# Trade-offs between bycatch and target catches in static versus dynamic fishery closures

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Edited by Nils Chr. Stenseth, Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biosciences, Universitetet i Oslo, Oslo, Norway; received August 18, 2021; accepted November 22, 2021

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**While there have been recent improvements in reducing bycatch in many fisheries, bycatch remains a threat for numerous species around the globe. Static spatial and temporal closures are used in many places as a tool to reduce bycatch. However, their effectiveness in achieving this goal is uncertain, particularly for highly mobile species. We evaluated evidence for the effects of temporal, static, and dynamic area closures on the bycatch and target catch of 15 fisheries around the world. Assuming perfect knowledge of where the catch and bycatch occurs and a closure of 30% of the fishing area, we found that dynamic area closures could reduce bycatch by an average of 57% without sacrificing catch of target species, compared to 16% reductions in bycatch achievable by static closures. The degree of bycatch reduction achievable for a certain quantity of target catch was related to the correlation in space and time between target and bycatch species. If the correlation was high, it was harder to find an area to reduce bycatch without sacrificing catch of target species. If the goal of spatial closures is to reduce bycatch, our results suggest that dynamic management provides substantially better outcomes than classic static marine area closures. The use of dynamic ocean management might be difficult to implement and enforce in many regions. Nevertheless, dynamic approaches will be increasingly valuable as climate change drives species and fisheries into new habitats or extended ranges, altering species-fishery interactions and underscoring the need for more responsive and flexible regulatory mechanisms.**

static and dynamic closures | bycatch mitigation | fisheries management | marine protected areas

Fisheries are among the most important sources of employment (1) and food security in many coastal nations and small islands. In 2017, fish consumption represented 17% of the animal protein intake globally (2). Over the past 70 y, worldwide wild marine capture fisheries production increased from around 20 million metric tons in 1950 to almost 85 million metric tons in 2018 (2). A major impediment to ensuring that fisheries are sustainable is the impact of fishing practices on both targeted and nontargeted species, including bycatch of marine megafauna such as sea turtles, seabirds, sharks, and marine mammals (3, 4). We define bycatch for the purpose of this study as any unwanted catch, which is discarded alive, injured, or dead (modified from ref. 5). Target catch is defined here as the species with higher commercial value that, in general (except in some small-scale artisanal fisheries), comprise the largest fraction of catch kept and sold or consumed.

Fisheries bycatch has been identified as one of the main threats to the populations of many species around the world. For example, bycatch in longline fisheries is thought to be the largest threat to albatross and large petrel populations, many of which are threatened or endangered (6). Pelagic drift gillnet

## Significance

The incidental catch of threatened species is still one of the main barriers to fisheries sustainability. What would happen if we closed 30% of the ocean to fishing with the goal of reducing bycatch? Analyzing 15 different fisheries around the globe, we found that under static area management, such as classic no-take marine area closures, observed bycatch could be reduced by 16%. However, under dynamic ocean management based on observed bycatch and closing the same total area but fragmented in smaller areas that can move year to year, that reduction can increase up to 57% at minimal or no loss of target catch.

Author contributions: M.P. and R.H. designed research; J.T.W., D.O., S.A., S.B., A.D., M.F., R.F., M.H., E.L.H., J.E.J., M.H., S.J., D.M.K., S.K., J.L., J.M., L.P., L.R., K.R., R. Sant'Ana, R. Sharma, J.A.S., and K.S. analyzed data; and M.P., J.T.W., D.O., S.A., S.B., A.D., M.F., R.F., M.H., E.L.H., J.E.J., M.H., S.J., D.M.K., S.K., J.L., J.M., L.P., L.R., K.R., R. Sant'Ana, R. Sharma, J.A.S., K.S., and R.H. wrote the paper.

Competing interest statement: Some of the authors are involved in fisheries management or provide fisheries advice in ways that can be viewed as competing interests. Many are employed by national fisheries agencies (J.T.W., A.D., M.F., R.F., E.L.H., J.E.J., S.J., J.M., K.R., and K.S.), intergovernmental (J.L. and M. Hall) and nongovernmental organizations (S.A., L.P., L.R., and R. Sharma) or fishing industry (M. Herrera) that advocate for specific fisheries policies. The academic scientists have received funding from sources that include government fisheries agencies (M.P., D.O., S.B., R. Sant'Ana, J.A.S., and R.H.), fishing companies (M.P., D.O., and R.H.), and nongovernmental organizations (M.P., D.O., R. Sant'Ana, and R.H.).

This article is a PNAS Direct Submission.



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This article contains supporting information online at http://www.pnas.org/lookup/suppl/doi:10.1073/pnas.2114508119/-/DCSupplemental.

Published January 20, 2022.

fisheries, which account for around 34% of Indian Ocean tuna catches, have caught an estimated cumulative total of 4.1 million small cetaceans between 1950 and 2018 (7). Meanwhile, the vaquita porpoise (*Phocoena phocoena*) population has declined 92% between 1997 and 2015 due to incidental mortality in Mexican gillnet fisheries (8), leaving fewer than 19 individuals in 2018 (9). Among small cetaceans, bycatch is the greatest threat for 11 out of 13 species listed as critically endangered by the International Union for Conservation of Nature (IUCN) (10). In addition, bycatch of juvenile fish in trawl shrimp fisheries is a major concern, as shrimp fisheries account for 27% of the total recorded discards in commercial fisheries globally (11).

Area and temporal closures are a generic mitigation measure that can help reduce bycatch of multiple species that overlap in space and time and are often used to reduce fisheries bycatch (5, 12, 13). For example, depth-based, seasonally varying, gear-specific Rockfish Conservations Areas (RCAs) were implemented by the Pacific Fishery Management Council in 2002 to reduce incidental catch of overfished rockfish species along the west coast of the United States. Following the recovery of multiple rockfish species, the trawl RCAs off Oregon and California were reopened in 2020. Similarly, numerous spatial and temporal closures exist in tuna fisheries, typically to control juvenile mortality and/or bycatch (14). In the Eastern Pacific Ocean (EPO), the Inter-American Tropical Tuna Commission (IATTC) implements a spatial closure known as the "Corralito" (96° to 110°W between 4°N and 3°S) from 29 September to 29 October that was designed to reduce the catch of juvenile bigeye (*Thunnus obesus*) and yellowfin (*Thunnus albacares*) tunas. In terms of bigeye tuna conservation, the IATTC argues that this closure is equivalent to closing the whole EPO to purse-seine fishing for ∼3 d but with less effect on target yellowfin tuna, since most of the yellowfin catch occurs outside this area (15). Spatial closures have also been implemented in Brazil to protect multiple nontarget species from demersal gillnet fisheries targeting monkfish, *Lophius gastrophysus* (16). However, the effectiveness of these closures in reducing bycatch or targeted species has not been comprehensively evaluated.

A major concern for the efficacy of spatial and temporal closures is the extent to which, rather than reducing total fishing effort, they simply redistribute effort away from some areas/times while concentrating it in others (17–20). If fishing effort is displaced rather than removed, spatial and temporal closures can create trade-offs between reduced fishing mortality on bycatch and target species inside no-take protected areas or during protected times, and potentially increase fishing mortality of nontarget species in waters surrounding closures (19–21). For example, Abbot and Haynie (19) found that the implementation of large spatial closures in a North Pacific trawl fishery designed to protect red king crab (*Paralithodes camtschaticus*) promoted dramatic increases in Pacific halibut (*Hippoglossus stenolepis*) bycatch due to direct displacement effects and indirect effects from adaptations in fishermen's targeting behavior.

