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Paper:

Carvalho, P., Jupiter, S., JanuchowskiHartley, F., Goetze, J., Claudet, J., Weeks, R., Humphries, A. & White, C. (2019). Optimized fishing through periodically harvested closures. *Journal of Applied Ecology*

<http://dx.doi.org/10.1111/1365-2664.13417>

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1 **Optimized fishing through periodically harvested closures**

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25 **Summary**

- 26 1. Periodically harvested closures are a widespread, centuries-old form of fisheries management
27 that protects fish between pulse harvests and can generate high harvest efficiency by reducing
28 fish wariness of fishing gear. However, the ability for periodic closures to also support high
29 fisheries yields and healthy marine ecosystems is uncertain, despite increased promotion of
30 periodic closures for managing fisheries and conserving ecosystems in the Indo-Pacific.
- 31 2. We developed a bioeconomic fisheries model that considers changes in fish wariness, based
32 on empirical field research, and quantified the extent to which periodic closures can
33 simultaneously maximize harvest efficiency, fisheries yield, and conservation of fish stocks.
- 34 3. We found that periodic closures with a harvest schedule represented by closure for one to a
35 few years between a single pulse harvest event can generate equivalent fisheries yield and stock
36 abundance levels and greater harvest efficiency than achievable under conventional fisheries
37 management with or without a permanent closure.
- 38 4. Optimality of periodic closures at maximizing the triple objective of high harvest efficiency,
39 high fisheries yield, and high stock abundance was robust to fish life history traits and to all
40 but extreme levels of overfishing. With moderate overfishing, there emerged a trade-off
41 between periodic closures that maximized harvest efficiency and no-take permanent closures
42 that maximized yield; however, the gain in harvest efficiency outweighed the loss in yield for
43 periodic closures when compared with permanent closures. Only with extreme overfishing,
44 where fishing under nonspatial management would reduce the stock to $\leq 18\%$ of its unfished
45 level, was the harvest efficiency benefit too small for periodic closures to best meet the triple
46 objective compared with permanent closures. ~~In addition, with overfishing the optimal harvest~~

~~cycle of periodic closures shifted to include longer closure periods between single pulse harvest events.~~

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 non-spatial 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: Fisheries Management, Bioeconomic Model, Marine Protected Areas, Conservation, Fish Behavior, 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

69 maintains high harvest efficiency, but at the price of reduced yield compared with what was
70 achievable without permanent closures (Hilborn *et al.* 2004). Thus, while permanent closures
71 certainly have value for overfished fisheries and provide control areas to investigate the impacts
72 of fishing and other anthropogenic effects on fish populations and ecosystems (Ballantine 2014),
73 they may be inappropriate in a well-managed fishery (no overfishing), because the displaced
74 fishing effort they generate can compromise either the economic or food-provisioning value of the
75 fishery, or both.

76 Although there is strong and growing advocacy among marine conservation groups and
77 scientists worldwide for the implementation of permanent closures (Lubchenco & Grorud-Colvert
78 2015), such closures are often controversial and can be met with intense opposition (Agardy *et al.*
79 2003). Alternatively, small-scale fishing communities around the world routinely use periodically
80 harvested closures (hereafter referred to as periodic closures) that receive far less attention (Cohen
81 & Foale 2013). Instead of permanently restricting access to fish stocks, periodic closures provide
82 temporary protection between periods of fishing. Communities throughout the Indo-Pacific have
83 been using periodic closures for centuries to promote occasional and efficient exploitation of fish
84 and invertebrate stocks (Fig. 1; Ayres 1979; Bess 2001; Williams *et al.* 2006; Govan *et al.* 2009;
85 Cohen & Foale 2013). As with permanent closures, periodic closures displace fishing effort and
86 thus may promote fish recovery (Game *et al.* 2009; Kaplan *et al.* 2010). However, this
87 displacement is not permanent and, importantly for the fishery, fish protected during the closure
88 period become less wary of fishing gear (Goetze *et al.* 2017). This behavioral change increases
89 fish catchability and thus harvest efficiency when the closed area is re-opened (Januchowski-
90 Hartley *et al.* 2014). Consequently, periodic closures may be capable of simultaneously supporting

91 high levels of yield, stock abundance, and harvest efficiency – perhaps to a greater extent than
92 attainable by permanent closures or non-spatial fisheries management.

