normalised ocean background irradiance, or each LED colour mode radiance $I(\lambda)$, integrated over 1 nm intervals across the visible light spectrum $d(\lambda)$(300-700 nm).

To understand how visible each LED colour mode was to animals in relation to the ocean background (background contrast), visual stimulation was calculated using the following equation (Crothers and Cummings, 2013),

$$\text{Visual stimulation} = \frac{\left(\frac{\sum Qc(light\ colour)}{\sum Qc(tank\ background)}\right)}{n(c)}$$

where the output is the predicted total number of photons reaching the eye of the animal, combined across all receptor types, when considering the ratio of the Qc of an LED against the Qc of the ocean background, and divided by the number of photoreceptor types $n(c)$ that an animal possesses. Therefore, the model output is the level of visual stimulation towards a light colour mode in shallow coastal waters at 5 m. For full quantum-catch modelling methodology, see for example; Endler and Miekle (2005); Stevens et al., (2009); Renoult et al., (2017).

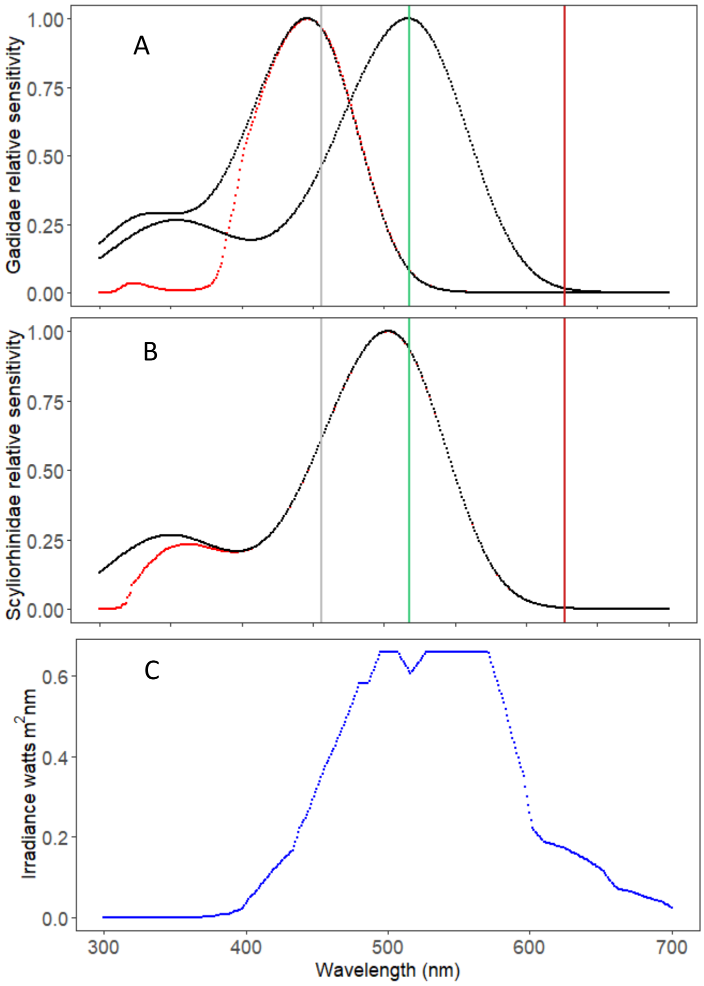


Figure 16:

Vision model components. Graphs **A)** and **B)** represent the sensitivity peaks of the Scyliorhinidae (502 nm) and Gadidae (446 & 517 nm) families respectively, where the small-spotted catshark (Gačić et al., 2006) and cod (Bowmaker, 1990) were used to represent the families. Their peak sensitives were fitted with the Govardovskii et al. (2000) model template to standardise curves. Vertical coloured lines are the peak sensitivities of white (456 nm), green (519 nm) and red (640 nm) light respectively. Ocular media transmissions were obtained for catsharks and cod from Thorpe et al. (1993). Graph **C)** represents a coastal background at 5 m depth, based on Jerlov's (1968) quantification of coastal water type 3C. Data for irradiances was extracted from Sticklus et al., (2018)**.** All irradiance data and ocular media transmissions were extracted from the literature using the free online programme Graphreader (Larson, 2022)**.**

BRUVs

BRUVS were deployed in five sites along the coastline around Falmouth and Helford in Cornwall, United Kingdom (Figure 16) from between August-February in 2021 to 2023. The locations were as follows; Castle beach (50°08'50.1"N 5°03'16.6"W), Pendennis (50°08'36.1"N 5°02'39.8"W), Gylly Beach (50°08'31.6"N 5°04'08.3"W), Swanpool (50°08'22.0"N 5°04'34.6"W) and Durgan (50°06'11.9"N 5°06'55.8"W), where habitats had rocky reef, kelp, seagrass (particularly Durgan) and sandy substrate. A total of 34 site visits took place over three years, with video footage obtained from 83 BRUV drops. BRUVs with lights were paired with a control BRUV, which had a light attached that was switched off. However, for one occasion at Durgan, the camera did not record for the control treatment. The number of location visits for BRUV deployments were as follows: 9 in Durgan (1 in 2023, 8 in 2021), 2 in Swanpool (2 in 2022), 6 in Gylly beach (2 in 2022, 2 for in 2021), 14 in Castle beach (2 in 2023, 2 in 2022 and 10 in 2021) and 3 in Pendennis (1 in 2023, 2 in 2022).

BRUV drops

For 2021 data (the pilot design) 22 drops consisted of two BRUV deployments, which were a control BRUV paired with a BRUV with a white light attached. For 2022 data, the hypothesis of whether more visually conspicuous light colours (as inferred by the visual model) would cause the greatest observations and maxN values of species to the family level, was explored. For this, the following BRUV drops took place: white light, 6 BRUV drops; green light, 5 BRUV drops; red light, 6 BRUV drops and control, 7 BRUV drops. For 2023 data, where the hypothesis of whether higher flash rates would have fewer observations and maxN values of species to the family level was tested, the following BRUV drops with white light took place: 32 Hz, 5 drops; 4 Hz; 4 drops; 0 Hz, 4 drops and control, 3 drops. Lights that were switched on had the highest brightness setting to maximise visibility (white light: 212 mW, green light: 110 mW and red light: 140 mW).

Observer bias

For each of the three years, footage was watched by a different observer, where there were slight differences in metrics and BRUV designs over the years (see below for BRUV design information), as each observer was a different Master's student conducting their individual project. This was with the view to have an optimal design for dropping BRUVs in summer 2023, but due to unforeseen circumstances (see Author's declaration), further data collection could not be conducted. The observer for 2021 data collection (which was a pilot design) did not record maxN values, meaning observation data is possibly an overestimation of abundance. However, to account for potential pseudo-replication, the observer did not include individuals of the same species that re-entered the video frame within 30 seconds.

To account for observer bias in general over the years, I re-watched a randomised subset of footage from BRUV drops to confirm consistency. The 2023 data had very few abundances of species, which is likely due to data collection taking place in January and February (where abundances of species are lower than summer), as well as fewer BRUV drops taking place compared to previous years. However, an observer difference cannot be completely ruled out over the years as I did not watch all of the videos, and so the year of data collection was used in models to account for this (see *Statistical analysis*).

BRUV design

BRUV stations were custom-built from white polyvinyl chloride (PVC) pipe frames (approximately 70 cm x 80 cm x 70 cm), and were weighted with four 1kg weights to sit on the seafloor (Figure 17). BRUVs had a baited arm of 1 m in length, which was fitted with a plastic bait cage and an LED (*Pisces*; SafetyNet Technologies), where bait was 100 grams of chopped Atlantic mackerel (*Scomber scombrus*). GoPro video cameras (3 x HERO 8, 1 x HERO 9) were used to gather video data using high-quality (4K, 30 fps) footage to maximise the ability to identify species. However, for the 2021 pilot data, control BRUVs used a Vemont full HD 2.0 inch action camera, which was mounted in dive housing. To account for differences in fields of view, the observer in 2021 only looked at species that were in close proximity to the bait arm and camera. For each year of data collection, BRUVs had a slight modification in terms of light placement. As 2021 data was a pilot design, the LED was placed next to the camera, which was behind the bait arm. In 2022, the LED was attached to the bait cage on the bait arm, and in 2023, the LED placed adjacent to the bait cage (Figure 17 & 18). BRUVs had a buoy attached and were deployed at approximate depths of between 2 to 10 m, where sampling took place at dawn on flat, calm days with no wind, to maximise visibility and species identification. BRUVs were between 10-250 m apart to minimize the potential for overlap of bait plumes and to reduce the chance of fish moving between BRUVs. Repeats of sample sites were made at least four days apart to reduce the risk of species becoming habituated to the bait. Cameras recorded for around an hour, where 83 hours of footage was watched by three different observers (one observer per year from 2021-2023) in real-time to ascertain species identity, observations and/or maxN. Individuals were included if they were on the screen for at least three seconds. As sand eels (family Ammodytidae) were seen passing in the background in large shoal numbers (100+), they were left out of analysis as model selection was not possible with their inclusion, due to such a high range in abundances of species.

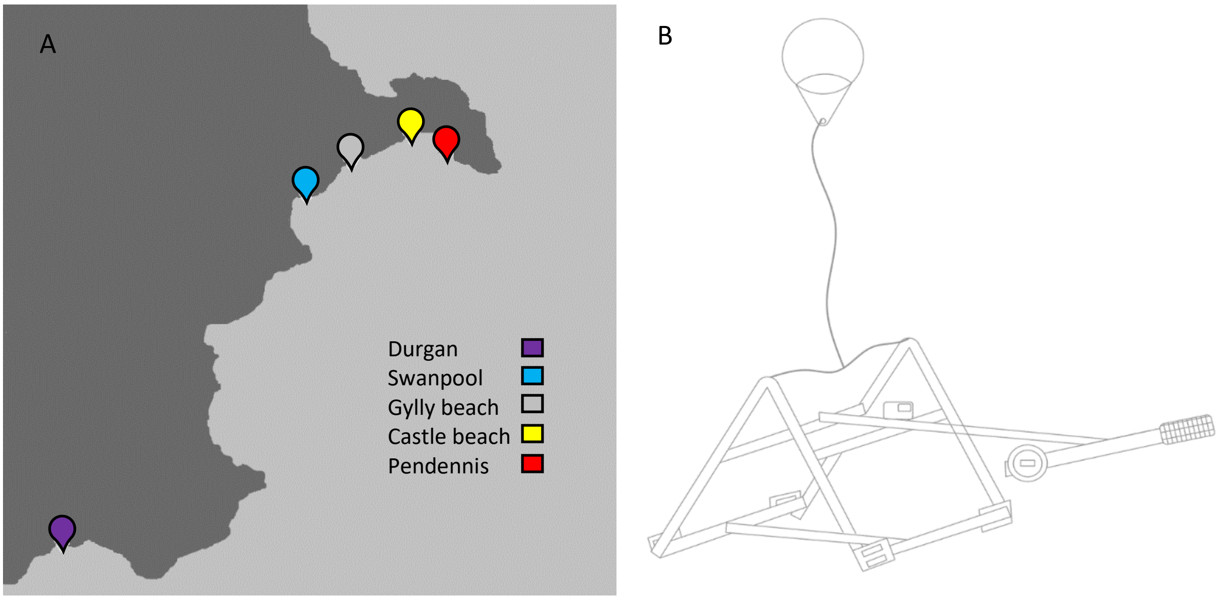


Figure 17:

BRUV drop sites and BRUV design. A) Drop sites were all within Cornwall, UK, in the North East Atlantic. This included Durgan, which is situated in the Helford. All other drops were located in Falmouth, which were; Swanpool; Gylly beach; Castle beach and Pendennis. BRUVs were taken to deployment sites on a paddleboard or small RIB, and were no more than 250 m away from the shore. **B)** The BRUV shown depicts the 2023 design, where previous years had the LED placed adjacent to the camera (2021) and on the bait cage (2022). All BRUVs were equipped with an LED, where control BRUVs had lights switched off. The illustration of the BRUV was provided by Oscar Millar, who collected the 2023 data.

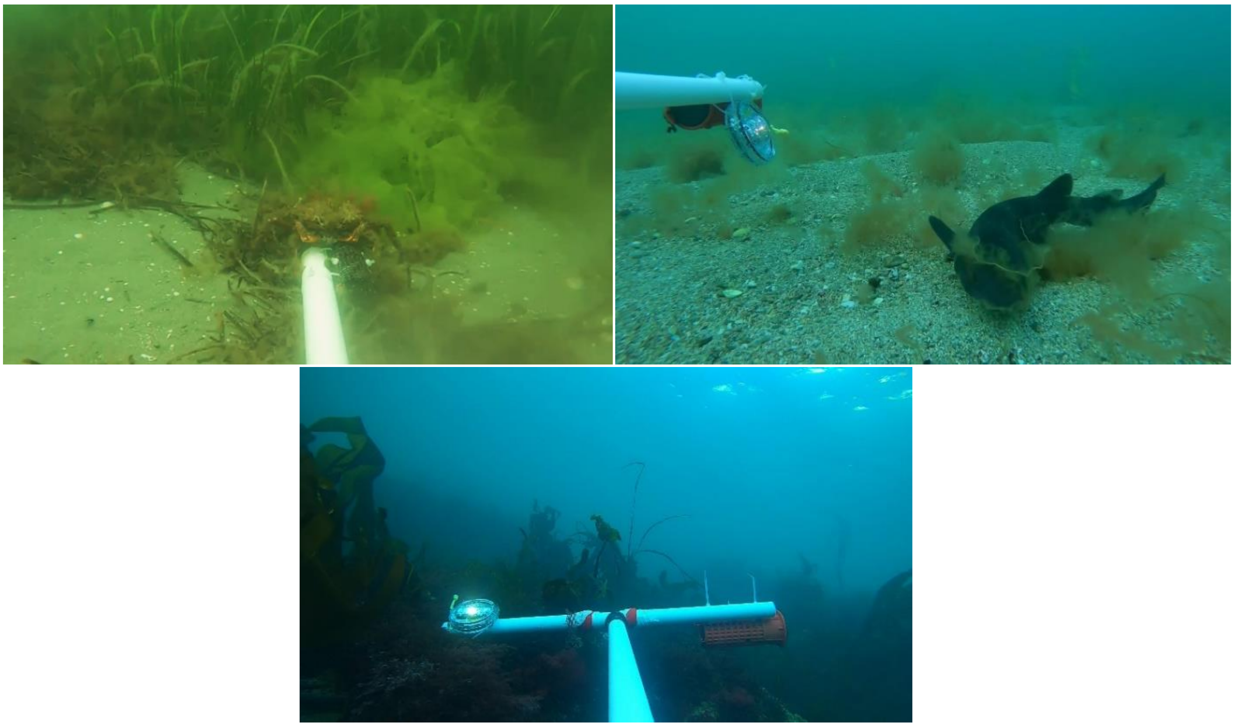


Figure 18:

BRUV video stills from each year of data collection. From left to right, top to bottom; Footage from 2021, where a spider crab (*Maja brachydactyl*) is on the bait; 2022, where a nursehound (*Scyliorhinus stellaris*) is swimming in view, and 2023, where white light is shown. Each year showcases the differences in BRUV design, where the LEDs have slightly different placements (the LED for 2021 data collection was behind the bait arm).

Statistical analysis

I used the statistical programme R (R Core Team, 2021) to generate general linear mixed models (GLMMs) with a Poisson distribution, as observations and maxN data was right skewed. As there was an unbalanced sampling design across sites, year and families, each of these variables were added as a random effect. ANOVAs were also used to further assess the effect of light colour and flash rate on abundances for 2022 and 2023 data respectively.

For assessing whether BRUVs with lights on compared to lights off (light versus control) attracted more species to the family level in terms of increased observations, I used data from three years, and for maxN data, I used data from 2 years (2022 and 2023), which can be presented in the following model:

glmer(maxN/observation~ light_control + (1|year) + (1|family) + (1|location), family='poisson'(link=log)).

For assessing whether more visually stimulating light colours were more effective at attracting species to the family level with the 2022 data, I used an ANOVA to compare maxN and observation data between lights-on BRUVs and control BRUVs, for both. I also used an ANOVA to assess whether flashing light frequencies (32 Hz, 4 Hz, and 0 Hz, compared to control) affected maxNs, and observations of species to the family level with the 2023 data.

Results

Vision modelling

For the quantum-catch model, the family representatives for vision were Gadidae and Scyliorhinidae, where I modelled their vision in shallow coastal conditions at 5m, which were similar to BRUV conditions (Figure 19) Scyliorhinidae had rod-dominated retina (Gačić et al., 2006), whereas Gadidae had two cone cells (dichromatic) (Bowmaker, 1990). In terms of behaviour, I predicted that BRUVs with white light would have the highest maxN and observations of species to the family level, followed by green and then red.

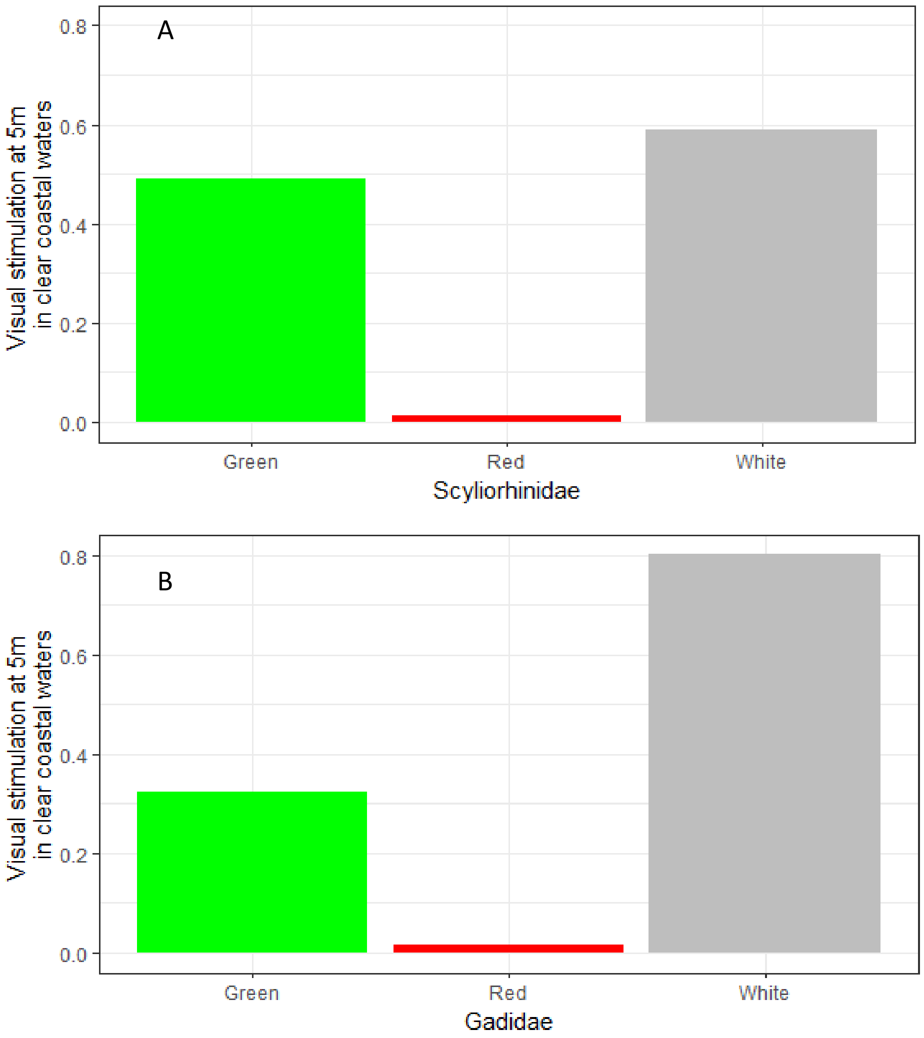


Figure 19:

Vision model output. A) Represents the visual stimulation output for the Scyliorhinidae family in 5 m, and **B)** is the visual stimulation output for Gadidae in 5 m. For both families, white is the most visually stimulating light, followed by green and then red. At 5 m depth, which are comparable to BRUV conditions, visual stimulation values are much lower than what they would be at depth (**see Chapter 2**, Figures 7-10), where ambient conditions would be much darker. Gadidae are more visually stimulated than Scyliorhinidae in general.

BRUVs

From the 83 BRUV deployments over 34 location visits and across three years, 33 marine species were identified from 26 families.

Observations

Observations of species to the family level slightly increased in lights on BRUVs (total observations of 680 across 22 families, mean= 11.33 ± SD 19.35) versus control BRUVs (total observations of 390 from 15 families, mean= 10.00 ± SD 15.85). However, due to high variation in observations (Table 6) across locations (Figure 20), family and year (Figure 21), inferences should be taken with caution about the effect of light. General patterns show that average observations were higher in 2022 and 2021, and at Swanpool and Castle beach (Figure 20 & 21). The random effects showcase high variance, which is likely due to the unbalanced sample sizes across locations over the years (Table 6).

Table 6:

GLMM results for observations of families in lights on and control BRUVs. There was a slight increase in abundances for lights on BRUVs, shown with a significant but small positive estimate. The variation from the random effects is high, suggesting little consistency in the results over year, location and across families.

