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► **To cite this version:**

Adrien Lagarde, Luc Doyen, Joachim Claudet, Olivier Thébaud. Stochastic Multi-species MSY to Achieve Ecological-Economic Sustainability of a Coral Reef Fishery System in French Polynesia. *Environmental Modeling & Assessment*, 2022, 27 (5), pp.771-789. 10.1007/s10666-022-09847-0 . hal-03783309

HAL Id: hal-03783309

<https://hal.science/hal-03783309v1>

Submitted on 22 Sep 2022

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Stochastic Multi-species MSY to Achieve Ecological-Economic Sustainability of a Coral Reef Fishery System in French Polynesia

Adrien Lagarde¹ · Luc Doyen¹ · Joachim Claudet² · Olivier Thebaud³

Abstract

This paper investigates the ecological-economic sustainability of coral reef socio-ecological systems under fishing and environmental pressures. To achieve this, a dynamic, spatially explicit, multi-species, multi-fleet fisheries model is developed. Stochastic environmental shocks are assumed to alter coral cover and consequently the entire coral reef social-ecological system. The model is calibrated using ecological, socio-economic and environmental data in French Polynesia. Four exploratory fishing strategies and a goal-seeking strategy entitled Stochastic Multi-Species Maximum Sustainable Yield (SMMSY) are compared in terms of ecological-economic outcomes and sustainability of the socio-ecological system. The SMMSY turns out to promote ecological-economic sustainability. It is characterised by a global increase in fishing effort pointing to the relative current under-exploitation of the fishery. SMMSY balances the trophic level of catches after natural shocks and sustains the fundamental herbivore grazing process. SMMSY strategies are also more diversified in terms of temporality, gears, spatial distribution of fishing and target species.

Keywords Ecological-economics · Biodiversity · Ecosystems · Scenarios · Small-scale fisheries · Sustainability · Resilience · French Polynesia

1 Introduction

Indo-Pacific coral reefs are among the most complex ecosystems worldwide. Most of these coral reefs are currently undergoing rapid changes and degradations due to an increase in both anthropogenic and natural disturbances [1, 2]. In particular, natural disturbances play an important role in the long-term dynamics of coral reefs, often causing periods of decline in coral cover potentially followed by periods of recovery [3, 4]. As a result of the human footprint on the planet, these disturbances should increase in intensity and occurrence in the foreseeable future [5]. Indeed, climate change and environmental shocks such as species invasions or

cyclones contribute to creating, or intensifying existing risks, uncertainties and vulnerabilities in marine systems [6–8]. As a consequence, ensuring the socio-economic sustainability of fisheries while preserving marine biodiversity and ecosystem services have become a major challenge for regional, national and international agencies [7]. To implement these objectives, multidimensional and integrative management models are emerging, and a large number of scientists advocate the use of ecosystem approach or ecosystem-based fishery management (EBFM) in order to take into account and integrate the various ecological and economic complexities and uncertainties at play [9–13].

Operationalising the EBFM approach requires new models or to adapt existing models. In that respect, the use of monospecies reference points in multi-species fisheries is increasingly criticised [14]. For instance, monospecies Maximum Sustainable Yield (MSY) targets have been shown to alter the structure of harvested ecosystems [15]. Moreover, although maximum economic yield (MEY) favours higher biomasses than MSY policies in single-species fisheries [16, 17], it does not account for potential ecological interactions in mixed fisheries [18]. As an alternative to single-species management strategies, there have been attempts at

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designing multi-species MSY (MMSY) and MEY (MMEY) policies, in which total catches or total profits are maximised [19, 20]. Such global harvesting policies may however enhance biodiversity losses: while MMSY policies are likely to threaten low-productivity species, MMEY policies induce the overexploitation of stocks with low economic value [21–23].

Beyond the complexities underlying normative strategies such as MMSY or MMEY, the integration of climate change is another challenge for EBFM. Indeed, as highlighted by [24–26] and [27] exploring the influence of climate change on marine resource dynamics is a key issue. Indeed, climate change may have strong impacts on ecological processes such as population distributions or population dynamics [28, 29]. However, accounting for these dynamics in models of population dynamics remains a challenge [30, 31]. Brander [32] and Cheung et al. [33] argue that climate change and global warming, in particular through their effects on sea temperature, may be the strongest drivers of stock dynamics and harvest levels in the future. Diop et al. [34] and Lagarde et al. [35] highlight the bioeconomic benefits of fishing strategies accounting for climate change. In that respect, the case of tropical fisheries is especially challenging, since a decrease of diversity is projected with climate warming [33, 36, 37].

Here, we focus on a case study in French Polynesia, the coral reef system of Moorea. In this system, ecological complexity emerges from the interplay between coral and algae cover, the different trophic groups of fishes including coral-ivores, herbivores and piscivores along with migration of fish between the fore reef and lagoon. The diversity of fishing techniques (diving, canoe, motorised boats) and tourism activities interacting with this ecological system contribute to the complexity of the fishery system as in many fisheries worldwide [38, 39].

Several studies have emphasised the difficulty to model such complex social-ecological systems, notably when also seeking to account for the effects of global change's effects [40, 41]. Our research proposes an intermediate complexity approach [37, 42] to the modelling of the Moorea social-ecological reef fishery system, allowing to estimate and compare fishing management strategies in ecological-economic terms in a context of environmental shocks. A dynamic, spatially explicit, multi-species, multi-fleet fishery model is developed and calibrated using ecological, economic and environmental data collected in Moorea. This ecological-economic model is strongly inspired by [43] and [44] as regards marine habitat dynamics of coral versus algae covers and by [45] regarding trophic interactions between fishes. Stochastic environmental shocks are assumed to alter coral cover and consequently the entire coral reef social-ecological system in line with [46]. From the calibrated model, four exploratory, forward-looking fishing management strategies and a normative, target-seeking strategy are compared in terms of their ecological-economic outcomes and with respect

to the sustainability and resilience of the system [47, 48]. More specifically, we evaluate and compare biodiversity, catch and fishing effort performances of these management strategies. To do so, we adopt a multi-criteria perspective in line with EBFM. The normative strategy entitled “Stochastic Multi-Species Maximum Sustainable Yield” (SMMSY) relies on the optimisation of expected harvests over time. This strategy echoes few studies [49–52] which attempt to evaluate sustainable marine food production for regions that highly depend on this, such as for insular populations. A major originality of our study is to present stochastic results based on an MSY-oriented approach at the scale of a coral reef fishery system.

The rest of the article is structured as follows. Section 2 presents the case study in French Polynesia. Section 3 describes the ecological-economic model as well as the five fishing management strategies. Ecological-economic results across the management strategies are analysed in Sect. 4. Section 5 concludes.

2 The Moorea Island Small-scale Fishery

Moorea Island (17°30'S, 149°50'W; French Polynesia), as illustrated by Fig. 1, is surrounded by a barrier reef characterised by a rich coral and fish diversity. Long of 61 km and wide of 750 m, the coral reef of Moorea has been subject to long-term monitoring and therefore displays one of the longest data sets on the evolution of a coral reef ecosystem in the world, beginning in the early 1980s [53].

Moorea experienced a great number of disturbances over the past decades affecting the tridimensional structure of the reef. This includes cyclones (1991, 2010) and crown-of-thorns seastar (COTS) outbreaks in particular (1979–1984, 2006–2009) as well as several bleaching events (1983, 1987, 1991) which cause variable degrees of decline and recovery in coral cover and diversity ([3]). Despite these perpetual shifts in coral reefs along with changes in the associated fish assemblages, fish functional diversity remains stable. Indeed, natural shocks play a fundamental role in the dynamics of Moorea's reef system.

Another key driver of changes in this system is human population growth [1, 4], which has been high in French Polynesia over the past decades, with an estimated 2% per year increase (Statistics Institute of French Polynesia, ISPF) although a slowdown in population growth is currently observed¹. Economically and socially, fishing activities are of key importance to local populations of Moorea, as in most small islands of the Pacific [54, 55]. However, the extent of the pressures entailed by fishing on coral reef ecosystems of Moorea, as well as the ensuing sustainability of

¹ Less than 1% between 2007 and 2017 [81].

Fig. 1 Moorea Island



observed fishing activities, remains poorly known. Indeed, fish landing levels remain highly uncertain as the few analyses [56–59] attempting to assess global fishing catches in Moorea providing very different estimates over the years, whereas fishermen ascertain they harvest the same amount of fish than before [60].

A large proportion of landings from the reef fishery is self-consumed², the rest being sold in the so-called “tui”³ [61] to contribute to cash earnings of households. The weight of a tui is about 3 kg and is sold around 1500 XPF⁴. Aubanel [56] observes the same price than nowadays (pers. observation) suggesting that the socio-economic system relating to fishing displays a very stable pattern. More detailed analysis of tui composition and prices [61, 62] show however the potential for some heterogeneity in the prices of individual species, with implications for the changes in the composition of landings over time, following environmental perturbations and impacts of fishing (see Table 1).

3 The Ecological-Economic Model

3.1 Conceptual Model

Figure 2 represents the conceptual ecological-economic model developed, which is dynamic, spatially explicit, multi-species and multi-fleet, and highlights the main interactions

² More than 50% in average according to social surveys.

³ A tui is “A wreath of fish consisting of one or more species, tied together with plant fibre drawn through their gills and then suspended on a metal holder, which forms the sales unit.” [60].

⁴ Around 12€.

between the ecological, economic and social components of the fishery. Table 2 in the Appendix details the species composition of the different functional groups considered in the model. It also provides the notations used hereafter for these groups.