93 Here we tested the value of periodic closures using a bioeconomic fisheries model that
94 incorporates change in fish behavior during closed periods. Empirical studies show that periodic
95 closures can increase biomass, abundance, and average size of target species compared with areas
96 always open to fishing (Goetze *et al.* 2018), and that periodic closures can provide an ephemeral
97 boost in harvest efficiency when re-opened to fishing due to changes in fish behavior during the
98 closure period (Januchowski-Hartley *et al.* 2014; Goetze *et al.* 2017). Modeling research on
99 rotational closures, a related form of management where the closure area is moved iteratively
100 throughout the fishing domain, found that this management strategy is capable of enhancing
101 conservation and sometimes yield, particularly in an overfished system (Myers *et al.* 2000; Hart
102 2003; Valderrama & Anderson 2009; Plagányi *et al.* 2015).

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

113 protection, parameterized using empirical data on changes in fish behavior in periodic closures,
114 permanent closures and areas permanently open to fishing.

115 **Materials and methods**

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

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

$$124 \quad x_{i,t+1} = \frac{\sum_{j=1}^N D_{ji} A_j e_{j,t}}{A_i}. \quad \text{eqn 1}$$

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

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

$$132 \quad g(x_{i,t}) = x_{i,t} + r_d x_{i,t} \left(1 - x_{i,t} / K_i\right), \quad \text{eqn 2}$$

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

$$143 \quad h_{i,t} = g(x_{i,t})f(E_{i,t})A_i, \quad \text{eqn 3}$$

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

$$146 \quad f(E_{i,t}) = 1 - \exp(-E_{i,t}q_{i,t}). \quad \text{eqn 4}$$

147 The escaped stock density after harvest is thus

$$148 \quad e_{i,t} = g(x_{i,t})(1 - f(E_{i,t})). \quad \text{eqn 5}$$

149 The catchability coefficient ($q_{i,t}$) is a function of how long the patch had been previously
 150 closed to fishing (i.e., never for permanently open patches under all three management scenarios,
 151 and 1-10 years for the periodic closure patch, depending on its closed period). We generated a
 152 catchability curve using empirical data on the distance reef fish initiated a flight response from
 153 simulated spearfishers (flight initiation distance). Data came from studies that measured flight
 154 initiation distance for families Acanthuridae and Labridae (subfamily Scarinae) in four Indo-
 155 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). 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:

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

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):

$$q_{i,t} = \frac{F_{i,t}^{\alpha}(C_{i,t})}{F_{i,t}^{\alpha}(C_{i,t}=0)}, \quad \text{eqn 7}$$

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

179 of catchability curves. To do this we introduced the scalar α to modulate the rate and magnitude
 180 of change in fish catchability in relation to years closed (Fig. S3). Thus, the functions in eqn 7 are:

$$181 \quad F_{i,t}^{\alpha} = \alpha * \beta + 0.431 \quad \text{eqn 8}$$

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

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

$$193 \quad \mathbf{D}^{cp} = \begin{bmatrix} Q_{1,1} & Q_{1,2} \\ Q_{2,1} & Q_{2,2} \end{bmatrix}, \quad \text{eqn 9}$$

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

$$199 \quad \mathbf{D}^{cp} = \begin{bmatrix} 0.7 & 0.3 \\ 0.7 & 0.3 \end{bmatrix}. \quad \text{eqn 10}$$

