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ECOSYSTEMS AND SUSTAINABILITY

Variability in behaviour of four fish species attracted to baited underwater cameras in the North Sea

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Abstract Baited underwater camera (BUC) systems to estimate demersal fish abundance are becoming increasingly considered as an alternative to traditional survey methods, particularly in environments that contain sensitive habitats or protected species. Based on 27 replicate deployments of BUCs at 100 m depth in the northern North Sea, in rank order of abundance, hagfish (*Myxine glutinosa*), flatfish mainly dabs (*Limanda limanda*), whiting (*Merlangius merlangus*) and haddock (*Melanogramus aeglefinus*) were observed consistently at baits. Higher maximum numbers ($N_{\max}$) occurred during daytime in all species with the most significant effect in flatfish, 18 in daytime and 5 at night-time. Bottom current had no significant effect on numbers of whiting, flatfish or haddock. The $N_{\max}$ of hagfish was strongly related to current speed in a non-linear way with an increase in numbers up to 10 cm s^{-1} and then decrease in $N_{\max}$ at higher water speeds. Understanding and accounting for such species-specific influences is important in the design of long term monitoring surveys using baited cameras.

Keywords Baited camera · Current · Demersal fish · North Sea · Fisheries

Introduction

Baited underwater cameras (BUC) are a potential non-extractive alternative to traditional sampling tools, such as trawling and long lines, for generating metrics of abundance and diversity in inaccessible areas or where the habitat and/or populations are protected. This sampling method has been used successfully in deep sea environments (Priede & Bagley, 2001; Jones et al., 2003), marine protected areas (Willis et al., 2003), shallow temperate and

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tropical habitats (Ellis & Demartini, 1994; Cappo et al., 2004; Harvey et al., 2007) and juvenile fish habitats (Laurel et al., 2009).

All sampling methods have inherent selectivity bias related to the specific behaviour of different fish, and the design and efficiency of the gear. BUCs are static systems based on attracting fish to bait in the same way as fishing pots, traps and longlines. Fish attracted to the bait are photographed but do not need to be hooked or trapped. This reduces some of the "near field" selective bias compared to extractive methods but not the "far field" biases. The attraction of fish to bait depends on a variety of environmental and biological factors that affect the detection and reaction thresholds of fish to the odour plume from the bait. The active space of the bait (Bossert & Wilson, 1962) will be defined by the chemical properties of the bait itself, the olfactory detection thresholds of different species and environmental factors that influence the propagation of the odour plume such as current speeds, tidal patterns and seabed topography (Olsen & Laevastu, 1983; Engås & Løkkeborg, 1994). The reaction threshold of fish, the point at which it chooses to search for the source of the odour, will be influenced by factors such as time of day, current speeds in relation to general activity level and swimming ability, hunger level and the presence of other potential prey and predators (e.g. Løkkeborg et al., 1995; Stoner, 2003). The active area will also shrink over time as rate of release of attractants declines (Løkkeborg, 1990), and most fish will be attracted within the first few hours (Løkkeborg & Pina, 1997). The influence of these factors on the performance of baited fish gears was reviewed by Stoner (2004) who concluded that temperature, light level and current speed were likely to have large impacts on fish catchability. Most baited camera studies to date have either been carried out during daylight hours in shallow, well lit environments, or depths well beyond the level of sunlight penetration and variation in light levels has not been investigated. The impact of current speed has also received limited attention, although Heagney et al. (2007) demonstrated an effect on fish abundance estimates and assemblage structure in a pelagic environment using an area-based approximation for plume dispersal.

A number of metrics can be derived from baited camera studies including first arrival time, maximum number of fish observed at any one time, time to maximum number and variations on initial arrival rate at the bait. First arrival time has successfully been used in deep sea studies (Priede & Merrett, 1996) where fish densities are relatively low and arrival times are in the range of tens of minutes to hours. In shallower environments with higher fish densities, this metric has been found to be less useful where arrival times are consistently short (Willis et al., 2000; Stoner et al., 2008). Stoner et al. (2008) also found time to TFA (time of first arrival) was not as well correlated with comparative seine net catches as $N_{\max}$ or NFA; total number of fish observed arriving within a fixed time period. Farnsworth et al. (2007) estimated absolute abundances with a modelling approach which included regression-based prediction from the initial (rising) slope of numbers at the bait, the rate of departure during the declining phases and a hidden Markov model estimate of the number of fish out of the field of view. Given the relatively shallow depth in this study and the use of stills images rather than video footage, $N_{\max}$ was chosen as the most suitable index for estimating relative abundances despite its likely conservative reflection of true abundance. It is also one of the most widely used indices and in this paper we investigated the potential effects of current speed and light level (day/night) on this index of abundance of fish attracted to a baited camera system in a shallow water environment in the North Sea. The species chosen for investigation were those most commonly observed in photographs, and displaying differing behavioural traits.

