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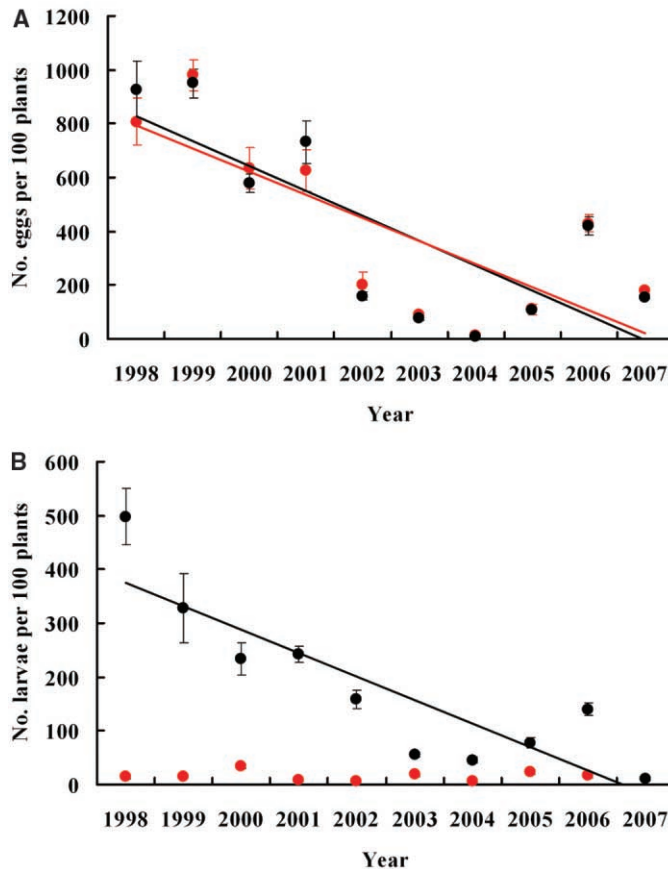
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**Fig. 3.** Egg and larval densities of *H. armigera* on cotton at Langfang site, Hebei Province, China, from 1998 to 2007. **(A)** Relation between egg density on Bt cotton (red circles) and non-Bt cotton (black circles) and planting year of Bt cotton. Linear model on Bt cotton (black line),  $y = 185,476.90 - 92.42x$ ,  $F = 69.05$ ,  $df = 1,58$ ,  $P < 0.0001$ ,  $R^2 = 0.54$ . Linear model on non-Bt cotton (red line),  $y = 171,365.94 - 85.37x$ ,  $F = 62.59$ ,  $df = 1,58$ ,  $P < 0.0001$ ,  $R^2 = 0.52$ . **(B)** Relation between larval density on Bt cotton (red circles) and survey years. Linear model on non-Bt cotton (black line),  $y = 87,107.86 - 43.41x$ ,  $F = 97.56$ ,  $df = 1,58$ ,  $P < 0.0001$ ,  $R^2 = 0.63$ . Data are means  $\pm$  SEM. There are six samples for each point in the graphs.



farmers. In China, a multiple cropping system consisting of soybeans, peanuts, corn, and vegetables is common. These crops also serve as hosts for *H. armigera*, and, because they do not express Bt toxin, they serve as refuges for non-resistant insects (10). Because cotton is not the only host crop, Bt cotton comprises about 10% of the major host crops in any province or throughout northern China. This accidental approach to refuge management appears to have,

so far, warded off the evolution of resistance (10). Nevertheless, as a result of decreased spraying of broad-spectrum pesticides for controlling cotton bollworm in Bt cotton fields, mirids have recently become key pests of cotton in China (18, 19). Therefore, despite its value, Bt cotton should be considered only one component in the diversified cropping systems common throughout China.

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Supporting Online Material

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 15 May 2008; accepted 8 August 2008  
 10.1126/science.1160550

# Can Catch Shares Prevent Fisheries Collapse?

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Recent reports suggest that most of the world's commercial fisheries could collapse within decades. Although poor fisheries governance is often implicated, evaluation of solutions remains rare. Bioeconomic theory and case studies suggest that rights-based catch shares can provide individual incentives for sustainable harvest that is less prone to collapse. To test whether catch-share fishery reforms achieve these hypothetical benefits, we have compiled a global database of fisheries institutions and catch statistics in 11,135 fisheries from 1950 to 2003. Implementation of catch shares halts, and even reverses, the global trend toward widespread collapse. Institutional change has the potential for greatly altering the future of global fisheries.

