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Optimized fishing through periodically harvested closures

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Abstract :

1. Periodically harvested closures are a widespread, centuries-old form of fisheries management that protects fish between pulse harvests and can generate high harvest efficiency by reducing fish wariness of fishing gear. However, the ability for periodic closures to also support high fisheries yields and healthy marine ecosystems is uncertain, despite increased promotion of periodic closures for managing fisheries and conserving ecosystems in the Indo-Pacific.

2. We developed a bioeconomic fisheries model that considers changes in fish wariness, based on empirical field research, and quantified the extent to which periodic closures can simultaneously maximize harvest efficiency, fisheries yield and conservation of fish stocks.

3. We found that periodic closures with a harvest schedule represented by closure for one to a few years between a single pulse harvest event can generate equivalent fisheries yield and stock abundance levels and greater harvest efficiency than achievable under conventional fisheries management with or without a permanent closure.

4. Optimality of periodic closures at maximizing the triple objective of high harvest efficiency, high fisheries yield, and high stock abundance was robust to fish life history traits and to all but extreme levels of overfishing. With moderate overfishing, there emerged a trade-off between periodic closures that maximized harvest efficiency and no-take permanent closures that maximized yield; however, the gain in

harvest efficiency outweighed the loss in yield for periodic closures when compared with permanent closures. Only with extreme overfishing, where fishing under nonspatial management would reduce the stock to ≤18% of its unfished level, was the harvest efficiency benefit too small for periodic closures to best meet the triple objective compared with permanent closures.

5. Synthesis and applications. We show that periodically harvested closures can, in most cases, simultaneously maximize harvest efficiency, fisheries yield, and fish stock conservation beyond that achievable by no-take permanent closures or nonspatial management. Our results also provide design guidance, indicating that short closure periods between pulse harvest events are most appropriate for well-managed fisheries or areas with large periodic closures, whereas longer closure periods are more appropriate for small periodic closure areas and overfished systems.

Keywords : bioeconomic model, conservation, fish behaviour, fisheries management, marine protected areas, marine reserves, periodically harvested closures, population dynamics

Introduction

Spatial fisheries closures are used widely as a management tool for mediating overfishing and promoting stock recovery (Gerber *et al.* 2003), but their ability to enhance the value of well-managed fisheries may be limited (Hilborn *et al.* 2004). This perception of the mixed utility of spatial closures is driven by scientific inquiry focused on permanent closures, a type of protected area that restricts all fishing indefinitely (Horta e Costa *et al.* 2016). Under management with permanent closures, displaced fishing effort from the protected area can produce negative consequences for fisheries value. In these instances, displaced effort is crowded into the remaining fishing grounds, potentially maintaining high yields (Hastings & Botsford 1999), but at the price of reduced harvest efficiency and thus excess fishing costs (White *et al.* 2008). Alternatively, displaced effort is removed from the system (i.e., fishers exit the fishery), which potentially maintains high harvest efficiency, but at the price of reduced yield compared with what was achievable without permanent closures (Hilborn *et al.* 2004). Thus, while permanent closures certainly have value for overfished fisheries and provide control areas to investigate the impacts of fishing and other anthropogenic effects on fish populations and ecosystems (Ballantine 2014), they may be inappropriate in a well-managed fishery (no overfishing), because the displaced fishing effort they generate can compromise either the economic or food-provisioning value of the fishery, or both.

Although there is strong and growing advocacy among marine conservation groups and scientists worldwide for the implementation of permanent closures (Lubchenco & Grorud-Colvert 2015), such closures are often controversial and can be met with intense opposition (Agardy *et al.* 2003). Alternatively, small-scale fishing communities around the world routinely use periodically harvested closures (hereafter referred to as periodic closures) that receive far less attention (Cohen & Foale 2013). Instead of permanently restricting access to fish stocks, periodic closures provide temporary protection between periods of fishing. Communities throughout the Indo-Pacific have been using periodic closures for centuries to promote occasional and efficient exploitation of fish and invertebrate stocks (Fig. 1; Ayres 1979; Bess 2001; Williams *et al.* 2006; Govan *et al.* 2009; Cohen & Foale 2013). As with permanent closures, periodic closures displace fishing effort and thus may promote fish recovery (Game *et al.* 2009; Kaplan *et al.* 2010). However, this displacement is not permanent and, importantly for the fishery, fish protected during the closure period become less wary of fishing gear (Goetze *et al.* 2017). This behavioural change increases fish catchability and thus harvest efficiency when the closed area is re-opened (Januchowski-Hartley *et al.* 2014). Consequently, periodic closures may be capable of simultaneously supporting high levels of yield, stock abundance, and harvest efficiency – perhaps to a greater extent than attainable by permanent closures or non-spatial fisheries management.

Here we tested the value of periodic closures using a bioeconomic fisheries model that incorporates change in fish behaviour during closed periods. Empirical studies show that periodic closures can increase biomass, abundance, and average size of target species compared with areas always open to fishing (Goetze *et al.* 2018), and that periodic closures can provide an ephemeral boost in harvest efficiency when re-opened to fishing due to changes in fish behaviour during the closure period (Januchowski-Hartley *et al.* 2014; Goetze *et al.* 2017). Modelling research on rotational closures, a related form of management where the closure area is moved iteratively throughout the fishing domain, found that this management strategy is capable of enhancing conservation and sometimes yield, particularly in an overfished system (Myers *et al.* 2000; Hart 2003; Valderrama & Anderson 2009; Plagányi *et al.* 2015).

