## Marine Opportunity Costs:

 a method for calculating opportunity costs to multiple stakeholder groupsVanessa M Adams, Morena Mills,

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## EXECUTIVE SUMMARY

Research for this study was carried out under a two-year project to support the implementation of Ecosystem-Based Management (EBM) at two catchment-to-reef sites on Vanua Levu, Fiji, during which conservation planning approaches were trialled using EBM tools to evaluate options for re-designing marine protected area (MPA) networks. Current approaches in systematic conservation planning have focused on developing tools to maximize conservation benefits while minimizing socio-economic costs to users of a landscape or seascape area. In this study, we present a novel method for calculating the opportunity costs of conservation actions to multiple gear type users arising from fisher displacement due to the establishment of MPAs in Kubulau District, Vanua Levu, Fiji. The method builds upon those applied in land conservation in which the probability of land conversion to alternate functions is used to estimate opportunity costs to multiple stakeholders, which differs from previous approaches by providing information about costs of currently unused areas that may be of potential future benefit. We model opportunity costs of establishing a network of MPAs as a function of food fish abundance, probability of catch as function of gear type and market value of species. Count models (including Poisson, Negative Binomial and two zero-inflated models) were used to predict spatial distribution of abundance for preferred target fish species and validated against underwater visual census (UVC) surveys and biophysical predictor variables (reef type, reef exposure, depth, distance to shore, protection status). Spatial distributions of targeted fish within the three most frequently sighted food fish families (Acanthuridae, Lutjanidae, Scaridae) varied considerably: Lutjanidae had the highest abundance on barrier reefs; Acanthuridae on inshore fringing and patch reefs; and Scaridae on fringing reefs. Modeled opportunity cost, estimated as a function of abundance and probability of catch by gear type, indicated highest cost to fishers would arise from restricting access to the fringing reef between the villages of Navatu and Kiobo and the lowest cost would arise from restricting access to the Cakaunivuaka reef. The opportunity cost layer was added to Marxan models to identify optimum areas for protection to meet fisheries objectives in Kubulau's traditional fisheries management area with: (a) the current MPA network locked in place; and (b) a clean-slate approach. The opportunity cost method presented here gives an unbiased estimate of opportunity costs to multiple gear types in a marine environment that can be applied to any region using existing species data.

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## INTRODUCTION

The rapid degradation of marine resources resulting from human activity has instigated a global movement to increase the protection of the oceans (IUCN 2009). The establishment of protected areas is a widespread and acknowledged tool for conserving biodiversity and the provisioning of ecosystem services (MEA 2005). In the marine environment, the positive benefits of marine protected areas (MPAs) are widely reported and include increases in: biomass of fisheries resources; size of target species; and species richness (Lester et al. 2009). However, these benefits rely on effective reserve design as well as compliance and enforcement.

There has been considerable discussion on differences in design criteria for reserves and reserve networks with explicit goals of biodiversity conservation versus fisheries production (Halpern \& Warner 2003; Hastings \& Botsford 2003; Almany et al. 2009): optimum designs to meet both objectives may ultimately require trade-offs between size, spacing and representation. Systematic conservation planning can account for these trade-offs during the selection of areas for conservation (Margules \& Pressey 2000) and is currently the preferred approach to designing MPA networks in developed countries (Sala et al. 2002). Historically driven by biological goals and data, the technical ability to design effective protected area networks has evolved rapidly (Margules \& Pressey 2000). Despite this progress, recent research highlights the need to include socio-economic data in conservation planning as it will influence the likely outcomes of plans (Naidoo et al. 2006; Polasky 2008).

Use of socio-economic criteria is especially important in the context of developing countries where social acceptance is a critical factor in determining MPA success and data is generally limited (Ban et al. 2009; Johannes 1998). While inclusion of socio-economic factors in the design of MPAs has increased in the last decade (Ban \& Klein 2009), the spatial variation in costs to stakeholder groups needs to be better understood and incorporated into conservation plans (Adams et al. in press; Klein et al. 2008; Klein et al. 2009). This is especially important in Pacific Island countries where: communities are highly dependent on marine resources for subsistence (Adams et al. 1997); fishers have limited spatial and occupational mobility (Aswani \& Lauer 2006); and customary marine tenure institutions set social and governance constraints on MPA network design (Aswani \& Hamilton 2004). For example, research from the Western Province of the Solomon Islands suggests that success of MPA networks relies on their placement within secure sea tenure regimes and the perception of equitable distribution of biological and social costs and benefits by resource users (Aswani \& Hamilton 2004). Any type of conservation planning approach to MPA network design for the Western Pacific needs to be particularly sensitive to these cultural needs.

The most prevalent type of socio-economic data included in conservation planning is fisheries catch data (Ban \& Klein 2009). Catch per unit effort (CPUE) data included are typically derived from socio-economic survey questions such as fishing location, gear used and the type and amount of fish caught. These data both enable assessment of the spatial distribution of fishing effort and can be combined with ecological surveys to examine the effects of fishing effort on reef fish community composition (Jennings \& Polunin 1996). The
collection of CPUE data is becoming standard practice, particularly for commercial fisheries within developed countries (Klein et al. 2008; Richardson et al. 2006), and national-scale collection of artisanal and subsistence CPUE data can be done at relatively low-cost in developing countries (Fiji Locally Managed Marine Area network, unpublished data). Recent studies have also examined how to use CPUE data to plan for multiple fisheries to ensure that the impact of MPAs is not displaced onto a single stakeholder group (Klein et al. 2008; Klein et al. 2009).

One limitation of CPUE data is that they only capture the current fishing effort, which may result in areas with no identified effort. To respond to these issues, some conservation planning exercises have defined the cost to be a function of effort and area to ensure that these areas are not considered without socio-economic cost for conservation (Game et al. 2008; Stewart et al. 2003). However, for areas with no current fishing effort, assuming homogenous costs (i.e. allowing costs to be a function of area alone) does not capture what is likely to be heterogeneous effort. Areas may have no current fishing effort for several reasons, including: survey data did not capture the seasonality of fishing distributions due to the timing of data collection; and, particularly in developing countries, access to offshore areas may be restricted due to lack of current economic capacity to purchase motorised transportation (Salas \& Gaertner 2004).

As access to motor boats increases, it is reasonable to expect that fishing effort will change and move further offshore to areas currently not fished. Therefore, a method for estimating opportunity costs of areas currently not fished is needed so that conservation plans take into account the heterogeneous opportunity costs to fishers. A method for calculating opportunity costs in transitional landscapes has been developed (Naidoo \& Adamowicz 2006), however an analogous method is not currently described for marine environments. In response to this need, we present a novel method for calculating the opportunity costs to multiple gear type groups arising from fisher displacement due to the establishment of marine protected areas and apply the method to a region in Fiji. We then demonstrate an application of using the opportunity cost layer within a conservation planning software framework to present recommendations for reconfiguring an existing community-managed MPA network in Kubulau District, Fiji Islands, to improve its social acceptance.

Through this study, we seek to address 5 main questions:
(1) Where are the preferred target species located and what spatial models serve as the best predictors of species abundance;
(2) Where in Kubulau is current fishing effort focused and how does it vary by gear;
(3) What are the differences in opportunity costs across users of different fishing gear, based on current and potential costs;
(4) Where would be the best areas to modify the current MPA network to reduce conflict and improve fisheries benefits and which users would be most affected by these changes; and
(5) How can this model be applied to other resource management decisions?

## METHODS

## Study area

Kubulau District is an administrative unit of Bua Province, in south west Vanua Levu, Republic of Fiji Islands (Figure 1). The traditional fishing grounds (qoliqoli) have been legally demarcated by the Fiji Native Lands and Fisheries Commission. The $261.6 \mathrm{~km}^{2}$ of inshore waters within the Kubulau qoliqoli contain a diverse array of habitats, including reef flats, seagrass beds, coastal fringing reefs, soft bottomed lagoons, patch reefs, offshore barrier reefs and deep channels. Fish diversity estimates from rapid surveys in 2003 showed comparable numbers to sites in Indonesia and Papua Guinea (Marnane et al. 2003), with endemics represented by nearly $5 \%$ of all fish observed (WCS 2009). Measurements of targeted food fish from underwater visual census (UVC) surveys along Kubulau forereefs range from 0.002 to 12.1 tonnes ha ${ }^{-1}$ (WCS, unpublished data).


