



Status and Solutions for the World's Unassessed Fisheries

Christopher Costello *et al.*
Science **338**, 517 (2012);
 DOI: 10.1126/science.1223389

This copy is for your personal, non-commercial use only.

If you wish to distribute this article to others, you can order high-quality copies for your colleagues, clients, or customers by [clicking here](#).

Permission to republish or repurpose articles or portions of articles can be obtained by following the guidelines [here](#).

The following resources related to this article are available online at www.sciencemag.org (this information is current as of October 26, 2012):

Updated information and services, including high-resolution figures, can be found in the online version of this article at:

<http://www.sciencemag.org/content/338/6106/517.full.html>

Supporting Online Material can be found at:

<http://www.sciencemag.org/content/suppl/2012/09/26/science.1223389.DC1.html>

A list of selected additional articles on the Science Web sites **related to this article** can be found at:

<http://www.sciencemag.org/content/338/6106/517.full.html#related>

This article **cites 26 articles**, 8 of which can be accessed free:

<http://www.sciencemag.org/content/338/6106/517.full.html#ref-list-1>

This article has been **cited by 1** articles hosted by HighWire Press; see:

<http://www.sciencemag.org/content/338/6106/517.full.html#related-urls>

This article appears in the following **subject collections**:

Ecology

<http://www.sciencemag.org/cgi/collection/ecology>

highlights the relative increase in infraspinous breadth (table S10).

These developmental patterns further inform the link between shoulder morphology and locomotor behavior. Arboreal hominoids possess narrower infraspinous regions, in contrast to the broad fossae displayed by modern humans (6, 19, 26). Further, the increase in infraspinous breadth during *Pan* and *Gorilla* ontogeny corresponds with a behavioral shift from a principally arboreal lifestyle at younger ages to an adult locomotor repertoire predominated by terrestrial knuckle-walking (27, 28). The infraspinatus muscle is consistently recruited to stabilize the shoulder joint during both suspensory and knuckle-walking behaviors in chimpanzees (20, 29), so the change in African ape infraspinous fossa shape might represent an adaptive optimization of the scapular blade. A narrow infraspinous region with an obliquely oriented scapular spine is a more effective configuration for infraspinatus' role in stabilizing the shoulder joint during suspensory activities (19, 20). In contrast, an enlarged infraspinous fossa allows the muscle to pass broadly behind the humeral head, which might facilitate joint integrity when the arm is loaded from below as individuals engage more regularly in knuckle-walking activities (19).

The change in infraspinous fossa shape during African ape ontogeny may represent a response to the changing loading regimes of a dynamic locomotor repertoire. This interpretation is supported by experimental evidence, where differences in shoulder activity during growth corresponded with significant infraspinous fossa shape changes in mice (30). Thus, in addition to a more cranially oriented shoulder joint and an oblique scapular spine, we propose that DIK-1-1's relatively narrow infraspinous region is a functionally meaningful characteristic. This configuration further highlights its overall apelike appearance while also distinguishing it from juvenile modern humans and the considerably more derived KNM-WT 15000 adolescent.

Comparing the DIK-1-1 scapulae to those of adult conspecifics suggests that growth of the *A. afarensis* shoulder may have followed a developmental trajectory more like that of African apes than modern humans. This conclusion is consistent with evidence purporting that *A. afarensis* dental development was also apelike (31). Additionally, behavioral changes that occur throughout African ape ontogeny could be linked with morphological shifts, indicating that some scapular blade characteristics track locomotor habits, even during an organism's lifetime. The apelike appearance of the most complete *A. afarensis* scapulae strengthens the hypothesis that these hominins participated in a behavioral strategy that incorporated a considerable amount of arboreal behaviors in addition to bipedal locomotion.

