ICES Journal of Marine Science, 2022, **79**, 1467–1480
DOI: 10.1093/icesjms/fsac067
Advance access publication date: 6 May 2022
Original Article

Modelling the effect of habitat and fishing heterogeneity on the performance of a Total Allowable Catch-regulated fishery

Julie D. Pourtois[1,2,*], Mikaela M. Provost[1,2], Fiorenza Micheli[1,2,3] and Giulio A. De Leo[1,2]

[1] Hopkins Marine Station, Stanford University, Pacific Grove, CA 93950, USA
[2] Department of Biology, Stanford University, Stanford, CA 94305, USA
[3] Stanford Center for Ocean Solutions, Stanford University, Pacific Grove, CA 93950, USA

[*] *Corresponding author: tel: 6093569325; e-mail:* jp22@stanford.edu

Fisheries are often characterized by high heterogeneity in the spatial distribution of habitat quality, as well as fishing effort. However, in several fisheries, the objective of achieving a sustainable yield is addressed by limiting Total Allowable Catch (TAC), set as a fraction of the overall population, regardless of the population's spatial distribution and of fishing effort. Here, we use an integral projection model to investigate how stock abundance and catch in the green abalone fishery in Isla Natividad, Mexico, are affected by the interaction of heterogeneity in habitat quality and fishing effort, and whether these interactions change with Allee effects—reproductive failure in a low-density population. We found that high-quality areas are under-exploited when fishing pressure is homogeneous but habitat is heterogeneous. However, this leads to different fishery outcomes depending on the stock's exploitation status, namely: sub-optimal exploitation when the TAC is set to maximum sustainable yield, and stability against collapses when the fishery is overexploited. Concentration of fishing effort in productive areas can compensate for this effect, which, similarly, has opposite consequences in both scenarios: fishery performance increases if the TAC is sustainable but decreases in overexploited fisheries. These results only hold when Allee effects are included.

Keywords: abalones, Allee effect, fisheries, over-capacity, spatial heterogeneity, TAC.

Introduction

Accounting for spatial heterogeneity in habitat quality and in the distribution of target stocks is increasingly being recognized as an essential part of fisheries management (Caddy, 1975; Seijo *et al.*, 2004; Castello *et al.*, 2013; Kaplan *et al.*, 2014; Pérez-Jiménez and Mendez-Loeza, 2015; Voss *et al.*, 2018; Okamoto *et al.*, 2019; Woodson *et al.*, 2019). Patchy distributions of fish stocks may arise from spatial variation in habitat quality and productivity, and can also be driven by complex hydrographic processes regulating dispersal and local retention of fish larvae over convoluted coastlines, marine shoals, banks and seamounts, as well as by adult movement and spawning behaviour (Ciannelli *et al.*, 2010; Skjæraasen *et al.*, 2011; Huserbråten *et al.*, 2018; Barth *et al.*, 2019; Norderhaug *et al.*, 2021). In sedentary species, areas with low-quality habitats are generally characterized by low recruitment, which then influences spatial patterns in mature adults (Charton and Ruzafa, 1999). Even highly mobile species can exhibit complex spatial structures, with populations composed of multiple sub-stocks using different spawning grounds or travelling over long distances (Reich and DeAlteris, 2009; Kaplan *et al.*, 2014).

Disregarding spatial heterogeneity in the dynamics of substocks within large areas increases the risk of local overexploitation, reduces yield (Voss *et al.*, 2018) and can obscure early warnings of population collapse (Charton and Ruzafa, 1999; Reich and DeAlteris, 2009; Kaplan *et al.*, 2014; Okamoto *et al.*, 2019). Unfortunately, gathering fine-scale spatial information on habitat quality and sub-stock structure is time-consuming and costly. As a consequence, many fisheries have been traditionally managed over large areas without accounting for the fine scale spatial distribution of sub-stocks nor for heterogeneities in the quality of the fishing ground. A common non-spatial management system used in fisheries sets a Total Allowable Catch (TAC) for the entire stock. In response to declining catches in the 1980s (Ye and Gutierrez, 2017), managers of open-access commercial fisheries limited catches by setting a yearly TAC for the management unit, with the fishery closing once the quota is met (Plummer *et al.* 2012; Morgan, 1997; Batstone and Sharp, 1999; Daw and Gray, 2005; Ye and Gutierrez, 2017). Owing to their simplicity, many fisheries have maintained their TAC regulations, which have since also been implemented in other fisheries across the world (Lokani *et al.*, 1995; Hernandez and Kempton, 2003; Branch and Clark, 2006; Ryu *et al.*, 2006; Matsuda *et al.*, 2010).

Many challenges are associated with TAC-regulated fisheries, however. Because the fishery closes when the quota is reached, this system inherently puts fishers in competition against each other for a share of the quota, resulting in an "Olympic race to fish" (Hilborn, 2007). This race to fish can also be caused by the steep price of some fishing licenses, leading to fishers having to put their personal assets at risk. In the absence of more complex management systems based on individual transferable quotas (ITQ) and territorial use rights for fishing (TURF), the race to fish inevitably creates incentives to boost harvesting effort by increasing the size and number of fishing vessels, ultimately leading to over-capitalized fleets and strong political pressure to further increase exploitation rates (Branch *et al.*, 2006; Beddington *et al.*, 2007; Antica-

Received: October 15, 2021. **Revised:** March 16, 2022. **Accepted:** March 21, 2022

mara *et al.*, 2011; Rust *et al.*, 2016). This pressure to maximize short-term catch and the challenges of stock assessment often result in TAC limits set higher than would be needed in order to achieve the maximum sustainable yield (MSY) or other, more conservative fishery targets (Daw and Gray, 2005; Villasante *et al.*, 2011). However, even when the TAC is set at conservative levels relative to MSY, fisheries can still experience a decline in stocks over time. This happens, for example, when stocks are managed over broad management areas, overriding the underlying spatial heterogeneity. Mismatches between ecological and management spatial scales can lead to overexploitation of sub-stocks and deplete the entire stock over time, even for exploitation rates deemed sustainable at the broader geographical scale (Rose and Kulka, 1999; Spies *et al.*, 2015; Voss *et al.*, 2018; Okamoto *et al.*, 2019). Species subject to Allee effects, i.e. reproductive failure in a low density population, are especially sensitive to local overfishing, as high exploitation rates increase the chance that the local population density drops below the threshold required for successful reproduction (Frank and Brickman, 2000). These local collapses might get ignored so long as the annual quota in the larger management unit is achieved, but can progressively erode the reproductive stock and, even when the fishery is globally stable, they may affect other species in the ecosystem and vulnerable communities that interact with the fishery at local spatial scales (Okamoto *et al.*, 2019).

Previous studies on spatial management typically explored different assessment and enforcement strategies (eg. Spies *et al.*, 2015; Voss *et al.*, 2018), but not the potential different human responses to these strategies. However, spatial heterogeneity in fishing mortality must also be considered in order to fully understand the impact of habitat heterogeneity, as fishers respond to ecological cues in an effort to maximize net economic gains (Hilborn and Ledbetter, 1979; Wilen *et al.*, 2002; Branch *et al.*, 2006). In order to maximize benefits, fishers use information about fish density from previous experiences or available information on habitat quality to focus their fishing effort in high-yield areas (Hilborn and Ledbetter, 1979; Branch *et al.*, 2005). This is most likely to happen for less mobile species and for species that aggregate in spawning areas at certain times of the year (Sadovy and Domeier, 2005; Erisman *et al.*, 2012). In addition, management strategies that create incentives for a race to fish and lead to over-capitalized fleets—such as in TAC-regulated fisheries—can further encourage a shift of fishing effort from less productive towards more productive areas (Gorfine and Dixon, 2001). This behaviour provides the potential for a negative feedback loop, as fishing mortality increases in more productive areas, thus reducing the abundance of larger and disproportionally more reproductive individuals (De Leo and Micheli, 2015). This can sometimes be consistent with management goals by homogenizing the population across space (Gorfine and Dixon, 2001), but can also cause declines in the stock and reduce recovery potential (De Leo and Micheli, 2015), especially for species that reproduce at spawning aggregations (Sadovy and Domeier, 2005; Erisman *et al.*, 2012). Finally, fishers may account for distance from port when distributing their fishing effort, in order to minimize fuel and labor costs (Sampson, 1992; Caddy and Carocci, 1999).

The risk of habitat heterogeneity causing overfishing within a TAC-regulated fishery is thus influenced by (1) the extent to which fishing mortality is evenly distributed or aggregated around high-quality habitat patches, and (2) how important high-quality habitat patches are to supporting overall stock productivity. If good habitat is aggregated, and these areas are important for maintaining overall stock productivity, then fishing mortality concentrated in these few areas may lead to an overfished stock (Hilborn *et al.*, 2006). If, however, there is uncertainty about the spatial distribution of fish and expected catches, and fishing mortality is more evenly distributed across a heterogeneous habitat, it is unclear what the overfishing risks are to the fishery.

In this work, we investigate how the interaction between heterogeneity in habitat quality and in the distribution of fishing effort affects fishery performance in a TAC-regulated fishery. Previous studies have examined the benefits of spatial management (Kaplan *et al.*, 2014; Voss *et al.*, 2018; Okamoto *et al.*, 2019) and compared fisheries performance when fishing is distributed evenly throughout the management area and when fishing effort is proportional to fish abundance (Caddy, 1975; Seijo *et al.*, 2004). Here, we use a spatially-explicit Integral Projection Model (IPM) to study the effect of fishing effort aggregation—allowing for a more flexible response of fishers to spatial heterogeneity in habitat quality—on an over-capitalized TAC-regulated fishery, and for a species with and without the Allee effect. IPMs allow assessments to explicitly account for relevant non-linearities associated with the well documented increase in per-capita survival, fecundity, and fishing mortality with body size in many marine species of commercial and conservation interest (De Leo and Micheli, 2015), and their compounded effect with reduced recruitment caused by reproductive or settlement failure at low population density (Aalto *et al.*, 2019).