Figure 1. Survey sites for biological surveys and villages surveyed for CPUE data in Kubulau district, Vanua Levu, Fiji. Reef habitats for the Kubulau qoliqli and current tabu and MPAs are mapped. Underwater visual census (UVC) survey sites are shown and villages for CPUE data are labelled. Reef names of significant reefs are shown for reference.

In response to concerns about declining marine resources, the Kubulau chiefs established a district fisheries committee, who in 1997 banned commercial fishing by non-resource owners within the qoliqoli. The committee also informally declared a community-managed, no-take marine reserve around Namenalala Island. Despite the early success of the Namena Marine Reserve, the Kubulau communities recognized by 2003 that they needed some external assistance to halt the decline in key food fish species. In order to additionally address the impacts of unsustainable land use on water quality and the health of downstream ecosystems, the chiefs established the Kubulau Resource Management Committee (KRMC) to promote integrated management of marine, freshwater and terrestrial resources throughout the district. In 2005, the communities of Kubulau formally established a network of MPAs, including 17 village-managed (tabu) areas and 3 no-take district marine reserves (Namena, Nasue and Namuri).

The initial design of the protected areas network, and its subsequent reconfiguration, were informed by both socioeconomic and biological research undertaken by the KRMC and its conservation partners - the Wildlife Conservation Society, WWF, Wetlands InternationalOceania and the Coral Reef Alliance. A ridge-to-reef management plan was completed for Kubulau District in July 2009 and has been endorsed by the council of chiefs (WCS 2009). However, lack of consideration for village traditional fishing rights areas (kanakana) has created conflict over access to certain closed areas, which in at least one case has resulted in violent altercations between community fish wardens trying to prevent locals from fishing in a designated protected area (Clarke \& Jupiter in press).

The total population of Kubulau District is approximately 1,000 people distributed across 10 villages and 1 settlement. The 7 coastal villages have a higher dependence on marine resources than the 3 inland villages and 1 settlement, though presently only 4 of the coastal villages (Navatu, Namalata, Kiobo, Natokalau) have motorized vessels used for fishing. Preferred fishing gear types include: gill nets; spearguns; hand spears; hook and line; and Hawaiian slings (see Table 1 for full listing).

## Target species data

Shortly after the establishment of the protected area network, underwater visual census (UVC) surveys were carried out at 99 locations within the Kubulau qoliqoli between October and December 2005 to measure fish abundance and size of the following families:
Acanthuridae, Ephippidae, Haemulidae, Lethirinidae, Lutjanidae, Mullidae, Scaridae, Serranidae (groupers only), Siganidae. Sites were chosen to maximize spatial representation across reef habitats, resulting in low replication at the individual location level that we acknowledge may have high instantaneous variation in reef community assemblages (McClanahan et al. 2007). Measurements of fish size (total length) and abundance were scored along $5 \mathrm{~m} \times 50 \mathrm{~m}$ belt transects at deep ( $12-15 \mathrm{~m}$ ) and shallow depths ( $5 \mathrm{~m}-8 \mathrm{~m}$ ) at most forereef sites, and at shallow depths only at backreefs sites. Each sighted fish $>2 \mathrm{~cm}$ was classified to species level within size categories (2-5, 6-10, 11-15, 16-20, 21-25, 26-30, $31-35,36-40 \mathrm{~cm}$ ). The length of fishes $>40 \mathrm{~cm}$ was recorded to the nearest cm to improve estimates of biomass. Biomass was calculated from size class estimates of length ( $\mathrm{L}_{\mathrm{T}}$ ) and existing published values from Fishbase (Froese \& Pauly 2009) used in the standard weightlength expression $M=a L_{T}{ }^{\mathrm{b}}$, with $a$ and $b$ values preferentially selected from sites closest to Fiji (e.g. New Caledonia). If no length-weight (L-W) conversion factor was present for the
species, the factors for a species of similar morphology in the same genus was used (Jennings \& Polunin 1996). If a suitable similar species could not be determined, averages for the genera were used. As most of the New Caledonia fishes were measured to fork length (FL), a length-length (L-L) conversion factor was obtained from Fishbase where possible to convert from total length ( TL ) to FL before biomass estimation. Food fish species ( $n=148$ of 190 recorded) were identified from the families recorded to be used for spatial modeling of abundance throughout the qoliqoli (see Species abundance models sub-section below).

Table 1. List of transport and gear types from CPUE surveys completed by trained Kubulau community representatives between May 2008 to February 2009. The largest area report for each transport and gear type is listed. For combinations of transport and gear type with polygons unavailable, the area was set to equal to the next closest combination of gear and transport.

| Transport | Gear type | Area of largest associated |
| :--- | :--- | :--- |
| Walk | Gill net | 1.651 |
| Walk | Handspear | 0.989 |
| Walk | Speargun | 0.609 |
| Walk | Handline | $1.763^{*}$ |
| Boat | Gill net | 1.752 |
| Boat | Handline | 1.763 |
| Boat | Speargun | 1.111 |
| Boat | Trolling | 1.717 |
| Boat | Hawaiian sling | $1.111^{\dagger}$ |
| Boat | Diving | 1.417 |
| Boat | Handspear | $0.989^{\S}$ |
| Paddle | Speargun | 0.179 |
| Bilibili | Gillnet | 1.918 |
| Bilibili | Handline | $1.763^{*}$ |
| Bilibili | Speargun | $0.179^{\ddagger}$ |
| Bilibili | Handspear | $0.989^{\ddagger}$ |
| Paddle | Hawaiian sling | $1.111^{\dagger}$ |
| Paddle | Gill net | 0.257 |
| Swim | Speargun | 0.180 |
| Swim | Hawaiian sling | 0.180 |

* Data unavailable. Assumed the largest area used is the same as handline and boat.
† Data unavailable. Assumed to be the same as speargun and boat.
$\ddagger$ Data unavailable. Assumed to be the same as speargun and paddle.
§ Data unavailable. Assumed to be the same as hand spear and walk.


## Habitat data

Exposed and submerged coral reefs were digitized by the Fiji Department of Lands from aerial photographs captured in 1994 and 1996. Where data were missing, we digitized exposed reef only from Fiji topographic map sheets at 1: 50,000 scale. We used a decision rule classifier to divide the Kubulau qoliqoli habitats into barrier reef, patch reef, and
fringing reef (Table 2). Conservation targets for each habitat class for minimum representation in reserve design models (see Application sub-section below) are listed in Table 2. To derive biophysical predictor variables for species abundance models, we further scored the the reef types by: exposure to tides (submerged $=1$, exposed $=0$ ); exposure to waves (forereefs $=1$, other reef $=0$ ); and depth (depth $\leq 5 \mathrm{~m}=0$, depth $>5 \mathrm{~m}=1$ ). Depth was calculated from digitized nautical charts. Linear distance from shore for each survey location was calculated in GIS.

Table 2. Habitat type, percentage by area of qoliqoli and percentage of survey sites. The data oversample barrier reefs ( $84.5 \%$ of survey sites as compared to only $53 \%$ of qoliqoli).

| Habitat | Percentage area of <br> qoliqoli | Percentage of <br> survey sites | Conservation <br> Target <br> $(\%)$ | Conservation <br> Target $\left(\mathrm{km}^{2}\right)$ |
| :--- | :--- | :--- | :--- | :--- |
| Barrier | $54 \%$ | $84.5 \%$ | $30 \%$ | 11.1 |
| Fringing | $17 \%$ | $15.5 \%$ | $30 \%$ | 6.0 |
| Patch | $29 \%$ | $6.0 \%$ | $30 \%$ | 3.5 |

## Socio-economic data

Between May 2008 and February 2009, area specific catch per unit effort (CPUE) information (in catch person $\mathrm{hr}^{-1} \mathrm{~m}^{-2}$ ) was collected from fishers from four villages (Raviravi, Navatu, Kiobo, Nakorovou) within Kubulau District. Trained community volunteers recorded information once a week from all fish landings in the village during a 24 hour period. Fishers were asked for information on the total number fish caught, the number of fishers who went out fishing, the time spent fishing, the gear used for fishing and the transport used for fishing. All participants ( $\mathrm{n}=126$ total) were asked to indicate where they fished on a map. Of the 126 fishers, 54 drew polygons for fishing areas and the remaining fishers identified their fishing spots using points. In cases where one of the polygons was associated with more than one gear type or method of transport, only the most efficient gear type and method of transport was chosen to represent the polygon.