Materials and methods

Study site

The study area lies 55 km northeast of Peterhead, Scotland (57°48′N, 0°58′W) between the "Fladden" and "Bosies Bank" fishing grounds (Fig. 1). It is a flat, sandy area of approximately 100 m depth. Data were obtained on three cruises: 25th April to 2nd of May 2005 on board of *FRV Scotia* (length: 68.6 m), 23rd to 30th April 2007 on board of the fishing charter vessel *MFV Prowess* (length: 50 m) and 8th May to 4th June 2008 on board of the *VOS Lismore* (length: 54 m). Details of deployments are given in Table 1.

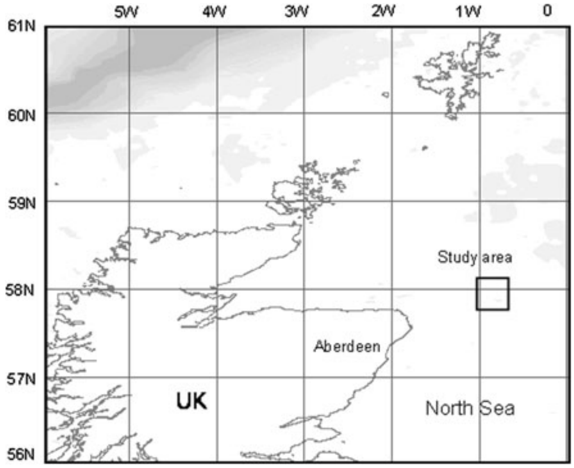

Fig. 1 Map showing sampling location, Central North Sea within ICES division IVa lower confine, 50 nautical miles NE of Aberdeen, Scotland

Baited underwater camera system

The BUC used for these experiments was based on the Robust BIOdiversity (ROBIO) lander designed for deep water research (Jamieson & Bagley, 2005). A downward facing Kongsberg 5 mega pixel underwater camera OE14-208 and flash unit OE11-242, with 24 V battery pack were mounted on an aluminium frame (height 1.8 m, base 1.3 m; Fig. 2) suspended 2.1 m above the seafloor by flotation attached to a mooring line and a 120 kg ballast weight tethered to the frame. The camera and flash were orientated to view approximately 3.2 m^2 of the seafloor. A standard bait (500 g) of fresh mackerel (*Scomber scombrus*) was attached to a reference scale fixed to the ballast weight. A current meter (Aquadopp, Nortek Ltd) was also attached to measure temperature, depth, speed and direction of the current. A scanmar depth sensor was used to provide real-time readings of the depth of the camera frame. A mooring line to a surface marker buoy and flag allowed recovery of the camera frame and ballast at the end of each deployment. An acoustic ballast release system was used as a back-up method for retrieving the BUC.

The camera was programmed to take one picture every minute and the current meter recorded measurements every 30 s. The current was averaged for the first 2 h of deployment, discarding readings where the current meter indicated excessive tilt or spin of the BUC system. All fish observed in the photos were identified (to species level where possible) and counted. Flatfish were consistently difficult to identify to species level as a direct result of the poor contrast between the seabed and the flatfish's colouration. Sub-sampling of particularly high quality images suggested that over 97% of the flatfish attracted to the baited camera were common dab (*Limanda limanda*), with occasional plaice (*Pleuronectes platessa*) and long-rough dab (*Hippoglossodes platessoides*). Deployment times varied from 49 to 423 min but only those over 2 h in duration were considered. The time period from which $N_{\max}$ (maximum number) was taken was standardised to the first 2 h. Deployments were classed as day or night as defined by rising and setting sun times for the day and location obtained from the U.S. Navy Observatory Astronomical Applications (http://www.usno.navy.mil/).

Data analysis

All statistical analyses were performed using R software version 2.4. Non-parametric univariate Kruskal–Wallis rank sum tests were performed to test for differences in water current speed and temperature with the factor year. Temperature did not vary significantly between years and was not included in any further analyses. Factors affecting $N_{\max}$ for the four most abundant species observed at the bait were analysed using generalised linear models (GLMs) and generalised additive models (GAMs). Current velocity at the seabed was treated as a continuous explanatory variable with light level (day/night) and year treated as categorical variables. $N_{\max}$ is a count data type and therefore was assumed to follow a Poisson distribution. When necessary, models were corrected for overdispersion. Models were optimised with backward selection (drop1 and step functions in R). The effects of adding interactions were also considered. Where necessary, nested models were compared and the model with the lowest AIC (Akaike Information Criteria) accepted. During the process of model selection and when the models showed very similar AIC values (differences in AIC <2), an F test was performed to compare and select between nested models. The influence of possible outliers or influential points in each model was evaluated by Cook's distance (values >1). Only the final optimal models are reported, provided no outliers were detected and no serious patterns remained in the residuals.

