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Scallops caught in the headlights: swimming escape behaviour of the Atlantic sea scallop (*Placopecten magellanicus*) reduced by artificial light

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Quantifying the distribution and abundance of the Atlantic sea scallop (*Placopecten magellanicus*) is a fishery management priority, and stock assessments increasingly rely on video surveys. Interpreting the results of these surveys requires understanding the inherent biases introduced as a result of target animal behaviour. Our study investigated the effect of artificial lights on the behaviour of Atlantic sea scallops during a video survey using a towed benthic sled. Swimming and stationary scallops were counted in survey videos using event logging software. In addition, the locations, orientations, and swimming directions of the scallops were noted in a subset of the videos. The proportion of scallops that swam when an artificial light was turned on was significantly smaller than the proportion that swam when the light was off. Further analysis using a logistic model showed that only light state (off or on) predicted the likelihood of scallop swimming responses. Possible reasons for this unexpected behaviour are discussed, with a focus on the scallop visual system.

Keywords: benthic sled, bivalve vision, survey bias, underwater video, visual survey.

Introduction

The Atlantic sea scallop (*Placopecten magellanicus*) is the focus of one of the most valuable fisheries on the east coast of the United States, with US scallop landings exceeding 24 000 t or $500 million annually from 2003 to 2012 (NEFSC, 2014). Quantifying the distribution and abundance of this species is a fishery management priority (Hart and Chute, 2004). In earlier years, research towards this goal relied on surveys using mobile fishing gear (NEFSC, 2014). Although these traditional surveys still play an important role in scallop stock assessments, studies on scallop distribution and abundance increasingly rely on the visual surveys using drop cameras (Stokesbury *et al.*, 2004; Somerton and Glendhill, 2005; Carey and Stokesbury, 2011; NEFSC, 2014; NJSGC, 2014), towed sleds (Rosenkranz and Byersdorfer, 2004; Somerton and Glendhill, 2005; NEFSC, 2014; NJSGC 2014), and automated underwater vehicles (Somerton and Glendhill, 2005; Singh *et al.*, 2013; NJSGC, 2014). Interpreting the results from these relatively new survey techniques requires understanding any biases introduced because of scallop behaviour (Stoner *et al.*, 2008; Ryer *et al.*, 2009).

Quantifying the catchability of target species in fishing gear has long been a concern in fisheries surveys (Arreguín-Sánchez, 1996). The catchability of a species, animals caught per unit effort relative to the actual population size, depends largely upon the animal's behaviour in the presence of the fishing gear (Arreguín-Sánchez, 1996; He, 2010). Recent attempts to quantify the catchability of fish in visual surveys have noted that this is a complicated endeavour because reactions of fish to light and sound vary widely across species (Trenkel *et al.*, 2004; Marchesan *et al.*, 2005; Stoner *et al.*, 2008; Ryer *et al.*, 2009). A review of research on marine fish behaviour in the presence of underwater vehicles concluded that most species react to the vehicles, but the details of their reactions vary widely, and determining how behaviour biases surveys is not straightforward (Stoner *et al.*, 2008). Species-specific reactions to artificial light may depend on their predatory and predator-avoidance behaviours, their normal activity levels, or their visual systems and adaptations to low- and high-light conditions (Marchesan *et al.*, 2005; Lorance and Trenkel, 2006; Ryer *et al.*, 2009).

Although scallops are often treated as sessile animals when modelling their density in gear surveys (Rago *et al.*, 2006), their swimming escape response is well documented (Caddy, 1968; Brand, 2006; Wilkens, 2006). Furthermore, they have many eyes along the margin of their mantle, and their swimming behaviour is visually influenced (Wilkens, 2006; Speiser and Johnsen, 2008). Therefore, their catchability in visual surveys could be affected by their swimming behaviour. Our study investigated the effect of artificial lights on the behaviour of Atlantic sea scallops during a video survey using a towed benthic sled.

Material and methods

Study sites

The research was conducted at two sites in southern New England waters east of Long Island in September 2014 (Figure 1). Each survey site covered an area of ca. 2 km^2, and the sites were located 1.7 km apart. The substrate at site 1 (40.9422°N 71.6834°W) was primarily a patchy mix of sand and gravel, while the substrate at site 2 (40.9278°N 71.6893°W) had a higher percentage of silt. The average depth at site 1 was 45 m, and the average depth at site 2 was 49 m. Average bottom temperature at both sites was 14.5°C. This area is open to scallop fishing, and scallops are regularly found there during yearly assessment surveys (NEFSC, 2014).

