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Fish behaviour effects on the accuracy and precision of underwater visual census surveys. A virtual ecologist approach using an individual-based model

Miguel Pessanha Pais*, Henrique N. Cabral

MARE – Marine and Environmental Sciences Centre, Faculdade de Ciências, Universidade de Lisboa, Campo Grande, 1749-016 Lisboa, Portugal

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A B S T R A C T

Underwater visual census (UVC) methods are used worldwide to monitor shallow marine and freshwater habitats and support management and conservation decisions. However, several sources of bias still undermine the ability of these methods to accurately estimate abundances of some species.

The present study introduces FishCensus, a spatially-explicit individual-based model that simulates underwater visual census of fish populations. The model features small temporal and spatial scales and uses a movement algorithm which can be shaped to reflect complex behaviours and effects of diver presence. Four different types of fish were used in the model, featuring typically problematic behavioural traits, namely schooling behaviour, cryptic habits, shyness and boldness. Corresponding control types were also modelled, lacking only the key behavioural traits. Sampling was conducted by a virtual diver using four true fish densities and employing two distinct methods: strip transects and stationary point counts.

Comparisons with control fish have shown that schooling and bold behaviours induce positive bias and reduce precision, while cryptic and shy behaviours induce negative bias and increase precision, although shy behaviour did not have a significant effect on precision in transects. By looking at deviations from true density, however, schooling, shy and bold fish densities were strongly overestimated by both methods, while cryptic fish were slightly underestimated. Schooling and bold fish had the lowest precision overall, followed by shy fish. Fish rarity decreased precision, but had no effect on bias. Stationary points had less precision than transects for all fish types, and led to much higher counts, resulting in greater overestimation of density overall.

By modelling complex behaviour, it was possible to separate the contributions of detectability and non-instantaneous sampling on bias, and gain a deeper understanding of the effect of behavioural traits on UVC estimates. The model can be used as a tool for planning and optimization of monitoring programs or to calculate conversion factors for past or ongoing surveys, assuming behavioural patterns are well replicated.

1. Introduction

Methods to quantify the abundance of populations and communities are key in Ecology, determining the way a state or process of the system is perceived by observers (Zurell et al., 2010). When the entire area of interest or population cannot be surveyed, as is often the case, the choice of method and sampling design can be crucial, particularly if observations support conservation and management decisions (Blanchard et al., 2008; Pais et al., 2014).

Underwater visual census (UVC) methods are a cost-effective way to survey shallow marine and freshwater habitats. In addition, the fact that they are non-destructive makes them ideal choices for protected areas, supporting important management and conservation decisions worldwide, particularly on temperate and coral reefs (Colvocoresses and Acosta, 2007; Di Franco et al., 2009; Edgar et al., 2004; Henriques et al., 2013; McClanahan et al., 2007a,b). As with any sampling method, UVC methods estimate the true state of the observed system, but are affected by two kinds of uncertainty: precision and bias. Precision is the width of the dispersion of estimates around the mean and bias is the deviation of the mean from the true value we are estimating. Precision can be quantified by doing replicate measurements, and to a certain extent it can be reduced by

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* Corresponding author.
E-mail address: mppais@fc.ul.pt (M.P. Pais).

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increasing sampling effort (Pais et al., 2014), however, bias is very difficult to quantify and can only be minimised by changing sampling design, or applying a correction factor to field data (Kulbicki et al., 2010).

UVC methods are subject to several sources of bias, such as observer experience (Thompson and Mapstone, 1997), low detectability of organisms (MacNeil et al., 2008a), observer movement (Lincoln Smith, 1988), non-instantaneous sampling (Ward-Paige et al., 2010) and underwater visibility (Bozec et al., 2011). In fact, even if we ensure that divers are experienced and the sampling method is standardised across space and time, estimates may still be completely false, even if very precise (Sale and Sharp, 1983). While UVC methods are known for their tendency to underestimate due to imperfect detectability (Katsanevakis et al., 2012), Ward-Paige et al. (2010) used a simulation model to show that shark densities are systematically overestimated due to their high mobility. In either case, bias can have devastating effects, because managers and scientists may spend unnecessary resources to protect species which are not actually endangered, or may be unaware when population sizes reach threateningly low levels. Accurate estimates are particularly important for fisheries stock assessments (Jennings and Polunin, 1995), or to parameterise dynamic community and population models that support management decisions (Pelletier et al., 2008).

Several studies on UVC have concluded that bias is strongly linked to species behavioural traits (Bozec et al., 2011; Kulbicki et al., 2010; MacNeil et al., 2008a; Samoilys and Carlos, 2000; Willis et al., 2000). In fact, some traits such as cryptic habits (Christensen and Winterbottom, 1981; Willis, 2001), schooling behaviour (MacNeil et al., 2008a) and reaction to divers (Edgar et al., 2004; Kulbicki, 1998) have been pointed out as particularly difficult to deal with when using UVC.

The quantification of sampling bias can be very useful, not only because it can be used to reshape sampling designs to better suit our subject, but also because it allows us to apply correction factors to existing data, or to standardised long-term monitoring programmes (Christensen and Winterbottom, 1981; Pierucci and Cózar, 2015; Sale and Sharp, 1983). This of course requires that we know the true density of fish at a given time, which is a challenge that many have tried to overcome. The majority of studies dealing with bias in UVC used an alternative method (usually more destructive) to represent the true state of the system, which include traps (Edgar et al., 2004) or fish poisoning in an enclosed pool (Christensen and Winterbottom, 1981) or caged area (Willis, 2001). Other approaches include distance sampling (Bozec et al., 2011; Buckland et al., 2012) and predictive models that use data from different transect widths and extrapolate to a zero-width theoretical scenario (Sale and Sharp, 1983). However, these alternative methods have their own bias (Mahon and Hunte, 2001), and some can seriously affect or kill fish from the assemblages of interest, defeating the purpose of a non-destructive method.

Another alternative approach is to use a controlled environment, which can be a fish tank or even a natural enclosed area, where a known number of fish are introduced (e.g. Biro, 2013). Of course, the logistics of such an approach hinder its use, but even if feasible, fish behaviour can be affected by conditions in captivity and artificial gathering of fish near walls can affect counts if the tank is too small.

A third alternative is to use computer simulation. This requires the effort of programming the model, but can ultimately meet the requirements of being cost-effective and non-destructive, while also continuing to serve as a tool for future use and improvement. A suitable modelling approach to answer sampling-related questions is what has been labelled by Zurell et al. (2010) as the “virtual ecologist” approach. In such models, more realistic output values can be drawn by also modelling the data collection procedure, where a “virtual ecologist” records measurements and observations in a similar way a real ecologist would do in the field. For the specific case of UVC, two models have been built to study observation bias, both opting for a spatially-explicit individual-based model of fish movement, with divers added as agents responsible for observing and recording the number of fish according to pre-determined rules and limitations. The Reefex model was developed by Watson et al. (1995) to study the influence of fish speed and approach angle on transects and stationary point counts. It featured grid-based fish movement and a time step of 10 s. While the movement model was simplified, many complex processes were included, such as fish avoidance, different behaviours with pre-defined frequencies and observation error.

More recently, Ward-Paige et al. (2010) studied the effect of bias due to observer speed and non-instantaneous sampling in UVC of sharks, creating a new model that improved on some of the limitations faced by the Reefex model to answer these questions. The resulting AnimDens model uses a correlated random walk for sharks and a much smaller time step of 1 or 2 s. Because the movement model is simplified down to two parameters, speed and maximum turning angle, it is meant to be generically adaptable to visual counts of any moving animal.