We build the analysis by using an existing demographic and management IPM model of the green abalone fishery (*Haliotis fulgens*) in Isla Natividad, Baja California, Mexico (Rossetto *et al.*, 2015; Aalto *et al.*, 2019). The *Haliotis* genus includes more than 30 abalone species of high commercial or conservation interest in all continents (except for Antarctica) (Gordon and Cook, 2004). *Haliotis fulgens* is a good reference model for other marine invertebrate species whose life cycle is characterized by broadcast spawning, dispersal via a larval stage, adults with limited mobility, natural mortality that decreases and fecundity that increases with body size respectively, and potential for reproductive failure at low population density. We used the model to analyse the effect on fisheries' performance—measured in terms of abundance and catch—of alternative assumptions about (i) habitat heterogeneity, (ii) fishing effort heterogeneity, (iii) presence of the Allee effect, (iv) other spatial constraints to the distribution of fishing effort such as distance from port, and (v) level of exploitation. Specifically, we asked how the impact of habitat heterogeneity on fishery performance varies with heterogeneity in fishing effort and for species with and without Allee effects, compared to a homogeneous fishery. While we parameterize the model with respect to the abalone fishery in Baja California to ground it in reality, our model does not consider certain environmental variables—such as sea surface temperature—that affect abalone population dynamics. Our goal for this work is thus to provide insights into the impact of habitat heterogeneity under different conditions, and the relative effect size of these conditions, rather than provide direct management advice for this fishery.

Methods

We adapted an existing integral projection model (IPM), describing the spatially explicit dynamics (see **Spatial config-**

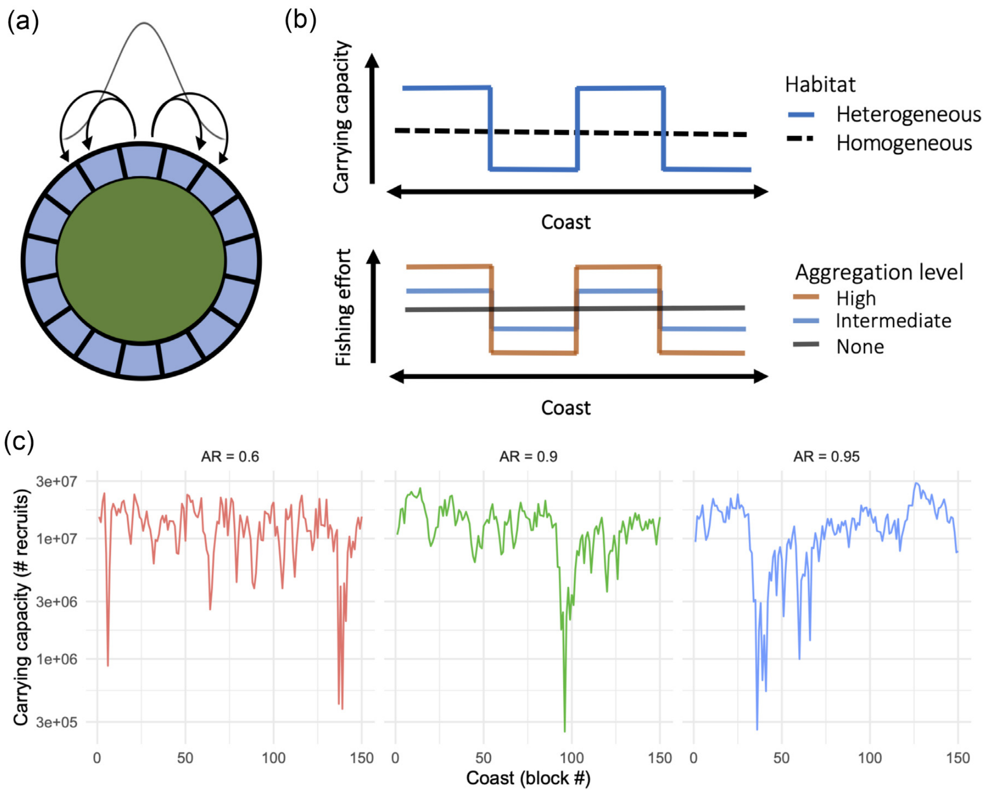

Figure 1. (a) Spatial configuration of the coastline. The circular coast is divided into blocks that are linked through larvae dispersal. (b) Top: carrying capacity for a homogeneous habitat and a simplified heterogeneous habitat with two high-quality and two low-quality areas. Bottom: fishing effort for three levels of fishing effort aggregation. (c) Carrying capacity across the coast for coefficients of spatial auto-correlation of 0.6, 0.9, and 0.95. The three coastlines have the same overall carrying capacity 150·k (k being the mean carrying capacity in the homogeneous case, set to 10^7).

uration and habitat quality) of the abalone fishery of Isla Natividad, Mexico (see **Study system**) (Aalto *et al.*, 2019). We use the same model parameterization as in Aalto *et al.* (2019) for fecundity, dispersal, recruitment, growth and survival, and introduced different levels of heterogeneity in both habitat quality (affecting recruitment rates) and fishing mortality across space (see **Model description** and **Model parameterization**). We then assessed fishery performance for different combinations of habitat and fishing effort heterogeneity (see **Analysis**).

Study system

Green abalones (*H. fulgens*) are marine gastropods that can be found in crevices and under rocks of coastal environments in Southern California, USA, and along Baja California, Mexico (NOAA, n.d.). They have two separate sexes and are broadcast spawners, which can make them susceptible to reproductive failure at low densities (Babcock and Keesing, 1999), a phenomenom also known as the Allee effect (Allee *et al.*, 1949). Habitat quality and heterogeneity is determined by many factors, including wave energy, ocean currents, water temperature, and geology (Miller *et al.*, 2019).

Abalone fisheries in Mexico are co-managed by the government and fishery cooperatives (McCay *et al.*, 2014). The Federal government established concession boundaries for cooperatives and determines minimum size limits and annual quotas per cooperative. Cooperatives can enforce regulations more stringent than that of the Federal government, decide when and where abalones are effectively fished, and establish no-take reserves within the concession. Isla Natividad is a small island in Baja California, Mexico. While no-take reserves have been successfully implemented by the cooperative of Isla Natividad (Rossetto *et al.*, 2015), we do not consider them in this work.

Spatial configuration and habitat quality

Following previous modelling effort of abalone dynamics in Isla Natividad, population dynamics and fishery management were simulated over a 15 km circular coastline divided in 150 blocks of 100 × 500 m each, alongshore and offshore, respectively (Figure 1a). We numbered each block of this circular coastline from 1 to 150, with block #1 and #150 being adjacent to each other. We assumed that all boats left from one port, located in block 75. Each block $z = 1, 2, \ldots, 150$, has unfished recruit carrying capacity K_z, which modulates recruitment into that block. In all simulations, the mean carrying capacity over the entire coast is k. To simulate a homogeneous habitat across the coastline, we set $K_z = k$ for any z (Figure 1b). Consistent with Aalto *et al.* (2019), we set the mean recruit carrying capacity k to produce an unfished density of 0.2 ind/m^2. To simulate habitat heterogeneity, we generated 150 values from an autoregressive model of order 1 and coefficient ϕ, which can vary between 0 and 1:

$$K_{z+1} = \phi K_z + w_{z+1}, \tag{1}$$

where w is a white noise (random, uncorrelated) sequence. These values represent different carrying capacities associated with blocks. We first standardized these carrying capacities by shifting the distribution to set the minimum K to 0.1 (to avoid null values), and then rescaled them to ensure a constant mean carrying capacity across the blocks for the different habitat scenarios.

Model description

Abalone population density at time $t + 1$ for each block z at length l is determined by the growth of individuals to size l from time t to $t + 1$, where t is in years. Following Ellner and Rees (2006), we take the integral with respect to l' of the density of surviving individuals growing from length l' to length l. This expression is dependent on the density for length l' at time t $n_{z,\ t}(l')$, the probability of growing from length l' to l $G(l|l')$, the probability of survival when growing from length l' to l $\sigma(l,\ l')$, and the fishing mortality at length l in block z $H(z,\ l)$. Finally, we add to this expression the number of recruits $R_{z,\ t}$ growing to size l.

$$n_{z,t+1}\ (l) = \ G(l|L_0)R_{z,t} + \int \sigma\left(l, l'\right)\left(1 - H\left(z, l\right)\right) G(l|l')n_{z,t}\left(l'\right) dl'. \tag{2}$$

We assume that harvest occurs at the end of the year.

Fecundity

The number of eggs $E_{z,\ t}$ produced in each block z and at time t depends on the biomass of mature females and the probability of aggregation of both sexes (representing the Allee effect). The biomass of mature females at length l is obtained by dividing the population density $n_{z,\ t}(l)$ by two, under the assumption of 1:1 sex ratio, and multiplying this by the proportion of mature individuals $p_{mature}(l)$ and their weight $w(l)$. We integrate this expression with respect to l. We then multiply the total biomass of mature females by the fecundity ψ_w and the fertilization success $Allee_{z,t}$:

$$E_{z,t} = \ Allee_{z,t}\psi_w \int p_{mature}\left(l\right) w\left(l\right) \frac{n_{z,t}\left(l\right)}{2} dl. \tag{3}$$

Abalone biomass w was assumed to scale allometrically with length l as follows:

$$w\ \left(l\right) = a_w\ l^{b_w}, \tag{4}$$

where b_w is the scaling exponent and a_w is the body mass when $l = 1$.

The proportion of mature individuals is defined as a function of the length l, a scaling parameter a_{mat} and the length L_{mat}, at which half of the individuals are mature (Aalto *et al.*, 2019):

$$p_{mature}\ \left(l\right) = \frac{1}{1 + exp\left(\frac{L_{mat} - l}{a_{mat}}\right)}\ . \tag{5}$$

Finally, fertilization success $Allee_{z,t}$ is an increasing and saturating function of the mean aggregation size $Agg_{z,t}$, which is itself determined by two parameters a_{agg} and b_{agg}, and the total density of mature individuals (see Aalto *et al.*, 2019 for details):

$$Allee_{z,t} = \ 1 - 0.5^{Agg_{z,t} - 1}. \tag{6}$$

$$Agg_{z,t} = b_{agg}\ + a_{agg} \int p_{mature}\left(l\right) n_{z,t}\left(l\right) dl. \tag{7}$$

Dispersal and recruitment

From each block, the fraction of larvae ρ dispersing n blocks away is determined by a Gaussian distribution with mean dispersal distance $d(t)$ that varies from year to year according to a gamma distribution with shape d_s and rate d_r. The number of settlers $S_{z,t}$ is defined as the sum of the number of eggs $E_{j,t}$ from each block j that dispersed to this block z, and that survived with a probability σ_E. This survival rate is modified by a random variable $r(t)$ that follows a lognormal distribution with a mean of 0 and a standard deviation of 0.7 on the log-scale, representing variations from environmental fluctuations:

$$S_{z,t} = \ r\left(t\right)\sigma_E \sum_j E_{j,t}\rho\left(\left|j - z\right|\right). \tag{8}$$

We finally calculated the number of recruits $R_{z,t}$ using a Ricker function (Ricker, 1954) with settler survival rate σ_s and settler carrying capacity K_z:

$$R_{z,t} = \sigma_s\ S_{z,t}exp\left(\frac{-S_{z,t}}{K_z}\right). \tag{9}$$

Growth and survival

Following Bardos (2005), Rossetto *et al.* (2015), and Aalto *et al.* (2019b), we used a probabilistic non-negative Gompertz growth function to calculate the probability $G(l|l')$ of growing to length l from length l'. A description of this function is available in Supplementary Text S1.