In the last decades, momentum has grown for the use of spatial restrictions, such as no-take marine protected areas (MPAs), to conserve ocean biodiversity. The main goals of MPAs are commonly protecting and restoring spatially defined ecosystems or specific habitats (e.g., seamounts and coral reefs), conserving and preserving cultural heritage, creating opportunities for education and research, preserving unaltered habitats as reference areas against global change, providing benefits for recreation and tourism, or seeking to improve outcomes for adjacent fisheries through "spillover" of fish or larvae from inside the MPA to outside (with this spillover effect needing to be greater in magnitude than the impacts of lost fishing grounds to provide a net increase in fishing outcomes) (22–24). Today, many nations are calling for protection (MPAs safe from some or all forms of human exploitation) for 30% of the world's ocean by 2030, a call endorsed by a resolution of the IUCN World Conservation Congress in 2016 (25). Even though this "30 × 30" proposal is not based solely on a desire to reduce bycatch, protection of biodiversity is a key objective of this proposed expansion of protected areas, and a key task in protecting biodiversity is reducing bycatch.

In this study, we build on the concepts of 30 × 30 by analyzing what might happen to both bycatch and target species if 30% of the fishing areas in a database of fisheries around the world were closed to exploitation. We focus on differences in potential outcomes resulting from protecting a static or dynamic portion—in the range of 30%—of evaluated fishing grounds. The effectiveness of permanent static area closures at reducing bycatch is still an open question (13, 26, 27). Static area closures identify a fixed area of the ocean to be placed in a permanent protected area based on perceptions of current or future threats and objectives. However, the optimal habitats of mobile species can shift within and across years due to environmental variability and climate change, thereby modifying interactions between fisheries and bycatch species in space and time. Dynamic ocean management is an emerging tool in which management measures (e.g., closures) can change across space and time in response to environmental variability and ocean uses (28), helping to balance bycatch and economic opportunity for fisheries (18, 29, 30). Ideally, dynamic management tools can integrate near-real-time environmental data to track multiple species' habitats to optimize bycatch to target catch ratios (31, 32).

Some studies have considered the general advantages of dynamic ocean management (29, 31, 33) and provided assessments of the role of spatial closures in bycatch reduction in specific case studies (18). Along with bycatch reduction alone, a key consideration is how policies can be designed to minimize bycatch while maintaining the economic, nutritional, and cultural benefits obtained by sustainably managing target species (34–36). In this study, we make an important advance to this literature by producing an empirical multigear evaluation of the potential effects of different spatial, dynamic, and temporal closures on not only bycatch but target species outcomes across 15 global fisheries (Fig. 1).

We specifically address the following questions: 1) How effective are static no-take areas and temporal closures in reducing bycatch compared to dynamic time and area closures? 2) What are the trade-offs among bycatch reduction, changes in fishing effort, and target species catch under static versus dynamic closures? 3) How much reduction in bycatch would be achieved by closing 30% of fishing areas under static or dynamic scenarios? We used data collected by on-board observers or declared in detailed logbooks to identify areas in which the ratio of bycatch to target catch is high and explored the potential impacts of static and dynamic closures of these areas under different configurations (Fig. 2). A critical feature of our study is that we account for the simultaneous impacts of effort displacement across multiple bycatch and target species using two possible fleet models: constant effort and constant catch. Under constant effort, total fishing effort remains constant with or without closures. When closures are in effect, the constant total fishing effort is concentrated in the remaining areas open to fishing. Under the constant catch scenario, fishing effort is allowed to change to maintain the same level of total target catch with or without closures. So, when closures are in effect, total effort can increase or decrease outside the closures to maintain the same fishery-wide total catch. Under both scenarios, we distribute fishing effort in the open areas in proportion to the spatial distribution of effort in the open areas preclosures.

We also considered scenarios in which fishing efficiency (i.e., catch per unit of effort [CPUE]) remains the same after

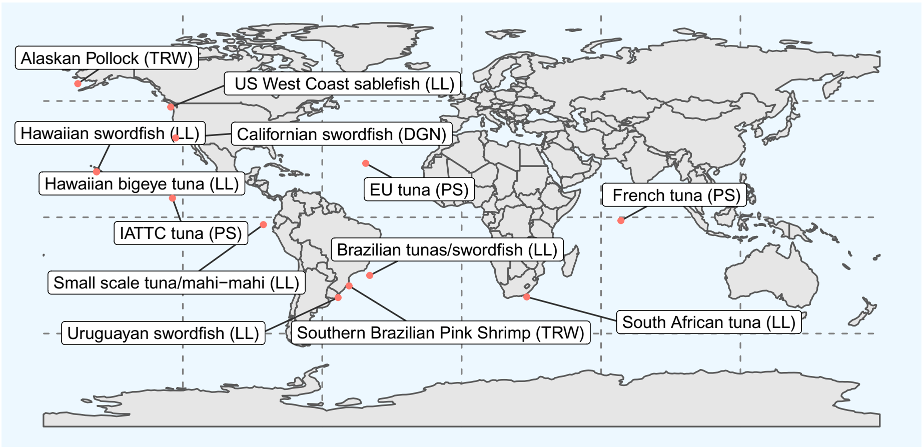


**Fig. 1.** Location of the fishery case studies used in the analysis. LL: Longline; DGN: Drift Gillnet; TRW: Trawling; PS: Purse-seine.

closures and in which fishing efficiency for target species decreases in response to more intense fishing outside of closures (*SI Appendix*, Fig. S1).

## Results

A total of 15 fisheries around the globe (Fig. 1 and *SI Appendix*, Table S1) were analyzed, and the commonalities across these case studies were summarized. We then considered the potential impacts to bycatch and target species of a range of spatial and temporal closures, defined by whether a feature can change over time (dynamic versus static) and whether the feature must be contiguous in space (mosaic versus centroid). A dynamic mosaic design is the most similar to a dynamic ocean management approach, while a static centroid design is the most similar to a classic no-take MPA. Given perfect information, a dynamic approach will always perform as well or better than a static approach. Similarly, a mosaic area shape will always perform as well or better than a centroid shape (Fig. 2). Nonetheless, the detailed information from our case studies allowed us to quantify the potential magnitude of these differences in a variety of real-world scenarios.

