Absolute abundance estimates from shallow water baited underwater camera surveys; a stochastic modelling approach tested against field data

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Abstract

Baited underwater cameras are becoming a popular tool to monitor fish and invertebrate populations within protected and inshore environments where trawl surveys are unsuitable. Modelling the arrival times of deep-sea grenadiers using an inverse square relationship has enabled abundance estimates, comparable to those from bottom trawl surveys, to be gathered from deep-sea baited camera surveys. Baited underwater camera systems in the shallow water environments are however, currently limited to relative comparisons of assemblages based on simple metrics such as Max_N (maximum number of fish seen at any one time). This study describes a stochastic simulation approach used to model the behaviour of fish and invertebrates around a BUC system to enable absolute abundance estimates to be generated from arrival patterns. Species-specific models were developed for the tropical reef fishes the black tip grouper (*Epinephelus fasciatus*) and moray eel (*Gymnothorax* spp.) and the Antarctic scavengers; the asteroid (*Odontaster validus*) and the nemertean worm (*Parbolasia corrugatus*). A sensitivity analysis explored the impact of input parameters on the arrival patterns (Max_N, time to the arrival of the first individual and the time to reach Max_N) for each species generated by the model. Sensitivity analysis showed a particularly strong link between Max_N and abundance indicating that this model could be used to generate absolute abundances from existing or future Max_N data. It in effect allows the slope of the Max_N vs. abundance relationship to be estimated. Arrival patterns generated by each model were used to estimate population density for the focal species and these estimates were compared to data from underwater visual census transects. Using a Bland-Altman analysis, baited underwater camera data processed using this model were shown to generate absolute abundance estimates that were comparable to underwater visual census data.

Highlights:

- Modelling the behaviour of fish and invertebrates around a baited camera system
- Models developed for tropical fish and Antarctic invertebrates
- Abundance estimates calculated and compared to data from visual census transects

- Comparable abundance estimates generated by the model and transects

Keywords: baited underwater cameras; modeling; fish and invertebrate surveys; underwater visual census

Abbreviations:

BUC: Baited underwater camera

Max_N: Maximum number of individuals, of the same species, appearing on the field of view in any one frame over the whole deployment

$T_{arrival}$: Time to the arrival of the first individual from each species

T_{maxN}: Time to the maximum number of individuals observed at one time

UVC: Underwater visual census

1. Introduction

Abundance estimates of marine populations, that are both accurate, close to the true abundance, and precise, repeatable under the same conditions, are important to understand changes in marine populations or communities (Farnsworth et al., 2007) and to help achieve sustainable management and effective conservation objectives (Collins et al., 2002). For marine fish and invertebrate populations the majority of this data has been collected using trawl surveys (Fitzpatrick et al., 2012; Johnson et al., 2012), which are difficult in abyssal environments and unsuitable in marine protected areas (Bailey et al., 2007). Baited underwater camera (BUC) systems have therefore been used in many studies to gather data on deep-sea scavenging fauna (Farnsworth et al., 2007) and fish assemblages in protected areas (Willis and Babcock, 2000; McLean et al., 2010). However, to use BUC data to produce absolute abundance estimates of fish and invertebrate populations requires a detailed understanding of the physical and biological parameters involved in the process of animals detecting and following the bait plume to the camera (Priede et al., 1994; Bailey et al., 2007).

Bait plume dispersal from a point source, its detection by fish or invertebrates and their arrival at the source, is influenced by a number of environmental and biological factors (Collins et al., 2002; Stoner, 2004). The odour from the bait disperses as a plume into the surrounding water on currents (Reidenbach and Koehl, 2011). The velocity and direction of currents will affect the length and lateral dispersal of the plume as well as its dispersal direction (Bailey and Priede, 2002; Dorman et al., 2012). The dispersal of odour plumes is also affected by turbulence within the aquatic environment (Meager and Batty, 2007), the topography over which it travels (Collins et al., 1999; Collins et al., 2002; Reidenbach and Koehl, 2011) and the characteristics and persistence of the bait (Bailey and Priede, 2002; Stoner, 2004). Fish and invertebrates have evolved olfactory organs with chemosensory abilities that allow them to detect odour plumes and follow them to their source (Reidenbach and Koehl, 2011). The area within the odour plume where the odour concentration is above the threshold which organisms can detect is known as the 'active space' (Sigler, 2000; Stoner, 2004). The probability of the fish entering the active space of the bait plume will be dependent on their search behaviours (Dorman et al., 2012), including their swimming speed and position in the water when foraging (Stoner, 2004), as well as the abundance and distribution of the

population (Armstrong et al., 1992). Once the plume has been detected, the fish will decide whether to follow it based on the feeding motivation that the bait provides (Dorman et al., 2012). The time that individuals remain at the bait will be determined by the availability of food within the environment (Charnov, 1976) as well as the competition and interactions with other scavengers at the bait (Armstrong et al., 1992; Bailey and Priede, 2002; Dunlop et al., 2014).

The process of bait plume detection, attraction and arrival of the deep sea grenadier *Coryphaenoides armatus* at a BUC was modelled using an inverse square relationship:

$$n = c/t_{arr}^{2}$$

where n is the number of fish per square kilometre and c is a constant, dependent upon the current velocity and through water swimming speed of the fish towards the BUC system (Priede et al., 1990; Priede and Bagley, 2000). t_{arr} represents the time elapsed between the beginning of the camera deployment and the arrival of the first fish. The model was developed by Priede et al., (1990) to allow scavenger density to be estimated from their arrival rates at the BUC in conjunction with information on the odour plume spreading characteristics, current velocities and fish swimming speed. The staying time of deep-sea grenadiers at the BUC can be estimated using the relationship:

$$N_{\beta} = \frac{\alpha_0}{x}(1 - e^{-\beta x})$$

where N_{β} is the maximum number of fish present after a certain period of time, α_0 the initial rate of fish arrival at time zero, e the exponential constant and x a constant representing the decay of the odour plume from dilution and bait consumption (Priede et al., 1990). Arrival rates are of interest as a bait placed amongst an abundant scavenger population has a greater chance of being reached by an individual quickly (Bassett and Montgomery, 2011). The arrival times of deep-sea grenadiers at a BUC in two sites in the North Atlantic were modelled in the above manner to produce estimates of abundance which were comparable to those from bottom trawl surveys from approximately the same area and time (Armstrong et al., 1992; Priede and Merrett, 1996). However, when applied to fish arrival times on the Mid-Atlantic Ridge there was no correlation between BUC generated abundances and those estimated from trawls (Bailey et al., 2007).

The use of BUC systems in shallow waters have enabled relative comparisons of both fish and invertebrate assemblages in the tropical (McLean et al., 2010; Moore et al., 2010), temperate (Willis et al., 2003) and the Antarctic environments (Smale et al., 2007) between areas of different protection status (Willis and Babcock, 2000; Westera et al., 2003), habitat type (Moore et al., 2010) and disturbance pressure (Smale et al., 2007). The majority of studies have used the maximum number of individuals, of the same species, appearing in the field of view in any one frame over the whole deployment (Max_N) as an index of relative abundance (Willis and Babcock, 2000; Stoner et al., 2008). Max_N avoids the repeated recording of individuals that leave and re-enter the camera field of view and usually less than the count of all animals

