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Paul G Carvalho, Stacy D Jupiter, Fraser Januchowski-hartley, Jordan Goetze, Joachim Claudet, et al.. Optimized fishing through periodically harvested closures Author affiliation. *Journal of Applied Ecology*, 2019, 56 (8), pp.1927-1936. 10.1111/1365-2664.13417 . hal-03033915

HAL Id: hal-03033915

<https://hal.science/hal-03033915v1>

Submitted on 1 Dec 2020

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

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

55 **Keywords:** Fisheries Management, Bioeconomic Model, Marine Protected Areas, Conservation,
56 Fish Behavior, Periodically Harvested Closures, Population Dynamics

57 **Introduction**

58 Spatial fisheries closures are used widely as a management tool for mediating overfishing
59 and promoting stock recovery (Gerber *et al.* 2003), but their ability to enhance the value of well-
60 managed fisheries may be limited (Hilborn *et al.* 2004). This perception of the mixed utility of
61 spatial closures is driven by scientific inquiry focused on permanent closures, a type of protected
62 area that restricts all fishing indefinitely (Horta e Costa *et al.* 2016). Under management with
63 permanent closures, displaced fishing effort from the protected area can produce negative
64 consequences for fisheries value. In these instances, displaced effort is crowded into the
65 remaining fishing grounds, potentially maintaining high yields (Hastings & Botsford 1999), but
66 at the price of reduced harvest efficiency and thus excess fishing costs (White *et al.* 2008).
67 Alternatively, displaced effort is removed from the system (i.e., fishers exit the fishery), which
68 potentially maintains high harvest efficiency, but at the price of reduced yield compared with
69 what was achievable without permanent closures (Hilborn *et al.* 2004). Thus, while permanent

70 closures certainly have value for overfished fisheries and provide control areas to investigate the
71 impacts of fishing and other anthropogenic effects on fish populations and ecosystems
72 (Ballantine 2014), they may be inappropriate in a well-managed fishery (no overfishing),
73 because the displaced fishing effort they generate can compromise either the economic or food-
74 provisioning value of the fishery, or both.

75 Although there is strong and growing advocacy among marine conservation groups and
76 scientists worldwide for the implementation of permanent closures (Lubchenco & Grorud-
77 Colvert 2015), such closures are often controversial and can be met with intense opposition
78 (Agardy *et al.* 2003). Alternatively, small-scale fishing communities around the world routinely
79 use periodically harvested closures (hereafter referred to as periodic closures) that receive far
80 less attention (Cohen & Foale 2013). Instead of permanently restricting access to fish stocks,
81 periodic closures provide temporary protection between periods of fishing. Communities
82 throughout the Indo-Pacific have been using periodic closures for centuries to promote
83 occasional and efficient exploitation of fish and invertebrate stocks (Fig. 1; Ayres 1979; Bess
84 2001; Williams *et al.* 2006; Govan *et al.* 2009; Cohen & Foale 2013). As with permanent
85 closures, periodic closures displace fishing effort and thus may promote fish recovery (Game *et*
86 *al.* 2009; Kaplan *et al.* 2010). However, this displacement is not permanent and, importantly for
87 the fishery, fish protected during the closure period become less wary of fishing gear (Goetze *et*
88 *al.* 2017). This behavioral change increases fish catchability and thus harvest efficiency when the
89 closed area is re-opened (Januchowski-Hartley *et al.* 2014). Consequently, periodic closures may
90 be capable of simultaneously supporting high levels of yield, stock abundance, and harvest
91 efficiency – perhaps to a greater extent than attainable by permanent closures or non-spatial
92 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
96 areas always open to fishing (Goetze *et al.* 2018), and that periodic closures can provide an
97 ephemeral boost in harvest efficiency when re-opened to fishing due to changes in fish behavior
98 during the closure period (Januchowski-Hartley *et al.* 2014; Goetze *et al.* 2017). Modeling
99 research on rotational closures, a related form of management where the closure area is moved
100 iteratively throughout the fishing domain, found that this management strategy is capable of
101 enhancing conservation and sometimes yield, particularly in an overfished system (Myers *et al.*
102 2000; Hart 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
105 cucumbers). We take a more general approach in order to cover a broad range of fishery species
106 and fishing conditions. The aims of our bioeconomic model were to: (i) quantify harvest
107 efficiency, yield, and stock abundance under periodic closure management, (ii) identify optimal
108 periodic closure designs (percentage domain in the closure, and its closed-open cycle) for
109 maximizing efficiency, yield and stock, and (iii) compare these optimized levels of efficiency,
110 yield and stock with the maximum levels achievable with permanent closures and non-spatial
111 fisheries management. In our bioeconomic model, we considered a range of life history traits
112 characterizing growth rates and mobility, as well as the potential for a temporary increase in the
113 catchability of fish following their protection, parameterized using empirical data on changes in
114 fish behavior in periodic closures, 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
117 simulate periodic closures, permanent closures, and non-spatial fisheries management. The
118 model 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
120 fishing. The proportional area of the domain represented by the patch that could be closed is c ,
121 with the remaining area $(1 - c)$ always open to fishing.

