Rethinking spatial costs and benefits of fisheries in marine conservation

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ABSTRACT

Fishing catch is often used as a cost in marine conservation planning to avoid areas of high fishing activity when identifying potential marine reserve locations. However, the theory of marine reserves indicates that reserves are more likely to benefit fisheries in areas of heavy fishing activity that would otherwise be overfished. Whether or not fishing catch is calculated as a cost depends on the balance of conservation and fisheries goals for a reserve, and thus is critical for policymakers to consider when designing marine reserve networks. This research shows the utility of running an inverted cost model of fishery catches during marine reserve spatial prioritization as a first step in a marine planning process oriented towards stabilizing local fisheries. This technique serves as a heuristic tool that may help conservation planners explore regions that would otherwise be overlooked if fisheries data were absent or integrated purely as a cost in the planning process. Drawing on data from Madagascar to illustrate our approach, this research demonstrates that the regions most frequently selected using the inverted cost model not only meet conservation targets, but are also those most accessible to community-based resource managers, the dominant management paradigm in Madagascar as well as in many developing countries.

1. Introduction

Marine ecosystems provide food and income for billions of people world-wide (Roe and Elliott, 2004), as well as other ecosystem services, including erosion and flood control, nutrient cycling, and recreation, amongst others (Peterson and Lubchenco, 1997). Ecosystem services, the multiplicity of benefits people derive from ecosystems, highlight the tensions as well as the potential compatibility of economic development and biodiversity conservation objectives (Tallis et al., 2008). Many marine ecosystems are under mounting pressure from consumption of marine products, climate change, and pollution (Brander, 2010; Shahidul Islam and Tanaka, 2004). The trade-offs and synergies between biodiversity conservation and ecosystem service provision in the marine realm are often unclear, thus pointing to the need to devise strategies that help policymakers examine the compatibility and conflicts between multiple objectives (Raudsepp-Hearne et al., 2010). In addition, highlighting trade-offs will help make conservation efforts more efficient (Lester et al., 2013), and the decision-making process more transparent (White et al., 2012), thus likely increasing buy-in to decision-making outcomes.

Increasing the area of marine ecosystems under protection has become a dominant strategy in international environmental policy to help conserve and sustainably use the oceans (Rees et al., 2017). Marine reserves (or no-take zones) are thought to buffer the sustainable delivery of key ecosystem services, specifically those related to fisheries, while also protecting marine biodiversity (Lubchenco et al., 2003). Currently, one approach in regional-scale marine reserve network planning for biodiversity is to avoid areas of high fishing activity (Ban et al., 2013; Ban and Klein, 2009). Fishing areas are avoided to minimize the economic cost and social impacts of reserve networks (Weeks

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et al., 2010; Ban and Klein, 2009). Heavy fishing can significantly reduce, alter, or destabilize the abundance, size and biomass of both targeted and non-targeted species (Sobel and Dalgren, 2004) and possibly lead to local extinction (Jackson, 2001), results diametrically opposed to the goal of biodiversity protection.

In addition to improving biodiversity conservation, marine reserves might help buffer against any negative effect of over harvesting on fisheries (Leslie, 2005), with evidence that both sets of goals can be simultaneously achieved (Abesamis and Russ, 2005; Green et al., 2014). Despite this evidence, considerable debate remains in the marine conservation literature concerning the conditions under which a reserve can meet both marine biodiversity protection and fisheries objectives (Thorpe et al., 2011; Devillers et al., 2015; Boon and Beger, 2016).

Here we bring these key debates to bear on the way in which conservation planners are using marine spatial planning software to select the size and location of marine reserves. A variety of software (e.g. Marxan, Zonation, C-Plan, and ResNet) has been developed to help managers decide where to locate new reserves in terrestrial and marine environments. However, in the past few decades, Marxan has become the dominant software used globally, guiding managers to select reserve configurations that efficiently meet biodiversity targets while also considering various costs within the land or seascape (Ball et al., 2009; Janβen et al., 2019). In its selection of potential reserve designs, Marxan algorithm finds sets of areas that meet biodiversity targets at minimum cost (Sala et al., 2002). For marine reserves, fishing catch models or actual fishing data are frequently used to generate a spatial cost layer. Recent examples where this is the case include marine reserve network design in Rodrigues Island in the Western Indian Ocean (Pasnin et al., 2016), Baja California (Arafeh-Dalmau et al., 2017), Papua New Guinea (Tulloch et al., 2016), and the English Chanel (Metcalfe et al., 2015).