While these two previous models succeed at answering specific questions about UVC bias, the representation of fish behaviour in either of them is very simplified. It is impossible or very difficult to accurately represent the movement of a fish species with complex behaviours such as schooling and shoaling, diver avoidance/attraction or cryptic habits. This can lead to bias estimates from these models being more accurate for certain species than for others, depending on how the real species fits the grid-based or correlated random walk assumptions.

In the present study, a new individual-based model is presented, building upon some of the concepts behind the Reefex and AnimDens models but featuring complex fish movement and behaviour. The FishCensus model can have a very small time step (0.1 s) to allow for precise modelling of fish reactions to their surroundings, and can be used to simulate counts using the most common UVC methods. This study focuses on four behavioural traits which are typically problematic for UVC, namely schooling behaviour, cryptic habits, shyness and boldness towards divers. Four generic fish types representing these key traits were simulated and placed in the environment at four densities. Virtual divers performed strip transects and stationary point counts and reported an estimated density, which was used to calculate accuracy and precision. The isolated effect of each behavioural trait was also calculated using control fish types. The FishCensus model is proposed as a tool to aid in sampling design for monitoring and research, and to calculate correction factors for densities of species estimated with standardised methods.

2. Materials and methods

2.1. Model description

The FishCensus model was programmed in NetLogo version 5.3.1 (Wilensky, 1999). The latest model versions are freely available at https://www.openabm.org/model/5305/. Model version 1 was used in this study. A full description following the ODD (Overview, Design concepts, Details) protocol for describing individual-based models (Grimm et al., 2010, 2006) is available as supplementary material (S1).

2.1.1. Purpose

The FishCensus model simulates how different fish behaviours affect density estimates in common underwater visual census methods. By adapting a flexible fish movement model to the desired species or group, the model can help calculate correction factors for past and ongoing surveys or decide the best sampling method for an upcoming field assessment.

2.1.2. Landscape and scales

The model is spatially explicit, two-dimensional and has two types of moving agents, divers and fish. The model landscape is represented by a grid of squares with 1 m sides that have no variables directly affecting agents. Depth is ignored (assumed constant) and maximum underwater visibility was set to 6 metres and remained constant in time and space. The landscape size was set to 20 × 80 squares (1600 m^2). Divers and fish wrap around when they reach the edges to avoid artificial gatherings near walls. The origin of the coordinate system is located in the centre of the bottom left square, so that integer coordinate values always correspond to square centres, even though agents move in continuous space.

There are two levels on the time scale. Fish and diver movements use a time step representing 1/10 of a second and all other procedures in the model are based on a time step of one second. Model runs stop when finishing conditions are met for the sampling method chosen (i.e. diver reaches a fixed distance or sampling time).

2.1.3. Agents

2.1.3.1. Diver. The diver is a single agent, responsible for performing a chosen sampling method with pre-defined input parameters. Diver state variables are their x and y coordinates, heading (degrees) and a constant speed (metres per minute). There is a fixed view angle value that defines a field of view in front of the divers and is set to 180° for transects and 160° for stationary points (Ward-Paige et al., 2010). The diver keeps record of all counted fish in a list and a list of unique fish ID numbers is used as short term memory to prevent immediate recounts. Fish that leave the field of view are removed from the memory list.

2.1.3.2. Fish. Fish can belong to different “species” or types that share the same attributes and size. Besides species name and size, there are several other attributes of fish agents that stay constant during model runs. Every fish type has a maximum ID distance to the diver (in metres), within which they can be seen and correctly identified. There is also a maximum approach distance (m), which is the distance to divers or predators that triggers evasive movement. Another important attribute is detectability, which is the probability of a fish being visible to the diver. Fish visibility is determined in every behaviour change (10 model seconds by default; see section 2.1.6.4). A detectability below 1 means fish can become hidden from the diver, even if within ID distance (e.g. to simulate cryptic behaviour or mimicry).

Fish sensing capabilities are described by a perception distance (m) and a perception angle (degrees), which encompasses short distance detection of visual, tactile and chemical stimuli. A Boolean attribute establishes if fish will exhibit schooling behaviour. If true, a distance to schoolmates (in body lengths) must be specified and a list of schoolmates (conspecifics within perception angle and distance) is updated every time step for every fish. Fish state variables include their x and y coordinates, heading (degrees), the x and y components of their velocity vector and the x and y components of their acceleration vector. The magnitude of the vectors is limited by three attributes: maximum sustained speed (maximum velocity magnitude for continuous movement), maximum burst speed (maximum velocity magnitude in evasive movement) and maximum acceleration (maximum increase in speed that can occur in a second).

2.1.4. Initialization

The total number of fish to place is calculated from the predefined true density and the area of the environment. Fish are placed with random coordinates and headings and both velocity and acceleration vector components set to 0. All attributes are set per fish type and all fish are visible. Then, the behaviour change sub-model (section 2.1.6.4) is run to select the starting behaviour for every fish. The movement model is then run for 200 cycles (20 model seconds) to stabilise the starting positions for fish (form schools, gather in patches, etc.). Further behaviour changes do not occur during this stabilization phase and the model clock is not advanced.

The diver is then placed on the environment. For the stationary point count method, the diver is placed in the centre of the world, for transects, the diver starts on the centre of the 6th patch from the bottom, at the same distance from both margins of the world. Diver starts with a heading of 0° (facing upwards) for both methods.

2.1.5. Model schedule

Every model run represents a single sample, using a single method of choice and sampling for a given time or distance. A cycle (one second in model time) starts with a check to see if the diver has reached the end conditions of the survey. If the diver is finished, then outputs are calculated and the model run ends. If not, the model cycle continues.

The model cycle starts with the diver counting the fish that are eligible (see section 2.1.6.2), which happens every second in model time. Then all the agents move (10 movement cycles per model second), starting with the diver and following with all the fish, in an order that is randomly picked each cycle. In its turn to move, a fish will perform all vector calculations, determine the new velocity vector and move to the new position, then the next fish is picked.

There is no limit for the number of fish stored in memory, but when the movement cycle ends, fish listed on the diver’s memory that left the field of view are removed from the list. Every 10 model seconds all fish pick a behaviour from the behaviour list. In case there are fish with detectability smaller than 1, visible status is re-calculated for the next 10 s (see section 2.1.6.4). The sequence of events and sub-models on every time step is represented in a diagram in Fig. 1.

2.1.6. Sub-models

2.1.6.1. Diver movement. Diver movement is much simpler than fish movement, however, since the position of the diver can influence the response of fish, it also moves every tenth of a model second (by default), even though counts are only made every second (see 2.1.6.2).

The movement sub-model differs with the chosen sampling method. For fixed distance transects, the diver maintains a heading of 0° and moves forward at a pre-defined constant speed. For stationary point count, the diver starts with heading 0° and rotates clockwise at a pre-defined constant speed (in degrees/second). The default diver movement models and parameters for the stationary point count and random path methods were adapted from Ward-Paige et al. (2010), with added spatial and temporal resolution. Transect diver swim speed was set to 8 m per minute based on average swim speeds in real transects on temperate reefs (Pais et al., 2014).

2.1.6.2. Fish counting. This is a diver procedure that simulates the observation and recording of fish during the virtual sampling method. Some parts of the counting sub-model differ with the chosen sampling method.

