



When does spillover from marine protected areas indicate benefits to fish abundance and catch?

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Abstract

Spillover is a term commonly applied to the dispersal of fish and/or larvae from inside a closed area to areas open to fishing. The presence of spillover is often quantified by measuring gradients in attributes such as abundance or catch rates near the boundaries of closed areas or by measuring higher abundance inside closed areas compared to outside. It is commonly assumed that such gradients or ratios indicate that the closed area has benefitted the fishery and the total abundance of fish. We explore this assumption using a spatially explicit model of closed areas with different intensities of fishing and fish movement, and we find that such gradients will be expected any time there is higher abundance inside the closed area. However, such gradients do not necessarily indicate a benefit to the fishery either in terms of total catch or catch rate, and unless pre-closure fishing was intense, total abundance is not expected to rise significantly. We examine case studies that argue that spillover exists and leads to fishery benefits. We then evaluate the evidence for net benefits in these case studies and find those with evidence of net benefits all come from places where fishing pressure was intense. While most analysis come from quite small coastal closed areas, two studies of very large open-ocean closed areas are discussed, and we find that both suggest little overall impact on the tuna populations that support the main commercial fisheries affected by the closures in question.

Keywords Closed areas · MPA · Marine protected areas · Spillover · Papahānaumokuākea Marine National Monument PMNM

Introduction

MPAs are often advocated as a way to prevent or reduce overfishing and at the same time increase food production from fisheries (Gaines et al. 2010; Partnership for Interdisciplinary Studies of Coastal Oceans 2002). The primary mechanism by which closed areas could benefit fished areas is often described as “spillover.” Spillover occurs when the increase of abundance inside closed areas combined with fish movement will cause fish or larvae to “spill over” across

the boundary of the closed area and become available to the fishery. Some degree of spillover will always be expected if there was fishing inside the closed area except for the most sessile of species. The key question then is not does spillover occurs, but how much spillover occurs and what can it tell us about the magnitude of conservation and fishery impacts of closed areas. Because the term MPA can be used to describe areas with many different forms of restrictions, we will use the term closed area to be more specific about forms of MPA that are closed to fishing.

Two indications that spillover may be taking place are higher abundance or catch per effort (CPUE) inside or near the boundary of the closed area and “fishing the line” in which effort tends to concentrate near the boundary of the closed area (Reithe 2003; Cabral et al. 2017; Chen et al. 2020; Van Der Lee et al. 2013; Kellner et al. 2007). The creation of a closed area that results in an increase in abundance inside the closed area should be expected to produce spillover and a subsequent density gradient so long as movement is not low relative to the size of the closed area (all else being equal, e.g., habitat). This can lead to

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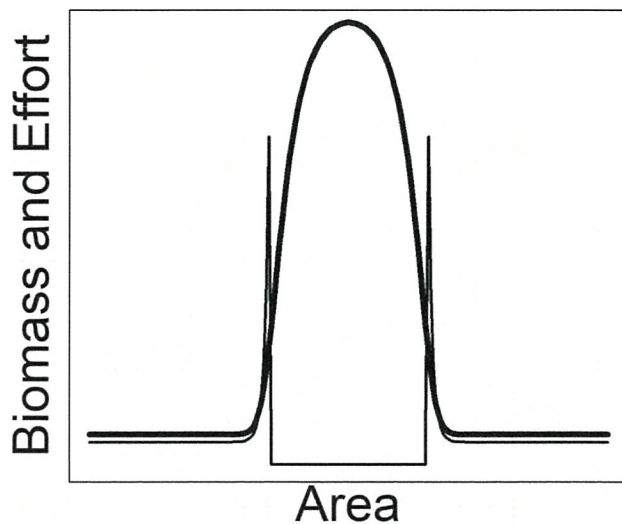


Fig. 1 The density of fish (thick line) and fishing effort (thin line) in a closed area model of a linear coastline. Redrawn from Hilborn et al. (2006)

boats concentrating near the boundary of closed areas, a phenomenon known as “fishing the line.” Fig. 1, redrawn from Hilborn et al. (2006), shows the simulated abundance of fish and the distribution of boats across a linear coastline of 100 areas with 40 areas closed to fishing in the middle. It shows a very strong density gradient across the closed area boundary and a clear pattern of “fishing the line.” Similar results can be found in Fig. 3 of White et al. (2011). The simulated scenario shown in Fig. 1 portrays a fishery that was seriously overfished, in which a closure of 40% of the area led to a rough doubling of both the total abundance of fish and the catch. This is a simple demonstration of how closed areas can benefit both biodiversity and catch through spillover when overfishing is intense.

There are many papers that measure these types of gradients with distance from closed area border, and by inference, spillover. Di Lorenzo et al. (2020) showed gradients at the boundary of 23 closed areas around the world. Harmelin-Vivien et al. (2008) showed density gradients in abundance at closed boundaries across six closed areas in the western Mediterranean. Halpern et al. (2009) reviewed 14 studies showing density gradients. Gradients in abundance are a near-universal phenomenon near closed areas as long as abundance has increased inside it. Ignoring habitat effects, the intensity of the gradient will depend on how much higher the abundance is inside and on the movement rate of each species. However, only Halpern et al. (2009) provided evidence for benefits to the total catch. Neither Di Lorenzo et al. (2020) nor Harmelin-Vivien et al. (2008) showed the causal effect of the closure on biomass and only show that abundance was higher closer to the closed areas than farther away. In the absence of appropriate controls, gradients could

simply reflect pre-existing habitat gradients reflecting closed area placement choices. Ferraro et al. (2019) and Ovando et al. (2021) discuss these and other challenges of causal inference in spatial policies.

There are some examples that do provide evidence for benefits to catch. Kerwath et al. (2013) provide strong evidence for an overall increase in catch due to a closed area in South Africa, and Goñi et al. (2010) show that the closed area allowed for individual lobsters to grow larger which benefits the fishery at the edge. Both of these areas had been intensively overfished, exactly the circumstances where theory suggests that abundance and catch would benefit from the closed areas.

Closed areas can benefit catch either by reducing recruitment overfishing or growth overfishing. Closed areas can reduce recruitment overfishing by increasing the total reproductive output of the population when it has been driven low enough so as to limit recruitment, which is normally the case for heavily exploited populations but often not the case for lightly or even moderately exploited ones (Sissenwine and Shepherd 1987). Growth overfishing occurs when the fishing gear captures individuals at a small size while they are rapidly growing (Hilborn and Walters 1992). Postponing capture to a larger size may increase the total yield with the same level of fishing effort if the benefits of larger fish size outweigh the negative effect of additional cumulative natural mortality. The closed area may facilitate this effect by allowing the individuals to grow larger inside the closed area and then be captured when they move out of it. Under these conditions, the closed area essentially acts to shift the population selectivity curve. However, fish size will be expected to increase inside a closed area simply because fish live longer and larger size inside the closed area does not necessarily mean growth overfishing was occurring.

Closed areas will benefit total abundance in the same two ways, but also by simply reducing the fraction harvested. This will occur if the closed area causes some fishing effort to leave the entire region or if the fishing effort is forced into a smaller area where competition is more intense, reducing the fraction of the population harvested. However, while population increases will be expected so long as the closed area reduces total mortality on the population, increases in catch are only possible if recruitment and/or growth overfishing would have occurred in the absence of the closed area. Higher yields would require that the protected area is large enough to stop overfishing but not so large as to reduce catches through lack of fishing grounds. A closed area covering 100% of the fishing grounds will halt overfishing but not increase catch.

Goñi et al. (2010) provide an example of a closed area potentially reducing growth overfishing. They showed that the average size of fish caught near the closed area boundary was considerably larger than elsewhere although the

number of fish caught decreased. The net effect of lower numbers but higher weight provided a catch benefit. Kerwath et al. (2013) argue that the closed area benefited the fishery by both adult and larval spillover. In this same area, Götz (2005) showed that the target species was significantly larger inside the closed area. There was no direct evidence for an increase in total spawning stock size, but the doubling of catch per unit of fishing effort and increase in total catch compared to the same species in other areas suggests that it is likely the stock was also subject to recruitment overfishing.

