Crop rotations in the sea: Increasing returns and reducing risk of collapse in sea cucumber fisheries

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Rotational harvesting is one of the oldest management strategies applied to terrestrial and marine natural resources, with crop rotations dating back to the time of the Roman Empire. The efficacy of this strategy for sessile marine species is of considerable interest given that these resources are vital to underpin food security and maintain the social and economic wellbeing of small-scale and commercial fishers globally. We modeled the rotational zone strategy applied to the multispecies sea cucumber fishery in Australia's Great Barrier Reef Marine Park and show a substantial reduction in the risk of localized depletion, higher long-term yields, and improved economic performance. We evaluated the performance of rotation cycles of different length and show an improvement in biological and economic performance with increasing time between harvests up to 6 y. As sea cucumber fisheries throughout the world succumb to overexploitation driven by rising demand, there has been an increasing demand for robust assessments of fishery sustainability and a need to address local depletion concerns. Our results provide motivation for increased use of relatively low-information, low-cost, comanagement rotational harvest approaches in coastal and reef systems globally.

rotational harvest | beche-de-mer | pulse fishing | spatial management | Great Barrier Reef

The sustainable management of natural resources is a fundamental challenge in the face of increasing human population and related demand for food, limited research and management capacity, and the drive for short-term economic development. Benthic organisms that are shallow and have limited motility can be particularly susceptible to overharvesting, especially, such as in the case of sea cucumbers, when they are comparatively valuable and easy to harvest and store and where communities rely on these resources for food and income (1, 2). The value and demand for sessile marine resources, such as sea cucumber, are rising (3), resulting in the general overexploitation and even high extinction risk for some sea cucumber populations globally (3, 4), even in seemingly well-managed fisheries, such as in the Great Barrier Reef Marine Park (GBRMP) (5, 6). Globally, there is a need to assess fishery sustainability to meet increasingly stringent requirements for ecological sustainability, particularly in regions with high conservation value. However, gathering and analyzing suitable fishery-dependent and -independent data are often beyond the financial and logistical capacities of the fishery, particularly for multispecies fisheries.

In our study, we estimated the benefits of a rotational zone strategy (RZS) applied to the sea cucumber fishery of Australia's Great Barrier Reef (GBR) (Fig. 1), which has a 3-y rotation cycle through 154 zones. Under pressure from management over historical overexploitation of high-value species and a perceived high risk of overexploitation of other species, the fishers of the GBR sea cucumber fishery designed and implemented an RZS in 2004, where the entire GBR fishery area was split into 154 zones, with each zone fished only one time every 3 y (6, 7). This strategy together with fishing limits within zones, minimum size limits, and total allowable catches (TACs) for some high-value species were meant to reduce the risk of localized and overall overexploitation—but the RZS has not yet been rigorously tested (8). The zone size and rotation periodicity were determined by industry using a common sense approach to suit their operations (7, 8). The modeling approach that we applied to this data-poor multispecies fishery included testing across a broad range of uncertainty by using alternative models [a reference set (RS)], stochastic replicates, and alternative life histories (nine species). Our modeling approach (*Methods* and *SI Methods*) aimed to comprehensively test the hypothesis that an RZS can contribute to more sustainable management of sedentary small-scale fisheries generally. The model time period is 1995–2012, with a 20-y future projection time period. For each of 154 zones where each of the nine species occurs, 160 population projections are run under each of a range of future harvest scenarios with different periodicity and magnitude. We use a risk management approach, because it is a pragmatic and proactive means of evaluating tradeoffs in managing variable and difficult to predict data-poor stocks (9–11).

Management strategy evaluation (MSE) (12) is widely used in fisheries as a decision support tool for evaluating the consequences of a range of management strategies, while acknowledging system uncertainty. Briefly, it involves developing a model to describe the fishery, with a focus on identification and modeling of uncertainties as well as portraying different representations of resource dynamics (13). Alternative management strategies are then simulated, and the consequences are predicted using performance statistics: for example, to quantify the biological and economic status corresponding to alternative options. MSE enables evaluation of the tradeoffs in performance of management strategies, and although mostly applied to single-species harvest strategies, more recently, it is being applied to more complex

Significance

Rotating the harvest of natural resources is a management strategy that humans have used on land for centuries, but it is less commonly applied to marine resources. Marine animals, such as sea cucumbers, scallops, and abalone, may be particularly suited for this form of management. Although highly important to many communities worldwide, they are often severely overexploited, underlining the need for effective and easy to manage harvest strategies. We modeled the rotational zone strategy applied to the multispecies sea cucumber fishery in Australia's Great Barrier Reef Marine Park and show a substantial reduction in the risk of localized depletion, higher long-term yields, and improved economic performance. Hence, our results support the use of rotational harvests to better manage these marine resources.

