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10 **Optimized fishing through periodically harvested closures**

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34 **Abstract**

- 35 1. Periodically harvested closures are a widespread, centuries-old form of fisheries management
36 that protects fish between pulse harvests and can generate high harvest efficiency by
37 reducing fish wariness of fishing gear. However, the ability for periodic closures to also
38 support high fisheries yields and healthy marine ecosystems is uncertain, despite increased
39 promotion of periodic closures for managing fisheries and conserving ecosystems in the
40 Indo-Pacific.
- 41 2. We developed a bioeconomic fisheries model that considers changes in fish wariness, based
42 on empirical field research, and quantified the extent to which periodic closures can
43 simultaneously maximize harvest efficiency, fisheries yield, and conservation of fish stocks.
- 44 3. We found that periodic closures with a harvest schedule represented by closure for one to a
45 few years between a single pulse harvest event can generate equivalent fisheries yield and
46 stock abundance levels and greater harvest efficiency than achievable under conventional
47 fisheries management with or without a permanent closure.
- 48 4. Optimality of periodic closures at maximizing the triple objective of high harvest efficiency,
49 high fisheries yield, and high stock abundance was robust to fish life history traits and to all
50 but extreme levels of overfishing. With moderate overfishing, there emerged a trade-off
51 between periodic closures that maximized harvest efficiency and no-take permanent closures
52 that maximized yield; however, the gain in harvest efficiency outweighed the loss in yield for
53 periodic closures when compared with permanent closures. Only with extreme overfishing,
54 where fishing under nonspatial management would reduce the stock to $\leq 18\%$ of its unfished
55 level, was the harvest efficiency benefit too small for periodic closures to best meet the triple
56 objective compared with permanent closures.
- 57 5. *Synthesis and applications.* We show that periodically harvested closures can, in most cases,
58 simultaneously maximize harvest efficiency, fisheries yield, and fish stock conservation
59 beyond that achievable by no-take permanent closures or non-spatial management. Our
60 results also provide design guidance, indicating that short closure periods between pulse
61 harvest events are most appropriate for well-managed fisheries or areas with large periodic
62 closures, whereas longer closure periods are more appropriate for small periodic closure
63 areas and overfished systems.

64 **Keywords:** Fisheries Management, Bioeconomic Model, Marine Protected Areas, Conservation,
65 Fish Behavior, Periodically Harvested Closures, Population Dynamics, Marine reserves

66 **Introduction**

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

84 Although there is strong and growing advocacy among marine conservation groups and
85 scientists worldwide for the implementation of permanent closures (Lubchenco & Grorud-
86 Colvert 2015), such closures are often controversial and can be met with intense opposition
87 (Agardy *et al.* 2003). Alternatively, small-scale fishing communities around the world routinely
88 use periodically harvested closures (hereafter referred to as periodic closures) that receive far
89 less attention (Cohen & Foale 2013). Instead of permanently restricting access to fish stocks,
90 periodic closures provide temporary protection between periods of fishing. Communities
91 throughout the Indo-Pacific have been using periodic closures for centuries to promote
92 occasional and efficient exploitation of fish and invertebrate stocks (Fig. 1; Ayres 1979; Bess
93 2001; Williams *et al.* 2006; Govan *et al.* 2009; Cohen & Foale 2013). As with permanent

94 closures, periodic closures displace fishing effort and thus may promote fish recovery (Game *et*
95 *al.* 2009; Kaplan *et al.* 2010). However, this displacement is not permanent and, importantly for
96 the fishery, fish protected during the closure period become less wary of fishing gear (Goetze *et*
97 *al.* 2017). This behavioural change increases fish catchability and thus harvest efficiency when
98 the closed area is re-opened (Januchowski-Hartley *et al.* 2014). Consequently, periodic closures
99 may be capable of simultaneously supporting high levels of yield, stock abundance, and harvest
100 efficiency – perhaps to a greater extent than attainable by permanent closures or non-spatial
101 fisheries management.

