Reproductive hyperallometry and managing the world's fisheries

Dustin J. Marshall[a,1,2], Michael Bode[b,1] , Marc Mangel[c,d,e] , Robert Arlinghaus[f,g] , and E. J. Dick[h]

[a]Center for Geometric Biology, Monash University, Melbourne VIC 3800, Australia; [b]School of Mathematical Sciences, Queensland University of Technology, Brisbane QLD 4000, Australia; [c]Department of Biology, University of Bergen, 9020 Bergen, Norway; [d]Institute of Marine Sciences, University of California, Santa Cruz, CA 95064; [e]Puget Sound Institute, University of Washington, Tacoma, WA 98402; [f]Department of Biology and Ecology of Fishes, Leibniz Institute of Freshwater Ecology and Inland Fisheries, 12587 Berlin, Germany; [g]Division of Integrative Fisheries Management, Faculty of Life Sciences, Humboldt-Universität zu Berlin, 10115 Berlin, Germany; and [h]Fisheries Ecology Division, Southwest Fisheries Science Center, National Marine Fisheries Service, Santa Cruz, CA 95060

Marine fisheries are an essential component of global food security, but many are close to their limits and some are overfished. The models that guide the management of these fisheries almost always assume reproduction is proportional to mass (isometry), when fecundity generally increases disproportionately to mass (hyperallometry). Judged against several management reference points, we show that assuming isometry overestimates the replenishment potential of exploited fish stocks by 22% (range: 2% to 78%) for 32 of the world's largest fisheries, risking systematic overharvesting. We calculate that target catches based on assumptions of isometry are more than double those based on assumptions of hyperallometry for most species, such that common reference points are set twice as high as they should be to maintain the target level of replenishment. We also show that hyperallometric reproduction provides opportunities for increasing the efficacy of tools that are underused in standard fisheries management, such as protected areas or harvest slot limits. Adopting management strategies that conserve large, hyperfecund fish may, in some instances, result in higher yields relative to traditional approaches. We recommend that future assessment of reference points and quotas include reproductive hyperallometry unless there is clear evidence that it does not occur in that species.

reproduction | marine protected areas | life history

Humans rely on fish for protein and micronutrients, and seafood consumption continues to grow. Seafood is generally less environmentally destructive than other animal protein sources (1), and global consumption of seafood is projected to increase to 180 million tons in the next 10 y (2). However, the global catch of wild-caught seafood has plateaued despite increasing effort and improved technology (3), and many fisheries are at or beyond their limit (4). More than a third of fisheries for which there are stock assessment data are overfished, and another third are exploited at maximum levels (5). Increasingly, active management can and does successfully rebuild once-depleted stocks (6, 7), but in some cases, actively managed fisheries can still suffer declines (8). Partly offsetting the limits set by capture fisheries, aquaculture has expanded massively to meet rising seafood demands, but aquaculture is not without its own inherent limits (2, 9). Recently discovered widespread patterns in fish reproductive biology present new challenges but also novel opportunities to balance management and conservation in capture fisheries.

A meta-analysis of over 300 marine fish species (10) revealed that for 95% of species studied, fish reproductive output scaled disproportionately with individual fish mass. That is, a doubling of mass of an individual fish more than doubles its reproductive output. While this pattern may seem innocuous, it contradicts a fundamental assumption present in most models that fisheries managers use to determine exploitation levels (11, 12). For 32 of the world's largest fisheries (each more than 100,000 tons caught per annum, totaling around a third of global catch; *SI Appendix, Table S1*), almost all (95%) of the stock assessment models used

to set target catches assume that fecundity is isometric, that is, strictly proportional to fish mass (*SI Appendix*, Table S1). In other words, the key tools used to manage fisheries and set catches assume that the total mass of reproductive fish determines the total egg production of the population, regardless of the size structure in that population. However, when reproduction scales hyperallometrically, assuming isometry will systematically overestimate the reproductive output of populations of smaller fish relative to populations of larger fish of the same total mass. While others have noted this may be an issue (13), in practice, the overwhelming majority of contemporary stock assessments for these large fisheries rely on total spawner biomass alone, either as a reference point or during the assessment process to estimate other reference points (e.g., the fishing mortality rate that maximizes yield, F_{MSY}) or both (*SI Appendix*, Table S1).

Fishing alters the size distribution of fished populations (14) such that reproductive hyperallometry matters. An inevitable consequence of increasing mortality (whether it be natural or fishing mortality) is that fish are less likely to reach an older age, such that the largest members of the population are rarer in exploited stocks (15). Fishing therefore reduces the average age and size of individuals in a population, and standard yield models suggest

Significance

We find that a ubiquitous assumption in fisheries models for predicting population replenishment introduces systematic overestimates of replenishment in fished populations. For 32 of the world's major fisheries, these biases result in harvest thresholds being set too high: in most cases, reference points based on spawning potential ratios are more than 2.5 times higher than those necessary to achieve the desired level of replenishment. When we use the more biologically appropriate assumption of reproductive hyperallometry, we find that management tools such as spatiotemporal closures and harvest slots can outperform traditional approaches in terms of yield. Failing to consider reproductive hyperallometry overestimates the efficacy of traditional fisheries management and underestimates the benefits of approaches that create reservoirs of larger individuals.

SUSTAINABILITY SCIENCE

www.manaraa.com

optimal exploitation is achieved by letting the fish grow until an optimal age and then harvesting them intensively (16). What is overlooked is that the standard assumption of isometry in fecundity systematically underestimates the loss of egg production caused by the loss of larger fish (17).

We examined how two standard management reference points (population parameters used to guide management decisions), spawning potential ratio (SPR; *SI Appendix*, Fig. S1) and maximum sustainable yield (MSY), change when reproductive hyperallometry is incorporated. SPR and MSY are used as reference points for almost every fishery considered here (*SI Appendix*, Table S1). In essence, we estimate egg production the same way as standard modeling approaches but we couple size-frequency distributions to estimates of reproductive scaling to create a more accurate estimate of egg production. Although the idea of protecting the natural size and age structure has been raised before (see ref. 12 for a review), the relative importance of hyperallometry in fecundity has not been formally assessed across a range of stocks. We modeled how species-specific estimates (*SI Appendix*, Table S2) of hyperallometric scaling alter standard fisheries-management benchmarks of the world's 32 major fisheries relative to making the traditional assumption of reproductive isometry.

First, we consider the SPR as a reference point, which is the ratio of the egg production of an exploited population to the egg production that would occur in the absence of exploitation. We found that SPR is by far the most common reference point in fisheries management, even for relatively high-information stocks (*SI Appendix*, Table S1), but it does not explicitly consider density-dependent recruitment. Thus, second, we consider MSY, a less commonly used reference point (*SI Appendix*, Table S1) but one that incorporates density-dependent recruitment via either assuming or estimating "steepness," which is the fraction of unfished recruitment when the spawning biomass is reduced to 20% of its unfished size (18). Higher steepness values imply stronger density dependence. Calculating MSY requires more parameters and constitutes an internationally agreed-upon management objective if the aim is to achieve highly productive fisheries in terms of yield. SPR and MSY, and variants of them, are used to inform target removals of almost all the world's managed stocks, and in practice, these reference points almost always assume reproductive isometry (*SI Appendix*, Table S1).

We find the assumption of reproductive isometry results in systematic overestimates of population replenishment potential, such that removal-based reference points are inadvertently too high (see *Results*). Fortunately, the solution to this problem is as simple as estimating the degree of hyperallometry in a species' reproductive output—these analyses have often been done for commercially harvested species (*SI Appendix*, Table S2 and Fig. S2)—and altering the exponent of the reproductive relationship in the stock-assessment model. Next, we explored how incorporating reproductive hyperallometry changes the predicted benefits of alternative management approaches that seek to maintain reservoirs of larger females in the population and choose two possible tools: spatiotemporal closures (STCs) and harvest slots (HSs).