References and Notes

- E. H. Ashton, C. E. Oxnard, *Proc. Zool. Soc. Lond.* **142**, 49 (1964).
- V. Inman, J. Saunders, L. Abbott, *J. Bone Joint Surg. Am.* **26**, 1 (1944).
- C. E. Oxnard, *Am. J. Phys. Anthropol.* **26**, 219 (1967).
- D. Roberts, Structure and function of the primate scapula, in *Primate Locomotion*, F. A. Jenkins, Ed. (Academic Press, New York, 1974), pp. 171–200.
- A. Schultz, *Hum. Biol.* **2**, 303 (1930).
- N. M. Young, thesis, Harvard University (2002).
- N. M. Young, *Am. J. Phys. Anthropol.* **136**, 247 (2008).
- Z. Alemseged *et al.*, *Nature* **443**, 296 (2006).
- C. V. Ward, *Yearb. Phys. Anthropol.* **5** **35**, 185 (2002).
- S. G. Larson, *Evol. Anthropol.* **16**, 172 (2007).
- B. Latimer, in *Origine(s) de la bipédie chez les hominidés*, Y. Coppens, B. Senut, Eds. (CNRS, Paris, 1991), pp. 169–176.
- C. O. Lovejoy, *Sci. Am.* **259**, 118 (1988).
- J. T. Stern, *Evol. Anthropol.* **9**, 113 (2000).
- R. L. Susman, J. T. Stern, in *Origine(s) de la bipédie chez les hominidés*, Y. Coppens, B. Senut, Eds. (CNRS, Paris, 1991), pp. 121–131.
- Y. Haile-Selassie *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **107**, 12121 (2010).
- The new *A. sediba* shoulder blade from Malapa, South Africa (32) was not included in the present study, but represents another significant addition to the scapular fossil record.
- Materials and methods are available as supplementary materials on Science Online
- K. D. Hunt, *Am. J. Phys. Anthropol.* **86**, 521 (1991).
- S. G. Larson, *Am. J. Phys. Anthropol.* **98**, 13 (1995).
- S. G. Larson, J. T. Stern Jr., *Am. J. Anat.* **176**, 171 (1986).
- S. G. Larson, J. T. Stern Jr., W. L. Jungers, *Am. J. Phys. Anthropol.* **85**, 71 (1991).
- S. E. Inouye, B. T. Shea, *Int. J. Primatol.* **18**, 629 (1997).
- R. P. Mensforth, B. Latimer, S. Senturia, *Am. J. Phys. Anthropol.* **81**, 267 (1990).
- S. G. Larson *et al.*, *J. Hum. Evol.* **53**, 718 (2007).
- M. J. Morwood *et al.*, *Nature* **437**, 1012 (2005).
- D. J. Green, thesis, The George Washington University (2010).
- D. M. Doran, *J. Hum. Evol.* **23**, 139 (1992).
- D. M. Doran, *J. Hum. Evol.* **32**, 323 (1997).
- S. G. Larson, J. T. Stern Jr., *J. Zool.* **212**, 629 (1987).
- D. J. Green, B. G. Richmond, S. L. Miran, *J. Exp. Zool. B Mol. Dev. Evol.* (2012).
- C. Dean *et al.*, *Nature* **414**, 628 (2001).
- L. R. Berger *et al.*, *Science* **328**, 195 (2010).

Acknowledgments: We thank C. Kiarie and the staff at the National Museum of Ethiopia for help during the preparation of these fragile fossils. We greatly appreciate critical comments offered by B. Richmond, B. Wood, R. Bernstein, M. Hamrick, L.P. Hernandez, and three anonymous reviewers on this manuscript and A. Gordon for analytical assistance. We thank D. Hunt, L. Gordon, E. Westwig, I. Tattersall, G. García, J. Chupasko, M. Omura, Y. Haile-Selassie, L. Jellema, M. Harman, A. Gill, E. Mbua, S. Muteti, M. Yilma, P.V. Tobias, B. Zipfel, S. Potze, and T. Perregil for coordinating museum visits. We also acknowledge the NSF IGERT grant (9987590), NSF Doctoral Dissertation Improvement Grant (BCS-0824552), NSF (BCS-0914687), The Leakey Foundation, the Wenner-Gren Foundation, The George Washington University, Midwestern University, and the California Academy of Sciences for funding support. This paper was written by D.J.G. and Z.A. Fossil data were collected and described by D.J.G. and Z.A. Extant primate data were collected and analyzed by D.J.G. The data reported in this paper are summarized in the supplementary materials; raw data are available on request to D.J.G.