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

$$203 \quad \mathbf{D} = \begin{bmatrix} Q_{1,1} + (1 - Q_{1,1})S & Q_{1,2} - Q_{1,2}S \\ Q_{2,1} - Q_{2,1}S & Q_{2,2} + (1 - Q_{2,2})S \end{bmatrix}, \quad \text{eqn 11}$$

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

$$209 \quad \mathbf{D} = \begin{bmatrix} 0.76 & 0.24 \\ 0.56 & 0.44 \end{bmatrix}. \quad \text{eqn 12}$$

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

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

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

243 For each model parameterization analyzed (characterized by c , S , r , harvest cycle, level of
244 overfishing and management scenario) we recorded fishery yield, harvest efficiency, and stock

245 abundance – the triple objective. We quantified harvest efficiency as catch-per-unit-effort (CPUE)
246 and evaluated equilibrium model results to achieve the fisheries objective of long-term
247 sustainability.

248 **Results**

249 For our case study ($c = 0.3$, $S = 0.2$, $r = 0.3$) under a well-managed fishery we found that
250 regulating the area using a periodic closure with a 1- to 2-year closed period between single, short
251 fishing events enabled the fishery to generate average annual levels of fishery yield and stock
252 abundance equivalent to the highest levels attainable under either permanent closure or non-spatial
253 management (Fig. 2). Additionally, the periodic closure achieved an average annual harvest
254 efficiency 3% greater than what could be achieved by non-spatial management and 9% greater
255 than that achievable by permanent closure management (Fig. 2). This superiority of periodic
256 closures over the other two forms of management held across a range of fish population growth
257 rates (Fig. S4). Without considering change in fish behavior during closure periods ($\alpha = 0$), the
258 value of the periodic closure collapsed to the levels achievable by permanent closures and non-
259 spatial management (Fig. S5-S6).

260 The case study results were robust to all but extreme levels of overfishing. Consideration
261 of moderate overfishing (30% ~~increased effort from effort in a well-managed system~~overfishing:
262 fishing effort that achieves maximum sustainable yield for each patch and year, increased by 30%)
263 revealed a trade-off between periodic and permanent closures in their improvement over non-
264 spatial management: the optimal periodic closure harvest cycle (closed for 2 years between short
265 fishing bouts) maximized harvest efficiency, but a permanent closure maximized stock abundance
266 and fishery yield (Fig. 2). Harvest efficiency under periodic closure management was 5% greater
267 than that achieved by permanent closures, and yield and stock abundance were only 1% and 2%

268 less than those by permanent closures, respectively (Fig. 2). Extending the closed period made it
269 more similar to a permanent closure (i.e., harvest efficiency decreased and stock abundance and
270 yield increased), but even with a lengthy closed period (10 years), harvest efficiency remained
271 proportionally greater (2%) than the loss in yield and stock abundance (< 1%), compared with
272 values generated by permanent closure management (Fig. 2). In contrast, with extreme overfishing
273 (65% ~~increased effort~~overfishing), the advantages of harvest efficiency for periodic closures
274 eroded and permanent closures became optimal for achieving the triple objective (Fig. 2). In this
275 case, harvest efficiency was equivalent for permanent and periodic closures (with a 10-year closed
276 period and 1-year open period), but yield and stock were each 2% greater for permanent closures
277 (Fig. 2).

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

290 achievable by non-spatial management (Fig. S7). Harvest efficiency under periodic closure
291 management increased as site-fidelity of the target species increased.

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

313 of permanent closures for species with higher site-fidelity ($S > 0.2$; Fig. S7) due to the high
314 conservation value for stock abundance generated by permanent closures.

