



EARTHJUSTICE

ALASKA CALIFORNIA FLORIDA MID-PACIFIC NORTHEAST NORTHERN ROCKIES
NORTHWEST ROCKY MOUNTAIN WASHINGTON, DC INTERNATIONAL

C.M. "Rip" Cunningham, Jr., Chairman
 Paul Howard, Executive Director
 New England Fishery Management Council
 50 Water Street, Mill 2
 Newburyport, MA 01950

October 8, 2012

RE: Atlantic Herring Fishery Specifications for FY 2013-2015

Dear Chairman Cunningham and Director Howard:

We are writing on behalf of our clients Michael Flaherty, Captain Alan Hastbacka, and the Ocean River Institute,¹ the plaintiffs in *Flaherty v. Bryson*, regarding the Atlantic herring fishery specifications for the 2013-2015 fishing years. The work completed to date on this specifications package does not satisfy the Courts' Memorandum Opinion and Order.² The Order requires that a range of alternatives to the existing interim ABC control rule be considered in the specifications package, or another appropriate action to be completed within one year, including at least one alternative "based on the most recent best available science for setting ABC control rules for herring and other forage fish." The Order also requires consideration of a "range of alternatives to the current AMs for the fishery."³ Neither of these requirements has been met.

In order to comply with the Court's remedial order and August 2, 2012 deadline, we request that the Council consider the following:

1. A reasonable range of alternative ABC control rules for Atlantic herring as part of the River Herring⁴ catch cap framework, which also must be completed by August 2, 2012 under the Order.⁵ Two alternatives based on the most recent scientific studies on forage fish (Pikitch et al 2012; Smith et al 2011; Cury et al 2011; Tyrrell et al 2011) are outlined below for the Council's consideration. These alternatives were developed in consultation with scientists familiar with this work. The referenced papers are attached for your convenience. Please add this letter and the studies to the records for both the 2013-15 specification action and the River Herring catch cap framework action.
2. Additional AM alternatives as part of the 2013-15 specifications action and/or as part of the River Herring catch cap framework as appropriate.

¹ See *Flaherty v. Bryson*, 850 F. Supp.2d 38 (D.D.C. 2012).

² The Memorandum Opinion and Order are found behind Tab #1 to the NEFMC Council Meeting Materials for the Herring Committee Report for Wednesday, September 26, 2012, available at <http://www.nefmc.org/herring/index.html>; see also Letter from John Bullard to Rip Cunningham at 3 ("Consistent with the Court's remedial order, I recommend the NEFMC consider, as part of the 2013-2015 Atlantic herring specifications, a range of alternatives for the Atlantic herring ABC control rule and AMs.") also behind Tab #1.

³ *Id.* at pp. 12-13.

⁴ The term River Herring includes blueback herring, alewives, hickory shad, and American shad.

⁵ See Order at 13.

An ABC Control Rule Informed By The Best Available Science On Forage Fish

Our clients and others have requested on many occasions that the Council consider an ABC control rule for Atlantic herring based on the best available science for forage fish.⁶ By definition, a control rule should specify an *approach* that sets appropriate harvest levels under a wide range of stock conditions and protects the stock from overfishing by becoming increasingly conservative as stock biomass departs from a specified target biomass.⁷ During the development of Amendment 4 and the last (2010-2012) specifications process, the Council declined to develop an actual control rule consistent with the revised Magnuson-Stevens Act and National Standard 1 Guidelines due to the absence of a benchmark assessment. The public was assured, however, that the “interim” control rule (average of most recent 3 years catch) would be replaced by an appropriate control rule in the next specifications package.⁸

The new benchmark assessment was completed in July 2012. As discussed at the recent Council meeting, this assessment is a significant improvement over prior assessments because it used the best available scientific information on predation to specify natural mortality (m) in the assessment model); however, more is required when determining the acceptable biological catch for forage fish like Atlantic herring. Recent scientific studies, using different models to look at forage fish within many different ecosystems, conclude that both a realistic treatment of natural mortality in the stock assessment and determination of MSY, *and* a forage-appropriate control rule are needed. *See* Pikitch et al 2012; Smith et al 2011; Cury et al 2011; Tyrrell et al 2011. This is necessary to account for the special risks associated with fisheries for forage fish, including the risk of dependent predator-populations collapsing and the particular vulnerability of forage species to over-exploitation. Herring are particularly vulnerable to over-exploitation because of their schooling behavior and because they undergo substantial population shifts even without fishing, making the risk of overfishing during down cycles even higher. Forage stocks must be given special consideration, above and beyond proper treatment of natural mortality in assessments, in order to avoid collapsing the forage stock and / or dependent predator populations, and causing destructive impacts on ecosystems. *See* Pikitch et al 2012; Smith et al 2011.

The Science and Statistical Committee (SSC) met on September 12, 2012 in order to develop its ABC recommendations for catch in the 2013-2015 fishing years and to discuss ABC control rules for the fishery. The SSC concluded that the two approaches for setting ABC developed by the Herring Plan Development Team (PDT) were nearly equivalent from a biological perspective

⁶ *See inter alia* January 13, 2009 Letter from Marine Fish Conservation Network to NEFMC; March 19, 2009 Letter from Herring Alliance to NEFMC; June 19, 2009 Letter from Herring Alliance to NEFMC; January 13, 2010 Letter from Herring Alliance to NEFMC; January 13, 2010 Letter from National Coalition for Marine Conservation to NEFMC. These comment letters and others pointed the Council toward a large body of science indicating that herring’s role as forage must be taken into account in stock assessments, as well as in ABC control rules in order to protect their forage base.

⁷ 50 C.F.R. §§ 600.310(e)(3)(iv)(C), (f)(1).

⁸ *See* AR 6069 Final Amendment 4 to the Herring FMP at p. 22 (“The interim control rule serves as a placeholder until a more appropriate control rule is developed. In addition to the ABC advice, the SSC also recommended that a new benchmark assessment should be scheduled as soon as possible, preferably in advance of the next management cycle. This would allow the SSC to create an ABC control rule for the next specifications process. In the future the SSC will develop the ABC control rule when further information becomes available.”).

(similar spawning stock biomass in 2015), thus the SSC gave the Council the choice of the two approaches for setting catch. However, many SSC members at that meeting recognized that both of these alternatives fell short of a proper control rule. *See* SSC discussion, September 12, 2012.

When the Council in turn considered only these two approaches for the 2013-15 specifications package, the Council failed to consider an ABC control rule alternative based on the best available science for setting ABC for forage fish and failed to meet the National Standard One guidelines for setting ABC for forage fish. The first approach, the 75% F_{msy} approach, is simplistic and undifferentiated from the default control rule used for many of the non-forage stocks (such as New England groundfish): ABC is based upon a fishing mortality rate (F) of 75% F_{msy} . The second approach, the “constant catch-based approach,” is similar to the interim approach used for setting ABC during the 2010-2012 specifications (average catch 2006-2008). This approach (based on the maximum catch that will still have less than a 50% chance of overfishing in any of the three years) allows for more herring to be caught (342 mt as compared to 320 mt), is not based upon the above default control rule (75% F_{msy}), and was not part of the peer-reviewed material developed for the benchmark assessment. This approach fishes at twice MSY justified in part by a single year class (the strength of which can often be overestimated in the short-term⁹), and has no buffer for scientific uncertainty in its third year.

The SSC requested guidance from the Council regarding how it would like to see this Atlantic herring stock managed in the future, as would be appropriate to develop a permanent ABC control rule, yet none was provided.¹⁰ As the SSC noted, neither approach in the specifications package may be acceptable beyond the next three years and neither is a control rule that considers a wide range of possible stock conditions with a known objective – instead both rely on a single year class that will ultimately move out of the population.¹¹ Although the recommendations might meet ecosystem needs “by default if not by design,” these approaches are not an ABC control rule based on the best available science for forage fish that would have “reduced fishing rate and [maintained] higher stock size to account for its role in the ecosystem.”¹²

Based on the best available science, an appropriate control rule for Atlantic herring should:

- Offset ABC from the estimated OFL according to scientific uncertainty in the estimate.
- Establish a target Biomass at or greater than 75% B_0 (virgin biomass)(*see* papers Pikitch et al 2012; Smith et al 2011; National Standard 1 guidelines)

⁹ *See* DRAFT Atlantic Herring Specifications 2013-2015 at § 5.2.2 at p. 19 (2008 Atlantic Herring Year Class).

¹⁰ The SSC requested guidance in their written report and Dr. Legault reiterated this request in the oral presentation at the September 26, 2012 NEFMC Meeting. *See* September 21, 2012 Memorandum from SSC to Paul Howard entitled *Herring ABC for FY2013-2015* (“However, the SSC requests guidance from the Council as to how it would like to see this stock managed, i.e., as a typical fishery with MSY-based reference points, or a reduced fishing rate and higher stock size to account for its role in the ecosystem. This would ensure that the next time herring are assessed, a control rule could be created which meets the needs of the Council. A control rule which could be set for more than three years would need to consider a wide range of possible stock conditions and have a known objective.”); *see also* September 26, 2012 Council Meeting Audio Recording #12 *Scientific and Statistical Committee Report*

¹¹ *Id.*

¹² *Id.*

- Establish a limit cut-off biomass at or above 40% B_0 ; cut-off biomass is used now for Antarctic krill, Alaska herring, U.S. West Coast sardine, and mackerel.
- Set a maximum fishing rate (F) corresponding to 50% F_{msy} or 50% of natural mortality (m), whichever is smaller; F should be low compared to m.
- Establish a declining mortality rate as Biomass declines below the target level, so that fishing ends when the limit Biomass is reached (i.e., $F=0$).

Requested ABC Control Rule Alternatives

Alternative 1 (Lenfest Forage Fish Task Force): Harvest control rule (i.e., *hockey stick* harvest control rule) based on conventional single species assessment (i.e. most recent for Atlantic herring) and MSY reference points (see references at note #1):

If $B \geq (0.75)*B_0$ {Target is $\frac{3}{4} B_0$ }
 ABC = B associated with $0.5F_{MSY}$

If $(0.4)*B_0 < B < (0.75)*B_0$ {B is below target, ABC should decrease as B decreases, to B_{LIM} , by decreasing F with decreasing B}

ABC increases with B, when $B > B_{LIM}$

If $B \leq (0.4)*B_0$ {B too low}
 ABC = 0 (No Fishing)

Where:

B = current Spawning Stock Biomass

B_0 = Biomass expected to exist without any fishing, *virgin biomass*

$B_{LIM} = (0.4)*B_0$ {when $B \leq B_{LIM}$ the stock is overfished}

$B_{Target} = 0.75*B_0$

Hockey stick rule

The same minimum biomass limits as the step function rules apply, but fishing mortality is decreased gradually instead of all at once as fish biomass decreases.

- 20% minimum biomass limit to 100%
- 40% minimum biomass limit to 100%

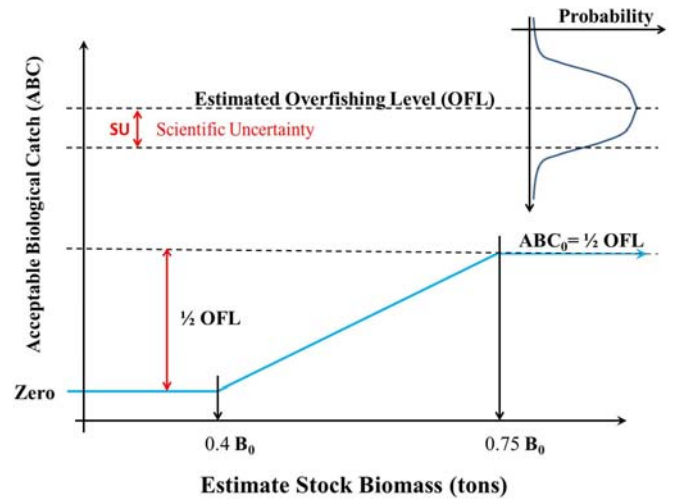
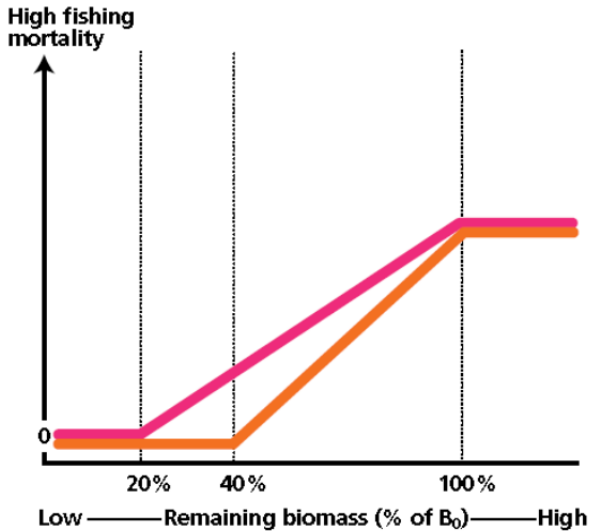


Figure 6.1 from Pikitch et al 2012 (left)

illustrating the type of control rule that they recommend for forage stocks – presented here in terms of fishing mortality as a function of stock biomass. The orange curve corresponds to the recommendation that would apply to Atlantic herring as a stock in the intermediate information tier. A depiction of the same sort of control rule in terms of Acceptable Biological Catch (ABC; right).

Alternative 2: A harvest control strategy for forage fish modeled after the Pacific Fishery Management Council’s approach for Coastal Pelagic Species, as described in previous correspondence with the New England Council.¹³

$$ABC = \{B - (CUTOFF + BUFFER)\} \times \text{Fraction}$$

B: the biomass determined by the most recent stock assessment

BUFFER: Buffer for scientific uncertainty, reflecting the uncertainty in the estimate of OFL and any other scientific uncertainty.

¹³ See AR 4565 Letter from Herring Alliance to Council Executive Director Paul Howard, January 13, 2010 (referencing similar letter sent on June 19, 2009); AR 4517 Letter from Marine Fish Conservation Network, January 12, 2009; see also Pacific Fishery Management Council (2009). Status of the Pacific coast coastal pelagic species fishery and recommended acceptable biological catches. Stock assessment and fishery evaluation, section 4.3.1 *General MSY Control Rule for Actively Managed Species* (p 19).

CUTOFF: the minimum stock size threshold, estimated from consumption data, or set at $0.4B_0$
Fraction: a conservative fishing mortality strategy designed to maintain biomass at a level above B_{msy} that provides adequate forage for the ecosystem (e.g., $0.5F_{MSY}$ or $F = 0.5 * M$).

The New England Council is yet to consider an Atlantic herring ABC control based on the best available science for establishing an ABC control rules for forage fish, as required by the *Flaherty v. Bryson* Remedial Order. We therefore request that you provide terms of reference to the SSC to consider a range of alternatives for setting an ABC control rule for this fishery, including alternatives based on those provided here, as part of the River Herring catch cap framework to be completed by the Council by August 2, 2013.

Range of Alternative for Accountability Measures

NOAA General Counsel advised the Council at its September 26, 2010 meeting that it needed to consider a “reasonable range of alternatives” to the current AMs in order to comply with the Court’s Order in *Flaherty v. Bryson*.¹⁴ Although Amendment 4 initially identified three different measures in the Atlantic herring FMP as AMs for the fishery, the court found that only two of these (management closures and overage deductions) could be considered AMs for the Atlantic herring fishery. *See* Opinion at 58 (haddock incidental catch cap is not an AM for herring because it does not limit the ACL of herring). Moreover, the Court held that Amendment 4 and its environmental assessment “demonstrate[] a total failure to consider the environmental impacts of alternatives to the proposed ABC control rule or AMs.”

Therefore, the Council must at a minimum analyze a reasonable range of alternatives to the two existing AMs for the fishery listed below:

1. Management Area Closures - 50 C.F.R. § 648.201(a)(1) (prohibits vessels from catching more than 2000 lbs of Atlantic herring per day once NMFS has determined that catch will reach 95% of the annual catch allocated in a given management area).
2. Overage Deduction - 50 C.F.R. § 648.201(a)(3) (mitigates ACL overages by deducting the amount of any overage from the relevant ACL or sub-ACL for the fishing year following NMFS’s determination of the overage).

Overages occur in this fishery frequently and are significant. For example, from 2003-2011, numerous overages occurred in Areas 1A or 1B in 6 out of 9 years, and likely occurred in Area 1A for the third year in a row in 2011.¹⁵ In 2010 (the last year for which catch totals are final), the quota caught in Area 1A was 107% and the quota caught in Area 1B was a whopping 138%, despite “closure” at 95%. These facts demonstrate that the current AMs are ineffective at

¹⁴ *See* Council Audio Wednesday September 26, 2012, #15 Herring Committee Report. *See also* Opinion at 70 (In the absence of consideration of a range of alternatives to the accountability measures chosen in Amendment 4, NMFS had failed to take a “hard look” at the environmental impacts of Amendment 4).

¹⁵ *See* Tab #2 Draft Discussion Document Atlantic Herring Fishery Specifications for the 2013-2015 Fishing Years, Tables 2, 3, and 4 and discussion on pp. 5-7.

constraining ACLs, sub-ACLs in particular, because they allow ACLs to be exceeded and for rolling overages to occur -- both counter to the requirements of the Magnuson-Stevens Act.

The Council identified two AM alternatives for consideration in the 2013-2015 specifications package:¹⁶

1. A “proactive” AM that would close the directed fishery in a given management area when the catch is projected to reach 92% of the area annual catch limits under the following two conditions:

- a) the stock is overfished or overfishing is occurring and;
- b) the sub-ACL for a management area has been exceeded in either of the preceding two years.

2. A “reactive” AM providing that if overfishing is not occurring and the stock is rebuilt (spawning stock biomass exceeds the target), the accountability measure (a pound for pound payback) will not be triggered until the sub-ACL is exceeded by 5% or more.

These alternatives do not constitute a “reasonable range of alternatives” consistent with the National Environmental Policy Act.¹⁷

At best, the first alternative might require an earlier closure to the fishery under very limited circumstances (the fishery must be both overfished (or overfishing is occurring) *and* the area in question has suffered its second overage in three years). The second alternative is less restrictive than the current reactive AM for the fishery because it would eliminate the requirement for overage paybacks in many circumstances and makes unclear what the effective limit for the fishery is – in fact, it appears to provide an incentive to fish harder as the area catch limit is approached in order to catch up to 5% more than the ACL without having to mitigate the overage. Moreover, neither alternative addresses the overall ACL for the fishery. This set of AM alternatives is inconsistent with NEPA, the Court’s Order to consider a “range” of AM alternatives, and the Magnuson-Stevens Act requirements to prevent ACLs from being exceeded and mitigate overages if they occur.¹⁸ The Magnuson-Stevens Act requires ACLs to set *specific limits* on the total fish caught in each fishery to prevent overfishing. 16 U.S.C. §§ 1851(a)(1), (15); 50 C.F.R. § 600.310(f)(1).