Supplementary Materials

www.sciencemag.org/cgi/content/full/338/6106/514/DC1
Materials and Methods
Supplementary Text
Figs. S1 to S4
Tables S1 to S10
References (33–41)

9 July 2012; accepted 31 August 2012
10.1126/science.1227123

Status and Solutions for the World's Unassessed Fisheries

Christopher Costello,^{1*} Daniel Ovando,¹ Ray Hilborn,² Steven D. Gaines,¹ Olivier Deschenes,³ Sarah E. Lester^{1,4}

Recent reports suggest that many well-assessed fisheries in developed countries are moving toward sustainability. We examined whether the same conclusion holds for fisheries lacking formal assessment, which comprise >80% of global catch. We developed a method using species' life-history, catch, and fishery development data to estimate the status of thousands of unassessed fisheries worldwide. We found that small unassessed fisheries are in substantially worse condition than assessed fisheries, but that large unassessed fisheries may be performing nearly as well as their assessed counterparts. Both small and large stocks, however, continue to decline; 64% of unassessed stocks could provide increased sustainable harvest if rebuilt. Our results suggest that global fishery recovery would simultaneously create increases in abundance (56%) and fishery yields (8 to 40%).

When sustainably managed, marine fisheries provide a major source of food and livelihoods for hundreds of millions of people worldwide (1). When poorly man-

aged, these benefits to people and ecosystems are severely compromised (2). Despite this tremendous global impact, there is considerable debate among conservation and fisheries scientists about the status of global fisheries [e.g., (3)]. To date, assessing the biological status of fisheries has relied either on detailed stock assessments, which combine structural population models with data to estimate a species' population size and trajectories under different harvest scenarios, or on local knowledge and less formal analysis (4). A recent synthesis of global fisheries with formal assessments

¹Bren School of Environmental Science and Management, University of California, Santa Barbara, CA 93106, USA. ²School of Aquatic and Fishery Sciences, University of Washington, Seattle, WA 98195, USA. ³Department of Economics, University of California, Santa Barbara, CA 93106, USA. ⁴Marine Science Institute, University of California, Santa Barbara, CA 93106, USA.