In recent years, the most significant trend in closed area establishment has been to close large open-ocean areas, often encompassing hundreds of thousands of square kilometers, in contrast to most of the smaller closed areas (often only a few square kilometers) where spillover has historically been measured (Halpern et al. 2009; Di Lorenzo et al. 2020). The largest five are the Ross Sea (1.9 M km²), Papahānaumokuākea Marine National PMNM in Hawaii (1.5 M km²), the US Pacific Remote islands (1.3 M km²), Pitcairn Islands (0.8 M km²), and Palau (0.8 M km²) (Marine Conservation Institute 2024). Many of these large closed areas were very lightly fished prior to establishment. For example, the Ross Sea was only fished by a handful of vessels for one species (Beer et al. 2011), the Pitcairn Islands MPA was almost unfished (Alger and Dauvergne 2017), and a set of MPAs in Brazil encompassing almost 1 M km² was very lightly fished (Giglio et al. 2018). So the expectation for these and other large, lightly fished areas would have little impact on fish abundance. Medoff et al. (2022) suggested that spillover from the Papahānaumokuākea Marine National PMNM benefited local fisheries, and they suggested such benefits could be expected from these large closed areas. They state that “If a large MPA was providing protection to a number of migratory fish species and subsequently providing a spillover benefit beyond its boundaries, one would expect to observe an increase in CPUE near the MPA relative to any changes in CPUE far from the MPA.” The closed area examined in Medoff et al. (2022) was first established in 2006 by a declaration of President George W. Bush and was expanded in 2016 by President Obama to be four times larger and to encompass all of the US economic zone west of the main Hawaiian Islands and it is the impact of this expansion that we examine.

The purpose of this paper is to explore the extent to which a gradient in abundance and/or biomass with increasing distance from the border of a closed area indicates that the fishery closure has provided any benefits to the abundance of fish and to the catch achieved. We will do this first with a range of theoretical models, then with a review of meta-analyses and studies of spillover, and finally, critically examine the evidence that there were indeed benefits to catch or

total abundance. We will look in detail at the two studies of the impact of very large closed areas.

Methods

Model description

Table 1 gives the notation and values of parameters.

Basic population dynamics

The fish population and fishing fleet are modeled in a linear grid tracking the biomass of fish (B_a) and the number of vessels (V_a) by area.

The fish population dynamics are governed by the Deriso-Schnute delay difference model (Hilborn and Walters 1992) which fully replicates an age-structured model so long as the age of recruitment and full vulnerability to fishing are the same, and the somatic growth follows the Brody relationship. The Brody relationship is a plot of the weight at age + 1 vs weight at age, and two parameters from that relationship, the y-intercept (α) and the slope (ρ).

In the absence of movement of juveniles or adults, the model equations are

$$S_{t,a} = s(1 - u_{t,a}) \quad (1)$$

where $S_{t,a}$ is the total survival from t to $t + 1$ in area a , s is the survival from natural mortality, and $u_{t,a}$ is the harvest rate at time t in area a . The number of individuals year t area a ($N_{t,a}$) depends on survival, numbers of fish the previous year, and recruitment l years before ($R_{t-l,a}$).

$$N_{t,a} = S_{t-1,a}N_{t-1,a} + R_{t-l,a} \quad (2)$$

Biomass depends upon survival, growth, and recruitment.

$$B_{t,a} = S_{t-1,a}(\alpha N_{t-1,a} + \rho B_{t-1,a}) + wR_{t-l,a} \quad (3)$$

The total egg production ($E_{t,a}$) is assumed to be the same as the mature biomass.

$$E_{t,a} = B_{t,a} \quad (4)$$

As seen in Eq. 14, the actual larval settlement in each area $E'_{t,a}$ depends on how the larval movement model shifts the larval production in space. The recruitment follows the Beverton-Holt stock-recruitment relationship, with recruits entering the population l years after spawning as seen in Eqs. 2 and 3.

$$R_{t,a} = \frac{E'_{t,a}}{e + bE'_{t,a}} \quad (5)$$

Table 1 Notation and values

Quantity	Symbol	Value
Biomass (mature and vulnerable to fishing) of fish time t , area a	$B_{t,a}$	
Number of vessels time t , area a	$V_{t,a}$	
Number of mature individuals time t , area a	$N_{t,a}$	
Survival from natural mortality	s	0.8
Fraction harvested time t , area a	$u_{t,a}$	
Total survival of fish time t to $t+1$, area a	$S_{t,a}$	
Recruits generated at time t , area a	$R_{t,a}$	
weight of an individual recruits	w	3.0738
Intercept of the Brody growth equation	α	2.3678
Slope of the Brody growth equation	ρ	0.8738
Egg production time t , area a	$E_{t,a}$	
Larval settlement after larval movement	$E'_{t,a}$	
Parameter of the Beverton-Holt stock-recruitment curve which is the inverse initial slope of the relationship	e	4.47
Parameter of the Beverton-Holt stock-recruitment curve corresponding to the inverse of the maximum recruitment	B	0.0008929
Catching power of each unit of vessel	q	
Age of recruitment and maturity	l	3
Index of an area is open to fishing (1) or closed to fishing (0)	O_a	
Total number of vessels	V^{tot}	100
Vessel aggregation parameter	c	4
Unfished recruitment per area	R_0	100
Spawner recruit steepness	h	0.7
Unfished population size in an area	B_0	4168
The distance between area a and area i	$D_{a,j}$	
The standard deviation of adult dispersal distance	σ_{adult}	3, 10, 20
The standard deviation of larval dispersal distance	$\sigma_{juvenile}$	3
The proportion of adults moving from area a to area j	$p_{a,j}^{adult}$	
The proportion of juveniles moving from area a to area j	$p_{a,j}^{juv}$	

The harvest rate in each area depends on the number of vessels in the area and the vessel efficiency parameter q .

$$u_{t,a} = 1 - \exp(-qV_{t,a}) \quad (6)$$

Prior to the establishment of closed areas, the number of vessels is the same in all areas, and the value of q is calculated to achieve the desired harvest rate from Eq. 6. However, when fishing to a quota, the assumption is that each vessel exerts more effort to achieve the quota as abundance outside the closed area declines and q needs to increase. In each year, the value of q is calculated so that the quota will be achieved. In other words, we assume that the quota operates as a target for the fishery, not a ceiling. However, we constrain the maximum harvest rate in each area to 80%, which means that when stocks are heavily fished outside the closed areas, the target harvest rate may not be achieved.

The catch in an area is the harvest rate times the biomass.

$$C_{t,a} = u_{t,a}B_{t,a} \quad (7)$$

The unfished population size in an area (B_0) is found by simulating forward with no fishing and a recruitment of R_0 . The Beverton-Holt recruitment parameters e and b are derived from input values of R_0 , the recruitment per area in the absence of fishing, and h the “steepness” a measure of the extent of compensation in the recruitment process.

$$e = \frac{B_0}{R_0} \left(1 - \frac{h - 0.2}{h0.8} \right) \quad (8)$$

$$b = \frac{h - 0.2}{0.8R_0h} \quad (9)$$

Movement calculations

Equation 10 shows how the proportion of adult fish or larvae moving from area a to area j is related to the distance between them ($D_{a,j}$) and the dispersal parameters σ_{adult} and σ_{juvenile} (denoted simply σ). Fish that move off one end of the region wrap around to the other end as if the region was a circle.

$$P_{a,j}^* = \frac{1}{\sigma\sqrt{2\pi}} \exp\left(-0.5\left[\frac{D_{a,j}}{\sigma}\right]^2\right) \quad (10)$$

The proportional movement matrix is then normalized so it adds to 1 for each a .

$$P_{a,j} = \frac{P_{a,j}^*}{\sum_j P_{a,j}^*} \quad (11)$$

There is a P matrix for adults and juveniles and an associated σ .