When areas of high fishing catch or fishing effort weigh against the selection of an area in Marxan, biodiverse areas that also have high catch or effort data associated with them are less likely to be selected in the prioritization process. Here, we advance the argument that during the initial phase of reserve planning, prioritizing areas of high biodiversity and high fishing activity, in other words selecting *for* important fishing grounds instead of the common method of *avoiding* important fishing grounds, may help conservation planners meet biodiversity conservation goals, restore intensely harvested stocks, and accommodate a decentralized management strategy. This novel approach is predicated on three interrelated findings in the marine reserve literature.

First, models indicate that marine reserves are more likely to benefit adjacent fisheries that are intensively harvested (Gerber et al., 2003; Hilborn et al., 2004; Hart, 2006). Numerous meta-analyses have shown that reserves are effective at increasing abundance and diversity of coastal fish assemblages when exploitation levels are high and the fishery is not already well managed (Micheli et al., 2004; Lester et al., 2009; Claudet et al., 2010; Vandeperre et al., 2011). These findings indicate that reserves located in highly biodiverse and highly fished areas may help stabilize fisheries production via spillover, thus balancing the cost of removing productive regions from fishing (Worm et al., 2006; Colléter et al., 2014; Hart, 2006).

Second, areas of historically high fishing activity signal likely areas of high-productivity and possible source populations (Crowder et al., 2000). Generally, marine species diversity correlates with habitat diversity (Komyakova et al., 2013; Fischer et al., 2019) and fisheries productivity (Worm et al., 2006), indicating that there are situations where there is a correspondence, not conflict, between conservation and fisheries benefits. This theoretical and empirical evidence suggests that in some situations, prioritizing, not avoiding, areas of high fishing intensity is the best way to incorporate fisheries goals into spatial planning exercises. For example, important fishing areas such as embayments are often nursery areas or spawning aggregation sites

(Dorenbosch et al., 2005; Abrantes et al., 2015; Hamer et al., 2011), but excluding these source areas from a reserve network would be short sighted.

Third, a disproportionate number the world's most biodiverse and threatened marine ecosystems are found in emerging or developing countries (Marinesque et al., 2012). In these contexts, where resource-intensive top-down management of marine protected areas is often impractical, the participation from adjacent coastal communities in the monitoring and enforcement of reserves is vital (Costello and Kaffine, 2010; López-Angarita et al., 2014; Bruner et al., 2004; Marinesque et al., 2012). Furthermore, establishing a network of small fisheries-oriented reserves with the consent and participation of local fishers is often the most politically viable strategy for the survival and success of the marine reserves (Afflerbach et al., 2014; Johannes, 2002; Rocliffe et al., 2014). These findings therefore suggest locating reserves adjacent to, instead of distant from fishing communities.

Establishing marine reserves in areas of high resource use in order to benefit adjacent fishing represents a fundamental shift away from an ideology that leads to separate natural areas from areas of human use. This ideological shift is bolstered by empirical studies of marine reserve spillover. However, the benefits from establishing reserves in areas with high fishing activity may not always outweigh the costs of taking that area out of production or be able to overcome the political pushback from fishers. The context in which one would expect the benefits of reserve placement to outweigh the costs include areas where 1) the fishery would otherwise be overfished, 2) a significant portion of the fishery targets short-ranging species (e.g. reef-based tropical fisheries), 3) there is flexibility in either fishers' livelihoods or alternative fishing zones that enable fishers to sustain the short-term cost of a given reserve, and 4) monitoring and enforcement of the reserves relies in part or entirely on adjacent fishing communities.

