Analysis of functional response in presence of schooling phenomena: An IBM approach

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ABSTRACT

The aim of this paper is to analyse the emergence of functional response of a predator–prey system starting from diverse simulations of an Individual-Based Model of schooling fish. Individual characteristics can, indeed, play an important role in establishing group dynamics. The central question we address is whether or not aggregation influences predator–prey relationships.

To answer this question, we analyse the consequences of schooling when estimating functional response in four configurations: (1) no schooling of either prey nor predators; (2) schooling of prey only; (3) schooling of predators only; and (4) schooling of both prey and predators. Aggregation is modelled using the rules of attraction, alignment and repulsion.

We find important differences between the various configurations, highlighting that functional response is largely affected by collective behaviour. In particular, we show: (1) an increased predation efficiency when prey school and (2) different functional response shapes: Holling type II emerges if prey do not school, while Holling type III emerges when prey aggregate.

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Introduction

The scientific community today is called upon to solve many compelling challenges dealing with crucial issues such as climate changes, overexploitation of resources and the necessity of sustainable economic development. In addition, there is a need for intelligent management of living resources. This goal requires a deep knowledge of the interactions within different species as well as between species and the environment. In particular, predation is one of the most important factors influencing the ecological structure and the development of communities, as already stressed by Bax (1998) and Geritz and Gyllenberg (2013), who showed that predation is a key process in ecosystem functioning which must not be neglected in longer-term management. This is especially true in marine ecosystems due to both the complexity of the food net and to intensive fishing activities, which could cause marked cascading effects (Scheffer et al., 2005). Predator–prey dynamics are usually represented by a functional response, which is the amount of prey eaten per predator and per unit of time. This function is a proxy of the flux of matter from one trophic level to another as it determines the transfer of biomass in the food chain (Poggiale, 1998). Typically, a predator–prey model focuses on the interactions between two isolated species (Geritz and Gyllenberg, 2013), taking into account some aspects that are considered nodal to explain the dynamics. These interactions depend on the nature of the studied species. Crucial among these characteristics are collective behaviours, especially in the context of marine ecosystems. In fact, in these ecosystems, schooling and swarming are dominant features (over 50% of bony fish species school (Shaw, 1978; Major, 1978)).

Over the last three decades, considerable attention has been paid to this phenomenon in the literature. Aggregates displaying collective behaviours are present in many different systems, from non-living ones (such as nanoparticles clusters) to living ones (schooling fish, swarming ants or flocking birds). Important common features can be identified in all these cases (Giardina, 2008):

- collective behaviour emerges in the absence of centralised control;
- the mechanism of group formation is very general and transcends the detailed nature of its components;
- some collective properties, known as emergent properties, arise from the set of individuals.

From a modelling point of view, the challenge is to build a model that begins with the description of individual interactions and goes on to reproduce the group formation and predict its dynamics.

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Many examples of clustering modelling can be found in the literature. A statistical physics approach was introduced by Vicsek et al. and became known as the "Vicsek Model" (VM) (Vicsek et al., 1995; Vicsek and Zafiris, 2012). This model is based on the assumption that the movements of living organisms are the result of self-propulsion, of interactions with neighbours and of randomness (Vicsek et al., 1999). In the literature, other models presenting additional rules governing interaction can be found. Hubbard et al. (2004) add an environmental gradient and Czirok et al. (1999) provide an extra spatial dimension (3D model). Other authors have built models characterised by the rules of attraction and repulsion. Couzin et al. (2002), for example, formulate a model for three-dimensional schooling fish (or flocking birds) in which repulsion, alignment and attraction interactions take place (the so-called "A/R/A model"). They test how behavioural differences among organisms influence aggregation processes. Moreover, they demonstrate sharp transitions between four collective behaviours (swarm, torus, dynamic parallel group, highly parallel group) by changing model parameters. Attraction–repulsion rules are also present in the work of Inada and Kawachi (2002) and Grégoire et al. (2003). The first study analyses order and flexibility in the motion of fish schools by changing the number of interacting neighbours and the randomness of motion. Simulations show that school order is strongly affected by randomness and by the number of interacting fish. High interconnection among fish leads to patterns of escape in the presence of a predator. Grégoire et al. (2003) combine Lennard-Jones potential with alignment and study phase transitions in such a system of self-propelled particles.

Improvements in the description of collective behaviours has been made possible by the huge development of Individual-Based Models (IBM). These models are interesting because of the novel way in which they approach the topic: they describe the dynamics at the individual level, by setting the rules of movement and the characteristics of every individual agent, while their outputs provide a representation of the whole system. One can actually see collective properties emerging from individual behaviours. Moreover, by simply testing different values of the parameters, it is possible to estimate how a change at individual scale can impact the whole system.

Consequently, IBMs are widely used to study aggregation phenomena of animals. Nevertheless, the majority of individual-based schooling models presented in the literature rarely focus on functional response to determine whether schooling, or more generally aggregation, has consequences for predator–prey dynamics. Attention is often paid to either aggregate behaviour under attack, such as Inada and Kawachi (2002) and in Lee et al. (2006), or to evolutionary topics. In this regard, Wood and Ackland (2007) consider the evolution of various aggregating features to examine which flock configurations may be selected in optimising foraging, or in defending against predation. They find that two types of flocks emerge when predators are present. The first is a slow-moving, milling group, characterised by a low orientation radius and a high turning angle. The second is a fast moving, dynamic group, with a large orientation zone.

Concerning functional response, we can cite (Tyutyunov et al., 2008; Cosner et al., 1999; Poggiale, 1998). The first paper analyses the way in which different assumptions about individual movements lead to various kinds of functional response. Aggregation is not explicitly expressed in this IBM, but predator prey-taxis and evasion of predators by prey individuals is considered, in addition to random displacement. The taxis stimulus of each species is the odour of the other species. The distribution of the odour of several individuals is obtained by superimposing all individual odours. Consequently, denser zones exist that mainly attract (or repulse) individuals. Depending on the intensity of taxis and on predator density, the predator population exhibits varying degrees of interference. Hence, functional response results as being prey-

dependent if no directional movements are considered, and predator-dependent if predators actively hunt the prey. Moreover, for particular values of predator density and taxis, ratio-dependent responses appear. The latter two papers do not deal with IBM. Cosner et al. (1999) examine how existing predator–prey models (from "traditional" to ratio/dependent models) can be derived in a unified way from mass action principles. Indeed, the authors start from a generalisation of the functional response and analyse how the total encounter rate between predator and prey is influenced by their spatial heterogeneity. However, this theoretical work does not explain how individual behaviours lead to different kinds of clustering. Poggiale (1998) studies spatial heterogeneity effects on functional response when different time scales occur. By using aggregation methods, this work links functional response to individual behaviour in a multi-patch environment.

Published works have thus either focused primarily on possible aggregate responses to predator attacks or they have explored the theoretical formulation of functional response.

The objectives of this paper are: (1) to test the emergence of functional response and its qualitative properties in the presence of schooling phenomenon, with no prior hypothesis concerning defence or attack strategies and (2) to compare these properties with the emerging functional response in the absence of schooling.

For this purpose, we first consider interactions between two species, then we define a set of aggregation rules according to the A/R/A model and finally we analyse the consequences of schooling in predator–prey dynamics. We make the assumption that predators are attracted by prey situated within a visual-range distance.

We analyse four cases: (i) a simple predator–prey model in which no schooling behaviour is present; (ii) the presence of schooling prey only; (iii) predators only school; and (iv) both prey and predators school.

In the first part of this paper we explain the model rules (Section 'Material and methods'). In the second part we provide various model studies and results (Section 'Results'). Finally, we discuss the results (Section 'Discussion') and conclude (Section 'Conclusions').

Material and methods

State variables and rules

The state variables we are dealing with are agents, virtually representing fish, moving in a two dimensional space, a disk of radius L (see Table 1 for numerical values) and split in two types: prey and predators. The position of each agent is defined in polar coordinates by a radius and an angle (Eq. (1)):

$$\vec{r_i^p}(t) = (r_i^p(t), \theta_i^p(t)) \quad i = 1, \ldots, N \tag{1}$$
$$\vec{r_j^{Pr}}(t) = (r_j^{Pr}(t), \theta_j^{Pr}(t)) \quad j = 1, \ldots, P$$

where p stands for *prey* and Pr for *Predators*. If we note $I \subset \mathbb{R}$, $I = [0; L]$, we have both $r^p \in I$ and $r^{Pr} \in I, \theta^p$ and $\theta^{Pr} \in [0; 2\pi]$ and finally $t \in \mathbb{R}$. Their time evolutions provide information of the modulus of displacement and the direction of motion respectively. Predators and prey total numbers are denoted by P and N respectively.