¹⁶ See September 28, 2012 NEFMC News Brief at 2, available at: <http://www.nefmc.org/> (Council Meeting Brief); see also Council Audio # 15 Herring Committee Report.

¹⁷ See 40 C.F.R. § 1502.14. “The phrase ‘range of alternatives’ ...includes all reasonable alternatives, which must be rigorously explored and objectively evaluated, as well as those other alternatives, which are eliminated from detailed study with a brief discussion of the reasons for eliminating them. For some proposals there may exist a very large or even an infinite number of possible reasonable alternatives. For example, a proposal to designate wilderness areas within a National Forest could be said to involve an infinite number of alternatives from 0 to 100 percent of the forest. When there are potentially a very large number of alternatives, only a reasonable number of examples, covering the full spectrum of alternatives, must be analyzed and compared in the EIS. An appropriate series of alternatives might include dedicating 0, 10, 30, 50, 70, 90, or 100 percent of the Forest to wilderness. What constitutes a reasonable range of alternatives depends on the nature of the proposal and the facts in each case.” NEPA See NEPA’s Forty Most Asked Questions, Nos. 1a. -1b. Council on Environmental Quality, 46 Fed. Reg. 18026 (1981). *Ed. Note.* (March 16, 1981), available at <http://ceq.hss.doe.gov/nepa/regs/40/40P1.HTM>.

¹⁸ 16 U.S.C. § 1853(a)(15); 50 C.F.R. § 600.310(g)(1).

Given the history of recent overages in this fishery, ranging as high as 138% of the sub-ACL, a closure at even 92% of the limit is unlikely to prevent the ACL's from being exceeded. A reasonable range of alternatives to the management area closure should include options that close the fishery when the catch is projected to reach 85% and 90% of the sub-ACL. A reasonable range of alternatives to the overage deduction should include an option that would deduct overages in the next fishing year. Although NMFS has taken the position in the past that it cannot monitor catch accurately enough to implement the pound for pound overage deduction in anything less than a one-year lag, under current regulations NMFS appears to be able to monitor Canadian catch in near real time in order to return 3,000 mt to the U.S. catch within the same fishing year. It has also been argued that the industry needs certainty in order to business plan, thus estimating potential overages and adjusting the amounts if necessary once the data is final is not feasible. This argument does not stand up given the fact specifications are regularly not finalized prior to the start of the fishing year, yet industry has been unaffected. Given the further improvements to the fisheries monitoring and reporting measures included in Amendment 5, next year overage paybacks is a reasonable alternative that would increase accountability in the fishery.

In sum, the identified AM alternatives in the specifications package do not represent a reasonable range of alternatives under NEPA and do not meet the requirements of the Magnuson-Stevens Act. “[A]ctions that violate the MSA cannot be reasonable alternatives to consider.” Opinion at 71 (*citing American Oceans Campaign v. Daley*, 183 F. Supp. 2d 1, 20). In order to comply with the Court’s Order, the Council should immediately develop new accountability measure alternatives and analyze them expeditiously for implementation with this specifications package. Alternative AMs that cannot be completed as part of the specifications should be considered in the bycatch cap framework, consistent with the Court’s Remedial Order.

At its September 26, 2012 meeting, the Council selected an ABC for 2013-15 based on a constant catch approach without considering an ABC control rule “based on the most recent best available science for setting ABC control rules for herring and other forage fish.” It also failed to consider a reasonable range of alternatives for AMs in the fishery consistent with NEPA and that achieve the requirements of the Magnuson-Stevens Act. Thank you for considering these recommendations for complying with the *Flaherty v. Bryson* Court Order. The recommended measures could significantly improve management of the Atlantic herring resource and help ensure accountability in the fishery.

Sincerely yours,

/s/ Roger Fleming
Roger Fleming, Attorney
Erica Fuller, Attorney
Earthjustice

on behalf of its clients
Michael Flaherty

Captain Alan Hastbacka
Ocean River Institute

Cc: John Bullard, Regional Administrator
Gene Martin, NOAA General Counsel
Mitch McDonald, NOAA General Counsel
Carrie Nordeen, NERO Sustainable Fisheries Division
Dr. Chris Legault, Chairman of SSC
Rick Robbins, Chairman, MAFMC
Lori Steele, Fishery Analyst Herring FMP

-3, into which the fluorescent proteins enhanced green fluorescent protein (EGFP) or mCherry were introduced to distinguish between the two cell lines. These cells were sparsely cultured to allow the formation of independent colonies. When their colony edges came into contact with one another, their boundaries were examined. Cells expressing identical nectin types did not intermingle at the border, whereas those expressing nectin-1 and -3 mutually invaded the counter colony, resulting in the formation of a mosaic pattern (Fig. 4, A to E, and fig. S6). We also performed time-lapse video microscopy using a coculture of MDCK cells expressing nectin-1 or -3 (N1- and N3-MDCK cells). In the supporting movie (movie S1 and Fig. 4E), one N1-MDCK cell (arrowhead) initially adhered to one of a pair of N3-MDCK cells (asterisks); subsequently, the former cell invaded the space between the two N3-MDCK cells. As a result, N1- and N3-MDCK cells were rearranged into a mosaic pattern. Similar behavior of cells was repeatedly observed in multiple experiments.

Thus, we propose that the heterophilic interactions between nectin-1 and -3 are critical for establishing the checkerboard-like pattern of hair cells and supporting cells. The molecular interaction between nectin-1 and -3 is the strongest of all possible combinations of the three nectins, which is likely to be responsible for the checkerboard-like assembly of these cells (Fig. 4F), as predicted by the mathematical model (8). The loss of nectin-3 removed such biased cell-cell adhesion, leading to cell rearrangement, including attachments between hair cells (Fig. 2D), as explained by the differential adhesiveness hypothesis (18). Nectin-1 KO mice displayed milder phenotypes. In these mice, the relatively strong interaction between nectin-3 and -2 probably retained the adhesion between hair cells and supporting cells; on the other hand, the adhesion between supporting cells should have been enhanced as a result of the redistribution of nectin-3 to these sites. These combinatorial situations probably suppressed adhesion between hair cells (Fig. 4F). In nectin-2 KO mice, the heterophilic interactions between nectin-1 and -3 persisted; this explains the absence of a phenotype in these mice. In the absence of nectins, the cell junctions were not disrupted. This is most likely due to the coexpression of classic cadherins in the auditory epithelia. Hair cells and supporting cells are thought to be segregated through the process of lateral inhibition mediated by Notch-Delta signaling (4, 19), and such processes themselves might contribute to the spatial separation of these cells (20–22). However, genetic inactivation of Notch signaling does not impair the checkerboard-like pattern, although it does result in an increase in the number of hair cells (4). This suggests that lateral inhibition is insufficient to create the checkerboard-like cellular pattern, stressing the importance of nectins in this patterning process. It is of note that heterophilic interactions be-

tween Hibris and Roughest, other members of the immunoglobulin superfamily, also contribute to the cell arrangement in the *Drosophila* eye (23, 24), suggesting that similar mechanisms are conserved for cellular patterning across species.

References and Notes

- H. I. Yamanaka, H. Honda, *Int. J. Dev. Biol.* **34**, 377 (1990).
- R. L. Gulley, T. S. Reese, *J. Neurocytol.* **5**, 479 (1976).
- E. McKenzie, A. Krupin, M. W. Kelley, *Dev. Dyn.* **229**, 802 (2004).
- P. J. Lanford *et al.*, *Nat. Genet.* **21**, 289 (1999).
- P. Chen, J. E. Johnson, H. Y. Zoghbi, N. Segal, *Development* **129**, 2495 (2002).
- M. Montcouquiol *et al.*, *Nature* **423**, 173 (2003).
- M. Montcouquiol, M. W. Kelley, *J. Neurosci.* **23**, 9469 (2003).
- H. Honda, H. Yamanaka, G. Eguchi, *J. Embryol. Exp. Morphol.* **98**, 1 (1986).
- M. Takeichi, *Science* **251**, 1451 (1991).
- B. M. Gumbiner, *Nat. Rev. Mol. Cell Biol.* **6**, 622 (2005).
- Y. Takai, H. Nakanishi, *J. Cell Sci.* **116**, 17 (2003).
- Y. Takai, W. Ikeda, H. Ogita, Y. Rikitake, *Annu. Rev. Cell Dev. Biol.* **24**, 309 (2008).
- Y. Takai, J. Miyoshi, W. Ikeda, H. Ogita, *Nat. Rev. Mol. Cell Biol.* **9**, 603 (2008).
- K. Satoh-Horikawa *et al.*, *J. Biol. Chem.* **275**, 10291 (2000).
- H. Togashi *et al.*, *J. Cell Biol.* **174**, 141 (2006).
- N. Okabe, K. Ozaki-Kuroda, H. Nakanishi, K. Shimizu, Y. Takai, *Dev. Dyn.* **230**, 174 (2004).
- F. D. Nunes *et al.*, *J. Cell Sci.* **119**, 4819 (2006).
- M. S. Steinberg, *Science* **141**, 401 (1963).
- M. W. Kelley, D. R. Talreja, J. T. Corwin, *J. Neurosci.* **15**, 3013 (1995).
- J. Kimble, P. Simpson, *Annu. Rev. Cell Dev. Biol.* **13**, 333 (1997).
- R. Kopan, R. Cagan, *Trends Genet.* **13**, 465 (1997).
- J. Lewis, *Curr. Opin. Neurobiol.* **6**, 3 (1996).
- S. Bao, R. Cagan, *Dev. Cell* **8**, 925 (2005).
- S. Bao, K. F. Fischbach, V. Corbin, R. L. Cagan, *Dev. Biol.* **344**, 948 (2010).

Acknowledgments: This work was supported by the Global Centers of Excellence Program “Global Center for Education and Research in Integrative Membrane Biology” and the Targeted Proteins Research Program from the Ministry of Education, Culture, Sports, Science and Technology in Japan; by Grants-in-Aid from the Japan Society for the Promotion of Science; and by the Core Research for Evolutional Science and Technology from the Japanese Science and Technology Agency.

Supporting Online Material

www.sciencemag.org/cgi/content/full/science.1208467/DC1
Materials and Methods
Figs. S1 to S6
References (25–27)
Movie S1

16 May 2011; accepted 8 July 2011
Published online 28 July 2011;
10.1126/science.1208467

Impacts of Fishing Low-Trophic Level Species on Marine Ecosystems

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Low-trophic level species account for more than 30% of global fisheries production and contribute substantially to global food security. We used a range of ecosystem models to explore the effects of fishing low-trophic level species on marine ecosystems, including marine mammals and seabirds, and on other commercially important species. In five well-studied ecosystems, we found that fishing these species at conventional maximum sustainable yield (MSY) levels can have large impacts on other parts of the ecosystem, particularly when they constitute a high proportion of the biomass in the ecosystem or are highly connected in the food web. Halving exploitation rates would result in much lower impacts on marine ecosystems while still achieving 80% of MSY.

Concerns about the trophic impact of harvesting marine species were recognized more than three decades ago (1). Despite recent successes in reducing exploitation rates in some marine ecosystems (2), concerns remain over the effects of fishing on the structure and function of marine ecosystems (3, 4).

Low-trophic level (LTL) species in marine ecosystems comprise species that are generally plankton feeders for the larger part of their life

cycle. They are often present in high abundance and tend to form dense schools or aggregations. They include small pelagic “forage” fish such as anchovy, sardine, herring, mackerel, and capelin but also invertebrate species such as krill. Humans harvest across the trophic levels in marine food webs, and landings of LTL species have been increasing generally in proportion with global catches (5). Forage fish account for over 30% of global fish landings, most of which is

now used for fishmeal production as feed for livestock industries and aquaculture rather than being consumed directly (6). However, LTL species also contribute directly to food security in many developing countries, and between 10 and 20% of global landings are consumed directly by humans (7). One species alone, Peruvian anchovy, contributes up to 50% of global landings used for fishmeal production. Driven by global markets for fertilizer, animal feed, and increases in the production of seafood from aquaculture, demand for fishmeal continues to increase (8).

LTL species play an important role in marine food webs because they are the principal means of transferring production from plankton to larger predatory fish and to marine mammals and sea-

birds. Several studies have raised concerns about the impacts on seabirds of local depletion of forage fish [anchovy in Peru (9), sand eels in the North Sea (10), and anchovy and sardines in South Africa (11)]. Similar concerns have been raised about the prospects of a large increase in catch of krill in the Southern Ocean and its potential impact on recovery of depleted marine mammals such as whales (12). Of particular concern are “wasp waist” systems, where a large part of the plankton production is funnelled through a small number of LTL species to higher trophic levels (13, 14).

Although studies in individual ecosystems have raised concerns about the ecological effects of fishing LTL species, there has been no systematic attempt to examine and summarize what these broader effects might be or under what circumstances various effects might be expected to arise. In this study, we used ecosystem models in five well-studied regions to examine systemic effects of fishing LTL species. The regions include three eastern boundary current ecosystems—the northern Humboldt, the southern Benguela, and the California current—and two systems less dominated by upwelling, including the North Sea and the southeast Australian shelf and continental slope (Fig. 1). To avoid conclusions being dominated by structural assumptions in particular types of model, we used three different ecosystem models to explore the responses: Ecopath with EcoSim (EwE) (15, 16), OSMOSE (17, 18), and Atlantis (19, 20). For each ecosystem and model, we selected up to five LTL species or groups and subjected them one by one to a range of fishing pressures, resulting in depletion levels

relative to unfished biomass from zero (no fishing) to 100% (extirpated). The LTL species selected included some that are currently fished (such as anchovy) and others that are not currently exploited in those ecosystems (such as krill and mesopelagic fishes). We did not include harvested shellfish such as scallops and prawns, notwithstanding their commercial importance (21), because most of the models did not resolve these species well. Impacts on other ecological groups in the ecosystem were measured relative to biomass levels of those groups produced by simulations in which the focal LTL species was unfished, and all other groups were fished at current levels. Details of the ecosystems, models, groups, and experiments are provided in (22).

We found widespread impacts of harvesting LTL species across the ecosystems and LTL species selected (Fig. 2). The percent of ecological groups exhibiting effects greater than 40% increased with the level of depletion of the LTL species, but the extent of impact also varied across LTL species. Impacts on other ecological groups were both positive and negative (fig. S1), ranging up to very severe impacts for some groups (>60% change in biomass) even at relatively low levels of depletion (25% below unfished levels)—that is, biomass reduced to 75% of unfished levels) of the LTL species. Negative impacts (reductions in abundance) tended to predominate for marine mammals and seabirds, although the majority of impacts on such groups were small. Some commercial species could also be negatively affected, although again impacts on most commercial species were small. Results

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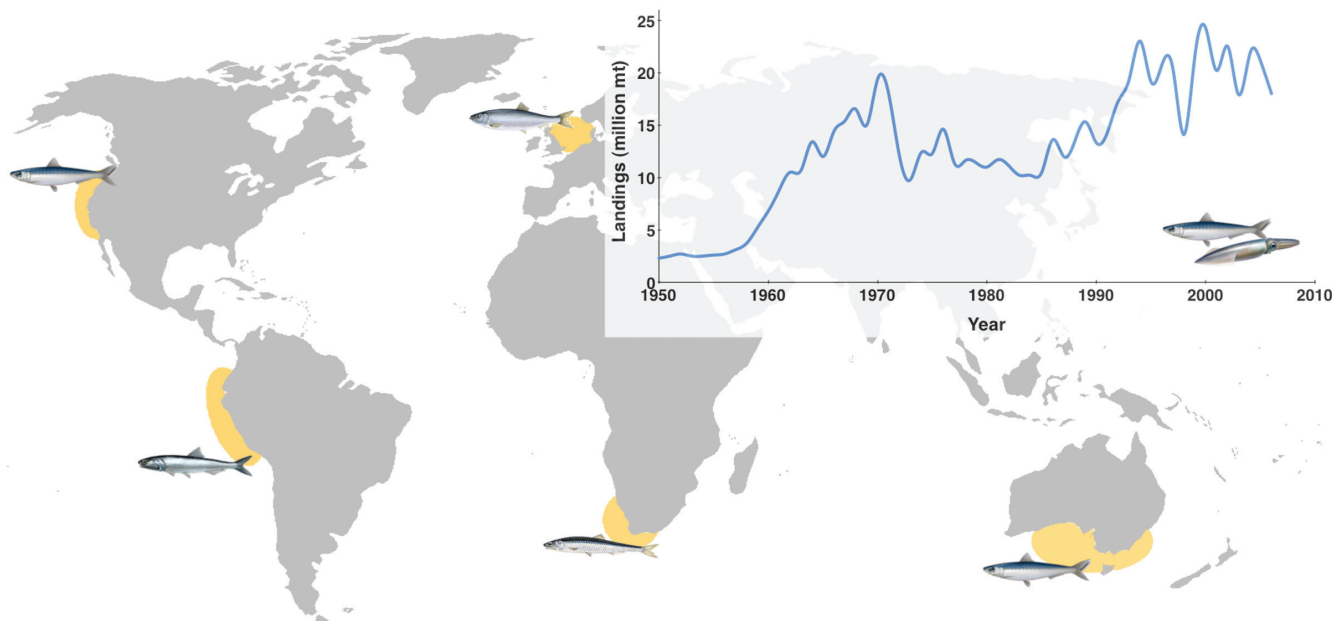


Fig. 1. Global map showing location of study ecosystems. From left to right are the California current, northern Humboldt, North Sea, southern Benguela, and southeast Australia. Graph shows trend in landings of forage species from

1950 to 2009. [Source: Sea Around Us Project, www.seaaroundus.org/global/1/3.aspx. Images of forage fish are copyright Casson Trenor, 2010, at www.sustainablesushi.net]

were generally robust to the three types of model used in the analysis (fig. S2).

The variation in impact of harvesting different LTL species has potentially important management implications; large impacts may require a change in harvest levels, whereas LTL species

with small impacts could be harvested at conventional single-species levels. In each ecosystem, harvesting several of the LTL species was found to have high impacts, although the species with high impacts were not always consistent across ecosystems (Fig. 2). For example, in the

northern Humboldt ecosystem, harvesting anchovy had high impacts, and harvesting sardine had low impacts, but in the southern Benguela ecosystem, harvesting sardines had the larger impact, whereas the impacts of fishing both species were low in the southeast Australian and California current ecosystems. Impacts of harvesting mesopelagic fishes (a group not currently targeted in any of these ecosystems or generally in global fisheries) were consistently high across ecosystems, and impacts of harvesting krill (large zooplankton), also not currently exploited in these ecosystems, also tended to be medium to high. Fishing sand eels had the highest impact in the North Sea.