To create a single layer to represent fishing effort, all fishing spots identified as points were translated into polygons by creating a circle around each identified point with an area equivalent to that of the largest drawn polygon with the same combination of transport and gear (Table 1). When determining the size of the polygon to correspond with points we chose the largest fishing area as we felt this was a conservative method of identifying key fishing areas. Polygons were overlaid in geographic information system (GIS) to form one layer for each gear type and one layer for all gear types. A final uniform CPUE was calculated for each polygon by dividing the catch by the number of people fishing, time spent and fishing area.

## Opportunity cost model

In order to model opportunity costs of fishing sites we consider the stakeholder groups in the region. We define stakeholder groups by the type of fishing gear used (Table 1). In Kubulau there are seven stakeholder groups identified by the types of fishing gear. For each stakeholder group we identify key species, $i$. We define the opportunity cost to stakeholder group $j$ to be $c_{j}$
$c_{j}=\sum_{i=1}^{n} p_{j i} a_{i} b_{i} m_{i}$
Where $p_{j i}$ is the percentage catch for gear type $j$ of species $i, a_{i}$ is the abundance of species $i$, $b_{i}$ is the expected biomass of species $i$ and $m_{i}$ is the market value of species $i$.

The opportunity cost, c , of a fishing site is the sum of opportunity costs to all stakeholder groups weighted by the current proportion , $w_{j}$, of the total fleet of gear types and fishers currently in the fishery:
$c=\sum_{j=1}^{J} w_{j} c_{j}$
We calculate the opportunity cost as a weighted sum to capture the current distribution of gear types in the fleet. Additionally, a fishing site is not exclusively available for fishing by any one gear type, therefore calculating the opportunity cost to be equal to the most profitable gear type at that site is not accurate for marine environments. We calculate the opportunity costs to each stakeholder group as well as the full opportunity cost of each fishing site.

The abundance and percentage catch components were modeled separately. Each model is described in full detail below. Biomass was estimated based on average size of fish by species from the UVC data. Market value, or sales price, was obtained by the closest Fiji Department of Fisheries district office in Savusavu. The most recent fish prices from 2009 by family are provided in Table 3.

Table 3. Fish price as set by Fiji Department of Fisheries branch office in Savusavu, Vanua Levu.

| Class | Price (FJD/kg) | Family |
| :--- | :--- | :--- |
| A | $\$ 3.00$ | Lethrinidae, Serranidae, Siganidae |
| B | $\$ 2.50$ | Carangidae, Haemulidae, Lutjanidae, Mullidae |
| C | $\$ 2.00$ | Acanthuridae, Scaridae |

## Species abundance models

Because species abundance data is often characterized by a large number of zeros, a number of zero-inflated models have recently been developed which allow for the concurrent estimation of occurrence and abundance (Joseph et al. 2009; Warton 2005; Welsh et al. 1996; Wenger \& Freeman 2008). To ensure a rigorous treatment of the abundance modelling, we compared four count models for each species abundance model: Poisson (P), Negative Binomial (NB), zero-inflated Poisson (ZIP) and zero-inflated Negative Binomial (ZINB) (see supplementary materials for mathematical details). The Poisson and Negative Binomial models are standard count models used to estimate abundance whereas the zero-inflated models simultaneously model probability of detection and abundance. Because Poisson models may be sensitive to low occurrence numbers we selected only species that had at least $15 \%$ occurrence in the data resulting in 35 species from 17 genera (see Appendix 1 for equations).

The models were fit using the general linear model (glm) and zero-inflated model (zeroninfl) functions in R ( $R$ Development Core Team 2005). These packages use maximum likelihood to estimate coefficients for the generalized linear models (Poisson and negative binomial) as well as for the zero-inflated models. We used forward and backwards removal to select the best subset of predictors for each model (see Table 4 for list of predictors). For each species we selected the best model by comparing proportion of zeros (predicted zeros/observed zeros) and Akaike's information criterion (AIC; Akaike 1974):

AIC $=2 \mathrm{k}-2 \log \mathrm{~L}$
where $L$ is the likelihood and $k$ is the number of parameters in the fit. The best-fitting model has the lowest AIC. In the case where models had similar AIC the model with the closest predicted number of zeros was selected (Thompson \& La Sorte 2008; Warton 2005; Wenger \& Freeman 2008) (see Appendix 2 for model details). Abundance was predicted for each species across the qoliqoli based on the selected model. Abundance was then summed by family and fish class to produced expected abundances for these groupings of species.

Table 4. Biophysical and anthropogenic predictors of fish species abundance. The type of variable is listed (binary or numeric).

| Predictor | Variable name | Variable type |
| :--- | :--- | :--- |
| Reef Type | Fringing | Binary |
|  | Barrier | Binary |
|  | Patch | Binary |
| Seagrass | Seagrass | Binary |
| Exposure to tides | Submerged | Binary |
| Exposure to waves | Forereef | Binary |
| Depth > 5m | Deep | Binary |
| Distance to shore | Distance | Numeric |
| Protection status | MPA | Binary |

The predictor variables were selected based on available data representing biophysical anthropogenic factors that influence abundance (Table 4). Note that all predictors were considered for both the Bernoulli, Poisson and negative binomial processes in the mixture models. However, the best subsets of predictors were selected for each of the processes in the mixture models.

## Percentage catch models

For each gear type group we compared the predicted abundance of key species to the number of fish caught as reported in CPUE surveys (WCS, unpublished data). For each gear type the genera included are based on the CPUE data and are in line with previous reports of species caught (Teh et al. 2009). Percentage catch (catch/abundance) was modeled by gear type using regression analysis, using AIC to determine the best subset of predictors (Table 5, Appendix 3).

## Opportunity cost model validation

The modeled opportunity costs were compared to the Kubulau CPUE data for 250 m grid cells. The opportunity cost by gear type and CPUE by gear type was recorded for each 250
$m$ grid cell in the study region that had CPUE recorded ( $n=713$ ). A spearman's rank correlation was calculated by gear type group to determine how similar the relative value of each grid cell was using the traditional socio-economic data and our opportunity cost model.

Table 5. Predictor variables for percentage catch models.

| Predictors | Description |
| :--- | :--- |
| time | The amount of time spent fishing per fisher, determined from CPUE data |
| time2 | The amount of time spent fishing per fisher squared |
| fisher | Number of fishers fishing together, determined from CPUE data |
| area | Area in km2 |
| ab | Abundance |
| abperkm2 | Abundance per km2 |

## Application

We used Marxan software (Possingham et al. 2000) to explore options for design and reconfiguration of a cost-effective MPA network for Kubulau that met the conservation targets for all habitat types (Table 2). Marxan uses a simulated annealing algorithm to find good solutions to the mathematical problem which is:
$\operatorname{minimize} \sum_{i=1}^{N s} x_{i} c_{i}+b \sum_{i}^{N s} \sum_{h}^{N s} x_{i} *\left(1-x_{h}\right) c v_{i h}$
subject to the constraint that all the representation targets are met
$\sum_{i}^{N s} x_{i} r_{i j} \geq T_{j} \forall j$
and x is either zero or 1
$x_{i} \in\{0,1\} \forall i$
where $r_{i j}$ is the occurrence level of feature $j$ in site $i, c_{i}$ is the cost of site $i, N_{s}$ is the number of sites, $N_{f}$ is the number of features, and $T_{j}$ is the target level for feature $j$. The control variable $\mathrm{x}_{i}$ has value 1 for sites selected for the reserve network and value 0 for sites not selected (Ball et al. 2009).