Video surveys

The video surveys were conducted at the two sites during a 2-d period, with ten survey transects at site 1 and nine survey transects at site 2. The surveys were carried out in late afternoon at the first site and in late morning at the second site. Survey transect lengths were estimated using vessel GPS coordinates and averaged 649.5 m (range 367–1887 m). Survey tracks were roughly parallel ca. 150 m apart, with the sled running in the opposite direction for alternative tracks. It is unlikely that any scallops encountered the sled more than once.

The surveys were conducted using a bottom-contacting benthic sled (Figure 2) towed off the starboard quarter of a 17.4-m fishing vessel at an average speed of 2.8 knots. The sled was constructed of welded steel round bar with attached steel runners (total length = 1.33 m, length of runner contact = 1.02 m, width = 1 m, weight = 123 kg). Cross-beams were added to support cameras and lights.

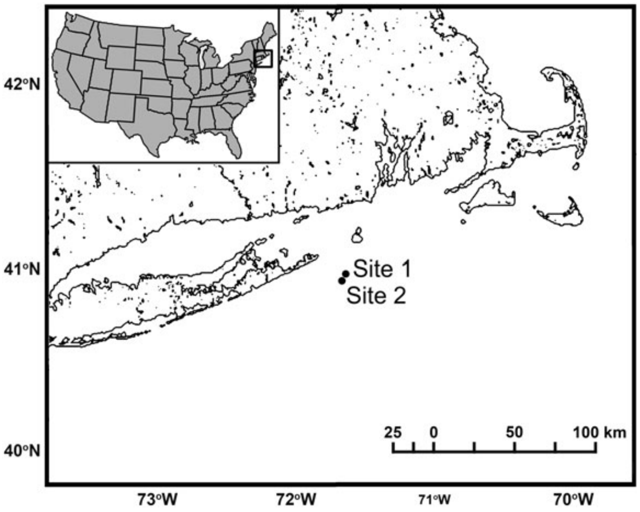


Figure 1. Map showing the locations of the study sites in southern New England waters east of Long Island.

An underwater video camera (Outland Technology UWC-325) was mounted 77 cm above the bottom of the runners. This fixed-focus camera has low light sensitivity (0.001 lux), and it successfully recorded video footage with no added lighting. The camera was focused at the seabed at a 39.5° angle, capturing the area between the runners that ran from ca. 1 m in front of the sled to the start of the flat portion of the runners (Figure 2). An underwater LED light (Outland Technology UWL-401) was mounted 44 cm above and slightly in front of the camera (121 cm above the bottom of the runners) and could be turned off and on by the sled operator during video recording. This 2150-lumen light has a beam angle of 100° and an output of 960 lux at 1 m. During the surveys, turbidity near the bottom must have been low because backscatter from the artificial lights was minimal.

Video analysis

During the video survey transects, the camera and light set-up were being evaluated. As such, video footage was recorded with and without artificial lighting. Fourteen of 19 survey transects were conducted with artificial lighting off or on for the entire recording. Five survey transects had the light turned off and on during recording, so the videos for these transects included both light-off and light-on segments. Overall, 44% of the video was recorded with artificial lighting (45% at site 1, 43% at site 2).

Video was analysed using Behavioral Observation Research Interactive Software (BORIS), an open-source event logging software that utilizes VLC media player (http://penelope.unito.it/boris and http://www.videolan.org/vlc/index.html). All videos were annotated by the same person, and events on each video were coded twice for accuracy. Large scallops were located and tracked until they reached the bottom edge of the screen before being classified as stationary or swimming (examples in Figure 3).