At every second in model time, the diver lists eligible fish that meet the following criteria:

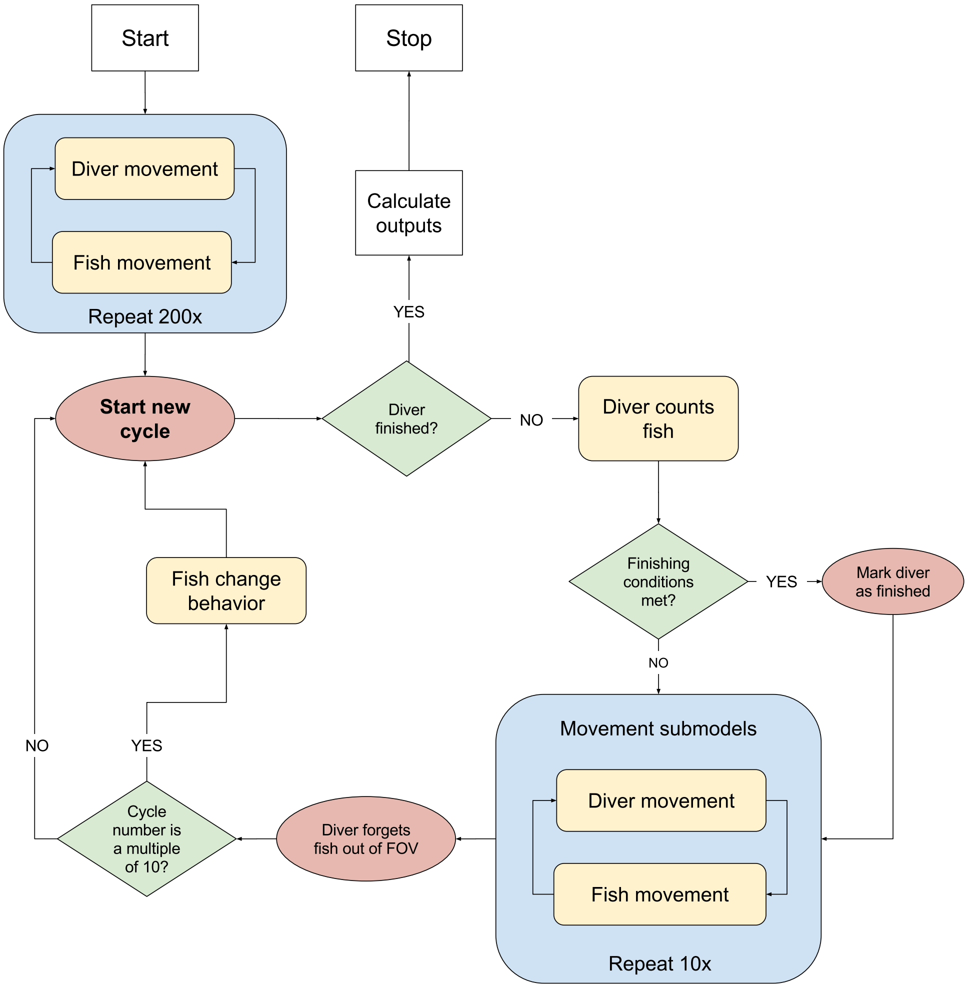

Fig. 1. Overview of the FishCensus model schedule. Each cycle (between initialization and outputs) represents 1 model second. Legend: FOV- Field of view.

1) Their coordinates fall within the field of view (defined by view angle and maximum visibility);
2) Their coordinates fall within the sample area (transect length and width or point count radius);
3) They are closer than their ID distance (distance at which an individual is identifiable);
4) They are visible (Boolean variable based on detectability);
5) Their unique ID is not in the diver's memory (only new or forgotten fish can be counted).

Besides maximum visibility and memory, counts are also limited by a saturation value. Count saturation is the maximum number of fish that a diver can register in a second, with priority given to closest fish. This is set to 3 fish based on visual working memory studies (Luck and Vogel, 1997). The "species name" value of the new fishes is then added to the diver's list of counted fish and their unique ID is added to the memory list. Counted fish remain recorded until the end of the sample, but fish in the memory list are removed from memory if they leave the diver's field of view.

2.1.6.3. Fish movement. The parameterisation of the movement model at such a small scale relies heavily on real time observation of model runs and comparison with field observations or video footage. Parts of the movement sub-model code are based on the NetLogo implementation by Wilensky (2005) of the flocking model of Spector et al. (2005). A set of urges are translated into two-dimensional acceleration vectors of magnitude 1 m/s^2 that are multiplied by weight coefficients given to different urges. Finally, a vector representing deceleration due to drag (A_d) is added. All vectors are then summed to generate a resultant acceleration vector (A) that is added to the velocity vector from the previous cycle to generate the new velocity vector:

$$A = \sum_{i=1}^{8} (w_i.A_i) + A_d$$

where w_i and A_i are the weight and the acceleration vector for urge i. The magnitude of the velocity vector is limited by two attributes, the maximum cruise speed and the maximum burst speed. These are very important values for fish movement simulation and can either be based on real measurements or estimated from the caudal fin aspect ratio and total length (Sambilay Jr, 1990). The acceleration vector is also limited to a maximum value.

If the magnitude of the resultant acceleration vector exceeds the maximum acceleration, it is scaled down to this value and then added to the velocity vector on the previous cycle to calculate the x and y components of the new velocity. To avoid erratic movement at low speed, a minimum speed threshold was arbitrarily set at 0.2 m/s for all fish types in this study, below which no movement occurs. The only time a velocity vector magnitude can exceed the maximum cruise speed is when a diver is within the approach distance and covered by the perception angle, and the diver avoidance urge weight is greater than zero. In this case, the maximum burst speed becomes the limit.

Table 1
Detailed description of the urge vectors used in the fish movement model.

Urge	Description	Vector calculation
Wander	Urge to move around randomly.	x and y components drawn from a uniform distribution between −1 and 1.
Cruise	Urge to maintain current heading.	Vector in the direction of velocity on the previous cycle.
Rest	Urge to stop moving.	Vector in the opposite direction of velocity on the previous cycle.
Align	Urge to align with schoolmates.	Mean of the x components and y components of the velocity vector of schoolmates.
Spacing	Urge to move away from schoolmates that are too close.	Sum of the vectors pointing away from schoolmates that are closer than the schooling distance, their magnitude being equal to the distance to each schoolmate.
Centre	Urge to centre the position relative to schoolmates.	Vector in the direction of the point defined by averaging x and y coordinates of all schoolmates.
Avoid diver	Urge to move away from the diver. Urge weight can be negative for attraction to divers.	Vector in the opposite direction of a diver who enters the area defined by approach distance and perception angle.
Patch centre	Urge to move to the centre of the picked patch if a fish moves outside the picked patch distance.	Vector in the direction of the picked patch centre.

Fish can be stationary for long periods and often move with short bursts, followed by a coasting phase. This is a very important aspect of fish movement and is greatly influenced by drag forces (Videler, 1981). Since length is constant for a fish type in the model, the magnitude of the acceleration due to drag in a movement cycle can be written in the form $a_d = k\,v^2$, with v being the speed on the previous cycle. The constant k is calculated from the total length (L) in meters using the formula

$$k = \frac{\frac{1}{2} \times D \times d \times cL^2}{aL^b}$$

where D is the drag coefficient, d is the density of the fluid (1027 kg/m^3 for surface seawater), c is the coefficient for the length − surface area relationship and a and b are coefficients for the length − weight relationship (see supplementary material S2 for details on the calculation). The coefficients a, b and c must be converted so the formulas reflect relationships in meters and kilograms. This formula establishes the magnitude of the acceleration vector, while its direction is always opposite to the velocity vector on the previous cycle.

While the values to estimate drag forces can be taken from real values measured for each fish type in the model, they are only available for a reduced number of species, and when using generic fish types, it can be difficult to opt for one value over another. Given this, the extensively studied movement of the cod *Gadus morhua* Linnaeus, 1758 was used as an approximation for simplicity. Videler (1981) estimated that the drag coefficient of a coasting cod with 0.3 m total length is approximately 0.011. The length-weight relationship for cod can be converted to Kg and m from Coull et al. (1989) to $W = 10.3\,L^{2.857}$ and the coefficient for the length − surface area relationship (in metres) is approximately 40 (O'shea et al., 2006).

