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Santa Barbara

Effects of fish movement and environmental variability in the design and success of a marine
protected area

A dissertation submitted in partial satisfaction of the
requirements for the degree Doctor of Philosophy
in Marine Science

by

Jorge Fernando Cornejo Donoso

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March 2016

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March 2016

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protected area

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by

Jorge Fernando Cornejo Donoso

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Jorge F. Cornejo Donoso
University of California, Santa Barbara
March 2016

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ABSTRACT

Effects of fish movement and environmental variability in the design and success of a marine
protected area

by

Jorge Fernando Cornejo Donoso

Marine Protected Areas (MPA) are broadly used to protect marine ecosystems, restore biomass, and increasingly as tools in fisheries management for benthic stocks. Nevertheless, MPAs are seldom used to target pelagic species due the challenges of designing an effective MPA in a highly dynamic environment. It is believed that highly mobile organisms will get few benefits, since they leave the protected area too frequently. One possible solution is to compensate for such movement with larger MPAs. Nevertheless, uncertainty about the benefits in the face of vagaries about fish movement make it unlikely that such efforts would be successfully pursued.

Although it is a generally accepted that MPAs provide multiple benefits if well designed, empirical demonstrations of benefits from MPA are hard to obtain. They require long term evaluations, and as a consequence, comparisons between alternative MPA designs are almost nonexistent. Simulation models provide an alternative to empirical approaches that allow tests of designs and forecasts of potential outcomes. To date, most of the simulation models of MPAs have been developed for benthic systems, where simplified assumptions about fish

and fisherman movement are reasonable. Fortunately, with the advent of more realistic fish movement models, new approaches are now possible that can combine complex individual-based models of movement, population dynamics and virtual MPA systems. The use of these new complex simulation models can guide the optimization of MPA design to increase both stock sizes and fisheries yields.

The goal of the research presented in this dissertation is to study the potential of a large MPA to protect a pelagic stock and determine how fish movement characteristics and complex environmental dynamics influence the optimal design criteria for a successful pelagic MPA. The findings are timely given increasing interest in developing large no fishing zones to protect overfished pelagic stocks, especially for those taxa whose distribution spans more than one exclusive economic zone or resides in international waters. For this purpose I implemented a simulation model that incorporates detailed fish movement and their responses to complex environmental forcing to study the effect of fish movement on the efficacy of MPAs of different size and location.

In Chapter 1, I examined the effects of movement assumptions on the effectiveness of different MPA sizes on fish stocks and fisheries yields. I compared the results to prior modelling studies of MPA design that assumed simple random movement. I explored four movement assumptions with increasing behavioural complexity: a) random, diffusive movement, b) aggregations, c) aggregations that respond to environmental forcing (sea surface temperature), and d) aggregations that respond to environmental forcing and are transported by currents. I found that MPAs can protect pelagic stocks and increase fisheries yields. The optimal MPA size to maximize fisheries benefits increased with fish movement complexity from an area of ~10% when diffusive movement was assumed to ~30% when the

movement included aggregations, responses to the sea surface temperature (SST) and transport by currents.

In Chapter 2, I studied the effect of spatial environmental variability in the design of the MPA. For this purpose, I specifically explored the same four movement assumptions with increasing behavioural complexity: a) random, diffusive movement, b) aggregations, c) aggregations that respond to environmental forcing (sea surface temperature), and d) aggregations that respond to environmental forcing and are transported by currents, to compare the outcomes from several MPA designs in terms of placement and size. The goal was to analyse how complexities of fish movement and environmental dynamics theoretically affect the predicted outcomes from different MPA designs. In this chapter I found that increasing the size of an MPA reduces the risk of selecting poor or suboptimal placements and protects a larger fraction of the stock while maintaining similar fisheries yields. Simplified movement assumptions (e.g. diffusive movement) underestimated the relative importance of MPA placement and overestimated both the expected stock size and the mean time to recovery. These findings highlight the value of understanding fish movement dynamics and their responses to environmental forcing, providing further evidence that MPAs have the potential to protect, rebuild and manage pelagic stocks.

In Chapter 3, I included the effects of temporal variability in environmental forcing. I used the MPA model to simulate a complex pelagic environment with a spatially and temporally heterogeneous sea surface temperature that drove the organism's movement dynamics. The goal was to include the effects of a highly variable environment on MPA design and successfully increase stock size and fisheries yields. The results suggested that when temporal environmental variability occurs, the expected fisheries benefits are

significantly reduced relative to simulations with constant environments. The reduced fishery benefits occur even when the stock density levels were similar, suggesting that in highly variable pelagic environments MPAs may require more of a tradeoff between protect the stocks and increasing fisheries yields.

The results of this research suggest that MPAs can effectively be used to protect and rebuild pelagic stocks, and have the potential to increase fisheries yields. Nevertheless, to effectively design MPAs with conservation and management goals, it is necessary to understand the organism's movement dynamics and how they respond to environmental forcing. Models like the one used in this dissertation have the potential to inform future management decisions and help to design future pelagic MPAs that produce multiple benefits in a variety of environmental settings.

TABLE OF CONTENTS

I.	Effects of movement assumptions on the success of a marine protected area.....	1
	Abstract:	1
	Introduction.....	2
	Material and methods.....	4
	Results.....	15
	Discussion.....	16
	References.....	18
II.	Effects of movement assumptions on the optimal placement of a marine protected area.....	28
	Abstract.....	28
	Introduction.....	29
	Material and methods.....	31
	Results.....	37
	Discussion.....	40
	References.....	43
	Appendix: MPA properties.....	52
III.	Effects of the temporal environmental variability on the success of a marine protected area.....	63
	Abstract.....	63
	Introduction.....	64
	Methods.....	66
	Results.....	73
	Discussion.....	74
	References.....	76

LIST OF TABLES

Chapter I

Table 1: Model input values.	22
Table 2: Summary of results per Scenario and MPA size. Int: Interaction between organisms, SST: Responses to the sea surface temperature, and Cur: Transport by currents.....	23

Chapter II

Table 1: Model input values.	47
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Appendix:

Table 1: Residence time for each MPA placement and scenario.	57
Table 2: t-test results between scenarios using the same MPA placement.	57
Table 3: t-test results between placements for the same scenario.	58
Table 4: Exposure time for each MPA placement and scenario. placement.	58
Table 5: t-test between MPA placement for the same scenario.	59
Table 6: t-test between scenarios for the same MPA placement.....	59

Chapter III

Table 1: Model input values.	80
-----------------------------------	----

LIST OF FIGURES

Chapter I

Figure 1: Zones of interaction of particle k. Ak is the zone of attraction (light grey area), Ok is the zone of orientation (medium grey) and Rk if the zone of repulsion (dark grey area). Each zone has a radius of ra, ro and rr respectively.	24
Figure 2: Representation of a relative stock density (dashed line) and fisheries yields (doted line) time series. The figure shows when: the fishing start (year 10), the MPA is implemented (year 20), the recovery start (year 35, Figure 3a), the density and yield is increasing fast (year 40, Figure 3b), and the recovery is at its maximum and has reached the equilibrium (year 65 , Figure 3c).	24
Figure 3: Mean landings values by MPA size and scenarios after a) 15, b) 20, and c) 45 years of MPA implementation. Aggr: Aggregation behavior, SST: Responses to the sea surface temperature, and Cur: Transport by currents.	25
Figure 4: Mean densities by MPA sizes and scenario after a) 15, b) 20, and c) 45 years of the implemented MPA. Aggr: Aggregation behavior, SST: Responses to the sea surface temperature, and Cur: Transport by currents.	26
Figure 5: Accumulated landings for the whole period after MPA implementation (50 years). Aggr: Aggregation behavior, SST: Responses to the sea surface temperature, and Cur: Transport by currents.	27

Chapter II

Figure 1: Time series of average densities obtained with an MPA of 10%. a) diffusive movement, b) aggregations, c) aggregations responding to the SST, and d) aggregations responding to SST and transported by the currents. Lines in red represent the mean of densities, in dark green the median and in thin red, orange and yellow, the 3 best placement optimized considering the most complex environmental movement scenario. Variability in the density estimation was not included to simplify the figure.	48
Figure 2: Time series of average densities obtained with an MPA of 20%. a) diffusive movement, b) aggregations, c) aggregations responding to the SST, and d) aggregations responding to SST and transported by the currents. Line in red represent the mean of densities, in dark green the median and in thin red, orange and yellow, the 3 best placement optimized considering the most complex environmental movement scenario. Variability in the density estimation was not included to simplify the image.	48
Figure 3: Time series of average landings with an MPA of 10%. a) diffusive movement, b) aggregations, c) aggregations responding to the SST, and d) aggregations responding to SST and transported by the currents. Line in red represent the mean of densities, in dark green the median and in thin red, orange and yellow, the 3 best placement optimized considering the most complex environmental movement scenario. Variability in the landings estimation was not included to simplify the image.	49
Figure 4: Time series of average landings with an MPA of 20%. a) diffusive movement, b) aggregations, c) aggregations responding to the SST, and d) aggregations responding to SST and transported by the currents. Line in red represent the mean of densities, in	

dark green the median and in thin red, orange and yellow, the 3 best placement optimized considering the most complex environmental movement scenario.	
Variability in the landings estimation was not included to simplify the image.....	49
Figure 5: Mean landings predicted by each MPA placement using diffusion movement assumption (y axis) and using the full environment scenarios that include aggregation, responses to SST and transport by currents.	50
Figure 6: Time series of the predicted densities obtained with the full environment assumption for the MPA placements that resulted on the highest densities using the diffusion, aggregation, and SST forcing scenarios.	50
Figure 7: Trade off between protection of the stock (densities) and increasing landings for both MPA sizes using the most complex environmental movement scenario. 10% MPA size in blue and 20% MPA size in red.	51
Appendix	

Figure 1: Boxplot of the mean residence time for each MPA placement and scenario standardize to the generation time, the time required for an organism to reproduce.....	60
Figure 2: Bloxplot of the fraction of the life of the fish spended outside of the protection of the MPA.....	60
Figure 3: Mean density (in blue) and CPUE (in red) function of the distance to the border of an MPA of 20% assuming aggregation, response to SST and transport by current as movement (negative distances indicate the pixel is inside the MPA).	61
Figure 4: Mean density (in blue) and CPUE (in red) function of the distance to the border of an MPA of 20% assuming aggregation and response to SST as movement (negative distances indicate the pixel is inside the MPA).	61
Figure 5: Mean density (in blue) and CPUE (in red) function of the distance to the border of an MPA of 20% assuming only aggregations as movement (negative distances indicate the pixel is inside the MPA).	62
Figure 6: Mean density (in blue) and CPUE (in red) function of the distance to the border of an MPA of 20% assuming diffusion movement (negative distances indicate the pixel is inside the MPA).....	62

Chapter III

Figure 1: Monthly Sea Surface Temperature (SST) used as environmental forcing.....	81
Figure 2: Time series of the mean densities (upper panel) and mean landings (lover panel) comparing between MPA placement optimized to increase densities (left side) and for landings (right side; errors bars represent the standard deviation of the mean).	82
Figure 3: Density and landings time series for scenarios using alternative temperature preferences.	83

I. Effects of movement assumptions on the success of a marine protected area

Cornejo-Donoso, J., Einarsson, B., Birnir, B., Gaines, S.D.

Abstract:

Marine Protected Areas (MPA) are important management tools to protect marine organisms, restore biomass and increase fisheries yields. MPAs have been widely used for relatively sedentary species, but it is believed that highly mobile organisms will get few benefits from such spatial protection, since they leave the protection of the MPA too frequently. Creating very large MPAs to compensate for extensive movement is challenging, especially if there is large uncertainty about the vagaries of fish movement and consequently the benefits of large closures. Given the recent development of more realistic models of fish movement, we explore whether better knowledge of the details of fish movement could reduce the MPA size needed to generate a given level of conservation or fisheries benefits.

Here we present results from an individual based model that simulates the movement and population dynamics of a highly mobile fish in settings with MPAs and fishing. Using a set of interconnected models, we explore the effects of movement assumptions on the effectiveness of MPAs of different size on fish stocks and fishery yields. We explore four movement assumptions with increasing behavioural complexity: a) random, diffusive movement, b) aggregations, c) aggregations that respond to environmental forcing (sea surface temperature), and d) aggregations that respond to environmental forcing and are transported by currents. Prior modelling studies of MPA design and effectiveness have largely assumed random movement.

The results indicate that it is possible to implement MPAs that provide significant benefits to pelagic stocks and increase fisheries yields. The optimal MPA size to maximize fisheries benefits increases as movement complexity increases from ~10% for the diffusive assumption to ~30% when full environment forcing was used.¹

Introduction

Marine Protected Areas (MPAs) are a spatial management tool commonly used to restore and protect marine organisms. When scaled to the proper size or combined as an interconnected network, they can effectively protect fisheries stocks and increase fisheries yields (Botsford et al., 2003). But to be successful for both conservation and fisheries, MPA designs must adequately address the consequences of species movement, including the swimming behaviour of adults and the dispersal of larvae (Gaines et al., 2010; Kellner et al., 2008).

Theoretical studies suggest that a well-designed MPA can provide comparable benefits to those obtained with perfect management of the catch. For example, Hastings and Botsford (1999) showed that for species with sedentary adults and larval dispersal, the optimal MPA size can offer identical stock protection and yield to that provided by the optimal fishing mortality rate. Hilborn and colleagues (2006) found similar results and concluded that most MPA fisheries benefits occur when adults have medium to low annual movement. More recently, Rassweiler and collaborators (2012) used a bioeconomic model with more complex

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larval and juvenile movement to show that it is possible to strategically design a spatial management plan that exceeds the value of a fully optimized non-spatial management (i.e. restrictions of the total allowable catch).

Although these studies highlight some impacts of the movements of organism on MPA outcomes, they still rely on very simplified abstractions of movement. For example, most MPA studies still commonly assume simple diffusive and advective movement with the rationale that it is a reasonable depiction of the passive dispersal of particles like eggs or larvae (Codling, 2008). Yet, a wide body of literature shows that more actively moving organisms in spatially and temporally heterogeneous environments can have movement dynamics that are far more complex and poorly approximated by simple advection and diffusion (Benhamou, 2007; Codling, 2008). For example, Codling (2008) uses an individual movement model and a simple virtual marine reserve-fishery system to highlight situations where assuming movement by advection or diffusion is not reasonable, because it can lead to dramatic differences to the apparent effectiveness of an MPA. In addition, a number of studies have successfully simulated individual fish movement in a heterogeneous space, with the underlying assumption that fish movement is governed by the tendency to imitate the motion of other fish in a local neighbourhood and that the resulting aggregations respond to external forcing such as temperature gradients or food density (Hubbard et al., 2004). Because the movement in these models can be simulated in a fine spatial and temporal scale (Huse et al., 2004), they have successfully captured migration dynamics (Barbaro et al., 2009; Magnússon et al., 2004), predicted the spatial distribution of highly mobile fish (e.g. blue fin tuna; Royer *et al.*, 2005) and simulated the spatial interactions between predators and prey (Huse et al., 2004). Although a number of studies have argued that the predictions from

MPA simulations can be strongly sensitive to the assumptions about movement (Gaines et al., 2003; Gerber et al., 2003; Kellner et al., 2008), these major advances in modelling the dynamics of fish movement have not been integrated with models of marine conservation or fisheries.

Here we take a first step toward integrating more realistic models of fish movement with spatial management models of fisheries. We explore how different movement dynamics change the optimum MPA size that maximizes fisheries benefits and the relative fisheries benefits of managing with MPAs versus managing average fishing mortality rates. To this end we link an individual based model (IBM) of movement to a spatially explicit fisheries model patterned after a small pelagic fish in a spatially heterogeneous environment.

Material and methods

The Model

We follow the Overview, Design concepts, and Details (ODD) protocol to describe individual based models (Grimm et al., 2006) – first providing an overview of the model, followed by a description of the underlining biological processes, including fishery activities, and finally the detailed mathematical description of the particle movement.

The Individual Based Model (IBM) used is an adaptation of the particle interaction model introduced by Vicsek and colleagues (1995), extended by Czirók and Vicsek (2000), and modified by Magnússon (Hubbard et al., 2004). A dynamical system analysis of the corresponding ODE model was done by Birnir (2007). The simulations were run using the infrastructure provided by the UCSB Center for Scientific Computing.

The model was used to explore the effects of movement assumptions of a pelagic organism on the success of MPAs as a fisheries management tool. For this goal, we developed a complex movement model for individual fish, which incorporates schooling, responses to a spatially heterogeneous environmental forcing, population dynamics, and the effect of spatially dynamic fishing on population mortality. We defined four models with assumptions of different movement (scenarios) of increasing complexity: a) random, diffusive movement, b) aggregations that move randomly, c) aggregations that respond to environmental forcing [sea surface temperature (SST)], and d) aggregations that respond to environmental forcing and are transported by currents.

In all scenarios the particles state variables were position, speed, movement direction, and developmental stage (i.e. egg/larvae, juvenile and adults). In the most complex model, the particles sensed the position of nearby particles and the local temperature gradient. Then, based on these stimuli, the direction and speed of the particle movement was actively adjusted for the next time step, while currents passively transported the particles.

At the population level, the state variables were the intrinsic growth rate, carrying capacity, natural mortality rate, and fishing mortality rate (F ; Table 1).

The model incorporated stochasticity in several components including: the initial direction and movement speed when a new fish is added to the system (age 0), the timing of the individual death and reproduction. Natural and fishing mortality rates were implemented as a daily probability of death for each particle; therefore, at any given time t , the natural and fishing mortality of an individual particle were unknown, but the daily mean of these two variables was predefined and known.

Simulation Scenarios

- i) *Random movement of adults and eggs/larvae*: this scenario was equivalent to movement by diffusion, with a mean diffusion coefficient of 0.0069 sectors, of 4000 sectors total for the MPA, per day. Eggs, juveniles and adults had the same pattern of movement, which is completely independent of neighbouring fishes, maximum speed increasing until maturation.
- ii) *Aggregation*: in this scenario the adults interacted with their neighbours, coordinating their speed and direction, forming aggregations. The direction and speed of the school was not influenced by any environmental forcing, nor transported by currents.
- iii) *Aggregation, and environmental forcing*: in this case, the adults interacted with their neighbours, forming aggregations that coordinated their swimming direction and speed. These aggregations reacted to environmental forcing (SST) by adjusting their direction and speed.
- iv) *Aggregation, environmental forcing, and transport by currents*: this was the most complex scenario used for movement. In this case, the adults interacted with their neighbours, forming aggregations that coordinated their swimming direction and speed. These aggregations reacted to environmental forcing (SST) by adjusting their direction and speed and were transported by currents. Eggs/larvae were also transported by the currents, but did not form aggregations.