The spatial domain is limited, so once an individual reaches the limits of the simulation area, it reappears on the opposite radius, with the same movement orientation it had in the previous time step. This individual is regarded as a new one: it has no memory of the interactions it had before with other agents. By this way, we can consider a domain in which individuals can enter or exit randomly as if we were considering a part of the ocean but with

Table 1
Summary of the parameters used in the model and range tested in the sensitivity analysis.

Parameter	Value	Sensitivity range	Unit of measurement
Initial T	0		[T]
Δt	1		[T]
T_{max}	380		[T]
T_{start} for predation	350		[T]
Prey number	$10 \rightarrow 1260$		♯ prey
Predator number	20		♯ predator
Repetitions	50		–
Spatial domain radius	[0; 400]		[L]
Initial position range (prey)	[0; 250]	Initial position range (predator)	[0; 50]
Prey parameters			
Attraction range R_{att}	100.0	±10%	[L]
Alignment range R_{al}	50.0	±10%	[L]
Repulsion range R_{rep}	10.0	±10%	[L]
Empty space R_e	0.05	–	[L]
Attraction interaction			
α	10.0	±10%	$\frac{[L]}{[T]}$
β	0.03	±50%	$[L]^{-1}$
Repulsion interaction			
c	5.0	±10%	$\frac{[L]^2}{[T]}$
Alignment interaction			
$|\vec{v}_{al}|$	1.0	±50%	$\frac{[L]}{[T]}$
k_{al}	200	±10%	–
Noise component			
$|\vec{v}_{rnd}|$	3.0	±10%	$\frac{[L]}{[T]}$
k_{rand}	200	±10%	–
Predator parameters			
Attraction range R_{att}	300.0	±10%	[L]
Alignment range R_{al}	90.0	±10%	[L]
Repulsion range R_{rep}	60.0	±10%	[L]
Empty space R_e	0.05	–	[L]
Attraction interaction			
α'	10.0	±10%	$\frac{[L]}{[T]}$
β'	0.03	±10%	$[L]^{-1}$
Repulsion interaction			
c'	5.0	±10%	$\frac{[L]^2}{[T]}$
Alignment interaction			
$|\vec{v'}_{al}|$	1.0	±50%	$\frac{[L]}{[T]}$
$k_{al'}$	200	±10%	–
Noise component			
$|\vec{v'}_{rnd}|$	3.0	±10%	$\frac{[L]}{[T]}$
k_{rand}	200	±10%	–
Predator–prey interaction			
Predation–detection range R_{pred}	500	±10%	[L]
Capture range R_{capt}	5	±10%	m
m (max number of ingested prey)	2		♯ prey
Prey			
λ	2.0	±10%	$\frac{[L]}{[T]}$
ζ	0.025	±50%	$[L]^{-1}$
Predator			
ϕ	1.0	±50%	$\frac{[L]}{[T]}$
μ	0.01	±50%	$[L]^{-1}$

estimation of agent density, because no fixed area can be defined. As previously mentioned, we considered four different cases: (a) predator–prey interaction in absence of any kind of aggregation (random displacement); (b) predation in presence of schooling prey; (c) predation of schooling predators on prey which move randomly; and (d) predation of schooling predators on schooling prey. During the simulation time, agents move according to the following rules, detailed in the next sections:

1. two kinds of events describe the interactions among agents of different types: encounters and consumption. When they meet each other, they escape (prey) or try to capture the other (predator) moving in the direction of each other. Predators are considered hungry while they have not captured a number m of prey (Table 1);
2. if a predator captures a prey individual, that individual is removed and the number of prey is set to $N - 1$ at the following time step;
3. if schooling process is present, agents are mutually attracted, they align with neighbours or they repulse each other depending on their mutual distance, see (Fig. 1(a));
4. agents move randomly in different directions drawn accordingly from a von Mises distribution (Eq. (4)). This first stochastic part of the movement expresses the uncertainty in establishing agent displacement;
5. we hypothesised that individuals do not perfectly perceive neighbours; therefore, alignment direction has a degree of uncertainty. This second stochastic component is linked to the fish's imperfect perception of the surrounding world.

At the beginning of each simulation, initial positions are uniformly distributed. Initial radius moduli are in a range of 0–250 for prey and 0–50 for predators (see Table 1). For every simulation, the predator–prey dynamics starts only after a certain period of time (T_{start}), in order to allow prey to form schools and avoid arbitrary initial condition effects. To be sure of analysing an instantaneous phenomena, we stopped simulations after a few time steps (for $t = T_{max}$, see Table 1).

Instantaneous prey density $\rho_{inst}(t)$ is calculated at each time step as the sum of prey over the spatial domain. The average density is then given by Eq. (2):

$$\rho(T_{max}) = \frac{1}{T_{max} - T_{start}} \int_{T_{start}}^{T_{max}} \rho_{inst}(t)dt. \tag{2}$$

Random displacement

Animal movements cannot only be described by the action of a given number of deterministic factors. Since we cannot be aware of the entire set of forces acting in a defined environment, neither predict completely the behaviour of living organisms, we prefer to include a random component which deviates the deterministic walk of agents. The amplitude of the random component is constant (Eq. (3)), while the direction θ_{rnd} is a realisation of a random variable Θ following the von Mises distribution g (Fisher et al., 1993) defined by Eq. (4):

$$\|\vec{v}_{rnd}\| = v_0 \tag{3}$$

$$g(\theta, \kappa, \theta_\mu) = \frac{1}{2\pi I_0(\kappa)} e^{(\kappa \cos(\theta - \theta_\mu))} \tag{4}$$

where I_0 denotes the modified Bessel function of the first kind and order 0 (Eq. (5)):

$$I_n(\kappa) = \frac{1}{2\pi} \int_{-\pi}^{\pi} e^{\kappa \cos\theta} \cos(n\theta)d\theta \tag{5}$$

a constant density. Since we are dealing with pelagic aggregates in a general configuration, we prefer to work with such a no closed area. On the contrary, a no limited domain (that is, a domain big enough to guarantee that agents never reach its boundaries during the simulation time) adds computational complications for the
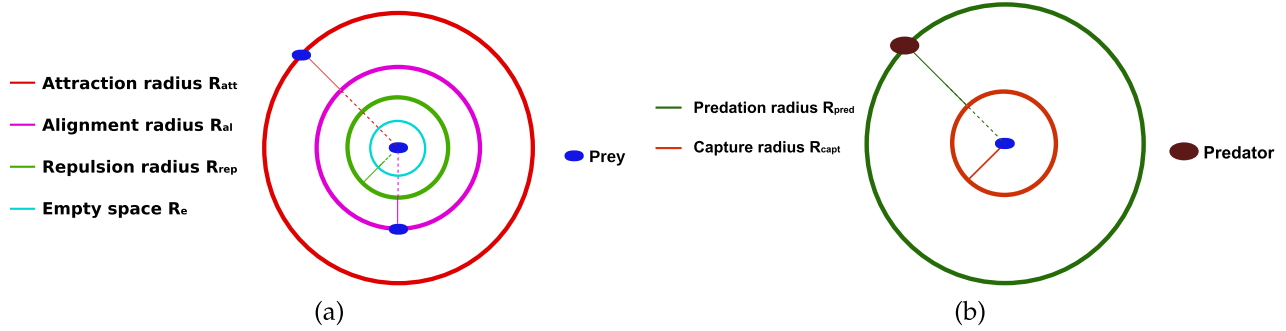
Fig. 1. (a) The A/R/A model. Interaction ranges: if two individuals are closer than R_{att} they are attracted each other, they align in the range of alignment R_{al} and repulse each other in R_{rep}. The final displacement for an individual i is given by the result of the vectorial sum of the interactions over all the individuals lying in the interaction range. (b) Predator–prey interaction ranges: if a predator is closer than R_{pred} to a prey, it is attracted and prey escapes. If they are closer than R_{capt} and the predator is hungry, prey is eaten. The final displacement for a predator (prey) is given by the result of the vectorial sum of the interactions over all prey lying in the predation range.

The von Mises distribution function (Eq. (4)) can be regarded as the circular analogue of the normal distribution on the line, centred at the mean angle θ_μ. In our model, the latter is given by the direction of the same individual at the previous time step, since it is quite unlikely to see abruptly changes in the direction of cruising fish. At each time step, non-interacting individuals will then deviate from their main cruise direction with a probability that depends on the concentration parameter κ: the higher is κ, the bigger will be the probability to have an angle θ close to the mean θ_μ.

