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

Éva Elizabeth Plagányi1, Timothy Skewes, Nicole Murphy, Ricardo Pascual, and Mibu Fischer

Oceans and Atmosphere Flagship, Commonwealth Scientific and Industrial Research Organisation, Brisbane, QLD, Australia 4102

Edited by Stephen Polasky, University of Minnesota, St. Paul, MN, and approved April 8, 2015 (received for review April 11, 2014)

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.

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.

1To whom correspondence should be addressed. Email: Eva_Plaganyi-Lloyd@csiro.au.

Author contributions: E.E.P. and T.S. designed research; E.E.P., T.S., and N.M. performed research; E.E.P., T.S., and R.P. contributed new reagents/analytic tools; E.E.P., T.S., N.M., R.P., and M.F. analyzed data; and E.E.P. and T.S. wrote the paper.

The authors declare no conflict of interest.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1406689112/-/DCSupplemental.
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. S3 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...
For the same risk to the resource, the difference between the average catch and value with increasing rotation-cycle length was maintained in some zones, and the spawning biomass of the target 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). 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). 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 (235%), despite a decrease in the zones fished (Fig. 4). 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). 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. 4B).
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 management 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, if, 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 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

<table>
<thead>
<tr>
<th>Species</th>
<th>RZS</th>
<th>No RZS</th>
<th>RZS</th>
<th>No RZS</th>
<th>RZS</th>
<th>No RZS</th>
<th>RZS</th>
<th>No RZS</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Black teatfish</td>
<td>0.10</td>
<td>0.14</td>
<td>0.93</td>
<td>0.87</td>
<td>45.3</td>
<td>44.8</td>
<td>1.303</td>
<td>1.290</td>
<td>305.1</td>
</tr>
<tr>
<td>Brown sandfish</td>
<td>0.00</td>
<td>0.00</td>
<td>1.00</td>
<td>1.00</td>
<td>0.2</td>
<td>0.2</td>
<td>0.003</td>
<td>0.003</td>
<td>0.000</td>
</tr>
<tr>
<td>White teatfish</td>
<td>0.01</td>
<td>0.16</td>
<td>1.00</td>
<td>0.96</td>
<td>17.2</td>
<td>18.5</td>
<td>0.497</td>
<td>0.532</td>
<td>1.6</td>
</tr>
<tr>
<td>Prickly redfish</td>
<td>0.00</td>
<td>0.01</td>
<td>1.00</td>
<td>1.00</td>
<td>20.1</td>
<td>19.5</td>
<td>0.361</td>
<td>0.351</td>
<td>0.2</td>
</tr>
<tr>
<td>Golden sandfish</td>
<td>0.05</td>
<td>0.05</td>
<td>0.98</td>
<td>0.95</td>
<td>3.0</td>
<td>2.8</td>
<td>0.110</td>
<td>0.103</td>
<td>0.05</td>
</tr>
<tr>
<td>Curryfish hermanni</td>
<td>0.02</td>
<td>0.09</td>
<td>1.00</td>
<td>0.93</td>
<td>17.2</td>
<td>17.6</td>
<td>0.309</td>
<td>0.317</td>
<td>0.9</td>
</tr>
<tr>
<td>Curryfish vartus</td>
<td>0.01</td>
<td>0.02</td>
<td>0.98</td>
<td>0.97</td>
<td>6.7</td>
<td>6.5</td>
<td>0.121</td>
<td>0.117</td>
<td>0.02</td>
</tr>
<tr>
<td>Deepwater blackfish</td>
<td>0.03</td>
<td>0.04</td>
<td>0.98</td>
<td>0.96</td>
<td>1.6</td>
<td>1.4</td>
<td>0.028</td>
<td>0.026</td>
<td>0.02</td>
</tr>
<tr>
<td>Burrowing blackfish</td>
<td>0.17</td>
<td>0.21</td>
<td>0.96</td>
<td>0.83</td>
<td>193.8</td>
<td>184.9</td>
<td>3.488</td>
<td>3.327</td>
<td>3.27</td>
</tr>
<tr>
<td>Total</td>
<td>305.1</td>
<td>296.2</td>
<td>6.220</td>
<td>6.070</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
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 fishery areas (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, they only offer 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.

Ecosystems 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. 1A). 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 cucumbers.

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 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 over-exploited 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 MSE 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 function that underlies the underlying parameter (i.e., deterministic), and (iii) 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 (12, 40). It allows us to explore 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 boiled) (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. 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, and for each of the nine cycles, 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 ECDMFP as well as the average catch rates of white teatfish and prickly redfish when averaged across the 9-y pre-RZS implementation period (1993–2003) with the 8-y post-RZS implementation period (SI Methods).

ACKNOWLEDGMENTS. The authors thank the participants of the Stakeholder Workshop held as part of the project. Fishers, entitlement holders, processors, industry scientists, and managers all contributed. Particular thanks to Phil Gaffney, Susan Theiss, and the team in the Queensland Department of Agriculture, Fisheries and Forestry Data Section for provision of fishery data. Great Barrier Reef Marine Park Authority, facilitated by Randall Ove and spatial Great Barrier Reef Marine Park Zonation Schemes, and reef habitat data. M. Haddon, R. Hillary, R. Buckworth, and two anonymous reviewers provided helpful comments on an earlier version of the manuscript. This project was funded by Australia’s Fishery Research and Development Corporation. Scientific and Industrial Research Organisation Oceans and Atmosphere Flagship.
Supporting Information

Plagányi et al. 10.1073/pnas.1406689112

SI Methods

Data.