To explain this range of impacts across LTL species, we looked for more generic properties of these groups (other than taxonomy) that might explain and predict the variation. Three potential predictors were the relative abundance of the group in the ecosystem (for example, Peruvian anchovy accounts for up to 35% of the consumer biomass in the northern Humboldt ecosystem), the trophic level of the group, and the connectivity of the group in the food web. Trophic level was not a good predictor of impact, but the other two factors appear to be important. Abundant groups have consistently large impacts, whereas smaller groups can have either small or large impacts (Fig. 3A). There appears to be a threshold effect for connectance (the proportion of total trophic connections in the food web for each LTL species), with species that have a connectance value greater than ~0.04 having larger impacts (Fig. 3B). However, factors other than total connectance are likely to be important, including the presence of groups with trophic niches similar to those of the exploited species that can dampen the ecosystem effects of depleting the targeted species.

There are important tradeoffs to examine in considering the wider implications of these results for exploitation of LTL species. In particular, impacts on other parts of the ecosystem will be smaller at lower exploitation rates, but yields also will be lower (Fig. 4). There is a tension here between achieving broader goals of protecting and maintaining biodiversity (including ecosystem structure and function) and global food security. LTL species support the latter both through direct human consumption and through providing feed for livestock and aquaculture production. Considerable reductions in impact can be achieved by moving from exploitation at MSY levels (achieved at close to 60% depletion levels) to a target of 75% of unexploited biomass (25% depletion) for an LTL species, as shown in Fig. 4. The cost of such a change would be slightly less than 20% of long-term yield. This target could be achieved at significantly lower exploitation rates (mostly less than half MSY rates) (fig. S3), which would imply much lower fishing effort and may be closer to long-term economic optimum levels. There could also be some benefit of a reduction in harvest rate of LTL species to yields for other

Fig. 2. Effects of level of depletion of LTL species on the proportion of other trophic groups whose biomass varied by more than 40% relative to their level where the LTL species was not fished. Results are shown for a variety of LTL species fished in each modeled ecosystem.

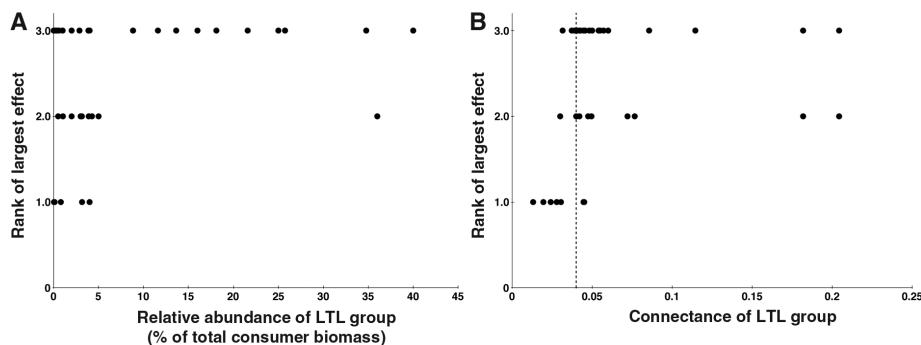
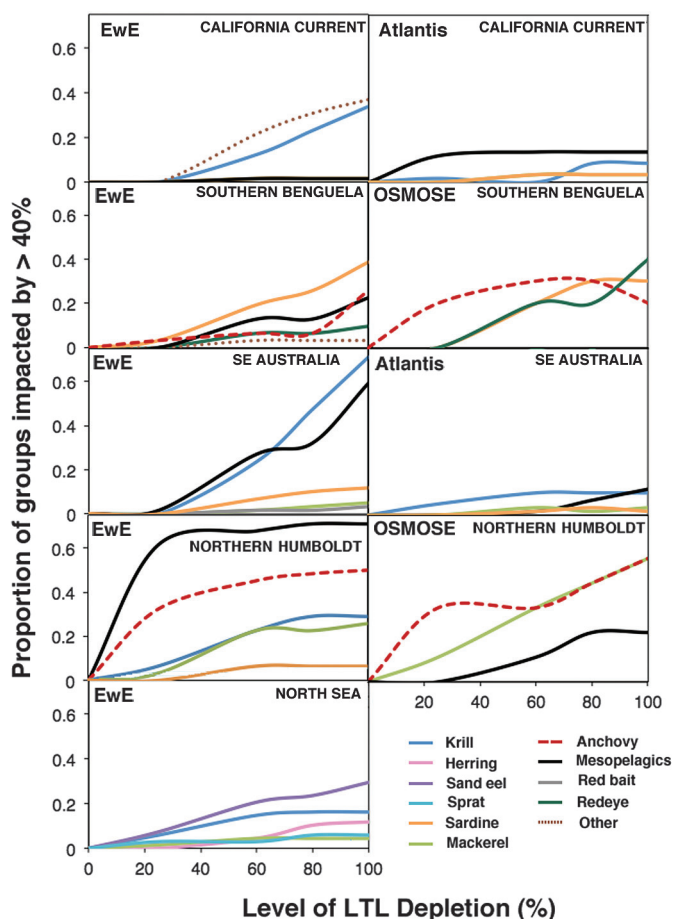
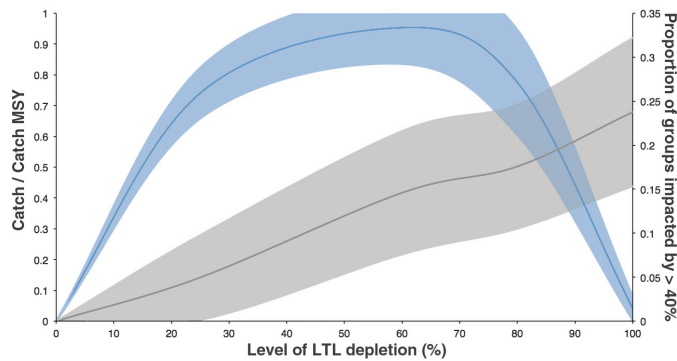


Fig. 3. Relationships between attributes of depleted LTL species and their ecosystem impact. Impacts are scored as the rank of the largest effect: rank 1, no change greater than 20% in any other ecological group; rank 2, no change greater than 60% in any other ecological group; and rank 3, change greater than 60% in at least one other ecological group. Each point corresponds to one ecosystem, model, and LTL species. All LTL species are depleted by 60%. (A) Impact of relative biomass of LTL species (biomass as a percent of total consumer biomass in the ecosystem) on rank of largest effect. (B) Impact of connectance (proportion of all ecosystem trophic links involving the LTL species) on rank of largest effect.

Fig. 4. Tradeoff between yield and ecological impact as level of LTL depletion varies. Yield (blue) is shown as a proportion of MSY. Ecological impact (gray) is measured as the proportion of other ecological groups whose biomass varied by more than 40%. Shaded zones show ± 1.96 times SE. Results are for all ecosystems, models, and LTL species.



commercially targeted species (fig. S1). Although we did not explicitly examine multi-species harvest strategies, exploitation rates well below MSY levels are consistent with previous findings that lower exploitation rates should be adopted for most species (2).

These results are based on model predictions. Each of the models has been validated against time-series data from well-studied systems, and additional empirical validation for impacts on seabirds and marine mammals is provided in (22). Clearly, the details of which groups respond to depletion of LTL species is sensitive to both model parameterization and to choice of model structure (22). For this reason, we do not consider that these models should be used to determine tactical management decisions. However, the overall findings reported here are robust to details of model choice.

The conclusion that lower exploitation rates are needed for forage species also finds support from a wider set of model types (23). Spatial structure in marine ecosystems is an important factor in species interactions, and local prey depletion may be particularly important for land-based predators such as penguins and seals (24). Two of the models used in this study (OSMOSE and Atlantis) incorporate spatial structure, but not always at the resolution needed to address such issues. All of the models incorporate environmental forcing and variability, which is also an important feature driving the dynamics of many LTL species (25, 26). The finding that connectance influences which species are likely to have larger impacts is potentially important, but although the measure of connectance is easily derived in models, it may be more difficult to determine empirically (and the empirical validity of the indicator would need verification). Previous studies have shown that the ways in which species are connected in the food web can influence system properties (27, 28). Previous studies have also emphasized that additional protection may be needed for forage species (29).

The exploitation patterns examined in this study have involved constant fishing mortality rates. Initial explorations of other forms of exploitation, including use of biomass thresholds

or “set asides” (biomass levels below which no exploitation will occur), suggest that lower ecological impacts could be achieved for similar long-term average yields, but at the cost of higher year-to-year variation in catches. Use of such set asides is already a feature of some LTL fisheries, including a 5-million-ton-minimum spawning stock biomass level for Peruvian anchovy (30) and 150,000 tons for California sardine (31). Closed areas are also used in some fisheries so as to reduce impacts on predators, such as closures for sand eels in some parts of the North Sea to improve the breeding success of sea birds (32).

Although harvest strategies for LTL species vary widely, many stocks are currently fished at levels below the biomass that achieves MSY (22). The results of this study combined with set asides and targeted spatial closures should help inform harvest strategies that achieve ecological objectives while ensuring ongoing substantial yields from LTL groups in support of the ongoing challenge of feeding the global human population (33).

References and Notes

- R. M. May, J. R. Beddington, C. W. Clark, S. J. Holt, R. M. Laws, *Science* **205**, 267 (1979).
- B. Worm *et al.*, *Science* **325**, 578 (2009).
- D. G. Ainley, L. K. Blight, *Fish Fish.* **10**, 13 (2009).
- M. Llope *et al.*, *Glob. Change Biol.*, published online 14 October 2010 (10.1111/j.1365-2486.2010.02331.x).
- T. A. Branch *et al.*, *Nature* **468**, 431 (2010).
- J. Alder, B. Campbell, V. Karpouzli, K. Kaschner, D. Pauly, *Annu. Rev. Environ. Resour.* **33**, 153 (2008).
- A. G. J. Tacon, M. Metian, *Ambio* **38**, 294 (2009).
- G. Merino, M. Barange, C. Mullon, *J. Mar. Syst.* **81**, 196 (2010).
- J. Jahncke, D. M. Checkley, G. L. Hunt, *Fish. Oceanogr.* **13**, 208 (2004).
- M. Frederiksen *et al.*, *Mar. Ecol. Prog. Ser.* **300**, 201 (2005).
- R. J. M. Crawford, L. G. Underhill, L. Upfold, B. M. Dyer, *ICES J. Mar. Sci.* **64**, 570 (2007).
- A. J. Constable *et al.*, *ICES J. Mar. Sci.* **57**, 778 (2000).
- P. Cury *et al.*, *ICES J. Mar. Sci.* **57**, 603 (2000).
- L. J. Shannon, P. M. Cury, A. Jarre, *ICES J. Mar. Sci.* **57**, 720 (2000).
- C. Walters, D. Pauly, V. Christensen, J. F. Kitchell, *Ecosystems (N. Y.)* **3**, 70 (2000).
- V. Christensen, C. J. Walters, *Ecol. Modell.* **172**, 109 (2004).
- Y.-J. Shin, P. Cury, *Can. J. Fish. Aquat. Sci.* **61**, 414 (2004).
- M. Travers *et al.*, *Ecol. Modell.* **220**, 3089 (2009).
- E. A. Fulton *et al.*, *Ecol. Modell.* **173**, 371 (2004).
- E. A. Fulton, A. D. M. Smith, A. E. Punt, *ICES J. Mar. Sci.* **62**, 540 (2005).
- S. C. Anderson, J. M. Flemming, R. Watson, H. K. Lotze, *PLoS ONE* **6**, e14735 (2011).
- Materials and methods are available as supporting material on Science Online.
- M. C. Tyrrell, J. S. Link, H. Moustahfid, *Fish. Res.* **108**, 1 (2011).
- J. A. Santora, C. S. Reiss, A. M. Cossio, R. R. Veit, *Fish. Oceanogr.* **18**, 20 (2009).
- R. T. Barber, F. P. Chavez, *Science* **222**, 1203 (1983).
- F. P. Chavez, J. Ryan, S. E. Lluch-Cota, M. Niquen C, *Science* **299**, 217 (2003).
- T. Gross, L. Rudolf, S. A. Levin, U. Dieckmann, *Science* **325**, 747 (2009).
- J. M. Montoya, G. Woodward, M. C. Emmerson, R. V. Solé, *Ecology* **90**, 2426 (2009).
- C. J. Walters, V. Christensen, S. J. Martell, J. F. Kitchell, *ICES J. Mar. Sci.* **62**, 558 (2005).
- P. Freon, M. Bouchon, C. Mullon, C. García, M. Niquen, *Prog. Oceanogr.* **79**, 401 (2008).
- K. T. Hill *et al.*, Assessment of the Pacific Sardine Resource in 2008, for U.S. Management in 2009 (2009); available at www.pcouncil.org/wp-content/uploads/2009_CPS_SAFE_APP1_Sardine.pdf.
- S. P. R. Greenstreet *et al.*, *ICES J. Mar. Sci.* **63**, 1530 (2006).
- H. C. J. Godfray *et al.*, *Science* **327**, 812 (2010).

Acknowledgments: This work was partly funded by the Marine Stewardship Council (MSC) to investigate “Developing best practice management for low trophic level fisheries: evaluation of harvest strategies.” The authors also acknowledge funding from the Commonwealth Scientific and Industrial Research Organization (Australia), National Oceanographic and Atmospheric Administration (USA), Institut de Recherche pour le Développement (France), and Instituto del Mar del Perú (Perú). I.C.K. (not funded by MSC) and E.A.F. acknowledge support from the Gordon and Betty Moore Foundation and the David and Lucile Packard Foundation. S.M. acknowledges support from European Union (EU) FP7 grant FACTS (Forage Fish Interactions), grant agreement 244966, and Department of Environment Food and Rural Affairs contract M1202. L.S. acknowledges the support of the South African Research Chair Initiative, funded through the South African Department of Science and Technology and administered by the South African National Research Foundation (NRF). Y.J.S. acknowledges support from EU FP7 project MEECE (Marine Ecosystem Evolution in a Changing Environment), grant agreement 212085. J. Field kindly provided the EcoSim model for the northern California current and advised on its use. C. de Moor provided information on management targets for sardines and anchovy in the Southern Benguela.

Supporting Online Material

www.sciencemag.org/cgi/content/full/science.1209395/DC1

Materials and Methods

SOM Text

Figs. S1 to S3

Table S1

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6 June 2011; accepted 12 July 2011

Published online 21 July 2011;

10.1126/science.1209395



The global contribution of forage fish to marine fisheries and ecosystems

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Abstract

Forage fish play a pivotal role in marine ecosystems and economies worldwide by sustaining many predators and fisheries directly and indirectly. We estimate global forage fish contributions to marine ecosystems through a synthesis of 72 published Ecopath models from around the world. Three distinct contributions of forage fish were examined: (i) the ecological support service of forage fish to predators in marine ecosystems, (ii) the total catch and value of forage fisheries and (iii) the support service of forage fish to the catch and value of other commercially targeted predators. Forage fish use and value varied and exhibited patterns across latitudes and ecosystem types. Forage fish supported many kinds of predators, including fish, seabirds, marine mammals and squid. Overall, forage fish contribute a total of about \$16.9 billion USD to global fisheries values annually, i.e. 20% of the global ex-vessel catch values of all marine fisheries combined. While the global catch value of forage fisheries was \$5.6 billion, fisheries supported by forage fish were more than twice as valuable (\$11.3 billion). These estimates provide important information for evaluating the trade-offs of various uses of forage fish across ecosystem types, latitudes and globally. We did not estimate a monetary value for supportive contributions of forage fish to recreational fisheries or to uses unrelated to fisheries, and thus the estimates of economic value reported herein understate the global value of forage fishes.

Keywords Ecosystem service, ecosystem-based management, fisheries value, forage fish, supportive values, trade-offs

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Received 21 Feb 2012

Accepted 26 Jul 2012

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Introduction

'Forage fish' species are small or intermediate-sized pelagic species (e.g. sardine, anchovy, sprat, herring, capelin, krill) that are the primary food source for many marine predators, including mammals (Thompson *et al.* 1996; Pauly *et al.* 1998; Weise and Harvey 2008), seabirds (Crawford and Dyer 1995; Jahncke *et al.* 2004; Furness 2007; Daunt *et al.* 2008) and larger fish (Walter and Austin 2003; Butler *et al.* 2010; Logan *et al.* 2011; Magnussen 2011). Forage fish feed on zooplankton and phytoplankton and are important conduits of energy transfer in food webs for many marine ecosystems, from the tropics to the Earth's poles (Cury *et al.* 2000, 2003; Fréon *et al.* 2005; Bakun *et al.* 2010).

Fisheries for forage fish occur across broad latitudinal ranges (FAO 2010) and constitute a large and growing fraction of the global wild marine fish catch (Alder *et al.* 2008). In addition, five of the top ten fish species caught (by weight) in 2008 were forage fish species. Notably, the Peruvian anchoveta (*Engraulis ringens*, Engraulidae) supports the largest fishery in the world (FAO 2010). Nearly 90% of the global forage fish catch is used by reduction industries, which produce fish meal and fish oil (Alder *et al.* 2008). While economic studies of forage fish have focused primarily on their role as a directly harvested commodity (Herrick *et al.* 2009; Mullon

et al. 2009; Tacon and Metian 2009), few have attempted to quantify the indirect economic contributions that these species provide (Hannesson *et al.* 2009; Herrick *et al.* 2009; Hannesson and Herrick 2010). Accounting for the indirect or support service values that prey species provide to other fisheries is inherently more difficult (Hannesson *et al.* 2009; Hannesson and Herrick 2010; Hunsicker *et al.* 2010), but doing so can provide important information to assess the trade-offs between exploiting forage fish and other species in the same marine ecosystem.

There has been growing scientific consensus for the application of ecosystem-based management approaches (Pikitch *et al.* 2004; McLeod *et al.* 2005; McLeod and Leslie 2009) in contrast to traditionally applied single-species approaches (Beddington *et al.* 2007; FAO 2010). Single-species management generally seeks to maintain populations of a target species yet ignores most ecosystem factors. Even in cases where forage fish are well managed from a single-species perspective (i.e. overfishing is not occurring), a form of 'ecosystem overfishing' *sensu* Murawski (2000) can occur, whereby depleted abundance of forage fish may negatively affect the ecosystem (Gislason 2003; Coll *et al.* 2008). Implementing an ecosystem-based approach to the management of forage fisheries seems especially warranted (Pikitch *et al.* 2004; Richerson *et al.* 2010; Smith *et al.* 2011), as these

species exhibit strong trophic linkages and fluctuate in abundance along with seasonal, annual and inter-decadal variations in oceanographic forces (Barber and Chavez 1983; Francis *et al.* 1998; Polovina *et al.* 2001; Chavez *et al.* 2003).