102 Here we tested the value of periodic closures using a bioeconomic fisheries model that
103 incorporates change in fish behaviour during closed periods. Empirical studies show that
104 periodic closures can increase biomass, abundance, and average size of target species compared
105 with areas always open to fishing (Goetze *et al.* 2018), and that periodic closures can provide an
106 ephemeral boost in harvest efficiency when re-opened to fishing due to changes in fish behaviour
107 during the closure period (Januchowski-Hartley *et al.* 2014; Goetze *et al.* 2017). Modelling
108 research on rotational closures, a related form of management where the closure area is moved
109 iteratively throughout the fishing domain, found that this management strategy is capable of
110 enhancing conservation and sometimes yield, particularly in an overfished system (Myers *et al.*
111 2000; Hart 2003; Valderrama & Anderson 2009; Plagányi *et al.* 2015).

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

124 **Materials and methods**

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

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

$$133 \quad x_{i,t+1} = \frac{\sum_{j=1}^N D_{ji} A_j e_{j,t}}{A_i}. \quad \text{eqn 1}$$

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

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

$$141 \quad g(x_{i,t}) = x_{i,t} + r_d x_{i,t} (1 - x_{i,t} / K_i), \quad \text{eqn 2}$$

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

$$152 \quad h_{i,t} = g(x_{i,t}) f(E_{i,t}) A_i, \quad \text{eqn 3}$$

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

$$155 \quad f(E_{i,t}) = 1 - \exp(-E_{i,t}q_{i,t}). \quad \text{eqn 4}$$

156 The escaped stock density after harvest is thus

$$157 \quad e_{i,t} = g(x_{i,t})(1 - f(E_{i,t})). \quad \text{eqn 5}$$

158 The catchability coefficient ($q_{i,t}$) is a function of how long the patch had been previously
159 closed to fishing (i.e., never for permanently open patches under all three management scenarios,
160 and 1-10 years for the periodic closure patch, depending on its closed period). We generated a
161 catchability curve using empirical data on the distance reef fish initiated a flight response from
162 simulated spearfishers (flight initiation distance). Data came from studies that measured flight
163 initiation distance for families Acanthuridae and Labridae (subfamily Scarinae) in four Indo-
164 Pacific countries: Papua New Guinea, Vanuatu, Philippines, and Chagos (Table S1; Feary *et al.*
165 2011; Januchowski-Hartley *et al.* 2015). Flight initiation distance was quantified in periodic
166 closures, permanent closures, and non-spatial management areas ($n = 24$), and in relation to the
167 length of time the area had been protected from fishing prior to the empirical study (0-39 years).
168 Using the mean and variance in flight initiation distance observed for each family at each site
169 (Table S1), we generated a normal cumulative probability distribution indicating the probability
170 of observing fish initiate flight at a distance less than or equal to a specified distance from the
171 simulated spearfisher. We then evaluated this distribution in relation to the mean effective range
172 required to catch a fish using the type of rifle-style speargun commonly used in the Indo-Pacific
173 (323.75 cm, Januchowski-Hartley *et al.* 2015; for example, see Fig. S1 and Table S1 in
174 Supporting Information). We repeated the evaluation for each of the 24 study sites, then used
175 least squares to fit a Logarithmic curve to the data describing the normal cumulative probability
176 in relation to the number of consecutive years the site had been closed to fishing prior to the
177 empirical study:

$$178 \quad F_{i,t} = 0.172 * \log(C_{i,t}) + 0.431, \quad \text{eqn 6}$$

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

181 Given that a fish needs to be within speargun range to be harvested by that gear, we
182 assumed the catchability of fish in patch i during a particular year ($q_{i,t}$) to be a function of $F_{i,t}$. To

183 maintain generality, we set catchability equal to $F_{i,t}$ scaled relative to the level calculated when
 184 an area is always open to fishing and thus fish catchability is not enhanced (Fig. S3):

$$185 \quad q_{i,t} = \frac{F_{i,t}^{\alpha}(C_{i,t})}{F_{i,t}^{\alpha}(C_{i,t} = 0)}, \quad \text{eqn 7}$$

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

$$192 \quad F_{i,t}^{\alpha} = \alpha * \beta + 0.431 \quad \text{eqn 8}$$

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

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

$$204 \quad \mathbf{D}^{cp} = \begin{bmatrix} Q_{1,1} & Q_{1,2} \\ Q_{2,1} & Q_{2,2} \end{bmatrix}, \quad \text{eqn 9}$$

