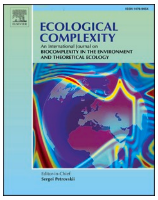
Ecological Complexity 44 (2020) 100876

Contents lists available at ScienceDirect

Ecological Complexity

journal homepage: www.elsevier.com/locate/ecocom



Effects of cooperation and different characteristics of Marine Protected Areas in a simulated small-scale fishery

Kwabena A. Owusu [a,b], Esteban Acevedo-Trejos [a], Mouhamed M. Fall [b], Agostino Merico [*,a,c]

[a] Department of Theoretical Ecology and Modelling, Leibniz Centre for Tropical Marine Research (ZMT), Bremen, Germany
[b] African Institute for Mathematical Sciences, Mbour, Senegal
[c] Department of Physics and Earth Sciences, Jacobs University Bremen, Germany

ARTICLE INFO

Keywords:
Marine reserves
Agent-Based Model
Small-scale fishery
Sustainability
Conservation

ABSTRACT

Marine fisheries are a critically important source of food, nutrition, and employment for millions of people. As the global population increases, new and expanding pressures are created on fish resources. Marine Protected Areas (MPAs) have been widely promoted as valuable tools for rebuilding or maintaining fish stocks around the world. The success of MPAs, however, widely depends on their particular configuration and management and their effectiveness is often object of contentious debates in both scientific and political arenas. Since fisheries management is a collective action problem, some forms of human cooperation in terms of fishing behaviour can lead to sustainable fisheries and can represent, in theory, a complementary or even an alternative approach to the establishment of no-take marine reserves. We present here a new Agent-Based Model (ABM) that captures the main characteristics of an idealised small-scale fishery. We then use the model to investigate the combined effects of different fishing strategies (expressed by a cooperative trait associated to fishing effort) and various configurations of no-take reserves (including presence or absence of MPA, size of MPA, age of MPA, i.e. time elapsed since its establisment, and distance between two MPAs) on fish abundance and catch under an overfishing regime. Our results show that high cooperation without an MPA can be as effective as lower levels of cooperation combined with an MPA in maintaining fish stocks and catches at relatively high levels. The mobility of our fish agents implies that, contrary to current belief, these results may not be limited to sedentary species. We also found that the greatest impacts on fish abundance and catch are produced by the size of an MPA and the time elapsed since its establishment. Furthermore, the distance between two MPAs has no significant effect, regardless of the cooperation levels characterising the fishing agents. Despite its simplicity, the ABM presented here provides insights on the most plausible effects that combinations of different MPA designs and human cooperation strategies can produce on overexploited small-scale fisheries. When appropriately adapted with a realistic, fishery-specific parameterisation, this model can constitute a valuable tool for evaluating the impact of different resource management strategies. We make the model available as open-source software with the aims of fostering reproducibility, transparency, and flow of ideas.

1. Introduction

Global fish catches increased in the period from 1950 to 1990 and started to decline after that, with about 53 % of the global fish stocks being currently below a recovery target of 80 % of the maximum sustainable yield (Costello et al., 2016). The cumulative impacts of the increasing global population and the ever expanding range of access to marine fisheries threaten fish resources and the economies that rely on them (Halpern et al., 2008; Kildow and McIlgorm, 2010; Sale et al., 2005). These are aspects of great concern because fish proteins represent an essential nutritional component in many countries and in particular in countries where total protein intake levels are low (Guillen et al., 2019). In the tropics, for example, fish constitutes the major source of proteins, essential micronutrients, and fatty-acids for millions of people (Golden et al., 2016). How can we ensure food and nutritional securities for everyone and at the same time maintain or rebuild fish stocks to sustainable levels ?

Marine Protected Areas (MPAs) have become a common tool for managing marine resources as their use has expanded rapidly since they were first introduced around the end of the nineteenth century (Wells

---

[*] Corresponding author.
E-mail address: agostino.merico@leibniz-zmt.de (A. Merico).

https://doi.org/10.1016/j.ecocom.2020.100876
Received 17 February 2020; Received in revised form 7 October 2020; Accepted 24 October 2020
Available online 4 November 2020
1476-945X/© 2020 Elsevier B.V. All rights reserved.

et al., 2016). MPAs may also be referred to as marine parks, sanctuaries, reserves, or closures. The terms reserve and closure are used most commonly in the context of fisheries management. Many conservation groups and scientists have called for the establishment of MPAs as a way of mitigating the overexploitation of marine resources (Claudet et al., 2006; Nelson and Bradner, 2010; Pauly et al., 2002). The success and achievement of MPAs, however, can vary widely, depending on their configuration (Ban et al., 2017) and management (Gill et al., 2017). Critical aspects for the design of effective MPAs remain their spatial scales and the socio-cultural, political, and legislative contexts (Giakoumi et al., 2018).

MPAs, in their most restrictive form, i.e. as no-take fishery reserves, are often opposed by fishermen and other stakeholders due to the displacement of fishing activities and reduced catches (Bennett and Dearden, 2014; Caveen et al., 2014). Consequences of no-take reserves include social, economic, and cultural conflicts among the involved groups and communities (Bavinck and Vivekanandan, 2011; Christie, 2004). How much catch is lost due to spatial closures in both the short and the long term is a difficult, albeit critically important, issue (O'Leary et al., 2018). Additionally, debates about whether a single large no-take fishery reserve is more effective than several smaller ones of the same total area (SLOSS), or whether closely spaced no-take areas are more effective than distantly spaced ones, remain contentious (Ovaskainen, 2002).

Fisheries management is a collective action problem (Jones, 2006). Neoclassical economic theories of human behaviour predict the "tragedy of the commons" when resources such as marine stocks are managed in the absence of a third-party enforcement of agreements or if practical difficulties prevent privatisation (Hardin, 1968). In other words, although everyone benefits from an intact common resource, there is always a tendency to cheat (i.e. to overharvest) at the individual level, because cheating brings economic advantages to the individual whereas the costs (e.g. an ocean stripped of its resources) are distributed among everybody. However, laboratory simulations of such social dilemmas (Fehr and Gächter, 2000; Janssen et al., 2010; Owusu et al., 2019), field studies of commonly managed resources (Cárdenas and Ostrom, 2004; Prediger et al., 2011; Rustagi et al., 2010), and mathematical modelling (Brandt and Merico, 2013; Brandt et al., 2012; Janssen and Baggio, 2017) all indicate that humans do not universally maximize short-term personal gains but can cooperate to produce shared, long-term benefits.

From a mathematical point of view, game theory provides an analytical framework for understanding how cooperation evolves among strictly-assumed rational players. Nowak (2006) proposed five mechanisms for cooperation to evolve based on game theoretic reasoning, which involve fixed matrices of interactions among players. While game theory leads to rigorous and elegant conclusions, applications and extensions of the results to the real world are, to the least, very problematic, especially in explaining social facts under the rational choice axiom. Common Pool Resource (CPR) experiments unveiled many shortcomings about conventional theories of collective action that assume rational, self-interested behaviours (Dietz et al., 2003) and highlighted the full spectrum of dimensions involved, including those related to personal emotions, social and environmental conditions, and ethical and existential issues. Given these complexities, many scholars have recently called for a paradigm shift to overcome the limitations of the standard economic tools and models (Bookstaber, 2017; Burgess et al., 2020; Helbing and Kirman, 2013). A bottom-up modelling approach that incorporates the behaviour of many heterogeneous individuals and that aims at investigating the emerging macroscopic patterns arising from individual decisions, appears most promising. Such an approach is available and is called Agent-Based Modelling. These models have advantages also with respect to mean-field, dynamic system models (such as those based on diffusion processes or equilibrium theories), especially when dealing with inhomogeneous populations of agents and complex interactions among agents (Bonabeau, 2002).

Forms of human cooperation that lead to sustainable fisheries can be, in theory, a complementary or even an alternative approach to the establishment of no-take reserves. However, the relative impacts and consequences of the two approaches have received little attention by the scientific community. We present here an Agent-Based Model (ABM) that captures, in broad terms, the main characteristics of a small-scale fishery (by comprising a relatively small fleet and parameter values scaled proportionately with respect to small, traditional fishing craft representative of West Africa). We then use the model to disentangle the combined effects of fishing behaviour, expressed by a cooperative trait associated to fishing effort, and different designs of no-take areas, including presence or absence, size, distance, and age (i.e. time elapsed since its establishment), on fish abundances and catches under an overfishing regime. This study presents a first idealised application of this new model and, as such, we see it as a proof-of-concept rather than as an effort oriented towards the development of fishery theories. Also, the number and diversity of stakeholders involved, even in small-scale fisheries (e.g. Belhabib et al., 2014), which often include an important illegal component (Ferraro and Brans, 2009; Niasse and Seck, 2011), and the uncertainties related to real fish stock and catch data (Belhabib et al., 2014) pose a variety of challenges to mathematical modelling. Therefore, our aim is not to pin down the exact trajectories of fish abundance and catch produced by the different management scenarios but rather to provide a qualitative insight on the most plausible effects that such scenarios can produce with a model of minimal complexity. We provide the numerical code of our model as open-source software (https://github.com/systemsecologygroup/CoopFishABM) so that it can be used, modified, and redistributed freely. This, we hope, will foster reproducibility, transparency, and flow of ideas.

2. Model description

We developed an Agent-Based Model (ABM) to investigate the combined effects of varying levels of cooperation and different configurations of MPAs on an idealised fishery comprising a reatively small fishing fleet of 20 boats, thus reflecting a small-scale fishery, and a variable number of fish agents. The boats in our model could be thought of as pirogues, i.e. large wooden canoes, powered by outboard motors, typical of West African small-scale fisheries (Belhabib et al., 2018; Diankha et al., 2017), we will thus use this terminology hereafter.

2.1. Fishing ground

The fishing ground Fig. 1 is simulated as a finite two-dimensional space represented by a square with area $A = 2$. The boundaries of the virtual fishing ground are wrapped so that when a fishing agent go out from one side of the area, a new one re-enter from the opposite side. This aspect accounts for pirogues leaving the fishing ground to return to shore and for new ones entering the fishing ground, under the assumption that the entering pirogues have the same cooperative characteristics of those exiting. The carrying capacity, K, of the fishing ground, i.e. the maximum number of fish that the ground can sustain, is set to 200 individuals. MPAs are simulated as no-take subregions of the fishing space. Their key characteristics are: 1) size, 2) distance, when two MPAs are considered, and 3) age. The size of an MPA is expressed as percentage of total fishing ground.