This research draws on coarse scale data from Madagascar to show that by analyzing fisheries cost data in several ways at the national level (where often only coarse data are available), conservation planners are able to better match reserve design to regional and local ecosystem needs and management capacity. Our investigation here serves primarily as a heuristic tool, and its strength is in its simplicity. As a first step, a coarse scale analysis can help identify regions where subsequent fine scale work can be done.

2. Methods

2.1. Case study area

Our study area comprises the coastal waters surrounding the island of Madagascar, a developing country highly reliant on fisheries as a source of protein, income, and foreign exchange (UN, 2010; Harris, 2011; Le Manach et al., 2012). In 2014, the Malagasy president vowed to triple the country's marine environment under protection (Amia, 2014); a vow that exponentially increased marine reserve coverage in the country. Important marine conservation work planned at the local level currently occurs throughout the island; however, numerous governmental and non-governmental organizations are working towards integrating efforts on a national scale in order to form a cohesive marine reserve network that is both comprehensive and representative (SAPM, 2009; Allnutt et al., 2012).

The study area boundary combines five bioregions (IOC, 2010) that occur along the coast, which generally correspond to Madagascar's neritic zone, a sublittoral zone that extends from the coastline to a depth of roughly 200 m at the edge of the insular shelf. Ninety-nine percent of the study area is within Madagascar's Exclusive Economic Zone (EEZ). Small portions also fall within the Juan de Nova and Glorieuses EEZ, both territories of France (Fig. 1). The total study area is 187,366 km^2.
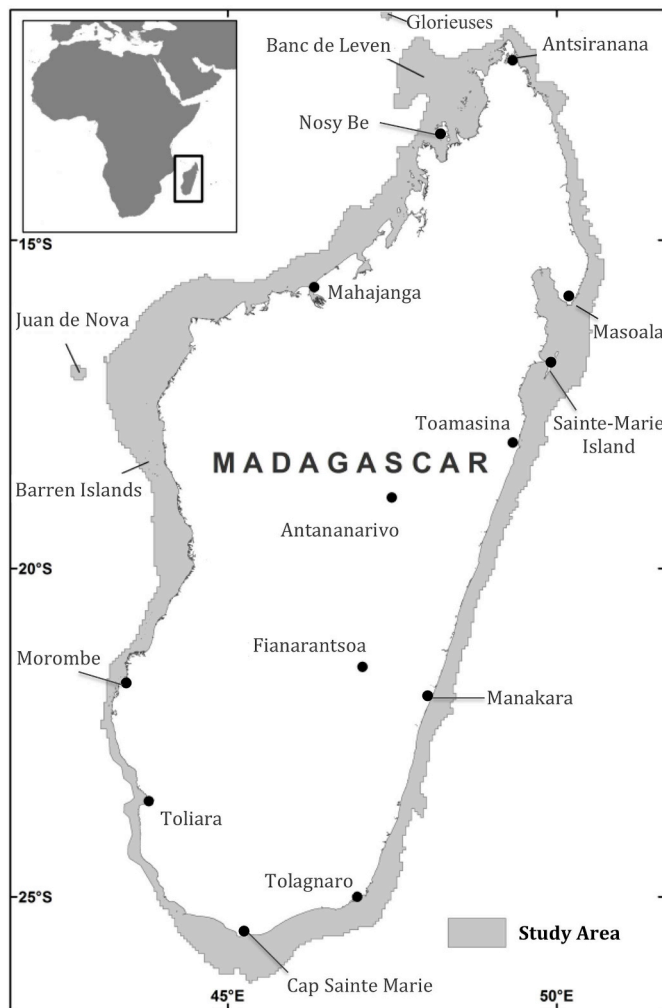
Fig. 1. Map of study area. Most of the study area is in Madagascar's Exclusive Economic Zone with the exception of small areas that fall in the Glorieuses Islands and Juan de Nova Islands.

2.2. Data sources

The fish catch model is a combination of motorized and non-motorized coastal fishing activity using anthropogenic drivers of marine change for the West Indian Ocean (Lagabrielle et al., 2009). This model combines spatial data on global fisheries catches (Watson et al., 2006; Watson et al., 2004), tuna purse seine catch data supplied by the Indian Ocean Tuna Commission (IOTC) and data on coastal fisheries derived from national fisheries statistics and population density data. See Fig. S1 for a map of modeled fish catch.