A fish can have up to 8 urges acting simultaneously (Table 1) and all vectors are given a magnitude equal to their weight coefficient. Weights define the relative importance of urges and are characteristic of fish types, with a set of urge weights defining a behaviour for a fish type (see section 2.1.6.4). Weight for the diver avoidance urge can be set to negative values to simulate attraction to divers.

2.1.6.4. Fish behaviour change.

The way behaviour change is implemented in FishCensus is based on the Reefex model by Watson et al. (1995), including the default 10 s interval. This seems like a reasonable value for a parameter that must be arbitrarily set, given that behavioural states are independent of external stimuli.

Attributes for up to four behavioural states, their names and frequencies are stored as fish variables. Stored attributes for a behavioural state are detectability, schooling (Boolean), schooling distance, urge weights (align, centre, spacing, wander, rest, cruise, patch gathering, diver avoidance) and picked patch distance.

Table 2
Fixed attributes for the four types of fish used in the experiments.

	Schooling	Cryptic	Shy	Bold
Size (m)	0.2	0.1	0.3	0.3
ID distance (m)	4	1	6	6
Approach distance (m)	1.0	0.7	3.0	3.0
Perception distance (m)	0.35	–	–	–
Perception angle (degrees)	320	360	320	320
Max. acceleration (m/s^2)	0.2	0.1	0.1	0.1
Max. sustained speed (m/s)	0.5	0.3	0.4	0.4
Burst speed (m/s)	2.6	1.1	2.2	2.2

Behavioural state frequencies are used every 10 model seconds to perform a weighted random selection with replacement. Every fish, in a randomised order, picks the next state. If a fish has schoolmates, it will act as a leader and the others will immediately pick the same state, even if some of them may already have picked on that turn.

Once the next behaviour is picked, and if detectability is smaller than 1, the fish runs a Bernoulli trial to determine if it will be visible to the diver for the next 10 model seconds. This Bernoulli trial occurs with every behaviour change, always in a randomised order, while detectability remains smaller than 1. Visible status in schools is independently set for every fish.

The last step of the behaviour change sub-model takes place only if the weight given to the patch gathering urge is greater than 0. If this is the case, then it is assumed that the behavioural state requires a fixed patch. If a fish has not picked a patch on a previous state or commanded by a schoolmate on the present turn, it must choose the patch that stands 2 metres ahead. Once more, if there are schoolmates, they will skip the queue and pick the same patch immediately. If the weight given to the patch gathering urge is 0, the picked patch fish variable is cleared or replaced with a null value.

The behaviour change turn ends when all fish have picked the next behavioural state, set their visible status (if applicable) and picked a patch (if applicable).

2.2. Fish types and parameterisation

To test the influence of behavioural traits on the accuracy and precision of estimated density, four generic types of fish were created, representing four typically problematic behaviours for underwater visual census, namely a "schooling" type, a "cryptic" type, a fish that is attracted to divers ("bold" type) and a fish that evades divers ("shy" type). Fixed attribute values for these types

Table 3
Behavioural states, frequencies and attributes for the four fish types used in the experiments. BL: body lengths.

		Schooling			Cryptic				Shy		Bold	
	Behavioural state	wandering	feeding	stationary	guarding	feeding	nested	patrolling	wandering	stationary	wandering	stationary
	Frequency	0.5	0.2	0.3	0.25	0.2	0.1	0.45	0.6	0.4	0.6	0.4
	Detectability	1	1	1	0.3	0.6	0.1	0.5	1	1	1	1
	Schooling?	TRUE	TRUE	TRUE	FALSE	FALSE	FALSE	FALSE	FALSE	FALSE	FALSE	FALSE
	Schooling distance (BL)	1	1	1	–	–	–	–	–	–	–	–
	Patch distance (m)	–	1	–	0.5	3	0.5	2	–	–	–	–
Urge weights	Align	5	1	5	–	–	–	–	–	–	–	–
	Centre	6	2	6	–	–	–	–	–	–	–	–
	Spacing	15	5	15	–	–	–	–	–	–	–	–
	Wander	3	1	1	3	3	0	3	7	7	7	7
	Rest	0	1	7	2	1	15	2	0	6	0	6
	Cruise	0	0	0	0	0	0	0	10	0	10	0
	Patch gathering	0	10	0	6	6	15	6	0	0	0	0
	Diver avoidance	10	10	10	4	10	0	10	10	10	−1	0

are specified in Table 2 and behavioural states and parameters for each type are summarised in Table 3.

All four fish types were parameterised based on real species or groups that are familiar to the authors, so that observation experience could aid in parameterising the model. While some data exist to support parameterisation, it is not easy to find a direct value to input into the model, and some assumptions are unfortunately unavoidable. Fish speed is among the most important values for a UVC simulation (Ward-Paige et al., 2010; Watson et al., 1995). For this study the values were calculated from the caudal fin aspect ratio of representative fish species, using the equations from Sambilay Jr (1990), and validated through comparison with video footage and field observations. Maximum acceleration was parameterised by first establishing maximum speeds and adjusting while the model runs in real time until expected movement patterns are matched, since blindly fitting a value here is difficult and may lead to unrealistic movement. Perception angle for cryptic fish was assumed to be 360°, due to the position of the eyes on top of the head and the predominantly sedentary behaviour. For all other fish types, a value of 320° was adopted, since it encompasses both visual and lateral line perception, in accordance with observations by Partridge and Pitcher (1980). ID distance, approach distance, schooling distance and some behaviour frequencies and patterns were parameterised based on the authors' experience from more than 250 UVC dives in temperate reefs, complemented by underwater video. In this qualitative assessment, it is important to compare details such as fish spacing in schools, the school shape and horizontal spread, the approximate distance from a threat that triggers evasive movement, or how erratic or directed the movement is (e.g. fish changing location or looking for food).

The "schooling" type is based on sparids from the genus *Diplodus*. These species usually form small to medium-sized schools and can often be found stationary, or feeding in shoals around rock patches (Gonçalves et al., 2014). There is an extensive literature on the movement of sparids at larger scales, using acoustic telemetry, but fine scale movement data is scarce. Given this handicap, behaviours and frequencies for the "schooling" type were based on the authors' experience from field observations. Perception distance has a strong effect on school sizes, therefore the value was set by matching the resulting school sizes with real observations of *Diplodus* spp. (approximately 2–15 fish; personal observation). Video 1 (available in the online version) illustrates the movement of the "schooling" type with the model running in real time.

The "cryptic" type is based on blenniids, mostly on the genus *Parablennius*. These are small (8–10 cm) benthic fish that tend to be very approachable by divers. They hide in holes and crevices and males can have territorial behaviour in the reproductive season. Behaviours and frequencies were based on a study by Almada et al. (1987) on the behaviour of territorial males of *Parablennius pilicornis*. The main parameters that vary according to behaviour are detectability and the maximum distance to the patch centre. Detectability has been quantified for some blenniids to be in the range 0.1–0.4 (MacNeil et al., 2008a), but these values take into account other factors that are modelled separately in FishCensus, such as water visibility, maximum ID distance, count saturation, observer speed, among others (Bozec et al., 2011). For this reason, while the lowest value was set at 0.1 for a nested fish, the highest value was set at 0.6 for feeding behaviour, to compensate for other factors in the model that can increase the probability of missing a fish. Video 2 (available in the online version) shows an example of the "cryptic" type.