We assumed that the natural mortality rate μ scaled with body mass w according to a power law with scaling parameters $\theta > 0$ and $\alpha < 0$, namely:

$$\mu\left(l\right) = \ exp\left(\theta + \alpha ln\left(w\left(l\right)\right)\right). \tag{10}$$

We calculated annual survival by integrating from starting length l_0 to ending length l_1 (corresponding to l and l' in Eq. (2)):

$$\sigma\left(z, l_0, l_1\right) = \int_{l_0}^{l_1} e^{-\mu(l)} dl\ . \tag{11}$$

Fishing effort and mortality

We assumed the fishery to be at over-capacity, and set the total number of boats B_{tot}, representing the maximum total fishing effort in all blocks around Isla Natividad, to three times the fishing effort (number of boats) needed to achieve the MSY (see **Analysis**). While data are not available for Isla Natividad specifically, Garcia and Newton (Garcia *et al.*, 1995) estimated that global fishery capacity would need to be reduced by 53% to reach maximum economic yield. This figure can often be higher, especially in small-scale fisheries, which are more complex and difficult to manage (Yap, 1997; Pomeroy, 2012).

Boats were allocated over the fishing ground based on stock abundance and distance from the port. Specifically, we attributed to each block z at time t a weight $W_{z,\ t}$, which decreases with distance from the port and increases with the relative abundance of harvestable individuals in the block with respect to the overall stock, namely

$$W_{z,t} = e^{-\beta\left(1 - \frac{n_{z,t}}{\sum n_t}\right) - \gamma\ \frac{\left|z_{port} - z\right|}{z_{port}}}\ , \tag{12}$$

where β is a fleet-aggregation parameter (the higher β, the higher the aggregation of the fishing fleet in the blocks with highest abalone abundance, Hilborn *et al.*, 2006) and γ is a parameter proportional to the cost of navigation to distant fishing grounds (so, the higher γ, the closer the fishing fleet to the port). At each time step t, fishing boats were

Table 1. Parameter values

Process	Symbol	Meaning	Value	Units
Spatial configuration	ϕ	Auto-regressive coefficient	0–1	
	k	Mean carrying capacity	1.29×10^7	larvae
Growth	G	Gompertz growth parameter	0.5635	
	L_n	Maximum length mean	150.39	mm
	σ_L^2	Maximum length variance	55.95	
	β_G	Mean scaling	1.478	
	γ_G	Variance scaling	1.719	
Fecundity	ψ_w	Fecundity	3772	eggs g^{-1}
	a_w	Weight scaling value	2.24×10^{-5}	g mm^{-bw}
	b_w	Weight exponent	3.36	
	L_{mat}	Length for 50% maturity	135.99	mm
	a_{mat}	Maturity scaling value	30.2	mm
	a_{agg}	Aggregation slope	11.6	
	b_{agg}	Aggregation intercept	1	
Dispersal and recruitment	d_s	Dispersal distance gamma shape	3	
	d_r	Dispersal distance gamma rate	0.006	
	σ_E	Egg survival	0.005704	
	σ_S	Recruit survival	0.02	
	θ	Mortality intercept	0.635	
	α	Mortality scaling	−0.317	
Fishing effort and mortality	q	Catchability	0.1	
	β	Biomass scaling factor	0/100/200	
	γ	Distance scaling factor	0/2	
	L_{min}	Minimum legal length	155	mm

then distributed over the fishing ground proportionally to the normalized weights $W_{z,t}$:

$$B_{z,t} = B_{tot} \frac{W_{z,t}}{\sum_z W_{z,t}}. \quad (13)$$

The potential catch P_t at time t is a function of the fishing effort $B_{z,t}$ and catchability q summed across all blocks:

$$P_t = \sum_z \int_{l_{min}}^{\infty} H_{z,t}(l)\, n^*_{z,t}(l)\, dl \quad (14)$$

$$= \sum_z \int_{l_{min}}^{\infty} \left(1 - e^{-qB_{z,t}}\right) n^*_{z,t}(l)\, dl,$$

where $H_{z,\,t}\ (l) = \ 1 - e^{-qB_{z,t}}$ is the fishing mortality, i.e. the *fraction* harvested at size l, in block z at time t, $f_{z,t} = qB_{z,\,t}$ is the fishing mortality *rate*, l_{min} is the legal minimum length at which abalones are exploited in the fishery, and $n^*_{z,t}$ is the post-growth pre-fishing abalone density from Eq. (2).

If the catch that would have occurred without regulation (P_t) was lower than the TAC_t, then the regulations had no effect, and the actual catch A_t was equal to P_t. If P_t exceeded the TAC_t, then the catch in each block z was reduced by a factor $s_t = TAC_t/\mathrm{P}_t$, so that the actual catch A_t was equal to the TAC_t, namely

$$H_{z,t} = s_t \ \left(1 - e^{-qB_{z,t}}\right), \quad (15)$$

where

$$s_t = \begin{cases} 1 & if\ P_t \le TAC_t \\ \frac{TAC_t}{P_t} & if\ P_t > TAC_t \end{cases} \quad (16)$$

and

$$n_{z,t+1}\ (l) = \begin{cases} (1 - H_{z,t})\, n^*_{z,t}(l) & if\ l \ge l_{min} \\ n^*_{z,t}(l) & if\ l < l_{min} \end{cases}. \quad (17)$$

Therefore, s_t can be seen as a parameter that is proportional to the length of the fishing season: if P_t exceeds the TAC_t, then fishing activities end as soon as the total allowable quota is reached.

Model parameterization

Parameter values are reported in Table 1. Life history parameters, i.e. size-dependent natural mortality, fecundity, maturation, and growth rate, and the parameters describing abalone dispersal in the planktonic phase around Isla Natividad were obtained from Aalto *et al.* (2019). We ran our model with and without Allee effects. Unless stated otherwise, Allee effects are included.

We generated three different heterogeneous habitats with spatially auto-correlated carrying capacities that had coefficients ϕ equal to 0.6, 0.9, and 0.95 (Figure 1c) as well as a homogeneous habitat. In the main text, we present our results for one randomly generated coastline for each ϕ but we show in Figure S1 that our results are general and do not depend on a specific coastline. Unless stated otherwise, $\phi = 0.9$.

The parameter β, proportional to the aggregation of fishers in high-density blocks where the catch is expected to be higher, was set to 0 (uniform distribution), 100 and 200 for medium and high aggregation, respectively. The parameter γ, proportional to the aggregation near the harbour, was set to $\gamma = 0$ (no aggregation, distance of the fishing ground from the harbour is irrelevant) or 2 (distant fishing ground is less harvested than fishing ground near the harbour).

Analysis

First, we numerically calculated the fishing mortality H_{MSY} required to achieve MSY for a homogeneous habitat with and without Allee effects, using a recursive method with 1% increments in fishing mortality and setting the total allowable quota at each time step t as follows:

$$TAC_{t,MSY} = \sum_z \int_{l_{min}}^{\infty} H_{MSY} n^*_{z,t}(l)\, dl\ . \quad (18)$$

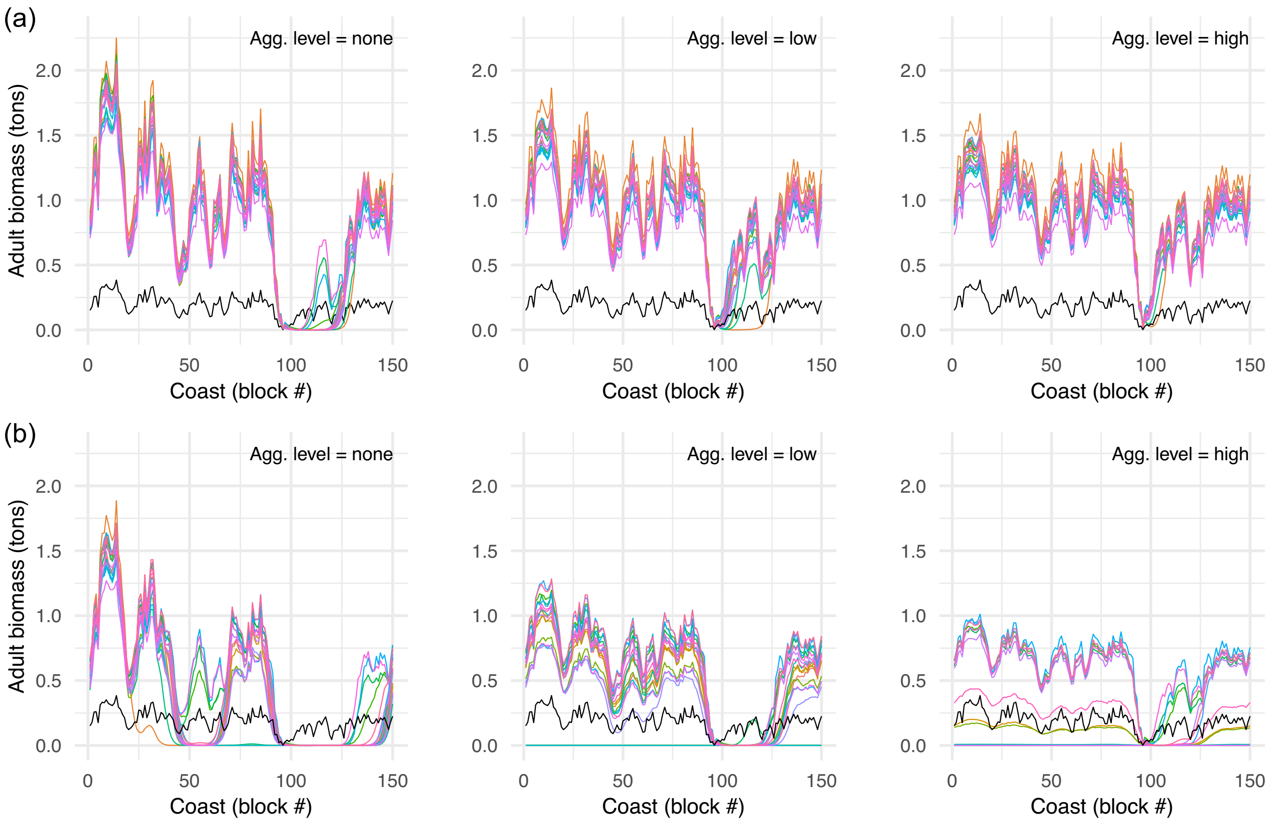

Figure 2. Total biomass of mature adults along the coast for different levels of fishing effort aggregation, for (a) a TAC set at MSY and (b) above MSY. Each colour line represents one of 20 replicates. The black line represents the collapse threshold for each block (10% of the unfished biomass).