The first equation minimizes the penalties associated with the cost of a network and the configuration or shape of the reserve network. The parameter $c v_{i h}$ reflects the cost of the connection, in this case simply the shared boundary, of planning units $i$ and $h$. The parameter $b$, is the boundary length modifier (BLM), a user-defined variable that controls the importance of minimizing the total boundary length of the selected areas. A small BLM will result in a reserve network that minimizes cost but might be quite fragmented. A large BLM will place greater emphasis on minimizing boundary length to produce a more compact reserve network but at a likely greater cost.

We consider four scenarios:

Scenario 1- We use CPUE as the cost layer and do not require that current tabu areas and MPAs be included in the selection of representative areas (clean slate \#1).

Scenario 2 - We use CPUE as the cost layer and require that current tabu areas and MPAs be included in the selection of representative areas (locked in \#1).

Scenario 3- We use opportunity cost as the cost layer and do not require that current tabu areas and MPAs be included in the selection of representative areas (clean slate \#2).

Scenario 4 - We use opportunity cost as the cost layer and require that current tabu areas and MPAs be included in the selection of representative areas (locked in \#2).

For the each habitat type (barrier, fringing and patch reefs), we set a representative target of $30 \%$. For each scenario, we selected the BLM with the method described Stewart \& Possingham (2005). To implement this method, we ran Marxan with the simulated annealing schedule and performed 100 repeat runs for each scenario. The repeat runs used progressively larger values for BLM, varied incrementally from 0 to 10 . This allowed us to identify, for each scenario, a good BLM that minimizes the trade-off between boundary length and cost. For each scenario we ran Marxan with the simulated annealing schedule and 1,000 repeat runs.

## RESULTS

Table 6. Best performing predictive abundance model by fish species.

|  |  |  |  |
| :--- | :--- | :--- | :--- |
| Name | Model | Name | Model |
| Acanthurus lineatus | ZINB | Macolor niger | ZIP |
| Acanthurus nigroris | ZINB | Monotaxis grandoculis | ZINB |
| Acanthurus olivaceus | ZINB | Naso lituratus | ZINB |
| Cephalopholis argus | ZIP | Naso unicornis | ZINB |
| Cetoscarus bicolor | ZINB | Parupeneus barberinus | ZINB |
| Cephalopholis urodeta | NB | Parupeneus bifasciatus | ZINB |
| Chlorurus bleekeri | ZINB | Parupeneus cyclostomus | ZIP |
| Chlorurus microrhinos | ZINB | Parupeneus multifasciatus | ZINB |
| Chlorurus sordidus | ZINB | Plectropomus leopardus | ZIP |
| Ctenochaetus striatus | ZINB | Scarus altipinnis | NB |
| Epinephelus merra | NB | Scarus dimidiatus | ZIP |
| Hipposcarus longiceps | NB | Scarus ghobban | ZINB |
| Lutjanus bohar | ZINB | Scarus niger | ZINB |
| Lutjanus fulvus | ZINB | Scarus oviceps | NB |
| Lutjanus gibbus | ZINB | Scarus schlegeli | ZINB |
| Lutjanus monostigma | ZIP | Siganus doliatus | ZIP |
| Lutjanus semicinctus | ZIP | Siganus punctatus | ZIP |
| Macolor macularis | ZINB |  |  |

The zero-inflated models outperformed the negative binomial and Poisson models for 86\% of the species considered. The zero-inflated negative binomial was the best performing model (selected for 21 of the 35 species, Table 6) and zero-inflated poisson was the second best model (selected for 9 of 35 species, Table 6).

Acanthuridae, Lutjanidae and Scaridae were the most abundant families in the qoliqoli in terms of numbers of their targeted food fish sighted (Figure 2). Species abundance model results indicate that abundance of fish within these three families varies spatially with highest abundance occurring in different habitats for each. Acanthurids have the highest abundance on inshore fringing and patch reefs (Figure 2a); lutjanids have the highest abundance on barrier reefs (Figure 2b); while scarids have the highest abundance on fringing reefs (Figure 2c).


Figure 2. Modeled abundance per $2,500 \mathrm{~m}^{2}$ for the three most abundant families: Acanthuridae, Lutjanidae, Scaridae. (a) Acanthuridae abundance per 2,500 m² (b) Lutjanidae abundance per 2,500 $\mathrm{m}^{2}$ (c) Scaridae abundance per $2,500 \mathrm{~m}^{2}$

Abundance by market class also varied spatially (Figure 3). Fish in Class C were most abundant, with widespread distribution across all habitats in the qoliqoli, particularly on seaward facing slopes of fringing reefs and forereef slopes of barrier reefs (Figure 3c). Class $B$ fish were found in greatest numbers on outer barrier forereefs, while Class $A$ fish had the lowest abundance in these areas (Figure 3a,b). Class A fish had distinctly higher abundance on inshore fringing and patch reefs (Figure 3a).


Figure 3. Abundance per $2,500 \mathrm{~m}^{2}$ by market class A, B, C. (a) Market Class A Abundance. Families included are Lethrinidae, Serranidae and Siganidae. (b) Market Class B Abundance. Families included are Carangidae, Lutjanidae and Mullidae. (c) Market Class C Abundance. Families included are Acanthuridae and Scaridae.

CPUE, as indicated by fisher survey records, was relatively uniform across all inshore reefs with the highest effort occurring on fringing reef near villages, particularly near areas where multiple villages are in close proximity (Figure 4a). However, by gear type CPUE was spatially dissimilar (Figure 5, Table 6a). Actual spatially distributed CPUE from trolling, diving and hand line were most similar ( $\rho$ ranging from 0.125 to 0.314 , Table 6a). Hawaiian sling and speargun CPUE were the most dissimilar ( $\rho=-0.235$, Table 6a).

Table 6. Comparison of gear type effort (per $2,500 \mathrm{~m}^{2}$ ) across qoliqoli. Bold values indicate significance at $p<0.001$, all other values non-significant. (a) Spearman's rank correlation ( $\rho$ ) of CPUE by gear type (b) Spearman's rank correlation ( $\rho$ ) of opportunity costs by gear type ( $p<0.001$ ).
(a) Correlations between CPUE by gear type

|  | dive | handline | handspear | Hawaiian | gillnet | speargun | trolling |
| :--- | ---: | ---: | ---: | ---: | :--- | :--- | :--- |
| handline | 0.061 |  |  |  |  |  |  |
| handspear | 0.043 | -0.128 |  |  |  |  |  |
| hawaiian | -0.079 | -0.121 | 0.007 |  |  |  |  |
| gillnet | -0.159 | -0.066 | -0.023 | -0.144 |  |  |  |
| speargun | -0.132 | -0.225 | -0.227 | -0.235 | -0.044 |  |  |
| trolling | 0.314 | $\mathbf{0 . 1 2 5}$ | -0.074 | -0.070 | -0.133 | -0.016 |  |
| total | -0.236 | $\mathbf{0 . 1 9 3}$ | $\mathbf{0 . 0 7 9}$ | $\mathbf{0 . 0 9 8}$ | $\mathbf{0 . 3 6 6}$ | $\mathbf{0 . 3 4 8}$ | $-\mathbf{0 . 1 6 9}$ |

## (Table 6 cont.)

## (b) Correlations between Opportunity Cost by gear type

|  | dive | handline | handspear | Hawaiian | gillnet | speargun | trolling |
| :--- | ---: | ---: | ---: | ---: | :--- | :--- | :--- |
| handline | 0.797 |  |  |  |  |  |  |
| handspear | 0.988 | 0.836 |  |  |  |  |  |
| hawaiian | 0.85 | 0.93 | 0.892 |  |  |  |  |
| gillnet | 0.958 | 0.906 | 0.982 | 0.939 |  |  |  |
| speargun | 0.939 | 0.931 | 0.955 | 0.924 | 0.98 |  |  |
| trolling | 0.9 | 0.852 | 0.932 | 0.903 | 0.945 | 0.916 |  |
| total | 0.945 | 0.93 | 0.968 | 0.939 | 0.994 | 0.995 | 0.934 |



Figure 4.Total CPUE and modeled Opportunity Cost for all gear types in Kubulau district. (a) Catch per unit effort (CPUE) calculated as catch person ${ }^{-1}$ hour $\mathrm{m}^{-2}$. (b) Opportunity cost to all gear types in Fiji Dollars (FJD) per 2,500 m².