The biomass and numbers after movement are simply the summed biomass or numbers before and the proportion moving from area a to area j .

$$B'_{t,j} = \sum_a B_{t,j} P_{a,j}^{\text{adult}} \quad (12)$$

$$N'_{t,j} = \sum_a NP_{a,j}^{\text{adult}} \quad (13)$$

Juvenile movement may occur before or after the density dependence process of Eq. 5.

$$E_{t,j}' = \sum_a E_{t,j} P_{a,j}^{\text{juvenile}} \quad (14)$$

Fishing fleet dynamics

When a closed area is implemented in the simulation, a fixed number of areas (M) in the middle of the modeled areas are closed to fishing. Vessels are assumed to distribute themselves in relation to the abundance of fish in each area. An initial allocation to vessels in each area is governed by the following equation used in Hilborn et al. (2006). The parameter c controls how much the fleet tends to aggregate around high-density sites with a high c value (e.g., 10), causing most boats to fish in the highest abundance site, whereas a c value of zero would cause effort to be uniformly distributed regardless of the abundance.

$$V_{ta}^* = \exp\left(-c \left[1 - \frac{B_{t,a}}{\max(B_{t,a})}\right]\right) \quad (15)$$

Then, if the area is closed to fishing, no vessels are assigned to the area.

$$V_{ta}^* = O_a V_{ta}^* \quad (16)$$

And finally, the total number of vessels is distributed in proportion to this quantity.

$$V_{ta} = V^{\text{tot}} \frac{V_{ta}^*}{\sum_a V_{ta}^*} \quad (17)$$

Calculation procedure

The simulation has three major steps. First, the value of B_0 is calculated by running the model without fishing for 100 time periods by which time the model has come to equilibrium; then, the starting biomass for each cell is set to those values. The model is run without fishing for 10 years, then with fishing but no closed area for another 40 years, then with the closed area for 50 years. These time intervals allow the system to be near equilibrium before the closed areas are implemented at the end of the simulation.

A general analysis of when spillover occurs

For our demonstration, we simulate a circular coastline of 200 areas, with 30% of the areas in the middle set as a closed area. Biologically, the fish in the model mature at 3 years of age, have an annual survival rate from natural mortality of 80%, and a spawner recruit steepness of 0.7. These parameters are roughly similar to many commonly exploited species such as cod, pollock, and hake.

We ran nine combinations of three different adult movement rates and three levels of exploitation. The adult movement rates were low, medium, and high, corresponding to $\sigma_{\text{adult}} = 3, 10$, and 20 . The levels of exploitation were controlled by the number of vessels V^{tot} and the values of q . The number of vessels was adjusted to produce a total fishing mortality rate u (see Eq. 6) prior to closed area establishment of 0.5, 1, and 2, relative to u_{msy} which is the fishing mortality rate that would maximize long-term yield in the absence of closed areas. These values correspond to lightly fished, fished at u_{msy} , and overfished cases.

Impact of the expansion of the Papahānaumokuākea Marine National Monument (PMNM)

Medoff et al. (2022) proposed to measure the presence of spillover from the PMNM by comparing CPUE of bigeye (*Thunnus obesus*) and yellowfin (*Thunnus albacares*) tuna near and far and before and after expansion of the PMNM, with alternative definitions of “near” and “far” explored. This

technique is generally termed a “difference-in-difference” or “before-after-control-impact” model, and conditional on the validity of the model assumptions controls for unobserved differences in baseline CPUE between the near and far areas as well as unobserved but commonly shared temporal trends in CPUE between the before and after periods.

However, the difference-in-difference framework used in Medoff et al. (2022) makes some strong assumptions that we explore here. We had two sources of data on catch and effort for bigeye (*Thunnus obesus*) and yellowfin tuna (*Thunnus albacares*) in the region of the PMNM. Logbook data were available for each 1-degree square from 2011 to 2021, with the exception of squares where there were fewer than three boats fishing in an individual year, which were unavailable for reasons of confidentiality (but which made up less than 3% of the effort in all years of the reference time period). These data were supplied by one of the authors (JH). One of us, MF, had access to the NOAA observer data for the Hawaii-based deep-set longline fishery on a set-by-set basis from 2011 to 2022. The observer coverage target was 20% of trips.

Our first step was simply to map the spatial distribution of effort (Fig. S1), catch, and the catch per hook (CPUE) before and after PMNM expansion from the 1-degree square data (Figs. S2 and S3). Then, we used the data from the observer program to look at trends in CPUE for yellowfin and bigeye tuna before and after the establishment of the closed area as a function of distance from the closed boundary.

The difference-in-difference model used by Medoff et al. (2022) estimates the closed area effect for distance bin d (E_d), first by calculating the change in CPUE after expansion to before expansion as a function of distance from the PMNM boundary (Eq. 18). They then calculated the spillover as the difference between E_d “near” and “far” from the PMNM boundary (Eq. 19), with a range of definitions of near and far considered.

$$E_d = (CPUE_{d,after} - CPUE_{d,before}) \quad (18)$$

$$spillover = E_{near} - E_{far} \quad (19)$$

The rationale for use of this difference-in-difference style model is that it controls for both baseline differences in the pre-PMNM CPUE near and far, as well as shared additive changes in CPUE after the PMNM. In other words, if some environmental shock caused the overall abundance of tuna to increase by X in both the near and far areas, this difference-in-difference model would control for that change when calculating the effect of the PMNM above and beyond these environmental changes.

We believe it is more appropriate in this context to compare the change in CPUE as measured in ratios, rather than absolute value. Fishery data from the region show that there

were (and are) gradients and heterogeneity in CPUE in space prior to the expansion of the PMNM, suggesting that tuna abundance may be consistently higher in some areas than others. For YFT, areas near the expanded PMNM boundary had over twice the CPUE of areas 500 nautical miles away which corresponds to a latitudinal gradient in CPUE. Further, the overall CPUE of yellowfin in the overall region doubled beginning just prior to the expansion of the PMNM. This is inconsistent with the additive effect assumed by Eq. 19. If tuna redistribute themselves in space in proportion to habitat, given an environmental event that increased abundance in the region, we would have expected different areas to have the same proportional change in CPUE, not different absolute changes in CPUE. If this is indeed the case, then Eq. 19 will not properly control for environmentally driven changes in tuna abundance. The effect size used by Medoff et al. (2022) in Eq. 19 would suggest that an area with low CPUE should have risen absolutely as much as an area with high CPUE in response to an exogenous shock to tuna abundance. If Eq. 20 is correct, then we would expect that if abundance rose exogenously by 50%, then CPUE in each area also would rise by 50%.

$$E_d = (CPUE_{d,after} / CPUE_{d,before}) \quad (20)$$

We then look at the values of E_d as a function of distance from the PMNM boundary.

Results

The impact of fishing pressure and movement distance

Figure 2 shows the results for the nine cases that were run with the assumption that the fishery has a fixed annually updated quota based on a target harvest rate times the total biomass. The graphs and tables show results after 50 years of closed area implementation with 30% of the area closed.