We found that with the current model parameterization, the fraction of the abalone stock to be harvested to achieve MSY in the case of a homogeneous habitat is $H_{MSY} = 9\%$ of fish abundance above the minimum legal size with Allee effects, and 18% of the fish abundance without Allee effects. We then considered two exploitation levels, namely $H = H_{MSY}$, where the TAC is set to achieve MSY, and $H = H_{OVER}$, which exceeds H_{MSY} by 33%, i.e. 12 and 24% of fish population with and without Allee effects, respectively. Fisheries sometimes set more conservative quotas, in order to better protect populations against uncertainty in stock evaluation and imperfect enforcement. We found similar patterns when using $H = \frac{2}{3} H_{MSY}$ as when using $H = H_{MSY}$ (Supplementary Figure S2), and we only present the latter here.

As our goal here was to assess long-term performance, we ran simulations for the combination of exploitation levels (H_{MSY} and H_{OVER}), heterogeneity of the fishing ground (ϕ = 0.6, 0.9, and 0.95), scaling factors ($\beta = 0, 10, 200$ and $\gamma = 0, 2$), and with or without Allee effect, for 250 years. This was enough to reach long-term equilibrium in all cases considered. For each simulation, we ran 20 replicates with all model parameters constant in time, except for stochastic dispersal and recruitment strength in each block at time t. We kept track of the population density at each size l in each block z through time (the output of the simulation is a 3-D matrix with time, fish length and fishing block number as its dimensions). We reset the random generator seed before each simulation in order to have paired observations of alternative scenarios under the same stochastic sequence for dispersal, recruitment strength, and fishing mortality (for example, replicate 1 has exactly the same parameters across all scenarios).

Long-term fishery performance was assessed as the 10-year average catch and the total biomass of mature adults over the coastline. For each replicate, we also calculated the proportion of collapsed blocks, defined as blocks where the biomass of mature adults at equilibrium is 10% or less of the unexploited mature adult biomass. We then compared the distribution of adult biomass between the heterogeneous and the homogeneous habitat scenarios (homogeneous fishing) using Cohen's d to evaluate the effect size. Effect size is typically considered small, medium, and large for $d = 0.2, 0.5,$ and 0.8 respectively (Cohen, 1988). We then used a linear mixed-effects model to assess the effect of fishing effort aggregation on adult biomass, with random effects for replicates.

All simulations and analysis were run using R (version 3.6.1) (R Core Team, 2019).

Results

Effort aggregation in high-quality areas improves fishery performance at sustainable exploitation rates when Allee effects are included

There were no *global* collapses—defined as 10% or less remaining of the overall unexploited mature adult biomass (Worm *et al*., 2006)—in a heterogeneous environment when the TAC was set to achieve MSY (Figure 2a) in the case of Allee effect and homogeneous distribution of fishing effort. However, areas with lower carrying capacities (blocks 100–125) had an adult population close to 0 in many replicates. As low adult abundance in a block may be either a consequence of overfishing or simply reflects a low natural carrying capac-

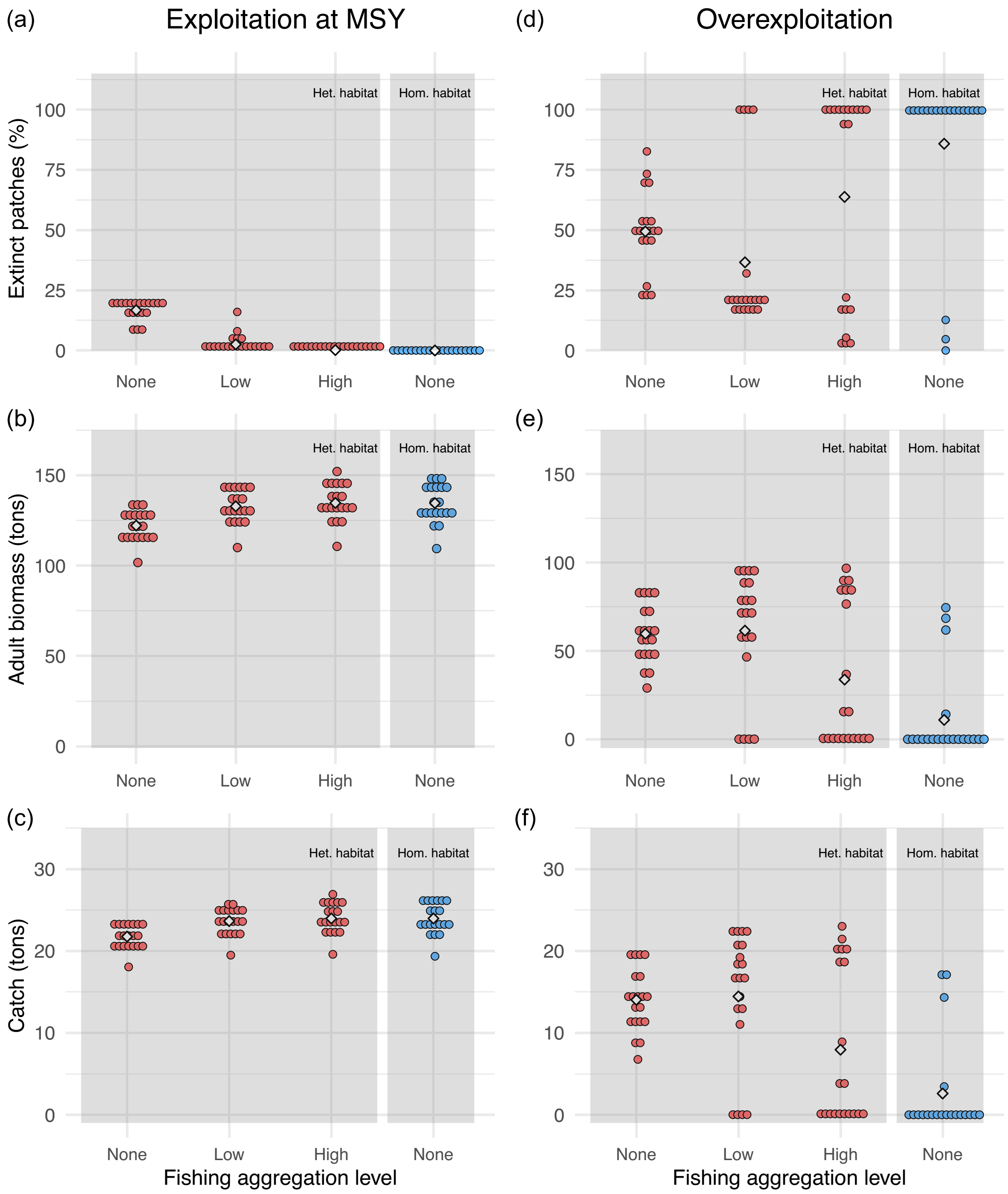

Figure 3. Percent of extinct patches, adult biomass, and catch for stocks exploited at MSY (a, b, and c respectively) and overexploited (d, e, and f respectively). Each dot represents a replicate. White diamonds show means. All simulations in this figure were performed by assuming reproductive failure at low population density (Allee effect).

ity (low habitat quality), we calculated the number of blocks that collapsed, corresponding to a decrease below 10% of the unfished adult biomass in each block (Worm *et al.*, 2006). In most of the replicates, 15–20% of blocks collapsed according to this criterion (Figure 3a). In comparison, there were no collapsed blocks in any of the replicates when fishing in a homogeneous environment. This difference was also reflected in the adult biomass and the catch (Figure 3b and c), which both decreased by 9.2 ± 1.2% in the heterogeneous habitat with homogeneous fishing (Cohen's d, $d > 1$ for both biomass and catch).

The proportion of collapsed patches decreased, and the adult biomass and catch increased in the heterogeneous environment when fishers were able to target areas with higher densities of abalone (Figures 2a and 3a–c, Table 2). The largest marginal increase in fishery performance occurred for low aggregation fishing, with only a small additional increase for high aggregation fishing effort. In addition, increasing levels of fishing aggregation reduced heterogeneity in abalone biomass between different blocks as well as between replicates, as the high-quality blocks were increasingly more exploited than the low quality blocks (Figures 2a and 3a): areas with high densi-

Table 2. Summary statistics for mixed-effects models with adult biomass as the response variable and aggregation level (A.L.) as the predictor variable.