Although the potentially harmful consequences of mismanaged fisheries were forecast over 50 years ago (1, 2), evi-

dence of global declines has only been seen quite recently. Reports show increasing human impacts (3) and global collapses in large predatory fishes

(4) and other trophic levels (5) in all large marine ecosystems (LMEs) (6). It is now widely believed that these collapses are primarily the result of the mismanagement of fisheries.

One explanation for the collapse of fish stocks lies in economics: Perhaps it is economically optimal to capture fish stocks now and invest the large windfall revenues in alternative assets, rather than capturing a much smaller harvest on a regular basis. Although this remains a theoretical possibility for extremely slow-growing species

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(7), it remains rare in reality. A recent study reports that under reasonable economic parameterization, extinction is suboptimal (even with low growth rates) and that biomass under economically optimal harvest is larger than that under maximum sustainable yield (8).

If global fisheries contain large potential profits [perhaps a present value of \$1 trillion (9)], yet the profits are only realized if the fisheries are managed sustainably, why are actively managed fisheries systematically overexploited? The answer lies in the misalignment of incentives. Even when management sets harvest quotas that could maximize profits, the incentives of the individual harvester are typically inconsistent with profit maximization for the fleet. Because individuals lack secure rights to part of the quota, they have a perverse motivation to “race to fish” to outcompete others. This race can lead to poor stewardship and lobbying for ever-larger harvest quotas, creating a spiral of reduced stocks, excessive harvests, and eventual collapse.

Examining specific cases, Beddington *et al.* (10), Hilborn *et al.* (11), Grafton *et al.* (12), and Griffith (13) argue that rights-based fisheries reforms offer promising solutions. Rather than only setting industry-wide quotas, fishermen are allocated individual rights. Referred to as catch shares or dedicated access privileges, these rights can be manifest as individual (and tradable) harvest quotas, cooperatives, or exclusive spatial harvest rights; the idea is to provide—to fishermen, communities, or cooperatives—a secure asset, which confers stewardship incentives. Most readily implemented within national jurisdictions (that is, inside 200 miles), some international agreements attempt to serve a similar function in international waters. Although both theory and

empirical evidence suggest a robust link between catch shares and economic performance of a fishery (14, 15), the link with ecological performance is more tenuous. Even so, Sanchirico and Wilen (16) argue that “It is widely believed and supported by anecdotal evidence that once fishers have a financial stake in the returns from sensible investment in sustainable practices, they are more easily convinced to make sacrifices required to rebuild and sustain fisheries at high levels of economic and biological productivity.” A recent report provides examples consistent with this widely held belief (17). We tested the hypothetical causal link between the global assignment of catch shares and fisheries sustainability.

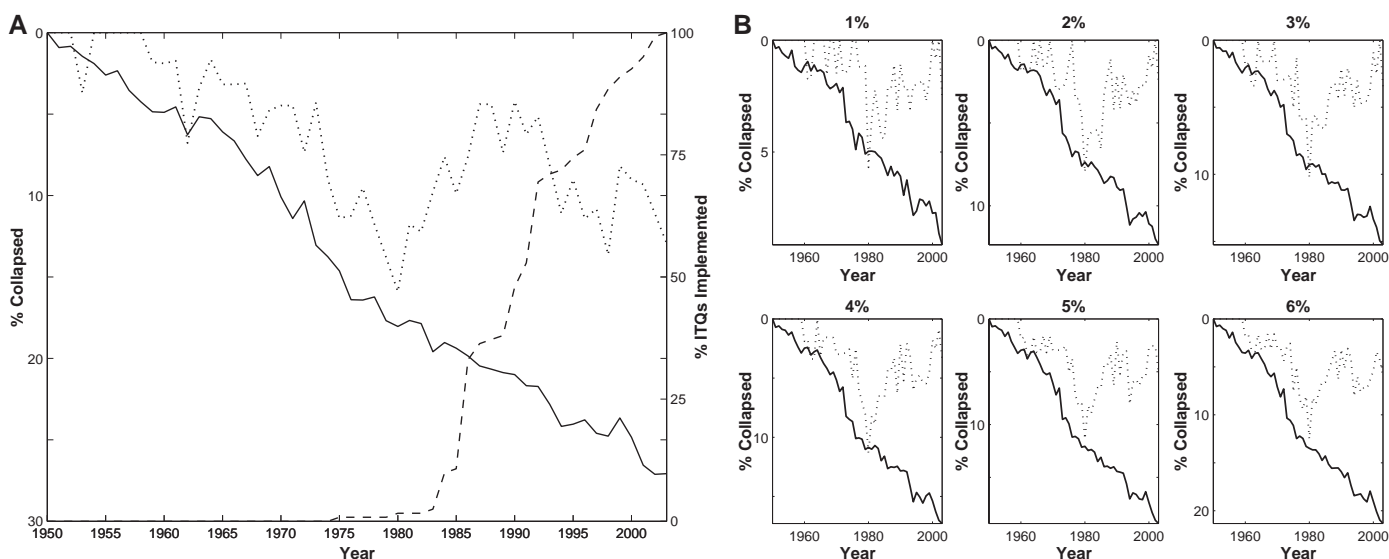
Whereas individual fishing rights have been implemented on small spatial scales in traditional cultures for millennia, the adoption rate in major fisheries has accelerated since the late 1970s. To test the efficacy of catch shares, we assembled a global database of 11,135 commercial fisheries and determined which fisheries had instituted catch shares from 1950 to 2003. We matched this institutional database to the same harvest database (18) used to assess fisheries collapse by Worm *et al.* (6). Our objective is to answer the question: Can catch shares prevent fisheries collapse?