Explanatory variable	**Fixed effects**	**Estimate + STd. error**	**z value**	**P value**
Observations (intercept lights off)	Intercept	0.522 ± 0.631	0.828	0.4074
	Lights on	0.172 ± 0.07	2.550	**0.0108***

Random effect	SD	Variance
Family (26)	1.038	1.077
Location (5)	0.358	0.128
Year (3)	0.976	0.952

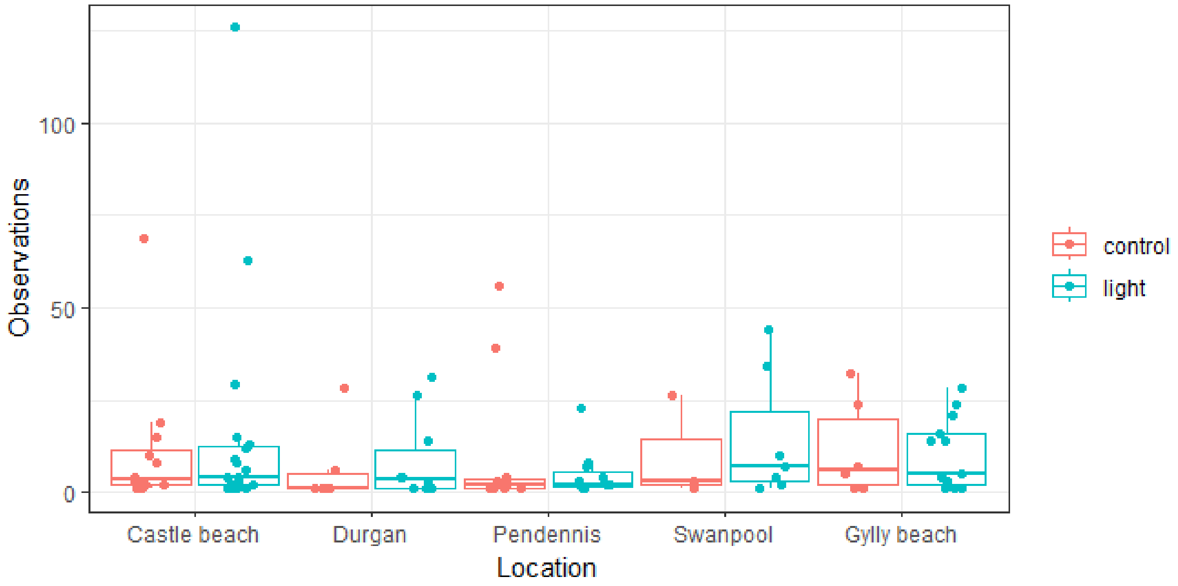


Figure 20:

Observations of species to the family level in lights on and control BRUVs across different locations. Each data point represents the observations of different families for each of the five BRUV locations, where average observations + SD are as follows; Castle beach control: 11.42 ± 19.05 light 16.00 ± 30.38; Durgan control: 6.33 ± 10.80 light 8.6 ± 11.25 Pendennis control: 9.58 ± 18.10 light 4.91 ± 6.46; Swanpool control: 10.00 ± 13.89 light 14.57 ± 17.20; Gylly beach control: 11.67 ± 13.11 light 10.31 ± 9.68. For each location, total observations equated to: Castle beach (441), Durgan (124), Pendennis (169), Swanpool (132), Gylly beach (204).

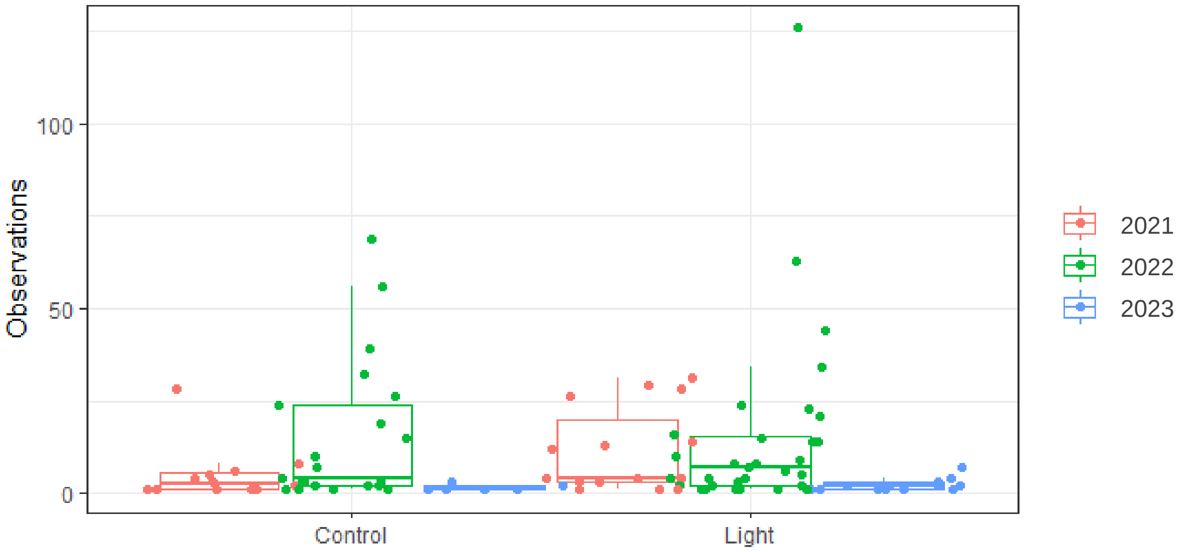


Figure 21:

Observations of species to the family level in lights on and off BRUVs over each year. Each data point represents the total observations of different families over three years for all locations. Mean observations + SD are as follows; 2021 control 5.08 ± 7.59: light 11.60 ± 11.41; 2022 control 15.24 ± 19.51: light 15.29 ± 24.90; 2023 control 1.50 ± 0.84: light 2.29 ± 1.73. For each year, total species observations were as follows: 2021 (235), 2022 (794), 2023 (41). The high observation counts in BRUVs with light in 2022 was due to many occurrences of pollock.

When testing if BRUVS with white light had the greatest observations to the family level compared to green, red, and control BRUVs using the 2023 data, I found no difference between colour modes (F(3, 101) = 2.527, p = 0.06), where total observations across light colour modes were as follows; white: 145 across 11 families (mean= 1.67 ± SD 1.87), green: 172 across 9 families (mean= 2.35 ± SD 3.15), red: 157 across 11 families, (mean= 1.81 ± SD 4.23), and control: 320 across 12 families (mean =1.91 ± SD 4.30). Similarly, for flashing light, I also found no difference between flash rates 32 Hz, 4 Hz, 0 Hz and control (F(3, 30) = 0.564, p = 0.643) when using the 2022 data, where total observations were as follows: 32 Hz: 9 across 6 families (mean = 2.11 ± SD 1.36), 4 Hz: 9 across 4 families (mean = 1.67 ± SD 1.41), 0 Hz: 9 across 4 families (mean = 8.00 ± SD 15.97), control: 9 across 4 families (mean = 5.70 ± SD 7.89).

MaxN

The maxN values of 835 species were recorded, which were slightly higher at BRUVs with lights on (506 maxN values, mean=1.97 ± SD 3.99) versus lights control BRUVs (329 maxN values, mean=1.91 ± SD 4.12), over two years of data (2022 with 794 maxN values and 2023 with 41 maxN values; Table 7). However, due to high variation in maxN values (Table 7) across locations (Figure 22), family (Figure 23) and year, inferences should be taken with caution about the effect of light. In terms of families of commercial interest, Clupeidae (comprised of sprat *Sprattus sprattus*) were only present in lights on BRUVs, and Moronidae had a generally higher presence in light conditions compared to control, where this family was comprised of European bass *Dicentrarchus labrax* (Figure 23). Additionally, Mullidae (comprised of striped red mullet *Mullus surmuletus*) were only present in light conditions (Figure 23). However, sample sizes were small, and so inferences should be tentative.

Table 7:

GLMM results for maxN of families in lights on versus control BRUVs. Location and family significantly affected the maxNs of species to the family level. The variation from the random effects is high, suggesting little consistency in the results over year, location and across families.

Explanatory variable	**Fixed effects**	**Estimate + STd. error**	**z value**	**P value**
MaxN values (intercept lights off)	Intercept	0.709 ± 0.398	1.780	0.07516
	Lights on	0.171 ± 0.060	2.849	**0.00439 ****
Random effect	SD	Variance		
Family (22)	0.880	0.774		
Location (25)	0.725	0.525		
Year (2)	0.115	0.013		

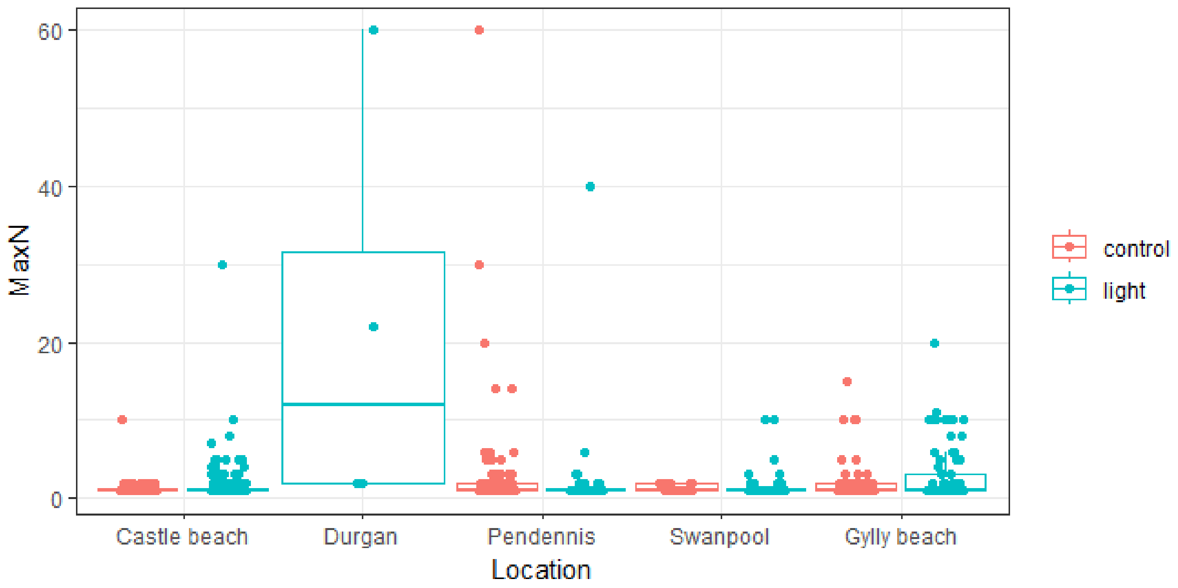


Figure 22:

MaxN values across locations in lights off (control) versus on BRUVs. Average maxN values across families + SD for each location were as follows: Castle beach: control, 1.18 ± 0.87, light, 1.52 ± 2.12; Durgan: control, 0 (due to the control BRUV not recording here), light, 21.50 ± 27.34; Pendennis: control, 2.74 ± 6.56, light, 2.00 ± 5.33; Swanpool: control, 1.30 ± 0.47, light, 1.32 ± 1.34; Gylly beach: control, 2.06 ± 2.60, light, 3.00 ± 3.65. Sample sizes were as follows: Castle beach (368), Durgan (4), Pendennis (169), Swanpool (132), Gylly beach (162).

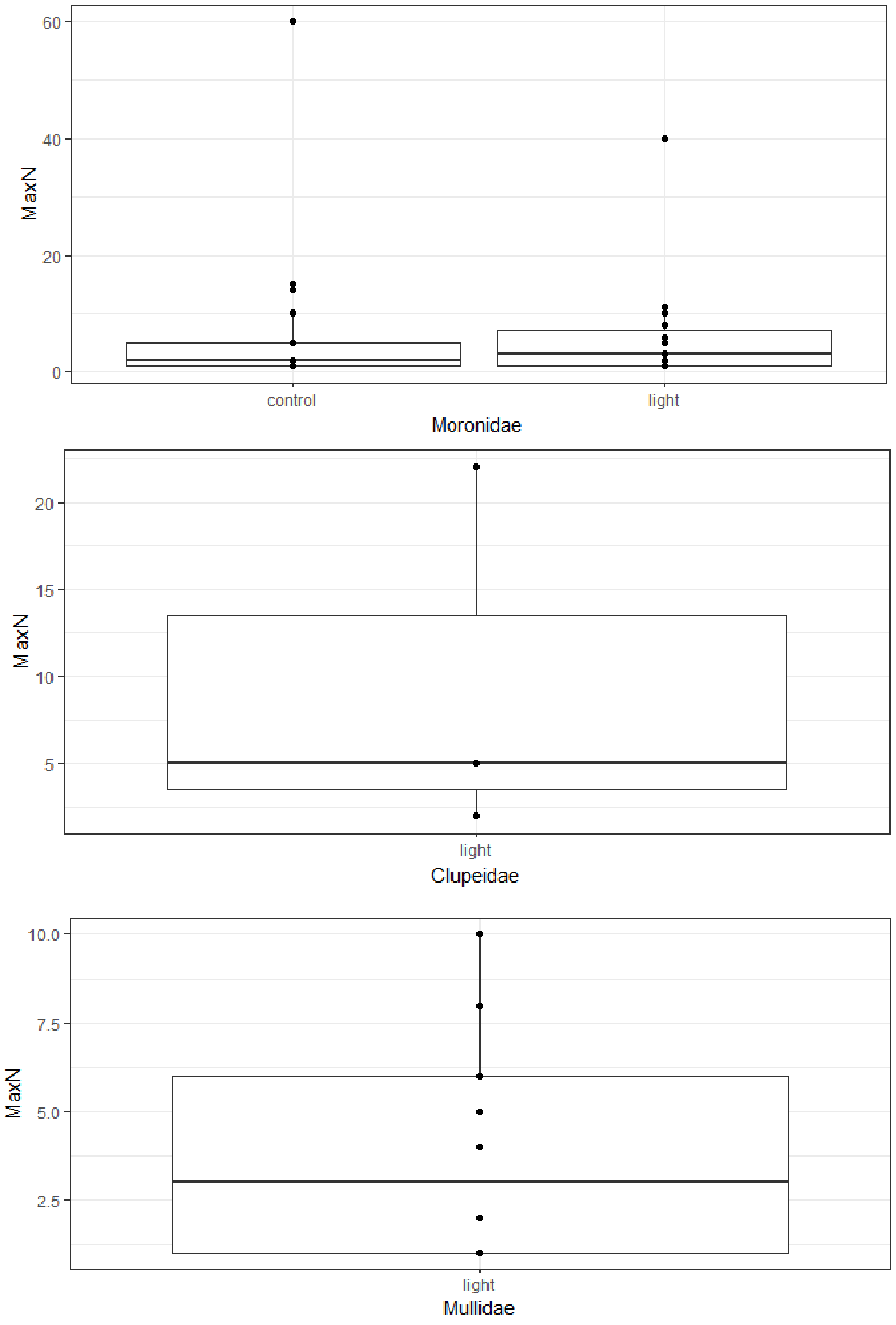


Figure 23:

MaxN values for species of commercial interest. Average maxNs (+ SD) across light modalities and locations were as follows: Moronidae: control, 5.77 ± 11.62; light, 5.89 ± 8.96; Clupeidae: control, 0 and light, 9.67 ± 10.79 and Mullidae: control, 0 and light: 4.07 ± 3.45. Sample sizes were as follows: Moronidae (46) Clupeidae (3) and Mullidae (14).

When testing if BRUVS with white light had the highest maxN values compared to green, red, and control BRUVs, I found no difference across colour modes (F(3, 790) = 0.293, p = 0.83), where average maxN was as follows: white 1.59 ± SD 1.73, green 1.93 ± SD 2.65, red 1.85 ± SD 4.04 and control 1.86 ± SD 4.10. Similarly, for flashing light, I also found no difference between flash rates 32 Hz, 4 Hz and 0 Hz (F(3, 38) = 0.988, p = 0.409), where average maxN was as follows: 32 Hz: 2.11 ± SD 1.36; 4 Hz: 1.66 ± SD 1.41, 0 Hz: 8.00 ± SD 15.97, control: 3.67 ± SD 4.85.

Discussion

This study aimed to test if light (flashing and continuous) could behaviourally stimulate marine species in a wild, non-invasive context, and whether a vision model could predict behaviour towards light colours, as shown in a previous laboratory setting. I found that observations and aggregations (maxN) of species to the family level were slightly higher in the presence of BRUVs with lights on compared to control BRUVs over three years of data, but light colour and flash rate had no further effect on behaviour. However, high variation in abundances across years, location and families were evident, which is likely due to unbalanced sample sizes, and so any inferences about the effect of light on behaviour should be taken cautiously.

The year that data was collected influenced maxN values and observations, where 2021 had the greatest difference in means between light and control BRUVs for observation data (Figure 20). This may be partly due to the increased number of site visits and thus sampling effort that took place in 2021 (22), compared to 2022 (7) and 2023 (5). This may also be due to a potential sampling bias in 2021, as the cameras used to record species in control and light conditions were different, meaning the field of view could have influenced observations. Although this was accounted for by excluding species that were beyond the bait arm or camera, without knowing exact distances (which cannot be recorded with mono-BRUVs), a sampling bias cannot be completely ruled out. However, the other years show similar patterns in observation data (e.g. a slight increase in observations around lights on BRUVs), suggesting some level of accuracy. For maxN data, there was no effect of year, but abundances and sample sizes were much lower in the 2023 data, which is likely due to the lower prevalence of marine life in January and February during 2023 data collection.

The location of BRUVs also seemed to be important for influencing the abundances of families. The mean highest observations in BRUVs with lights on were at Castle beach, and for maxN, it was Durgan. However, Durgan only had four data points due to one visit there, and so any inference from this location is tentative. Castle beach also had the greatest total observations compared to all other locations, as well as the greatest number of site visits. Hence, sampling effort may have contributed to the location effect.

As Castle beach is also surrounded by rocks, and can often be inaccessible at high tide, it is likely to have fewer anthropogenic disturbances such as swimmers and paddleboarders, compared to the other beaches. Although I did not measure anthropogenic disturbances, previous studies have found that this can negatively impact fish assemblages, communities and behaviour (Candolin and Rahman, 2023; Henriques et al., 2013), where fewer disturbances could have also contributed to higher observations of families at Castle beach.

In addition to location, the placement of BRUVs may have influenced the abundances of species. In some cases, BRUVs were only 10 m apart, due to time constraints when deploying them. This could mean that observations of species were repeated if individuals moved between BRUVs. However, as I was assessing the effect of light and light colours, if light (and certain light colours) were indeed more attractive to individuals, then we would have expected less crossover between BRUVs next to eachother. Hence, repeated visits of individuals would still have been insightful.

For observation data, many families had low observations of species in 2023 compared to other years, which is likely due to the time of year that sampling took place in 2023 (February). For some families - particularly those of commercial interest (Mullidae, Moronidae and Clupeidae) - maxN was higher in the presence of light. Moronidae and Clupeidae (bass and herring family) are shoaling species, where previous studies have found that shoaling species can aggregate around light (Becker et al., 2013; Dragesund, 1958). One reason for this could be that the light increased the visibility of the surroundings, and hence, facilitated more foraging opportunities or increased access to the bait (Becker et al., 2013).

However, the greatest maxN value was 60 in control conditions for Moronidae (Figure 23), showing that maxN values were highly variable, which was similar with Clupeidae and Mullidae. Additionally, only four data points were sampled for Clupeidae, suggesting that more deployments will be needed to determine any family-specific light-mediated behaviour. In general, it seems that light may have the potential to be mildly attractive across families, which is in line with previous studies where light has been tested in a passive context (Bryhn et al., 2014; Ciriaco et al., 2003; Enever et al., 2022; Nguyen and Winger, 2019b) and previous chapter findings.

Interestingly, there was no effect on behaviour across all families when BRUVs had flashing light or different light colours. It may be the case that sample sizes were too small for an effect to be seen between light colours with the 2022 data, and for flashing light with the 2023 data. Another reason for a general pattern not being observed with flashing light may be because cFFF values can be variable within and between species (McComb et al., 2010). For example, within a species of crustacean *Nematocelis megalops*, average cFFF was 28 ± 2.0 SE over a sample of five individuals (Frank, 2003). Variation also exists between species, where crustacean species *Plesionika rossignoli* and *Stylocheiron maximum* had respective cFFF values of 14 and 34 Hz (Frank, 2003). The same study also found that cFFF values in species varied between light and dark conditions (Frank, 2003). Hence, variability in cFFF values may have meant more variable responses towards flashing light between and within species, and less of a trend to the family level, which may also be the case for light colours.

Alternatively, the absence of an effect for light colours on behaviour across species may be due to the low visual stimulation values for all colour modes in shallow waters. When comparing the vision model results to deeper water conditions in previous chapter (**Chapter 2**, Figures 7-10), the outputs are much higher, as LEDs become much more contrasted to the darker background. In a previous chapter (**Chapter 3**) where a link between behaviour and the vision model was shown, the ambient background conditions were darker than the shallow BRUV conditions. Hence, a lower ambient light level may be necessary in order to allow for more pronounced visual and behavioural differences between species across colour modes. This may also be why there was only a slight increase in abundance in lights on BRUVs compared to control BRUVs, as light was potentially not visually and thus behaviourally stimulating enough.

Even though both modelled family representatives had the same rankings for visual stimulation values (e.g. being most stimulated by white, followed by green and then red) it may be the case that shallow water species are not as affected by variable light wavelengths. Within shallow waters, most of the light from the sun is transmitted, compared to deeper waters where certain wavebands can be absorbed, particularly longer wavelength light (Warrant and Locket, 2004). Thus, in shallow waters, variable light spectra may not be as novel, and less likely to invoke behavioural responses, regardless of visual stimulating rankings.

Unlike laboratory conditions where light output can be controlled, there is a potential for light to vary in the wild (Yochum et al., 2022). As the model background was based on irradiance from the sun on a clear, cloudless day (Jerlov, 1968; Sticklus et al., 2018), the possible background elements from the BRUV footage such as kelp, rocks and the BRUV itself, were not taken into account. This could mean that the LED visibility varied between BRUV deployments, which in turn, could have impacted behaviour (Utne-Palm, 1999). Along with light variability, many other sensory stimulants can affect the abundances of species at BRUVs, such as other flora and fauna (Coghlan et al., 2017), as well as the presence of bait (Whitmarsh et al., 2017). Therefore, variability in LED visibility and the presence of other sensory stimulants may be why there was only a slight increase in abundances of species in lights on BRUVs, which supports the idea that light in a wild context is less effective (Ryan et al., 2017) .

It is important to note that in the previous chapter, behaviour towards light in the laboratory was measured with individual fish and their interactions with an LED, whereas in this shallow-water context, abundances of species were used to quantify behaviour. Hence, the two studies are not directly comparable. For light-specific behaviour, I did not use an LED interaction as a metric, as the LED placement was not fixed on BRUVs over the three years of data collection, due to changes in BRUV design. Additionally, with BRUV data, there is a possibility of pseudo-replication when assessing the behaviour of individuals, as they can exit and re-enter the camera field of view (Whitmarsh et al., 2017). However, maxN can try and account for this by considering the maximum number of individuals of a species seen at one time, although this can in turn lead to an underestimation of species (Sherman et al., 2018). MaxN also does not take into account repeat location visits, which could mean the same individuals are sampled over time. However, the same area was only sampled again after four days, to minimise pseudo-replication.