Catch data. Nine focus species of the MSE, selected in consultation with stakeholders (1), have made up over 92% of the catch since 1995 (Table S1).

The primary data source was spatial logbook data from the ECBDMF. Catch data for sea cucumber fisheries can be reported in various forms: from live to processed and dried beche-de-mer. Most tropical sea cucumber fisheries report catches as dried beche-de-mer. The ECBDMF mostly records landed weight in logbooks and buyer returns (sometimes mistakenly called gutted weight), which is the form currently used for quota management and catch reporting. Number caught is also used for catch reporting in logbooks. Landed weight is either gutted and salted or gutted, parboiled, and frozen. Conversion data for these forms are not available for all species, but salted form conversion factors are available for several species (2) and average about 0.85 of gutted weight (range = 0.76–0.92). No conversion factors are available for parboiled and frozen product. However, perusal of average landed weights indicates similar weight loss factors for several species.

The current logbook database does not contain any spatial catch data from before the 1995–1996 fishing year (3). For ease of referencing, we refer to all split-year fishing seasons using the start year (i.e., model year 1995 corresponds to fishing year 1995–1996). To date, management agencies and industry have focused on mitigating risk to fishery populations through harvest strategies that have limited and spread effort, such as the RZS of the ECBDMF, where each of 154 rotational zones is allocated a limited number of fishing days (15 d) only one time every 3 y on a rotational basis (1).

Population parameters and model inputs. Estimates of species growth, age at maturity, and age at maximum size for fished animals are summarized in Table S1. Knife-edge functions are assumed for the species-specific fecundity vectors, with the age at first maturity \(a_m\) as shown in Table S1. Similarly, the MLS limits shown in Table S1 are converted to age estimates using the equations below, and a knife-edge fishing selectivity is assumed. Hence, it is assumed that animals of 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). There are several problems associated with constructing an age–length key for holothurians, including the difficulties of accurately measuring individuals, their malleable shape, the fact that they cannot be tagged, and the fact that they are able to shrink in size (3, 4). There were also little data to fit a growth curve for each species, and hence, a simpler linear approach was preferred in this study based on the data presented in Table S1 and with relationships computed as described below.

The length (in millimeters) of an individual of species \(s\) at age \(a\) is computed as

\[
L_{s,a} = \kappa_s \cdot a, \tag{S1}
\]

where

\[
\kappa_s = \ell_{\infty,s} / \ell_{\text{max}} \tag{S2}
\]

under the assumption that individuals attain their maximum length \(\ell_{\infty,s}\) at age \(\ell_{\text{max}}\).

The mass (in grams) of an individual of species \(s\) and age \(a\) is given by

\[
w_{s,a}^{\text{raw}} = c_s \cdot (L_{s,a})^b, \tag{S3}
\]

where the constants \(c_s\) and \(b\) were estimated by fitting to available length–weight data for five species (1). Parameter values for the remaining species are assumed to be the same as those for the most similar of five species for which data were available. The mass of animals is assumed to remain constant after attaining the maximum age of five set in the model.

Detailed scientific information on the density of harvested holothurian species on the GBR is very limited; however, there were some robust density data for two species: black teatfish and burrowing blackfish. Black teatfish were surveyed from late 1998 to early 2000 (around the time of the fishery closure) (3, 5). Seventy-two reefs throughout the GBR were sampled, including closed and open reefs. Industry-sponsored surveys of burrowing blackfish populations have taken place at several locations in the ECBDMF where burrowing blackfish have been prospected by the fishers (6, 7). Starting (1995) density estimates input into the model were computed as described in the work by Skewes et al. (1) and are summarized in Table S2.

MSE Approach. The spatial units used in the MSE are the RZS zones of the ECBDMF (154 zones) plus 3 original burrowing blackfish zones (Fig. 1). 2 offshore reefs (Saumarez and Marion Reefs), and 1 general fishery permit for Ashmore Reef, resulting in a total of 160 zones; plus, there are open and closed areas outside these zones (lumped into two categories), resulting in 162 zones that are explicitly represented in the model.

Given the large amount of detailed output available from a spatial multispecies model, selected summaries only are presented of typical and key results. We assume that 1995 represents the pristine (no fishing) condition, because there were only fairly minor catches before this time (apart from black teatfish but see below). Collectively, the model includes a broad range of starting values given that there are nine species and 162 zones. We use the starting biomass values as a proxy for an average unfished level \(K\), but the populations are highly variable, and hence, in good years, the biomass may exceed \(K\). Moreover, the RS as described below incorporates simulations that use a different starting biomass estimate.

The MSE approach shows the tradeoffs between different strategies and hence, informs which strategies reduce the risk to the resource as a whole as well as individual species of concern as well as those that are more efficient. This approach is particularly suited to assessing the effectiveness of an RZS, especially for reducing the risk of localized stock depletion. Simulation of a range of alternative implementations, such as the time between rotations, has the potential to inform improvement in management practices.

Spatial Model of Sea Cucumber Populations. Below is a description of the population model, which is based on an earlier model developed by Plagányi et al. (8). The model includes nine sea cucumber species with populations distributed across 162 zones. The time period is 1995–2012, with a 20-y future projection time period. A full description of the age-structured population model is provided in the work by Skewes et al. (1).
An age-structured production model (examples in refs. 9 and 10) is simultaneously applied to each of nine species, with sub-populations simulated at each of 162 zones.