3.2 Mathematical Model

We now describe the ecological-economic model in mathematical terms. It is inspired by [43, 46] and [44]. The dynamics of the five functional groups are assumed to be governed by Lotka-Volterra type interactions including trophic (for fishes) or competition (for habitats) mechanisms. The model is spatially explicit with two patches to account for the movements of fishes between the Lagoon and the Fore Reef. In each patch p (Lagoon or Fore Reef), we describe three distinct dynamics: the first for Coral (Eq. (1)), the second for Algae (Eq. (2)) and the third one for the three functional groups of fish (Eqs. (6) and (7)), namely the piscivores, the herbivores and the corallivores. The stochasticity in the model arises from shocks (cyclones, cots outbreaks) damaging the coral cover on the fore reef.

Habitat Dynamics The dynamics of coral cover $x_{1,p}(t)$ in patch p at time t reads as follows:

$$x_{1,p}(t+1) = x_{1,p}(t) \left(1 + r_1 - s_{1,1}x_{1,p}(t) - s_{1,2}x_{2,p}(t) - s_{1,5}x_{5,p}(t) \right) (1 - \Delta r_p(\omega(t))), \quad (1)$$

where r_1 stands for the intrinsic growth rate of the coral cover, $s_{1,1} > 0$ relates to carrying capacity of coral while $s_{1,2} > 0$ represents the competition between coral and algae cover $x_{2,p}$ on the same patch p and $s_{1,5} > 0$ corresponds to

Table 1 SMMSY fishing effort evolution per comity Δe_{fc} . The detailed SMMSY fishing effort evolution structure is displayed by type of fishing. The efforts are gathered and averaged per geographical units underlying the case study. Furthermore, its evolution is here

		Comity	Haapiti	Papetoai	Paopao	Teavaro	Afarcaitu	Mean per fleet
Lagoon	No Boat		39%	91%	-3%	22%	64%	43%
	Unmotorised Boat		51%	104%	49%	75%	89%	73%
	Motorised Boat		18%	97%	72%	46%	47%	56%
	Non Resident		50%	87%	-27%	72%	49%	46%
Reef	Unmotorised Boat		30%	75%	15%	47%	60%	45%
	Motorised Boat		68%	109%	-28%	93%	12%	51%
	Non Resident		56%	100%	8%	39%	60%	53%
Mean per Comity			45%	95%	12%	56%	54%	

the trophic interaction between corallivore biomass $x_{5,p}$ in patch p and coral. The variable rate $\Delta r_p(\omega(t))$ captures the environmental disturbances (cots outbreak, cyclones) on coral cover in patch p depending on stochastic scenarios $\omega(t)$. We assume that shocks only impact the coral group on the fore reef as it has been observed historically as described in Sect. 2.

The dynamics of algae cover $x_{2,p}(t)$ in patch p at time t reads as follows:

$$x_{2,p}(t+1) = x_{2,p}(t)(1 - s_{2,3}x_{3,p}(t)), \quad (2)$$

where $s_{2,3} > 0$ relates to the trophic interaction between herbivore biomass $x_{3,p}$ in patch p and algae. State $x_{2,p}(t)$ is also constrained by a surface inequality:

$$x_{2,p}(t) \leq g(K_p - x_{1,p}(t)), \quad (3)$$

where the parameter g stands for the percentage of reef grazed (only algae) as in [43] and K_p represents the carrying capacity for habitats in patch p , i.e. the entire available area which can be colonised by algae and coral (canal and sandy floor/depth excluded⁵). In other words, K_p is the carrying capacity for habitats in patch p .

Fish Dynamics The dynamics of corallivores $x_{5,p}(t)$ in patch p at time t reads as follows:

$$x_{5,p}(t+1) = x_{5,p}(t) \left(1 + r_5 - \gamma_p(x_{1,p}(t))s_{5,4}x_{4,p}(t) + s_{5,1}x_{1,p}(t) \right), \quad (4)$$

where parameter $s_{5,1} > 0$ stands for the consumption of coral by corallivores. Parameter $s_{5,4} > 0$ stands for the predation of piscivores on corallivores and $\gamma_p(x_{1,p}(t))$ represents the

presented per capita such as: $\Delta e_{fc} = \frac{e_{fc}(t_n) - e_{fc}(t_h)}{(1+l_f)^{n-h}}$ where $e_{fc}(T)$ stands for the estimated fishing effort per fleet f and per comity c in 2049 and l_f the demographic growth rate. We observe than the fishing effort increases

refuge effect as explained in Eq. (5). In that regard, following [46], we capture the effect of habitat refuge⁶ for predation intensity by the difference between the carrying capacity of Coral (maximum of Coral cover depending on patches) and the percentage of Coral cover at time t such as:

$$\gamma_p(x_{1,p}(t)) = K_p - x_{1,p}(t) \geq 0, \quad (5)$$

where $K_p - x_{1,p}(t)$, also presented above in Eq. (2), stands for the non-coral area where finding a refuge is harder for grazers/small herbivores.

Regarding the dynamics of mobile and harvested fish groups, namely herbivores $x_{3,p}(t)$ and piscivores $x_{4,p}(t)$ in patch p at time t , we first write it without accounting for dispersion mechanisms between the lagoon and the fore reef as follows:

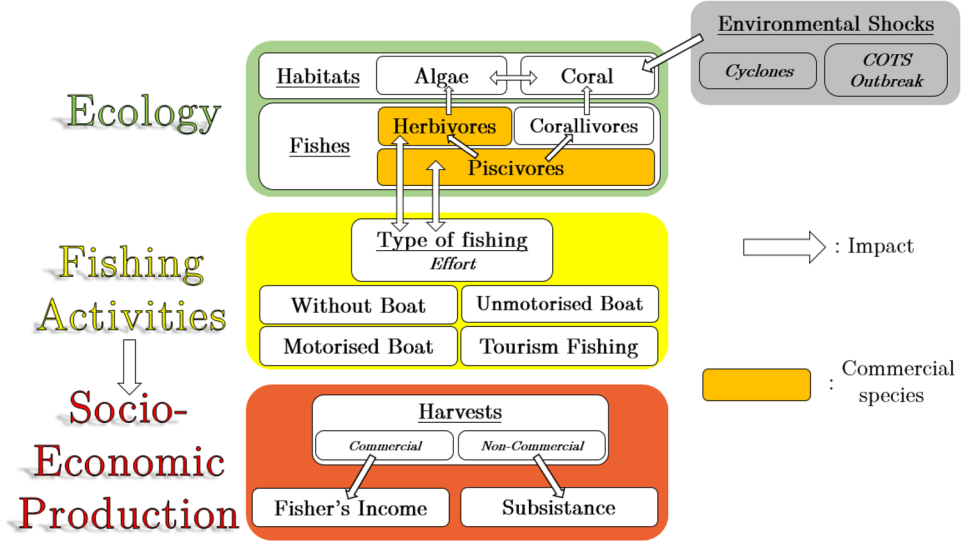
$$\begin{cases} \widetilde{x}_{3,p}(t+1) = x_{3,p}(t) \left(1 + r_3 + s_{3,2}x_{2,p}(t) - \gamma_p(x_{1,p}(t))s_{3,4}x_{4,p}(t) \right) - H_{3,p}(t) \\ \widetilde{x}_{4,p}(t+1) = x_{4,p}(t) \left(1 + r_4 + \gamma_p(x_{1,p}(t))s_{4,3}x_{3,p}(t) - s_{4,4}x_{4,p}(t) + \gamma_p(x_{1,p}(t))s_{4,5}x_{5,p}(t) \right) - H_{4,p}(t) \end{cases}, \quad (6)$$

where $H_{3,p}(t)$ and $H_{4,p}(t)$ are the fishing harvests of herbivores and corallivores respectively. Again r_3 and r_4 stand for the intrinsic growth rates of the herbivores and piscivores. Parameter $s_{3,2} > 0$ represents the consumption by herbivores of algae. Symetric parameters $s_{3,4} > 0$ and $s_{4,3} > 0$ stand for

⁵ K_{lagoon} equals 50% for the lagoon and K_{reef} is set at 98% for the fore reef.

⁶ Basically, all things equal, the higher the coral cover, the less predation there is and the more herbivores there are.

Fig. 2 Conceptual model



the predation of herbivores by piscivores and $s_{4,4} > 0$ for the intra-specific competition, i.e. cannibalism within piscivores group. Again $\gamma_p(x_{1,p}(t))$ models the refuge effect generated by the coral $x_{1,p}(t)$.

Spatially Explicit Dynamics In order to capture the spatial movements of fishes between the lagoon and the fore reef, a diffusion factor depending on the mobile species and on the patch is implemented as in [63]. The parameters $d_{i,p,p'}$ stand for the share of the biomass of group i which moves from patch p to patch p' . We assume that herbivores and piscivores are mobile species while the corallivores remain within their initial patch ($d_{5,lagoon,reef} = 0$). Dispersion dynamics thus reads:

$$\begin{cases} x_{3,p}(t+1) = \sum_{p'=lagoon}^{reef} d_{3,p',p} \widetilde{x}_{3,p'}(t+1) \\ x_{4,p}(t+1) = \sum_{p'=lagoon}^{reef} d_{4,p',p} \widetilde{x}_{4,p'}(t+1) \end{cases}, \quad (7)$$

where $d_{3,lagoon,reef} > 0$ and $d_{4,lagoon,reef} > 0$ and $x_{i,p'}(t+1)$ defined in (6).