*To whom correspondence should be addressed. E-mail: costello@bren.ucsb.edu

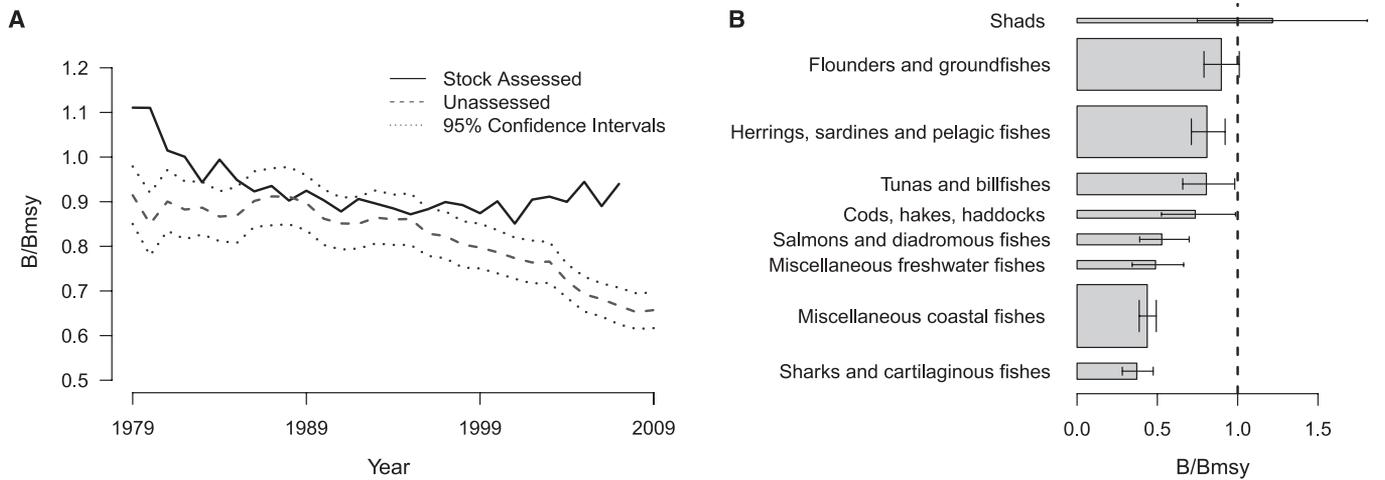


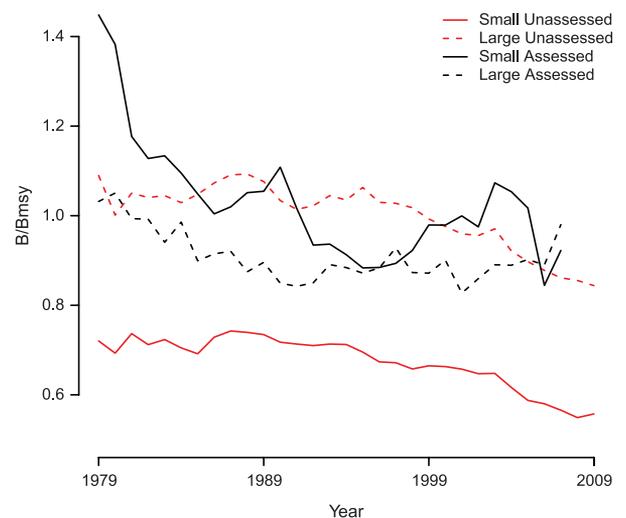
Fig. 1. (A) Time trend of median B/B_{msy} for stock assessed and unassessed fisheries. **(B)** Histogram of median predicted B/B_{msy} in 2009 for species categories of unassessed fisheries. Bar widths are proportional to the number of fisheries in each category.

reveals that although 63% have a biomass (B) below what would produce maximum sustainable yields (MSY), nearly half of these (45%) have lowered exploitation rates sufficient for recovery (3). A complementary analysis by the U.N. Food and Agriculture Organization (FAO) found that 32% of 441 studied stocks are either overexploited (28%), depleted (3%), or recovering (1%) (4). However, it is unclear whether these results extend to the remainder of global fisheries; although 20% of global catch comes from assessed species (5, 6), <1% of species have assessments, largely owing to intensive data requirements and cost. Here, we explore the status of thousands of previously unassessed fisheries and use the estimates to inform the challenges and benefits surrounding global fisheries recovery.

The scientific literature includes widespread speculation on global fisheries status because of considerable ecological, social, and food security implications. One approach relies on indirect measures of fishery status (e.g., fraction of fisheries with declined catch, mean trophic level of catch, percentage of primary production appropriated by fishery catches) (2, 7–12), but these approaches have many potentially confounding explanations. For example, declining catch is a necessary but not sufficient indicator of collapsed fisheries, resulting in unreliable estimates of stock status (13). A different approach uses status estimates from a smaller collection of “data-rich” fisheries (with formal assessments) as indicators for all fisheries (13), which also leads to unreliable predictions if data-rich fisheries differ fundamentally from unassessed fisheries (3).

Building on this literature, we developed a multivariate regression approach to identify predictors of stock status (B/B_{msy}) from assessed fisheries and use these models to estimate the status of unassessed fisheries (14). We couple the compilation of existing stock assessments (5) to an extensive database of characteristics of each unassessed fishery, such as time series of catch

Fig. 2. Time trend of median B/B_{msy} for unassessed fisheries (red) and assessed fisheries (black) with small landings (i.e., lifetime landings for a fishery is less than the median lifetime landings for all fisheries; solid line) and large landings (dashed line).



and fishery development (6) and species’ life-history traits (15). Building on fishery science, our method assumes that the status of a population is a function of its life-history traits and harvest history, and the manner in which these variables collectively affect fishery status is consistent across species with similar characteristics.

Our approach uses the same kinds of variables (life history, fishery catch, etc.) as do stock assessments. Yet the approach departs fundamentally from traditional stock assessment because at no time do we specify a structural model linking these variables to stock status and we have no indices of abundance trends. By building a panel (i.e., longitudinal data set), our approach captures both time-series effects (e.g., how long the fishery has operated) and cross-sectional effects (e.g., anchovies and sharks may respond differently to the same series of catch). This approach does not produce precise estimates for individual fisheries and therefore is not a substitute for formal assessment. However, it does provide a method for es-

timating the status of collections (including the global status) of previously unassessed stocks.

Regression models estimating $\log(B/B_{msy})$ predict stock status for assessed fisheries; we use six models of varying complexity (14) that are consistent with the scientific literature [e.g., (16–18)]. Specifically, B/B_{msy} is higher when catch shows an upward trajectory and lower when current catches are consistently lower than historic levels. Small, quickly maturing species that can recover rapidly from mismanagement have higher B/B_{msy} than slow-growing species that take longer to reach sexual maturity and have lower sustainable exploitation rates.