120 visiting the bait (McLean et al., 2010; Harvey et al., 2012). Some surveys have also used the time to the
121 arrival of the first individual from each species ($t_{arrival}$) and time to the maximum number of individuals
122 observed at one time (t_{maxN}) (Willis and Babcock, 2000; Jones et al., 2003). In the shallow water
123 environment however, the development of models of the process of fish or invertebrate arrival at BUCs has
124 been limited (Stoner et al., 2008; Langlois et al., 2012). Heagney et al., (2007) investigated whether abyssal
125 scavenger arrival models could be applied to shallow mid-water baited underwater video data. Existing
126 models appropriate for deep-sea BUC studies with long soak times and where scavengers approached more
127 slowly, were found unsuitable for shallow water BUC studies with much shorter soak times and which
128 attract many fast moving species (Heagney et al., 2007). Rapid arrival patterns of shallow water fish result
129 in overestimated abundance due to the inverse square law of the abyssal model (King et al., 2006; Stobart et
130 al., 2007). Compared to the shallow water environment, currents in the abyss are relatively constant, so an
131 assumption of a constant current speed and direction is more suitable (Heagney et al., 2007; King et al.,
132 2008). The assumptions of deep-sea models also cannot be applied to describe the foraging behaviours of
133 shallow water fish species, which also use sight, as well as chemoreception, to find food (Ellis and
134 DeMartini, 1995; Stobart et al., 2007). The time related metrics used in the deep-sea such as, $t_{arrival}$ and t_{maxN},
135 have not correlated well with other surveys methods in some shallow water BUC surveys (Stoner et al.,
136 2008; Willis and Babcock, 2000).
137
138 The area sampled by the active space of the odour plume is largely unknown in shallow BUC surveys.
139 Concerns have been raised regarding the effect of localised environmental conditions, such as topography
140 and current conditions, on plume dynamics making it difficult to make comparisons between areas (Taylor
141 et al., 2013; Watson et al., 2009). Surveys assume that a comparable area is sampled by each deployment,
142 however, this will often be untrue if current conditions vary (Heagney et al., 2007). The importance of the
143 currents on the dynamics of bait plume dispersal and subsequent fish arrival patterns have been highlighted
144 in several studies in the mid water (Heagney et al., 2007) and demersal environments (Dorman et al., 2012).
145 The unknown sample area of shallow water BUC surveys also makes it difficult to make comparisons with
146 abundance estimates from other survey methods. Several studies have investigated the differences in fish
147 and invertebrate studies recorded by BUC and UVC surveys (Langlois, 2006; Watson et al., 2010),
148 however, conclusions regarding comparisons have been difficult as the area sampled cannot be directly
149 compared (Langlois et al., 2010).
150
151 A model to determine the absolute measures of shallow water fish or invertebrate abundance from
152 arrival patterns at a BUC would involve developing an area based bait dispersion model using in-situ
153 measurements of current speed and direction (Heagney et al., 2007). The mechanistic models outlined by
154 Priede et al., (1990) to estimate the abundance of deep-sea demersal fish from first arrival times are
155 deterministic. However, the arrival rate of fish is stochastically related to population abundance and the
156 factors governing aspects of shallow water fish movement are often assumed to be well represented by
157 random distribution (Farnsworth et al., 2007). This means it is important to include stochastic elements to
158 mechanistic models. The physical factors, current distribution and velocity, observed around the camera
159 system also have a random distribution within a particular range. Therefore it is important to introduce this

160 random aspect into models to describe fish attraction and arrival at a BUC system. Stochastic models that
161 incorporate both the predictable and random aspects of a process, are increasingly being used to build our
162 understanding of complex natural ecosystems (Brown and Kulasiri, 1996). Farnsworth et al., (2007) also
163 modelled the arrival process of deep-sea demersal scavengers at the BUC using the addition of stochastic
164 elements to deterministic models. Farnsworth's (2007) models unfortunately did not include a mechanism
165 to reverse the process and calculate abundances from arrival patterns. The models also required a very large
166 number of assumptions and parameters, making them difficult to implement for many BUC users.
167
168 The primary objective of the present study was to develop a stochastic modelling approach to enable the
169 estimation of the absolute abundance of fish and invertebrates using arrival data collected using a shallow
170 water BUC system. This involved the development of species-specific models for two fish and two
171 invertebrate species observed in tropical and Antarctic BUC surveys. A global sensitivity analysis was used
172 to determine the impact of model parameters on the arrival pattern produced by the model. A secondary
173 objective, following the development of an effective modelling methodology, was to demonstrate how
174 absolute abundance estimates can be generated from BUC data using the methodology. The achievement of
175 this objective was assessed by comparing the model absolute abundance outputs to those from
176 corresponding underwater visual census (UVC) transects. It was hypothesised that 1), the sensitivity
177 analysis would show which model variables have an effect upon the arrival pattern of fish or invertebrates at
178 the BUC and what aspects of the arrival pattern variable are affected the most (i.e. Max_N, $t_{arrival}$ and t_{maxN})
179 and 2), that the modelling methodology would generate absolute abundance estimate that were comparable
180 to those from corresponding UVC surveys.
181
182 **2. Materials and Methods**
183
184 *2.1. Model outline*
185
186 The simulation was built in MATLAB (R2010b) using the movement of an individual fish around a
187 BUC system within a designated area. A bait plume was plotted and the area covered (B_a, m^2) was
188 described as a sector of a circle, using the three equations below. The length of the plume (L_{pl}, m) was
189 calculated using a radius described as the mean current speed (V_w, ms^{-1}) recorded throughout the
190 deployment multiplied by the simulation time (T, seconds). The plume therefore expanded with every time
191 step of the simulation. The plume angle (Pl_θ, radians) was calculated from the inverse tangent of the
192 diffusional velocity (B_y, ms^{-1}), divided by the current speed (V_w, ms^{-1}). The relationship between these
193 model parameters is described in the equations:

$$L_{pl} = V_w T$$

$$Pl_\theta = 2tan^{-1}\left(\frac{B_y}{V_w}\right)$$

$$B_a = \left(\frac{\theta}{2}\right) L_{pl}^2$$

194 Simulations depict the movement of a population of a fixed abundance within a defined area (A, m^2). Prior
195 to detection of the bait plume fish move at a cruising speed (V_{cr}, ms^{-1}) or are stationary, and turned a random

196 number of times (T_r) within a set time period known as the turning interval (Int_{tr}, seconds). The direction
197 within which the fish travels after each turn (D_r, radians) was randomly selected (independently for each
198 individual).
199
200 $$D_r = rand(0, 360)$$
$$Int_{tr} = rand\ (0, T_r) * T_r$$
201
202 The starting point ($P_{st}, (x, y)$) was selected (again independently for each individual) from a random
203 position within the simulation area (A, m^{-2}) using the formula below:
204
$$\left(P_{st}, (x, y)\right) = rand\ (-\frac{A}{2}, \frac{A}{2})$$
205
206 The distance travelled per time step (D_s, m) was calculated by dividing the cruising speed by the time
207 resolution (T_r, seconds). Distance travelled in the x and y axis ($D_s\ (x, y)$) was found by multiplying the
208 cruise speed divided by the simulation time resolution (length of the time-step used in simulations) and
209 multiplying this by sine and cosine of the direction (D_r , radians):
210
211 $$D_s(x) = \frac{V_{cr}}{T_r} \sin(D_r)$$
212 $$D_s(y) = \frac{V_{cr}}{T_r} \cos\ (D_r)$$
213
214 The distance to the camera ($D_{cm}\ (x, y)$) was calculated by taking the square root of the distance travelled in
215 the x and y axis:
$$D_{cm}\ (x, y) = \sqrt{D_s(x, y)^2}$$
216
217 When the distance to the camera ($D_{cm}\ (x, y)$) is less than the radius associated with the circular bait area
218 (B_a, m^2) the fish is considered to have encountered the bait plume area. On encounter the fish turns into an
219 approach angle $app(\theta)$ calculated using:
220
$$app\ (\theta) = (180, 360, 0, -180\ \tan^{-1} D_s\ \left(\frac{x}{y}\right))$$
221
222 (the angle used in this equation depends upon the position on the fish when the bait plume is encountered).
223 This change in direction causes the fish to swim directly upstream towards the bait at a through-water
224 approach speed up the plume towards the camera (V_{fsa}, ms^{-1}). This speed is faster than the cruising
225 swimming speed and was calculated from observation of fish max swimming speed in previous published
226 studies. Current speed (V_w, ms^{-1}) is subtracted to account for the fish swimming upstream against the
227 current. Once in the bait plume the distance travelled towards the camera and its relation to the camera
228 position is recalculated using the through-water approach speed (V_{fsa}, ms^{-1}):
229

$$D_s(x) = \frac{V_{fsa}}{T_r}\sin(D_r)$$

$$D_s(y) = \frac{V_{fsa}}{T_r}\cos\ (D_r)$$

Upon reaching the bait the individual will remain there for a "staying time" (S_t, seconds) found by taking a random time between a pre-determined interval. This was multiplied by the time resolution (T_r, seconds) of the simulation:

$$S_t = rand([1800, T_r])$$

After remaining at the camera for the staying time the fish is removed from the simulation as it is assumed to have reached satiation or decided to forage elsewhere. Simulations run for 60 or 90 minutes and record the total number of fish, or invertebrates, present at the bait every 30 seconds, the same interval is used in the in-situ BUC studies. For the invertebrates studied here staying time was set till the simulation end. The model is depicted in as a diagram in Fig. 1.