Simulation area

The simulation area was defined as a rectangular grid of 100 by 40 sectors that represented a large region of the ocean. This simulated ocean is designed to cover a

geographic area larger than the expected distribution range of the simulated stock. Therefore, the space is defined as a closed system with no immigration or emigration (i.e. all borders are repelling). Temperature and currents fields were used to force the fish movement inside the grid. No vertical movement was included.

Population dynamics

The fish demographic parameters used in the simulations are based on the Peru-Chile anchovy (*Engrulis ringens* Jenyns, 1942). This small pelagic fish has a common length of ~15 cm, a short, iteroparous life cycle, and a main spawning event occurring around the second half of the year (Table 1). Our theoretical fish was based on the anchovy, because they represent one of the most important fisheries in the world, have been subject to intense fishing for decades, have a short life cycle and fast reproduction (Froese and Pauly, 2000), all characteristics that would make it an ideal study case for the potential use of a pelagic MPA to protect and manage the stock.

The reproduction is defined as a population event normally distributed with mean 250 (September 7) and a standard deviation of 20 days (Table 1). As the fish is added to the system a reproduction day is assigned where reproduction will occur when mature with a defined fecundity of 10 eggs per individual. After a reproduction event, the new added organisms (eggs) are subject to a density dependent natural mortality (Z) which is adjusted to satisfy the dynamics as predicted by a Gordon Schaefer model (Gordon, 1954).

Based on the difference between the expected number of fish for next year (N_{t+1}), the effective number of recruited fish (N_R) and the number of eggs/larvae (N_{eggs}), the probability of survival of an individual egg/larvae is calculated as follows:

$$N_{t+1} = N_R + N_R \cdot r \cdot \left(1 - \frac{N_R}{K}\right) \quad \text{Eq. 1}$$

In this way, the number of organisms that can be recruited is:

$$Rec = N_{t+1} - N_R \quad \text{Eq. 2}$$

And therefore the probability of survival ($S_{prob.}$) is:

$$S_{prob.} = \frac{Rec}{N_{eggs}} \quad \text{Eq. 3}$$

Adult natural mortality was defined for two age class ranges –one to four years old and five years and older (Table 1).

Fish Age Classes

Three different age classes of fish are included in the model: eggs/larvae, juveniles and adults. Each age class is defined by distinct swimming capacities, aggregation behaviours, and responses to environmental forcing.

- a) *Eggs/Larvae* are not active swimmers; therefore, they cannot form aggregations or respond to temperature fields. Their movements in the system are a consequence of transport by currents and an initial slow movement that spreads them from the spawning point.
- b) *Juveniles* have limited swimming capacity; they form aggregations and respond to temperature fields. Their maximum speed is slower than adults. Juveniles are not fished (fishing mortality, F , set to zero).
- c) *Adults* swim faster than juveniles. They are recruited to the fishery ($F > 0$) and reproduce once a year.

Process scheduling

All simulations started by assigning a random position, speed, direction, day of future reproduction, and age to each particle (Table 1). Each simulation ran for 70 years, the first 20 without fishing to let the system reach equilibrium and remove potential effects of the initial conditions. At year 20 fishing starts and continues for 10 years without any management (i.e. open access). As a result, overfishing is inevitable. At year 30, an MPA is implemented as an east-west strip of different widths at the centre of the simulated region. A fixed fraction of the area is therefore excluded from fishing.

For each time step ($\frac{1}{5}$ day), fish interact with their neighbours and respond to the temperature field by adjusting their heading and speed. As the fish swim, they are also transported by currents. At the beginning of every day, each fish ages by one day, natural mortality (Z) and reproduction occur within the entire fish population, and then the fishing fleet redistributes and imposes fishing mortality (F).

When a fish reproduces, the new eggs/larvae are given random headings and movement speeds for their birthday (as shown in Table 1). Eggs and larvae are only transported by currents, while juveniles also swim with limited abilities during their first six months. If they survive this juvenile development period, a fish's swimming capacity progressively increases until they are one year old when maturity is reached and fisheries recruitment occurs (*Engraulis* spp; Froese and Pauly, 2000). At this point, fish are susceptible to fishing mortality based upon the daily patterns of fish and the fleet. If a fish survives to its designated reproduction date, it releases offspring to complete the cycle.

Spatial distribution of fishing boats

The movement of the fishing fleet was modelled as in Hilborn *et al.* (2006). A total of 5,000 fishing boats are allocated in the grid based on fish abundance using the following two-step process:

$$B'_{ijt} = \begin{cases} \exp \left[-c \left(1 - \frac{N_{ijt}}{M_{Nt}} \right) \right] & \text{if } ij \text{ is outside the MPA} \\ 0 & \text{if } ij \text{ is inside the MPA} \end{cases} \quad \text{Eq. 4}$$

$$B_{ijt} = 5,000 \frac{B'_{ijt}}{\sum_{ij} B'_{ijt}} \quad \text{Eq. 5}$$

Where:

B'_{ijt} : Intermediate relative number of boats in sector ij at time t

B_{ijt} : Number of fishing boats in sector ij at time t

c : Aggregation parameter for fishing boats – determines how boats respond to fish abundance

M_{Nt} : Maximum abundance of fish in the grid outside the MPA at the time t

N_{ijt} : Number of fish in sector ij at time t before the redistribution takes place

Equation 4 explains how the fishing boats concentrate in response to fish densities in each sector. The parameter c was set to 3 for all simulations, which represents an intermediate level of fishing boat aggregation in areas of high fish densities (Hilborn *et al.*, 2006). For each sector in the simulation area, the adjusted fishing mortality is obtained by multiplying the daily fishing mortality rate by the number of boats in a particular sector and by a scaling factor that characterizes the likelihood of capture for a given density of fish and a given effort of fishing (calculated as in White & Costello 2014). As a result, the realized fishing mortality is spatially heterogeneous.

The annual fishing mortality for our theoretical fishery was set to 1.27 per year as the mean for the space and time, equivalent to the F for the Peru-Chile anchovy fishery (CeDePesca, 2010; Leal and Bucarey, 2009; Serra et al., 2009). This high F value is appropriate for driving the stock to collapse and provides the conditions to test the benefits of the MPA to induce recovery and later the protection of the stock

MPA management

Simulations were run with an increasing fraction of the total area closed as an MPA to find the optimal size in terms of fisheries yields. All fishing is excluded from the MPA. Outside the MPA the fishing fleet is allowed to operate all year around.

Fish Movement

The fish movement is simulated using a discrete interaction particle model where each particle (i.e. fish) sense their surroundings and determine the neighbours heading and speed to define their own, which results in coordinated movement and aggregations behaviour. To simulate this interactions among neighbouring fishes, three sensory zones are defined (Figure 1; Aoki, 1982; Barbaro *et al.*, 2009; Huth and Wissel, 1992). The innermost region is the *zone of repulsion* (R_k , light grey area). In this region fish head away from each other, thereby avoiding collisions. The next region is the *zone of orientation* (O_k , medium grey area). In this region fish align in speed and direction. Finally, in the *zone of attraction* (A_k , dark grey area) the fish head toward each other, forming aggregations.

The number of fish in the repulsion, orientation and attraction zones is denoted by N_{R_k} , N_{O_k} and N_{A_k} , respectively; $\mathbf{q}_k(t) = (x_k(t), y_k(t))^T$ is the fish position, $v_k(t)$ is its speed, and ϕ_k is the direction of fish k at time t .

A fish k updates its speed by:

$$v_k(t + \Delta t) = \frac{1}{N_{O_k}} \sum_{j \in N_{O_k}} v_j(t) \quad \text{Eq. 6}$$

and its position is updated by:

$$\mathbf{q}_k(t + \Delta t) = \mathbf{q}_k(t) + \Delta t \cdot v_k(t + \Delta t) \begin{pmatrix} \cos(\phi_k(t + \Delta t)) \\ \sin(\phi_k(t + \Delta t)) \end{pmatrix} \quad \text{Eq. 7}$$

where ϕ_k is the directional angle of fish k . For each time step (Δt), the heading and direction of the fish is recalculated based on the previous position and the positions of neighbouring fish. Movement occurs in continuous space. A weighted average of the direction and speed is taken over the zone of orientation and $\phi_k(t + \Delta t)$ is calculated as

$$\begin{pmatrix} \cos(\phi_k(t + \Delta t)) \\ \sin(\phi_k(t + \Delta t)) \end{pmatrix} = \frac{\mathbf{d}_k(t + \Delta t)}{\|\mathbf{d}_k(t + \Delta t)\|} \quad \text{Eq. 8}$$

where:

$$\begin{aligned} \mathbf{d}_k(t + \Delta t) := & \frac{1}{N_{R_k} + N_{O_k} + N_{A_k}} \\ & \times \left(\sum_{r \in N_{R_k}} \frac{\mathbf{q}_k(t) - \mathbf{q}_r(t)}{\|\mathbf{q}_k(t) - \mathbf{q}_r(t)\|} + \sum_{o \in N_{O_k}} \begin{pmatrix} \cos(\phi_o(t)) \\ \sin(\phi_o(t)) \end{pmatrix} \right. \\ & \left. + \sum_{a \in N_{A_k}} \frac{\mathbf{q}_a(t) - \mathbf{q}_k(t)}{\|\mathbf{q}_a(t) - \mathbf{q}_k(t)\|} \right) \quad \text{Eq. 9} \end{aligned}$$

Environmental forcing

A spatially heterogeneous environment, without temporal variability, was used to force the movement dynamics of the fish. As a first step the environment is spatially heterogeneous but kept constant in time. This captures reasonable well the influence of the heterogeneous

environment during one season. The plan is to include the full temporal environmental variation in future simulations. The environment was incorporated into the model as a grid of currents and temperature data.

Currents move the fish directly, and this translation movement is independent of the fish's own movements in response to other fish and to temperature. The current field is denoted by $C(i,j)$. Fish also respond to the temperature field $T(i,j)$ by seeking to find locations within their preferred temperature range, T_1 to T_2 . The fish adjust to the surrounding temperatures according to the gradient of the function r

$$r(t) := \begin{cases} -(T - T_1)^2 & \text{if } T \leq T_1 \\ 0 & \text{if } T_1 \leq T \leq T_2 \\ -(T - T_2)^2 & \text{if } T_2 \leq T \end{cases} \quad \text{Eq. 10}$$

Including the effects of the environmental fields on the particle's positions ($\mathbf{q}_k(t)$) we obtain

$$\mathbf{q}_k(t + \Delta t) = \mathbf{q}_k(t) + \Delta t \cdot v_k(t + \Delta t) \frac{\mathbf{D}_k(t + \Delta t)}{\|\mathbf{D}_k(t + \Delta t)\|} + \mathbf{C}(\mathbf{q}_k(t)) \quad \text{Eq. 11}$$

where:

$$\mathbf{D}_k(t + \Delta t) := \alpha \frac{\mathbf{d}_k(t + \Delta t)}{\|\mathbf{d}_k(t + \Delta t)\|} + \beta \frac{\nabla r(T(\mathbf{q}_k(t)))}{\|\nabla r(T(\mathbf{q}_k(t)))\|} \quad \text{Eq. 12}$$

and the speed (v_k) is calculated as in equation 3, \mathbf{d}_k is the same unit vector as in equation 5, and the weights satisfy the following

$$\alpha + \beta = 1 \quad \text{Eq. 13}$$

where, α corresponds to the particles' interactions with their neighbours and β defines the responses to the temperature field.

This grid includes the border as areas of extreme temperature values, which repel the fish and contain within the grid.

Initialization

The simulation started with *ca.* 25,000 randomly distributed fish. Because of stochasticity in their heading, speed, day of reproduction, and natural and fishing mortality, there is variation among simulations. Eleven replicates were run to explore this variability.

Datasets

A monthly mean *SST* for August of 2009 was obtained from the global dataset provided by NASA (OceanColor web site)², this month had significant spatial *SST* variability with values above and below the range used to force the movement (Eq. 7 and 9). This resulted in a spatially heterogeneous environmental, but the temporal variability is fixed. The satellite image selected was the daytime *SST* 11 μ 4x4 km processed from the data obtained with the MODIS-Aqua sensor. A subset of the global image was selected of the coast of Peru and Chile that covers the Peru-Chile anchovy stock distribution area, approximately between the 18° and 24° Lat S, a mask was applied to remove and reshape the land and ocean areas, making them equivalent to the defined simulation area. The resulting temperature field was used as the environmental forcing in the simulations.

Ocean currents were modelled as the annual mean of AVISO/geostrophic currents (obtained from NOAA's Coastwatch service³) for the same region of the Peruvian and Chilean coasts. These data have a resolution of 0.25° and were interpolated and reshaped to make them compatible with the simulation area (using kriging in R). This current field was used to passively transport the particles.

² <http://oceancolor.gsfc.nasa.gov/>

³ <http://coastwatch.pfeg.noaa.gov/coastwatch/CWBrowserWW360.jsp>

Results

MPAs smaller than 10% of the area had little benefits under any movement patterns (Figures 3 and 4). The optimal MPA sizes that maximized fisheries yields at equilibrium, across all simulated classes of patterns of movement, was between 10% and 30% of the area (Figure 3), or 20% to 30% when accumulated yields were considered (Figure 5). This MPA sizes range suggests that the optimum size for an MPA resulting from a diffusive model can be close to the optimal size obtained with more realistic movement assumptions.

Although the differences in the optimal MPA size to increase fisheries yields were modest across movement scenarios at equilibrium (Figure 3c), the trend was that larger MPAs were required as movement complexity increased; the maximum fisheries yields were obtained with an MPA of 10% for the diffusion scenario (~90% of maximum sustainable yield⁴ (MSY)), 20% for aggregations and aggregation and SST (~80% of MSY), and 30% when aggregation, SST and currents transport were assumed (~80% of MSY). On the other hand, the mean recovery time was reduced as the movement complexity increased (Figures 4a and b). The slowest recovery occurred with the diffusive model (Figures 3b and 4b). These differences in the mean recovery times have significant effects on the total expected fisheries benefits and underestimate yields by *ca.*30% when the optimal MPA size is used (Figure 5).

Our results also show that when 60 to 80% of the area was protected, the reduction of fishing grounds was compensated by a larger fish stock and the consequent spill-over effect, resulting in relatively constant fishing yields (Figure 3). But, even when the protection of

⁴ Defined as $MSY = \frac{K \cdot r}{4}$

areas larger than those that maximize fisheries yields was suboptimal, they provided other benefits like a reduction in the variability of density and yields and constant yields over time (Figure 4).

Discussion

Managing highly mobile species is an immense challenge due to the tremendous complexity of movement in a three dimensional environment. It is impossible to model such movement without sacrificing some details. The key question is which details are crucial for capturing the movement dynamics. In this paper we explore how incorporating additive details on movement complexity, ranging from simple diffusion to full environmental forcing, changes outcomes and predicted fish distribution when an MPA is used to protect and manage the stock. Our results indicate that simplified movement models (e.g. random walk, diffusion, complete redistribution) overestimate the expected protection and fisheries benefits as well as underestimate the required MPA size to protect the stock, giving suboptimal results. However, if it is not feasible to implement a complex model due to data constraints or other limitations, the oversimplified movement assumption provides guidelines to select the minimum MPA size that would protect the stock and benefit the fisheries. For example, when optimizing the MPA size using the diffusion model, the stock rebuilds to $\sim 1/3$ of the unfished densities, while doubling the protection area (i.e. full environment optimum size) the protected stock increased to $\sim 1/2$ of unfished densities with yields of $\sim 80\%$ of MSY (Table 2).

Even though optimum MPA sizes described here were equivalent or smaller than previously reported as optimal for fisheries benefits (Gaines et al., 2010), these areas are not small in absolute terms. For instance, considering the distribution area described for the

anchovy stock shared by Peru and Chile (Alheit and Ñiquen, 2004), an MPA of 20% would be of $\sim 40,000 \text{ km}^2$ which is equivalent to 40 times the total area of the Channel Islands Marine Protected Areas network in California, or *ca.* 10% the size of the U.S. Marine National Monument Papahānuamokuākea. Nevertheless, the use of a large MPA as a fisheries management tool would be considerably less intensive in data requirements relative to current practices. Annual stock assessments and minimum size quotas are economically expensive, time consuming and subject to high natural variability, particularly for small-pelagic fisheries with periodic regime shifts. Previously, MPAs have been used for small-scale management or for sedentary, benthic species. However, our results provide evidence for the potential success of large MPAs for pelagic stocks protection. By showing the incremental gains from information, this contribution also illustrates that lack of data to strategically design them is not crucial, or complete knowledge of fish movement is not a requirement for a successful MPA implementation (Game et al., 2009).

This paper is an important contribution that expands our understanding of MPAs as management tools and the potential benefits of implementing large pelagic MPAs, that has thus far been ignored in the academic and management venues. Further, our methodology and results spur exciting research avenues that can expand the applicability of MPAs. For example, including temporal variability, climate change or economics drivers of the fishing fleet could provide additional realism as well further insight into the value of MPAs for a range of biological and social outcomes. These simulations are the first step toward a new generation of models that would incorporate more realistic assumptions of environmental heterogeneity (spatial and temporal), fisheries dynamics and trophic interactions, among others. Increasing the realism of these models will allow scientists to test and compare

between potential MPA implementations, optimize their design, and obtain insight with potential fisheries policy and management implications.

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Table 1: Model input values.

Parameter	Initial Value	Units
Number of Fish	$\sim 25,000$	<i>ind.</i>
Reproduction Day	$N(250, 20)$	<i>day</i>
Fish Heading	$U(0, 360)$	<i>deg</i>
Adult Fish Speed	$U(0, 50)$	<i>sector d⁻¹</i>
Eggs/Larvae speed	$U(0, 0.1)$	<i>sector d⁻¹</i>
Initial fish age	$U(1, 3)$	<i>year</i>
Diffusion Coefficient	0.0069 [0.0000, 0167]	<i>sector d⁻¹</i>
Natural mortality (<i>Z</i>)		
1 to 4 years old	7×10^{-4}	<i>d⁻¹</i>
5+ years old	3×10^{-3}	<i>d⁻¹</i>
Fishing mortality (<i>F</i>)	1.27	<i>y⁻¹</i>
Fishing activity start	20	<i>year</i>
Management activity start	30	<i>year</i>
Total simulation length	70	<i>year</i>
Fecundity	10	<i>eggs ind⁻¹</i>
Radius of		
Repulsion r_r	0.02	<i>sector</i>
Alignment r_o	0.10	<i>sector</i>
Attraction r_a	0.10^5	<i>sector</i>
Temperature preferences [T_1, T_2]	[16, 18]	$^{\circ}C$
Weighted influence of		
Neighbors (α)	0.995	
Temperatures (β)	0.005	
Boat aggregation index (<i>c</i>)	3	
Fish carrying capacity (<i>K</i>)	30,000	<i>ind.</i>
Intrinsic rate of increase (<i>r</i>)	1.2	<i>ind. year⁻¹</i>
Simulation time-step Δt	0.2	<i>day</i>

⁵ This means that the area of attraction was not considered.