STCs, in which fishing is excluded from specific areas or times, are one way to maintain larger-sized fish within a metapopulation. Well-enforced STCs allow some fish to avoid fishing mortality and continue to grow such that, on average, STCs generate fish that are around twice the mass of fish outside the STC (19, 20). An often-cited benefit for fisheries is that recruits produced by spawners within STCs will replenish exploited populations outside protected areas (21). Indeed, dispersing larvae from STCs can enhance replenishment up to 185 km away [though typical estimates are around 18 to 30 km (22–24)]. Twenty years ago, theory suggested that STCs could be as effective at managing exploited fished populations (at least, in terms of numerical yield)

as traditional fisheries approaches that control fishing mortality directly, such as through quotas (25), but the effects of reproductive hyperallometry were not considered. We compare two types of STC: one where the closure is permanent and unmoving in space (i.e., akin to a standard no-take marine protected area), the other where the closure is temporary (we chose illustrative periods of 5 and 10 y) and moves through space at the end of every period, creating what is known as rotating harvest. Both approaches mimic current management tools and either may be more appropriate depending on social-ecological context. We augmented standard models of catch restriction (the setting of maximum catch by fishers) and STC-managed fisheries to include hyperallometric reproduction and size-dependent natural mortality, another key biological dimension that is often disregarded in fisheries-management models given the difficulty in estimating it precisely under fished conditions (see *Methods*). We solved these models to maximize yield of biomass, rather than numbers; we refer to the solution as the optimal STC approach.

The use of STCs as a fisheries-management tool remains contentious, and the traditional approach of limiting catch remains the dominant tool (26, 27). HSs, in which there are maximum and minimum limits to the size of fish that can be taken (28) rather than the standard approach of minimum-length limits, are another way of maintaining larger-sized fish within a population. Some gear types produce natural HSs, such as gill nets with lower and upper bounds on mesh sizes. We therefore also examined the possible value of HSs in achieving optimal catch when reproduction is hyperallometric. Although HSs are less utilized in commercial fisheries, the regulation may work well in small-scale commercial or recreational fisheries. We thus include HSs here to highlight their potential value more broadly.

Results

We compared models that use standard assumptions of reproductive isometry to those that use the scaling exponents appropriate to each species (see *SI Appendix*, Fig. S1 for an illustration). We find that assuming reproductive isometry systematically underestimates the contribution of larger individuals to egg production, and even though they are rare, large fish make very strong contributions to total egg production (*SI Appendix*, Table S2). For example, assuming a fishing mortality of 0.2 for yellowfin tuna *Thunnus albacares* (a species with moderate reproductive hyperallometry), fish older than 3 y in a fished population will constitute only around 7% of the population. Under the (incorrect) assumption of isometry, these older fish are still responsible for roughly 58% of total egg production. Yet, under the assumption of hyperallometry, these same rather rare fish are responsible for 68% of total egg production. For species with more extreme hyperallometry (e.g., the European pilchard *Sardinops sagax*), the error introduced by assuming isometry in egg production is exacerbated: older (>3 y) fish are predicted to produce only 30% of eggs under isometry but 97% of eggs after accounting for hyperallometry.

The systematic underestimation of the contribution of larger individuals introduced by assuming reproductive isometry results in the systematic overestimation of spawning potential of fished stocks relative to virgin stocks (the SPR). In our analysis for 32 exploited stocks, the intended SPR calculated under the assumption of isometry was found to be 22% higher on average than the actual SPR based on hyperallometry, but there was significant variation from species to species (3% to 78%; *SI Appendix*, Table S2). We found the degree to which assuming isometry overestimated SPR increasing with reproductive scaling. For example, SPR estimates for *Euthynnus affinis*, with relatively low reproductive scaling, were barely different from each other (~3% difference) regardless of whether isometry or hyperallometry was assumed, whereas *S. sagax* with its very steep reproductive scaling

www.manaraa.com

resulted in large discrepancies (~78%) between the intended SPR under isometry and the actual SPR under hyperallometry.

The misestimation of spawning potential due to assuming reproductive isometry leads to management reference points being set too high relative to when hyperallometry is accounted for (*SI Appendix*, Table S2). Using SPR as a reference point, simulating replenishment in a model under reproductive isometry resulted in target catches that were ~2.7 times higher, on average, than what they would be based on reproductive hyperallometry (Fig. 1*A*). Using MSY as a reference point and incorporating a density-dependent stock-recruitment relationship (SRR), we find that assuming reproductive isometry results in reference points that are around 30% higher than they should be once reproductive hyperallometry is incorporated (Fig. 1*B*). The relationship between reproductive scaling and the degree to which target catches are set too high is more variable using this reference point because other elements (e.g., steepness) affect MSY calculations.

Comparing STCs and catch-restriction management with hyperallometric reproduction, the biomass yields of optimal STCs always exceeded those based on optimal catch-restriction management (Fig. 2 shows results assuming steepness = 0.7; see *SI Appendix*, Table S3 for other steepnesses). The yield benefits of STCs were found to be particularly pronounced for species with "slow" life histories (i.e., low natural mortality, slow growth) and relatively high reproductive scaling exponents. For example, for Atlantic cod *Gadus morhua*, yields were predicted to be 1.92 times higher using STCs rather than traditional quota-based management. By contrast, for species with very fast life histories, there is little to no benefit of management by STC relative to traditional management (Fig. 2). Yields from optimal STCs exceeded that of catch restriction by an average of 30% for 32 of the world's major fisheries. Permanent, static closures outperformed temporary, mobile closures, and longer closures outperformed shorter closures (*SI Appendix*, Table S3). However, the differences between STCs of varying duration were trivial for some species, particularly those with fast life histories (*SI Appendix*, Table S3). For species with slow life histories, major benefits of STCs only emerged over closure periods of 10 y relative to 5 y (*SI Appendix*, Table S3). These dynamics suggest that STCs must be relatively long lasting to provide major benefits relative to traditional catch restriction management. Note the benefits of STCs emerged in our models under the realistic assumption that fishing effort was displaced to unprotected sites, increasing fishing pressure elsewhere.

When we modeled management using HSs and incorporated reproductive hyperallometry, we again found the benefits of HS relative to traditional management were species specific (Fig. 3). Management by an HS always improved catch in terms of number of fish caught [a mean increase of 9%, similar to previous studies (28, 29)] but only improved biomass yields by around 2% on average, and even then, HSs were only superior to traditional (minimum length limit only) approaches when scaling exponents for the mass-fecundity relationship were relatively high (29): Reproductive scaling exponents above 1.6 yielded biomass benefits of the HSs relative to traditional management using minimum-landing sizes, and for very high reproductive scaling exponents (e.g., 3+), the benefits of HS can exceed 25%.