A/R/A model

As we said before, interactions concern the tendency of individuals to gather and to align with neighbours. Hence two elements have to be defined: the neighbourhood and the adopted behaviour among neighbour agents. Different kinds of neighbourhood have been already analysed in previous studies. As in the work of Vicsek et al. (1999), Vicsek et al. (1995) and Couzin et al. (2002), we consider a symmetric area around agents, without blind zones (this latter is present, instead, in the work of Couzin et al. (2002), which is moreover a three dimensional model).

The way of representing interactions have also been widely explored in literature. As in the paper of Couzin et al. (2002), we choose to take into account attraction, alignment and repulsion, but we do not maintain a constant speed for agents. On the contrary, we explicitly calculate attraction, alignment and repulsion speeds (called $\|\vec{v}_{att}\|$, $\|\vec{v}_{al}\|$ and $\|\vec{v}_{rep}\|$ respectively, see below).

Since the goal of this study is to study the behaviour of a general aggregating species, we try to keep rules as simple as possible, letting an hypothetical future users the possibility of adjusting the parameters in his/her particular case. We define the attraction, alignment and repulsion interactions as mechanisms appearing in different and non overlapping circular zones, centred on the individual and of fixed different radius $R_{att} > R_{al} > R_{rep}$ respectively (Fig. 1(a)).

Attraction is defined as follows: if a fish j enters in the attraction area of individual i, i starts to move towards it as described by Eq. (6):

$$\|\vec{v}_{att}\| = \alpha \cdot p e^{(-\beta\|\vec{r}_{ij}\|)}$$
$$\vec{r}_{ij} = \vec{r}_j - \vec{r}_i \tag{6}$$

where $\|\vec{r}_{ij}\|$ is the distance between the two individuals.

Attraction interaction takes place if $R_{al} < \|\vec{r}_{ij}\| \leqslant R_{att}$. The exponential shape of Eq. (6) has been chosen because attraction in a school seems to be primarily driven by the sense of sight, which is exponentially attenuated in water (Aksnes and Utne, 1997): a fish sees the others and then decides to move towards them (Partrige and Pitcher, 1980; Hemmings, 1966). The movement

direction is the same as $\vec{r}_{ij}$. If several fish are present in the attraction range, the final movement is given by the vector addition of all the attraction components.

Furthermore, agents adjust their cruise direction to the mean direction θ_{mean} of all the organisms present in the alignment zone, that is within a distance $R_{rep} < \|\vec{r}_{ij}\| \leqslant R_{al}$. This distance is smaller than the previous one since alignment apparently depends on the pressure receptors of the lateral line (Partrige and Pitcher, 1980). Alignment speed modulus $\|\vec{v}_{al}\|$ is constant (Table 1). Since perception of external world is not perfect, fish do not align perfectly with the others; consequently, the alignment angle is a realisation of the von Mises distribution function, centred at $\theta_\mu = \theta_{mean}$.

Finally, repulsion takes place for $R_e \leqslant \|\vec{r}_{ij}\| \leqslant R_{rep}$; also repulsion depends on pressure stimulations and decreases as distance increases. The direction of movement is the same of $\vec{r}_{ij}$, but in the opposite sense:

$$\|\vec{v}_{rep}\| = \frac{c}{\|\vec{r}_{ij}\|} \tag{7}$$

A range of no interaction is defined too (R_e), in order to guarantee an empty space around each agent.

Predator–prey interactions

The relationship among different type of agents depends on distance and on how prey (predators) respond to attacks (detection of food). We establish a circular domain of radius R_{pred} centred at each prey agent (Fig. 1(b)). If the distance $\|\vec{r}_{pP}\|$ between a predator (Pr) and a prey individual (p) (Eq. (8)) is less than R_{pred} and bigger than R_{capt}, both the organisms start to react. In particular, predator goes towards prey agent (Eq. (10)), while the latter escapes, as described by Eq. (9).

$$\vec{r}_{pPr} = \vec{r}_p - \vec{r}_{Pr} \tag{8}$$

$$\|\vec{v}_{esc}\| = \lambda e^{(-\zeta\|\vec{r}_{pPr}\|)} \tag{9}$$

$$\|\vec{v}_{Pred}\| = \phi e^{(-\mu\|\vec{r}_{pPr}\|)} \tag{10}$$

The movement direction is the same as $\vec{r}_{pPr}$.

Visual speeds are summed up together. So, if e.g. two prey lie both at a distance $R_{capt} < \|\vec{r}_{pP}\| \leqslant R_{pred}$, the resulting $\|\vec{v}_{Pred}\|$ is the vectorial sum over the two catching speeds. The same rule is applied if more than two prey are present in the interaction range R_{pred}. Likewise, the escape speed of a prey agent is given by the vectorial sum over all the interactions with detected predators.

A predator eats a prey individual when it is close enough (distance $\|\vec{r}_{pPr}\|$ smaller than R_{capt}) and if it is still hungry. Again, relationships have been established in regard to biological features: at small distance, the main sense leading fish is sight, which decreases exponentially with distance in water. Once simulation time reaches the T_{start} value, predators attack when they are hungry, while prey always try to avoid predators.

At each time step, the displacement of an agent is defined by the vectorial sum of all these components: the escape/capture component, the random displacement, and the interaction components if individuals school.

Model outputs and analysis

The outputs of the models we are interested in are the emerging functional responses in different configurations. To analyse them, we run the model for different numbers of prey N and estimate the number of eaten prey per predator and per unit of time for increasing prey densities. Since simulation time is short, prey density does not change considerably. Thus, we can consider having a value of functional response that corresponds to a single value of density.

Our main goal is to analyse the model outputs and compare the emerging functional response to study the influence of schooling phenomena on predator–prey relationships. First, we effectuate a non-parametric regression, without any assumption on the shape of the functional response (Simonoff, 1998). Then, we make a parametric regression analysis in order to express our results with simple equations. In particular, we find that the shapes of our curves are expressed by the Holling type II Eq. (11) or a two-parameters Holling type III Eq. (16) (see Appendix B for more details).

Let the Holling type II functional response be:

$$f_{H_{II}}(n) = \frac{a \cdot n}{1 + b \cdot n} \tag{11}$$

where n is the density of prey, a represents the 'discovery rate' parameter, or the proportion of prey killed by a single predator per unit of time at low prey density, and finally b is the capturing efficiency. This functional response, called the disc equation (Holling, 1959), is built upon the hypothesis that predation time T can be split in searching and handling time (T_s et T_h respectively). Let Y be the number of prey consumed by one predator during a given time period $T = T_s + T_h$, and t_h the handling time for a single prey individual, that is, the time spent on processing it. Then:

$$Y = a \cdot T_s n \tag{12}$$

$$T_h = t_h Y \tag{13}$$

$$T_s = T - T_h \tag{14}$$

Combining Eqs. (12), (14) and (13) one derives Eq. (15),

$$\frac{Y}{T} = \frac{a \cdot n}{1 + a \cdot t_h n} \tag{15}$$

which represents the amount of prey eaten by one predator per unit of time and corresponds to the Holling type II functional response. There is a linear relationship between parameters a and $b : b = t_h a$ (Holling, 1959; Dawes and Souza, 2013).

In the other cases, that is when Holling type II equation does not fit properly the data, we fit a two parameters logistic Eq. (16):

$$f(n) = \frac{c \cdot n^2}{1 + d \cdot n^2} \tag{16}$$

This is a specific form of the more general Holling type III Eq. (17):

$$f_{H_{III}}(n) = \frac{\alpha \cdot n^2}{1 + \beta \cdot n + \gamma \cdot n^2}. \tag{17}$$

Eq. (17) has not been built upon biological hypothesis as the previous Eq. (11). However, we know that this kind of functional response occurs when predators change their behaviour in order to improve their feeding success. In particular, Eq. (17) arises if predators learn to handle in a more efficiently way, or they discover where more prey can be found, or they just switch target species in order to catch the more abundant one (Real, 1977; Cordoleani et al., 2013). Anyway, we briefly remind that an enzyme-predator analogy has been actually proposed by Real (1977) in order to give a biological interpretation to parameters c and d of the simplest Eq. (16).