Fishing The fishery production is represented by a standard Schaefer function where harvest is a linear function of both fishing efforts and resource biomass as follows:

$$H_{i,f,p}(t) = q_{i,f,p} e_{f,p}(t) L_f(t) x_{i,p}(t) \quad i = 3, 4. \quad (8)$$

Here the parameter $q_{i,f,p}$ measures the catchability of group i by fishing pattern/fleet f in patch p per hour. The fishing effort $e_{f,p}(t)$ is the number of hour per year spent by one

fisherman of the fleet f in patch p while $L_f(t)$ stands for labor⁷ engaged within fleet f (in number of fishers per km²).

Uncertainty We assume that shocks only impact the coral group on the fore reef. In other words, the environmental impact on the lagoon is null as follows:

$$\Delta r_{lagoon}(t) = 0.$$

We also assume that the environmental shocks $\Delta r_{reef}(t)$ follow a Bernoulli distribution of parameter μ and p . Therefore, the probability of the natural disturbance μ ($0 < \mu < 1$) on the fore reef for the coral is described by:

$$\mathbb{P}(\Delta r_{reef}(t) = \mu) = p, \quad \mathbb{P}(\Delta r_{reef}(t) = 0) = 1 - p, \quad (9)$$

where μ is the magnitude of shocks on coral reef. The Bernoulli distribution is supposed to be independantly and identically distributed (i.i.d) over time.

Uncertainty is here expressed by a probability of occurrence of a natural disturbance. We assume that COTS outbreak and cyclone (which are the two main shocks that affect coral cover) have the same impact based on historical observations and in order to simplify the model. The natural shocks on the fore reef induced by cyclones or COTS outbreaks strongly affect the dynamics of the whole coastal ecosystem, at least in the short term, as exemplified by the historical trajectories plotted in Fig. 3.

⁷ Historical Labor (2005–2016) is presented in Table 4. Estimated labor is assumed to grow linearly following an estimated demographic rate noted l_f : $L_f(t+1) = l_f * L_f(t_h)$ with $t_h = 2016$.

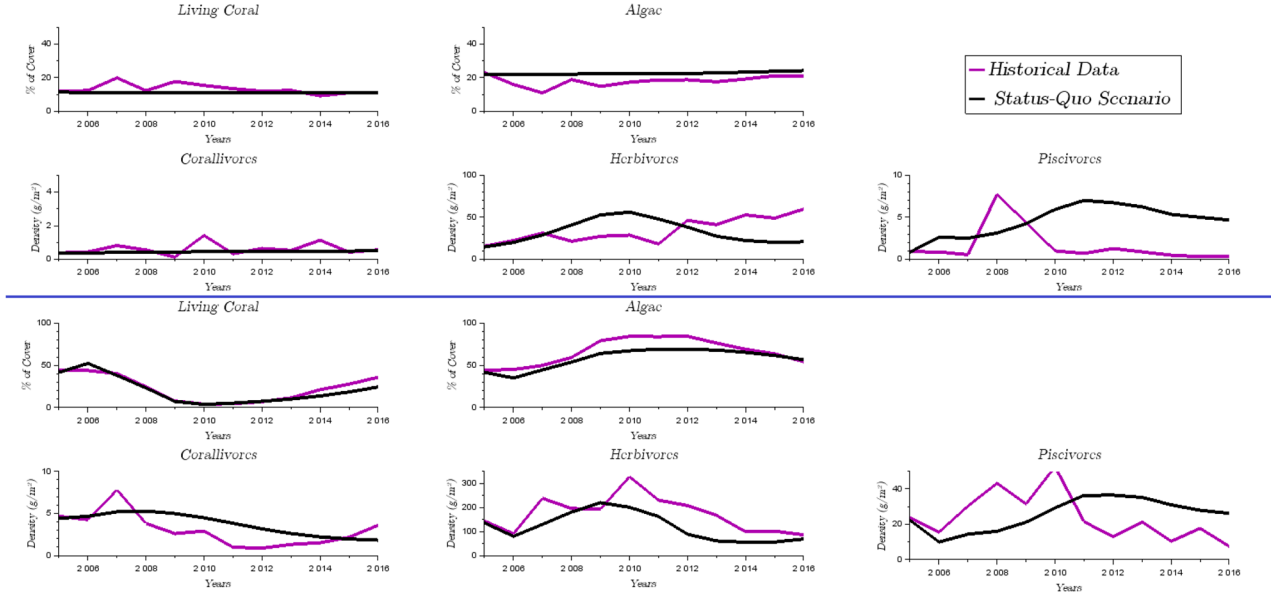


Fig. 3 Calibration — The five first figures (top) account for the lagoon and the five following figures (bottom) stand for the fore reef

Thus, it was important to account for such processes. Moreover, the historical paths (Fig. 3) shows a recovery of coral, and more globally of the ecosystem as a whole, which occurs after some years. Such recovery relates to the historical resilience mentioned in the paper. At this stage, a first question that arises is whether changes in the fishing effort as those underlying the different fishing strategies of the paper (Status-Quo, MMSY, Closure...) can alter such complex dynamics and recovery. This is a major issue of the paper. A second question arising is whether more frequent (or damaging) shocks can be detrimental to such dynamics and recovery as the resilience of coral depends on the frequency and magnitude of shocks. In particular, the climate change could significantly modify the parameters of such stochasticity. This last issue, beyond the scope of this paper, is investigated in the fourth chapter of the PhD thesis of Adrien Lagarde⁸.

3.3 Calibration

We calibrate the model using ecological, economic and environmental data from French Polynesia and in particular Moorea island [53, 58]. In this study, we are focusing on the thirteen areas defined by the previous Maritime Space Management Plan⁹ (2005–2019). Biological data such as fish density, % of cover of habitats, area in km² stem from the long-term monitoring carried out by the CRIOBE¹⁰ within the framework of the PGEM from 2005 to 2016. Economic

data (capturability coefficients, fishing effort, fleets composition) are obtained from the PROCFish report [64], through the ANR ACROSS project and surveys which have been done in Maatea (one of the Moorea’s communes).

The estimated ecological parameters to estimate include the intrinsic growth rates r_i of groups, the interaction coefficients s_{ij} between groups and the diffusion rate $d_{i,p,p'}$ of mobile species between patches for each species i . The method to estimate the ecological parameters consists in minimising the mean square error between the annually observed $x^{hist}(t)$ and states $x(t)$ simulated by the model. We rely on data from different zones z along the coast in Moorea as follows:

$$\min_{r,s,d} \left[\sum_{t=t_0}^{t_h} \sum_i \sum_p \sum_z \left(x_{i,p,z}^{hist}(t) - x_{i,p,z}(t) \right)^2 \right], \quad (10)$$

with $t_0 = 2004$ and $t_h = 2016$ stands for first and the last year of observed data. The nonlinear optimization problem in Eq. (10) was solved numerically using the Scilab¹¹ software and algorithms based on genetic optimization (optim_ga).

Based on the historical records from Moorea’s monitoring, we consider that external shocks such as cyclones, COTS outbreak or bleaching event have a major impact only on coral cover on the fore reef¹².

¹¹ <https://www.scilab.org/>.

¹² The biological dimension embeds these phenomena through a forcing of the coral cover in 2006, 2007, 2008 (COTS) and 2010 (cyclone OLI) to its historical and observed % of cover

$x_{1,reef}(t_{shock}) = x_{1,reef}^{hist}(t_{shock})$ with $t_{shocks} = [2007, 2008, 2009, 2010]$.

⁸ <http://www.theses.fr/2020BORD0214>.

⁹ PGEM (Plan de Gestion de l’Espace Maritime) in French — [82].

¹⁰ <http://www.criobe.pf/>.

In the [Appendix](#), Table 3 summarises the different biological parameters of the model while Table 4 displays the fishing parameters. The stochasticity parameters relating to the coral dynamics and Eq. (9) are $\mu = 0.7$ and $p = 10\%$. These values¹³ have been chosen according to historical and reconstructed data from [53].

Regarding the quality of the calibration, we observe in Fig. 3 that, the deviation of the estimation from the data is better on the fore reef than on the lagoon where an inertia is observed. This may be explained by the fact that other ecological drivers apply in the lagoon. In particular, other human activities (terrestrial inputs, physical development, navigation and tourism) whose nature is not known to negatively impact the piscivores notably in the second part of the historical period. Furthermore, as the smaller size of the fore reef implies a higher overall density (fishes) and cover (habitats), it is difficult to compare them on the same scale. Moreover, collected data (notably for herbivores and piscivores) on the fore reef are likely to be more biased given the very high density and diversity in this particular patch.

Given the large number of parameters, a sensitivity analysis was carried in order to assess the robustness of the calibration and therefore of the results. Figure 12, in the [Appendix](#), displays the simulated trajectories of all functional groups for both patches with a variation [-10%,+10%] of all calibrated parameters. We see that, even if the densities or cover rates are either higher or lower according to parameters variation, the trends and paths remain qualitatively similar. This result reinforces the relevance of the model and its calibration in the sense that the model seems to get a good representation of the ecosystem structure and interactions.

3.4 Fishing Strategies

We consider different fishing strategies in order to compare them in terms of simulated trajectories over the period $t_h = 2016$ to $t_n = 2049$. Following [65] and IPBES [66], we distinguish between exploratory and goal-seeking strategies for fishing. The three first strategies are theoretical and would not be applicable as management models but allow us to explore how the system responds to shocks depending on the fishing closures.