We compiled biodiversity data (Table 1) from a related study (Allnutt et al., 2012) and includes spatial distribution data for four biodiversity features: bioregions (IOC, 2010), coral reef geomorphological types (Andréfouët et al., 2009), mangroves (Harper et al., 2007; Moat and Smith, 2007) and individual fish species (see Allnutt et al., 2012). There are two key differences between this and the related 2012 study, the research presented here: 1) we mapped biological variables across Madagascar's waters instead of just along the western coast, and 2) we did not convert fish species distribution models to presence/absence, but instead used the continuous values directly from maximum entropy species distribution models (Phillips and Dudík, 2008).

2.3. Spatial analysis and comparison

We divided the study area into 7895 square planning units, each approximately 25 km^2 in area, and we measured the number of every fish species, habitat, and bioregion distribution found in each. We selected a 25 km^2 grid to match the scale at which data were available. Then fish catch data were used to assign an economic value or selection "cost" to each planning unit according to two scenarios.

We ran Marxan 100 times for each cost scenario, and compared both summed solutions ("selection frequency" maps) and the "best" run (the one with the lowest overall objective function score across runs). In both cost scenarios, feature targets were as follows: 10% of each fish species distribution and bioregion, 30% of mangroves and each reef geomorphology type. In addition, we ran a null model with cost set to 1 in every planning unit as a point of comparison. Given the primarily heuristic function of this analysis, and in order to be able to better test the basic cost inversion hypothesis, we used minimal options wherever possible, e.g. equivalent "species penalty factor" on all conservation, no "boundary length modifier" for clustering, no "minimum separation distance."

In the first cost scenario, fish catch data were used directly as a cost, which is a common way that catch data are used in marine planning (Fig. S1). In the second scenario, the catch data were inverted (cost = 1/modeled catch data) so that the planning units with the highest catch have the lowest cost, and vice-versa (Fig. S1). In the null model, no cost was included (Fig. 4).

We calculated a Cohen's Kappa statistic (Cohen, 1960) to conduct pairwise comparisons between the three models: fisheries as a cost, fisheries as an inverted cost, and the null model (Table 2). Kappa coefficients are used to assess classification accuracy between maps, and thus help describe the level of agreement of two maps by chance (Monserud and Leemans, 1992; Richardson et al., 2006).

3. Results

3.1. Marxan analysis

In the scenario where fisheries catch data were used as a cost, areas of higher selection frequency tend to be further offshore (Fig. 2). Remote islands and offshore banks also feature prominently in this scenario, as well as remote regions of the continental shelf off the southern, northeastern, and western coasts (Fig. 3).

In the inverted scenario, where regions of high fisheries catch data have low cost (Fig. 2), the map shows a generally diffuse selection frequency spread from the coastline out to 20–50 km, with notable concentration in the southwestern coast, and numerous bays and inlets of the northwestern coast (Fig. 3).

The number of planning units required to achieve the conservation targets under the best run of each scenario were 861 for the fisheries as a cost model, 824 for the fisheries as an inverted cost model, and 824 for the null model.[1]

3.2. Kappa comparison

Observed overall agreement between the fisheries as cost scenario and inverted scenario was 44.4%, with a chance agreement of 48.9%, and a Kappa coefficient of −0.08. Observed overall agreement between the fisheries as a cost scenario and the null model was 49.9% with a chance agreement of 47.3%, and a Kappa coefficient of 0.05. Observed overall agreement between the fisheries as an inverted cost scenario and the null model was 63.8% with a chance agreement of 49.4%, and a

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[1] Despite similar required planning unit numbers for each scenario, there was not a great deal of overlap in planning unit selection. A total of 56 units were selected by all 3 models, 114 selected by both the fisheries as a cost model and the fisheries as an inverted cost model, 149 selected by both the fisheries as a cost model and the null model, and 175 selected by both fisheries as an inverted cost model and the null model.

Table 1
Biodiversity data used in the analysis.