In their widely cited contribution, Worm *et al.* (6) correlate the species richness of LMEs with fisheries collapse. They define a fishery as collapsed in year  $t$  if the harvest in year  $t$  is <10% of the maximum recorded harvest up to year  $t$ . Using this definition, ~27% of the world’s fisheries were collapsed in 2003. Extrapolating this trend into the future, Worm *et al.* (6) find that 100% of the world’s fisheries could be collapsed

by 2048. Although this highly controversial projection (19) captured most of the attention from this article, a larger focus of the work was the role of ecosystem biodiversity in preventing collapse. Fisheries in more biodiverse regions were less likely to be collapsed at any given point in history. Unfortunately, however, this greater resilience to human exploitation does not change the ultimate conclusion. Biodiversity does not prevent collapse; it merely delays it.

In our analysis, we expanded beyond the characteristics of the ecosystem to consider the characteristics of the regulating fisheries institutions, simultaneously controlling for the ecosystem, genus, and other covariates. To assemble our catch-share database, we searched the published literature and government reports, interviewed experts on global fisheries, and vetted our final database with a diverse array of researchers. In total, we identified 121 fisheries managed using catch shares—defined as variations on individual transferable quotas (ITQs)—by 2003 (20). These work by allocating a dedicated share of the scientifically determined total catch to fishermen, communities, or cooperatives. This provides a stewardship incentive; as the fishery is better managed, the value of the shares increases. By analyzing the data at the fishery level [rather than the aggregate level, as in (6)], we facilitate inclusion of fisheries institutions as independent variables in our model specification.

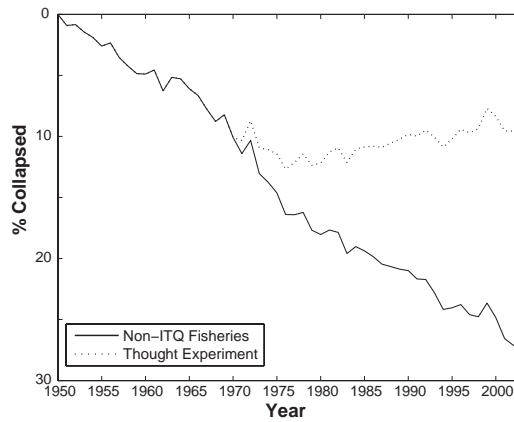
We adopt the Worm *et al.* (6) definition of collapse. Although a better measure would be based on stock (21), no systematic database of global fish biomass exists. This collapse metric may overestimate the frequency of collapsed fisheries (22), which creates a conservative test for the benefits of catch shares. Sensitivity analyses that



**Fig. 1.** (A) Percent of fisheries collapsed with (dotted line) and without (solid line) ITQ management using the Worm *et al.* (6) collapse threshold (10% of historical maximum). The number of ITQ fisheries increases through time (right y axis and dashed line), and the rate of

implementation has been accelerating. (B) Percent of fisheries collapsed with (dotted line) and without (solid line) ITQ management using more conservative collapse thresholds: 1 to 6% of historical maximum catch.

**Fig. 2.** Simulation of trend in fisheries collapse if all non-ITQ fisheries switched to ITQs in 1970 (dotted line), compared with the actual trend (solid line). The thought experiment assumes that the annual ITQ benefit counterbalances the global trend toward complete collapse, which is consistent with the observed trends in actual ITQs (Table 1). Fluctuations in the simulation arise from estimated interannual variability.