Closure (C) Strategy The first exploratory strategy named Closure bans fishing for all fleets and patches p as follows:

$$e_{f,p}^C(t) = 0 \quad \forall t = t_h + 1, \dots, t_n \quad \forall f, p.$$

This strategy makes it possible to focus on the ecological dynamics of the ecosystem in the long run. Although theoretical, it constitutes a benchmark regarding the ecological performances of the ecosystem.

Closure on Lagoon and a 100% Increase in Effort on the Fore Reef (2R) The second exploratory strategy bans fishing on the lagoon and double the fishing effort on the fore reef to compensate the closure within the lagoon:

$$e_{f,lagoon}^{2R}(t) = 0 \quad e_{f,reef}^{2R}(t) = 2 * e_{f,reef}(t_h) \quad \forall t = t_h + 1, \dots, t_n \quad \forall f, p.$$

Closure On Fore Reef and a 100% Increase in Effort On the Lagoon (2La) Symmetrically, the third strategy explores a situation where fishing is stopped on the fore reef while it doubles within the lagoon:

$$e_{f,lagoon}^{2La}(t) = 2 * e_{f,lagoon}(t_h); \quad e_{f,reef}^{2La}(t) = 0 \\ \forall t = t_h + 1, \dots, t_n \quad \forall f, p.$$

Status-Quo (SQ) Strategy The fourth exploratory fishing strategy entitled Status-Quo (SQ) maintains fishing efforts at the current level (of year $t_h = 2016$) throughout the period of interest for every fleet f and every patch p . In other words, it assesses the consequences of maintaining the current management of the fishery such that:

$$e_{f,p}^{SQ}(t) = e_{f,p}(t_h) \quad \forall t = t_h + 1, \dots, t_n \quad \forall f, p.$$

Stochastic Multi-species Maximum Sustainable Yield (SMMSY) Strategy This strategy differs from the exploratory fishing strategies (such as SQ) in the sense that it is a goal-seeking (or normative) strategy aimed at achieving specific goals in the future. The objective of this SMMSY strategy is to reach a maximum sustainable yield over all harvested species, that is to say, to maximise long-term landings induced by the different types of fishing f . To account for the uncertainty of shocks $\Delta r_{reef}(t)$ affecting coral reef dynamics in Eq. (1), we consider the expected value of the sum of the landings over time as follows:

$$\max_{e^{(\dots)}} \mathbb{E} \left[\sum_{t=t_h+1}^{t_n} \left(\sum_i \sum_f \sum_p H_{i,f,p}(t) \right) \right]. \quad (11)$$

In this strategy, we assume that only two fishing effort choices e_0 et e_1 are identified at the start of two periods $t_h + 1$ and $t_1 + 1$. Moreover, to deal with feedback controls and uncertainties, the choice of these two efforts relies on a ‘non-anticipative’ control strategy [9, 67]. Feedback controls mean that management accounts for the uncertainty through the different possible states induced by the stochastic dynamics. Thus, at the first period $[t_h + 1, t_1]$ of the

¹³ When a relevant natural shock occurs, coral cover on the fore reef decreases of 70% in average and it happens once every decade in average for the last 30 years.

decision process, the fishing effort is assumed to depend only on the information on the initial state $x(t_h + 1)$ available throughout the period. Thereby, at the start of the second period $t_1 + 1$, we have a number of possible states of the ecosystem induced by the different replicates drawn randomly. For each of these possible states $B(t_1 + 1)$, a new decision about fishing effort is taken $e(t_1 + 1, x(t_1 + 1))$ again in the form of a feedback control depending on the state of the ecosystem at time $t_1 + 1$. Here, we postulate that the fleets will potentially change their fishing effort with SMMSY every 16 years (because $t_1 = 2032$). Such a slow schedule captures the inertia of decisions and adaptations.

4 Results

Figures 4 to 8 show the ecological trajectories of the fish functional groups aggregated over the two patches for the five different effort scenarios. In the Appendix, the dynamics of Coral and Algae cover are described in Fig. 11. Figure 9a displays catch performances of the four fleets and (b) plots the global catches trajectories over time. Each strategy is then analysed from ecological and economic viewpoints. The five management strategies are displayed using a colour code (Grey: SQ, Green: Closure, Blue: 2R, Red: 2La, Brown: SMMSY). The greater variability observed for the herbivore group is explained by a higher spawning stock and density in comparison to other

functional groups and by a likely higher bias in historical data.

4.1 Status-Quo (SQ): Ecologically and Socially Sustainable

Plotted in grey on Fig. 4, the SQ strategy displays a relatively diversified ecosystem. The density of commercial species (piscivores and herbivores) remains at sustainable levels. From the economic and fishing viewpoints as displayed by Fig. 9, catches increase throughout the time horizon. Thus, the potential demographic growth of human populations does not seem to strongly alter the socio-ecosystem structure, sustainability and resilience.

4.2 Closure (CL): Limited Ecological Gains and Not Socially Sustainable

Drawn in green on Fig. 5, the CL projections are characterised by the same habitat dynamics than in the SQ projection, while it significantly differs for fish density trajectories of the herbivores and piscivores groups. It turns out that preventing every zone from fishing does not improve the ecological status of the ecosystem, in particular in terms of fish biomass. This counter-intuitive result is due to the fact that the fishing ban reinforces the top predators, namely the piscivores, which affects the herbivores because of trophic interactions. Moreover, this closure strategy is obviously not economically and socially viable given the high dependency of the local inhabitants on fishing.

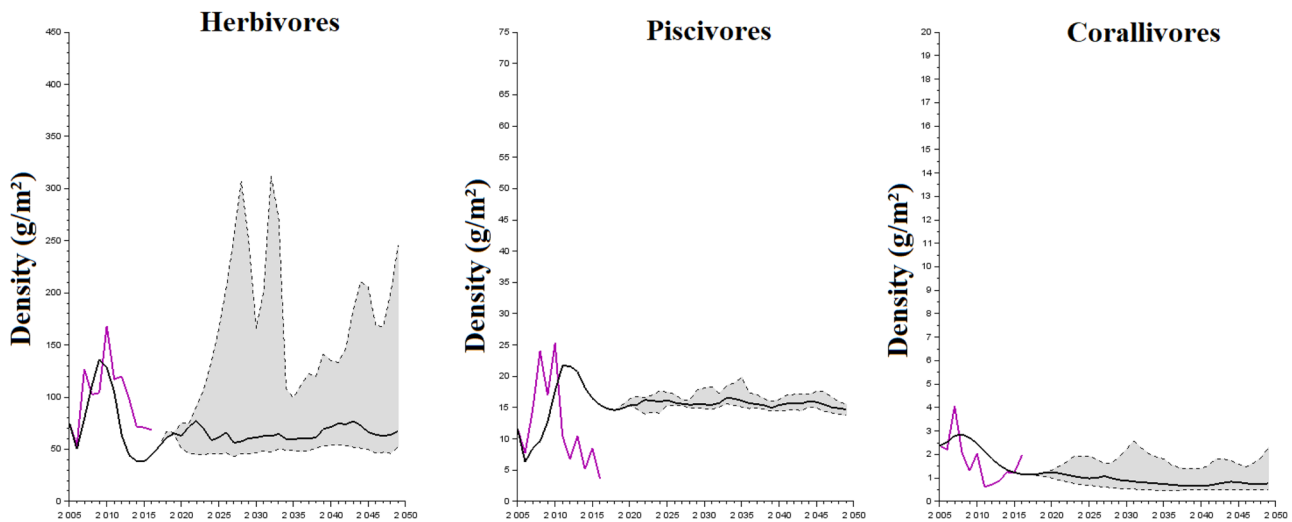


Fig. 4 Status-Quo strategy — Ecological Trajectories — The three figures account for the aggregated (Lagoon/Fore Reef) fish densities. The 100 simulated trajectories are represented by the grey area. The

solid lines display the average of these 100 trajectories and the purple line stands for the historical data

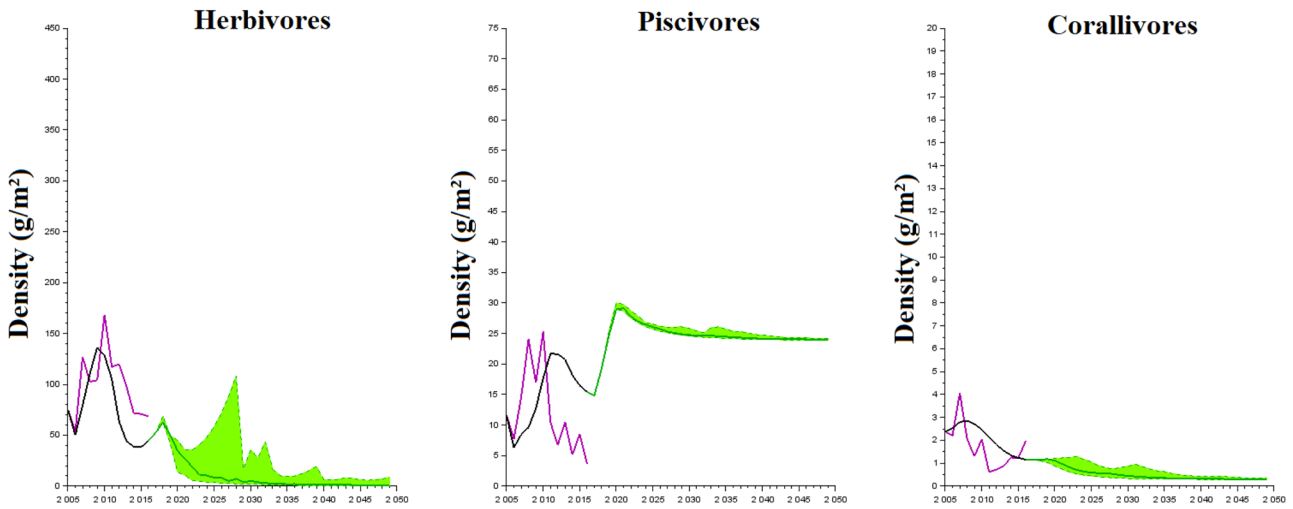


Fig. 5 Closure strategy — Ecological Trajectories — The three figures account for the aggregated (lagoon-fore reef) fish densities. The 100 simulated trajectories are represented by the green area. The

solid lines display the average of these 100 trajectories and the purple line stands for the historical data