The above studies focused on a subset of fisheries species – benthic marine invertebrates that are sessile and without changes in wariness to fishing gear (e.g., scallops and sea cucumbers). We take a more general approach in order to cover a broad range of fishery species and fishing conditions. The aims of our bioeconomic model were to: (i) quantify harvest efficiency, yield, and stock abundance under periodic closure management, (ii) identify optimal periodic closure designs (percentage domain in the closure, and its closed-open cycle) for maximizing efficiency, yield and stock, and (iii) compare these optimized levels of efficiency, yield and stock with the maximum levels achievable with permanent closures and non-spatial fisheries management. In our bioeconomic model, we considered a range of life history traits characterizing growth rates and mobility, as well as the potential for a temporary increase in the catchability of fish following their protection, parameterized using empirical data on changes in fish behaviour in periodic closures, permanent closures and areas permanently open to fishing.

Materials and methods

We developed a fish population model coupled with an economic harvest model to simulate periodic closures, permanent closures, and non-spatial fisheries management. The model contained two patches, one of which could be designated as a protected area (periodic or permanent). For non-spatial fisheries management, both patches were open permanently to fishing. The proportional area of the domain represented by the patch that could be closed is c, with the remaining area $(1 - c)$ always open to fishing.

The general model format follows that by White & Costello (2014); the equation of spatial population dynamics in patch i is:

$$x_{i,t+1} = \frac{\sum_{j=1}^{N} D_{ji} A_j e_{j,t}}{A_i}. \qquad \text{eqn 1}$$

The timing is thus: the present stock density in each patch ($x_{j,t}$) grows ($g(x_{j,t})$), and then is harvested ($h_{j,t}$), giving residual (i.e., escaped) stock density ($e_{j,t}$). Following conversion to stock abundance (via multiplication by patch area, A_j), the escaped stock disperses between patches (D_{ji}). The resulting stock abundance is divided by patch area (A_i) to indicate stock density at the beginning of the subsequent time step ($x_{i,t+1}$).

We simulated population growth using a discrete-time logistic population growth function (Schaefer 1957):

$$g(x_{i,t}) = x_{i,t} + r_d x_{i,t}(1 - x_{i,t}/K_i), \qquad \text{eqn 2}$$

where K_i is the carrying capacity and r_d is the discrete population growth rate. We assumed a carrying capacity of $K_i = 1$ unit biomass density without losing generality. Discrete population growth rate is derived from the intrinsic rate of population growth: $r_d = \exp(r) - 1$ (Gotelli 1995). We assumed as a baseline intrinsic rate of population growth $r = 0.3$, which represents fish with moderate resilience (Froese & Pauly 2012), such as those in families Acanthuridae and Labridae (subfamily Scarinae), which are often primary target fishes in Indo-Pacific coral reef systems (Williams *et al.* 2006; Jupiter *et al.* 2012; Abesamis *et al.* 2014). In addition, we examined outcomes for species with low and high intrinsic population growth rates, $r = 0.1$ and 0.5, respectively (Froese & Pauly 2012). Harvest (i.e., yield) is a function of stock density after growth, fishing effort in each patch ($E_{i,t}$), and patch area:

$$h_{i,t} = g(x_{i,t}) f(E_{i,t}) A_i, \qquad \text{eqn 3}$$

where $f(E_{i,t})$ is the fraction of stock harvested and calculated using an exponential survival function:

$$f(E_{i,t}) = 1 - \exp(-E_{i,t} q_{i,t}). \qquad \text{eqn 4}$$

The escaped stock density after harvest is thus

$$e_{i,t} = g(x_{i,t})(1 - f(E_{i,t})). \qquad \text{eqn 5}$$

The catchability coefficient ($q_{i,t}$) is a function of how long the patch had been previously closed to fishing (i.e., never for permanently open patches under all three management scenarios, and 1-10 years for the periodic closure patch, depending on its closed period). We generated a catchability curve using empirical data on the distance reef fish initiated a flight response from simulated spearfishers (flight initiation distance). Data came from studies that measured flight initiation distance for families Acanthuridae and Labridae (subfamily Scarinae) in four Indo-Pacific countries: Papua New Guinea, Vanuatu, Philippines, and Chagos (Table S1; Feary *et al.* 2011; Januchowski-Hartley *et al.* 2015). Flight initiation distance was quantified in periodic closures, permanent closures, and non-spatial management areas (n = 24), and in relation to the length of time the area had been protected from fishing prior to the empirical study (0-39 years). Using the mean and variance in flight initiation distance observed for each family at each site (Table S1), we generated a normal cumulative probability distribution indicating the probability of observing fish initiate flight at a distance less than or equal to a specified distance from the simulated spearfisher. We then evaluated this distribution in relation to the mean effective range required to catch a fish using the type of rifle-style speargun commonly used in the Indo-Pacific (323.75 cm, Januchowski-Hartley *et al.* 2015; for example, see Fig. S1 and Table S1 in Supporting Information). We repeated the evaluation for each of the 24 study sites, then used least squares to fit a Logarithmic curve to the data describing the normal cumulative probability in relation to the number of consecutive years the site had been closed to fishing prior to the empirical study:

$$F_{i,t} = 0.172 * \log(C_{i,t}) + 0.431, \qquad \text{eqn 6}$$

where $F_{i,t}$ is the probability of fish initiating flight at a distance less than the mean effective speargun range, and $C_{i,t}$ is years protected from fishing (Fig. S2).