**Table 1.** Fishery-specific analyses of ITQ benefits. Each fishery is treated as a time series of collapse, with some fisheries converting to ITQ during the interval. Propensity score matching (25) controls for the effects of LME, genus, or species to further isolate biases that may arise from the particular places and fisheries where ITQs have been implemented. Columns 2 to 5 provide regression model results for four different propensity score models. Rows 2 and 3 provide the regression coefficients and SEs (in parentheses). Fisheries without ITQ management had an average annual percentage change of 0.54. For all comparisons, the annual benefit of ITQs roughly counters the current rate of decline in other fisheries (23). All estimated coefficients are statistically significant at the 1% level.

Parameter used to match fisheries	None	LME	Genus	Species
Percent ITQ difference (SE)	-7.06 (0.49)	-7.41 (0.428)	-6.79 (0.443)	-6.87 (0.441)
Annual percent ITQ effect (SE)	-0.49 (0.136)	-0.37 (0.137)	-0.54 (0.136)	-0.51 (0.139)

consider alternative thresholds for collapse and address other potential biases yield unchanged or stronger conclusions (23).

By 2003 the fraction of ITQ-managed fisheries that were collapsed (dotted line in Fig. 1A) was about half that of non-ITQ fisheries (solid line in Fig. 1A). Accelerated adoption of ITQs began in the late 1970s (dashed line and right y axis in Fig. 1A). In the preadoption period, would-be ITQ fisheries were on trajectories toward collapse, similar to non-ITQ fisheries. In the adoption period, the two curves diverge as ITQs are increasingly adopted (24). This disparity grows over time (23).

Demonstrating statistically a causal linkage between rights-based management and fisheries sustainability is complicated by three competing effects. First, the number of ITQ fisheries is growing, and new ITQ fisheries are drawn from a global pool with an ever-increasing fraction of collapsed fisheries. Random selection from this global pool could mask some benefits of rights-based management. Second, the conversion of fisheries to ITQs may involve a biased selection. For example, ITQs may be implemented disproportionately in fisheries that are already less collapsed, possibly giving a misleading perception of benefits from rights-based management. Finally, there may be temporal benefits of an ITQ (for instance, the longer an ITQ is in place in a given fishery, the less likely

that fishery is to collapse). All of these mechanisms would lead to differences between ITQ and non-ITQ fisheries, but only the last mechanism implies a benefit from the management change.

An initial regression of the data in Fig. 1 suggests that implementing an ITQ reduces the probability of collapse by 13.7 percentage points (23). Because ITQs have been disproportionately implemented in a few global ecosystems such as Alaska, Iceland, New Zealand, and Australia (25), regional or taxonomic biases could generate misleading results. To account for potential selection bias, we used a variety of estimation strategies: (i) We restricted the sample to only those ecosystems or taxa that have experienced ITQ management. (ii) We used propensity score methods to match ITQ fisheries to appropriate control fisheries (26). (iii) We used fixed-effects estimation to identify the benefit of ITQs within each fishery.

The results are remarkably similar across all specifications and estimation techniques (23). The propensity score results are summarized in Table 1. Consistent with Fig. 1, ITQ fisheries perform far better than non-ITQ fisheries. Switching to an ITQ not only slows the decline toward widespread collapse, but it actually stops this decline. Each additional year of being in an ITQ (row 2 of Table 1) offsets the global trend (0.5%

increase) of increasing collapse in non-ITQ fisheries (23). Other estimation techniques suggest even larger benefits. For example, fishery fixed-effects results suggest that ITQs not only halt the trend in global collapse, but they may actually reverse it (23).

Although bioeconomic theory suggests that assigning secure rights to fishermen may align incentives and lead to significantly enhanced biological and economic performance, evidence to date has been only case- or region-specific. By examining 11,135 global fisheries, we found a strong link: By 2003, the fraction of ITQ-managed fisheries that were collapsed was about half that of non-ITQ fisheries. This result probably underestimates ITQ benefits, because most ITQ fisheries are young.

The results of this analysis suggest that well-designed catch shares may prevent fishery collapse across diverse taxa and ecosystems. Although the global rate of catch-share adoption has increased since 1970, the fraction of fisheries managed with catch shares is still small. We can estimate their potential impact if we project rights-based management onto all of the world's fisheries since 1970 (Fig. 2). The percent collapsed is reduced to just 9% by 2003; this fraction remains steady thereafter. This figure is a marked reversal of the previous projections.

Despite the dramatic impact catch shares have had on fishery collapse, these results should not be taken as a carte blanche endorsement. First, we have restricted attention to one class of catch shares (ITQs). Second, only by appropriately matching institutional reform with ecological, economic, and social characteristics can maximal benefits be achieved. Nevertheless, these findings suggest that as catch shares are increasingly implemented globally, fish stocks, and the profits from harvesting them, have the potential to recover substantially.