Human decision-making is often influenced by comparisons of monetary values or trade-offs between different products or services (Polasky and Segerson 2009). By quantifying the value of these ecosystem products and services, such trade-offs, and the impacts of degrading ecosystems, are made more explicit (Costanza *et al.* 1997; Balmford *et al.* 2002; Barbier *et al.* 2011). The majority of economic analyses conducted for forage fish fisheries have been one dimensional (Herrick *et al.* 2009), focusing on factors or management strategies affecting the direct value of these species as a landed commodity. Only a handful of studies have enumerated the indirect values that species targeted by fisheries provide (Hannesson *et al.* 2009; Hannesson and Herrick 2010; Hunsicker *et al.* 2010; Kamimura *et al.* 2011). Because of their key position in marine food webs, the overall global importance of forage fish to fisheries and ecosystems has likely been significantly understated.

This study provides the first global estimate of forage fish value to commercially important marine fisheries and enumerates the contributions of forage fish to ecosystem predator production. We synthesized data obtained from Ecopath models representing marine ecosystems around the world. This approach allowed for broad relationships to be detected and described by summarizing data from multiple independent studies (Gurevitch and Hedges 1999), including information on feeding habits, production and catch rates. We estimated the contribution that forage fish species make to: (i) the diets and production of all forage fish predators within each modelled ecosystem, (ii) forage fish fisheries, in terms of catch and catch value and (iii) the catch and value of other commercially targeted predator species (e.g. tunas, cod, striped bass), based on their diet dependence on forage fish. We compared and contrasted these contributions and values, and investigated the effects of model structure, ecosystem type and latitude (Table 1). Finally, we use the relationships and properties revealed by these models, together with estimates of catch values at the scale of economic exclusive zones (EEZ) and high seas areas (HSA), to estimate the total value that forage fish contribute to global marine fisheries.

Methods

Compilation and synthesis of Ecopath models

Of the more than 200 Ecopath models that have been published (Fulton 2010), 72 were obtained and selected for this synthesis. The requirements for inclusion in our analysis were that the Ecopath models had to represent a marine or estuarine ecosystem in a relatively recent state (within the last 40 years), include at least one forage fish model group, and have all the necessary data and parameters openly available. The majority of Ecopath models used (90%, 65 out of 72) represented ecosystems within the past 30 years. We obtained Ecopath models from peer-reviewed publications ($n = 33$), technical reports ($n = 36$) and theses/dissertations ($n = 3$) (Table 1). Ecopath models that were not included failed to have at least one forage fish model group, did not have data openly available, represented older time periods (>40 years old), or a combination of all three. Collected models spanned a wide geographical range and provided relatively good global coverage of most coastal ocean areas and marine ecosystem types, with the exception of the Indian Ocean, which is poorly studied compared with other ocean areas (De Young 2006) (Fig. 1). When available, we also obtained Ecopath pedigree index information (Christensen and Walters 2004; Christensen *et al.* 2005) to assess data quality of the models.

To examine the patterns in forage fish contributions and values, we grouped Ecopath models by latitude and by ecosystem type. Latitude groupings consisted of three categories: Tropical-Subtropical (less than 30° N – less than 30° S), Temperate (greater than or equal to 30° N – 58° N and greater than or equal to 30° S – 58° S) and High latitude (greater than 58° N and greater than 58° S). We separated upwelling ecosystem models from the latitude groupings due to the dominant roles forage fish catches play in these ecosystems. Ecosystem types included: upwelling ecosystems, semi-enclosed ecosystems, non-upwelling coastal ecosystems, tropical lagoon ecosystems, open ocean ecosystems, Arctic high latitude ecosystems, and Antarctic ecosystems. All models were categorized into only one ecosystem type and latitude group (Table 1).

In this analysis we define 'forage fish' as species that occupy an important intermediary trophic position and that retain that ecological role throughout their life. We thus excluded from our

Table 1 List of the 72 Ecopath models used in this synthesis. Full model references can be found in Appendix S1 (available in the online version of this article).

Model No.	Model name	Model year(s)	Latitude group	Ecosystem type	Model area (km ²)	Pedigree index	No. of MG	No. of PMG	No. of FFMG	Value data	Krill MG	Citation
1	Western Bering Sea ¹	1980s–1990s	High latitude	Arctic high latitude	254 000	–	48	22	3	Yes	Yes	Aydin <i>et al.</i> (2002)
2	Eastern Bering Sea (1)	1980s	High latitude	Arctic high latitude	484 508	–	25	14	1	Yes	No	Trites <i>et al.</i> (1999)
3	Eastern Bering Sea (2)	1980s–1990s	High latitude	Arctic high latitude	485 000	–	38	19	2	Yes	No	Aydin <i>et al.</i> (2002)
4	Prince William Sound, Alaska (1) ²	1980–89	High latitude	Arctic high latitude	8800	0.351	19	6	2	Yes	No	Dalsgaard and Pauly (1997)
5	Prince William Sound, Alaska (2) ³	1994–96	High latitude	Arctic high latitude	9000	0.675	48	20	5	Yes	No	Okey and Pauly (1999)
6	Hecate Strait, Northern British Columbia	2000	High latitude	Non-upwelling coastal	70 000	–	50	34	5	Yes	Yes	Ainsworth <i>et al.</i> (2002)
7	Northern California Current	1990	Upwelling	Upwelling	69 176	–	63	38	3	Yes	Yes	Field <i>et al.</i> (2006)
8	Gulf of California	1978–79	Tropical-Subtropical	Semi-enclosed	27 900	–	25	8	1	Yes	No	Arreguin-Sánchez <i>et al.</i> (2002)
9	Huizachi-Caimanero lagoon complex, Mexico	1970–2000	Tropical-Subtropical	Tropical lagoon	175	0.750	26	6	1	Yes	No	Zetina-Rejón <i>et al.</i> (2003)
10	Golfo de Nicoya, Costa Rica	1980s–1990s	Tropical-Subtropical	Tropical lagoon	1530	–	20	10	1	Yes	No	Wolff <i>et al.</i> (1998)
11	Golfo Dulce, Costa Rica	1960–90s	Tropical-Subtropical	Tropical lagoon	750	–	20	9	1	No	No	Wolff <i>et al.</i> (1996)
12	Eastern Subtropical Pacific Ocean ⁴	1993–97	Tropical-Subtropical	Open ocean	32 800 000	–	40	31	2	Yes	No	Olson and Watters (2003)
13	Northern Humboldt Current ⁵	1995–96	Upwelling	Upwelling	165 000	0.638	32	15	3	Yes	No	Tam <i>et al.</i> (2008)
14	Northern Humboldt Current ⁶	1997–98	Upwelling	Upwelling	165 000	0.638	32	16	3	Yes	No	Tam <i>et al.</i> (2008)
15	Sechura Bay, Peru	1996	Upwelling	Upwelling	400	0.462	22	5	1	Yes	No	Taylor <i>et al.</i> (2008)
16	Central Chile	1998	Upwelling	Upwelling	50 042	–	21	8	5	Yes	Yes	Neira <i>et al.</i> (2004)
17	Tongoy Bay, Chile	1980s–1990s	Upwelling	Upwelling	60	–	17	5	1	No	No	Wolff (1994)
18	Falkland Islands	1990s	Temperate	Non-upwelling coastal	527 000	–	44	32	2	Yes	Yes	Cheung and Pitcher (2005)
19	South Brazil Bight	1998–99	Tropical-Subtropical	Non-upwelling coastal	97 000	–	25	6	2	Yes	No	Gasalla and Ross-Wongtichowski (2004)

Table 1 Continued.

Model No.	Model name	Model year(s)	Latitude group	Ecosystem type	Model area (km ²)	Pedigree index	No. of MG	No. of PMG	No. of FFMG	Value data	Krill MG	Citation
20	Caeté Estuary, Brazil	1999	Tropical-Subtropical	Non-upwelling coastal	220	–	18	4	1	Yes	No	Wolff <i>et al.</i> (2000)
21	Gulf of Paria	1980s–1990s	Tropical-Subtropical	Tropical lagoon	7600	–	23	11	1	No	No	Manickchand-Heileman <i>et al.</i> (2004)
22	Northeastern Venezuela shelf	1970s–1980s	Tropical-Subtropical	Non-upwelling coastal	30 000	–	16	10	1	Yes	No	Mendoza (1993)
23	Gulf of Salamanca	1997	Tropical-Subtropical	Tropical lagoon	955	0.743	18	6	1	Yes	No	Duarte and García (2004)
24	Celestun lagoon, Mexico	2001	Tropical-Subtropical	Tropical lagoon	28	0.362	19	1	2	Yes	No	Vega-Cendejas and Arreguín-Sánchez (2001)
25	Terminos lagoon, Mexico	1980s–1990s	Tropical-Subtropical	Tropical lagoon	2500	–	20	5	1	No	No	Manickchand-Heileman <i>et al.</i> (1998a)
26	Southwestern Gulf of Mexico	1980s–1990s	Tropical-Subtropical	Tropical lagoon	65 000	–	19	9	1	No	No	Manickchand-Heileman <i>et al.</i> (1998b)
27	Laguna Alvarado, Mexico	1991–94	Tropical-Subtropical	Tropical lagoon	62	0.500	30	9	2	Yes	No	Cruz-Escalona <i>et al.</i> (2007)
28	Tampamachoco lagoon, Mexico	1980s–1990s	Tropical-Subtropical	Tropical lagoon	15	–	23	6	1	No	No	Rosado-Solórzano and Guzmán del Prío (1998)
29	Gulf of Mexico	1950–2004	Tropical-Subtropical	Non-upwelling coastal	1 530 387	–	61	23	6	No	No	Walters <i>et al.</i> (2008)
30	West Florida shelf	1980s–1990s	Tropical-Subtropical	Non-upwelling coastal	170 000	–	59	18	2	No	No	Okey <i>et al.</i> (2004)
31	Chesapeake Bay	2000	Temperate	Non-upwelling coastal	10 000	0.450	45	17	5	Yes	No	Christensen <i>et al.</i> (2009)
32	Gulf of Maine	1977–86	Temperate	Non-upwelling coastal	90 700	–	30	12	2	Yes	No	Heymans (2001)
33	Northern Gulf of St. Lawrence	1985–87	Temperate	Non-upwelling coastal	103 812	0.651	31	19	3	Yes	No	Morissette <i>et al.</i> (2003)
34	Newfoundland	1995	Temperate	Non-upwelling coastal	495 000	0.396	50	30	4	Yes	No	Heymans and Pitcher (2002)
35	Lancaster Sound region, Canada	1980s	High latitude	Arctic high latitude	97 698	–	32	2	1	No	No	Mohammed (2001)
36	West Greenland	1991–92	High latitude	Arctic high latitude	63 500	0.439	12	4	1	Yes	No	Pedersen (1994)

Table 1 Continued.

Model No.	Model name	Model year(s)	Latitude group	Ecosystem type	Model area (km ²)	Pedigree index	No. of MG	No. of PMG	No. of FFMG	Value data	Krill MG	Citation
37	Icelandic shelf	1997	High latitude	Arctic high latitude	115 000	0.295	21	10	2	No	No	Mendy (1999)
38	Barents Sea (1)	1990	High latitude	Arctic high latitude	1 400 000	–	41	18	5	Yes	No	Blanchard <i>et al.</i> (2002)
39	Barents Sea (2)	1995	High latitude	Arctic high latitude	1 400 000	–	41	18	5	Yes	No	Blanchard <i>et al.</i> (2002)
40	Baltic Sea	1974–2000	Temperate	Semi-enclosed	396 838	–	16	5	4	Yes	No	Harvey <i>et al.</i> (2003)
41	North Sea	1981	Temperate	Non-upwelling coastal	570 000	–	25	8	4	Yes	Yes	Christensen (1995)
42	English Channel	1995	Temperate	Non-upwelling coastal	89 607	–	48	15	4	Yes	No	Stanford and Pitcher (2004)
43	Western English Channel	1994	Temperate	Non-upwelling coastal	56 452	–	52	20	4	Yes	No	Araujo <i>et al.</i> (2005)
44	Bay of Mont. St. Michel, France	2003	Temperate	Non-upwelling coastal	250	–	19	1	1	Yes	No	Arbach Leloup <i>et al.</i> (2008)
45	Cantabrian Sea shelf	1994	Temperate	Non-upwelling coastal	16 000	0.669	28	9	2	Yes	No	Sánchez and Olaso (2004)
46	Azores Archipelago	1997	Temperate	Non-upwelling coastal	584 000	0.409	44	15	1	Yes	No	Guénette and Morato (2001)
47	Northwestern Mediterranean Sea	1994	Temperate	Semi-enclosed	4500	–	23	10	3	Yes	No	Coll <i>et al.</i> (2006)
48	Orbetello lagoon, Italy	1996	Temperate	Non-upwelling coastal	27	–	9	4	1	Yes	No	Brando <i>et al.</i> (2004)
49	Northern & Central Adriatic Sea	1990s	Temperate	Semi-enclosed	55 500	0.657	40	16	3	Yes	No	Coll <i>et al.</i> (2007)
50	Black Sea	1989–91	Temperate	Semi-enclosed	423 000	–	11	4	1	Yes	No	Örek (2000)
51	Atlantic coast of Morocco	1984	Upwelling	Upwelling	586 900	0.382	38	19	2	Yes	No	Stanford <i>et al.</i> (2004)
52	Banc d'Arguin, Mauritanie	1988–98	Tropical-Subtropical	Non-upwelling coastal	10 000	0.537	22	7	1	Yes	No	Sidi and Diop (2004)
53	Cape Verde Archipelago	1981–85	Tropical-Subtropical	Non-upwelling coastal	5394	–	31	9	1	Yes	No	Stobberup <i>et al.</i> (2004)
54	Central Atlantic Ocean	1997–98	Temperate	Open ocean	18 419 191	–	39	14	1	Yes	No	Vasconcelos and Watson (2004)
55	Gambian continental shelf	1995	Tropical-Subtropical	Non-upwelling coastal	4000	–	23	7	2	No	No	Mendy (2004)

Table 1 Continued.

Model No.	Model name	Model year(s)	Latitude group	Ecosystem type	Model area (km ²)	Pedigree index	No. of MG	No. of PMG	No. of FFMG	Value data	Krill MG	Citation
56	Guinea-Bissau continental shelf	1990–92	Tropical-Subtropical	Non-upwelling coastal	40 816	–	32	12	2	Yes	No	Amorim <i>et al.</i> (2004)
57	Senegambia	1990	Tropical-Subtropical	Non-upwelling coastal	27 600	–	18	7	2	Yes	No	Samb and Mendy (2004)
58	Guinean continental shelf	2005	Tropical-Subtropical	Non-upwelling coastal	42 969	–	35	21	2	Yes	No	Gascuel <i>et al.</i> (2009)
59	Southern Benguela Current	1990	Upwelling	Upwelling	220 000	–	32	15	4	Yes	No	Shannon <i>et al.</i> (2003)
60	South Orkneys/South Georgia	1990s	High latitude	Antarctic	1 880 000	–	30	22	2	Yes	Yes	Bredesen (2004)
61	Antarctic Peninsula	1991–2001	High latitude	Antarctic	3400	–	39	20	2	Yes	Yes	Erfan and Pitcher (2005)
62	Kerguelen Archipelago EEZ	1987–88	Temperate	Non-upwelling coastal	575 100	–	23	15	2	Yes	Yes	Pruvost <i>et al.</i> (2005)
63	Maputo Bay, Mozambique	1980s–1990s	Tropical-Subtropical	Non-upwelling coastal	1100	–	10	4	1	Yes	No	Paula e Silva <i>et al.</i> (1993)
64	Great Barrier Reef, Australia	2000	Tropical-Subtropical	Tropical lagoon	325 848	–	30	12	2	No	No	Gribble (2005)
65	Darwin Harbour, Australia	1990–2000	Tropical-Subtropical	Non-upwelling coastal	250	0.375	21	5	1	No	No	Martin (2005)
66	Brunei Darussalam	1989–90	Tropical-Subtropical	Tropical lagoon	7396	–	13	4	1	Yes	No	Silvestre <i>et al.</i> (1993)
67	Terengganu, Malaysia	1980s	Tropical-Subtropical	Tropical lagoon	1050	–	13	2	2	Yes	No	Liew and Chan (1987)
68	Hong Kong, China	1990s	Tropical-Subtropical	Non-upwelling coastal	1680	–	37	12	1	No	No	Buchary <i>et al.</i> (2002)
69	Tapong Bay, Taiwan	1999–2001	Tropical-Subtropical	Tropical lagoon	4	0.820	18	1	2	No	No	Lin <i>et al.</i> (2006)
70	East China Sea	1997–2000	Tropical-Subtropical	Open ocean	770 000	0.636	45	19	6	Yes	No	Jiang <i>et al.</i> (2008)
71	Bohai Sea	1982–83	Temperate	Non-upwelling coastal	77 000	–	13	5	1	Yes	No	Tong <i>et al.</i> (2000)
72	Central North Pacific	1990s	Tropical-Subtropical	Open ocean	9 888 350	–	25	20	2	No	No	Cox <i>et al.</i> (2002)

¹48 group model, ²pre-oil spill model, ³post-oil spill model, ⁴ETP7 model, ⁵La Niña model, ⁶EI Niño model. MG = Model groups, PMG = Predator model groups, FFMG = Forage fish model groups.

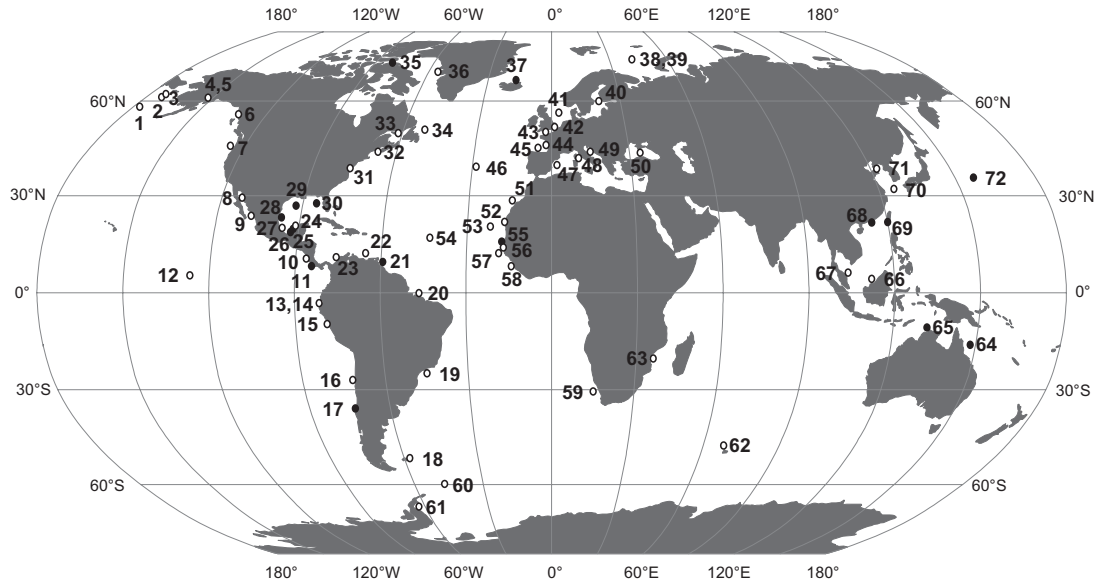


Figure 1 Approximate locations of the 72 Ecopath models used in this synthesis. Ecopath models where monetary value could (white circles) and could not (black circles) be calculated. Model numbers correspond to Table 1.

definition species that assume this role early in life but later move into higher trophic categories as they age (e.g. North Pacific hake, Blue whiting, Alaska pollock).