2.2. Characteristics of fish agents

At time $t = 0$, a total of $N = 200$ fishes are randomly distributed over the fishing ground. The reproduction of fishes is simulated as a stochastic process depending on a reproduction probability and on a logistic-type growth restriction, which is given by

$$R(n) = g_{max} \cdot n \cdot \left(1 - \frac{n}{K}\right), \tag{1}$$

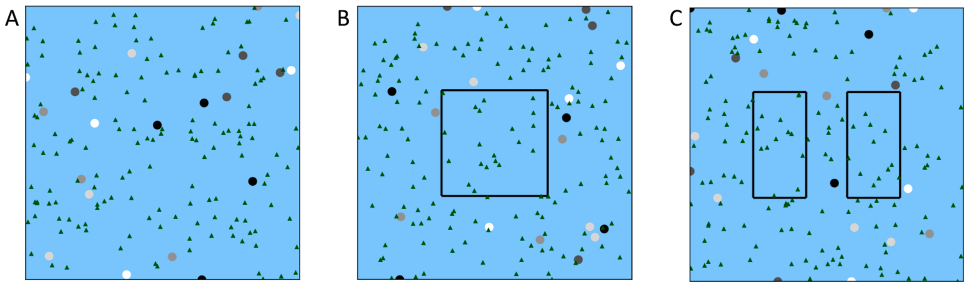


Fig. 1. Simulated fishing grounds reflecting three management designs (MPAs are represented as areas bounded by black solid lines): no MPA (A), single large MPA (B), and two spaced MPAs (C). Fishing agents (i.e. pirogues marked with circles) and fishes (marked with triangles) are initially randomly distributed on a finite 2-D space. The different colours of the pirogues reflect the associated cooperative trait level, ranging from fully cooperative (black) to fully non-cooperative (lightest grey), see Fig. 3 and main text for more details.

where n is the current fish population (in number of individuals), K is the carrying capacity of the fishing ground (in number of individuals), and g_{max} is the maximum intrinsic growth rate (in per time). Therefore, every time a fish agent is randomly picked, a random number is drawn between 0 and 1 and compared to the current reproduction rate $R(n)$; if the random number is smaller than $R(n)$, reproduction occurs (i.e. a new fish agent is added to the population), otherwise reproduction does not occur (no fish agent is added to the population). This formulation ensures that, as the number of fish agents increases and the population size gets closer to the carrying capacity K, it becomes less likely that fish agents reproduce.

Fishes are fished at a rate H that is controlled by the harvesting characteristics of the fishing agents, which is formulated according to the classic Schaefer's model (Clark, 2010; Schaefer, 1954), see subsection 2.3 for further details.

The movement of a fish is characterised by a speed v_i. Following previous works (Aoki, 1982; Cornejo-Donoso et al., 2017; Huth and Wissel, 1992), the direction of movement is simulated by using three sensory zones around the fish, they are: repulsion zone (with radius r_r), parallel-orientation zone (with radius r_o), and attraction zone (with radius r_a), Fig. 2. The repulsion zone reflects the fact that fishes in a school generally do not collide. Probability distribution analysis shows that the nearest neighbour fishes in a school never come closer than a certain minimum distance. If a neighbour fish comes too close to other fishes, the neighbour fish tries to avoid a collision by moving away from the other fishes. In our model, this is implemented by finding the midpoint of all neighbouring fish agents within the repulsion zone, computing the direction to go towards that midpoint, and taking the opposite direction (i.e. away from the midpoint). The parallel-orientation zone reflects the fact that fishes in a school also maintain a preferred distance from its neighbour fishes. In our model, this is implemented by changing the direction of a fish in order to match its average direction to that of all other fishes found within the parallel-orientation zone. The attraction zone makes fishes swimming towards a school. This is implemented by computing the midpoint of all the fishes found within the attraction zone and changing the direction of a nearby fish towards that midpoint.

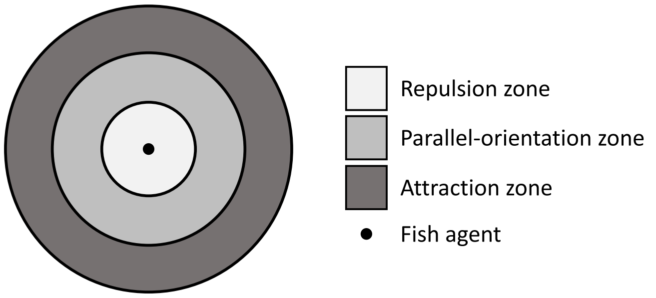


Fig. 2. Sensory zones of our fish agents. To avoid collisions, a fish swims away from fishes located within its repulsion zone (radius r_r). A fish aligns to swim in the same direction of fishes located within its parallel-orientation zone (radius r_o). Finally, a fish heads towards fishes located within its attraction zone (radius r_a), thus forming aggregations.

Following Cornejo-Donoso et al. (2017), the position of fish agent i at time $t + \Delta t$ is calculated as

$$\underbrace{q_i(t+\Delta t)}_{\text{new position}} = \overbrace{q_i(t)}^{\substack{\text{previous}\\ \text{position}}} + \underbrace{v_i(t+\Delta t)}_{\text{speed}} \cdot \overbrace{\begin{pmatrix} cos(\phi_i(t+\Delta t)) \\ sin(\phi_i(t+\Delta t)) \end{pmatrix}}^{\text{directional angle}} \cdot \underbrace{\Delta t}_{\text{time step}}, \quad (2)$$

where $q_i(t) = (x_i(t), y_i(t))^T$ is the vector indicating the position of a fish agent at time t, v_i is the speed, and ϕ_i is the direction. Fish offspring are initially located in the position of the parents.

2.3. *Characteristics of fishing agents*

In our model, a single fishing agent is represented by a single pirogue (or boat). The model simulates a fixed number of pirogues (P=20), which are randomly distributed over the virtual fishing ground at time t=0. Each pirogue is characterised by a cooperative trait value (over a scale of five values) and a corresponding fishing effort (Fig. 3A). The relationship between cooperation and effort is based on previous works (Akpalu, 2008; Clark, 1973; Kramer, 1986; Roch and Samuelson, 1997) and reflects the fact that a high preference for immediate gain (here

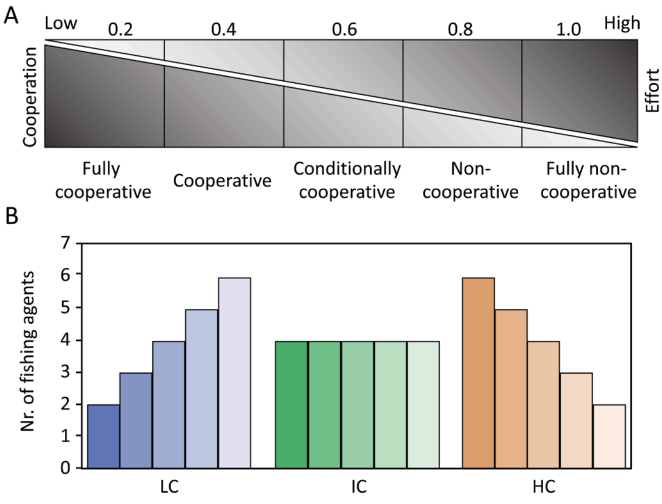


Fig. 3. Attributes of cooperation and fishing effort considered in our model (A). Fully cooperative pirogues are characterised by the lowest fishing effort, whereas fully non-cooperative pirogues are characterised by the highest fishing effort. Three cases are considered (B): (1) the low cooperation (LC) case in which 10 % of the pirogues are fully cooperative, 15 % are cooperative, 20 % are conditionally cooperative, 25 % are non-cooperative, and 30 % are fully non-cooperative; (2) the intermediate cooperation (IC) case in which fully cooperative, cooperative, conditionally cooperative, non-cooperative, and fully non-cooperative account each for 20 % of the total; and (3) the high cooperation (HC) case, in which fully cooperative, cooperative, conditionally cooperative, non-cooperative, and fully non-cooperative pirogues are, respectively, 30 %, 25 %, 20 %, 15 %, and 10 % of the total.

intended as low cooperative behaviour) is associated with a high fishing effort, whereas a low preference for immediate gain (here intended as high cooperative behaviour) is associated with a low fishing effort. These high or low preferences for immediate gain are called intertemporal choices as they involve trade-offs between costs and benefits occurring at different times. Intertemporal choices are importat and ubiquitous, both among humans and animals, and constitute a fundamental concept in economics, also known as discounting (Dasgupta and Maskin, 2005; Frederick et al., 2002). Our own work suggested that, by giving more weight to the future productivity of the resource, a lower discount rate among resource users (corresponding to a lower effort) relates to higher cooperation, to more sustainable use of the resource, and to higher harvest on the long-term (Brandt and Merico, 2013; Brandt et al., 2012). In contrast, a higher discount rate (corresponding to higher effort) relates to lower cooperation, to lower harvest on the long-term, and even to a collapse of the user-resource system (Brandt and Merico, 2013; Brandt et al., 2012).

Following these arguments, we designed three main types of pirogues characterised by different and fixed cooperative levels: fully cooperative (lowest fishing effort), intermediate cooperative (intermediet fishing effort), and fully non-cooperative (highest fishing effort). These three different cooperative types are assembled according to five cooperative trait values (Fig. 3B). They are: 1) the low cooperation (LC) case, in which fully cooperative, cooperative, conditionally cooperative, non-cooperative, and fully non-cooperative pirogues are, respectively, 10 %, 15 %, 20 %, 25 %, and 30 % of the total; 2) the intermediate cooperation (IC) case, in which fully cooperative, cooperative, conditionally cooperative, non-cooperative, and fully non-cooperative pirogues are equally distributed, each accounting for 20 % of the total; and 3) the high cooperation (HC) case, in which fully cooperative, cooperative, conditionally cooperative, non-cooperative, and fully non-cooperative pirogues are, respectively, 30 %, 25 %, 20 %, 15 %, and 10 % of the total. Although agents are characterised by fixed cooperation traits, this particular cooperation design leads to a trade-off, whereby high fishing effort (i.e. low cooperation) creates immediate and abundant harvest but at a cost of rapid resource depletion; and low fishing effort (i.e. high cooperation) has an immediate cost of reduced harvest but with the benefit of keeping the resource at sustainable levels, in accordance to discounting principles (Brandt and Merico, 2013; Brandt et al., 2012).

The harvest rate of a pirogue is formulated according to the Schaefer's model (Clark, 2010; Schaefer, 1954):

$$H(n') = q \cdot E_k \cdot n' , \tag{3}$$

where q is the catchability coefficient (in pirogue^{-1} time^{-1}), n' is the number of fishes in a fixed neighbourhood, and E_k is the fishing effort, ranging from 0.2 (for low effort) to 1.0 (for high effort) and associated to a specific cooperative trait value (Fig. 3A). The catchability coefficient is the same for all pirogues and specifies the efficiency of the fishery (Arreguín-Sánchez, 1996). A pirogue can only harvest the fishes present in the neighbourhood (with radius r_n), reflecting the area covered by the fishing net.

