Environmental market design for large-scale marine conservation

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It is commonly agreed that marine conservation should expand considerably around the world. However, most countries have not yet implemented large-scale no-take Marine Protected Areas (MPAs). When a country closes a large fraction of its waters to fishing, it stands to lose a considerable level of fishery revenue. Although biodiversity and spillover fishing benefits may far exceed these losses, benefits from large-scale MPAs typically accrue to other countries or to the high seas. Here, to overcome this dilemma, we simulate and test an international fisheries management scheme with transferable fishing rights that incentivizes, rather than hinders, large-scale marine conservation. By combining a bioeconomic model of cross-country trading of fishing rights with vessel-level tracking data before and after a large-scale conservation action is implemented, we show that transferable fishing rights and a biomass-based allocation rule are pivotal to incentivize conservation under this market-based setting. Our work focuses on the Vessel Day Scheme (VDS)—an environmental market that is employed by the Parties to the Nauru Agreement (a group of nine Pacific Island nations) to manage their tuna fisheries—and areas in which large-scale conservation interventions have taken place. Overall, these results provide a template for how to incentivize countries to engage in large-scale marine conservation within a market-based setting.

ecognizing the need to protect marine biodiversity and ecosystem services, various international bodies have committed to substantially expand marine protection around the world by protecting 30% of the oceans^{1,2}, with a focus on no-take MPAs^{3,4}. Although most MPAs implemented to date have been small, it is widely recognized that very large MPAs must also be part of the strategy if we are to meet these goals. But would any country rationally close 30%, 80% or even 100% of its waters to fishing if this means losing all fishing revenue from within the closed area? At first glance, the answer is probably 'no'. Losing this important source of revenue would cripple many fishing-dependent economies, particularly the Pacific Island nations, which are viewed by many as viable candidates for large closures⁵. By contrast, the closure may generate substantial spillover of larvae and adult fish6,7, as well as other benefits, into adjacent waters that could, in principle, offset these losses. The problem with this argument is that for very large MPAs, these spillover benefits could accrue to other nations and to the high seas⁸, with no obvious mechanism for the conserving country to recoup them. International fishing-effort markets, in which nations trade the right to fish across international boundaries, may offer a viable solution. The design and effectiveness of fishing-effort markets for fisheries management have been explored previously^{9,10}, but little attention has been given to the role that these markets can play in conservation. Here we show how new fishing-effort markets can be designed or existing ones modified to incentivize the implementation of large-scale MPAs.

We are motivated by a real-world, albeit relatively understudied, institution called the Parties to the Nauru Agreement (PNA). The PNA is a coalition of nine Pacific Island nations that collectively manages purse seine fishing of tuna in the waters of its members^{10,11} (Fig. 1). These waters account for 14.5 million km² (an area that is four times larger than the continental United States) and more than 60% of the skipjack tuna caught in the Western Central Pacific¹⁰. The PNA manages this tuna purse seine fishery using a VDS in which

total annual fishing effort is capped at around 45,000 vessel-days. Vessel-days are allocated across the nine nations, which then lease the vessel-days to fishing vessels, most of which are foreign. Generally, a vessel-day grants a fishing vessel the right to fish for 24h within one of the nine Exclusive Economic Zones (EEZs) within the PNA. Member nations derive enormous benefits from leasing these fishing rights to foreign fleets, in some cases exceeding half of a country's GDP¹². In addition to highly productive tuna fisheries, the PNA waters provide a wealth of ecosystem benefits; there is therefore a focus on largescale conservation efforts in the region⁵. In 2015, Kiribati-a PNA member-created the Phoenix Islands Protected Area (PIPA), which is one of the largest protected areas on Earth (408,250 km²), and Palau will close 80% of its national waters to fishing by January 2020. Here we draw from the PNA's market-based approach to managing tuna fisheries and build on it to show how an environmental market can be designed to incentivize conservation.

Not all market-based approaches to environmental management contain the same conservation incentives. A pervasive finding across a range of natural resources is that features of markets, such as the allocation of rights, can have implications for the market's functioning¹³. In the context of fishing-effort markets, we found that two market design features are pivotal in determining the incentives for large-scale marine conservation-trading and allocation rules. But why would these design features of a fisheries market affect the incentives for conservation? Consider the incentives for a country to close 100% of its waters. Such a closure might benefit other countries through the spillover of fish from the protected area to the waters of neighbouring countries. If the conserving country could trade the rights to that spillover to adjacent countries, this could offset the foregone fisheries revenue. But if the conserving country was not allowed to trade these rights, then it would lose all of its fishing revenue. The rules for how fishing rights are allocated across countries are equally important. Given that rights are allocated each year on the basis of the previous year's fishing effort,

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Fig. 1 | Exclusive Economic Zones and Marine Protected Areas in the PNA. A map of the EEZs and MPAs in the PNA. Inset: a reference for the area. PNA nations are shown in blue, whereas all of the others are indicated by empty polygons. The red box outlines the three EEZs of Kiribati. The red shaded polygons show the PIPA implemented in 2015 and the proposed PNMS that is due to be implemented in 2020. Land masses are shown in grey. The labels indicate ISO3 country codes for PNA members. PLW, Palau; PNG, Papua New Guinea; FSM, Federal States of Micronesia; SLB, Solomon Islands; NRU, Nauru; MHL, Marshal Islands; KIR, Kiribati; TUV, Tuvalu; TKL, Tokelau.

the more a country fishes, the more it gets allocated the next year. This would clearly disadvantage a conservation-minded country and, in fact, might reward undesirable behaviour. In the following section, we show how trading and allocation rules can shape the incentives that can facilitate or hinder large-scale conservation. We then utilize vessel-tracking data to analyse a real-world case of large-scale marine conservation under fishing-effort markets.