Overall, this study shows evidence for the potential of light to be mildly attractive towards species within a non-invasive, shallow water context. However, despite being demonstrated in previous laboratory studies, the results from a vision model could not be linked to behavioural responses towards light in this ocean context. Although light was tested in shallower waters that are less comparable to fishing contexts, this study provided a first step for testing the vision model assumptions in the field, through utilising easily accessible coastline and using a form of inexpensive data collection. Future studies should explore vision modelling predictions and behaviour in deeper water conditions to maximise the visibility of LEDs, and to subsequently test if light has a greater behavioural effect. Hence, a consideration of ambient light may be needed in the future when deploying lights in a fishing context.

Chapter 5: No evidence that artificial light deters a UK shark species from capture in an experimental trawling scenario

Abstract

Artificial light can be used in fishing to reduce non-target catch (bycatch) from nets through highlighting the gear or repelling species from nets. Previous chapter work on light and behaviour in a laboratory context has shown that vision modelling can help to predict the most behaviourally stimulating light colour mode to species. As this was demonstrated with royal blue light and the small-spotted catshark (*Scyliorhinus canicula*) - where sharks showed increased interactions with more visually stimulating colour modes – I therefore aimed to see if this link could be applied to an experimental trawling scenario to reduce their capture. I hypothesised that, by adding lights to the headline of an otter trawl (where lights

have previously reduced bycatch of fish), royal blue light would be an optimal colour for reducing catshark bycatch. However, the results showed no difference in catshark abundance when comparing between hauls with lights on (n=8) and off (n=8). Coupled with video footage, I also found that the majority of catsharks (98.8%) were not able to swim out of the trawl once they had entered the net. The results showcase the complexities of testing lab-based predictions in the field, particularly in active fishing settings where many other factors can influence behaviour. Future trials would still benefit from testing the vision model-behaviour link in fisheries where lights have been successful in reducing bycatch, to see if reduction can be further optimised. Specifically, a passive fishing scenario may be best to further test light colours, to remove the influence of movement stimuli on behaviour.

Introduction

Natural light in both terrestrial and marine ecosystems can mediate behaviour and physiology in species (Russart and Nelson, 2018). At a general level, light is a key component for circadian rhythm, which is where the presence or absence of light can dictate activity levels of animals (Sigholt et al., 1995). For example, particular phases of the lunar cycle can kick-start spawning events for many coral species (Davies et al., 2023). For other marine species, light can aid predator detection, where species like cuttlefish can perceive predators in turbid conditions via planes of light that are not visible to the human eye (light polarization; Schroer and Hölker, 2016). Additionally, some species instinctively orientate themselves towards or away from light, in a process known as phototaxis (Jékely, 2009). Phototaxis in prey species can also have a knock-on aggregation effect across species in higher trophic levels, which are attracted to prey (Utne-Palm et al., 2018).

Due to the importance of light in ecosystems, it has subsequently been exploited in a number of marine industries, including aquaculture and fishing (Nguyen and Winger, 2019a). In aquaculture, studies have found that continuous artificial light combined with shortened photoperiods (day to night cycles) can affect the physiology of farmed salmon by increasing their growth rate (Sigholt et al., 1995). As well as physiology, light can affect the swim behaviour of penned salmon, where illuminated conditions help to reduce movement to unfavourable parts of the water column for fish, which in turn maximises their growth (Juell and Fosseidengen, 2004).

In fisheries, light use is thought to have started thousands of years ago, where fishers would make fires on beaches to increase catch to shallow waters (Arimoto et al., 2010). In present times, light is still used for this purpose, but technology has now moved towards the use of light-emitting diodes (LEDs), which are energy-efficient and battery powered (Nguyen and Winger, 2019a). LEDs for attraction purposes are prominent in squid jigging (Chen et al., 2008), and more recently, researchers discovered that scallops can be attracted to light in pots (Enever et al., 2022).

Now, research is increasingly focusing on whether lights can manipulate behaviour to reduce the capture of non-target species in fishing (Nguyen and Winger, 2019a), which is known as bycatch (Alverson et al., 1994; Lewison et al., 2004). Bycatch stems from unselective methods of fishing, which can be influenced by gear types that are indiscriminate between species (Alverson et al., 1994; Anderson et al., 2011; Lewison et al., 2004). For example, seabirds are highly susceptible to being caught on the baited hooks of longlines, as the lines take time to sink to deeper waters (Anderson et al., 2011). As such, seabird mortalities related to pelagic longline fisheries are estimated to be between one hundred and sixty thousand to three hundred and twenty thousand annually (Anderson et al., 2011). Other marine species that have experienced population declines as a direct result of bycatch include megafauna such as cetaceans and elasmobranchs (Lewison et al., 2004).

Across various trials, LEDs have successfully reduced bycatch in a range of taxa and gear types (Bielli et al., 2020; Lomeli et al., 2018; Ortiz et al., 2016; Wang et al., 2007). For example, in trawl scenarios, lights have reduced the bycatch of whiting (*Merlangius merlangus*) through illuminating a size-specific escape panel (Southworth et al., 2020). Other studies have illuminated the footrope of a trawl, which reduced eulachon bycatch (Hannah et al., 2015) and in static gears, lights have reduced the bycatch of turtles and cetaceans (Bielli et al., 2020), as well as elasmobranchs (Senko et al., 2022). Proposed mechanisms for the success of lights is that they can highlight an escape route on nets, or increase the visibility of the surroundings, which enables fish to escape or avoid capture (Hannah et al., 2015; Southworth et al., 2020).

Marine taxa that are particularly susceptible to population declines from fishing are elasmobranchs (sharks, skates and rays) due to their slow-growth and long gestation periods (Cailliet, 2015). Whether they are targeted or incidentally caught, research has estimated that fishing threatens one-quarter of all elasmobranchs species, and as such, they are more at risk of extinction compared to other marine taxa (Dulvy et al., 2014).

As outlined above, elasmobranch bycatch was reduced when adding lights to gillnets, where green lights achieved a 95% reduction in shark, ray and skate bycatch (Senko et al., 2022). Other research has also tested lights and repellents in a more controlled laboratory setting with sharks. For example, lights in combination with sound reduced bait uptake by sharks at a bait station (Ryan et al., 2017), and in a previous chapter (**Chapter 3**), I found that small-spotted catsharks (*Scyliorhinus canicula*) had a greater number of interactions with LEDs that should be more stimulating to their vision (white, blue and green LEDs, compared to red and amber). In **Chapter 3**, visual stimulation was quantified using a vision model, which considers a species' vision and their light environment, with the aim to narrow down the most visible LED colour mode (for quantum-catch details see Figure 11, and Endler and Miekle, (2005) and Stevens et al., (2009) for methodology). However, for the other elasmobranch species tested in **Chapter 3** the skates (*Raja* spp.) were inactive during light exposure trials. Hence, lights are not as behaviourally stimulating for some elasmobranch species.

For the small-spotted catshark, although they are labelled as 'Least Concern' on the IUCN Red List (International Union for Conservation of Nature) (Ellis et al., 2005), catsharks are still highly susceptible to being caught as bycatch in a range of fisheries that use active and static gears (Papadopoulo et al., 2023). For example, a recent study conducted in Welsh waters found that catsharks were the dominant bycatch species in baited crab pots (Moore et al., 2023). In Europe, a number of small-scale fisheries also exist for the small-spotted catshark (Alonso-Fernández et al., 2022). Within fisheries which target sharks in Europe, catsharks have been categorised as overexploited (Papadopoulo et al., 2023). Additionally, catsharks are closely related to the bull huss (*Scyliorhinus stellaris*), which is IUCN listed as 'decreasing' (Finucci et al., 2021), and have a similar habitat and ecology to spurdog (*Squalus acanthias*), which have been historically overfished (De Oliveira et al., 2013). These three coastal shark species are found in North-East Atlantic waters, where they can be caught as bycatch in demersal fisheries (Parton et al., 2020).

As work from **Chapter 3** showcased that skates were not as behavioural stimulated by light, I chose to focus on the small-spotted catshark as a bycatch representative for this study. To my knowledge, the use of lights to reduce shark bycatch in an active fishing context has not yet been tested. Therefore, based on the previous trials that show 1) that sharks are receptive to light from **Chapter 3** and a previous study (Ryan et al., 2017), and 2) that certain light colours can invoke greater reactions in catsharks, I aimed to apply this to field trials. Specifically, I aimed to reduce the capture of small-spotted catsharks by adding royal blue lights to a net in an experimental trawling scenario. I chose to use royal blue light compared to other colours because a greater number of catsharks reacted to this colour in previous laboratory trials, and the royal blue LED had the brightest output (Appendix Table 1), which is likely to increase visibility in potentially turbid waters. To also compare whether vision in previous laboratory conditions would be similar in coastal water conditions, I also modelled catshark vision in the latter environment using a quantum-catch model.

As sharks are unlikely to fit through standard UK escape panels, lights were placed on the headline of the trawl. Previous studies have found that lights at the front of the trawl can reduce bycatch (Hannah et al., 2015; Lomeli et al., 2018) which is likely due to fish being able to retain their swimming ability at the front of the trawl compared to other parts (Hannah et al., 2015). Hence, I predicted that royal blue light would give sharks the best chance at either 1) avoiding initial capture in the net, or 2) escaping once captured in the net, by highlighting an exit via the mouth of the trawl. To test this, alternate trawls with lights on versus lights off were performed, to assess whether less catsharks were caught when royal blue lights were on. I also made use of a new underwater video camera (*CatchCam*, SafetyNet Technologies) which is specifically designed for trawling gear, to further assess how catsharks responded to lights.

Materials and methods

Catsharks were captured from 30 minute short hauls via an otter trawl with a headline of 15 m and an 80 mm cod-end (the closed end of a trawl net where catch is contained), at a vessel speed of two to three knots. The net was 10 m in length from the footrope of the net to the cod-end. Trawls were conducted by the Research Vessel *MBA Sepia* from the Marine Biological Association (MBA) in Plymouth, UK, at approximate depths of 33-40 m in Bigbury bay (50°15'56.7"N 3°53'32.3"W) across daylight hours in June and September 2023. This area was chosen due to the large elasmobranch population, which has previously been recorded from the MBA's inshore fishing surveys.

From crew knowledge and camera footage on the gear, it was deemed that catsharks were more likely to enter the net via the middle section of the net mouth. Five royal blue LED lights were therefore positioned *(Pisces* lights*,* peak wavelength 447 nm, SafetyNet Technologies) on the trawl headline, with one light in the centre and each successive light being 1 m apart (Figure 24). Each light emitted approximately 370 mW, which was measured using a spectroradiometer (JETI specbos 1211-2) from a distance of 50 cm in air within a dark room at the University of Exeter, Penryn Campus.

The camera used on the net (*CatchCam*) has a small red LED within the unit when recording is activated, and is also paired with a separate white LED lamp (brightness 124 lumens) to help illuminate the surroundings. The white LED was therefore set to "on" for both control and experimental trawls. To offset a possible influence on fish behaviour with the LED lamp, *CatchCam* was placed on the net extension (Figure 24), as it was at an optimal distance (5.5 m from the footrope to the camera) to observe the trawl mouth, whilst being far enough away so that fish would unlikely be able to swim back out of the net once reaching the camera, if fish were indeed influenced by the white light. The LED lamp and camera unit were housed in a green trawling unit, which was attached on the inside of the net via the upper part of the net extension with nylon rope and cable ties. A buoy was also attached above the unit and net to allow the net to remain open during trawling (see Appendix Figure 5). With *CatchCam* footage, I recorded whether catsharks could escape out of the mouth of the trawl once they had entered, which was recorded at 25 fps (frames per second) with a resolution of 480p (640 by 480 pixels).

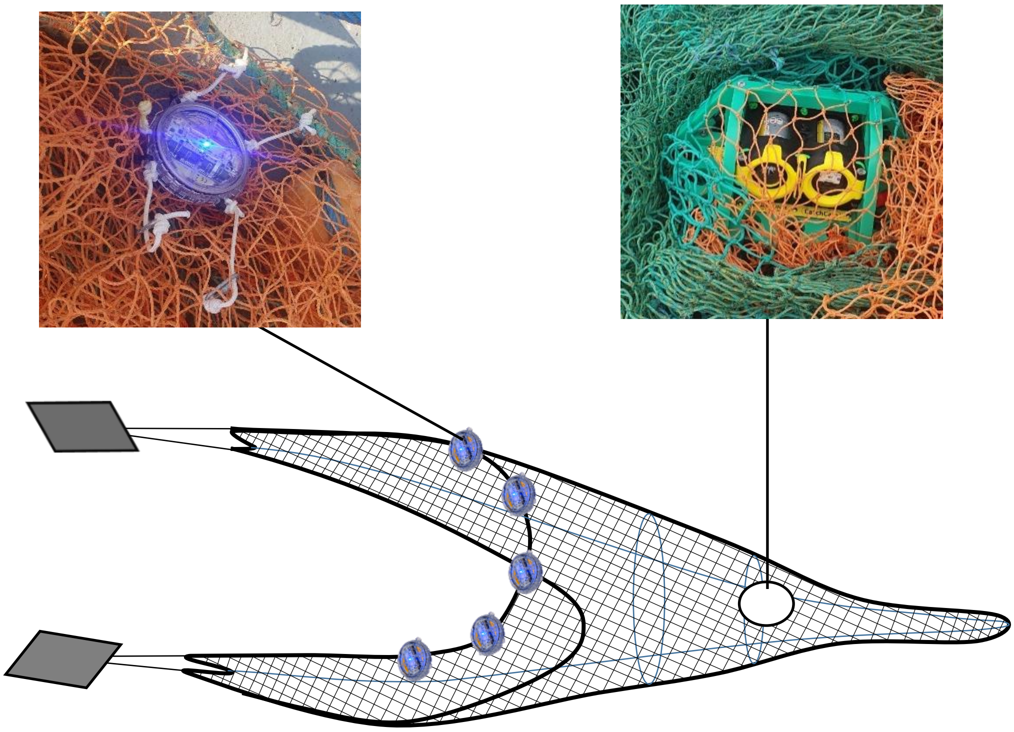


Figure 24:

Otter trawl diagram with experimental net set up. Five LEDs were placed on the headline of the trawl, each 1 m apart. Lights were attached to the headline via nylon string, carabineers and cable ties. The camera *CatchCam* was attached inside the net via a trawl attachment, where it recorded catch entering the net for experimental and control trawls, and was accompanied by a white LED lamp.

A total of 16 hauls were conducted across five days, where two days of trials took place in June, and three in September. For each day, two or four hauls were performed, which were alternated between experimental hauls (lights on, n=8) and control hauls (lights off, n=8). I also alternated whether trials started with lights on or lights off for the first haul, to avoid a time of day bias.

For catshark data, I recorded their abundance, sex, length and weight. However, as there is no quota or MCRS (minimum conservation reference size) with this species, I mainly focused on abundance. For environmental data, I recorded the sea-surface temperature using a CTD (conductivity, temperature and depth measuring instrument) for each day of trials, apart from one day where the CTD did not record. In this case, I used the Sea Temperatures database (Sea Surface Temperatures, 2005). Turbidity was also recorded with a secchi disk, at the beginning of each trial day (n=5). For the full list of species caught and their subsequent abundances, see Appendix Table 3.

On one of the hauls, catshark abundance was not recorded, which is where *CatchCam* provided a back-up for observations of fish entering in the net.

Vision modelling

To assess whether the quantum-catch model from previous laboratory trials in **Chapter 3** corroborated with what catshark vision would be like in an ocean context, I quantified the potential visibility of the stimuli to catsharks in water conditions similar to Bigbury bay. The model components were:

the photoreceptor sensitivity of catsharks *Scyliorhinus canicula* (Gačić et al., 2006) and their ocular media transmittance (Thorpe et al., 1993); the irradiance of ocean waters at 50 m depth based on the Jerlov (1968) quantification of ocean type IB, and the spectrum of light emitted from six LED colour modes of SafetyNet Technologies' LED light device *Pisces*. This can be represented as the following

$$Qc = \int_{300}^{700} I(\lambda) Ac(\lambda)\, d(\lambda)$$

where Qc is the summed photoreceptor quantum catch for the background, or each LED colour mode. Qc is calculated from the normalised product of photoreceptor sensitivity type *c* of catsharks $Ac(\lambda)$ (derived from the product of ocular media transmission and photoreceptor sensitivity at every 1 nm interval) and the normalised ocean background irradiance, or each LED colour mode radiance $I(\lambda)$, integrated over 1 nm intervals across the visible light spectrum $d(\lambda)$(300-700 nm).

To understand how visible each LED colour mode was to catsharks in relation to the ocean background (background contrast), visual stimulation was calculated using the following equation (Crothers and Cummings, 2013),

$$\text{Visual stimulation} = \frac{\left(\frac{\sum Qc(light\ colour)}{\sum Qc(tank\ background)}\right)}{n(c)}$$

where the output is the predicted total number of photons reaching the eye of the catshark, combined across all receptor types, when considering the ratio of the Qc of an LED against the Qc of the ocean background, and divided by the number of photoreceptor types $n(c)$ that the catshark possesses. Therefore, the model output is the level of visual stimulation towards a light colour mode in coastal waters at 50 m. For full quantum-catch modelling methodology, see for example; Endler and Miekle (2005); Stevens et al., (2009); Renoult et al., (2017).

Ethics

Experiments did not fall under regulated procedures in the Animals (Scientific Procedures) Act 1986, and therefore did not require a home office license, as the species identification and measurement did not breach the lower-threshold for procedures. All captured catsharks survived and were released back into the sea via the MBA’s special dispensation license. Where possible, other fish species caught were returned to the sea immediately after measurement, before trawling started in a new location within Bigbury bay. All fish that were in a compromised condition were euthanized via schedule 1 by crew members that are trained by the Named Animal Care and Welfare Officer (NACWO) at the MBA. Ethics were approved by external (MBA) and internal (University of Exeter) ethical reviews, which are combined in the following ethics application: ID 1135017.

Statistical analysis

All data exploration and statistical analysis were conducted in the programme R (R Core Team, 2021). As catshark abundance was count data and slightly right skewed, I performed a General Linear Model (GLM) with a Poisson distribution, and compared total catshark abundances in each haul in lights off versus lights on conditions. Fixed variables included sea surface temperature, secchi disk depth visibility reading, depth for each haul, haul number, and haul month.

The following R code was used, where light mode was either “on”, or “off”:

```
glm(abundance~ light_mode +depth+surface_water_temp +haul_month
+secchi, family="poisson", data=catsharks_abundance)
```

Results

Catshark abundance

Catsharks (n=160) were captured and obtained across the five days and 16 hauls (Figure 25). For lights on hauls (n=8), 76 were caught, and for lights off hauls (n=8) 84 were caught. Catshark abundance ranged from 0 to 23 (mean =12 ± SD 7.55) for control hauls, and 6 to 23 (mean =9.5 ± SD 6.44) for experimental hauls. There was no significant difference between experimental and control hauls for catshark abundance, and the fixed variables did not have an effect on the abundance of catsharks (Table 8).

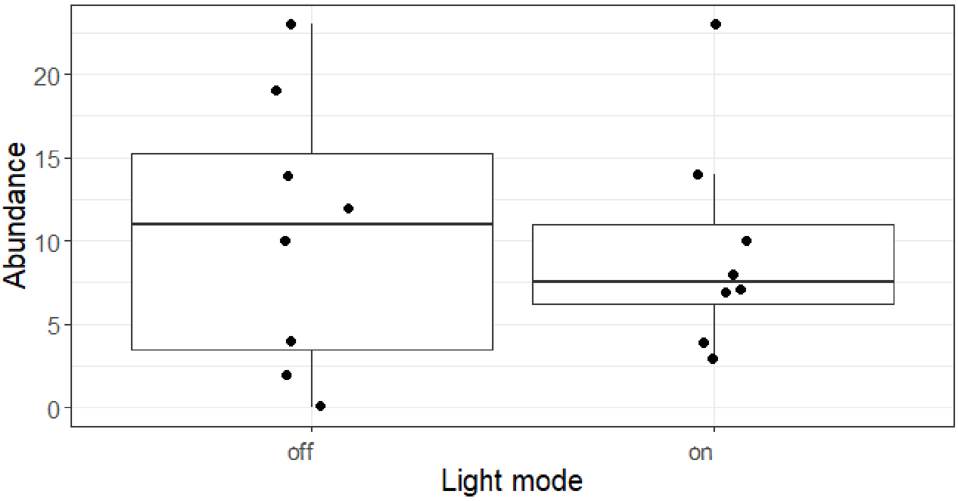


Figure 25:

Catshark abundance in lights off versus lights on hauls. Each data point represents the number of catsharks caught per haul, where there was 16 hauls in total. Abundances ranged from 0 to 23 for lights off hauls, and 6 to 23 for lights on hauls.

Table 8:

GLM results for catsharks. Fixed effects did not influence the abundances of catsharks, and catshark numbers did not significantly change between lights on and off hauls.

Fixed effects	***Estimate + STd. error***	***z value***	***P value***
Catshark abundance (Intercept)	7.424 ± 2.679	2.771	0.0056**
Light mode (on)	-0.030 ± 0.185	-0.165	0.8690
Depth	-0.035 ± 0.048	-0.738	0.4606
Sea surface temperature	-0.166 ± 0.122	-1.360	0.1737
Haul month (September)	-0.762 ± 0.430	-1.773	0.0763
Secchi	-0.073 ± 0.093	-0.789	0.4303

Catshark escape ability

From the video footage (8 hours), two catsharks escaped the trawl; one from burying out of the net (Figure 26), and the other from out-swimming the trawl and escaping from the wing. Therefore, based on catch data, 162 catsharks were originally captured, with 98.8% of them being retained. However, from video footage, 159 were observed entering the net. Some catsharks may have been missed on video footage due to the net being obscured in some of the earlier videos. Net entanglement of catsharks was observed in almost every haul (14 out of 16 hauls), with a total of 27 catsharks becoming entangled across all hauls.

It is possible that more catsharks entered and potentially escaped the net, but were missed by the obscured camera in some of the footage. However, it was evident that the vast majority of catsharks were not able to outswim the net, and so therefore more catshark escapement is unlikely. From the observations of catsharks at the mouth of the trawl, many could only maintain speed at the mouth of the trawl for a short period of time, but did not have the endurance for prolonged swimming, and would often lose energy after alternating between sides of the trawl mouth.