According to Huff et al. (2015), Agrawal et al. (2013), and Little and McDonald (2007), sharing information is a relevant factor in resource harvest decisions. In our model, movement decisions are influenced by the information on fish catch that a pirogue shares with other neighbouring pirogues. This is implemented by making the pirogue moving towards the direction of a neighbouring pirogue exhibiting a greatest catch. If no such pirogue is present in the neighbourhood, then the pirogue moves in a random direction and for a distance of 0.3 unit length. This assumption is roughly consistent with activities in small-scale fishery, where fishermen of different pirogues may know each other or may even be relatives and can thus exchange information (for example, via radio or mobile telephone) on various aspects, including weather conditions, situations of distress, and catches.

Following Cornejo-Donoso et al. (2017), the change in the position of a pirogue j is updated as follows:

$$\underbrace{p_j(t+\Delta t)}_{\text{new position}} = \overbrace{p_j(t)}^{\substack{\text{previous}\\ \text{position}}} + \underbrace{v_j(t+\Delta t)}_{\text{speed}} \cdot \overbrace{\begin{pmatrix} cos(\phi_j(t+\Delta t)) \\ sin(\phi_j(t+\Delta t)) \end{pmatrix}}^{\text{directional angle}} \cdot \underbrace{\Delta t}_{\text{time step}} , \tag{4}$$

where $p_j(t) = (x_j(t), y_j(t))^T$ is the vector indicating the previous position, v_j is speed of the pirogue, and ϕ_j is the direction of the pirogue pointing, as explained above, towards the pirogue exhibiting the highest catch or to a random direction and for a distance of 0.3 unit length if no pirogues are present in the neighbourhood. Fishing within the marine protected areas is prohibited and pirogues are forced to comply with this regulation, thus cheating is not considered in our experiments.

2.4. Handling of events and time

For the sake of generality, time is treated in abstract terms. A single model time step is thus one unit of time. The flow diagram in Supporting Information Fig. S1 illustrates the events that occur over a single time step. Initially, all agents (fishes and pirogues) are randomly distributed over the fishing ground. In each time step: 1) fishes are randomly picked and allowed to reproduce with a certain probability and to move to a new position, and 2) pirogues are randomly picked and allowed to harvest and to move to a different position. Since the number of fishes varies over time while the number of pirogues remains fixed, the state of our system (number of fishes and pirogues) is updated in an asynchronous manner (Caron-Lormier et al., 2008; Cornforth et al., 2005). We thus assume that in each asynchronous updating, $1/(n+P)$ of a time step passes by, where $n+P$ is the total number of agents (fishes and pirogues) at the time of updating. With this method, each agent (whether fish or pirogue) is updated once, on average, in each time step.

The full list of model parameters is given in Table 1.

2.5. Numerical experiments

For each simulation, the model runs over a spin-up phase of 50 time steps to allow the system to reach an equilibrium. This is followed by a second phase of 100 time steps, which we consider for our analysis.

We examined the impacts of establishing a single MPA on fish abundance and catch. We considered three cases of cooperation levels (low, intermediate, and high) and two fish ground management configurations (with and without MPA), see Model description for details on how cooperation is operationalised in the model. For these numerical experiments, we considered an MPA that covers 15 % of the fishing ground. In total, we tested six combinations, i.e. the two management configurations for each of the three cooperation cases and, to account for the stochastic nature of the ABM model, we run four replicate simulations for each of the six combinations, for a total of 24 runs.

We also investigated the separate impacts of MPA size, MPA age, and distance between two MPAs on fish abundance and catch. For these investigations, we considered three scenarios. In the first scenario, we increased the size of a single MPA from 10 % to 80 % of total fishing area in steps of 10 % while keeping the age fixed to 100 time steps. In the second scenario, we increased the distance between two MPAs from 0.1 to 0.8 in steps of 0.1 while fixing the total size of the two MPAs to 15 % of the total fishing ground and the age to 100 time steps. In the third scenario, we increased the age of a single MPA (which size was fixed to 15 % of total fishing ground) from 10 to 80 time steps in steps of 10. We run 4 replicate simulations for each of the 8 levels of each simulation scenario (i.e. 4 replicates for each of the 24 cases). Furthermore, we investigated the combined impacts of MPA size (10 %, 25 %, and 40 % of total fishing area), age (25, 50, and 75 time steps), and distance between two MPAs (0, 0.2, and 0.4) on fish abundance and catch (the design of these experiments is shown in Supporting Information Fig. S2).

Finally, our model simulations are run under an overexploitation regime, reflected by a relatively high catchability coefficient q (which is set to 60 % of the number of fishes present in the neighbourhood radius r_n, Table 1), because otherwise there will not be any need for considering fishing ground management strategies. However, the implications of this choice on the model results are investigated with additional simulations reflecting decreasing levels of exploitation (i.e. with decreasing catchability values).

2.6. Sensitivity analysis

Given the uncertainties involved in the parameterisation of this idealised model application (see Table 1), we assessed the sensitivity of our model results to changes in parameter values. The model configuration for the sensitivity analysis is as follows: two MPAs covering 25 % of the total fishing ground, placed at a distance of 0.2, and with an age of 100 time steps. Standard parameter values are changed, independently, one by one, by ±50 % (see Table 1). The sensitivity of the model is analysed by comparing the results (averages of four replicates and over time of fish abundance and catch) obtained with standard parameter values with those obtained with changed parameter values using the following sensitivity index:

$$S = \frac{X^{'}(p^{'}) - X(p)}{X(p)} \cdot 100\,, \qquad (5)$$

where $X(p)$ is the average result obtained with the standard parameter value p and $X^{'}(p^{'})$ is the average result obtained with the changed parameter value $p^{'} = p \pm 50\,\%$.

In addition, since our results are obtained on the base of four replicate simulations for each combination of fishing ground managment configuration and cooperation level, we run simulations with an increasing number of replicates (4, 8, 16, and 32, respectively) for the case of different cooperation levels in combination with presence and absence of single MPA (covering 15 % of the fishing ground and an age of 100 time units), to investigate if the number of replicates has an effect on the model results.

3. Results

3.1. Effects of cooperation levels with and without an MPA

The first round of experiments aimed at investigating the impacts that different levels of cooperation (low, intermediate, and high) and presence or absence of single MPA have on fish abundance and catch. We observed that with an MPA fish abundance and catch are higher under all cooperation levels than without an MPA (Fig. 4). Similarly, an increasing level of cooperation leads to higher fish abundance and catch (Fig. 4). The biggest difference is observed between treatments with the presence of an MPA and high cooperation levels and with the absence of an MPA and low cooperation levels (Fig. 4).

Our results also show that the case of high cooperation without MPA leads, on average, to the same fish abundance and catch as the case of intermediate cooperation with MPA (Fig. 4). Similarly, intermediate cooperation without MPA leads to same fish abundance and catch as the case of low cooperation with MPA (Fig. 4). These results reflect our specific assumptions and are consistent with the trade-off we considered between cooperation and fishing effort. This trade-off results in a form of cooperation that is more effective than no-take zones in keeping fish abundance and catch at sustainable levels. We note here that the incentive of fishermen to maximise short-term profits under the open-access regime may be driven by the fact that this regime and the associated negative externalities give fishermen less control over the future of the stock rather than by the possibility that fishermen care less about the future of the stock.

3.2. Individual effects of cooperation levels and different characteristics of MPAs

Increasing the size of a single MPA, with age fixed to 100 time step, produced a significant increase in fish abundance regardless of cooperation levels (Fig. 5A). However, increasing the size of a single MPA produced a significant increase in catch until the MPA size reached approximately 60 % of total fishing area, beyond which catch began to

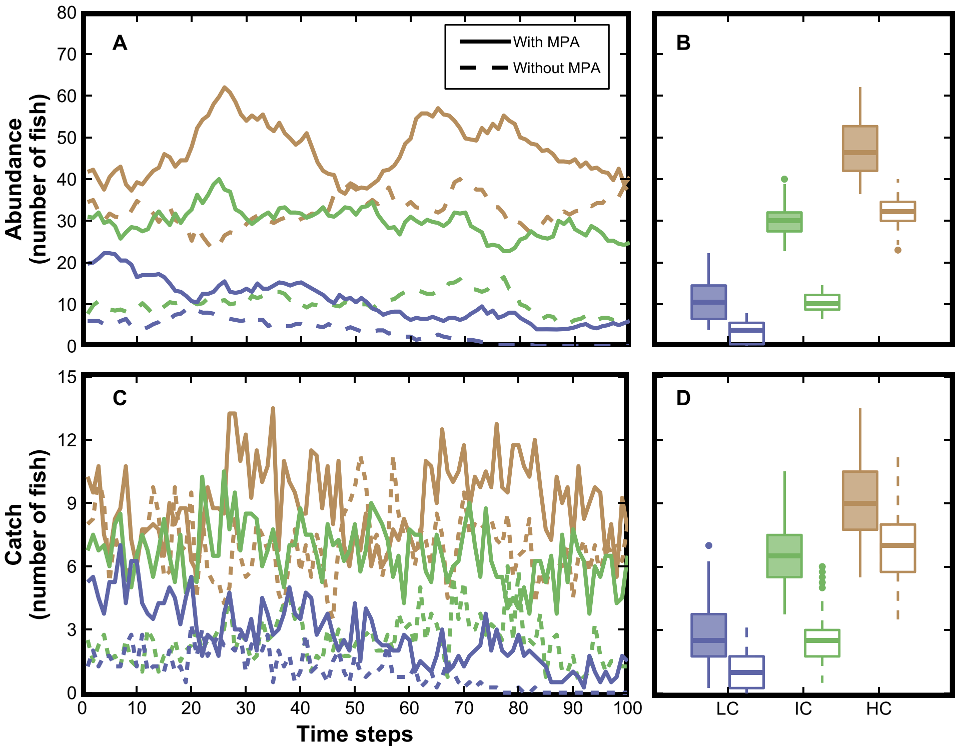


Fig. 4. Temporal dynamics of fish abundance (**A**) and catch (**C**) resulting from different cooperation levels and presence or absence of a single MPA. Each line (**A, C**) is an average of four replicate simulations for the different levels of cooperation (LC, IC, and HC for, respectively, low, intermediate, and high cooperation). The boxplots show the variability of the four replicates for abundance (**B**) and catch (**D**). Dashed whiskers and empty boxes represent simulations without MPA; solid whiskers and filled boxes represent simulations with MPA.