4.3 Closure on Lagoon and + 100% on Reef (2R): Ecologically Limited and Not Socially Sustainable

As shown by trajectories in blue on Fig. 6, closing only the lagoon induces similar trends as compared to the CL closure strategy. Indeed, given the size of the fishing area in the lagoon, banning fishing in this area increases top predator density and as a consequence strongly and negatively impacts the herbivore biomass. Economically, as displayed by Fig. 9, the level of

catches is lower than under the SQ strategy mainly because the lagoon represents 90% of Moorea’s coastal ecosystem.

4.4 Closure on Fore Reef and Increase of 100% on Lagoon (2La): Ecologically and Socially Sustainable

As illustrated by trajectories in red on Fig. 7, closing the fore reef implies similar ecological consequences as compared to

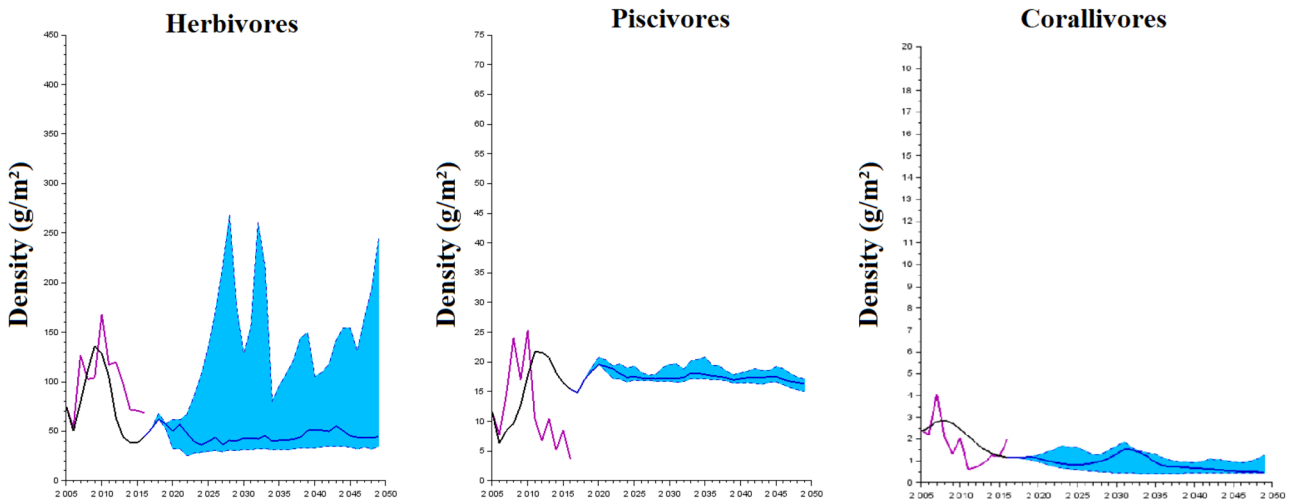


Fig. 6 2R strategy — Ecological Trajectories — The three figures account for the aggregated (Lagoon/Fore Reef) fish densities. The 100 simulated trajectories are represented by the blue area. The solid

lines display the average of these 100 trajectories and the purple line stands for the historical data

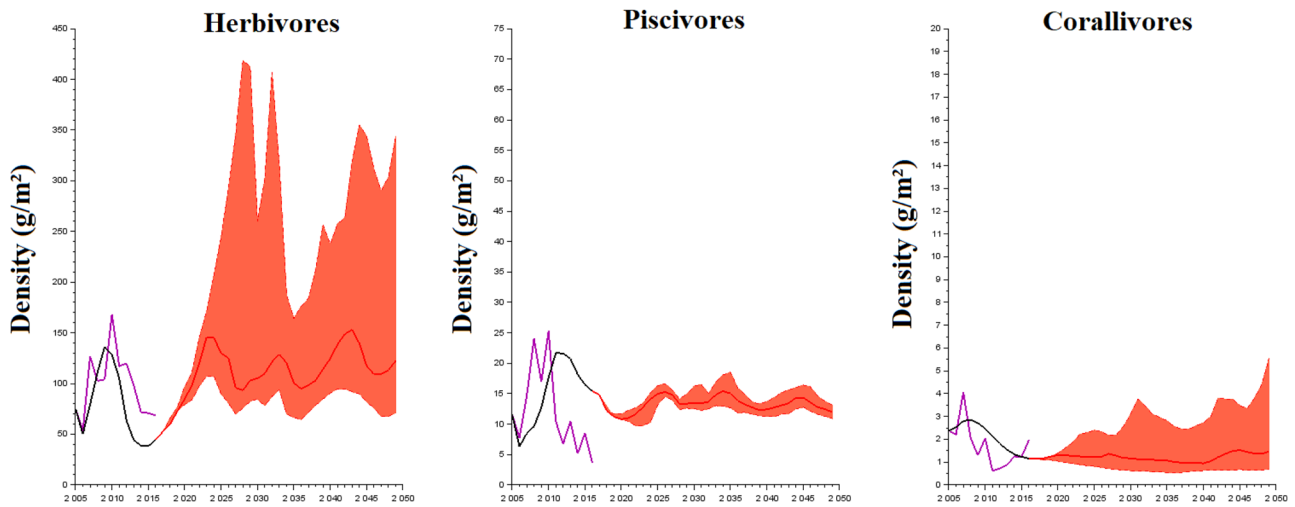


Fig. 7 2La strategy — Ecological Trajectories — The three figures account for the aggregated (lagoon/fore reef) fish densities. The 100 simulated trajectories are represented by the red area. The solid lines

display the average of these 100 trajectories and the purple line stands for the historical data

the SQ strategy. Within the fore reef, the piscivores density is slightly higher than in SQ and does not significantly affect the herbivore biomass. Regarding catches, plotted in Fig. 9, the size of the lagoon and the refuge effect that emerges from the closing of the fore reef entails a high level of catches, notably higher than under the previous strategy. Therefore, stop fishing in the fore reef and reallocating fishing effort to the lagoon leads to a stronger ecological and economic sustainability than the previous strategy 2R closing the lagoon.

4.5 SMMSY: Ecologically and Socially Sustainable

As highlighted by trajectories in brown on Fig. 8, the SMMSY strategy displays ecological paths similar to the previous strategy 2La but with a lower density of piscivores. From economic and social perspectives (Fig. 9), catches are higher than with all other strategies, since this is the strategy maximising catches. If we examine more closely the structure of fishing effort (Table 1), notably for the type of fishing, we find that