Results

Designing markets for conservation. To examine how market design incentivizes or hinders large-scale conservation, we developed a 10-country spatial bioeconomic model that mirrors the strategies and spatial connections among the nine PNA nations and the high seas. Countries 1-9 represent the PNA countries, which operate under a vessel-day scheme in which vessel-days are capped for each country and closely tracked. Country 10 represents the high seas, where fishing days are unregulated and are determined by prevailing economic conditions. We examined the effects of largescale conservation in a single country (country 1) under markets with and without trading between countries. In all cases, we solved the bioeconomic model for the equilibrium vessel-day price, fishing-effort redistribution across countries and fish stock that would be expected to occur in the market. We quantified the change in revenue to country 1 and compared each scenario with a benchmark scenario in which no conservation action was taken. We simulated these outcomes across a range of reserve sizes and assumptions about within-country stock movement (see Methods).

We first simulated a fishery in which trading between countries is not allowed. This represents the status quo of any nation that unilaterally engages in large-scale conservation. Intuitively, we found that a spatial closure in country 1 will always result in a loss in revenues for this country (Fig. 2a). Higher within-country stock movement ($\theta = 0$ implies no within-country movement and $\theta = 1$ implies that fish are well-mixed within the fishing season) allows vessels to harvest the stock within the remaining open area, lowering the



Fig. 2 | Cost of spatial closures in a vessel-day fishery. a,b, Costs for country 1 when there is no trading (**a**) and when trading is allowed (**b**; note the change in axis limits). **c**, Costs avoided by trading. For **a**-**c**, each line represents a possible value of within-country stock movement (θ ; line colours), where θ =0 represents a stock that does not move and θ =1 represents a stock that continuously moves between the reserve and the fishing zone. The revenue losses to country 1 (**a** and **b**, *y* axis) are relative to a fishery with no spatial closures, and are shown as a function of reserve size (R; *x* axis), on a scale of no reserve (R=0) to closing the entire EEZ (R=1). The dashed red line in **a** is a 1:1 line. When trading between countries occurs, 88% to 99% of revenue losses can be avoided.

cost to country 1. Even for a highly mobile stock in which fish can move in and out of the reserve, a spatial closure reduces the amount of biomass that is available for harvest in the conserving country (that is, biomass outside of the reserve), reducing the willingness of vessels to pay to fish in such waters (Supplementary Fig. 1). When countries cannot trade, the costs of conservation are incurred by country 1, but the benefits are received by the eight other countries (revenues increase between 0% and 6% each; Supplementary Fig. 2) and the high seas. This benchmark simulation highlights the misalignment of incentives—a conservation-minded country incurs large costs and provides public benefits to other nations but has no mechanism for recouping these benefits.

How does trading between countries change these results? We next simulated the same fishery, but allowed for the trade of



Fig. 3 | Costs of a spatial closure for country 1 under different allocation rules. Each line represents the revenue losses for a combination of allocation rules (α ; solid, dashed and dotted lines) and movement (θ ; colours) for different reserve sizes (R; x axis). A value of $\alpha = 1$ implies that allocations are based entirely on historical effort, whereas a value of $\alpha = 0$ implies a 100% biomass-based allocation rule. A value of $\theta = 0$ represents a stock that does not move and $\theta = 1$ represents a stock that continuously moves between the reserve and the fishing zone. The proportion of the EEZ closed to fishing is given by R. An effort-based allocation and low within-country movement values result in the highest costs. Cost can be minimized for all movement values if allocation is based on biomass within the waters of each country.

vessel-days across countries (which is the case for the PNA). As before, a closure in country 1 reduced the value of vessel-days in that country (because the fishable area shrinks). By contrast, increased biomass in the other countries caused their vessel-day prices to increase. As a result, vessel-days from country 1 were traded to countries 2–9 until prices equalized across countries (Supplementary Fig. 3). Under this market design, revenue losses to country 1 were less than 1% compared with the base case with no reserve (Fig. 2b; note that the *y* axis scale is 0–0.8% rather than 0–100% as in Fig. 2a). This shows that, with trading, the relative revenue drop will always be smaller than the relative effort drop, and the opposite is observed when there is no trading (Supplementary Fig. 4). Overall, this shows that 88% to 99% of the costs of conservation can be avoided if markets are designed to allow trading (Fig. 2c).