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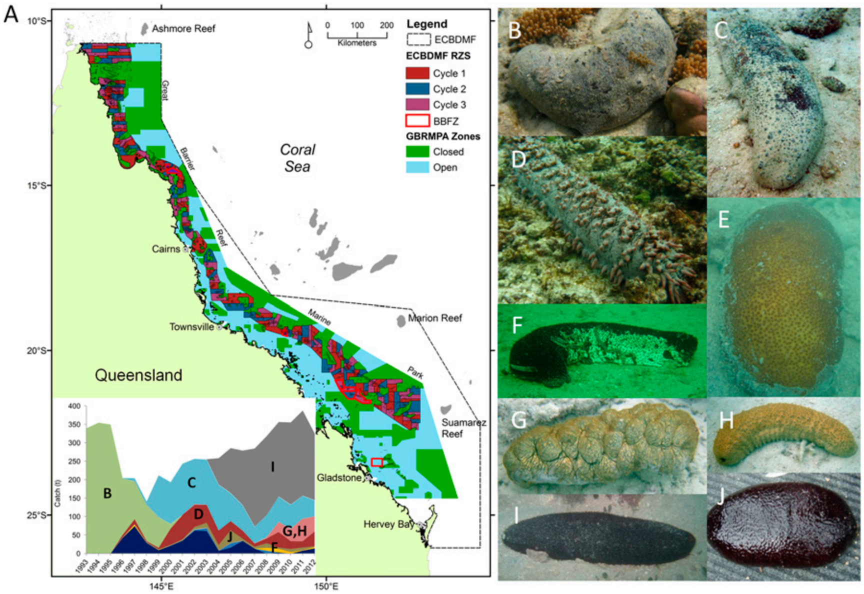

Fig. 1. (*A*) Map of the ECBDMF showing 154 RZS zones, existing burrowing blackfish zones (BBFZs), 2 ECBDMF offshore fishing zones (Suamarez and Marion Reefs), and 1 general fishery permit area (Ashmore Reef). The remainder of the Great Barrier Reef Marine Park (GBRMP) area is divided into open and closed zones (to sea cucumber fishing) (Fig. S1). Main fishery species include (*B*) black teatfish *Holothuria whitmaei*, (*C*) white teatfish *Holothuria fuscogilva*, (*D*) prickly redfish *Thelenota ananas*, (*E*) brown sandfish *Bohadschia vitiensis*, (*F*) golden sandfish *Holothuria lessoni*, (*G*) curryfish vastus *Stichopus vastus*, (*H*) curryfish herrmanni *Stichopus herrmanni*, (*I*) burrowing blackfish *Actinopyga spinea*, and (*J*) deepwater blackfish *Actinopyga palauensis*. *A*, *Inset* shows the estimated historic catch by (fiscal) year (in tons landed weight—gutted, salted, or parboiled and frozen) per species (indicated by *B*–*J*) and a lumped other species category [catch and fishery logbook data (28)]. *A* data © Commonwealth of Australia (Great Barrier Reef Marine Park Authority) 2010; *B*–*J* images courtesy of the Commonwealth Scientific and Industrial Research Organisation (Canberra, Australia).

multispecies fisheries (10). We use this approach to assess and compare the tradeoffs and risk of overexploitation under alternative management strategies for nine fishery species of the Queensland East Coast Sea Cucumber (Bêche-de-mer) Fishery (ECBDMF) (Fig. 1 and Fig. S1).

Dating back to the early 1800s (6), it is a multispecies fishery from the family Holothuriidae, with several higher-valued species making up the bulk of the catch. The species composition of the catch has varied over the years (Fig. 1) for a number of reasons, including species depletions, precautionary management, changes in market value, emerging markets, and fishery and processing technology. For example, before 2008, curryfish were not heavily fished, because they are difficult to process because of disintegration during handling, resulting in a low-grade end product, but techniques have now improved (14).