Scenario					
Adult biomass	Fixed effects	Estimate	SE	CI (95%)	Cohen's *d*
H_{MSY} Allee effect AR = 0.9 Figure 3b	Low A.L.	10.6	0.57	9.46–11.8	1.18
	High A.L.	12.5	0.57	11.3–13.6	1.32
Adult biomass	Fixed effects	Estimate	SE	CI (95%)	Cohen's *d*
H_{MSY} No Allee effect AR = 0.9 Figure 4a	Low A.L.	−0.644	0.062	−0.769–(−0.520)	−0.10
	High A.L.	−1.298	0.062	−1.42–(−1.17)	−0.21
Adult biomass	Fixed effects	Estimate	SE	CI (95%)	Cohen's *d*
H_{OVER} No Allee effect AR = 0.9 Figure 4b	Low A.L.	−0.791	0.065	−0.923–(−0.660)	−0.13
	High A.L.	−1.51	0.065	−1.64–(−1.38)	−0.25
Adult biomass	Fixed effects	Estimate	SE	CI (95%)	Cohen's *d*
H_{MSY} Allee effect AR = 0.6 Figure 5b	Low A.L.	1.47	0.489	0.484–2.46	0.15
	High A.L.	0.516	0.489	−0.474–(− 1.51)	0.05
Adult biomass	Fixed effects	Estimate	S.E.	CI (95%)	Cohen's *d*
H_{MSY} Allee effect AR = 0.95 Figure 5b	Low A.L.	4.79	0.575	3.63–5.96	0.56
	High A.L.	8.51	0.575	7.34–9.67	0.98

ties of abalone decreased in density, whereas most areas with low densities increased in density when fishing effort was aggregated along the coastline.

Overexploited fisheries have an increased chance of global collapse at high levels of fishing aggregation when Allee effects are included

Unlike the scenarios in which harvesting was managed to achieve MSY, fisheries in overexploited scenarios performed consistently better in a heterogeneous habitat than in a homogeneous one (Figure 3d–f). Increasing the TAC by 30% above MSY levels led to global collapses in nearly all replicates for the homogeneous habitat (Figure 3d). Overexploited fisheries with a heterogeneous habitat performed better than fisheries with a homogeneous habitat, especially when fishing was distributed homogeneously across the coast. In the case of homogeneous fishing effort, all replicates had a higher proportion of collapsed blocks than when managed for MSY, but none of the replicates showed a global collapse. Low levels of fishing aggregation led to global collapse in some replicates, while decreasing the proportion of collapsed blocks in others. This heterogeneity between replicates was even more pronounced at high levels of fishing aggregation, and was also observed for adult biomass and catch. The highest mean adult biomass and catch were achieved with intermediate levels of aggregation, despite the global collapse of a few replicates. As for the lower exploitation rate H_{MSY}, increasing levels of aggregation led to a decrease in heterogeneity in abalone biomass across space (Figure 2b). However, differences between replicates increased rather than decreased, with the standard deviation of adult biomass increasing from 8 643 to 10 232 tonnes between homogeneous fishing and high fishing aggregation.

Allee effects drive most of the difference in adult biomass between homogeneous and heterogeneous systems

Since it can be hard to detect the presence of Allee effects in wild populations and not all populations may experience Allee effects, we also ran simulations without Allee effects to see the impact of this assumption on our results. In the absence of Allee effects, 18% of the abalone stock needed to be harvested to achieve MSY. Without the Allee effect, adult biomass in the heterogeneous habitat was slightly lower than in homogeneous habitat (Figure 4a, difference: −1.21 ± 0.16%, Cohen's *d*, $d = 0.15$). We observed a similar outcome for an overexploited fishery (Figure 4b), with a small decrease of 1.60 ± 0.20% between the homogeneous and heterogeneous habitats (Cohen's *d*, $d = 0.17$). Unlike the increase in adult biomass observed when Allee effects are included, we found a small decreasing trend in adult biomass as aggregation strength increased (Figure 4a, Table 2). A similar outcome was detected also when the fishery was overexploited (Figure 4b, Table 2). When comparing cases with and without an Allee effect, both catch and adult biomass were at their lowest when abalones were sensitive to Allee effects and overexploited (Figure 4c). Abalone that are not sensitive to Allee effects were less affected, with overexploitation leading to small decreases in adult biomass. Highest adult biomass was achieved for populations sensitive to Allee effects but exploited at MSY levels.

Differences between homogeneous and heterogeneous habitats are small for habitats with low spatial auto-correlation

We quantified different degrees of spatial heterogeneity by generating auto-correlated sequences of carrying capacity with coefficient ϕ equal to 0.6, 0.9, and 0.95 (Figure 1c). These coefficients are a measure of the similarity between neighbour-

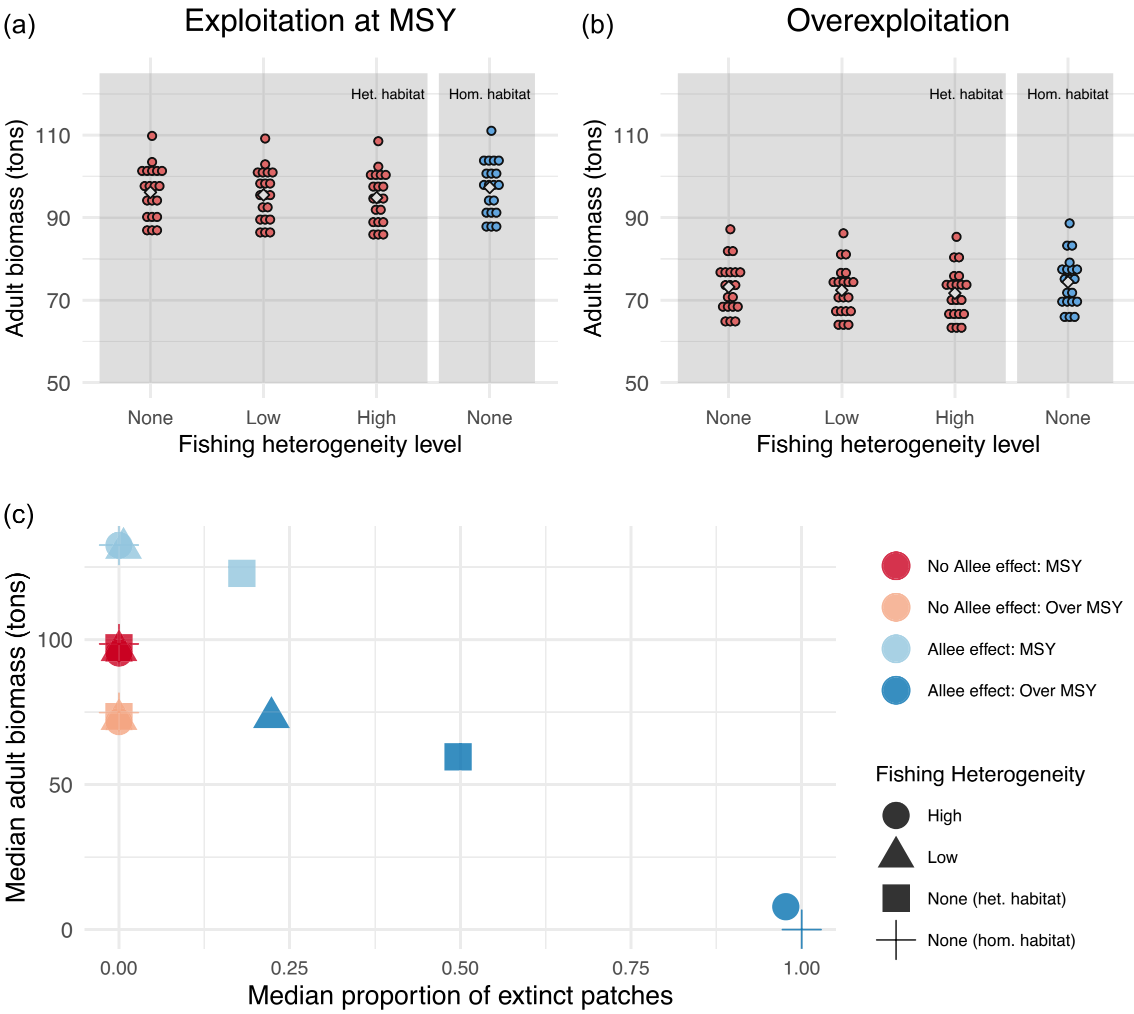

Figure 4. Total adult biomass in tonnes for a TAC at MSY (a) and above MSY (b), and for different levels of fishing heterogeneity when no Allee effect is included in the model. Each point represents one replicate. (c) Comparison of the median adult biomass with and without Allee effect, for different fishing mortalities (TAC at or above MSY) and different levels of fishing heterogeneity (including a homogeneous habitat for comparison).

ing blocks with larger values indicating higher similarity. All results presented this far are for $\phi = 0.9$.

For lower spatial correlation in habitat quality (auto-correlation coefficient $\phi = 0.6$), there were no collapsed blocks for most replicates in a heterogeneous habitat managed for MSY (Figure 5a). Relative to biomass in the homogeneous habitat, adult biomass at MSY was 3.17 ± 0.10% lower in the heterogeneous habitat (Figure 5b, Cohen's d, $d = 0.38$), compared to 9.2% in the case of high spatial correlation in habitat quality ($\phi = 0.9$). For higher spatial correlations ($\phi = 0.95$), adult biomass at MSY showed a large decrease of 7.16 ± 1.40% (Cohen's d, $d = 0.76$) and the number of collapsed patches increased to 20% in the heterogeneous habitat compared to the homogeneous one (assuming homogeneous fishing effort). In the case of high spatial correlation in habitat quality ($\phi = 0.95$) adult biomass and catch increased as fishing effort aggregation increased. For $\phi = 0.6$, adult biomass increased slightly with low aggregation but did not show any change at high aggregation (Table 2). When TAC was set above $\mathrm{TAC}_{\mathrm{MSY}}$, the standard deviation of the proportion of collapsed blocks and adult biomass was lowest for the heterogeneous habitat fished homogeneously, and increased with fishing aggregation, for all auto-correlation coefficients. However, habitats with a higher auto-correlation coefficient maintain a higher average adult biomass as fishing aggregation increases (Figure 5b).

Minimizing distance travelled by fishers leads to lower fishery performance

When accounting for the assumed decreased profits of fishing in distant fishing grounds from the port (located in block 75), a higher number of fishing blocks collapsed, especially close to the port (Figure 6a and b). This resulted in lower total adult biomass as well. Increasing the strength of fishing aggregation decreased the proportion of collapsed patches and increased adult biomass (Figure 6b and c). In addition, we observed an increase in variation between replicates at low and high levels of aggregation.