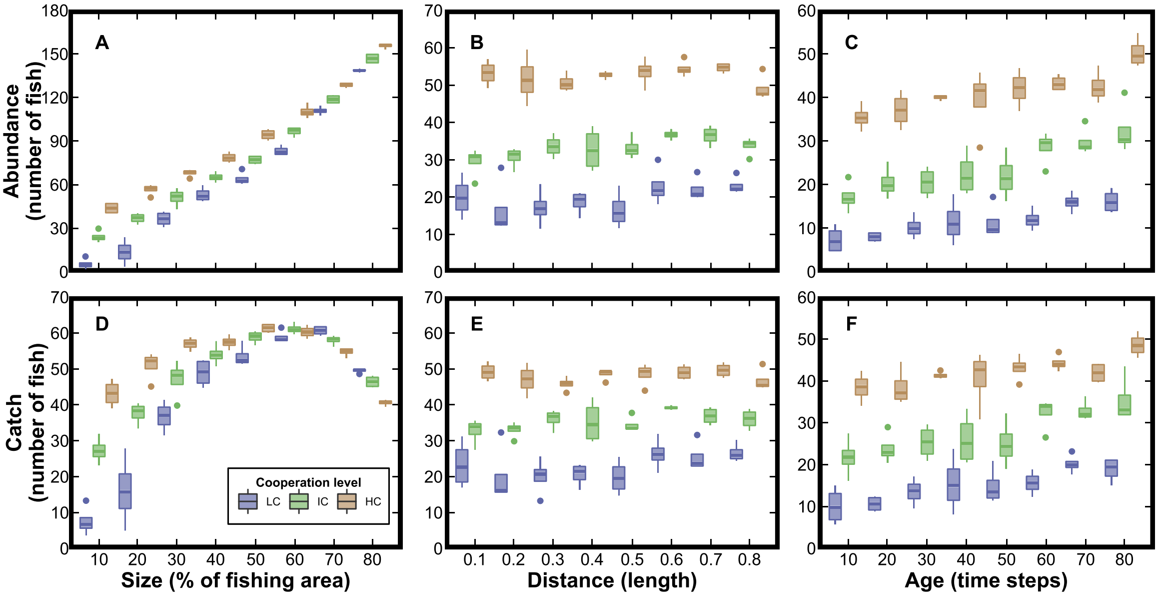


Fig. 5. Fish abundance (**A, B, C**) and catch (**D, E, F**,) for increasing size of a single MPA (with age fixed to 100 time steps), increasing distance between two MPAs (for a total size of 15 % of total fishing area, i.e. 7.5 % for each MPA and both with age fixed to 100 time steps), and increasing age of a single MPA (with size fixed to 15 % of total fishing area) and at different levels of cooperation (LC = low cooperation, IC = intermediate cooperation and HC = high cooperation). The boxplots show the variability of four replicate simulations.

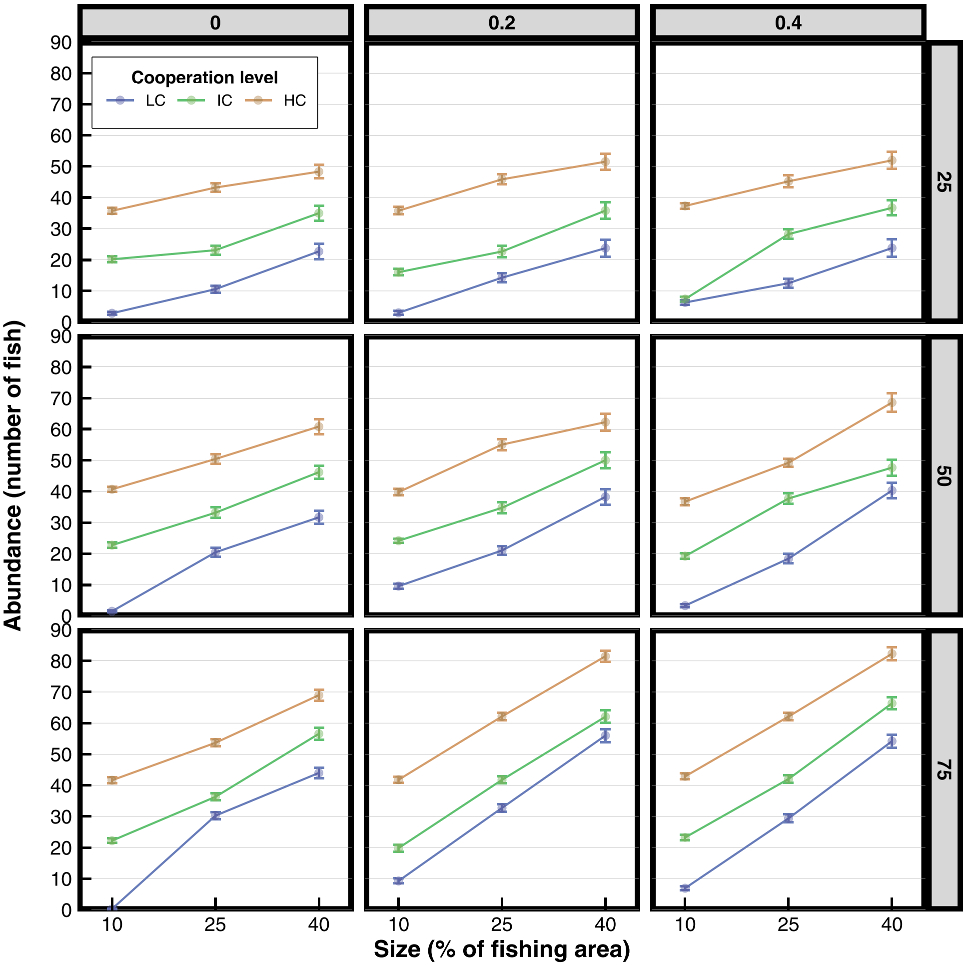


Fig. 6. Fish abundance for varying (1) size of a single MPA, (2) distance between two MPAs (columns), and (3) age of a single MPA (rows), and at different cooperation levels. Each treatment of size, distance, and age (i.e. each panel), corresponds to a set of 9 runs, each run replicated 4 times, for a total of 324 runs. The experimental design with the corresponding sets of 9 runs per treatment is illustrated in Supporting Information Fig. S2.

decline (Fig. 5D).

We found a non-significant change in both fish abundance (Fig. 5B) and fish catch, at all cooperation levels (Fig. 5E), when the distance between two MPAs (with a fixed total MPA size of 15 % of total fishing area and fixed ages of 100 time steps) is increased. Increasing the age of a single MPA of fixed size (15 % of total fishing area) produced a slight increase in both fish abundance (Fig. 5C) and catch (Fig. 5F).

3.3. Combined effects of cooperation levels and different characteristics of MPAs

Increasing the size of a single MPA produced positive effects on fish abundance (Fig. 6) and catch (Fig. 7) under all cooperation levels. Similarly, increasing the age of a single MPA produced positive effects on fish abundance (Fig. 6) and catch (Fig. 7) under all cooperation levels. In contrast, increasing the distance between two MPAs had almost no effects on fish abundance (Fig. 6) and catch (Fig. 7) under all cooperation levels.

In summary, the size of a single MPA and the time elapsed since its establishment have stronger impacts on abundance and catch than the distance between two MPAs, regardless of the cooperation level.

3.4. Effects of different exploitation regimes

As explained at the end of subsection 2.5, our model investigations are conducted under an overexploitation regime. Under the most positive scenario (high cooperation with a single MPA), fish abundance oscillates around 45 individuals (Fig. 4), representing a fish population that is approximately 75 % smaller than the carrying capacity (which is set to 200 fishes). This overfishing regime produces results (in all experiments, fish abundances are higher with MPAs than without, Fig. 4) that are consistent with the general understanding of MPAs (Gerber et al., 2003; Guénette et al., 1998). Relaxing the fishing pressure, i.e. decreasing the catchability coefficient q, produces fish abundances increasingly closer to the carrying capacity (Fig. 8A). Reduced catchabilities increase catches overall (Fig. 8B), because of the higher fish abundances resulting from the less aggressive fishing regimes. In addition, the presence of an MPA does not produce beneficial effects on catches when the fishery is underexploited (i.e. at catchabilities below 0.3). Therefore, the model is able to reproduce a key feature in MPA theory (Halpern, 2003; Lester et al., 2009) whereby the presence of no-take fishery reserves do not enhance catches unless the system is overfished.

3.5. Results of sensitivity analysis

We examined the sensitivity of fish abundance and catch to changes in parameters values under the different cooperation levels using the sensitivity index reported in equation 5. For all cooperation levels (Fig. 9), increasing the initial number of pirogues (P), neighbourhood radius for pirogues (r_n), catchability coefficient (q), and speed of fishes (v_i) produced a decrease in fish abundance and catch. In contrast,

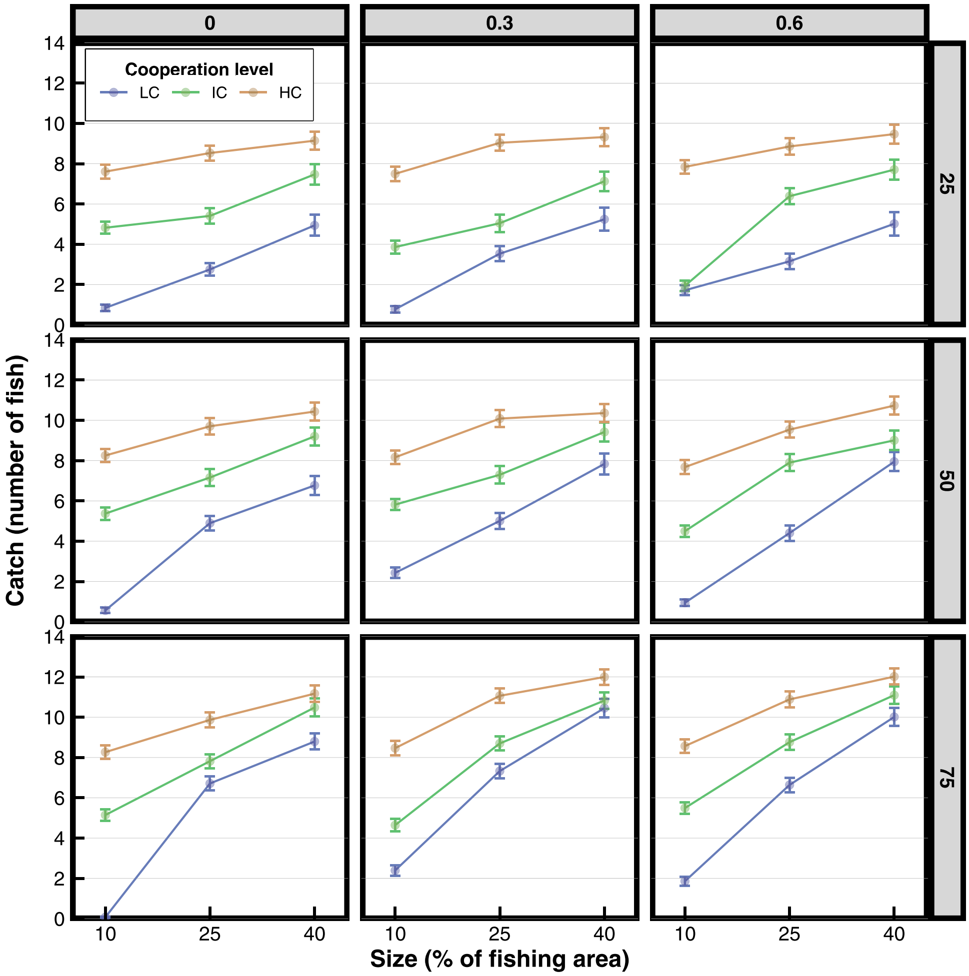


Fig. 7. Fish catch for varying (1) size of a single MPA, (2) distance between two MPAs (columns), and (3) age of a single MPA (rows), and at different cooperation levels. Each treatment of size, distance, and age (i.e. each panel), corresponds to a set of 9 runs, each run replicated 4 times, for a total of 324 runs. The experimental design with the corresponding sets of 9 runs per treatment is illustrated in Supporting Information Fig. S2.