The resource dynamics are modeled by the following set of population dynamics equations:

\[ N_{s,r+1,y} = R_{s,r+1,y}, \]

\[ N_{s,r+1,y+1} = \left( N_{s,r,y} e^{-3M_t/4} - C_{s,r,y} \right) e^{-M_t/4} \quad \text{for } 1 \leq a \leq m - 2, \]

\[ N_{s,r+1,m,y} = \left( N_{s,r,y} e^{-3M_t/4} + N_{s,r,y} e^{-3M_t/4} - C_{s,r,y} \right) e^{-M_t/4}, \]

where \( N_{s,r,y} \) is the number of holothurians of species \( s \) and age \( a \) in zone \( r \) at the start of year \( y \) (which refers to a calendar year), \( R_{s,r} \) is the total recruitment (number of 0-y-old holothurians) in zone \( r \) of species \( s \) at the start of year \( y \), \( M_t \) denotes the (age-independent) natural mortality rate of species \( s \), \( C_{s,r,y} \) is the predicted number of holothurians of age \( a \) and species \( s \) caught in zone \( r \) in year \( y \), and \( m \) is the maximum age considered (taken to be a plus group and set equal to five for all species). The population model used here assumes pulse fishing [Pope’s approximation (11)], and the approximation of the fishery as a pulse catch three-quarters into each year is because zones are approximated (11), and the approximation of the fishery as a deterministic is the proportion of the virgin recruitment that is realized at a spawning biomass level of 20% of the virgin spawning biomass:

\[ \beta_4 = \frac{(K^p)(1 - 5h_{t0},2)}{5h_t - 1} \]

and

\[ \alpha_5 = \frac{\beta + K^p}{SPR_{syr}} \]

where

\[ SPR_{syr} = \sum_{a=1}^{m} f_{s,y} \omega_{s,a}^s \rho_{s,a}^{virg} \]

with

\[ N_{s,a}^{virg} = 1, \]

\[ N_{s,a} = N_{s,a-1} e^{-M_t} \quad \text{for } 2 < a < m - 1, \]

\[ N_{s,m} = N_{s,m-1} e^{-M_t} \left( 1 - e^{-M_t} \right). \]

Total catch and catches at age. The catch by mass in year \( y \) is given by

\[ C_{s,y} = \sum_{a=1}^{m} w_{s,a}^y e^{-3M_t/4} S_{s,a} F_{s,y}, \]

where \( \omega_{s,a}^y \) is the mass of a holothurian of species \( s \) and age \( a \) at the time that it is exploited (i.e., September), \( C_{s,y} \) is the number of holothurian of species \( s \) and age \( a \) caught in zone \( r \) in year \( y \), \( S_{s,a} \) is the fishing selectivity at age \( a \) for species \( s \)—assumed not to vary spatially (note that, when \( S_{s,a} = 1 \), it implies that age class \( a \) is fully selected)—and \( F_{s,y} \) is the fished proportion of a fully selected age class of species \( s \) in zone \( r \).

The model estimate of the exploitable (available) component of biomass during the third quarter is given by

\[ B_{s,y}^p = \sum_{a=1}^{m} w_{s,a}^y e^{-3M_t/4} S_{s,a} \]

Initial conditions. The resource is assumed to be at deterministic equilibrium (corresponding to an absence of harvesting) at the start of 1995 (the initial year considered here). Given a value for the preexploitation spawning biomass \( B_{s,0}^p \) of each species \( s \) together with the assumption of an initial equilibrium age structure, it follows that

\[ B_{s,0}^p = \sum_{a=1}^{m} f_{s,a} w_{s,a}^y \exp(-M_t \cdot m) \exp(-M_t \cdot m) \exp(-M_t \cdot m), \]

which can be solved for \( R_{s,0} \).
Natural mortality rates have not been well-established for sea cucumber species. Mortality rates for several sea cucumber species have been reported in the literature (1). These data are comparable with values calculated for sea cucumber species from the MSE model using Hoenig’s Method (using maximum age) (13). We used a conservative approach to selecting natural mortality rate parameters, including an annual $M = 0.3$ (resulting in a longevity of 15 y using Hoenig’s Method) as the lower rate scenario for teatfish species and prickly redfish and $M = 0.4$ for all other species (Table S1).

**M:** Natural mortality. Natural mortality rates have not been well-established for sea cucumber species. Mortality rates for several sea cucumber species have been reported in the literature (1). These data are comparable with values calculated for sea cucumber species from the MSE model using Hoenig’s Method (using maximum age) (13). We used a conservative approach to selecting natural mortality rate parameters, including an annual $M = 0.3$ (resulting in a longevity of 15 y using Hoenig’s Method) as the lower rate scenario for teatfish species and prickly redfish and $M = 0.4$ for all other species (Table S1).

**ML:** The lower bounds of the mortality estimates were used for each species, and because this simulation is a slow-growth scenario, they were combined with slow-growth assumptions for two teatfish species for which slow growth has been proposed as likely (5).

**H. Steepness parameter.**

$HH$: The average mortality estimates for each species were used together with the growth parameters (length–weight–age relationships) computed as shown in Table S1.

$HL$: The lower bounds of the mortality estimates were used for each species, and because this simulation is a slow-growth scenario, they were combined with slow-growth assumptions for two teatfish species for which slow growth has been proposed as likely (5).

**R. Recruitment frequency.**

$RH$: Recruitment is assumed to be stochastic, with random fluctuations about the underlying stock–recruit curve.

$RL$: Recruitment is assumed to be deterministic, with the recruitment for each species in each of the zones determined by the stock–recruit relationship.

**K. Starting biomass.**

$K$: The starting (1995) biomass was fixed at the input values calculated as described above, except for black teatfish, for which one-half of the value was used.