Table 1 Deployment, date, time of deployment (GMT), light level (D = day, N = night) and mean bottom current speed (cm s^{-1}) during the 2 h of deployment

Deploy	Date	Time (GMT)	Light	Current (cm s^{-1})
S0506	27/04/2005	15:58	D	8.3
S0508	28/04/2005	11:21	D	12.8
S05010	29/04/2005	23:03	N	5.8
S0509	29/04/2005	16:59	D	9.2
S05011	30/04/2005	09:13	D	8.8
S05012	30/04/2005	15:39	D	15.3
S05013	30/04/2005	23:35	N	5.7
S05014	01/05/2005	07:39	D	15.0
J07010	24/04/2007	12:31	D	16.3
J07011	24/04/2007	17:57	D	16.8
J07012	25/04/2007	23:17	N	13
J07013	25/04/2007	04:10	D	14.4
J07014	25/04/2007	09:59	D	21.1
J07015	25/04/2007	15:19	D	11.9
J07016	25/04/2007	20:28	N	16.6
J07017	26/04/2007	01:36	N	13.2
J07018	26/04/2007	06:45	D	19
J07019	26/04/2007	12:01	D	20.2
J07021	27/04/2007	22:59	N	12.1
J07022	27/04/2007	04:09	D	11.8
J07023	27/04/2007	09:18	D	15.5
J07024	27/04/2007	14:25	D	23.2
Lis08_10	17/05/2008	10:23	D	13.8
Lis08_11	19/05/2008	08:00	D	11.3
Lis08_13	20/05/2008	08:40	D	15.9
Lis08_14	21/05/2008	08:28	D	9.4
Lis08_17	22/05/2008	08:30	D	9.8

In addition to the models, the effect of light level on median $N_{\max}$ values is presented using boxplots for each of the four species.

Results

Four species of fish consistently appeared at the baits: haddock (*Melanogramus aeglefinus*), whiting (*Merlangius merlangus*), common dab (*Limanda limanda*) and hagfish (*Myxine glutinosa*). Plaice (*Pleuronectes platessa*) also co-occurred with the dabs from which they could not always be reliably distinguished so dabs and plaice are treated together in this analysis as flatfish.

A total number of 27 deployments (April 2005, $n = 8$, April 2007, $n = 14$ and May 2008, $n = 5$) were used for analysis, of which 6 deployments took place at night. Mean water current speed (cm s^{-1}) during the first 2 h of baited camera deployments ranged from 5.7 to 23.2 cm s^{-1} (Table 1) and was significantly greater in 2007 than in 2005 and 2008 (K–W, $P = 0.006$). The results of the GLMs and GAMs of $N_{\max}$ for the four species as a function of the chosen variables are presented in Table 2.

First arrival times were short, with 50% of the fish observed occurring during the first 10 min of deployment. The majority of arrival times (~90%) occurred within 40 min for whiting, 30 min for flatfish, 15 min for hagfish and 50 min for haddock. Although in general terms arrival times were shorter for higher $N_{\max}$ values, this was not true in the case of whiting and flatfish. Arrival times also were not significantly different between diurnal and nocturnal deployments regardless the magnitude of $N_{\max}$. Therefore, it was considered that $N_{\max}$ was a better reflection on the relative changes in fish population.

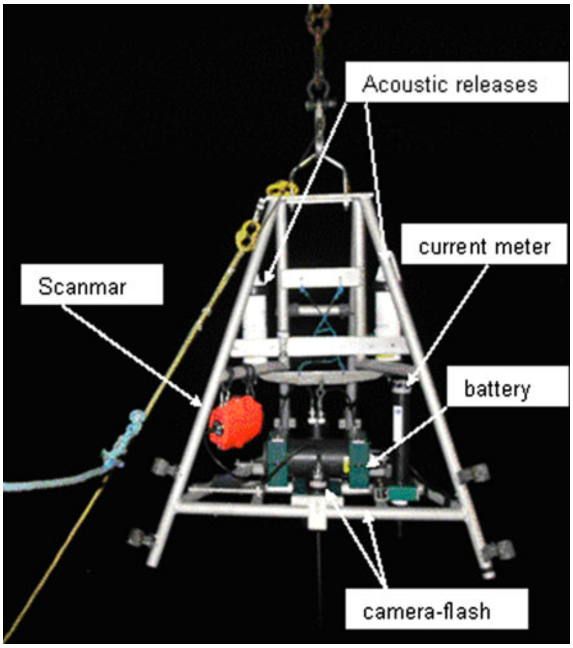

Fig. 2 Marine Scotland–Marine Laboratory baited camera system. Lander aluminium frame fitted with a Kongsberg stills camera and flash gun, battery and a Nortek Aquadopp current meter. Two acoustic releases where fitted as back up recovery system together with a scanmar unit to assess for frame tilt

Whiting were observed in 26 of the 27 deployments with maximum numbers of up to 31. When a Poission-GLM was fitted, overdispersion was detected, therefore, the standard errors were corrected using a quasi-GLM model (Zuur et al., 2009) with current speed, light level and year included as explanatory variables. The effect of current speed was not significant (Fig. 3a) and was dropped from the model. The optimal model showed that the two remaining explanatory variables (day/night and year) had a significant effect, explaining 37.2% of the deviance. *P* values for the factors were obtained by comparing nested models (Table 2). The model estimated fewer whiting during night deployments (Fig. 3b) and a higher $N_{\max}$ in 2005. The possible outlier (whiting $N_{\max} = 31$) had a Cook's distance <0.5 and was therefore retained in the model.