Both the "shy" and "bold" types share parameters from labrids from the genus *Labrus*. These species are usually solitary and reaction to divers usually varies per species, sex and age (personal observation). Even though some males guard nests in the reproductive season (Villegas-Ríos et al., 2013), this was not included in the model since it was not the key behaviour under study. As a simplification, only two behavioural states were included for this type, with a slightly higher probability for the "wandering" state (Table 3). As with the "schooling" type, the available data is mostly from acoustic telemetry, so fine scale behaviour frequencies for "shy" and "bold" types were set based on what the authors perceive from field observations. Videos 3 and 4 (available in the online version) illustrate the movement of the "shy" and "bold" types, respectively, particularly their reaction to the diver.

2.3. Experiments and data analysis

To calculate the effect of behaviour on accuracy and precision of density estimates, three control types were created that were identical to their counterparts in all parameters, except those shaping the behaviours under study. For the schooling type, the control had schooling set to false for all behaviours, thus align, centre and spacing urges are ignored. For the cryptic type, control had detectability set to 1 for all behaviours. Finally, for both the shy and bold types, the control had the diver avoidance weight set to zero, being indifferent to the diver.

Experiments were run for transect and stationary point counts. Transects were 2 m wide and 40 m long and the diver swam at 8 m/minute, stationary points used a 5 m observation radius, 4° per second clockwise rotation and a total observation time of 5 min. Both methods sampled an area of approximately 80 m^2.

To assess the effect of true density on the estimates, and to understand if the effects of behaviour are affected by true density, four pre-determined densities were tested, namely 0.05, 0.1, 0.2 and 0.3 fish/m^2. 10 surveys with 10 replicates each were run for all four fish types and three controls at each true density, for each of the two methods. To ensure sample independence, fish were replaced and reshuffled before every replicate and a new random seed was used. Precision per survey was calculated as the coefficient of variation of the estimates, which is obtained by dividing the standard deviation of the density estimates from the 10 replicates by the true density. The inaccuracy of each survey was calculated as the average difference between estimated and true density for the 10 replicates, divided by true density. Both precision and inaccuracy were then multiplied by 100 to reflect percentages of true density

The effect of true density on inaccuracy and precision irrespective of behaviour was tested through a mixed nested analysis of covariance, with true density (continuous) nested within behaviour (four levels, random). The significance of the effects of isolated behavioural traits was tested with one-way analysis of covariance, with true density as a covariate and behaviour as a two-level fixed factor (behaviour vs control).

2.4. Model sensitivity

In order to understand how sensitive the output of the model is to small changes in parameters, a local sensitivity analysis was run using 30 × 2 m transects, a diver swimming at 8 m per minute with a visibility of 6 m and true density of fish fixed at 0.2 fish per m^2. 15 replicates were run for each parameter. Fish types were created specifically for sensitivity analysis and details can be seen in the supplementary material (S3).

3. Results

3.1. Effect of behaviour on inaccuracy and precision

Fig. 2 shows the average inaccuracy (a1 and b1) and precision (a2 and b2) for all types at different true densities. In general, inaccuracy was not affected by true density within fish types ($F_{1,3} = 2.87$, $p > 0.05$), even though a slight increase is visible with decreasing density of schooling fish (Fig. 2a1). Precision, however, is severely affected by decreasing density ($F_{1,3} = 10.62$, $p < 0.05$), a relationship that is more pronounced for bold fish, where the coefficient of variation goes from 98% at 0.3 fish/m^2 to 256% at 0.05 fish/m^2.

The diver systematically underestimated the density of cryptic fish by about 80% of true density in stationary points and 40% in transects (Fig. 2 a1 and b1, respectively). All other types had overestimated densities, with stationary counts leading to approximately two times more bias when compared to transects for bold and shy fish. Bold fish estimated density was biased by almost 500% of true density in transects and by more than 900% in stationary points. For schooling fish, the difference between methods was more pronounced, going from more than 130% in transects to about 400% in stationary counts.

Precision was higher (lower coefficient of variation) on transects, with stationary counts having almost two times more variation for all fish types (Fig. 2a2 and b2). Cryptic fish, particularly on stationary counts, had the highest precision, and this type was the least affected by density. The remaining fish types had similar precision, with schooling and bold fish showing a slightly larger variation.

Since inaccuracy is stable across different true densities, it is possible to use a "correction factor" approach without much concern about true density (which is unknown in the field). This can be useful to correct densities for past or ongoing surveys, by simply multiplying the correction factor by the estimated density. This correction factor can be obtained with the formula $1/(\delta+1)$, where δ is inaccuracy. In the case of this study, correction factors should not be directly applied to every species sharing these behavioural traits, since that would carry an assumption that the behaviours were well represented across all species. Nevertheless, calculated correction factors for these fish types are shown in Table 4 for demonstration, based on the data from Fig. 2 for a true density of 0.2 fish/m^2.

Table 4
Average inaccuracy and correction factors (CF) for all fish types, calculated from 10 surveys with 10 replicates using a true density of 0.2 fish/m^2.

method	type	inaccuracy	CF
stationary	schooling	400%	0.20
	cryptic	−79%	4.74
	shy	609%	0.14
	bold	974%	0.09
transect	schooling	142%	0.41
	cryptic	−37%	1.60
	shy	259%	0.28
	bold	504%	0.17

Fig. 3 shows the average difference between the fish types and their controls, which represents the absolute effect size attributable only to the key behavioural trait in each case. ANCOVA results revealed that true density, treated as a covariate, only had a significant effect on inaccuracy for bold ($F_{1,76} = 5.15$, $p < 0.05$), shy ($F_{1,76} = 10.22$, $p < 0.05$) and schooling ($F_{1,76} = 12.45$. $p < 0.05$) fish when using stationary counts. For schooling and shy fish, effect size decreased with density, while for bold fish the pattern was opposite (Fig. 3a1). All behavioural traits significantly affected inaccuracy, over and above the effect of true density, for both methods, and there was no significant effect of the interaction term. In general, schooling and bold behaviours affected bias positively on both methods, with bold behaviour contributing to nearly 200% positive bias in transect surveys and even surpassing that on stationary counts. The effect of cryptic behaviour alone accounts for only 5–10% negative bias in stationary point counts ($F_{1,76} = 19.67$, $p < 0.05$), whereas in transects this value increases to more than 40% ($F_{1,76} = 444.97$, $p < 0.05$).

The effect of behaviour on precision was much more variable among replicate surveys, as evidenced by the standard error bars, particularly in low densities (Fig. 3 a2, b2). However, the effect of isolated behaviour traits on precision was still significant for most fish types in both methods, except for shy fish sampled with transects ($F_{1,76} = 0.29$, $p > 0.05$). Interaction between true density and behaviour was significant for cryptic ($F_{1,76} = 9.81$, $p < 0.05$) and bold ($F_{1,76} = 4.48$, $p < 0.05$) fish when using stationary points, evidenced by an increase in effect size with decreasing density (Fig. 3b2). For both methods, schooling and bold behaviours tend to decrease precision (increasing variability), while cryptic and shy behaviours increase precision.

3.2. Model sensitivity

Behaviour change interval (10 s) and count saturation (3 fish per second) are two structural parameters of the model that had to be somewhat arbitrarily set. Increasing behaviour change interval by 1 s (10%) led to an average increase of 15.2% on the estimated density, while decreasing this parameter by 1 s led to an increase of 4.1%. These values suggest the output is relatively robust to small changes in this model simplification parameter. For the count saturation, counting 1 less fish per minute led to an increase in 0.4% in the output and counting one more fish led to a 1.6% increase.