315 In the case of extreme overfishing (65% ~~increased effort~~ overfishing), permanent closures
316 achieved equal or greater harvest efficiency than periodic closures, along with greater yield and
317 stock abundance (Fig. 3 and S7). Periodic closures were superior at balancing the triple objective
318 when overfishing was ~~less than 35%~~ < 55%, which under nonspatial management would reduce the
319 stock to 37% of its level at MSY and 18% of its unfished level (Fig. 4). At 55% overfishing and
320 greater, permanent closures were able to simultaneously maximize yield, stock abundance and
321 harvest efficiency (Fig. 4). ~~When overfishing surpassed 35%, permanent closures were able to~~
322 ~~attain equivalent harvest efficiency and greater yield and stock abundance than periodic closures~~
323 ~~(Fig. 4).~~

324 Discussion

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

334 Empirical studies have found greater harvest efficiency (catch-per-unit-effort) inside
335 periodic closures upon their re-opening compared with areas always open to fishing (Januchowski-

336 Hartley *et al.* 2014; Goetze *et al.* 2017). Our theory-based analysis extends the implications of the
337 empirical results by showing that periodic closure management is capable of enhancing average
338 harvest efficiency measured across the entire fishing domain and harvest schedule. We also
339 quantify the strength of this effect size in relation to its underlying mechanism – the level of change
340 in fish wariness to fishing gear following temporary protection.

341 Modeling studies suggest that rotational closures can enhance yield compared with non-
342 rotational fisheries management, particularly when overfishing occurs (Myers *et al.* 2000; Hart
343 2003; Plagányi *et al.* 2015). Our results support these findings, as we found that periodic closures
344 with long closure periods (10 years) between 1-year open periods were capable of generating
345 greater yield than non-spatial management, even when overfishing was high ($> 30\%$ overfishing).
346 If age-structure was integrated into our model, it is possible that periodic closures would enhance
347 yield more by protecting larger individuals during closure periods that are exploited upon re-
348 opening. Similarly, consideration of age-structure and thus protection of larger individuals might
349 also generate conservation of greater average annual stock biomass with periodic closures, as
350 indicated empirically (Cinner *et al.* 2005; Bartlett *et al.* 2009) and with modeling (Myers *et al.*
351 2000; Hart 2003; Game *et al.* 2009).

352 While we show periodic closures to excel in achieving the triple objective when fishers
353 behave rationally and optimize effort for maximizing yield, excessive fishing effort and
354 overharvesting is a common problem worldwide (Costello *et al.* 2012), including in some
355 communities that use periodic closures (e.g., on Kia Island, Fiji; Jupiter *et al.* 2012, 2017). With
356 consideration of moderate overfishing in our case study scenario, we found a tradeoff in
357 performance between periodic closures, which maximize harvest efficiency, and permanent
358 closures, which maximize yield and stock abundance. In most of our evaluations for moderate

359 levels of overfishing, the proportional gain in harvest efficiency from management with a periodic
360 closure over that with a permanent closure was greater than the proportional loss in yield and stock
361 abundance, indicating the tradeoff to be biased in favor of periodic closures. This bias also was
362 robust to the length of closure period (up to 10 years). When moderate overfishing was considered
363 in our sensitivity analysis, we saw the same tradeoff as in the case-study above. For fisheries
364 targeting fish with low to moderate site-fidelity ($S \leq 0.4$), which include common target species
365 throughout the Indo-Pacific (Meyer *et al.* 2010; Jupiter *et al.* 2012; Abesamis *et al.* 2014),
366 management with permanent closures occupying a moderate to large proportion of the
367 management area ($c \geq 0.25$) generated higher average annual yield compared with that attainable
368 by periodic closures (Fig. S7). However, the percentage gain in yield by permanent closures was
369 always less than the loss in harvest efficiency (Fig. 3 and S7). If fishers target more sedentary
370 species, then spillover of fish from a permanent closure to an open area is limited, thus generating
371 less yield than attainable under periodic closures, causing the tradeoff to dissolve in favor of
372 periodic closure management (Fig. S7). In regard to stock abundance, its tradeoff with harvest
373 efficiency was balanced between periodic and permanent closure management for fisheries
374 targeting species with low to moderate site-fidelity ($S \leq 0.2$), and unbalanced in favor of permanent
375 closures for species with higher site-fidelity ($S > 0.2$; Fig. S7). The above sensitivity analysis
376 results held true for species with high and low resilience to fishing (Fig. S8-S10). When
377 overfishing was increased ~~(beyond 35 to $\geq 55\%$ increase in fishing effort from effort under a well-~~
378 ~~managed fishery, which under nonspatial management would reduce stock abundance to $\leq 37\%$ of~~
379 ~~its level at MSY (and $\leq 18\%$ of its unfished level),~~ the above trade-offs between periodic and
380 permanent closures faded, and instead permanent closures maximized yield, stock and harvest
381 efficiency. Approximately $< 25\%$ of global fisheries fall within this extreme range of overfishing