Table 2: Summary of results per Scenario and MPA size. Int: Interaction between organisms, SST: Responses to the sea surface temperature, and Cur: Transport by currents.

MPA(%)	Scenarios											
	Diffusion			Interaction			Int+SST			Int+SST+Cur		
	Dens±SD	Yield±SD		Dens±SD	Yield±SD		Dens±SD	Yield±SD		Dens±SD	Yield±SD	
2	11 ±9	16 ±14		8 ±7	11 ±9		7 ±5	9 ±8		4 ±4	2 ±1	
4	124 ±87	114 ±74		29 ±12	35 ±13		43 ±26	44 ±33		5 ±3	4 ±4	
6	1.854 ±3.03	1.508 ±2.48		72 ±23	77 ±23		710 ±367	800 ±404		8 ±5	7 ±5	
10	13.89 ±814	8.288 ±472		2.650 ±690	2.982 ±1.20		7.851 ±1.93	3.997 ±2.83		4.706 ±5.55	435 ±683	
20	19.33 ±568	6.487 ±462		16.07 ±1.19	7.487 ±687		12.71 ±1.62	6.262 ±988		10.75 ±1.73	5.625 ±2.42	
30	21.14 ±409	5.045 ±412		16.15 ±8.00	3.656 ±1.88		15.98 ±1.27	5.333 ±656		14.14 ±1.15	6.297 ±1.02	
40	24.67 ±571	1.604 ±499		22.02 ±655	4.275 ±669		20.57 ±839	3.286 ±418		18.09 ±558	4.292 ±467	
60	25.22 ±515	1.884 ±478		24.62 ±442	2.358 ±605		23.24 ±548	938 ±223		21.97 ±869	936 ±180	
80	26.29 ±401	855 ±218		25.58 ±619	2.183 ±489		24.31 ±755	1.056 ±230		21.74 ±557	1.147 ±162	
90	26.29 ±268	881 ±335		26.07 ±373	1.336 ±389		25.15 ±327	611 ±127		22.00 ±697	1.234 ±206	
96	26.94 ±251	126 ±25		26.90 ±358	210 ±76		25.44 ±380	222 ±61		23.19 ±409	1.547 ±168	
98	27.12 ±335	0 ±0		26.77 ±229	0 ±0		25.81 ±218	2 ±1		24.26 ±410	375 ±157	

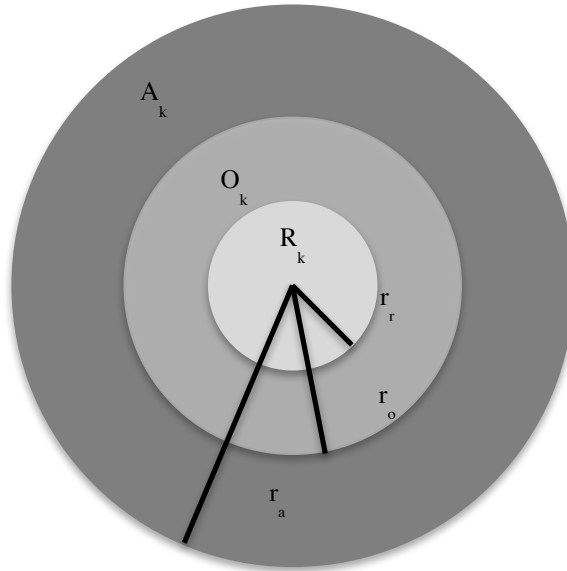


Figure 1: Zones of interaction of particle k . A_k is the *zone of attraction* (light grey area), O_k is the *zone of orientation* (medium grey) and R_k is the *zone of repulsion* (dark grey area). Each zone has a radius of r_a , r_o and r_r respectively.

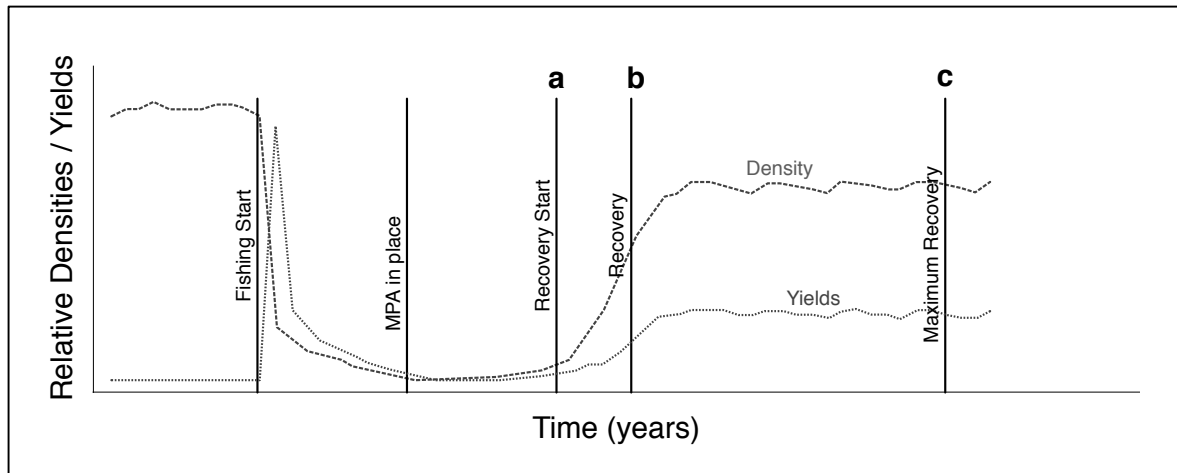


Figure 2: Representation of a relative stock density (dashed line) and fisheries yields (dotted line) time series. The figure shows when: the fishing start (year 10), the MPA is implemented (year 20), the recovery start (year 35, Figure 3a), the density and yield is increasing fast (year 40, Figure 3b), and the recovery is at its maximum and has reached the equilibrium (year 65, Figure 3c).

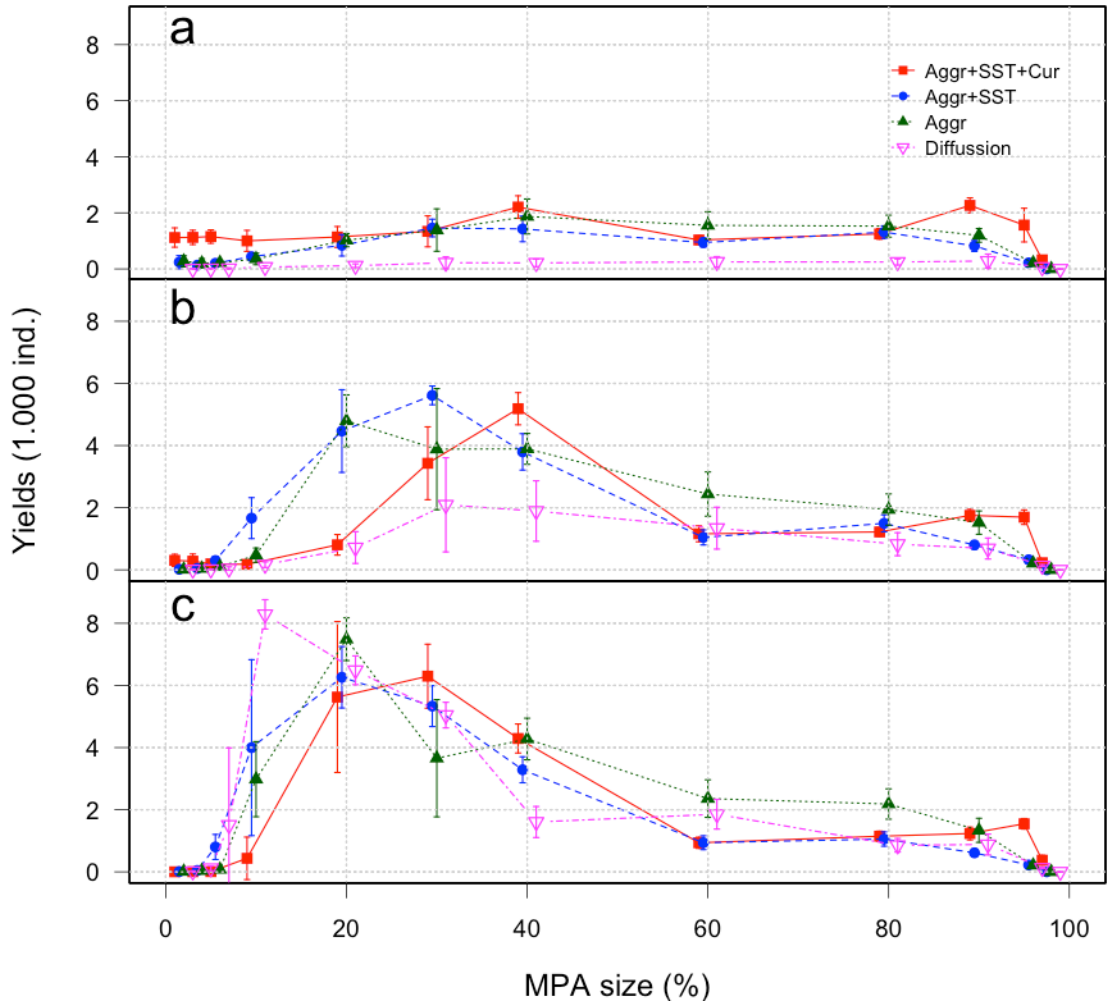


Figure 3: Mean landings values by MPA size and scenarios after a) 15, b) 20, and c) 45 years of MPA implementation. Aggr: Aggregation behavior, SST: Responses to the sea surface temperature, and Cur: Transport by currents.

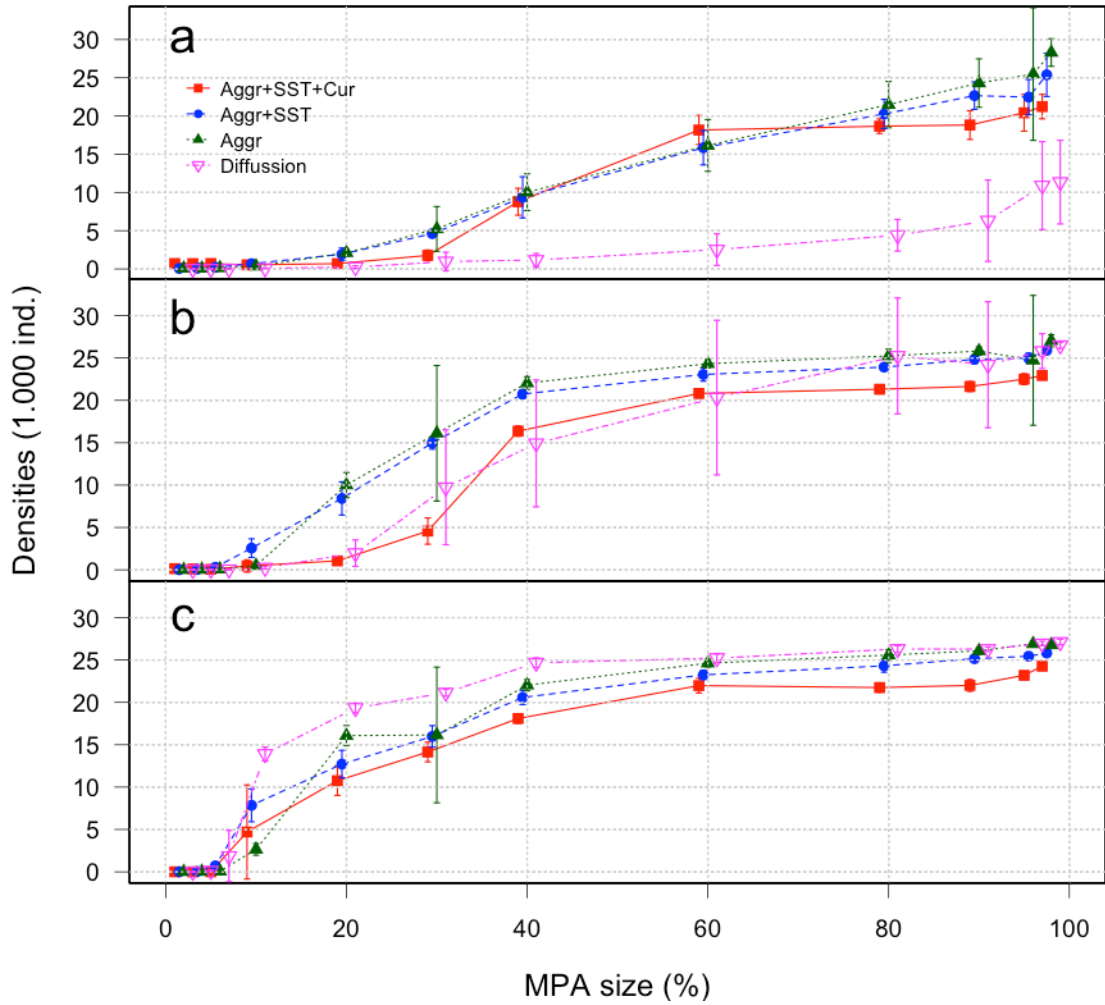


Figure 4: Mean densities by MPA sizes and scenario after a) 15, b) 20, and c) 45 years of the implemented MPA. Aggr: Aggregation behavior, SST: Responses to the sea surface temperature, and Cur: Transport by currents.

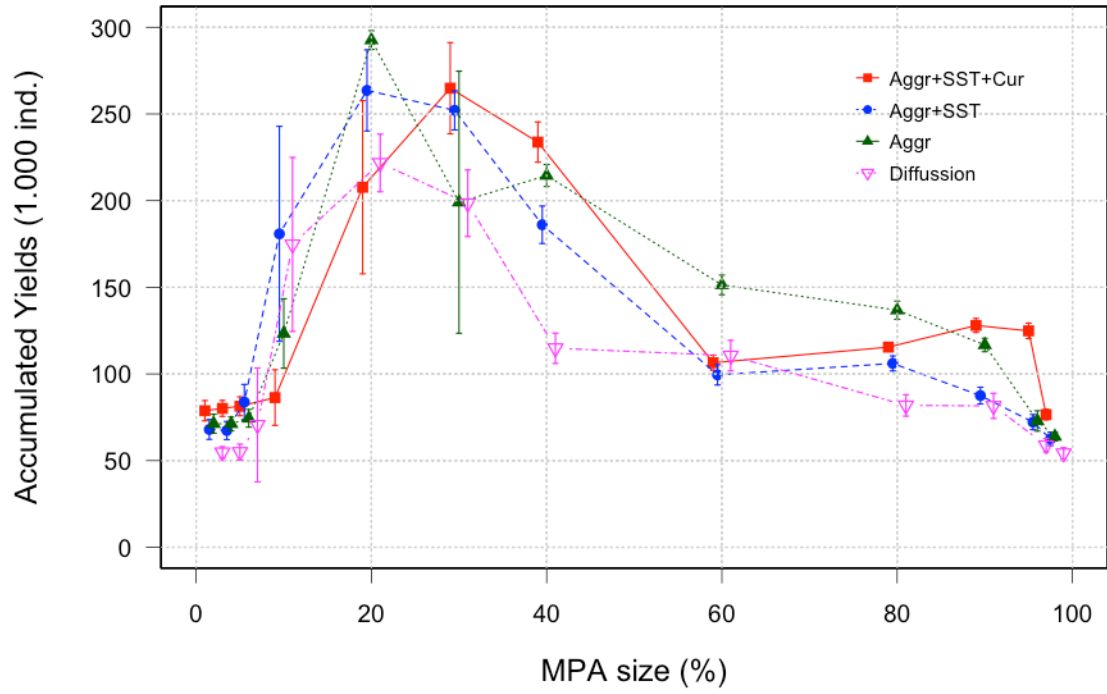


Figure 5: Accumulated landings for the whole period after MPA implementation (50 years). Aggr: Aggregation behavior, SST: Responses to the sea surface temperature, and Cur: Transport by currents

II. Effects of movement assumptions on the optimal placement of a marine protected area

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Abstract

Marine protected areas (MPA) are increasingly considered as important tools for managing fisheries due to benefits such as ease of management and increases in ecosystem resilience. Empirical demonstrations of benefits from different MPA designs are hard to obtain, because they require long term evaluations across multiple settings. Simulation models have been proposed as a complementary alternative to overcome these limitations and allow us to explore a broader diversity of MPA design issues.

In this paper we study how complexities of fish movement and environmental dynamics theoretically affect the predicted outcomes from different MPA designs. To this end, we compared MPA designs, in terms of placement and size, using an individual based model under four fish movement scenarios that span a range of increasing behavioral complexity: a) random, diffusive movement, b) aggregations, c) aggregations that respond to the environmental forcing (sea surface temperature), and d) aggregations that respond to the environmental forcing and are transported by currents.

Our results indicate that increasing the size of an MPA reduces the risk of selecting poor or suboptimal placements and protects a larger fraction of the stock while maintaining similar fisheries yields. Simplified movement assumptions (e.g. diffusive movement) underestimated the relative importance of the MPA placement and overestimated both the expected stock size and the mean time to recovery.

These findings highlight the value of understanding fish movement dynamics and their responses to environmental forcing. The impacts of different MPA designs depend greatly on these key biological traits. Finally, our results provide further evidence that large MPAs can be effective tools to protect, rebuilt and manage pelagic stocks.⁶

Keywords: IBM, Model, MPA, Marine Protected Area, management

Introduction

Marine protected areas (MPA) has been commonly used to protect and restore marine resources from ecosystem-wide changes caused by human activities (Grorud-Colvert et al., 2010) and are increasingly considered as tools for managing fisheries (McClanahan and Mangi, 2000) due to benefits such as ease of management, spillover of larvae and adults, and the increases in yields, abundance, and species diversity (Gaines et al., 2010; Gerber et al., 2003; Halpern, 2003). Although it is a generally accepted that MPAs can provide multiple benefits if well designed, it is a challenge to link any gains specifically to the MPA, because it requires a long time series of inside/outside and before/after data (Halpern, 2003). As a result, empirical evaluations of different MPA designs have made slow progress.