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

$$210 \quad \mathbf{D}^{cp} = \begin{bmatrix} 0.7 & 0.3 \\ 0.7 & 0.3 \end{bmatrix}. \quad \text{eqn 10}$$

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

$$214 \mathbf{D} = \begin{bmatrix} Q_{1,1} + (1 - Q_{1,1})S & Q_{1,2} - Q_{1,2}S \\ Q_{2,1} - Q_{2,1}S & Q_{2,2} + (1 - Q_{2,2})S \end{bmatrix}, \quad \text{eqn 11}$$

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

$$220 \mathbf{D} = \begin{bmatrix} 0.76 & 0.24 \\ 0.56 & 0.44 \end{bmatrix}. \quad \text{eqn 12}$$

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

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

233 To represent a 'well-managed' fishery, fishing effort was optimized in each fishable
234 patch and for each annual time step in the model to achieve maximum sustainable yield (MSY)
235 across the two-patch management area. That is, under non-spatial management a constant effort
236 level was optimized in both patches to achieve MSY, and under management with a permanent
237 closure a constant effort level was optimized in the fishable patch to achieve MSY. Under
238 management with a periodic closure, effort was optimized for each year and patch to achieve
239 MSY, with one patch always open to fishing and the other open periodically in accordance with

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

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

260 **Results**

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

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

272 The case study results were robust to all but extreme levels of overfishing. Consideration
273 of moderate overfishing (30% overfishing; fishing effort that achieves maximum sustainable
274 yield for each patch and year, increased by 30%) revealed a trade-off between periodic and
275 permanent closures in their improvement over non-spatial management: the optimal periodic
276 closure harvest cycle (closed for 2 years between short fishing bouts) maximized harvest
277 efficiency, but a permanent closure maximized stock abundance and fishery yield (Fig. 2).
278 Harvest efficiency under periodic closure management was 5% greater than that achieved by
279 permanent closures, and yield and stock abundance were only 1% and 2% less than those by
280 permanent closures, respectively (Fig. 2). Extending the closed period made it more similar to a
281 permanent closure (i.e., harvest efficiency decreased and stock abundance and yield increased),
282 but even with a lengthy closed period (10 years), harvest efficiency remained proportionally
283 greater (2%) than the loss in yield and stock abundance (< 1%), compared with values generated
284 by permanent closure management (Fig. 2). In contrast, with extreme overfishing (65%
285 overfishing), the advantages of harvest efficiency for periodic closures eroded and permanent
286 closures became optimal for achieving the triple objective (Fig. 2). In this case, harvest
287 efficiency was equivalent for permanent and periodic closures (with a 10-year closed period and
288 1-year open period), but yield and stock were each 2% greater for permanent closures (Fig. 2).

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

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

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

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

331 permanent closures were able to simultaneously maximize yield, stock abundance and harvest
332 efficiency (Fig. 4).

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333 **Discussion**

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

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

350 Modelling studies suggest that rotational closures can enhance yield compared with non-
351 rotational fisheries management, particularly when overfishing occurs (Myers *et al.* 2000; Hart
352 2003; Plagányi *et al.* 2015). Our results support these findings, as we found that periodic closures
353 with long closure periods (10 years) between 1-year open periods were capable of generating
354 greater yield than non-spatial management, even when overfishing was high ($> 30\%$
355 overfishing). If age-structure was integrated into our model, it is possible that periodic closures
356 would enhance yield more by protecting larger individuals during closure periods that are
357 exploited upon re-opening. Similarly, consideration of age-structure and thus protection of larger
358 individuals might also generate conservation of greater average annual stock biomass with
359 periodic closures, as indicated empirically (Cinner *et al.* 2005; Bartlett *et al.* 2009) and with
360 modelling (Myers *et al.* 2000; Hart 2003; Game *et al.* 2009).