Flatfish were observed in all 27 deployments, with the $N_{\max}$ ranging from 2 to 54 individuals. A quasi-GLM model was fitted to the data to correct for overdispersion. No relationship was found between the $N_{\max}$ of flatfish and the explanatory variables current speed and year. However, time of day had a significant influence on flatfish $N_{\max}$ (Table 2) and the model explained 30% of the deviance. Higher numbers of flatfish were observed during the daylight deployments (Fig. 4b). The possible outlier ($N_{\max} = 54$) had a Cook's distance <0.5 and was therefore retained in the model.

Hagfish were present in all deployments with an $N_{\max}$ ranging from 2 to 204 individuals. A negative binomial-GAM was used to correct for overdispersion and model $N_{\max}$ of hagfish. The effect of light and year were not significant (Fig. 5b) but the model showed a significant non-linear relationship between current speed and $N_{\max}$. The optimal model explained 36% of the deviance and the significance level of the smoother term was $P = 0.03$ (Table 2). The model predicts higher numbers of hagfish with medium current speeds (9–14 cm s^{-1}) and a decline at higher current speeds (Fig. 5a). Cook's distance for the two possible outliers (hagfish $N_{\max}$ 204 and 137) was less than 0.5 in each case, these data points were retained after being shown to have little influence on the model.

Table 2 Results of GLMs and GAMs for data on maximum number ($N_{\max}$) of the four most abundant species and mean bottom current speed during 2 h deployments in cm s^{-1} (S_{2h}), light level (day/night) and interannual effect (2005, 2007, 2008)

Species	Model formula	*P* values			
		S_{2h}	Light	Year	Dev explained
Whiting	q-glm (whi.max ∼ light + year)	–	0.021	0.006	37.2
Hagfish	nb-gam (hag.max ∼ s(S_{2h}))	0.03	–	–	36
Flatfish	q-glm (flat.max ∼ light)	–	0.014	–	30.4
Haddock	p-glm (had.max ∼ S_{2h})	<0.001	–	–	29.2
	p-glm (had.max ∼ light + year)	–	0.03	<0.001	67

Haddock shows the two alternative models. Table gives values of probability (*P*) for each parameter in the model and the explained deviance. (p-glm = poisson-glm, q-glm = quasipoisson-glm and nb-gam = negative-binomial-gam)