Data extraction

We extracted model groups, catch data, diet composition matrices, biomass data, production-to-biomass ratios and model area (km^2) from tables in Ecopath model publications and transferred them into separate Microsoft[®]Excel spreadsheets. When necessary, we converted all Ecopath catch and biomass data not conforming to the standard Ecopath units for catch ($\text{tonne km}^{-2} \text{ year}^{-1}$) and biomass (tonne km^{-2}).

The majority (83%) of Ecopath models in this analysis had data on total catch (landings plus discards). The remaining 17% (12 out of 72) of the models only published landings data with no estimates of discards. For these 12 models we assumed that discards were zero in our analysis. Discards represent approximately 8% of the marine fisheries catch by weight globally but vary greatly among species and ecosystems (Kelleher 2005).

Ecopath models contain interactive 'groups' which can be composed of either single or multiple species that share similar life histories or ecological functions (Polovina 1984). We used the Ecopath models assembled with the original model groups as

specified by the model authors. The published models generally included a list of species or taxa constituting each model group. When such taxonomic information was provided, we used this information to create an inventory of all species. In this study, we classified a model group as a forage fish group whenever at least one forage fish species was included. For instance, if an anchovy species was a component of a larger model group called 'Small Pelagics', along with gobies and juvenile mackerels, then we considered this group as a forage fish group, even though other species in that group may not necessarily meet our definition of forage fish. The majority (65% or 105 out of 161) of forage fish model groups consisted entirely of forage fish species. Of the remaining 56 forage fish model groups, 30 were discerned to be dominated by forage fish species, while information on the preponderance of forage fish species was lacking for the other 26 model groups. The one exception to our classification of forage fish model groups applied to krill (Order: Euphausiacea), which were only represented as separate model groups in 9 of the 72 Ecopath models in this analysis (Table 1). In the few remaining Ecopath models where krill were present in the ecosystem but not as a separate model group, they were grouped into various 'Zooplankton' groups. We chose to exclude these 'Zooplankton' model groups as forage fish groups in this analysis and only included contributions of krill from models

with defined krill model groups. We acknowledge that this modelling approach may cause differences between ecosystems in terms of forage fish contributions (i.e. those that have a separate krill group and those that do not) but assumed in this analysis that if model authors grouped krill separately it was due to their perceived importance in the ecosystem. We considered it was more appropriate to include krill groups as forage fish in this analysis when present than to completely exclude them.

Importance of forage fish to ecosystem predators

We identified forage fish predators in all models and their dependence on forage fish (percent of forage fish in diet) from the respective model diet matrix. We defined forage fish predators as model groups whose diets contained any fraction of one or more forage fish model groups (i.e. diet of >0% forage fish). This definition allowed for forage fish species to be included as forage fish predators, if their diet consisted of forage fish. This rarely occurred, with only 3.9% (35 out of 895) of forage fish predators also included as forage fish. Forage fish predators were then categorized into the following dependence groups: (i) low dependence on forage fish (>0 to <25%), (ii) moderate dependence (≥ 25 to <50%), (iii) high dependence (≥ 50 to <75%) and (iv) extreme dependence on forage fish ($\geq 75\%$).

We estimated the portion of each forage fish predator's production supported by forage fish across all ecosystem models using equations modified from Hunsicker *et al.* (2010). First, we calculated the total annual production (P_j , units: tonne km⁻² year⁻¹) of each forage fish predator group j in each Ecopath model using Equation (1), in which predator group j 's biomass (B_j , units: tonne km⁻²) was multiplied by that respective predator group's production-to-biomass ratio (P/B , units: year⁻¹).

$$P_j = B_j \left(\frac{P}{B} \right)_j \quad (1)$$

Second, we found the portion of each predator group's total annual production ($P_{i,j}$) supported by forage fish prey groups (i), by multiplying predator group j 's respective diet dependence on forage fish ($D_{i,j}$) by P_j using Equation (2).

$$P_{i,j} = D_{i,j} P_j \quad (2)$$

The total support service contribution of forage fish to ecosystem predator production (S_z) therefore can be found using Equation (3), as the product of

($D_{i,j}$) and (P_j) summed over all forage fish groups (i) and predator groups (j) in an ecosystem.

$$S_z = \sum_j \sum_i D_{i,j} P_j \quad (3)$$

Hunsicker *et al.* (2010) showed that $D_{i,j}$ is equivalent to the contribution of prey group i to predator group j 's production ($P_{i,j}$) when assimilation and energy content of prey items are roughly equivalent. In the absence of detailed data on these variables, we assumed they were equal to one another but note that our analysis underestimates $P_{i,j}$ because of the generally high energy content of forage fish species (Van Pelt *et al.* 1997; Anthony *et al.* 2000) compared to most predators. Thus, our estimates for the support service contribution of forage fish to ecosystem predator production can be considered conservative in this regard.

Direct and support service contributions of forage fish to commercial fisheries

We calculated the contributions of forage fish to fisheries in terms of catch (tonne km⁻² year⁻¹) for all 72 Ecopath models and catch value (2006 USD km⁻² year⁻¹) for a subset of models that had adequate taxonomic information ($n = 56$). Ecopath models were grouped into categories based on ecosystem type and latitude of the model (Table 1). We used a global ex-vessel price database, developed by Sumaila *et al.* (2007) to obtain ex-vessel 'real' price data for all fished species in our Ecopath models. Ex-vessel 'real' price is defined as the actual prices that fishermen receive for their products before processing and is hereafter simply referred to as price. In this analysis, we use 'value' to refer to ex-vessel fish price times quantity (gross returns) and not economic profit (net returns).

We obtained total catch data for every country participating in fisheries in a respective Large Marine Ecosystem (LME) in year 2006 from the Sea Around Us project LME database (Watson *et al.* 2004; www.seaaroundus.org), and used the ex-vessel price database to compile country specific ex-vessel price data for every species in the 56 models. Information on every fishing country in each LME and their respective total catch can be accessed on the Sea Around Us project LME database website (www.seaaroundus.org). To account for differences in prices between countries operating in a given LME, we calculated a weighted average based on the total catch in 2006 of all participating countries within that LME. When

model groups consisted of two or more species, the ex-vessel price for the model group was found by averaging the ex-vessel prices for all respective species within, which were each weighted by the catches of participating countries. We used these averaged ex-vessel model group prices to calculate fisheries value (2006 USD km⁻² year⁻¹) for each respective model group in all 56 Ecopath models.

For small geographic areas (e.g. estuaries, lagoons, and small coastal areas), we assumed that only the country surrounding these waters fished them. We made this assumption because detailed information about which specific countries fish within an Ecopath model area is not usually published. For the few Ecopath models that were located outside a defined LME area (e.g. Central North Pacific Ocean, Central Atlantic Ocean and Eastern Subtropical Pacific Ocean), we assumed participating fishing countries to be those nearest to, and surrounding, the model locations. Ecopath models of island countries and territories that fell outside of LME boundaries (e.g. the Azores Archipelago) were assumed to be fished only by that country, or the country of which it is a territory.

We estimated forage fish catch by summing the catch of all forage fish model groups in each respective ecosystem model. Catch value (2006 USD km⁻² year⁻¹) was estimated for each respective forage fish model group by multiplying the catch (tonne km⁻² year⁻¹) by the respective ex-vessel price (2006 USD tonne⁻¹) (Sumaila *et al.* 2007). Similarly, we summed catch values for all forage fish model groups to find the total forage fish catch value (2006 USD km⁻² year⁻¹) for each Ecopath model. We estimated the support service contributions of forage fish to the catch (S_c) and catch value (S_v) of other commercially targeted model groups by using Equation (3), except that the predator group's total annual production (P_j) was replaced by the catch (C_j , Equation 4) and catch value (V_j , Equation 5) of each predator group j .

$$S_c = \sum_j \sum_i D_{i,j} C_j \quad (4)$$

$$S_v = \sum_j \sum_i D_{i,j} V_j \quad (5)$$

Forage fish contribution to global fisheries value

Forage fish species contribute to the value of global fisheries in two important ways: (i) by their

direct catch value and (ii) by their support service as prey to the value of other commercially targeted species. Using forage fish value estimates for these contributions from each Ecopath model, we extrapolated to Exclusive Economic Zone (EEZ) or High Seas Area (HSA) regions to derive global estimates. We worked at the scale of EEZs and HSAs because independent estimates of forage fish catch values were available at this scale (Sumaila *et al.* 2007) to complement the values we estimated in Ecopath models. We assumed that a single Ecopath model representing an area within an EEZ or HSA region provided a reasonable depiction of the relationship between the support service value of forage fish and the total fisheries value for the entire region. A breakdown of the actual area covered by our Ecopath models as a percentage of the total EEZ/HSA area or the total Inshore fishing area (IFA) can be found in Table S1 (see Appendix S2). The IFA is defined by the Sea Around Us Project database (www.seaaroundusproject.org) as the area between the shoreline and whichever comes first, either the 200 m bathycline or a distance of 50 km from the shoreline. The majority of the global marine fisheries catch value (78%) and forage fish catch value (97%) is derived from IFAs (Sumaila *et al.* 2007) (www.seaaroundusproject.org). A summary of Ecopath model coverage in terms of EEZ/HSA or IFA area and fisheries value is provided in Table S2 (see Appendix S2). When multiple Ecopath models were available for a given EEZ or HSA region, we used average values weighted by the geographic area covered by each ecosystem model. We quantified global forage fisheries value by summing the value of forage fish across all EEZs and HSAs in the Sea Around Us project database. The majority of forage fish species in these databases were separated into two commercial groups, 'Herring-likes' and 'Anchovies'. We assumed that the total direct forage fish catch value for each respective EEZ and HSA was the sum of these two commercial groups. When data on 'Herring-likes' and 'Anchovies' were missing from this database, we used data available for forage fish categorized by species group. This method may slightly underestimate forage fisheries value, as it did not include some forage fish species that were grouped into other non-forage fish commercial groups.

To estimate the global support service value of forage fish to other commercially targeted species, we extrapolated the values estimated for each

Ecopath model to each corresponding EEZ and HSA region. To do this, we used Ecopath models with value data available and calculated an Ecopath value ratio (EVR) using Equation (6). In Equation (6), the catch value of forage fish predators supported by forage fish (S_v) was divided by the total fishery catch value (y) of the Ecopath model, excluding non-cephalopod, non-krill invertebrates (e.g. other decapods, bivalves). By assuming that EVRs found in our Ecopath models are representative of the larger EEZs or HSAs in which they are located, we calculated the total support service value (\$Supportive) of forage fish in each EEZ and HSA. Using Equation (7) we multiplied the respective EVR for an EEZ or HSA by the total fishery catch value (excluding non-cephalopod, non-krill invertebrates) for that area calculated from the Sea Around Us database (\$SAUP).

$$\text{EVR} = \frac{S_v}{y} \quad (6)$$

$$\text{\$Supportive} = \text{EVR} \times \text{\$SAUP} \quad (7)$$

Ecopath models were available for 25% (64 out of 257) of the world's EEZs and HSAs, which represents 33% of the total EEZ/HSA area (Table S2, Appendix S2). In the majority (36 out of 64) of these EEZ/HSA areas, Ecopath model coverage was >50% of the respective EEZ/HSA area (see Appendix S2, Tables S1 and S2). These EEZ/HSAs constitute 39% of the global marine catch value (2006 \$USD) excluding non-cephalopod and non-krill invertebrates (i.e. other decapods, bivalves) and 53% of the global forage fish catch value (2006 \$USD) (Table S2, Appendix S2). Ecopath model coverage of IFAs was even greater, representing 47% of the total area (km²) (Table S2, Appendix S2). An additional 86 EEZs and HSAs (see Table S1, Appendix S2), which did not have Ecopath models, were included under the assumption that the Ecopath model in the EEZ or HSA immediately adjacent was representative of that neighbouring EEZ or HSA. These EEZs and HSAs represented an additional 28% of the global forage fish catch value to fisheries. The remaining 107 EEZs or HSAs did not have Ecopath models or an adjacent neighbour with an Ecopath model (e.g. isolated islands) and represented only 19% of the global forage fish value to fisheries. In these EEZ/HSA areas, we applied an EVR based on the average of EVRs from other Ecopath models in the same latitudinal group. We calculated all values

as ex-vessel price values in 2006 \$USD and summed all support service values and forage fisheries catch values across all EEZs and HSAs. This produced our estimate of forage fish contribution to global fisheries value.

Results

Quality of Ecopath models

Ecopath pedigree indices (Christensen and Walters 2004) were available for 22 models (Table 1). The Ecopath pedigree index varies with the quality of data within Ecopath models, and values can range from 0 (not reliable) to 1 (highly reliable) (Christensen and Walters 2004; Christensen *et al.* 2005). Ecopath pedigree indices in this analysis ranged from 0.295 to 0.820 with the majority (55%, 12 out of 22) exceeding 0.5 (Table 1). Differences were observed in pedigree indices of models published in peer-reviewed journals (Ecopath pedigree mean = 0.625, median = 0.638, $n = 11$) and technical reports (Ecopath pedigree mean = 0.450, median = 0.408, $n = 11$). None of our indices were in the poorest quality level grouping, wherein data are considered to be no better than guesses (<0.2; Christensen and Walters 2004; Christensen *et al.* 2005). Moreover, the average and median pedigree indices observed in this study (0.518 and 0.537, respectively) were substantially higher than those for other studies (0.441 and 0.439, respectively) (Morissette *et al.* 2006; Morissette 2007).

Extent of predator dependence on forage fish

Seventy-five percent (54 out of 72) of the Ecopath models used in this analysis had at least one model group that was highly ($\geq 50\%$ but <75% of diet) or extremely dependent ($\geq 75\%$ of diet) on forage fish. Twenty-nine percent (21 out of 72) of the models included at least one extremely dependent predator group. We found extremely dependent predators present across all latitude groups and ecosystem types, with the exception of open ocean ecosystems. Extremely dependent predators accounted for only 5.8% (52 out of 895) of all forage fish predators and consisted of fishes ($n = 30$), seabirds ($n = 12$), marine mammals ($n = 9$) and one species of squid (*Loligo gahi*, Loliginidae). Amongst conspecific predator groups, however, seabirds had the highest percentage of extremely dependent predators, with

19% (12 out of 62) of all seabird predators having diets $\geq 75\%$ forage fish. Extremely dependent predators groups were most commonly found in upwelling and Antarctic ecosystem types, with an average of two and five extremely dependent predators per model, respectively. Many of these extremely dependent predator species were also listed on the IUCN Red List (Table 2).

We evaluated the relative frequency of various levels of forage fish dependencies and how they varied across ecosystem types by combining data from all models. Pooled data across all ecosystem models

indicated that on average, 49% of all predator groups in our models relied on forage fish for at least 10% of their dietary requirements (Fig. 2). Forage fish predators that are highly or extremely dependent on forage fish account for 16% of all predator groups in marine ecosystem models on average. Predators with diets consisting of more than 90% forage fish were also found but represented fewer than 5% of all predator groups in this analysis.

When comparing across ecosystem types, Antarctic ecosystem models generally had the greatest

Table 2 Extremely dependent forage fish predators ($\geq 75\%$ forage fish in their diets) found in this synthesis that have taxonomic information and are evaluated by the International Union for Conservation of Nature (IUCN) Red List. Model numbers correspond to model names in Table 1.

Common name	Scientific name	Family	IUCN Status ¹	Population trend	Model No(s)
<i>Marine Mammals</i>					
Sei Whale	<i>Balaenoptera borealis</i>	BALAENOPTERIDAE	Endangered	Unknown	(1, 60)
Blue Whale	<i>Balaenoptera musculus</i>	BALAENOPTERIDAE	Endangered	Increasing	(1, 60)
Fin Whale	<i>Balaenoptera physalus</i>	BALAENOPTERIDAE	Endangered	Unknown	(1, 60)
Common Minke Whale	<i>Balaenoptera acutorostrata</i>	BALAENOPTERIDAE	Least Concern	Stable	(1, 60)
Southern Right Whale	<i>Eubalaena australis</i>	BALAENIDAE	Least Concern	Increasing	60
Grey Seal	<i>Halichoerus grypus</i>	PHOCIDAE	Least Concern	Increasing	40
Crabeater Seal	<i>Lobodon carcinophagus</i>	PHOCIDAE	Least Concern	Unknown	60
Humpback Whale	<i>Megaptera novaeangliae</i>	BALAENOPTERIDAE	Least Concern	Increasing	(1, 60)
Ringed Seal	<i>Phoca hispida</i>	PHOCIDAE	Least Concern	Unknown	40
<i>Seabirds</i>					
Black-browed Albatross	<i>Thalassarche melanophrys</i>	DIOMEDEIDAE	Endangered	Decreasing	18
Macaroni Penguin	<i>Eudyptes chrysolophus</i>	SPHENISCIDAE	Vulnerable	Decreasing	(60, 62)
Humboldt Penguin	<i>Speriscus humboldtii</i>	SPHENISCIDAE	Vulnerable	Decreasing	17
Peruvian Pelican	<i>Pelecanus thagus</i>	PELECANIDAE	Near Threatened	Decreasing	(13–14, 15, 17)
Guanay Cormorant	<i>Phalacrocorax bougainvillii</i>	PHALACROCORACIDAE	Near Threatened	Decreasing	(13–14, 15)
Sooty Shearwater	<i>Puffinus griseus</i>	PROCELLARIIDAE	Near Threatened	Decreasing	1
Gentoo Penguin	<i>Pygoscelis papua</i>	SPHENISCIDAE	Near Threatened	Decreasing	(60, 62)
King Penguin	<i>Aptenodytes patagonicus</i>	SPHENISCIDAE	Least Concern	–	62
Rhinoceros Auklet	<i>Cerorhinca monocerata</i>	ALCIDAE	Least Concern	–	1
Southern Rockhopper Penguin	<i>Eudypte schrysocome</i>	SPHENISCIDAE	Least Concern	Decreasing	62
Tufted Puffin	<i>Fratercula cirrhata</i>	ALCIDAE	Least Concern	–	1
Southern Giant-petrel	<i>Macronectes giganteus</i>	PROCELLARIIDAE	Least Concern	Decreasing	18
Cassin's Auklet	<i>Ptychoramphus aleuticus</i>	ALCIDAE	Least Concern	–	1
Peruvian Booby	<i>Sula variegata</i>	SULIDAE	Least Concern	–	(13–14, 15, 17)
Common Guillemot	<i>Uria aalge</i>	ALCIDAE	Least Concern	–	1
<i>Fish</i>					
Yellowfin Tuna	<i>Thunnus albacares</i>	SCOMBRIDAE	Near Threatened	Decreasing	(13–14, 56)
Common Dolphin	<i>Coryphaena hippurus</i>	CORYPHAENIDAE	Least Concern	Stable	(13–14)
West African Ladyfish	<i>Elops lacerta</i>	ELOPIDAE	Least Concern	Unknown	56
Skipjack Tuna	<i>Katsuwonus pelamis</i>	SCOMBRIDAE	Least Concern	Stable	56
North Pacific Hake	<i>Merluccius productus</i>	MERLUCCIIDAE	Least Concern	Unknown	7
Sockeye Salmon	<i>Oncorhynchus nerka</i>	SALMONIDAE	Least Concern	Stable	(4–5)
Pacific Bonito	<i>Sarda chiliensis</i>	SCOMBRIDAE	Least Concern	Decreasing	(13–14)

¹IUCN (2011) IUCN Red List of Threatened Species. Version 2011.2 <http://www.iucnredlist.org> Downloaded on 2 December 2011.