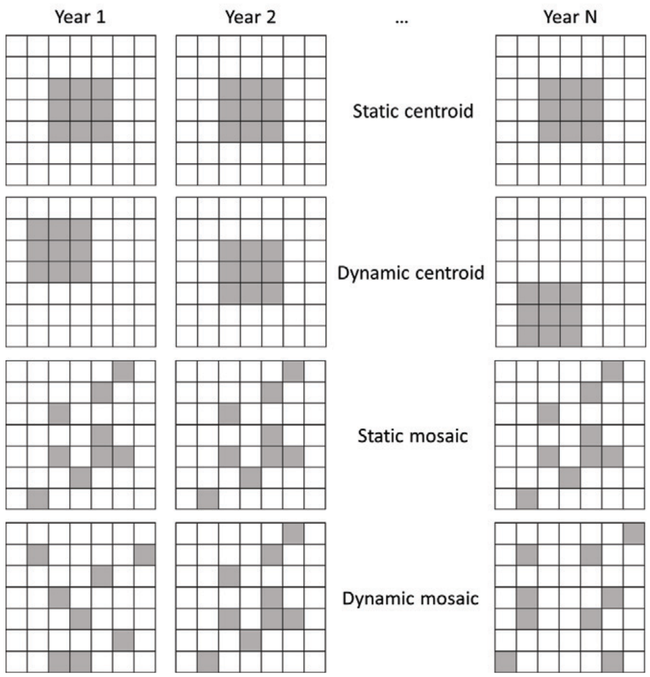


**Fig. 2.** Representation of 1) a static area closed around a centroid (no movement from year to year; first row) or dynamic (moves from year to year; second row); and 2) a mosaic area, static (third row) and dynamic (fourth row).

**How Effective Are Static No-take Areas and Temporal Closures in Reducing Bycatch Compared to Dynamic Time and Area Closures?** In general, bycatch (summed across all species) declined as more of the area or time was closed (Fig. 3, *Top*). A static closed area around a centroid (pink line in Fig. 3, *Top*), which is analogous to permanent no-take areas, resulted in a greater reduction in bycatch than temporal closures (even when closing 5 mo to fishing; gray line in Fig. 3, *Top*). With a static closure of 30% of the total fishing zone (assuming that fishing effort is displaced but fishing efficiency remains the same), bycatch was reduced by 17% (*SI Appendix*, Table S2). Alternatively, if we assume constant catch and constant fishing efficiency, the decrease in bycatch was 20% on average. With constant catch but reduced fishing efficiency, bycatch was reduced by only 10% (Fig. 4, *Top* and *SI Appendix*, Table S2). Bycatch reduction was much higher (~28% on average) if the centroid closure was allowed to be dynamic in both space and time (i.e., moves from year to year) (green line and box in top panels in Figs. 3 and 4, respectively). For the dynamic mosaic closure, in which independent areas with high bycatch-to-target ratios can be closed and shifted year to year, the potential bycatch reduction was considerably higher than scenarios with static closures (orange line in Fig. 3, *Top*). For a 30% closure under dynamic mosaic management, bycatch could be reduced by 56% under constant effort and constant fishing efficiency and 59% under constant catch and constant fishing efficiency (top panel in Fig. 4 and average percentage values in *SI Appendix*, Table S2). Thus, mosaic designs were more effective than centroid designs in reducing bycatch (50% compared to 22% on average for all scenarios; *SI Appendix*, Table S2), and dynamic management, in which those areas can move year to year (Fig. 2), was more effective than static management approaches (48% compared to 29% on average for all scenarios; *SI Appendix*, Table S2). In addition, area closures were more effective in general than temporal closures, which, on average for 3-mo closures, for example, only reduced bycatch by 4% averaged across all scenarios (Fig. 3).

**What Are the Trade-offs among Bycatch Reduction, Changes in Fishing Effort, and Target Species Catch under Static versus Dynamic Closures?** Overall, when assuming constant fishing efficiency and constant effort, reductions in bycatch were achieved

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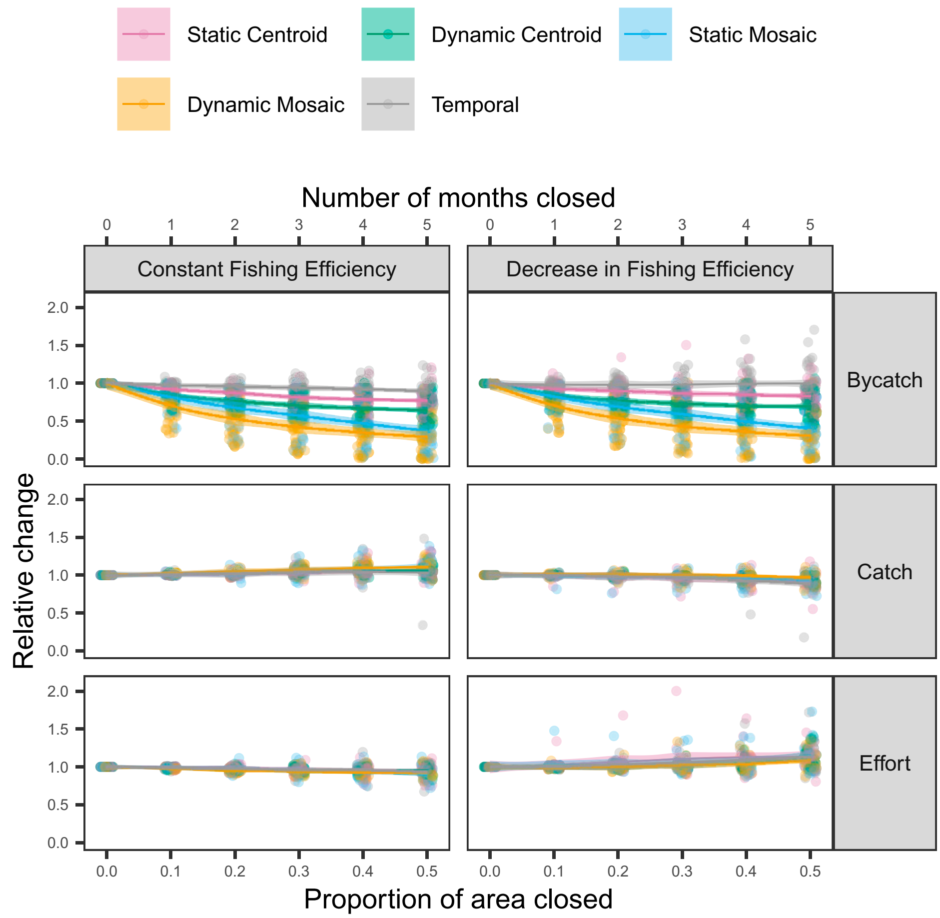


**Fig. 3.** Relative changes for each type of closure for bycatch (*Top*), target catch when total effort remains the same (constant effort, *Middle*), and effort when total catch remains the same (constant catch, *Bottom*). For bycatch, relative changes for both constant effort and constant catch scenarios were combined for simplicity and because there were almost no differences between them (*SI Appendix*, Fig. S11). Points represent individual case studies; lines are a smooth curve with the band around them representing one SD. The column on the left represents when fishing efficiency remain constant, and the column on the right when fishing efficiency (target species CPUE) decreases. The primary *x*-axis shows the proportion of area closed from 0.1 or 10% to 0. 5 or 50% of the fishing zone. For temporal closures, the number of months closed are represented on the secondary *x*-axis at the top (gray line only).

without large changes in the capture of the target species (left panel on the middle row in Figs. 3 and 4). This is because we preferentially closed areas in which the ratios of bycatch to target species were higher. The catch of target species was 3% more for permanent or stationary closures under constant effort and fishing efficiency or 7% more for dynamic mosaic closures under the same scenario (Fig. 4 and *SI Appendix*, Table S1). However, if we assume that fishing efficiency was negatively affected by an increase in effort outside the closed area, the catch of target species was 4% lower than without any closure for static centroid areas or remained the same for dynamic mosaic closures (right panel on the middle row in Figs. 3 and 4 and average percentages in *SI Appendix*, Table S2). In general, the potential of reducing bycatch without reducing the catch of target species (no matter the configuration of the area or assumptions of changes in fishing efficiency) was slightly higher for dynamic closures (~3% more) than for static closures (~1% less; *SI Appendix*, Table S2).