Data type	Dataset	Source
Bioregions	5 Madagascar bioregions	Indian Ocean Commission (2010)
Habitats	Mangroves	Harper et al.(2007), Moat and Smith (2007)
	Reef geomorphology: Atoll rim	Andréfouët et al. (2009)
	Reef geomorphology: Bank barrier	Andréfouët et al. (2009)
	Reef geomorphology: Bank lagoon	Andréfouët et al. (2009)
	Reef geomorphology: Coastal barrier reef complex	Andréfouët et al. (2009)
	Reef geomorphology: Coastal/fringing patch	Andréfouët et al. (2009)
	Reef geomorphology: Continental lagoon	Andréfouët et al. (2009)
	Reef geomorphology: Diffuse fringing	Andréfouët et al. (2009)
	Reef geomorphology: Fringing of coastal barrier complex	Andréfouët et al. (2009)
	Reef geomorphology: Intra-lagoon patch-reef complex	Andréfouët et al. (2009)
	Reef geomorphology: Intra-seas exposed fringing	Andréfouët et al. (2009)
	Reef geomorphology: Intra-seas patch-reef complex	Andréfouët et al. (2009)
	Reef geomorphology: Lagoon exposed fringing	Andréfouët et al. (2009)
	Reef geomorphology: Ocean exposed fringing	Andréfouët et al. (2009)
	Reef geomorphology: Outer barrier reef complex	Andréfouët et al. (2009)
	Reef geomorphology: Shelf patch-reef complex	Andréfouët et al. (2009)
	Reef geomorphology: Shelf slope	Andréfouët et al. (2009)
Species	251 fish species models generated using Maxent	REBIOMA[a], unpubl. data

[a] Réseau de la Biodiversité de Madagascar http://www.rebioma.net/index.php/en.

Table 2
Percent of total area for each mapping scenario that falls within each of 10 selection frequency categories. The higher the selection frequency the more essential the site is for meeting biodiversity targets. Also indicated is the percent of overlap between the three maps within each selection frequency category.

Selection frequency	Fisheries as Cost	Inverted Fisheries as Cost	Percent overlap Fisheries as Cost and Inverted Cost	Percent overlap Fisheries as Cost and Null	Percent overlap Inverted Cost and Null
0–10	70.0	65.6	42.6	70.1	65.6
11–20	9.5	25.6	1.5	9.5	25.6
21–30	8.4	4.7	0.1	3.0	0.8
31–40	4.3	1.3	< 0.1	8.3	4.7
41–50	2.9	0.8	< 0.1	4.3	1.3
51–60	1.4	0.7	< 0.1	1.4	0.7
61–70	0.7	0.5	< 0.1	0.9	0.3
71–80	0.9	0.3	< 0.1	1.0	0.2
81–90	0.9	0.3	< 0.1	0.7	0.5
91–100	0.9	0.2	< 0.1	0.9	0.3

Kappa coefficient of 0.28. The Kappa coefficients for all comparisons indicate that the three scenarios produced maps highlighting very different areas.

When comparing overlap in different categories of selection frequency (Table 2), a high degree of overlap between the three maps (42.6%, 70.1% and 65.6% respectively) occurred only for sites with low selection frequency scores (0–10) over 100 runs. There was substantially less overlap in the next lowest selection frequency category between the three maps, and overlap remains below 10% through the remaining categories as selection frequency increases. In other words, only sites that were not selected frequently by either scenario overlapped substantially between the fisheries as cost, fisheries as inverted cost, and null scenarios.

4. Discussion

Our results suggest that marine reserves oriented towards enhancing fisheries can also have biodiversity value, and that collectively, a network of such reserves may represent the same conservation targets as a network selected only for a conservation objective.

In the scenario where fisheries catch data were used as a cost, and areas of higher selection frequency tend to be further offshore, our findings are likely to be consistent across nations where small-scale near-shore fishing constitutes the majority of fishing effort (Chuenpagdee et al., 2006). The remote islands and offshore banks that feature prominently in the fishing catch as cost scenario could be ideal for conservation planners to establish larger reserves dedicated primarily to biodiversity conservation with a focus on monitoring long-range motorized vessels (e.g. industrial fishing). Finer scale analysis of these areas, including measuring the diversity of marine life and verifying fishing intensity levels, is important because some of these areas might already function as de facto reserves if little fishing activity occurs there. Identifying de facto reserves would be cost-effective, eliminate the occurrence of residual reserves (Devillers et al., 2015; Boon and Beger, 2016), both of which are especially important in countries where monitoring infrastructure and funds are scarce.