$KL$: The starting (1995) biomass was assumed to be 0.5 times the $K$ values.

Given key uncertainties regarding major considerations of resource status and productivity, the full RS of 16 operating models (OMs) spanning these uncertainties, rather than a single OM, was constructed for the sea cucumber resource (Table S3).

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 (12). These different replicates vary because of stochastic effects, namely recruitment variability.

**Performance Statistics.** The following performance statistics, related to the objectives above, were computed for each harvest strategy tested to assess the use and optimal configuration of the RZS for mitigating localized depletion, reducing risks to overall sustainability, and maximizing efficiency and profits of this multi-species fishery. Projections were conducted over 20 y.

**Resource status-related.**

$B^P_{2012}/B^P_{0}$: The expected spawning biomass at the end of the projection period relative to the starting (1995) level (used as a proxy for $K$) for each species averaged across the entire area and for each zone.

$B^P_{2012}/B^P_{0}$: 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 and for each zone.

Risk of local depletion: Percentage of all individual runs that ended below $B^P_{0} = 0.2$ of the comparable no fishing reference case at the end of the projection period.

Risk of depletion below 40% unfished: As above but a more conservative risk measure.

**Utilization-related.**

Average catch: $1/20\sum C_i$ over 2012–2032 (for each zone as well as the entire area and for three groups of species: very high, high, and medium value).

Average annual revenue (million dollars): Computed as the landed weight of each species multiplied by current average market prices.

**Computing revenue.** Average annual revenue (million dollars) is computed as the landed weight of each species multiplied by current average market prices. Golden sandfish were regarded as 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 (1). We used the relative values of very high, high, and medium (no low-value species are included here) and their relative catches (Table S1). This revenue estimate does not account for costs of monitoring and adaptive management.

**Validating the Model.** 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. Unfortunately, there are no relative indices of abundance to which to fit the model; however, we were able to test the model against the assumption of the pristine (pre-1995) biomass for black teatfish being the application of closed area density (in 2000) to all reef areas in the northern GBR fishery area (5). These data indicate that the black teatfish population decreased to 38% of the 1995 estimate by year 2000 in the fished zones, and the preliminary model was not able to match this decrease for most zones—at least not in such a way that the population would subsequently recover in the absence of fishing. Detailed sensitivity analyses suggested that there were two main problems with the black teatfish model fit—the starting biomass estimates are too high in some zones, and the recruitment is a bit too optimistic. The catches (after converting to tons) were a small percentage only of the biomass estimates in most zones, which is incompatible with the observed population declines; hence, the biomass estimates may be overly optimistic, and model starting estimates ($K$) for black teatfish were adjusted to one-half of these values. It is also likely that the catch estimates for black teatfish underestimate true removals given that fishing of this high-value species occurred for several years before the catch data were available. Data on the total catch of black teatfish between 1987 and 1999 are not available but have been estimated at 2,500 t (quoted in ref. 4) compared with 593 t as per the logbook data between 1995–1996 and 1999. For the other species, the survey biomass estimate is used for one-half of the RS, and one-half of this value is used for the other eight OMs.

A second challenge in the modeling involved balancing recruitment with population growth. For teatfish species in particular, where slow-growth scenarios are considered likely, under extreme scenarios, such as pulsed and sporadic recruitment, local black teatfish populations were unable to sustain themselves in the model and continue to decline, even if future catches are set to zero. A model diagnostic that was used was that a recovery is expected with no fishing, even if slow. However, if we have...
constant (albeit variable) recruitment, it is hard to see the impact of catches that were taken in a few years only, because only the older age classes are targeted, and there are sufficient incoming recruits to fill the gap. However, black teatfish populations have been observed declining rapidly in response to fishing (4, 5). Hence, to more accurately calibrate the model for black teatfish and white teatfish, the recruitment variability has been skewed slightly, so that, in some (randomly determined) years, the recruitment is lower than average (but not zero). Collectively, these changes to the preliminary model yielded a more realistic population trajectory for black teatfish that compares better with the survey relative index (1).

An important model diagnostic was that the model populations had the same features as observed in the field—for example, high natural variability, even in the absence of fishing, and the ability to replicate boom-and-bust cycles under fishing. Although realistic, this variability confounds understanding of the impacts of fishing over and above natural variability, and hence, we included a performance statistic that compared each projected population depletion with an equivalent no fishing projection.

To assess whether the modeled population fluctuations were realistic, we compared them with survey data available for four of the same species in Torres Strait, where there have been several surveys of sea cucumber populations (15, 16). In all four cases (black teatfish, blackfish, white teatfish, and prickly redfish), the extent of modeled variability compared well with observed variability from field observations (1) (Fig. S5), further validating the usefulness of the model.

An additional model diagnostic that was used for all species to assess whether the modeled populations were as realistic as possible was to examine the historic fishing proportion estimates (catch as a proportion of population numbers of all ages exceeding the age at first capture), because these fishing proportions are bounded by zero and a maximum of one. Hence, very low values suggest the biomass estimates used may be too high, whereas consistently high values suggest that the biomass may have been underestimated (which was the case for white teatfish in some zones) (1).

Finally, a realistic black teatfish population recovery under no fishing was modeled under both starting biomass and low-K starting biomass scenarios. This simulation shows a recovery under both starting biomass scenarios, with recovery taking about 15–20 years under the more likely low-K scenario (1).