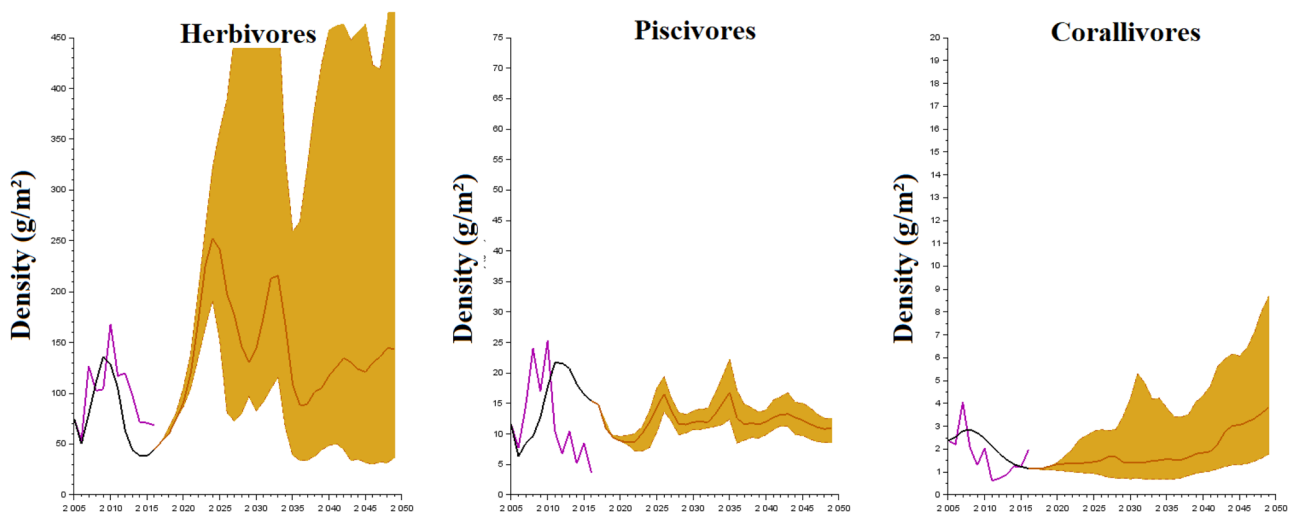
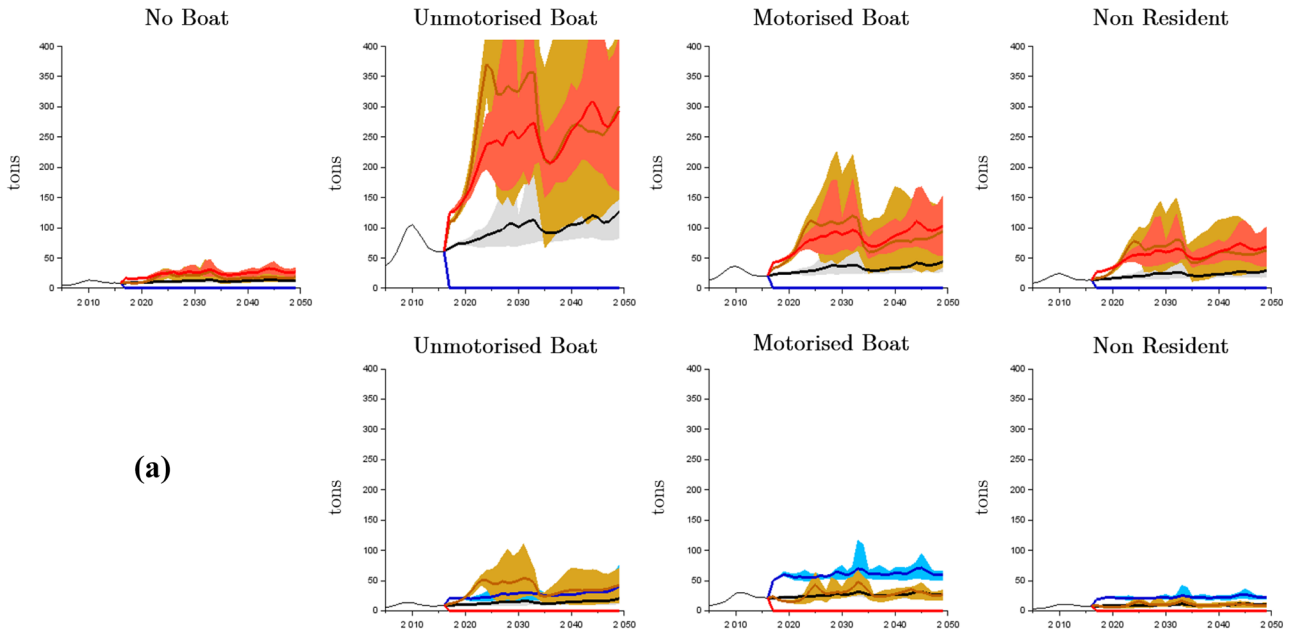


Fig. 8 SMMSY strategy — Ecological Trajectories — The three figures account for the aggregated (lagoon-fore reef) fish densities. The 100 simulated trajectories are represented by the brown area. The

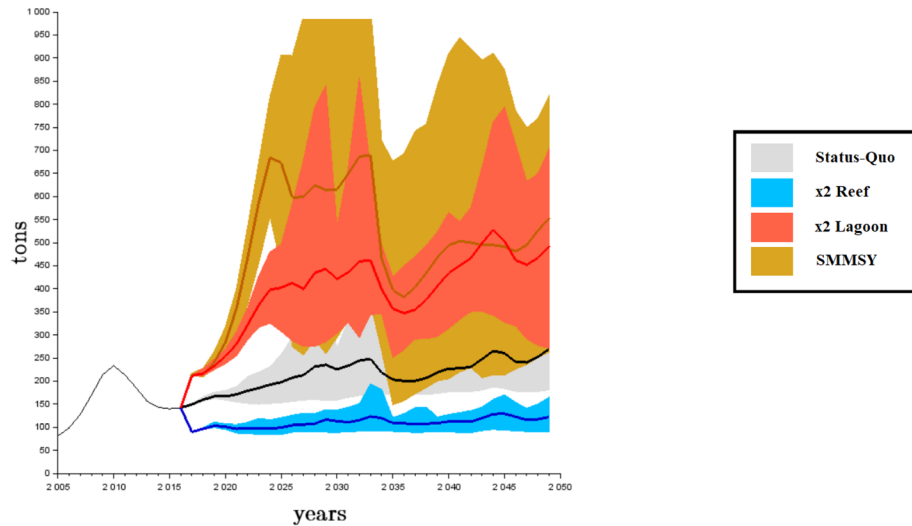
solid lines show the average of these 100 trajectories and the purple line stands for the historical data

Catches per Fleets



(a)

Catches



(b)

Fig. 9 a Catches per fleets trajectories: The 100 simulated trajectories are represented by the coloured areas depending on the management strategy. The solid lines display the average of these 100 trajectories. The four first fleets (up) operate on the lagoon and the three other ones (down) operate on the fore reef (with “no boat” it is impossible

to fish on the fore reef). **b** Aggregated catches trajectories: the 100 simulated trajectories are represented by the coloured areas depending on the management strategy. The solid lines display the average of these 100 trajectories

fishing effort is higher for unmotorised boats on the lagoon when compared to other types of fishing. Such an outcome could be explained by a lower mobility (represented in this model by a lower catchability) of this fleet on the fore reef

mainly because the fore reef is smaller and further away from the coast than the lagoon. Thus, it is more profitable to increase the effort of this fleet in a patch where it has a higher catchability, i.e. the lagoon.

5 Discussion

5.1 MICE Modelling to Operationalise Ecosystem-Based Fishery Management

The model we developed in this paper is in line with Models of Intermediate Complexity (MICE) advocated in [9, 37, 42] to deal with ecosystem-based fishery management. Indeed, this model is question-driven, and aims to limit complexity by restricting the focus on the minimum components and interactions needed to address the main effects of the management question under consideration. While more focused than whole-of-ecosystem models, such as Atlantis [68] or Ecopath with Ecosim (EwE — [69]), such models still integrate complex marine ecosystem dynamics under global changes, the economic processes driving the evolution of marine fisheries, and their interactions with marine ecosystem services and human well-being. An advantage of these models is that they remain simple enough to allow easy adaptation and facilitate communication between disciplines and stakeholders, including non-scientists. In that respect, our model accounts for the major ecological complexities of coral reef ecosystems by articulating habitat dynamics, trophic interactions between fishes and environmental perturbations such as cyclones or COTS outbreaks. By placing emphasis on fishing outcomes, it also accounts for the economic and social drivers as well as management issues. In that regard, the comparison between the different fishing strategies and the Status-Quo gives important insights into potential improvements over the current system state and its management.

5.2 SMMSY to Promote Ecological-Economic Sustainability

Our simulation of the normative strategy SMMSY turns out to be very informative in terms of reconciling ecological-economic objectives and fostering resilience of the reef fishery social-ecological system. By maximising (expected) catches, such a strategy indeed sustains commercial species in the long run and also induces the persistence of all the ecosystem components. Commercial species indeed represent a major share (>80%) of the entire ecosystem and play an essential ecological role for sustaining coral reefs, in particular via grazing by herbivores (grazers). Therefore, the SMMSY emerges as an EBFM relevant to manage both large-scale [35] but also small-scale fisheries such as those encountered in coral reef systems. In Fig. 10, we synthesise the ecological-economic scores (Share of Herbivores Biomass, Catches, Marine Trophic Index, Fish Biomass Increase)

and display the average and global fishing effort evolution of the five¹⁴ management strategies. If we use the surface of the radar plots (fishing effort excluded, so set at one to allow the comparison of surface), we can then rank the strategies in terms of these ecological-economic results:

$$2R < SQ < 2La < SMMSY$$

While weighting the 5 indices presented above according to a substitutability factor could be used to further rank the alternative strategies, implementing such a weighting would imply a strong assumption of weak sustainability [70] which is increasingly considered irrelevant [71]. Analysis of the ranks obtained following this approach shows that the SMMSY strategy performs better ecologically with a higher increase in fish biomass but also economically and socially, with a stronger amount of catches and a lower effort than the 2La strategy, which is the second best. With a greater share of herbivores, the grazing function is also preserved thus promoting the resilience of the ecosystem. Nonetheless, a lower Marine Trophic Index (MTI) indicates a potential tipping point where some high trophic level could be at risk. A spatially explicit management strategy, such as the 2La scenario, could also deal with this issue (further addressed in Sect. 5.4). More globally, the SMMSY strategy emerges as the most sustainable management strategy among the different strategies investigated here including the SQ. In particular, the gains of SMMSY with respect to SQ make it possible to identify margins of improvement with respect to the current situation.

Using the resilience analysis and 3Rs metrics proposed in [48], we can also claim that the system remains resilient under this strategy because it resists and retains its functional and diversified identity; it is also robust because it does not fall below a critical threshold where a functional group could be extinct; and its recovery time is very low for coral (a few years) and null for herbivores and piscivores. The determinants of this system's resilience could be further explored, building on these results, to identify the key determinants of its resilience. However, we are aware that the sustainability of MSY based strategies is disputed [72]. Instead of MSY, many resource economists advocate the use of maximum economic yield (MEY) targets, at which profits are maximised [17]. Although it depends on the discount rate,

¹⁴ The Closure scenario displays an empty radar plot except for the Share of Herbivores Biomass (51%) and as a consequence is not plotted here.