The areas frequently selected in the inverted scenario (e.g. the southwestern coast and numerous bays and inlets of the northwestern coast), could be ideal for conservation planners to establish smaller reserves focused primarily on fisheries management. The three pairwise Kappa comparisons demonstrate that the fisheries as an inverted cost model has a higher correspondence with the null model (0.28) than the fisheries as a cost model and the null (0.05). Given that the null model is strictly selecting for areas of high fish diversity, habitat and bioregional representation, one would expect these areas to be correlated to productivity. Although a 0.28 correspondence is considered low (Lourival et al., 2011), the slightly higher correspondence with the null model may indicate that the areas selected in the inverted cost model also correlate to areas of high productivity, aligning with the goal of fisheries stabilization.

The diffuse nature of priority areas in the inverted cost model means that the economic benefits are well spread through the region, corresponding with theoretical work that shows a system of smaller reserves covering a greater fraction of the coast is an optimal fisheries solution

Fisheries as a Cost

Fisheries as an Inverted Cost
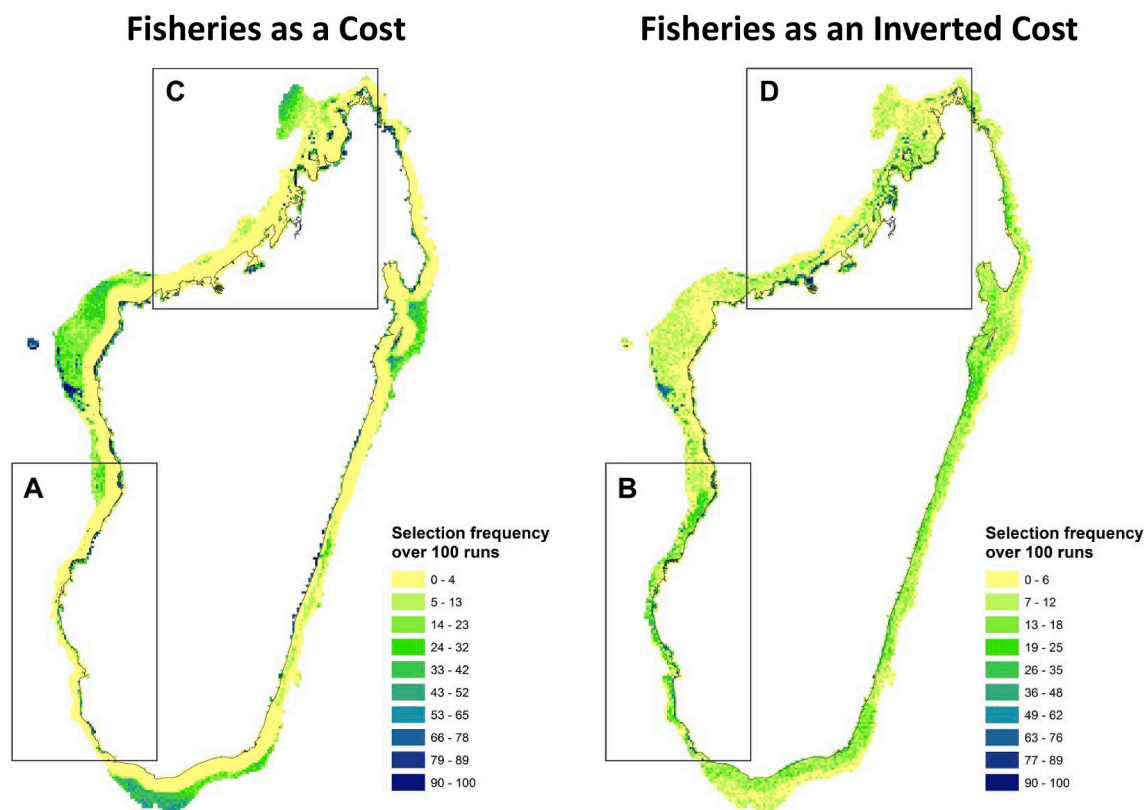
Fig. 2. Marxan frequency selection map. Left map indicates where fisheries are calculated as cost, thus maximizing biodiversity values while minimizing the area selected with high fishery values. Right map indicates where fisheries are calculated as an inverted cost, thus selecting for high biodiversity values while maximizing areas included with high fisheries values. The darker the shades of green and blue indicate higher selection frequency, lighter shades of yellow indicate lower selection frequency. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