361 While we show periodic closures to excel in achieving the triple objective when fishers
362 behave rationally and optimize effort for maximizing yield, excessive fishing effort and
363 overharvesting is a common problem worldwide (Costello *et al.* 2012), including in some

364 communities that use periodic closures (e.g., on Kia Island, Fiji; Jupiter *et al.* 2012, 2017). With
365 consideration of moderate overfishing in our case study scenario, we found a tradeoff in
366 performance between periodic closures, which maximize harvest efficiency, and permanent
367 closures, which maximize yield and stock abundance. In most of our evaluations for moderate
368 levels of overfishing, the proportional gain in harvest efficiency from management with a
369 periodic closure over that with a permanent closure was greater than the proportional loss in
370 yield and stock abundance, indicating the tradeoff to be biased in favour of periodic closures.
371 This bias also was robust to the length of closure period (up to 10 years). When moderate
372 overfishing was considered in our sensitivity analysis, we saw the same tradeoff as in the case-
373 study above. For fisheries targeting fish with low to moderate site-fidelity ($S \leq 0.4$), which
374 include common target species throughout the Indo-Pacific (Meyer *et al.* 2010; Jupiter *et al.*
375 2012; Abesamis *et al.* 2014), management with permanent closures occupying a moderate to
376 large proportion of the management area ($c \geq 0.25$) generated higher average annual yield
377 compared with that attainable by periodic closures (Fig. S7). However, the percentage gain in
378 yield by permanent closures was always less than the loss in harvest efficiency (Fig. 3 and S7). If
379 fishers target more sedentary species, then spillover of fish from a permanent closure to an open
380 area is limited, thus generating less yield than attainable under periodic closures, causing the
381 tradeoff to dissolve in favour of periodic closure management (Fig. S7). In regard to stock
382 abundance, its tradeoff with harvest efficiency was balanced between periodic and permanent
383 closure management for fisheries targeting species with low to moderate site-fidelity ($S \leq 0.2$),
384 and unbalanced in favour of permanent closures for species with higher site-fidelity ($S > 0.2$; Fig.
385 S7). The above sensitivity analysis results held true for species with high and low resilience to
386 fishing (Fig. S8-S10). When overfishing was increased to $\geq 55\%$, which under nonspatial
387 management would reduce stock abundance to $\leq 37\%$ of its level at MSY (and $\leq 18\%$ of its
388 unfished level), the above trade-offs between periodic and permanent closures faded, and instead
389 permanent closures maximized yield, stock and harvest efficiency. Approximately $< 25\%$ of
390 global fisheries fall within this extreme range of overfishing (Costello *et al.* 2016). Our
391 conclusions of trade-offs between periodic and permanent closures assumed that managers care
392 equally about yield, stock and harvest efficiency. However, managers may value one outcome
393 more than others, and thus draw different qualitative conclusions from the trade-offs.

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

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

417 We demonstrate that periodic closures can be more, or at least equally, effective
418 compared with permanent closures for fisheries that are well-managed to moderately overfished.
419 We also show that the benefits of periodic closures dissolves when overfishing is extreme. These
420 results may explain the range of effectiveness of periodic closures used in practice (Cinner *et al.*
421 2005; Jupiter *et al.* 2012). Communities often harvest periodic closures too frequently or exceed
422 harvest targets, or both (Goetze *et al.* 2018), and thus the successful management of periodic
423 closures depends on enforcement of appropriate harvest targets (within periodic closures and

424 surrounding management areas) and harvest cycles, and consistent monitoring of fish
425 populations.

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

437 **Authors' contributions**

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

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445 previous drafts.