**Sensitivity Tests.** To further test the sensitivity of the MSE outputs to variation in basic assumptions, numbers of sensitivity tests were run using the 3-y RZS scenario as the reference case for comparisons. These tests are described in more detail in ref. 1 and support the finding that the RZS with current TAC levels performs well and is robust across a range of sensitivities tested. Below, we describe two key sensitivity tests that were done.

1. Age at first maturity: Increase the age at first maturity by 1 year (equivalent to increasing the size at first maturity), so that there is a longer time before individuals can contribute to the spawning biomass, but the age/size at first capture remains as current.

2. Age at first maturity with higher TAC: As above but also assume higher future TACs ($\times 3$).

The model outputs were sensitive to even a small change in the age at maturity. The risk of depletion increases markedly for burrowing blackfish and black teatfish (Table S4). This result highlights the importance of good data to inform choice of an MLS, which takes into account the age or size at maturity. Fortunately, the current catch levels are sufficiently conservative that no major risk was predicted to the resource as a whole if there is some error in the best estimates of the age at first maturity. However, if simulations are run with much higher TACs and these more conservative age at maturity estimates, several local populations are predicted to crash, and overall population depletion is substantially worse (Table S4). This poor performance is particularly the case for the species with younger age/size at first maturity, such as golden sandfish and burrowing blackfish (Table S1).

**Risk–Revenue Tradeoff Curve for RZS with Different Cycle Times.** For each of the RZS-cycle lengths tested, we simulated future fishing by assuming that it would take place in a similar manner to recent fishing but with relative increases in catches, so that, for each scenario, the average annual catch over the 20-y projection period would be roughly equivalent to the commercial TAC of no more than 361 t landed form (salted/frozen and boiled). The TAC is comprised of 0 t black teatfish, 53 t white teatfish (divided into 40 and 13 t for northern and southern areas, respectively), and 308 t other species (including some minor species not included in our model). However, as before, we used a hypothetical future TAC for black teatfish of 45.3 t for illustrative purposes. Note that the actual realized catches in each model scenario may be less than the planned catch if insufficient exploitable biomass is available in a zone.

For each cycle-length scenario, we compute the average realized catch and value as well as the risk performance statistics (SI Methods, Performance Statistics).

Fig. S6 shows the risk–revenue tradeoff for each of the rotation cycles as indicated, with the individual symbols representing nine different species and the individual points highlighted for the two high-value species (black teatfish and white teatfish) and the medium-value burrowing blackfish. Comparing across each species suggests a reduction in the risk as the cycle time is increased (illustrated in Fig. 3 for example). Although the catch per species is similar for different cycle times, there are some small differences in catch and hence, revenue—for example, for white teatfish, the 3-y cycle average revenue (US$0.96 million) exceeds the no RZS and 5- and 6-y cycle revenues (US$0.93, US$0.74, and US$0.76 million, respectively) but is less than the 2-y cycle revenue (US$1.01 million). However, the 2-y cycle and no RZS scenarios have high associated risk statistics (Fig. S6), and hence, there is a tradeoff between achieving a high revenue and reducing risk. A similar result is seen for black teatfish (i.e., the risk associated with the 2-y cycle and no RZS scenarios exceeds 10%). For burrowing blackfish, however, the target catch could not be caught under the no RZS and 2-y cycle scenarios, which thus, show lower revenue and higher risk than the longer cycle times. To illustrate the risk–revenue tradeoff, we first computed the total revenue (by summing the revenue of all species) for each cycle time scenario, because in a multispecies fishery, total revenue is an important indicator of economic performance. Next, we considered the risk associated with each revenue total. We used as our risk statistic the median risk from all species and also, computed the SD to highlight that the risk statistics are variable across species. The median risk–total revenue tradeoff curve (Fig. 2) suggests that the 3-y cycle time results in the greatest total revenue with a low associated median risk, and it is, thus, considered optimal in this fishery given the mix of species, their life histories, management regulations (such as MLS relative to age at maturity), and relative value.

**Empirical Validation of the RZS.** We analyzed all available cleaned logbook data 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 when averaged across the 9-y pre-RZS implementation period (1995–2003) with the 8-y post-RZS implementation period (Fig. 4/4). We also computed the average number of zones that was fished each year for all nine species as a rudimentary measure of fishing effort. Relevant management changes over this period include the 1999 closure of the black teatfish fishery (because of concerns over its status) and the overall TAC being reduced from 500 to 380 t (wet gutted weight)
in 1998 to 361 t (landed weight—salted or parboiled and frozen) in 2006 because of the catch being reported as landed (green salted and parboiled and frozen) weight (17). For white teatfish, a TAC of 127 t (increased to 138 t for one season) was introduced in 1999 and has been reduced over the years, mainly because of concerns about the sustainability of the catch and the loss of fishing areas through GBRMP zoning, to the current 64 t (17). Moreover, in 2003, the fishery began targeting a new species, burrowing blackfish, after exploratory surveys found high densities in specific locations. Also, during 2008–2009, curryfish increased in the catch because of rising interest in the commercial market for this species and improved processing techniques (17).

In light of the above, the two species that have been most consistently fished in the pre- and post-RZS periods are white teatfish (a high-value species) and prickly redfish (a medium-value species). For these two species, we, therefore, used available logbook data to compare the average catch rates (numbers per day) during the pre-RZS (1995–2003) and post-RZS (2004–2011) periods (Fig. 4B). We used an unpaired t test to test the hypothesis that the post-RZS catch rate exceeds the pre-RZS catch rate.