Figure 5. Catch per unit effort to gear type groups. (a) CPUE of trolling users in catch person ${ }^{-1}$ hour ${ }^{-1}$ $\mathrm{m}^{-2}$ (b) CPUE of speargun users in catch person ${ }^{-1}$ hour $\mathrm{m}^{-1}$ (c) CPUE of hand line users in catch person ${ }^{-1}$ hour ${ }^{-1} \mathrm{~m}^{-2}$ (d) CPUE of gillnet users in catch person ${ }^{-1}$ hour $\mathrm{m}^{-1}$.

The modeled opportunity cost was highest for inshore fringing and patch reefs, with one section of high value fringing reefs occurring offshore in the Namena MPA (Figure 4b). Modeled opportunity costs were variable both in magnitude and spatial distribution for the different gear types used (Figure 6). Speargun users had the highest opportunity cost of all gear types with a maximum value of $\$ 11.88$ FJD $/ 2,500 \mathrm{~m}^{2}$, and opportunity costs were positively correlated with speargun CPUE (Figure 6b, Table 6b). Opportunity costs to speargun users were, on average, higher than all other gear types across all offshore reefs (Figure 6b). Users of gill nets and hand lines had the next highest opportunity costs, respectively, with highest values for both occurring on inshore fringing and patch reefs (Figure $6 \mathrm{c}, \mathrm{d}$ ). Users who troll for catch had the lowest opportunity cost of all gear types (Figure 6a) with the greatest potential loss occurring on barrier forereefs.

Table 7. Comparison of modeled opportunity costs by gear type to CPUE data across qoliqoli ( $\mathrm{n}=$ 713). Spearman's rank correlation ( $\rho$ ) of opportunity costs and CPUE by gear type ( ${ }^{* * *} \mathrm{p}<0.001,{ }^{* *}$ $\left.p<0.01,{ }^{*} p<0.05\right)$.

| Gear Type | Spearman's rank correlation $(\rho)$ |
| :--- | ---: |
| Gillnet* | 0.075 |
| Diving ${ }^{* *}$ | -0.092 |
| Hawaiian*** | 0.096 |
| Hand line | -0.018 |
| Hand spear | 0.046 |
| Speargun*** | 0.170 |
| Trolling | -0.052 |
| Total*** | 0.303 |

Modeled opportunity costs were positively correlated for all users of gear types (Table 6b). Opportunity costs to speargun and gillnet users were most similar to total effort for the modeled opportunity costs ( $\rho=0.995$ and 0.994 respectively, Table 6b). Total modeled opportunity cost was positively correlated with total CPUE ( $\rho=0.303, p<0.001$, Table 7). Speargun had the highest correlation between the modeled opportunity cost and catch per unit effort data ( $\rho=0.170, p<0.001$ ) and hand line had the lowest correlation ( $\rho=-0.018$; Table 7).

The current network of tabu and MPAs in Kubulau qoliqoli cover 40\% of all barrier reefs, $36 \%$ of fringing reefs and $2 \%$ of patch reefs. For the reconfiguration scenarios 2 and 4 with the protected area network locked in, areas selected by Marxan analyses were predominantly the patch reefs within Cakaunivuaka Reef (Figure 7b,d). The selection frequency for these two scenarios had a strong, positive correlation (Spearman's rank correlation coefficient $\rho_{2,4}=0.848, p<0.001$ ). Selection frequency for the clean slate scenarios 1 and 3 was also positively correlated (Spearman's rank correlation coefficient $\rho_{1,3}$ $=0.847, p<0.001$ ). The frequency of areas selected under the clean slate versus locked in scenarios using CPUE were negatively correlated (Spearman's rank correlation coefficient $\rho_{1,2}=-0.012, \mathrm{p}<0.035$ ), while the frequency of areas selected using opportunity costs data was positively correlated ( $\rho_{3,4}=0.312, p<0.001$ ). Clean slate areas provided more spatial


Figure 6. Opportunity costs to gear type groups. (a) Opportunity cost to trolling users in Fiji Dollars (FJD) per 2,500 m ${ }^{2}$ (b) Opportunity cost to speargun in Fiji Dollars (FJD) per 2,500 m${ }^{2}$ (c) Opportunity cost to hand line in Fiji Dollars (FJD) per 2,500 $\mathrm{m}^{2}$ (d) Opportunity cost to gill net in Fiji Dollars (FJD) per $2,500 \mathrm{~m}^{2}$.
options and are notable in particular for their virtual exclusion of reefs within the Namuri MPA (Figure 7a,c). Best solutions from the clean slate Marxan analyses also indicate that Namuri MPA plus some of the inshore community tabu could be eliminated, while adding protection to Nakadamalevu and Cakaunivuaka reefs (Figure 8a, c). The locked in model also
indicates possible additions to the network from the northwest, central, and southwest portions of Cakaunivuaka reefs (Figure 8b,d).


Figure 7. Marxan Selection Frequency (a) Selection frequency for scenario 1. Current MPAs were not locked in and CPUE was used as the cost layer. (b) Selection frequency for scenario 2. Current MPAs were locked in and the boundaries are shown in black. CPUE was used as the cost layer. (c) Selection frequency for scenario 3. Current MPAs were not locked in and opportunity cost was used as the cost layer. (b) Selection frequency for scenario 4. Current MPAs were locked in and the boundaries are shown in black. Opportunity cost was used as the cost layer.


Figure 8. Marxan best solutions. (a) Best solution for scenario 1. Current MPAs were not locked in and CPUE was used as the cost layer. (b) Best solution for scenario 2. Current MPAs were locked in and the boundaries are shown in black. CPUE was used as the cost layer. (c) Best solution for scenario 3. Current MPAs were not locked in and opportunity cost was used as the cost layer. d) Best solution for scenario 4. Current MPAs were locked in and the boundaries are shown in black. Opportunity cost was used as the cost layer.

## DISCUSSION

## Species abundance and opportunity costs models

The best models selected for species abundance were predominantly zero-inflated models. The zero-inflated negative binomial was the dominant model across the 35 species which is in line with model selection in other studies (Joseph et al 2009). When aggregated to the family level, abundance was higher for Acanthuridae, Lutjanidae and Scaridae. This result is consistent with previous reports of acanthurids and scarids accounting for a large percentage of catch in Fijian and other tropical Western Pacific fisheries (Jennings \& Polunin 1995; Kuster et al. 2005; Rhodes et al. 2007). The highest predicted abundance for these families occurs in lagoon reefs (acanthurids and scarids) and on outer reef sleeps (lutjanids; Figure 2), which is comparable to previous reports of highest CPUE on lagoon reefs and outer reef slopes and open seas (Jennings \& Polunin 1995).