Given that a fish needs to be within speargun range to be harvested by that gear, we assumed the catchability of fish in patch i during a particular year ($q_{i,t}$) to be a function of $F_{i,t}$. To maintain generality, we set catchability equal to $F_{i,t}$ scaled relative to the level calculated when an area is always open to fishing and thus fish catchability is not enhanced (Fig. S3):

$$q_{i,t} = \frac{F^{\alpha}_{i,t}(C_{i,t})}{F^{\alpha}_{i,t}(C_{i,t} = 0)}, \qquad \text{eqn 7}$$

where the denominator is the probability of fish initiating flight at a distance within speargun range in an area permanently open to fishing. To account for variance in changes in fish wariness to fishing gear in relation to protection period, we examined the sensitivity of our results to a range of catchability curves. To do this we introduced the scalar α to modulate the rate and magnitude of change in fish catchability in relation to years closed (Fig. S3). Thus, the functions in eqn 7 are:

$$F^{\alpha}_{i,t} = \alpha * \beta + 0.431 \qquad \text{eqn 8}$$

where $\beta = 0.172 * \log(C_{i,t})$ and $0 \leq \alpha \leq 1.5$. If $\alpha = 0$, fish catchability is held constant at $q_{i,t} = 1$ regardless of closure period. If $\alpha = 1$, then catchability changes in relation to closure period in accordance with the baseline estimate derived from the empirical studies (i.e., equation 6 and 7). If $\alpha > 1$, then the increase in catchability with closure period is enhanced over that estimated from the empirical studies. In addition to variance in fish behaviour, the scalar α also indirectly accounts for variation in fishing gear, such that $\alpha > 1$, for example, represents a more effective speargun with a longer range. Thus, the scalar helps maintain generality in our model.

Dispersal of stocks between patches was calculated proportional to patch size ("common pool" dispersal), and then modified to reduce dispersal with an enhanced site-fidelity parameter (S), following White & Costello (2014). In the common pool model, dispersal between patches is proportional to the size of each patch:

$$\mathbf{D}^{cp} = \begin{bmatrix} Q_{1,1} & Q_{1,2} \\ Q_{2,1} & Q_{2,2} \end{bmatrix}, \qquad \text{eqn 9}$$

where rows indicate source patches and columns indicate destination patches ($Q_{s,d}$). Each row-column cell represents the fraction of the population that disperses from row patch to column patch. The model system is closed, thus rows sum to 1. For example, we evaluated a case study where 30% of the total management area is protected ($c = 0.3$); in this situation common pool dispersal is:

$$\mathbf{D}^{cp} = \begin{bmatrix} 0.7 & 0.3 \\ 0.7 & 0.3 \end{bmatrix}. \qquad \text{eqn 10}$$

Introduction of site-fidelity parameter S increases the fraction of the population that remains in a given patch (e.g., via self-recruitment and/or territoriality), with a commensurate decrease in cross-patch movement. The dispersal matrix is thus:

$$\mathbf{D} = \begin{bmatrix} Q_{1,1} + (1 - Q_{1,1})S & Q_{1,2} - Q_{1,2}S \\ Q_{2,1} - Q_{2,1}S & Q_{2,2} + (1 - Q_{2,2})S \end{bmatrix}, \qquad \text{eqn 11}$$

where $0 \leq S \leq 1$. If $S = 0$, enhanced site fidelity is removed and dispersal is represented by the common pool model (i.e., equation 9). If $S = 1$, site-fidelity is 100% and no dispersal occurs between the patches (i.e., in the dispersal matrix **D**, diagonal values equal 1 and off-diagonal values equal 0). For the $c = 0.3$ case study, the target species has moderate site-fidelity ($S = 0.2$), making the dispersal matrix:

$$\mathbf{D} = \begin{bmatrix} 0.76 & 0.24 \\ 0.56 & 0.44 \end{bmatrix}. \qquad \text{eqn 12}$$

Thus, 44% of the stock in the periodic closure exhibits self-recruitment (56% spillover to the fished area), and 76% of the stock within the fished area exhibits self-recruitment (24% spillover to the periodic closure) annually.

We tested the value of periodic closure management with an example case study: the periodic closure constitutes 30% of the total management area ($c = 0.3$), and the target species has moderate site-fidelity ($S = 0.2$) and a relatively high population growth rate ($r = 0.3$), which represents fish with moderate resilience, such as those in families Acanthuridae and Labridae (subfamily Scarinae). We also conducted a sensitivity analysis, in which we considered the full factorial combination of values for the proportion of area protected (c = 0–50%), enhanced site-fidelity (S = 0–1) and intrinsic rates of population growth (r = 0.1–0.5). The range of closure size in relation to total area (c = 0–50%) was chosen to be consistent with the proportional sizes of periodic closures used in practice (e.g., in Fiji; Mills *et al.* 2011).

To represent a ‘well-managed’ fishery, fishing effort was optimized in each fishable patch and for each annual time step in the model to achieve maximum sustainable yield (MSY) across the two-patch management area. That is, under non-spatial management a constant effort level was optimized in both patches to achieve MSY, and under management with a permanent closure a constant effort level was optimized in the fishable patch to achieve MSY. Under management with a periodic closure, effort was optimized for each year and patch to achieve MSY, with one patch always open to fishing and the other open periodically in accordance with a prescribed closed-open harvest cycle (here on a yearly time scale). Fishing effort displaced by a periodic closure can shift to the open area, rather than simply being removed from the fishery. In all cases, MSY was measured at model equilibrium, and across the study system (i.e., both patches) and over the complete management cycle (i.e., one year for non-spatial and permanent closure management, and the closed plus open periods for periodic closure management). For periodic closures, we considered a range of harvest cycles, ranging from 1-10 years closed in combination with 1-10 years open. We also assessed the sensitivity of our results to overfishing. In this case, we increased the optimal harvest effort (effort that achieves MSY) in each patch and year by 5 – 65% (referred to as percent overfishing). A moderately low value in this range, 20%, represents the median level of overfishing observed globally, where, under non-spatial management, the stock is reduced to about 75% of the stock in a well-managed fishery (Costello *et al.* 2016). The upper bound of this range, 65%, represents an extreme level of overfishing that, under non-spatial management, reduces the stock to 25% of the stock in a well-managed fishery. This extreme scenario represents about a quarter of the world's fisheries (Costello *et al.* 2012 and references therein).

For each model parameterization analysed (characterized by *c, S, r,* harvest cycle, percent overfishing and management scenario) we recorded fishery yield, harvest efficiency, and stock abundance – the triple objective. We quantified harvest efficiency as catch-per-unit-effort (CPUE) and evaluated equilibrium model results to achieve the fisheries objective of long-term sustainability.