To predict the status of unassessed fisheries, we compiled a companion database of 7721 marine fisheries from the FAO landings database (6). There are strong caveats around aspects of these data (19), but they remain the best source of global fisheries catch records. This database determines the finest resolution for analysis—species caught by a country within an FAO region (fig. S2).

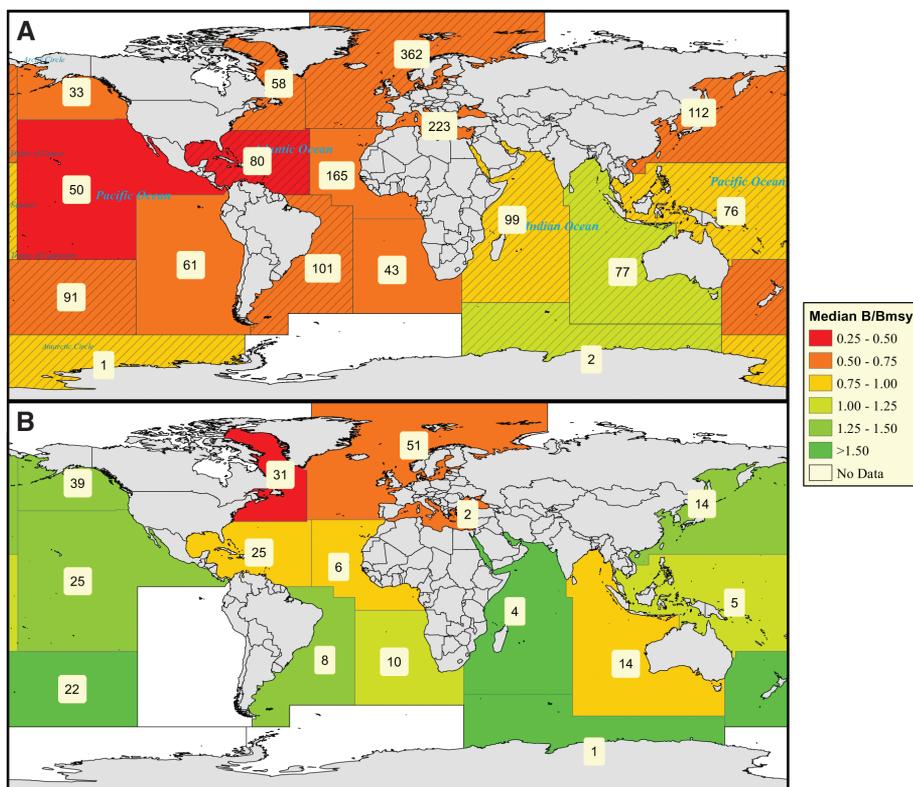


Fig. 3. Map of median B/B_{msy} of (A) unassessed fisheries in 2009 and (B) stock assessed fisheries (2000 to 2007) for FAO regions. Hashing indicates the model accounts for less than 40% of total reported landings in that region.

After focusing exclusively on finfish and aggregating across countries for highly mobile species, our final data set contains 1793 distinct unassessed marine fisheries from around the world, comprising 23% of global landings (6). For each unassessed fishery, we applied the most data-rich model possible, yielding time-series estimates of B/B_{msy} for each fishery.

We found that 64% of unassessed fisheries have a stock biomass less than B_{msy} (14)—nearly identical to the comparable statistic (63%) for assessed fisheries (3). We also found that 18% [confidence interval (CI): 0.17 to 0.20] of unassessed stocks are collapsed (i.e., $B/B_{msy} < 0.2$), which is intermediate to other estimates [5% by (17), 14% by (3), and 30% by (7)]. Overall, we predict a median B/B_{msy} of 0.64 (CI: 0.61 to 0.69) for the world’s unassessed fisheries in 2009—substantially lower than the median value of 0.94 exhibited by assessed fisheries in 2007, the nearest year for which data are available (Fig. 1A). Trends in assessed and unassessed stocks diverged in the mid-1990s; one possible explanation is a shift of effort from assessed (and well-managed) fisheries to unassessed ones (20).