In terms of movement parameters and vector urges, the model is particularly sensitive to fish speed (maximum speed and the magnitude of the rest urge). The rest urge adds additional drag to fish movement, regardless of their maximum speed, so changing this urge can drastically change the average speed and thus impact the visual counts. Maximum speed, however, is one of the most important attributes in the model, requiring a particularly

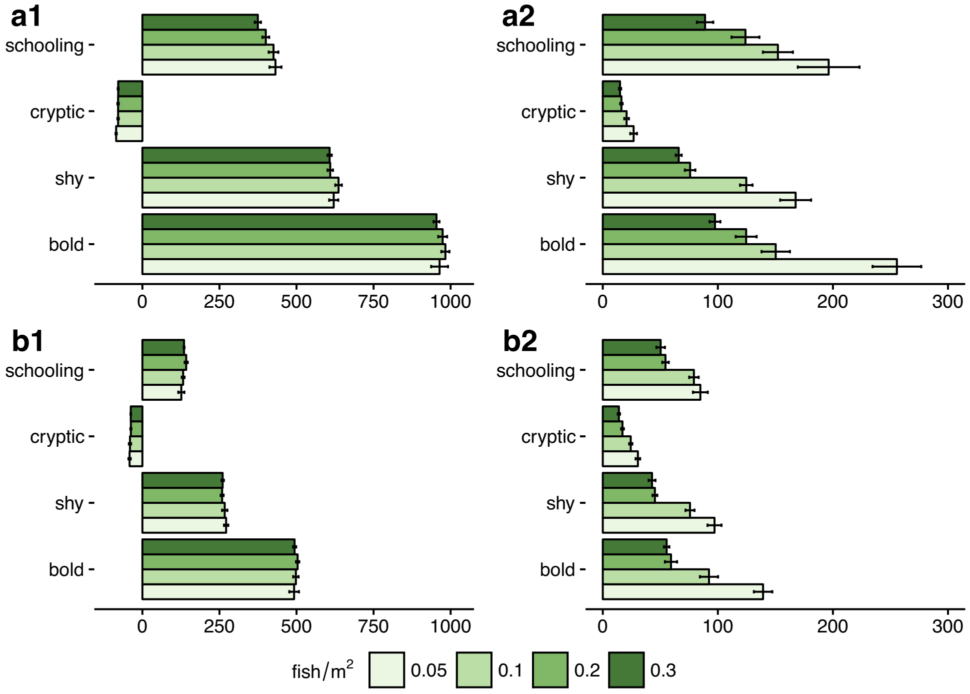

Fig. 2. Inaccuracy (1) and precision (2) at four different true densities (fish/m^2) for stationary point counts (a) and transects (b), expressed as percentages of true density. Average values from n = 10 surveys, each survey with 10 replicates. Error bars denote the standard error of the mean.

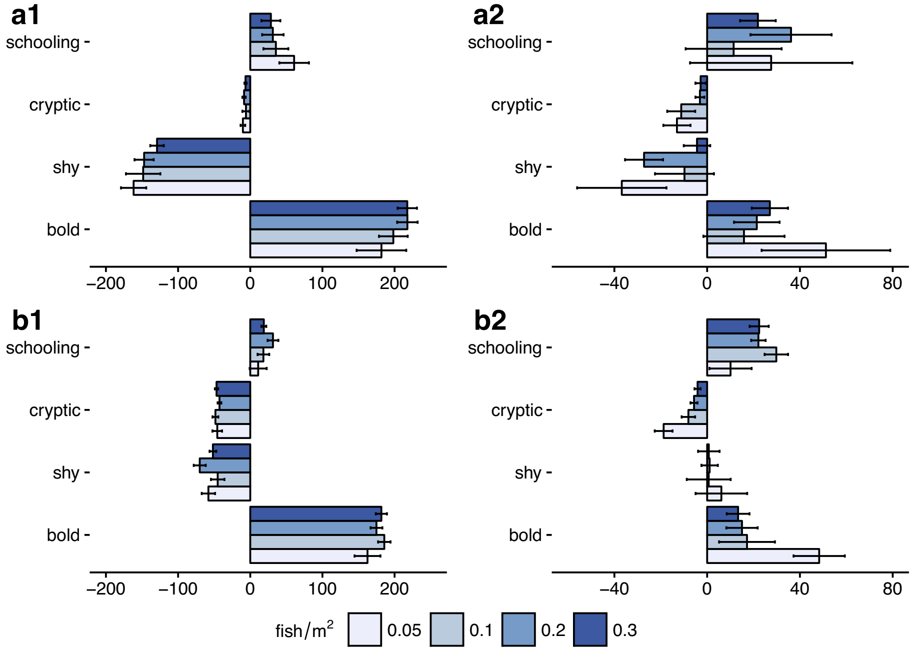

Fig. 3. Isolated effect of key behavioural traits on inaccuracy (1) and precision (2) at four different true densities (fish/m^2) for stationary point counts (a) and transects (b), expressed as percentages of true density. Average values from n = 10 surveys, each survey with 10 replicates. Error bars denote the standard error of the mean.

informed parameterisation, either from laboratory measurements, video analysis or by using a proxy such as the caudal fin aspect ratio approach implemented in the model interface.

For schooling behaviour, the output seems to be particularly sensitive to the spacing between schoolmates. Decreasing or increasing the distance by 20% led to a decrease or increase in estimated density by about 20%, respectively. Because increasing the "centre" urge vector leads to more compact schools, it is analogous to decreasing the distance in terms of sensitivity.

A decrease in fish view angle of a non-schooling fish led to a 2.0% average increase in estimated density, while an increase led to an average increase of the output in 1.8%. Changing the view angle on a schooling fish tends to affect the shape and size of schools, and therefore model sensitivity is probably affected differently (for more details on sensitivity analysis see supplementary material S3).

4. Discussion

4.1. Assumptions, simplifications and parameterisation

Most methods used to estimate bias in UVC in the field share a common problem: they are calculating bias based on approximations to true density, which can be biased themselves (Sale and Sharp, 1983; Willis et al., 2000). Computer simulation is a cheaper alternative to laboratory experiments in aquaria, and a non-destructive alternative to fishing, poisoning or explosives in reefs. However, it does come with disadvantages, one of them being the simplification process associated with modelling. In field-based methods the actual species, with all their behaviours and particularities, are used to estimate bias, while in individual-based models results arise from simplified representations. The first simplification in this study is the lack of individual variability in terms of size, behaviour repertoire and ID distance. This ignores the existence of smaller fish that would have lower detectability and thus the model may be slightly overestimating their densities. This is, however, an option for the current study and not a limitation of the model, since FishCensus allows for multiple fish types to populate the model simultaneously and these types can represent different size classes of the same "species", with different behaviours and detectability. Another simplification is the absence of topographic complexity in the environment, which would make detectability vary spatially. This can be seen as an advantage for generalisation, since calculations can be made in an abstract sense, detached from a particular location with all its habitat patchiness. Additionally, the detectability parameter can be used as a proxy to represent a species likely to be missed due to topography. Another important aspect is the lack of a third dimension. While it is possible to include a vertical dimension, computational power requirements would increase greatly, and likely without significant gains. One of the most important aspects to consider is the shape of schools, since the spacing urge and the schoolmate distance only account for horizontal distance. If a species of interest tends to form schools of vertically stacked individuals, spacing urge should be set to low values to allow for more overlap in two-dimensional space. This is particularly important because model output was shown to be particularly sensitive to school shaping parameters.