SI Discussion

Our study uses a realistic multispecies and spatial model of sea cucumber populations to show the yield and revenue benefits of rotations, even when recruitment is uncertain and stochasticity is added and integrated across a range of species with different life history (and hence, yield per recruit) characteristics. Moreover, we show that an RZS can substantially reduce the risk of localized depletion in a fishery. Our model uses all data available for the fishery and tests the robustness of model results to a broad range of parameter and model structural uncertainty.

At the simplest level, the benefits of an RZS arise because of the fallow period, enabling individuals to grow to the size where the somatic growth rate is largest relative to natural mortality $M$. For most species, $M$ declines with age, whereas somatic growth rate increases with age before reaching a maximum and declining as individuals approach their maximum size. For faster-growing species (generally, shorter-lived with higher $M$), the rate of production of biomass is, thus, achieved sooner than for slow-growing species (longer-lived with lower $M$). Similarly, faster-growing species need less time to mature and contribute to breeding, and hence, shorter rotation cycles may work better for them than for longer-lived species. Our results provide some support for this notion, although they are confounded by a range of additional variables that need to be considered (which, indeed, they are in our model), including the MLS.

Fig. S2. Average annual projected catch when applying the fishing strategy as shown for 20 y into the future to nine major targeted species.

Fig. S3. The average annual projected catch under each fishing strategy for the same level of risk as the 3-y RZS strategy shown together with the difference in the total annual value (million dollars) and the 3-y RZS strategy.

Fig. S4. Risk performance statistics (defined as the probability of biomass being reduced below 40% of the comparable no fishing scenario) for nine major species targeted when future catches are set at triple the current level compared between scenarios with no RZS, a 3-y cycle time of RZS implementation, and a strategy with catches spread spatially with a fishing mortality proportion (F) of 20% per zone. (A) Blackfish, (B) teatfish, (C) curryfish, and (D) sandfish and redfish species.
Fig. S5. Illustrative examples of (A) black teatfish, (B) deepwater blackfish, (C) white teatfish, and (D) prickly redfish spawning biomass model trajectories for selected zones in the ECBDMF compared with survey biomass data from Torres Strait zones to compare the range of variability that can be expected in sea cucumber populations. Survey sites labelled as North (Nth), South (Sth), South-East (SE), Reef (Rf), and Great Barrier Reef (GBR).

Fig. S6. The risk–revenue tradeoff for each of the rotation cycles as indicated, with the individual symbols representing nine different species and the individual points highlighted for the two high-value species (black teatfish (BTF) and white teatfish (WTF) and the medium-value burrowing blackfish (BBF)). The risk performance statistic is defined as the probability of biomass being reduced below 40% of the comparable no fishing scenario, and the revenue (million dollars) is computed as the product of catch (tons) and value.
Table S1. Growth and age parameter starting estimates and alternative mortality rates (years\(^{-1}\)) for sea cucumber species used in the population model (note that sandfish are included for comparison only)

<table>
<thead>
<tr>
<th>Common name</th>
<th>Species</th>
<th>MLS (mm)</th>
<th>Age of maturity (y)</th>
<th>Size at maturity (mm)</th>
<th>Size at maturity (kg)</th>
<th>Size maximum length (mm)</th>
<th>Size maximum weight (kg live)</th>
<th>Age at maximum length (y)</th>
<th>Natural mortality (Hoenig’s; MSE_minimum; MSE_maximum)</th>
<th>Value (multiplier)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sandfish</td>
<td>Holothuria scabra</td>
<td>200(^*)</td>
<td>2(^†)</td>
<td>150(^†)</td>
<td>0.184(^§)</td>
<td>400(^*)</td>
<td>2(^*)</td>
<td>To 10; 6(^+)</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Black teatfish</td>
<td>Holothuria whitmaei</td>
<td>300(^*)</td>
<td>4(^*)</td>
<td>260(^†)</td>
<td>0.09(^§)</td>
<td>560(^*)</td>
<td>3(^*)</td>
<td>5–10(^1)</td>
<td>0.44; 0.3; 0.6</td>
<td>H (0.8)</td>
</tr>
<tr>
<td>Brown sandfish</td>
<td>Bohadschia vitiensis</td>
<td>150(^*)</td>
<td>3(^†)</td>
<td>150(^†)</td>
<td>2.5(^*)</td>
<td>260(^*)</td>
<td>3(^*)</td>
<td>7.3; 0.4; 0.8</td>
<td>M (0.5)</td>
<td></td>
</tr>
<tr>
<td>White teatfish</td>
<td>Holothuria fuscogillva</td>
<td>400(^*)</td>
<td>4(^*)</td>
<td>320(^†)</td>
<td>1.175(^§)</td>
<td>570(^*)</td>
<td>5(^*)</td>
<td>12(^+)</td>
<td>0.44; 0.3; 0.6</td>
<td>H (0.8)</td>
</tr>
<tr>
<td>Prickly redfish</td>
<td>Thelenota ananus</td>
<td>500(^*)</td>
<td>4(^*)</td>
<td>300(^†)</td>
<td>1.23(^§)</td>
<td>800(^*)</td>
<td>12(^*)</td>
<td>10–15(^1)</td>
<td>0.44; 0.3; 0.6</td>
<td>M (0.5)</td>
</tr>
<tr>
<td>Golden sandfish</td>
<td>Holothuria lessoni</td>
<td>150(^*)</td>
<td>2(^†)</td>
<td>150(^†)</td>
<td>0.73(^§)</td>
<td>460(^*)</td>
<td>3(^*)</td>
<td>6(^i)</td>
<td>0.73; 0.4; 0.8</td>
<td>VH (1)</td>
</tr>
<tr>
<td>Curryfish hermanni</td>
<td>Stichopus hermanni</td>
<td>350(^*)</td>
<td>3(^†)</td>
<td>220(^†)</td>
<td>4.5(^*)</td>
<td>550(^*)</td>
<td>7(^*)</td>
<td>0.62; 0.4; 0.8</td>
<td>M (0.5)</td>
<td></td>
</tr>
<tr>
<td>Curryfish vastus</td>
<td>Stichopus vastus</td>
<td>150(^*)</td>
<td>2(^†)</td>
<td>150(^†)</td>
<td>6(^i)</td>
<td>360(^*)</td>
<td>4.5(^*)</td>
<td>6(^i)</td>
<td>0.73; 0.4; 0.8</td>
<td>M (0.5)</td>
</tr>
<tr>
<td>Deepwater blackfish</td>
<td>Actinopyga palauensis</td>
<td>200(^*)</td>
<td>3(^†)</td>
<td>400(^*)</td>
<td>2(^*)</td>
<td>400(^*)</td>
<td>2(^*)</td>
<td>6(^i)</td>
<td>0.73; 0.4; 0.8</td>
<td>M (0.5)</td>
</tr>
<tr>
<td>Burrowing blackfish</td>
<td>Actinopyga spinea</td>
<td>150(^*)</td>
<td>3(^†)</td>
<td>380(^*)</td>
<td>1.5(^*)</td>
<td>380(^*)</td>
<td>2(^*)</td>
<td>6(^i)</td>
<td>0.73; 0.4; 0.8</td>
<td>M (0.5)</td>
</tr>
</tbody>
</table>