2.2. General assumptions

Fish or invertebrates are assumed to act independently of each other at all stages of the simulation and to always react to the bait plume on encounter. The bait plume was always spread from the origin of the coordinate system used in the simulations and assumed to disperse in a single direction. The present model assumes a constant plume concentration and represents a framework that can be combined with fluid dynamics models of bait plume dispersal from a point source in the future to enable the dilution of the plume concentration and changes in current direction to be incorporated into the models.

Simulations were developed for four species; the grouper *Epinephelus fasciatus* and moray eels of the genus *Gymnothorax* spp. recorded in the tropical Gulf of Aqaba and the Antarctic scavenging invertebrates *Odontaster validus* and *Parbolasia corrugatus*. The BUC system consisted of a digital stills camera (SeaLife DC800 or DC1000) enclosed in an underwater housing. No additional light was required for work in the Gulf of Aqaba, but in Antarctica the camera was synchronized, via optical cables, with two variable-power digital slave strobe light units (Epoque ES-23DS). The camera was placed in time lapse mode (30 s intervals). The camera equipment was supported on an L-shaped frame of aluminium tubing. A u-shaped bracket holding the camera was bolted to the vertical element of the frame and angled downwards at 60˚ to view the mesh bait bag attached to the far end of a horizontal pole. 200 g of either chopped fish (*Sparus aurata* and *Dicentrarchus labrax*) in the Gulf of Aqaba or chopped Antarctic invertebrates (*Ophionotus victoriae*, *O. validus*, *Sterechinus neumayeri* and *Laternula elliptica*) were used as bait. The system was deployed from a boat and lowered to the seabed or placed by a SCUBA diver. A ballast weight (c10kg) held the camera system to the seabed and it was held upright in the water column by two small mid-water buoys. At the end of deployments the camera system was recovered either by hauling on a recovery line or by attachment and inflation of a lifting bag by SCUBA divers.

Data on swimming or crawling speeds, the turning frequency and aspects of the foraging behaviours for each species were determined from published studies (Fulton, 2007; D'Aout and Aerts, 1999; Clarke and Prothero-Thomas, 1997; Kidawa, 2001; Bshary et al., 2006) (Table 1). Estimations of staying time were based on observation of individuals in BUC deployments. For the tropical species it was difficult to identify individuals to calculate their staying time at the bait and estimations were taken from observation of the number of consecutive images an individual of that species was observed in. Current velocity was recorded during Antarctic deployments using a Nortek Aquadopp Acoustic Doppler current meter (Aquadopp Current Meter, Nortek, USA) while for the Gulf of Aqaba data an Acoustic Doppler Current Profiler between 10 m and 1 km from BUC deployments was used. Current meter measurements provided the current ranges within which the simulation could operate.

All BUC deployments had a matching underwater visual census (UVC) transect at the same location and depth making up on station. In the Gulf of Aqaba an area of 100 m^2 was swum once (50 x 2 m transect) and the numbers of *E. fasciatus* and *Gymnothorax.* spp. were recorded on a slate (32 stations total, eight at each at 5, 10, 15 and 20 m). In Antarctica the density of *O. validus* and *P. corrugatus* was recorded from analysis of images from a 25 x 0.5 m UVC transect of continuous stills images (18 stations total, six each at 5, 10 and 25 m).

The ranges of input parameters for each model are described in Table 1. The current speeds observed during the BUC deployments in both the Antarctic and the Gulf of Aqaba were approximately comparable to the current speeds measured in the deep-sea environment by Sainte-Marie and Hargrave, (1987). Therefore, due to the lack of measurements of the diffusional velocities the same velocity, 10^{-3} m s^{-1}, used to model the arrival of scavengers at a baited camera by Sainte-Marie and Hargrave, (1987) was used.

Moray eels of the genus *Gymnothorax* and blacktip groupers (*E. fasciatus*) are ambush predators highly associated with rocky reefs and crevices and will defend a small territory (Gibran, 2007). Therefore in simulations of *Gymnothorax.* spp. and *E. fasciatus* movement around the BUC system individuals were relatively slow moving prior to the detection of the bait plume. Antarctic invertebrate scavengers are slow moving compared to the tropical fish therefore BUC deployments in the shallow water Antarctic environment lasted for 1.5 h. The invertebrates also crawl along the seabed so current velocity was not subtracted from the approach velocity. Both Antarctic scavengers remained stationary prior to the detection of an odour plume and on reaching the bait scavengers remained there till the end of the simulation as observed in BUC deployments.

2.3. Data analysis

Models generated an arrival patterns for fish or invertebrates at the bait based on a predicted number present every 30 s, to produce a dataset in the same form as that from in-situ BUC deployments. Max_N, $t_{arrival}$ and t_{maxN} were used to describe the arrival pattern of fish or invertebrates at the BUC. This sensitivity analysis enabled the dependence of the fish or invertebrate arrival pattern output by the model on input parameters to be determined and was used to test hypothesis one. A global sensitivity analysis was

307 performed on each species-specific model to determine the impact of the input parameters; population
308 abundance, current speed, diffusional velocity, swimming speed before contact with the odour plume,
309 approach speed and staying time (Table. 1). Each input parameter was set to be randomly selected from the
310 full range of potential values and each of the four models was run 300 times to ensure that the full range of
311 potential input parameters was considered. This was checked by plotting a histogram of the distribution of
312 the input parameters and was also used to ensure that the range of input values had a random distribution.
313 Both the marginal and bivariate simulated factor distributions were explored to ensure that coverage of the
314 factor space was extensive (Saltelli, 2000).
315
316 A stepwise regression was performed in R (version 3.0.2, The R Development Core Team, 2013) to
317 examine the relationship between the input parameters and the model output abundance indices; Max_N,
318 $t_{arrival}$ and t_{maxN}. The relationship between any input parameter identified as having a significant effect on
319 Max_N, $t_{arrival}$ and t_{maxN} was plotted in a scatter plot. The relationship between the model parameters and the
320 BUC abundance indices were unknown as this early stage of model development and the stepwise
321 regression was used as a tool to explore these relationships. The analysis of the influence of model input
322 parameters on the resultant fish or invertebrate arrival pattern highlighted which parameters were important
323 to calibrate with in-situ measurements.
324
325 *2.4. Producing absolute abundance estimates from BUC data*
326
327 Any parameters with a significant effect were parameterised using an in-situ measurement of this
328 variable where available. For example, if current speed had a significant impact on the Max_N then the
329 current speed from the in-situ BUC deployment providing the camera data was used to produce an
330 abundance estimate was used as a model input. Those identified as having no significant impact on the
331 model output were set to be selected randomly from a range of suitable values for that measure. However,
332 for some parameters an in-situ measurement was not available and values within the models had to remain
333 as the estimates ranges. These parameters were highlighted as those requiring future measurement to
334 improve the accuracy of the model outputs.
335
336 To produce absolute abundance estimates using the modelling methodology a suitable range of estimated
337 population abundances must be first input into the model. In practice these estimates could be derived from
338 previous surveys using other methods, literature for similar areas or be best guesses. In the case of this
339 validation exercise corresponding UVC surveys from the same position and approximately the same time as
340 the BUC deployments were used to find a suitable abundance range for the tropical and Antarctic models.
341 Each single population abundance input into the model produced a BUC arrival pattern. For example, if an
342 abundance range of 1 - 100 individuals was used 99 arrival patterns would be produced. The arrival
343 patterns produced by the model were compared to the arrival patterns produced by the corresponding BUC
344 survey. The R-squared value of the slope fitted to the arrival curve of individuals at the camera with time
345 was used to find a match between model and BUC arrival patterns. Once a match was found the population
346 abundance input into the model to produce that arrival pattern is recorded as the model's best estimate of the

absolute abundance of the fish or invertebrate population surveyed by the BUC system. This process is illustrated in Fig. 2 where the arrival pattern from five model runs of the model of *E. fasciatus* movement around the BUC can be compared to that of the in-situ BUC arrival pattern.