Simulation approaches have been proposed as a complementary way to compare among MPAs designs, but they are not exempt from challenges. It is known that simulations are highly sensitive to the assumptions describing the biology of larval dispersal and adult

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movement (Gaines et al., 2003; Gerber et al., 2003; Hilborn et al., 2006; Kellner et al., 2008) as well as to the complexity of the natural environment and human systems for which are been considered (McGilliard and Hilborn, 2008). Therefore, a successful simulation model that studies the optimal reserve design requires a considerable effort to include the role of young and adult dispersal (Gaines et al., 2003; Gerber et al., 2003; Hilborn et al., 2006; Kellner et al., 2008) and MPA configurations (i.e. size, placement and shape; Hilborn et al. 2006).

Several studies have successfully modeled detailed movement dynamics to predict such diverse outcomes as: fish migration (Barbaro et al., 2009; Magnússon et al., 2004), spatial trophic interactions between predators and prey (Huse et al., 2004), and optimal MPA size to maximize fisheries yields (Cornejo-Donoso et al. 2016). Including detailed movement dynamics and environmental complexity have the potential to improve MPA simulation models and enhance their success as tools for management.

Here we explore how different assumptions about fish movement affect the impact of MPAs on multiple outcomes. Although fish movement can have very complex dynamics (Helfman et al., 1997), most MPA models have made highly simplified assumptions about how fish move. If different movement dynamics greatly alter the outcomes from MPA creation, simple models may be creating misperceptions of MPA impacts. To explore this question, we built on the work of Cornejo-Donoso and collaborators (2016) to compare the expected impacts of MPAs using four scenarios with increasing movement complexity and realism.

Material and methods

The Model

We follow the Overview, Design concepts, and Details (ODD) protocol to describe individual based models (Grimm et al., 2006) - first providing an overview of the model, followed by a description of the underlining biological processes, including the fishery activities, and finally the detailed mathematical description of the underlying particle movement.

The Individual Based Model (IBM) used is an adapted version of the particle interaction model introduced by Vicsek and colleagues (1995), extended by Czirik and Vicsek (2000), and modified by Magnússon (Hubbard et al., 2004). All simulations were run using the infrastructure of the UCSB Center for Scientific Computing.

We explored how MPA placement affects expected outcomes with four movements assumptions (scenarios) of increasing complexity: a) random, diffusive movement, b) aggregations that move randomly, c) aggregations that respond to environmental forcing [sea surface temperature (SST)], and d) aggregations that respond to environmental forcing and are transported by currents. For this goal we use a particle movement model centered on the individual (i.e. the fish; Youseff et al. 2008), which incorporates schooling, environmental forcing, population dynamics, fishing mortality and a virtual MPA system (Cornejo-Donoso et al. 2016).

The state variables for each particle are position, velocity, and development stage (i.e. egg/larvae, juvenile and adults). In the most complex scenario, fish sense the position of nearby fish and the gradient of local SST. Then, based on those stimuli, the movement

direction and speed are actively adjusted for the next time step, while currents passively transport the fish.

At the population level, the state variables are the intrinsic growth rate (r), carrying capacity (K), natural mortality (Z), and fishing mortality rate (F ; Table 1).

The model incorporates stochasticity in several components including: the day of reproduction, initial movement direction and speed when the fish is added to the system (age 0), and timing of the individual death. The natural and fishing mortality are implemented as a daily probability of death for each particle.

Simulation scenarios

- v) *Random movement of adults and eggs/larvae*: this scenario is equivalent to movement by diffusion, with a mean diffusion coefficient of 0.0069 sectors per day. Eggs, juveniles and adults have the same movement patterns, which is completely independent of neighbouring fishes, with maximum speed increasing until maturation.
- vi) *Aggregation*: in this scenario the adults interact with their neighbours, coordinating their speed and direction, forming aggregations. The direction and speed of the school is not influenced by any environmental forcing, nor transported by currents.
- vii) *Aggregation, and environmental forcing*: In this case, adults interact with their neighbours, forming aggregations that coordinate their swimming direction and speed. The aggregations react to the local gradient of environmental forcing (SST) by adjusting their direction and speed.
- viii) *Aggregation, environmental forcing, and transport by currents*: this is the most complex movement assumption. In this case, the adults interact with their

neighbours, forming aggregations that coordinate their swimming direction and speed. These aggregations react to the local gradient of environmental forcing (SST) by adjusting their direction and speed and are transported by currents. Eggs/larvae are also transported by currents, but do not form aggregations. This scenario is considered the closest representation of nature, and therefore is used as a reference to compare the results obtained with other movement assumptions.

Simulation area

The simulation area is a rectangular grid of 100 by 40 sectors that represents the ocean. The simulated ocean covers a geographic extension larger than the expected distribution area of the simulated stocks. This area is defined as a closed system with no immigration or emigrations (i.e. repelling borders). Temperature and current fields are used to force the fish movement inside this grid. No vertical movement is included.

Population dynamics

Following the same approach of Cornejo-Donoso *et al.* (2016) the demographic parameters for the theoretical simulated fish are based on the Peru-Chile anchoveta (*Engraulis ringens* Jennyns, 1942), which is the world's largest fishery. Anchoveta have an adult length of ~15 cm, a short iteroparous life cycle, and a main spawning event during the second half of the year (Table 1). Reproduction is defined as a population event occurring around September 7, normally distributed with mean 250 and a standard deviation of 20 days (Table 1). Fecundity was defined as 10 eggs per individual, which after been added to the system were subject to a density dependent natural mortality (Z) which is adjusted to satisfy the population dynamics as predicted in the Gordon-Shafer model (Equations 1, 2 and 3 in

Chapter I; Gordon 1954). Adult natural mortality is defined and fix for two age class groups – one to four years old versus five years and older (Table 1).

Fish Age Classes

Three different types of particles are included on the simulations: eggs/larvae, juveniles and adults, each defined with distinct swimming capacities, aggregation behaviors, and responses to the environmental forcing.

- d) *Eggs/Larvae* are not active swimmers; therefore, they cannot form aggregations or respond to temperature fields. Their movements in the system are consequence of the transport done by currents and an initial slow movement to spread them from the spawning point.
- e) *Juveniles* have a limited swimming capacity; they formed aggregations and respond to temperature fields. Their maximum speed is slower than adults. Juveniles are not fished.
- f) *Adults* swim faster than juveniles. They are recruited to the fishery ($Z > 0$) and reproduce once a year.

Process scheduling

The simulations start by assigning a random position, speed, direction, day of reproduction and age (Table 1). Each simulation runs for 70 years. The first 20 years are without fishing to let the system reach equilibrium and to remove any potential effects of the initial conditions. At year 20, fishing starts and continues for 10 years without any fisheries management (i.e. open access). As a result, overfishing is inevitable. At year 30 an MPA of 20x20 (10% of the area) or 20x40 (20% of the area) is established that excludes all fishing,

which were the MPA areas that gave the largest yields in Chapter I (Jorge Cornejo-Donoso et al., 2016). Twenty-one systematically chosen locations for the MPA of 10% were explored by subsequently moving the MPA every 10 sectors in the x and y direction, and 15 locations for the MPA of 20% every 10 sectors in the x direction and every 20 sectors in the y direction. A buffer area of 10 sectors was left in the y axis border to minimize the border effect. Fishing boats operate without any restriction outside the MPA area.

For each time step ($\frac{1}{5}$ of a day), the fish interact with neighboring fish and respond to the temperature field by adjusting their heading and speed to seek preferred temperatures. As fish swim, they are also transported by currents. At the beginning of each day the fish ages by one day and natural mortality (Z) and reproduction occurs. Following reproduction and mortality, the fishing fleet is redistributed and imposes fishing mortality (F).

When a fish reproduces, the new egg/larvae is assigned with a birthday and given a random heading and movement speed (Table 1). Currents alone transport eggs/larvae and limited movement juveniles during the first six months as they do not self propel. If they survive this development period, their swimming capacity is progressively increased until they are one year old, when maturity is reached and recruitment to the fishery occurs (e.g. *Engraulis* spp; Froese and Pauly, 2000). Reproduction occurs annually.

Because there is stochasticity in the heading, speed, reproduction day, and in the timing of individual's deaths, there is variation among repeated simulations. Sixteen replicates were run to capture the extent of variability.

Fishing fleet distribution model

The fishing fleet is built into the model as a relocation dynamic that uses a total of 5,000 vessels that are spatially distributed based on the fish densities in each sector (Eq. 4 and 5,

Chapter I) as described in Hilborn and collaborators (2006) and modified by Cornejo-Donoso *et al.* (2016). An adjusted fishing mortality is obtained by multiplying the daily F by the number of boats in a particular sector and by a scaling factor that characterizes the likelihood of capture for a given density of fish and a given effort of fishing (calculated as in White & Costello 2014), in this way the realized fishing mortality is spatially heterogeneous.

The annual F for the simulated fishery was set to 1.27 per year as the mean for the space and time, equivalent to the F for the Peru-Chile anchovy fishery (CeDePesca, 2010; Leal and Bucarey, 2009; Serra *et al.*, 2009), which is an F high enough to overfish the stock and provide the conditions to test potential MPA benefits.

For details on the assumptions and equations used in the underlying fishing fleet model please see Chapter I.

Fish Movement

The fish movement is simulated using a discrete interaction particle model where each particle (i.e. fish) sense their surroundings to determine the neighbour's velocity to define its own, resulting in coordinated movement and aggregation behaviour. To simulate this interaction process three sensory zones are defined (Figure 1, Chapter I; Aoki, 1982; Barbaro *et al.*, 2009; Huth and Wissel, 1992); a) the innermost region (repulsion zone) where fish head away from each other to avoid collisions, b) the intermediate region (orientation zone) where fish coordinate their speed and direction, and c) the most external regions (attraction zone) where fish attract to each other and form aggregations (Figure 1, Chapter I).

For each time step, the heading and direction of the fish is recalculated based on the previous position and the positions of neighbouring fish, with a maximum speed of $10 \text{ km } d^{-1}$ for adult fish (James and Probyn, 1989; van der Lingen, 1995). Movement occurs in

continuous space and a weighted average of the direction and speed of the zone or orientation is taken.

For details on the assumptions and equations used in the underlying fish movement model please see Chapter I.

Environmental forcing

The environmental forcing is incorporated as a spatially heterogeneous grid of currents and temperature data, without temporal variability. This grid includes the coastline as areas of extreme temperature values. The SST mean for August of 2009 was obtained from the global dataset provided by NASA OceanColor web site⁷. This month had significant spatial SST variability with values above and below the range used to force the movement. A subset of the global image (18° and 24° Lat S) was selected of the coast of Peru and Chile, and a mask was applied to reshape the land and ocean areas into a form equivalent to the defined simulation area. An annual mean of the current circulation of AVISO/geostrophic currents for the same area was obtained from the NOAA's Coastwatch service⁸. These data had a resolution of 0.25° and were interpolated and reshaped to make them compatible with the simulation area (using kriging in R). This current field is used to passively transport the fish.

Results

Under all simulation scenarios, a strategically designed MPA protecting 10% or 20% of the area rebuilt the stock and increased fisheries yields. The larger MPA performed better in terms of densities but not in landings (Figures 1, 2, 3 and 4). Overall, for some outcomes

⁷ Daytime SST 11 μ 4x4 km processed from the data obtained with the MODIS-Aqua sensor (<http://oceancolor.gsfc.nasa.gov/>)

⁸ <http://coastwatch.pfeg.noaa.gov/coastwatch/CWBrowserWW360.jsp>

simplified movement models made similar forecasts for the benefits of an MPA relative to the full movement model. For other outcomes, however, simplified models either underestimated or overestimated the benefits of an MPA (Figure 5).

When 10% of the area was protected, the most complex environmental movement scenario had an average density recovery equivalent to 19% of unfished levels (Figure 1d), but the level of recovery varied substantially among MPA locations. At the best location for density recovery, densities reached 61% of unfished levels. Across the different movement scenarios, average densities varied greatly, but peak densities for the best MPA locations under each scenario have very similar final densities. As expected, the protection increased when 20% of the area was closed to the fisheries. In this case, peak densities at equilibrium reached *ca.* 80% of unfished levels (Figure 2d) under all movement scenarios (Figure 2). As with the smaller MPA, average densities varied greatly among the movement scenarios.

When the MPA placement was optimized to maximize fisheries benefits the most complex environmental movement scenario predicted peak sustainable landings equivalent to 86% of MSY for both MPA sizes (10% MPA Figure 3d and 20% MPA Figure 4d). For this outcome, the simplified movement models tended to overestimate the potential peak yields (Figure 5). For example, expected peak sustainable yields under the diffusion scenario with a 20% MPA size reached 98% of MSY.

In terms of the time required to recover the stock, larger MPAs and more complex movement dynamics drove faster recoveries. The optimized MPA placement for the most complex environmental movement scenario predicted a recovery time between 1.5 and 4 times faster than the best placement under the other scenarios (Figures 1 and 2). Mean recovery times were 8, 12, 21, and 33 years for the 10% MPA and 5, 10, 10 and 20 years for

the 20% MPA for the most complex environmental movement, SST, aggregations, and diffusion movement respectively. All simplified movement scenarios greatly overestimate the time to stock and fisheries recovery relative to expected results with more realistic patterns of movement.

The results above compared outcomes from the best MPA locations under different movement scenarios. Such analyses may be masking larger differences between model predictions, because the best MPA locations may differ among the four movement models. Therefore, even for outcomes where the models predicted similar best responses, the choice of MPA locations could be very different. Therefore, the simplified model could recommend placements that do not perform optimally when subject to all movement dynamics (Figure 5). To explore this issue and simplify the comparison between the four movement scenarios, we identified the three best MPA placements that maximized the stock size under each movement scenario (Figures 1 and 2). Then we used these “best” MPA locations to predict outcomes under the full movement model. In the case of the 10% MPA, the three best locations obtained from the diffusion and aggregation scenarios produced highly variable and often suboptimal outcomes. In each case, one MPA location did not produce any recovery of the stock, a second MPA location produced a suboptimal recovery, while the final MPA location did well to maximize stock recovery (Figure 6a). For the MPA locations suggested by the SST movement model, two of the three MPAs produced results that maximized densities, while one was suboptimal. By definition, all three locations suggested by the most complex environmental movement scenario produced very high recovery densities. Relative to the peak MPA location in terms of maximal equilibrium densities, the average responses

of the four movement models (diffusion, aggregation, SST, full movement) were 34%, 21%, 28% and 19%.

When the same analyses were run for the 20% MPA in all the scenarios, the variability among sites was smaller. Unlike the smaller MPA case, there were no “best” locations that failed to achieve significant stock recovery (Figure 6b). Therefore, the risk of choosing a poor location from a simplified movement model was reduced with a larger MPA.

Another factor influencing MPA location is the objective for the MPA. Locations that maximize recovery density (conservation objective) versus maximize yield (fisheries objective) may differ. If so, such tradeoffs in choice of MPA location have important management implications. Using the most complex environmental movement scenario to maximize recovered stock density, MPAs of 10% and 20% could maintain constant stock densities of 56% and 70% of unfished stock levels respectively. The MPAs that produce these peak stock recoveries only generate fisheries yields equivalent to ~68% and ~11% of MSY respectively. By contrast, when MPAs was placed in locations to maximize yields, the stock recovery was reduced to 40% and 41% of the unfished stock size respectively, but yields increased to ~86% of MSY for both MPA sizes (Figure 7).

Discussion

There is increasing evidence that large to very large MPAs can effectively protect stocks of highly mobile organisms, increase fisheries yields and increase fishery profits (Apostolaki et al., 2002; Game et al., 2009; White and Costello, 2014). Nevertheless, the MPA designs and locations that best meet these objections are difficult to evaluate empirically given the long times to recovery and the inability to compare competing designs. As a result, most of our insight on MPA design criteria comes from model analyses. This creates challenges when

dealing with MPA designs for highly mobile, pelagic species, because the behavioral and environmental drivers of movement are quite complex. The pelagic environment is a complex three dimensional system undergoing constant change. This complexity has driven modelers to make numerous simplifying assumptions about pelagic fish movement. The question is whether these simplifications have captured the key complexities that influence the efficacy of MPA designs. In this paper we addressed this question by comparing predictions about stock recovery and fisheries benefits from alternative model designs that are derived from an increasingly complex set of movement assumptions.

Our results suggest that simplified models of fish movement can generate predictions that are inconsistent with expectations from more complex models. In particular, simplified movement models tended to overestimate the potential fisheries yield benefits from an MPA and overestimate the time it would take to achieve these benefits (Figure 5). These misrepresentations would likely have opposing effects within an MPA planning process since one would suggest larger benefits, while the other would suggest the time to capture those benefits would increase substantially. Some predicted outcomes, such as the ultimate recovered density, were more consistently predicted by the competing movement models.

Perhaps the biggest challenge from using simplified movement models is the finding that they can predict very different locations for the optimal siting of an MPA. In some cases, prime sites under a simple movement model (e.g. diffusion or aggregation) showed no stock recovery when movement included more complex environmental drivers. If this finding is robust to other fisheries and environmental settings, it suggests caution in identifying optimal MPA designs from simple movement models.

Fortunately, the propensity for simple models to occasionally identify poor sites for MPAs when movement is more complex is countered by a key MPA characteristic – MPA size. Larger MPAs reduce the risks of suboptimal placement of MPAs. With a larger MPA the details of oceanographic flows and environmental gradients were less critical to performance, and even the simplest movement assumptions produced generally good results. Some simple rules of thumb derived from these findings are: a) when detailed stock movement dynamics are available it is possible to design small and efficient MPA with models that capture movement dynamics; and b) when knowledge of stock movement is limited, a larger MPA designed with simpler models can still yield very good results. These conclusions support previous findings indicating that MPA benefits are sensitive to the assumptions about fish movement (Gaines et al., 2003; Gerber et al., 2003; Kellner et al., 2008). In practical terms this means that gaining better insight on the details of fish movement could have important benefits to MPA designs, but in the absence of such information, a good alternative is to implement larger MPAs.

The MPAs simulated in this study were capable of rebuild an overfished stock and provide fisheries benefits, even when they were proportionally smaller than sizes previously reported as optimal to obtain these benefits (McClanahan and Mangi 2000, Gaines et al. 2010). Although these benefits accrue with MPAs that are 10% or 20% of the area, this area represent the entire stock distribution range. In absolute terms, the creation of an MPA of this dimension for the Peru-Chile anchovy stock would be of $\sim 40,000 \text{ km}^2$ in area, which is not a small MPA.