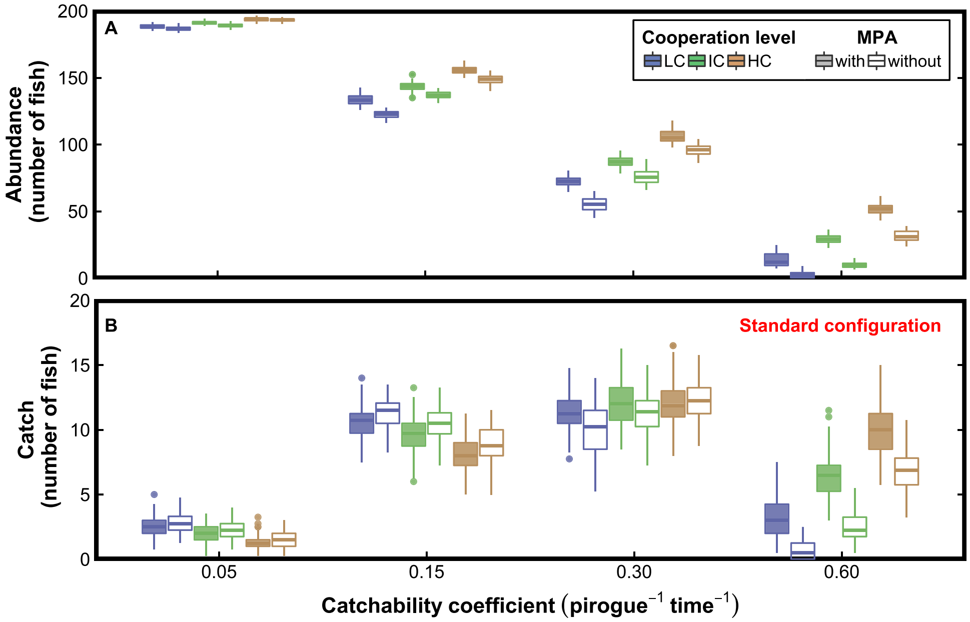


Fig. 8. Fish abundances (A) and catches (B) under different exploitation regimes characterised by increasing catchability. Results obtained with the standard model configuration (overfishing regime) are those corresponding to a catchability coefficient q equal to 0.6 pirogue^{-1} time^{-1}.

increasing the intrinsic growth rate of fishes (g_{max}) and carrying capacity (K) resulted in an increase in fish abundance and fish catch. Increasing or decreasing the speed of the pirogues (v_j) produced a positive change in abundance and catch. In general, the sensitivity of the model becomes less pronounced when moving from low cooperation (Fig. 9A,D) to intermediate (Fig. 9B,E) and high cooperation (Fig. 9C,F). Parameters that show a fairly consistent high impact over the different cooperation levels are catchability (q), intrinsic growth rate of fishes (g_{max}), and number of pirogues (P). This implies that such parameters have to be carefully quantified or evaluated when the model is applied to real fisheries. In addition, since fish abundance and catch respond quite sensitively to catchability, this parameter can be used effectively for management purposes.

Another important parameter in our model is the initial number of fishes (N). For the purpose of demonstrating the capabilities of the model in reproducing qualitatively different results under varying MPA characteristics and cooperative scenarios, we used 200 fishes as initial standard condition (with a corresponding carrying capacity of 200 fishes) because this number allowed us to perform many different experiments over a reasonable amount of time. We therefore explored the sensitivity of the model results to different initial number of fishes (and corresponding carrying capacities, which are set equal to the initial number of fishes) and for each case we provide the required computing time (Fig. 10).

This analysis shows that the model results are qualitatively the same for different numbers of initial fishes (and corresponding carrying capacities). Specifically, for all initial conditions, the presence of an MPA produces higher fish abundance and catch under all cooperation levels compared to when an MPA is absent. Also, for all initial conditions, higher cooperation levels produce higher fish abundance and catch with

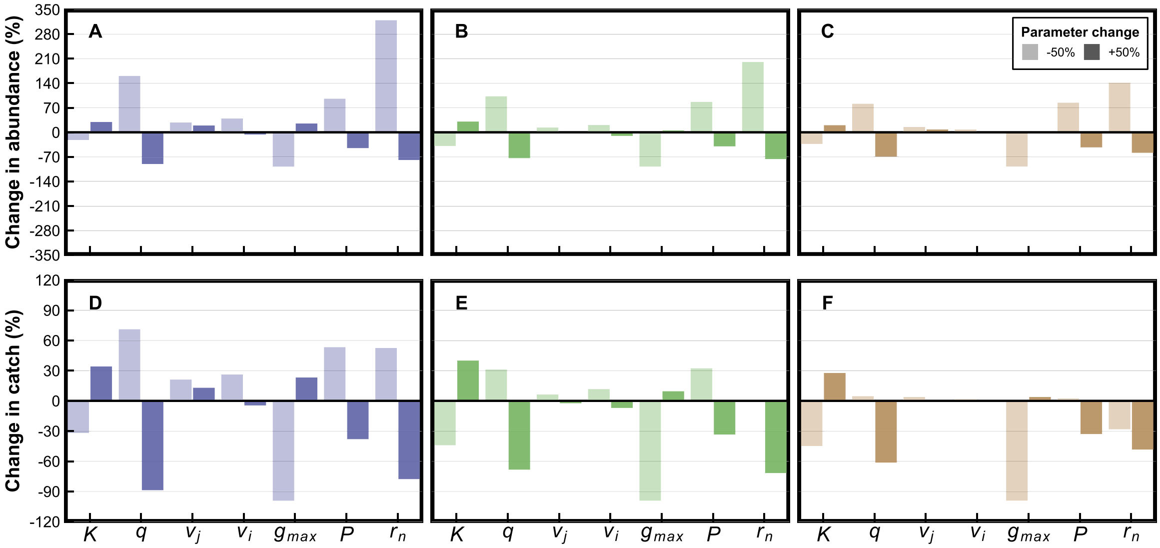


Fig. 9. Sensitivity of abundance (**A, B, C**) and catch (**D, E, F**) under different cooperation levels (blue = low cooperation, green = intermediate cooperation, and orange = high cooperation) and for two MPAs covering a total of 25 % of fishing area, placed at a distance of 0.3 from one another, and each with an age of 100 time steps. The height of the bars indicates deviations from the results obtained with standard parameter values (as in Table 1).

Table 1
List of parameters used in the model. For the sake of generality, the units of the model are defined in abstract terms so that distances are expressed in ’length’, which are fractions of the square root of 2 (2 being the area of the idealised fishing ground) and time is expressed in model time steps. The specific values of the parameters are chosen to be adaptable to a real-case scenario and according to consistency arguments. All parameters related to length (speeds of agents and radii of interaction) are scaled to the size of the fishing ground in a way that is consistent with a small-scale fishery typical of West Africa. For example, the speed of the simulated pirogue is 0.3 length · time^{-1}. Since the fishing ground is set to a size of 2 length^2, it follows that the virtual pirogue can cover about 21 % of a linear distance on the fishing ground (assuming a squared ground) in a model time step. Pirogues of small-scale fisheries operate at an average speed of about 72 km · day^{-1} (Metcalfe et al., 2017). If we considered a fishing ground of 158000 km^2, corresponding to the Exclusive Economic Zone of Senegal (Pauly and Zeller, 2016), then a real pirogue could cover about 18 % of a linear distance of this area in a day time, comparably to our idealised parameter setting. Analogous arguments are applied to deduce the other parameter values.

Symbol	Description	Standard value	Unit
Characteristics of fish agents			
N	initial number of fish agents	200	nr of individuals
g_{max}	maximum intrinsic growth rate	0.26	time^{-1}
v_i	speed of fish	0.2	length · time^{-1}
r_r	radius of repulsion zone	0.025	length
r_o	radius of orientation zone	0.06	length
r_a	radius of attraction zone	0.1	length
Characteristics of fishing agents			
P	total number of fishing agents	20	nr of pirogues
v_j	speed of a pirogue	0.3	length · time^{-1}
r_n	neighbourhood radius	0.2	length
q	catchability coefficient	0.6	pirogue^{-1} · time^{-1}
Fishing environment			
K	carrying capacity of fishing ground	200	nr of individuals
A	size of fishing ground	2	length^2

and without the MPA.

Our results are obtained on the base of four replicate simulations for each combination of fishing ground managment configuration and cooperation level. Simulations with combinations of different cooperation levels and presence and absence of a single MPA obtained with increasing number of replicates show that model results are very robust with respect to number of replicates (Fig. 11).

4. Discussion

MPAs have been promoted as a tool to preserve fish stocks, to safeguard biodiversity, and to secure other vital ecosystem services (Balmford et al., 2004; Mellin et al., 2016; Rodrigues et al., 2004). Their effectiveness in achieving ecological and societal objectives, however, has provoked debates in scientific and conservation circles (Bennett and Dearden, 2014; Chaigneau and Brown, 2016; Gerber et al., 2011; Pendleton et al., 2018). There is also a divide between those who argue in favour of no-take reserves and those who promote sustainable fishing through forms of participation and cooperation among resource users (Fulton et al., 2012). Mathematical models can help in the design of no-take reserves by integrating a diverse array of relevant scientific information into a common framework and by providing insights into the alternative scenarios that could emerge under different MPA configurations and human cooperation strategies (Fulton et al., 2015). Using an Agent-Based Model that captures the characteristics of a small-scale fishery in broad terms, we investigated here the combined effects of fishing behaviours (reflected by levels of cooperation associated to fishing efforts) and different features of MPA design (including presence or absence of MPA, size, age, and distance between two MPAs) on fish abundance and catch under an overfishing regime.