Results

For our case study ($c = 0.3$, $S = 0.2$, $r = 0.3$) under a well-managed fishery we found that regulating the area using a periodic closure with a 1- to 2-year closed period between single, short fishing events enabled the fishery to generate average annual levels of fishery yield and stock abundance equivalent to the highest levels attainable under either permanent closure or non-spatial management (Fig. 2). Additionally, the periodic closure achieved an average annual harvest efficiency 3% greater than what could be achieved by non-spatial management and 9% greater than that achievable by permanent closure management (Fig. 2). This superiority of periodic closures over the other two forms of management held across a range of fish population growth rates (Fig. S4). Without considering change in fish behaviour during closure periods (α =

0), the value of the periodic closure collapsed to the levels achievable by permanent closures and non-spatial management (Fig. S5-S6).

The case study results were robust to all but extreme levels of overfishing. Consideration of moderate overfishing (30% overfishing; fishing effort that achieves maximum sustainable yield for each patch and year, increased by 30%) revealed a trade-off between periodic and permanent closures in their improvement over non-spatial management: the optimal periodic closure harvest cycle (closed for 2 years between short fishing bouts) maximized harvest efficiency, but a permanent closure maximized stock abundance and fishery yield (Fig. 2). Harvest efficiency under periodic closure management was 5% greater than that achieved by permanent closures, and yield and stock abundance were only 1% and 2% less than those by permanent closures, respectively (Fig. 2). Extending the closed period made it more similar to a permanent closure (i.e., harvest efficiency decreased and stock abundance and yield increased), but even with a lengthy closed period (10 years), harvest efficiency remained proportionally greater (2%) than the loss in yield and stock abundance (< 1%), compared with values generated by permanent closure management (Fig. 2). In contrast, with extreme overfishing (65% overfishing), the advantages of harvest efficiency for periodic closures eroded and permanent closures became optimal for achieving the triple objective (Fig. 2). In this case, harvest efficiency was equivalent for permanent and periodic closures (with a 10-year closed period and 1-year open period), but yield and stock were each 2% greater for permanent closures (Fig. 2).

We examined the sensitivity of our results to relative size of the closure (c = 0 to 50% of the total management area, consistent with periodic closures in practice; Fig. 3; Mills *et al.* 2011) and site-fidelity of target fishery species (S = 0 to 1, representing the full range of movement patterns, from "common pool" dispersal to sedentary; Fig. 3 and S7). For each combination of c and S, we identified the closed-open harvest cycle that maximized yield, and if more than one combination maximized yield, we selected the harvest cycle that maximized harvest efficiency. For a well-managed fishery (no overfishing), we found the optimal periodic closure to have closed periods ranging from 1 year (typical result) to at most 4 years (only for very small periodic closures, $c \leq 5\%$, and fisheries targeting sedentary species, $S = 1$), between 1-year pulse harvest events. Among these optimal periodic closure designs, all generated an average annual harvest efficiency exceeding that achievable by non-spatial or permanent closure management (Fig. 3), concurrent with average annual yield and stock abundance levels equivalent with the highest levels achievable by non-spatial management (Fig. S7). Harvest efficiency under periodic closure management increased as site-fidelity of the target species increased.

Similar to the case study, results from the sensitivity analysis were relatively unchanged with consideration of overfishing, up to a point. Consideration of moderate overfishing (e.g., 30% overfishing) did not change the range of optimal closed-open harvest cycles that maximized yield (1-4 years closed and 1-year open), but now 4-year closures were not limited to only very small closures targeting sedentary species. In general, the optimal closure period increased with decrease in the size of the closure. Also, across all closure sizes and levels of fish site-fidelity, management with periodic closures again generated greater harvest efficiency than management with permanent closures or non-spatial management, despite harvest efficiency decreasing with decreasing site-fidelity. As with the case study, there was a tradeoff between periodic closures, which maximized harvest efficiency (Fig. 3), and permanent closures, which maximized yield and stock abundance (Fig. S7). For fisheries targeting fish with low to moderate site-fidelity ($S \leq 0.4$), management with permanent closures occupying a moderate to large proportion of the management area ($c \geq 0.25$) generated higher average annual yield compared with that attainable by periodic closures (Fig. S7). However, for a given set of S and c values, the percentage gain in yield over periodic closures was always less than the percentage loss in harvest efficiency. With more sedentary target species ($S \geq 0.6$), spillover of fish from the permanent closure to the open area is limited, enabling for less yield than attainable under periodic closures (Fig. S7), causing the tradeoff to dissolve in favour of periodic closure management. In regard to stock abundance, its tradeoff with harvest efficiency was balanced between periodic and permanent closure management for fisheries targeting species with low to moderate site-fidelity ($S \leq 0.2$), and unbalanced, for the only time in our analysis given moderate overfishing, in favour of permanent closures for species with higher site-fidelity ($S > 0.2$; Fig. S7) due to the high conservation value for stock abundance generated by permanent closures.

In the case of extreme overfishing (65% overfishing), permanent closures achieved equal or greater harvest efficiency than periodic closures, along with greater yield and stock abundance (Fig. 3 and S7). Periodic closures were superior at balancing the triple objective when overfishing was < 55%, which under nonspatial management would reduce the stock to 37% of its level at MSY and 18% of its unfished level (Fig. 4). At 55% overfishing and greater, permanent closures were able to simultaneously maximize yield, stock abundance and harvest efficiency (Fig. 4).

Discussion

We show that management with periodic closures can simultaneously achieve high yield, high harvest efficiency, and high stock abundance, and that using periodic closures could enable fisheries management to perform better in achieving this triple objective than management with permanent closures or non-spatial management. In well-managed fisheries, optimal periodic closures achieved equivalence in maximum yield and stock abundance, while providing enhanced harvest efficiency, compared with permanent closures and non-spatial management. This superiority of periodic closures emerges due to reduction in fish wariness of fishing gear during the closure period, which fishers exploit to increase harvest efficiency upon the closure's re-opening.