446 **Data accessibility**

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

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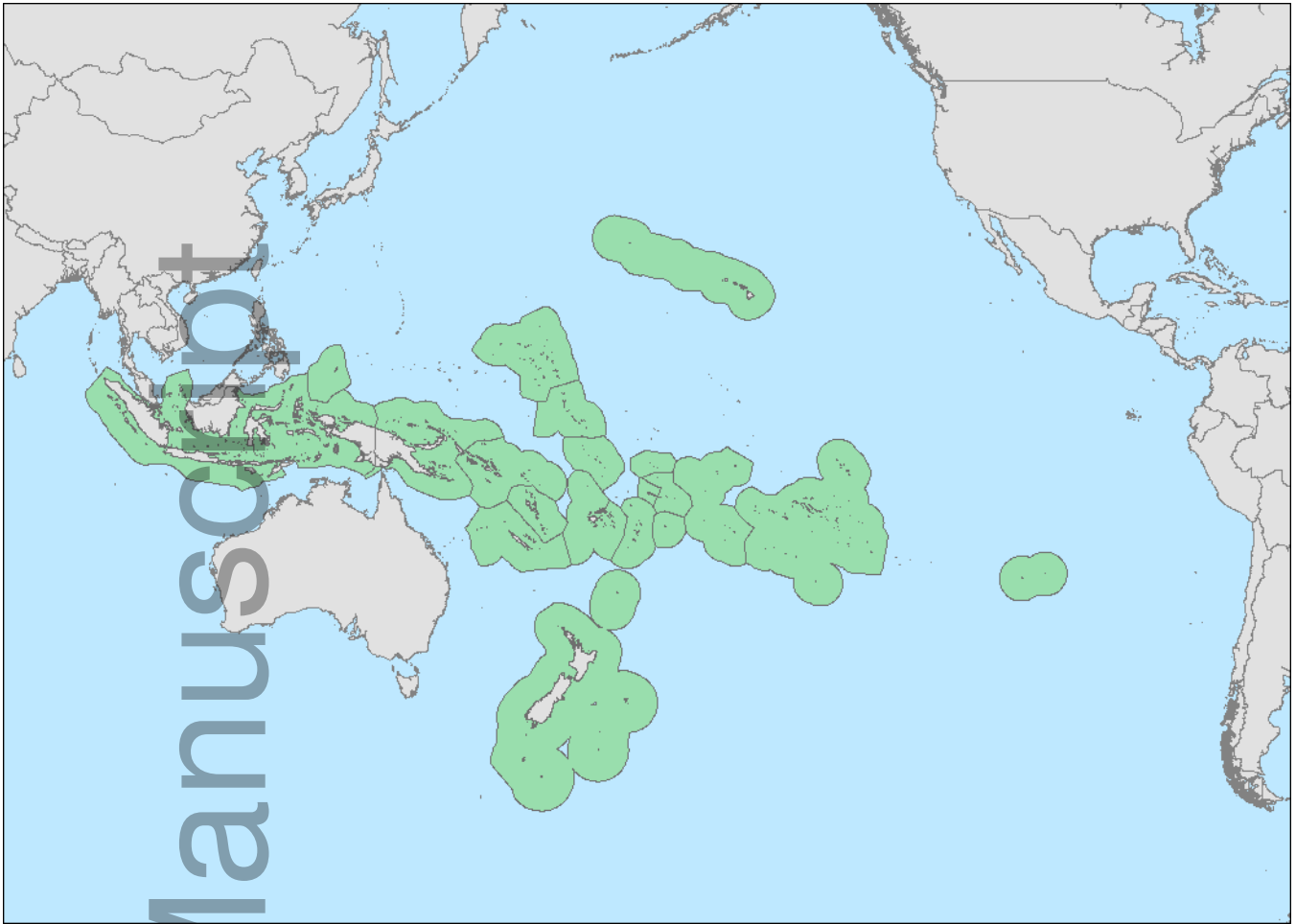
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554 **Figure 1:** Map of the Exclusive Economic Zones (*green*) of regions that practice periodic
555 closures for marine resource management. Locations identified from a comprehensive literature
556 search (Ayres 1979; Bess 2001; Williams *et al.*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