In agreement with the views that an MPA can effectively maintain fish stocks to sustainable levels (Gell and Roberts, 2003; Micheli et al., 2004; Russ et al., 2008), the results of our simulations show that the presence of an MPA would produce higher levels of fish abundance and catch compared to the case in which the MPA is absent (Fig. 4). However, our model also suggests that human cooperation, expressed in terms of fishing effort, whereby low effort reflects high cooperation and high effort reflects low cooperation, is an important determinant of fish

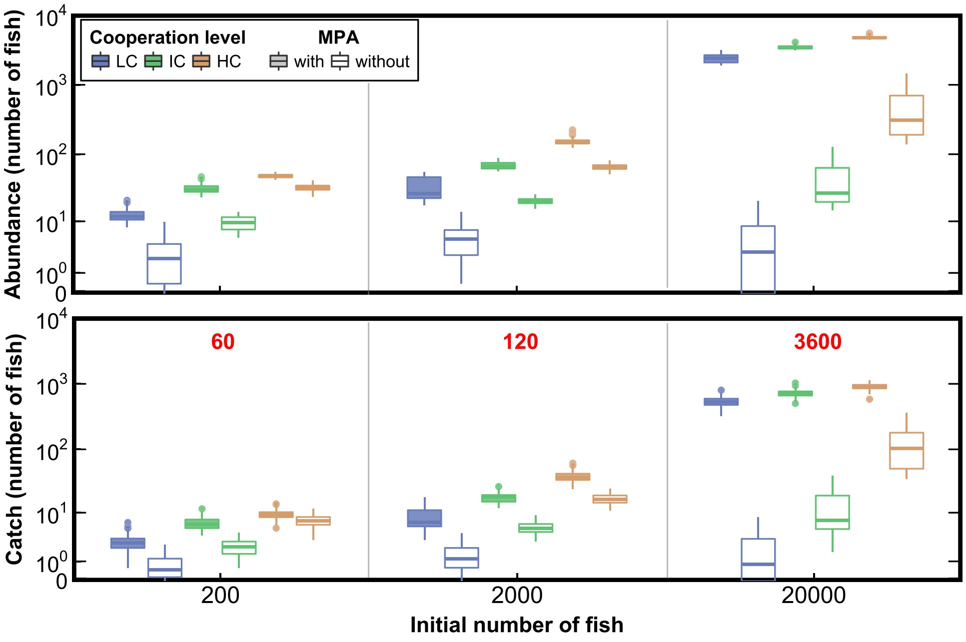


Fig. 10. Sensitivity of fish abundance and catch to increasing number of initial fish agents (N) and corresponding carrying capacities. The numbers in red indicates the approximate computing time (in minutes) required to generate the results for producing each set of 6 boxplots (24 simulations per set). Computing times are relative to a computer system with the following characteristics: macOS with 2.8 GHz Intel Core i7 processor and 16 GB 1600 MHz DDR3 memory.

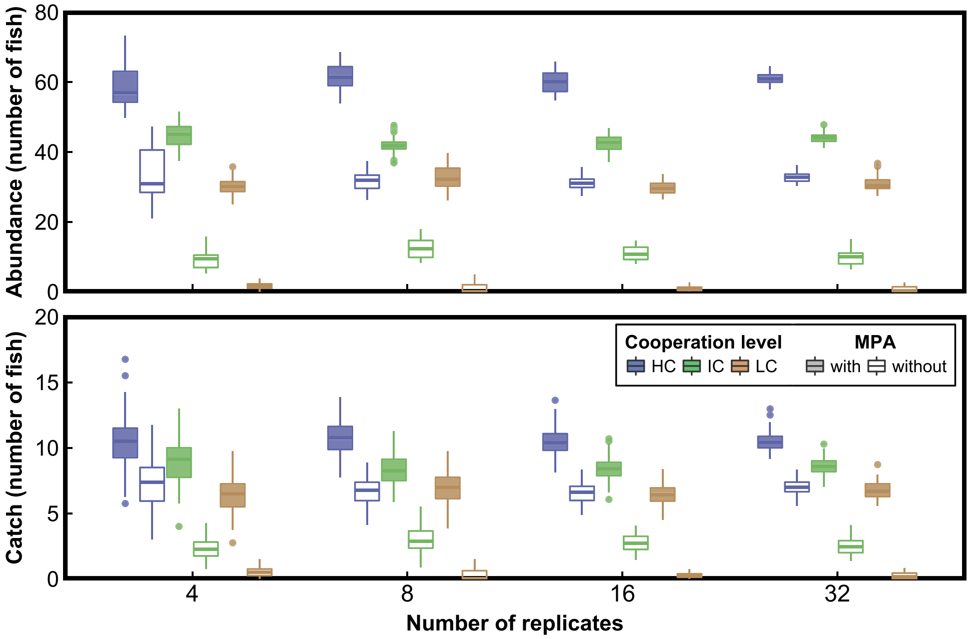


Fig. 11. Sensitivity of fish abundance and catch to increasing number of replicates for three cooperation levels in combination with presence and absence of a sinlge MPA covering 15 % of the fishing ground and with an age of 100 units of time.

abundance and catch. More specifically, we find that high cooperation, i.e. when the distribution of different cooperative attributes peaks towards fully cooperative pirogues (Fig. 3), in the absence of an MPA can sustain levels of fish abundance and catch equivalent to those produced under intermediate cooperation, i.e. when the different cooperative attributes are homogeneously distributed among the pirogues (Fig. 3), and in the presence of an MPA (Fig. 4). Similarly, intermediate cooperation and in the absence of an MPA is as effective as low cooperation, i.e. when the distribution of different cooperative attributes peaks towards fully non-cooperative pirogues (Fig. 3), and in the presence of an MPA (Fig. 4). These findings support the concerns raised by earlier studies showing that advantages derived from MPAs are outweighed by those obtained with effort reduction (Steele and Beet, 2003) or that the effectiveness of no-take reserves is reduced without additional measures of restraining fishing efforts outside the reserve (Hannesson, 1998). Given the relatively high mobility of our fishes, which cover 10 % of the fishing ground at each time step, these results imply that the advantages in the absence of an MPA and under high cooperation may not be limited to sedentary species, as thought in the past (e.g. Hastings, 1999).

The size of an MPA is another debated issue, with some suggesting that the effects of an MPA on fish stocks is independent of its size (Côté et al., 2001; Guidetti and Sala, 2007; Halpern, 2003) and others sustaining that a large MPA performs better than small ones (e.g. Claudet et al., 2008). However, many studies seem to agree on the fact that an MPA should cover between 20 and 40 % of a fishing ground, because a reserve smaller than 20 % would bring no benefits and a reserve larger than 40 % would prevent fish larvae to reach areas outside the reserve thus making fishery goals unachievable (Bohnsack, 1990; Cornejo-Donoso et al., 2017; Gell and Roberts, 2003; Roberts, 2000). We found that an MPA covering around half of the fishing ground would achieve both goals of maintaining fish abundance (Fig. 5A) and ensure highest fish catches (Fig. 5D), although this result may be fishery-specific and in this first, abstract version of the model fish agents are not characterised by different life stages. Increasing the MPA size well beyond half of the fishing ground further increases the fish stock (Fig. 5A) but this comes at the cost of reduced catches (Fig. 5D). Past studies suggested that the size of an MPA should be constrained by the scale of fish movement (Botsford et al., 2003; Gaines et al., 2010; Gell and Roberts, 2003; Polacheck, 1990). This is because highly mobile fishes would frequently move across the boundaries of the reserve into the fished areas, an effect called spill-over (Rowley, 1994). Our sensitivity analysis showed lower fish abundance and catch when the speed of fishes is increased by 50 % and higher fish abundance and catch when the speed of fishes is decreased by 50 %, although both these effects are offset by high cooperation (Fig. 9). We found no differences between a single, large MPA and two interspaced MPAs, regardless of their distance (Fig. 5B,E). Increasing the distance between two MPAs had almost no effects on fish abundance (Fig. 6) and catch (Fig. 7) under all cooperation levels. Fish agents in our model are characterised by only two properties: the maximum intrinsic growth rate and the speed with which they move. Therefore, this result suggests that both these properties do not have an impact on fish biomass and catch when the distance between two MPAs is varied. This numerical experiment can provide relevant insights in a more sophisticated version of the model, for example in one that includes life history traits of fish, such as those related to larval dispersal or to differential fish movements when a distinction is introduced between juveniles and adults.

The age of the reserve can have a variety of effects ranging from no impacts on fish abundances (Côté et al., 2001; Mosquera et al., 2000), to slow recovery of fish abundances after the establishment of an MPA (Claudet et al., 2006; Guidetti and Sala, 2007; Molloy et al., 2009; Russ et al., 2005), and to fast recovery of fish abundances soon after the establishment of an MPA (Halpern and Warner, 2002). The time period to restore abundance levels after the establishment of an MPA depends on the biological characteristics of the fish species involved (Claudet et al., 2008; Vandeperre et al., 2011). Our simulations showed only a slight increase in fish abundance and catch when the age of the MPA is increased (Fig. 5C,F), although (as mentioned in the previous paragraph) this first version of the model does not characterise fish agents with life-history traits, which could influence the results. We also found that, under low cooperation, a longer period of closure is required to attain the same levels of fish abundance and fish catch reached under intermediate or high cooperation levels (Fig. 5C,F).

There are, of course, limitations about the relevance of simple models to complex ecological and socioeconomic issues. Our ABM represents an initial, minimal treatment of the problems associated to ecosystem management and human behaviour and, as such, it has to be intended as a proof-of-concept. The flexibility offered by this type of models, however, allows for continuing developments and implementations (Bonabeau, 2002). For example, more agents can be added or the complexity of the agents can be increased in terms of behaviour and rules of interactions. Avenues of future development include a dynamic and flexible treatment of cooperation (instead of the static form of cooperation adopted in this first version) and the implementation of multiple fish species with different behavioural attributes and life-history traits. A dynamic and flexible treatment of cooperation has the potential to produce valuable insights, which may not be easily anticipated. For example, a treatment of cooperation based on heuristics, whereby individuals adaptively and independently choose their cooperation level dynamically and based on experience, optimisation, or rule of thumbs (Bookstaber, 2017; Gigerenzer and Brighton, 2009; Gigerenzer and Gaissmaier, 2011), can allow non-ergodic dynamics, as typically experienced in real fisheries (Burgess et al., 2020), to emerge. Distinguishing between mobile and sedentary fish and subdividing fish agents according to their commercial value (Di Lorenzo et al., 2016), for example, would allow to (1) test the spill-over effect in specific locations and (2) assess the proportion of fish biomass that is fished around MPAs. Complexity can be also added to fishing agents to investigate in more detail cooperative self-governance, which can be achieved with a variety of mechanisms (Ostrom, 1990), including monitoring, sanctioning, and reciprocity. Rule compliance, which can be implemented as a function of fishing effort, is often an important limitation to the success of MPAs (Rife et al., 2013) and represents, therefore, another interesting line of model development and research. Finally, considering a large number of agents can be extremely computation intensive. Our sensitivity runs with 20,000 fish agents, for example, required 2.5 days (3600 minutes) of computation on a relatively fast computer. Several solutions, whether technological or mathematical, can be adopted when facing a large number of agents. One that we plan to implement in the future is based on the so-called super-individual approach (Scheffer et al., 1995), which can reduce computation time dramatically but it requires a careful consideration of individual variability (Parry and Evans, 2008).