The ECBDMF has a limited participation base and modest annual catch [387 tonnes (t) in 2010–2011] (14). However, with the value of beche-de-mer rising because of the increased demand from a growing China and the widespread overexploitation of sea cucumber populations across the globe (4), this fishery provides an important livelihood and foreign exchange opportunity for local fishing communities. The fishery has been the subject of some concern for management agencies in the past (it has the only fishery species closed in the GBRMP because of overexploitation—black teatfish) and has faced criticisms of insufficient monitoring and lack of transparency (5) (the small number of operators means that detailed catch and effort data are confidential in Australia and hence, reported in aggregate form only in our analyses).

Worldwide, rotational fishing has been used for abalone, corals, geoduck clams, sea urchins, and scallop species (15–19). Moreover, there is a need for pretested management approaches that can readily be applied in the numerous coastal and island nations where sea cucumber or similar harvests occur. Globally, sea cucumber fisheries are one of the most important for indigenous fishers; although spatial rotation techniques were implemented historically, many stocks have now crashed because of overfishing (4), but additional opportunities exist. A 3-y rotational harvest and modest exploitation rate (~6% annualized) have, so far, proved successful for maintaining populations and providing fishery efficiencies for the Alaskan and Canadian west coast sea cucumber fishery (*Parastichopus californicus*) (20, 21). There is some limited evidence of successful performance for reef fish and trochus (*Tectus niloticus*) based on empirical studies (22, 23). Modeling studies, such as those based on yield per recruit analysis of rotational fishing applied to the sea scallop, suggest a slight increase in both yield and biomass per recruit (15, 24, 25). Other recorded benefits include increased protection from fishing and reduced likelihood of irreversible decline (26); increased abundance, mean age, and size; and enhanced local reproductive potential and improved probability of larval export to surrounding areas (27).

In our study, we test the RZS of the ECBDMF and conclude that it achieves its objectives of reducing localized depletion and reducing the risk to overall fishery sustainability (Fig. 2). In addition, we evaluate the performance of rotation cycles of different length and show an improvement in biological and economic performance with increasing time between harvests up to 6 y.

Results

When averaged across all model simulations (using the median and 90th percentiles of 160 simulations for each of 154 zones where each of nine species occurs), the RZS system emerges as substantially reducing the risk of local depletion compared with a nonrotational system with similar overall total catch (Fig. 3 and Fig. S2). There was a consistently greater (or equivalent) risk with no RZS for all species, with a substantial increase in the risk of localized depletion for three highly targeted species (white teatfish, black teatfish, and burrowing blackfish) (Fig. 3). In zones where catches are high relative to standing stock, an RZS allows those catches to be sustained, because biomass accumulates below

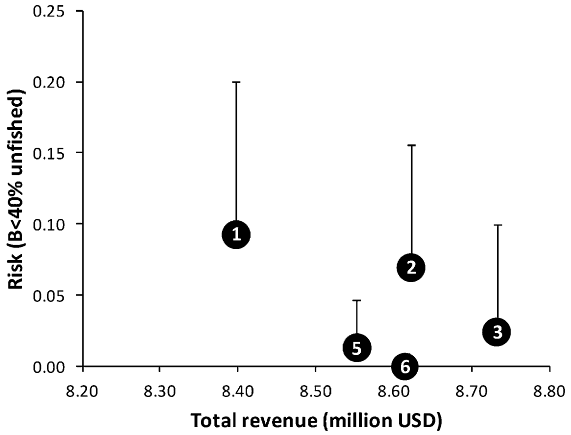

Fig. 2. Tradeoff curve between median risk performance (defined as probability of biomass being reduced below 40% of the comparable no fishing scenario; +1 SD encompasses variation across nine species) and total revenue (million dollars) for RZSs with the different cycle times (year) as indicated on the symbols.

the minimum legal size (MLS) and younger cohorts have time to grow to breed between fishing cycles. This biomass accumulation is particularly the case for slower-growing species, such as the white teatfish, for which risk of local depletion decreases exponentially with increasing time between harvests (Fig. 3). In contrast, in the absence of an RZS, high catches could not be maintained in some zones, and the spawning biomass of the teatfish species declines to very low levels.