Discussion

For 32 of the world's largest fisheries, reproductive isometry is usually assumed when setting reference points. We show that this assumption introduces systematically overoptimistic predictions of egg production and population replenishment in fished populations because it underestimates the impact of removing larger females from the population. Consequently, recommended catches based on such modeling results in levels of population replenishment that are less than intended. The level of bias introduced by assuming reproductive isometry increases with the actual
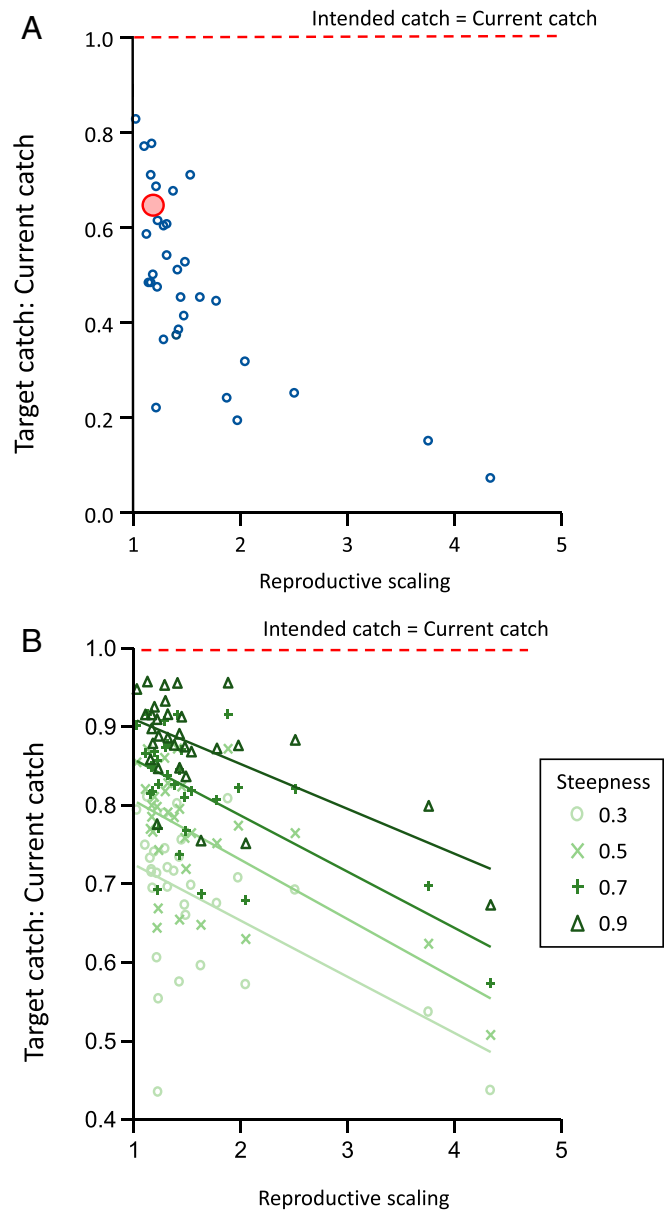
Fig. 1. Relationship between reproductive scaling and mismatch between target harvest and actual reference point when reproductive hyperallometry is included for 32 of the world's major fisheries (each dot represents a species). All values fall below the horizontal dashed line, indicating that reference points currently exceed intended target levels once reproductive hyperallometry is incorporated. (*A*) Estimates based on SPR with no assumptions about recruitment. The red circle represents the average reproductive scaling for marine fishes. (*B*) Estimates based on MSY. Shading indicates different assumptions about steepness (the relationship between egg production and recruitment [see *Methods* for details]).

reproductive exponent of that particular species. Applying the global average for reproductive exponents (1.18) from ref. 10 to the rest of the world's fisheries suggests that SPR-based fishing mortality reference points are around twice what is intended. The average value of the exponent in ref. 10 likely represents the lower bound of reproductive scaling for most species because it is based on batch fecundity alone, not absolute fecundity, which is likely to have an even greater exponent (30) and is the parameter of interest when calculating management thresholds (30). In other words, simply to achieve the target level of egg production
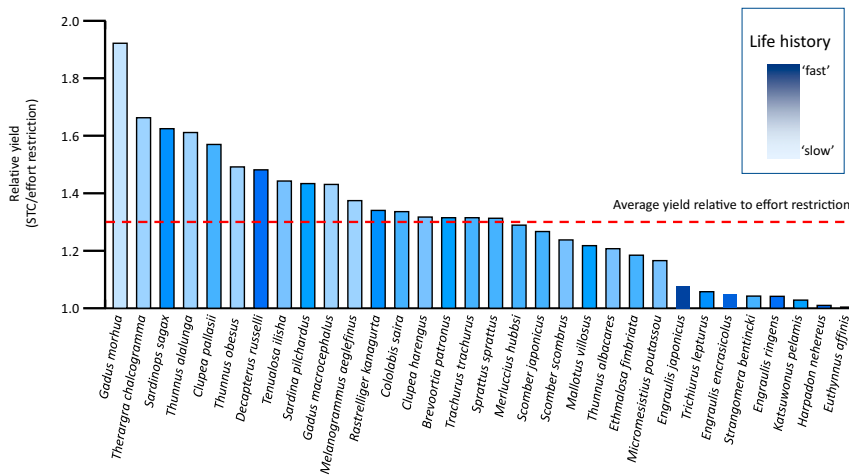
www.manaraa.com

Fig. 2. Benefits of STCs for biomass yield relative to traditional fisheries management approaches for 32 of the world's major fisheries. The bars represent the ratio of maximum yield based on management using optimal STCs versus traditional management. The red dashed line indicates the average increase in yield offered by STCs across all 32 species. Bars are arranged in order of benefit and are color-coded according to the von Bertalanffy maturation parameter (*k*), with darker colors indicating slower maturation.

from the population that is intended (31), fishing mortality would need to be more than halved, at least initially. This systematic error could help to explain why some stocks have collapsed despite active management (12). Beverton and Holt cautioned against assuming reproductive isometry over 60 y ago (32), and there have been repeated suggestions since then (11, 33). However, effectively incorporating reproductive hyperallometry necessitates more information about stock size structure, which may have impeded its widespread adoption. Researchers and managers may have also undervalued the relevance of even small changes in the exponent of the mass-fecundity relationship and opted for the easier assumption of isometry instead. Given our results here, we suggest future stock assessments include reproductive hyperallometry wherever possible and, in the absence of species-specific reproductive scaling estimates, an exponent of 1.18 for the mass-fecundity relationship be used as a default rather than 1, as is presently the case in most stocks.

Here, we focus on egg production—we do not consider the effects of maternal size on the quality of eggs or recruits. Larger mothers tend to produce larger offspring that may have a greater chance of recruiting or coping with intraspecific competition than the offspring of smaller mothers (13, 34). When larger mothers do produce offspring of greater quality, these effects will enhance the effects of hyperallometric egg production. Likewise, we do not consider spawning duration, though recent reviews suggest that larger mothers may spawn for a greater proportion of the season (30)—again, this effect of female size would exacerbate the consequences of ignoring reproductive hyperallometry.

While we always found that assuming isometry introduces overestimates reference points, the magnitude of the overestimate depends on the reference point (SPR versus MSY) that is used. The consequences of assuming reproductive isometry using SPR as a reference point are more severe than when MSY is used as a reference point because MSY approaches assume or include density-dependent recruitment effects, which tend to dampen recruitment when populations are at a higher density, particularly when high values of steepness are assumed (Fig. 1*B*). Thus, the reference points differ systematically in their sensitivity to misestimating the reproductive output of a population. Yet, SPR remains overwhelmingly the most common reference point in the fisheries we considered, so we would argue our findings for SPR are the most relevant for contemporary management (*SI Appendix*, Table S1).

Our results are compatible with the observation that many stocks are stable or even increasing in managed fisheries. Harvest levels that are around or even above the MSY still allow a population to persist, even if that threshold is inadvertently higher than the intended goal and biomasses are lower than at MSY (16). Instead, our results suggest that harvest rates set assuming isometry may be set higher than they should be to maximize either long-term yield or facilitate recovery. Setting harvest levels higher than optimal would then cost yield. Consequently, reductions in the short term may be necessary to bring removals into line with the intended reference points. Such reductions could have negative repercussions in the short term for both food security and the economy but will yield positive benefits in the long term. Importantly, reproductive hyperallometry provides opportunities for improving long-term catches relative to current practices.