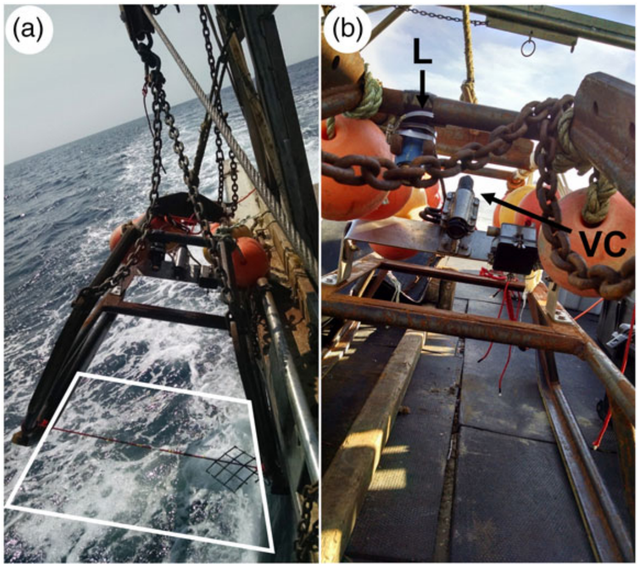


Figure 2. The bottom-contacting sled used in the video surveys. (a) The sled hanging off the side of a scallop vessel before launch, with the approximate trapezoidal area of view for the camera highlighted in white. (b) A close-up view of the video camera (VC), light (L), and mount. This figure is available in black and white in print and in colour at *ICES Journal of Marine Science* online.

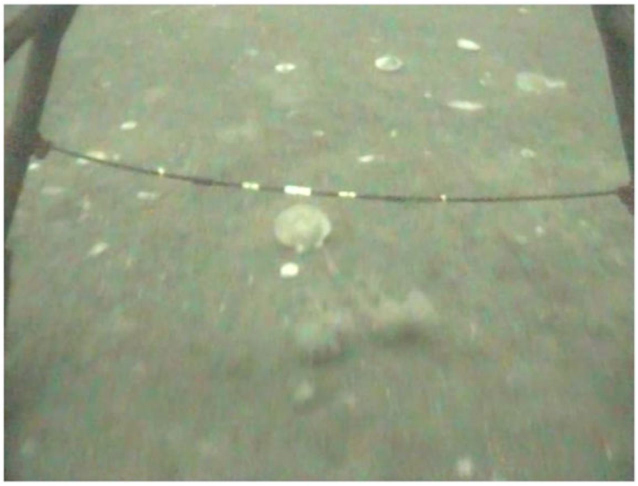
Only medium–large scallops were counted because small scallops were difficult to locate when not swimming. The approximate sizes of the largest and smallest annotated scallops were determined from a subset of screenshots using Adobe Photoshop after compensating for the trapezoidal distortion created by the oblique viewing angle of the camera (Wakefield and Genin, 1987).

Additional analysis was done on four videos that had long segments of footage with the artificial light off or on for part of the video. The location (left, right, or centre) and settled orientation were recorded for each scallop. If a scallop started swimming, the swimming direction was also noted. Settled orientations and swimming directions were recorded in compass degrees rounded to the nearest 10°.

Statistical analysis

The scallop count data from each survey site and from both sites combined were analysed with a χ^2 test for independence to determine if there was a significant association between scallop swimming behaviour and the artificial light being off or on.

(a) Light off



(b) Light on

Figure 3. Screenshots taken from the video survey footage. (a) Image from video with the artificial light turned off showing the sediment clouds created as a scallop begins to swim. (b) Image from video with the light turned on showing three stationary scallops.

To examine other factors that might influence scallop swimming behaviour, we used a binomial logistic regression model in the package "lme4" (generalized linear mixed model function "glmer" with link = "logit") in R (Bates *et al.*, 2014; R Core Team, 2014). The likelihood of swimming behaviour was modelled as a function of light (off or on), location relative to sled runners (in the centre of the sled path or near a runner), orientation relative to the approaching benthic sled (away vs. towards the sled, with the shell hinge defined as the back of the scallop), and an interaction effect for location and orientation. A random effect for survey track was included to account for correlation between observations along a single benthic sled survey track due to variables like ambient light levels, bottom sediment type, tow direction relative to currents, and current strength. The initial model included all variables and the interaction between location and orientation. The final model was determined after backward elimination of non-significant variables and evaluation based on the Akaike information criterion (AIC) and likelihood ratio tests (Akaike, 1973). To determine if the random effect of track was required in the final model, a caterpillar plot of the 95% prediction intervals for each track-specific random intercept was examined for zero crossings relative to the global mean over all tracks (Bates, 2010).