(Hastings and Botsford, 2003; Gell and Roberts, 2003). In general, the higher the fishing pressure and/or the mobility of the target species in a given area (Watson et al., 2000), the greater the number of small reserves necessary to maintain connectivity for propagules, juveniles and adults between individual reserves (Moffitt et al., 2011; Gaines et al., 2010). Similarly, this diffuse model has been suggested for ecosystem services that flow from small patches of natural habitat over local scales, such as pollination services (Brosi et al., 2008).

The theoretical arguments underpinning the inverted scenario is congruent with the existing marine conservation paradigm in southwestern Madagascar, a region known for extremely high fishing effort and a fringing coral reef with high levels of biodiversity. Numerous governmental and non-governmental organizations in conjunction with local communities have already established several dozen small $(0.1–4 km^2)$ permanent and temporary-rotational marine reserves in this region. Many of these primarily locally managed marine reserves are contained within larger marine protected areas (from several tens of kilometers up to $300 km^2$) that allow or promote "sustainable use" of marine resources. The small marine reserves in this area aim to enhance adjacent subsistence as well as commercial fisheries for species with known rapid growth and reproduction rates such as octopus (Harris, 2011; Oliver et al., 2015).

One key similarity between the two cost scenarios is the selection of areas with particularly high biodiversity levels, where biodiversity target requirements outweigh the fishery costs that would otherwise count against the selection of these areas. For example, notable areas of overlap include the Barren Islands off Western Madagascar, and a few mangrove-dense bays on the northwestern coast. These areas may account for the slight increase in percentage overlap values at the higher end of the selection frequency table (Table 2). Although the Barren Islands are far from the coast, islands in this zone are seasonally

frequented by migratory fishers that come primarily from the southwestern coast of Madagascar. Blue Ventures, a marine conservation and development organization, along with the Malagasy regional government, recently established a suite of marine reserves in the Barren Islands area (Cripps and Gardner, 2016).

The coarseness of the data available to us for Madagascar led us to fix our grid at $25 km^2$, however by no means does this imply that establishing reserves at the $25 km^2$ scale is ideal. In data poor regions of the world, including in many developing countries, a coarse scale analysis will help identify regions where subsequently, finite resources can be used to collect data at a much finer scale, evaluate overall network connectivity, and engage local stakeholders.