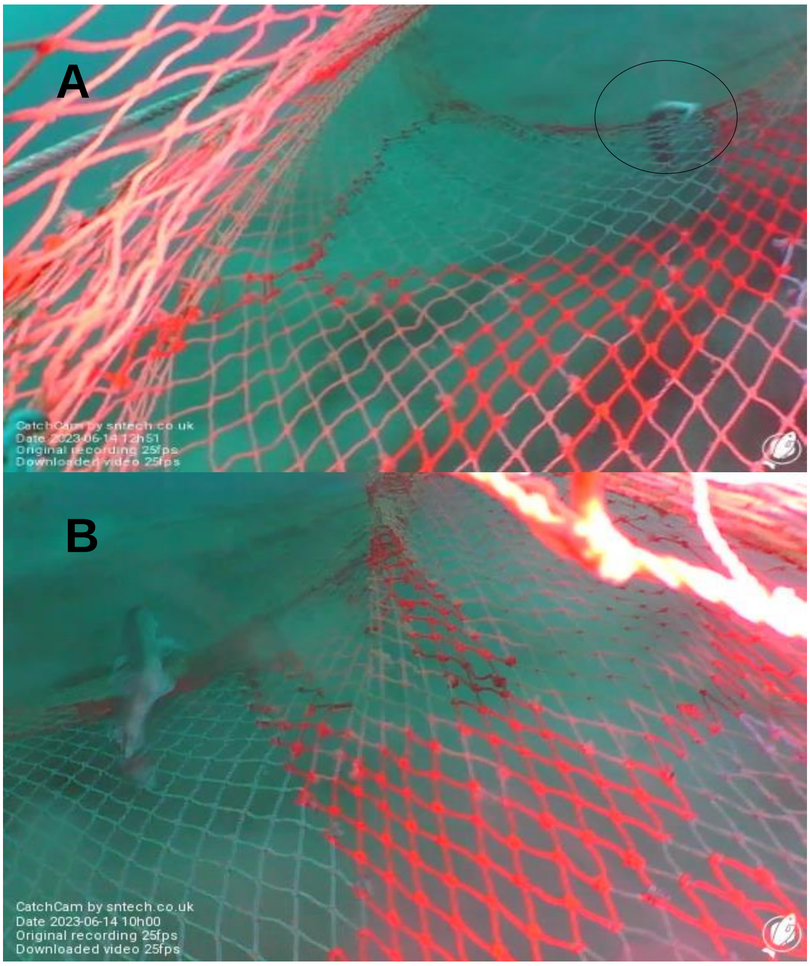


Figure 26:

Catsharks within the trawl. Video footage from *CatchCam* which showcases different behaviours of catsharks whilst in the trawl. **A)** One of the two catsharks that escaped from the trawl by burying through the mesh. **B)** A catshark swimming towards the mouth of the trawl.

Vision modelling

The vision model outputs were similar for both the laboratory and ocean contexts, with white LEDs being the most visually stimulating, followed by green, blue, royal blue, amber and then red. The tank conditions had slightly higher visual stimulation values, which is likely because ambient conditions were darker.

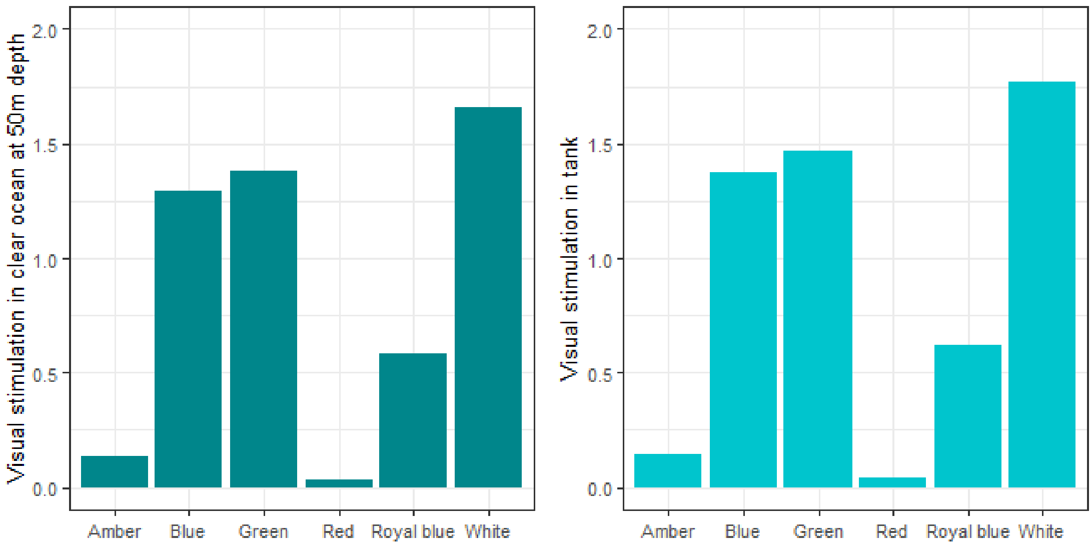


Figure 27:

Visual stimulation values in different ambient light contexts.The left graph is visual stimulation outputs for catsharks in clear ocean conditions at 50 m. Ocean irradiance data was based on the Jerlov, (1968) quantification (open ocean type IB) and extracted from Sticklus et al., (2018) using Graphreader (Larson, 2022). The right graph is the vision model based on laboratory tank conditions in **Chapter 3**.

Discussion

The study set out to use prior knowledge of a link between vision and behaviour in catsharks towards light within a laboratory context, to test whether lighting could reduce their capture in an otter trawl. The results found no evidence for an effect of light in the field, despite previous work showing that sharks are interested in blue light (**Chapter 3**) and that shark bycatch can be reduced with light in a passive fishing context (Senko et al., 2022). However, with the use of a camera on the net, I was able to observe catshark behaviour within the trawl, which suggests possible reasons as to why lights may have been ineffective.

Firstly, this trial was the first to test lights to reduce shark bycatch in an active fishing scenario, as opposed to a passive one (Senko et al., 2022). Catsharks in particular were assessed due to their active responses to light in **Chapter 3** compared to other species of elasmobranchs (skates), which were more stationary in the presence of light (see Appendix Table 3 for trawl results with skates, where light also didn't have an effect).

Due to previous assumptions in trawling scenarios on light-avoidance behaviour of bycatch species (Hannah et al., 2015), I hypothesised that the lights would either help catsharks to avoid initial capture, or allow them to swim out of the net once captured, by highlighting an escape route via the mouth of the trawl. However, from video footage, it seems that catsharks could not sustain prolonged swimming speeds and were unable to orientate themselves out of the net. In previous research, small-spotted catsharks have had their swim speeds predicted in relation to their muscle fibre capacity (Curtin and Woledge, 1988). Researchers proposed that when considering maximum muscle fibre energy output, catshark maximum speed would be 4.2 m per second (Curtin and Woledge, 1988). However, the study did not measure speed in a fishing context and also did not consider muscle fatigue (Curtin and Woledge, 1988). Although 4.2 m per second is faster than the two to three knots of the research vessel in these trials, it was evident that catsharks could not sustain speed for a prolonged period in the trawl. Hence, in a fishing scenario, catshark swimming capacity is likely reduced, which was shown from the high retention of catsharks in the trials.

From video footage, it also appeared that catsharks were potentially disorientated in the net, as they would switch between sides of the trawl mouth whilst swimming. As *Pisces* lights have a translucent casing, light can be seen from both sides of the device; however, the brightest output was facing away from the inside of the net (Figure 24). Hence, catsharks may not have clearly seen the lights once captured in the net. The importance of light placement has been demonstrated in other fishing with light trials, where one study found that lights on an escape panel increased eulachon (*Thaleichthys pacificus*) bycatch, whereas lights on the headline reduced their bycatch (Hannah et al., 2015). As one catshark was able to escape via the trawl wings, future trials could benefit from placing lights on the inside of the trawl (Figure 28) to allow for a better visual pathway for net escapement.

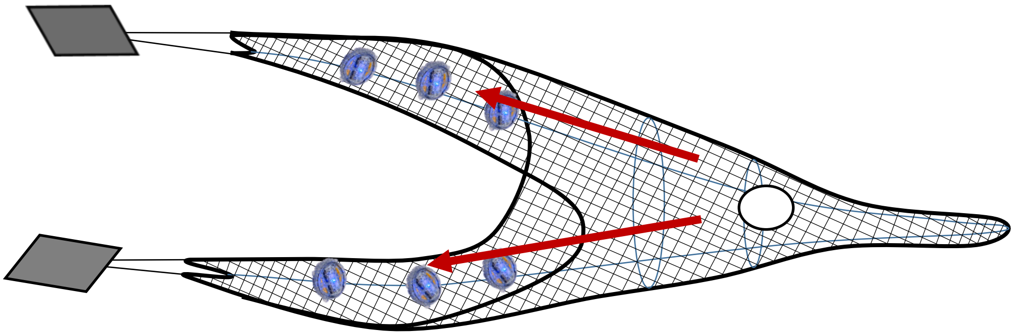


Figure 28:

Alternative light placement suggestion. Future trials may benefit from placing lights on the inside of the trawl wings, so that catsharks have more visual direction for escape, as they were seemingly disorientated at the mouth of the trawl when trying to escape.

Another observed escapement method which was successful for one catshark and attempted by many, was burrowing and twisting through the net mesh, where the successful individual was small enough to squeeze through the mesh holes. Curling is a common defence mechanism among catsharks in the wild when they feel threatened (The Shark Trust, 2019). However, this behaviour led to nearly 17% of observed catsharks becoming entangled in the net. Entanglement may have also been more likely for catsharks as they have tiny tooth-shaped structures that are unique to elasmobranchs, known as dermal denticles (Southall and Sims, 2003), which could be more susceptible to snagging in the net material. Future net designs could consider increasing mesh size at the entrance of the trawl for catsharks, where many were observed swimming. However, this could end up with a loss of target catch in commercial trials (Hendrickson, 2011). The behaviour of target species would therefore need to be observed in future trawling trials, which wasn’t assessed in these trials as the trawling was experimental (not commercial), and catches were mainly elasmobranch species (see Appendix Table 3).

The curling response of catsharks after coming into contact with the net and their lack of response to light potentially showcases that sharks were not using visual cues in this fishing context. Another prominent sense that sharks possess is the ability to detect electrical currents from biological and non-biological sources, via electrosensory receptors in their skin (Jordan et al., 2013). Studies have subsequently trialled magnets and electrical deterrents to cause an aversive response in sharks for bycatch-reduction in longline fishing, but with varied success (Jordan et al., 2013). However, a more recent trial found a 91% reduction in blue shark (*Prionace glauca*) bycatch with SharkGuard, which is a small device that attaches to baited hooks and emits an electric pulse to deter sharks (Doherty et al., 2022). It may be the case that electrical pulses are a better sensory stimulant for sharks compared to light, although this would need to be tested in an active fishing scenario.

For the second prediction, I hypothesised that lights would allow sharks to avoid initial capture in the net. Although there was a slightly greater abundance of catsharks in control hauls, there was no significant difference compared to experimental hauls. This may have been down to the visibility of the LEDs on the headline, where in the video footage from field trials, the ambient light levels seemed higher than light levels in previous laboratory trials. To account for this, I modelled the LED colour modes of *Pisces* in coastal waters at similar depths to where fishing took place, which showed that royal blue would be the same ranking as the laboratory vision model in terms of catshark visual stimulation towards light (Figure 27).

The laboratory model yields slightly higher visual stimulation values for catsharks, which is likely due to the darker background conditions in the tank, and therefore an increased contrast of LEDs to the background. It may also be the case that the ambient light conditions used in the ocean model (Jerlov’s clear ocean type IB; Jerlov, 1968) were darker than the actual conditions in Bigbury bay, as the trials had the additional white light from the camera. This may have further reduced the contrast of the royal blue LEDs to the background, meaning they would be less visually stimulating, which could explain why catsharks were more responsive to light in laboratory conditions, although this is unlikely to be the only factor. However, the visual model does not tell us whether there is a brightness threshold that needs to be met for a behavioural reaction to occur. Ambient conditions have previously been shown to be important in fish and light studies, where researchers found that the use of light in night-time conditions compared to day-time conditions increased the ability of red snapper (*Lutjanus campechanus*) to find an illuminated escape chamber (Parsons et al., 2012). In future fishing-with-light trials, studies might therefore benefit from fishing at greater depths or at night, to increase visibility of LEDs and the chances of responses in fish.

It may also be the case that another LED colour would work better in the field. I chose to use royal blue for field trials as the most catsharks responded to this colour in **Chapter 3**, which could potentially be due to this colour mode having the greatest brightness output. It may be that white (which is the most visually stimulating colour mode according to laboratory and field models; Figure 27) would have been the most behaviourally stimulating to use, which would need to be tested in future trials. However, from video footage, the overriding stimulus that catsharks were subjected to was the movement of trawl, where the majority off catsharks were unable to outswim the trawl once captured. Hence, a change of light colour in these trials is unlikely to change the results.

This chapter has demonstrated the difficulties of replicating laboratory-based behaviours in a field context. In particular, the study highlights the many sensory factors at play in an active fishing scenario, such as the sustained speed of a vessel, BRD placement, ambient light conditions, and optimal sensory systems to target in study species. However, previous laboratory evidence of a link between vision and behaviour could still be applied in further fishing with light trials; for example, for use in fisheries where light has been shown to be successful, in order to further optimise bycatch-reduction with light colour. The trials also show the importance of observing behaviour in a fishing context, where the camera helped to quantify catshark behaviour, as well as showcasing the difficulties that they face in escaping the net once caught. Further gear innovation trials may be needed to enable this species (and other sharks) to escape trawl nets, such as an evaluation of the best sensory system to target, the placement of BRDs and net mesh design.

Chapter 6: General Discussion

Due to the current lack of methodology for selecting an optimal light colour to invoke responses in bycatch species within particular fishing contexts, and the variability in outcomes for bycatch-reduction trials with light, my thesis aimed to address these issues using a sensory ecology approach. Specifically, I explored whether bycatch-reduction with light could be optimised with the use of a vision model, which aimed to predict the most visible light colour to bycatch species when considering their vision underwater.

Summary of results

As sensory ecology is the discipline of how animals perceive and respond to stimuli (Stevens, 2013), I separated bycatch-reduction with light into two parts. For the first part, I considered light as a visual stimuli in different ocean types and depths, by modelling the vision of target and bycatch species in these environments using a quantum-catch model in **Chapter 2**. The results showed that lights are likely viewed differently by target and bycatch species, and ocean type and depths can affect how visible LEDs are to species. Specifically, darker ambient conditions should make LEDs more visually stimulating. In terms of light colours, white light is most visible in all fishing scenarios to all species, whereas red is the least. Differences in visual stimulation values between species are more likely to be observed between short and medium-wavelength colour modes.

As it is impossible to know how species really view lights, and the model only makes predictions based on certain vision parameters, the second part of the sensory ecology approach was to see if empirical behavioural data could match model predictions. Therefore, in **Chapter 3**, I explored whether the model predictions about the visibility of LEDs to target and bycatch species could be linked to behaviour (i.e. whether behavioural responses were more pronounced in the presence of more visually stimulating LED colour modes) through behavioural observations of plaice, skates and catsharks in a controlled tank setting. I found evidence to suggest that LED visibility is linked to behaviour in catsharks, where they had increased interactions with LED colours that should be more stimulating to their vision in tank conditions. This link was less obvious in plaice, but both skates and plaice showed increased stationary behaviour in the presence of more visually stimulating colour modes.

When testing the model predictions about LED visibility by using BRUVs in a non-invasive wild context in **Chapter 4**, the link with behaviour was not as evident. In general, there was a slight increase in the abundances of species to the family level in the presence of BRUVs with lights on, compared to lights off. However, there was no preference for the most visually stimulating light colour (white). The model values for LED visibility in shallow water contexts were also much lower compared to previous chapter models where background conditions were darker, highlighting how LEDs are less contrasting to backgrounds where there is more ambient light.

In Chapters **3 and 4**, behavioural responses of fish to light were also unaffected by flash rate. However, this may have been due to the flash rate settings of the LED product *Pisces*, as the highest flash rate setting of 32 Hz may have been perceived as continuous by some species in **Chapter 4**. Likewise, the next lowest flash rate (4 Hz) may have been to slow to be aversive for fish in both chapters. In future versions of *Pisces*, it may be useful to have a flash rate between 4 and 32 Hz, as this would be within the elasmobranch range of 16 to 25 Hz (McComb et al., 2010) and the teleost range of 30 to 60 Hz (Horodysky et al., 2010).

For the second wild context in **Chapter 5**, I aimed to find empirical data to support the model predictions in an experimental trawling scenario, where the objective was to reduce the capture of catsharks when using lights. Catsharks were chosen as the focus due to their increased responsiveness to light compared to skates and plaice in **Chapter 3**. As the previous laboratory experiments had found that there was no difference in interactions numbers for white, green and blue light in catsharks (potentially due to a visibility and behavioural threshold having being reached for these colours), I chose to trial royal blue light. Additionally, royal blue was also the brightest colour mode out of the LED options, which is likely to maximise the visibility of the LED to catsharks in an ocean setting. By attaching five LEDs to the headline of the trawl, and conducting alternate trawls with lights on versus lights off, I found no difference in catshark abundances between trawls. Hence, the use of royal blue light did not manage to reduce the capture of the bycatch representative.

Although a sensory ecology approach has been successful for managing other conservation issues such as invasive species control (Cruz et al., 2009) and the reduction of bird strike and collisions (Swaddle et al., 2016), the approach was not as successful for reducing bycatch with lights in the trawling scenario that I tested. I therefore discuss aspects of the sensory ecology approach, as well as its applicability to a dynamic fishing environment.

Model evaluation

The use of a quantum-catch model to make predictions about behaviour in a laboratory environment worked well for an active species (catsharks), where evidence for a link was found. Within a laboratory environment, external stimuli such as light, sound and movement are much more easily controlled compared to wild contexts (Campbell et al., 2009). With this reduction in sensory stimuli in captivity (Swaisgood, 2010), if a change to the environment is introduced, it enables easier observation of behaviour (Swaisgood, 2010). As the ambient light environment was constant in the tank trials in **Chapter 3** and the tank area was confined, it meant that the LED was the main object in the field of view for fish. Hence, when assessing links between the vision and model, behaviour that was solely in response to the LEDs could be observed and quantified.

Although the observer bias may have contributed to the lack of evidence for a link between the model and behaviour in **Chapter 4**, evidence to support the link in **Chapter 5** was also lacking. One reason for this could be that the quantum-catch model was not enough to explain behaviour in these ocean contexts, potentially because the model needed more parameters in wild scenarios. Although I considered light availability by using irradiance data from different depths and water types (Jerlov, 1968), other factors like the composition of a background can influence a visual scene (Akkaynak et al., 2017). For example, in the BRUV experiments, kelp, rock and sediment compositions would have been variable depending on BRUV location and position, and in the trawling scenario, the background composition would also be subject to change as the gear moved across the ground. In both BRUV and fishing scenarios, the LEDs were also attached to other equipment such as PVC pipes or fishing gears. Hence, the backdrop to the LED was variable, which the model didn’t account for.

Variable background components have previously been considered in vision models by using a metric known as just noticeable differences (JNDs) (Silvasti et al., 2021). Specifically, JNDs help to predict the ability of an animal to detect the smallest colour difference between an object and the background by assigning discrimination thresholds based on the animal’s vision (Silvasti et al., 2021;

Zanker, 1995). Future models could aim to quantify and categorise background types with different habitats and gear types, to make more accurate predictions about how visible LEDs would be in certain environments. However, as thin filament nets are often designed to be inconspicuous to fish (Battisti et al., 2019) it may be the case that nets would not affect the background as much as other components.

To assess whether variable backgrounds can affect responses of species to LEDs, empirical behavioural data would still be needed to ascertain whether new model assumptions are correct (Olsson et al., 2018). With catsharks and their apparent attraction to light in **Chapter 3**, future tests in a laboratory environment could look at catshark detection speed of LEDs within variable backgrounds, through the "nudging" metric that they showcased. In a fishing scenario, future trials could also test whether bycatch-reduction with light is effected by background composition. This could be trialled in fisheries where light has already successfully reduced bycatch, like with turtles and static gears (Wang et al., 2013). However, for some species, it might be harder to measure the effect of backgrounds on behaviour if they have previously shown little interest in lights (like skates and plaice) or if prior behaviour towards light is unknown.

Another additional model parameter that could be considered in wild contexts is the distance of species from LEDs. As species within the tanks in **Chapter 3** were never more than 2.5 m away from the LED in clear water conditions, it was likely that fish were always able to see the light. I didn't include distance in the model as I assumed fish would be close to LEDs, even within a confined net space. However, to further understand when fish are most likely to notice lights, especially in a trawling scenario where they haven't yet been captured, future models could consider detection distance. This could be achieved through considering visual acuity, which is a parameter of vision that describes the ability of animals to see details within a scene at a given distance (Caves and Johnsen, 2018). A high acuity means that animals are able to see a scene with clarity at a set distance, and a lower acuity means that they are unlikely to define objects (Caves et al., 2020). Much like other vision adaptations, visual acuity can be measured anatomically or behaviourally, where the former would be through photoreceptor density, and the later through optomotor responses, which assesses the head tracking movement of animals when they view a moving object (Caves et al., 2017).

Interestingly, an R package has been produced that predicts how different animals might view a visual scene based on their visual acuity at a given distance (Caves and Johnsen, 2018; Figure 29). If applied to fishing with light trials, it may provide a basis for making clearer predictions on behaviour, by determining what distance marine species would be most likely to notice an LED, and whether they can then react in time before capture.