382 [\(Costello *et al.* 2016\)](#). Our conclusions of trade-offs between periodic and permanent closures
383 assumed that managers care equally about yield, stock and harvest efficiency. However, managers
384 may value one outcome more than others, and thus draw different qualitative conclusions from the
385 trade-offs.

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

395 We used available data on fish flight initiation distance to model changes in fish behavior
396 (Table S1; Feary *et al.* 2011; Januchowski-Hartley *et al.* 2015). Although these data focus on the
397 flight response of fish when approached by a simulated spearfisher, other studies have documented
398 changes in fish behavior and catchability for other gear types as well (Alós *et al.* 2015; Goetze *et*
399 *al.* 2017). For example, target species in periodic closures where a drive-in gillnet was the
400 predominant fishing gear displayed significant changes in wariness during closed periods, which
401 was correlated with enhanced harvest efficiency when the closure was opened (Goetze *et al.* 2017).
402 In addition, in the Mediterranean increased avoidance of hook and line fishing gear by the painted
403 comber (*Serranus scriba*) was correlated with recreational fishing pressure (Alós *et al.* 2015).
404 However, another species in the Mediterranean did not display a significant change in gear

405 avoidance (Alós *et al.* 2015). Change in fish behavior may be species- or family-dependent; more
406 research on the rate and magnitude of behavioral change across taxa will provide valuable insight
407 for the design and implications of periodic closures, which aim to exploit this trait.

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

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

426 **Author contribution:** PC and CW designed and analyzed the models with input from other
427 authors; SJ, RW and FJH provided data for bioeconomic model; PC and CW wrote the first draft
428 of the paper and all authors contributed substantially to revisions.

429 **Acknowledgements**

430 Project support was provided by grant #2014—39332 from the David and Lucile Packard
431 Foundation (SJ and CW) and the National Science Foundation Graduate Research Fellowship
432 Award (PC). We thank R. White for assistance with ArcGIS and A. MacNeil for input on previous
433 drafts.

434 **Data accessibility statement:** Should the manuscript be accepted, data and code supporting the
435 results will be archived in an appropriate public repository.