In each year, a quota was set based on the total biomass inside and outside the closed area times a target harvest rate, $0.5 u_{msy}$, u_{msy} , and $2 u_{msy}$. The amount of effort each boat exerted was adjusted by changing q to achieve the overall target quota, provided it was possible to achieve that quota. This is equivalent to assuming that each boat fished more days each year when abundance in open areas declined. All scenarios showed higher abundance inside the closed area. Given a low dispersal rate, areas inside the center of the closed area end up at the unfished population size. Given a medium dispersal rate, the very center of the PMNM has the highest abundance but is well below the unfished population size. Given a high dispersal rate, the difference in abundance inside and out is relatively little. All cases show a gradient of

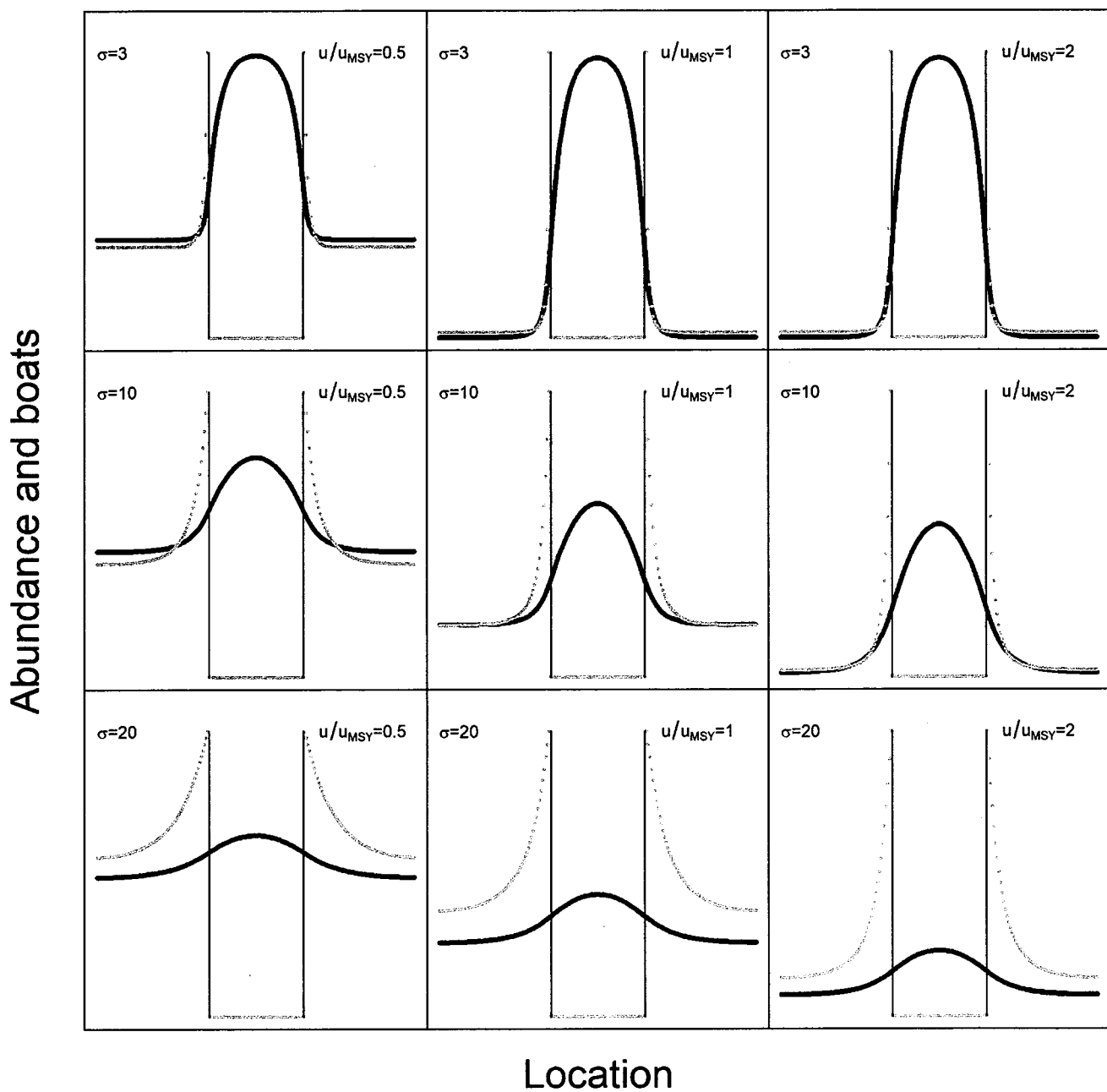


Fig. 2 The abundance of fish and boats across 200 areas with combinations of adult dispersal rate σ and u/u_{MSY} when the fishery catch is a quota set from a harvest rate times total abundance. The fish abun-

dance is a solid black line, and the distribution of boats gray dots. The two vertical black lines are the closed area boundaries

abundance at the edge of the closed area and a concomitant concentration of fishing boats adjacent to it.

In the two lowest dispersal rate cases and when the fishery mortality rate is at or above the level that would produce maximum sustainable yield (second and third columns), the fishery essentially collapses outside the closed area because the quota, which is set on the basis of the total population, cannot be achieved.

Table 2 shows the impact of a closed area on catch and total abundance as the ratio of the catch or total abundance after the closed area is implemented, compared with before. The last two columns show the catch as a fraction of the maximum sustainable yield. In none of these cases, when fishing to a quota, does the establishment of the closed area increase the catch, even though the quota would increase as abundance increases? When there is a large biomass within the closed area, the 80% harvest rate for areas close to the

Table 2 Results for the case where the fishery is managed to a quota

σ	U/U_{MSY}	Catch after/catch before	Change in biomass	Change in CPUE	Catch/MSY before	Catch/MSY after
3	0.5	0.94	0.94	0.63	0.81	0.76
3	1	0.20	0.80	0.01	1.00	0.20
3	2	0.24	2.25	0.00	0.79	0.19
10	0.5	0.98	0.98	0.84	0.81	0.80
10	1	0.91	0.92	0.57	1.00	0.91
10	2	0.69	1.45	0.11	0.79	0.54
20	0.5	1.00	1.00	0.92	0.81	0.81
20	1	0.98	0.99	0.83	1.00	0.98
20	2	0.97	1.10	0.56	0.79	0.76

closed area constrains the total harvest rate to be less than the target. In many of the cases, the reduction in catch is very small, but this is achieved by increased fishing effort. In all cases, when overfishing is occurring ($u/u_{MSY}=2$), the abundance increases. Yet without overfishing, the total abundance declines because the same total catch is taken from the open areas, while any increase in abundance inside the closed areas does not compensate for the decrease in abundance outside the closed areas.

Figure 3 shows the results of the nine cases where the total amount of fishing effort is fixed. Again, we always see a gradient in the abundance of fish near the closed area boundary with a concentration of fishing effort at the boundary. The major difference with these results compared to “fishing to a quota” scenario is that the fishery outside of the closed area does not collapse with increased fishing pressure. Although the fishing pressure outside the closed area does increase when the closure is implemented, the effort does not continue to increase in order to try to catch the quota. This has been discussed in earlier papers on closed area modeling (e.g., Ovando et al. (2021)), but the key result relevant to the topic of this paper is that regardless of the dispersal rate or the level of fishing pressure, there will be gradients in abundance at the edge of a closed area.

In Table 3, we see that in all cases, abundance goes up because the effective harvest rate declines when effort is concentrated outside the closed area, and unlike in the fixed quota scenario, the fishing effort stays constant. The catch increases in the cases where the fishing mortality rate before the closed area was well above u_{MSY} , except in the low dispersal case, where most of the biomass in the system is locked up in the closed area. In all other cases, catch declines because outside the closed area, the CPUE declines, and while effort remains constant, the harvest rate on the total population declines leading to lower catch and higher total abundance.

Literature evidence for spillover and impact on catch and abundance

Di Lorenzo et al. (2020) is the only meta-analysis of addressing spillover from closed areas and examined 23 closed areas primarily looking directly at gradients in density and/or abundance inside and outside of the closed areas. The closed areas were very small, with only 1 greater than 20 km² and 10 less than 1 km². Almost all their findings were totally consistent with the modeling presented earlier; they found that high-value commercial species were 80% higher inside the closed areas, but non-commercial species (presumably unfished) were no higher, and that the difference between inside and outside was much greater for sedentary species than for more mobile species. They found average biomass to be 54% higher close to the closed area boundary (within 200 m) compared to far away. They claim that the gradient in abundance between inside, outside close to the boundary, and outside far away is evidence for increased yield and revenue to the fishery via spillover. They say “spillover directly benefits fishery yields and revenues” without any evidence that either total abundance or catch has increased.