Overall, similar trends were observed under the constant catch scenario (Figs. 3 and 4, *Bottom*). When we assumed that fishing efficiency decreased for a 30% area closure, effort had to increase to reach the same total catch (Fig. 4 and *SI Appendix*, Table S2). Specifically, for mosaic dynamic closures, effort had to increase by 2% when closing 30% of the fishing area to achieve the same total catch, but it had to increase by 11% under a traditional static centroid closure (Fig. 4, *Bottom Left* and *SI Appendix*, Table S2).

**How Much Reduction in Bycatch Would Be Achieved by Closing 30% of Fishing Areas under Static or Dynamic Scenarios?** A mosaic dynamic design is closest to dynamic ocean management, while a centroid static design is most similar to a classic no-take marine protected area (Fig. 2). In general, a closure of 30% of the fishing area reduced bycatch by an average of 57% with a mosaic dynamic design without sacrificing the catch of target species, compared to a 16% average by a centroid static area closure. Thus, dynamic ocean management was substantially more effective in reducing bycatch than classic static approaches for area closures. Even when we allowed a static centroid area to be a mosaic (closing multiple small areas), bycatch was reduced by 42% compared to the 57% achieved under the mosaic dynamic design. Adding the dynamic component to the mosaic design accounted for the extra 15% of the bycatch reduction (*SI Appendix*, Table S2). If we allow the static centroid area to be dynamic, the bycatch reduction can increase from 16 to 28% (*SI Appendix*, Table S2).

**Differences among Case Studies.** The trends and magnitude of the relative changes for all fisheries combined varied among case studies (Figs. 5 and 6). For example, in the Hawaiian swordfish (*Xiphias gladius*) and Hawaiian bigeye tuna fisheries,

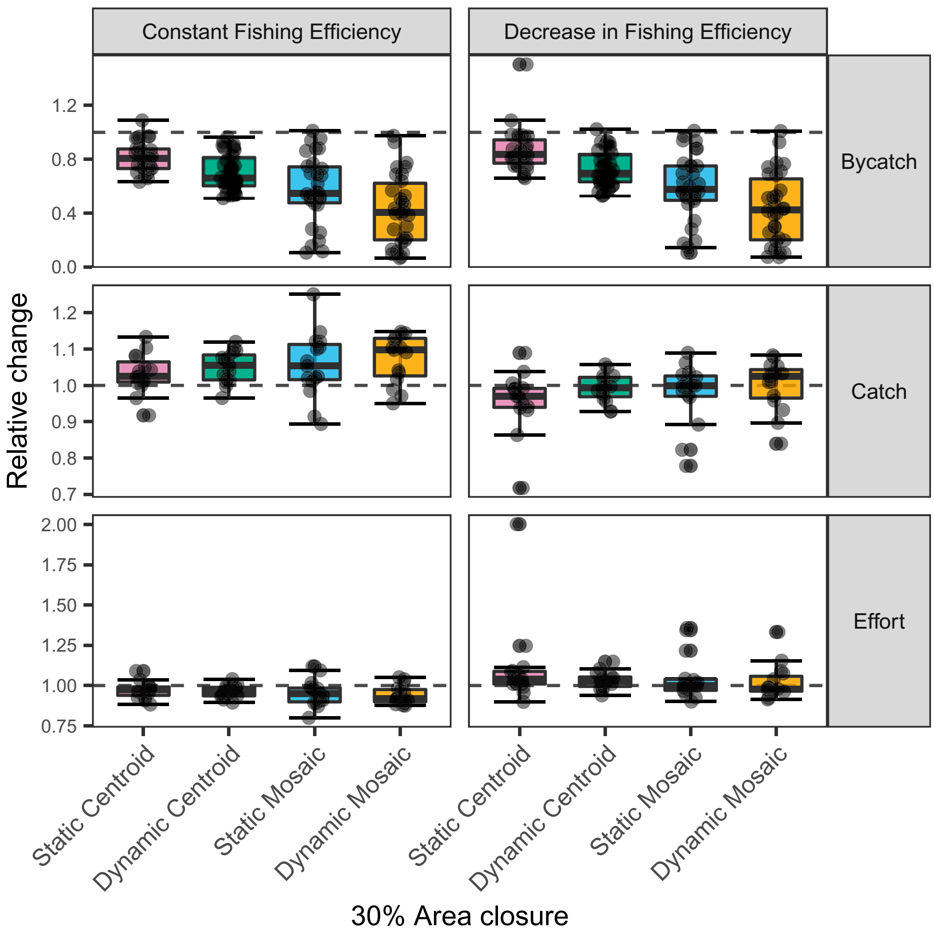


**Fig. 4.** Relative changes for each type of closure when closing 30% of the total area to fishing for bycatch (*Top*), target catch when total effort remains the same (constant effort, *Middle*), and effort when total catch remains the same (constant catch, *Bottom*). For bycatch, both constant catch and constant effort scenarios were combined for simplicity and because there were almost no differences between them (*SI Appendix*, Fig. S12). The column on the left represents when fishing efficiency is constant, and the column on the right when fishing efficiency decreases. The box represents the quartiles (25, 50, or 75 percentiles) in which 50% (horizontal line in the box) is the median. The upper whisker is the maximum value of the data that is within 1.5 times the interquartile range over the 75th percentile. The lower whisker is the minimum value of the data that is within 1.5 times the interquartile range under the 25th percentile. Each case study is represented by the gray dots. The horizontal dashed line is the status quo.

a dynamic mosaic closure drastically reduced bycatch without major consequences on the total catch of target species when fishing effort remained constant (Fig. 5). However, for some oceanic purse-seine tuna fisheries, like in the Indian and Atlantic oceans, spatial closures of any kind had almost no effect on bycatch when closing 30% of the area.

The differences among case studies were partially associated with the spatiotemporal correlations between target and bycatch species. When the correlation between catch of target species and bycatch was high (e.g., European Union Atlantic purse-seine tuna fishery), the relative difference in bycatch reduction to target catch loss was smaller than if the correlation was low (Fig. 7). As an example, if we have one target species and one bycatch species, we will have the least impact on the target catch if there is a low or negative correlation between catches of target species and bycatch species. However, if multiple bycatch species have similar spatial and temporal hot spots, then dynamic or static closures will work comparably well. In some of our case studies, closing areas to protect one species dislocated effort in ways that resulted in increased bycatch of other species. For the case study of the small-scale/artisanal surface fishery for tuna and mahi-mahi in the EPO, under mosaic closures, bycatch decreased for almost every species (particularly for leatherback sea turtles, *Dermochelys coriacea*) but with a slight increase in seabird bycatch, which was higher for static than dynamic closures (*SI Appendix*, Fig. S9). Despite this, seabird bycatch in this fishery is very low (~0.004% of the total).