Let be the functional response a generic sigmoid function as in Eq. (18):

$$f(n) = \frac{\alpha n^m}{1 + \beta n^m} \tag{18}$$

where, following the enzyme reaction analogy, m becomes the number of encounters (binding sites) a predator (enzyme) must have with its prey (molecule) before it learns to be efficient at feeding on it (the reaction takes place). L.A. Real named the parameter $c = \alpha n^{m-1}$ the rate of potential detection of prey. In this way, this rate depends on the number of encounters m. He then considered the Holling disc equation as the particular case of Eq. (18) in which $m = 1$ and $\beta = \alpha n^{m-1} T_h = c T_h$. We have to notice that this kind of threshold mechanism, common in enzyme reactions, is not necessarily representative of predator–prey interactions. L.A. Real interpretation, indeed, suggests that predators are unable to feed if they meet a single isolated prey individual.

We perform the Hotelling T-squared test (see Appendix B) in order to test the difference of the parameter distribution (a, b) (or (c, d)) between the cases in which the disc equation (or the Holling type III equation) fits.

Results

Hereafter we analyse the functional responses obtained from simulations. We display simulation data for all four cases and data trend estimated by non parametric regression over 50 simulations (bandwidth selected by cross validation (Simonoff, 1998)). Moreover, we present the mean of the 50 Holling type II and III functional responses.

In Fig. 2(a) the simplest configuration is presented, where no schooling phenomenon takes place. For schooling predators and no schooling prey, illustrated in Fig. 2(b), the function increases slowly, similarly to the simplest no schooling case in Fig. 2(a). Functional response in the schooling prey case is displayed in Fig. 2(c). The curve rises quite abruptly. The same situation has been found for the case in which prey and predator school, Fig. 2(d).

We note that Fig. 2(a) and (b) have a shape similar to the Holling type II functional response, while Fig. 2(c) and (d) have a sigmoid shape. We then make a parametric regression and fit Eqs. (11) and (17) respectively, as showed in Fig. 3(a)–(d). This illustrates how our approach can be used to build model formulation at population level by using IBMs.

In Fig. 4(a) an example of the relationship between parameters a and b (Eqs. (11)) is shown. Fig. 4(b) concerns parameters c and d (Eq. (16)). Black dots are values of estimated parameters a and b (or c and d) found with the regression analysis, under the hypothesis of parameters' Gaussian distribution. The ellipse represents the 95%-variance isocline. a and b seem to have a linear dependence, as suggested by model hypothesis (15). Also parameters c and d show the same linear relationship. In Fig. 4(c) and (d) we compare parameter values for the four different cases (two by two). These graphics give a visual highlight of the Hotelling T-squared test
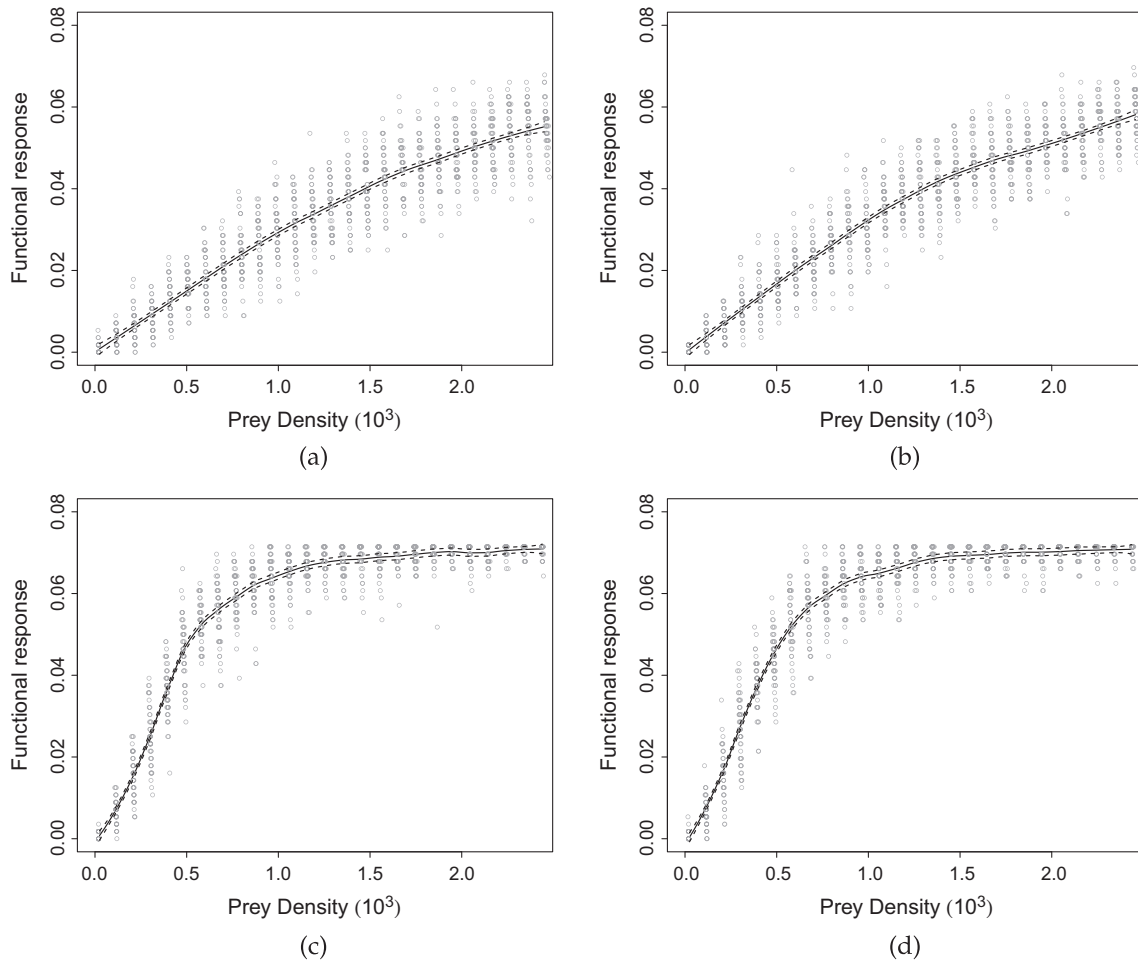
Fig. 2. Functional responses in the four different cases. Black lines represent the trend of the data (grey points) estimated by non-parametric regression over data generated from 50 simulations of the IBM with 95% confidence interval (dashed lines). (a) No schooling of either prey nor predators. (b) Schooling of predators only. (c) Schooling of prey only. (d) Schooling of both prey and predators.

results. In fact, this test gives a *p*-value of zero when we compared the case characterised by the absence of schooling with the one in which predators school. This means that the distributions of *a* and *b* are different and the two cases give different functional responses. On the other side, the *p*-value of the test comparing the distribution of *c* and *d* is approximately of 0.5. We can say that the case of schooling of prey and the one of schooling of both prey and predators are represented by the same curve.

A comparison is conducted between the different configurations (see (Fig. 5)). When prey aggregate functional responses are higher.

The sensitivity analysis (see Appendix A) highlights the importance of schooling in predator–prey interactions: among the parameters that most influence the models, three of them are linked to aggregation (α, β, R_{al}) and show how attraction among prey and the increment of functional response are directly proportional, see Fig. 6(a) and (b). Furthermore, results depend also on ϕ, μ and v_{rnd}.

Discussion

Consumer–resource interactions are basic in ecology. In many modelling studies, attention is primarily focused on collective behaviour facing a single predator, or on different schooling escape strategies, or again on the theoretical formulation of functional response in population dynamics. However, in this paper we focus on the emergence of functional response using an individual-based approach. We realise simulations of predator–prey interactions to verify if the schooling process could affect this response, with no *a priori* hypothesis concerning prey defence strategy.

Herein we present two main results. First of all, the model suggests that predation is more efficient when faced with aggregated prey. Secondly, prey aggregation appears to influence the shape of the functional response.

We will start our discussion with the first point: when prey school, predation tends to be more efficient. In fact, our results show that there is little difference between the case of schooling predators and the case of a lack of aggregation. Moreover, the two other scenarios (in which only prey school and in which both prey and predator school) are different from the previous two. High density populations attract hungry individuals which are able to quickly satisfy their food needs, because once a prey agent has been found, many others will be near. Thus, once a predator has located an individual, it is able to detect other prey in a short distance-range, which avoids spending time searching for food, thus leading to better catch efficiency. It is interesting to note that the sensitivity analysis (see Appendix A) also highlights this result. In fact, an increase in attraction among prey favours predation, while a rise in alignment range causes the opposite tendency. This suggests that the more coordinated the school is, the more difficult will be the capture. Globally, this analysis also allows us to conclude that the presented model is sensitive to a small number of parameters and that it is therefore fairly robust.