Lester et al. (2009) is a major meta-analysis of the abundance difference inside and outside closed areas and has been cited over 1700 times as evidence for benefits of closed areas. This study concentrated solely on abundance or density inside vs outside, and not gradients, but did discuss that spillover would likely result from this difference. No attempt was made to estimate changes in catch, CPUE, or total abundance.

There is strong empirical data to show that the relative abundance inside and outside of closed areas depends primarily on fishing pressure (Cinner et al. 2018; California Department of Fish and Wildlife 2022), and this is supported by the modeling presented earlier. Di Lorenzo et al. (2020) provided no data on the intensity of fishing in the study areas, which would, a priori, be the most likely indicator of fishery benefits.

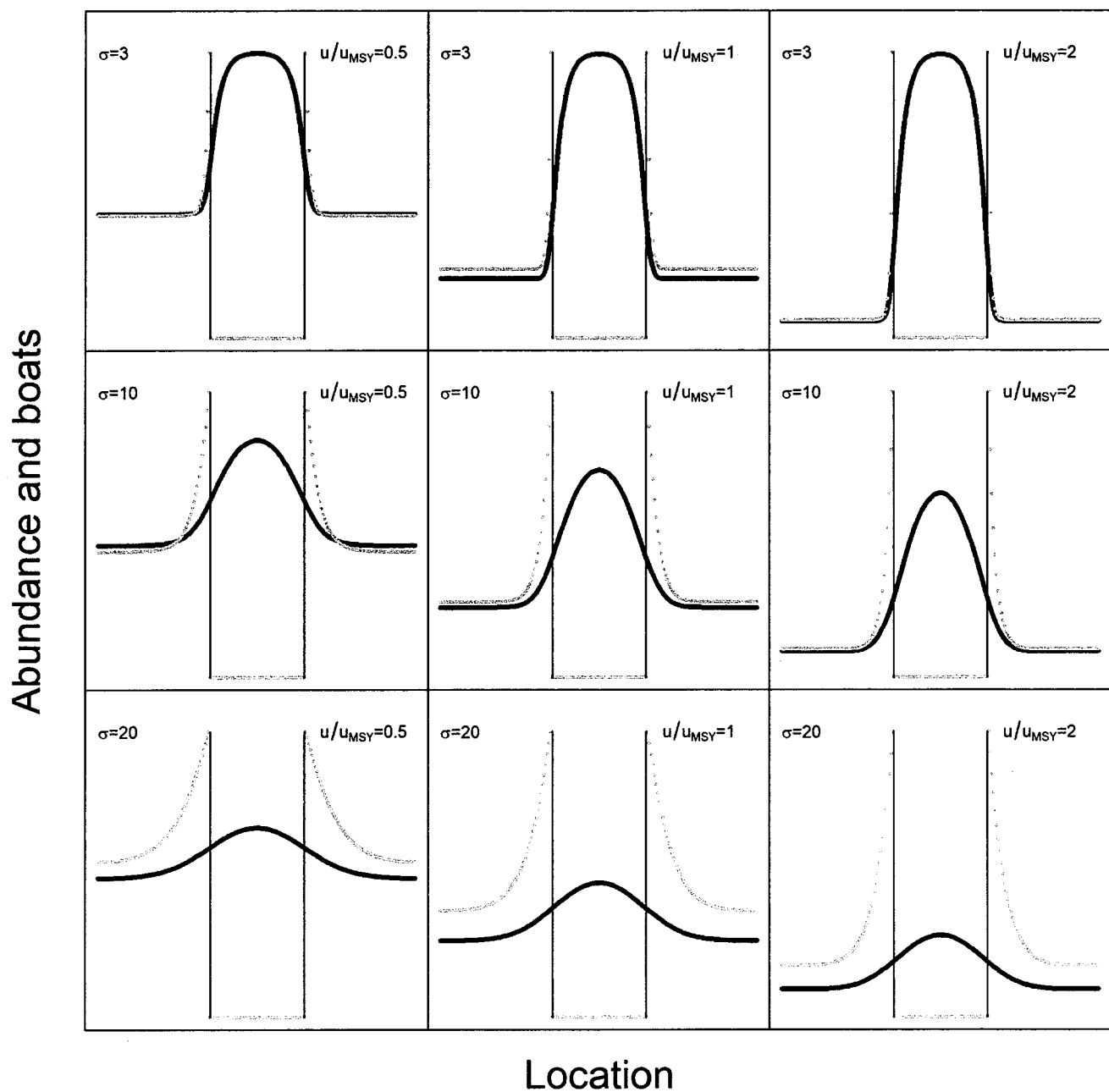


Fig. 3 The abundance of fish and boats across 200 areas for combinations of adult dispersal rate σ and u/u_{MSY} when the fishery has a fixed amount of effort. The fish abundance is a solid black line, and

the number of boats gray dots. The two vertical black lines are the closed area boundaries

The impact of the Papahānaumokuākea Marine National PMNM on bigeye and yellowfin tuna

The major US commercial fishery in the region is the longline fishery for bigeye tuna that caught an average of 4500 metric tonnes (MT) per year between 2005 and 2021. The initial PMNM in 2006 had no effect on the longline fishery as the area was already closed to longlining. From 2007 to 2015 (after the initial PMNM establishment but before the

PMNM expansion), an average of 317 MT of bigeye, that is 7% of US longline landings, were caught in the subsequently expanded area. The status of the bigeye stock in the stock assessment (Ducharme-Barth et al. 2020) for Region 2 (NE portion of the area assessed including all of the US Hawaii EEZ) is considered to be very healthy, at 60% of the unfished spawning abundance compared to 23% that would be the MSY target abundance. This suggests that fishing mortality on bigeye in Region 2 is well below u_{msy} .

Table 3 Results of the case where the fishery has fixed total effort

σ	U/U_{MSY}	Catch after/catch before	Change in biomass	Change in CPUE	Catch/MSY before	Catch/MSY after
3	0.5	0.85	1.09	0.85	0.81	0.69
3	1	0.77	1.35	0.77	1.00	0.77
3	2	0.77	2.78	0.77	0.79	0.60
10	0.5	0.92	1.06	0.92	0.81	0.75
10	1	0.91	1.21	0.91	1.00	0.91
10	2	1.07	2.12	1.07	0.79	0.84
20	0.5	0.96	1.03	0.96	0.81	0.78
20	1	0.97	1.12	0.97	1.00	0.97
20	2	1.14	1.58	1.14	0.79	0.89

The yellowfin tuna stock in Region 2 is even more lightly fished (Vincent et al. 2020), with current abundance estimated to be 90% of the unfished stock size. The abundance of yellowfin tuna in all the Western and Central Pacific, including Region 2, has increased since the PMNM expansion. In Region 2, which includes Hawaii, in 2014, the available biomass was 43,000 MT, rising to 51,000 MT in 2015, 60,000 MT in 2016, and 69,000 MT by 2018. This increase was a result of an increase in recruitment throughout the Western Pacific.

Medoff et al. (2022) estimate that the catch per hook (CPUE) of yellowfin and bigeye tuna close to the expanded PMNM increased faster than CPUEs far from the border and ascribed this result to spillover from an increase in the population inside the PMNM area due to the expansion of the closed area. This is a surprising result because there was so little fishing inside the PMNM prior to expansion, and movement rates for both yellowfin and bigeye tuna are high (Vincent et al. 2020; Ducharme-Barth et al. 2020).

Medoff et al. (2022) estimated the strongest gradient in CPUE for yellowfin tuna. Whereas almost any closed area is expected to show a gradient in abundance at the boundary, the elimination of an average annual catch of 59 MT of yellowfin tuna (0.0015 of the regional biomass) from the expanded PMNM for a stock that is so lightly fished, seems unlikely to have been responsible for a gradient in abundance at the edge of the PMNM of this magnitude.