The absolute abundance estimate produced using the model methodology and field BUC data were compared to those generated by corresponding UVC surveys to validate the ability of the model to produce accurate abundance estimates. Models describing the movement of the two tropical fish species and the two Antarctic invertebrate scavengers in relation to the BUC system were validated using transect data. BUC absolute abundance estimates were compared to those from the corresponding UVC surveys using a Bland-Altman analysis (Bland and Altman, 1986). A Bland-Altman analysis is used to compare two methods of measurement, usually a new method with an established one (Bland and Altman, 1986). In this study the UVC represents the established method for measuring fish and invertebrate absolute abundance and the BUC the new method. The Bland-Altman plots show the mean difference between the two corresponding measurements from both methods, known as 'the bias', and the 95% limits of agreement as +/- 1.95 SD of the mean difference. The plot enables visual judgement of the agreement between the measurements and the smaller the range between the measurements the better the match (Bland and Altman, 1986; Bland and Altman, 1995). An analysis showing no significant systematic bias between the two methods would show the majority of the data points within the confidence limits and that points would have a symmetrical around zero. A Bland and Altman analysis was performed in the R package 'MethComp' and a Bland-Altman plot and measures of the test bias test were produced to compare the measurements of absolute abundance using the UVC and tropical and Antarctic BUC models (Fig. 3).

3. Results

3.1. Sensitivity analysis

The input parameters (abundance, current speed, approach speed, cruising speed, diffusional velocity and staying time) produced by 300 runs of the 4 models were plotted in frequency histograms and their distribution was random and encompassed the full range of potential input parameters. Sensitivity analysis revealed that the model input parameters explained a large proportion of the variability in the Max_N output of the 4 models. Input parameters explained less of the variability in the time-based metrics ($t_{arrival}$ and t_{maxN}). Abundance was the model input parameter that had the greatest impact on the Max_N, $t_{arrival}$ and t_{maxN} outputs from the model for all 4 species.

For both tropical models the parameter population abundance explained a large proportion of the variability in the Max_N output; *E. fasciatus* ($y = 0.73x + 0.71$; R-sq (adj) = 91.74; $P < 0.0001$) and for *Gymnothorax* spp. ($y = 0.57x + 0.49$; R-sq (adj) = 97.99; $P < 0.0001$). Input parameters explained less of the variability in the $t_{arrival}$ of tropical fish at the bait. Population abundance had a small but significant effect on *E. fasciatus* ($y = 61.81x + 217.89$; R-sq (adj) = 18.16; $P < 0.0001$) and *Gymnothorax. spp.* $t_{arrival}$ ($y = -54.21x + 83.89$; R-sq (adj) = 30.17; $P < 0.0001$). Current speed also had a significant impact on

Gymnothorax. spp. $t_{arrival}$ (y = 135.45x + 42.94; R-sq (adj) = 1.47; $P = 0.02$). Current speed explained 1.8% of the *Gymnothorax. spp*. t_{maxN} (y = 315.57x + 191.45; R-sq (adj) = 1.8; $P = 0.018$) and population abundance had a significant impact on *E. fasciatus* t_{maxN} (y = 1792.8x + 6614.5; R-sq (adj) = 6.71%; $P < 0.0001$). Staying time had no effect upon indices for both tropical models.

Only population abundance input into models of the Antarctic asteroid *O. validus* movement around the BUC explained a significant proportion of the Max_N values generated (y = 0.53x – 0.92; R-sq (adj) = 49.32; $P < 0.0001$). *O. validus* $t_{arrival}$ and t_{MaxN} values were also only significantly affected by input abundance (y = -234.17x + 5199.6 and y = -23.84 + 4915.4; R-sq (adj) = 19.14 and 3.37; $P < 0.0001$ and P = 0.0008). For *P. corrugatus* input abundance accounted for 34.48% of the variability in Max_N (y = 0.2241 – 0.0985; R-sq (adj) = 34.4; $P < 0.0001$) and $t_{arrival}$ and t_{maxN} 19.29% and 1.49% (y = -163.74 + 4879.5 and y = -15.179 + 4662.0; R-sq (adj) = 19.29 and 1.49; $P < 0.0001$ and $P = 0.03$). Current speed and *P. corrugatus* approach speed had no significant effect upon Max_N, $t_{arrival}$ and t_{maxN} values.

3.2. Comparison to baited underwater camera data

The Max_N output of the models developed to describe the behaviour of the two tropical fish and Antarctic invertebrate species were all primarily affected by the input parameter population abundance. Therefore, Max_N was only used to match arrival patterns from the in-situ BUC deployment and the multiple model arrival patterns. $T_{arrival}$ and t_{maxN} were also significantly related to abundance and could also be potentially used to select model arrival patterns. There was limited evidence from the sensitivity analysis of the effect of the other model parameters on the model abundance indices therefore parameters were kept within the ranges reported in Table 1.

For 10 of the BUC deployments the corresponding UVC recorded no groupers and for three of the UVC transects that observed groupers none were observed in corresponding BUC deployments. 10 corresponding UVC and BUC pairs both recorded *E. fasciatus* and for 9 of these pairs the BUC model produced the same or slightly higher abundance estimates (Fig. 3a). The Bland Altman plot provides little evidence of systematic bias between the abundance estimates of the grouper *E. fasciatus* generated by the BUC model methodology and the UVC surveys. This is concluded as all data points are within the +/- 1.96 SD limits of agreement in the plots and points are distributed symmetrically around the mean (Fig.4a). Only 4 corresponding UVC and BUC pairs both observed moray eels of the genus *Gymnothorax* and the BUC model produced higher or the same abundances. Moray eels were only observed in BUCs in 8 of the corresponding UVC and BUC pairs and only in UVC in 4 pairs. The Bland-Altman plot show that points are symmetrically distributed around the mean and that all point were within the +/- 1.96 SD limits of agreement (Fig.4b).

In all 18 UVC and BUC pairs *O. validus* was observed and there was no clear pattern of differences between the abundance estimates recorded by each method (Fig.3c). All the data points for *O. validus* abundance estimates from the BUC model and the UVC were within or on the +/- 1.96 SD limits of

agreement. From the plot it would however, appear that the plots were slightly asymmetrical to the zero and that average abundances from the model are slightly less than those recorded by the UVC as the abundance of *O. validus* increases (Fig.4c). For 8 of the 18 corresponding transect and BUC model pairs abundance estimates for *P. corrugatus* were only recorded by the BUC model and in a further 6 pairs the BUC model estimates were much larger than in the UVC surveys (Fig.3d). In the Bland-Altman plots two outliers were removed where abundances > 100 individuals were recorded by the BUC. All points were within the 1.96 SD limits of agreement but they were not symmetrically distributed around the mean indicating that higher abundances were measured by the BUC (Fig.4d).

4. Discussion

Results from the sensitivity analysis indicate that for tropical and Antarctic models of fish and invertebrate movement around the BUC system the abundance of the surveyed population was the factor most strongly related to the Max_N. These models allow a BUC user to determine the relationship between Max_N and the abundance of the focal species and allow the commonly collected Max_N unit of relative abundance to be converted to absolute units. Two other commonly-recorded indices of abundance, $t_{arrival}$ and t_{maxN} appear to be less closely related to absolute abundance than might have been assumed, but might usefully contribute to model parameter selection where more than one abundance value results in the observed Max_N. Within the range of species used here, estimates of their searching speed and staying time had relatively little influence on the model Max_N. This is a reassuring finding as it is relatively difficult to estimate these behavioural values in wild animals.