With no spatial rotation, the fishery yielded a median annual landed catch and value of 296 t and US$6.07 million, respectively (Table 1). The 3-y RZS achieved improved performance (to 305 t and US$6.22 million, respectively) with reduced risks to sustainability (Table 1). Simulations that estimated the total catch for a range of alternative harvest strategies when tuning to the same reference risk level showed an exponential increase in 20-y average catch and value with increasing rotation-cycle length (Fig. S3). For the same risk to the resource, the difference between the no RZS and 3-y RZS strategies was 140 t and US$2.9 million. Hence, even under relatively conservative catch levels, there was an economic benefit to implementing an RZS, and this benefit increases further as catch levels increase (Fig. S4). In addition, if the costs of harvesting are taken into account, the net economic benefits of an RZS may be even greater, because it would not be necessary to travel to all zones every year and allowing biomass to increase between harvests would improve catch rates and therefore, fishing efficiency.

We compared the maximum total revenue (all species combined) and associated median risk (defined as the probability of biomass being reduced below 40% of the comparable no fishing scenario) for RZSs with different cycle times and found that a 3-y cycle was optimal (Fig. 2 and more details in *SI Methods*). Total revenue starts to decline for longer cycles, although risk is reduced further. This result arises in this instance because of the combination of species fished, their relative growth, maturation and mortality rates, MLS, and catch level as well as differences in the value of the species being targeted (Table S1) and hence, may not be the optimal rotation-cycle time for all systems.

We tested the robustness of our finding that an RZS is beneficial in reducing the risk of local depletion using several additional sensitivity tests, including mortality, growth estimates, and patterns and scales of recruitment variability (28) (Tables S2 and S3). Our analysis suggests that, even when including these major uncertainties, it is possible to reliably discriminate between alternative management strategies in the case of data-poor fisheries.

We also tested alternative catch limits and fishing strategies, such as applying a fixed (low) fishing mortality rate continuously to all zones vs. a higher fishing mortality (but with the same overall TAC) periodically only (28). Model results were sensitive to higher catch levels (Fig. S4) and alternative settings for age at maturity and its relationship with the minimum size limit implemented (*SI Methods* and Table S4), emphasizing the enhanced benefits of using an MLS limit and cap on total catch (or effort) to supplement an RZS.

Empirical validation of the results of our modeling study is complicated because of a number of factors, including changes in fisheries legislation and target species (*SI Methods*). Nonetheless, we compared the aggregate catches (numbers landed) by species for the ECBDMF when averaged across the 9-y pre-RZS implementation period (1995–2003) with the 8-y post-RZS implementation period (Fig. 4*A*). The average annual catches have increased for all species, except black teatfish (closed since 2004), white teatfish, and prickly redfish. In light of changes in species targeting (*SI Methods*), it is not surprising that the average annual catches of curryfish and burrowing blackfish have increased substantially (by a factor >100) (Fig. 4*A*). Brown and golden sandfish catches have increased (125% and 203%, respectively) for roughly the same number of zones fished, and blackfish catches have increased substantially (233%), despite a decrease in the zones fished (Fig. 4*A*). White teatfish (−33%) and prickly redfish (−20%) catches have declined, and there have been small changes in the average number of zones fished (Fig. 4*A*). These two species have been the most consistently fished pre- and post-RZS, so that it is also possible to compare their catch rates (average number per day), and in both cases, the average catch rates have increased significantly (by 28% and 10%, respectively) since implementation of the RZS (Fig. 4*B*).