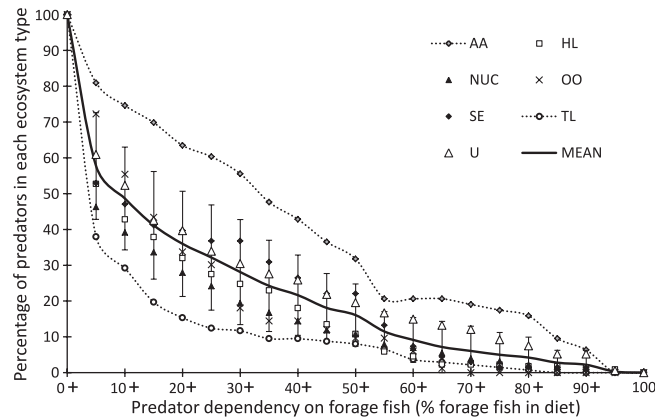


Figure 2 Percentage of forage fish predators in analysed ecosystems ($n = 72$) and their dependence on forage fish (% forage fish in diet). Solid line represents the Mean \pm SD for all predators in this analysis. Ecosystem types: AA, Antarctic; OO, open ocean; U, upwelling current; HL, Arctic high latitude; SE, semi-enclosed; NUC, non-upwelling coastal; TL, tropical lagoon.

proportion of forage fish predators in their models for any level of forage fish dependence compared to other ecosystem model types (Fig. 2). Upwelling ecosystems had the second highest percentage of predators with 90% forage fish dependence levels. Tropical lagoon ecosystem types had the lowest proportion of predators for a given forage fish dependence level (Fig. 2).

Support service contribution to ecosystem predator production

The total predator production (tonne $\text{km}^{-2} \text{year}^{-1}$) supported by forage fish varied greatly among the 72 models in this analysis (Fig. 3). Supported predator production was the largest for two upwelling ecosystem models, the northern California Current model and central Chile model, and one non-upwelling coastal ecosystem (Falkland Islands model). Forage fish contributed 52 and 17 tonne $\text{km}^{-2} \text{year}^{-1}$ to predator production in northern California Current and central Chile models respectively, and the contribution in the Falkland Islands model was 18.9 tonne $\text{km}^{-2} \text{year}^{-1}$. When the contribution of krill to the production of other forage fish (e.g. krill, sardines, anchovies) was removed in the northern California Current and Falkland Islands models, the support service to predators dropped to 32 and 3.3 tonne $\text{km}^{-2} \text{year}^{-1}$ respectively.

Across ecosystem types, the greatest support service contribution of forage fish to predator production was seen in upwelling and Antarctic eco-

systems (Fig. 4a). The support service contribution to predator production in both these ecosystem types exceeded 9 tonne $\text{km}^{-2} \text{year}^{-1}$, and were more than three times greater than values seen for Arctic ecosystems and non-upwelling coastal ecosystems and more than an order of magnitude greater than open-ocean, tropical lagoon and semi-enclosed ecosystem types (Fig. 4a). In terms of latitude groupings (with upwelling ecosystems excluded), we found the greatest support service contributions to predator production in high latitude regions (3.79 tonne $\text{km}^{-2} \text{year}^{-1} \pm 1.23$ SE), followed by temperate latitudes (1.81 tonne $\text{km}^{-2} \text{year}^{-1} \pm 0.59$ SE) and finally tropical-sub-tropical latitudes (1.18 tonne $\text{km}^{-2} \text{year}^{-1} \pm 0.17$ SE; Fig. 4b).

Importance of forage fish to commercial fisheries

Forage fish catch varied greatly among models examined, both in tonnage and ex-vessel price value. In some models, we found no forage fish catch reported (e.g. Central Atlantic Ocean), while others had extremely large forage fish catches (e.g. Sechura Bay, Peru). The highest forage fish catches were found in the Humboldt Current models where the Peruvian anchoveta fishery operates. Of the three Humboldt Current models, the Sechura Bay (Peru) model had an extraordinarily high level of forage fish catch (81 tonne $\text{km}^{-2} \text{year}^{-1}$) valued at \$35 497 (USD $\text{km}^{-2} \text{year}^{-1}$), whereas in the northern Humboldt Current models for El Niño and La Niña periods, forage fish catches



Figure 3 Support service of forage fish to ecosystem predator production across all Ecopath models in this analysis ($n = 72$).

were 20 tonne km⁻² year⁻¹ (\$934 USD km⁻² year⁻¹) and 39 tonne km⁻² year⁻¹ (\$2020 USD km⁻² year⁻¹), respectively.

Forage fish contributed important support to other commercial fisheries in all models that contained such fisheries. Of the ecosystems we examined, forage fish were most important as prey, in terms of tonnage, to commercial fisheries in central Chile (3.82 tonne km⁻² year⁻¹), Prince William Sound (pre-oil spill model; 3.58 tonne km⁻² year⁻¹) and the northern California Current (3.13 tonne km⁻² year⁻¹; Fig. 5). In terms of value, forage fish provided the greatest support service to fisheries in the Prince William Sound

model (pre-oil spill model) at a value of \$5942 USD km⁻² year⁻¹, followed by the Chesapeake Bay at a value of \$3095 USD km⁻² year⁻¹. The high support service values in these ecosystems are due to the large contribution of forage fish to the diets of salmon (*Oncorhynchus* spp., Salmonidae) in Prince William Sound and striped bass (*Morone saxatilis*, Percichthyidae) in Chesapeake Bay, both of which have relatively high ex-vessel price values.

In 13 out of 56 models, 100% of the total forage fish value was derived from support to other fisheries (i.e. there were no forage fish fisheries reported in these 13 ecosystems). In more than half the models (30 out of 56), the value of the fisheries

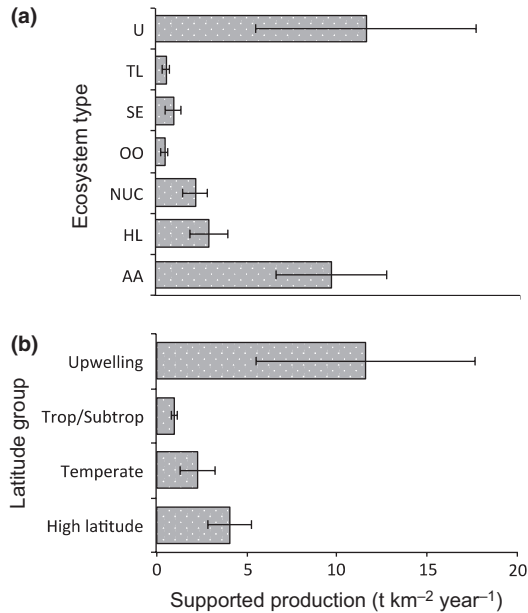


Figure 4 Mean forage fish contribution to (non-commercial) ecosystem predator production by ecosystem type (a) and latitude grouping (b) with standard error plotted. Ecosystem types: U, upwelling current; TL, tropical lagoon; SE, semi-enclosed; OO, open ocean; NUC, non-upwelling coastal; HL, Arctic high latitude; and AA, Antarctic.

supported by forage fish was greater than the value of forage fish catch (Fig. 6).

Comparisons across latitude groups and ecosystem types

The largest forage fish catches were found in the tropical-subtropical latitude group (4.95 tonne km⁻² year⁻¹ ± 2.5 SE) and decreased monotonically as polar regions were approached. In contrast, the level of other commercial catch supported by forage fish was the lowest in the tropical-subtropical latitude group (0.23 tonne km⁻² year⁻¹ ± 0.05 SE) but greater in temperate (0.63 tonne km⁻² year⁻¹ ± 0.2 SE) and high latitude ecosystems (0.35 tonne km⁻² year⁻¹ ± 0.29 SE). We separated upwelling ecosystem models from these latitude groupings, as forage fish catches play a dominant role in these ecosystems. We found that temperate models had the highest forage fish fisheries catch when compared with the remaining two latitude groups (Fig. 7a). Forage fish catch value (excluding upwelling ecosystems) was the greatest in the tropical-subtropical latitude group and diminished poleward (Fig. 7b). The sup-

port service provided by forage fish for other commercial fisheries, in both catch and catch value, increased poleward so that it was equivalent (in catch) or exceeded (in catch value) the forage fish catch or catch value in high latitudes (Fig. 7a,b).

Forage fish catch (tonne km⁻² year⁻¹) was the highest in upwelling ecosystems (Fig. 8a), exceeding that of all other ecosystem types combined by a factor of four. Forage fish catch exceeded the catch of other model groups that preyed on forage fish for all ecosystem types (Fig. 8a). Similarly, forage fish had the highest catch value in upwelling ecosystems at \$5660 USD km⁻² year⁻¹ ± \$4980 SE (Fig. 8b). Other ecosystem types had substantially lower forage fish catch values, each contributing < \$830 USD km⁻² year⁻¹. The value of forage fish catches was the smallest in high latitude Arctic and Antarctic ecosystems (\$184 USD km⁻² year⁻¹ and \$149 USD km⁻² year⁻¹, respectively). In contrast, the support service value of forage fish was the greatest in the Arctic ecosystems (HL, mean = \$706 USD km⁻² year⁻¹) – over 3.5 times greater than the forage fish value for that ecosystem type (Fig. 8b).

Global estimate of forage fish value to fisheries

The estimated total ex-vessel price value of forage fish to global commercial fisheries was \$16.9 billion (USD). This estimate combines global forage fish fishery value of \$5.6 billion (33%, USD) with a support service value to other fisheries of \$11.3 billion (67%, USD). This value represents nearly 20% (\$16.9b/\$85b) of the ex-vessel catch values of all world fisheries, estimated at between \$80 and 85 billion USD year⁻¹ (Sumaila *et al.* 2007; FAO 2010). Importantly, we found that the value of commercial fisheries supported by forage fish (e.g. cod, striped bass, salmon) was twice the value of forage fish fisheries at a global scale.

Discussion

We recognize that using Ecopath models, like any mathematical representation of an ecosystem, has certain limitations. However, our approach was built around the idea that, within the constraints of the model assumptions, averaging across many models will at least reduce the effects of stochastic uncertainty. Ecopath models provide only a single spatial and temporal representation of an ecosystem and they contain numerous assumptions

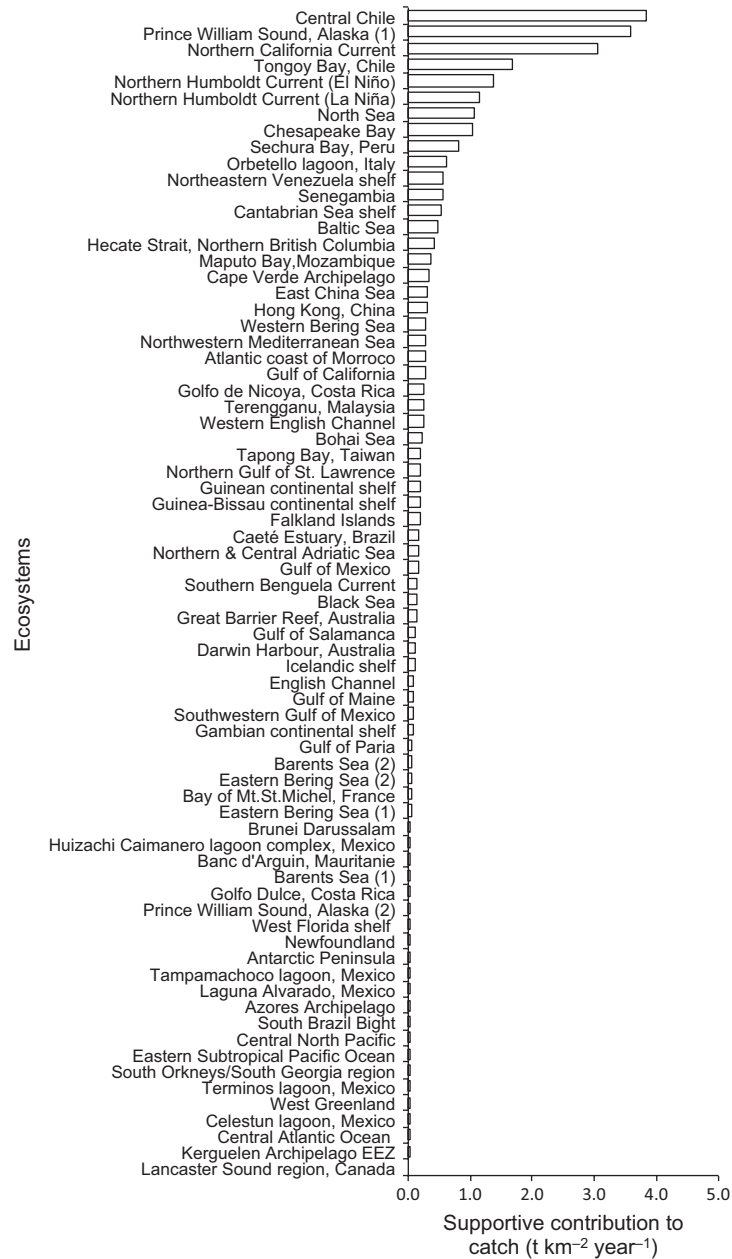


Figure 5 Support service contributions of forage fish to other fisheries catch across all Ecopath models ($n = 72$).

whose consequences are often impossible to assess and could be important. This means, at the very least, that they do not capture changes in ecosystem dynamics and fisheries effort over space and time. Models are constructed based on data availability and the author's understanding of the ecosystem and research objectives, allowing for a gradient in model complexity and quality. The models contain simplified diet information of predators included in the models, which needs to be

considered when interpreting or using the results of this study. For example, some Ecopath models lacked predators that are known to prey on forage fish, and in other cases, investigators pooled individual predator species together into a single trophic group. Nearly 30% (21 out of 72) of the models in our study did not have any seabird model groups, while 33% (24 out of 72) did not have a marine mammal group. Our estimates for predator production therefore are likely conserva-

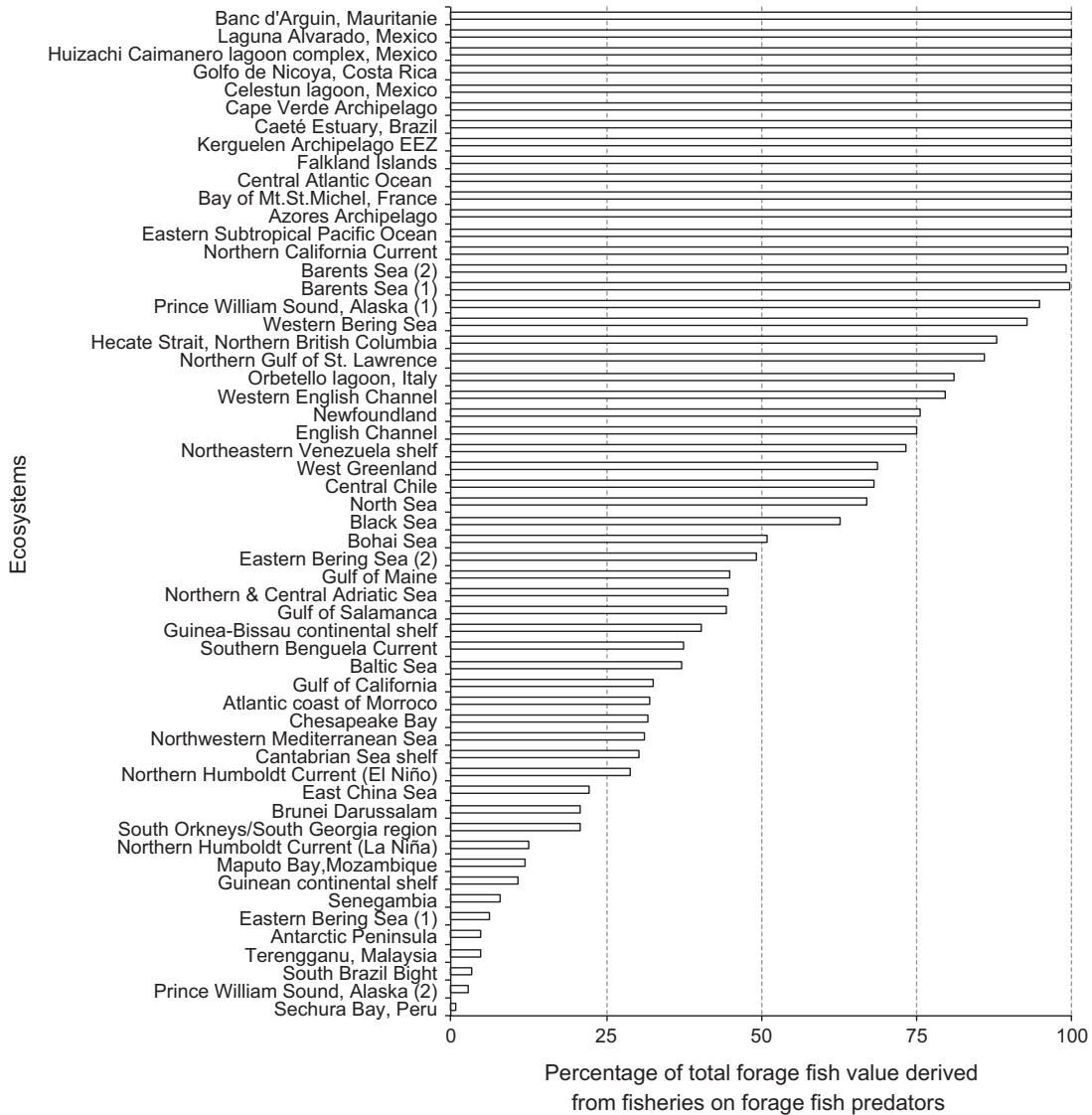


Figure 6 Percentage of total forage fish values (forage fish fisheries value + support service value to other fisheries) across Ecopath models ($n = 56$) derived from forage fish support service to other commercial fisheries. Ecosystems with 100% support service to other commercial fisheries do not have active forage fish fisheries in their respective ecosystem model.

tive, as we were not able to capture the importance of forage fish to these predators not included in the models. Likewise, aggregating predator species into model groups results in an averaged diet dependence on forage fish for the model group, which may mask high diet dependence for one or more individual species in that group. Averaging diet dependence for a single species over a large geographic area may also mask high diet dependencies that occur on smaller spatial or temporal scales. Validating every model to determine how

well it represents its respective ecosystem and biological components was beyond the scope of this analysis, but Ecopath pedigree index information for a subset of models shows that the majority used in this analysis are of acceptable quality (Table 1). Using published models provided us with a large number of models covering the widest range of ecosystems and latitudes possible.