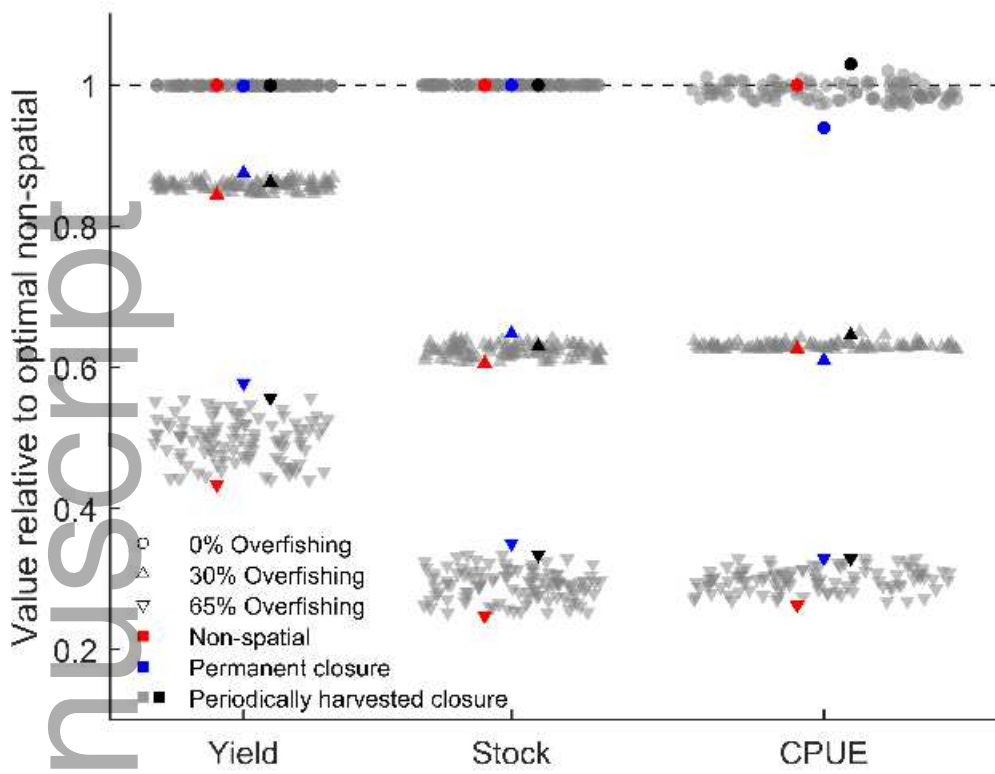
557 **Figure 2:** Average annual yield, stock abundance, and harvest efficiency (catch-per-unit-effort
558 [CPUE]) under non-spatial, permanent closure, and periodic closure management. Black, filled
559 markers indicate optimal periodic closure designs for 0% (1 year closed, 1 year open), 30% (2
560 years closed, 1 year open), and 65% overfishing (10 years closed, 1 year open). Gray markers
561 indicate outcomes for the full range of closed-open harvest cycles (all combinations of 1, 2, 3 ...
562 10 years each). $S = 0.2$; $r = 0.3$; $c = 0.3$ (for permanent and periodic closures).