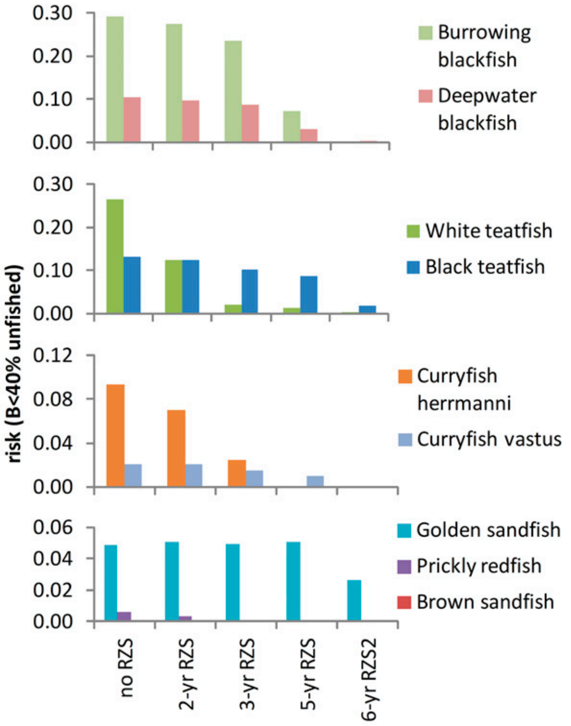

Fig. 3. Comparison of risk performance statistics (defined as the probability of biomass being reduced below 40% of the comparable no fishing scenario) for nine major species targeted in the absence of an RZS compared with different cycle times of RZS implementations as indicated and for the same catch.

Table 1. Comparison of performance with a 3-y RZS and without an RZS but with similar overall catch

Species	Risk of depletion below 40% unfished		Depletion $B^{sp}_{2032}/B^{sp}_{2012}$		Average annual landed catch (tons)		Average annual profit (million dollars)	
	RZS	No RZS	RZS	No RZS	RZS	No RZS	RZS	No RZS
Black teatfish	0.10	0.14	0.93	0.87	45.3	44.8	1.303	1.290
Brown sandfish	0.00	0.00	1.00	1.00	0.2	0.2	0.003	0.003
White teatfish	0.01	0.16	1.00	0.96	17.2	18.5	0.497	0.532
Prickly redfish	0.00	0.01	1.00	1.00	20.1	19.5	0.361	0.351
Golden sandfish	0.05	0.05	0.98	0.95	3.0	2.8	0.110	0.103
Curryfish herrmanni	0.02	0.09	1.00	0.93	17.2	17.6	0.309	0.317
Curryfish vastus	0.01	0.02	0.98	0.97	6.7	6.5	0.121	0.117
Deepwater blackfish	0.03	0.04	0.98	0.96	1.6	1.4	0.028	0.026
Burrowing blackfish	0.17	0.21	0.96	0.83	193.8	184.9	3.488	3.327
Total					305.1	296.2	6.220	6.070

Risk considers the percentage of simulations for each of nine species shown that are depleted below a specified level relative to the comparable no fishing reference case [depletion is the expected spawning biomass at the end of the projection period relative to the current (2012) level] for each species averaged across the entire area together with a summary of the average annual catch landed (in terms of tons landed product) and the average value of the catch ignoring any costs of monitoring and adaptive management.

Discussion

We evaluate the performance of rotation cycles of different length and show an improvement in biological and economic performance with increasing time between harvests up to 6 y. The RZS system emerges as substantially reducing the risk of local depletion, particularly for slow-growing species, compared with a nonrotational system with similar overall total catch. We, therefore, conclude that the RZS of the ECBDMF achieves its objectives of reducing localized depletion and reducing the risk to overall fishery sustainability, and hence, we recommend increased use of rotational harvest approaches for managing sessile marine resources in coastal and reef systems globally. There is an urgent need to improve management of high-value sessile marine resources, such as sea cucumber, because of ever-increasing demand and overexploitation (3). Globally, these fisheries are under pressure but are typically data-poor and lack the more conventional fishery-dependent and -independent data that are used to inform fishing limits. Our method integrates conventional fishery data with expert knowledge from fishers to fill in gaps, and hence, it also provides a good model for low-data stock assessment and fishery management in other places.

In general, rotation harvest strategies have the advantage that they are low cost (in terms of information needs and the need to conduct fishery-independent surveys) and easy to implement [for example, it is easier to restrict access to an area rather than enforcing individual limits on boats or fishers (15)], particularly in a comanagement context with good cooperation. Indeed, rotating spatial harvest or pulse fishing is increasingly recognized as a socially acceptable and locally implementable effective control to manage small-scale fisheries (29). Moreover, the ECBDMF also provides some benefits and efficiencies to fishing, management, and research by reducing the number of locations where fishing, enforcement, and surveys take place (15, 21).