Our results thus suggest that schooling is not the best strategy to adopt by prey from a population point of view. However, it is
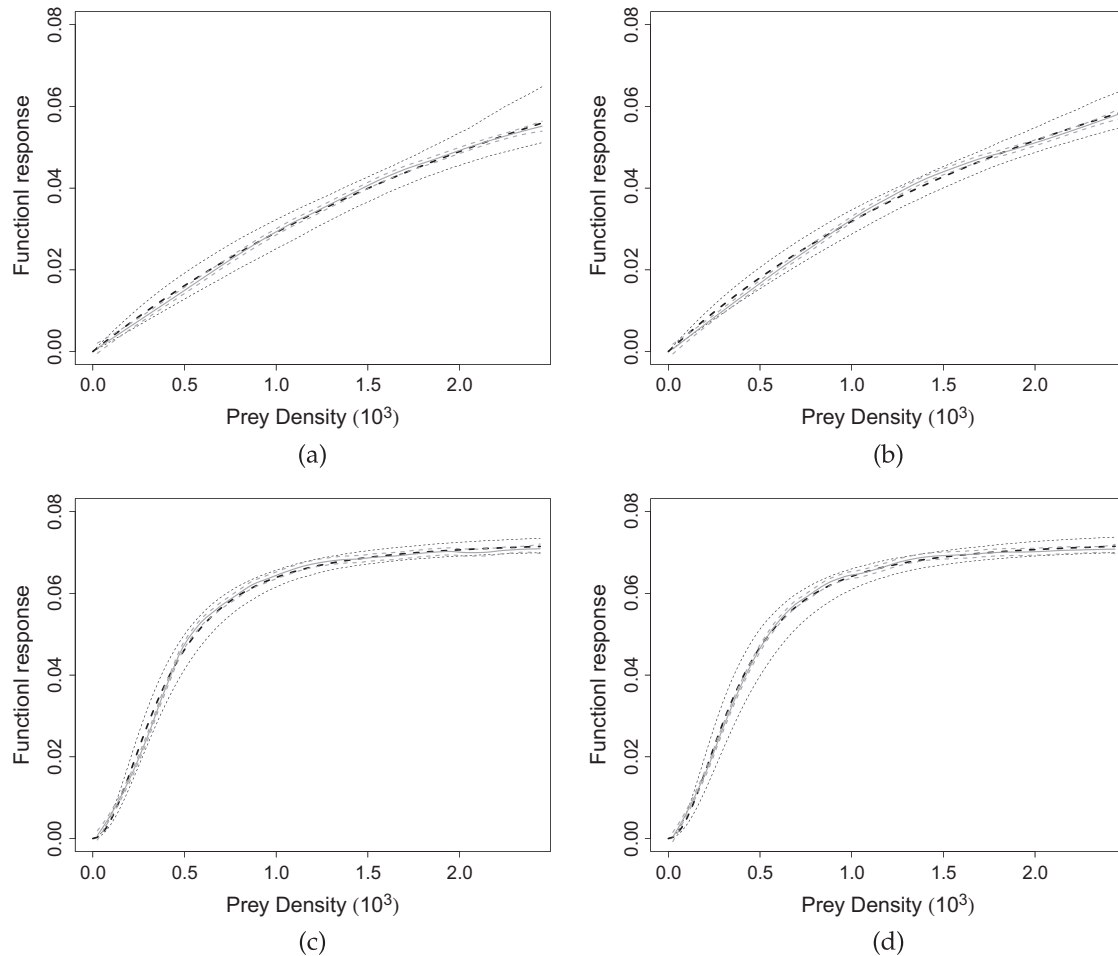
Fig. 3. Fits of functional responses in the four cases. Grey lines represent the trend of the data estimated by non-parametric regression from data generated with 50 simulations of the IBM. Black dashed lines are the means of 50 Holling II (a–b) or Holling III (c–d) functional responses fitted on each simulation dataset. Dotted black and dashed grey lines limit the 95% confidence interval of the parametric and non parametric regression curves respectively. (a) No schooling of either prey nor predators. (b) Schooling of predators only. (c) Schooling of prey only. (d) Schooling of both prey and predators.

important to stress that we are analysing only a two-species-system and that simulations do not reflect the complexity of animal interactions. Moreover, even if aggregation is not advantageous in protecting from predation, collective behaviour could be a good strategy for other reasons. Indeed, the hypothesis of schooling as a strategy against predation has to be considered carefully.

First of all, there is no straightforward evidence that the risk of predation decreases (Ioannou et al., 2012). This is the case in special configurations, or for prey situated in the centre of the group. Riffenburgh (1960) showed that advantage of schooling for prey depends on both prey sighting ranges in relation to the distance among prey individuals and on prey number. Major (1978) studied interactions between the jack *Caranx ignobilis* and the Hawaiian anchovy *Stolephorus purpureus*. The jack is a facultative schooling species, while the anchovy is an obligate schooling species. Major concluded that schooling habit confers advantages to both predators and prey. Predators attacked the easier prey-the ones that made "mistakes", that is, the prey which appeared or behaved differently from the others, and were frequently found on the fringes. Increasing numbers of predators caused an increasing number of isolated prey individuals. Those prey became accessible sooner, because prey schools were broken with greater ease. Moreover, a recent study on stomach content of the shortfin mako shark *Isurus oxyrinchus* found its preferred prey to be the Atlantic saury *Scomberesox saurus* (87% of teleost prey), a species which lives in schools (Porsmoguer et al., 2014).

Secondly, schooling could be an advantage at the individual level by decreasing the probability of an individual being captured. However, since aggregates are more easily detected, this may not be the case at the population level. Further research to analyse the consequences of schooling at different organisation levels would undoubtedly be of the utmost interest. Our results thus show that schooling appears to be unfavourable for prey, so the natural question to consider is from which point of view is this unfavourable. In a biological system many species interact. Perhaps a better feeding strategy offsets losses due to predation. If not, perhaps schooling developed for other evolutionary reasons. We know, indeed, that obligate schooling species have large geographical ranges and that they migrate. Moreover, large aggregations appear during spawning seasons, to guarantee great reproductive success within restrict spatial and temporal limits (Cushing and Harden Jones, 1968). Fully understanding the evolutionary meaning of school formation still remains a challenge to this day.