For all species-specific, models Max_N appeared to be the measure which accounted for most of the variability in the input population abundance fish or invertebrates. Measurements of $t_{arrival}$ and t_{maxN} would however, reflect more about aspects of fish approach swimming speed and the current velocity observed around the BUC deployment. Stoner et al., (2008) found that a poor correlation exists between BUC time based metrics and abundance estimates of juvenile Pacific cod from corresponding seine net trawls, while Max_N measures correlated well with trawl survey results. Time based metrics from BUC studies in the abyssal environment have however, been used successfully to calculate the absolute abundance of scavenging fish populations (Priede and Merrett, 1996). The current speeds observed around the BUC deployments and that were used for model ranges were relatively slow. If BUC deployments were within environments experiencing high current speeds then possibly variation in current speed would likely have a greater affect on BUC output indices and detailed current speed measurements during BUC deployments would be essential. The model framework presented here allows these different scenarios to be tested against field data. Estimates of the range of diffusional velocities experienced in the tropical and Antarctic environments were not available to investigate its potential effect upon arrival patterns, but again the framework allows easy incorporation of new field or laboratory data on diffusion to be incorporated as it becomes available. The incorporation of fluid dynamics modelling into the methodology would enable the potential effects of current speed and diffusional velocity on the arrival of fish or invertebrates at the BUC to be explored in more detail. Unlike previous models an odour plume of any shape or concentration can be

467 incorporated into this framework to replace the "pie segment" used here. Animals contacted by the plume or
468 walking/swimming into the side of it would respond in the same way as those in the existing models.
469 Refinements such as animals resuming random movement if they leave an irregularly shaped plume would
470 be added at this stage.
471
472 Staying time had no impact on abundance metrics even though it had been shown to affect Max_N values
473 in the deep-sea BUC studies (Priede et al., 1990). The majority of BUC studies in the abyssal northeast
474 Atlantic found the mean staying time of the deep-sea grenadier (*C. armatus*) to be approximately 2 hours
475 (Priede et al., 1994; Henriques et al., 2002). In the shallow water BUC fish arrive more rapidly and
476 frequently, causing the staying time to likely have less of an impact on Max_N values. With longer staying
477 times the number of fish at the camera will accumulate to reach Max_N and the total meaning that Max_N will
478 have more of a linear relationship with the numbers visiting the BUC. However, in the shallow water
479 environment where more fish are coming and going from the field of view there maybe a larger difference
480 between Max_N and the total number of animals visiting the camera. These results therefore indicate that in
481 these models accurate estimate of fish or invertebrate staying time, cruising speed or diffusional velocity are
482 not important to the output of the model and therefore all that is necessary is the selection of a suitable
483 range. More important factors such as fish and invertebrate approach speed and the current speed should be
484 prioritised. The latter is certainly directly measurable at the camera, though in complex habitats the current
485 experienced by the fauna might be quite different. Approach speed is harder to ascertain, though stereo
486 camera systems such as BRUVS can probably provide useful information if the system lands facing
487 downstream at the point at which animals arrive. With downward-looking cameras the field of view is often
488 too small to get good estimates of movement speed, but not impossible, especially for slow-moving species.
489 In our Antarctic studies we were able to directly measure invertebrate walking speed across the seabed.
490
491 The absolute abundance estimates of *E. fasciatus* and *O. validus* generated by the BUC model
492 methodology were found to be most comparable to the abundance estimates from corresponding UVC
493 surveys. This is because these species are visible to the UVCs as well as to the BUC. The other two species
494 tend to be hidden in rocks (Clarke and Prothero-Thomas, 1997) or within the coral reef (Bshary et al., 2006)
495 except when bait is present, with their occasional appearance in the open probably being caused by recent
496 feeding or disturbance. Moray eels of the genus *Gymnothorax* are generally nocturnal hunters and during
497 the day they will remain hidden within rocky refuge (Bshary et al., 2006; Bardach et al., 1959) making it
498 difficult for daytime UVC surveys to detect them. In a number of BUC and UVC corresponding pairs the
499 BUC survey observed moray eels when the UVC surveys recorded none causing the BUC model to estimate
500 abundances when the UVC estimate equalled zero. The abundance estimates generated by the BUC models
501 for the nemertean worm *P. corrugatus* were higher than those within the higher abundance estimates were
502 produced by the BUC models for *P. corrugatus* due to the BUC recording *P. corrgutus* but none being
503 observed in the corresponding UVC survey. This can be attributed to the species taking refuge under rocks
504 during the day (Clarke et al., 1997) causing few to be observed in daytime transects. This will result in the
505 model parameters being calibrated to artificially low populations densities. Little is known about the
506 behaviour of *P. corrugatus* and it is possible that large groups of individuals congregate within refuges

(Clarke and Prothero-Thomas, 1997), violating the assumption of the model that individuals are randomly distributed and act independently of each other.

Models also assume that all fish react and follow the bait plume once encountered, however factors such as satiation state, olfactory capabilities and the availability of other food sources in the environment will impact upon their decision. Due to the comparability of absolute abundance estimates from the BUC model and the UVC, it would appear that a large proportion of the nearby animals from these species reacted to the bait plume. Model assumptions include that individuals react independently of each other however, competitive behavioural interactions have been observed to occur between fish at the bait of BUC systems (Armstrong et al., 1992; Stoner et al., 2008; Dunlop et al., 2014). It has been suggested that these interactions discourage some fish from approaching the bait due to the increased chance of competition (Jones et al., 2013; Willis et al., 2003; Cappo et al., 2004) or predation (Lampitt et al., 1983; Harvey et al., 2007) presented by the other fish. It is therefore evident that in both the fish species studied competitive interactions around the BUC could potentially impact upon the arrival patterns of individuals at the bait. The effect of other species interactions on the arrival patterns of fish and invertebrates at the BUC should also be considered. Effects may include particular species posing a higher predation risk at the bait reducing the number of the other species observed. Further studies of the impact of these interactions would allow this information to be added to modelling approaches. Unlike previous models our framework would allow multiple species models to be combined using information on the species composition and potentially the effects of interactions on bait approach and staying times. Also when foraging individuals become close to the bait they are potentially attracted by the movement and sounds of others feeding (Bailey and Priede, 2002). For shallow water fish species that reply heavily upon sight for foraging and hunting (Stoner et al., 2008) this has the potential to impact on their behaviour in relation to the BUC system and thus arrival patterns. Further valuable research would be the investigation of the application of this modelling approach to other marine species, which have been found to be attracted to BUC systems. This would primarily include the large, predatory mobile species that BUC surveys have been found to effectively survey (Malcolm et al., 2007; Watson et al., 2010).

Preliminary results show that this stochastic modelling approach can generate absolute abundance estimates of some shallow water fish and invertebrate populations from BUC deployments and that these estimates are comparable to an established survey method. Discrepancies were apparently due to cryptic behaviour in some species resulting in underestimates of abundance during underwater visual census surveys. The generation of absolute abundance estimates from shallow BUC surveys improves the application of the method substantially and makes the results comparable to those of other survey methods, such as trawl surveys and transects commonly used in stock assessments and monitoring programmes. This also enables previously-collected BUC data to be reanalysed and diversity indices for these deployments to be recalculated based on the abundances of the animals present rather than combinations of Max_N values.

In conclusion, the spatial, stochastic modelling approach described and tested in this study represents one of the first attempts to model the arrival process of shallow water marine species at a BUC system.

Initial results for a small set of tropical and Antarctic species-specific models show that this method has the potential to generate absolute abundance estimates from BUC data that are comparable to UVC data. The model could be used retrospectively to re-analyse existing Max_N data. This development combined with the existing ability of BUCs to generate data in a time-and-cost efficient and non-destructive manner can significantly improve the value of this method to monitor inshore marine populations.

Figure and Table Legends

Fig. 1. Diagram illustrating the general input and output parameters of the model simulation describing the behaviour of fish and invertebrate populations in relation to a baited underwater camera system.

Fig. 2. Example plot of the arrival pattern of the black tip grouper (*Epinephelus fasciatus*) at the baited underwater camera system (BUC) produced by 5 model runs and the arrival pattern from an in-situ BUC deployment.

Fig. 3. Histograms and scatter plots comparing the absolute abundance estimates generate from UVC transects (open bars) and BUC models (closed bars) for a) the grouper (*Epinephelus fasciatsus*), b) the moray eel species (*Gymnothorax* spp.), c) the Antarctic asteroid (*Odontaster validus*) and d) the Antarctic nemertean worm (*Parbolasia corrugatus*).