Mechanistically, the benefits of implementing an RZS arise, because fishing alters population age compositions, with associated changes in so-called yield per recruit caused by changes in average fecundities and individual body size (30). For example, the best-sized fish to harvest is that where somatic growth is largest relative to natural mortality, and the best population size to aim for is that which yields the maximum total reproductive effort. By not fishing the same area every year, these effects result in a greater yield per recruit, because the overall biomass of animals over the minimum size limit accumulates along with the reproductive capacity of the population (particularly if the MLS limit protects at least the first age at maturity) (*SI Discussion*). Also, faster-growing species need less time to mature and contribute to breeding. In general, it, therefore, follows that longer-lived species may need longer rotation cycles. A previous study (15) used a theoretical deterministic model of scallop yield and spawning stock biomass to show that a rotational strategy should theoretically provide equal or greater yield than a nonrotational strategy.

Our results suggest the following guidelines for rotational harvest strategies applied to data-poor species in regions where more sophisticated management controls are difficult to implement. (*i*) Use a rotational cycle (with longer cycle time for longer-lived species). (*ii*) An MLS limit enhances benefits (and where data are available to inform the choice of this, selected to protect at least the first age at maturity). (*iii*) Use a cap on total catch or effort per locality (if feasible to monitor). Our aim was to simulate a realistic fishery and make recommendations that could also be applied to other more data-poor regions around the world. Hence, although theoretically, the spatial distribution of the catch could be optimized, in practice, this exercise would require detailed (and very expensive) monitoring information to annually determine the optimal spatial distribution of the harvest—this monitoring challenge is also because fishery-dependent data, such as catch per unit effort, are considered unreliable indicators of sea cucumber abundance and because recruitment variability means that it is difficult to predict which areas will have high recruitment from 1 y to the next. However, provided that there is some overall and reasonable cap on catch or effort, our analysis suggests that an RZS provides a less data-hungry method to reduce risk to the resource and improve (but not necessarily optimize) economic performance. Moreover, we simulated actual legal size limits as

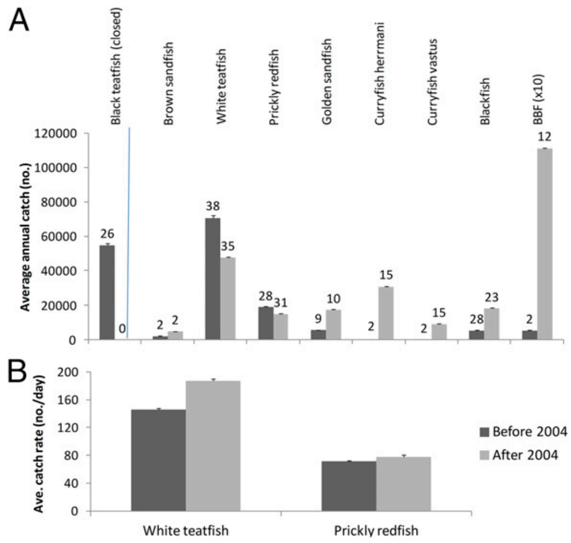

Fig. 4. (*A*) Comparison of the observed average annual catch (number + SE) for nine species (all zones combined) during the pre-RZS period (1995–2003) compared with post-RZS implementation (2004–2011). The burrowing blackfish (BBF) catch has been divided by 10 for ease of viewing on the same scale. The numbers above each bar are the average numbers of zones fished per species for each period. (*B*) Comparison of the observed average catch rates (numbers/day + SE) of white teatfish and prickly redfish during the pre-RZS (n = 4,096 and n = 2,183, respectively) and post-RZS (n = 2,263 and n = 1,749, respectively) periods.

well as reduced size limits and found that the best outcomes are obtained when an RZS is used combined with a size limit that protects at least the first age at maturity (*SI Methods* and Table S4), because the RZS allows the biomass of larger, more fecund animals to accumulate, thereby boosting overall yields as well as enhancing catch rates (in turn, an indicator of the cost of fishing).