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

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

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

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

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

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
142 growth, 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.*
156 2011; Januchowski-Hartley *et al.* 2015). Flight initiation distance was quantified in periodic
157 closures, permanent closures, and non-spatial management areas ($n = 24$), and in relation to the
158 length of time the area had been protected from fishing prior to the empirical study (0-39 years).
159 Using the mean and variance in flight initiation distance observed for each family at each site

160 (Table S1), we generated a normal cumulative probability distribution indicating the probability
 161 of observing fish initiate flight at a distance less than or equal to a specified distance from the
 162 simulated spearfisher. We then evaluated this distribution in relation to the mean effective range
 163 required to catch a fish using the type of rifle-style speargun commonly used in the Indo-Pacific
 164 (323.75 cm, Januchowski-Hartley *et al.* 2015; for example, see Fig. S1 and Table S1). We
 165 repeated the evaluation for each of the 24 study sites, then used least squares to fit a Logarithmic
 166 curve to the data describing the normal cumulative probability in relation to the number of
 167 consecutive years the site had been closed to fishing prior to the empirical study:

$$168 \quad F_{i,t} = 0.172 * \log(C_{i,t}) + 0.431, \quad \text{eqn 6}$$

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

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

$$175 \quad q_{i,t} = \frac{F_{i,t}^\alpha(C_{i,t})}{F_{i,t}^\alpha(C_{i,t}=0)}, \quad \text{eqn 7}$$

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

$$182 \quad F_{i,t}^\alpha = \alpha * \beta + 0.431 \quad \text{eqn 8}$$

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

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

$$194 \quad \mathbf{D}^{cp} = \begin{bmatrix} Q_{1,1} & Q_{1,2} \\ Q_{2,1} & Q_{2,2} \end{bmatrix}, \quad \text{eqn 9}$$

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

$$200 \quad \mathbf{D}^{cp} = \begin{bmatrix} 0.7 & 0.3 \\ 0.7 & 0.3 \end{bmatrix}. \quad \text{eqn 10}$$

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

204
$$\mathbf{D} = \begin{bmatrix} Q_{1,1} + (1 - Q_{1,1})S & Q_{1,2} - Q_{1,2}S \\ Q_{2,1} - Q_{2,1}S & Q_{2,2} + (1 - Q_{2,2})S \end{bmatrix},$$
 eqn 11

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

210
$$\mathbf{D} = \begin{bmatrix} 0.76 & 0.24 \\ 0.56 & 0.44 \end{bmatrix}.$$
 eqn 12

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

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

223 To represent a ‘well-managed’ fishery, fishing effort was optimized in each fishable
 224 patch and for each annual time step in the model to achieve maximum sustainable yield (MSY)
 225 across the two-patch management area. That is, under non-spatial management a constant effort

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

245 For each model parameterization analyzed (characterized by c , S , r , harvest cycle, level
246 of overfishing and management scenario) we recorded fishery yield, harvest efficiency, and stock
247 abundance – the triple objective. We quantified harvest efficiency as catch-per-unit-effort

248 (CPUE) and evaluated equilibrium model results to achieve the fisheries objective of long-term
249 sustainability.