Fig. 4. Bland Altman plots illustrating the agreement between the abundance estimates generated by the baited underwater camera model (BUC) and the underwater visual census survey (UVC) for a) *Epinephelus fasciatus*, b) *Gymnothorax* spp., c) *Odontaster validus* and d) *Parbolasia corrugatus*.

Table 1 Input parameters ranges for *Epinephelus fasciatus*, *Gymnothorax* spp., *Pollachius virens*, *Scyliorhinus canicula*, *Odontaster validus* and *Parbolasia corrugatus*.

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Figure 1

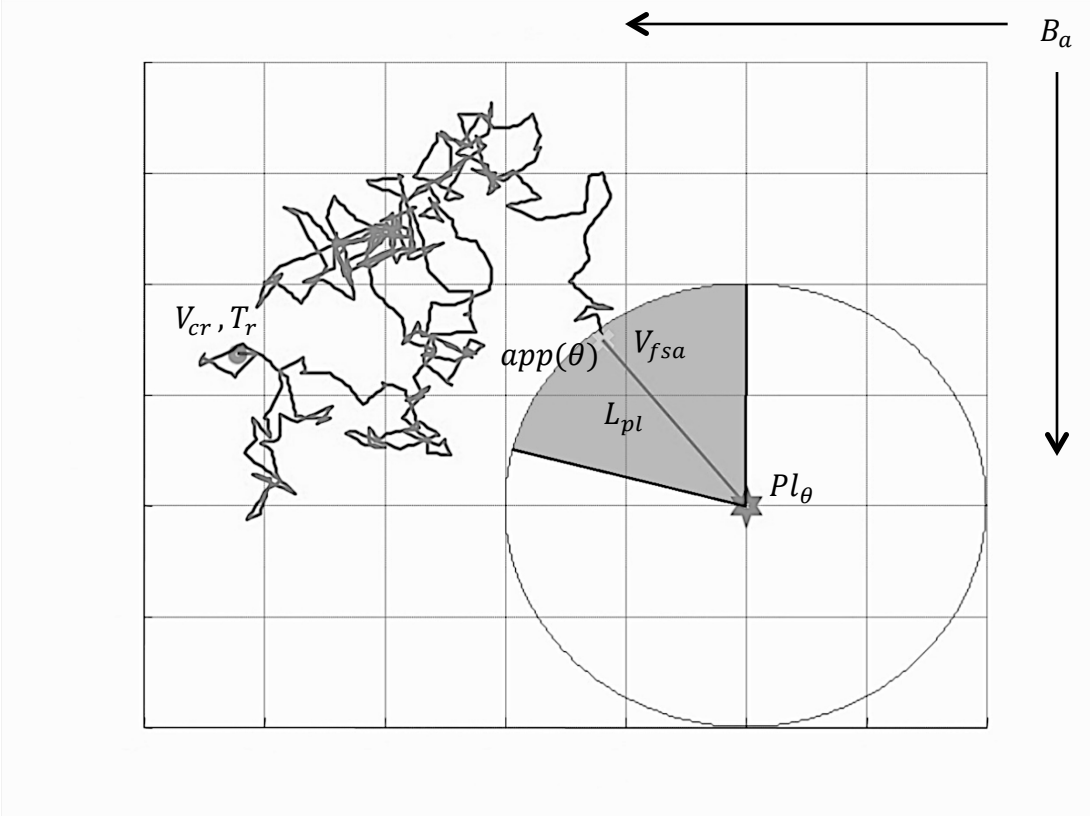


Figure 2

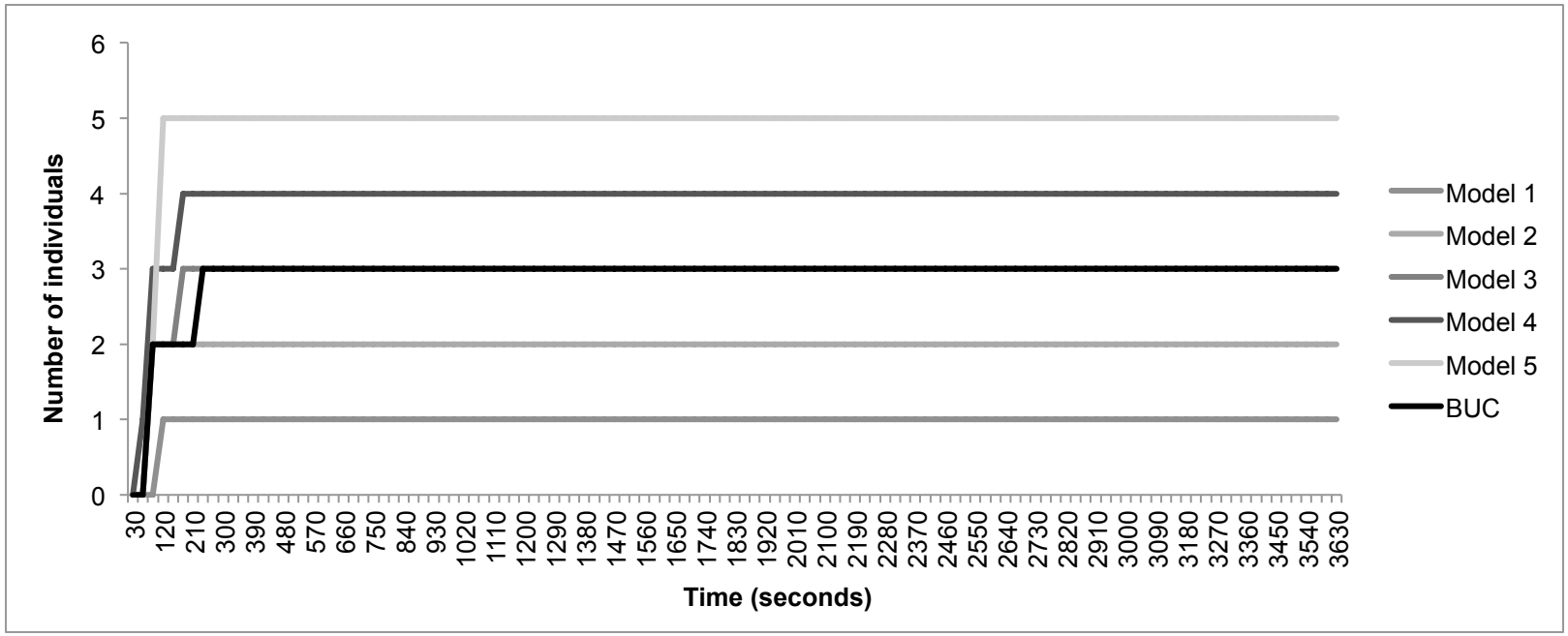
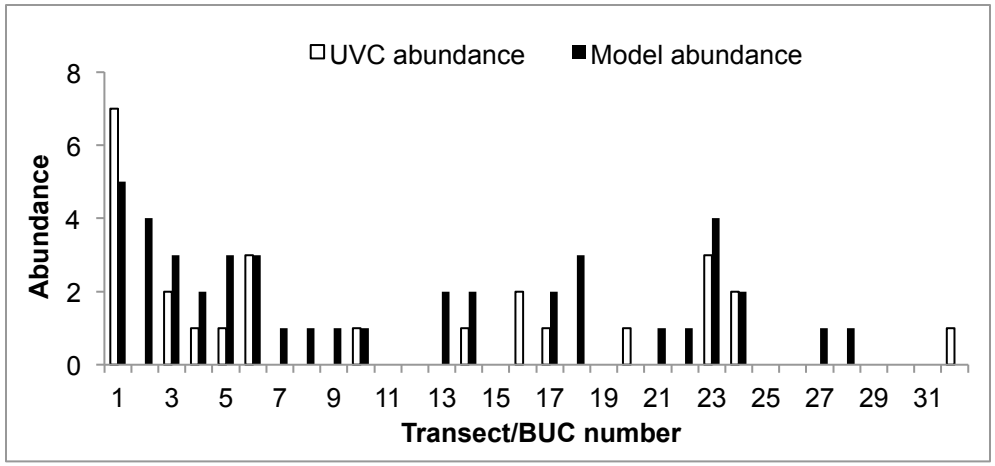
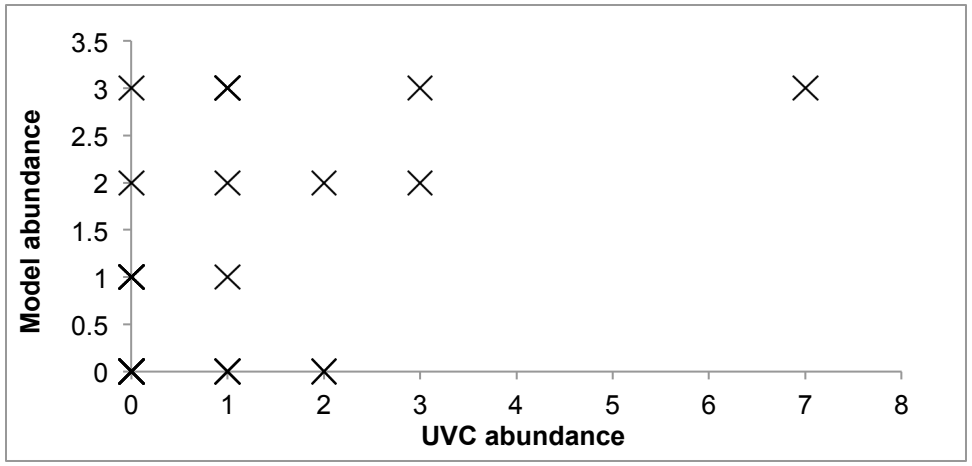