To narrow the gap between real and simulated fish, the FishCensus model attempts to unite two different modelling approaches, virtual ecologist approaches to bias estimation and complex movement models with emergent behaviour and interactions. Previous virtual ecologist approaches to bias estimation in animal counts used simplified behaviour models, which is better for computational performance and allows them to isolate particular aspects of movement, such as the speed or approach angle of the animals being counted (Ward-Paige et al., 2010; Watson et al., 1995). However, fish behaviour can be very complex and it has been shown repeatedly that behaviour is one of the main factors responsible for bias in counts (Biro, 2013; Kulbicki, 1998; Kulbicki et al., 2010; Lincoln Smith, 1989; Sale and Sharp, 1983). The simulation of collective movement in water and air (swarming, flocking and schooling) has been around for decades, from the simple "boids" model of Reynolds (1987) and its generic entities with the urges to cohere, align and separate, to more complex and species-specific models that include elements of flight physics (e.g. Hemelrijk and Hildenbrandt, 2012). To produce fish movement and schooling behaviour without unnecessary complexity, FishCensus uses a "boids" approach.

The only addition to the FishCensus movement model that borrows from physics simulation is the drag vector. In fact, while drag does not need to be specifically modelled for schooling behaviour of constantly moving fish, or flocking of birds, it is very important when modelling behaviour changes and avoidance bursts in animals that move in a dense medium. When a fish evades a nearby diver its speed increases but, as a consequence, the amount of drag countering the movement also increases, causing the fish to drastically reduce the speed a small distance ahead (Videler, 1993).

The purpose of this study was to test the influence of behavioural traits, and not to calculate inaccuracy for a particular species, thus the use of generic fish types representing key behaviours is sufficient, with the added advantage of more flexibility in finding data to parameterise. There are, however, still several assumptions and arbitrariness when establishing some parameters. One of the main difficulties found is the scarcity of information for direct, objective parameterisation of the movement model. It is very difficult to objectively know how much weight the urge to align has over the urge to avoid a diver in fish decision-making. What we can observe is the movement patterns emerging from those weights in different situations, and compare them to real observed patterns (Kramer-Schadt et al., 2007). This kind of "pattern-oriented modelling" (Grimm and Railsback, 2012) that relies heavily on observation benefits from a user interface to control parameter values in real time and observe changes instantly, a feature of the NetLogo modelling environment where FishCensus is implemented. While parameterisation relies heavily on observation, local sensitivity analysis revealed a greater sensitivity of the output to speed and school shaping parameters, which are among the easiest patterns to extract from observation.

The amount of time a fish spends on each behavioural "state" can also be quantified to a certain extent with observations or video recordings in the field or in aquaria. While this was achievable to a certain extent with the cryptic type, using literature on the behaviour of territorial males (Almada et al., 1987), parameterisation of the other types relied heavily on the authors' experience, due to lack of small scale movement data. While this is not ideal, FishCensus seems to better represent the intricacies of complex fish behaviour than previous models, in a way that can be visually compared to real patterns.

The diver movement model for both methods was similar to the AnimDens model implementation. However, AnimDens divers are able to count fish without saturation limits and remember all fish counted, showing that even a perfect observer would still report biased estimates (Ward-Paige et al., 2010). In FishCensus memory implementation intends to be more realistic, but can also be seen as unforgiving, in a sense that all fish that leave the field of view are immediately forgotten. In a real UVC a diver may remember some fish that are very site-attached, rare or unique in some way (pers. obs.), but these nuances were simplified into a mechanistic process and may artificially lead to a slightly increased overestimation, which is assumed to be negligible.

Validation, as in attempting to "fit" values to field data, is a difficult task, and one that would require an artificial setting without guarantees of matching field conditions. In addition, in the case of the present study, using generic types may lead to combinations of parameters which do not exist in a single species. Even though speeds are estimated from the caudal fin aspect ratio of real species, as well as other parameters, the main goal was not to exactly mimic one species, but to achieve a certain level of realism that can make typical behavioural patterns plausible and results useful. Since the model is created exactly because bias in the field is unknown, and traditional approaches to calculate bias focus on detectability alone, confidence on the bias estimates comes from confidence on the representation of behaviour patterns and the modelled sampling method. Nevertheless, the results of the experiments here presented agreed with known patterns and orders of magnitude observed in the field, as detailed in the next section, which supports the validity and usefulness of emergent, larger scale patterns in the model.

4.2. Effect of behavioural traits on density estimates

The coefficients of variation estimated using transects were slightly below the ranges estimated by McClanahan et al. (2007a,b) for within site variation in coral reefs. This lower variability is expected since natural spatial and temporal variability is not explicitly modelled in FishCensus. The observed increase in variability with fish rarity is also a known issue in fisheries stock assessments (Blanchard et al., 2008), posing a serious problem for impact assessment and monitoring, because as a population declines, the decline becomes harder to detect in statistical tests. Bias, on the other hand, seems to stay unaffected by true density. This has also been observed by Watson and Quinn II (1997) using the Reefex model for both stationary points and transects. This observation is important for monitoring purposes, because it supports the idea that a “correction factor” can be applied to reduce bias, irrespective of true density (Christensen and Winterbottom, 1981; Sale and Sharp, 1983; Ward-Paige et al., 2010).

By looking at the available literature on UVC bias estimation, there seems to be a generalised idea that abundances tend to be underestimated (e.g. Christensen and Winterbottom, 1981; Edgar et al., 2004; Jennings and Polunin, 1995; Willis, 2001). For this reason, it may come as a surprise that three out of four fish types studied were severely overestimated by transects and point counts. In fact, field-based methods of bias estimation attempt to correct for bias due to fish detectability or reaction to the diver (Bozec et al., 2011; Edgar et al., 2004; Sale and Sharp, 1983). However, a very important component of bias is due to non-instantaneous sampling (Ward-Paige et al., 2010). Swimming along a transect or rotating in a fixed point as fish move freely in and out of the sample area can lead to biased estimates, particularly with fast-moving fish. Estimating this component of bias is difficult in the field and benefits greatly from computer models (Pierucci and Cózar, 2015).

The cryptic fish type was the only one whose density was underestimated, mostly in transects. This has been witnessed by several studies and has been one of the major criticisms of using UVC for cryptic fish. Willis (2001) reported underestimations by 44–91% for common cryptic species even when using exhaustive UVC searches compared with rotenone poisoning and Sale and Sharp (1983) estimated a negative bias of 21% when comparing wide with narrow transects. These estimates are in the same order of magnitude of the results obtained with FishCensus, even though bias varies with the particularities of each cryptic species and a swim speed of 8 m per minute may not be ideal for cryptic fish (Lincoln Smith, 1989). The agreement of computer models with field methods in bias estimation for these species is likely due to their limited movement. If detectability is set to 1, they almost function as stationary objects, so bias due to non-instantaneous sampling is negligible (Ward-Paige et al., 2010). This means that the amount of bias in estimates will be almost entirely linked to detectability, which is what field methods of bias estimation focus on.