Discussion

Spatial heterogeneity within fishing grounds is common. Here we analysed the performance of an overcapitalized TAC-

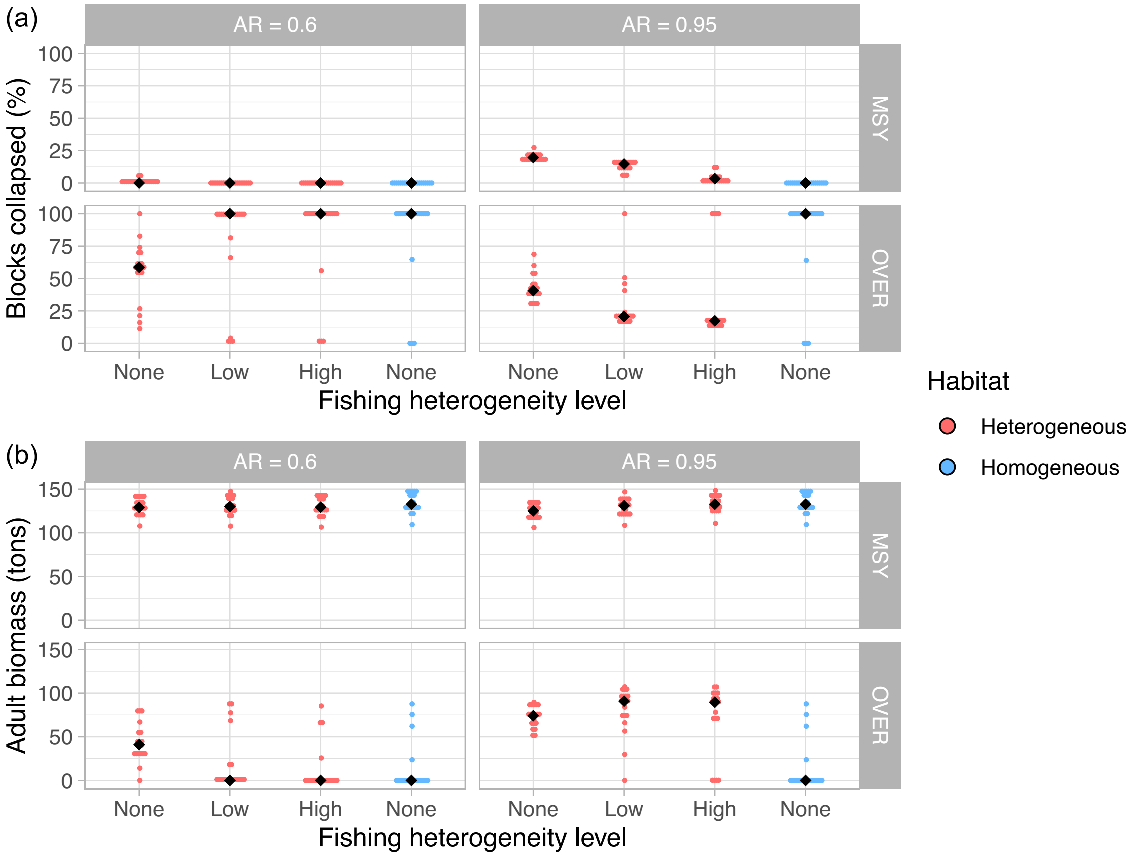

Figure 5. (a) Percent of blocks collapsed and (b) adult biomass for different habitat and fishing heterogeneity, for a TAC at or above MSY and for habitats with auto-regression coefficients of 0.6 and 0.95. Medians are shown with black diamonds.

regulated fishery when the total allowable quota is estimated as a fraction of the overall fish stock, the fishing ground is characterized by marked heterogeneity in habitat quality, and fishing effort tends to aggregate over high-quality, highly productive habitats. We found that, for a species characterized by the Allee effect, i.e. reproductive failure at low population density in a heterogeneous habitat, the aggregation of fishing effort where abundance is highest can improve fishery performance in comparison with a fishery in which fishing effort is uniformly distributed along the coastline. However, this result did not hold for overexploited fisheries, for which aggregation in fishing effort increases the risk of global stock collapse. A summary of our results can be found in Table 3. These results suggest that not accounting for spatial heterogeneity in fisheries management may lead to inefficiencies or misestimations of the risk of collapse.

When fishing effort is distributed evenly over the coastline regardless of habitat quality, local extinction may occur in low quality patches as fishing pressure may drive population density below the threshold at which reproductive failure is likely to occur (Allee effect). Conversely, high-quality fishing grounds may be under-harvested. As areas of the fishing ground are systematically either over- or under-harvested, fishery performance in a heterogeneous habitat, as measured via catch and adult biomass, is lower than in the case of a homogeneous habitat. Therefore, computing the TAC by averaging out spatial heterogeneity leads to lower fishery output even when the overcapitalized fishery is not overexploited. This was observed also in other studies (Voss *et al.*, 2018; Okamoto *et al.*, 2019).

The same patterns of under/overexploited patches of high-/low-quality habitat, respectively, apply to overexploited fisheries, but with a different outcome. When the TAC is computed by setting the fishing effort 30% higher than that needed to achieve MSY, a fishery with homogeneous habitat quality and fishing effort evenly distributed along the coastline does very poorly, with global collapses resulting in most replicates as overexploitation drives the population density near or below the critical Allee threshold across the coast. On the other hand, a heterogeneous habitat leads to a reduced number of local and global collapses and higher biomass, when fishing effort is distributed evenly along the coast. In this scenario, the under-harvesting of high-quality patches reduces the chances of collapse and therefore provides some stability to the fishery.

Fishing effort is rarely homogeneous because fishers tend to target high-quality habitat, especially for sedentary species (Gorfine and Dixon, 2001; Branch *et al.*, 2006). This results in an increase of the fishing effort in these areas and in a decrease of the fishing effort in remaining areas. Effectively, this brings fishing mortality in each block closer to the fishing mortality corresponding to MSY, and the fishery performance closer to the performance observed in homogeneous fisheries for both sustainably exploited and overexploited fisheries.

In the case of fisheries exploited at MSY, our results show that aggregation of fishing effort increased adult biomass and decreased collapses, leading to high performance equivalent

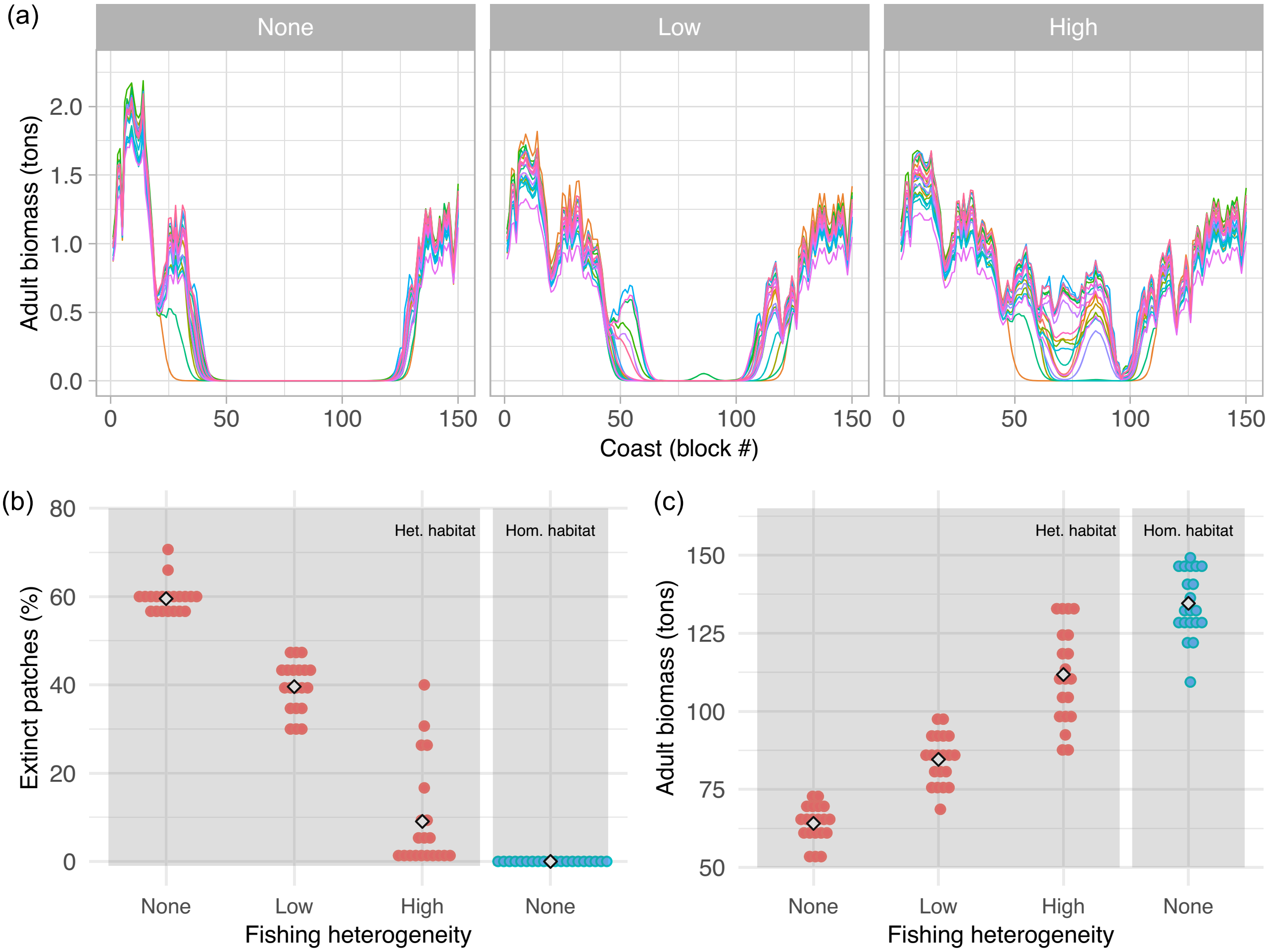

Figure 6. Fishery performance when fishers account for distance from port, located at block 75. (a) Adult biomass across space for three different levels of effort aggregation at H_{MSY}, (b) percent of blocks collapsed, and (c) total adult biomass for different habitat and fishing heterogeneity at H_{MSY}. Medians are shown with white diamonds.

to that of a fishery with a homogeneous habitat. Fishers can take advantage of the larger potential of high-quality patches, which also provides some relief to the lower-quality patches. On the other hand, heterogeneous fishing effort led to an increase in variation between replicates in overexploited fisheries, with total fishery collapse in some replicates. The probability of total collapse increases with the level of fishing effort aggregation in high-quality patches. In these scenarios, even the high-quality patches are overfished to the point of collapse, and the decrease in fishing effort in low-quality patches is insufficient to maintain population density above the critical Allee threshold.