Incorporating hyperallometric reproduction recalibrates the estimation of how different management approaches affect the replenishment potential of a population. We find that the reduction in catch necessary to properly account for hyperallometric reproduction could be partly offset by implementing STC-based
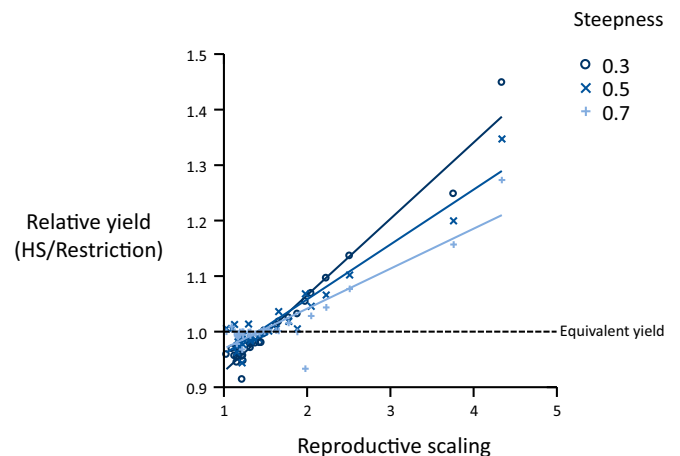
Fig. 3. Benefits of HS management for biomass yield relative to traditional catch restriction approach for 32 of the world's major fisheries. Each dot is a different species, and the three symbols represent predictions for different values of steepness in the SRR (see *Methods*). Dots above the dashed line increase the relative yield of fisheries.

Marshall et al.
Reproductive hyperallometry and managing the world's fisheries
www.manaraa.com

management for certain species. Because STCs create a reservoir of larger fish, under hyperallometry, their contribution to population replenishment is far higher than was previously calculated. Summed across all the fisheries considered here and based on simple ex-vessel prices, STC-driven offsets could amount to millions of tons per annum and billions in additional revenue relative to traditional effort-control approaches. For species with slow life histories, the benefit of STC management is particularly high—for Atlantic cod, switching to an STC approach is predicted to increase long-term catch by ~90% relative to the current management strategy.

Our models suggest that STCs may be an underestimated tool for fisheries management when reproduction is hyperallometric, but they are contentious. The use of STCs has long been focused on coastal habitats and species with limited adult dispersal, but increasingly, the role of STCs in the open ocean (so-called "Blue Water MPAs") and migratory species is being considered (35, 36). We therefore include a consideration of STCs for all species regardless of life history, habitat, or adult dispersal for completeness and in recognition of the fact that STCs may be more applicable than has been appreciated previously. Nevertheless, in some instances, STCs will likely be impractical and instead, HS might be a more useful alternative.

We found that the costs or benefits of HS relative to traditional approaches of minimum-size limits varied from species to species. For species with reproduction roughly proportional to mass, HS approaches often decreased biomass yields relative to traditional approaches (29, 37). Nevertheless, nontrivial gains are associated with HS relative to traditional size-based management for some species (e.g., big eye tuna, *Thunnus obesus*, catch in biomass increases by ~5% worth ~$34 million p.a.). In fisheries where numerical yield generates more benefits than biomass yield (e.g., for some recreational fisheries), HS generally promise to outperform minimum-length limits. Because HS may be impractical for commercial fisheries with significant discard mortality (e.g., trawling) or small-bodied targets (e.g., clupeids), their benefits may best be realized for stocks that are primarily targets of recreational anglers (37) or small-scale fisheries operating with gill nets or traps, such as many fisheries in coastal areas. Importantly, small-scale commercial fisheries and recreational fisheries constitute key sources of fish mortality in many areas of the world (37). Relative to industrial fisheries, these fisheries may be more amenable to HSs because most gear types used in small-scale fisheries either can tailor size selectivity directly on intermediate sizes (e.g., gill nets with minimum and maximum mesh sizes) or they allow the release of too small or too large bycatch in proper condition, allowing survival post release (e.g., fish from fyke nets or angling gear). While we explored two specific approaches (STCs and HSs), hyperallometric reproduction means that any strategy that protects and retains larger fish in a population despite intensive fishing should generate a disproportionate dividend for the total egg production of the population and, to some extent within limits set by density dependence, its replenishment.

Our results are based on a number of simplifying assumptions (for sensitivity analyses, see *SI Appendix*, Table S3). For example, in the STC models, we assume that adults move very little relative to the size of closed areas and that larval fish can move very far, so that closures can replenish fishing grounds from a great distance. These assumptions are reasonable (22–24) but are unlikely to be met for some species (38). Furthermore, we also assume no discard mortality in the HS models, which can strongly affect the performance of any size limit (28, 37). As such, we view our predictions regarding the relative benefit of STCs or HSs as a best-case scenario, and their performance should be explored in more detail with specific life history and movement data. For example, we compared predictions based on our approach here to a much more detailed model that includes specific larval connectivity

for coral trout *Plectropomus leopardus*, a commercially exploited species on the Great Barrier Reef (GBR; see *Methods*). Using the more generic approach, we predict a benefit of STCs of ~31% relative to catch restriction approaches. By contrast, the more explicit model predicts a benefit of only 16% of STCs over catch restriction, indicating that our generic approach overestimates the benefits of STCs in this species by around 12%. A benefit of 16% is still nontrivial, and our models indicate that for some species (particularly those with slow life histories, limited adult movement, larval dispersal, and steep scaling exponents), size-reservoir approaches outperform catch restrictions by such margins such that our results are robust to relaxing some assumptions.

It is important to note that we measure the benefits of STCs and HSs under the assumption of a steady state. Catches may vary in the period between the establishment of STCs or HSs and when these stocks reach equilibrium. Subject to these caveats, STCs and HSs, which have emerged as a tool for the recovery of stocks (39), also emerge as a means for improving the sustainable yield of fisheries worldwide. We do not argue that STCs and HSs are the sole means to improving yields. Gear with different size selectivity, for example, could be used to target different size classes. Rather, we suggest that the differential role in replenishment that larger fish play should be better recognized and incorporated in future management approaches.

The discovery of widespread hyperallometry in egg production provides a significant challenge to contemporary fisheries management. Our work suggests that modern management could respond to this challenge by better leveraging the reproductive potential of larger, older fish in exploited stocks more so than is presently the case, using relatively simple policy innovations. Policy makers and managers may consider moving from effort restriction to STCs and HSs where possible, and thereby policy makers and managers may consider moving from effort restriction to STCs and HSs where possible, and thereby more effectively achieve their intended management goals. At the very minimum, efforts are required to increasingly measure and integrate size-fecundity relationships into assessment models.

Methods

This section contains descriptions of 1) the life history (demographic parameters), including lifetime egg production (LEP) and SPR, a metric of resilience based only on demographic parameters; 2) the population dynamics, with both natural and fishing mortality and a Beverton-Holt SRR (BH-SRR); 3) the spatially homogenous model for the fishery corresponding to HSs; and 4) the spatially explicit model for the fishery corresponding to STCs. We use a standard age-structured fishery model (16, 40, 41), choosing the rate of fishing mortality to maximize yield in either numbers or biomass.