As introduced above, the second interesting result of this paper concerns the shape of functional responses. The parametric regression shows that two types of function emerge: the Holling disc Eq. (11) and a sigmoid function. In particular, the Holling type II equation has been fitted in the two cases of schooling predators and in the case of no schooling. We chose this function primarily because its shape was recognisable in our results. Furthermore, only two parameters determine the shape of this functional response and
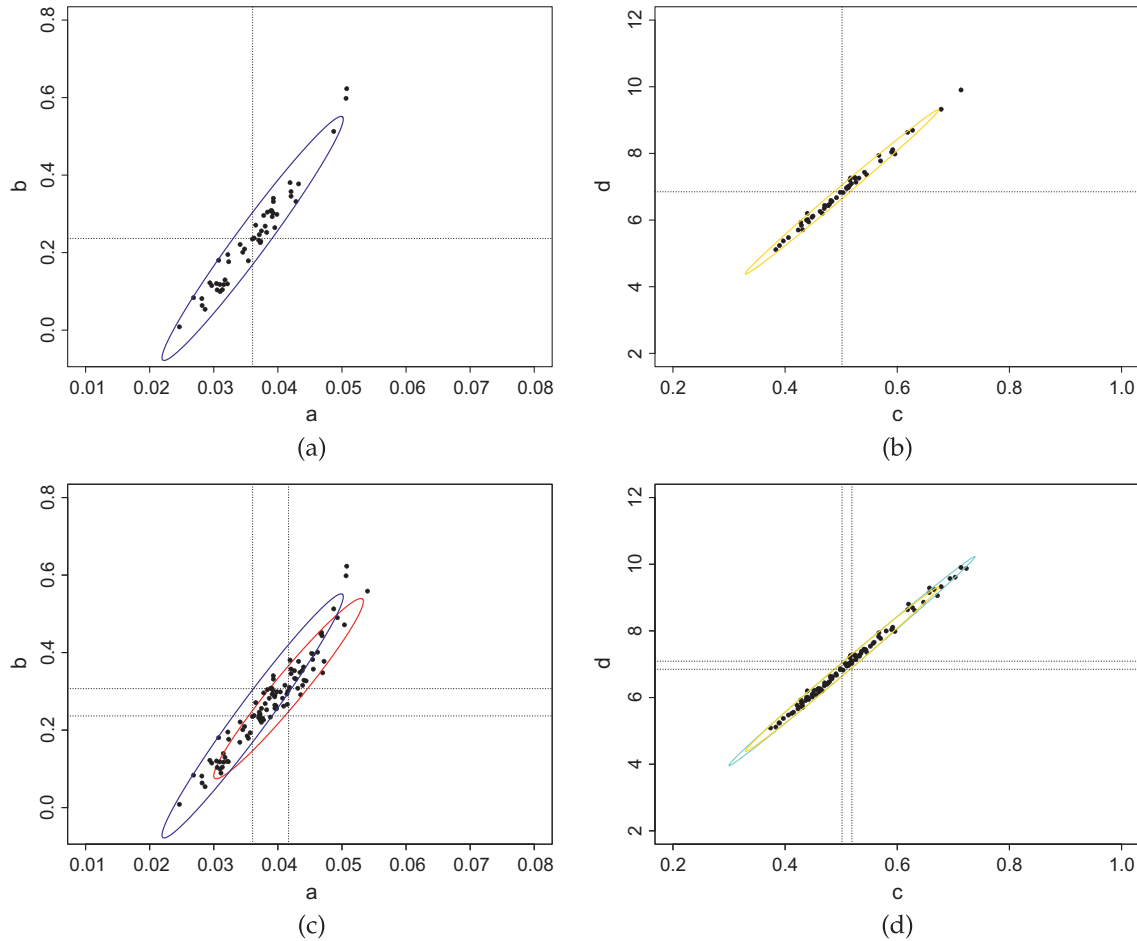
Fig. 4. Bivariate Gaussian distance. Each black point is a value of the couple of the estimated parameters (a, b) or (c, d). The ellipse is the isocline that contains the 95% of the values under Gaussian assumption. (a) No schooling phenomena. We can see a linear relationship between a and b, as predicted by the Holling type II model. (b) Schooling of prey. We can see a linear relationship between c and d. (c) Comparison between the values of the case without aggregation (blue ellipse) and the one of predator aggregation (red ellipse). The two ellipses are not completely overlapping, so the couple of parameters is significantly different between the two cases. (d) Comparison between the values of the case of prey aggregation (yellow ellipse) and the one of predator and prey aggregation (azure ellipse). The two ellipses are completely overlapping. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
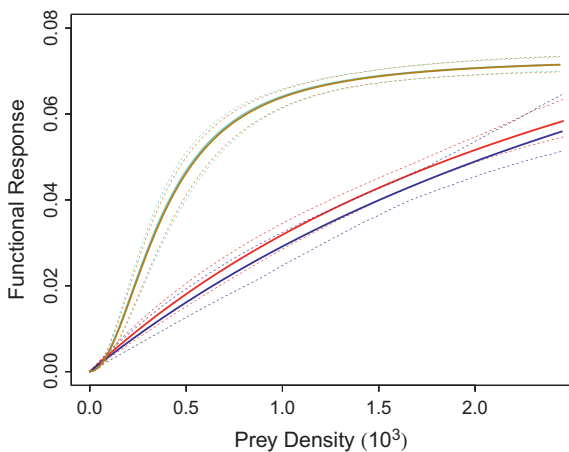

Fig. 5. Comparison among the four cases. Parametric regression curves of Fig. 3(a)–(d)) are shown. Yellow curve: schooling of prey; azure curve: schooling of both prey and predators; red curve: schooling of predators; blue curve: absence of schooling phenomena. The dynamics primarily depends on prey aggregation. Dashed lines limit the 95% confidence interval of the parametric regression curves. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

they can be easily linked to biological/behavioural characteristics. In the other cases, model outputs exhibit patterns similar to the Holling type III function, represented by Eq. (17). The presence of prey aggregates thus causes a change in functional response shape. When prey school, predators become more efficient, once a certain threshold of prey density has been reached. We suppose that this shift in functional responses occurs when aggregates appear. However, we are not yet able to determine why this sigmoid shape appears, because every behavioural aspect of predation needs to be confirmed by data whereas the main goal of this paper is to compare emerging functional responses when aggregation occurs. Nevertheless, it would be interesting to fit a general function to model data. Indeed, when dealing with high variability, such as in aggregated populations, using a simple function – namely the disc equation or the Holling type III equation – is not the best possible choice (Cordoleani et al., 2011; Morozov et al., 2012). A better choice might be a linear combination of different classical equations, with various parameters linked to the model at the individual scale. These parameters could be chosen in accordance with real data. Ideally, different types of functional response (Holling type II, type III, etc.) would emerge by changing parameter values. In this way, it would then be possible to link IBMs to population dynamics. Further analysis in this direction to define
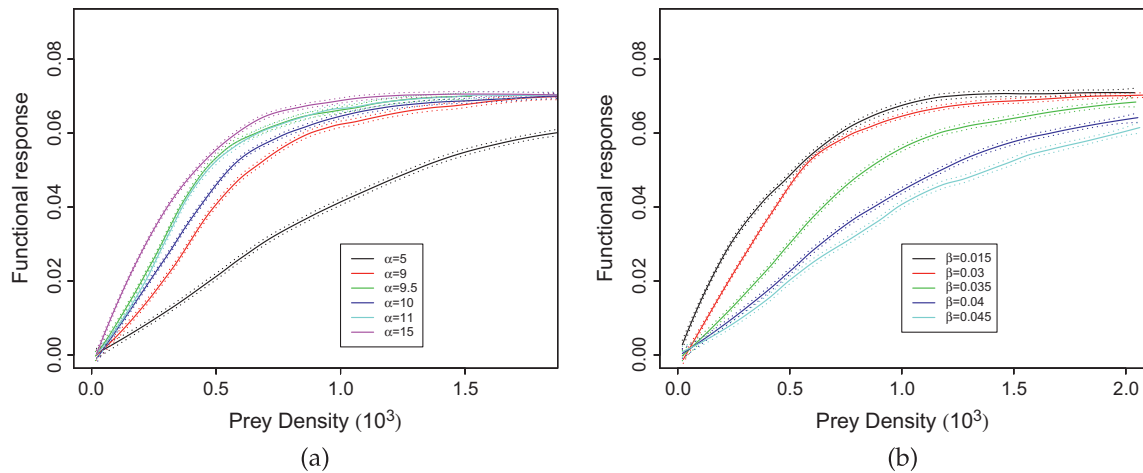
Fig. 6. Curves are estimated by non-parametric regression over data generated from 50 simulations of the IBM with 95% confidence interval (dotted lines). (a) Sensitivity analysis to parameter α. Schooling prey. Different values of α have been tried. The blue curve is the model one: $\alpha = 10.0$. The bigger is α, the more efficient is predation in the zone before the *plateau*. (b) Sensitivity analysis to parameter β. Schooling prey. Different values of β have been tried. The red curve is the model one: $\beta = 0.03$. The bigger is β, the less efficient is predation. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the best model that fits our results, would undoubtedly be very enriching.

We compared the parameter distributions among the four curves using the Hotelling T-squared test. This analysis confirmed that the distribution of parameters (a, b) is significantly different for the two curves describing predation without aggregated prey. On the contrary, the distribution of (c, d) is the same for the two sigmoid curves. Prey schooling is the major factor influencing predation efficiency.

The IBMs presented in this paper allow to check possible trends of functional response in different configurations of marine ecosystems in the presence of schooling. This phenomenon, despite its common occurrence, is still misunderstood and should be studied further. Although IBMs are powerful tools for achieving this goal, they alone are insufficient. They can be very useful in two situations, both of which could be explored starting from our model. The first situation, linked to the choice of functional response discussed above, is when IBMs represent a starting point for a larger spatio-temporal scale work, in order to take into account individual-based processes in population dynamics. In this case, the interpretation of the functional response in population growth dynamics becomes a crucial point. Indeed, the problem of the representation of macroscale interactions starting from a microscale model is a central topic in theoretical ecology. Other studies have stressed how a global functional response can emerge from local functional responses with different shapes (Cordoleani et al., 2013; Morozov et al., 2012; Poggiale, 1998). In this work we use classical functional responses (Holling II, III) because even if these mathematical objects are only approximations of reality, they are well known and easy to interpret and manipulate. Nevertheless, they are based on hypotheses that must always be checked to ensure the best possible approximation. We are referring, in particular, to hypotheses relating to the different time scales encompassing the various processes of an organism's life. In our cases, time scales can be considered to be very fast with respect to population dynamics, because we are dealing with short predation processes. However, if the aim is to better understand population dynamics when schooling species are involved, a deeper reflection upon the form of functional responses is needed.