Even though models like the most complex environmental movement scenario used in this study are fairly complex, they are still abstractions of the complexities of movement by

pelagic fish, and they might not be good predictor of the real natural behavior. Our work suggests that the simple models of movement typically employed to study MPAs can be relatively poor abstractions of even slightly more complex models of movement. Although there are still many unresolved questions about the dynamics of fish movement, these findings suggest the need for caution in placing too much emphasis on predictions details from simple models and to keep working to improve the realism of fish movement simulations. These simulations are a good start in the search for the key movement characteristics that functionally impact MPA designs for conservation and fisheries benefits. Fortunately, in the absence of such knowledge, reasonably good outcomes for multiple objectives seem to arise by implementing larger MPAs.

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Table 1: Model input values.

Parameter	Initial Value	Units
Number of Fish	~25,000	<i>ind.</i>
Reproduction Day	$N(250, 20)$	<i>day</i>
Fish Heading	$U(0, 360)$	<i>deg</i>
Adult Fish Speed	$U(0, 10)$	$km\ d^{-1}$
Eggs/Larvae speed	$U(0, 0.02)$	$km\ d^{-1}$
Initial fish age	$U(1, 3)$	<i>year</i>
Diffusion coefficient	0.0069 [0.0000, 0167]	<i>sector\ d^{-1}</i>
Natural mortality (Z)		
1 to 4 years old	7×10^{-4}	d^{-1}
5+ years old	3×10^{-3}	d^{-1}
Fishing mortality (F)	1.27	y^{-1}
Fishing activity start	20	<i>year</i>
Management activity start	30	<i>year</i>
Total simulation length	70	<i>year</i>
Fecundity	10	<i>eggs\ ind^{-1}</i>
Radius of		
Repulsion r_r	0.02	<i>km</i>
Alignment r_o	0.10	<i>km</i>
Attraction r_a	0.10 ⁹	<i>km</i>
Temperature preferences [T_1, T_2]	[16, 18]	$^{\circ}C$
Weighted influence of		
Neighbors (α)	0.995	
Temperatures (β)	0.005	
Boat aggregation index (c)	3	
Fish carrying capacity (K)	30,000	<i>ind.</i>
Intrinsic rate of increase (r)	1.2	<i>ind.\ year^{-1}</i>
Simulation time-step Δt	0.05	<i>day</i>

⁹ This means that the area of attraction was not considered.

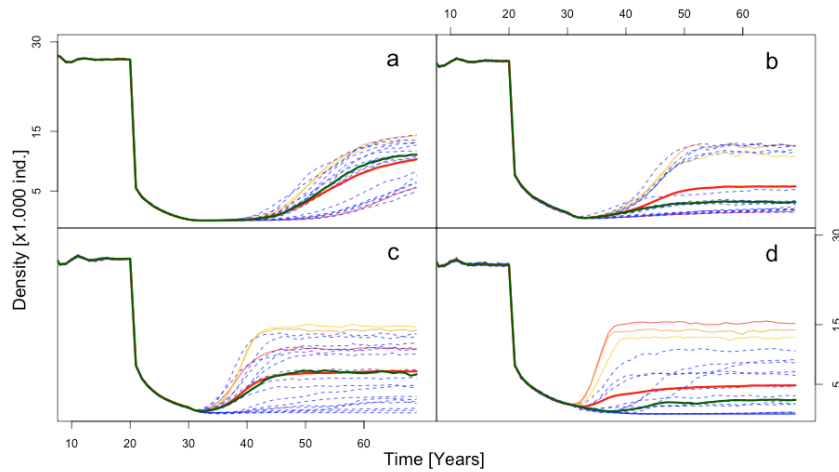


Figure 1: Time series of average densities obtained with an MPA of 10%. a) diffusive movement, b) aggregations, c) aggregations responding to the SST, and d) aggregations responding to SST and transported by the currents. Lines in red represent the mean of densities, in dark green the median and in thin red, orange and yellow, the 3 best placement optimized considering the most complex environmental movement scenario. Variability in the density estimation was not included to simplify the figure.

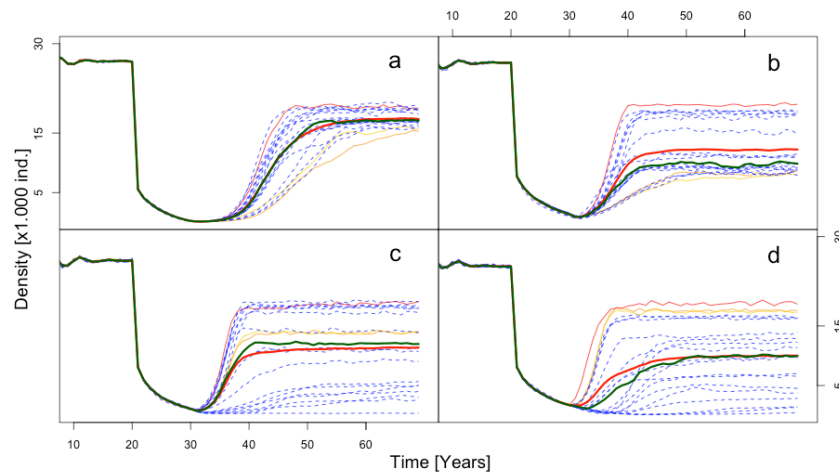


Figure 2: Time series of average densities obtained with an MPA of 20%. a) diffusive movement, b) aggregations, c) aggregations responding to the SST, and d) aggregations responding to SST and transported by the currents. Line in red represent the mean of densities, in dark green the median and in thin red, orange and yellow, the 3 best placement optimized considering the most complex environmental movement scenario. Variability in the density estimation was not included to simplify the image.

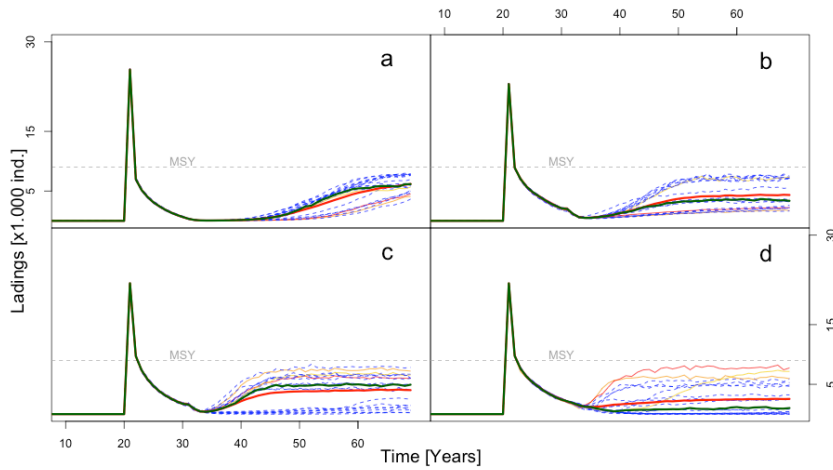


Figure 3: Time series of average landings with an MPA of 10%. a) diffusive movement, b) aggregations, c) aggregations responding to the SST, and d) aggregations responding to SST and transported by the currents. Line in red represent the mean of densities, in dark green the median and in thin red, orange and yellow, the 3 best placement optimized considering the most complex environmental movement scenario. Variability in the landings estimation was not included to simplify the image.

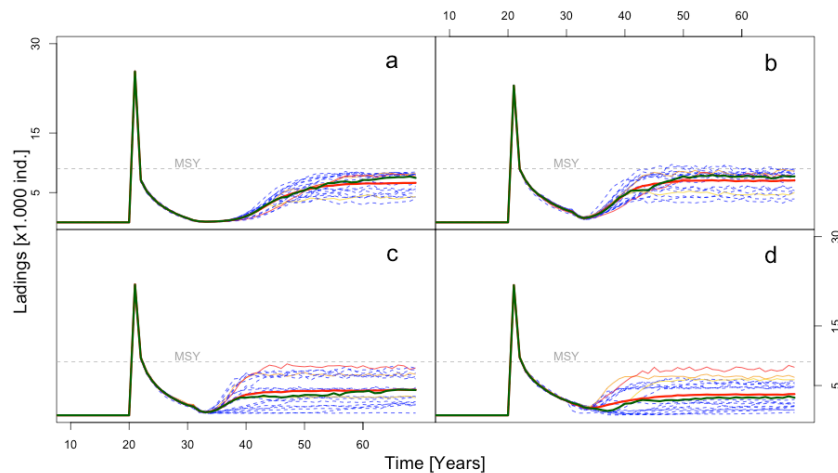


Figure 4: Time series of average landings with an MPA of 20%. a) diffusive movement, b) aggregations, c) aggregations responding to the SST, and d) aggregations responding to SST and transported by the currents. Line in red represent the mean of densities, in dark green the median and in thin red, orange and yellow, the 3 best placement optimized considering the most complex environmental movement scenario. Variability in the landings estimation was not included to simplify the image.

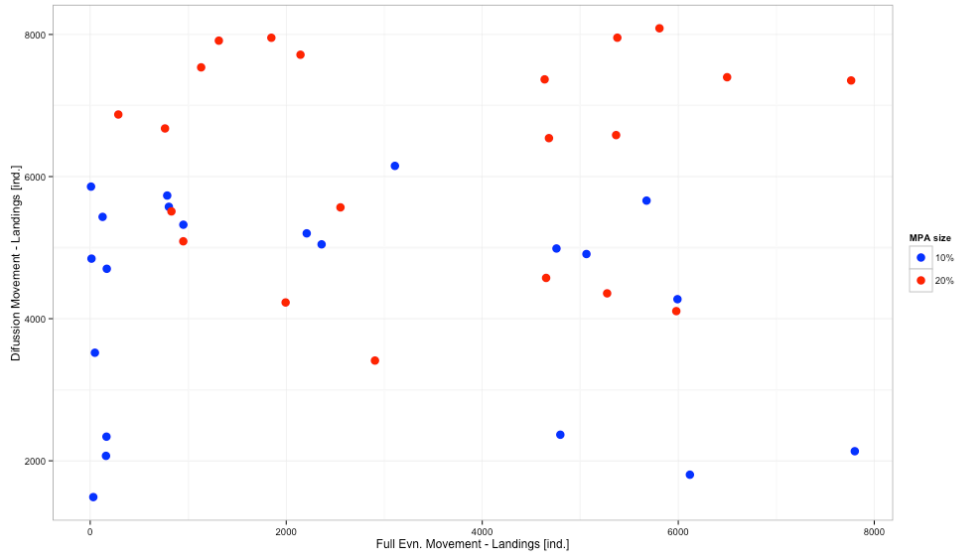


Figure 5: Mean landings predicted by each MPA placement using diffusion movement assumption (y axis) and using the full environment scenarios that include aggregation, responses to SST and transport by currents.

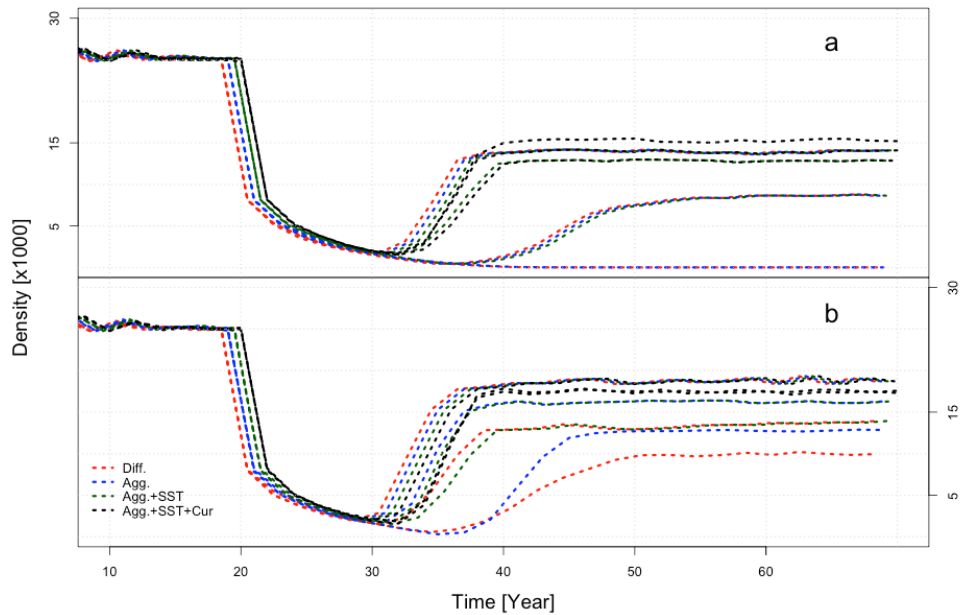


Figure 6: Time series of the predicted densities obtained with the full environment assumption for the MPA placements that resulted on the highest densities using the diffusion, aggregation, and SST forcing scenarios.

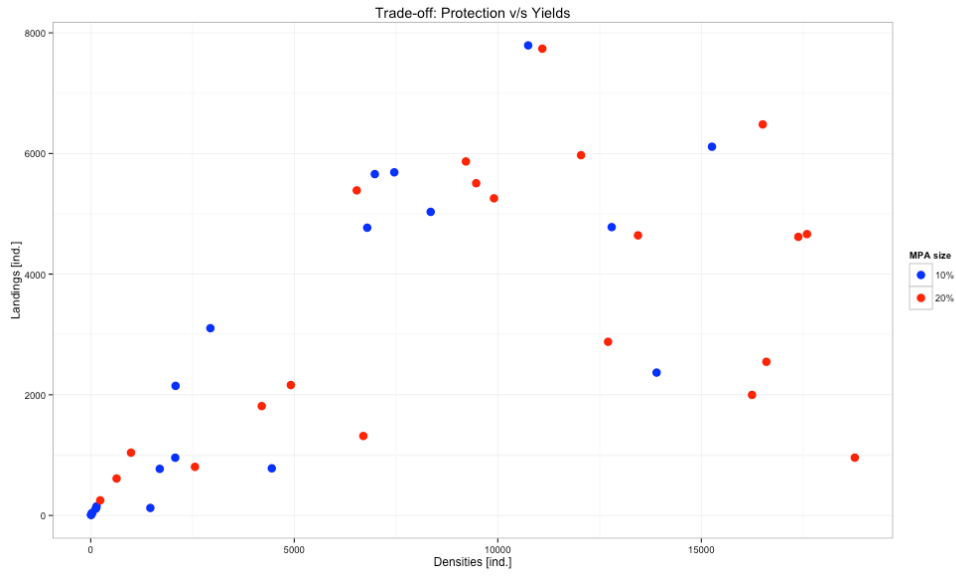


Figure 7: Trade off between protection of the stock (densities) and increasing landings for both MPA sizes using the most complex environmental movement scenario. 10% MPA size in blue and 20% MPA size in red.

Appendix: MPA properties

Residence time:

The residence time was calculated for each scenario¹⁰ and five MPA placements, which included the placement that resulted in the largest stock density, the largest yields and three other randomly selected. The daily fish position (as x, y coordinates) for the adults between the year 40 and to the last day of year 44 was obtained in each simulation. The total number of days that the fish was inside the protected area, and the total days in the fish life were computed, dropping all the organisms were never inside the MPA. The mean residence time for each MPA placement and scenario was obtained in days, years and as a fraction of the total fish life (Table 1).

The results of these simulations show that in all scenarios and placements analyzed a fraction of the organisms in the stock had a residence time larger than 1 year (Figure 1), giving them the opportunity to reproduce and sustain the stock. If a large fraction of the stock stays inside the protected area for a year or more, the MPA shows to be an effective management tool for protection and to increase their densities. Such is the case of the two MPA placements ($x: 10-30 y:20-60$ and $x:20-40 y:20-60$) with mean residence times larger than one year (Table 1) that gave the largest densities for the full environment scenario (i.e. aggregations that respond to SST and are transported by the currents) in Chapter II.

A *t-test* was used to identify if the differences in residence time between scenarios in the same placement and between placements for the same scenario. Our results indicate that

¹⁰ The movement scenarios used were aggregation with SST and Currents, aggregations and diffusion movement. Most of the simulations runs for aggregation movement that respond to the SST failed, probable as a consequence of a node in the cluster that went down.

differences in residence times between scenarios are significant (Table 2). Similarly, in most cases, the differences between placements for the same scenarios are also significant (Table 3). If we focus on the full environment scenario as a representative example, we can see that there are only two MPA placements (x:10-30 y:30-70 and x:20-40 y:50-90) where the mean residence time (305 and 307 days respectively) is not significantly different. As expected these two placements produced similar densities levels.

Exposure to the fishery

The exposure time was calculated for each scenario and three placements, including the MPA that produced the largest densities and medium yields (x:10-30 y:20-60; blue in Figure 2), the largest yields and medium densities (x:10-30 y:30-70; red in Figure 2), and a randomly selected MPA that produced low densities and yields (x:10-30 y:40-80; green in Figure 2). For each of these MPA placements and scenarios a simulation was run to obtain the daily position (as x, y coordinates) of all adult fishes in the system between the year 20 and the last days of year 24.

To obtain the maximum time that an individual fish spends outside the protected area (i.e. exposed to the fishery) the fishing mortality was removed ($F=0$). This allows fish to move in and out of the MPA without increasing their total mortality rate. The fishes that spend all their life inside or outside the MPA were dropped from the analysis. The individual exposure time was calculated as the total number of days that a fish was found outside the protected area, expressed in days, years and as a fraction of the total organism's life (Table 4).

One of the most interesting results about the exposure time is that the MPA with the lowest densities and yields had the largest exposure time (Table 4), which in combination with the reduced residence time (Table 1) could explain the low densities obtained for that

particular MPA placement (x:10-30 y:40-80) in Chapter II. On the other hand, the MPA with the largest yields showed the lowest exposure time, which is an unexpected result and probably an artifact of setting the fishing mortality to zero, reducing the density dependent spill-over and artificially increasing the residence time.

To detect significant differences between the scenarios for the same placement, and between placement for the same scenario, a pair-wise *t-test* was done. The results show significant differences (<0.01) for the full environment scenario between the three MPAs, and between scenarios for the same placement for two of the three MPA placements. MPA x:10-30 y:40-80, which produced the lowest densities and yields, did not have significant differences in the exposure time between scenarios.