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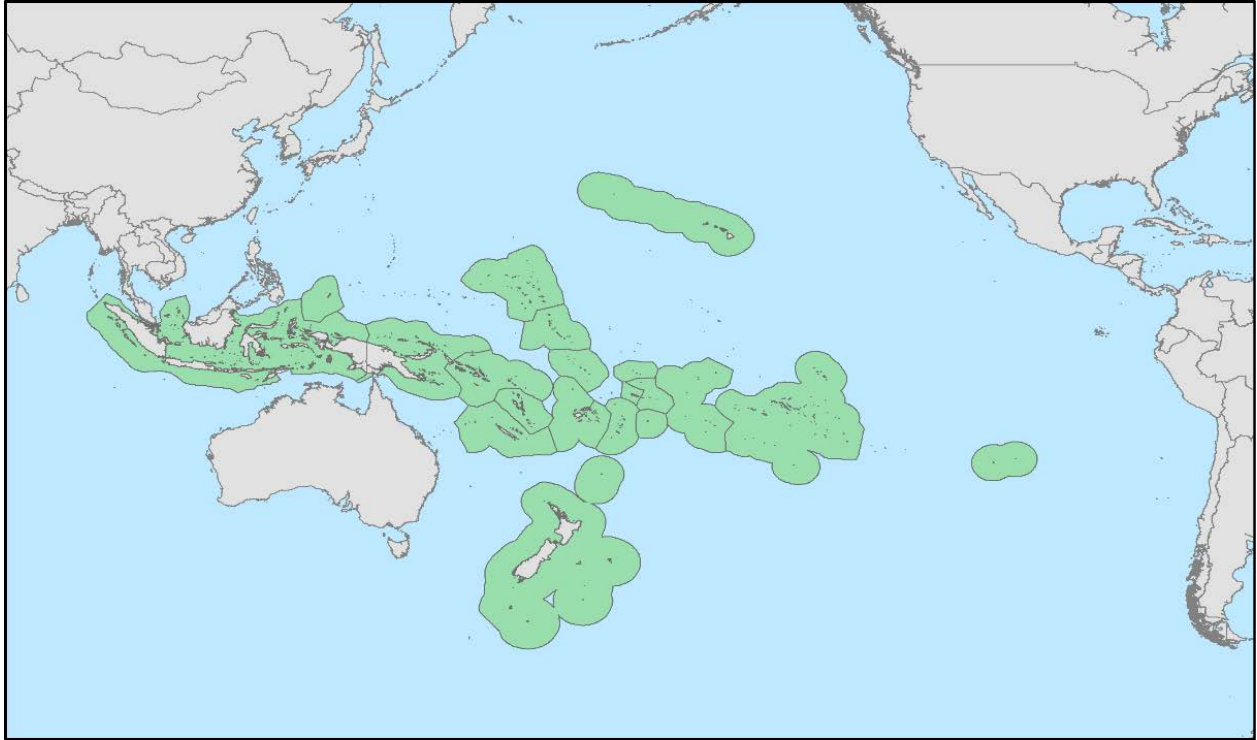
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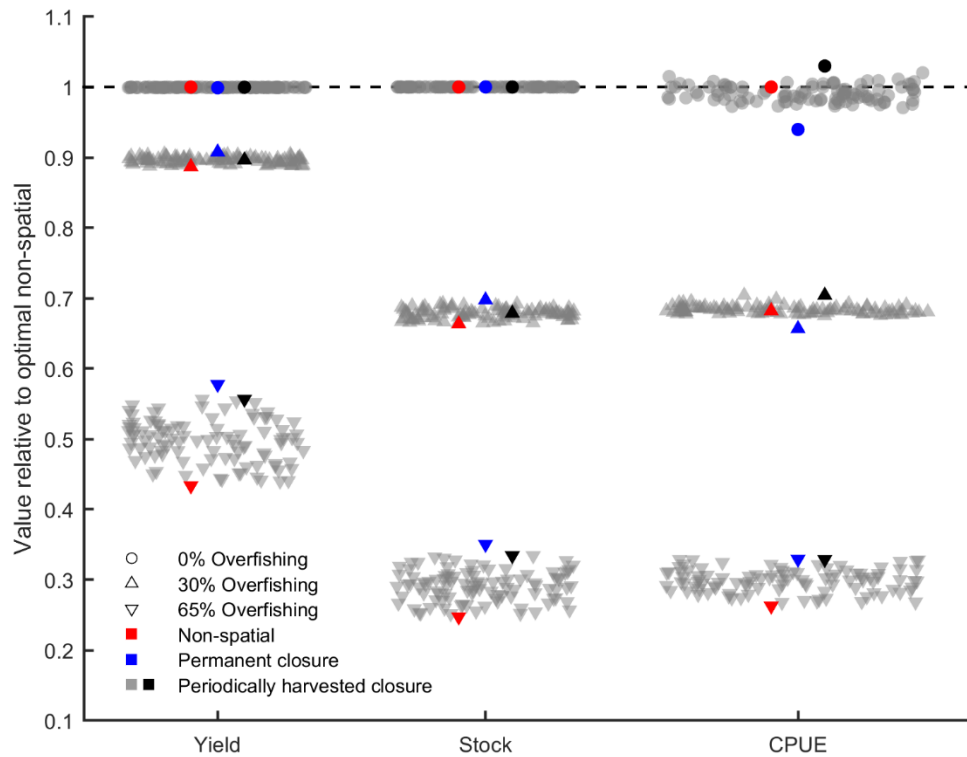
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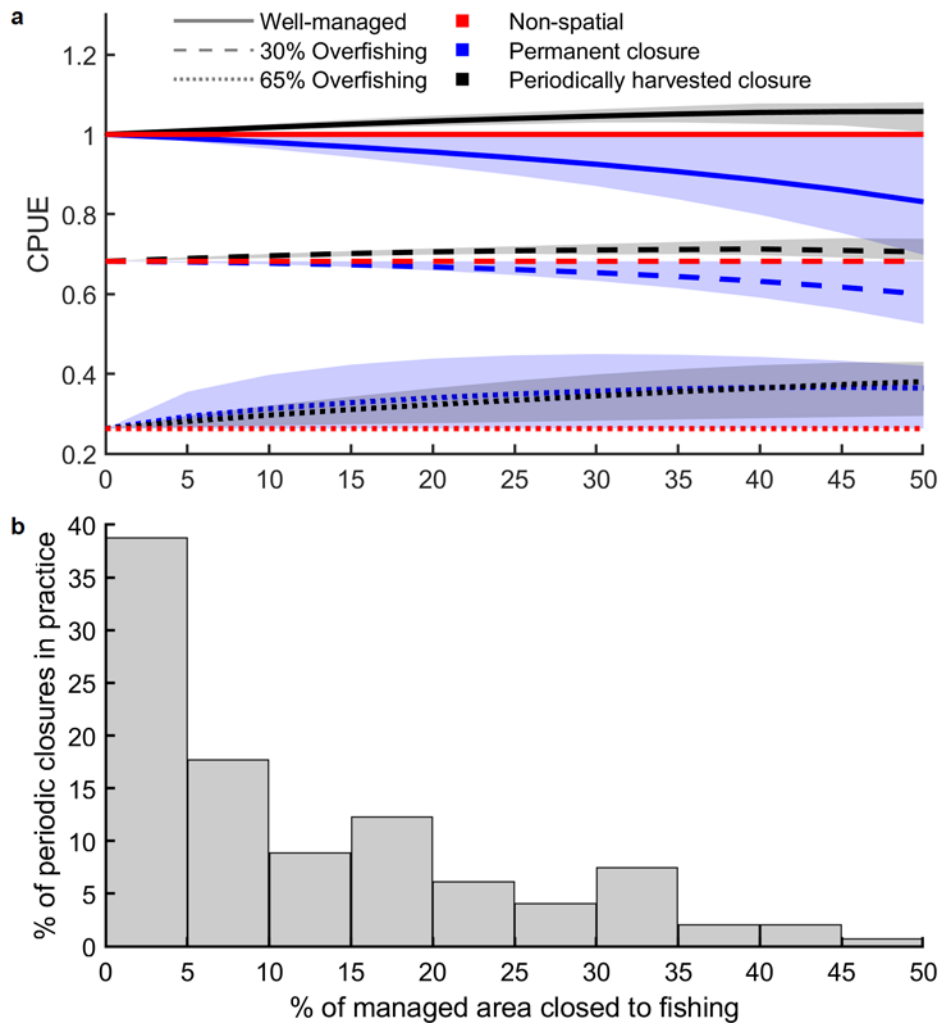
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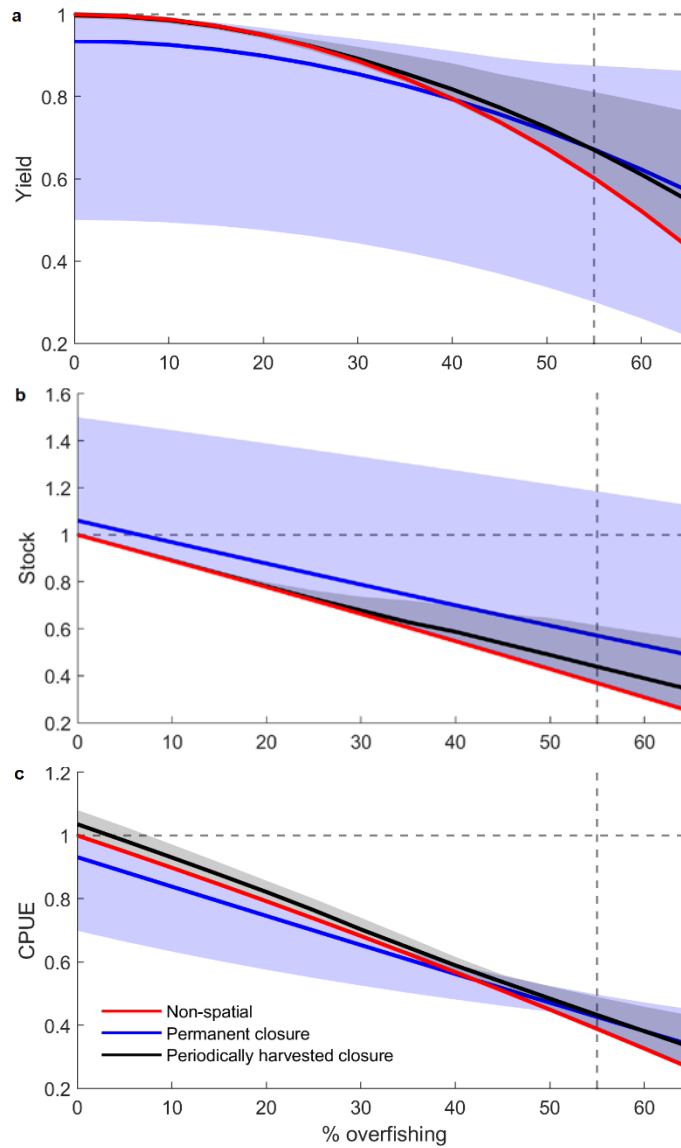
538 **Figure 1:** Map of the Exclusive Economic Zones (*green*) of regions that practice periodic
539 closures for marine resource management. Locations identified from a comprehensive literature
540 search (Ayres 1979; Bess 2001; Williams *et al.* 2006; Govan *et al.* 2009; Cohen & Foale 2013).