We have shown that trading significantly reduces the costs of conservation. However, a new question arises: how should rights be re-allocated every year once a country starts closing its waters to fishing? Customarily, the allocation of fishing-effort rights is a formula that combines historical fishing effort and biomass in a country's waters¹⁰. We tested a range of allocation rules that weighed effort (α) and biomass (1- α) differently as the basis for ongoing rights allocation. We simulated a fishery operating with closures for 50 years and compared the resulting revenues to a fishery without any closures. We found that when allocation is based on historical effort only (that is, $\alpha = 1$), implementing a reserve results in longterm losses to the conserving country of between 20% and 93%, depending on the size of reserve and stock movement (Fig. 3). However, a biomass-only allocation rule (that is, $\alpha = 0$) resulted in revenue losses that were as low as 0.1% to 0.7%, essentially eliminating the costs of conservation. This result implies that if allocation is based purely on the biomass within a nation's waters, and not on fishing intensity, the incentives for conservation can be sustained through time.

Markets and conservation in practice. A large-scale MPA was recently implemented in PNA waters, providing the ideal empirical setting to test our predictions. In January 2015, Kiribati closed



Fig. 4 | Change in spatial footprint of fishing activity by 318 tuna purse seiners. a,**b**, The normalized change in average fishing hours through time for displaced (**a**; n = 64) and non-displaced vessels (**b**; n = 254). **c**, The difference between **a** and **b**, highlighting areas where displaced vessels redistributed to, relative to non-displaced vessels. Note that displaced vessels allocated more hours to the Gilbert Islands and Line Islands (part of Kiribati's EEZs), but also Tuvalu and the high seas surrounding PIPA and Kiribati's EEZ. For **a-c**, the black lines show EEZs and the red box outlines the PIPA.

11.5% of its EEZ to implement the PIPA, effectively displacing all fishing effort within its boundaries^{14,15}. By protecting this important tuna spawning habitat⁷, PIPA may provide important recruitment and biomass benefits to the adjacent waters. We combined vessel-level tracking data¹⁶ and country-level licence revenue data reported by the Pacific Islands Forum Fisheries Agency (FFA)¹⁷ to quantify the displacement of vessel-days and the likely costs of conservation. Of the 318 tuna purse seine vessels that fished in PNA waters between 2012 and 2018, 64 'displaced' vessels had fished within PIPA at least once before its implementation and 254 'non-displaced' vessels had never fished in PIPA waters but had fished within PNA waters. We used vessel-level tracking data to calculate vessel-days using the same method as the PNA (see Methods). We present descriptive statistics on the redistribution of fishing activity before and after the implementation of PIPA.

Consistent with the prediction of our model, after PIPA was implemented, displaced vessels largely relocated to outside of Kiribati and into the waters of other PNA countries (Fig. 4). Indeed, from 2014 to 2015, displaced vessels spent 2,115 fewer vessel-days (a 25% reduction) in Kiribati and 2,298 fewer vessel-days in PNA waters (a 17% reduction; Fig. 5a,b). By contrast, non-displaced vessels spent 4,656 additional days in Kiribati during 2015 and an

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Fig. 5 | Effort displacement and licence revenues. a,b, Automatic-identification-systems (AIS)-derived annual vessel-days for Kiribati (**a**) and for all of the PNA (**b**) by 318 tuna purse seine vessels. Annual effort is broken down by displaced (n=64) and non-displaced (n=254) vessels. The dashed horizontal lines represent the total allowable vessel-days in Kiribati (11,000 vessel-days (ref. ³⁰)) and the PNA (45,000 vessel-days). **c**, Annual revenue from fishing licence fees by country and year (2008-2016). **d**, The correspondence between FFA-reported revenues and AIS-derived vessel-day observations (2012-2016). The dashed line in **d** represents a line of best fit, and the shaded area represents the s.e. around the regression. The colours in **c** and **d** represent ISO3 country codes for PNA members.

additional 9,598 vessel-days in PNA waters. By 2018, we observed a net decrease of vessel-days within Kiribati—from 12,671 in 2014 to just 7,677 in 2018—with displaced vessels driving the decrease (Fig. 5a). However, aggregate effort at the PNA level remained relatively constant and we did not observe a 'fishing-the-line' effect, where fishing effort builds up along MPA borders (Extended Data Figs. 1 and 2). The reduction in effort in Kiribati and the constant effort at the PNA level suggest that trading facilitated the redistribution of effort within PNA waters, as predicted by our model.

The decrease in vessel-days in Kiribati can be alternatively (or jointly) explained by changes in oceanographic conditions that drive the distribution of target species and fishing vessels. For example, as El Niño events develop, tuna species are known to shift longitudinally across PNA waters, causing vessels to redistribute^{11,18}. However, the aggregate decrease that we observed for Kiribati in Fig. 5a was driven by the relocation of vessels that historically fished within PIPA, not by the entire fleet. Oceanographic conditions should influence the entire fleet, whereas the closure of PIPA should have a stronger impact on vessels that used to fish in that region. The large decrease in effort within Kiribati for the displaced vessels (compared with the non-displaced vessels) is therefore consistent with the argument that PIPA displaced these vessels to waters outside of Kiribati. The differences in vessel characteristics between displaced and non-displaced vessels may influence their ability to redistribute or take advantage of different oceanographic conditions in Kiribati. It should be noted that, on average, displaced vessels have smaller crew sizes, more engine power, are larger than nondisplaced vessels, fished more in the PNA during 2014 and are more likely to be registered to the Republic of Korea (Supplementary