Number of individuals
0
1
2
3
4
5
6
30
120
210
300
390
480
570
660
750
840
930
1020
1110
1200
1290
1380
1470
1560
1650
1740
1830
1920
2010
2100
2190
2280
2370
2460
2550
2640
2730
2820
2910
3000
3090
3180
3270
3360
3450
3540
3630
Time (seconds)
Model 1
Model 2
Model 3
Model 4
Model 5
BUC

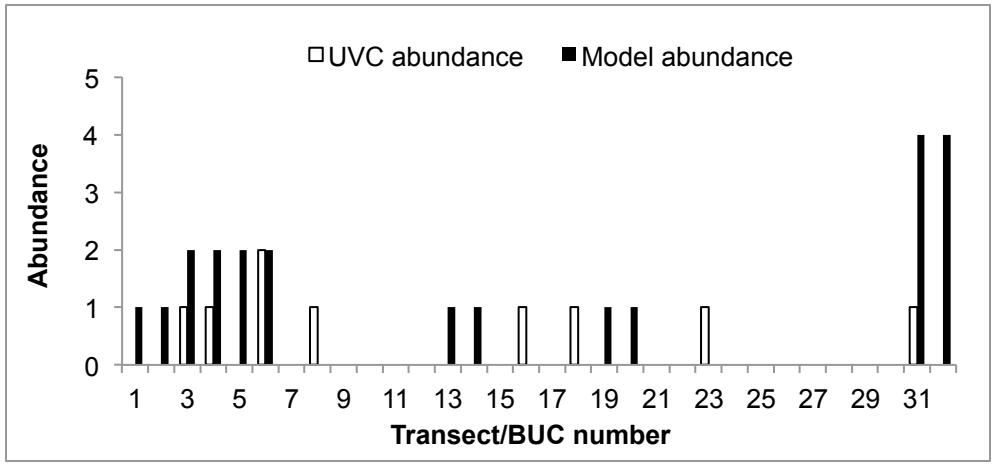
Figure 3

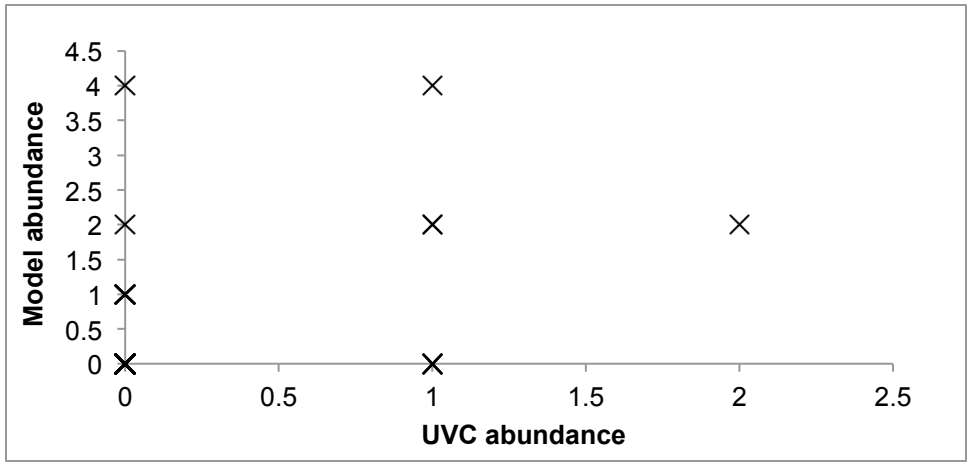
a) *Epinephelus fasciatus*



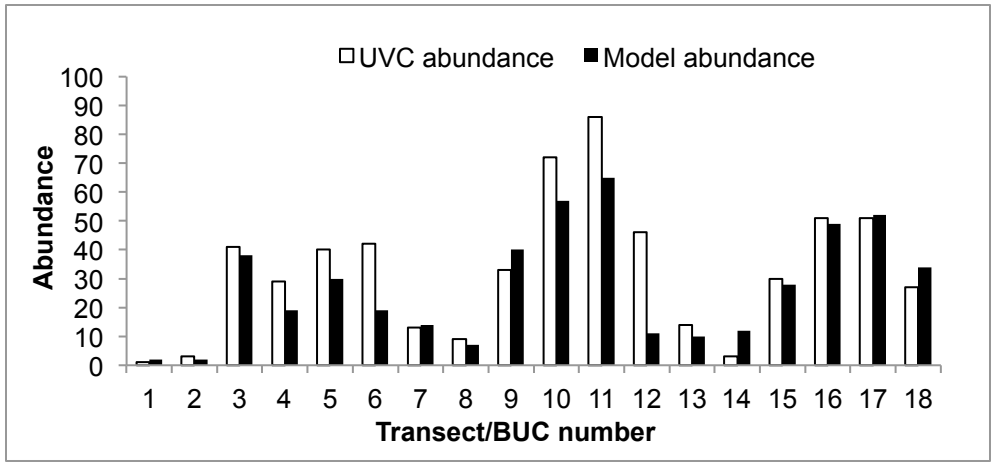


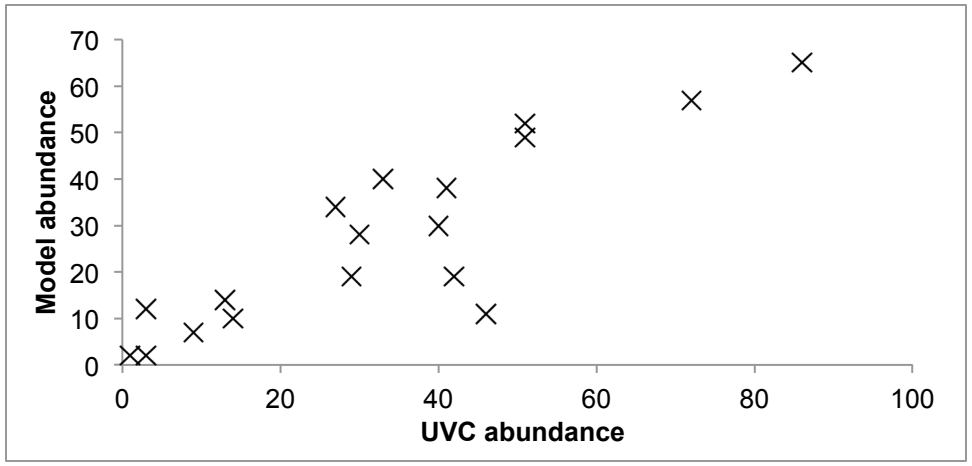
b) *Gymnothorax* spp.