Spatial distribution of capture per unit of effort (CPUE)

A spatially explicit grid containing fish density and capture per unit of effort (CPUE) was exported the last day of the year, between years 50 and 69 of the simulation. Using this grid, the distance to the closest point of the MPA border was calculated as:

$$D = \sqrt{(P_x - B_x)^2 + (P_y - B_y)^2} \times F$$

where:

P_x = Pixel position in the x axis

P_y = Pixel position in the y axis

B_x = Closest MPA border to the pixel in the x axis

B_y = Closest MPA border to the pixel in the y axis

F = Flag indicating if the pixel is inside (-1) or outside (1) the MPA

D = Minimum distance between a pixel and the MPA border

The mean fish density and mean CPUE was calculated for the pixels located at the same distance to the border. The resulting values are presented for the full environment scenarios

in figure 3, for aggregations that respond to the SST in figure 4, for aggregations that do not respond to the environment in figure 5 and for movement by diffusion in figure 6.

The results show the expected pattern known as fishing the line. In all the scenarios and placements, it is possible to observe that the fish densities are larger inside the MPA (negative values in the figures) where no fishing activities are allowed and decrease slowly towards the border. Outside the MPA the densities suffer a sharp decrease as consequence of the concentrated fishing activities close to the MPA border, where most of captures are found. This pattern was similar for all the MPA placements and scenarios.

The main changes in the spatial dynamics of fish density and CPUE were a consequence of the simplifications on the movement assumptions. As the movement is simplified the spatial distribution of fish densities is also simplified, which is then reflected on the spatial dynamics of the CPUE. We found three different patterns of the spatial distribution of density and CPUE depending on the movement scenario selected. For example the MPA on position x:10-30 y:20-60 for the scenarios that incorporate environmental forcing (both SST and SST and currents) shows high densities inside the MPA, with peaks and valleys of density and CPUE outside the MPA (Figures 3a and 4a). This same MPA position in the aggregation scenario shows a smooth decline of fish density from the MPA center to the outside areas (Figure 5a). Lastly in the scenario assuming movement by diffusion there is almost an homogeneous and flat density inside the MPA (Figure 6a). These results suggest the importance of the environmental forcing (SST and currents) to induce the heterogeneous spatial distribution of fish densities and their spill-over.

Conclusion

The right combination of a long residence time (close to a year) and a medium exposure time is required to generate the correct condition for an MPA to protect the stock and increase the yields at the same time. For example, with a high residence time the stock densities will increase, but these increases will not necessarily translate into large fisheries yields if the spill-over of adults is small. While a small residence time combined with a high exposure time will generate large initial yields followed by a sharp decline and posterior stock collapse. In this case the MPA does not retain the organisms for enough time to ensure at least one reproductive episode.

Understanding the relationship between spatial environmental heterogeneity and fish behavioral response (i.e. movement assumptions) is fundamental to predict the outcomes of an MPA placement in terms of stock densities and fisheries yields.

Table 1: Residence time for each MPA placement and scenario.

Placement	Scenario	Residence Time [Days]	Residence / Total [Life Span]	Life Span [days]
<i>x:10-30</i>	<i>Aggr+SST+Cur</i>	378±377	1.04±1.03	380±376
<i>Y:20-60</i>	<i>Aggr+SST</i>	-	-	-
	<i>Aggregation</i>	357±321	0.98±0.88	411±328
	<i>Diffusion</i>	426±430	1.17±1.18	456±427
<i>x:10-30</i>	<i>Aggr+SST+Cur</i>	313±319	0.86±0.87	334±318
<i>Y:40-80</i>	<i>Aggr+SST</i>	626±1039	1.71±2.85	626±1039
	<i>Aggregation</i>	192±243	0.53±0.66	323±306
	<i>Diffusion</i>	272±381	0.74±1.04	349±391
<i>x:20-40</i>	<i>Aggr+SST+Cur</i>	414±370	1.13±1.01	425±368
<i>Y:20-60</i>	<i>Aggr+SST</i>	-	-	-
	<i>Aggregation</i>	389±410	1.07±1.12	475±400
	<i>Diffusion</i>	449±455	1.23±1.25	479±445
<i>x:20-40</i>	<i>Aggr+SST+Cur</i>	307±315	0.84±0.86	330±315
<i>Y:50-90</i>	<i>Aggr+SST</i>	-	-	-
	<i>Aggregation</i>	387±413	1.06±1.13	476±411
	<i>Diffusion</i>	342±414	0.94±1.13	391±408
<i>x:10-30</i>	<i>Aggr+SST+Cur</i>	305±309	0.84±0.85	311±312
<i>Y:30-70</i>	<i>Aggr+SST</i>	-	-	-
	<i>Aggregation</i>	358±396	0.98±1.08	462±400
	<i>Diffusion</i>	414±453	1.13±1.24	453±438

Table 2: *t-test* results between scenarios using the same MPA placement.

Placement	Scenario / Scenario	t value	DF	p value
<i>x:10-30</i>	<i>Aggr+SST+Cur / Aggregation</i>	3.7036	7584	<0.001
<i>y:20-60</i>	<i>Aggr+SST+Cur / Diffusion</i>	-7.5289	11109	<0.001
	<i>Aggregation / Diffusion</i>	-15.683	22971	<0.001
<i>x:10-30</i>	<i>Aggr+SST+Cur / Aggregation</i>	72.052	111950	<0.001
<i>y:40-80</i>	<i>Aggr+SST+Cur / Diffusion</i>	18.37	82516	<0.001
	<i>Aggregation / Diffusion</i>	-37.596	72240	<0.001
<i>x:20-40</i>	<i>Aggr+SST+Cur / Aggregation</i>	12.243	153530	<0.001
<i>y:2060</i>	<i>Aggr+SST+Cur / Diffusion</i>	-15.916	133300	<0.001
	<i>Aggregation / Diffusion</i>	-26.209	140320	<0.001
<i>x:20-40</i>	<i>Aggr+SST+Cur / Aggregation</i>	-39.937	130640	<0.001
<i>y:50-90</i>	<i>Aggr+SST+Cur / Diffusion</i>	-12.592	50956	<0.001
	<i>Aggregation / Diffusion</i>	16.198	54303	<0.001
<i>x:10-30</i>	<i>Aggr+SST+Cur / Aggregation</i>	-27.401	129590	<0.001
<i>y:30-70</i>	<i>Aggr+SST+Cur / Diffusion</i>	-47.928	108260	<0.001
	<i>Aggregation / Diffusion</i>	-24.788	120610	<0.001

Table 3: *t*-test results between placements for the same scenario.

Placement / Placement	Aggr+SST+Currents			Aggregation			Diffusion		
	t value	DF	p	t value	DF	p	t value	DF	p
<i>x</i> :10-30 <i>y</i> :20-60									
<i>x</i> :10-30 <i>y</i> :40-80	12.3	5973	< 0.001	64.5	28073	< 0.001	37.1	19902	< 0.001
<i>x</i> :10-30 <i>y</i> :20-60									
<i>x</i> :20-40 <i>y</i> :20-60	-6.7	6065	< 0.001	-11.8	35886	< 0.001	-5.5	19300	< 0.001
<i>x</i> :10-30 <i>y</i> :20-60									
<i>x</i> :20-40 <i>y</i> :50-90	13.2	6087	< 0.001	-10.8	35468	< 0.001	19.1	24257	< 0.001
<i>x</i> :10-30 <i>y</i> :20-60									
<i>x</i> :10-30 <i>y</i> :30-70	13.7	6063	< 0.001	-0.1	33663	0.89	2.9	20065	0.004
<i>x</i> :10-30 <i>y</i> :40-80									
<i>x</i> :20-40 <i>y</i> :20-60	-54.5	137620	< 0.001	-108.4	127920	< 0.001	-70.4	104020	< 0.001
<i>x</i> :10-30 <i>y</i> :40-80									
<i>x</i> :20-40 <i>y</i> :50-90	2.8	112360	0.005	-107.8	131130	< 0.001	-23.4	61996	< 0.001
<i>x</i> :10-30 <i>y</i> :40-80									
<i>x</i> :10-30 <i>y</i> :30-70	4.1	112510	< 0.001	-94.9	133130	< 0.001	-55.1	101840	< 0.001
<i>x</i> :20-40 <i>y</i> :20-60									
<i>x</i> :20-40 <i>y</i> :50-90	55.2	122770	< 0.001	1.3	161150	0.2	36.4	63594	< 0.001
<i>x</i> :20-40 <i>y</i> :20-60									
<i>x</i> :10-30 <i>y</i> :30-70	56.9	123030	< 0.001	16.0	162010	< 0.001	13.7	128420	< 0.001
<i>x</i> :20-40 <i>y</i> :50-90									
<i>x</i> :10-30 <i>y</i> :30-70	1.2	104800	0.222	14.7	165850	< 0.001	-24.1	65994	< 0.001

Table 4: Exposure time for each MPA placement and scenario. placement.

Placement	Scenario	Exposure Time	Exposure Time	Life Span	Exposure time
		[Day]	[Year]	[Day]	[Proportion]
<i>x</i> :10-30 <i>y</i> :20-60	<i>Aggr+SST+Cur</i>	641±395	1.76±1.08	1,065±472	0.61±0.26
	<i>Aggr+SST</i>	371±278	1.02±0.76	568±406	0.64±0.10
	<i>Aggregation</i>	688±457	1.88±1.25	1,169±469	0.58±0.28
	<i>Diffusion</i>	608±432	1.67±1.18	1,104±450	0.54±0.28
<i>x</i> :10-30 <i>y</i> :40-80	<i>Aggr+SST+Cur</i>	683±389	1.87±1.07	989±403	0.66±0.24
	<i>Aggr+SST</i>	514±395	1.41±1.08	856±387	0.53±0.18
	<i>Aggregation</i>	606±494	1.66±1.35	1,103±505	0.54±0.32
	<i>Diffusion</i>	669±403	1.83±1.10	1,217±462	0.54±0.25
<i>x</i> :10-30 <i>y</i> :30-70	<i>Aggr+SST+Cur</i>	505±298	1.38±0.82	1,148±402	0.46±0.26
	<i>Aggr+SST</i>	-	-	-	-
	<i>Aggregation</i>	640±462	1.75±1.27	1,220±454	0.52±0.29
	<i>Diffusion</i>	679±464	1.86±1.27	1,206±491	0.55±0.28

Table 5: t-test between MPA placement for the same scenario.

Scenario	MPA placement								
	x:10-30 y:20-60			x:10-30 y:20-60			x:10-30 y:40-80		
	t value	DF	p	t value	DF	p	t value	DF	p
<i>Aggr+SST+Currents</i>	-3.1	3451	0.002	12.0	3441	<0.001	15.2	3028	<0.001
<i>Aggregation + SST</i>	-1.3	15	0.214	-	-	-	-	-	-
<i>Aggregation</i>	8.6	9937	<0.001	5.3	9996	<0.001	3.5	9954	<0.001
<i>Diffusion</i>	-7.2	9949	<0.001	-7.9	9948	<0.001	-1.2	9806	0.223

Table 6: t-test between scenarios for the same MPA placement.

MPA Placement		Scenarios	t value	df	p
<i>x:10-30 y:20-60</i>	<i>Agg+SST+Cur</i>	<i>Agg+SST</i>	8.41	96	<0.001
	<i>Agg+SST+Cur</i>	<i>Aggregation</i>	-4.16	3798	<0.001
	<i>Agg+SST+Cur</i>	<i>Diffusion</i>	3.02	3600	0.003
	<i>Agg+SST</i>	<i>Aggregation</i>	-10.08	88	<0.001
	<i>Agg+SST</i>	<i>Diffusion</i>	-7.55	88	<0.001
	<i>Aggregation</i>	<i>Diffusion</i>	8.99	9968	<0.001
<i>x:10-30 y:40-80</i>	<i>Agg+SST+Cur</i>	<i>Agg+SST</i>	1.59	13	0.135
	<i>Agg+SST+Cur</i>	<i>Aggregation</i>	6.42	3502	<0.001
	<i>Agg+SST+Cur</i>	<i>Diffusion</i>	1.26	2875	0.208
	<i>Agg+SST</i>	<i>Aggregation</i>	-0.87	13	0.397
	<i>Agg+SST</i>	<i>Diffusion</i>	-1.46	13	0.167
<i>x:10-30 y:30-70</i>	<i>Aggregation</i>	<i>Diffusion</i>	-6.90	9613	<0.001
	<i>Agg+SST+Cur</i>	<i>Aggregation</i>	-14.40	5473	<0.001
	<i>Agg+SST+Cur</i>	<i>Diffusion</i>	-18.57	5496	<0.001
	<i>Aggregation</i>	<i>Diffusion</i>	-4.27	9998	<0.001

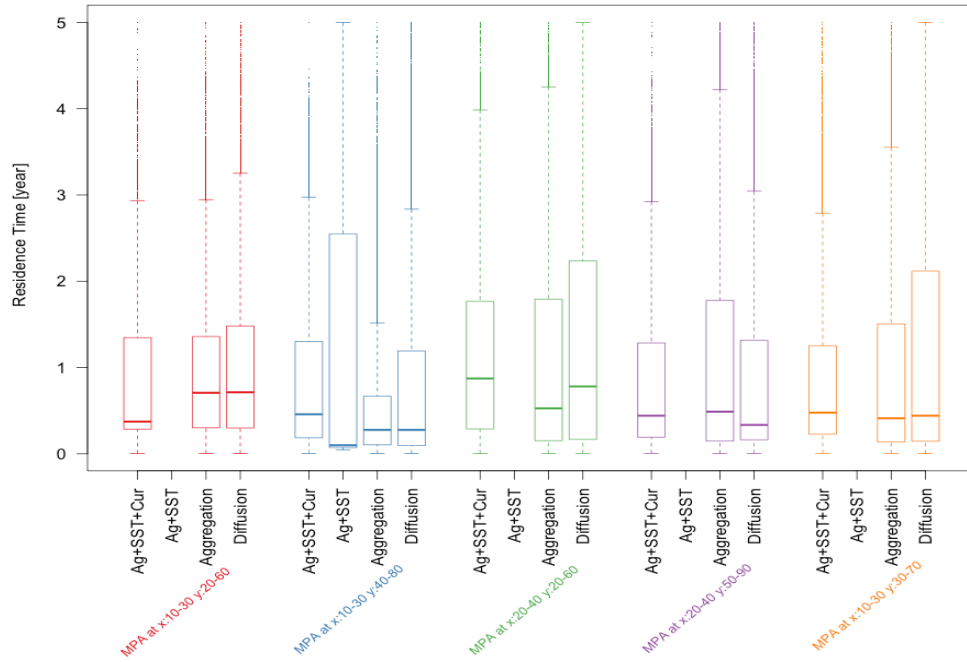


Figure 1: Boxplot of the mean residence time for each MPA placement and scenario standardized to the generation time, the time required for an organism to reproduce.

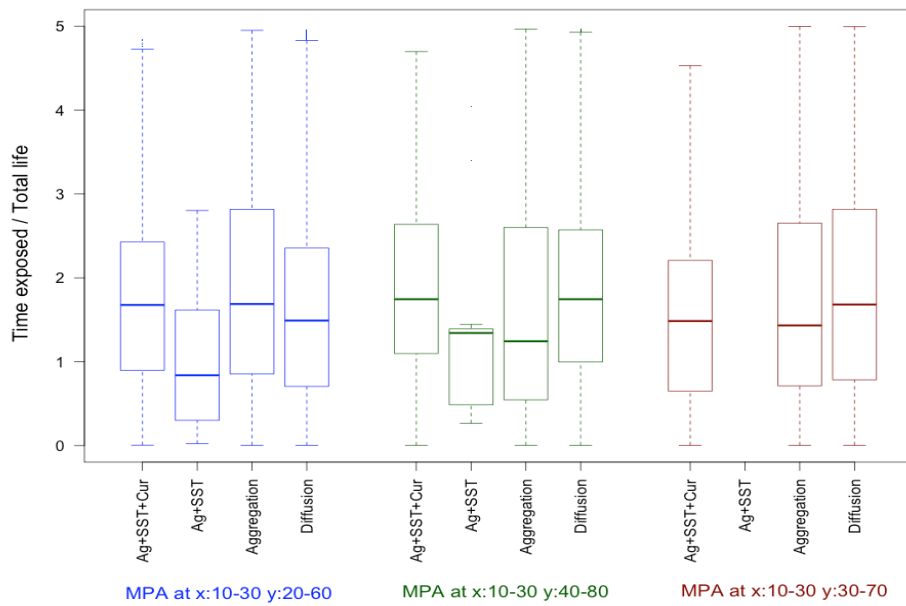


Figure 2: Boxplot of the fraction of the life of the fish spent outside of the protection of the MPA.

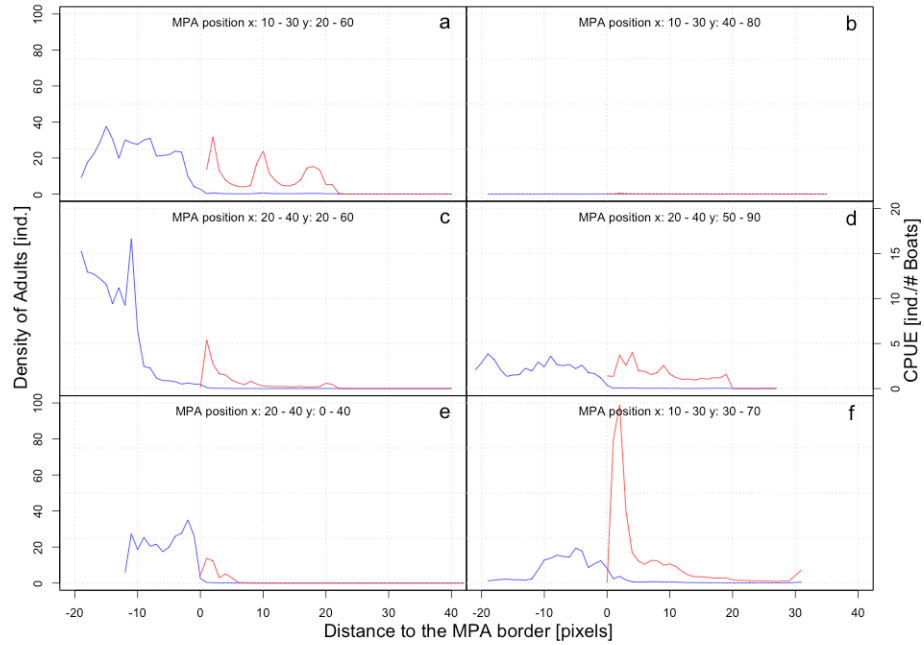


Figure 3: Mean density (in blue) and CPUE (in red) function of the distance to the border of an MPA of 20% assuming aggregation, response to SST and transport by current as movement (negative distances indicate the pixel is inside the MPA).