The second situation in which IBMs are extremely useful is reached when they are coupled with a conspicuous set of data pertaining to a particular species. In this case, they are able to simulate very different and credible configurations, saving researchers from undertaking expensive and not always feasible laboratory experiments. To this end, a frequently stressed problem concerning modelling of collective behaviour is its degree of abstraction (Vicsek and Zafiris, 2012): even if there is an attempt to collect data on aggregating species, our knowledge is still poor and no biological characteristics can confirm the existence of an attraction–repulsion zone or force, and nor can the number or the density of neighbours that an individual can perceive. Some authors have underlined the importance of describing organisms' features more precisely, arguing that in many models their representations, as well as definitions of their interactions, are so simplified that is not possible to link them to reality (Schellinck and White, 2011). It is important to underline that not only sight but other signals and senses such as olfaction or sound detection should be considered in the description of aggregation and predation. It would be interesting, for example, to add a hearing-dependent attraction to enable predators to hear prey before seeing them.

Some studies linking data and models already exist, but few deal with fish. Of those which do, experiments with animal behaviour in the presence of fish aggregating devices (FADs) (Robert et al., 2012; Capello et al., 2011), or studies using video tracks of fish shoaling in a tank (Gautrais et al., 2012; Hemelrijk et al., 2010) can be cited. To combine a verification of models with specific measurements is an interesting challenge. For example, behavioural information acquired from acoustic tagging (such as FADs) and from stomach contents (see Porsmoguer et al., 2014), could be integrated into the model. In order to adjust aggregation parameters, in-tank experiments might be required. In this way, it might be possible to test the coherency of mathematical expressions and to reflect upon the evolutionary meaning of schooling (Did aggregation appear primarily as a feeding strategy? What are the energy costs of such behaviour?) To evaluate individual energy budget and consequently strategies, it might be necessary to determine the balance between the costs and the benefits of schooling. Indeed, it is worth remembering that aggregation may be advantageous if only for hydrodynamic reasons, helping individuals in long and/or difficult migrations. This, like the above hypotheses, may explain why fish grouped together despite the ensuing higher mortality rate due to predation, or why predators school even when there is no evidence of improved success in feeding.

Conclusions

In this paper, our primary aim has been to show the consequences of school formations on predator–prey interactions and to show that the occurrence of inhomogeneous interacting groups influences predation efficiency. We propose an IBM describing predator–prey dynamics in the presence of schooling phenomena. Our rules have been built with the aim of constructing as simple a model as possible, one which can be adapted to different species simply by changing a few parameter values, or which can be generalised into a state variable model that takes individual interactions into account. Two main results emerge from our work, both of which are interesting from a modelling point of view and which underline the importance of biological features when modelling natural systems.

First, the notion that functional response, which characterises population dynamics and determines the biomass flux in the trophic chain, *emerges* from the description of individual interactions. Indeed, we have shown that the shape of this function depends on the rules governing agent motion (aggregation plus predator–prey interactions in movements).

Second, this work suggests that aggregation may be an important factor in ecosystem functioning which should thus be taken into account in future studies, even those concerning ecosystem management. Further research to put this predator–prey interaction into a larger spatio-temporal scale system, involving other species, would undoubtedly be constructive.

Acknowledgements

Appendix A. Sensitivity analysis

To analyse the sensitivity of our model to all parameters, we make different tests changing subsequently just one of them by 10–50% of its value, depending on if it was bigger or smaller than one respectively; in the third column of Table 1 we specified which increment has been chosen for each one. As for the main model, we ran 50 simulations for every new configuration and we remark that the model is sensitive just to a small number of parameters. Furthermore, in order to fully test the coherence and the stability of the model, we also check how it responds to wider variations concerning some crucial parameters. Hereafter we present the graphics obtained with those parameters that caused a substantial difference. Since the two cases concerning the presence of schooling prey are equivalent, we show the graphics of just one configuration, the one of aggregated prey. Even for the additional tests we illustrate just one emblematic case, the one of schooling prey, to briefly show the main results. We made a non-parametric regression to show the trend of data.

First of all, coefficient α, Eq. (6), which expresses the proportionality between the visual perception and the displacement due to attraction, shows some changes: the bigger is this parameter, the stronger is the attraction among fish in schooling process and the higher is the functional response. We tested a series of α values in order to verify the influence of attraction interactions among prey upon functional response (Fig. 6(a)).

Coefficient β, Eq. (6), is the second parameter which influences the strength of intra-species attraction: a low rise of β strongly attenuates the attraction among prey, because of exponential nature of the attraction function, and produces a lower functional response in the situations of aggregation of prey and aggregation of both prey and predators. Since prey's aggregation is responsible of a rise of predation efficiency, we expected this result. We made some tests concerning β too, see (Fig. 6(b)).

On the other side, changes on β' coefficient (in predators' aggregation) does not engender a statistically relevant difference.

Parameter ϕ, Eq. (10), is linked to predation attraction versus prey. When prey are not aggregated Fig. 7(b)), as well as if they are schooling Fig. (7(a)), an augmentation of ϕ causes a rise in functional response and conversely a decreases of this parameter engenders a lower curve.

Concerning the same equation, parameter μ has not a big influence in the dynamics, Fig. 8(a). However, if we halve its value the shape of the curve changes abruptly. This means that halving its value is a too strong change for the model. This also stresses the importance of the choice of parameter values.

Another parameter influencing the behaviour is the alignment range (R_{al}): a smaller R_{al} causes an higher functional response (Fig. 8(b)). This coefficient is responsible of the amplitude of coordination area, inside which individuals adjust their direction to their neighbours' one. Consequently, it seems that the larger is this region, the more hardly will be to catch a prey.

Parameter v_{rnd}, Eq. (3) has been modified separately in prey's and predator's equations. When prey are concerned and they school, a bigger random contribution means less aggregation, so a decrease of the parameter causes a rise in the curve (Fig. 8(c)). We also paid attention to how does the coefficient v'_{rnd} influence predator–prey dynamics, since if the random factor is more important than the searching/attacking ones, the latter behaviour could be hidden by the former ones. However, there were not important impacts on results.

Furthermore, we tested different values of parameter λ, which is responsible of the escape reaction, thinking that some important changes of its value in comparison to other predator–prey interaction parameters could influence the behaviour of our model. By the way, we did not find relevant differences.

Appendix B. Statistical tools

B.1. Non linear regression

Suppose that we dispose of a sample of q observations (n_i, y_i), $i = 1, 2, \ldots, q$, and that those data are connected through Eq. (11) such that

$$y_i = \frac{a \cdot pn_i}{1 + b \cdot pn_i} + \epsilon_i \tag{19}$$

where y_i is the number of prey eaten per unit of time per predator observed in a simulation, n_i is the mean prey density over short length of time and ϵ_i are random errors supposed to be Gaussian and such that $E[\epsilon_i] = 0$. Estimations of $\hat{a}$ and $\hat{b}$ of parameters a and b are determined by non-linear regression (Gauss–Newton algorithm), when minimising the sum of squares of the errors $S(a, b)$ (Seber and Wild, 2003):

$$S(a, b) = \sum_{i=1}^{q} \left[y_i - \frac{a \cdot pn_i}{1 + b \cdot pn_i} \right]^2 \tag{20}$$