Results

In total, just over 140 min of video footage was analysed, with the light turned off for 79.15 min and turned on for 61.21 min. A total of 2227 scallops were annotated in these videos, with 1655 at site 1 and 572 at site 2 (Table 1). At site 1, 18.7% of the scallops swam when the light was off, while only 1.8% swam when the light was on (Figure 4). Similar results were seen at site 2, where 28.2% of the scallops swam when the light was off and 4.6% swam when the light was on (Figure 4). The approximate sizes of the identified scallops ranged from 70 to 120 mm shell height, with most in the 70–100 mm size range. Scallops with shell heights >100 mm were observed swimming, which is notable because large scallops are more sedentary than smaller animals (Caddy, 1968).

A χ^2 test of independence was performed to examine the relationship between the light being off or on and the swimming response of scallops. There was a significant relationship between the presence of artificial light and the swimming behaviour of scallops [site 1: χ^2 $(2, n = 1655) = 124.915$, $p < 0.0001$; site 2: χ^2 $(2, n = 572) = 48.131$ $p < 0.0001$; both sites combined: χ^2 $(2, n = 2227) = 179.649$, $p < 0.0001$]. The proportion of scallops that swam when the artificial light was turned on was significantly less than the proportion that swam when the light was off.

To determine if potential variables other than light influenced scallop swimming responses to the approaching benthic sled, we included location relative to the sled runners and orientation of the scallop relative to the approaching sled in a generalized linear

Table 1. Summary of stationary and swimming scallop counts at both sites with the light turned off and on.

	Substrate type	Light off		Light on	
		Stationary	**Swimming**	**Stationary**	**Swimming**
Site 1	Sand/gravel	703	162	776	14
Site 2	Sand/silt	255	100	207	10
Total		958	262	983	24

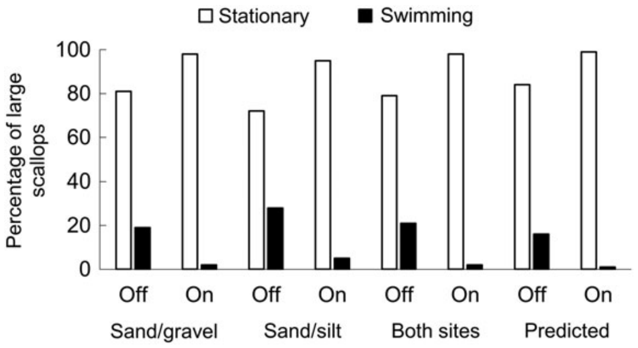


Figure 4. The percentage of large scallops (shell height >70 mm) counted as stationary or swimming when the light was turned off or on at site 1, site 2, and both sites combined. The model-predicted percentage of scallops that would swim when the light was off or on is shown on the far right.

Table 2. Results of the logistic regression analysis for likelihood of swimming behaviour.

	Initial GLMM model with all variables			
Fixed effects	**Coefficient**	**s.e.**	***z*-value**	***p*-value**
Intercept	−1.8446	0.3548	−5.199	<0.0001
Light (off/on)	−2.8131	0.5997	−4.691	<0.0001
Location (centre/runner)	0.3302	0.3515	0.939	0.348
Orientation (facing away/ towards sled)	0.0613	0.5209	0.118	0.906
Location × orientation	−0.2201	0.6417	−0.343	0.732
Random effect	**Variance**	**s.d.**		
Survey track	0.1251	0.3537		
Fixed effects	**Final GLM model (no random effect)**			
	Coefficient	**s.e.**	***z*-value**	***p*-value**
Intercept	−1.6474	0.1387	−11.879	<0.0001
Light (off/on)	−2.8524	0.5969	−4.779	<0.0001

Only the initial and final models are shown. The initial model was a generalized linear mixed model (GLMM) with three fixed effects, one fixed interaction effect, and one random effect. Only one fixed effect remained in the final generalized linear model (GLM).

mixed model. Only light had a significant effect on the likelihood of swimming behaviour (Table 2). The simpler model, including light as the only fixed variable and track as a random variable, had a lower AIC score (all fixed variables: AIC = 382.4; light: AIC = 377.5), and a likelihood ratio test confirmed there was no significant improvement to the model when additional variables were included [$\chi^2(3) = 1.0485$, $p = 0.79$]. Examination of the 95% prediction intervals for each survey track random intercept indicated that this variable was not needed in the model. All four of the track-specific intervals crossed zero (Figure 5). The final model, which included only light as a fixed variable, estimated that scallops had a 16.1% chance of swimming when the light was off and a 1.1% chance of swimming when the light was on based on the predicted odds ratios (Figure 4).