We used our model to estimate status by categories such as species category, fishery size, socioeconomic conditions of the host nation, and geographic region. Although most species categories would benefit from management reform, small schooling fish such as herrings and sardines

have relatively higher biomass than many slow-growing large-bodied fishes such as sharks (Fig. 1B). Larger-than-average unassessed fisheries have a median biomass near MSY ($B/B_{msy} = 0.83$; CI: 0.77 to 0.92; Fig. 2). Smaller stocks, which are critically important for biodiversity and small-scale seafood security, tend to be in much worse condition ($B/B_{msy} = 0.55$; CI: 0.51 to 0.60). These effects of fishery size hold over time, and both groups show continuing declines in biomass. We found that unassessed fisheries in the developing world ($B/B_{msy} = 0.70$, CI: 0.60 to 0.80) may have higher stock biomasses, on average, than those in developed countries (B/B_{msy} of 0.56; CI: 0.51 to 0.62; supplementary text). Geographically, the eastern Indian Ocean, including India, southern Indonesia, and Western Australia, have relatively high B/B_{msy} , whereas the Northwestern Atlantic, including the Northeastern United States and Canada, has among the lowest median B/B_{msy} (Fig. 3). In general, there are stark contrasts between the median status of assessed and unassessed stocks, even in regions noted for well-managed assessed stocks (e.g., New Zealand and Alaska; Fig. 3). However, our data coverage in some regions is low (Fig. 3), and thus geographical comparisons warrant caution.

We used five approaches to validate the accuracy of model predictions, including within sample validation for assessed fisheries, bias tests for fishery size and data errors, jackknife analy-

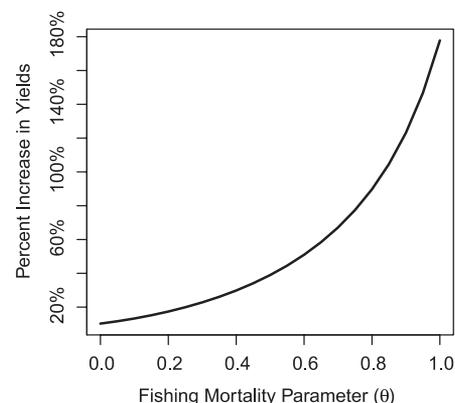


Fig. 4. Percentage increase in fishery yields from moving to B_{msy} across a spectrum of possible fishing mortality rates. θ measures the fractional difference between fishing mortality to hold current biomass in steady state and fishing mortality at collapse.

ses, comparisons with FAO assessments, and comparisons with B/B_{msy} estimates from inside and outside more than 50 marine reserves around the world. Each of these validations generally supported the value of this new assessment tool (supplementary text).

The ability to estimate the status of thousands of unassessed stocks allows us to address a number of globally important policy questions. An immediate consequence of $B/B_{msy} < 1.0$ is the increase in fishery yield and fish biomass that would result from recovery. Using B_{msy} as a target for rebuilding fisheries, the percentage increase in stock biomass that would result from reform is simply: %Increase = $100(B_{msy}/B - 1)$. For example, recovering the median fishery in our analysis ($B/B_{msy} = 0.64$) would generate a 56% increase in biomass left in the ocean.

Fishery recovery also ultimately increases yields. Many regions of the world with low B/B_{msy} also face pressing food security challenges, which will increase dramatically given projected changes in human populations and wealth in the coming decades (21). We find that in some fisheries, yields could more than double (supplementary text), although it is worth noting that total global seafood production is dominated by a small number of large stocks. Forecasting the potential response for the median fishery requires estimating the current fishing mortality. Using the very conservative assumption that current mortality would stabilize B/B_{msy} at its current value, recovering the median fishery would increase yield by 15% and recovering all fisheries would increase yield by 8%. The continued declines in biomass for both large and small unassessed stocks, however, suggest that current mortality is substantially higher. If instead we assume that unassessed fisheries are 50% closer to the fishing effort that would lead to their collapse, the predicted increase in yield from recovery is 51% for the median fishery and 40% globally (Fig. 4; supplementary text).

Our analysis suggests large potential conservation and food benefits from improving the management of the world's unassessed fisheries. To realize these benefits requires successful approaches for fisheries reform. Limiting entry and using individual transferable quotas have been shown to benefit data-rich fisheries within developed countries (22). These approaches, however, may prove more challenging to implement for unassessed fisheries in developing countries, because they inherently require strong governance, rule of law, and monitoring. Rather, approaches such as territorial user right fisheries (TURFs) (23), fisheries cooperatives (24), TURFs coupled with no-take reserves (25), and co-management approaches (26) are likely to be more broadly appropriate tools. In addition, coupling recent advances in data-poor assessment (27) with these management instruments will be critical to success.