Tables 2 and 3, Supplementary Fig. 5). Thus, a change in international relations between Kiribati (or other PNA countries) and the flag country of a particular vessel might represent another explanation for the observed changes in fishing patterns, although we are not aware of any such changes that occurred between 2012 and 2018. Ruling out alternative explanations for observed effects is an important component of careful empirical evaluation of MPAs¹⁹. Our results should therefore not be interpreted as the direct causal impacts of PIPA, but are better viewed as patterns that are consistent with the predictions of our theoretical model.

As predicted by our model, the implementation of PIPA resulted in a decrease in fishing effort within Kiribati's water without large revenue losses. Kiribati's reported revenue increased from US\$127.3 million in 2014 to US\$148.8 million in 2015, before decreasing to US\$118.3 million in 2016 (Fig. 5c). The increase and subsequent decrease in revenues matches the vessel-day patterns observed for Kiribati from 2014 to 2016 (Fig. 5d). Critically, the decrease in revenue in 2016 (20%) is smaller than the decrease in vessel-days (35%). This supports a key prediction of our model with trading, the relative revenue drop will be smaller than the relative decrease in effort but, without trading, the opposite relationship would hold (Supplementary Fig. 4). At the PNA level, total revenues showed a net increase of US\$64.7 million and US\$28 million for 2015 and 2016, respectively (Supplementary Fig. 6), despite the PIPA closure.

Discussion

Our findings may help to inform management and the implementation of existing and upcoming MPAs in the PNA. In January 2020,

Palau will close nearly 80% of its EEZ to commercial fishing to create the Palau National Marine Sanctuary (PNMS)—the 14th largest protected area in the world (Fig. 1). Vessel-tracking data (2012–2018) show that, on average, the proposed PNMS boundaries have historically contained $86 \pm 5.30\%$ (± 1 s.d.) of longline vessel-days (non-tradable) and $91.3 \pm 5.03\%$ (± 1 s.d.) of purse seine vessel-days (tradable) in Palauan waters (Extended Data Figs. 3 and 4).

Although trading would allow Palau, Kiribati and other PNA members to reduce revenue losses from large-scale conservation, our model indicates that moving from the present 40% biomassbased allocation rule to a 100% biomass-based rule would ensure long-term financial security in the presence of large-scale MPAs, and further incentivize conservation within the PNA. A 100% biomass-based allocation rule means that fishing rights will be distributed between nations on the basis of the proportion of total biomass within their waters, regardless of historical fishing intensity. By contrast, an effort-based allocation would reward undesirable behaviour by granting more fishing rights to the country that fishes the most. This is a model prediction that cannot be empirically tested in the PNA context because the allocation rule has not been experimentally modified. Nevertheless, the PNA countries have already shown that rights-based management of transboundary resources can result in large management and economic benefits^{10,11}. By facilitating trade and allocating rights on the basis of biomass, the PNA countries may also have become pioneers in effective large-scale marine conservation in a market-based setting.

However, there are a series of important considerations to take into account. First, in our model, only one of the countries considers the implementation of a protected area. An interesting extension of this could consider cooperative conservation. In such a cooperative setting, a group of countries could coordinate on an optimized, large-scale strategic closure-perhaps using vessel-day trading as a means of compensation-in a manner that is similar to the model described above. Future research could explore the role of heterogeneous costs and benefits between countries, and the manner in which these can shape conservation outcomes in a market-based setting. A second consideration is the role of the high seas; environmental markets require secure property rights, which are lacking in the high seas²⁰. Benefits accruing to the high seas could potentially be eroded by the prevailing open-access conditions. A conservation-minded nation therefore has no mechanism to capture the benefits provided to the high seas, highlighting the importance of empowering high-seas governance and transboundary cooperation^{11,20}. Finally, our research focused on fisheries and large-scale conservation, but the framework could potentially be expanded and applied to other systems and natural resources. For example, similar mechanisms could be implemented in markets for tradable water rights²¹ or game hunting²² for which secure property rights and the presence of a market may incentivize users to conserve the resource in question.

The use of environmental markets for conservation is a common but contentious approach among conservation scientists and resource managers²³. One of the driving concerns is that markets may create incentives that lead to undesirable outcomes, therefore emphasizing the need for careful design. We show that without cross-country markets, individual countries have little incentive to undertake large-scale marine conservation, but that this incentive can be reversed if those countries are in an appropriately designed market-based setting. For the market to create these incentives, certain design features are paramount. In the case of fishing rights and large-scale MPAs, cross-country transferable fishing rights and a biomass-based allocation rule are two conditions that are necessary to achieve the conservation incentive. International goals over the next decade have set ambitious targets for terrestrial and marine conservation; these goals will provide benefits that range from preserving biodiversity to enhancing human well-being^{1,2,24,25}. Our study shows how well-designed environmental markets can provide the right incentives for effective large-scale marine conservation.