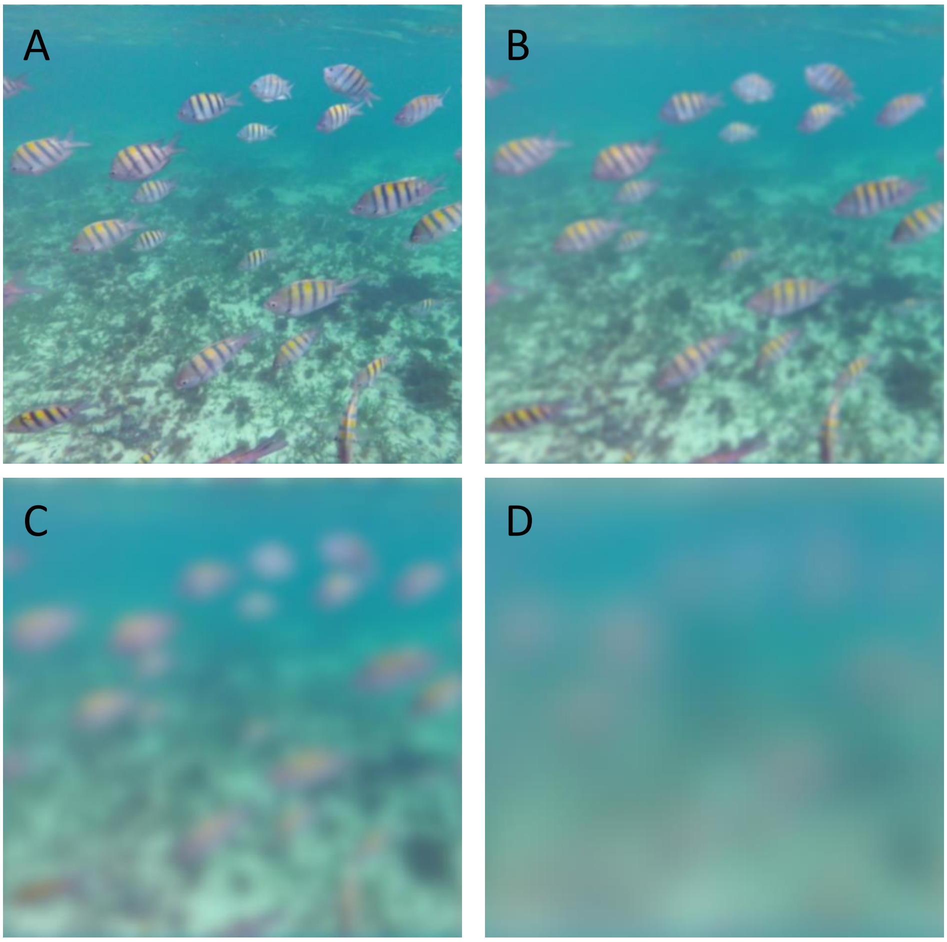


Figure 29:

The predicted visual scene for four commercial species based on their visual acuity from a distance of three metres, using the R package AcuityView (Caves and Johnsen, 2018). A lower degree score means a higher visual acuity. From A to F: **A)** Yellowfin tuna (*Thunnus albacares*), 0.06 degrees (Caves et al., 2017) **B)** Alaska pollock (*Gadus chalcogrammus*) (Caves et al., 2017) **C)** Common octopus, (*Octopus vulgaris*), 0.588 degrees (Hanke and Kelber, 2019) **D)** Blue crab (*Callinectes sapidus*), 1.8 degrees (Baldwin and

Johnsen, 2011). From this, tuna would be most likely to see objects clearly at this distance. This output also does not consider the colour vision capabilities of species.

It is important to note that neither the quantum-catch model in **Chapter 2** nor the AcuityView package considers the horizontal attenuation of light. As previously mentioned, I chose not to include this as 1) I assumed fish would be close to LEDs, and 2) the model was used as a baseline, due to being the first (to my knowledge) to be applied to fishing with light. Additionally, the conditions where I tested links between lights and behaviour were clear from video footage in all chapters, which suggests maximised light transmission through the water column. Although horizontal attenuation of light underwater can be predicted through attenuation equations depending on depth and water type (Aas et al., 2013; Williamson and Hollins, 2023), a more accurate way to assess underwater irradiance would be to take direct measurements using a spectroradiometer. However, deployment of spectroradiometers underwater can be costly due to the need for them to withstand pressure at depth and to be waterproof (Yu et al., 2017). Therefore, it was out of the scope of my PhD fund to use an underwater spectroradiometer, which is why I made use of publicly available irradiance data. However, future research could add the new suggested model parameters of 1) detection distance using visual acuity values from the literature, 2) horizontal attenuation, either by direct light measurements or attenuation equations and 3) background composition using JNDs. With this information, model outputs would potentially be more informative in wild scenarios, in terms of predicting when species are first likely to notice an LED on a net or in their environment. Hence, more informed behavioural predictions can be made based on new model assumptions, such as whether marine species have the swimming capabilities to actually avoid the net by the time they've see the light.

Behaviour evaluation

As previously mentioned, linking vision and behaviour was a key part of the sensory ecology approach. In general, the exploration of any type of stimuli and how they can be measured through behavioural parameters is assessed under the discipline of psychophysics (Akre and Johnsen, 2014; Blough and Yager, 1972). A key challenge with this method of measuring stimuli is that any link with behaviour will always be indirect, as there is no way to neurologically confirm how an animal thinks or sees (Blough and Yager, 1972). Therefore, ensuring that behavioural parameters are consistent across time is key for making assumptions about the given stimuli.

Captive scenario

The captive scenario showcased the importance of finding appropriate behavioural parameters for linking to visual stimuli. For catsharks in **Chapter 3**, the behavioural response to LEDs was quite evident, as there was a repeated nudging of the LED by catsharks. For skates and plaice, the most consistent behavioural response to light was stationary behaviour. As previously mentioned, it may be the case that there was a more subtle behavioural response that would have shown a stronger link with the vision model, such as camouflaging. If this was the case, a higher resolution camera may be needed in future trials to quantify colour changes in relation to the background (Akkaynak et al., 2017) as a measure of response to novel stimuli like LEDs for these species.

When assessing links between the model and behaviour in other species during future trials within a captive scenario, a prior consideration of species ecology may be useful. For example, as many commercial species can form shoals, it may be better to test the behavioural responses of a group rather than the individuals (Yochum et al., 2022). Within a shoal, the movement of conspecifics is often the stimuli that keeps the shoal cohesive (Nakayasu and Watanabe, 2014). Therefore, behavioural parameters such as distance from the light, distance from one another in the shoal, or average speed could be used (Yochum et al., 2022). This was previously explored with Chinook salmon, where five fish at a time were observed via video observation in a tank, to assess how they responded to light colours and different strobe intensities. The study found that with artificial light exposure, swimming speeds of the group increased, as well as distance from the light (Yochum et al., 2022).

For the assessment of speed and distance of fish in tanks, tracking software can be used (Panadeiro et al., 2021). Such software is developed by deep learning methods, where a computer is trained to track an individual in a given space from video footage (Mathis et al., 2018). However, the software can be expensive, and often requires specific lighting environments in order for tracking programmes to locate fish against the background (Panadeiro et al., 2021; Sridhar et al., 2019). Although free software exists (Panadeiro et al., 2021), the time it takes to train the software can be extensive, and as I was only testing individuals, I did not use tracking programmes for my experiments. However, as tracking software develops and becomes more user friendly, automated programmes may be a good way to quantify behaviour in future laboratory settings for fish and light interactions, depending on the species and their ecology.

Wild context

In terms of a behavioural proxy in **Chapter 4**, I chose to assess the abundance of species in the form of maxN and observations, to test if abundances increased in the presence of more visually stimulating light colours, as predicted by the model. As previously discussed, there was no evidence for a link with the model, which may be due to abundance variability across years and locations, as well as a potential observer bias. However, it may have also been the case that the behavioural parameters of abundance were not appropriate measures of visual stimuli in this BRUV context. Other behavioural parameters that could have shown a better link with model predictions may have been direct interactions with the LED on BRUVs, as this rules out other influences on abundances such as the bait. However, due to differences in BRUV designs across years, it would have been hard to conclusively say whether any light interactions were due to the LED colour itself, or differences in light placement. Hence, I chose to use abundance as a behavioural proxy. Future studies could deploy more BRUVs with the 2023 bait arm design (Figure 18), in order to assess the direct interactions of species with different coloured LEDs, as the LED is separated from the bait cage in this design.

Fishing scenario

In fishing contexts, current behavioural parameters for assessing the effects of any gear modification are normally indirectly quantified through catch composition (Pol and Eayrs, 2021). Although a good indicator of whether a gear modification has worked, catch composition does not elude to how the modification has worked. This poses a potential problem when trying to assess how fish respond to light on fishing gear, particularly if assessing different colours.

As previously mentioned, behavioural mechanisms have been proposed in studies that have successfully reduced bycatch with light. Specifically, light is thought to 1) either increase the visibility of nets so that species can avoid capture, 2) repel species away (Hannah et al., 2015; Melli et al., 2018), or 3) attract species to an escape panel. The latter was observed in one study, where a video camera recorded Chinook salmon exiting a net via an illuminated escape panel (Lomeli and Wakefield, 2012). However, to my knowledge, the majority of bycatch-reduction with light studies have not directly observed behaviour towards light in nets, or formerly analysed it. Therefore, it is impossible to say for certain how species may react to light in fishing contexts, without these direct observations.

Direct observations with cameras in a fishing context can be difficult to obtain due to the low light availability and harsh conditions at depth, which is why cameras are often not deployed on gears (Rose et al., 2005). For **Chapter 5**, with the use of a new camera that was specifically designed for trawling gear by my PhD funders, I was able to directly observe the behaviour of fish in the trawl. As previously mentioned, the footage showed that catsharks were unable to escape once captured in the net, and possibly unable to see the lights. Subsequently, behavioural parameters could not be linked to the visual stimuli of LEDs. However, even if future trials changed the position of the lights to maximise escape based on the swimming behaviour and orientation of catsharks, it could well be the case that lights are still not a strong enough sensory stimulant for these species in this dynamic context.

Alternative sensory stimulants

With the help of the video footage in **Chapter 5**, other sensory stimuli that potentially affected catsharks (and species in general) in the trawl could be identified. For catsharks, one such stimuli was touch, where individuals seemed very receptive to the net after coming into contact with it. However, as previously mentioned, contact with the net often induced burrowing and curling behaviour, and in many cases, lead to entanglement. One way to tackle this could be to trial new net material that is less likely to snag on the denticles of elasmobranchs. New net material has previously been trialled with the aim to reduce porpoise bycatch, where iron-oxide gillnets were found to reduce their capture compared to monofilament nets, as the iron-oxide was likely more detectable via porpoise echolocation (Larsen et al., 2007). In a more recent study, a replacement for the cod-end of a net has been designed called the Modular Harvesting System (MHS), which aims to increase the survival and welfare of fish in a trawl (Moran et al., 2023). The new design works by replacing the mesh material of conventional cod-ends with high strength composite fabric, which gives the net a new tubular shape with escapement holes (Moran et al., 2023). With this, water flow within the net is greatly reduced, which enables fish to maintain a normal swimming speed. As such, the net is likely to lead to fewer mortalities of fish as they are not fatigued by the time that they are brought up on deck, which could enable the survival and release of more bycatch species (Moran et al., 2023). Hence, a system like this may be more suitable for reducing shark bycatch in trawls compared to the use of lights.

Another sensory system that has been previously discussed is the unique electrosensory system that elasmobranchs possess (Curtin and Woledge, 1988). This has previously been exploited in a passive fishing scenario to repel shark bycatch with an electrical emitting device called SharkGuard (Doherty et al., 2022). Although electrosensory systems of catsharks were not tested in the trawl, the placement of an electrosensory device could be decided based on the observed swimming behaviour of catsharks. For example, SharkGuard could be placed on the wings of the trawl to repel sharks out of the net once captured, or on the headline of the trawl, to repel sharks from initial capture. However, further research would first need to understand the minimum distance at which electrical fields are first detected by sharks, as well as camera observations on how sharks may approach trawl nets. Hence, it can be determined whether sharks have enough time to react to electrosensory stimulants, given the speed of the vessel.

For bycatch species other than sharks, a similar approach could be taken in terms of using observations from camera footage to assess other appropriate sensory stimulants or BRD positioning. Even though I did not explicitly test skates in the trawling scenario, footage showcased interesting escape attempts, where several skates slowly undulated along the bottom of the net towards the net mouth in order to seemingly counteract the water flow (Figure 30) against their flat bodies. With this knowledge, escape panels could be designed for undersized skate and positioned on the bottom of trawl nets to help them escape. However, as previously mentioned, it could also lead to a loss of target catch, and so observations of target species would also be needed.

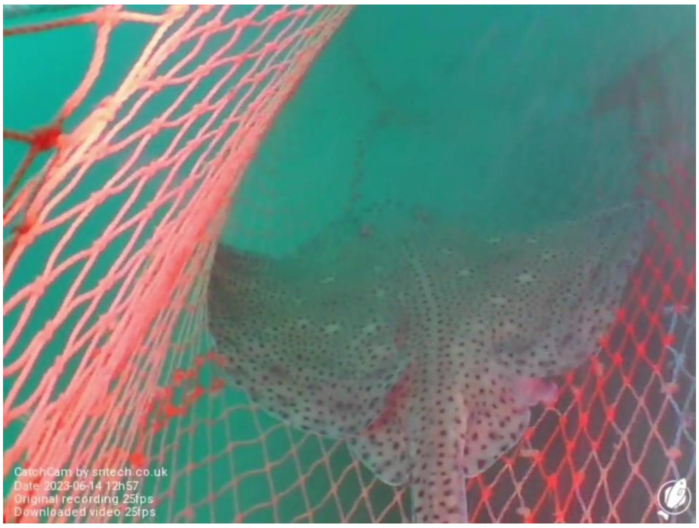


Figure 30:

A blonde ray (*Raja brachyura*) attempting escape in the trawl net. This skate (and several others) were observed laying low in the bottom of the net, in order to seemingly position their bodies to counteract the water flow, which allowed them to navigate back towards the mouth of the trawl.

Future sensory ecology application

Due to the dynamic environment in an active fishing scenario and the many sensory stimulants that can influence behaviour (Wardle, 1986), the sensory ecology approach may need to be altered in active contexts when considering BRDs. Specifically, the behaviour of species within the trawl may need to be assessed first via video observation, rather than starting with the exploration of a species' sensory system. This would mean an increase in deployments of underwater video cameras in future research, to assess behaviour in the net before the influence of a BRD. For example, from video footage obtained in **Chapter 5,** information such as how fish swim (including their orientation in the net and their escape attempts) could be used to choose appropriate sensory stimulants to maximise bycatch reduction in a dynamic fishing scenario (Jordan et al., 2013). Once a suitable behaviour to exploit has been identified, the appropriate sensory system could then be explored to optimise BRDs, such as the use of modelling for visual stimuli, as well as optimising the placement of BRDs when considering the swimming behaviour of bycatch species.

For lights specifically, the application of a vision model first may still be useful when trialling lights in new passive fishing scenarios. In passive environments, with the absence of a moving vessel and net, fewer sensory stimulants are likely to be effecting behaviour, and so assumptions about responses to light may be more accurate (i.e. species may avoid illuminated nets as they are more visible). The vision model may also be more accurate, as background conditions are less changeable compared to dynamic trawling environments. Hence, a better assessment of links between the vision model and behaviour may be made. However, this approach should be avoided in passive scenarios where bycatch species have shown a potential attraction to light, which was demonstrated when the bycatch of diving birds increased with green LEDs on gillnets (Sigurdsson, 2023).

Where light has previously worked to reduce bycatch, the application of a vision model could also still be used to further optimise light colour use and to maximise bycatch reduction. For example, in the studies where an illuminated escape panel has reduced the bycatch of undersized fish (Southworth et al., 2020), the model could be used in further trials to assess whether a particular light colour would improve bycatch-reduction across different depths and conditions. Similarly, the model could be applied to passive scenarios with turtles and gillnets, where light has consistently reduced their bycatch across numerous trials (Bielli et al., 2020; Ortiz et al., 2016; Virgili et al., 2018; Wang et al., 2013).

This application of the model was something that I had aimed to test in a trawling scenario in collaboration with ILVO (Flanders Research Institute for Agriculture, Fisheries and Food), Belgium, where researchers had previously shown a reduction of undersized plaice bycatch with lights when placing LEDs on the headline of an otter trawl in a paired trawl design (lights on versus lights off). The aim was to explore whether white light – which was the most visually stimulating light colour according to the model that I used, which considered plaice vision and fishing conditions - would reduce more plaice bycatch compared to blue light, which was not as visually stimulating. However, the vessel that was being used had equipment issues, and due to PhD time constraints, further trials could not be conducted. This optimisation could still be further explored in future trials, by using different light colours based on model predictions about visibility, to see if bycatch is further reduced.

Practical implications

In the case of **Chapter 5**, the experimental scientific trawls enabled repeated trials without the loss of target catch, as the operation was not commercial. This also allowed trials to continue, even when the lights were not having the desired effect. Subsequently, the practical implications of artificial light in a commercial fishing context were not assessed, such as how light can be adopted within normal fishing operations. This seems to be a widespread issue after initial testing of new gear technologies, where the monitoring of light uptake by fishing fleets after scientific trials is generally lacking in the literature. Lack of monitoring may be due to a lack of uptake in technologies by fishers, which could stem from socioeconomic factors such as the historic distrust between scientists and policy makers and the fishing community (Steins et al., 2023), as well as the potential financial risk to fishing fleets if target catch is lost or operational costs increase with new gear modifications (Eayrs and Pol, 2019).

The monitoring of artificial light-use over time is likely needed, as from the results in **Chapter 4**, the effect of light on fish abundance seems to vary across time, seasons and locations. This may be due to the unbalanced sampling design, where the differences in sampling effort across years and location contributed to the high variability in abundances of species. Future studies would need to alter the BRUV deployment methods used in **Chapter 4**, to ensure consistency across locations, observers and light modalities. However, a high level of variation was also demonstrated in **Chapter 3** with individual responses to light. Further research could assess individual differences in behaviour by considering repeatability, which assesses the potential of individuals to show consistent behavioural traits over time, and can highlight differences in personalities (Bell et al., 2009). For example, differences in boldness and exploration ability have previously been quantified among individual cichlid fish (Mazué et al., 2015). If personalities exist in commercially relevant species, then this could impact responses to light, and have implications for the overall effectiveness of lights as a BRD.

As is the case for many scientific trials, experiments in this thesis were limited by funds. An increase in replicates within wild contexts would have reduced the variation seen in behaviour and abundance. Therefore, the results across chapters also highlight the need for further year-round testing of light in fishing contexts, to assess whether light will be continually effective over time and across variable conditions. This in turn would inform fishers about the effectiveness of light as a BRD, depending on the effect found.

Model adoption

To account for some variability in a fishing context with regard to light-use, the sensory ecology approach was intended to help by considering the variability in the underwater light environment. If the vision model output was applied to further trials in the future, and was found to be helpful, a consideration of how fishing communities would actually adopt the model would be needed. A user friendly mobile app could potentially be created, where fishers could input their bycatch and target species, as well as their current fishing conditions (depth and location). The app could then give an output of the optimal light colour to use. Although this was out of the scope of my PhD project, I have included model components in my thesis and have provided code and data online (see Appendix Table 2 and Figure 11 captions) for any future developments.

Concluding remarks

Although I assessed a sensory ecology approach in two parts for my thesis, starting with vision in **Chapter 2** and then behavioural assessments in **Chapters 3**, **4**, and **5**, the results from fishing trials in **Chapter 5** showcase an additional third part to the sensory ecology approach is likely needed in future work. Specifically, the assessment of bycatch species' general behaviour in dynamic fishing gears, potentially before deciding on the BRD and placement. With this, BRDs in dynamic gears can be further optimised through understanding appropriate sensory systems to exploit.

With light in particular, the results from my thesis have shown that different colours can affect the behaviour of species in a laboratory context, which is in line with many other light studies in captivity (Ciriaco et al., 2003; Marchesan et al., 2005; Yochum et al., 2022). However, within the wild contexts that I tested, I found that light was less effective as a behavioural stimulant. In particular, lights did not reduce bycatch in a trawling scenario, which adds to the results of previous trawling studies, where light as a BRD has had variable success rates (Geraci et al., 2021; Lomeli and Wakefield, 2019; Melli et al., 2018; Southworth et al., 2020). It may be the case that LEDs are more effective in passive scenarios, where multiple studies have shown success with bycatch reduction, particularly with reducing turtle bycatch (Bielli et al., 2020; Ortiz et al., 2016; Virgili et al., 2018; Wang et al., 2013). However, there is a need to explore whether light can consistently achieve bycatch reduction over time, as this is currently lacking in the literature.

Within all fishing contexts, species are unlikely to be affected by only one stimulus such as light. Instead, it may be the case that a multi-sensory approach is needed in order to tackle bycatch in fishing gears. This could be achieved through a top down (sensory system exploration first) or bottom up (behavioural observations first) approach, depending on whether passive or dynamic gears are being used. In whichever case, the combined knowledge of species' sensory capabilities and observations of their behaviour are likely necessary in order to aid innovations in gear technologies, and to ultimately reduce bycatch.

Appendices

Appendix Tables

Appendix Table 1:

The brightness of each light colour mode of *Pisces.* This was measured at 50 cm distance in a dark room with spectroradiometer JETI specbos 1211-2 (300-700 nm). The numbers in bold are the brightness values for the LEDs used in **Chapter 3** tank experiments, which corresponds to the remote setting in the brightness column (low, normal, high or super).

Brightness (300-700nm) @50 cm	***Royal blue***	***Blue***	***Cyan***	***Green***	***Amber***	***Red***	***White***
[mW/sqm] - low	18.37	13.89	9.198	11.06	2.492	6.974	12.9
[mW/sqm] -normal	**68.11**	**52.93**	33.46	35.75	9.797	28.49	**50.64**
[mW/sqm] - high	114.9	90.21	55.62	**57.55**	16.7	**50.66**	86.03
[mW/sqm] - super	370.6	276.1	171.8	160.4	**49.63**	180.2	282.5

Appendix Table 2:

The photoreceptor sensitivities (λmax) of species of commercial interest. Species with * next to their common name have incomplete ocular media data. The ocular media graph column refers to whether lens transmissions were extracted from the literature using the online programme Graphreader (Larson, 2022). Graphs were either extracted from Thorpe et al. (1993), which included the ocular media curves of type A, B, C and D, or from studies that directly measured ocular media (see ocular media reference column). In some cases, a closely related species was chosen instead due to lack of data in the literature. For lens information, the metric used for lens absorption in the literature is **λ**50 (50% of light absorption), which is reported in this table. Columns with N/A either did not record relevant information in the referenced papers, or the information has not been found in the literature. See https://github.com/j-somerville/Light-Vision-Model for how this data was used in the **Chapter 2** model.