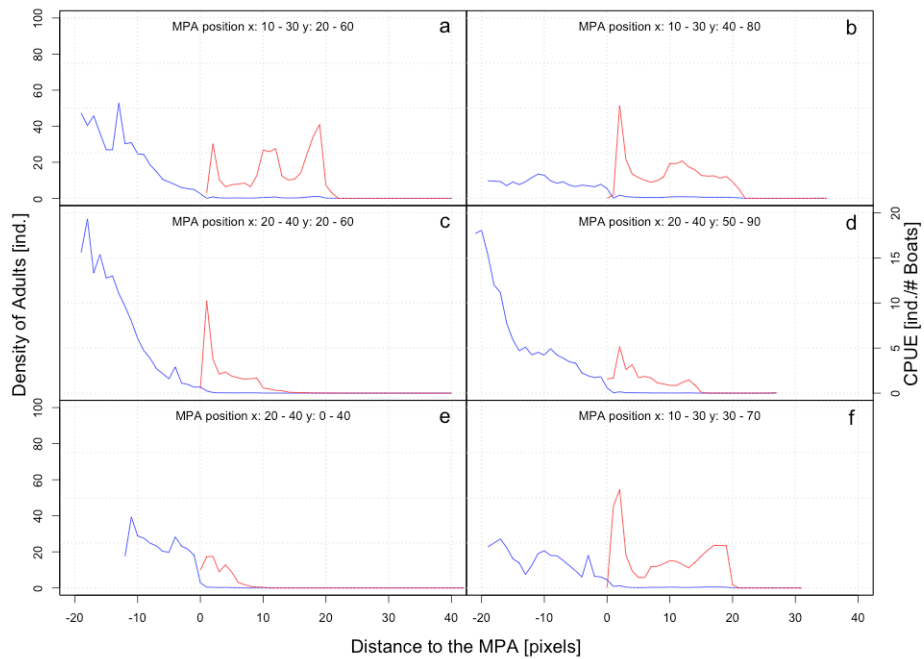


Figure 4: Mean density (in blue) and CPUE (in red) function of the distance to the border of an MPA of 20% assuming aggregation and response to SST as movement (negative distances indicate the pixel is inside the MPA).

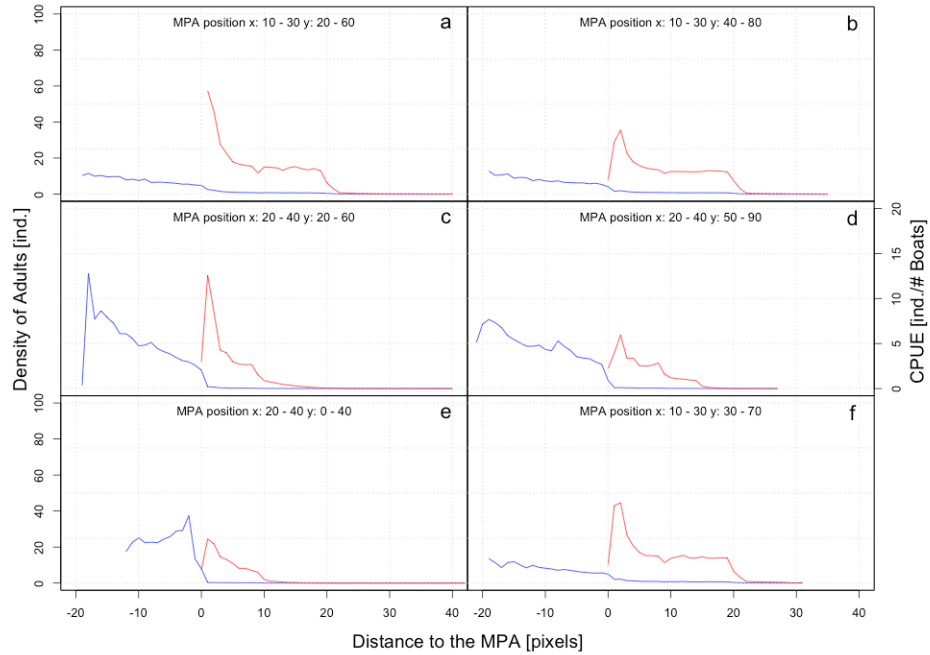


Figure 5: Mean density (in blue) and CPUE (in red) function of the distance to the border of an MPA of 20% assuming only aggregations as movement (negative distances indicate the pixel is inside the MPA).

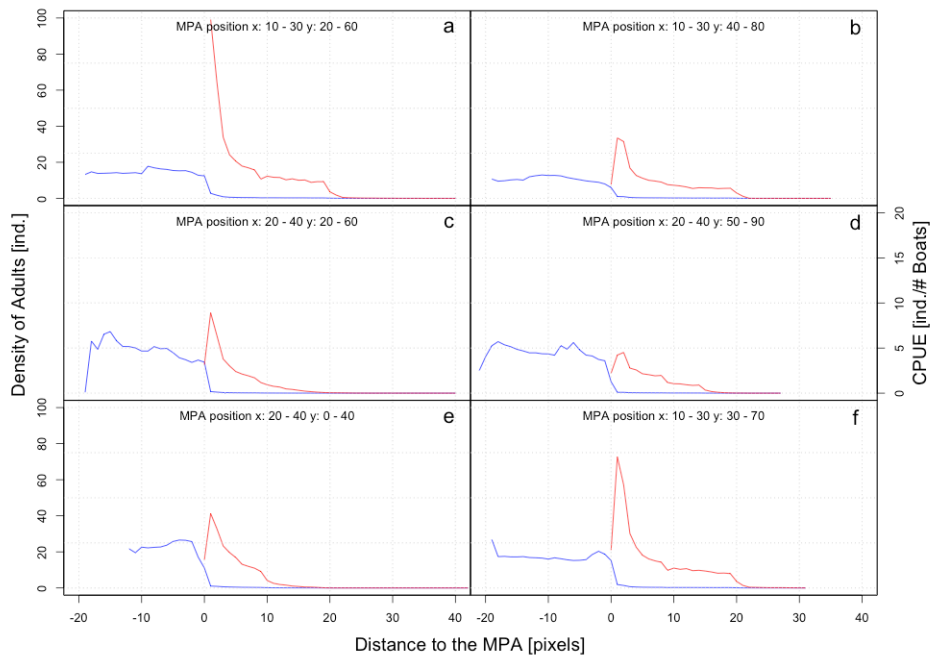


Figure 6: Mean density (in blue) and CPUE (in red) function of the distance to the border of an MPA of 20% assuming diffusion movement (negative distances indicate the pixel is inside the MPA).

III. Effects of the temporal environmental variability on the success of a marine protected area

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Abstract

Marine Protected Areas (MPA) are broadly used to protect benthic ecosystems and are increasingly considered in fisheries management, but they are seldom used to protect pelagic organisms because the design an effective MPA for a highly dynamic environment, where most organisms display complex movement patterns, has been a challenge.

Simulation models have been used to study the design of MPAs and to predict their outcomes. Nevertheless, most of the models have been developed for benthic systems where simplified assumptions about fish and fisherman movement can be used. Fortunately, scientific advances now allow the combination of complex individual-based models, population dynamics and virtual MPA system so new approaches, without the traditional simplified assumptions, are possible. Studies using these new complex simulation models have shown that it is possible to optimize the MPA design to increase both stock sizes and fisheries yields.

In this study we use an MPA model to simulate a complex pelagic environment with a spatially and temporally heterogeneous sea surface temperature that drives the organism's movement dynamics. The goal of these simulations was to study the effects of a highly variable environment on MPA design and success to increase stock size and fisheries yields.

Our results indicate that when temporal environmental variability is included, the expected fisheries benefits are significantly reduced relative to simulations with constant

environments, even when the stock density levels were similar. This suggests that in the case of a highly variable pelagic environment, a traditional MPA can protect the stocks, but it would not necessarily increase fisheries yields.¹¹

Keywords: IBM, MPA, Marine Protected Area, fisheries management

Introduction

Marine protected areas (MPA) are increasingly considered as an option within fisheries management (McClanahan and Mangi, 2000), because they protect and restore marine resources from ecosystem-wide changes (Gronrud-Colvert et al., 2010), are comparatively easy to manage, and when designed well can increase fisheries yields, abundance, and species diversity (Gaines et al., 2010; Gerber et al., 2003; Halpern, 2003). Although these benefits are widely touted, it is often a challenge to prove causality empirically since the benefits can arise over a moderately long time horizon (Halpern, 2003).

Simulation models are a complementary way to explore the likely impacts of MPA designs in more complicated fisheries scenarios (Jorge Cornejo-Donoso et al., 2016; Costello et al., 2010; Hilborn et al., 2004; Rassweiler et al., 2012). The challenge is identifying which complexities to include and which to ignore. Two of the main factors recognized to play an important role in this trade-off between simplification and realism are the organism's movement rates (Gaines et al., 2003; Gerber et al., 2003; Hilborn et al., 2006; Kellner et al.,

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2008) and the complexity/variability of the natural environment (McGilliard and Hilborn, 2008).

In the pelagic ecosystem, all organisms move at some point during their lives (Holyoak *et al.*, 2008; Lagler *et al.*, 1967), and the pattern of movement responds to changing environmental conditions both passively and actively (e.g. seeking foraging areas, avoiding predation or hostile conditions; Holyoak *et al.*, 2008). Understanding the magnitude and characteristics of movement is crucial to the design of effective marine reserves (Gaines *et al.*, 2003; Hilborn *et al.*, 2006). For instance, in areas with strong currents and dispersal by planktonic larvae, a network of multiple reserves can produce greater fisheries and conservation benefits than a single reserve of an equivalent total size (Gaines *et al.*, 2003). Furthermore, oversimplified movement assumptions can greatly underestimate MPA benefits and overestimate MPA costs, giving a false perception of MPAs as ineffective tools for management of pelagic stocks (Jorge Cornejo-Donoso *et al.*, 2016).

In this study we extend the work of Cornejo-Donoso and collaborators (Chapter I) to simulate a highly temporally and spatially variable environment to test the effectiveness of an MPA to rebuild a pelagic stock and increase fisheries yields. Previous simulations assumed a spatially heterogeneous environment that was constant over time. This is a reasonable assumption for certain ecosystems, but is not realistic for areas with marked seasonality or higher frequency variation, and therefore it may not be a reliable representation of the organism's movement and consequent impacts of spatial closures.

The importance of this challenge lies in the fact that some of the largest stocks and fisheries in the world are pelagic species with high movement rates and complex inter-

annual, seasonal and sub-seasonal oceanographic dynamics (e.g. ENSO¹², eddies, upwelling). Such variable oceanography drives variability in temperatures, salinity, food availability and other factors that can impact fish movement, stock distribution and density, which ultimately affect the stock availability to the fishery. An example of the consequences of drastic changes on the environmental conditions was described for the Chilean anchoveta during a strong El Niño event. The increase in sea surface temperature reduced the distribution area concentrating the fish, which resulted in an increase in fisheries captures, severe overfishing and finally several years of recruitments failures (Alheit and Ñiquen, 2004).

Models that do not incorporate at least some of the detailed environmental variability may not adequately represent the impacts of an MPA on fishery dynamics. Here we address these challenges by exploring the role of complex oceanography on fish movement and MPA impacts using a system similar to the Peru-Chile anchoveta fishery as a case study.

Methods

The Model

We follow the overview, design concepts, and details (ODD) protocol to describe individual based models (Grimm et al., 2006) - first providing an overview of the model, followed by a description of the underlining biological processes, including the fishery activities, and finally the mathematical description of the underlying particle movement.

The Individual Based Model (IBM) used is an adapted version of the particle interaction model introduced by Vicsek and colleagues (1995), extended by Czirók and Vicsek (2000),

¹² El Niño Southern Oscillation

and modified by Magnússon (Hubbard et al., 2004). All simulations were run using the infrastructure of the UCSB Center for Scientific Computing.

The purpose of these simulations was to study how seasonality in environmental forcing (temporal variability) can affect the MPA design, the effectiveness to rebuild an overfished stock and provide fisheries benefits. To this end, we used a particle movement model centered on the individual (i.e. the fish; Youseff *et al.*, 2008) which incorporates schooling, spatial and temporal environmental forcing, population dynamics, fishing mortality and a virtual MPA system (Jorge Cornejo-Donoso et al., 2016).

The state variables for each fish are position, velocity, and development stage (i.e. egg/larvae, juvenile and adults). The model design implies a fish sensing the position of nearby fishes and the gradient of local sea surface temperature (SST). Then, based on those stimuli, the movement direction and speed of the fish are actively adjusted for the next time step, while currents passively transported the fish.

At the population level, the state variables are the intrinsic growth rate (r), carrying capacity (K), natural mortality (Z), and fishing mortality rate (F ; Table 1).

The model incorporates stochasticity in several components including: the day of reproduction, initial movement direction and speed when the fish recruits to the system (age 0), and mortality rates. The natural and fishing mortality are implemented as a daily probability of death for each particle.

Simulation area

The simulation area is defined as a rectangular grid of 100 by 40 sectors that represented the ocean. The simulated ocean covers a geographic extension larger than the expected distribution area of the simulated stocks. This area is defined as a closed system with no

immigration or emigrations (i.e. repelling borders). Temperature and currents fields are used to force the fish movement inside the grid. No vertical movement is included.

Population dynamics

Following the same approach of Cornejo-Donoso *et al.* (2016b; Chapter I) the demographic parameters for the theoretical simulated fish are based on the Peru-Chile anchoveta (*Engraulis ringens* Jennyns, 1942), which is the world's largest fishery. Anchoveta have an adult length of ~15 cm, a short iteroparous life cycle, and a main spawning event during the second half of the year (Table 1). Reproduction is defined as a population event occurring around September 7, normally distributed with mean 250 and a standard deviation of 20 days (Table 1). Fecundity was defined as 10 eggs per individual, after been added to the system were subject to a density dependent natural mortality (Z) which is adjusted to satisfy the population dynamics as predicted in the Gordon-Shafer model (Equations 1, 2 and 3 in Chapter I; Gordon 1954). Adult natural mortality is defined and fix for two age class groups – one to four years old versus five years and older (Table 1).

Fish Age Classes

Three different types of particles are included on the simulations: eggs/larvae, juveniles and adults, each defined with distinct swimming capacities, aggregation behaviors, and responses to the environmental forcing (Table 1).

- g) *Eggs/Larvae* are not active swimmers; therefore, they cannot form aggregations or respond to temperature fields. Their movements in the system are consequence of the transport done by currents and an initial slow movement to spread them from the spawning point.

- h) *Juveniles* have a limited swimming capacity; they formed aggregations and respond to temperature fields. Their maximum speed is slower than adults. Juveniles are not fished.
- i) *Adults* swim faster than juveniles. They are recruited to the fishery ($Z > 0$) and reproduce once a year.

Process scheduling

The simulations start by assigning a random position, speed, direction, day of reproduction and age (Table 1). Each simulation runs for 70 years. The first 20 years are without fishing to let the system reach equilibrium and to remove any potential effects of the initial conditions. At year 20, fishing starts and continues for 10 years without any fisheries management (i.e. open access). As a result, overfishing is inevitable. At year 30 an MPA of 20x40 grid cells (20% of the area) is established that excludes all fishing. Fifteen systematically chosen locations were explored by subsequently moving the MPA every 10 sectors in the x direction and every 20 sectors in the y direction. A buffer area of 10 sectors was left in the y axis border to minimize the border effect. Fishing boats operate without any restriction outside the MPA area.

For each time step ($\frac{1}{5}$ of a day), the fish interact with neighboring fish and respond to the temperature field by adjusting their heading and speed to seek preferred temperatures. As fish swim, they are also transported by currents. At the beginning of each day the fish ages by one day and natural mortality (Z) and reproduction occurs. Following reproduction and mortality, the fishing fleet is redistributed and imposes fishing mortality (F).

When a fish reproduces, the new egg/larvae is assigned with a birthday and given a random heading and movement speed (Table 1). Currents alone transport eggs/larvae and

limited movement juveniles during the first six months as they do not self propel. If they survive this development period, their swimming capacity is progressively increased until they are one year old, when maturity is reached and recruitment to the fishery occurs (e.g. *Engraulis* spp; Froese and Pauly, 2000). Reproduction occurs annually.

Because there is stochasticity in the heading, speed, reproduction day, natural and fishing mortality there is variation among repeated simulations. Sixteen replicates were run to capture the extent of variability.

Fishing fleet distribution model

The fishing fleet is built into the model as a relocation dynamic that uses a total of 5,000 vessels that are spatially distributed based on the fish densities in each sector (Eq. 4 and 5, Chapter I) as described in Hilborn and collaborators (2006) and modified by Cornejo-Donoso *et al.* (2016b). An adjusted fishing mortality is obtained by multiplying the daily F by the number of boats in a particular sector and by a scaling factor that characterizes the likelihood of capture for a given density of fish and a given effort of fishing (calculated as in White & Costello 2014), in this way the realized fishing mortality is spatially heterogeneous.

The annual F for the simulated fishery was set to 1.27 per year as the mean for the space and time, equivalent to the F for the Peru-Chile anchovy fishery (CeDePesca, 2010; Leal and Bucarey, 2009; Serra *et al.*, 2009), which is an F high enough to overfish the stock and provide the conditions to test potential MPA benefits.

For details on the assumptions and equations used in the underlying fishing fleet model please see Chapter I.

Individual movement

Adult fish interact with their neighbors to form aggregations that coordinate their swimming direction and speed. Each time step the velocity is obtained as a weighed average of the velocity of neighboring fishes. For this purpose, three sensory zones around the particle are used; innermost zone of repulsion, where fish head away from each other, the zone of orientation, where the fish align their speed and direction, and the zone of attraction, where the fish heads toward the neighbors, forming the schools (Aoki, 1982; Barbaro et al., 2009; Huth and Wissel, 1992). For each time step, the heading and direction of the fish is recalculated based on the previous position and the positions of neighbouring fish, with a maximum speed of 10 km d^{-1} for adult fish (James and Probyn, 1989; van der Lingen, 1995). Movement occurs in continuous space and a weighted average of the direction and speed of the zone or orientation is taken.

These aggregations react to the local gradient of environmental forcing (SST) by adjusting their direction and speed, while passively being transported by currents.

Eggs/larvae are also transported by currents, but do not form aggregations.

For details the assumptions and equations used in the underlying model, please see Chapter I.

Environmental forcing

The environmental forcing is incorporated as a spatially heterogeneous grid of currents and a spatially and temporal heterogeneous SST data grid. This grid includes the coastline as areas of extreme temperature values. The SST monthly means for 2009 were obtained from

the global dataset provided by NASA OceanColor¹³. This year is assumed to represent the typical inter El Niño/La Niña environmental conditions for the system, and has significant spatial and temporal SST monthly variability with marked seasonality and values above and below the range used to force the movement. A subset of the global image (18° and 24° Lat S) was selected of the coast of Peru and Chile, and a mask was applied to reshape the land and ocean areas into a form equivalent to the defined simulation area. The final spatial temperatures times series was two thirds of the time between 15°C to 20°C, while only one third of the time it was on the warm side (20°C or higher; Figure 1).