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

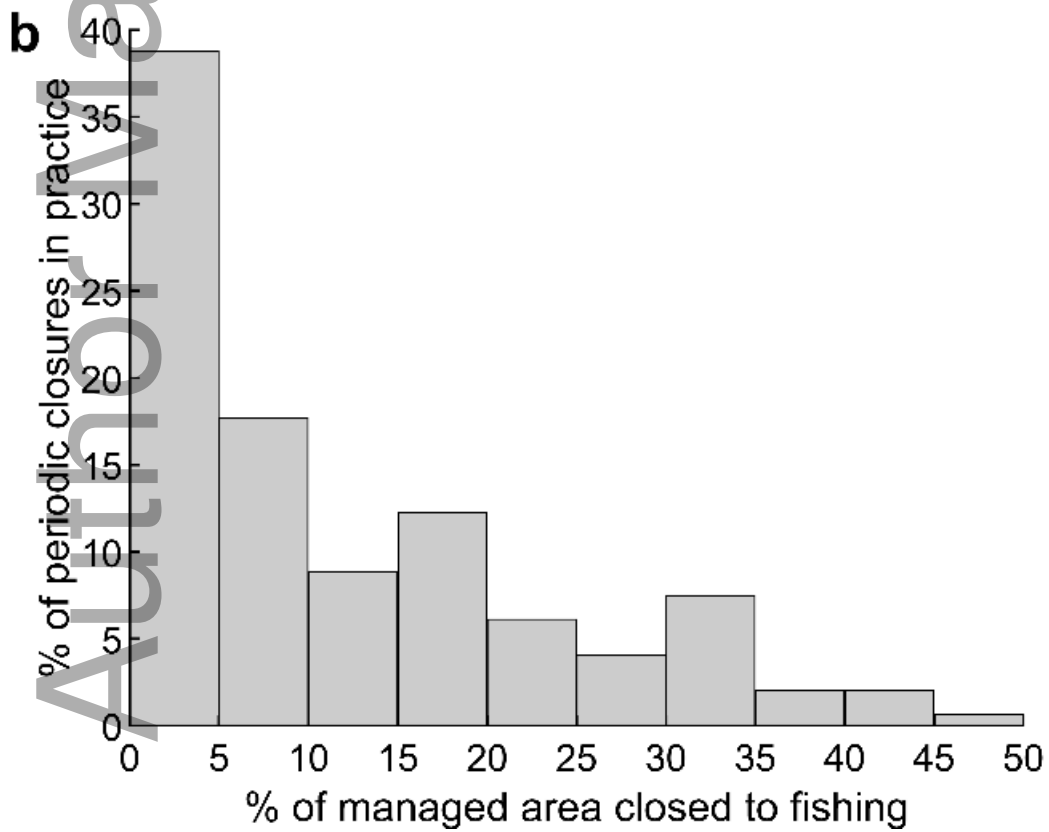
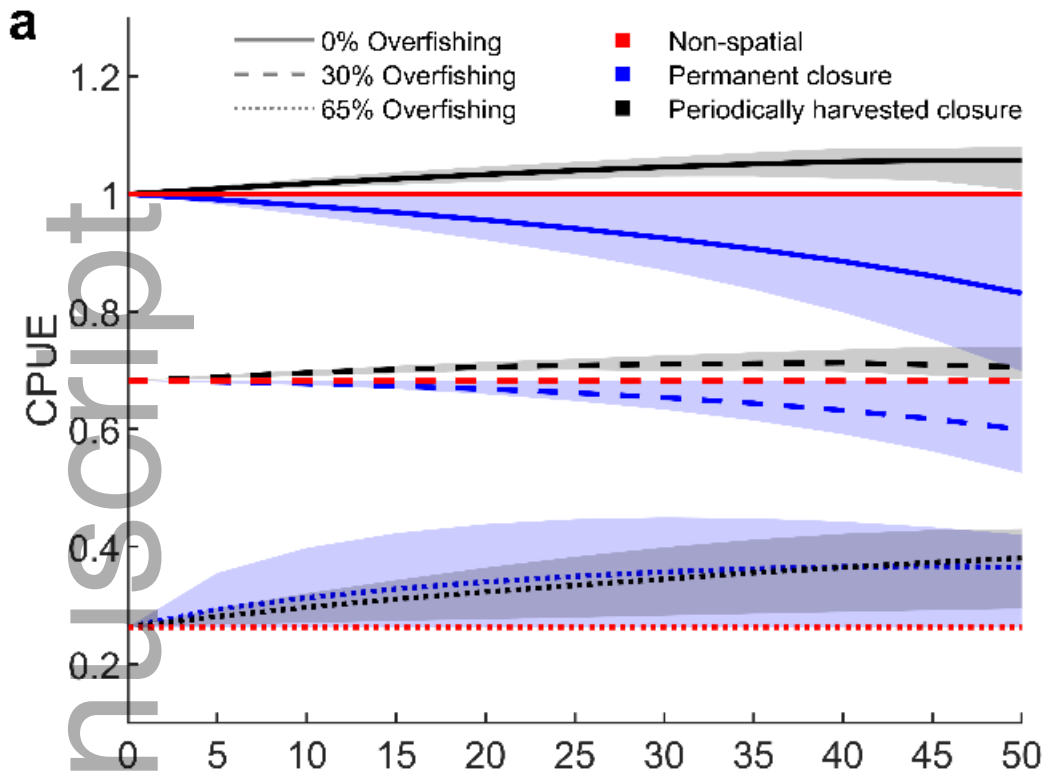
569 **Figure 4:** Yield, stock and harvest efficiency (CPUE) in relation to percent overfishing. All
570 values are relative to the outcome under well-managed non-spatial management (horizontal
571 dashed line). Shading represents the range of outcomes for different levels of fish site-fidelity (S
572 $= 0 - 1$) and proportion of total management area within closure ($c = 0 - 50\%$). The solid lines
573 indicate means of the range of values for all combinations of S and c . The vertical dashed line
574 indicates the range of overfishing ($0 - 55\%$) within which periodic closures were, on average,
575 superior over the other forms of management strategies at balancing the triple objective of high
576 harvest efficiency, high fisheries yield, and high stock abundance.



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