Here we used information on catches, catch values and food web connections to estimate the global contribution of forage fish to fisheries and

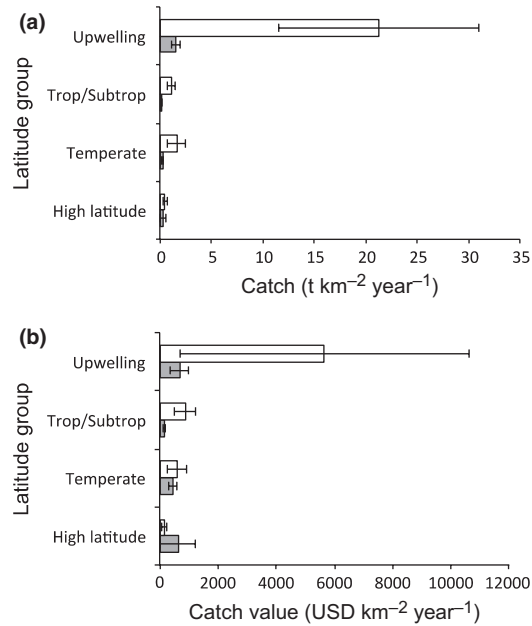


Figure 7 Mean catch (a) and mean catch value in 2006 USD (b) of forage fish (white bars) and mean supportive contribution of forage fish to other species' catch and catch value (grey bars), by latitude group. Bars indicate standard error. Upwelling ecosystem models were separated out to more clearly demonstrate latitudinal patterns.

ecosystems. While we find that the importance of forage fish varies geographically, it is clear that these species are of critical importance to many predators, including humans. We consider our approach as a reliable and relatively quick way of assessing the importance of forage fish in marine ecosystems and fisheries around the world. Ecopath models in this analysis covered 33% of the total EEZs and HSAs and covered 47% of the IFA (Table S2, Appendix S2), which is where 97% of the global forage fisheries catch value is derived (Sumaila *et al.* 2007). We acknowledge that geographic coverage is limited in the Indian Ocean. Although EEZ and HSA areas in the Indian Ocean account for 20% of the total EEZ and HSA area, they represent <15% of the total fisheries catch value (excluding non-cephalopod or non-krill invertebrates) and <12% of the total forage fish catch value. Furthermore, Indian Ocean EEZ and HSA areas accounted for <10% of the total global supportive value of forage fish. More robust fisheries information from this data-poor region (De Young 2006) would benefit future analyses.

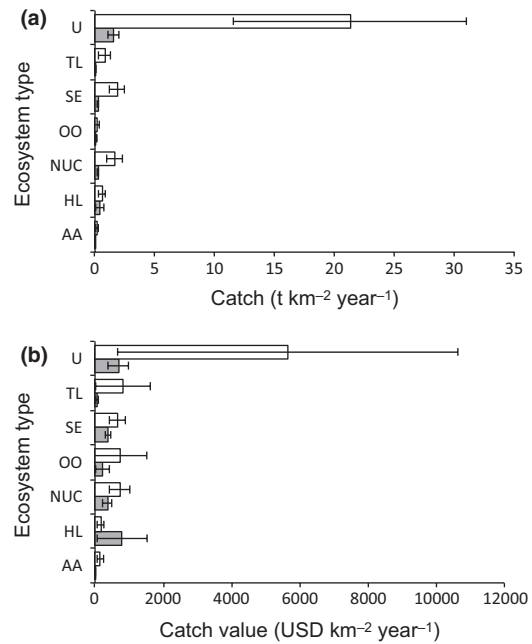


Figure 8 Mean catch (a) and catch value in 2006 USD (b) of forage fish (white bars) and mean supportive contribution of forage fish to other species' catch and catch value (grey bars). Bars indicate standard error. Ecosystem types: U, upwelling current; TL, tropical lagoon; SE, semi-enclosed; OO, Open ocean; NUC, non-upwelling coastal; HL, Arctic high latitude; and AA, Antarctic.

At the global scale the supportive value of forage fish to fisheries greatly exceeds their direct commodity value. We note that the estimated total ex-vessel value (\$16.9 billion USD annually) is likely an underestimate, because it does not take into account the contribution of forage species to early life history stages of predators that are not yet of commercial catch size (e.g. juvenile cod, juvenile striped bass). We also have not included in our analysis the contributions of species that are considered forage fish only during juvenile life stages (e.g. Alaska pollock). Accounting for these types of forage species would increase our estimates of support to ecosystem predator production and marine fisheries in certain ecosystems. More importantly, the ex-vessel value of commercial fisheries is only one of many other indicators of the economic contributions of forage fish, and thus is clearly an underestimate of total economic worth. We have not accounted for the potential economic value of forage fish to recreational fisheries, to ecotourism [e.g. the whale watching industry is estimated at \$2.5 billion 2009 USD

annually (Cisneros-Montemayor *et al.* 2010)], as bait for fisheries, and to the provision of other ecosystem services such as water filtration.

Forage fish are integral to marine food webs as prey for a wide variety of higher trophic-level species. For many predators, forage fish constitute a substantial percentage of their diet, possibly making them vulnerable to reductions or fluctuations in forage fish biomass. We found that many extremely dependent predators were species listed on the IUCN Red List as 'Near Threatened', 'Vulnerable' or 'Endangered' (Table 2). These predators were commonly found in upwelling ecosystems, where empirical evidence shows that changes in forage fish abundance – caused by fishing, the environment, or a combination of both – negatively impact predator reproduction (Sunada *et al.* 1981; Becker and Beissinger 2006), breeding (Crawford and Dyer 1995; Cury *et al.* 2011), abundance (Crawford and Jahncke 1999; Jahncke *et al.* 2004), and carrying capacity (Crawford *et al.* 2007). This analysis has identified ecosystems that are likely to have highly to extremely dependent forage fish predators and may assist in ecosystem-based management efforts that consider both commercial fisheries and effects on threatened or endangered species.

We provide the first global estimates of the importance of forage fish as support for predators in marine ecosystems. Quantifying forage fish catch, support service to other commercially targeted predators, and support to all other ecosystem predators allows for identification of potential trade-offs that may occur among uses (Fig. 9). Competition for the use of forage fish biomass among ecological and fisheries interests can result in trade-offs, which can lead to conflicts in the management of forage fish. This is especially important, as forage fish are an increasingly valued commodity (Naylor *et al.* 2009; Tacon and Metian 2009) and provide fundamental ecological support to many other species. Taking a holistic viewpoint of their value is a step towards quantification of the overall contributions forage fish make to marine ecosystems and to the global economy. A challenge that remains for fisheries managers and policy makers is determining acceptable levels of catch that account for the roles forage fish play in the larger marine environment.

The management of trade-offs in marine ecosystems can often be challenging (Okey and Wright 2004; Cheung and Sumaila 2008; Salomon *et al.*

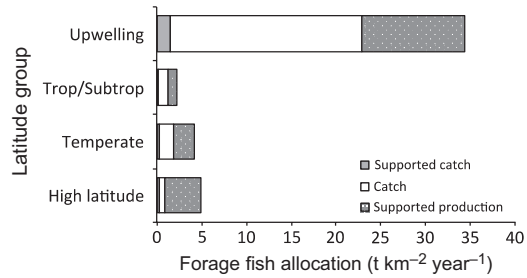


Figure 9 Forage fish allocation across latitude groups in terms of support service to fisheries (grey bars), forage fish catch (white bars) and support service to ecosystem predator production (dotted grey bars).

2011), but accounting for trade-offs is important and can lead to more sustainable levels of exploitation without compromising ecosystem integrity (Okey and Wright 2004). Ultimately, accounting for trade-offs between forage fish fisheries and conservation goals will require knowledge and understanding of the sensitivity to which commercially targeted and non-commercial predator species respond to fisheries induced changes in forage fish abundance. A combination of modelling (Okey and Wright 2004; Cheung and Sumaila 2008; Smith *et al.* 2011) and empirical (Read and Brownstein 2003; Brodziak *et al.* 2004) methods will likely be required to fully understand trade-offs in forage fishery management.

Acknowledgements

This work was supported by a grant from the Lenfest Ocean Program to E.K.P. and the research was conducted under the auspices of the Lenfest Forage Fish Task Force. This manuscript represents a portion of the Ph.D. dissertation research of K.J.R. at Stony Brook University. The authors would like to specifically thank the Sea Around Us project, a joint activity of the University of British Columbia and the Pew Environment Group, and L. Morissette for providing access to data essential to this work. Thanks also go to C. Perretti, S. Rahman and J. Rice for help in this analysis and fruitful discussions. Two anonymous reviewers are acknowledged and thanked for their comments which improved this manuscript.

References

- Alder, J., Campbell, B., Karpouzi, V., Kaschner, K. and Pauly, D. (2008) Forage fish: from ecosystems to markets. *Annual Review of Environment and Resources* **33**, 153–166.

- Anthony, J.A., Roby, D.D. and Turco, K.R. (2000) Lipid content and energy density of forage fishes from the northern Gulf of Alaska. *Journal of Experimental Marine Biology and Ecology* **248**, 53–78.
- Bakun, A., Babcock, E.A., Lluch-Cota, S.E., Santora, C. and Salvadeo, C.J. (2010) Issues of ecosystem-based management of forage fisheries in “open” non-stationary ecosystems: the example of the sardine fishery in the Gulf of California. *Reviews in Fish Biology and Fisheries* **20**, 9–29.
- Balmford, A., Bruner, A., Cooper, P. *et al.* (2002) Economic reasons for conserving wild nature. *Science* **297**, 950–953.
- Barber, R.T. and Chavez, F.P. (1983) Biological consequences of El Niño. *Science* **222**, 1203–1210.
- Barbier, E.B., Hacker, S.D., Kennedy, C., Koch, E.W., Stier, A.C. and Silliman, B.R. (2011) The value of estuarine and coastal ecosystem services. *Ecological Monographs* **81**, 169–193.
- Becker, B.H. and Beissinger, S.R. (2006) Centennial decline in the trophic level of an endangered seabird after fisheries decline. *Conservation Biology* **20**, 470–479.
- Beddington, J.R., Agnew, D.J. and Clark, C.W. (2007) Current problems in the management of marine fisheries. *Science* **316**, 1713–1716.
- Brodziak, J.K.T., Mace, P.M., Overholtz, W.J. and Rago, P.J. (2004) Ecosystem trade-offs in managing New England fisheries. *Bulletin of Marine Science* **74**, 529–548.
- Butler, C.M., Rudershausen, P.J. and Buckel, J.A. (2010) Feeding ecology of Atlantic bluefin tuna (*Thunnus thynnus*) in North Carolina: diet, daily ration, and consumption of Atlantic menhaden (*Brevoortia tyrannus*). *Fishery Bulletin* **108**, 56–69.
- Chavez, F.P., Ryan, J., Lluch-Cota, S.E. and Ñiquen, C.M. (2003) From anchovies to sardines and back: multi-decadal change in the Pacific Ocean. *Science* **299**, 217–221.
- Cheung, W.W.L. and Sumaila, U.R. (2008) Trade-offs between conservation and socio-economic objectives in managing a tropical marine ecosystem. *Ecological Economics* **66**, 193–210.
- Christensen, V. and Walters, C.J. (2004) Ecopath with Ecosim: methods, capabilities and limitations. *Ecological Modelling* **172**, 109–139.
- Christensen, V., Walters, C.J. and Pauly, D. (2005) *Ecopath with Ecosim: A User's Guide*. Fisheries Centre, University of British Columbia, Vancouver. November 2005 edition, 154 p. (available online at <http://www.ecopath.org>).
- Cisneros-Montemayor, A.M., Sumaila, U.R., Kaschner, K. and Pauly, D. (2010) The global potential for whale watching. *Marine Policy* **34**, 1273–1278.
- Coll, M., Libralato, S., Tudela, S., Palomera, I. and Pranovi, F. (2008) Ecosystem overfishing in the Ocean. *PLoS One* **3**, 1–10.
- Costanza, R., d'Arge, R., de Groot, R. *et al.* (1997) The value of the world's ecosystem services and natural capital. *Nature* **387**, 253–260.
- Crawford, R.J.M. and Dyer, B.M. (1995) Responses by 4 seabird species to a fluctuating availability of cape anchovy *Engraulis capensis* off South Africa. *Ibis* **137**, 329–339.
- Crawford, R.J.M. and Jahncke, J. (1999) Comparison of trends in abundance of guano-producing seabirds in Peru and southern Africa. *South African Journal of Marine Science* **21**, 145–156.
- Crawford, R.J.M., Underhill, L.G., Upfold, L. and Dyer, B.M. (2007) An altered carrying capacity of the Benguela upwelling ecosystem for African penguins (*Spheniscus demersus*). *ICES Journal of Marine Science* **64**, 570–576.
- Cury, P., Bakun, A., Crawford, R.J.M. *et al.* (2000) Small pelagics in upwelling systems: patterns of interaction and structural changes in “wasp-waist” ecosystems. *ICES Journal of Marine Science* **57**, 603–618.
- Cury, P., Shannon, L.J. and Shin, Y.-J. (2003) The functioning of marine ecosystems: a fisheries perspective. In: *Responsible Fisheries in the Marine Ecosystem* (eds M. Sinclair and G. Valdimarsson). CAB International, Wallingford, pp. 103–123.
- Cury, P.M., Boyd, I.L., Bonhommeau, S. *et al.* (2011) Global seabird response to forage fish depletion—One-third for the birds. *Science* **334**, 1703–1706.
- Daunt, F., Wanless, S., Greenstreet, S.P.R., Jensen, H., Hamer, K.C. and Harris, M.P. (2008) The impact of the sandeel fishery closure on seabird food consumption, distribution, and productivity in the northwestern North Sea. *Canadian Journal of Fisheries and Aquatic Sciences* **65**, 362–381.
- De Young, C. (2006) *Review of the State of World Marine Capture Fisheries Management: Indian Ocean*. FAO Fisheries Technical Paper, Food and Agriculture Organization, Rome, p. 458.
- FAO (2010) *The State of World Fisheries and Aquaculture 2010*. Food and Agriculture Organization, Rome, p. 197.
- Francis, R.C., Hare, S.R., Hollowed, A.B. and Wooster, W.S. (1998) Effects of interdecadal climate variability on the oceanic ecosystems of the NE Pacific. *Fisheries Oceanography* **7**, 1–21.
- Fréon, P., Cury, P., Shannon, L. and Roy, C. (2005) Sustainable exploitation of small pelagic fish stocks challenged by environmental and ecosystem changes: a review. *Bulletin of Marine Science* **76**, 385–462.
- Fulton, E.A. (2010) Approaches to end-to-end ecosystem models. *Journal of Marine Systems* **81**, 171–183.
- Furness, R. (2007) Responses of seabirds to depletion of food fish stocks. *Journal of Ornithology* **148**, 247–252.
- Gislason, H. (2003) The effects of fishing on non-target species and ecosystem structure and function. In:

- Responsible Fisheries in the Marine Ecosystem* (eds M. Sinclair and G. Valdimarsson). CAB International, Wallingford, pp. 255–275.
- Gurevitch, J. and Hedges, L.V. (1999) Statistical issues in ecological meta-analyses. *Ecology* **80**, 1142–1149.
- Hannesson, R. and Herrick Jr, S.F. (2010) The value of Pacific sardine as forage fish. *Marine Policy* **34**, 935–942.
- Hannesson, R., Herrick, S. and Field, J. (2009) Ecological and economic considerations in the conservation and management of the Pacific sardine (*Sardinops sagax*). *Canadian Journal of Fisheries and Aquatic Sciences* **66**, 859–868.
- Herrick, S.F., Norton, J.G., Hannesson, R., Sumaila, U.R., Ahmed, M. and Pena-Torres, J. (2009) Global production and economics. In: *Climate Change and Small Pelagic Fish* (eds D.M. Checkley, J. Alheit, Y. Oozeki and C. Roy). Cambridge University Press, Cambridge, pp. 256–274.
- Hunsicker, M.E., Essington, T.E., Watson, R. and Sumaila, U.R. (2010) The contribution of cephalopods to global marine fisheries: can we have our squid and eat them too? *Fish and Fisheries* **11**, 421–438.
- Jahncke, J., Checkley, D.M. and Hunt, G.L. (2004) Trends in carbon flux to seabirds in the Peruvian upwelling system: effects of wind and fisheries on population regulation. *Fisheries Oceanography* **13**, 208–223.
- Kamimura, Y., Kasai, A. and Shoji, J. (2011) Production and prey source of juvenile black rockfish *Sebastes cheni* in a seagrass and macroalgal bed in the Seto Inland Sea, Japan: estimation of the economic value of a nursery. *Aquatic Ecology* **45**, 367–376.
- Kelleher, K. (2005) *Discards in the World's Marine Fisheries*. An update. FAO Fisheries Technical Paper. No. 470. Food and Agriculture Organization of the United Nations (FAO), Rome, p. 131.
- Logan, J.M., Rodriguez-Marin, E., Goni, N. *et al.* (2011) Diet of young Atlantic bluefin tuna (*Thunnus thynnus*) in eastern and western Atlantic foraging grounds. *Marine Biology* **158**, 73–85.
- Magnussen, E. (2011) Food and feeding habits of cod (*Gadus morhua*) on the Faroe Bank. *ICES Journal of Marine Science* **68**, 1909–1917.
- McLeod, K.L. and Leslie, H. (2009) *Ecosystem-based Management for the Oceans*. Island Press, Washington, DC, USA, p. 368.
- McLeod, K.L., Lubchenco, J., Palumbi, S.R. and Rosenberg, A.A. (2005) Scientific Consensus Statement on Marine Ecosystem-Based Management. Signed by 217 academic scientists and policy experts with relevant expertise and published by the Communication Partnership for Science and the Sea at <http://compassonline.org/?q=EBM> (last accessed on 13 November, 2011).
- Morissette, L. (2007) *Complexity, cost and quality of ecosystem models and their impact on resilience: a comparative analysis, with emphasis on marine mammals and the Gulf of St. Lawrence*. PhD thesis, University of British Columbia, Vancouver, BC, 260 pp.
- Morissette, L., Hammill, M.O. and Savenkoff, C. (2006) The trophic role of marine mammals in the northern gulf of St. Lawrence. *Marine Mammal Science* **22**, 74–103.
- Mullon, C., Mittaine, J.F., Thebaud, O., Peron, G., Merino, G. and Barange, M. (2009) Modeling the global fishmeal and fish oil markets. *Natural Resource Modeling* **22**, 564–609.
- Murawski, S.A. (2000) Definitions of overfishing from an ecosystem perspective. *ICES Journal of Marine Science* **57**, 649–658.
- Naylor, R.L., Hardy, R.W., Bureau, D.P. *et al.* (2009) Feeding aquaculture in an era of finite resources. *Proceedings of the National Academy of Sciences of the United States of America* **106**, 15103–15110.
- Okey, T.A. and Wright, B.A. (2004) Toward ecosystem-based extraction policies for Prince William Sound, Alaska: integrating conflicting objectives and rebuilding pinnipeds. *Bulletin of Marine Science* **74**, 727–747.
- Pauly, D., Trites, A.W., Capuli, E. and Christensen, V. (1998) Diet composition and trophic levels of marine mammals. *ICES Journal of Marine Science* **55**, 467–481.
- Pikitch, E.K., Santora, C., Babcock, E.A. *et al.* (2004) Ecosystem-based fishery management. *Science* **305**, 346–347.
- Polasky, S. and Segerson, K. (2009) Integrating ecology and economics in the study of ecosystem services: some lessons learned. *Annual Review of Resource Economics* **1**, 409–434.
- Polovina, J.J. (1984) Model of a coral reef ecosystem: 1. The Ecopath model and its application to French Frigate Shoals. *Coral Reefs* **3**, 1–11.
- Polovina, J.J., Howell, E., Kobayashi, D.R. and Seki, M.P. (2001) The transition zone chlorophyll front, a dynamic global feature defining migration and forage habitat for marine resources. *Progress in Oceanography* **49**, 469–483.
- Read, A.J. and Brownstein, C.R. (2003) Considering other consumers: fisheries, predators, and Atlantic herring in the Gulf of Maine. *Conservation Ecology* **7**, 1–12.
- Richerson, K., Levin, P.S. and Mangel, M. (2010) Accounting for indirect effects and non-commensurate values in ecosystem based fishery management (EBFM). *Marine Policy* **34**, 114–119.
- Salomon, A.K., Gaichas, S.K., Jensen, O.P. *et al.* (2011) Bridging the divide between fisheries and marine conservation science. *Bulletin of Marine Science* **87**, 251–274.
- Smith, A.D.M., Brown, C.J., Bulman, C.M. *et al.* (2011) Impacts of fishing low-trophic level species on marine ecosystems. *Science* **333**, 1147–1150.
- Sumaila, U., Marsden, A., Watson, R. and Pauly, D. (2007) A global ex-vessel fish price database: construction and applications. *Journal of Bioeconomics* **9**, 39–51.