Estimating Reproductive Hyperallometry. Estimates of the relationship between female body mass and reproductive output were collated from the literature (as per ref. 10). Where multiple estimates for the same species were available, we used the estimate with the best replication. In some instances, studies provided raw data in a figure or table, and we calculated the scaling of mass to size ourselves. In others, a scaling relationship between size and fecundity was reported (fish lengths were converted to masses using species-specific scaling relationships from Fishbase (https://www.fishbase.de/). For one species (*S. sagax*), the relationship between mass and batch fecundity alone grossly underestimates reproductive scaling [though it is still hyperallometric (42)]. In this species, spawning frequency (number of spawns per season) increases female body size, and so we estimated size-specific reproductive output for this species incorporating both batch fecundity effects and spawning frequency.

All of the species considered here showed hyperallometric scaling (*SI Appendix*, Table S2). For those species for which the raw data were accessible, we provide the figures (*SI Appendix*, Fig. S2). For some species with low sample sizes, the CI of the estimate of the scaling exponent overlapped 1. Given that the global estimate of the relationship between mass and fecundity is 1.18 for over 300 marine fishes, we believe it would be anticonservative to ignore the hyperallometric scaling in the species for which the CIs of scaling exponent overlap 1, but we do suggest that these species are a priority for collecting further data.

Marshall et al.
Reproductive hyperallometry and managing the world's fisheries

PNAS | 5 of 8
https://doi.org/10.1073/pnas.2100695118

www.manaraa.com

The Demographic Parameters, LEP, and SPR. We assume von Bertalanffy growth in length at age a, $L(a)$:

$$L(a) = L_\infty \left(1 - e^{-k(a-a_0)}\right),\qquad [1]$$

where L_∞ is the theoretical asymptotic size of a fish (reached at infinite age)*, k is the von Bertalanffy growth rate (related to catabolic factors; see ref. 41), and $a_0 < 0$ is the theoretical age at which the fish has zero length [thus accounting for $L(0) > 0$].

Length is related to mass at age $W(a)$ via a species-specific allometric relationship:

$$W(a) = c_\omega L(a)^{b_\omega},\qquad [2]$$

where c_ω and b_ω are species-specific parameters. We denote the rates of natural mortality and fishing mortality at age a by $M(a)$ and $F(a)$, respectively. Note that while stock assessments do not always assume natural mortality is size dependent (43), given our focus on size-dependent reproduction and the general consensus that mortality is unlikely to be size independent, we assumed size-dependent mortality in order to generate more realistic size distribution. Thus, the fraction of fish surviving from age a to age $a + 1$ is $\exp[-(M(a) + F(a))]$. We let $\{F\}$ denote the age-dependent schedule of fishing mortality and $S(a|\{F\})$ denote survival to age a of an individual. Then $S(0|\{F\}) = 1$ and

$$S(a + 1|\{F\}) = S(a|\{F\})\exp(-M(a) - F(a)).\qquad [3]$$

We assume that there is a maximum age A after which no fish survives. For computations, we chose A sufficiently large that the probability of surviving to that age was exceptionally small.

To characterize reproduction, we let $p_m(L(a))$ denote the probability that an individual of length $L(a)$ is reproductively active and assume that its reproductive output is

$$\varnothing(W(a)) = c_f W(a)^{b_f},\qquad [4]$$

where c_f and b_f are species-specific fecundity parameters. If $bf = 1$, reproduction is isometric, that is, proportional to mass; if $bf > 1$, reproduction is hyperallometric.

The LEP of an individual, which we denote by $\Phi(\{F\})$ (thus suppressing all of the other life history parameters but keeping a focus on the schedule of fishing mortality), is the sum of its expected (accounting survival) reproduction across the length of its life. Thus,

$$\Phi(\{F\}) = \sum_{a=0}^{A} S(a|\{F\})p_m(L(a))c_f W(a)^{b_f}.\qquad [5]$$

The SPR compares LEP of the average individual in a population experiencing fishing mortality $\{F\}$ with that of an unfished population, that is,

$$\text{SPR}(\{F\}) = \frac{\Phi(\{F\})}{\Phi(\{0\})} = \frac{\sum_{a=0}^{A} S(a|\{F\})p_m(L(a))c_f W(a)^{b_f}}{\sum_{a=0}^{A} S(a|\{0\})p_m(L(a))c_f W(a)^{b_f}}.\qquad [6]$$

Higher values of SPR ($\{F\}$) correspond to more resilient stocks, populations, or species (40). SPR emerged as a reference point based on efforts to identify harvest rates that achieve high levels of yield while simultaneously maintaining a sufficient level of spawning to ensure stock. For example, 30% of the egg production of an unfished stock might be sufficient to maintain a stock when the adult population is reduced if we accept that recruitment success is about 3 times higher in a fished stock relative to an unfished stock due to the reduction of density-dependent mortality (e.g., refs. 31, 44–47).

Since the true relationship between the number of spawners and the expected number of recruits (the SRR; see *Population Dynamics and Yield for Knife Edge Fishing Mortality* section below) is unknown, Clark (31, 45) sought to identify sustainable harvest rates that come close to maximizing expected yield under a range of assumptions about overall stock productivity. We chose SPR = 0.3 as our reference point since it is often recommended in the absence of detailed knowledge of the SRR, but we explored a range of other values and found very similar results.

*As described in more detail below, for computations, we followed ref. 16 and gave a distribution to L1, thus introducing variation in size at age into the model. For simplicity, we suppress the notation characterizing the distribution of asymptotic size.

We wanted to measure the effect that an assumption of reproductive isometry would have on the ideal fishing mortality rate if we assumed that fishers were aiming for an SPR of 30%. We first calculated this target fishing rate under isometry, $F_{0.3}^{\text{Iso}}$, by assuming $b_f = 1$ and identifying the value of $0 \leq F \leq 1$ that yields SPR = 0.30. We then replaced the isometric mass-fecundity relationship with the appropriate species-specific hyperallometric relationship and identified the value of $F_{0.3}^{\text{Hyp}}$ that delivered the target value of SPR = 0.3.

A hyperallometric reproductive relationship produces more eggs for a given age population, since $W(a)^{b_f} > W(a)$ for any $b_f > 1$ if $W(a) > 1$. The resulting hyperallometric populations can invariably tolerate higher rates of fishing than isometric populations (*ceteris paribus*), but this is an unstandardized (and thus unhelpful) comparison. To make the contrast fair, we altered the value of c_f in the hyperallometric populations (i.e., we scaled the per-capita egg production). In particular, we chose c_f^{Hyp} to standardize the two populations (isometric and hyperallometric) by ensuring their total virgin recruitment was equal (i.e., the amount of recruitment occurring in the absence of additional fishing mortality was the same).

By comparing $F_{0.3}^{\text{Iso}}$ with $F_{0.3}^{\text{Hyp}}$, we can estimate how much the assumption of reproductive isometry alters the amount of fishing mortality required to generate a target SPR of 30%. The mismatch tells us how much we need to decrease catch in order to attain the intended SPR$_{0.3}$. We can also calculate the degree to which egg production is overestimated when isometry is assumed by comparing the difference between the intended SPR$_{0.3}$ under isometry to the actual SPR$_{0.3}$ based on $F_{0.3}^{\text{Iso}}$ but for a hyperallometric population. The difference between these two SPR$_{0.3}$s, relativized by 0.3 yields the spawning potential overestimate (SPO; reported in *SI Appendix*, Table S2). *SI Appendix*, Fig. S1 shows a hypothetical SPO before it has been relativized.