250 **Results**

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

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

271 permanent closure (i.e., harvest efficiency decreased and stock abundance and yield increased),
272 but even with a lengthy closed period (10 years), harvest efficiency remained proportionally
273 greater (2%) than the loss in yield and stock abundance (< 1%), compared with values generated
274 by permanent closure management (Fig. 2). In contrast, with extreme overfishing (65%
275 overfishing), the advantages of harvest efficiency for periodic closures eroded and permanent
276 closures became optimal for achieving the triple objective (Fig. 2). In this case, harvest
277 efficiency was equivalent for permanent and periodic closures (with a 10-year closed period and
278 1-year open period), but yield and stock were each 2% greater for permanent closures (Fig. 2).

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

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

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

323 **Discussion**

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

333 Empirical studies have found greater harvest efficiency (catch-per-unit-effort) inside
334 periodic closures upon their re-opening compared with areas always open to fishing
335 (Januchowski-Hartley *et al.* 2014; Goetze *et al.* 2017). Our theory-based analysis extends the
336 implications of the empirical results by showing that periodic closure management is capable of
337 enhancing average harvest efficiency measured across the entire fishing domain and harvest

338 schedule. We also quantify the strength of this effect size in relation to its underlying mechanism
339 – the level of change in fish wariness to fishing gear following temporary protection.

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

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

361 bias also was robust to the length of closure period (up to 10 years). When moderate overfishing
362 was considered in our sensitivity analysis, we saw the same tradeoff as in the case-study above.
363 For fisheries targeting fish with low to moderate site-fidelity ($S \leq 0.4$), which include common
364 target species throughout the Indo-Pacific (Meyer *et al.* 2010; Jupiter *et al.* 2012; Abesamis *et al.*
365 2014), management with permanent closures occupying a moderate to large proportion of the
366 management area ($c \geq 0.25$) generated higher average annual yield compared with that attainable
367 by periodic closures (Fig. S7). However, the percentage gain in yield by permanent closures was
368 always less than the loss in harvest efficiency (Fig. 3 and S7). If fishers target more sedentary
369 species, then spillover of fish from a permanent closure to an open area is limited, thus
370 generating less yield than attainable under periodic closures, causing the tradeoff to dissolve in
371 favor of periodic closure management (Fig. S7). In regard to stock abundance, its tradeoff with
372 harvest efficiency was balanced between periodic and permanent closure management for
373 fisheries targeting species with low to moderate site-fidelity ($S \leq 0.2$), and unbalanced in favor of
374 permanent closures for species with higher site-fidelity ($S > 0.2$; Fig. S7). The above sensitivity
375 analysis results held true for species with high and low resilience to fishing (Fig. S8-S10). When
376 overfishing was increased to $\geq 55\%$, which under nonspatial management would reduce stock
377 abundance to $\leq 37\%$ of its level at MSY (and $\leq 18\%$ of its unfished level), the above trade-offs
378 between periodic and permanent closures faded, and instead permanent closures maximized
379 yield, stock and harvest efficiency. Approximately $< 25\%$ of global fisheries fall within this
380 extreme range of overfishing (Costello *et al.* 2016). Our conclusions of trade-offs between
381 periodic and permanent closures assumed that managers care equally about yield, stock and
382 harvest efficiency. However, managers may value one outcome more than others, and thus draw
383 different qualitative conclusions from the trade-offs.

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

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

407 We demonstrate that periodic closures can be more, or at least equally, effective
408 compared with permanent closures for fisheries that are well-managed to moderately overfished.
409 We also show that the benefits of periodic closures dissolves when overfishing is extreme. These
410 results may explain the range of effectiveness of periodic closures used in practice (Cinner *et al.*
411 2005; Jupiter *et al.* 2012). Communities often harvest periodic closures too frequently or exceed
412 harvest targets, or both (Goetze *et al.* 2018), and thus the successful management of periodic
413 closures depends on enforcement of appropriate harvest targets (within periodic closures and
414 surrounding management areas) and harvest cycles, and consistent monitoring of fish
415 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
418 fish conservation (stock abundance) objectives. We also demonstrate that periodic closures can,
419 in most cases, be superior at balancing these objectives in a fishery with excessive fishing
420 pressure. Evaluation of this balance between the three objectives in relation to socioeconomic
421 priorities among yield, harvest efficiency and stock abundance – within and outside the Indo-
422 Pacific – would provide additional insight on the utility of periodic closures for meeting
423 ecosystem-based fisheries management goals. Our findings challenge the dogma that periodic
424 closures are simply a cultural legacy that are only valuable within the Indo-Pacific and with
425 limited outcomes, and instead suggest that they may be an optimal fisheries management strategy
426 with broad utility.