Methods

Bioeconomic model. We modelled a ten-country discrete-time meta-population system, in which country 1 considers a spatial closure. Countries 1–9 operate under a vessel-day scheme and country 10 represents the high seas and other areas that are not managed under a VDS. The stock of fish in each country is relatively stationary within a single fishing season, but growth from escapement redistributes across all countries annually. The price of fish *p* and catchability *q* were held constant across countries.

Fishery dynamics. In the absence of a reserve, the revenue for vessels in country *i* is given by pqE_iX_i where E_i and X_i are effort (vessel-days) and stock size, respectively, in country *i* at the beginning of a period. The cost of fishing in country *i* is given by cE_i^β where $\beta = 1.3$ matches commonly used cost functions that assume increasing units of effort are increasingly costly to apply²⁶.

Country 1 considers a spatial closure by implementing a reserve as a fraction R of the total country ($R \in [0,1)$). Fish move within a country on the basis of θ where $\theta = 0$ implies no movement within the country and $\theta = 1$ implies that fish move so much that they can be caught from anywhere within the country (see the 'Notes on within-country fish movement' section). In this country, revenues are given by $pqE_1X_1(\theta R + (1 - R))$. The parenthetical term is the fishable fraction of biomass in country 1. It assumes that fraction θ of fish inside the reserve at the beginning of the fishing season are fishable outside of the reserve at some point during the course of the fishing season. The parameterization of movement and reserve size implies that profit from fishing country 1 is given by:

$$\Pi_1(E_1, X_1, R) = pqE_1X_1\Omega_1 - cE_1^{\beta}$$

where $\Omega_1 = \theta R + (1 - R)$. Also note that $\Omega_{i\neq 1} = 1$ as only country 1 implements a reserve. Therefore, we can generalize the country-level profit equation to:

$$\Pi_i(E_i, X_i, R_i) = pqE_i X_i \Omega_i - cE$$

The above equations imply that the marginal profit from the last unit of effort in a country is given by:

$$\pi_i(E_i) = \frac{\partial \Pi_i}{\partial E_i} = pqX_i \Omega_i - \beta c E_i^{\beta - 1} \tag{1}$$

In practice, the effort levels in each country are allocated by management (so $E_1, E_2, ..., E_9$ are given) and the effort level on the high seas (E_{10}) is a result of openaccess dynamics. We therefore assumed that effort continues to enter country 10 until the profit from the last unit of effort is exactly zero, indicating that E_{10} is the value for which $\pi_{10}(E_{10}) = 0$. Setting Equation (1) (for i = 10) equal to zero and removing $\Omega_{10} = 1$ for simplicity, we can solve for E_{10} :

$$E_{10} = \left(\frac{pqX_{10}}{\beta c}\right)^{\frac{1}{(\beta-1)}} \tag{2}$$

However, under VDS-operated countries, profits from the marginal unit of effort should equate to the price of fishing in the country. Vessel-day price for countries under VDS (i = (1,9)) is therefore given by:

$$\pi_i = pqX_i\Omega_i - \beta cE_i^{\beta}$$

Solving for E_i we obtain:

$$E_i = \left(\frac{pqX_i\Omega_i - \pi_i}{\beta c}\right)^{\frac{1}{\beta - 1}}$$
(3)

Equation (3) tells us the country-level effort for a given country-specific stock size (X_i) and vessel-day price (π_i) . A vessel-day scheme establishes a cap on total effort allowed. This means that fishing effort from countries 1–9 must add up to this limit (45,000 vessel-days). Therefore, total allowable effort in the fishery is given by:

$$\overline{E} = \sum_{i=1}^{9} \left(\frac{pqX_i \Omega_i - \pi}{\beta c} \right)^{\frac{1}{\beta - 1}} \tag{4}$$

In Equation (4), vessel-day price is the same across all countries when trading is allowed; the subindex is dropped for this parameter.

Stock dynamics. Country-level harvest is then determined by effort and stock size:

$$H_i = q E_i X_i \Omega_i \tag{5}$$

Therefore, escapement in country *i* in time period *t* is the difference between initial stock size and harvest given by $e_{i,t} = X_{i,t} - H_{i,t}$ and total escapement is $e_t = \sum_{i=1}^{10} e_{i,t}$. The entire stock then grows logistically according to:

$$X_{t+1} = e_t \times \exp\left(r\left(1 - \frac{e_t}{K}\right)\right)$$

where *r* and *K* are species-specific intrinsic growth and carrying capacity parameters (the slope $\frac{dX_{i+1}}{de_i}|_{e_i=0} = \exp(r)$). After the stock grows, a constant and country-specific fraction f_i of the total stock redistributes to country *i*, such that:

$$X_{i,t+1} = f_i X_{t+1}$$
(7)

(6)

Vessel-day revenues. The vessel-day price that a country charges is given by π_i from Equation (1). Country-level licence revenues are therefore given by:

$$\omega_i = \pi_i E_i \tag{8}$$

Equation (5) shows that low values of θ and R > 0 would decrease harvest and increase escapement in country 1 for a given level of effort and stock size. This would result in an increase in total stock size (Equation (6)) and a benefit to all of the other countries. However, this would also cause the stock in the high seas (X_{10}) to increase, leading to increased effort being allocated to the high seas (Equation (2)) and a loss of these potential rents. Thus, the spillover benefits of increasing R are never completely captured. Information on model parameterization is provided in the Supplementary Information.