Using the IBM, $M = 50$ samples of size q have been simulated. We obtained a set of M pairwise values $(\hat{a}_m, \hat{b}_m)$, $m = 1, \ldots, M$ estimated by non linear regression. Under gaussianity assumptions it is possible to draw 95% confidence intervals of parameters (a, b) using the M samples to estimate the mean and the variance of the bivariate distribution of $(\hat{a}, \hat{b})$.
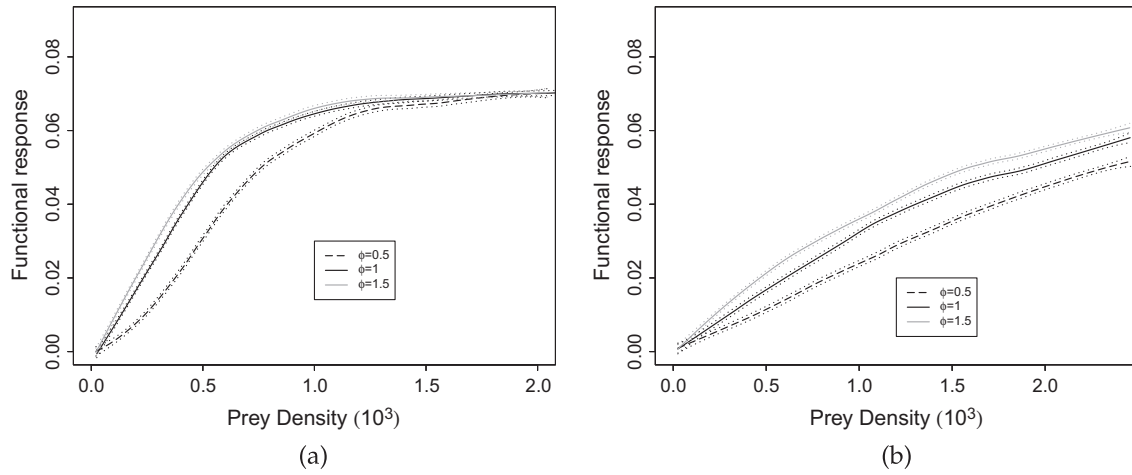
Fig. 7. Curves are estimated by non-parametric regression over data generated from 50 simulations of the IBM with 95% confidence interval (dotted lines). (a) Sensitivity analysis to parameter ϕ. Schooling prey. The black curve is the model one: $\phi = 1.0$. The bigger is predation coefficient, the more quickly the functional response rises. (b) Sensitivity analysis to parameter ϕ. Schooling predators. The black curve is the model one: $\phi = 1.0$. We can see the same trend.
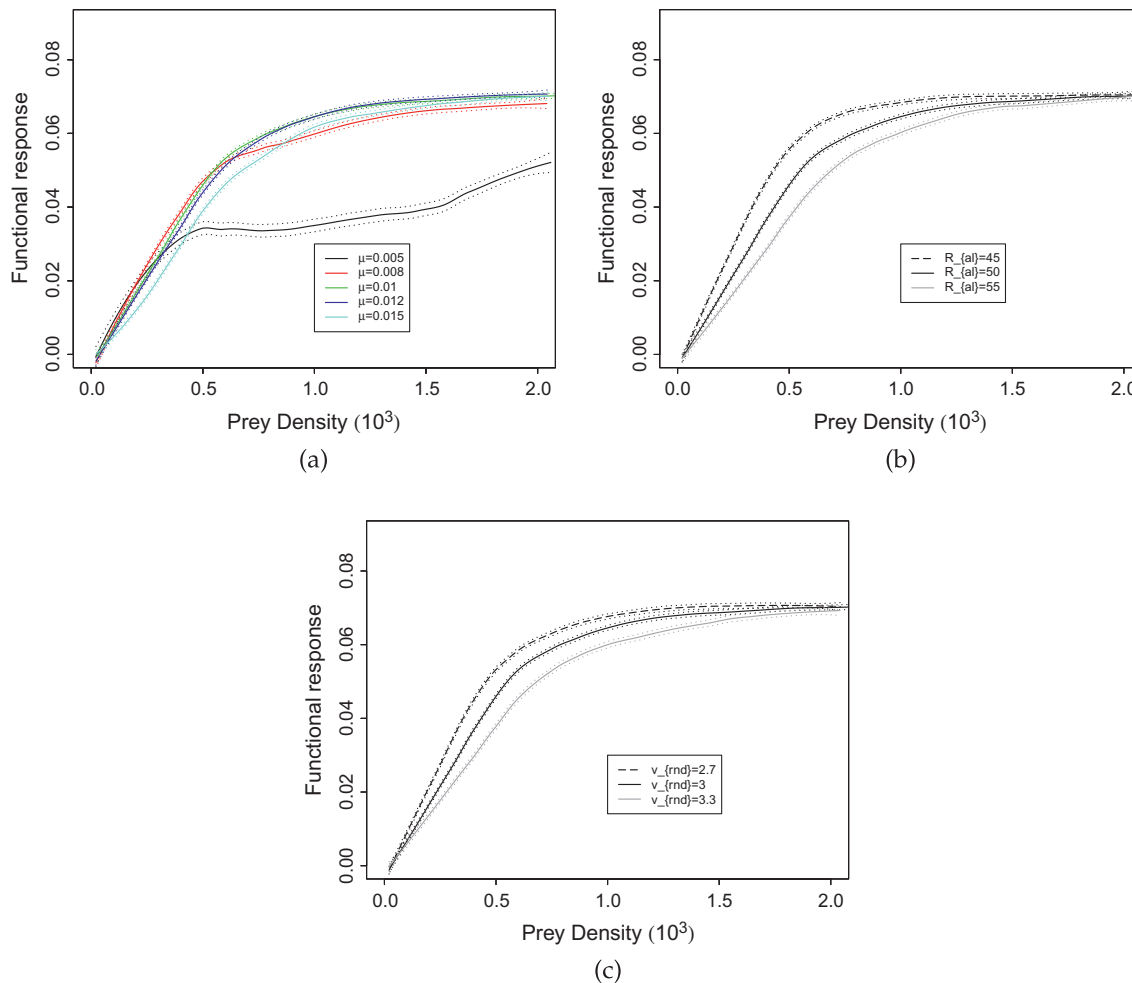

Fig. 8. Curves are estimated by non-parametric regression over data generated from 50 simulations of the IBM with 95% confidence interval (dotted lines). (a) Sensitivity analysis to parameter μ. Schooling prey. The green curve is the model result: $\mu = 0.01$. A different shape occurs when $\mu = 0.005$. (b) Sensitivity analysis to parameter R_{al}. Schooling prey. The black curve is the model result $R_{al} = 50.0$. The bigger is alignment range, the less efficient is the predator. (c) Sensitivity analysis to parameter v_{rnd}. Schooling prey. The black curve is the model result: $v_{rnd} = 3.0$. An increase in random displacement means less aggregation and consequently less predation. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Finally, the consequences of schooling when estimating functional responses in the four configurations (absence of schooling, schooling prey, schooling predators or schooling of both prey and predators) are studied through the comparison among all the different distributions of parameters $\{a, b\}$ (Hotelling T-squared test (Hotelling, 1931)).
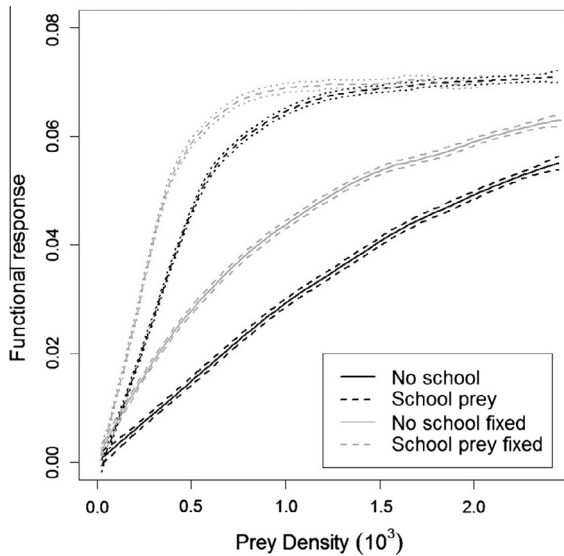
Fig. 9. Comparison among the "frozen" configuration and the one in which prey can escape (the model). Cases of prey aggregation and of absence of collective behaviours are represented.

Appendix C. Supplementary test

Potential consequence of non homogeneous prey distribution on predator–prey interactions has been already suggested several times (Arditi et al., 1991; Arditi and Saiah, 1992). However, nobody analysed systematically this topic as we have done in this paper. We propose here a supplementary test to investigate the influence of a non homogeneous distribution of prey on functional response. We calculated the functional response in a situation of "frozen prey". This means that when $T \geqslant T_{start}$, prey do not move any more. Consequently, predators catch in a patchy environment and their food is constituted by sessile organisms. In Fig. 9 we compare the results of this experience to the ones we have with the "normal model" (that is, when prey are allowed to escape). Both the configurations of schooling prey and of absence of aggregations are shown. Those tests show an equivalent difference between the two cases in which prey aggregate or not. Moreover, the figure suggests that the different functional responses found in the model can be explained to a large extent in terms of homogeneous or non-homogeneous distribution of prey. We expected this result, because we do not represent any defence behaviour. We can also see that there is a quantitatively difference among the frozen experiences and the model ones. The higher functional response in the first scenario is obviously due to the absence of prey escaping behaviour.

Appendix D. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.pocean.2015.02.002.

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