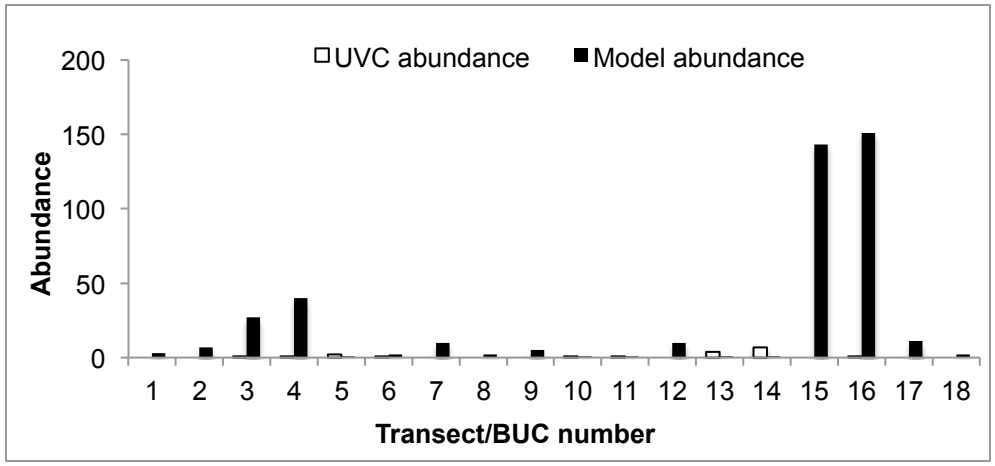


c) *Odontaster validus*





d) *Parabolasia corrugatus*



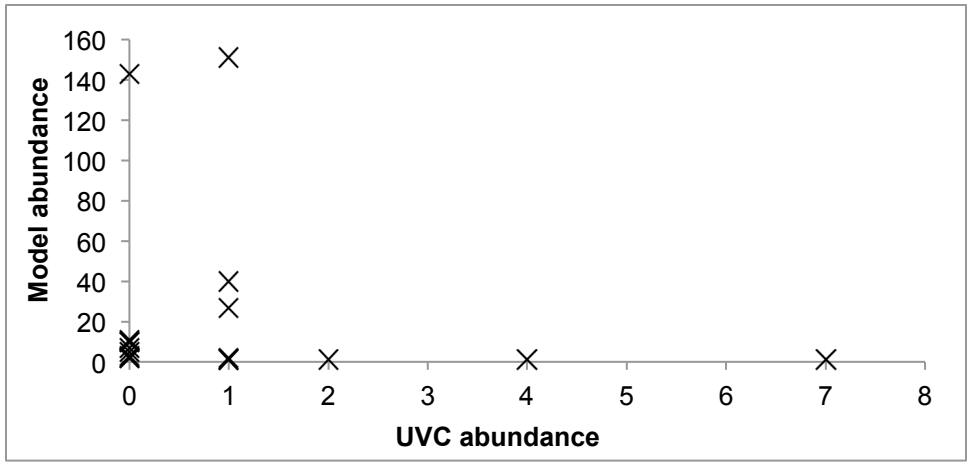


Figure 4

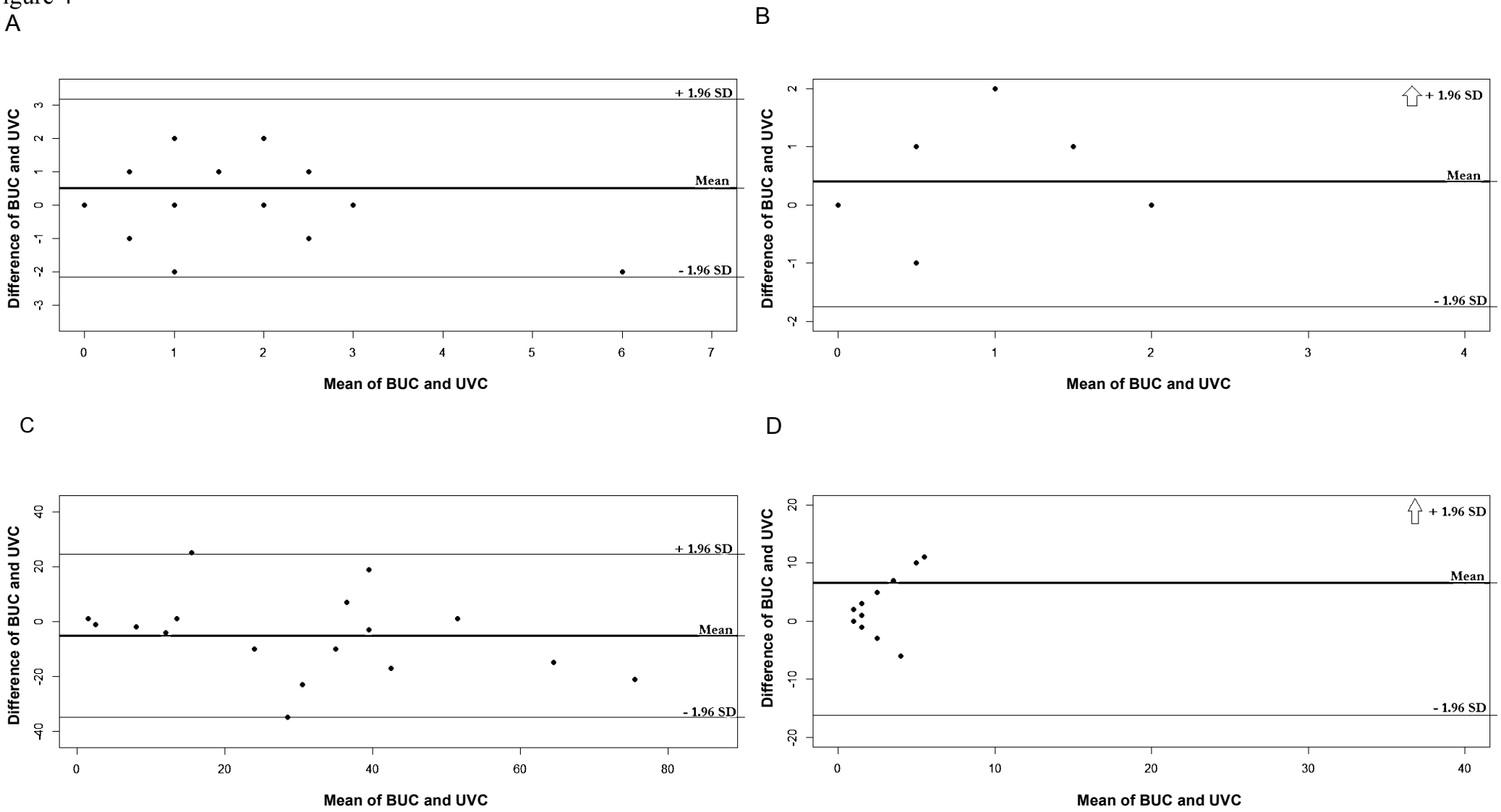

A
B
C
D
+ 1.96 SD
Mean
- 1.96 SD
Difference of BUC and UVC
Mean of BUC and UVC

Table 1

Parameters	Area (m^2)	Current speed ($m\ s^{-1}$)	Abundance (individuals)	Cruising speed ($m\ s^{-1}$)	Turning interval (s)	Approach speed ($m\ s^{-1}$)	Staying time (s)	References
Species								
Epinephelus fasciatus	1000	0.02 - 0.2	1 - 100	0 – 0.2	0 - 120	0.294 - 0.365	0 - 240	Fulton, 2007; Bshary et al., 2006
Gymnothorax spp.	1000	0.02 - 0.2	1 - 100	0	0 - 120	0.0935 - 0.318	0 - 180	D'Aout and Aerts, 1999; Gibran, 2007
Odontaster validus	6.25	0.01 - 0.1	1 - 100	0	n/a	0.0001 – 0.001	To simulation end	Kidawa, 2001
Parbolasia corrugatus	6.25	0.01 – 0.1	1 - 100	0	n/a	0.0001 – 0.0003	To simulation end	Clarke and Prothero-Thomas, 1997