Empirical studies have found greater harvest efficiency (catch-per-unit-effort) inside periodic closures upon their re-opening compared with areas always open to fishing (Januchowski-Hartley *et al.* 2014; Goetze *et al.* 2017). Our theory-based analysis extends the implications of the empirical results by showing that periodic closure management is capable of enhancing average harvest efficiency measured across the entire fishing domain and harvest schedule. We also quantify the strength of this effect size in relation to its underlying mechanism – the level of change in fish wariness to fishing gear following temporary protection.

Modelling studies suggest that rotational closures can enhance yield compared with non-rotational fisheries management, particularly when overfishing occurs (Myers *et al.* 2000; Hart 2003; Plagányi *et al.* 2015). Our results support these findings, as we found that periodic closures with long closure periods (10 years) between 1-year open periods were capable of generating greater yield than non-spatial management, even when overfishing was high (> 30% overfishing). If age-structure was integrated into our model, it is possible that periodic closures would enhance yield more by protecting larger individuals during closure periods that are exploited upon re-opening. Similarly, consideration of age-structure and thus protection of larger individuals might also generate conservation of greater average annual stock biomass with periodic closures, as indicated empirically (Cinner *et al.* 2005; Bartlett *et al.* 2009) and with modelling (Myers *et al.* 2000; Hart 2003; Game *et al.* 2009).

While we show periodic closures to excel in achieving the triple objective when fishers behave rationally and optimize effort for maximizing yield, excessive fishing effort and overharvesting is a common problem worldwide (Costello *et al.* 2012), including in some communities that use periodic closures (e.g., on Kia Island, Fiji; Jupiter *et al.* 2012, 2017). With consideration of moderate overfishing in our case study scenario, we found a tradeoff in performance between periodic closures, which maximize harvest efficiency, and permanent closures, which maximize yield and stock abundance. In most of our evaluations for moderate levels of overfishing, the proportional gain in harvest efficiency from management with a periodic closure over that with a permanent closure was greater than the proportional loss in yield and stock abundance, indicating the tradeoff to be biased in favour of periodic closures. This bias also was robust to the length of closure period (up to 10 years). When moderate overfishing was considered in our sensitivity analysis, we saw the same tradeoff as in the case-study above. For fisheries targeting fish with low to moderate site-fidelity ($S \leq 0.4$), which include common target species throughout the Indo-Pacific (Meyer *et al.* 2010; Jupiter *et al.* 2012; Abesamis *et al.* 2014), management with permanent closures occupying a moderate to large proportion of the management area ($c \geq 0.25$) generated higher average annual yield compared with that attainable by periodic closures (Fig. S7). However, the percentage gain in yield by permanent closures was always less than the loss in harvest efficiency (Fig. 3 and S7). If fishers target more sedentary species, then spillover of fish from a permanent closure to an open area is limited, thus generating less yield than attainable under periodic closures, causing the tradeoff to dissolve in favour of periodic closure management (Fig. S7). In regard to stock abundance, its tradeoff with harvest efficiency was balanced between periodic and permanent closure management for fisheries targeting species with low to moderate site-fidelity ($S \leq 0.2$), and unbalanced in favour of permanent closures for species with higher site-fidelity ($S > 0.2$; Fig. S7). The above sensitivity analysis results held true for species with high and low resilience to fishing (Fig. S8-S10). When overfishing was increased to ≥ 55%, which under nonspatial management would reduce stock abundance to ≤ 37% of its level at MSY (and ≤ 18% of its unfished level), the above trade-offs between periodic and permanent closures faded, and instead permanent closures maximized yield, stock and harvest efficiency. Approximately < 25% of global fisheries fall within this extreme range of overfishing (Costello *et al.* 2016). Our conclusions of trade-offs between periodic and permanent closures assumed that managers care equally about yield, stock and harvest efficiency. However, managers may value one outcome more than others, and thus draw different qualitative conclusions from the trade-offs.

Periodic closures used in practice vary in size, but are typically less than a quarter of the total management area (Fig. 4b; Mills *et al.* 2011; Cohen & Foale 2013). Our results suggest that many periodic closures used in practice may experience greater benefits through enhanced yield, stock and harvest efficiency if the closure area were to be expanded, perhaps to 50% of the total fishing area (Fig. 3 and S7). A recent comprehensive meta-analysis on periodic closures corroborates our finding and suggests increasing the size of periodic closures, and extending closure periods, for the purpose of long-term fisheries benefits and increasing fish stocks within closures (Goetze *et al.* 2018). Also, as the level of overfishing increases, the benefits of larger closures increases (Figs. 3, 4 and S7).

We used available data on fish flight initiation distance to model changes in fish behaviour (Table S1; Feary *et al.* 2011; Januchowski-Hartley *et al.* 2015). Although these data focus on the flight response of fish when approached by a simulated spearfisher, other studies have documented changes in fish behaviour and catchability for other gear types as well (Alós *et al.* 2015; Goetze *et al.* 2017). For example, target species in periodic closures where a drive-in gillnet was the predominant fishing gear displayed significant changes in wariness during closed periods, which was correlated with enhanced harvest efficiency when the closure was opened (Goetze *et al.* 2017). In addition, in the Mediterranean increased avoidance of hook and line fishing gear by the painted comber (*Serranus scriba*) was correlated with recreational fishing pressure (Alós *et al.* 2015). However, another species in the Mediterranean did not display a significant change in gear avoidance (Alós *et al.* 2015). Change in fish behaviour may be species- or family-dependent; more research on the rate and magnitude of behavioural change across taxa will provide valuable insight for the design and implications of periodic closures, which aim to exploit this trait.