References and Notes

1. R. Arnason, K. Kelleher, R. Willmann, *The Sunken Billions: The Economic Justification for Fisheries Reform* (World Bank, Washington, DC, 2009).
2. D. Pauly, R. Watson, J. Alder, *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **360**, 5 (2005).
3. B. Worm *et al.*, *Science* **325**, 578 (2009).
4. FAO, *The State of World Fisheries and Aquaculture 2010* (Food and Agriculture Organization of the United Nations, Rome, 2010).
5. D. Ricard, C. Minto, O. Jensen, J. Baum, *Fish. Fish.* **10**, 1111/j.14672011.00435.x (2011).
6. FAO, *FAO Statistics and Information Service of the Fisheries and Aquaculture Department. Total Fishery Production 1950-2009. FISHSTAT Plus* (Food and Agriculture Organization of the United Nations, Rome, 2011); www.fao.org/fishery/statistics/software/fishstat/en.
7. B. Worm *et al.*, *Science* **314**, 787 (2006).
8. U. T. Srinivasan, W. W. L. Cheung, R. Watson, U. R. Sumaila, *J. Bioecon.* **12**, 183 (2010).
9. W. Swartz, E. Sala, S. Tracey, R. Watson, D. Pauly, *PLoS ONE* **5**, e15143 (2010).
10. E. Chassot *et al.*, *Ecol. Lett.* **13**, 495 (2010).
11. T. A. Branch *et al.*, *Nature* **468**, 431 (2010).
12. D. Pauly, V. Christensen, J. Dalsgaard, R. Froese, F. Torres Jr., *Science* **279**, 860 (1998).
13. T. A. Branch, O. P. Jensen, D. Ricard, Y. M. Ye, R. Hilborn, *Conserv. Biol.* **25**, 777 (2011).
14. Materials and methods are available as supplementary materials on Science Online.
15. R. Froese, D. Pauly, *FishBase* (2010); www.fishbase.org.
16. M. L. Pinsky, O. P. Jensen, D. Ricard, S. R. Palumbi, *Proc. Natl. Acad. Sci. U.S.A.* **108**, 8317 (2011).
17. J. T. Thorson, T. A. Branch, O. P. Jensen, T. Quinn, *Can. J. Fish. Aquat. Sci.* **69**, 645 (2012).
18. T. R. McClanahan, J. O. Omukoto, *Conserv. Biol.* **25**, 945 (2011).
19. L. Garibaldi, *Mar. Policy* **36**, 760 (2012).
20. S. C. Anderson, J. M. Flemming, R. Watson, H. K. Lotze, *PLoS ONE* **6**, e14735 (2011).
21. D. Tilman, C. Balzer, J. Hill, B. L. Befort, *Proc. Natl. Acad. Sci. U.S.A.* **108**, 20260 (2011).
22. C. Costello, S. D. Gaines, J. Lynham, *Science* **321**, 1678 (2008).
23. J. Cancino, H. Uchida, J. E. Wilen, *Mar. Resour. Econ.* **22**, 391 (2007).
24. D. Ovando *et al.*, *Mar. Policy* (2012).
25. C. Costello, D. Kaffine, *Aust. J. Agric. Resour. Econ.* **54**, 321 (2010).
26. N. L. Gutiérrez, R. Hilborn, O. Defeo, *Nature* **470**, 386 (2011).
27. J. R. Wilson, J. D. Prince, H. S. Lenihan, *Mar. Coast. Fish.* **2**, 14 (2010).

Acknowledgments: We thank seminar participants at the University of British Columbia, S. R. Walton, A. Leland, T. Branch, Y. Ye, and T. Essington for helpful suggestions. We gratefully acknowledge the Waitt, Moore, Walton, Oak, and Packard Foundations, California Environmental Associates, and NSF grant 1041570 (to R.H.) for financial support. Detailed results, as well as the locations of source data used in this analysis, can be found in the supplementary materials and methods and text.