In conclusion, the success of an MPA entails a case-by-case understanding of the spatial structure of impacted fisheries, ecosystems, and human communities (Hilborn et al., 2004). Marine reserves, together with other management tools, including forms of participation and cooperation among resource users, can help maintain fish stocks to sustainable levels and, at the same time, achieve fishery objectives. When appropriately adapted to a particular system (for example, by adopting a realistic, fishery-specific parameterisation), our model can constitute a valuable addition to the suit of tools currently available for evaluating the impact of different resource management strategies.

CRediT authorship contribution statement

Kwabena A. Owusu: Conceptualization, Methodology, Software, Formal analysis, Investigation, Writing - review & editing. **Esteban Acevedo-Trejos:** Software, Formal analysis, Validation, Writing - review & editing. **Mouhamed M. Fall:** Methodology, Validation, Writing - review & editing, Supervision, Funding acquisition. **Agostino Merico:** Conceptualization, Methodology, Validation, Writing - original draft, Writing - review & editing, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that they do not have any financial or nonfinancial conflict of interests.

Acknowledgments

This research was funded by the the German Academic Exchange Service, DAAD, through the projects HARVEST (grant number 57142704) and COMPLEX (grant number 57384894). MMF and EA-T acknowledge, respectively, the Alexander von Humboldt Foundation and the Deutsche Forschungsgemeinschaft (grant number AC 331/1-1, as part of the Priority Programme 1704, DynaTrait) for financial support. Finally, we are grateful to two anonymous reviewers for their thoughtful and constructive comments that helped us to improve the paper.

Supplementary material

Supplementary material associated with this article can be found, in the online version, at 10.1016/j.ecocom.2020.100876

References

Agrawal, A., Brown, D.G., Rao, G., Riolo, R., Robinson, D.T., Bommarito, M., 2013. Interactions between organizations and networks in common-pool resource governance. Environmental Science & Policy 25, 138–146. https://doi.org/10.1016/j.envsci.2012.08.004.
Akpalu, W., 2008. Fishing regulations, individual discount rate, and fisherman behaviour in a developing country fishery. Environment and Development Economics 13, 591–606.
Aoki, I., 1982. A simulation study on the schooling mechanism in fish. Bulletin of the Japanese Society of Scientific Fisheries 48, 1081–1088. https://doi.org/10.2331/suisan.48.1081.
Arreguín-Sánchez, F., 1996. Catchability: a key parameter for fish stock assessment. Reviews in Fish Biology and Fisheries 6, 221–242.
Balmford, A., Gravestock, P., Hockley, N., McClean, C.J., Roberts, C.M., 2004. The worldwide costs of marine protected areas. Proceedings of the National Academy of Sciences 101, 9694–9697.
Ban, N.C., Davies, T.E., Aguilera, S.E., Brooks, C., Cox, M., Epstein, G., Evans, L.S., Maxwell, S.M., Nenadovic, M., 2017. Social and ecological effectiveness of large marine protected areas. Global Environmental Change 43, 82–91.
Bavinck, M., Vivekanandan, V., 2011. Conservation, conflict and the governance of fisher wellbeing: analysis of the establishment of the gulf of mannar national park and biosphere reserve. Environmental Management 47, 593–602.
Belhabib, D., Greer, K., Pauly, D., 2018. Trends in industrial and artisanal catch per effort in west african fisheries. Conservation Letters 11, e12360.
Belhabib, D., Koutob, V., Sall, A., Lam, V.W., Pauly, D., 2014. Fisheries catch misreporting and its implications: The case of senegal. Fisheries Research 151, 1–11.
Bennett, N.J., Dearden, P., 2014. Why local people do not support conservation: Community perceptions of marine protected area livelihood impacts, governance and management in thailand. Marine Policy 44, 107–116.
Bohnsack, J., 1990. The potential of marine fishery reserves for reef management in the US southern atlantic. NOAA. Tech. Rep. NMFS 261.
Bonabeau, E., 2002. Agent-based modeling: Methods and techniques for simulating human systems. Proceedings of the National Academy of Sciences 99, 7280–7287.
Bookstaber, R., 2017. Agent-based models for financial crises. Annual Review of Financial Economics 9, 85–100.
Botsford, L.W., Micheli, F., Hastings, A., 2003. Principles for the design of marine reserves. Ecological Applications 13, S25–S31.
Brandt, G., Merico, A., 2013. Tipping points and user-resource system collapse in a simple model of evolutionary dynamics. Ecological Complexity 13, 46–52.
Brandt, G., Merico, A., Vollan, B., Schlüter, A., 2012. Human adaptive behavior in common pool resource systems. PLoS ONE 7, e52763.
Burgess, M.G., Carrella, E., Drexler, M., Axtell, R.L., Bailey, R.M., Watson, J.R., Cabral, R. B., Clemence, M., Costello, C., Dorsett, C., et al., 2020. Opportunities for agent-based modelling in human dimensions of fisheries. Fish and Fisheries 21, 570–587.
Cárdenas, J.C., Ostrom, E., 2004. What do people bring into the game? experiments in the field about cooperation in the commons. Agricultural Systems 82, 307–326.
Caron-Lormier, G., Humphry, R.W., Bohan, D.A., Hawes, C., Thorbek, P., 2008. Asynchronous and synchronous updating in individual-based models. Ecological Modelling 212, 522–527.
Caveen, A., Polunin, N., Gray, T., Stead, S.M., 2014. The controversy over marine protected areas: science meets policy. Springer.
Chaigneau, T., Brown, K., 2016. Challenging the win-win discourse on conservation and development: analyzing support for marine protected areas. Ecology and Society 21, 36. https://doi.org/10.5751/ES-08204-210136.
Christie, P., 2004. Marine protected areas as biological successes and social failures in southeast asia. In: Shipley, J.B. (Ed.), Aquatic protected areas as fisheries management tools. American Fisheries Society, pp. 155–164.
Clark, C.W., 1973. The economics of overexploitation. Science 181, 630–634.
Clark, C.W., 2010. Mathematical bioeconomics: The mathematics of conservation, 3rd. John Wiley & Sons.
Claudet, J., Osenberg, C.W., Benedetti-Cecchi, L., Domenici, P., García-Charton, J.A., Pérez-Ruzafa, A., Badalamenti, F., Bayle-Sempere, J., Brito, A., Bulleri, F., et al., 2008. Marine reserves: size and age do matter. Ecology Letters 11, 481–489.
Claudet, J., Roussel, S., Pelletier, D., Rey-Valette, H., 2006. Spatial management of near shore coastal areas: the use of marine protected areas (MPAs) in a fisheries management context. Vie et Milieu 56, 301–305.
Cornejo-Donoso, J., Einarsson, B., Birnir, B., Gaines, S.D., 2017. Effects of fish movement assumptions on the design of a marine protected area to protect an overfished stock. PLoS ONE 12, e0186309.

Cornforth, D., Green, D.G., Newth, D., 2005. Ordered asynchronous processes in multi-agent systems. Physica D: Nonlinear Phenomena 204, 70–82.

Costello, C., Ovando, D., Clavelle, T., Strauss, C.K., Hilborn, R., Melnychuk, M.C., Branch, T.A., Gaines, S.D., Szuwalski, C.S., Cabral, R.B., et al., 2016. Global fishery prospects under contrasting management regimes. Proceedings of the National Academy of Sciences 113, 5125–5129.

Côté, I.M., Mosqueira, I., Reynolds, J.D., 2001. Effects of marine reserve characteristics on the protection of fish populations: a meta-analysis. Journal of Fish Biology 59, 178–189.

Dasgupta, P., Maskin, E., 2005. Uncertainty and hyperbolic discounting. The American Economic Review 95, 1290–1299.

Di Lorenzo, M., Claudet, J., Guidetti, P., 2016. Spillover from marine protected areas to adjacent fisheries has an ecological and a fishery component. Journal for Nature Conservation 32, 62–66.

Diankha, O., Demarcq, H., Fall, M., Thiao, D., Thiaw, M., Sow, B.A., Gaye, A.T., Brehmer, P., 2017. Studying the contribution of different fishing gears to the sardinella small-scale fishery in senegalese waters. Aquatic Living Resources 30, 27.

Dietz, T., Ostrom, E., Stern, P.C., 2003. The struggle to govern the commons. Science 302, 1907–1912.

Fehr, E., Gächter, S., 2000. Cooperation and punishment in public goods experiments. American Economic Review 90, 980–994.

Ferraro, G., Brans, M., 2009. Policy reforms and the politics of nature. the case of marine fisheries in china and senegal. Public management institute, katholieke universiteit leuven conference paper, MARE conference, amsterdam, p. 24.

Frederick, S., Loewenstein, G., O'donoghue, T., 2002. Time discounting and time preference: A critical review. Journal of Economic Literature 40, 351–401.

Fulton, E., Smith, A., Smith, D., van Putten, I., 2012. Human behaviour: the key source of uncertainty in fisheries management. Fish and Fisheries 12, 2–17.

Fulton, E.A., Bax, N.J., Bustamante, R.H., Dambacher, J.M., Dichmont, C., Dunstan, P.K., Hayes, K.R., Hobday, A.J., Pitcher, R., Plagányi, E.E., et al., 2015. Modelling marine protected areas: insights and hurdles. Philosophical Transactions of the Royal Society B 370, 20140278.

Gaines, S.D., White, C., Carr, M.H., Palumbi, S.R., 2010. Designing marine reserve networks for both conservation and fisheries management. Proceedings of the National Academy of Sciences 107, 18286–18293.

Gell, F.R., Roberts, C.M., 2003. Benefits beyond boundaries: the fishery effects of marine reserves. Trends in Ecology & Evolution 18, 448–455.

Gerber, L.R., Botsford, L.W., Hastings, A., Possingham, H.P., Gaines, S.D., Palumbi, S.R., Andelman, S., 2003. Population models for marine reserve design: a retrospective and prospective synthesis. Ecological Applications 13, 47–64.

Gerber, L.R., Estes, J., Crawford, T.G., Peavey, L.E., Read, A.J., 2011. Managing for extinction? conflicting conservation objectives in a large marine reserve. Conservation Letters 4, 417–422.

Giakoumi, S., McGowan, J., Mills, M., Beger, M., Bustamante, R., Charles, A., Christie, P., Fox, M., Garcia Borboroglu, P., Gelcich, S., et al., 2018. Revisiting 'success' and 'failure' of marine protected areas: a conservation scientist perspective. Frontiers in Marine Science 5, 223.

Gigerenzer, G., Brighton, H., 2009. Homo heuristicus: Why biased minds make better inferences. Topics in Cognitive Science 1, 107–143.