Although the orientations of scallops relative to the benthic sled did not significantly impact the likelihood of swimming responses, scallops consistently swam away from the approaching sled regardless of their settled orientation before swimming (Figure 6). This occurred although 26.2% of the scallops were facing towards the approaching sled before swimming.

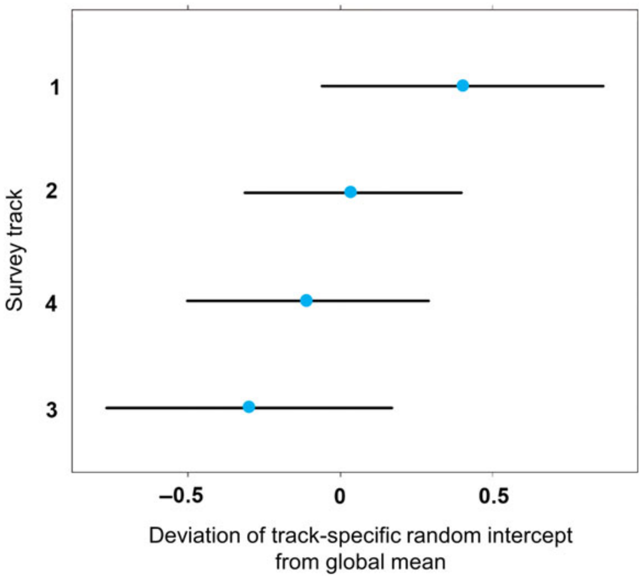


Figure 5. Caterpillar plot showing the 95% prediction intervals, estimated by the R package "lme4" function "glmer" and extractor "ranef", for the survey track-specific random intercepts. The *x*-axis is the deviation of each track-specific intercept from the global mean. Because all prediction intervals cross zero, the random effect of survey track was not included in the final model. The caterpillar plot was created using "dotplot" in the "lattice" graphics package in R (Sarkar, 2008). This figure is available in black and white in print and in colour at *ICES Journal of Marine Science* online.

Discussion

The χ^2 test and logistic regression model both clearly show that artificial light can significantly affect the swimming escape response of scallops. The percentage of Atlantic sea scallops that swam when approached by a benthic sled with artificial lighting was markedly less than the percentage that swam when approached by the same benthic sled operating in ambient light. This implies that artificial lights, which often improve the quality of underwater imagery, may also increase the likelihood that scallops will stay in place to be counted in a visual survey. This counterintuitive result contradicts anecdotal reports on the Antarctic scallop (*Adamussium colbecki*) and the saucer scallop (*Amusium balloti*) swimming in response to underwater camera lights (Ansell *et al.*, 1998; Dibden and Joll, 1998).

Scallop behaviour

The scallop swimming response is one of three locomotory behaviours observed for these bivalves. Scallops swim to escape predators or select habitat, and the swimming behaviours of different scallop species can be very similar (Brand, 2006; Wilkens, 2006). Some scallop species, including Atlantic sea scallops, can swim for long distances (over 5 m per swimming effort) by including a gliding component during the effort (Brand, 2006; Alejandrino *et al.*, 2011). Caddy (1968) investigated the swimming escape response of Atlantic sea scallops reacting to approaching divers. On average, the scallops swam 2.3 m (range 90 cm–4.3 m) away from approaching divers, rising 0.4 m above the sediment (Caddy, 1968). Smaller scallops (shell height <100 mm) swam away from approaching divers regardless of their original orientation, forming a semi-circular front ahead of the divers, while scallops >100 mm in size tended to remain recessed in the sand, often covered with a layer of fine sediment