Figure 9. Fiji fisherman with a traditional speargun (Hawaiian sling) trailing catch.
The highest value fish (Class A) have spatially dissimilar abundance distribution to the midvalue fish (Class B). However, this spatial dissimilarity does not seem to impact current fishing effort. Fishing effort summed across all gear types is highest on reefs closest to villages (inshore fringing and patch reefs), with low effort reported to occur on outer reef slopes. Based on overall species abundance distributions, opportunity cost models were highest for inshore fringing and patch reefs because there are both high value fish and high abundances of low value fish, validating our expectations. While this suggests that market value may be driving the spatial distribution of effort to some degree, market value does not appear to be the only consideration. For example, if market value were the only factor for spatial distribution of fishing, we would expect higher effort on outer reef slopes where the
mid-value fish have high abundances. Although spearguns are the most efficient gear type used (Figure 9), consistent with results from other artisanal catch surveys from coral reef fisheries (McClanahan \& Mangi; Cinner et al. 2009), and were used by Kubulau fishers on the outer reefs, due to economic constraints they are not owned by all fishers. If the market value of fishes were more spread out such that the large Class $A$ and $B$ fishes commonly found on the outer reef (e.g. Carangidae, Lutjanidae, Lethrinidae, Serranidae) had relatively greater value, there would likely be a displacement of fishing effort towards offshore areas, and other Kubulau residents might invest in spearguns, particularly if they have access to a reliable market. This type of market-driven fishing displacement has been observed in other multispecies fisheries, where the high value of catch has strongly influenced the location of fishing effort, particularly in situations with rising fuel prices and depletion of commercial stocks (Arellano \& Swartzman 2009).

Opportunity costs models are likely to have high values for areas that currently have high fishing effort as fishermen will likely choose to exploit the most abundant accessible fishing ground (Aswani 1998). Indeed, the modeled opportunity cost from this study was significantly, positively correlated to CPUE, indicating that if fishers are targeting high value reefs they will fish the inshore fringing and submerged patch reefs. However, the opportunity cost model also identified additional offshore regions of high value such as the fringing reef around Namenalala Island and the barrier forereef which are currently not fished. Additionally, different gear types have higher costs in areas distant from the inshore fringing reefs: for example, opportunity costs are highest for trolling on barrier forereefs. These differences reflect the differential efficiency of gear types across habitats (Kuster et al. 2005; Teh et al. 2009), which is reflected in the spatial heterogeneity of opportunity costs broken down by individual gear type. Speargun users are the most correlated with total opportunity cost. This is mainly due to the fact that due to its efficiency, speargun opportunity cost is often an order of magnitude larger than other opportunity costs to other gear types.

In contrast to the CPUE data, the estimated opportunity costs were all positively correlated for all gear types because the method demonstrates the expected cost of an area if a gear type were to be used. The model can therefore be used to examine expected distributions of fishing effort as access to gear types and modes of transport change. For example, we can use our opportunity cost model to examine how costs will change as more fishers gain access to spearguns and therefore change their spatial fishing effort. This type of analysis is not possible with the CPUE data as it only reflects current spatial distribution of effort and access to gear types. Our model can also be used to examine how fishing effort is expected to change as access to motorized transport increases (e.g. in Nicaragua, Daw 2008). The rapid uptake of motorized transport vessels, and subsequent change in fishing effort, has been observed in developing countries (Pauly 2006). This transition is also found in Fiji where the traditional outrigger canoe is being replaced by motor boats, resulting in a dramatic increase in catch rate (Kuster et al. 2005).

## MPA network reconfiguration options for Kubulau

There were notable similarities in the Marxan trials with the clean slate and locked in approaches where CPUE data and the opportunity cost data were used as alternative cost layers. Both locked in approaches indicated high priority additions to the network should
include areas within Cakaunivuaka Reef. Determination of the exact placement of new areas within the reef, however, will likely generate heated debate among resource users in Kubulau given that resource mapping exercises have indicated heavy use in the northeastern and southwestern portions of the reef (Figure 10).


Figure 10.
Resource map of preferred fishing locations during calm days. Colors indicate number of users reporting preference for fishing ground. Source: WCS 2008 and 2009 household surveys from Navatu, Natokalau, Nakorovou and Kiobo villages.

The clean slate approaches using both cost layers were also fairly similar and indicate other potential sites that could be added to the network, in particular, areas within Nakadamulevu Reef, a site originally proposed in 2005 for inclusion within the protected area network. Given that recent monitoring from the Namuri MPA suggests that it is being substantially affected by poaching (WCS 20010), and that the clean slate Marxan trials failed to select sites within Namuri, it would be worthwhile to suggest a trade-off to the community to open portions of Namuri in exchange for protection areas within Nakadamulevu and the adjacent Nakadamulailai reefs that are not heavily used for fishing. Closure of these areas could potentially also offset opening a portion of Namena Marine Reserve, which has been heavily contested by one of the Navatu clans with traditional fishing rights (kanakana) in the
area who have been repeated caught fishing in the Namena MPA in breach of community management rules (Clarke \& Jupiter in press). Because the clan has perceived inequity in the distribution of costs and benefits of the initial MPA network design, the Marxan solutions offer options for reconfiguration that may reduce conflict by producing a more socially acceptable configuration (Lal 2005). Some of this conflict may have arisen because environmental and social goals of management were ill-defined from the outset: having a clear understanding of these goals is critical to ensure that MPA design does not adversely impact current fishing industries and community identity (Ban et al. 2009; Klein et al. 2008).

While the two clean slate scenarios were spatially very similar ( $\rho_{1,3}=0.847, p<0.001$ ), there were some notable differences: for instance, the fringing reef around Namenalala Island was included in the Marxan scenario with CPUE as the cost layer but not when opportunity cost was considered. This is an example of how opportunity cost data allows for consideration of future fishing effort, which may be preferable to community managers who need to evaluate selections based on potential as well as current fishing effort. However, it is important to note that fishers may still fish even if costs are high because they fishing is a strong part of their cultural identity. These non-monetary benefits, which are not necessarily factored in to opportunity cost calculations, may make it hard for fishers to switch occupations (Pollnac \& Poggie 2008).

## Applications to other regions

The method for calculating opportunity costs to fishers presented here could be applied in any region with existing biological data, such as UVC surveys. We base our model on the assumption that catch size is a function of fish abundance and therefore closures to fishing in areas of high fish abundance will be of higher cost to fishermen. Therefore, our model differs from standard survey approaches that attempt to minimize impacts on current effort by deriving current preferred fishing grounds. Additionally, standard socio-economic survey methods often have issues such as ensuring representative gear type participation, full disclosure of fishing areas and lack of standardized methods for integrating spatial data (for methods on standardizing data collection with GIS see Close \& Brent Hall 2006; De Freitas \& Tagliani 2009). Our model may be useful when time and financial resources are limited or surveyors do not have adequate trust from fishers to receive accurate interview data regarding fishing effort. Additionally, CPUE data may not be appropriate for considering socio-economic goals for future fisheries usage if gear preferences or access to transport are expected to change dramatically (Salas \& Gaertner 2004), whereas models incorporating opportunity costs may be used in these cases to examine the spatial distributions of effort.

The opportunity cost model provides data that can directly be used in decision support tools such as Marxan and Marxan with Zones (Ball et al. 2009; Watts et al. 2009). It is increasingly clear that inclusion of this type of data in conservation planning is key in data poor regions or regions that are likely to be highly sensitive to socio-economic considerations (Ban et al. 2009; Ban \& Klein 2009). If we expect spatial distribution of fishing effort to be market driven then our opportunity cost model provides a good data set for including socioeconomic goals such as maximizing future fisheries returns or minimizing future impacts to preferred gear types. However, in developing countries studies have suggested that artisanal fishers are not always market driven (Pet-Soede et al 2001; Daw 2008). Factors
such as prestige associated with specific gear types, values placed on time versus money, risk aversion and restricted opportunities such as access to transport or marine tenure systems have been cited as affecting fisher behaviour (Bene \& Tewfik 2001; Montenegro et al. 2001; Salas \& Gaertner 2004). Therefore, when used for resource management decisions, the local context should factor heavily in what other information needs to be considered (e.g. considering the traditional divisions of fishing grounds or kanakana in Fiji). While these factors may weigh heavily in decision making, our model provides sound information regarding the economic considerations of designing MPAs and can be coupled with pertinent social information to provide informed decision making.

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## APPENDIX 1. Species Abundance Model Equations

Four models were compared for each species: Poisson (P), negative binomial (NB), zeroinflated Poisson (ZIP) and zero-inflated negative binomial (ZINB).