There are other area-restricting management strategies that are commonly implemented in fisheries, such as permanent or semipermanent fishery closures or marine protected areas (MPAs). Territorial user rights for fisheries rely on the assignment of spatial user rights and are increasingly recognized as valuable ancillary marine management approaches that improve the incentives for sustainable management (31). However, strategies, such as MPAs, differ markedly in that they rely on spillover of adults or larvae from closed areas to depleted fished zones (32, 33) rather than the RZS benefit inferred by a period of cessation in fishing and the resulting somatic growth and enhanced recruitment benefits. In fact, the ECBDMF also has substantial closed areas (Fig. 1 and Fig. S1) (8); however, we did not account for the additional benefits to the ECBDMF, because although the conservation benefits of MPAs are widely recognized, there are, as yet, few studies that have convincingly shown a benefit of MPAs to individual fisheries (34, 35), and the larval dispersal for tropical invertebrates, including holothurians, is poorly understood (32). Also, examples of commercial holothurians with high genetic diversity over short distances (36) and the slow recovery of depleted populations adjacent to protected populations (37) indicate the likelihood of a low rate of larval dispersal between RZS zones for holothurians. Moreover, the yield per recruit arguments above suggest that the overall yield from a number of intermittently closed areas should be greater than that from a combination of permanently open and closed areas (because the total reproductive outputs of a population will reduce as the population approaches its carrying capacity in a closed area). Goni et al. (35) quantified lobster adult spillover from an MPA and showed that it offset the loss of fishing grounds closed in an MPA, but this result holds for species with moderate movements rather than relatively sessile species, such as sea cucumbers. Finally, MPAs do not protect adjacent open areas from overfishing, whereas we show that an RZS substantially reduces the risk of local depletion.

Empirical observations provide some support that the fishery may be benefitting from implementation of an RZS given both increased catch and catch rate observations (Fig. 4). This benefit is despite the implementation of the 2004 GBRMP Zoning, resulting in an increase in the areas protected from extractive activities (such as fishing) from 4.6% to 33.3% and hence, approximately one-third of the shallow reef area being closed to sea cucumber fishing (Fig. 1*A*). Recently, Fletcher et al. (38) report that there has been no recovery in catch levels or catch rates of commercial fisheries since that time, but their analysis does not include collection fisheries, such as sea cucumber.

In summary, we use a quantitative modeling approach to show the advantages of a spatial rotational harvest strategy to improve management of Australia's GBR sea cucumber fishery. We find an improvement in biological and economic performance when implementing an RZS compared with no RZS as well as with increasing time between harvests up to 6 y. This result is robust across a suite of different species with different life history characteristics and fishing pressures, and it is supported by empirical observations of increases in average catches of most species and an increase in the average catch rate of white teatfish and prickly redfish over the 8-y period since implementation of an RZS as well as the results from other systems on species, such as scallops and abalone. These findings suggest that the benefits of an RZS might apply to marine benthic resources globally. The greatest improvement was obtained for slow-growing species and species under higher fishing intensity. Moreover, we show that these results are robust to a number of uncertainties in model parameterization and important structural assumptions, such as uncertain recruitment patterns, as well as under stochastic variability. Our results support the use of rotational harvests to better manage sessile marine resources that are often severely overexploited but highly important to many communities worldwide.

Methods

Full details of the methods are provided in *SI Methods*. We use a simulation method based on all available data and information from a sea cucumber fishery to test whether an RZS might, in general, reduce the risk of localized stock depletion in data-poor fisheries. Hence, we first describe the data and model inputs followed by the spatial multispecies model and methods used to test and compare alternative management strategies.

Area estimates for the fishery, zones, and reef habitats were assembled from available remote-sensed habitat data (3dGBR; www.deepreef.org), and spatial area estimates were calculated in a geographic information system (GIS). Spatial catch data from the ECBDMF logbook data (Queensland Department of Agriculture, Fisheries and Forestry) were then assigned to zones spatially using derived location data in the logbook data.

The focus species of the MSE were defined as the high- and medium-value species of the fishery based on the logbook data and input from fishers and managers at a stakeholder workshop (28). These species have made up over 92% of the catch since 1995 (Fig. 1).

Estimates of species growth, age at maturity, and age at maximum size for fished animals are summarized in Table S1. The same MLS limits are assumed in the RZS and no RZS simulations and shown in Table S1. Our base case model uses the actual MLS limits set for the fishery, but we also explore sensitivity to reducing these size limits and hence, increasing the availability of younger (often not reproductively mature) individuals to removal by the fishery. The MLS limits are converted to age estimates, and a knife-edge fishing selectivity is assumed. Hence, it is assumed that animals at or older than the age corresponding to the MLS are fully selected by the fishery and that there is good compliance with the MLS regulations. This assumption is likely to hold for the ECBDMF but not necessarily for many other sea cucumber fisheries. Age, length, and weight data for each species were also used to generate mass–length–age relationships as part of model simulations (Table S1).