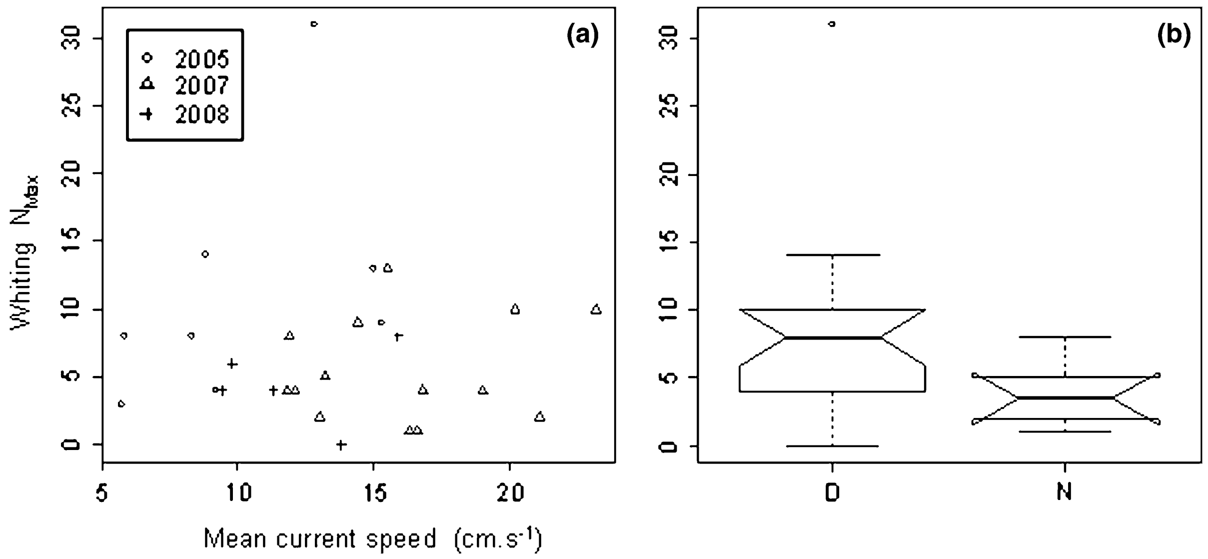

Fig. 3 **a** Whiting maximum number ($N_{\max}$) values for BUC deployments from surveys carried out over 3 years as a function of current speed. **b** Boxplot of $N_{\max}$ of whiting during the day (D) and night (N) time sampling. The midpoint of each box represents the median $N_{\max}$ value and the 25% quartiles define the hinges. Differences between hinges show the spread of the data with whiskers representing maximum and minimum values within 1.5 times the box size. Where notches overlap the two medians do not differ

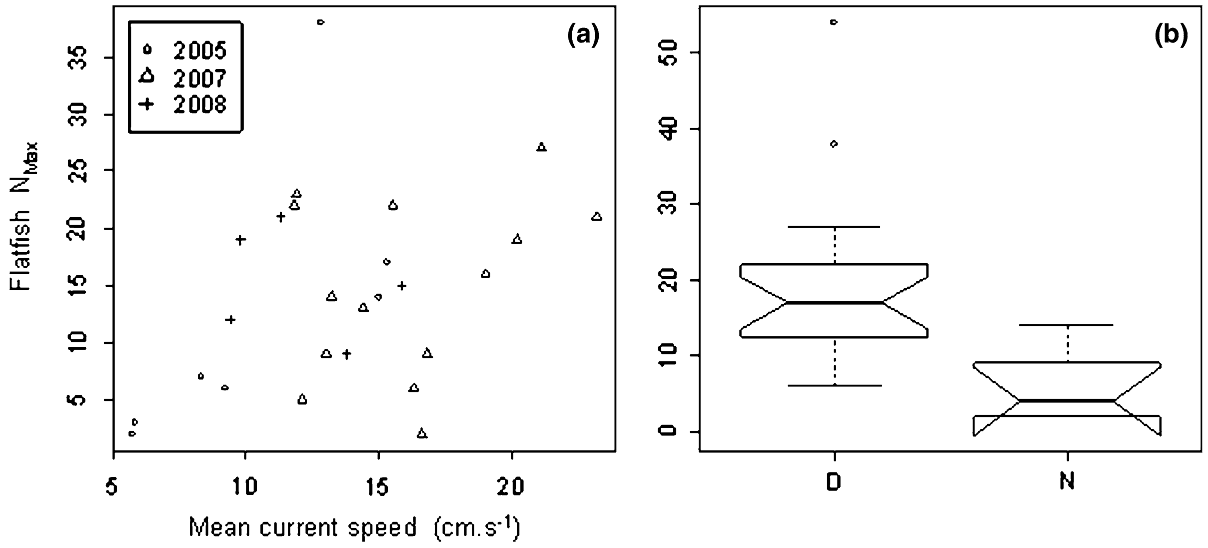

Fig. 4 **a** Flatfish maximum number ($N_{\max}$) values for BUC deployments from surveys carried out over 3 years as a function of current speed. **b** Boxplot of $N_{\max}$ of flatfish during the day (D) and night (N) time sampling. The midpoint of each box represents the median $N_{\max}$ value and the 25% quartiles define the hinges. Differences between hinges show the spread of the data with whiskers representing maximum and minimum values within 1.5 times the box size. Where notches overlap the two medians do not differ

Haddock were observed in 25 out of 27 deployments, and were the least abundant of the four species with an $N_{\max}$ of up to 9 individuals. Both year and current speed were able to explain the variance in the $N_{\max}$. However, the $N_{\max}$ of haddock and current speed have equivalent relationships with year, with