## Discussion

Sustainable fisheries are critical to securing the livelihoods and resources of millions of people. However, many fisheries, including both those with sustainable and those with unsustainable directed fishing, produce large amounts of bycatch that threaten the future of incidentally captured species. We analyzed target catch and bycatch data from 15 fisheries around the world to evaluate the potential effectiveness of different time and area closures as a bycatch mitigation measure. For these case studies, dynamic mosaic area closures were more effective in reducing bycatch while minimizing reductions in catch of target species, compared to static centroid area closures. For example, closing 30% of a fishing area under a mosaic dynamic approach could reduce bycatch by an average of 57% in comparison to 16% reductions in bycatch achievable under a static centroid closure. The magnitude of bycatch reduction possible is related to the correlation in space and time between target and bycatch species. The higher the correlation between target and bycatch species, the more challenging it is to find an area or temporal closure with a high reduction in bycatch without sacrificing catch of target species. Overall, the magnitude of bycatch reduction

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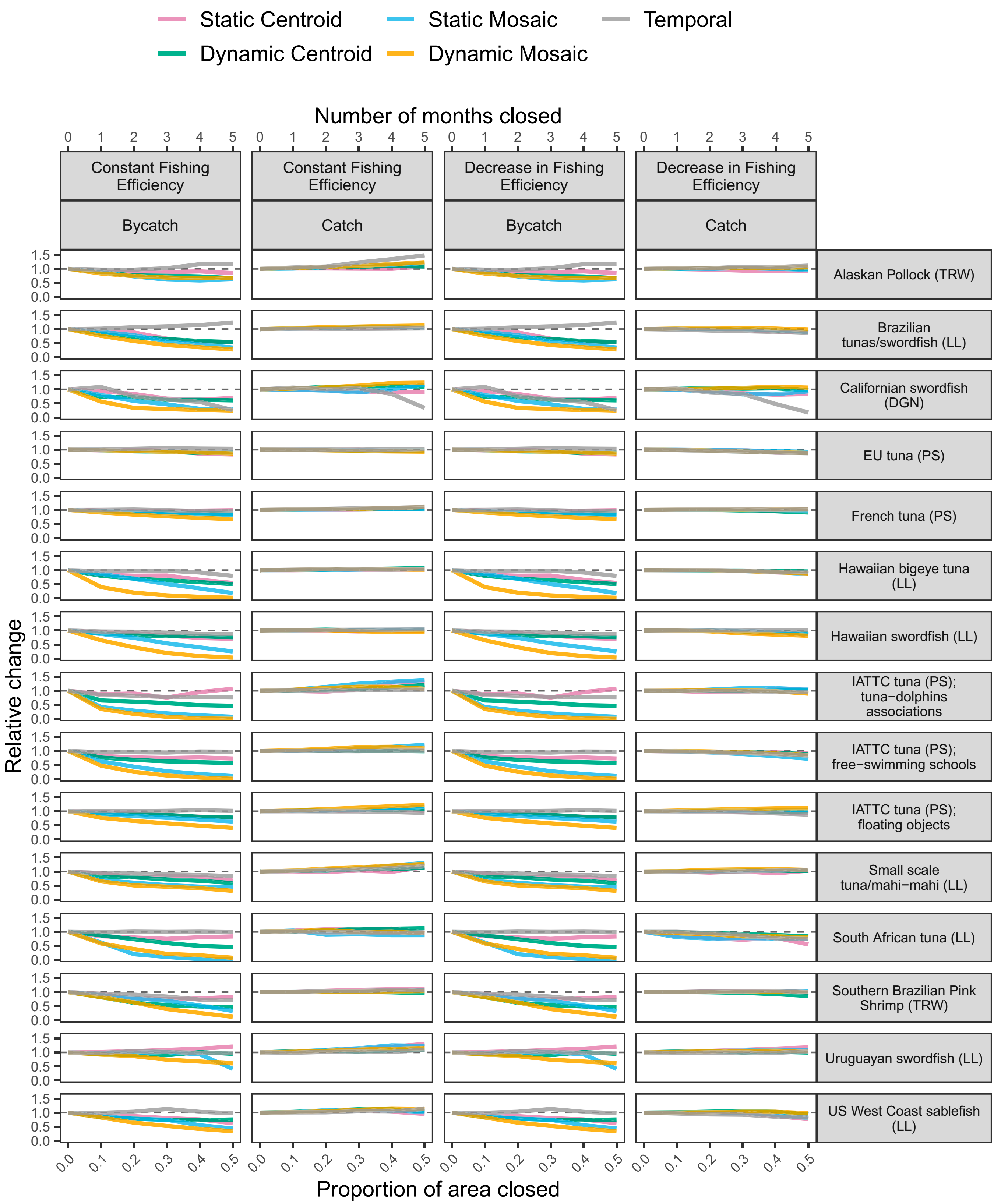


**Fig. 5.** Relative changes for each type of closure and each case study (rows) for total bycatch and catch of target species. These results are for the scenarios during which total effort remains the same (constant effort) and fishing efficiency decreases (*Right*) or remains constant (*Left*). The primary *x*-axis shows the proportion of area closed from 0.1, or 10%, to 0.5, or 50%, of the fishing zone. For temporal closures, the number of months closed are represented on the secondary *x*-axis at the top.