Notes on within-country fish movement. In our model parameterization, the proportion of biomass available for harvest in the conserving country is given by $\Omega_1 = (\theta R + (1 - R))$. This implies that, for a given country with stock size X_i , the total biomass available for harvest will be given by $\Omega_i X_i$. Consider the case of a sessile fish with $\theta = 0$. If the country were to close 50% of its waters to fishing (R = 0.5), only 50% of the stock would be available for harvest (that is, $(0 \times 0.5) + (1 - 0.5) = 0.5$). Now, consider the same closure is applied to a stock with high mobility, such as $\theta = 0.9$. In this case, despite the closure, fish frequently move between the reserve and fishing grounds making 95% of biomass available for harvest (that is, $(0.9 \times 0.5) + (1 - 0.5) = 0.95)$). As derived in the bioeconomic model above, a vessel's willingness to pay to fish in a given patch will be determined by the amount of biomass available for harvest. Within-patch stock movement therefore has an important role in determining a vessel's willingness to pay in the remaining open waters-a vessel will be willing to pay more to fish in waters in which 95% of biomass is available for harvest compared with what they are willing to pay to fish in waters in which only 50% of biomass is available for harvest.

Simulations. We ran simulations under various market designs and tested our model across a range of reserve sizes and within-country movement parameters. In the first scenario, we did not allow trading. In this case, total allowable effort (\overline{E}) and biomass B_{now} were known and were equally distributed among countries 1–9. For country 10, we solved Equation (2) until biomass converged to match B_{now} . We then closed a portion of country 1 and calculated the vessel-day price in country 1 given that only $X_s Q_s$ biomass was available for harvest. We compared vessel-day revenues of each scenario with a case in which there was no reserve (R=0). This produced a measure of the cost of implementing a spatial closure of size R in country 1.

In the second scenario, we allowed trading. We started again by solving Equation (2) for the high seas to obtain total effort. As a closure is not in effect and VDS-managed effort is equally distributed across the 9 countries, this equilibrium was the same as the first step described above. We then implemented a spatial closure in country 1. This lowered the price that fishers would be willing to pay to fish in a country with only biomass $X_s Q_s$ available for harvest, lowering demand for vessel-days in country 1. Countries 2–9 had a higher demand for vessel-days and, therefore, a portion of vessel-days from country 1 were sold to countries 2–9. This increased effort in these countries, reducing escapement and, therefore, biomass. This reduction in biomass in turn modified the marginal profit and willingness to pay to fish in each country. We iterated this process until biomass stabilized. As described above, we calculated vessel-day revenues for each country and compared them with a case in which there was no reserve in country 1.

Annual vessel-days are often allocated on the basis of a combination of historical within-country effort and biomass. In the PNA, 60% of the allocation is calculated on the basis of EEZ effort over the previous 7 yr and 40% is calculated on the basis of the 10 yr average of each country's share of estimated biomass (of skipjack and yellowfin tuna) within its EEZ (see Article 12.5 of the 2012 Amendment to the Palau Agreement and ref. ²⁷). Trading vessel-days to other countries would imply that historical within-country effort declines through time. The days allocated to a country with a full spatial closure would eventually be reduced to just the 40% on the basis of biomass.

In the trading scenario above, effort from country 1 (with the reserve) is traded to other countries. This means that its allocation will decrease as purse seine effort in country 1 is reduced. To analyse the consequences of different allocation rules when trading is allowed, we simulated a fishery 50 yr into the future, and annually re-allocated vessel-days on the basis of a 7 yr running mean of country-level effort

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and biomass. At the end of every time period (a year), vessel-days were re-allocated to each country on the basis of the following rule:

$$E_{i,t+1}^* = \alpha \left(\frac{\sum_{\tau=0}^r E_{i,t-\tau}}{\sum_{\tau=0}^{\hat{\tau}} \overline{E}_{t-\tau}} \right) + (1-\alpha) \left(\frac{\sum_{\tau=0}^r X_{i,t-\tau}}{\sum_{\tau=0}^{\hat{\tau}} \overline{X}_{t-\tau}} \right)$$

where α is a weight on historical effort (E_i) and $1 - \alpha$ is a weight on historical biomass (B_i). We used $\hat{\tau} = 6$ to obtain a moving mean of 7 yr for these measures. The difference between allocated days (E_i^*) and used days (determined by Equation (3)) for country 1 are the sales. We then calculated vessel-day revenues for each country over the 50 yr time horizon and compared these values with a case in which there is was reserve and allocations were based solely on biomass ($\alpha = 0$).