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#### Supporting Online Material

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22 April 2008; accepted 19 August 2008  
10.1126/science.1159478

## Parasite Treatment Affects Maternal Investment in Sons

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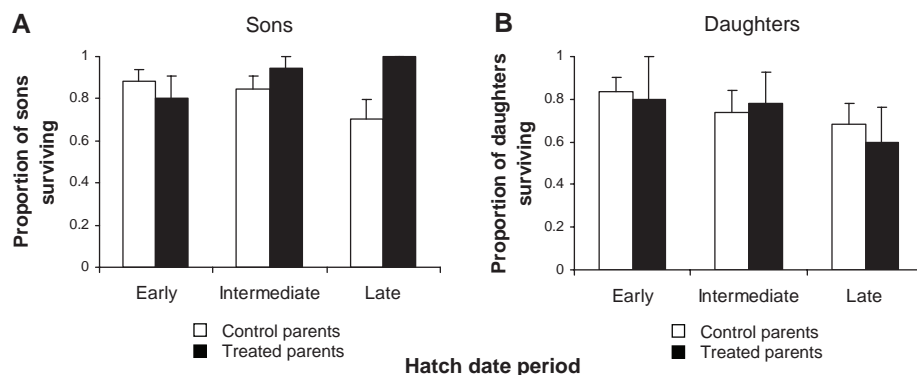
Parasitism can be a major constraint on host condition and an important selective force. Theoretical and empirical evidence shows that maternal condition affects relative investment in sons and daughters; however, the effect of parasitism on sex ratio in vertebrates is seldom considered. We demonstrate experimentally that parasitism constrains the ability of mothers to rear sons in a long-lived seabird, the European shag *Phalacrocorax aristotelis*. The effect contributes to the decline in offspring survival as the breeding season progresses and hence has important population-level consequences for this, and potentially other, seasonal breeders.

One key ecological factor influencing the condition of parents, and therefore the potential fitness of dependent offspring, is parasitism (1). In sexually dimorphic species, offspring of the larger sex often require higher nutritional investment and are more vulnerable to changes in parental condition (2). Moreover, sex allocation theory predicts that parents in good condition should bias investment toward offspring of the sex that stands to gain more from extra resources provided at critical developmental stages (3). We provide experimental evidence that parasites can constrain the ability of mothers, in particular, to rear offspring of the more expensive sex. This contributes to differential mortality of sons and daughters as the breeding season progresses and could explain the seasonal decline in offspring survival that is commonly observed in this and many other seasonal breeders.

Populations of the European shag *Phalacrocorax aristotelis* frequently suffer from severe infections of gastro-intestinal parasites, in particular anisakid nematodes [*Contracaecum rudolphi* and *Anisakis simplex* (4)]. Although their effects are usually sublethal, these parasites compete with the host for nutrients and trigger costly immune responses (5) that may impair host breed-

ing success. Shag chicks must be provisioned in the nest for ~50 days by both parents. Male-biased broods require more food than female-biased broods, and male nestlings grow faster, attain higher peak masses at fledging, and are about 20% larger than females as adults (4).

We experimentally manipulated parasitism levels in breeding adults just before chick hatching by treating both male and female parents with a broad-spectrum antiparasite drug (ivermectin), which removes gut parasites and prevents reinfection over a period of ~6 weeks and hence for most of the chick-rearing period. Throughout the laying period, nests were randomly allocated to either a treatment group, in which both parents were treated with ivermectin ( $n = 34$  nests), or a control (untreated) group in which parents were exposed to natural levels of parasitism ( $n = 83$  nests). Treated and control nests were matched for laying date, ensuring an equal spread of laying dates in each group spanning the natural range (~6 weeks). The survival of sons was higher when their parents had been treated (Fig. 1A) [generalized linear mixed model



**Fig. 1.** Differential effect of ivermectin treatment on survival of sons (A) and daughters (B), and interaction with hatch date. Black bars represent chicks from treated parents, and white bars chicks from control parents. Hatch dates are grouped into early, intermediate and late periods, based on thirds of the distribution and corresponding roughly to 2-weekly intervals. The decline in the survival of sons is not apparent when their parents have been treated. Parasite treatment did not appear to affect the success of rearing daughters. Overall, parasitism in parents accounted for ~37% of the natural seasonal decline in chick survival. Data are means  $\pm$  SEM. Effect sizes and statistics from logistic regression are given in the text.

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