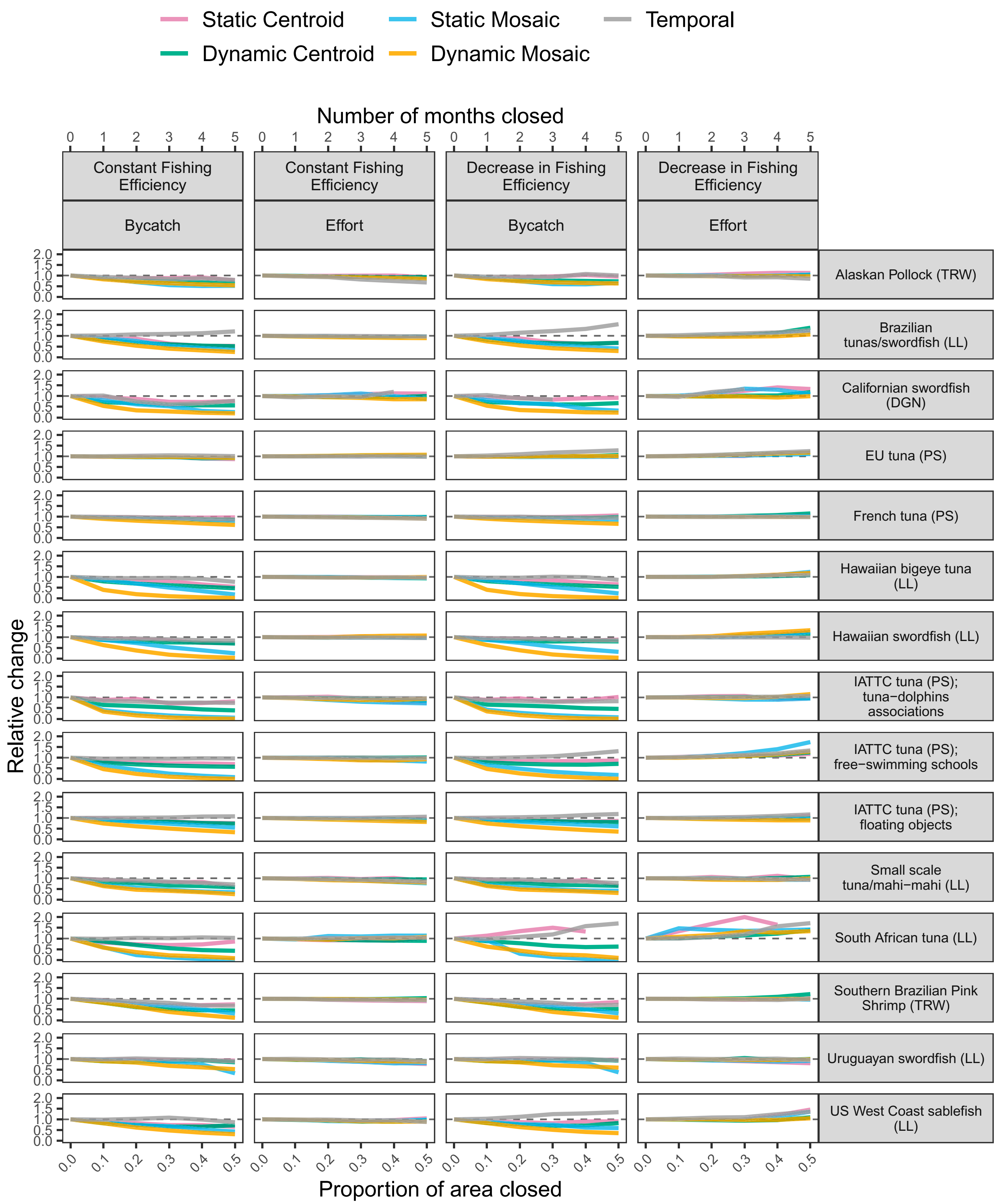


**Fig. 6.** Relative changes for each type of closure and each case study (rows) for total bycatch and effort. These results are for the scenarios when total catch of target species remains the same (constant catch) and fishing efficiency decreases (*Right*) or remains constant (*Left*). The primary *x*-axis shows the proportion of area closed from 0.1, or 10%, to 0.5, or 50%, of the fishing zone. For temporal closures, the number of months closed are represented on the secondary *x*-axis at the top.

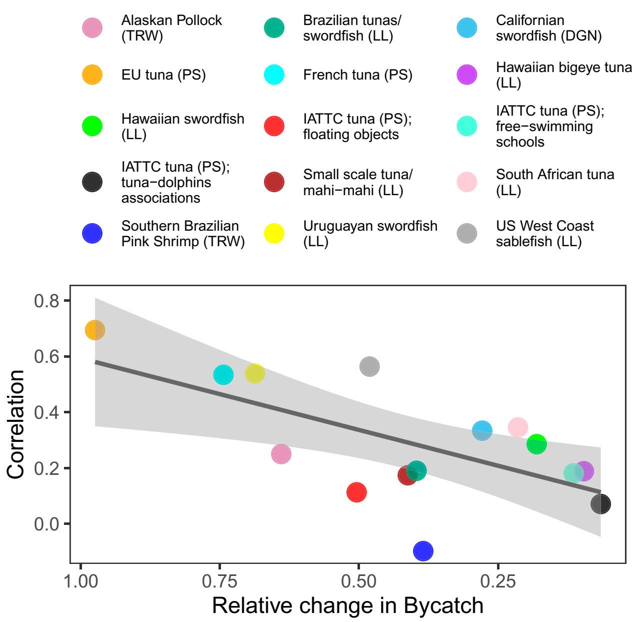


**Fig. 7.** Relationship between predicted bycatch reduction (*x*-axis) and correlation between total bycatch and total target species (*y*-axis). Bycatch reduction indicates relative change compared to no closure (= 1). Each dot represents a different case study, and this plot shows, as an example, the results from a 30% closed area in a dynamic mosaic approach. The solid line represents a simple regression and the gray area the 95% CI. LL: Longline; DGN: Drift Gillnet; TRW: Trawling; PS: Purse-seine. US: United satte; EU: European Union; IATTC: Inter-American Tropical Tuna Commission.

was different among fisheries, with significant variability in the potential effectiveness of both spatial and temporal closures.

Our results suggest that moving from centroid to mosaic closed-area designs (when static) facilitated a dramatic reduction in bycatch (from 16 to 42%), and moving to a mosaic dynamic approach, which is the closest approach to "real-time closures," allowed for further reductions in bycatch for mobile species (57% reduction; *SI Appendix*, Table S2). However, we emphasize that these results assume perfect knowledge of the distributions of effort and catch for different target and bycatch species. Real-world dynamic management must contend with the challenges of imperfect or sparse information, communication, and compliance. Yet there are several existing examples of dynamic real-time closures that address these challenges. Real-time closures for bycatch avoidance could be achieved through coordinated communication among fishers (13, 17, 37). This provides economic benefits to the industry by reducing the risk of exceeding bycatch thresholds while minimizing the reduction of target species catch. Gilman et al. (38) summarized the success of different fleet communication programs in the United States. They found that voluntary fleet communication programs substantially reduced fisheries bycatch and provided economic benefits. Although this type of bycatch mitigation measure can be successful without causing unintended impacts, it relies on participation from most fishing vessels and typically requires strong economic incentives (17, 38). It would also require real-time monitoring and reporting of bycatch, which is costly and logistically challenging and is difficult to implement and enforce in fisheries where economic resources, data collection, monitoring, and access to technology are limited.

Rather than relying on collective action and rapid communication alone, real-time dynamic closures could also be achieved by predicting and avoiding hot spots for bycatch by using environmental variables. Hazen et al. (31) developed habitat suitability models for target and bycatch species using satellite telemetry and fisheries observer data. Then, using daily satellite data to track ocean features, species movement, and fisheries, they predicted dynamic vulnerable habitats for bycatch species. They found that by tracking daily oceanographic conditions, the California swordfish drift gillnet fishery could access some of the currently closed fishing areas while still protecting leatherback sea turtles. Even if daily adjustments are not feasible, they suggested that annual adjustments to closed areas in response to interannual variability could achieve 80% of the successes of fully dynamic closures. Our study also demonstrates the potential benefits of dynamic annual adjustments over a static approach that does not change year to year.

Temporal closure scenarios were generally less effective for bycatch mitigation than spatial closures, though they still had efficacy under certain conditions. Temporal closures have been promoted to protect migratory routes for highly migratory and endangered species (14, 39) or to protect a specific life history stage of a population. For example, temporal closures may be particularly effective for protecting vulnerable life stages in single-species management, especially when the biology and ecology of all life history stages are known. In some case studies presented here (e.g., EU Atlantic purse-seine tuna fisheries), the life history plays a particularly complicated role as the same species transitions from bycatch as a juvenile to target catch as an adult (*SI Appendix*). The greater the correlation among these life stages, the more difficult it can be to design effective spatial or temporal closures (Fig. 7). High correlations between bycatch and target species (or life stages) are likely to be a common trend for some fisheries, and more sophisticated algorithms, such as Marxan, may help to reduce sensitivity to inter- and intraspecies correlations when designing area closures (40).