We demonstrate that periodic closures can be more, or at least equally, effective compared with permanent closures for fisheries that are well-managed to moderately overfished. We also show that the benefits of periodic closures dissolves when overfishing is extreme. These results may explain the range of effectiveness of periodic closures used in practice (Cinner *et al.* 2005; Jupiter *et al.* 2012). Communities often harvest periodic closures too frequently or exceed harvest targets, or both (Goetze *et al.* 2018), and thus the successful management of periodic closures depends on enforcement of appropriate harvest targets (within periodic closures and surrounding management areas) and harvest cycles, and consistent monitoring of fish populations.

This study demonstrates the enhanced value of periodic closures over conventional management in achieving fisheries productivity (yield), efficiency (catch-per-unit-effort), and fish conservation (stock abundance) objectives. We also demonstrate that periodic closures can, in most cases, be superior at balancing these objectives in a fishery with excessive fishing pressure. Evaluation of this balance between the three objectives in relation to socioeconomic priorities among yield, harvest efficiency and stock abundance – within and outside the Indo-Pacific – would provide additional insight on the utility of periodic closures for meeting ecosystem-based fisheries management goals. Our findings challenge the dogma that periodic closures are simply a cultural legacy that are only valuable within the Indo-Pacific and with limited outcomes, and instead suggest that they may be an optimal fisheries management strategy with broad utility.

Authors' contributions

PC and CW designed and analysed the models with input from other authors; SJ, RW and FJH provided data for bioeconomic model; PC and CW wrote the first draft of the paper and all authors contributed substantially to revisions.

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Data accessibility

Data and code available via the Dryad Digital Repository https://doi.org/10.5061/dryad.h7g27vc (Carvalho, Jupiter, Januchowski-Hartley, Goetze, Claudet, Weeks, *et al.*, 2019).

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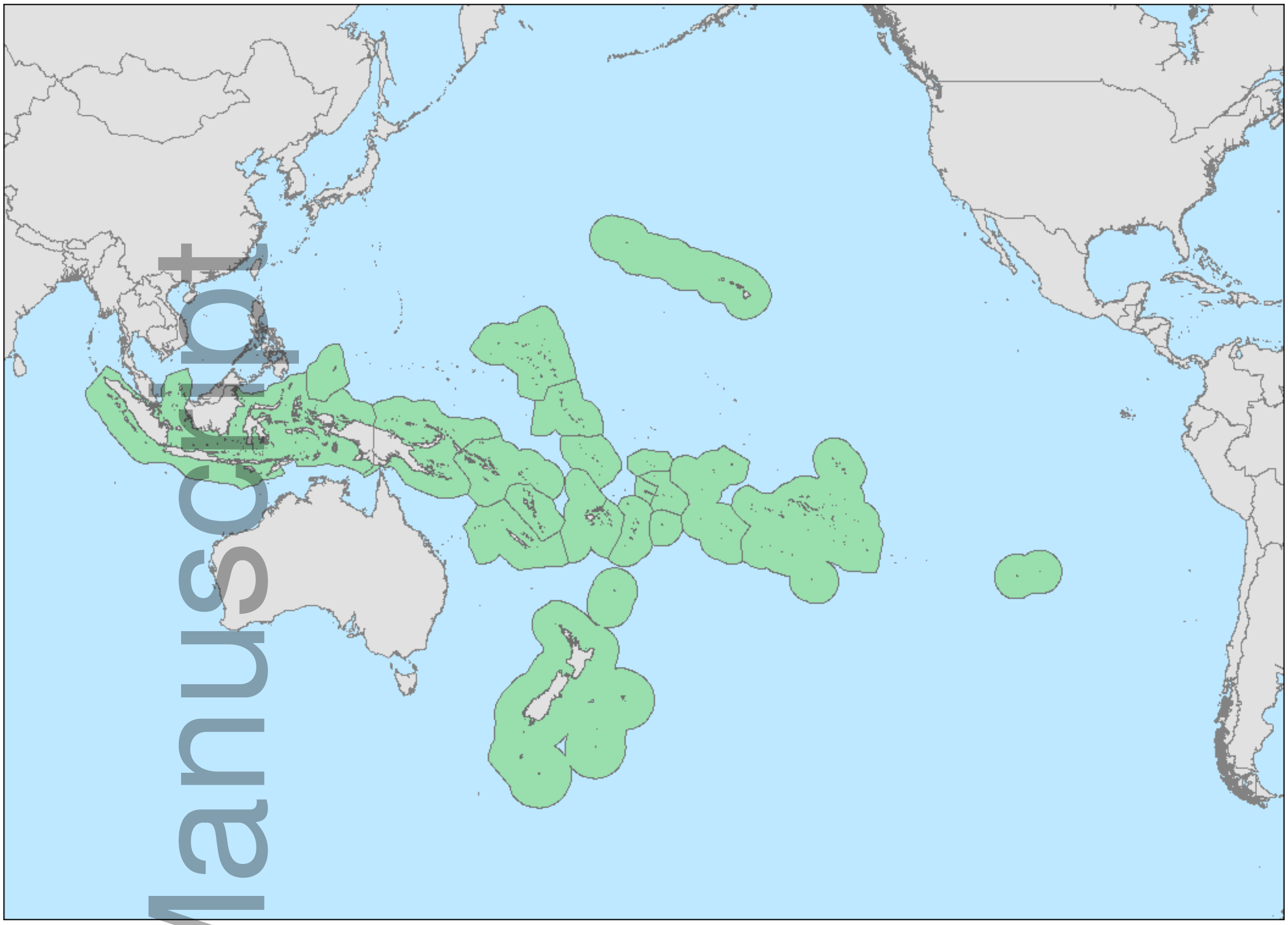
Figure 1: Map of the Exclusive Economic Zones (*green*) of regions that practice periodic closures for marine resource management. Locations identified from a comprehensive literature search (Ayres 1979; Bess 2001; Williams *et al.* 2006; Govan *et al.* 2009; Cohen & Foale 2013).