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

430 **Acknowledgements**

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

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

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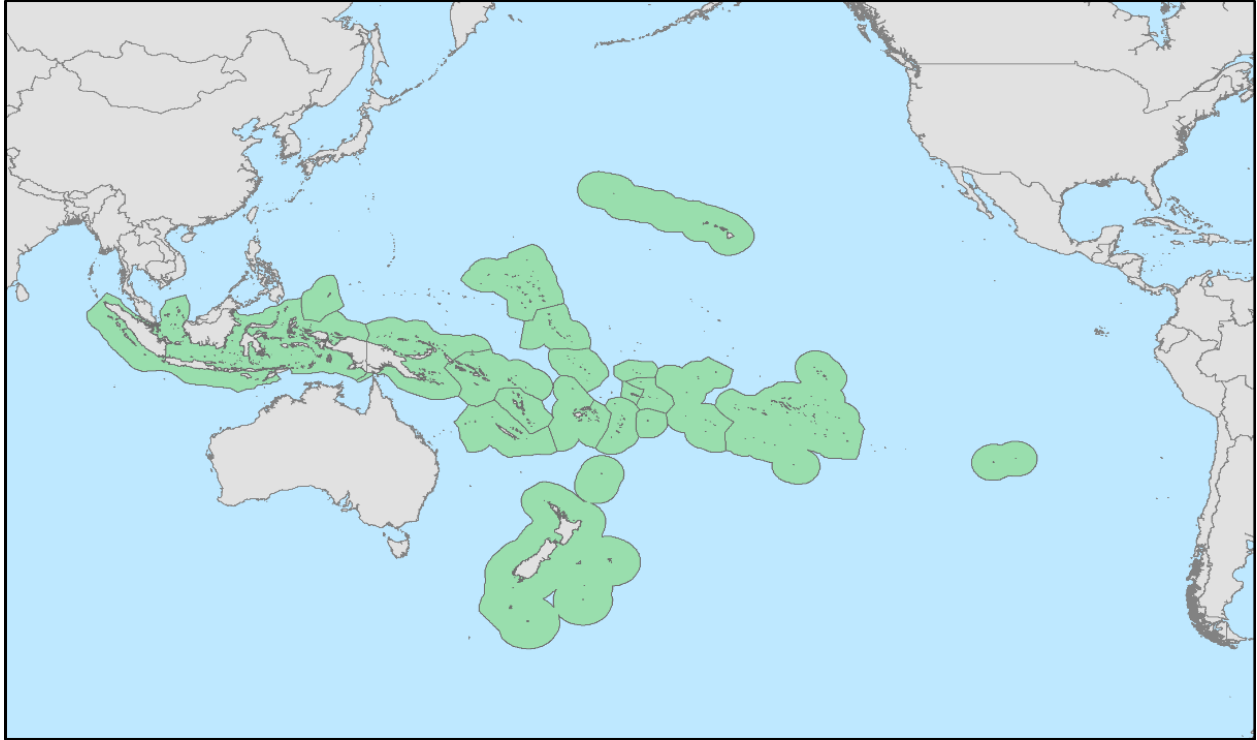
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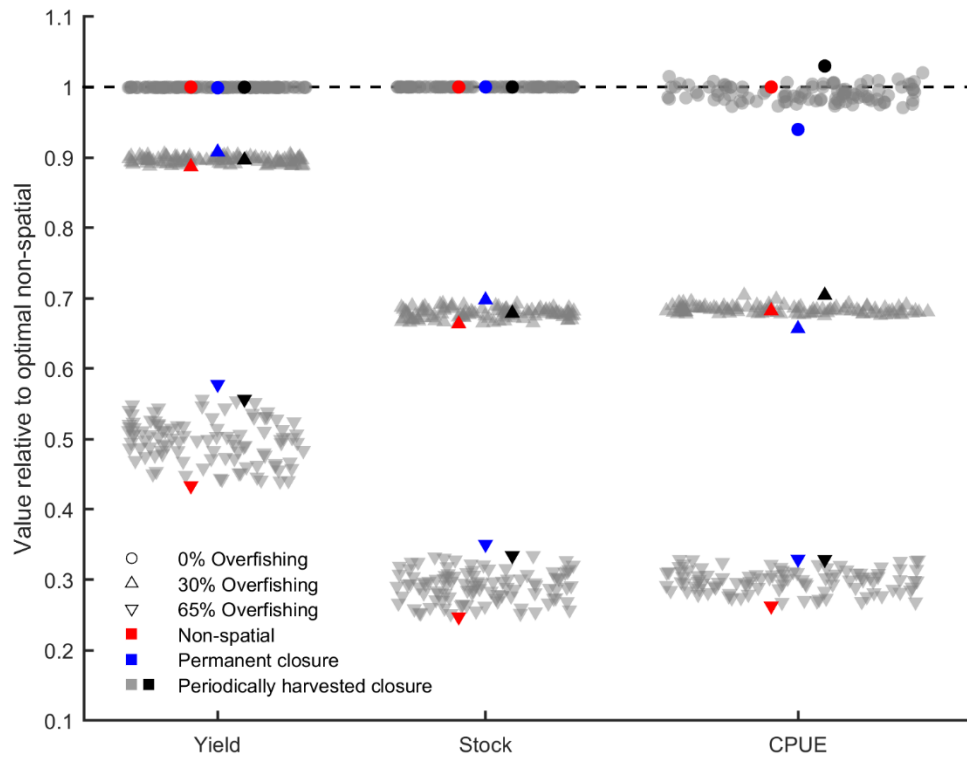
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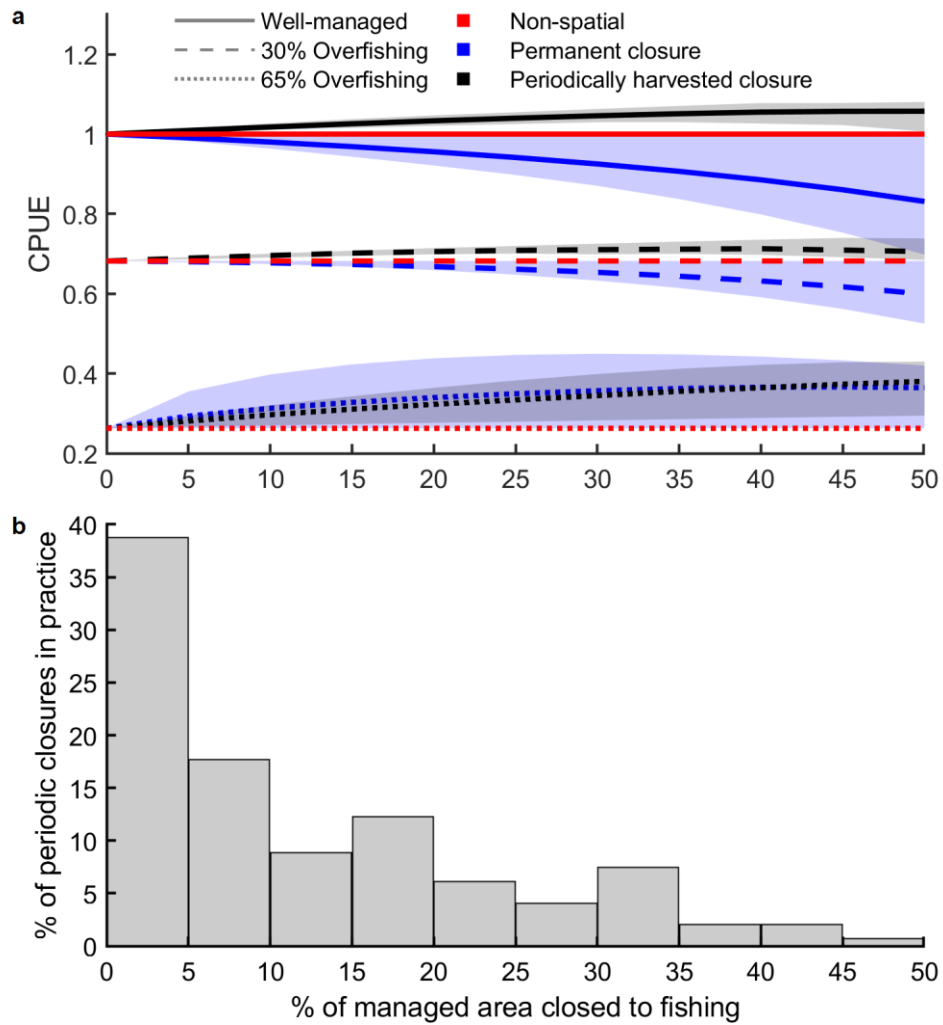
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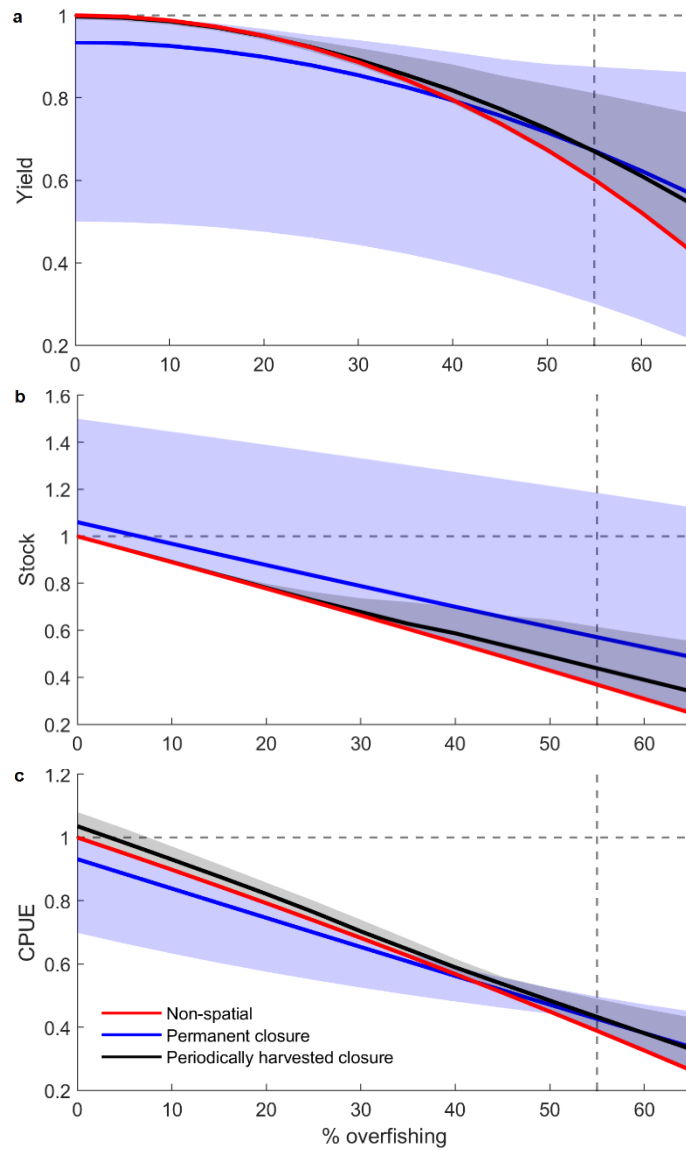
539 **Figure 1:** Map of the Exclusive Economic Zones (*green*) of regions that practice periodic
540 closures for marine resource management. Locations identified from a comprehensive literature
541 search (Ayres 1979; Bess 2001; Williams *et al.* 2006; Govan *et al.* 2009; Cohen & Foale 2013).



542 **Figure 2:** Average annual yield, stock abundance, and harvest efficiency (catch-per-unit-effort
543 [CPUE]) under non-spatial, permanent closure, and periodic closure management. Black, filled
544 markers indicate optimal periodic closure designs for 0% (1 year closed, 1 year open), 30% (2
545 years closed, 1 year open), and 65% overfishing (10 years closed, 1 year open). Gray markers
546 indicate outcomes for the full range of closed-open harvest cycles (all combinations of 1, 2, 3 ...
547 10 years each). $S = 0.2$; $r = 0.3$; $c = 0.3$ (for permanent and periodic closures).



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



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

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