Gigerenzer, G., Gaissmaier, W., 2011. Heuristic decision making. Annual Review of Psychology 62, 451–482.

Gill, D.A., Mascia, M.B., Ahmadia, G.N., Glew, L., Lester, S.E., Barnes, M., Craigie, I., Darling, E.S., Free, C.M., Geldmann, J., et al., 2017. Capacity shortfalls hinder the performance of marine protected areas globally. Nature 543, 665–669.

Golden, C.D., Allison, E.H., Cheung, W.W., Dey, M.M., Halpern, B.S., McCauley, D.J., Smith, M., Vaitla, B., Zeller, D., Myers, S.S., 2016. Fall in fish catch threatens human health. Nature 534, 317–320.

Guénette, S., Lauck, T., Clark, C., 1998. Marine reserves: from beverton and holt to the present. Reviews in Fish Biology and Fisheries 8, 251–272.

Guidetti, P., Sala, E., 2007. Community-wide effects of marine reserves in the mediterranean sea. Marine Ecology Progress Series 335, 43–56.

Guillen, J., Natale, F., Carvalho, N., Casey, J., Hofherr, J., Druon, J.N., Fiore, G., Gibin, M., Zanzi, A., Martinsohn, J.T., 2019. Global seafood consumption footprint. Ambio 48, 111–122.

Halpern, B.S., 2003. The impact of marine reserves: do reserves work and does reserve size matter? Ecological Applications 13, 117–137.

Halpern, B.S., Walbridge, S., Selkoe, K.A., Kappel, C.V., Micheli, F., D'agrosa, C., Bruno, J.F., Casey, K.S., Ebert, C., Fox, H.E., et al., 2008. A global map of human impact on marine ecosystems. Science 319, 948–952.

Halpern, B.S., Warner, R.R., 2002. Marine reserves have rapid and lasting effects. Ecology letters 5, 361–366.

Hannesson, R., 1998. Marine reserves: what would they accomplish? Marine Resource Economics 13, 159–170.

Hardin, G., 1968. The tragedy of the commons. Science 162, 1243–1248.

Hastings, A., et al., 1999. Equivalence in yield from marine reserves and traditional fisheries management. Science 284, 1537–1538.

Helbing, D., Kirman, A., 2013. Rethinking economics using complexity theory. Real-World Economics Review 64, 23–51.

Hilborn, R., Stokes, K., Maguire, J.J., Smith, T., Botsford, L.W., Mangel, M., Orensanz, J., Parma, A., Rice, J., Bell, J., et al., 2004. When can marine reserves improve fisheries management? Ocean & Coastal Management 47, 197–205.

Huff, E.S., Leahy, J.E., Hiebeler, D., Weiskittel, A.R., Noblet, C.L., 2015. An agent-based model of private woodland owner management behavior using social interactions, information flow, and peer-to-peer networks. PLoS ONE 10, e0142453.

Huth, A., Wissel, C., 1992. The simulation of the movement of fish schools. Journal of Theoretical Biology 156, 365–385.

Janssen, M.A., Baggio, J.A., 2017. Using agent-based models to compare behavioral theories on experimental data: application for irrigation games. Journal of Environmental Psychology 52, 194–203.

Janssen, M.A., Holahan, R., Lee, A., Ostrom, E., 2010. Lab experiments for the study of social-ecological systems. Science 328, 613–617.

Jones, P.J., 2006. Collective action problems posed by no-take zones. Marine Policy 30, 143–156.

Kildow, J.T., McIlgorm, A., 2010. The importance of estimating the contribution of the oceans to national economies. Marine Policy 34, 367–374.

Kramer, R.M., et al., 1986. Social values and cooperative response to a simulated resource conservation crisis. Journal of Personality 54, 576–582.

Lester, S.E., Halpern, B.S., Grorud-Colvert, K., Lubchenco, J., Ruttenberg, B.I., Gaines, S.D., Airamé, S., Warner, R.R., 2009. Biological effects within no-take marine reserves: a global synthesis. Marine Ecology Progress Series 384, 33–46.

Little, L., McDonald, A., 2007. Simulations of agents in social networks harvesting a resource. Ecological Modelling 204, 379–386.

Mellin, C., Aaron MacNeil, M., Cheal, A.J., Emslie, M.J., Julian Caley, M., 2016. Marine protected areas increase resilience among coral reef communities. Ecology Letters 19, 629–637.

Metcalfe, K., Collins, T., Abernethy, K.E., Boumba, R., Dengui, J.C., Miyalou, R., Parnell, R.J., Plummer, K.E., Russell, D.J., Safou, G.K., et al., 2017. Addressing uncertainty in marine resource management; combining community engagement and tracking technology to characterize human behavior. Conservation Letters 10, 460–469.

Micheli, F., Halpern, B.S., Botsford, L.W., Warner, R.R., 2004. Trajectories and correlates of community change in no-take marine reserves. Ecological Applications 14, 1709–1723.

Molloy, P.P., McLean, I.B., Côté, I.M., 2009. Effects of marine reserve age on fish populations: a global meta-analysis. Journal of Applied Ecology 46, 743–751.

Mosquera, I., Côté, I.M., Jennings, S., Reynolds, J.D., 2000. Conservation benefits of marine reserves for fish populations. Animal Conservation 4, 321–332.

Nelson, J., Bradner, H., 2010. The case for establishing ecosystem-scale marine reserves. Marine Pollution Bulletin 5, 635–637.

Niasse, M. L., & Seck, M. (2011). L'accaparement des ressources marines ouest africaines: sociétés mixtes de façade et licences de complaisance. expériences du sénégal et de la mauritanie.

Nowak, M., 2006. Five rules for the evolution of cooperation. Science 314, 1560–1563.

O'Leary, B.C., Ban, N.C., Fernandez, M., Friedlander, A.M., García-Borboroglu, P., Golbuu, Y., Guidetti, P., Harris, J.M., Hawkins, J.P., Langlois, T., et al., 2018. Addressing criticisms of large-scale marine protected areas. Bioscience 68, 359–370.

Ostrom, E., 1990. Governing the Commons: The Evolution of Institutions for Collective Action. Cambridge University Press.

Ovaskainen, O., 2002. Long-term persistence of species and the sloss problem. Journal of Theoretical Biology 218, 419–433.

Owusu, K.A., Kulesz, M.M., Merico, A., 2019. Extraction behaviour and income inequalities resulting from a common pool resource exploitation. Sustainability 11, 1–13. https://doi.org/10.3390/su11020536.

Parry, H.R., Evans, A.J., 2008. A comparative analysis of parallel processing and super-individual methods for improving the computational performance of a large individual-based model. Ecological Modelling 214, 141–152.

Pauly, D., Christensen, V., Guénette, S., Pitcher, T.J., Sumaila, U.R., Walters, C.J., Watson, R., Zeller, D., 2002. Towards sustainability in world fisheries. Nature 418, 689.

, 2016Global atlas of marine fisheries: A critical appraisal of catches and ecosystem impacts. In: Pauly, D., Zeller, D. (Eds.), 2016. Island Press.

Pendleton, L.H., Ahmadia, G.N., Browman, H.I., Thurstan, R.H., Kaplan, D.M., Bartolino, V., 2018. Debating the effectiveness of marine protected areas. ICES Journal of Marine Science 75, 1156–1159.

Polacheck, T., 1990. Year around closed areas as a management tool. Natural Resource Modeling 4, 327–354.

Prediger, S., Vollan, B., Frölich, M., 2011. The impact of culture and ecology on cooperation in a common-pool resource experiment. Ecological Economics 70, 1599–1608.

Rife, A.N., Erisman, B., Sanchez, A., Aburto-Oropeza, O., 2013. When good intentions are not enough... insights on networks of "paper park" marine protected areas. Conservation Letters 6, 200–212.

Roberts, C.M., 2000. Selecting marine reserve locations: optimality versus opportunism. Bulletin of Marine Science 66, 581–592.

Roch, S.G., Samuelson, C.D., 1997. Effects of environmental uncertainty and social value orientation in resource dilemmas. Organizational Behavior and Human Decision Processes 70, 221–235.

Rodrigues, A.S., Andelman, S.J., Bakarr, M.I., Boitani, L., Brooks, T.M., Cowling, R.M., Fishpool, L.D., Da Fonseca, G.A., Gaston, K.J., Hoffmann, M., et al., 2004. Effectiveness of the global protected area network in representing species diversity. Nature 428, 640.

Rowley, R.J., 1994. Marine reserves in fisheries management. Aquatic Conservation: Marine and Freshwater Ecosystems 4, 233–254.

Russ, G.R., Cheal, A.J., Dolman, A.M., Emslie, M.J., Evans, R.D., Miller, I., Sweatman, H., Williamson, D.H., 2008. Rapid increase in fish numbers follows creation of world's largest marine reserve network. Current Biology 18, R514–R515.

Russ, G.R., Stockwell, B., Alcala, A.C., 2005. Inferring versus measuring rates of recovery in no-take marine reserves. Marine Ecology Progress Series 292, 1–12.

Rustagi, D., Engel, S., Kosfeld, M., 2010. Conditional cooperation and costly monitoring explain success in forest commons management. Science 330, 961–965.

Sale, P.F., Cowen, R.K., Danilowicz, B.S., Jones, G.P., Kritzer, J.P., Lindeman, K.C., Planes, S., Polunin, N.V., Russ, G.R., Sadovy, Y.J., et al., 2005. Critical science gaps impede use of no-take fishery reserves. Trends in Ecology & Evolution 20, 74–80.

Schaefer, M.B., 1954. Some aspects of the dynamics of populations important to the management of the commercial marine fisheries. Inter-American Tropical Tuna Commission Bulletin 1, 23–56.

Scheffer, M., Baveco, J., DeAngelis, D., Rose, K.A., van Nes, E., 1995. Super-individuals a simple solution for modelling large populations on an individual basis. Ecological Modelling 80, 161–170.

Steele, J.H., Beet, A.R., 2003. Marine protected areas in 'nonlinear'ecosystems. Proceedings of the Royal Society of London B (Supplement) 270, S230–S233. https://doi.org/10.1098/rsbl.2003.0074.

Vandeperre, F., Higgins, R.M., Sánchez-Meca, J., Maynou, F., Goni, R., Martín-Sosa, P., Pérez-Ruzafa, A., Afonso, P., Bertocci, I., Crechriou, R., et al., 2011. Effects of no-take area size and age of marine protected areas on fisheries yields: a meta-analytical approach. Fish and Fisheries 12, 412–426.

Wells, S., Ray, G.C., Gjerde, K.M., White, A.T., Muthiga, N., Bezaury Creel, J.E., Causey, B.D., McCormick-Ray, J., Salm, R., Gubbay, S., et al., 2016. Building the future of MPAs – lessons from history. Aquatic Conservation: Marine and Freshwater Ecosystems 26, 101–125.