Another source of spatial heterogeneity in fishing behaviour emerges if fishers do not have equal access to all fishing grounds (Branch *et al.*, 2006). Here, we consider the scenario where all fishing boats have to travel each day from a single port on the island to reach the fishing grounds. Even when the TAC is set to achieve MSY, fishery outcomes are worse, compared to a homogeneous fishery and to a heterogeneous fishery where port access is not limiting. This occurs because high-quality patches far away from the port are not exploited to their full potential while low-quality patches close to the port are over-harvested. In this case, fishery performance increases when fishers focus their effort on the high-quality patches, which decreases the fishing pressure on the low-quality patches close to the port. This is consistent with results from Spies *et al.* (2015) who modelled the impact of different management practices on a fleet travelling from a single port for Pacific Cod and northern rockfish fisheries.

Because we modelled a fishery targeting abalone, which are characterized by larval, but not adult, dispersal, and possibly Allee effects, both Allee effects and dispersal characteristics were important when determining the effect of habitat and fishing heterogeneity. We found that Allee effects were responsible for the majority of observed model outcomes. Without Allee effects, the difference in adult biomass between the heterogeneous and the homogeneous fisheries was smaller than with Allee effects, but this difference increased as the aggregation in fishing effort increased. Reproductive failure at low densities has been shown to affect abalones (Babcock and Keesing, 1999). However, abalone behaviour and their environment can affect abalone aggregation and either amplify or decrease this effect (Catton and Rogers-Bennett, 2013). Our results emphasize the importance of understanding the full life cycle of target species, as presence or absence of reproductive failure at low population density might have unexpected consequences on the optimal distribution of fishing effort to maximize catch and minimize the risk of collapse.

The smaller difference we observed in our simulations between the homogeneous and heterogeneous habitats without

Table 3. Summary of results.

		Allee effect			
		With Allee effects		Without Allee effects	
		Het. habitat	Hom. habitat	Het. habitat	Hom. habitat
TAC = MSY	Hom. effort	–Local collapses –No global collapses –Lower biomass than hom. habitat	–No local collapses –No global collapses	–No local collapses –No global collapses	–No local collapses –No global collapses
	Het. effort	–Fewer local collapses –Similar biomass as hom. habitat	NA	–Lower biomass than hom. habitat	NA
TAC > MSY	Hom. effort	–Local collapses –No global collapses –Higher biomass than hom. habitat	–Global collapses	–No local collapses –No global collapses – Similar biomass as hom. habitat	–No local collapses –No global collapses
	Het. effort	–Global collapses	NA	–Lower biomass than hom. habitat	NA

Allee effects can be explained in part by the shape of the Ricker function regulating the number of larvae that successfully settle, which has a shallow slope around the maximum recruitment (Supplementary Figure S3). More specifically, the number of recruits decreases by only 18% when the number of potential settlers is 50% of the carrying capacity. Large decreases in adult density and eggs can thus be sustained with limited consequences for recruitment, as long as reproductive failure at low densities does not occur. These results suggest that modelling choices regarding density-dependence are particularly relevant when studying habitat heterogeneity and should be studied further. In addition, H_{MSY} does not change with the absolute density of the population when Allee effects are not included. A homogeneous distribution of fishing effort across space is thus equivalent to applying H_{MSY} in each block, which explains why fishery performance decreases when fishers aggregate in certain blocks.

Finally, larval dispersal distance relative to the level of habitat heterogeneity influenced the magnitude of the patterns we observed. Habitats with low auto-correlation coefficients exhibit high-frequency variations in carrying capacity (i.e. low-quality patches are likely to be surrounded by high-quality patches and vice versa), resulting in adult abalone biomass being smoothed out through larval dispersal. This resulted in much closer performance between the homogeneous and heterogeneous habitats. On the other hand, areas of high carrying capacity clumped together as the auto-correlation coefficients increased, leading to larger differences between the homogeneous and heterogeneous habitats. When this happens, larval dispersal only affects the dynamics of the patches close to boundaries between high- and low-quality areas. We expect that including adult dispersal, in the case of species with mobile adults, would further smooth out differences in fish densities across a heterogeneous landscape.

Our representation of fishers' behaviour in this model was phenomenological rather than mechanistic. While this approach allowed us to study the effect of fishing effort aggregation using few assumptions, considering the factors that directly affect fishers' behaviour (e.g. fixed and variable costs, profit, weather, and information sharing) could lead to more realistic outcomes and specific solutions. To build on the findings in this study, future research that investigates the performance of other fisheries characterized by spatial heterogeneity in habitat and fishing effort and susceptibility to Allee effects could help to ground-truth the model simulations presented here with observed data. This would involve partnering with scientists and managers from fisheries to use real data about the spatial heterogeneity of habitat quality and fishing effort, and dispersal distances of abalone in other fisheries. Geolocations of fishing vessels recorded from Vessel Monitoring Systems could be used to measure the actual relationships between distance travelled to fishing grounds, fishing effort, and amount of catch landed, all within the boundaries of management zones of a real fishery. Data of this kind exists for some of Australia (Mayfield *et al.*, 2011; Jalali *et al.*, 2015) and Tasmania's abalone fisheries (Tattersall, 2011). In addition to habitat quality and distance from port, there are other factors that influence where fishing occurs that could be considered, such as seasonal weather and market demand for large versus small-sized individuals. Once our modelling framework is grounded with spatial data for a specific TAC-regulated fishery, an important next step could be to test alternative measures to TAC to set sustainable levels of catch. For example, applying a management strategy evaluation approach would allow us to test the performance of setting spatially explicit catch quotas, as well as explore the sensitivity of different minimum length limits on overall fishery performance.

Conclusion

Using the Isla Natividad abalone fishery as a model system, we showed that certain characteristics of sedentary marine invertebrates—Allee effects and larval dispersal—interact with the level of fishery exploitation to shape the performance of our simulated fishery in significant ways. The presence of Allee effects, in particular, is a major driver of the effects of habitat heterogeneity on biomass and catch. Moreover, the effects of habitat heterogeneity on fisheries performance vary significantly with the level of fisheries exploitation. These results highlight the need to tailor the study of the impact of heterogeneity in fisheries to the life history characteristics of target species, to the level of heterogeneity of their habitat, and to the exploitation status of the fishery.

Supplementary material

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Author contributions

GDL and FM conceived the project, contributed to the design of the model and the writing of the manuscript. JP performed analysis and wrote the manuscript. All the authors contributed to writing.

Conflict of interest

The authors declare no competing interest.

Data availability statement

The R script underlying this article is available in the GitHub repository jpourtois/TAC_abalone.

Funding

JP acknowledges support from the Stanford Graduate Fellowship. MP, GADL and FM were supported by the National Science Foundation BIOOCE 1736830. FM and GADL were partially supported also by the National Science Foundation ICER-2108566.

Acknowledgements

We thank Emil Aalto for his technical assistance in the early stages of this project, and two anonymous reviewers for their review and suggestions, which greatly improved the manuscript.

References

Aalto, E. A., Micheli, F., Boch, C. A., Espinoza Montes, J. A., Woodson, C. B., and De Leo, G. A. 2019. Catastrophic mortality, Allee effects, and marine protected areas. The American Naturalist, 193: 391–408.

Plummer, M. L. Morrison, W. and Steiner, E. 2012. Allocation of fishery harvests under the Magnuson-StevensFishery Conservation and Management Act: Principles and practice. U.S. Dept. Commer., NOAA Tech. Memo. NMFS-NWFSC-115, 84 p.

Allee, W. C., Park, O., Emerson, A. E., Park, T., and Schmidt, K. P. 1949. Principles of Animal Ecology. 393–418 Saunders Company. PhiladelphiaPA

Anticamara, J. A., Watson, R., Gelchu, A., and Pauly, D. 2011. Global fishing effort (1950–2010): trends, gaps, and implications. Fisheries Research, 107: 131–136.

Babcock, R., and Keesing, J. 1999. Fertilization biology of the abalone *Haliotis laevigata* : laboratory and field studies. Canadian Journal of Fisheries and Aquatic Sciences, 56: 1668–1678.

Bardos, D. C. 2005. Probabilistic gompertz model of irreversible growth. Bulletin of Mathematical Biology, 67: 529–545.

Barth, J. M. I., Villegas-Ríos, D., Freitas, C., Moland, E., Star, B., André, C., Knutsen, H. *et al.* 2019. Disentangling structural genomic and behavioural barriers in a sea of connectivity. Molecular Ecology, 28: 1394–1411.

Batstone, C. J., and Sharp, B. M. H. 1999. New Zealand's quota management system: the first ten years. Marine Policy, 23: 177–190.

Beddington, J. R., Agnew, D. J., and Clark, C. W. 2007. Current problems in the management of marine fisheries. Science, 316: 1713–1716.

Branch, G. M., and Clark, B. M. 2006. Fish stocks and their management: the changing face of fisheries in South Africa. Marine Policy, 30: 3–17.

Branch, T. A., Hilborn, R., and Bogazzi, E. 2005. Escaping the tyranny of the grid: a more realistic way of defining fishing opportunities. Canadian Journal of Fisheries and Aquatic Sciences, 62: 631–642.

Branch, T. A., Hilborn, R., Haynie, A. C., Fay, G., Flynn, L., Griffiths, J., Marshall, K. N. *et al.* 2006. Fleet dynamics and fishermen behavior: lessons for fisheries managers. Canadian Journal of Fisheries and Aquatic Sciences, 63: 1647–1668.

Caddy, J. F. 1975. Spatial model for an exploited shellfish population, and its application to the Georges Bank scallop fishery. Journal of the Fisheries Research Board of Canada, 32: 1305–1328.

Caddy, J. F., and Carocci, F. 1999. The spatial allocation of fishing intensity by port-based inshore fleets: a GIS application. ICES Journal of Marine Science, 56: 388–403.

Castello, L., McGrath, D. G., Arantes, C. C., and Almeida, O. T. 2013. Accounting for heterogeneity in small-scale fisheries management: the amazon case. Marine Policy, 38: 557–565.