Common name	Scientific name	Target/bycatch	Fisheries area
Spurdog	*Squalus acanthias*	Bycatch	UK
Altantic Cod	*Gadus morhua*	Both	UK/Norway
***Black seabass**	*Centropristis striata*	Target	US/North Atlantic
***Atlantic herring**	*Clupea harengus*	Both	UK/Atlantic
Yellowfin tuna	*Thunnus albacares*	Both	South pacific/Panama
Scalloped hammerhead shark	*Sphyrna lewini*	Bycatch	South Pacific/Panama/North Pacific/Hawaii
***Pacific halibut**	*Hippoglossus stenolepis*	Both	North Pacific
Whiting	*Merlanguis merlangus*	Both	North Atlantic
Nephrops	*Nephrops norvegicus*	Target	North Atlantic
Atlantic mackerel	*Scomber scombrus*	Both	North Atlantic
Northern Krill	*Meganyctiphanes norvegica*	Target	North Atlantic
Pacific Bluefin Tuna	*Thunnus orientalis*	Both	Pacific
***Jack Mackerel**	*Trachurus symmetricus*	Target	Pacific
Common sole	*Solea solea*	Both	North Atlantic
Plaice	*Pleuronectes platessa*	Both	North Atlantic
***Chub mackerel**	*Scomber japonicus*	Target	Pacific
***European Anchovy**	*Engraulis encrasicolus*	Target	Atlantic
Thornback ray	*Raja clavata*	Both	North Atlantic
Common seal	*Phoca vitulina*	Bycatch	Pacific and North Atlantic
Catshark	*Scyliorhinus canicula*	Bycatch	North Atlantic
***Green turtle**	*Chelonia mydas*	Bycatch	Atlantic, Pacific, Indian
Blue crab	*Callinectes sapidus*	Target	Western Atlantic
American lobster	*Homarus americanus*	Target	Atlantic
Common cuttlefish	*Sepia officinalis*	Target	North Atlantic
Common octopus	*Octopus vulgaris*	Target	Eastern Atlantic
Sea scallop	*Placopecten magellanicus*	Target	Pacific
Chinook/chum/coho salmon	*Oncorhynchus tshawytscha*	Bycatch	Pacific
Alaska/walleye pollack	*Gadus chalcogrummus*	Target	Pacific

Appendix Table 2 continued

Common name	λmax (nm) & photoreceptor (1)	λmax (nm) & photoreceptor (2)	λmax (nm) & photoreceptor (3)	λmax & photoreceptor (4)	Dark/ light adapted
Spurdog	472, rod	520, cone	N/A	N/A	dark
Altantic cod	446, cone	517, cone	N/A	N/A	light
***Black seabass**	498, rod	463, cone	527, double cone	N/A	dark
***Atlantic herring**	501, rod	N/A	N/A	N/A	dark
Yellowfin tuna	483, rod	485, twin cone	426, cone	N/A	dark
Scalloped hammerhead shark	530, cone	N/A	N/A	N/A	dark
***Pacific halibut**	~530, cone	450, rod	N/A	N/A	dark
Whiting	501, N/A	N/A	N/A	N/A	dark
Nephrops	425, rhabdom	515, rhabdom	N/A	N/A	dark
***Atlantic mackerel**	422, cone	587, cone	N/A	N/A	dark
Northern Krill	490, rhabdom	N/A	N/A	N/A	dark
Pacific Bluefin Tuna	515, cone	423, cone	473, cone	N/A	light
***Jack Mackerel**	496, rod	N/A	N/A	N/A	dark
Common sole	472, cone	523,536, cones	559, cone	511, rod	dark
Plaice	440-460, cone	470-490, cone	560-590, cone	510-540, rod	dark
Chub mackerel	482, cone	525, cone	N/A	N/A	dark
European Anchovy	474, triple cone	502, triple cones	492	N/A	dark
Thornback ray	495-497, rod	N/A	N/A	N/A	unknown
Common seal	510, cone	N/A	N/A	N/A	light
Catshark	502.8, rod	N/A	N/A	N/A	dark
***Green turtle**	365, cone	440, cone	515, cone	560–565, cone	unknown
Blue crab	505, rhabdom	N/A	N/A	N/A	dark
American lobster	515, rhabdom	N/A	N/A	N/A	dark
Common cuttlefish	492, rhabdom	N/A	N/A	N/A	dark
Common octopus	475, rhabdom	N/A	N/A	N/A	dark
Sea scallop	488, rhabdom	513, rhabdom	N/A	N/A	dark
Chinook/chum/coho salmon	434, cone	510, cone	565, cone	508, rod	dark
Alaska/walleye pollack	498, N/A	N/A	N/A	N/A	dark

Appendix Table 2 continued

Common name	Ocular media graph	Lens transmission λ50 (nm)	Age photo-receptor	Age ocular media
Spurdog	Extracted (see ref)	300	Adult	Adult
Altantic cod	Extracted (whiting) type c	398-405	Adult	NA
***Black seabass**	N/A	N/A	Adult	NA
***Atlantic herring**	N/A	373-424	Both	NA
Yellowfin tuna	Extracted, (type D, extrapolated)	415	Adult	30 cm -juvenile
Scalloped hammerhead shark	Extracted, (see ref)	345-350	Juvenile	Juvenile
***Pacific halibut**	N/A	N/A	Adult	N/A
Whiting	N/A	383-397	Adult	N/A
Nephrops	N/A	N/A	Adult	N/A
Atlantic mackerel	Extracted, (type C)	360-402	N/A	N/A
Northern Krill	N/A	N/A	N/A	N/A
Pacific Bluefin Tuna	N/A	N/A	Juvenile	N/A
***Jack Mackerel**	N/A	N/A	N/A	N/A
Common sole	Extracted, (type A, extrapolated)	328-332.	Juvenile	N/A
Plaice	Extracted (type D, extrapolated)	399-408	Adult	N/A
***Chub mackerel**	N/A	N/A	Juvenile	N/A
***European Anchovy**	N/A	N/A	Adult	N/A
Thornback ray	Extracted (type A, extrapolated)	*Raja microocellata* (closest related info) 328	N/A	N/A
Common seal	Extracted (hooded seal, see ref)	350 (hooded seal)	N/A	Adult
Catshark	Extracted (type A, extrapolated)	316-340. Median=328. Same lens transmission as *Raja microocellata*	150-250 g potentially juveniles	N/A
***Green turtle**	N/A	N/A	N/A	N/A
Blue crab	N/A	N/A	N/A	N/A
American lobster	N/A	N/A	Adult	N/A
Common cuttlefish	N/A	N/A	N/A	N/A
Common octopus	N/A	N/A	N/A	N/A
Sea scallop	N/A	N/A	Adult	N/A
Chinook/chum/coho salmon	Extracted (type A,rainbow trout closest relative, between 322-334)	322-334. median =328.	Adult	N/A
Alaska/walleye pollack	Extracted, type C	whiting used (gadoid) 383-397	N/A	N/A

Appendix Table 2 continued

Common name	Ref ocular media	Ref photoreceptors	Comments
Spurdog	https://doi.org/10.1007/s00359-014-0950-y	https://doi.org/10.1007/s00359-014-0950-y	Lens diameter worked out from raw data, Spurdog caught during fishing, average from 87 data points of body length between 550 cm and 1140 cm. Cornea **λ50** is longer wavelength then lens (limiting factor may be cornea in this case).
Altantic cod	https://doi.org/10.1016/0042-6989(93)90085-B	https://doi.org/10.1007/978-94-009-0411-8_4	Gadoid lens transmission (used curve of whiting, as all have same max and similar **λ50**, cod's is slightly higher). Type c
***Black seabass**	N/A	https://doi.org/10.2307/1542188	
***Atlantic herring**	https://doi.org/10.1016/0042-6989(93)90085-B	https://doi.org/10.1017/S0952523807070459	
Yellowfin tuna	https://doi.org/10.1007/978-94-009-0411-8_4	https://doi.org/10.1080/1023624021000003826	Lamda max obtained after MSP in dark-adapted fish. Ocular media for small tuna, 30cm length
Scalloped hammerhead shark	https://doi.org/10.1086/648394	https://doi.org/10.1007/s00227-002-0919-1	Visual pigments not revealed, just spectral sensitivities (no template fitting). Juveniles 530 max and smaller peak at 480. Use 530 as main peak.
***Pacific halibut**	N/A	https://core.ac.uk/download/pdf/235400435.pdf	ERG responses of Pacific halibut to green wavelengths (≈520–580 nm) were diminished by 15 minutes of exposure to simulated sunlight. ERG taken in darkness and light. Photopigments not worked out - but cone may be receptive to longer wavelengths.
Whiting	https://doi.org/10.1016/0042-6989(93)90085-B	https://doi.org/10.1016/0042-6989(65)90057-X	
Nephrops	N/A	https://doi.org/10.1017/S0025315402006203	Nephrops norvegicus (when dark adapted) had absorption spectra which fit better when modelled as a single pigment eye as the superposition of light rays occurred on the proximal rhabdom. Likely to have a single pigment
***Atlantic mackerel**	N/A	https://doi.org/10.1016/0042-6989(65)90057-X	
Northern Krill	N/A	https://doi.org/10.1007/s003590050385	
Pacific Bluefin Tuna	N/A	https://doi.org/10.1007/s10695-011-9574-0	Juvenile photoreceptor vision. 138 mm in length
***Jack Mackerel**	N/A	https://doi.org/10.1016/0042-6989(65)90057-X	
Common sole	https://doi.org/10.1016/0042-6989(93)90085-B	https://doi.org/10.1002/cne.24893	180–250 days old; i.e., over 5 months after metamorphosis. Single and double cones. Two medium cone peaks
Plaice	https://doi.org/10.1016/0042-6989(93)90085-B	https://doi.org/10.1113/jphysiol.1968.sp008473	Two SW photoreceptors given in article, but for purpose of model, labelled longer-wavelength sensitivity one as MW. Also, ocular media chosen for model was type D - high concentrations of 360 and 320-30 nm pigment and around 400 nm for **λ50**.

***Chub mackerel**	N/A	https://doi.org/10.1007/s10695-008-9289-z	Some UV sensitivity, might not be UV cone but due to ocular media transmittance. Juveniles may possess more SW sensitivity. Munz 1964 also reported 491 nm sensitivity on visual pigment extraction. Possibly dichromatic species.
***European Anchovy**	N/A	http://dx.doi.org/10.1016/j.visres.2012.07.005	Visual pigment template best fittted, 474 and 502 nm.
Thornback ray	https://doi.org/10.1016/0042-6989(93)90085-B	https://pubmed.ncbi.nlm.nih.gov/868394/#:~:text=The%20retina%20possesses%20both%20the,540%2C%20502%20and%20476%20nm.	Unable to access full paper, getting information from abstract for photoreceptor sensitivity. For ocular media, using Thorpe et al 1993 lens transmission 'A' as closely related species has **λ50** that fits this category, with no pigment in lens
Common seal	https://doi.org/10.1242/bio.011304	https://doi.org/10.1139/z98-129	Some discrepancies between rod and cone cell sensitivity in pinniped studies. Likely to be colour blind/monochromatic but use rods and cones different for ambient light conditions. Hooded seal used for ocular media
Catshark	https://doi.org/10.1016/0042-6989(93)90085-B	https://doi.org/10.1007/s10695-006-9113-6	
***Green turtle**	N/A	http://dx.doi.org/10.1186/1472-6785-14-14	
Blue crab	N/A	https://link.springer.com/content/pdf/10.1007/BF00878449.pdf	
American lobster	N/A	https://link.springer.com/article/10.1007/BF00619310	
Common cuttlefish	N/A	https://doi.org/10.1016/j.visres.2005.09.035	
Common octopus	N/A	https://www.nature.com/articles/214572a0	
Sea scallop	N/A	https://doi.org/10.1242/jeb.048108	
Chinook/chum/coho salmon	https://doi.org/10.1016/0042-6989(93)90085-B	https://link.springer.com/content/pdf/10.1007/s00359-004-0573-9.pdf	Extracted (Type A, rainbow trout closest relative. Between 322-334) 328 medium.
Alaska/walleye pollack	https://doi.org/10.1016/0042-6989(93)90085-B	https://doi.org/10.1016/0042-6989(69)90107-2	Gadoid lens transmission (used curve of whiting, as all have same max and similar **λ50**, cod's is slightly higher). No mention of photoreceptor type, just pigment peak.

Appendix Table 3:

Species catch composition from experimental alternate trawling with lights on versus lights off. Measurement data includes length, weight, and disk length, where this latter measurement is for skates (*Raja* spp), which is the width between each wing tip. Light mode is whether lights were on or off for hauls. Sex was identified for elasmobranchs due to the presence or absence of claspers (male reproductive organ).

Haul ID	***Haul date***	***Species name***	***Length (cm)***	***Weight (g)***	***Disk (cm)***	***Sex***	***Light mode***
2023-001	13/06/2023	*Chelidonichthys cuculus*	302	272	0		off
2023-001	13/06/2023	*Chelidonichthys cuculus*	258	162	0		off
2023-001	13/06/2023	*Chelidonichthys cuculus*	275	188	0		off
2023-001	13/06/2023	*Chelidonichthys cuculus*	285	198	0		off
2023-001	13/06/2023	*Chelidonichthys cuculus*	202	88	0		off
2023-001	13/06/2023	*Conger conger*	1200	3300	0		off
2023-001	13/06/2023	*Conger conger*	835	1400	0		off
2023-001	13/06/2023	*Eutrigla gurnardus*	239	110	0		off
2023-001	13/06/2023	*Gobius spp.*	39	1	0		off
2023-001	13/06/2023	*Labrus mixtus*	310	382	0		off
2023-001	13/06/2023	*Labrus mixtus*	328	354	0		off
2023-001	13/06/2023	*Lepadogaster lepadogaster*	27	1	0		off
2023-001	13/06/2023	*Limanda limanda*	169	50	0		off
2023-001	13/06/2023	*Mustelus asterias*	720	1492	0	f	off
2023-001	13/06/2023	*Mustelus asterias*	744	1368	0	f	off
2023-001	13/06/2023	*Mustelus asterias*	660	1018	0	f	off
2023-001	13/06/2023	*Mustelus asterias*	711	1326	0	f	off
2023-001	13/06/2023	*Mustelus asterias*	725	1396	0	m	off
2023-001	13/06/2023	*Mustelus asterias*	710	1292	0	m	off
2023-001	13/06/2023	*Mustelus asterias*	801	1903	0	m	off
2023-001	13/06/2023	*Pleuronectes platessa*	340	414	0		off
2023-001	13/06/2023	*Pleuronectes platessa*	354	480	0		off
2023-001	13/06/2023	*Scophthalmus maximus*	376	1196	0		off
2023-001	13/06/2023	*Raja brachyura*	538	1182	380	f	off
2023-001	13/06/2023	*Raja brachyura*	848	5000	550	f	off
2023-001	13/06/2023	*Raja brachyura*	1010	7600	762	f	off
2023-001	13/06/2023	*Raja brachyura*	920	7000	672	f	off
2023-001	13/06/2023	*Raja brachyura*	821	4600	600	f	off
2023-001	13/06/2023	*Raja brachyura*	564	1472	401	f	off
2023-001	13/06/2023	*Raja brachyura*	598	1616	433	f	off
2023-001	13/06/2023	*Raja brachyura*	439	609	312	m	off
2023-001	13/06/2023	*Raja brachyura*	903	5900	680	f	off
2023-001	13/06/2023	*Raja brachyura*	563	1183	398	m	off
2023-001	13/06/2023	*Raja brachyura*	780	3800	558	m	off
2023-001	13/06/2023	*Raja brachyura*	945	7500	680	f	off
2023-001	13/06/2023	*Raja brachyura*	499	816	350	f	off
2023-001	13/06/2023	*Raja clavata*	665	1930	457	f	off
2023-001	13/06/2023	*Raja montagui*	499	732	317	m	off
2023-001	13/06/2023	*Raja montagui*	573	1400	390	f	off
2023-001	13/06/2023	*Scyliorhinus canicula*	595	694	0	m	off
2023-001	13/06/2023	*Scyliorhinus canicula*	610	808	0	m	off
2023-001	13/06/2023	*Scyliorhinus canicula*	651	944	0	m	off
2023-001	13/06/2023	*Scyliorhinus canicula*	625	826	0	m	off

2023-001	13/06/2023	*Scyliorhinus canicula*	619	848	0	m	off
2023-001	13/06/2023	*Scyliorhinus canicula*	591	846	0	m	off
2023-001	13/06/2023	*Scyliorhinus canicula*	592	736	0	m	off
2023-001	13/06/2023	*Scyliorhinus canicula*	632	926	0	m	off
2023-001	13/06/2023	*Scyliorhinus canicula*	598	796	0	m	off
2023-001	13/06/2023	*Scyliorhinus canicula*	588	736	0	m	off
2023-001	13/06/2023	*Scyliorhinus canicula*	658	1074	0	m	off
2023-001	13/06/2023	*Scyliorhinus canicula*	594	742	0	m	off
2023-001	13/06/2023	*Scyliorhinus canicula*	525	542	0	m	off
2023-001	13/06/2023	*Scyliorhinus canicula*	600	722	0	m	off
2023-001	13/06/2023	*Scyliorhinus canicula*	575	694	0	m	off
2023-001	13/06/2023	*Scyliorhinus canicula*	529	560	0	m	off
2023-001	13/06/2023	*Scyliorhinus canicula*	594	716	0	m	off
2023-001	13/06/2023	*Scyliorhinus canicula*	623	736	0	m	off
2023-001	13/06/2023	*Scyliorhinus canicula*	589	774	0	m	off
2023-001	13/06/2023	*Scyliorhinus canicula*	441	334	0	f	off
2023-001	13/06/2023	*Scyliorhinus canicula*	615	864	0	f	off
2023-001	13/06/2023	*Scyliorhinus canicula*	581	768	0	f	off
2023-001	13/06/2023	*Scyliorhinus canicula*	555	618	0	m	off
2023-001	13/06/2023	*Trisopterus minutus*	170	116	0		off
2023-001	13/06/2023	*Zeus faber*	230	188	0		off
2023-001	13/06/2023	*Zeus faber*	352	232	0		off
2023-001	13/06/2023	*Zeus faber*	243	226	0		off
2023-001	13/06/2023	*Zeus faber*	306	402	0		off
2023-002	13/06/2023	*Eutrigla gurnardus*	338	331	0		on
2023-002	13/06/2023	*Mustelus asterias*	753	1691	0	f	on
2023-002	13/06/2023	*Mustelus asterias*	772	1625	0	f	on
2023-002	13/06/2023	*Mustelus asterias*	790	1804	0	f	on
2023-002	13/06/2023	*Pleuronectes platessa*	295	305	0		on
2023-002	13/06/2023	*Raja brachyura*	566	1300	395	m	on
2023-002	13/06/2023	*Raja brachyura*	600	1584	421	f	on
2023-002	13/06/2023	*Raja brachyura*	828	4500	582	f	on
2023-002	13/06/2023	*Raja brachyura*	665	1900	470	f	on
2023-002	13/06/2023	*Raja brachyura*	542	1030	383	m	on
2023-002	13/06/2023	*Raja brachyura*	1007	8000	705	m	on
2023-002	13/06/2023	*Raja brachyura*	418	459	292	m	on
2023-002	13/06/2023	*Raja brachyura*	851	5000	618	f	on
2023-002	13/06/2023	*Raja clavata*	915	5800	650	f	on
2023-002	13/06/2023	*Raja montagui*	706	2500	458	f	on
2023-002	13/06/2023	*Scyliorhinus canicula*	592	674	0	m	on
2023-002	13/06/2023	*Scyliorhinus canicula*	520	577	0	m	on
2023-002	13/06/2023	*Scyliorhinus canicula*	632	808	0	m	on
2023-002	13/06/2023	*Scyliorhinus canicula*	579	675	0	m	on
2023-002	13/06/2023	*Scyliorhinus canicula*	608	824	0	f	on
2023-002	13/06/2023	*Scyliorhinus canicula*	586	670	0	f	on
2023-002	13/06/2023	*Scyliorhinus canicula*	636	851	0	f	on
2023-002	13/06/2023	*Scyliorhinus canicula*	580	697	0	f	on
2023-002	13/06/2023	*Trisopterus luscus*	273	280	0		on

2023-002	13/06/2023	*Trisopterus luscus*	242	177	0		on
2023-002	13/06/2023	*Zeus faber*	345	704	0		on
2023-002	13/06/2023	*Zeus faber*	316	487	0		on
2023-002	13/06/2023	*Zeus faber*	321	534	0		on
2023-003	14/06/2023	*Chelidonichthys cuculus*	305	276	0		on
2023-003	14/06/2023	*Chelidonichthys cuculus*	255	176	0		on
2023-003	14/06/2023	*Chelidonichthys cuculus*	265	202	0		on
2023-003	14/06/2023	*Chelidonichthys cuculus*	279	246	0		on
2023-003	14/06/2023	*Eutrigla gurnardus*	250	172	0		on
2023-003	14/06/2023	*Mustelus asterias*	810	1922	0	m	on
2023-003	14/06/2023	*Mustelus asterias*	785	1725	0	f	on
2023-003	14/06/2023	*Pleuronectes platessa*	512	1622	0		on
2023-003	14/06/2023	*Raja brachyura*	542	1202	299	m	on
2023-003	14/06/2023	*Raja brachyura*	595	1438	415	f	on
2023-003	14/06/2023	*Raja brachyura*	682	2624	450	m	on
2023-003	14/06/2023	*Raja brachyura*	655	2028	470	m	on
2023-003	14/06/2023	*Raja brachyura*	795	3700	565	m	on
2023-003	14/06/2023	*Raja brachyura*	641	1940	455	m	on
2023-003	14/06/2023	*Raja brachyura*	515	974	371	m	on
2023-003	14/06/2023	*Raja brachyura*	662	2309	480	f	on
2023-003	14/06/2023	*Raja brachyura*	758	3256	550	f	on
2023-003	14/06/2023	*Raja brachyura*	572	1370	305	f	on
2023-003	14/06/2023	*Raja brachyura*	854	4500	580	f	on
2023-003	14/06/2023	*Raja brachyura*	580	1400	410	f	on
2023-003	14/06/2023	*Raja brachyura*	700	2286	499	m	on
2023-003	14/06/2023	*Raja brachyura*	629	1702	442	m	on
2023-003	14/06/2023	*Raja brachyura*	765	3600	530	f	on
2023-003	14/06/2023	*Raja brachyura*	505	828	348	m	on
2023-003	14/06/2023	*Scyliorhinus canicula*	576	685	0	m	on
2023-003	14/06/2023	*Scyliorhinus canicula*	570	740	0	m	on
2023-003	14/06/2023	*Scyliorhinus canicula*	629	865	0	m	on
2023-003	14/06/2023	*Scyliorhinus canicula*	577	672	0	m	on
2023-003	14/06/2023	*Scyliorhinus canicula*	620	803	0	m	on
2023-003	14/06/2023	*Scyliorhinus canicula*	642	576	0	m	on
2023-003	14/06/2023	*Scyliorhinus canicula*	620	824	0	m	on
2023-003	14/06/2023	*Scyliorhinus canicula*	558	625	0	m	on
2023-003	14/06/2023	*Scyliorhinus canicula*	589	637	0	m	on
2023-003	14/06/2023	*Scyliorhinus canicula*	604	689	0	m	on
2023-003	14/06/2023	*Scyliorhinus canicula*	550	562	0	m	on
2023-003	14/06/2023	*Scyliorhinus canicula*	600	712	0	m	on
2023-003	14/06/2023	*Scyliorhinus canicula*	680	1064	0	m	on
2023-003	14/06/2023	*Scyliorhinus canicula*	536	519	0	m	on
2023-003	14/06/2023	*Scyliorhinus canicula*	564	642	0	f	on
2023-003	14/06/2023	*Scyliorhinus canicula*	620	807	0	m	on
2023-003	14/06/2023	*Scyliorhinus canicula*	610	836	0	m	on
2023-003	14/06/2023	*Scyliorhinus canicula*	615	815	0	m	on
2023-003	14/06/2023	*Scyliorhinus canicula*	629	835	0	m	on
2023-003	14/06/2023	*Scyliorhinus canicula*	552	583	0	m	on