The project included a stakeholder workshop to elicit fisher behavioral dynamics, field information, and management strategy test cases (including species and spatial management units) (28). Fishery-dependent (logbook), survey, and environmental data collected during the initial phases of the project were used to build and calibrate a spatial age-structured operating model.

The spatial and age-structured model includes nine sea cucumber species with populations distributed across 154 zones. The time period is 1995–2012, with a 20-y future projection time period (28). The following four factors were assumed to account for most of the uncertainty regarding the key considerations of resource status and productivity: (*i*) the natural mortality of each species, (*ii*) the steepness parameter of the stock-recruitment functions, (*iii*) the underlying recruitment pattern (stochastic and variable vs. deterministic), and (*iv*) the starting (1995) biomass (*SI Methods* and Table S3). An RS (39) was, thus, constructed to include a sufficiently representative range of potential estimates of current population status and productivity as summarized in Tables S1, S2, and S3. The RS was chosen based on multiple sensitivity analyses as well as the most up-to-date information on each species, and by placing reasonable bounds on key parameters, much of the uncertainty is accounted for in the analyses. Additional data and diagnostics used to validate the model are summarized in *SI Methods* and Fig. S5.

For each harvest strategy tested, 10 replicates of each of 16 RS cases (i.e., a total of 160 simulations) were projected over a 20-y period into the future. The different replicates represent alternative plausible future states of nature that are compatible with the available information (39). These different replicates vary because of stochastic effects, namely recruitment variability. For each species in each area, the median is based on all 160 projected simulations, and hence, each median incorporates both the uncertainty represented by the RS of 16 operating models as well as stochastic future environmental states. The same set of random numbers was used to test and compare the performance of future harvest strategies.

MSE is a powerful tool for investigating the efficacy of the RZS for mitigating risk to fishery populations and comparing alternative management strategies (10, 12, 40). It allows for the exploration of outcomes across a range of scenarios that address uncertainty in population parameters (growth, mortality, and recruitment) for fishery species. Our spatial multispecies model assumed that future fishing would take place in a similar manner to recent fishing, with a TAC of no more than 361 t landed form (salted/frozen parboiled) (Fig. 1). For illustrative purposes, we assumed that the (currently closed) black teatfish fishery would be reopened with a TAC set similar to the average of the last 3 y when a catch was taken. Moreover, the model simulates a 3-y (and other frequencies) rotational harvest, whereby an individual zone is fished only one time every 3 y, and compares this with a nonrotational fishing pattern that has the same total catch over a 20-y projection period (i.e., we simulate removing a bigger catch less frequently from a number of zones and compare this with smaller annual catches taken annually from these zones, which was the case before the implementation of the RZS) (Fig. S2). Finally, the 3-y RZS is used as a reference; the catches in the no RZS and other frequency RZS cases are calibrated to have the same risk as the reference case, and the difference in annual catch and value (averaged over 20 y) is computed (Fig. S3).

The primary risk metric that we used is the proportion of all individual runs across all zones that ended below 40% of the comparable no fishing reference case at the end of the projection period (i.e., when considering all possible future projection outcomes for a species over the entire fished area, how likely is it that local depletion will occur).

Average annual revenue (million dollars) was computed as the landed weight of each species multiplied by current average market prices. Golden sandfish are a very high-value species, and we assumed an average value of $200 per kg dry and an average conversion factor of 18% of salted landed weight (41). We used the relative values of very high, high, and medium (no low-value species were included here) and their relative catches (Table S1). This revenue does not account for costs of monitoring and adaptive management. For each of the nine species, we plotted the risk-revenue tradeoff under each of the rotation cycles examined (Fig. S6). Next, we plotted the median risk from all species corresponding to the total revenue (summed across all species) for each cycle time scenario (Fig. 2).

To test whether there was any empirical evidence to support our finding that an RZS performs better than a non-RZS system, we compared the aggregate catches (numbers landed) by species for the ECBDMF as well as the average catch rates of white teatfish and prickly redfish when averaged across the 9-y pre-RZS implementation period (1995–2003) with the 8-y post-RZS implementation period (*SI Methods*).

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