The Poisson distribution has a probability mass function of:
$\operatorname{Pr}(N=x \mid \lambda)=\dagger \quad \llbracket e^{\boldsymbol{\top}}(-\lambda) \lambda \boldsymbol{I}^{\boldsymbol{T}} x / x!\quad, \mathrm{x}=0,1,2, \ldots, \infty$
where $\lambda$ is the mean, which can be interpreted as the mean number of events occurring in an area or time. In this case we interpret $\lambda$ to be the number of fish counted in the $250 \mathrm{~m}^{2}$ survey area or in time units the number of fish counted in .33hrs. A limitation of the Poisson distribution is that the variance is equal to the mean. In biological data sets this is unlikely to be the case. In the case of over dispersed data, where the sample variance is greater than the sample mean, the negative binomial distribution can be used. The negative binomial distribution can account for larger variances with the use of the additional parameter $\vartheta$. The probability mass function of the negative binomial is:
$\operatorname{Pr}\left(N=x \mid \lambda_{\theta} \theta\right)=\downarrow(x+\theta-1)!f(\theta-1) \mid x!(\theta /(\theta+\lambda))^{\top}(-\theta)(\lambda /(\lambda+\theta))^{\dagger} x, \mathrm{x}=$ $0,1,2, \ldots, \infty$
where $\lambda$ is the mean, $\vartheta$ is the dispersion parameter and $N$ is the number of individuals in the survey site.

Environmental predictors were incorporated into the generalized linear regression and the log-linear transformation was applied:
$\log \left(\lambda_{i}\right)=\gamma_{0}+\sum_{j} \gamma_{j} x_{i}$
where $\lambda_{i}$ is the mean abundance at site $i, \gamma_{0}$ is the intercept coefficient, $x_{i}$ are the predictor variables for site $i$ and $\gamma_{j}$ are the predictor coefficients determined by maximum likelihood.

In zero-inflated mixture models the models are a mixture of a Bernoulli process (to model occupancy of sites) and Poisson or negative binomial process (to model site abundance). The mixture model assumes that some of the zeros occur due to the absence of a species at a site (captured by the Bernoulli process) and some of the zeros occur due to error in the count model (captured by the Poisson or negative binomial process). Therefore, the probability mass function for the zero-inflated Poisson process is:

```
\(\operatorname{Pr}\left(N_{1} i=0 \mid \lambda, \psi\right)=-\mid \psi+(1-\psi) e^{\top}(-\lambda)\)
\(\operatorname{Pr}\left(N_{1} i>0 \mid \lambda, \psi\right)=(1-\psi) \dagger \quad \llbracket e^{\dagger}(-\lambda) \lambda \rrbracket{ }^{\dagger} x / x!, \mathrm{x}=1,2, \ldots, \infty\)
```

where $N$ is the actual site abundance, $\psi$ is the probability that the site is occupied and $\lambda$ is the mean abundance. Similarly, the probability mass function for the zero-inflated negative binomial process is:
$\operatorname{Pr}\left(N_{1} i=0 \mid \lambda, \theta, \psi\right)=-\psi \psi+(1-\psi)(\theta /(\theta+\lambda))^{\mathrm{T}}(-\theta)$
$\operatorname{Pr}\left(N_{1} i>0 \mid \lambda, \theta, \psi\right)=-1(x+\theta-1)|f(\theta-1)| x \mid(\theta f(\theta+\lambda))^{\mathrm{t}}(-\theta)(\lambda /(\lambda+\theta))^{\mathrm{T}} x, \mathrm{x}=$ $1,2, \ldots, \infty$
where $N$ is the actual site abundance, $\psi$ is the probability that the site is occupied, $\lambda$ is the mean abundance and $\vartheta$ is the dispersion parameter of the negative binomial.

The log-linear transformation is applied to the Poisson and negative binomial components of the ZIP and ZINB. For the Bernoulli process a logistic regression is applied to predict occupancy:
$\log \mathbf{I}\left(\psi_{i}\right)=\beta_{0}+\sum_{j} \beta_{j} x_{i}$
where $\psi_{i}$ is the mean abundance at site $i, b_{0}$ is the intercept coefficient, $x_{i}$ are the predictor variables for site $i$, and $\beta_{j}$ are the predictor coefficients determined by maximum likelihood.

## APPENDIX 2. Species Abundance Models

Details of the model selected for each species is provided along with the AIC and proportion zeros. The variables considered are provided in Table 1 and correspond to the predictors discussed in the methods section.

| Name | Model | Equation | AIC | Proportio n zeros |
| :---: | :---: | :---: | :---: | :---: |
| Acanthurus lineatus | ZINB | $\begin{aligned} & \log (\lambda)=5803+1.1487 \mathrm{MPA}+1.0586 \text { Fringing }- \\ & 1.4808 \text { Seagrass } \\ & \operatorname{logit}(\psi)=2.2052-0.8246 \text { submerged } \end{aligned}$ | 308.6 | 1.007 |
| Acanthurus nigroris | ZINB | ```log(\lambda) = 1.5106 + 0.9843 MPA -1.9526 Barrier -2.8795 Fringing + 1.8929Seagrass + 1.2673forereef logit (\psi) = 2.5589-1.3350submerged``` | 299.2 | 1.000 |
| Acanthurus olivaceus | ZINB | $\begin{aligned} & \log (\lambda)=-0.3474+0.7258 \mathrm{MPA}+2.4137 \text { Barrier }+- \\ & 0.9574 \text { submerged }+0.8337 \text { forereef } \\ & \operatorname{logit}(\psi)=2.1313-0.9309 \text { submerged } \end{aligned}$ | 317.4 | 1.000 |
| Cephalopholis argus | ZIP | ```log(\lambda) = -0.4720-0.1657 MPA + 1.2758Barrier -0.3596 submerged -0.7076 Deep logit (\psi) = -3.1466-2.0674MPA + 4.3170Barrier - 1.6284Deep``` | 392.4 | 0.980 |
| Cetoscarus bicolor | ZINB | $\begin{aligned} & \log (\lambda)=-0.6338-0.6808 \text { Barrier }+2.9584 \text { Fringing } \\ & \operatorname{logit}(\psi)=0.1107-1.6391 \text { forereef } \end{aligned}$ | 604.4 | 1.000 |
| Cephalopholis urodeta | NB | $\log (\lambda)=-0.9562+-0.7682$ submerged | 296.06 | 0.992 |
| Chlorurus bleekeri | ZINB | $\begin{aligned} & \log (\lambda)=1.8949-0.2722 \text { Fringing } \\ & \operatorname{logit}(\psi)=0.9543-0.7221 \text { forereef }-0.7715 \text { submerged } \end{aligned}$ | 685.4 | 1.000 |
| Chlorurus microrhinos | ZINB | $\begin{aligned} & \log (\lambda)=0.8886+0.5502 \mathrm{MPA}+1.4201 \text { Fringing }- \\ & 2.4271 \text { Seagrass }+0.6926 \text { submerged } \\ & \operatorname{logit}(\psi)=0.1095-0.8022 \text { forereef }+0.5734 \text { Deep } \end{aligned}$ | 709.2 | 1.000 |
| Chlorurus sordidus | ZINB | $\begin{aligned} & \log (\lambda)=1.7369+0.4830 \text { forereef } \\ & \operatorname{logit}(\psi)=0.5712+-0.9308 \text { submerged } \end{aligned}$ | 935.2 | 1.000 |
| Ctenochaetus striatus | ZINB | $\log (\lambda)=2.7195+0.5222 \mathrm{MPA}-0.4206 \text { Barrier - }$ <br> 0.4757 Deep +0.5246 forereef $\operatorname{logit}(\psi)=-0.7085+1.6397 \mathrm{MPA}+1.4228 \text { Barrier }-$ <br> 0.7331 submerged | 751.4 | 1.000 |
| Epinephelus Merra | NB | $\log (\lambda)=-2.6165+1.0338$ submerged -1.0529forereef | 200.85 | 1.000 |
| Hipposcarus longiceps | NB | $\begin{aligned} & \log (\lambda)=-2.302+4.122 \text { Fringing }+-3.496 \text { Seagrass }+ \\ & 1.090 \text { submerged }+0.0008544 \text { distance } \end{aligned}$ | 331.04 | 1.000 |
| Lutjanus bohar | ZINB | $\begin{aligned} & \log (\lambda)=-0.0413+0.9142 \text { forereef } \\ & \operatorname{logit}(\psi)=0.4994-1.3889 B a r r i e r \end{aligned}$ | 619.4 | 1.000 |
| Lutjanus fulvus | ZINB | $\begin{aligned} & \log (\lambda)=1.1059+0.8658 \mathrm{MPA}+0.9638 \text { Fringing - } \\ & 1.0002 \text { Deep } \\ & \operatorname{logit}(\psi)=0.6349+0.6216 \text { submerged } \\ & \hline \end{aligned}$ | 242.6 | 0.993 |
| Lutjanus gibbus | ZINB | $\begin{aligned} & \log (\lambda)=1.2234+0.3343 \mathrm{MPA} \\ & \operatorname{logit}(\psi)=-0.6335+0.4480 \text { submerged } \end{aligned}$ | 769.8 | 1.000 |
| Lutjanus monostigma | ZIP | $\begin{aligned} & \log (\lambda)=-3.5860+1.4884 \mathrm{MPA}+2.5218 \text { Seagrass }+ \\ & 1.6865 \text { Fringing }+2.0503 \text { forereef } \\ & \operatorname{logit}(\psi)=0.03595+2.08250 \text { Seagrass } \end{aligned}$ | 189.2 | 1.000 |