Empirical case study. Vessel tracking data and MPAs. AIS are on-board devices that provide at-sea safety and prevent ship collisions by broadcasting vessel position, course and activity to surrounding vessels. These broadcast messages can be received by satellites and land-based antennas. We used AIS data provided by Global Fishing Watch¹⁶ to track 318 tuna purse seiners that fished within the PNA. For every georeferenced position, we observed the time spent (defined as the time since the last position) and whether the vessel was actively fishing versus only transiting. Of the 318 tuna purse seine vessels that fished in PNA waters between 2012 and 2018, 64 displaced vessels fished within PIPA at least once before its implementation, and the remaining 254 non-displaced vessels never fished in PIPA waters. Our dataset contains more than 37 million geo-referenced positions for these 318 tuna purse seiners. We used these data to calculate vessel-days (the metric used by the PNA), and to track the spatial redistribution of displaced vessels. A comparison of vessel characteristics between displaced and non-displaced vessels is provided in Supplementary Tables 2 and 3 and Supplementary Fig. 5.

We used these data to calculate the number of vessel-days that the 318 purse seiners spent fishing in each PNA country and in PNA waters as a whole (Fig. 5). The vessel-day equivalent of a day of fishing depends on vessel size—a measure used to control for effort creep. The Palau Arrangement for the Management of the Western Pacific Fishery Management Scheme²⁶ states that 1 d of activity by vessels with a length of less than 50 m counts as half of a vessel-day, 1 d day of activity by vessels with a length of 50–80 m counts as 1.5 vessel-days. Vessel length is an observable characteristic in our dataset and, therefore, vessel-days that were calculated in our analyses correspond to the PNA definition of vessel-days. Satellite reception of AIS messages increased with the addition of satellites to the constellation through time, which results in an apparent increase in effort (2012–2014). These temporal changes, however, affect displaced and non-displaced vessels equally and their relative effort should remain the same.

We also compared the location of fishing activity by displaced and nondisplaced vessels before and after the implementation of PIPA to better understand the redistribution of fishing effort. Non-displaced vessels serve as a plausible control group that was not subject to a spatial closure but might have redistributed in response to changing environmental conditions, such as El Niño^{11,18}.

We first filtered the data to keep only positions labelled as fishing events. We then created a gridded version of the data for each year and group (that is, displaced and non-displaced) by binning the coordinates to a 1° grid and summing all fishing hours for a given grid cell. We used a 1° grid as a reasonable compromise between higher resolutions that would result in a more granular but noisy footprint and the simple estimation of vessel-days at the EEZ-level (as shown in Extended Data Fig. 1, but represented spatially). This process resulted in 14 gridded datasets of fishing hours (7 yr, for two groups). For each group of vessels, we then calculated the average fishing hours before (2012–2014, inclusive) and after (2015–2018, inclusive) the implementation of PIPA; this resulted in 4 datasets of mean fishing effort (before and after for displaced and non-displaced vessels). We then calculated the change in effort allocation between these two periods (after – before) for each group, and normalized the value of each grid cell by diving it by the largest within-group absolute change:

$$h_{i} = \frac{(h_{i,a} - h_{i,b})}{\max(|(h_{i,a} - h_{i,b})|)}$$
(9)

where, for a given group of vessels, *i* is a subindex for each cell, and a and b indicate after and before. The resulting gridded differences are shown in Fig. 4a,b. The redistribution by non-displaced vessels (Fig. 4b) therefore provides a baseline of redistribution. We then compared the changes of displaced vessels to those of non-displaced vessels (Fig. 4c). The spatial redistribution patterns of displaced vessels relative to non-displaced vessels suggests that some of the displaced vessels relative to non-displaced vessels suggests that some of the displaced vessels relative to non-displaced vessels suggests that some of the displaced vessels relative to the Marshall Islands, Tuvalu, Nauru and the high seas.

Revenues. We obtained information on revenues from the Pacific Islands FFA Tuna Development Indicators 2016 report. Specifically, we used data compiled by the Pacific Islands FFA¹⁷ in which annual revenues from licence fees (for VDS and other access programs) are reported for each country (2008–2016; Fig. 5c,

Supplementary Figs. 6 and 7). For countries in the PNA, these revenues show a combination of vessel-day licence fees as well as joint-venture operations.

Shapefiles of EEZs were obtained through Marine Ecoregions of The World using World EEZ (v.10, released 21 February 2018; http://www.marineregions.org). Shapefiles for MPAs were obtained from the World Database of Protected Areas, and were downloaded in March 2019 from https://www.protectedplanet.net. All analyses were performed using R v.3.6.1 and RStudio v.1.2.5.001 (ref. ²⁹).

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

The data that support the findings of this study are available on GitHub at https://github.com/jcvdav/MPA_displacement.

Code availability

The code that support the findings of this study are available on GitHub at https://github.com/jcvdav/MPA_displacement.

Received: 18 September 2019; Accepted: 22 November 2019; Published online: 06 January 2020

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Acknowledgements

We thank R. Dacks for research assistance. J.C.V.-D. was supported by UCMexus-CONACyT (CVU, grant no. 669403) and the Latin American Fisheries Fellowship Program. J.L. was supported by the Conservation Strategy Fund, with a grant from the Pew Charitable Trusts and Pew Bertarelli Ocean Legacy. J.L. and C.C. acknowledge The Nature Conservancy.