Other studies have examined the economic impacts of PMNM and suggest either no benefit to the fishery or a negative effect. Lynham et al. (2020) argued that PMNM had no impact on the fishery when looking at the fleet as a whole, while Chan (2020) showed that vessels that had previously fished in the expanded PMNM had been significantly impacted. Chan said “The PMNM expansion caused the CPUE of this group of vessels to decrease by 7%. Revenue per trip decreased by 9%, \$3.5 million, during the first 16 months of the post-expansion period.”

Before we can consider the impact of the PMNM on the bigeye and yellowfin stocks, we need to understand the spatial distribution of effort, catch, and CPUE, and for this, we will use logbook data. The fishing effort is concentrated relatively close to the base of the fishing fleet in Oahu, and there was relatively little fishing effort in the PMNM (Fig. S1). There is no indication of effort concentrations near the PMNM boundary before or after expansion in 2016. Catch and CPUE for yellowfin before and after the expansion are shown in Fig. S2 and for bigeye in Fig. S3. The PMNM area

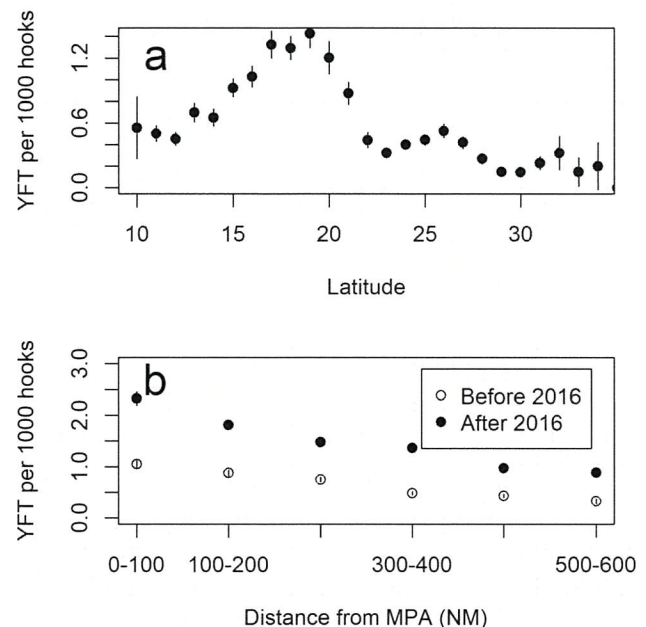


Fig. 4 The CPUE of yellowfin tuna by the deepest Hawaii longline fleet for different latitudes before the PMNM expansion (a) and as a function of distance from the expanded PMNM boundary (b). In b, the data are separated into years prior to the PMNM expansion (2010–2015) and after expansion (2017–2019). Vertical bars indicate 95% confidence intervals of the plotted means

was never an important part of the fishery for yellowfin and had minor importance for bigeye.

Medoff et al. (2022) found the strongest gradient, and thus spillover, for yellowfin. Yellowfin CPUE for the deep-set longline fleet prior to PMNM expansion showed a strong gradient in catch-per-hook of yellowfin associated with latitude which is clear in Fig. 4a, but harder to see when mapped in Fig. S2. Because the PMNM boundaries are primarily east–west, there was a strong gradient in CPUE as a function of distance from the boundary, with higher CPUE close to the boundary (Fig. 4b open circles). Areas within 100 NM of PMNM had a CPUE (fish per 1000 hooks) of 1.03, whereas areas 500–600 NM distance had a CPUE of 0.33.

Yellowfin CPUE at all latitudes and distances from the PMNM boundary increased roughly twofold after 2014. Figure 5 shows the amount of increase, both as an absolute catch per hook and as a proportion as a function of distance from the expanded PMNM boundary. While the method used in Medoff et al. (2022) theoretically accounted for pre-existing relationships between distance and CPUE, their method assumes that any changes in CPUE would be additive and that an area with a CPUE of 0.33 before the expansion of the PMNM would increase exactly as much as an area with a CPUE of 1.03.

Using the Medoff et al. (2022) model, if the areas next to the boundary doubled from 1 to 2, then for there to be no effect of the closed area, the far area would have needed to increase from 0.33 to 1.33—a fourfold increase. We would argue that as a population such as yellowfin tuna increased, we would expect that the stock would increase throughout the range, and it should be expected that all regions would have a similar proportional increase. Pre-existing differences

in abundance or catchability by latitude, longitude, distance from islands, etc. should be maintained. It is far more reasonable to expect a proportional change than an absolute one.

As seen in Fig. 5, there was actually a lower proportional increase near the closed area boundary than in areas 300 NM away. When measured in terms of proportional change, comparing areas 0–100 from the border to 200–300 suggests CPUE increased higher near the border compared to far from the border. But, comparing 0–100 to > 300 NM from the border suggests that CPUE actually increased more farther from the PMNM border than near it, which is inconsistent with the closed area effects hypothesized by Medoff et al. (2022).

Instead, when examined in terms of proportional change, yellowfin CPUE increased two- to threefold after the expansion of the PMNM throughout the areas where the US longline fishery took place. It is possible that some of this increase is due to the PMNM expansion, but when examined in terms of proportional changes with distance, we do not see evidence for this in the form of a clear gradient of changes in CPUE with distance from the PMNM border.

The bigeye CPUE within 100 NM of the PMNM boundary increased after 2014 and reached a peak in 2020, but has declined since then (Fig. S4). However, on average, bigeye CPUE closest to the boundary was 13% higher than CPUE beyond 100 NM, which may indicate a slight increase in abundance associated with the closure.

Discussion

Does spillover imply benefits to the catch or CPUE?

The results shown in Figs. 2 and 3 show that in a homogeneous spatial environment, closing areas to fishing will lead to increases in abundance inside the closed area, net movement from inside the closed area to outside, and a density gradient at the boundary. This is totally consistent with all previous closed area models going back to Beverton and Holt's (1957) classic work and including Polacheck (1990), Hastings and Botsford (1999), White et al. (2011), and Ovando et al. (2021). However, net movement from inside a closed area to outside does not necessarily demonstrate net benefits to either catch or CPUE (Tables 2 and 3). Indeed, these results are also consistent with past spatially explicit models that show that the only time catch or CPUE may benefit is when fishing pressure is exceedingly high and is more likely if the fishery is not fishing to a quota. The very few studies that have demonstrated a benefit to the fishery have been in places where fishing pressure was very high (Halpern et al. 2009; Goñi et al. 2010; Kerwath et al. 2013).

Density gradients indicate that benefits to the fishery potentially can occur, but by themselves do not provide

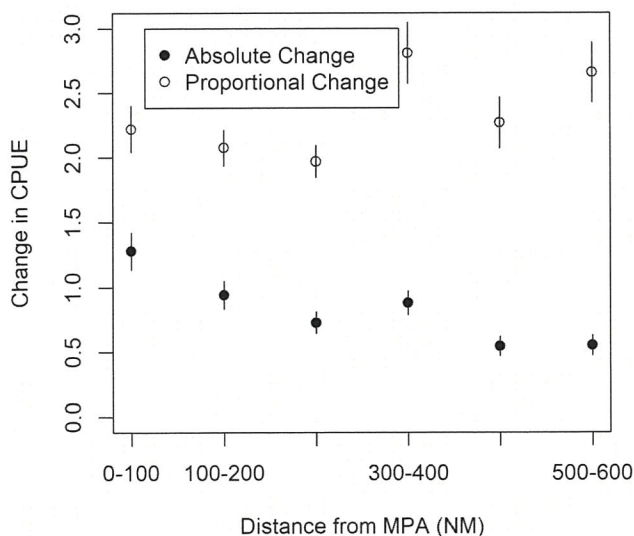


Fig. 5 Absolute increase in yellowfin CPUE plotted for different distances from closed area boundary (closed circles) and proportional increase (open circles). Vertical bars are 95% confidence intervals

strong evidence that there are such benefits. This is especially true when the level of exploitation is relatively low and the stocks are not overfished. Closing areas impacts gradients in two ways. Abundance inside the closed area will rise if there was significant fishing pressure prior to closure and the movement rate is low enough. This has been the focus of almost all closed area evaluations in the literature. Abundance outside the closed area will be expected to initially decrease due to increased fishing pressure as the fleet moves away from the closed area. The extent of this decline depends on how much effort was dislocated. As shown in Fig. 2, this is particularly extreme when the fleet is fishing to a fixed quota and movement rates are low, so that the harvest rate outside the closed area may rise greatly. Hopf et al. (2024) showed comparison of fish density inside-outside closures overestimated the impact of the closure by a factor of 2 when compared to before/after or BACI analysis.