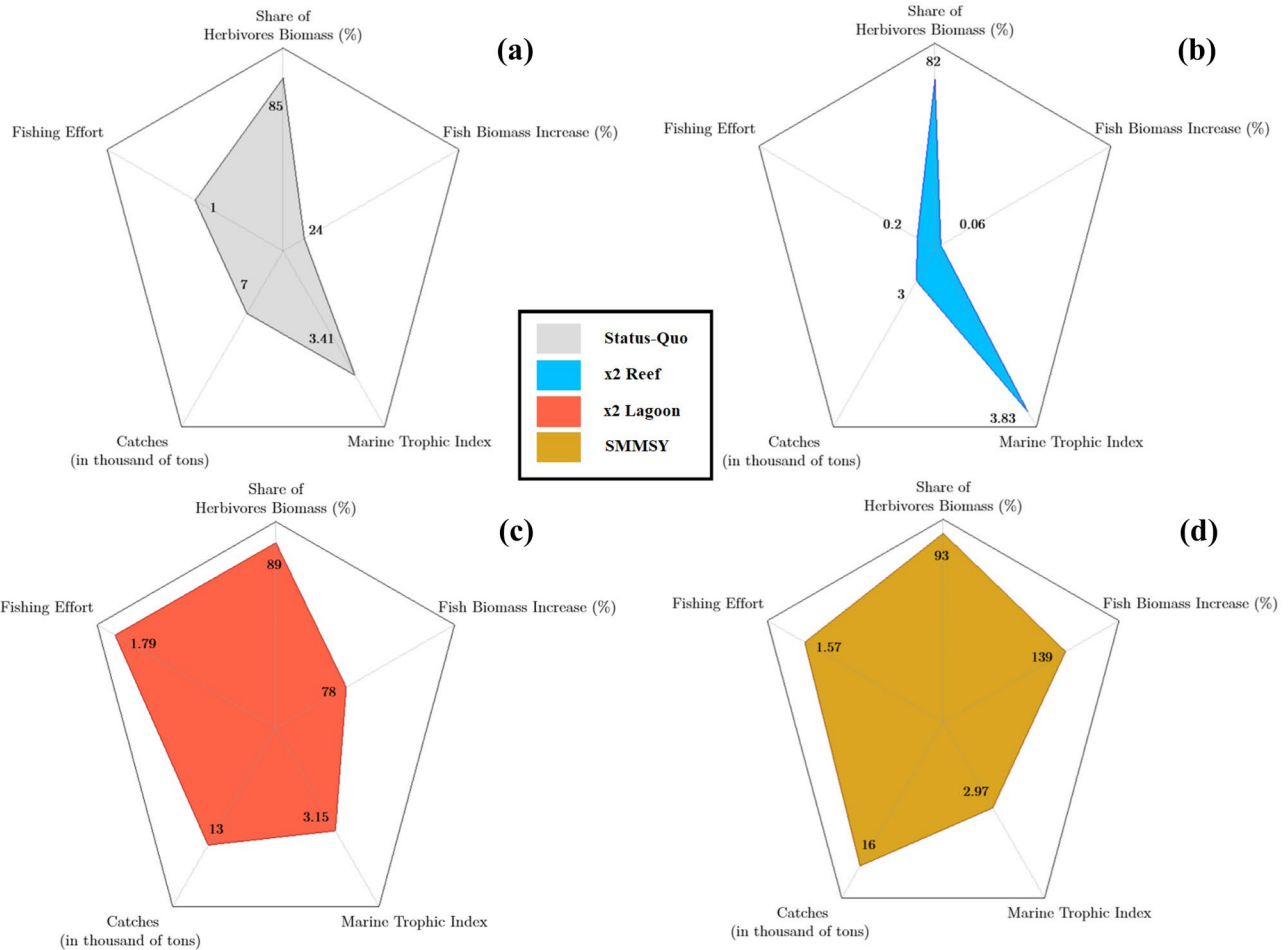


Fig. 10 Radar plot — The four radar plots are coloured according to the management strategies and the five components scales (SHB: 0–100%, Fishing Effort: 0–2, Catches: 0–20, Marine Trophic Index:

0–4, Fish Biomass Increase: 0–200%). Numbers within the radar plot represent the mean of the 100 simulations relating to its component. The five components are further described in Table 5, in the [Appendix](#)

the sensitivity of costs and revenues to biomass and harvest, and the marginal growth of the biomass, harvesting at MEY may favour higher biomass levels than MSY, for instance in the case of zero discounting [16, 73]. However, the extent to which MEY management can be adapted to the ecosystem approach remains an open question (Tromeur & Doyen, [22, 23]). Here a SMMEY (Maximum Economic Yield) could have been potentially considered. However, we have not used such a bioeconomic strategy in this paper mainly because of the limited economic data for the case study including the proportion of fishes sold vs. self-consumption as well the prices of fishes which are not fully known (only the price of fish combinations named ‘tui’ are known). Other alternative strategies to promote the sustainability and

resilience of fished coral systems include ecoviability strategies as advocated in [8, 9, 74]

5.3 Fishing as a Driver of Sustainability

As illustrated by the Closure scenario, an excessively strong decrease in fishing effort within a coral reef system can generate a high increase in top predator abundance. This is likely to entail a decline in preys notably in the herbivores group whose grazing function is an essential process driving the resilience of reef ecosystems [75–77]. For this reason, as shown by [44], it could be beneficial to maintain levels of fishing effort during specific periods of time such as during COTS outbreaks, notably because fishing leads to reducing the abundance

of predatory species, especially those preying on herbivores [78]. Maintaining a certain level of fishing notably targeting top predators enhances the grazer biomass and sustains the viability of corals thanks to algae feeders. In this sense, fishing can be a driver of system sustainability and resilience, compensating the negative effects of natural disturbances on the coral reef ecosystem.

5.4 Diffusion and Spatial Management

Regarding spatial issues, the major role of the diffusion process between patches for mobile species and the interest of spatial management are emphasised by the performances of the 2La and 2R strategies. These fishing scenarios indeed rely on a spatially explicit management. Closing the lagoon (2R) and its 90% share of the fishing area is obviously not economically or socially sustainable, but it is also ecologically non-sustainable as shown by the blue radar plot in Fig. 10. Closing the lagoon induces the same ecological outcome as under the full closure scenario: the increase of top predator abundance due to the fishing ban in the lagoon results in a decrease of herbivores (Fig. 10b).

Conversely, the 2La strategy displays better economic outcomes that even compete with the SMMSY, as highlighted by the magnitude of the radar plots in Fig. 10. This strategy seems to generate a refuge effect in the fore reef, which benefits to the top predators. This is, of course, highly dependent on the dispersion rates between the fore reef and the lagoon. Indeed, the Marine Trophic Index (the mean trophic level of catches) observed with this strategy is higher than for the SMMSY strategy ($3.15 > 2.98$). This patchy management strategy could then mitigate the fishing down effect [79] that seems to locally occur in Moorea with a decrease in catch sizes [55].

5.5 Policy Recommendations for Moorea Island

For many reasons, most of the MPAs implemented in Moorea have not produced biological benefits and in some zones, they even have had a negative impact on the biomass [80]. As a consequence, MPAs could be criticised as a policy to manage Moorea's coral reef social-ecological system. Nevertheless, the need to establish a management plan for a sustainable fishing activity has entailed the

revision of the current Maritime Space Management Plan (Fig. 1) where most of fully protected MPAs will be reopened but with new, more flexible restrictions. According to our results, such a management plan may indeed contribute to improving the sustainability of the system. However, we are aware that, the uncertainty surrounding model calibration, data collection and the extent to which environmental and ecological processes are understood may affect the validity of our conclusions. The width of the coloured areas surrounding the simulated trajectory figures attests this uncertainty in model predictions. However, the ecological-economic trends and management strategies discussed and analysed in this article indicate some likely sustainable paths for the system. We suggest a new and more adaptive way of managing the fishery, not only by zone, but also by patches and as a function of the types of fishing.

More globally, this paper puts forward the interest of a management strategy favouring diversity as a basis for adaptation coral reef social-ecological systems. We argue that fishing in such systems is likely to be more efficient by being more diversified in terms of temporality, gears, location and targets, and that such fishing might promote its sustainability and resilience facing environmental shocks. Longer and more precise data sets will surely provide more information enabling to further examine whether this can be demonstrated in small-scale fisheries management.