541 **Figure 2:** Average annual yield, stock abundance, and harvest efficiency (catch-per-unit-effort
 542 [CPUE]) under non-spatial, permanent closure, and periodic closure management. Black, filled
 543 markers indicate optimal periodic closure designs for 0% (1 year closed, 1 year open), 30% (2
 544 years closed, 1 year open), and 65% overfishing (10 years closed, 1 year open). Gray markers
 545 indicate outcomes for the full range of closed-open harvest cycles (all combinations of 1, 2, 3 ...
 546 10 years each). $S = 0.2$; $r = 0.3$; $c = 0.3$ (for permanent and periodic closures).



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



553 **Figure 4:** Yield, stock and harvest efficiency (CPUE) in relation to level of percent overfishing.
 554 All values are relative to the outcome under well-managed non-spatial management (horizontal
 555 dashed line). Shading represents the range of outcomes for different levels of fish site-fidelity (S
 556 = 0 – 1) and proportion of total management area within closure (c = 0 – 50%). The solid lines
 557 indicate means of the range of values for all combinations of S and c . The vertical dashed line
 558 indicates the range of overfishing (0 – 55%) within which periodic closures were, on average,

559 superior over the other forms of management strategies at balancing the triple objective of high
560 harvest efficiency, high fisheries yield, and high stock abundance.