Value categories are denoted very high (VH), high (H), or medium (M) and shown together with the revenue value multiplier for sea cucumber species in the catch.

\(^*\)Ref. 1.
\(^†\)Data from the Commonwealth Scientific and Industrial Research Organisation.
\(^‡\)Ref. 2.
\(^§\)Ref. 3.
\(^\}\)Ref. 4.
\(^\#\)Expert (workshop).
\(^k\)Data uncertain.
\(^+\)Ref. 5.
\(^1\)Ref. 6.
\(^2\)Ref. 7.

2. QDPIF (2004) Ecological Assessment of Queensland’s East Coast Bêche-de-mer Fishery (Queensland Department of Primary Industries and Fisheries, Brisbane, Australia).
Table S2. Starting model biomass estimates used in the MSE operational model

<table>
<thead>
<tr>
<th>Species</th>
<th>Habitat designation</th>
<th>Total biomass (tons gutted weight)</th>
<th>Closed area (tons gutted weight)</th>
<th>Status</th>
</tr>
</thead>
<tbody>
<tr>
<td>Black teatfish, 1980*</td>
<td>Dry reef area (mid- and outer reefs)</td>
<td>10,356</td>
<td>4,274</td>
<td>Virgin</td>
</tr>
<tr>
<td>Black teatfish, 2000†</td>
<td>Dry reef area (mid- and outer reefs)</td>
<td>6,921</td>
<td>4,274</td>
<td>Overexploited</td>
</tr>
<tr>
<td>White teatfish</td>
<td>Reef area (mid- and outer reefs)</td>
<td>3,425</td>
<td>1,667</td>
<td>Exploited</td>
</tr>
<tr>
<td>Brown sandfish</td>
<td>Reef area (midreefs, sectors 2–4)</td>
<td>2,335</td>
<td>717</td>
<td>Exploited</td>
</tr>
<tr>
<td>Prickly redfish</td>
<td>Reef area (mid- and outer reefs)</td>
<td>9,321</td>
<td>2,860</td>
<td>Exploited</td>
</tr>
<tr>
<td>Golden sandfish</td>
<td>BBF survey area</td>
<td>1,484</td>
<td>0</td>
<td>Near virgin</td>
</tr>
<tr>
<td>Curryfish herrmanni</td>
<td>Reef area (mid- and outer reefs)</td>
<td>5,544</td>
<td>1,511</td>
<td>Near virgin</td>
</tr>
<tr>
<td>Curryfish vastus</td>
<td>Reef area (mid- and outer reefs)</td>
<td>1,663</td>
<td>453</td>
<td>Near virgin</td>
</tr>
<tr>
<td>Blackfish</td>
<td>Reef area (mid- and outer reefs)</td>
<td>1,141</td>
<td>349</td>
<td>Exploited</td>
</tr>
<tr>
<td>Burrowing blackfish</td>
<td>BBFZ survey area and BBF fished areas</td>
<td>11,650</td>
<td>93</td>
<td>Near virgin</td>
</tr>
</tbody>
</table>

Includes all of the ECBDMF (including Saumarez and Marion Reefs) and Ashmore Reef, and burrowing blackfish zones (BBFZ). No density data are available for burrowing blackfish (BBF) or golden sandfish outside the surveyed areas.

†From the GBR-wide density survey (1), with average density applied to open and closed reefs in four sectors. Assumed as postfishery biomass.