Integrated, multispecies bycatch assessments should be incorporated into the decision-making process (21). We have shown that the decrease in bycatch of some species could produce an increase of bycatch of other species (*SI Appendix*, Fig. S9). Baum et al. (22) demonstrated this for a hypothetical area closure that reduced bycatch for most coastal and endangered shark species but increased bycatch rates of other oceanic sharks and threatened sea turtles. Species do not occur in isolation, and there is an increasing need to better consider the dynamic relationships among species and communities. These relationships, as well as the relationships among species and their environments, and target species and the fishers themselves, will all influence the efficacy of static or dynamic closures.

This study analyzed the consequences of temporal and area closures with the goal of reducing bycatch of mobile species. Our results are an estimation of what could happen to the bycatch, catch of target species, and fishing effort if we closed a certain area or month of the year to fishing within our case-study systems. However, we assumed that the behavior of bycatch species was not impacted by the redistribution of fishing effort. Seabirds, seals, orcas, and other such opportunistic predators are commonly attracted to fishing vessels, where they may feed on bait and/or discards (41). As a result, the reductions in bycatch associated with spatial closures may be modulated if such animals shift their distributions to follow fishing vessels. Even well-enforced area closures should be accompanied by other kinds of mitigation measures, such as gear modifications (19) and better handling and release practices to increase postrelease survival (35), where and when appropriate.

Our model allows for fishing efficiency, and hence target species CPUE, within a patch to either remain constant or decrease in response to increased effort resulting from spatial or temporal closures. Assuming that fishing efficiency decreases approximates a scenario in which increased fishing effort reduces fish biomass or reduces gear effectiveness. In the absence of spillover from closed areas, all else being equal, increased fishing effort must decrease abundance and therefore

CPUE, and so the scenario in which fishing efficiency remains unchanged reflects a scenario in which some spillover benefits are provided by the closed areas. However, it is also possible that spatial or temporal closures result in a net increase in CPUE if spillover is sufficient. While we do not consider such a scenario here, a "fishing efficiency increases" scenario could be considered in locations where the target species are heavily overfished (42).

Considering the ratio of bycatch to target species catch when deciding which area or month to close is one way to minimize socioeconomic impacts (43). Using this approach, we found that the relative change in target catch was minimal for almost all types of closures. It ranged from 4% less than business as usual for static centroid areas when fishing efficiency decreased (*SI Appendix*, Table S2) to 7% more for dynamic mosaic areas when fishing efficiency does not change (*SI Appendix*, Table S2). The implications of these differences are not only based in the type of area closure but in the assumptions that fishing efficiency can change. However, even if we assumed that fishing efficiency decreased in a dynamic mosaic approach, target catch remained unchanged. Beyond this, spatial closures in general can have differing impacts on fishers depending on their ports as well as added fuel costs and increased carbon footprints if further travel is required (18, 30, 44). We assumed that fishing effort inside the closed area would reallocate outside proportional to the effort that was outside the area before the closure. However, fisheries effort is not evenly distributed, with effort influenced by environment, vessel competition, fish availability and market, biological, cultural, and political factors (45). Moreover, we have not considered the economic costs of moving effort outside the closed area, which is a key assumption we have made, and the actual redistribution of effort observed will depend on the fishery and fishing grounds as well as subsidies and other economic incentives. The cost of traveling further from port could exacerbate impacts of both static and dynamic spatial closures (18), including impacts on the value of landed catch. Also, travel distance can increase safety risk to vessels, particularly small vessels forced farther offshore due to closed areas. However, this depends entirely on the spatial configuration of the fishery and the closure.

Most regulatory frameworks that establish time or area closures involve complex processes that are slow to implement and change. Thus, as the spatial distributions of some species shift in response to variable or changing climate conditions (44), the built-in flexibility associated with dynamic fishery closures becomes more valuable. Even at short timescales, the movement of most mobile species, associated with the dynamic characteristics of the ocean, highlights the greater efficiency of managing bycatch to target catch ratios via dynamic versus static closures.

Even though real-time closures are effective in reducing bycatch, we acknowledge that such dynamic approaches and their intensity might be very difficult to implement, particularly in fisheries where resources and/or management capacity are limited (19). The application of these dynamic approaches requires clear management goals and expensive or logistically challenging data provisions, which can include on-board observers, animal tracking and remote sensing information, sophisticated modeling techniques to predict species distribution, rapid data-sharing technology, advanced analytical processing power, continuous engagement with communities, and strong management and enforcement (28, 38).

## Conclusion

Spatial dynamic ocean management can be 3.6 times more effective than a static approach (such as a classic no-take area) when the main goal is to avoid bycatch. However, when the goal is to protect a critical habitat, a static biodiversity hot spot, or a unique feature, a static area closure could be more effective and easier to enforce. Therefore, when considering protecting a percentage of the ocean with conservation in mind, we must consider the ways in which closure strategies may achieve bycatch reduction as well as other conservation goals and the magnitude of associated trade-offs to the well-being of people who depend on the resources from those habitats.

## Materials and Methods

We analyzed the effect of area and temporal (monthly) closures using logbooks ($n = 3$ fisheries) and on-board observer data ($n = 12$ fisheries) collected from 15 fisheries around the globe (*SI Appendix*, Table S1). Our study included industrial and small-scale fisheries with surface- and bottom-fishing gears. Refer to *SI Appendix* for a brief description of each fishery. For most case studies, catch data were available at the resolution of individual deployments of fishing gear and for each species or group of species. We aggregated catch data by date (months and year) and spatial location (with a resolution of 0.5, 1, or 5 degrees of latitude and longitude depending on the resolution available for each fishery). For area closures, a range of 0 to 50% of the total fishing ground was considered for closure. For temporal closures, a range of 0 to 5 mo was explored. Each case study was analyzed independently, and results were combined to summarize general findings.

One reason why case studies were analyzed independently, besides the resolution and use of different fishing gears, is that species that are targeted in one fishery could be considered as bycatch in other fisheries and vice versa. For example, juvenile tunas in most purse-seine fisheries are targeted and marketed. However, for management purposes, juvenile tunas such as bigeye, *T. obesus*, could be considered bycatch (or at least unwanted catch), as avoiding juveniles would result in a more sustainable fishery. The purse-seine fisheries case studies presented in this paper considered both juvenile and adult bigeye tunas (depending on the case study; *SI Appendix*) as bycatch to explore the effect of spatial and temporal closures to minimize their catches.

Bycatch was analyzed in some cases at the species level and, in other cases, aggregated across species (e.g., in the EPO tuna/mahi-mahi fishery, the marine turtle group included loggerheads *Caretta caretta*, green turtles *Chelonia mydas*, olive ridley *Lepidochelys olivacea*, and hawksbill *Eretmochelys imbricate*, but leatherbacks were considered at the species level). Because not all species or groups of species have the same conservation concern, different conservation prioritization weights were assigned to each species or group to control their relative importance in informing closures. Individual bycatch species weights were assigned independently for each fishery, and the weighting criteria and species aggregations are described in *SI Appendix*.

Target species weights were primarily assigned based on economic importance or, potentially, other considerations (e.g., secondary target species, such as sharks, might have more importance in some fisheries than in others). Higher weights were given to those target species whose catches were to be maximized; similarly, larger weights were assigned to bycatch species whose catch we most sought to minimize. Analyses without the weighting process are presented in *SI Appendix* as a sensitivity examination (*SI Appendix*, Figs. S13–S17).