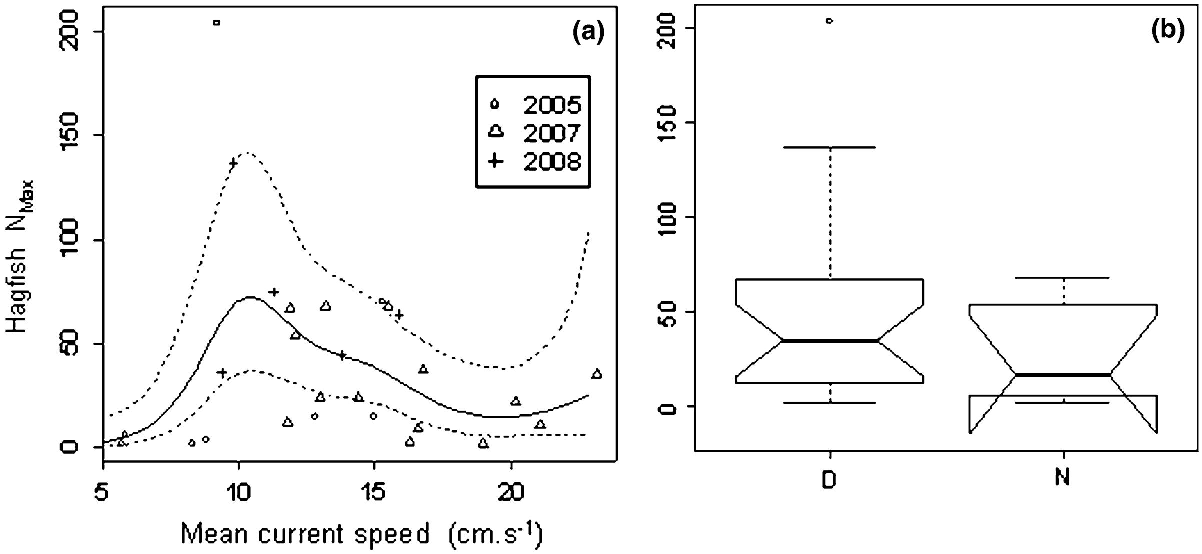

Fig. 5 **a** The effect of current speed on maximum number ($N_{\max}$) for hagfish from three surveys with fitted values (*continuous line*) and 95% confident intervals (*dotted line*) estimated by a negative binomial-GAM. **b** Boxplot of hagfish $N_{\max}$ during the day (D) and night (N) time sampling. The midpoint of each box represents the median $N_{\max}$ value and the 25% quartiles define the hinges. Differences between hinges show the spread of the data with whiskers representing maximum and minimum values within 1.5 times the box size. Where notches overlap the two medians do not differ

more haddock and higher current on 2007 and they could not be modelled simultaneously. As both predictor variables were plausible, the model was run twice, first with current speed and then with year. In both cases a GLM with Poisson distribution was fitted. Current speed had a significant positive effect on haddock $N_{\max}$, light (day/night) was not significant (Fig. 6; Table 2). The model explained 29.2% of the deviance. When year instead of current speed was used in the model, the light factor was borderline significant with a tendency towards higher $N_{\max}$ during the daytime (Fig. 6b) and year was highly significant with an increase in $N_{\max}$ in 2007. This model explained 67% of the deviance (Table 2).

Discussion

The hagfish *Myxine glutinosa*, the most abundant fish species attracted to the baits is known as a benthic scavenger that burrows in the sediment. The next most abundant were the flatfish, dabs *Limanda limanda* and plaice *Pleuronectes platessa* which are benthic foragers. Whiting (*Merlangius merlangus*) which are demersal and mainly piscivorous were next most abundant followed by the benthic foraging haddock (*Melanogramus aeglefinus*). These four species occurred in almost all deployments providing a basis for comparisons.

Priede et al. (1990) used 14–15 BUC deployments at each location to characterise the abyssal ichthyofauna of the Pacific Ocean, Armstrong et al. (1992) used 8–9 at each location in the abyssal Atlantic and 6–9 deployments per station enabled Priede et al. (2003) to discriminate seasonal differences. In the Mediterranean Sea Stobart et al. (2007) used 54–99 replicates per station to characterise a much more diverse fish assemblage with 21–36 species per location. Since this paper deals with only the 4 dominant species in the North Sea, 27 replicates is a sound basis for defining the differences between the species at this location. However the bias of sampling with only 6 of these deployments at night time limits the conclusions that can be drawn regarding day–night differences. All species showed lower numbers during night-time but this effect was only significant for whiting and flatfish. For future work all sampling should be standardised to occur during daylight hours, or a more balanced sampling protocol between day and night should be adopted with more deployments. Sampling was also uneven between years and different current speeds which meant that for haddock