Table S3. Summary of the reference set (RS) of 16 alternative model combinations of four primary uncertainties included in the operating model

<table>
<thead>
<tr>
<th>Case</th>
<th>Mortality (M)</th>
<th>S–R steepness (H)</th>
<th>Recruitment (R)</th>
<th>Growth (G)</th>
<th>Biomass (K)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>ML</td>
<td>HH</td>
<td>RH</td>
<td>GS</td>
<td>K</td>
</tr>
<tr>
<td>2</td>
<td>ML</td>
<td>HL</td>
<td>RL</td>
<td>GS</td>
<td>K</td>
</tr>
<tr>
<td>3</td>
<td>ML</td>
<td>HH</td>
<td>RL</td>
<td>GS</td>
<td>K</td>
</tr>
<tr>
<td>4</td>
<td>ML</td>
<td>HL</td>
<td>RH</td>
<td>GS</td>
<td>K</td>
</tr>
<tr>
<td>5</td>
<td>MH</td>
<td>HH</td>
<td>RH</td>
<td>GF</td>
<td>K</td>
</tr>
<tr>
<td>6</td>
<td>MH</td>
<td>HL</td>
<td>RL</td>
<td>GF</td>
<td>K</td>
</tr>
<tr>
<td>7</td>
<td>MH</td>
<td>HL</td>
<td>RH</td>
<td>GF</td>
<td>K</td>
</tr>
<tr>
<td>8</td>
<td>MH</td>
<td>HH</td>
<td>RL</td>
<td>GF</td>
<td>K</td>
</tr>
<tr>
<td>9</td>
<td>ML</td>
<td>HH</td>
<td>RH</td>
<td>GS</td>
<td>KL</td>
</tr>
<tr>
<td>10</td>
<td>ML</td>
<td>HL</td>
<td>RL</td>
<td>GS</td>
<td>KL</td>
</tr>
<tr>
<td>11</td>
<td>ML</td>
<td>HH</td>
<td>RL</td>
<td>GS</td>
<td>KL</td>
</tr>
<tr>
<td>12</td>
<td>ML</td>
<td>HL</td>
<td>RH</td>
<td>GS</td>
<td>KL</td>
</tr>
<tr>
<td>13</td>
<td>MH</td>
<td>HH</td>
<td>RH</td>
<td>GF</td>
<td>KL</td>
</tr>
<tr>
<td>14</td>
<td>MH</td>
<td>HL</td>
<td>RL</td>
<td>GF</td>
<td>KL</td>
</tr>
<tr>
<td>15</td>
<td>MH</td>
<td>HL</td>
<td>RH</td>
<td>GF</td>
<td>KL</td>
</tr>
<tr>
<td>16</td>
<td>MH</td>
<td>HH</td>
<td>RL</td>
<td>GF</td>
<td>KL</td>
</tr>
</tbody>
</table>

The low- (ML) and high-mortality (MH) scenarios are coupled with slow- (GS) and fast-growth (GF) scenarios, respectively. The stock-recruitment (S–R) steepness h options used are 0.7 (HH) and 0.5 (HL). RH and RL are the stochastic and deterministic recruitment options, respectively. K and KL represent the initial and 0.5 starting (1995) biomass options, respectively.
Table S4. Comparison between reference case and sensitivity scenarios assuming a 1-y older age at maturity to illustrate the worsening of performance statistics if age at maturity is larger (but MLS remains unchanged) and the same but threefold larger TAC.

<table>
<thead>
<tr>
<th>Species</th>
<th>Reference case (3-y RZS and current catch levels)</th>
<th>Increase age at maturity</th>
<th>Increase age at maturity with higher TAC</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Risk of depletion below $B_{lim}$ of 20% unfished</td>
<td>Risk of depletion below $B_{lim}$ of 40% unfished</td>
<td>Risk of depletion below $B_{lim}$ of 20% unfished</td>
</tr>
<tr>
<td></td>
<td>$B_{2012}/B_{1995}$</td>
<td>$B_{2032}/B_{2012}$</td>
<td>$B_{2012}/B_{1995}$</td>
</tr>
<tr>
<td>Black teatfish</td>
<td>0.03 0.10 0.88 0.93</td>
<td>0.11 0.13 0.86 0.87</td>
<td>0.21 0.23 0.77 0.78</td>
</tr>
<tr>
<td>Brown sandfish</td>
<td>0.00 0.00 1.00 1.00</td>
<td>0.00 0.00 1.00 1.00</td>
<td>0.00 0.00 1.00 1.00</td>
</tr>
<tr>
<td>White teatfish</td>
<td>0.00 0.01 0.87 1.00</td>
<td>0.02 0.10 0.80 0.99</td>
<td>0.02 0.13 0.75 0.98</td>
</tr>
<tr>
<td>Prickly redfish</td>
<td>0.00 0.00 0.99 1.00</td>
<td>0.00 0.00 0.99 1.00</td>
<td>0.00 0.01 0.96 0.98</td>
</tr>
<tr>
<td>Golden sandfish</td>
<td>0.04 0.05 0.94 0.98</td>
<td>0.06 0.06 0.93 0.97</td>
<td>0.15 0.18 0.80 0.85</td>
</tr>
<tr>
<td>Curryfish herrmanni</td>
<td>0.00 0.02 0.95 1.00</td>
<td>0.00 0.04 0.92 0.99</td>
<td>0.00 0.08 0.83 0.95</td>
</tr>
<tr>
<td>Curryfish vastus</td>
<td>0.01 0.01 0.98 0.98</td>
<td>0.01 0.02 0.98 0.94</td>
<td>0.04 0.08 0.90 0.87</td>
</tr>
<tr>
<td>Deepwater blackfish</td>
<td>0.02 0.03 0.96 0.98</td>
<td>0.04 0.04 0.96 0.96</td>
<td>0.05 0.05 0.94 0.94</td>
</tr>
<tr>
<td>Burrowing blackfish</td>
<td>0.08 0.17 0.81 0.96</td>
<td>0.20 0.21 0.75 0.82</td>
<td>0.35 0.37 0.60 0.66</td>
</tr>
</tbody>
</table>