To illustrate using a real species from our study, *Clupea harengus* has a reproductive scaling exponent of 1.54. Under the assumption of isometry, the predicted fishing mortality that yields and SPR$_{0.3}$ is F ~0.41. The actual SPR that this fishing mortality would produce under reproductive hyperallometry is 0.265, and thus, the SPR is ~11.6% lower than it should be than it should be relative to the intended SPR$_{0.3}$ ($\frac{0.035}{0.3} = 11.6\%$). In order to bring the SPR under hyperallometry to the intended level, the fishing mortality would therefore need to be reduced to ~0.28, yielding an overharvest ratio of ~1.44.

Population Dynamics and Yield for Knife Edge Fishing Mortality. Knife edge fishing mortality describes fishing effort that is applied only to individuals above a particular minimum age and then applies uniformly to all older ages. With knife edge fishing mortality, $F(a) = v(a) F$, where $v(a) = 0$ for individuals not taken by the fishery, $v(a) = 1$ for individuals taken by the fishery, and F is the maximum rate of fishing mortality. We follow the common assumption (16) that $v(a) = H(a - a_m)$ is a Heaviside step function, with the age at maturity a_m separating unharvested age classes $v(a) = 0$ from harvested age classes $v(a) = 1$. We let $N(a, t|F)$ denote the number of individuals of age a at time t when the rate of fishing mortality is F and assume that density dependence acts only on the zeroth age class (recruits). In this case, the fraction of fish surviving from age a to age $a + 1$ is $e^{-M(a)-Fv(a)}$ so that

$$N(a + 1, t + 1|F) = e^{-M(a)-Fv(a)}N(a, t|F).\qquad [7]$$

To characterize the zeroth age class (the recruits), $N(0, t + 1)$, we use the BH-SRR that has components of density-independent and density-dependent mortality during the egg and larval phase, before individuals are recruited to the population (see refs. 16, 18 for review). Offspring production by an individual of age a is $p_m(L(a))c_f W(a)^{b_f}$, and since there are $N(a, t|F)$ such individuals at time t, the total egg production by the population $\mathcal{E}(t|F)$ is

$$\mathcal{E}(t|F) = \sum_{a=0}^{A} N(a, t|F)p_m(L(a))c_f W(a)^{b_f}.\qquad [8]$$

For the BH-SRR,

$$N(0, \quad t + 1) = \frac{\alpha \mathcal{E}(t|F)}{\beta + \mathcal{E}(t|F)},\qquad [9]$$

where α and β are species-specific parameters.

When iterated forward in time, Eqs. 7–9 lead to a steady state for the number of individuals of age a in the population, which we denote by $\overline{N}(a|F)$ for $a = 0, 1, 2, \ldots A$. Associated with this steady state is a steady-state level of egg production,

$$\overline{\mathcal{E}}(F) = \sum_{a=0}^{A} \overline{N}(a|F) p_m(L(a)) c_f W(a)^{b_f}. \qquad [10]$$

Steepness h is defined as the fraction of unfished recruitment that is obtained when the egg production is reduced to 20% of its unfished level (see refs. 18, 48 for review). Many quantities of interest in fisheries science can be obtained from steepness (see Eq. **13** below). Following Walters and Martell (49), Martell et al. (Appendix B in ref. 50), and Quinn and Deriso (16), for a given steepness h, we first constructed the Goodyear Compensation ratio:

$$C_R = \frac{4h}{1-h}. \qquad [11]$$

Then, when fishing mortality is F, the number of recruits in the steady state is related to the number of recruits in the steady state of an unfished population by

$$\overline{N}(0|F) = \overline{N}(0|0) \; \frac{C_R - (\Phi(0)/\Phi(F))}{C_R - 1}, \qquad [12]$$

and all other population numbers are determined by the steady state version of Eq. **7**. Thus, specifying unfished recruitment, we rapidly obtain recruitment for any value of fishing mortality.

We focus on steady-state yields. The number of fish of age a not surviving to age $a + 1$ is $\overline{N}(a|F)(1 - e^{-M(a)-v(a)F})$. We assume the fraction of dead fish taken by the fishery is $\frac{v(a)F}{M(a)+v(a)F}$. Thus, the yield in numbers of fish of age a when the maximum rate of fishing mortality is F is

$$Y_N(a|F) = \overline{N}(a|F)(1 - e^{-M(a)-v(a)F}) \cdot \frac{v(a)F}{M(a) + v(a)F}. \qquad [13]$$

Note that if the exponential is Taylor-expanded to first order in $M(a) + v(a)F$, we have $YN(a|F) = v(a)F\overline{N}(a|F)$. The total yield in numbers is then

$$Y_{T,N}(F) = \sum_{a=0}^{A} Y_N(a|F). \qquad [14]$$

Since the mass of fish of age a is $c\omega L(a)^3$, the total yield in biomass is

$$Y_{T,B}(F) = \sum_{a=0}^{A} c_\omega L(a)^{b_\omega} Y_N(a|F). \qquad [15]$$

HSs: Age-Dependent Vulnerability to Fishing. To model HSs, we replace knife edge fishing mortality [i.e., $v(a) = 0$ for immature fish and $v(a) = 1$ for mature fish] by $v(a) = 0$ if length at age $L(a) < L_{min}$ or $L(a) > L_{max}$, where L_{min} and L_{max} are species-specific management choices, and $v(a) = 1$ for $L_{min} \le L(a) \le L_{max}$.

In computations, we assumed that asymptotic size had a normal distribution centered at a species-specific mean with SD equal to 10% of that mean, which generated a distribution of size at age, and that $h = 0.6$; we also explored results for $h = 0.3$ or $h = 0.7$ as a sensitivity analysis. To find the rate of fishing mortality that generated maximum sustainable (steady state) yield F_{MSY}, we conducted a numerical search, beginning with

$$F_{MSY} \approx M\left(\sqrt{\frac{4h}{1-h}} - 1\right), \qquad [16]$$

which (18) showed is a good approximation to F_{MSY} for an age-structured model with a given steepness h. For sensitivity analyses, see *SI Appendix*, Table S3.

STCs: Spatially Dependent Fishing Mortality. We extended the sedentary-adult, dispersive juvenile model of (25) to include multiple age classes and hyperallometric reproductive output. The rate of fishing mortality now depends upon space but not age; we denote it by $F(x)$, where x is the spatial variable, assuming a linear domain $0 \le x \le D$. We now must characterize the number of individuals by both age and spatial location, denoting this by $N(a, x, t|F)$, and Eq. **7** is replaced by

$$N(a + 1, x, t + 1|F) = e^{-M(a)-F(x)} N(a, x, t|F). \qquad [17]$$

The number of recruits is determined by the dispersal of eggs. We denote the dispersal kernel by $k(x, y)$, which is the probability that an egg spawned at

location y ends up at location x. Then, the total number of settling eggs/larvae at spatial point x is

$$S(x, t|F) = \sum_{a=0}^{A} \int_{y=0}^{D} N(a, y, t|F) p_m(L(a)) c_f L(a)^{b_f} k(x, y) dy. \qquad [18]$$

If θ is a measure of additional mortality during the dispersal phase, recruits at spatial point x are

$$N(0, x, t + 1|F) = \theta \frac{\alpha S(x, t|F)}{\beta + S(x, t|F)}. \qquad [19]$$

We explored three cases: 1) an effort-controlled fishery (25), 2) a marine reserve, and 3) temporary closures (rotational reserves).