2023-003	14/06/2023	*Scyliorhinus canicula*	538	537	0	f	on
2023-003	14/06/2023	*Scyliorhinus canicula*	587	761	0	f	on
2023-003	14/06/2023	*Scyliorhinus canicula*	602	763	0	m	on
2023-003	14/06/2023	*Trisopterus minutus*	136	56	0		on
2023-003	14/06/2023	*Zeus faber*	194	152	0		on
2023-004	14/06/2023	*Chelidonichthys cuculus*	261	175	0		off
2023-004	14/06/2023	*Chelidonichthys cuculus*	175	51	0		off
2023-004	14/06/2023	*Chelidonichthys cuculus*	261	175	0		off
2023-004	14/06/2023	*Chelidonichthys cuculus*	203	81	0		off
2023-004	14/06/2023	*Conger conger*	1005	1500	0		off
2023-004	14/06/2023	*Eutrigla gurnardus*	302	218	0		off
2023-004	14/06/2023	*Eutrigla gurnardus*	256	132	0		off
2023-004	14/06/2023	*Eutrigla gurnardus*	270	155	0		off
2023-004	14/06/2023	*Labrus bergylta*	371	1382	0		off
2023-004	14/06/2023	*Microstomus kitt*	355	950	0		off
2023-004	14/06/2023	*Mustelus asterias*	825	1760	0	m	off
2023-004	14/06/2023	*Mustelus asterias*	750	1496	0	f	off
2023-004	14/06/2023	*Mustelus asterias*	745	1564	0	f	off
2023-004	14/06/2023	*Mustelus asterias*	815	1882	0	f	off
2023-004	14/06/2023	*Mustelus asterias*	840	2202	0	f	off
2023-004	14/06/2023	*Mustelus asterias*	755	1534	0	m	off
2023-004	14/06/2023	*Mustelus asterias*	752	1492	0	m	off
2023-004	14/06/2023	*Pleuronectes platessa*	273	198	0		off
2023-004	14/06/2023	*Pleuronectes platessa*	290	238	0		off
2023-004	14/06/2023	*Pleuronectes platessa*	290	238	0		off
2023-004	14/06/2023	*Raja brachyura*	396	707	271	m	off
2023-004	14/06/2023	*Raja brachyura*	604	1966	436	f	off
2023-004	14/06/2023	*Raja brachyura*	609	1410	400	m	off
2023-004	14/06/2023	*Raja brachyura*	930	6500	668	f	off
2023-004	14/06/2023	*Raja brachyura*	748	3500	535	f	off
2023-004	14/06/2023	*Raja brachyura*	428	814	298	f	off
2023-004	14/06/2023	*Raja brachyura*	496	934	360	f	off
2023-004	14/06/2023	*Raja brachyura*	583	1520	424	f	off
2023-004	14/06/2023	*Raja brachyura*	1000	8500	705	m	off
2023-004	14/06/2023	*Raja brachyura*	520	1274	379	m	off
2023-004	14/06/2023	*Raja brachyura*	519	1292	368	m	off
2023-004	14/06/2023	*Raja brachyura*	214	66	143	m	off
2023-004	14/06/2023	*Raja brachyura*	820	4100	566	f	off
2023-004	14/06/2023	*Raja brachyura*	859	5000	609	m	off
2023-004	14/06/2023	*Raja brachyura*	541	1522	391	m	off
2023-004	14/06/2023	*Raja brachyura*	925	6500	651	m	off
2023-004	14/06/2023	*Raja microocellata*	760	3500	549	f	off
2023-004	14/06/2023	*Raja microocellata*	791	3400	513	m	off
2023-004	14/06/2023	*Raja montagui*	535	1355	371	f	off
2023-004	14/06/2023	*Raja montagui*	618	1878	435	f	off
2023-004	14/06/2023	*Raja montagui*	538	1346	380	f	off
2023-004	14/06/2023	*Raja montagui*	506	1088	321	f	off
2023-004	14/06/2023	*Raja montagui*	507	1242	360	f	off

2023-004	14/06/2023	*Raja montagui*	371	608	244	m	off
2023-004	14/06/2023	*Raja montagui*	474	990	314	m	off
2023-004	14/06/2023	*Raja montagui*	620	1790	399	m	off
2023-004	14/06/2023	*Scyliorhinus canicula*	641	1176	0	f	off
2023-004	14/06/2023	*Scyliorhinus canicula*	0	0	0		off
2023-004	14/06/2023	*Scyliorhinus canicula*	0	0	0		off
2023-004	14/06/2023	*Scyliorhinus canicula*	0	0	0		off
2023-004	14/06/2023	*Scyliorhinus canicula*	0	0	0		off
2023-004	14/06/2023	*Scyliorhinus canicula*	0	0	0		off
2023-004	14/06/2023	*Scyliorhinus canicula*	0	0	0		off
2023-004	14/06/2023	*Scyliorhinus canicula*	0	0	0		off
2023-004	14/06/2023	*Scyliorhinus canicula*	0	0	0		off
2023-004	14/06/2023	*Scyliorhinus canicula*	0	0	0		off
2023-004	14/06/2023	*Scyliorhinus canicula*	0	0	0		off
2023-004	14/06/2023	*Scyliorhinus canicula*	0	0	0		off
2023-004	14/06/2023	*Scyliorhinus canicula*	0	0	0		off
2023-004	14/06/2023	*Scyliorhinus canicula*	0	0	0		off
2023-004	14/06/2023	*Scyliorhinus canicula*	0	0	0		off
2023-004	14/06/2023	*Scyliorhinus canicula*	0	0	0		off
2023-004	14/06/2023	*Scyliorhinus canicula*	0	0	0		off
2023-004	14/06/2023	*Scyliorhinus canicula*	0	0	0		off
2023-004	14/06/2023	*Scyliorhinus canicula*	0	0	0		off
2023-004	14/06/2023	*Zeus faber*	200	103	0		off
2023-004	14/06/2023	*Zeus faber*	191	90	0		off
2023-004	14/06/2023	*Zeus faber*	209	117	0		off
2023-004	14/06/2023	*Zeus faber*	242	180	0		off
2023-004	14/06/2023	*Zeus faber*	328	440	0		off
2023-004	14/06/2023	*Zeus faber*	180	76	0		off
2023-005	14/06/2023	*Callionymus lyra*	201	64	0		on
2023-005	14/06/2023	*Chelidonichthys cuculus*	275	195	0		on
2023-005	14/06/2023	*Chelidonichthys cuculus*	201	85	0		on
2023-005	14/06/2023	*Chelidonichthys cuculus*	210	85	0		on
2023-005	14/06/2023	*Chelidonichthys cuculus*	334	347	0		on
2023-005	14/06/2023	*Eutrigla gurnardus*	220	91	0		on
2023-005	14/06/2023	*Eutrigla gurnardus*	215	85	0		on
2023-005	14/06/2023	*Eutrigla gurnardus*	203	68	0		on
2023-005	14/06/2023	*Eutrigla gurnardus*	184	64	0		on
2023-005	14/06/2023	*Hyperoplus immaculatus*	69	1	0		on
2023-005	14/06/2023	*Labrus bergylta*	331	677	0		on
2023-005	14/06/2023	*Mullus surmuletus*	161	63	0		on
2023-005	14/06/2023	*Mustelus asterias*	625	798	0	f	on
2023-005	14/06/2023	*Pleuronectes platessa*	292	277	0		on
2023-005	14/06/2023	*Pollachius pollachius*	465	867	0		on
2023-005	14/06/2023	*Raja brachyura*	600	1411	418	f	on
2023-005	14/06/2023	*Raja brachyura*	640	3000	525	f	on
2023-005	14/06/2023	*Raja brachyura*	910	6900	642	f	on
2023-005	14/06/2023	*Raja brachyura*	625	1799	438	m	on
2023-005	14/06/2023	*Raja brachyura*	952	7000	670	f	on

2023-005	14/06/2023	*Raja brachyura*	910	5200	620	m	on
2023-005	14/06/2023	*Raja brachyura*	835	4900	590	f	on
2023-005	14/06/2023	*Raja brachyura*	625	1732	448	f	on
2023-005	14/06/2023	*Raja brachyura*	705	2464	496	m	on
2023-005	14/06/2023	*Raja brachyura*	920	6500	650	f	on
2023-005	14/06/2023	*Raja brachyura*	990	7900	690	m	on
2023-005	14/06/2023	*Raja brachyura*	820	4458	4200	f	on
2023-005	14/06/2023	*Raja brachyura*	655	1744	445	m	on
2023-005	14/06/2023	*Raja brachyura*	732	3500	549	m	on
2023-005	14/06/2023	*Raja brachyura*	620	2007	449	f	on
2023-005	14/06/2023	*Raja brachyura*	790	4000	565	f	on
2023-005	14/06/2023	*Raja brachyura*	736	3142	537	m	on
2023-005	14/06/2023	*Raja brachyura*	487	693	325	m	on
2023-005	14/06/2023	*Raja brachyura*	940	6800	650	m	on
2023-005	14/06/2023	*Raja brachyura*	815	4900	582	f	on
2023-005	14/06/2023	*Raja brachyura*	654	1997	448	f	on
2023-005	14/06/2023	*Raja brachyura*	862	5000	635	f	on
2023-005	14/06/2023	*Raja brachyura*	480	863	360	f	on
2023-005	14/06/2023	*Raja brachyura*	680	2474	463	f	on
2023-005	14/06/2023	*Raja brachyura*	825	4500	605	f	on
2023-005	14/06/2023	*Raja brachyura*	580	1478	425	f	on
2023-005	14/06/2023	*Raja brachyura*	847	5000	592	f	on
2023-005	14/06/2023	*Raja microocellata*	729	2948	479	m	on
2023-005	14/06/2023	*Raja microocellata*	673	2242	496	f	on
2023-005	14/06/2023	*Raja montagui*	702	2734	465	f	on
2023-005	14/06/2023	*Raja montagui*	538	1092	362	f	on
2023-005	14/06/2023	*Raja montagui*	678	2552	458	f	on
2023-005	14/06/2023	*Raja montagui*	586	1360	390	f	on
2023-005	14/06/2023	*Raja montagui*	546	1142	367	m	on
2023-005	14/06/2023	*Raja montagui*	633	1790	427	m	on
2023-005	14/06/2023	*Raja montagui*	580	1288	380	m	on
2023-005	14/06/2023	*Raja montagui*	551	1196	370	m	on
2023-005	14/06/2023	*Raja montagui*	579	1520	388	f	on
2023-005	14/06/2023	*Scyliorhinus canicula*	623	858	0	m	on
2023-005	14/06/2023	*Scyliorhinus canicula*	629	912	0	m	on
2023-005	14/06/2023	*Scyliorhinus canicula*	612	758	0	m	on
2023-005	14/06/2023	*Scyliorhinus canicula*	564	676	0	m	on
2023-005	14/06/2023	*Scyliorhinus canicula*	458	332	0	m	on
2023-005	14/06/2023	*Scyliorhinus canicula*	588	768	0	m	on
2023-005	14/06/2023	*Scyliorhinus canicula*	519	588	0	m	on
2023-005	14/06/2023	*Scyliorhinus canicula*	630	844	0	f	on
2023-005	14/06/2023	*Scyliorhinus canicula*	623	854	0	f	on
2023-005	14/06/2023	*Scyliorhinus canicula*	625	882	0	m	on
2023-005	14/06/2023	*Trisopterus luscus*	261	246	0		on
2023-005	14/06/2023	*Trisopterus luscus*	239	168	0		on
2023-005	14/06/2023	*Trisopterus luscus*	251	283	0		on
2023-005	14/06/2023	*Trisopterus luscus*	242	187	0		on
2023-005	14/06/2023	*Trisopterus luscus*	273	245	0		on

2023-005	14/06/2023	*Trisopterus luscus*	307	374	0		on
2023-005	14/06/2023	*Zeus faber*	204	151	0		on
2023-005	14/06/2023	*Zeus faber*	151	74	0		on
2023-005	14/06/2023	*Zeus faber*	317	503	0		on
2023-005	14/06/2023	*Zeus faber*	230	189	0		on
2023-005	14/06/2023	*Zeus faber*	227	198	0		on
2023-006	14/06/2023	*Chelidonichthys cuculus*	208	60	0		off
2023-006	14/06/2023	*Chelidonichthys cuculus*	192	39	0		off
2023-006	14/06/2023	*Chelidonichthys cuculus*	279	169	0		off
2023-006	14/06/2023	*Eutrigla gurnardus*	281	194	0		off
2023-006	14/06/2023	*Eutrigla gurnardus*	227	81	0		off
2023-006	14/06/2023	*Mustelus asterias*	708	1346	0	f	off
2023-006	14/06/2023	*Mustelus asterias*	862	2248	0	f	off
2023-006	14/06/2023	*Mustelus asterias*	703	1268	0	f	off
2023-006	14/06/2023	*Pleuronectes platessa*	260	175	0		off
2023-006	14/06/2023	*Raja brachyura*	682	2278	495	m	off
2023-006	14/06/2023	*Raja brachyura*	579	1282	394	m	off
2023-006	14/06/2023	*Raja brachyura*	580	1370	415	f	off
2023-006	14/06/2023	*Raja brachyura*	517	990	383	f	off
2023-006	14/06/2023	*Raja brachyura*	642	1901	461	f	off
2023-006	14/06/2023	*Raja brachyura*	671	2403	490	f	off
2023-006	14/06/2023	*Raja brachyura*	686	2417	490	f	off
2023-006	14/06/2023	*Raja montagui*	577	1384	395	f	off
2023-006	14/06/2023	*Raja montagui*	575	1253	375	f	off
2023-006	14/06/2023	*Scyliorhinus canicula*	537	621	0	m	off
2023-006	14/06/2023	*Scyliorhinus canicula*	550	517	0	m	off
2023-006	14/06/2023	*Scyliorhinus canicula*	600	773	0	m	off
2023-006	14/06/2023	*Scyliorhinus canicula*	573	649	0	m	off
2023-006	14/06/2023	*Scyliorhinus canicula*	570	678	0	m	off
2023-006	14/06/2023	*Scyliorhinus canicula*	604	740	0	f	off
2023-006	14/06/2023	*Scyliorhinus canicula*	586	770	0	m	off
2023-006	14/06/2023	*Scyliorhinus canicula*	514	425	0	m	off
2023-006	14/06/2023	*Scyliorhinus canicula*	628	963	0	m	off
2023-006	14/06/2023	*Scyliorhinus canicula*	535	532	0	m	off
2023-006	14/06/2023	*Scyliorhinus canicula*	620	717	0	m	off
2023-006	14/06/2023	*Scyliorhinus canicula*	534	590	0	m	off
2023-006	14/06/2023	*Scyliorhinus canicula*	535	474	0	m	off
2023-006	14/06/2023	*Scyliorhinus canicula*	635	864	0	m	off
2023-006	14/06/2023	*Zeus faber*	351	680	0		off
2023-007	07/09/2023	*Mustelus asterias*	910	3000	0	f	on
2023-007	07/09/2023	*Pleuronectes platessa*	381	640	0		on
2023-007	07/09/2023	*Scophthalmus maximus*	357	1050	0		on
2023-007	07/09/2023	*Scyliorhinus canicula*	628	1002	0	m	on
2023-007	07/09/2023	*Scyliorhinus canicula*	612	822	0	m	on
2023-007	07/09/2023	*Scyliorhinus canicula*	569	706	0	f	on
2023-007	07/09/2023	*Scyliorhinus canicula*	613	902	0	m	on
2023-007	07/09/2023	*Scyliorhinus canicula*	710	1142	0	m	on
2023-007	07/09/2023	*Scyliorhinus canicula*	672	1023	0	m	on

2023-007	07/09/2023	*Scyliorhinus canicula*	562	734	0	m	on
2023-007	07/09/2023	*Scyliorhinus canicula*	625	843	0	m	on
2023-007	07/09/2023	*Scyliorhinus canicula*	641	1069	0	m	on
2023-007	07/09/2023	*Scyliorhinus canicula*	641	813	0	m	on
2023-007	07/09/2023	*Scyliorhinus canicula*	583	688	0	m	on
2023-007	07/09/2023	*Scyliorhinus canicula*	601	728	0	m	on
2023-007	07/09/2023	*Scyliorhinus canicula*	586	713	0	f	on
2023-007	07/09/2023	*Scyliorhinus canicula*	693	1375	0	m	on
2023-008	07/09/2023	*Arnoglossus imperialis*	213	59	0		off
2023-008	07/09/2023	*Callionymus lyra*	218	70	0		off
2023-008	07/09/2023	*Chelidonichthys cuculus*	250	124	0		off
2023-008	07/09/2023	*Chelidonichthys cuculus*	224	83	0		off
2023-008	07/09/2023	*Chelidonichthys cuculus*	270	235	0		off
2023-008	07/09/2023	*Labrus bergylta*	294	492	0		off
2023-008	07/09/2023	*Pleuronectes platessa*	526	1066	0		off
2023-008	07/09/2023	*Scyliorhinus canicula*	631	904	0	m	off
2023-008	07/09/2023	*Scyliorhinus canicula*	628	843	0	m	off
2023-008	07/09/2023	*Scyliorhinus canicula*	595	816	0	m	off
2023-008	07/09/2023	*Scyliorhinus canicula*	678	870	0	m	off
2023-008	07/09/2023	*Scyliorhinus canicula*	596	749	0	m	off
2023-008	07/09/2023	*Scyliorhinus canicula*	611	777	0	f	off
2023-008	07/09/2023	*Scyliorhinus canicula*	566	636	0	f	off
2023-008	07/09/2023	*Scyliorhinus canicula*	532	708	0	f	off
2023-008	07/09/2023	*Scyliorhinus canicula*	650	1042	0	m	off
2023-008	07/09/2023	*Scyliorhinus canicula*	533	524	0	m	off
2023-009	07/09/2023	*Labrus mixtus*	320	446	0		on
2023-009	07/09/2023	*Merlangius merlangus*	160	34	0		on
2023-009	07/09/2023	*Raja brachyura*	536	977	373	m	on
2023-009	07/09/2023	*Raja microocellata*	725	3000	485	m	on
2023-009	07/09/2023	*Raja microocellata*	764	3300	545	f	on
2023-009	07/09/2023	*Raja montagui*	566	1000	370	m	on
2023-009	07/09/2023	*Scyliorhinus canicula*	649	976	0	m	on
2023-009	07/09/2023	*Scyliorhinus canicula*	618	884	0	m	on
2023-009	07/09/2023	*Scyliorhinus canicula*	540	582	0	f	on
2023-009	07/09/2023	*Scyliorhinus canicula*	657	914	0	m	on
2023-009	07/09/2023	*Trisopterus minutus*	80	6	0		on
2023-009	07/09/2023	*Trisopterus minutus*	139	35	0		on
2023-009	07/09/2023	*Trisopterus minutus*	115	19	0		on
2023-009	07/09/2023	*Trisopterus minutus*	135	31	0		on
2023-010	07/09/2023	*Chelidonichthys cuculus*	352	433	0		off
2023-010	07/09/2023	*Chelidonichthys cuculus*	235	130	0		off
2023-010	07/09/2023	*Chelidonichthys cuculus*	330	382	0		off
2023-010	07/09/2023	*Conger conger*	870	1750	0		off
2023-010	07/09/2023	*Lophius piscatorius*	181	120	0		off
2023-010	07/09/2023	*Mustelus asterias*	620	1034	0	f	off
2023-010	07/09/2023	*Raja brachyura*	300	143	207	m	off
2023-010	07/09/2023	*Raja montagui*	255	71	165	f	off
2023-010	07/09/2023	*Zeus faber*	405	1222	0		off