Appendix

See Fig. 12

Table 2 The five functional groups. Underlined groups stand for commercial and mobile species

	Groups	Index (i)	Number of Species
Habitats	Coral (C)	1	24
	Algae (A)	2	10
Fish	<u>Herbivores</u> (H)	3	64
	<u>Piscivores</u> (P)	4	48
	Corallivores (Co)	5	7

Table 3 Calibrated parameters of the model, respectively (top) interactions matrix s_{ij} , (middle) species intrinsic growth rates r_i and the diffusion rates $d_{ip'p}$ of species i between patch p and p' . We also display

(bottom) the carrying capacity K_p of the habitat, i.e. the total area where algae and coral can evolve

Groups Interaction Matrix (s_{ij})	Coral	Algae	Herbivores	Piscivores	Corallivores
Coral	0.009	0.006	0	0	0
Algae	0	0	0.0005	0	0
Herbivores	0	0.022	0	0.001	0
Piscivores	0	0	6.10^{-5}	0.019	0.008
Corallivores	0.0045	0	0	0.0055	0

Species	Intrinsic Growth Rate (r_i)	Diffusion Rate ($d_{ip'p}$)	
Coral	0.25/0.92	Lagoon to Reef	Reef to Lagoon
Algae	-	-	-
Herbivores	0.01	0.25	0.5
Piscivores	0.40	0.45	0.75
Corallivores	0.01	-	-

	Carrying Capacity (K_p)	
	Lagoon	Fore Reef
Coral/Algae	0.38	0.98

Table 4 Fishing Parameters: catchabilities (top) q_{ifp} of fleet f on species i in patch p ; (top) fisherman per Km^2 in Maatea $L_f(t)$. The share of labor involved in each fleet as well as the global density of fish-

ermen in all areas are extrapolated from this distribution and also regarding the surface of the corresponding zone

Fisherman per Km^2 $L_f(t)$ in Maatea	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016
No Boat	9	9	9	10	10	10	10	10	11	11	11	11
Unmotorised Boat	16	17	17	18	18	18	19	19	20	20	20	20
Motorised Boat	4	4	4	4	4	4	4	4	5	5	5	5
Non Resident	10	10	10	11	11	11	11	11	12	12	12	12
No Boat	0	0	0	0	0	0	0	0	0	0	0	0
Unmotorised Boat	9	9	9	10	10	10	10	10	11	11	11	11
Motorised Boat	9	9	9	10	10	10	10	10	11	11	11	11
Non Resident	6	6	6	7	7	7	7	7	7	7	7	7

Catchabilities q_{ifp}	Lagoon		Fore Reef	
Fleets	Herbivores	Piscivores	Herbivores	Piscivores
No Boat	7.10^{-7}	3.10^{-5}	-	-
Unmotorised Boat	4.10^{-6}	4.10^{-5}	4.10^{-6}	2.10^{-5}
Motorised Boat	5.10^{-6}	4.10^{-5}	-	4.10^{-5}
Non Resident	5.10^{-6}	4.10^{-5}	-	4.10^{-5}

Fig. 11 Habitats Trajectories
— Both figures account for the aggregated (lagoon-fore reef) cover of Coral and Algae. The 100 simulated trajectories are represented by the coloured area. The solid lines show the average of these 100 trajectories depending on the fishing strategy

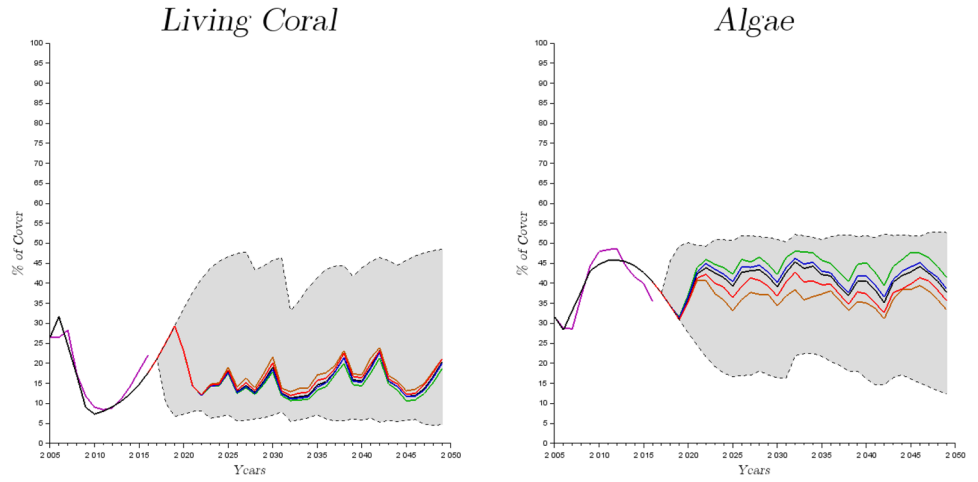


Table 5 Radar Plot Components' equations and remarks

Components	Equation and Remarks
Marine Trophic Index	$\frac{\sum MTL_i \cdot \bar{H}_i(t)}{\sum \bar{H}_i(t)}$ where MTL_i is the Marine Trophic Level of group i and $\bar{H}_i = \sum_f \sum_p H_{ifp}$ Only commercial species (Piscivores, Herbivores) are included in the calcul.
Fish Biomass Increase	$\frac{\sum_i \sum_p \bar{x}_{ip} - \sum_i \sum_p \bar{x}_{ip}^{hist}}{\sum_i \sum_p \bar{x}_{ip}^{hist}}$ where $\bar{x}_{ip}^{hist} = \frac{1}{t_h - t_0} * \sum_{t=t_0}^{t_h} x_{ip}^{hist}(t)$ and $\bar{x}_{ip} = \frac{1}{t_n - (t_h + 1)} * \sum_{t=t_h+1}^{t_n} x_{ip}(t)$ with $t_n = 2049$. This evolution index stands for the mean biomass increase of the simulated years (2017–2049) compared to the historical average biomass (2005–2016) and only concerns commercial species.
Share of Herbivores Biomass	$\frac{\sum_p \bar{x}_{3,p}}{\sum_i \sum_p \bar{x}_{ip}}$ This index calculates the average share of herbivores (2017–2049) based on the simulated average biomass of fish (2017–2049) and concerns all 3 fish groups.
Fishing Effort	$(PF(t_n - t_0)N)^{-1} * \left(\sum_{t=t_h+1}^{t_n} \sum_n \sum_f \sum_p e_{fp}(t, n) \right)$ where N is the number of simulation, F the number of fleet and P the number of patches. The fishing effort is the overall and temporal mean of the 100 simulations, 4 Fleets (F) and 2 patches.
Catches	$\sum_{t=t_h+1}^{t_n} \left(\sum_i \sum_f \sum_p H_{i,f,p}(t) \right)$ Catches are the temporal sum of the simulated years (2017–2049).

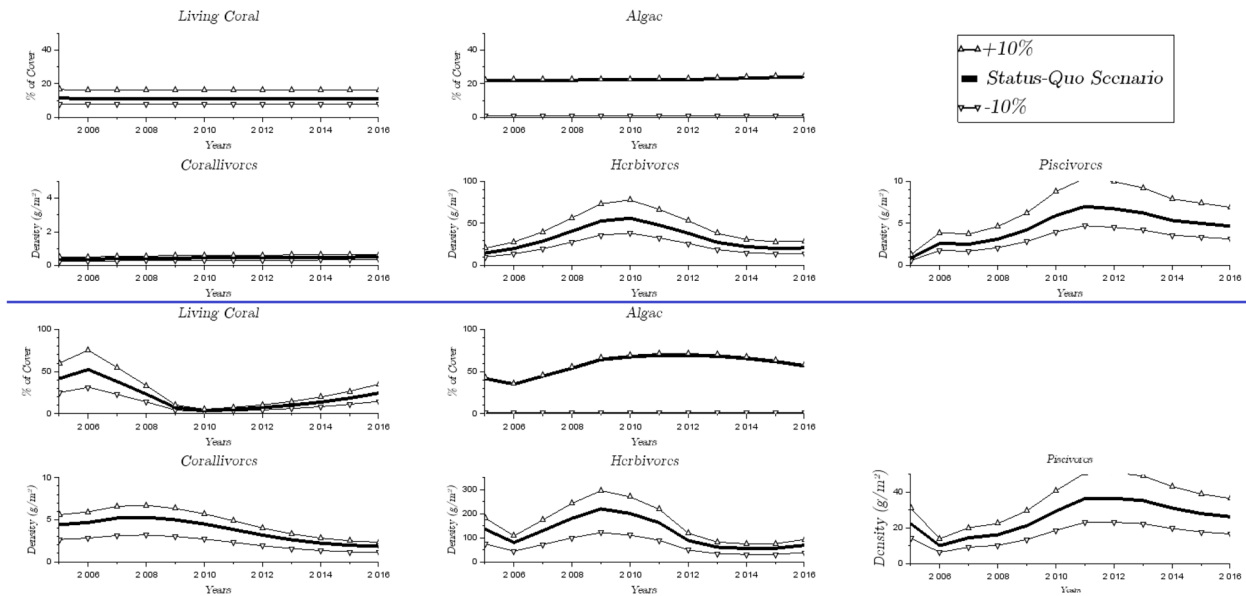


Fig. 12 Sensitivity analysis for the calibration. The five first figures (top) account for the lagoon and the five following figures (bottom) stand for the fore reef. The line filled with upside down triangles

represents a 10% decrease of all calibrated parameters while the line filled with “normal” triangles represents a 10% increase of all calibrated parameters

Author Contributions All authors contributed to the study conception, design, editing and conclusion. AL has written the paper, drawn the plots, and lead the article as a whole. LD and OT have realised the paragraphs, spelling and syntax corrections and modelled the equations with AL. JC and OT have helped the two previous authors on the analyses and conclusions. JC validated the ecological hypothesis. OT validated the economical concepts.

Funding This work has been carried out with the financial support of the research project ACROSS (ANR-14-CE03-0001). The role of the Belmont Forum through the network SEAVIEW (ANR-14-JPF1-0003) as well as the Cluster of Excellence COTE (ANR-10-LABX-45) through the project NAVIRE was also decisive. The main and unique authors of this study are A. Lagarde, L. Doyen, J. Claudet and O. Thebaud.

Data Availability All data and algorithms used in this study can be found at the Google Drive of the following mail address: these.algorithme.al@gmail.com with the password: eco-viability.

Declarations

Ethics Approval The study does not require ethics approval.

Consent to Participate and for Publication Not applicable

Conflict of Interest The authors declare no competing interests.

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