Effort-Controlled Fishery. In this case, which corresponds to management by catch restriction, the rate of fishing mortality is constant over both time and space. We numerically solved Eqs. **17**–**19** for the steady state $N(a, x|F)$ and used the Taylor expansion of Eq. **13** to approximate the yield of individuals of age a at spatial position x in numbers and biomass respectively by

$$Y_N(a, x|F) = F \cdot \overline{N}(a, x|F), \qquad [20]$$

$$Y_B(a, x|F) = F \cdot c_\omega L(a)^{b_\omega} \overline{N}(a, x|F). \qquad [21]$$

The total yield in numbers and biomass are then respectively

$$Y_{T,N}(F) = F \sum_{a=0}^{A} \int_{x=0}^{D} Y_N(a, x|F) dx, \qquad [22]$$

$$Y_{T,B}(F) = F \sum_{a=0}^{A} \int_{x=0}^{D} Y_B(a, x|F) dx. \qquad [23]$$

We chose F to maximize the yield, thus obtaining F_{MSY}.

Permanent Marine Reserve. In this case, we assumed that a permanently closed, perfectly enforced marine reserve exists between $x = 0$ and ended at $x = R$. Inside the reserve, the rate of fishing mortality was 0, and outside of the reserve, it was F, so that the rate of fishing mortality is a piecewise constant function of space:

$$F(x) = \begin{cases} 0 & \text{if } x > R \\ F_0 & \text{if } 0 \le x \le R \end{cases}. \qquad [24]$$

We numerically solved Eqs. **17**–**19** to the steady state and then computed the yields in analogy to Eqs. **20**–**23**. After that, we chose the value of F that maximized yield.

Temporal Closures. We modeled management with rotational (i.e., moving) reserves by defining the piecewise constant spatial function $F(x, t)$ in a time-dependent manner. We let the no-take reserve move each year at a fixed rate, treating the domain as periodic. Inside the reserve there is no fishing mortality but outside of the reserve maximum fishing mortality is F. If the width of a reserve is R and its rate of movement is s, then each location is part of the reserve for R/s years. Because the reserve is in continual motion, the population will achieve a steady state if $t >> R/s$ years.

Thus, we could use exactly the same procedures to compute yield and then determine the value of F that maximized steady-state yield. We then compared the steady-state yield under traditional fisheries management with the permanent closure and the rotating closure. For sensitivity analyses, see *SI Appendix*, Table S3.

Additional Computational Details. For computations, we assumed a uniform dispersal kernel so that $k(x, y) = 1/D$ and determined $M(a)$ from (51); $M(a) = k\left(\frac{Ltnqh_x 221e;}{L(a)}\right)^{1.5}$. We used species-specific parameters for 32 different exploited fishery species. For each species, we gathered allometric constants from the literature. Since a_0 was not generally available, we set it at the common value of -0.25.

Similarly, the BH-SRR parameters α and β are generally not known, so we chose values that represented four different intensities of density-dependent mortality based on steepness and using the method in ref. 48. We choose $\beta = 1$ and then varied α and θ to obtain $h = 0.3, 0.5, 0.7,$ or 0.9.

For the temporary closures, we chose values of $s = 5$ or 10.

Marshall et al.
Reproductive hyperallometry and managing the world's fisheries

SUSTAINABILITY SCIENCE

Comparing the Generic Model for STCs with a Detailed Model for *P. leopardus*. The assumption of a well-mixed larval pool that we used above allowed the model to be implicitly spatial, and we assumed that the habitat was of uniform quality. The economic aspects of the model were also kept simple, with spatially constant effort. It is possible that these assumptions will overestimate the benefits of STCs. For example, dispersal likely decays with increasing distance from the spawning location, which limits the benefits of larval spillover from no-take areas. Thus, 1) settlement enhancement will be localized around the STC and 2) a higher concentration of settlers will likely lead to higher density-dependent mortality rates; and 3) the benefits of higher recruitment densities will be counter acted by an increase in fishing effort.

To provide some indication of the magnitude and direction of the difference, we compared the predictions of our generic STC model to a spatially explicit bioeconomic fishery model, when both were parameterized for coral trout (*P. leopardus*) on Australia's GBR. The bioeconomic model is based on a spatially explicit marine metapopulation model, centered on midshore and offshore reefs on the southern GBR (52). Larval dispersal patterns were simulated using a coupled biological-oceanographic model of coastal flow, with the adult spawning and larval behavioral components chosen to match *P. leopardus* (or the most similar species for which data were available; see ref. 53). Additional details of the bioecononomic model are described in

detail in ref. 54. The key parameters shared by both models are a mass-based hyperallometric exponent 1.18, von Bertalanffy length parameters $k = 0.354$ and $L_\infty = 52.2$ cm, a length-biomass pre-exponential factor of 0.0079 and an exponent of 3.157, and a minimum reproductive size of 32 cm.

On the basis of these parameters, the generic model predicted that optimal spatial closures would deliver yields that were 31% larger than optimal effort controls. In contrast, the spatial bioeconomic model predicted that optimal spatial closures would deliver yields that are 16% larger than the optimal effort control. Thus, the generic model overestimated the benefits by a factor of ~12% (1.31/1.16 = 1.12).

Data Availability. All study data are included in the article and/or *SI Appendix*.