Another interesting case where a closed area has been suggested to increase the catch of lobsters (*Panulirus interruptus*) is seen in Lenihan et al. (2021) in California. A 15-km section of the coastline with 35% of the area put into closed areas showed a much higher increase in catch than areas 20–50 km away where there were no closures. Survey data showed an increase in abundance in both areas with and without closures. However, abundance rose faster in the areas with closures than in areas without closures (Lenihan et al. 2024). This contrasted this result with closed areas established farther south on the California coast, where no increase in catch was observed in areas that included closures. The authors ascribed this to differences in how the fishing fleets had responded to the changes in abundance, that is, in the northern region, it was by fishing the line which did not happen in the southern area. In the northern area, there was no size difference between lobsters inside and outside the closed area; thus, the only potential benefit to yield would come from larval spillover. However, the larval life history of the species includes a yearlong dispersive phase where larvae from the southern California coast down to the lower end of Baja California are thought to form a single larval source (Johnson 1960, 1974), and it is accepted that the entire coastline, encompassing both the areas where catch increases were seen and where they were not, are receiving the same larval settlement. Thus, it seems impossible that larvae from a closed area would differentially influence the areas with closures, and not the adjacent areas 15 or 20 km away that had no closures.

Limitations of the closed area modeling

The simple model used in the first part of this paper makes many unrealistic assumptions including deterministic population dynamics, no cost of travel, homogeneous habitat and carrying capacity, diffuse movement, and the harvest rate

policy that the fleet can expand its effort to reach the quota. We also only looked at a single life history. Factors such as habitat heterogeneity, multiple species, and multiple fleets will greatly complicate the effects of closed areas (Ovando et al. 2024). However, the results are totally consistent with previous modeling that included a much broader range of assumptions. Looking at the effort and catch distribution of bigeye and yellowfin around Hawaii (Figs. S1–S3), it is clear that a simple linear model is a useful tautological tool, but not a realistic model which could be used fit to a real-world situation. For almost any species, habitats are discontinuous, even in a pelagic system like these fisheries around Hawaii.

Do large ocean-closed areas generate spillover and benefit the fishery?

Given that both bigeye and yellowfin tuna in Region 2 are relatively lightly exploited, the a priori probability of fishery benefits from the PMNM must be low. Not enough harvest was removed from the expanded PMNM area to suggest that the population would be expected to increase significantly due to the closure and that this would provide a net benefit to the fishery. This is especially true for yellowfin, assessed to be in a near unfished condition in Region 2. Further, because the target species, bigeye, was limited by a quota, the dislocated effort simply caught the same amount of bigeye tuna outside the expanded PMNM.

We have shown that the strong gradient in change in yellowfin CPUE estimated by Medoff et al. (2022) was an artifact of their assumption that the increase in overall CPUE would be absolutely equivalent in all areas outside the closed area. If, instead, we assume that the difference in CPUE that existed before PMNM expansion was due either to spatial differences in abundance, movement into areas, or vulnerability to fishing, it would be natural to assume that an increase in overall yellowfin abundance would most likely cause a proportional increase in different areas. It is unrealistic to assume that an area with very low CPUE would increase just as much in absolute units as a high CPUE area. The fact that Medoff et al. (2022) found the largest effect for yellowfin, a stock around Hawaii in an almost unfished condition, is almost certainly due to the overall increase in abundance and the assumption they made about equal absolute CPUE increase as the default.

Beyond methodological questions, it is important to put the kinds of results presented by Medoff et al. (2022) into context. Medoff et al. (2022) estimated that the PMNM caused an increase in CPUE in a band near the borders of PMNM (0–100 NM in their primary results). Even if this result is correct, an increase in CPUE within this narrow band is not indicative of the overall effect of PMNM on total fishery catches or the total population size of these highly mobile species.

Another large ocean-closed area that has recently been evaluated is the Phoenix Islands Protected Area (PIPA) established by Kiribati. In contrast to the Hawaii example, fishing effort in PIPA had been intense prior to its establishment. Hampton et al. (2023) used a detailed ecosystem model fit to time series of abundance and environmental data and found that the benefit to stock-wide abundance is weak to non-existent. PIPA is about 1/2 the size of the PMNM, but had catches of bigeye tuna of 5000 MT compared to PMNM at 332 MT. The stock in the region of the PIPA was estimated to be much more depleted than around Hawaii (Ducharme-Barth et al. 2020). If closing Papahānaumokuākea benefited the abundance of bigeye, PIPA should have had a much bigger impact. Hampton et al. (2023) also explored the impact of a theoretically very large closed area that would include 1/3 of the range of the species in the western Pacific and estimated such a large closure would increase the bigeye abundance by 5–12%. Thus the work of Hampton et al. (2023) casts further doubt on the claims for benefits made by Medoff et al. (2022).

Conclusions

Gradients in abundance near closed area boundaries should be expected to occur any time abundance inside the closed area increases significantly above the abundance outside, animal movement is non-trivial, and habitat effects are controlled for. The extent and magnitude of the gradient will depend on how much the relative abundance has increased, which will in turn depend primarily on the intensity of fishing prior to closed area establishment and the amount of fish movement from inside to outside. However, the existence of such gradients does not indicate that there are benefits to the catch, CPUE, or total abundance of the species. Benefits to catch and CPUE are only likely when fishing pressure was extremely high. Benefits to total abundance are also much more likely if fishing pressure was high, but could also occur if there was a significant drop in the harvest.

We found that the majority of reviews of spillover have assumed gradients in abundance imply benefits to the fishery, but with some exceptions, provide no evidence for this. Our examination of the impact of the expansion of the Papahānaumokuākea Marine National PMNM shows that there was no evidence for a benefit to the fishery and only weak evidence of a gradient in abundance near the boundary for bigeye tuna.

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Author contribution R.H. M.F. J.H. and D.O. conceived the paper and contributed to the writing. R.H. did the simulation modelling. M.F. and R.H. did the analysis of the Hawaii marine reserve data.

Data availability All data used in this analysis are confidential. The code for the simulation model is available at github.com/RayHilborn/Spillover.

Declarations

Competing interests R.H. receives funding from a range of organizations including fishing industry groups that may be perceived as conflicts.