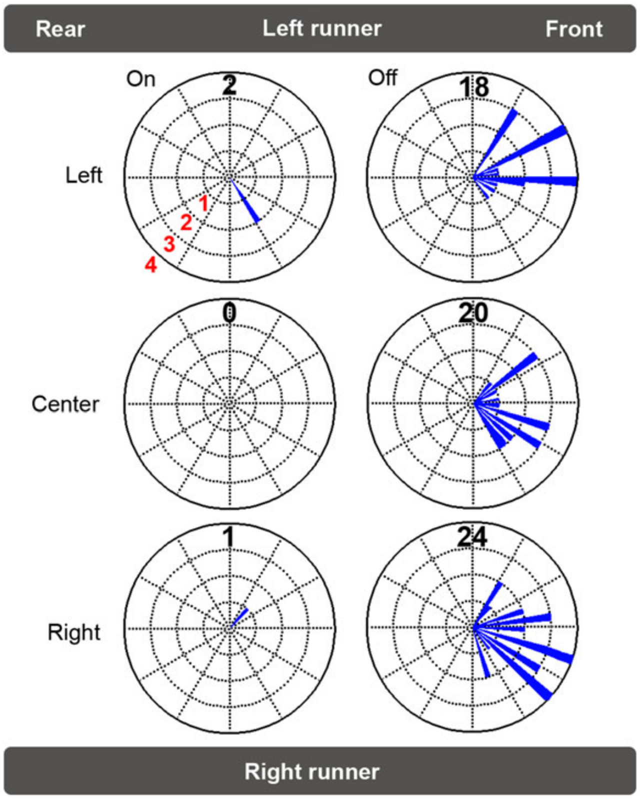


Figure 6. Rose plots showing the swimming directions of scallops when the light was on and off. Plots are shown for scallops located near the left runner, in the centre, and near the right runner, with the total number of scallops shown at the top of each plot. No scallops in the centre region were observed swimming when the light was turned on. Rose plots were generated in MATLAB (version R2012a). This figure is available in black and white in print and in colour at *ICES Journal of Marine Science* online.

(Caddy, 1968). A few larger scallops swam and travelled short distances (90 cm), rising <10 cm above the sediment (Caddy, 1968).

The scallops in our visual survey had a similar response, swimming in a direction away from the approaching sled regardless of their initial settled orientation (Figure 6). The majority of the swimming scallops observed during our surveys were <100 mm in size, and this included scallops with shell heights ranging from 70 to 100 mm as well as many small scallops not counted in the analysis. However, we did note larger scallops (shell heights >100 mm) swimming away from the sled. Often, large recessed scallops could be identified by their distinctive outlines, even when they were lightly covered with sediment. Yet perhaps more large recessed scallops were in our survey area if they were covered with a thick layer of sediment, making them difficult to identify and count.

Scallops have four main behaviours in response to visual stimuli: shell closure, swimming, orientation of their shells relative to something in their visual surroundings, and extension of their tentacles (Wilkens, 2006). Their most familiar visually driven behaviour is shell closure in response to decrease in light intensity or movement of a dark object, with more consistent reactions to movements over changes in light intensity (Gutsell, 1930; Wilkens, 2006). However, early research on the reactions of bivalves to changes in light intensity indicated that Atlantic calico scallops (*Arcopecten gibbus*) will respond to sudden increases in light by closing their valves (Wenrich, 1916). If Atlantic sea scallops have a similar reaction to sudden light increases, their swimming response would decrease in the presence of artificial lights.

Reactions to light

Artificial light can have a strong effect on animal behaviour. For example, many pelagic fish and cephalopod molluscs have strong positive phototactic responses that cause them to congregate in pools of light. This well-known behaviour has been exploited in fisheries that use light as an attractant (Ben-Yami, 1988). Research focused specifically on marine animal reactions to artificial light on underwater vehicles has been directed towards evaluating fish behaviour. Most fish in these studies were attracted to or avoided lights and underwater vehicles (Trenkel *et al*., 2004; Marchesan *et al*., 2005; Lorance and Trenkel, 2006; Ryer *et al*., 2009). Fish that were attracted to lights were typically species that fed on plankton that also have positive phototactic responses (Marchesan *et al*., 2005; Ryer *et al*., 2009). The most active fish species moved away from approaching artificial lights, and this reaction may be an avoidance behaviour triggered by a novel looming stimulus (Ryer *et al*., 2009). Fish that showed no response to vehicle artificial lights were typically ambush predators that use cryptic coloration (Ryer *et al*., 2009).