1. M. Clark, D. Tilman, Comparative analysis of environmental impacts of agricultural production systems, agricultural input efficiency, and food choice. *Environ. Res. Lett.* **12**, 064016 (2017).
2. World Bank, Fish to 2030: Prospects for fisheries and aquaculture. Agriculture and Environmental Services Discussion Paper 3, no. 3, Washington, D.C. http://documents.worldbank.org/curated/en/458631468152376668/Fish-to-2030-prospects-for-fisheries-and-aquaculture. Accessed 22 September 2020.
3. Y. Rousseau, R. A. Watson, J. L. Blanchard, E. A. Fulton, Evolution of global marine fishing fleets and the response of fished resources. *Proc. Natl. Acad. Sci. U.S.A.* **116**, 12238–12243 (2019).
4. D. Pauly et al., Towards sustainability in world fisheries. *Nature* **418**, 689–695 (2002).
5. FAO, *Fishery and Aquaculture Statistics, 2016* (Food and Agriculture Organization of the United Nations, Roma, Italy, 2016).
6. B. Worm, et al., Rebuilding global fisheries. *Science* **325**, 578–585 (2009).
7. R. Hilborn et al., Effective fisheries management instrumental in improving fish stock status. *Proc. Natl. Acad. Sci. U.S.A.* **117**, 2218–2224 (2020).
8. J. A. Hutchings, J. D. Reynolds, Marine fish population collapses: Consequences for recovery and extinction risk. *Bioscience* **54**, 297–309 (2004).
9. A. G. J. Tacon, M. Metian, Fishing for aquaculture: Non-food use of small pelagic forage fish—A global perspective. *Rev. Fish. Sci.* **17**, 305–317 (2009).
10. D. R. Barneche, D. R. Robertson, C. R. White, D. J. Marshall, Fish reproductive-energy output increases disproportionately with body size. *Science* **360**, 642–645 (2018).
11. C. T. Marshall, C. L. Needle, A. Thorsen, O. S. Kjesbu, N. A. Yaragina, Systematic bias in estimates of reproductive potential of an Atlantic cod (*Gadus morhua*) stock: Implications for stock-recruit theory and management. *Can. J. Fish. Aquat. Sci.* **63**, 980–994 (2006).
12. J. R. Beddington, D. J. Agnew, C. W. Clark, Current problems in the management of marine fisheries. *Science* **316**, 1713–1716 (2007).
13. M. A. Hixon, D. W. Johnson, S. M. Sogard, BOFFFFs: On the importance of conserving old-growth age structure in fishery populations. *ICES J. Mar. Sci.* **71**, 2171–2185 (2014).
14. R. J. Bell et al., Changes in the size structure of marine fish communities. *ICES J. Mar. Sci.* **75**, 102–112 (2018).
15. L. A. K. Barnett, T. A. Branch, R. A. Ranasinghe, T. E. Essington, Old-growth fishes become scarce under fishing. *Curr. Biol.* **27**, 2843–2848.e2 (2017).
16. T. J. Quinn, R. B. Deriso, *Quantitative Fish Dynamics* (Oxford University Press, 1999).
17. W. T. Cooper, L. R. Barbieri, M. D. Murphy, S. K. Lowerre-Barbieri, Assessing stock reproductive potential in species with indeterminate fecundity: Effects of age truncation and size-dependent reproductive timing. *Fish. Res.* **138**, 31–41 (2013).
18. M. Mangel et al., A perspective on steepness, reference points, and stock assessment. *Can. J. Fish. Aquat. Sci.* **70**, 930–940 (2013).
19. S. E. Lester et al., Biological effects within no-take marine reserves: A global synthesis. *Mar. Ecol. Prog. Ser.* **384**, 33–46 (2009).
20. G. J. Edgar et al., Global conservation outcomes depend on marine protected areas with five key features. *Nature* **506**, 216–220 (2014).
21. M. L. Baskett, S. A. Levin, S. D. Gaines, J. Dushoff, Marine reserve design and the evolution of size at maturation in harvested fish. *Ecol. Appl.* **15**, 882–901 (2005).
22. C. C. D'Aloia et al., Patterns, causes, and consequences of marine larval dispersal. *Proc. Natl. Acad. Sci. U.S.A.* **112**, 13940–13945 (2015).
23. H. B. Harrison et al., Larval export from marine reserves and the recruitment benefit for fish and fisheries. *Curr. Biol.* **22**, 1023–1028 (2012).
24. D. H. Williamson et al., Large-scale, multidirectional larval connectivity among coral reef fish populations in the Great Barrier Reef Marine Park. *Mol. Ecol.* **25**, 6039–6054 (2016).
25. A. Hastings, L. W. Botsford, Equivalence in yield from marine reserves and traditional fisheries management. *Science* **284**, 1537–1538 (1999).
26. R. Hilborn, Traditional fisheries management is the best way to manage weak stocks. *Proc. Natl. Acad. Sci. U.S.A.* **114**, E10610 (2017).
27. R. Hilborn, Are MPAs effective? *ICES J. Mar. Sci.* **75**, 1160–1162 (2018).
28. D. C. Gwinn et al., Rethinking length-based fisheries regulations: The value of protecting old and large fish with harvest slots. *Fish Fish.* **16**, 259–281 (2015).
29. R. N. M. Ahrens, M. S. Allen, C. Walters, R. Arlinghaus, Saving large fish through harvest slots outperforms the classical minimum-length limit when the aim is to achieve multiple harvest and catch-related fisheries objectives. *Fish Fish.* **21**, 483–510 (2020).
30. G. R. Fitzhugh, K. W. Shertzer, G. T. Kellison, D. M. Wyanski, Review of size- and age-dependence in batch spawning: Implications for stock assessment of fish species exhibiting indeterminate fecundity. *Fish Bull.* **110**, 413–425 (2012).
31. W. G. Clark, F-35% revisited ten years later. *N. Am. J. Fish. Manage.* **22**, 251–257 (2002).
32. R. J. H. Beverton, S. J. Holt, *On the Dynamics of Exploited Fish Populations* (Chapman & Hall, 1957).
33. E. Dick, S. Beyer, M. Mangel, S. Ralston, A meta-analysis of fecundity in rockfishes (genus *Sebastes*). *Fish. Res.* **187**, 73–85 (2017).
34. D. J. Marshall, S. S. Heppell, S. B. Munch, R. R. Warner, The relationship between maternal phenotype and offspring quality: Do older mothers really produce the best offspring? *Ecology* **91**, 2862–2873 (2010).
35. E. Gilman, M. Chaloupka, M. Fitchett, D. L. Cantrell, M. Merrifield, Ecological responses to blue water MPAs. *PLoS One* **15**, e0235129 (2020).
36. S. J. Bucaram et al., Assessing fishing effects inside and outside an MPA: The impact of the Galapagos Marine Reserve on the Industrial pelagic tuna fisheries during the first decade of operation. *Mar. Policy* **87**, 212–225 (2018).
37. R. Arlinghaus et al., Opinion: Governing the recreational dimension of global fisheries. *Proc. Natl. Acad. Sci. U.S.A.* **116**, 5209–5213 (2019).
38. S. Manel et al., Long-distance benefits of marine reserves: Myth or reality? *Trends Ecol. Evol.* **34**, 342–354 (2019).
39. M. P. Armstrong et al., The application of small scale fishery closures to protect Atlantic cod spawning aggregations in the inshore Gulf of Maine. *Fish. Res.* **141**, 62–69 (2013).
40. H. K. Kindsvater, M. Mangel, J. D. Reynolds, N. K. Dulvy, Ten principles from evolutionary ecology essential for effective marine conservation. *Ecol. Evol.* **6**, 2125–2138 (2016).
41. M. Mangel, *The Theoretical Biologist's Toolbox: Quantitative Methods for Ecology and Evolutionary Biology* (Cambridge University Press, 2006).
42. S. Martínez-Aguilar, F. Arreguín-Sánchez, E. Morales-Bojórquez, Natural mortality and life history stage duration of Pacific sardine (*Sardinops caeruleus*) based on gnomonic time divisions. *Fish. Res.* **71**, 103–114 (2005).
43. M. Mangel, The inverse life-history problem, size-dependent mortality and two extensions of results of Holt and Beverton. *Fish Fish.* **18**, 1192–1200 (2017).
44. M. P. Sissenwine, J. G. Shepherd, An alternative perspective on recruitment overfishing and biological reference points. *Can. J. Fish. Aquat. Sci.* **44**, 913–918 (1987).
45. W. G. Clark, Groundfish exploitation rates based on life history parameters. *Can. J. Fish. Aquat. Sci.* **48**, 734–750 (1991).
46. S. Ralston, West Coast groundfish harvest policy. *N. Am. J. Fish. Manage.* **22**, 249–250 (2002).
47. M. W. Dorn, Advice on West Coast rockfish harvest rates from Bayesian meta-analysis of stock–recruit relationships. *N. Am. J. Fish. Manage.* **22**, 280–300 (2002).
48. X. He, M. Mangel, A. MacCall, A prior for steepness in stock-recruit relationships, based on an evolutionary persistence principle. *Fish Bull.* **104**, 428–433 (2006).
49. C. J. Walters, S. J. Martell, *Fisheries Ecology and Management* (Princeton University Press, 2004).
50. S. J. Martell, W. E. Pine, C. J. Walters, Parameterizing age-structured models from a fisheries management perspective. *Can. J. Fish. Aquat. Sci.* **65**, 1586–1600 (2008).
51. E. L. Charnov, H. Gislason, J. G. Pope, Evolutionary assembly rules for fish life histories. *Fish Fish.* **14**, 213–224 (2013).
52. M. Bode, A. I. Tulloch, M. Mills, O. Venter, A. W. Ando, A conservation planning approach to mitigate the impacts of leakage from protected area networks. *Conserv. Biol.* **29**, 765–774 (2015).
53. M. Bode, P. R. Armsworth, H. E. Fox, L. Bode, Surrogates for reef fish connectivity when designing marine protected area networks. *Mar. Ecol. Prog. Ser.* **466**, 155–166 (2012).
54. D. J. Marshall, S. Gaines, R. Warner, D. R. Barneche, M. Bode, Underestimating the benefits of marine protected areas for the replenishment of fished populations. *Front. Ecol. Environ.* **17**, 407–413 (2019).

www.manaraa.com