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References

- Alger J, Dauvergne P (2017) The politics of Pacific Ocean conservation: lessons from the Pitcairn Islands marine reserve. *Pac Aff* 90:29–50
- Beer K, Brears R, Briars L, Roldan G (2011) A pragmatic utopia: should the Ross Sea be designated a marine protected area?. <https://ir.canterbury.ac.nz/server/api/core/bitstreams/87d9a919-f444-4d4a-98ad-1edc9b6abd2e/content>
- Beverton RJH, Holt SJ (1957) On the dynamics of exploited fish populations. Chapman and Hall, London
- Cabral RB, Gaines SD, Johnson BA, Bell TW, White C (2017) Drivers of redistribution of fishing and non-fishing effort after the implementation of a marine protected area network. *Ecol Appl* 27:416–428
- California Department of Fish and Wildlife (2022) California's marine protected area network decadal management review. <https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=209209&inline>
- Chan HL (2020) Economic impacts of Papahānaumokuākea Marine National Monument expansion on the Hawaii longline fishery. *Mar Policy* 115:103869
- Chen R, Baskett ML, Hastings A (2020) Fishing the line depends on reserve benefits, individual losing at boundary and movement preference. *bioRxiv* 09:15.299032
- Cinner JE, Maire E, Huchery C, MacNeil MA, Graham NA, Mora C, McClanahan TR, Barnes ML, Kittinger JN, Hicks CC (2018) Gravity of human impacts mediates coral reef conservation gains. *Proc Natl Acad Sci* 115:E6116–E6125

- Di Lorenzo M, Guidetti P, Di Franco A, Calò A, Claudet J (2020) Assessing spillover from marine protected areas and its drivers: a meta-analytical approach. *Fish Fish* 21:906–915
- Ducharme-Barth N, Vincent M, Hampton J, Hamer P, Williams P, Pilling G (2020) Stock assessment of bigeye tuna in the western and central Pacific Ocean. WCPFC, scientific committee 16th regular session SA-WP-03, pp 147. https://www.researchgate.net/publication/267936812_Stock_assessment_of_bigeye_tuna_in_the_western_and_central_Pacific_Ocean
- Ferraro PJ, Sanchirico JN, Smith MD (2019) Causal inference in coupled human and natural systems. *Proc Natl Acad Sci USA* 116:5311–5318
- Gaines SD, Lester SE, Grorud-Colvert K, Costello C, Pollnac R (2010) Evolving science of marine reserves: new developments and emerging research frontiers. *Proc Natl Acad Sci USA* 107:18251–18255
- Giglio VJ, Pinheiro HT, Bender MG, Bonaldo RM, Costa-Lotufo LV, Ferreira CE, Floeter SR, Freire A, Gasparini JL, Joyeux J-C (2018) Large and remote marine protected areas in the South Atlantic Ocean are flawed and raise concerns: comments on Soares and Lucas (2018). *Mar Policy* 96:13–17
- Gofi R, Hilborn R, Díaz D, Mallol S, Adlerstein S (2010) Net contribution of spillover from a marine reserve to fishery catches. *Mar Ecol Prog Ser* 400:233–243
- Götz A (2005) Assessment of the effect of Goukamma marine protected area on community structure and fishery dynamics. Rhodes University South Africa. <https://core.ac.uk/download/pdf/145047192.pdf>
- Halpern BS, Lester SE, Kellner JB (2009) Spillover from marine reserves and the replenishment of fished stocks. *Environ Conserv* 36:268–276
- Hampton J, Lehodey P, Senina I, Nicol S, Phillips JS, Tiamere K (2023) Limited conservation efficacy of large-scale marine protected areas for Pacific skipjack and bigeye tunas. *Front Marine Sci*. <https://doi.org/10.3389/fmars.2022.1060943>
- Harmelin-Vivien M, Le Diréac L, Bayle-Sempere J, Charbonnel E, García-Charton JA, Ody D, Pérez-Ruzafa A, Reñones O, Sánchez-Jerez P, Valle C (2008) Gradients of abundance and biomass across reserve boundaries in six Mediterranean marine protected areas: evidence of fish spillover? *Biol Cons* 141:1829–1839
- Hastings A, Botsford LW (1999) Equivalence in yield from marine reserves and traditional fisheries management. *Science* 284:1537–1538
- Hilborn R, Walters CJ (1992) Quantitative fisheries stock assessment: choice, dynamics and uncertainty. Chapman and Hall, New York
- Hilborn R, Micheli F, De Leo GA (2006) Integrating marine protected areas with catch regulation. *Can J Fish Aquat Sci* 63:642–649
- Hopf JK, Quennessen V, Ridgway J, Barceló C, Caltabellotta FP, Farnsworth Hayroyan S, Garcia D, McLeod M, Lester SE, Nickols K (2024) Ecological success of no-take marine protected areas: using population dynamics theory to inform a global meta-analysis. *Ecol Appl* e3027. https://esajournals.onlinelibrary.wiley.com/doi/pdf/10.1002/eap.3027?casa_token=vrZN3Q9L_MAAAAA%3Ahw53KfSSWVqdbGPryiNF5eubMy5QSEiypL1ZOTM8BOTmXATUtCWzkdYLkGjl_ax15BZsPvZ8B78w
- Johnson MW (1960) The offshore drift of larvae of the California spiny lobster *Panulirus interruptus*. *California Cooperative Oceanic Fish Invest Rep* 7:147–161
- Johnson MW (1974) On the dispersal of lobster larvae into the East Pacific Barrier (Decapoda, Palinuridea). *Fish Bull* 72:639–647
- Kellner JB, Tetreault I, Gaines SD, Nisbet RM (2007) Fishing the line near marine reserves in single and multispecies fisheries. *Ecol Appl* 17:1039–1054
- Kerwath SE, Winker H, Gotz A, Attwood CG (2013) Marine protected area improves yield without disadvantaging fishers. *Nat Commun* 4:2347. <https://doi.org/10.1038/ncomms3347>
- Lenihan HS, Gallagher JP, Peters JR, Stier AC, Hofmeister JK, Reed DC (2021) Evidence that spillover from Marine Protected Areas benefits the spiny lobster (*Panulirus interruptus*) fishery in southern California. *Sci Rep* 11:2663
- Lenihan HS, Reed DC, Vigo M, Leiphardt C, Hofmeister JK, Gallagher JP, Voss C, Moore P, Miller RJ (2024) Regional differences in fishing behavior determine whether a marine reserve network enhances fishery yield. *Sci Rep* 14:1242
- Lester S, Halpern B, Grorud-Colvert K, Lubchenco J, Ruttenberg B, Gaines S, Airamé S, Warner R (2009) Biological effects within no-take marine reserves: a global synthesis. *Mar Ecol Prog Ser* 384:33–46
- Lynham J, Nikolaev A, Raynor J, Vilela T, Villaseñor-Derbez JC (2020) Impact of two of the world's largest protected areas on longline fishery catch rates. *Nat Commun* 11:1–9
- Marine Conservation Institute (2024) Largest marine protected areas. <https://mpatlas.org/large-mpas/>
- Medoff S, Lynham J, Raynor J (2022) Spillover benefits from the world's largest fully protected MPA. *Science* 378:313–316
- Ovando D, Caselle JE, Costello C, Deschenes O, Gaines SD, Hilborn R, Liu O (2021) Assessing the population-level conservation effects of marine protected areas. *Conserv Biol* 35:1861–1870
- Ovando D, Bradley D, Burns E, Thomas L, Thorson J (2024) Simulating benefits, costs and trade-offs of spatial management in marine social-ecological systems. *Fish Fisheries* 25:218–234
- Partnership for Interdisciplinary Studies of Coastal Oceans (2002) The Science of marine reserves. <http://www.piscoweb.org>
- Polacheck T (1990) Year round closed areas as a management tool. *Nat Resour Model* 4:327–354
- Reithe S (2003) Quotas, marine reserves and fishing the line. When does marine reserve creation pay?. <https://munin.uit.no/bitstream/handle/10037/915/article.pdf?isAllowed=y&sequence=1>
- Sissenwine MP, Shepherd JG (1987) An alternative perspective on recruitment overfishing and biological reference points. *Can J Fish Aquat Sci* 44:913–918
- Van Der Lee A, Gillis D, Comeau P, Hurley P (2013) Fishing the line: catch and effort distribution around the seasonal haddock (*Melanogrammus aeglefinus*) spawning closure on the Scotian Shelf. *Can J Fish Aquat Sci* 70:973–981
- Vincent M, Ducharme-Barth ND, Hammer P, Hampton J, Williams P, Pilling G (2020) Stock assessment of yellowfin tuna in the western and central Pacific Ocean. WCPFC-SC16–2020/SA-WP-04 (Rev.3) M., <https://meetings.wcpfc.int/node/11694>
- White JW, Botsford LW, Baskett ML, Barnett LA, Barr RJ, Hastings A (2011) Linking models with monitoring data for assessing performance of no-take marine reserves. *Front Ecol Environ* 9:390–399