2023-010	07/09/2023	*Zeus faber*	284	324	0		off
2023-011	08/09/2023	*Chelidonichthys cuculus*	253	165	0		off
2023-011	08/09/2023	*Raja brachyura*	666	2500	465	f	off
2023-011	08/09/2023	*Raja brachyura*	850	4750	563	m	off
2023-011	08/09/2023	*Raja brachyura*	782	5000	565	m	off
2023-011	08/09/2023	*Raja brachyura*	673	2000	485	m	off
2023-011	08/09/2023	*Raja montagui*	511	850	341	f	off
2023-011	08/09/2023	*Scyliorhinus canicula*	600	912	0	f	off
2023-011	08/09/2023	*Scyliorhinus canicula*	561	661	0	f	off
2023-011	08/09/2023	*Scyliorhinus canicula*	517	493	0	f	off
2023-011	08/09/2023	*Scyliorhinus canicula*	636	863	0	m	off
2023-011	08/09/2023	*Scyliorhinus canicula*	615	809	0	m	off
2023-011	08/09/2023	*Scyliorhinus canicula*	591	842	0	f	off
2023-011	08/09/2023	*Scyliorhinus canicula*	558	727	0	f	off
2023-011	08/09/2023	*Scyliorhinus canicula*	554	612	0	f	off
2023-011	08/09/2023	*Scyliorhinus canicula*	573	619	0	f	off
2023-011	08/09/2023	*Scyliorhinus canicula*	581	648	0	m	off
2023-011	08/09/2023	*Scyliorhinus canicula*	681	1075	0	m	off
2023-011	08/09/2023	*Scyliorhinus canicula*	569	671	0	f	off
2023-011	08/09/2023	*Trisopterus minutus*	80	5	0		off
2023-011	08/09/2023	*Trisopterus minutus*	130	10	0		off
2023-011	08/09/2023	*Trisopterus minutus*	139	26	0		off
2023-011	08/09/2023	*Trisopterus minutus*	126	18	0		off
2023-012	08/09/2023	*Chelidonichthys cuculus*	327	315	0		on
2023-012	08/09/2023	*Raja montagui*	524	909	352	f	on
2023-012	08/09/2023	*Scyliorhinus canicula*	599	763	0	f	on
2023-012	08/09/2023	*Scyliorhinus canicula*	555	684	0	f	on
2023-012	08/09/2023	*Scyliorhinus canicula*	573	661	0	f	on
2023-012	08/09/2023	*Scyliorhinus canicula*	629	863	0	m	on
2023-012	08/09/2023	*Scyliorhinus canicula*	599	752	0	m	on
2023-012	08/09/2023	*Scyliorhinus canicula*	613	792	0	m	on
2023-012	08/09/2023	*Scyliorhinus canicula*	629	892	0	m	on
2023-012	08/09/2023	*Trisopterus minutus*	141	38	0		on
2023-013	12/09/2023	*Labrus mixtus*	330	516	0		on
2023-013	12/09/2023	*Raja brachyura*	755	3750	531	f	on
2023-013	12/09/2023	*Raja brachyura*	589	1560	424	f	on
2023-013	12/09/2023	*Raja brachyura*	361	263	316	m	on
2023-013	12/09/2023	*Raja microocellata*	532	1188	351	f	on
2023-013	12/09/2023	*Raja montagui*	546	1066	381	f	on
2023-013	12/09/2023	*Scyliorhinus canicula*	545	543	0	m	on
2023-013	12/09/2023	*Scyliorhinus canicula*	650	932	0	m	on
2023-013	12/09/2023	*Scyliorhinus canicula*	602	732	0	f	on
2023-013	12/09/2023	*Scyliorhinus canicula*	560	622	0	f	on
2023-013	12/09/2023	*Scyliorhinus canicula*	561	652	0	f	on
2023-013	12/09/2023	*Scyliorhinus canicula*	563	734	0	f	on
2023-013	12/09/2023	*Scyliorhinus canicula*	575	680	0	f	on
2023-014	12/09/2023	*Chelidonichthys cuculus*	228	123	0		off
2023-014	12/09/2023	*Chelidonichthys cuculus*	207	100	0		off

2023-014	12/09/2023	*Chelidonichthys cuculus*	240	144	0		off
2023-014	12/09/2023	*Chelidonichthys cuculus*	229	111	0		off
2023-014	12/09/2023	*Chelidonichthys cuculus*	206	76	0		off
2023-014	12/09/2023	*Chelidonichthys cuculus*	210	104	0		off
2023-014	12/09/2023	*Chelidonichthys cuculus*	222	108	0		off
2023-014	12/09/2023	*Raja brachyura*	641	2000	465	m	off
2023-014	12/09/2023	*Raja montagui*	575	1250	380	f	off
2023-014	12/09/2023	*Raja montagui*	610	1436	395	f	off
2023-014	12/09/2023	*Scyliorhinus canicula*	603	675	0	f	off
2023-014	12/09/2023	*Scyliorhinus canicula*	639	945	0	m	off
2023-014	12/09/2023	*Scyliorhinus canicula*	575	670	0	f	off
2023-014	12/09/2023	*Scyliorhinus canicula*	554	555	0	m	off
2023-014	12/09/2023	*Trisopterus minutus*	133	35	0		off
2023-015	12/09/2023	*Arnoglossus imperialis*	221	103	0		on
2023-015	12/09/2023	*Chelidonichthys cuculus*	285	268	0		on
2023-015	12/09/2023	*Chelidonichthys lucerna*	109	11	0		on
2023-015	12/09/2023	*Raja brachyura*	765	3250	535	f	on
2023-015	12/09/2023	*Scyliorhinus canicula*	610	786	0	f	on
2023-015	12/09/2023	*Scyliorhinus canicula*	585	733	0	f	on
2023-015	12/09/2023	*Scyliorhinus canicula*	603	762	0	f	on
2023-015	12/09/2023	*Trachurus trachurus*	83	11	0		on
2023-015	12/09/2023	*Trachurus trachurus*	87	6	0		on
2023-015	12/09/2023	*Trachurus trachurus*	90	10	0		on
2023-015	12/09/2023	*Trachurus trachurus*	75	6	0		on
2023-015	12/09/2023	*Trachurus trachurus*	80	10	0		on
2023-015	12/09/2023	*Trachurus trachurus*	75	10	0		on
2023-015	12/09/2023	*Trachurus trachurus*	75	8	0		on
2023-015	12/09/2023	*Trachurus trachurus*	78	11	0		on
2023-015	12/09/2023	*Trachurus trachurus*	85	7	0		on
2023-015	12/09/2023	*Trachurus trachurus*	84	10	0		on
2023-015	12/09/2023	*Trachurus trachurus*	91	14	0		on
2023-015	12/09/2023	*Trachurus trachurus*	86	6	0		on
2023-015	12/09/2023	*Trachurus trachurus*	79	6	0		on
2023-015	12/09/2023	*Trachurus trachurus*	84	9	0		on
2023-015	12/09/2023	*Trachurus trachurus*	85	8	0		on
2023-015	12/09/2023	*Trachurus trachurus*	76	6	0		on
2023-015	12/09/2023	*Trachurus trachurus*	75	5	0		on
2023-015	12/09/2023	*Trachurus trachurus*	90	11	0		on
2023-015	12/09/2023	*Trachurus trachurus*	87	8	0		on
2023-015	12/09/2023	*Trachurus trachurus*	83	6	0		on
2023-015	12/09/2023	*Trisopterus minutus*	121	21	0		on
2023-016	12/09/2023	*Chelidonichthys cuculus*	207	94	0		off
2023-016	12/09/2023	*Chelidonichthys cuculus*	242	138	0		off
2023-016	12/09/2023	*Labrus bergylta*	360	925	0		off
2023-016	12/09/2023	*Labrus bergylta*	306	583	0		off
2023-016	12/09/2023	*Mullus surmuletus*	195	108	0		off
2023-016	12/09/2023	*Mullus surmuletus*	203	113	0		off
2023-016	12/09/2023	*Raja brachyura*	650	1075	460	f	off

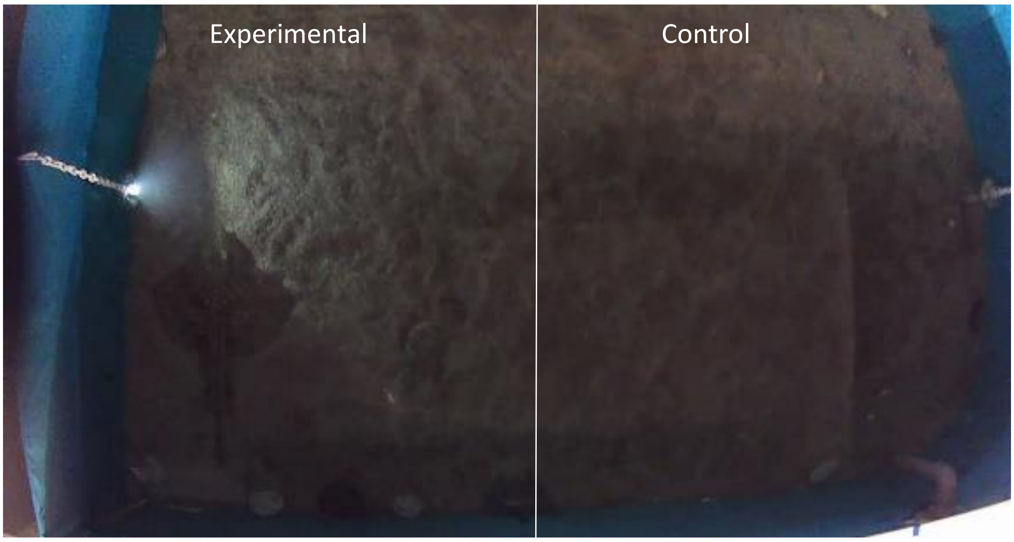
2023-016	12/09/2023	*Scyliorhinus canicula*	588	702	0	off
2023-016	12/09/2023	*Scyliorhinus canicula*	575	777	0	off
2023-016	12/09/2023	*Trisopterus minutus*	138	36	0	off

Appendix Table 4:

GLM results for comparing the abundance of skates in lights on versus lights off trawls. The results show skate abundance was not affected by the presence of light, where there were no differences in skate numbers between royal blue light trawls (n=8) and no light trawls (n=8). Other factors such as sea surface temperature affected abundances though, where less skates were present in colder temperatures. Additionally, the abundances of species differed – there were less *Raja clavata* (thornback ray), *R. microocellata* (small-eyed ray) and *R. montagui* (spotted ray) compared to the intercept of *R. brachyura* (blonde rays).

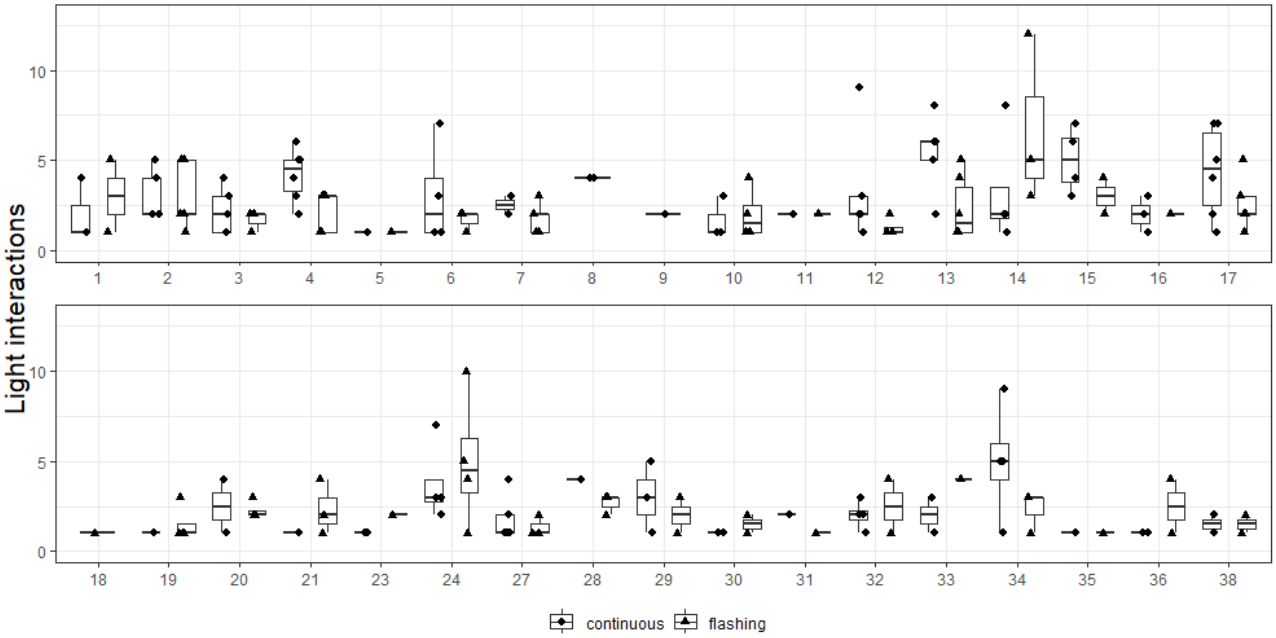
Fixed effects	***Estimate + STd. error***	***z value***	***P value***
Skate abundance (Intercept)	5.177 ± 4.345	1.191	0.23351
Light mode (on)	0.192 ± 0.297	0.645	0.51913
Depth	-0.003 ± 0.074	-0.042	0.96652
Sea surface temperature	-0.320 ± 0.145	-2.203	0.02759*
Haul month (September)	-0.291 ± 0.525	-0.554	0.57977
Species: Raja clavata	-1.516 ± 0.742	-2.043	0.04109*
Rajas microocellata	-1.064 ± 0.406	-2.622	0.00875**
Raja montagui	-0.626 ± 0.218	-2.878	0.00401**
MCRS (below)	0.029 ± 0.186	0.156	0.87607
Secchi	0.135 ± 0.142	0.951	0.34158

Appendix Figures



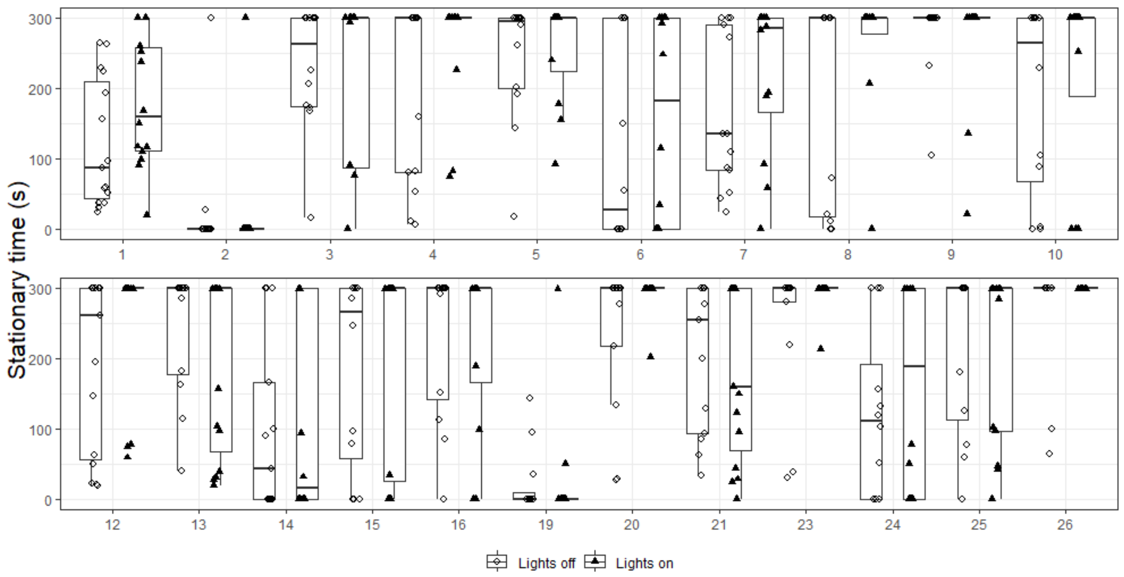
Appendix Figure 1:

The tank set up. The sides in which each LED was either on or off were defined as the experimental or control side of the tank respectively. The halfway point in the tank was approximated from markers, measured before trials started. The species in the tank is a spotted ray (*Raja montagui*).



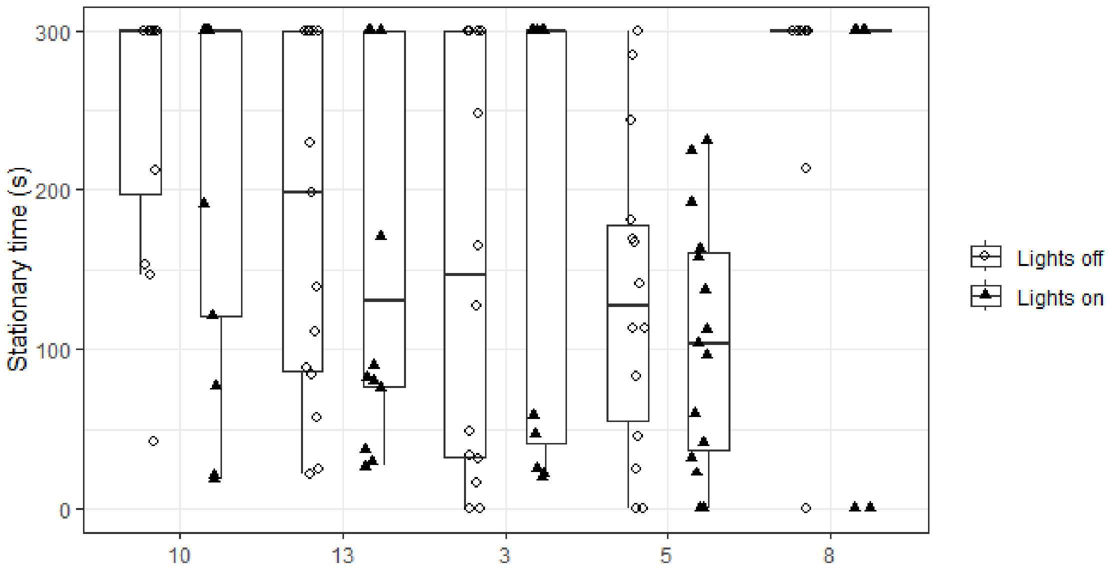
Appendix Figure 2:

Variation between catsharks in the number of light interaction numbers for the experimental light when it was turned on for all colour modes. The x axis on each graph represents a trial number (1-17 in the top graph and 18-38 in the bottom) and therefore an individual catshark. Each trial has the possibility of two box plots, which either represent continuous or flashing trials. Continuous trials are the left hand plots for each catshark, where data points are represented by black diamonds, and flashing trials have black triangles and are the right-hand side plot. The y axis represents the number of light interactions that each catshark had for either flashing or continuous trials for a particular colour mode. If trial numbers are missing on the x axes, it is because a particular catshark did not interact with the light for entire trials (both flashing and continuous, for all light colour modes),



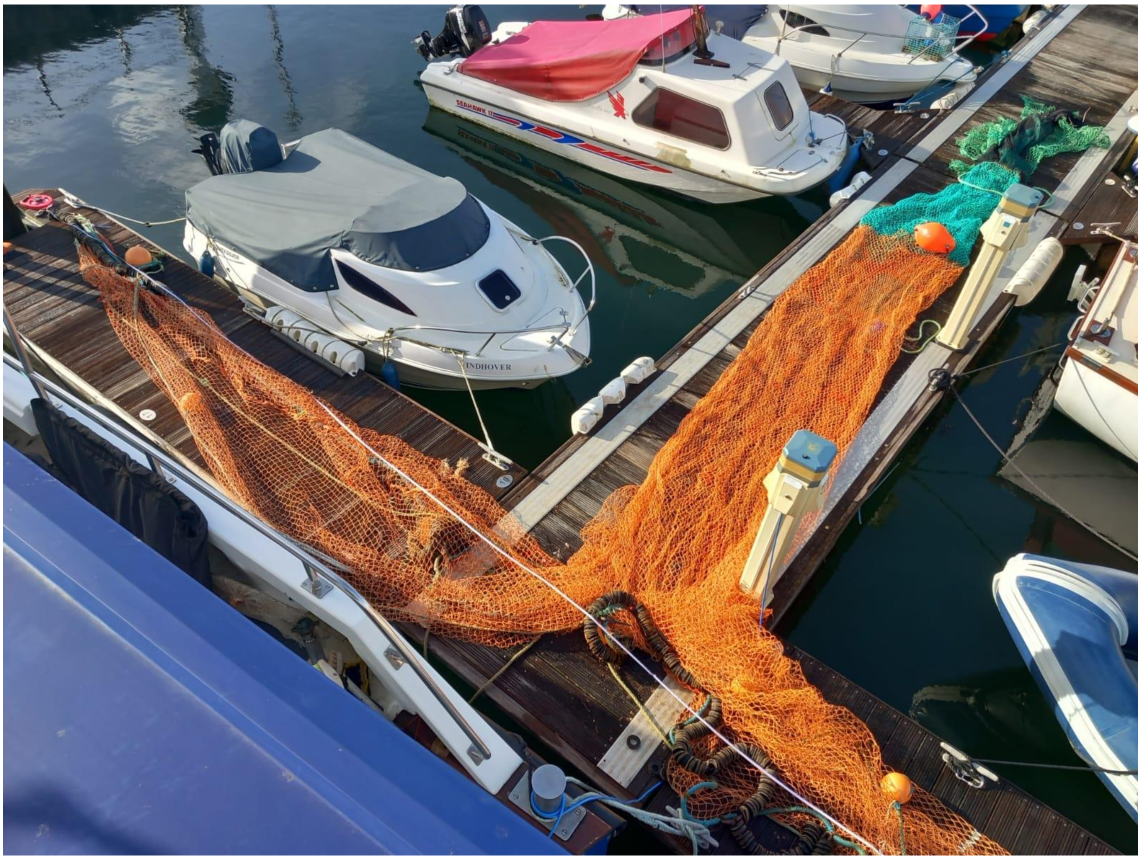
Appendix Figure 3:

Variation between skates in the time spent stationary (s) during flashing and continuous trials in lights off versus on conditions. Lights on is represented by black triangles, and lights off by white circles. The x axis is the trial number/individual skates (1 – 10 in the top graph, 11 – 26 in the bottom). Each trial has the possibility of two box plots for lights off and on data respectively. The y axis represents the time spent stationary (s) for each skate, in either control or experimental sides of the tank in flashing and continuous conditions, across all colour modes. If trial numbers are missing on the x axes, it is because a particular skate was stationary for entire trials (both flashing and continuous, for all light colour modes), which was 5 skates out of 27.



Appendix Figure 4:

Variation between plaice in the time spent stationary (s) during flashing and continuous trials in lights off versus on conditions. Lights on data points are represented by black triangles, and lights off by white circles. The x axis is the trial number/individual plaice. Each trial has the possibility of two box plots for lights off and on data respectively. The y axis represents the time spent stationary (s) for each plaice, in either control or experimental sides of the tank in flashing and continuous conditions, across all colour modes. If trial numbers are missing on the x axes, it is because a particular plaice was stationary for entire trials (both flashing and continuous, for all light colour modes), which was 9 plaice out of the 14 tested.



Appendix Figure 5:

The net used for trawling trials in Chapter 5. The net was 10 m in length from the codend to the footrope, with a 15 m headline. The orange buoy in this photograph is where the camera *CatchCam* was placed, with the camera unit attached inside the net. The buoy was attached to the camera unit via nylon rope and cable ties, which were looped through from the outside of the net. This was in order to keep the net open during fishing, as the camera and housing unit were not neutrally buoyant. Frankie Perry gave me permission to use this photograph, which she took, for my thesis.

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