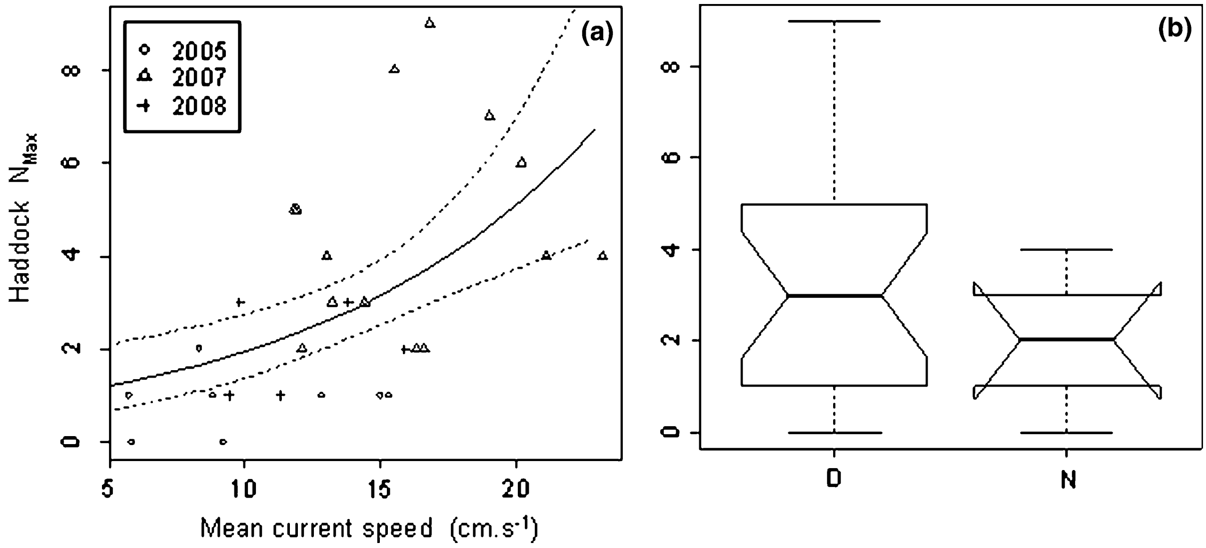

Fig. 6 **a** The effect of current speed on maximum number ($N_{\max}$) for haddock from three surveys with fitted values (*continuous line*) and 95% confident intervals (*dotted line*) estimated by a Poisson GLM. **b** Boxplot of $N_{\max}$ of haddock during the day (D) and night (N) time sampling. The midpoint of each box represents the median $N_{\max}$ value and the 25% quartiles define the hinges. Differences between hinges show the spread of the data with whiskers representing maximum and minimum values within 1.5 times the box size. Where notches overlap the two medians do not differ

it was not possible to determine whether the trend of increase in $N_{\max}$ with current speed was a real effect or the result of higher numbers of haddock in 2007. There had been a major recruitment of young haddock in 2005 resulting in high spawning stock biomass in that year. In 2007 spawning stock biomass was 25% of the biomass in 2005 suggesting the effect of current is a real effect (ICES, 2009). Many more samples over a number of years would help resolve the effect of year versus currents.

Light level had a significant effect on the $N_{\max}$ of whiting and a marginally significant effect for haddock in one of the two alternative models explored. For both species, the trend was for higher $N_{\max}$ during daytime deployments. These results fit well with what is known about their foraging behaviour. Using low light video observations, Fernö et al. (1986) also found a clear diurnal pattern for whiting attracted to baited hooks where increased activity was observed between dawn and dusk during May/June. A similar experiment with haddock and cod, noted higher numbers of haddock during the day, although the difference was not as pronounced as for cod (Løkkeborg et al., 1989). Higher day time trawl catches have also been reported for haddock in the North and Barents Sea (Engås & Soldal, 1992; Aglen et al., 1999; Petrakis et al., 2001; Adlerstein & Ehrich, 2002) and small whiting in the North Sea (Wieland et al., 1998). These activity patterns are most likely related to diel feeding migrations. Adult whiting are largely demersal, daytime foragers targeting piscivorous prey (Hislop et al., 1991; Bromley et al., 1997; Greenstreet et al., 1997) but also disperse and feed in the water column at night (Patterson, 1985; Mergardt & Temming, 1997; Pedersen, 2000; Onsrud et al., 2005). Variation in behaviour is most likely related to local environmental conditions and particular prey assemblages such as vertically migrating sand eels, the preferred prey of both haddock and whiting at certain times of the year (Temming et al., 2004). Haddock also prey on benthic species, feeding on molluscs, polychaetes, echinoderms and crustaceans and thus more closely associated with the seafloor than whiting.

Light level also had a significant effect in the flatfish model with higher $N_{\max}$ observed during daytime deployments. Common dab, the dominant species attracted to the bait, are not thought to make extensive vertical migrations (Gibson, 1973) which would make them unavailable to the baited camera. In fact, trawl catches are often much greater at night, potentially due to improved gear efficiency in low light conditions where avoidance is minimal (Petrakis et al., 2001; Adlerstein & Ehrich, 2002). Dab has a varied, benthivorous diet feeding mainly on invertebrates, in addition to small fish and fishery discards (Kaiser & Ramsay, 1997). It is generally classed as a visual daytime-feeder (Stevens, 1930; de Groot, 1969) although some studies have also observed feeding at other times (Knust, 1986; Carter et al., 1991). The diurnal differences observed in $N_{\max}$ most likely reflect a lack of nocturnal feeding activity by common dab in this area and/or at this particular time of year.

Although it is clear from $N_{\max}$ values that attraction to the bait can be influenced by the light level for some species, the first arrival time did not change significantly for the species observed in this study. This is in accordance with other studies in shallow waters (Willis et al., 2000) were the high population densities mean that the likelihood of a fish being close to the bait when it lands is high regardless of time of day.