Supplementary Materials

www.sciencemag.org/cgi/content/full/science.1223389/DC1
Materials and Methods
Supplementary Text
Figs. S1 to S13
Tables S1 to S12
References (28–32)

16 April 2012; accepted 4 September 2012
Published online 27 September 2012;
10.1126/science.1223389

The APC/C Inhibitor XErp1/Emi2 Is Essential for *Xenopus* Early Embryonic Divisions

Thomas Tischer,* Eva Hörmanseder,* Thomas U. Mayer†

Mitotic divisions result from the oscillating activity of cyclin-dependent kinase 1 (Cdk1). Cdk1 activity is terminated by the anaphase-promoting complex/cyclosome (APC/C), a ubiquitin ligase that targets cyclin B for destruction. In somatic divisions, the early mitotic inhibitor 1 (Emi1) and the spindle assembly checkpoint (SAC) regulate cell cycle progression by inhibiting the APC/C. Early embryonic divisions lack these APC/C-inhibitory components, which raises the question of how those cycles are controlled. We found that the APC/C-inhibitory activity of XErp1 (also known as Emi2) was essential for early divisions in *Xenopus* embryos. Loss of XErp1 resulted in untimely destruction of APC/C substrates and embryonic lethality. XErp1's APC/C-inhibitory function was negatively regulated by Cdk1 and positively by protein phosphatase 2A (PP2A). Thus, Cdk1 and PP2A operate at the core of early mitotic cell cycles by antagonistically controlling XErp1 activity, which results in oscillating APC/C activity.

After fertilization and a prolonged first cell cycle, *Xenopus* embryos progress through 11 rapid divisions devoid of gap phases. Cycle 13 marks mid-blastula transition (MBT), when cycles become longer and gap phases are resumed (1–3). Although it is clear that cyclin-

dependent kinase 1 (Cdk1) is the universal cell cycle regulator, it remains unknown how pre-MBT divisions lacking inhibitory phosphorylations of Cdk1 (2, 4) as well as the anaphase-promoting complex/cyclosome (APC/C)-inhibitory activities of Emi1 and SAC (3, 5, 6) are controlled. Before fertilization, XErp1 mediates the metaphase II arrest of mature *Xenopus* eggs by directly inhibiting the APC/C (7). Surprisingly, XErp1 is completely degraded at fertilization but reaccumulates in early embryos (8–12), yet egg extract studies suggest that XErp1 has no function in mitosis (9).

To understand the regulation of early mitotic divisions, we first examined XErp1 levels in *Xenopus* embryos by immunoblot analyses. After its destruction at fertilization, XErp1 reaccumulated to levels comparable to those in unfertilized eggs and started to disappear again at MBT, which is marked by the destruction of cyclin E1 and replacement of cyclin A1 by cyclin A2 (Fig. 1A). To test whether XErp1 expression is critical for early mitotic cycles, we injected antisense morpholino-oligos (MO) targeting *XErp1* mRNA (XErp1-MO) or control sense MO into one-cell embryos (13). At 24 hours post-fertilization (hpf), 92% of the control MO-injected embryos displayed small blastopores (Fig. 1, B and C), revealing that these embryos completed the first major morphogenetic transformation (i.e., blastopore closure). In contrast, 90% of XErp1-depleted embryos failed to undergo blastopore closure but underwent apoptosis at gastrulation (Fig. 1, B to D; fig. S1, A and B; and movie S1). To confirm that loss of XErp1 accounted for the observed phenotype, we co-injected embryos with XErp1-MO and wild-type (WT) *XErp1* mRNA (myc-XErp1^{WT}) that was not targeted by the MO (Fig. 1D). Expression of myc-tagged full-length XErp1^{WT} efficiently rescued blastopore closure in XErp1-depleted embryos (Fig. 1, B and C). Thus, XErp1 is essential for *Xenopus* early embryonic cycles.

Next, we analyzed whether these divisions depend on XErp1's APC/C-inhibitory activity. Indeed, the majority of XErp1-depleted embryos expressing XErp1 mutated in its zinc-binding region (ZBR⁻) or destruction box (Abox⁻)—both of

Department of Biology and Konstanz Research School Chemical Biology, University of Konstanz, Universitätsstr. 10, 78457 Konstanz, Germany.

*These authors contributed equally to this work.

†To whom correspondence should be addressed. E-mail: thomas.u.mayer@uni-konstanz.de