| Name | Model | Equation | AIC | Proportio n zeros |
| :---: | :---: | :---: | :---: | :---: |
| Lutjanus semicinctus | ZIP | $\log (\lambda)=-0.2692+0.4870 \text { Barrier }+0.2934 \text { Deep }+$ <br> 0.4761 submerged <br> $\operatorname{logit}(\psi)=-0.5401+0.5682$ submerged | 464.6 | 1.000 |
| Macolor macularis | ZINB | $\begin{aligned} & \log (\lambda)=-0.07471+0.59082 \mathrm{MPA}+0.65725 \text { forereef } \\ & \operatorname{logit}(\psi)=0.9892+0.3582 \text { submerged } \end{aligned}$ | 385 | 1.000 |
| Macolor niger | ZIP | $\log (\lambda)=-0.4586-2.0081$ Seagrass +0.9562 Deep + 0.8967 forereef <br> logit $(\psi)=0.7255+0.3972$ submerged | 364.2 | 1.000 |
| Monotaxis grandoculis | ZINB | $\begin{aligned} & \log (\lambda)=1.3511+0.4766 \text { Barrier } \\ & \operatorname{logit}(\psi)=-0.9505+0.7344 \text { Deep } \\ & \hline \end{aligned}$ | 970.4 | 1.021 |
| Naso lituratus | ZINB | $\begin{aligned} & \log (\lambda)=0.6517-0.8754 \text { Seagrass }+0.6542 \text { submerged } \\ & \operatorname{logit}(\psi)=2.8808+0.7895 \text { MPA - } 1.4811 \text { Barrier - } \end{aligned}$ <br> 2.9400 Seagrass -1.3792 forereef | 476 | 1.000 |
| Naso unicornis | ZINB | $\begin{aligned} & \log (\lambda)=1.6970+0.5318 \text { MPA }-1.7404 \text { Barrier }-1.3671 \\ & \text { Fringing }+-2.1027 \text { Seagrass }+0.4097 \text { Deep }+ \\ & 0.7369 \text { submerged } \\ & \operatorname{logit}(\psi)=0.4458+1.2541 \text { Barrier } \end{aligned}$ | 393.2 | 1.008 |
| Parupeneus barberinus | ZINB | $\log (\lambda)=0.6229+0.6542$ Barrier +0.8605 Fringing - <br> 0.4130 forereef +0.3984 submerged <br> $\operatorname{logit}(\psi)=0.7172+1.0368$ MPA - 1.3364 Seagrass | 506 | 1.000 |
| Parupeneus bifasciatus | ZINB | $\begin{aligned} & \log (\lambda)=0.7428-0.3592 \mathrm{MPA}+0.5858 \text { forereef } \\ & \operatorname{logit}(\psi)=1.4764+15.8825 \text { Patch } \end{aligned}$ | 387.4 | 1.000 |
| Parupeneus cyclostomus | ZIP | $\begin{aligned} & \log (\lambda)=-0.8861+0.2751 \text { Barrier } \\ & \operatorname{logit}(\psi)=-0.03607+1.47221 \text { Seagrass } \\ & +0.88298 \text { forereef } \end{aligned}$ | 264 | 1.000 |
| Parupeneus multifasciatus | ZINB | $\begin{aligned} & \log (\lambda)=1.1328-0.7618 \text { Patch }+0.5895 \text { Deep }-0.7456 \\ & \text { forereef } \\ & \text { logit }(\psi)=0.28-1.9591 \text { Patch } \end{aligned}$ | 360.6 | 1.000 |
| Plectropomus leopardus | ZIP | $\begin{aligned} & \log (\lambda)=0.2179-1.2473 \text { Barrier }-1.1920 \text { submerged } \\ & \operatorname{logit}(\psi)=0.2729+2.0921 \text { Barrier }-13.1578 \text { submerged } \end{aligned}$ | 169.2 | 1.007 |
| Scarus altipinnis | NB | $\log (\lambda)=0.3414+1.6554$ MPA -2.9865 Barrier -5.3612 Seagrass -1.1627 Deep +2.9682 forereef | 433 | 0.992 |
| Scarus dimidiatus | ZIP | $\begin{aligned} & \log (\lambda)=1.0516+0.3694 \text { Fringing } \\ & \operatorname{logit}(\psi)=0.04855+1.27836 \text { Barrier } \end{aligned}$ | 288 | 1.000 |
| Scarus ghobban | ZINB | $\log (\lambda)=0.8256-0.6094 \mathrm{MPA}+0.6855$ forereef + 0.6042 submerged <br> $\operatorname{logit}(\psi)=-1.3009+1.7594$ submerged | 536 | 1.000 |
| Scarus niger | ZINB | $\begin{aligned} & \log (\lambda)=0.9487-0.3020 \mathrm{Deep}+0.4657 \text { forereef logit }(\psi) \\ & =-0.1108-0.9279 \text { forereef } \end{aligned}$ | 769.4 | 1.000 |
| Scarus oviceps | NB | $\log (\lambda)=-0.08557-0.00005078$ distance -.5996Deep | 460.61 | 0.964 |
| Scarus schlegeli | ZINB | $\begin{aligned} & \log (\lambda)=1.2882+0.5543 \mathrm{MPA}-0.5613 \text { Barrier }- \\ & 0.9916 \text { Seagrass }+0.9265 \text { submerged } \\ & \text { logit }(\psi)=0.4658-0.8336 \text { submerged } \end{aligned}$ | 804 | 1.000 |
| Siganus doliatus | ZIP | $\log (\lambda)=1.5476-0.7184 \mathrm{MPA}-5.2078$ Barrier -5.0360 <br> Fringing 0.4987 forereef <br> $\operatorname{logit}(\psi)=0.04286+1.11709$ MPA -3.67213 Fringing + <br> 0.78589 Deep | 205.18 | 1.000 |
| Siganus punctatus | ZIP | $\begin{aligned} & \log (\lambda)=1.0359-0.4874 \mathrm{MPA}+0.3208 \text { submerged } \\ & \operatorname{logit}(\psi)=1.8378+1.0406 \text { submerged } \end{aligned}$ | 290 | 0.995 |

## APPENDIX 3. Percentage Catch Models

Models of percentage catch by gear type. Model details and $R^{2}$ values are given as well as the genera included, based on CPUE surveys.

| Gear type | Model | R^2 | NA* |
| :--- | :--- | :--- | :--- | | Genera included |
| :--- |
| Diving |
| Gillnet |

*Because sample size was too small, average catch percentage was used