Data that are currently missing at the national level in Madagascar, but would be more feasible to collect at a regional or local level include (but are not limited to): the location of key community fishing grounds, village-level commercial and subsistence catch values, sites of cultural importance, areas with high community-management interest, local knowledge of ecological features in the seascape such as fish spawning aggregation sites or the location of frequent endangered species sightings, key tourism sites, and the location of previous coral bleaching events. With these finer scale data, the use of software such as Marxan with Zones becomes more feasible (Watts et al., 2009). Marxan with Zones, as its name implies, allows managers to establish different zones in the ocean, not just reserved or unreserved, each with its own objectives (e.g. preserve 80% of known community fishing grounds) and constraints (e.g. distance from a village as a proxy for community-management access cost). Recent examples of fine-scale application of Marxan with Zones include the establishment of Tun Mustapha Marine Park in Malaysia (Jumin et al., 2018) and the Raja Ampat marine protected area network in Eastern Indonesia (Grantham et al., 2013).
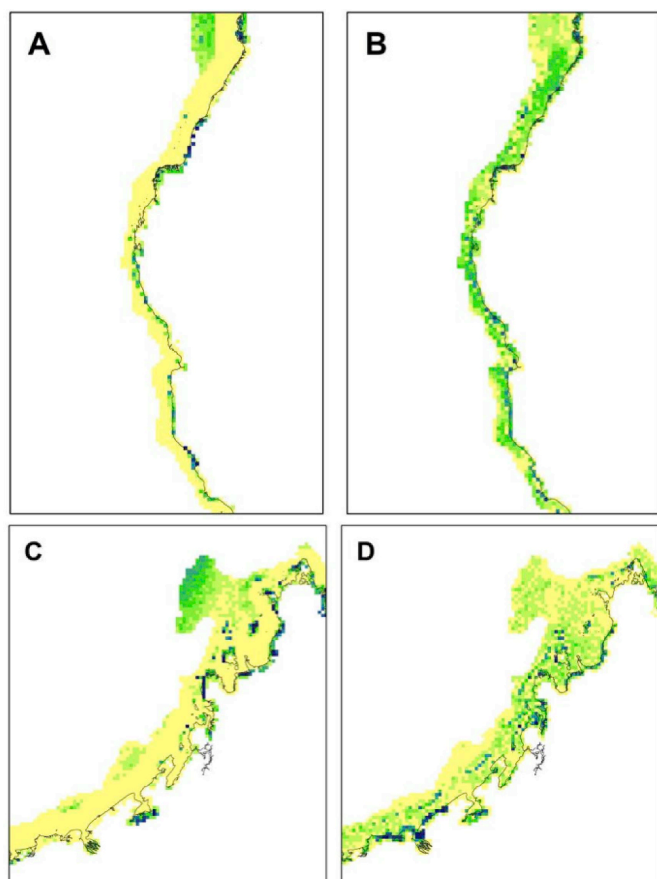
Fig. 3. Magnified Marxan frequency selection maps of southwest and northwest areas of Madagascar depicting the fisheries-as-cost scenario, where high catch is avoided (A & C), and the inverted scenario where low catch is avoided (B & D). The darker the shades of green and blue indicate higher selection frequency, lighter shades of yellow indicate lower selection frequency. These maps are not clear opposites in terms of selecting priorities. A notable difference includes the large bank well off the northwest coast (C), notable similarities include many of the bays and inlets in both regions. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

5. Conclusion

Our conclusions are two-fold. First, this heuristic exploration shows that by highlighting areas with high biodiversity and heavy fishing activity, in addition to areas of high biodiversity and low fishing activity, conservation planners can focus more directly on multiple objectives with their marine reserve network. Exploring alternative scenarios at multiple levels of conservation planning and implementation will ultimately help reduce incongruity of goals asserted at different scales within the planning process and improve reserve effectiveness. Additionally, examining multiple cost scenarios (an inverted fisheries cost, a null model) will help policymakers explore regions that would otherwise be overlooked if fisheries data were used primarily as a cost in the planning process.

Second, this research helps underscore that incorporating areas of high fishing activity in reserves can fit well with community-based management schemes. This is especially true in developing countries where management structure and resources are sparse, and local communities may be the best, or in some cases only, potential monitors and enforcers of marine protected area rules (McCay et al., 2014; Johannes, 2002; Rocliffe et al., 2014).

Our results may have important implications in the terrestrial realm concerning the scale at which localized ecosystem service provision

Fig. 4. Null model map. Planning units' costs are equal, catch data is not included. Red dots are areas that meet biodiversity targets. Best result depicted, Marxan was run 100 times for this scenario. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

aligns with biodiversity protection (Chan et al., 2006; Andam et al., 2010). Natural or semi-natural areas in human-dominated landscapes such as urban or agricultural zones may often be overlooked in spatial prioritization modeling. However, they may contribute to biodiversity protection to some degree, while contributing more substantially to localized ecosystem service benefits such as pollination (Kremen et al., 2002), tourism revenue, or storm mitigation (O'Farrell et al., 2012). In contrast, protected areas in sparsely populated places may contribute to the preservation of biodiversity, but the majority of the associated ecosystem services are enjoyed by remote beneficiaries, and the majority of costs are borne by local communities (Balmford and Whitten, 2003; Kremen et al., 2000).

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ocecoaman.2019.104824.

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