Author contributions

All of the authors contributed equally.

Competing interests

The authors declare no competing interests.

Additional information

Extended data is available for this paper at https://doi.org/10.1038/s41893-019-0459-z.

Supplementary information is available for this paper at https://doi.org/10.1038/ s41893-019-0459-z.

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Extended Data Fig. 1 | Annual country-level vessel-days for all PNA countries by 318 tuna purse seiners. Colors indicate ISO3 codes for each country (PLW: Palau, PNG: Papua New Guinea, FSM: Federal States of Micronesia, SLB: Solomon Islands, NRU: Nauru, MHL: Marshal Islands, KIR: Kiribati, TUV: Tuvalu, TKL: Tokelau). After 2015, vessel-days decrease for Kiribati and Increase for Papua New Guinea. Note that total vessel-days do not decrease at the PNA-level.

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Extended Data Fig. 2 | Annual fishing effort (hours) on a 1-degree grid around PIPA (red polygon) and Kiribati (black polygons). There is no clear evidence of a "fishing the line" effect, with the greatest effort applied on the Gilbert islands (Kiribati) after 2015.

ARTICLES **NATURE SUSTAINABILITY** Longlines Purse seines 12°N 12°N 10°N 10°N Vessel-days Vessel-days 1 10 8°N 8°N 0.1 1 0.01 6°N 0.1 6°N 0.001 0.01 4°N 4°N 0.001 0.0001 2°N 2°N 130°E 132°E 134°E 136°E 130°E 132°E 134°E 136°E

Extended Data Fig. 3 | Longline and purse seine vessel-days in Palau during 2018 at a 0.5 degree resolution. The red polygon shows the proposed Palau National Marine Sanctuary, containing 85.7% and 95.3% of longline and purse seine vessel-days, respectively. Note that the colorbars are presented in log10-transformed scale for better visualization.

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Extended Data Fig. 4 | Time series of the annual proportion of longline and purse seine vessel-days within the proposed PNMS boundaries. The proposed PNMS boundaries have historically contained $86 \pm 5.30\%$ (± 1 SD) of longline vessel-days and $91.3 \pm 5.03\%$ (± 1 SD) of purse seine vessel-days.

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Last updated by author(s): Nov 18, 2019

Reporting Summary

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| | | Our web collection on <u>statistics for biologists</u> contains articles on many of the points above. | | | | |

Software and code

| Policy information at | pout <u>availability of computer code</u> |
|-----------------------|---|
| Data collection | Data are publicly available through the Pacific Islands Forum Foreign Fishing Agency (www.ffa.int/economic_indicators) and Global Fishing Watch (globalfishingwatch.org). |
| Data analysis | All analyses were performed in R v.3.6.1 and RStudio V.1.2.1335. Version control on development of code was done via git v.2.19.1.windows.1 All code is available on GitHub at https://github.com/jcvdav/MPA_displacement |

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All studies must disclose on these points even when the disclosure is negative.

| Study description | We develop a spatially-explicit bioeconomic model of a fishery uperating under an effort cap. We evaluate the market structure conductive to large-scale marine conservation. We compare our model predictions to a real-world case using vessel-tracking data for a fishery managed under a vessel-day scheme, where a country implemented a conservation area. |
|----------------------------|--|
| Research sample | For the empirical portion of the paper, we fuse vessel-tracking data via AIS to track 313 tuna purse seine vessels that fished in the Exclusive Economic Zones of the nine countries that belong to the Parties to the Nauru Agreement (PNA). |
| Sampling strategy | All vessels with AIS were included. As part of the PNA regulations, vessels must have AIS in order to legally fish in PNA waters. |
| Data collection | Data were made available to us via Global Fishing Watch (globalfishingwatch.org). Global Fishing Watch uses on-board Automatic Identification Systems that broadcast the location and identity of vessels on open radio frequency. AIS messages are captured by land-based antennas and satellites and processed by Global Fishing Watch to identify fishing vessels, type of gear, and fishing activity. |
| Timing and spatial scale | AIS data are continuously collected and processed by GlobalFishingWatch. We use data from January 2012 to December 2018 for all vessels that fished within the Exclusive Economic Zones (EEZ) of the Parties to the Nauru Agreement. Since we are interested in aggregate measures of effort that match the management of the fishery (i.e. the vessel-day scheme), we calculate total vessel-days for each EEZ. |
| Data exclusions | No data were excluded from the analyses |
| Reproducibility | We do not employ experiments, but simulation. Our documented code is availabel in our GitHub repository, were we clearly state what each simulation tests for. |
| Randomization | Our study design did not involve experiments and did not require randomization |
| Blinding | Vessels voluntarily broadcast their position and identity as an at-sea safety measure, and to comply with the tracking requirements by the PNA. However, we are not interested in vessel-level location, but on the aggregate measure of at-sea hours. |
| Did the study involve fiel | d work? Yes X No |

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| \boxtimes | Eukaryotic cell lines | |
| \boxtimes | Palaeontology | |
| \boxtimes | Animals and other organisms | |
| \boxtimes | Human research participants | |
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