We considered three different approaches to determine closure areas or seasons that minimize 1) amount (numbers or kilos) of bycatch species, 2) bycatch rates (bycatch/effort) or 3) the ratio of bycatch to target species. In the last case, we sought to reduce as much of the bycatch as possible with the lowest losses in target catch. However, there are often trade-offs between these objectives. We did not find large differences among the minimization methods used (*SI Appendix*, Fig. S2), so for simplicity, and because we were interested in the trade-off between reducing bycatch without compromising the catch of target species, we presented the results from the third minimization method.

A factorial design (*SI Appendix*, Fig. S1) was considered to analyze scenarios. As the first factor, we considered two different closure configurations or shapes. For the centroid strategy, we selected a quadrant as a centroid and then calculated the amount of bycatch caught in the cells closest to the centroid (that constitute a certain percentage of areas closed). We then identified which centroid minimized bycatch the most. For instance, if we closed 30% of the area, we found which cells had the most bycatch in the 30% of quadrants closest to the cell. In the mosaic strategy, we closed independent quadrants to minimize bycatch, without the constraint that each quadrant had to be connected to the others (Fig. 2).

The second factor determined if the area was 1) static (fixed and permanent for the entire period) or 2) dynamic (mobile and potentially shifting spatially year to year). A combination of mosaic and dynamic area would be the closest to a real-time management approach; see Fig. 2 (29, 31, 38).

As a third factor, we considered two different approaches for fisheries management: 1) fishing effort is displaced but total effort remains constant

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https://doi.org/10.1073/pnas.2114508119

(constant effort). In this case, the catch of the target species changes based on the catch rates outside the area closed. This scenario is based on fisheries that are managed by effort controls. For fisheries managed under catch or quota controls, 2) fishing effort changes to achieve the preclosure total catch of target species in the remaining locations outside the closed areas (constant catch). The total catch of target species before and after the closure remains the same (see *SI Appendix* for more details on the calculations). Under both scenarios, the total amount of effort is distributed in the remaining open areas in proportion to the distribution of effort in the open areas preclosure.

Finally, our fourth factor considered two scenarios for the relationship between effort and fishing efficiency. In the first, we assumed the fishing efficiency of the fleets remains the same regardless of the concentration of fishing effort, which means that the CPUE of the target species does not change when effort is displaced outside the closed area (constant fishing efficiency). Thus, an increase in effort would produce an increase in catch proportional to the target CPUE. As an alternative, we assumed that the fishing efficiency (~CPUE) would be reduced by an increase in effort in the open areas, so an increase in effort would produce a decrease in the abundance of the target species outside the closed area and subsequently a decrease in catch (reduced fishing efficiency). Refer to *SI Appendix* for details on calculations.

Most of the datasets used in this study are confidential due to privacy restrictions associated with fishing locations. Thus, analyses were performed by the individual authors of each case study using a set of standardized R functions (code available at https://github.com/maitepons/MPA_tool). If needed, additional analyses can be performed upon request to the authors. In addition, an interactive web application is available in which users can input their own data to get results with the methods proposed in this paper here: https://maitepons.shinyapps.io/Spatial_temporal_closures_bycatch_reductions/.

**Data Availability.** R code has been deposited on Github (https://github.com/maitepons/MPA_tool). Some data cannot be shared directly; most of the datasets used in this study are confidential due to privacy restrictions associated with fishing locations. Guidelines for researchers interested in accessing/requesting each dataset: 1) Alaskan pollock: anonymized data used in the study is available at https://github.com/jordanwatson/Pons_PNAS; 2) Brazilian tunas/swordfish and Southern Brazilian Pink Shrimp: the datasets used in this analysis are subject to confidentiality requirements, so the raw data cannot be shared publicly. To request this data from Brazilian fisheries used in this analysis, please contact the Applied Marine Studies Laboratory of the School of the Sea, Science and Technology of the University of Vale do Itajaí; 3) Californian swordfish: The fisheries-dependent data from the Drift Gillnet (DGN) observer program were collected by the National Oceanic and Atmospheric Administration (NOAA) National Marine Fisheries Service and are confidential US government data. To request access to data from the West Coast Region Observer Program, please contact Charles Villafana (Charles.Villafana@noaa.gov); 4) EU tuna: this data can be shared upon request to miguel.herrera@opagac.org; 5) French tuna: this data are confidential. To request access to it, please contact David Kaplan at david.kaplan@ird.fr; 6) Hawaiian bigeye tuna and Hawaiian swordfish: the data from the Pacific Islands Regional Observer Program used in this analysis are subject to confidentiality requirements, so the raw data cannot be shared publicly. To request nonconfidential observer data from this program, contact the coauthor Mark Fitchett (mark.fitchett@wpcouncil.org); 7) IATTC tuna: tuna–dolphin associations and free-swimming schools and floating objects datasets: the raw data cannot be shared publicly, but there is a simplified version of the data used in this study available at the following link: https://www.iattc.org/PublicDomainData/IATTC-Catch-by-species1.htm. The raw data with higher resolution used in this study could be formally requested to IATTC at datahandlers@iattc.org; 8) Small-scale tuna/mahi-mahi: these data were collected under confidentiality and mutual trust agreements with individuals, associations, and fishing sectors of nine countries, and their use will require the approval of each of them in each country to be accessed by third parties. For further analysis and research collaboration, please contact Sandra Andraka (sandrakag@gmail.com); 9) South African tuna: this dataset is restricted and only accessible after approved written request to Sven Kerwath, Department of Forestry, Fisheries and the Environment: Fisheries Research and Development at SKerwath@dffe.gov.za; 10) Uruguayan swordfish: the data from the observer program ("Programa Nacional de Observadores a bordo de la flota atunera uruguaya") of the Uruguayan pelagic longline fishery used in this study are considered confidential under the Uruguayan decree N° 115/018, chapter XI, so the raw data cannot be shared publicly. On reasonable request of nonconfidential observer data, please contact Andrés Domingo (adomingo@mgap.gub.uy); 11) US West Coast sablefish: the data from the West Coast Groundfish Observer Program (WCGOP) used in this analysis are subject to confidentiality requirements set forth in The Magnuson-Stevens Act at section 402(b), 16 U.S.C. 1881a(b), so the raw data cannot be shared publicly. To request nonconfidential observer data from the WCGOP, contact the Fisheries Observation Science Program at the Northwest Fisheries Science Center.

**ACKNOWLEDGMENTS.** We thank all the fisheries observers who collected the valuable data necessary for this project. For D.M.K. and the French Indian Ocean (IO) purse, we thank the IRD-Ob7 pelagic observatory of the MARBEC laboratory for French IO tropical tuna logbook and observer data management and preparation, particularly L. Floch and P. Sabarros. Bycatch data for the French IO purse-seine fishery were collected under the auspices of the European program "Data Collection Framework" (Reg [EC] 1543/2000 and 199/2008) and the French "Observateur Commun Unique et Permanent" observation program supported by French purse-seine companies (Orthongel, a professional organization of the French tropical tuna purse-seine fishery). We would also like to thank Charles Villafana and the West Coast Observer Program for their help with the California Drift Gillnet fishery, Alan Haynie for valuable comments on an earlier draft, and Nicole Baker Loke for helping us during the submission process. The scientific results and conclusions, as well as any views or opinions expressed herein, are those of the authors and do not necessarily reflect the views of NOAA or the Department of Commerce.

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