An annual mean of the current circulation of AVISO/geostrophic currents for the same area was obtained from the NOAA's Coastwatch service¹⁴. These data had a resolution of 0.25° and were interpolated and reshaped to make them compatible with the simulation area (using kriging in R). This current field is used to passively transport the fish.

To test how sensitive is the model to the temperature preferences, eight simulations scenarios were run using the MPA placement that produces the largest landings and different fish temperature preferences. Four scenarios used a 4°C preferences range between 14°C and 24°C, and four used 2°C range between 16°C and 24°C. The temperature preference of 16°C to 18°C used in Chapter I and II (J. Cornejo-Donoso et al., 2016; Jorge Cornejo-Donoso et al., 2016) was the reference to compare between simulation.

¹³ Daytime SST 11µ 4x4 km processed from the data obtained with the MODIS-Aqua sensor (<http://oceancolor.gsfc.nasa.gov/>)

¹⁴ <http://coastwatch.pfeg.noaa.gov/coastwatch/CWBrowserWW360.jsp>

Results

When the temporal variability was included as part of the environmental forcing (i.e. SST seasonality) some MPA placements did not induce any stock recovery, some resulted in larger densities but not increased landings, and only a few placements resulted in both larger densities and landings. The predicted landings were smaller than those observed for similar densities when no temporal SST variability was included and an area of 20% was protected (Cornejo-Donoso *et al.*, 2016a; Chapter II). For instance, the largest stock recovery obtained, between the 15 MPA placements tested, was equivalent to ~65% of the unfished stock, while landings only recovered to values close to 10% of the maximum sustainable yield¹⁵ (MSY). When placement was selected based on fisheries benefits, the best placement provided a smaller stock size (~30% of the unfished stock) with a three-fold increase in fisheries landings (~35% of MSY; Figure 2).

We examined the outputs of our model considering a variety of temperature preferences and found that the results were not sensitive to the temperature parameter for temperatures within the range observed in SST. Scenarios with temperature preferences in the lower range of the observed SST (15°C to 20°C) did better in general, as their preferred temperatures were commonly found in the area.

As could be expected, scenarios with a broader range of temperature preferences (4°C) gave the organisms more environmental plasticity, even when the preferences included uncommon temperatures. The simulation scenario with temperature preferences of 20° to 24°C is special, in this case the stock collapsed in all but one of the replicates, which drove the mean stock densities and landings to higher values and also increased the variability

¹⁵ Defined as $MSY = \frac{K \cdot r}{4}$

around the mean (Figure 3). In scenarios with a smaller temperature preference range, the trends in density and landings were similar to those with a broader range, unless the preferences were close to 20°C (uncommon temperatures). In the latter cases the densities did not recover and no increases in fisheries landings were possible (Figure 3).

Discussion

The evidence showing that large MPAs are effective management tools to protect pelagic organisms is increasing and supports the idea that it is possible to design an MPA to recover pelagic stocks and benefit fisheries at the same time (Apostolaki et al., 2002; Jorge Cornejo-Donoso et al., 2016; Game et al., 2009; White and Costello, 2014). Nevertheless, most MPA simulation models have been developed for benthic environments and commonly use assumptions like sessile adults (Hilborn et al., 2006), diffusive movement of larvae and adults (Hilborn et al., 2006; McGilliard et al., 2010; Walters, 2000) and/or a homogeneous environment (Hilborn et al., 2006; McGilliard et al., 2010; Stefansson and Rosenberg, 2006), assumptions that are less reasonable for pelagic species. With the development of new models that allow the inclusion of detailed and complex movement dynamics and environmental forcing, it is now possible to improve MPA models and used them as reliable tools to study the MPA potential to protect pelagic stocks.

Our results suggest that when temporal SST variability is considered, it is possible to design an MPA that increases the mean residence time inside the protected area and therefore induces the recovery of an overfished pelagic stock. Between the 15 MPAs placements tested to increase stock protection and/or fisheries yields, some of them induced stock recovery, but these density increases resulted in smaller fisheries yields than those predicted with similar simulations where no SST seasonality was included (Chapter II). These results suggest that

the temporal environmental variability plays a fundamental role in the spatial distribution and also how the organism's movement responds to a changing environment.

In terms of the effects of temperature preferences in the outcomes of the simulated scenarios we conclude that the model is robust. In the case of drastic increases or decreases in SST beyond the preferred temperature range the organisms get trapped, which makes their stock more susceptible to fishing pressure. This explain why simulation scenarios that used high temperature preferences (above 20°C) did not recover after implementing the MPA. But even when the model seems to be robust to the temperature preferences and responds to the environmental forcing as was be expected, there could be some limitations. Our model did not include the effects of SST on reproduction success, organisms development, natural mortality or recruitment, all factors known to be affected by the environmental forcing (Morales-Bojórquez et al., 2003; Pauly, 1980; Pepin, 1991; Sabatés et al., 2006). Including the effects of environmental forcing on the population dynamics represent an interesting research avenue to explore, especially considering potential future ocean temperatures in the light of climate change.

The results in this study provide evidence that the movement dynamics of pelagic organisms, as well how that movement responds to environmental variability, need to be considered to design an effective pelagic MPA. Failing to include the environmental spatial and temporal variability and/or using oversimplified assumptions for the movement can mislead managers and policy makers, making decision based on incorrect or biases predictions. For instance, an MPA size that yielded very good outcomes with a constant world (i.e. no seasonality), did not work as well with this variable world. Future MPA simulations research should include all these details to improve realism, to guide the design

of pelagic MPAs, and give insight on potential scenarios to prepare alternative management options, preventing overfishing in situations as those experienced by the Chilean anchoveta stock.

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Table 1: Model input values.

Parameter	Initial Value	Units
Number of Fish	~25,000	<i>ind.</i>
Reproduction Day	$N(250, 20)$	<i>day</i>
Fish Heading	$U(0, 360)$	<i>deg</i>
Adult Fish Speed	$U(0, 10)$	$km\ d^{-1}$
Eggs/Larvae speed	$U(0, 0.02)$	$km\ d^{-1}$
Initial fish age	$U(1, 3)$	<i>year</i>
Natural mortality (Z)		
1 to 4 years old	7×10^{-4}	d^{-1}
5+ years old	3×10^{-3}	d^{-1}
Fishing mortality (F)	1.27	y^{-1}
Fishing activity start	20	<i>year</i>
Management activity start	30	<i>year</i>
Total simulation length	70	<i>year</i>
Fecundity	10	$eggs\ ind^{-1}$
Radius of		
Repulsion r_r	0.02	<i>km</i>
Alignment r_o	0.10	<i>km</i>
Attraction r_a	0.10^{16}	<i>km</i>
Temperature preferences	$[T_1, T_2]$	
Scenario 1	[14,18]	$^{\circ}C$
Scenario 2	[16, 20]	$^{\circ}C$
Scenario 3	[18, 22]	$^{\circ}C$
Scenario 4	[20, 24]	$^{\circ}C$
Scenario 5	[16, 18]	$^{\circ}C$
Scenario 6	[18, 20]	$^{\circ}C$
Scenario 7	[20, 22]	$^{\circ}C$
Scenario 8	[22, 24]	$^{\circ}C$
Weighted influence of		
Neighbours (α)	0.995	
Temperatures (β)	0.005	
Boat aggregation index (c)	3	
Fish carrying capacity (K)	30,000	<i>ind.</i>
Intrinsic rate of increase (r)	1.2	$ind.\ year^{-1}$
Simulation time-step Δt	0.05	<i>day</i>

¹⁶ This means that the area of attraction was not considered.

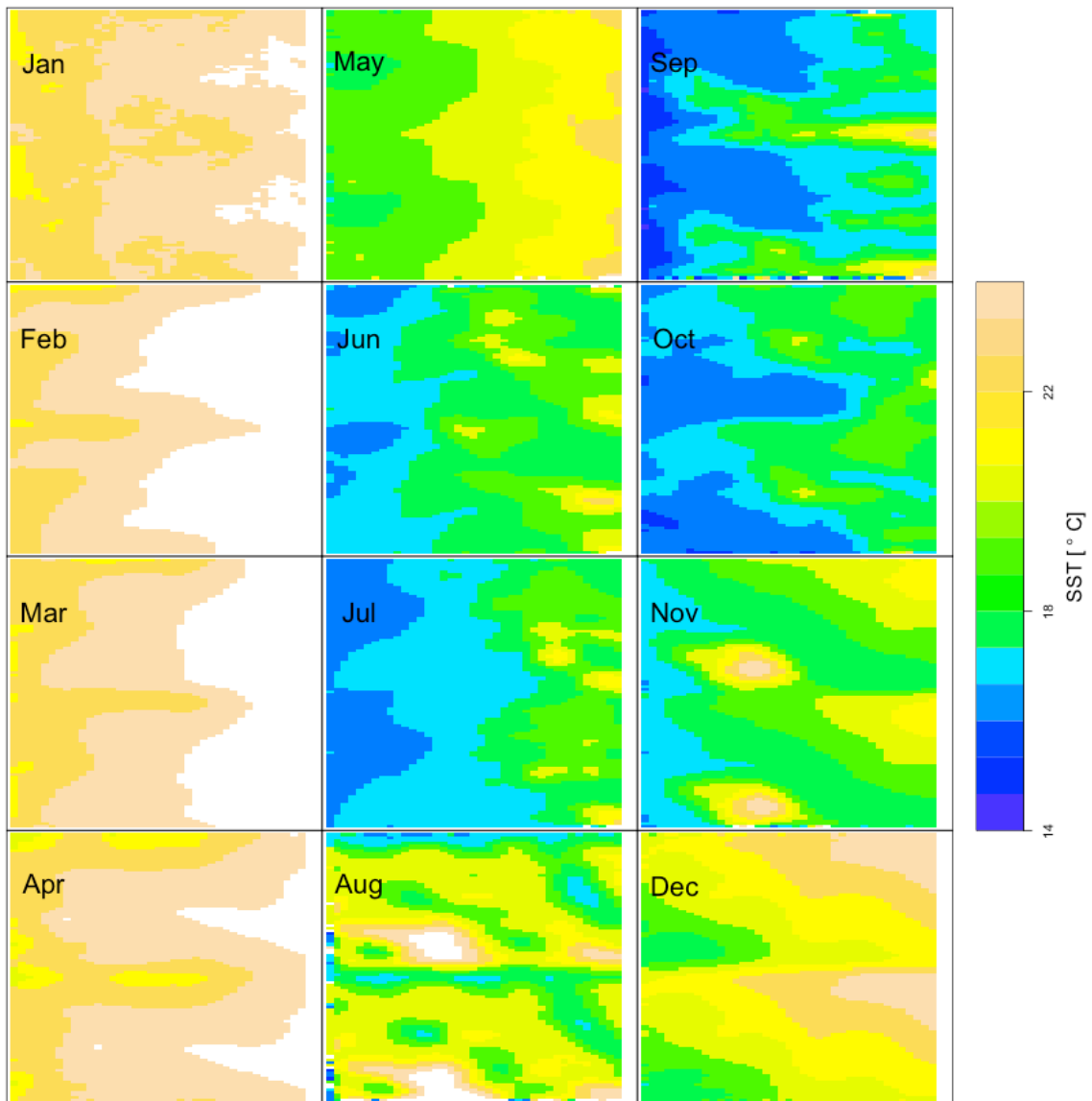


Figure 1: Monthly Sea Surface Temperature (SST) used as environmental forcing.

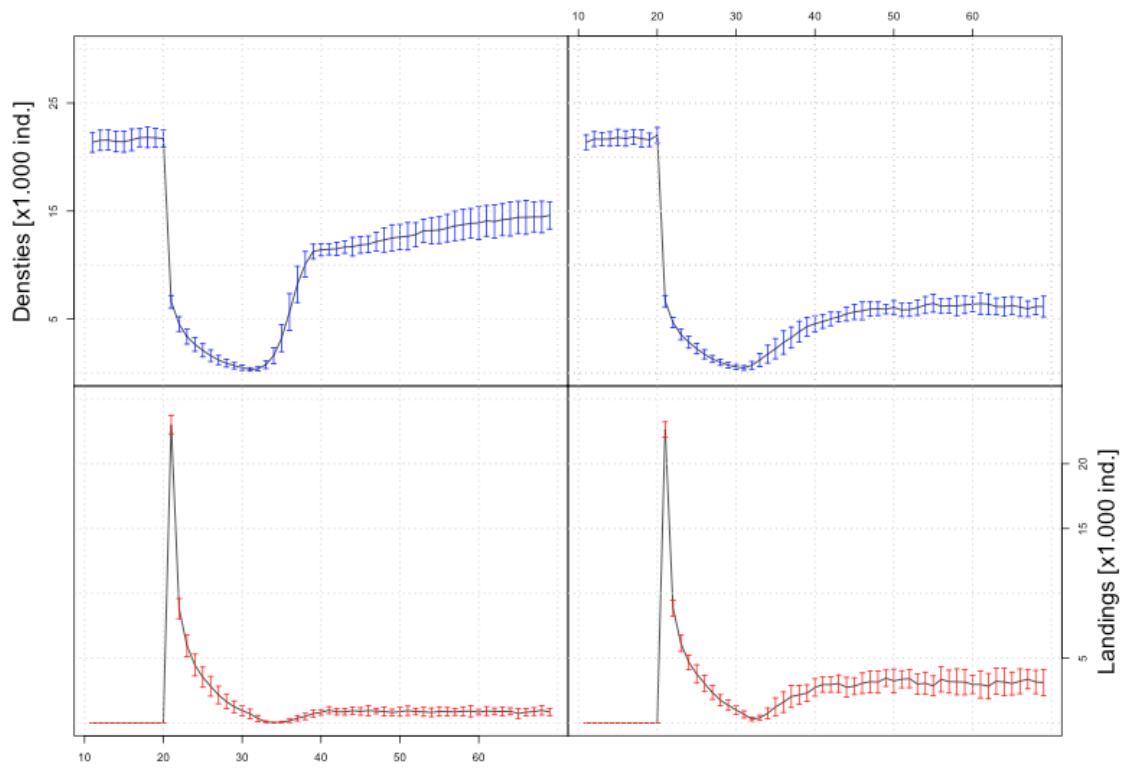


Figure 2: Time series of the mean densities (upper panel) and mean landings (lower panel) comparing between MPA placement optimized to increase densities (left side) and for landings (right side; errors bars represent the standard deviation of the mean).

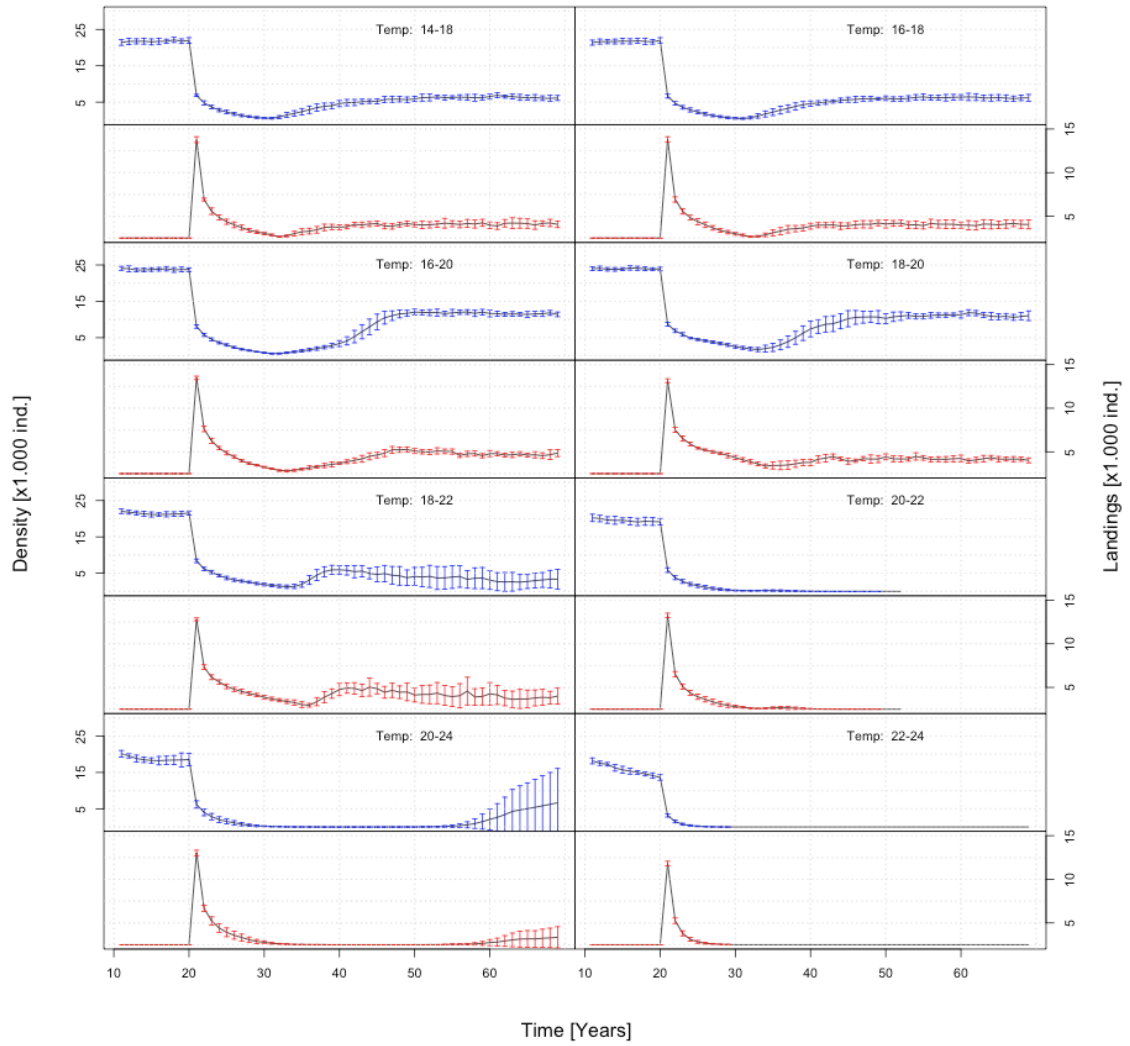


Figure 3: Density and landings time series for scenarios using alternative temperature preferences.