We found no reported cases of marine animals swimming away from vehicles when artificial lights were turned off while remaining stationary when lights were turned on. This behaviour is reported more often in terrestrial mammals that have visual systems adapted for low-light conditions. For example, deer are most active during crepuscular periods, and their eyes, with high concentrations of light-sensitive rods in the retina and a reflective layer behind the retina, are well suited for vision in dim light (Blackwell and Seamans, 2009). These animals freeze in front of oncoming cars with bright headlights when light oversaturates their retinal pigments and makes them temporarily blind. Similarly, if sudden bright lights temporarily blind a scallop, this could cause a decrease in swimming behaviour.

Further examination of the scallop visual system and parallels between the scallop two-layer retina system and the vertebrate rod and cone system supports this possibility (McReynolds and Gorman, 1970; Fain *et al*., 2010). Scallops have many small concave mirror eyes along the margins of their upper and lower shells (Wilkens, 2006; Speiser and Johnsen, 2008). The inside surface of each eye has a highly reflective argentea located behind two distinct retinal layers, and images are focused onto the retina by the reflective surface of the spherical interior of the eye (Land, 1965, 1966a; Wilkens, 2006; Speiser and Johnsen, 2008; Speiser *et al*., 2011). Because of the relatively short focal length in scallop eyes relative to pupil size, they have high light-gathering power despite their small size (Warrant and Locket, 2004; Colicchia *et al*., 2009). The low-light sensitivity of scallop eyes is enhanced by the characteristic photoreceptors and phototransduction pathways in this system (McReynolds and Gorman, 1970; Wilkens, 2006; Fain *et al*., 2010).

The two retinal layers in scallop eyes have different photoreceptor types, and these use distinct phototransduction pathways (McReynolds and Gorman, 1970; Kojima *et al*., 1997; Wilkens, 2006; Fain *et al*., 2010). The distal retinal layer, closest to the lens, includes ciliary photoreceptors that hyperpolarize in response to light (the "off" response), and these cells are thought to be responsible for detecting decreases in illumination from passing predator shadows and dark objects (Speiser and Johnsen, 2008; Fain *et al*., 2010). Like vertebrate cone cells, the distal retinal layer photoreceptors have low sensitivity and respond in bright light (McReynolds and Gorman, 1970; Shichida and Matsuyama, 2009). In contrast, the proximal retinal layer contains highly sensitive microvillar photoreceptors that depolarize in response to light (the "on" response; McReynolds and Gorman, 1970; Wilkens, 2006; Fain *et al*., 2010). Like vertebrate rod cells, these are high-gain photoreceptors that can respond to a single photon, allowing vision in dim light (McReynolds and Gorman, 1970; Nasi and Gomez, 1992; Fain *et al*., 2010). Dark-adapted scallop proximal photoreceptors are temporarily inactivated after exposure to bright light, failing to respond to additional flashes for periods of 45 s to minutes (Land, 1966b; McReynolds and Gorman, 1970). Comparable inactivity is characteristic of saturated vertebrate rod cells (Aguilar and Stiles, 1954; Fain *et al*., 2010) and causes the temporary blindness of deer that are "caught in the headlights".

Implications and future research

Differences in the behaviours of target and unintentionally caught species are often utilized to design fishing gear modifications (He, 2010). The fish recorded in our videos were difficult to identify because they were only observed swimming rapidly away from or towards the sides of the approaching sled. This occurred when the lights were off and on, in contrast to the behaviour of the scallops, suggesting that artificial light might be used to impact fish bycatch in scallop fisheries. Yet it should be noted that artificial illumination has been more successful in bycatch reduction when used as an attractant to encourage escapement of incidentally caught fish species (Lomeli and Wakefield, 2014; ODFW, 2014).

Our future research will explore details about how scallops react to approaching bright lights and the importance of the intensity and wavelength of that light. We hypothesized two reasons why scallop swimming behaviour might be inhibited by artificial lights: (i) light caused the scallops to close their shells and therefore not swim, or (ii) light temporarily blinded the scallops causing them to freeze. Laboratory-based studies will help us determine if either explanation seems likely. Additional fieldwork with the benthic sled will supplement controlled behavioural experiments in tanks, so that we can further explore the potential value of this unexpected scallop behaviour.

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