Current speed was not found to significantly improve the performance of the models for either whiting or flatfish. However, it was the only significant explanatory variable in the haddock model when the factor year was excluded. Current speed affects baited gear in two ways; through determining the active space of the bait and through its impact on the foraging behaviour of the fish. Fernö et al. (1986) found higher foraging activity levels for whiting during periods of medium to strong current speed compared to little or no current speed. Whilst stronger water currents will disperse the odour plume over a greater area, they may also reduce the effective area through greater dilution (McQuinn et al., 1988) and require greater energy to swim against (Weihs, 1987). Løkkeberg et al. (1989) found that at current velocities between 18 and 27 cm s^{-1}, activity levels for cod and haddock around a baited hook were 30% of those at lower current speeds. Below 18 cm s^{-1} there was no clear influence on activity levels. The mean length of hooked fish in the Løkkeberg et al. study was large; nearly 50 cm for haddock and 56 cm for cod. The current speeds recorded during the present study were largely below 18 cm s^{-1} but the mean size of fish attracted to the bait was smaller with whiting and haddock maximum lengths of 45 cm and mean sizes between 20 and 30 cm (unpublished data).

Sustainable swimming speeds (U_{ms}) for haddock have been estimated at 38–60 cm s^{-1} or 3.16–1.51 BL s^{-1} (body length) for 16–42 cm fish (Breen et al., 2004). These were considered low compared to values for cod (*Gadus morhua*) and saithe (*Pollachius virens*) estimated using a similar method (He & Wardle, 1988; He, 1991). A study of whiting in situ swimming speeds in a Norwegian fjord recorded swimming speeds 14–16 cm s^{-1} during the day and 10–11 cm s^{-1} at night, thought to reflect a change from visually based daytime feeding to olfactory feeding (Onsrud et al., 2005). The length of tracked individuals in this study was not known but trawl catches gave a length frequency with modal peaks at around 10–15 and 30–35 cm. Although no experiments have compared haddock and whiting swimming ability directly, Steinhausen et al. (2005) estimated optimum swimming speed (U_{opt}) for whiting and saithe and suggested that whiting was a stronger swimmer than haddock, but not as strong as saithe. It is possible that the different results of the two models might reflect differing swimming abilities or foraging strategies of the two species; whiting is a piscivorous forager targeting active prey whilst haddock feeds predominantly on slower moving benthic prey. If we accept current speed was the main influence on haddock numbers attracted to the bait, the model suggests an exponential relationship with more fish arriving as current speed increases up to $\sim$25 cm s^{-1}. This pattern, however, does not fit that of Løkkeberg et al. (1989) although only a small number of deployments were carried out where mean current speed was above the 18 cm s^{-1}.

The alternative haddock model with factors "year" and "time of day" is also highly plausible and explains a large proportion of the variance. There is high, annual variability in recruitment of haddock within the North Sea. ICES data reported a relatively high recruitment of the 2005 cohort, and North Sea-wide trawl survey data showed a peak in haddock numbers in 2007 before a decline in 2008 (unpublished data, Marine-Scotland data). This wider population fluctuation could be reflected in the numbers of haddock observed at the study site and might override any effect that the current speed could have on the $N_{\max}$ of fish observed.

Current speed was not a significant explanatory variable in the flatfish model. No published estimates of swimming endurance for common dab were found, but this species is known to be closely associated with the seafloor and unlikely to spend large amounts of time swimming off the seabed (Gibson, 1973). It is likely that the active space for this species was much smaller than for the gadoids and less influenced by current speeds.

Hagfish, *Myxine glutinosa*, showed a pattern unlike all the other species examined. The optimal model indicated increasing numbers of hagfish with increasing bottom current up to a maximum current speed of 11 cm s^{-1}, after which the numbers declined. This primitive, jawless eel-like scavenger lives buried in muddy areas (Whitehead et al., 1984) preying on dead or disabled fish. The lack of functional eyes means that olfactory cues are the main sensory mode of attraction to bait by positive rheotaxis. The pattern of response seen in this study was as would be expected for this type of olfactory based feeder. Hagfish are unlikely to be as strong swimmers as whiting or haddock and is clearly reflected in the current speed threshold above which N_{max} declines. Straham (1963) indicate a slow swimming speed for this species, 25 cm s^{-1} although it can be increased up to 1 m s^{-1} when alarmed by divers (Foss, 1968). It is also likely that hagfish have a patchily distribution, with a level of aggregation close to a previous feeding area, which may account for some of the high numbers (>100 individuals) observed in a single picture. No inter-annual variability was found, and the effect of time of day was negligible.

Conclusion

Our analysis has shown that, depending on the species, an index derived from baited cameras can be strongly influenced by the time of deployment and/or the current speed. Such influences can confound temporal and spatial trends in relative abundance if they are not controlled for or factored into the analysis of results. Understanding these influences and accounting for them in the design of long term monitoring surveys using baited cameras is critical.

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