Figure 2: Average annual yield, stock abundance, and harvest efficiency (catch-per-unit-effort [CPUE]) under non-spatial, permanent closure, and periodic closure management. Black, filled markers indicate optimal periodic closure designs for 0% (1 year closed, 1 year open), 30% (2 years closed, 1 year open), and 65% overfishing (10 years closed, 1 year open). Gray markers indicate outcomes for the full range of closed-open harvest cycles (all combinations of 1, 2, 3 … 10 years each). $S = 0.2$; $r = 0.3$; $c = 0.3$ (for permanent and periodic closures).

Figure 3: Average annual harvest efficiency (catch-per-unit-effort [CPUE]) for a range of relative closure sizes (a) and relative periodic closure sizes in practice (b). (a) CPUE in relation to size of the closure ($c = 0$ to 50% of the total management area), where 1 equals the outcome under non-spatial management in a well-managed system. Values for CPUE are with consideration of fish site-fidelity ($0 \leq S \leq 1$, *shading*). (b) Frequency distribution of periodic closure sizes used in practice in Fiji (Mills *et al.* 2011).

Figure 4: Yield, stock and harvest efficiency (CPUE) in relation to percent overfishing. All values are relative to the outcome under well-managed non-spatial management (horizontal dashed line). Shading represents the range of outcomes for different levels of fish site-fidelity ($S = 0 – 1$) and proportion of total management area within closure ($c = 0 – 50\%$). The solid lines indicate means of the range of values for all combinations of S and c. The vertical dashed line indicates the range of overfishing (0 – 55%) within which periodic closures were, on average, superior over the other forms of management strategies at balancing the triple objective of high harvest efficiency, high fisheries yield, and high stock abundance.



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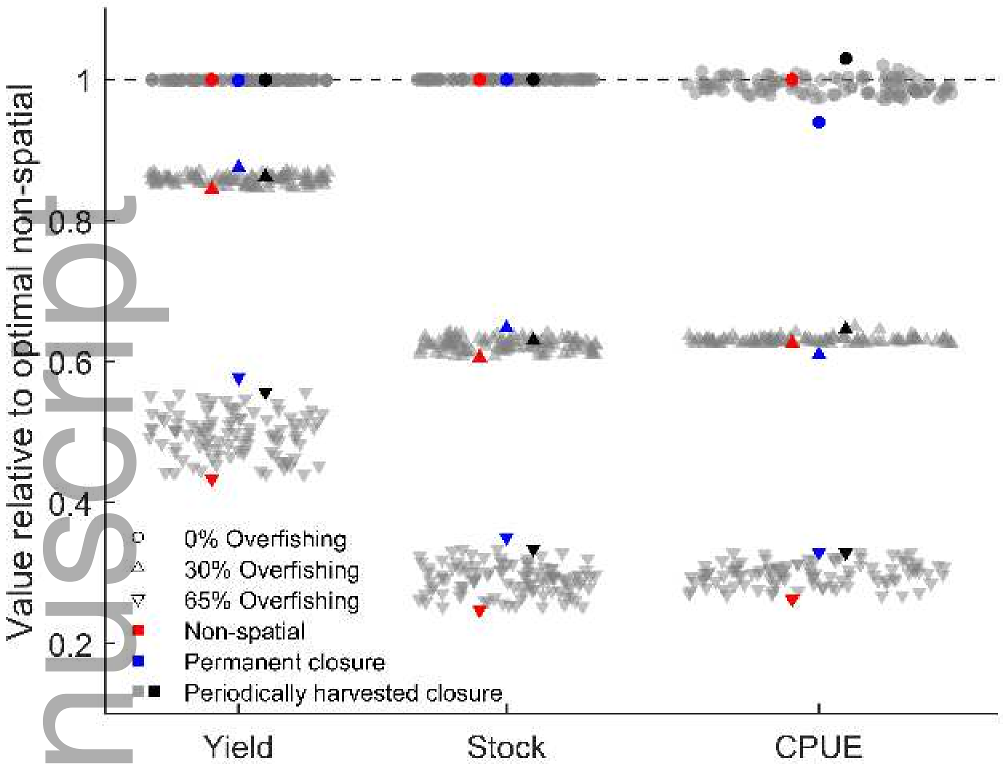