Bias due to schooling behaviour can be attributed to both spatial clustering and movement. This study revealed that schooling behaviour alone leads to less precision and accuracy in estimates for both methods. While gregarious behaviour usually helps with detectability (Kulbicki, 1998; MacNeil et al., 2008b), finding a school will have a much greater effect on total counts than when counting solitary fish. This can lead to a more erratic behaviour of predictions between transects (Cheal and Thompson, 1997) and also to more counts due to inconspicuousness (MacNeil et al., 2008b). This study predicted overestimations due to schooling behaviour alone to be under 50% for both methods, however, the actual difference from true density reached much larger values simply because the simulated fish were moving relatively fast when wandering around the sample area. In transects bias was smaller, likely because the simulated fish had a 50% chance of staying on the same area (either stationary or feeding), effectively reducing bias due to movement (Ward-Paige et al., 2010). In contrast, some field studies still conclude that schooling fish are underestimated by UVC. Christensen and Winterbottom (1981) found that only an average of 57% of schooling fish were counted in pools, and this was attributed to the observer being overwhelmed by the numbers and failing to make an accurate estimate. This was also pointed out by Lincoln Smith (1988). In a real field survey, divers will tend to count the whole school even if some fish fall out of the sample area, and will try to estimate numbers faster by counting small clusters at a time (personal observation). In FishCensus, the counting submodel does not change in the face of a schooling fish, so fish outside the field of view or sample area are simply ignored. In addition, the limit of 3 fish per second leads to a slower count that may end up missing some fish that leave before being counted. For small schools, such as the ones in the present study (size 2–15), this is likely not an issue, however, large schools may lead to unrealistic counts in the model and there is still room for improvement, which may include the addition of probabilities of counting errors, as suggested by Watson et al. (1995), which can be a function of fish density in the field of view.

One would expect shy fish to be systematically underestimated, and field observations point to that conclusion (Bozec et al., 2011; Kulbicki, 1998; Kulbicki et al., 2010). In the simulations, when compared to the control fish, shy behaviour led to underestimation in both methods. These findings matched the orders of magnitude found by Christensen and Winterbottom (1981) of up to 40% underestimation, or even the 90% underestimation reported by Edgar et al. (2004). Despite this, the simulated deviation between survey results and true density was still strongly positive for both methods, which is likely due to a cruise speed of 0.4 m/s, for which Ward-Paige et al. (2010) found overestimations by up to 700% (albeit with a slower observer swim speed). In fact, the AnimDens model demonstrated that, in non-instantaneous sampling, overestimation is directly proportional to fish speed relative to the diver, as more fish will potentially enter the sample area during the survey (Ward-Paige et al., 2010). The simulated shy fish avoided the diver when it got closer than 3 m, however, they represent large inconspicuous fish that are still visible and identifiable up to 6 m. This can attenuate bias in transects, since fish can cross the sample area in front of the diver and still be counted, while still at a safe distance (Bozec et al., 2011).

Bold or curious behaviour alone can lead to overestimation for two reasons. The first is the creation of a cluster around the diver that creates a false notion of density, the second one is the high probability of recounts this generates (Colton and Swearer, 2010; Kulbicki et al., 2010). In the modelled bold fish type the results of these effects led to about 200% positive bias when compared to the control type for both methods. However, when compared to true density, the total overestimation reached near an astounding 1000% in stationary points. This value can be inflated by the way memory works in FishCensus, since the diver is rotating at 4° per second for 5 min (more than three and a quarter rotations), favouring possible recounts of forgotten fish.

The difference between shy and bold behaviour has been pointed out by several authors as problematic, particularly in marine protected areas (MPAs) where UVC is frequently used for monitoring. In fact, the same species can display diver avoidance behaviour outside MPAs (e.g. due to spear fishers) or diver attraction or indifference inside MPAs, leading to an artificial increase of the perceived “reserve effect” (Edgar et al., 2004; Willis et al., 2000). In this study the differences in effect size were around 200%, favouring bold fish over shy or indifferent (control) fish in either method, which is a very significant difference in perception, considering a scenario where the true densities are equal.

In this study transects had less bias and more precision than point counts for all species, but point counts led to higher counts due to a greater overestimation. However, in some field studies comparing transects to point counts, counting more fish has been seen as a sign of better performance (Colvocoresses and Acosta, 2007; Samoilys and Carlos, 2000), a conclusion poisoned by the possibly erroneous assumption that UVC methods systematically underestimate. The relative performance of transects and point counts is of course only valid for the dimensions and sample times adopted for the experiments. While a 40 × 2 m transect or a 5 m radius point may be suited for some types of fish, the same may not be true for other types. In fact, while results could be satisfactory in point counts for the cryptic or schooling type, the shy and bold types would be strongly overestimated. It is nevertheless important to stress that the dimensions and times used are within common practice for a visibility of 6 m, and could easily be picked arbitrarily for a monitoring study (Colvocoresses and Acosta, 2007; Henriques et al., 2013; Lincoln Smith, 1988; Pais et al., 2014). This study supports the need for a careful selection of sampling methods and designs to suit behavioural traits of the species of interest (Kulbicki et al., 2010; Lincoln Smith, 1989), and FishCensus can be a valuable tool for that purpose.

There are two main components of UVC bias, namely detectability and the effect of fish movement due to the non-instantaneous nature of sampling methods. Cryptic or sedentary fish allow for better field estimations of true density, using methods such as rotenone collections or exhaustive searches in enclosed areas. However, bias for these species is almost only affected by detectability. On the other hand, field methods that try to estimate bias for mobile fish in the water column are either biased by gear selectivity (e.g. capture-resight, baited video) or also suffer from non-instantaneous sampling bias (distance sampling, varying transect widths, video transects). For these species, computer models such as AnimDens and Reefex have shown that UVC methods overestimate densities of mobile organisms. With FishCensus, by introducing complex behaviour into the model, it was possible to separate the contributions of both components of bias, and gain a deeper understanding of the effect of behavioural traits on UVC estimates.

4.3. Applicability of FishCensus as a tool

Due to the lack of information for direct, “blind” parameterisation, FishCensus benefits from the experience of the person estimating parameter values. Therefore, the model’s ability to represent realistic behaviour can be increased by using parameter values estimated (and shared) by experts on the species being modelled. While the model has abstract parameters that cannot be directly measured (e.g. vector weights), they can be parameterised based on observed movement patterns and qualitatively or quantitatively calibrated, as found necessary.

More than a simulation model of UVC to answer the questions posed by this study, FishCensus intends to be a tool to aid in picking the best protocol for an upcoming survey, or a complement to past or ongoing surveys by permitting the calculation of correction factors for real field data. Even if the detectability parameter in FishCensus is not a function of distance to the centre of the transect or fixed point, it can be used in conjunction with distance sampling theory if a uniform detection function can be assumed (Buckland et al., 2012). In the future, non-uniform detection functions can be added to FishCensus if required, although processes and attributes such as diver avoidance, maximum ID distance and count saturation are already contributing to a decay in detectability in areas further from the diver.

By modelling different transect dimensions, observation radiuses, swim speeds or sampling times, it is possible to test the response of bias or precision for a species to these parameters. It is also possible to apply search algorithms and approach survey planning as an optimisation problem, fitting the best possible method to a species and using bias or precision as fitness.

Similarly to the models that preceded it, FishCensus is an abstraction from variability due to external factors such as temporal patterns or habitat features (Irigoyen et al., 2013; Pais et al., 2014, 2013). For this reason, it is still important to consider between-site variability, since no two sites are the same. This variability needs to be captured in the field, and sampling design is key. This issue has been approached by the authors in the past (Pais et al., 2014, 2013), and some key aspects, besides site selection, are to 1) try to match the assessment scale to between-site variability and 2) adjust the sampling effort so that the most variable sites are considered.

Despite its simplifications inherent to a modelled environment, FishCensus can also be used to estimate residual variability due to fish movement and calculate sample sizes for a method and species, in order to optimise statistical power to detect expected effect sizes. This can be a good alternative between a fully theoretical *a priori* power analysis and an expensive pilot study.

The latest model versions are freely available at https://www.openabm.org/model/5305/, along with tutorials and instructions on how to collaborate, use the model and contribute with new species.

While the model is still in its infancy in terms of practical application, there is hope that it can help researchers and managers have a better idea about the true state of a system. Nevertheless, it will continue to be very difficult to know exactly how close to the truth we are getting.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolmodel.2016.12.011.

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