Catton, C. A., and Rogers-Bennett, L. 2013. Assessing the recovery of pink abalone (*Haliotis corrugata*) by incorporating aggregation into a matrix model. Journal of Shellfish Research, 32: 181–187.

Charton, J. A. G., and Ruzafa, Á. P. 1999. Ecological heterogeneity and the evaluation of the effects of marine reserves. Fisheries Research, 42: 1–20.

Ciannelli, L., Knutsen, H., Olsen, E. M., Espeland, S. H., Asplin, L., Jelmert, A., Knutsen, J. A. *et al.* 2010. Small-scale genetic structure in a marine population in relation to water circulation and egg characteristics. Ecology, 91: 2918–2930.

Cohen, J. 1988. Statistical Power Analysis for the Behavioral Sciences. Routledge, NY.

Daw, T., and Gray, T. 2005. Fisheries science and sustainability in international policy: a study of failure in the European Union's Common Fisheries Policy. Marine Policy, 29: 189–197.

De Leo, G. A., and Micheli, F. 2015. The good, the bad and the ugly of marine reserves for fishery yields. Philosophical Transactions of the Royal Society B: Biological Sciences, 370: 20140276.

Ellner, S. P., and Rees, M. 2006. Integral projection models for species with complex demography. The American Naturalist, 167: 410–428.

Erisman, B., Aburto-Oropeza, O., Gonzalez-Abraham, C., Mascareñas-Osorio, I., Moreno-Báez, M., and Hastings, P. A. 2012. Spatio-temporal dynamics of a fish spawning aggregation and its fishery in the Gulf of California. Nature Scientific Reports, 2: 1–11.

Frank, K. T., and Brickman, D. 2000. Allee effects and compensatory population dynamics within a stock complex. Canadian Journal of Fisheries and Aquatic Sciences, 57: 513–517.

Garcia, S. M., and Newton, C. 1995. Current Situation, Trends and Prospects in World Capture Fisheries. FAO, Fisheries Department. Rome.

Gordon, H. R., and Cook, P. A. 2004. World abalone fisheries and aquaculture update: supply and market dynamics. Journal of Shellfish Research, 23: 935–940.

Gorfine, H., and Dixon, C. D. 2001. Diver behaviour and its influence on assessments of a quota managed abalone fishery. Journal of Shellfish Research, 20: 8.

Hernandez, A., and Kempton, W. 2003. Changes in fisheries management in Mexico: effects of increasing scientific input and public participation. Ocean & Coastal Management, 46: 507–526.

Hilborn, R., and Ledbetter, M. 1979. Analysis of the British Columbia salmon purse-seine fleet: dynamics of movement. Journal of the Fisheries Research Board of Canada, 36: 384–391.

Hilborn, R., Micheli, F., and De Leo, G. A. 2006. Integrating marine protected areas with catch regulation. Canadian Journal of Fisheries and Aquatic Sciences, 63: 642–649.

Hilborn, R. 2007. Moving to sustainability by learning from successful fisheries. AMBIO: A Journal of the Human Environment, 36: 296–303.

Huserbråten, M. B. O., Moland, E., and Albretsen, J. 2018. Cod at drift in the North Sea. Progress in Oceanography, 167: 116–124.

Jalali, M. A., Ierodiaconou, D., Gorfine, H., Monk, J., and Rattray, A. 2015. Exploring spatiotemporal trends in commercial fishing effort of an abalone fishing zone: a GIS-Based hotspot model. PLoS One, 10: e0122995.

Kaplan, D. M., Dueri, S., Chassot, E., Amande, J. M., Dagorn, L., and Fonteneau, A. 2014. Spatial management of Indian Ocean tropical tuna fisheries : potential and perspectives. ICES Journal of Marine Science, 71: 1728–1749.

Lokani, P., Polon, P., and Lari, R. 1995. Fisheries and management of beche-de-mer fisheries in Western Province of Papua New Guinea. SPC Integrated Coastal Fisheries Management, 11: 267–275.

McCay, B. J., Micheli, F., Ponce-Díaz, G., Murray, G., Shester, G., Ramirez-Sanchez, S., and Weisman, W. 2014. Cooperatives, concessions, and co-management on the Pacific coast of Mexico. Marine Policy, 44: 49–59.

Matsuda, H., Makino, M., Tomiyama, M., Gelcich, S., and Castilla, J. C. 2010. Ecological Research, 25: 899–907.

Mayfield, S., Chick, R. C., Carlson, I. J., and Ward, T. M. 2011. Invertebrate dive fisheries can be sustainable: forty years of production from a greenlip abalone fishery off southern Australia. Reviews in Fisheries Science, 19: 216–230.

Miller, A. D., Hoffmann, A. A., Tan, M. H., Young, M., Ahrens, C., Cocomazzo, M., Rattray, A. *et al.* 2019. Local and regional scale habitat heterogeneity contribute to genetic adaptation in a commercially important marine mollusc (*Haliotis rubra*) from southeastern Australia. Molecular Ecology, 28: 3053–3072.

Morgan, G. R. 1997. Individual Quota Management in Fisheries: Methodologies for Determining Catch Quotas and Initial Quota Allocation. Food & Agriculture Organization of the United Nations.Rome

NOAA. (n.d.). Green Abalone| NOAA Fisheries. https://www.fisheries.noaa.gov/species/green-abalone#overview (last accessed 28 December 2021).

Norderhaug, K. M., Nedreaas, K., Huserbråten, M., and Moland, E. 2021. Depletion of coastal predatory fish sub-stocks coincided with the largest sea urchin grazing event observed in the NE Atlantic. Ambio, 50: 163–173.

Okamoto, D. K., Hessing-Lewis, M., Samhouri, J. F., Shelton, A. O., Stier, A., Levin, P. S., and Salomon, A. K. 2019. Spatial variation in exploited metapopulations obscures risk of collapse. Ecological Applications, 0: 1–16.

Pérez-Jiménez, J. C., and Mendez-Loeza, I. 2015. The small-scale shark fisheries in the southern Gulf of Mexico: understanding their heterogeneity to improve their management. Fisheries Research, 172: 96–104.

Pomeroy, R. S. 2012. Managing overcapacity in small-scale fisheries in southeast Asia. Marine Policy, 36: 520–527.

R Core Team. 2019. R: A Language and Environment for Statistical Computing. Vienna, Austria.

Reich, D. A., and DeAlteris, J. T. 2009. A simulation study of the effects of spatially complex population structure for Gulf of Maine Atlantic cod. North American Journal of Fisheries Management, 29: 116–126.

Ricker, W. E. 1954. Stock and recruitment. Journal of the Fisheries Research Board of Canada, 11: 559–623.

Rose, G. A., and Kulka, D. W. 1999. Hyperaggregation of fish and fisheries: how catch-per-unit-effort increased as the northern cod (*Gadus morhua*) declined. Canadian Journal of Fisheries and Aquatic Sciences, 56: 118–127.

Rossetto, M., Micheli, F., Saenz-arroyo, A., Antonio, J., Montes, E., and Leo, G. A. De. 2015. No-take marine reserves can enhance population persistence and support the fishery of abalone. Canadian Journal of Fisheries and Aquatic Sciences, 72: 1503–1517.

Rust, S., Jennings, S., and Yamazaki, S. 2016. Excess capacity and capital malleability in a fishery with myopic expectations. Marine Resource Economics, 31: 63–81.

Ryu, J. G., Nam, J., and Gates, J. M. 2006. Limitations of the Korean conventional fisheries management regime and expanding Korean TAC system toward output control systems. Marine Policy, 30: 510–522.

Sadovy, Y., and Domeier, M. 2005. Are aggregation-fisheries sustainable? Reef fish fisheries as a case study. Coral Reefs, 24: 254–262.

Sampson, D. B. 1992. Fishing technology and fleet dynamics: predictions from a bioeconomic model. Marine Resource Economics, 7: 37–58.

Seijo, J. C., Pérez, E. P., and Caddy, J. F. 2004. A simple approach for dealing with dynamics and uncertainty in fisheries with heterogeneous resource and effort distribution. Marine and Freshwater Research, 55: 249–256.

Skjæraasen, J. E., Meager, J. J., Karlsen, Ø., Hutchings, J. A., and Fernö, A. 2011. Extreme spawning-site fidelity in Atlantic cod. ICES Journal of Marine Science, 68: 1472–1477.

Spies, I., Spencer, P. D., and Punt, A. E. 2015. Where do we draw the line? A simulation approach for evaluating management of marine fish stocks with isolation-by-distance stock structure. Canadian Journal of Fisheries and Aquatic Sciences, 72: 968–982.

Tattersall, K. 2011. Tracking Fishermen : Using GIS to Characterize Spatial Distribution of Fishing Effort in the Tasmanian Abalone Fishery.University of Tasmania,Australia

Villasante, S., Do Carme García-Negro, M., González-Laxe, F., and Rodríguez, G. R. 2011. Overfishing and the common fisheries policy: (un)successful results from TAC regulation? Fish and Fisheries, 12: 34–50.

Voss, R., Quaas, M. F., Schmidt, J. O., Stoeven, M. T., Francis, T. B., Levin, P. S., Armitage, D. R. *et al.* 2018. Quantifying the benefits of spatial fisheries management – an ecological-economic optimization approach. Ecological Modelling, 385: 165–172.

Wilen, J. E., Smith, M. D., Lockwood, D., and Botsford, L. W. 2002. Avoiding surprises: incorporating fisherman behavior into management models. Bulletin of Marine Science, 70: 553–575.

Woodson, C. B., Micheli, F., Boch, C., Al-Najjar, M., Espinoza, A., Hernandez, A., Vázquez-Vera, L. *et al.* 2019. Harnessing marine microclimates for climate change adaptation and marine conservation. Conservation Letters, 12: e12609.

Worm, B., Barbier, E. B., Beaumont, N., Duffy, J. E., Folke, C., Halpern, B. S., Jackson, J. B. C. *et al.* 2006. Impacts of biodiversity loss on ocean ecosystem services. Science, 314: 787–790.

Yap, W. G. 1997. Can the philippines produce enough fish for the multitude. Aquaculture Asia, 2: 32–38.

Ye, Y., and Gutierrez, N. L. 2017. Ending fishery overexploitation by expanding from local successes to globalized solutions. Nature Ecology & Evolution, 1:0179.

Handling Editor: David Kaplan