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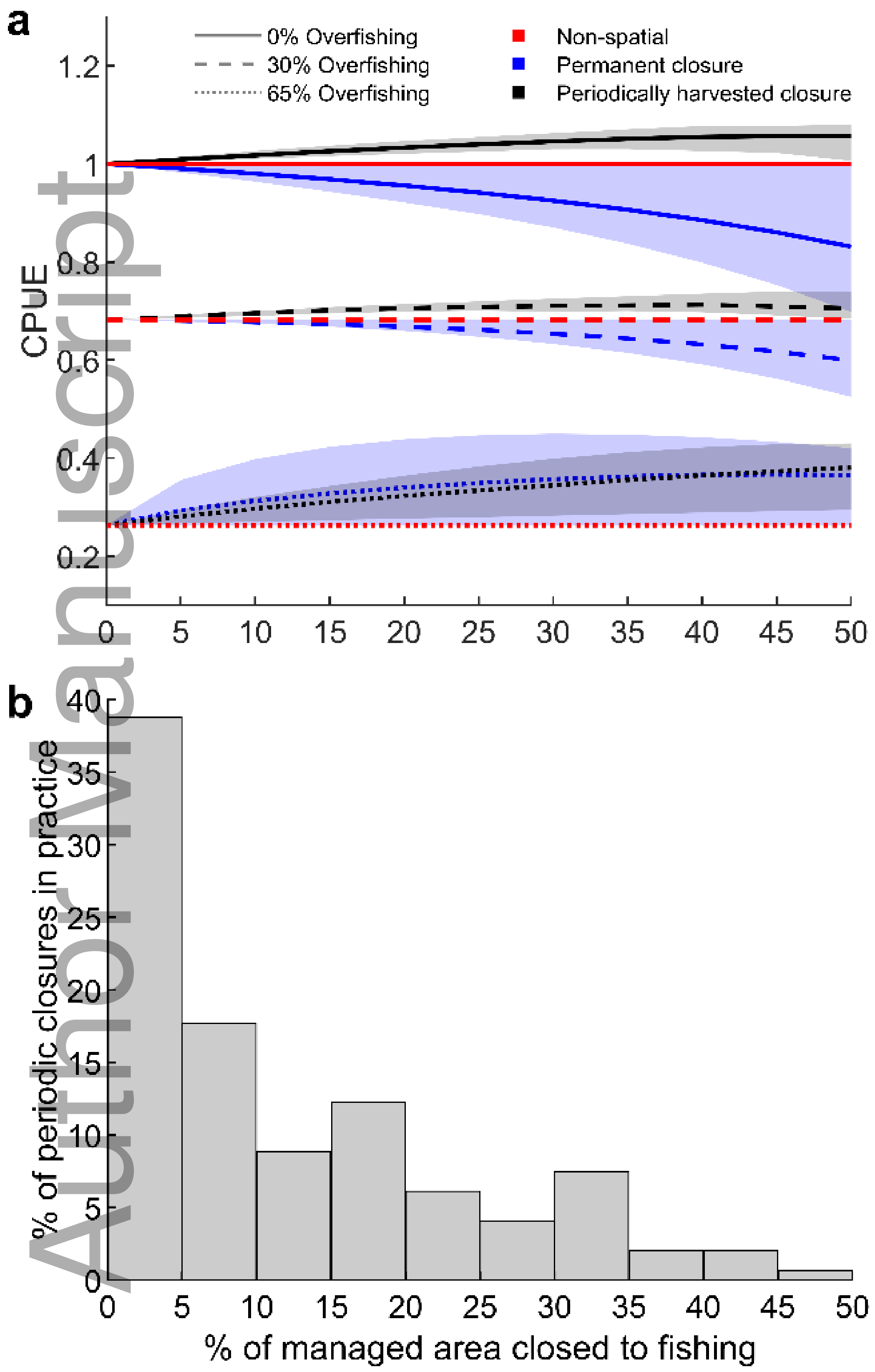

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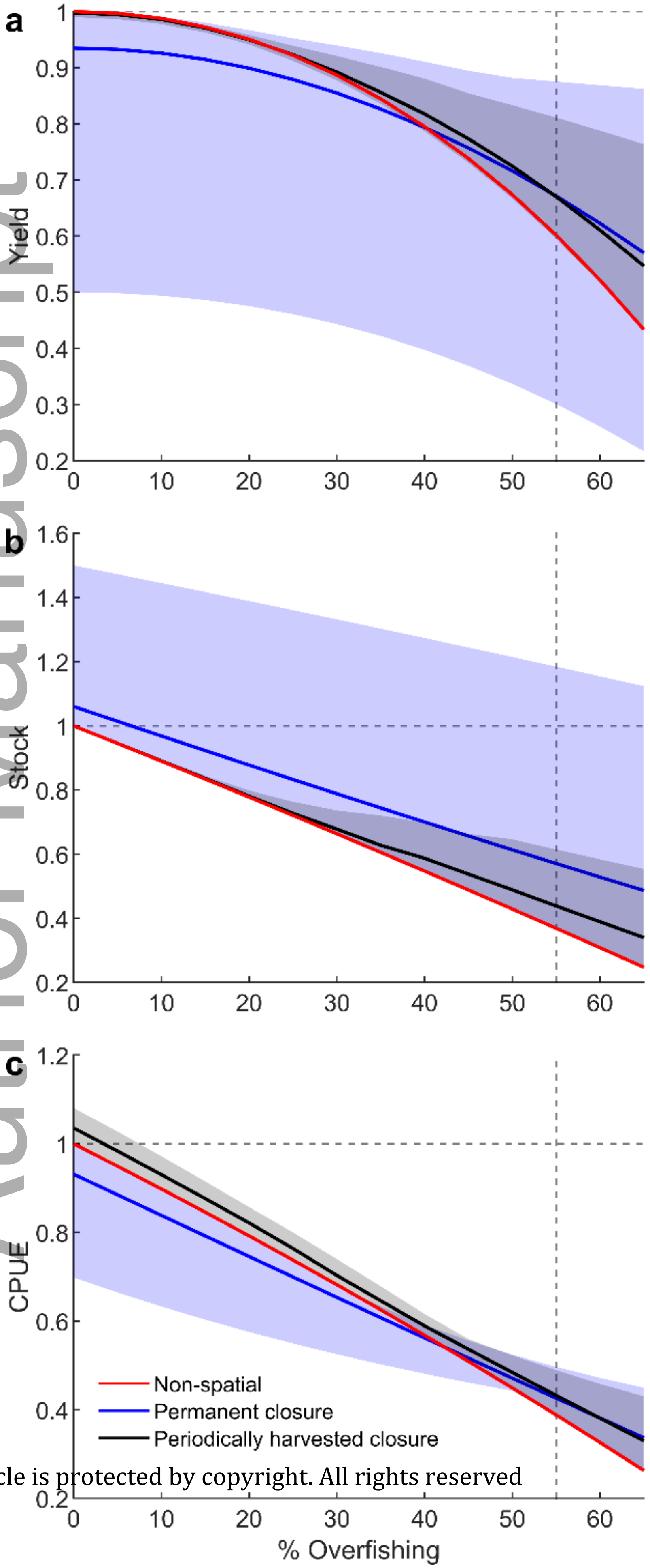
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Stock
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0.8
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CPUE
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% Overfishing
Non-spatial
Permanent closure
Periodically harvested closure