- Sunada, J.S., Kelly, P.R., Yamashita, I.S. and Gress, F. (1981) The brown pelican as a sampling instrument of age group structure in the northern anchovy population. *California Cooperative Oceanic Fisheries Investigations Reports* **22**, 65–68.
- Tacon, A.G.J. and Metian, M. (2009) Fishing for feed or fishing for food: increasing global competition for small pelagic forage fish. *Ambio* **38**, 294–302.
- Thompson, P.M., McConnell, B.J., Tollit, D.J., Mackay, A., Hunter, C. and Racey, P.A. (1996) Comparative distribution, movements and diet of harbour and grey seals from the Moray Firth, NE Scotland. *Journal of Applied Ecology* **33**, 1572–1584.
- Van Pelt, T.I., Piatt, J.F., Lance, B.K. and Roby, D.D. (1997) Proximate composition and energy density of some north pacific forage fishes. *Comparative Biochemistry and Physiology Part A: Physiology* **118**, 1393–1398.
- Walter, J.F. and Austin, H.M. (2003) Diet composition of large striped bass (*Morone saxatilis*) in Chesapeake Bay. *Fishery Bulletin* **101**, 414–423.
- Watson, R., Kitchingman, A., Gelchu, A. and Pauly, D. (2004) Mapping global fisheries: sharpening our focus. *Fish and Fisheries* **5**, 168–177.
- Weise, M.J. and Harvey, J.T. (2008) Temporal variability in ocean climate and California sea lion diet and biomass consumption: implications for fisheries management. *Marine Ecology-Progress Series* **373**, 157–172.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Full references for Ecopath models used in this analysis in alphabetical order.

Appendix S2. Supplementary Tables (Tables S1 and S2).

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Viewpoint article

The importance of including predation in fish population models: Implications for biological reference points

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ARTICLE INFO

Article history:

Received 2 November 2010

Received in revised form

16 December 2010

Accepted 17 December 2010

Keywords:

Multispecies models

Ecosystem models

Forage species

Predation

Mortality

Recruitment

Stock assessment

Biological reference points

ABSTRACT

A suite of applications utilizing various fisheries models have demonstrated that natural mortality due to predation is: (1) temporally and ontogenetically variable and (2) especially for forage species, generally higher than assumed in traditional single species stock assessments. Here we demonstrate that biological reference points generated by explicitly incorporating predation mortality into population dynamic models are generally more conservative (e.g., recommend higher standing biomass) than those produced using traditional assessment methods. Because biological reference points are the benchmark against which fisheries management decisions are made, they should reflect the ecological realities faced by each species to the fullest extent possible. We suggest much broader consideration of the more conservative biological reference points produced by explicitly incorporating predation mortality as a component of natural mortality to population models. This approach could implement a powerful yet tractable facet of ecosystem based fisheries management and is especially important for those stocks where predation mortality is known or suspected to be important.

Published by Elsevier B.V.

1. Introduction

Continued anthropogenic impacts have led to calls for a more holistic approach to marine resource management (Larkin, 1996; Micheli, 1999; Garcia et al., 2003; Browman and Stergiou, 2004). Several recent high profile papers have indicated globally serious situations for many marine species, in effect calling for more ecological factors to be considered (e.g., Jackson et al., 2001; Pauly et al., 2002; Myers and Worm, 2003; Pikitch et al., 2004; Worm et al., 2009). Admittedly these observations have not been without their critics and caveats (e.g., Hilborn, 2006). Regardless, there remains a recognized need to examine marine resource management from a more holistic, ecosystem-based perspective (Constable, 2001; Walters et al., 2005; Link, 2010). Central to this ecosystem-based perspective is accounting for all factors that can influence a fisheries stock, including ecological interactions.

There have been calls for fisheries managers to account for species interactions in fish population assessments for at least several decades (e.g., May et al., 1979) yet incorporating basic ecological processes (such as predation) into fisheries stock assess-

ments is still uncommon (Link, 2002; Townsend et al., 2008). Implementing a precautionary, ecosystem-based approach to fisheries management (EBFM) is becoming increasingly advisable for the sustainable harvest of marine capture fisheries (Botsford et al., 1997; Pauly et al., 2002; Garcia et al., 2003; Jennings, 2004). The accumulation of novel approaches to account for ecological interactions in fisheries models (e.g., Hollowed et al., 2000; Whipple et al., 2000; Hvingel and Kingsley, 2006), which have recently begun to be extensively reviewed (Plaganyi, 2007; Townsend et al., 2008), verify that the tools to do so are extant.

Forage species are a particularly germane instance where such ecological interactions should be given due consideration. Such species usually occupy middle trophic levels, serve as a mechanism of converting lower trophic level energy or biomass into forms suitable for upper trophic level consumption, are common prey for a wide range of such upper trophic level species, and can be an important source of standing biomass in an ecosystem. As such, forage species—which are often subject to both predation pressure and to commercial harvesting—are a logical starting point for demonstrating the efficacy of incorporating predation into fisheries population dynamics models. Various authors have found that when consumption of a particular forage species is calculated, the predation mortality values that had been assumed as a part of the total natural mortality in traditional stock assessments were underestimates (e.g., ICES, 1997; Hollowed et al., 2000; NEFSC, 2006) and, unsurprisingly, that predation mortality is temporally and ontogenetically variable (e.g., Gislason and Helgason, 1985; Mohn and

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Bowen, 1996; Tsou and Collie, 2001b). For forage species in particular, careful examination of traditional assumptions regarding predation mortality is needed because the abundance of their major predators (e.g., demersal fish, marine mammals, etc.) could reasonably be expected to increase in the next several years as stocks are rebuilt to meet legal requirements (e.g., Overholtz et al., 2008).

Biological reference points (BRPs) are values assigned to a fishery stock that indicate its status (e.g., biomass, fishing mortality, etc.) and are then used to make fisheries management decisions and actions. BRPs are often compared to signposts with target reference points depicting desirable conditions and limit reference points indicating conditions that should be avoided. There are many types of BRPs (e.g., Restrepo et al., 1998; Restrepo, 1999). Some of the most common limit BRPs are production based and are designed to prevent recruitment overfishing. Examples of these types of reference points are maximum sustainable yield (MSY), and the biomass and fishing rate, B_{MSY} and F_{MSY} respectively, at MSY. Yield per recruit based BRPs are intended to avoid growth overfishing (fishing a stock so heavily that individuals fail to reach their full growth potential). Some examples of these types of reference points are: F_{MAX} (the fishing mortality rate that will produce the maximum yield per recruit) and $F_{0.1}$ (the fishing mortality rate at which a small increase in fishing effort will bring only an additional 10% of the yield per recruit that would occur in an unfished population with the same increase in effort). MSY and its related or proxy reference points can be difficult to pinpoint due to a lack of contrast in survey or landings data and the dynamic nature of fisheries populations (e.g., Mace, 2001), so the International Council for the Exploration of the Seas (ICES) had adopted a precautionary approach to management. These precautionary reference points for biomass, B_{pa} , and fishing mortality, F_{pa} , are respectively higher than and lower than the limit reference points B_{lim} and F_{lim} (ICES, 1998). Yet despite all the caveats among particular BRPs, they remain widespread in their use for fisheries management.

One way to facilitate implementation of EBFM is to calculate BRPs that reflect and account for important ecological interactions. Biological reference points are expected to differ between single and multispecies contexts (ICES, 2001; Walters et al., 2005; Brodziak et al., 2008) and predation mortality in particular can exert a strong influence on BRPs (ICES, 1997). Additionally, the sensitivity of a wide variety of BRPs to trophic interactions has been explored (Collie and Gislason, 2001); thus an appraisal of the effects of incorporating predation or multispecies interactions to BRPs seems warranted to further support EBFM as an operational concept. Our objectives in this manuscript were to: (1) demonstrate the need to consider predation mortality for some stocks by examining example (i.e., not exhaustive, but certainly illustrative) instances where doing so has been significant, (2) elucidate the consequences of failing to do so, particularly for forage species, and (3) note that the tools and approaches to do so are extant as informed by the well studied/high data availability situations discussed herein and that these approaches could be applied to similar but less studied/lower data availability situations.

Here we examine the results of multiple modeling approaches that explicitly incorporated predation mortality for one or more forage species (Table 1). Predation mortality, M_2 , is a component of natural mortality, M . Other sources of natural mortality (M_1) are due to factors such as disease, senescence and injury. Thus, total natural mortality is a combination of M_1 and M_2 :

$$M = M_1 + M_2$$

which in turn is only one facet of total mortality Z , which also includes fishing mortality F :

$$Z = F + M$$

Some of the approaches used thus far for explicit consideration of predation mortality include: production models such as biomass dynamic (e.g., Overholtz et al., 2008; Moustahfid et al., 2009b) and “minimally realistic models” (Punt and Butterworth, 1995), single species age structured models (e.g., Livingston and Methot, 1998; Hollowed et al., 2000; Moustahfid et al., 2009a), multispecies VPA (MSVPA) (e.g., Gislason and Helgason, 1985; Livingston and Jurado-Molina, 2000; Tsou and Collie, 2001a; Tyrrell et al., 2008; Garrison et al., 2010), stochastic multispecies model (SMS; Koster et al., 2009), an area, age and length structured model MULTSPEC (Bogstad et al., 1997), multispecies statistical catch-at-age (e.g., Jurado-Molina et al., 2005), and a flexible, multispecies, spatially explicit statistical model, GADGET (Globally applicable Area-Disaggregated General Ecosystem Toolbox; Begley and Howell, 2004). Again, these examples are meant to be illustrative, not exhaustive. A subset of these investigations compared BRPs calculated using traditional single species methods with those derived with explicit consideration of predation mortality or from aggregated biomass approaches. For these applications, we compare the ratio between BRPs produced by each approach.

2. Observations on BRPs with and without predation

2.1. Interaction between fishing and predation mortality

As noted above, traditional approaches to stock assessment that underestimate the magnitude and dynamic nature of natural mortality for forage species lead to biomass and yield projections that are too optimistic and therefore, not precautionary. There are many geographically diverse examples of a species being subject to substantial predation pressure in addition to being commercially exploited (e.g., capelin, *Mallotus villosus*, in the Barents Sea (Hjermann et al., 2004), walleye pollock, *Theragra chalcogramma*, in the Gulf of Alaska and the Bering Sea (Jurado-Molina and Livingston, 2002) and herring, *Clupea harengus*, in the Northeast US (Overholtz and Link, 2007)). Heavy fishing pressure on species such as these that occupy mid-to-lower trophic levels could lead to competition between humans and other predators for the same relatively low valued fish (e.g., Overholtz et al., 2000; Hjermann et al., 2004). The consequence of this situation could be forgone biomass of higher trophic level species (Gamble and Link, 2009) - which are usually more economically valuable - due to the exploitation of lower trophic levels species.

The relative magnitude of fishing vs. natural mortality, in addition to the timing of peak predation mortality relative to fishing mortality, can also affect productivity estimates of a stock. For example, at low fishing mortality levels, predation mortalities that are only 50% of the fishing mortality value will lead to substantially inaccurate BRPs if predation mortality is not explicitly incorporated into the stock assessment model (ICES, 1997). If landings and consumptive removals are approximately equal, this is even more the case, with predator consumption typically influencing younger age classes of prey species and the resultant changes to BRP estimates (NEFSC, 2007; Overholtz et al., 2008). Similarly, if timing of high commercial exploitation and predatory removals are out of sync and dynamic over the year, traditional single species models that assume constant natural mortality rates will overestimate the stock's recovery potential (e.g., Moustahfid et al., 2009b).

2.2. Traditional assumptions about predation mortality should be carefully examined

Estimates of natural mortality range widely between species and with different modeling approaches (Fig. 1). Nevertheless, from the examples in Fig. 1 (and others, see below) a geographi-

Table 1

Examples of population models that have explicitly accounted for predation mortality and the salient observations derived from doing so. Superscript letters reference natural mortality estimates from different models presented in Fig. 1.

Authors	Predator species	Prey species	Ecosystem	Model type	Observations from including predation
Gislason and Helgason (1985)	10 fish species	e.g., herring, sandeel, sprat, mackerel	North Sea	MSPVA	Amount of biomass killed via predation is 1.6 times greater than the amount taken by fisheries
Punt and Butterworth (1995)	Fur seals, Cape hake, other predatory fish	Cape hake, deep water hake	South African west coast	Minimal realistic model	The effect of seal culls could be small or even detrimental to the hake fishery because of increased predation of one hake species on a congeneric resulting in diminished hake biomass overall
^a Bogstad et al. (1997)	Cod, harp seal, minke whale	Capelin, herring, cod	Barents Sea	MULTSPEC	Increases in marine mammal populations will affect herring, capelin and cod
^g Livingston and Methot (1998)	Walleye pollock, cod, northern fur seals	Walleye pollock	Eastern Bering Sea	SS age structured	Cannibalism by walleye pollock strongly affects recruitment of this species to the fishery.
Hollowed et al. (2000)	Arrowtooth flounder, halibut and Stellar sea lion	Walleye pollock	Gulf of Alaska, USA	SS age structured	Models that failed to account for uncertainty in natural mortality underestimated stock biomass by 20%
^g Livingston and Jurado-Molina (2000)	5 fish and 1 seal species	e.g., Walleye pollock, cod, herring	Eastern Bering Sea, USA	MSVPA	Predation and cannibalism important influences on walleye pollock, especially age 0
Constable (2001), Constable et al. (2000)	Patagonia toothfish	Krill	Antarctic	Generalized yield	Precautionary catch limits for Patagonia toothfish were revised to take into account other predators' demands for krill
^c Tsou and Collie (2001b)	6 demersal fish	Silver hake, herring, mackerel, sand lance	Georges Bank, USA	MSVPA	For all important prey except mackerel, predation mortality was high compared to residual natural mortality
^h Garrison and Link (2004), NEFSC (2006)	Striped bass, weakfish, bluefish	Menhaden	Eastern US coast	MSVPA-X	Predation mortality increased with increased predator populations and has a notable impact on the menhaden
Jurado-Molina et al. (2005)	Walleye pollock, cod	Walleye pollock	Eastern Bering Sea	MS statistical catch-at-age	For older age classes, the statistical model, MSVPA and SSVPA all provide similar population estimates
^f NEFSC (2007)	18 predator species	Northern shrimp	NE US Continental Shelf	Biomass dynamic	Consumptive removals of shrimp were higher than the amount of exploitable biomass estimated from the biomass dynamic model
Harvey et al. (2008)	Pacific hake	3 rockfish species	U.S. Pacific coast	2 species age structured	Estimated time to rebuild was substantially increased by incorporating predation and spatio-temporal overlap (bycatch)
^d Overholtz et al. (2008)	29 species inc. fish, mamm, seabirds	Herring	Georges Bank/Gulf of Maine, USA	Biomass dynamic	Predation mortality rate of herring is related to both its abundance and that of its predators.
^b Tyrrell et al. (2008)	11 demersal fish species	Herring, mackerel	NE US Continental Shelf	MSVPA-X	Predation mortality on youngest age classes of herring and mackerel substantially higher than values used in traditional single species assessments
Koster et al. (2009)	Cod	Juvenile cod, herring, sprat	Eastern Baltic Sea	Age-length SMS	BRP's need to be revised to account for environmental regime shifts and the effects of incorporating cannibalism varies with different assumptions re: environment and recruitment interactions
^e Moustahfid et al. (2009a)	13 demersal fish species	Mackerel	NE US Continental Shelf	SS age structured	Magnitude and uncertainty of mackerel's SSB and recruitment underestimated when predation is not explicitly modeled

MSVPA: multispecies virtual population analysis, MULTSPEC: an area, age and length structured multispecies simulation model, SS age structured: single species age structured, MSVPA-X: expanded multispecies virtual population analysis, MS statistical catch at age: multispecies statistical catch at age, Age-length SMS: age-length-structured multispecies model.

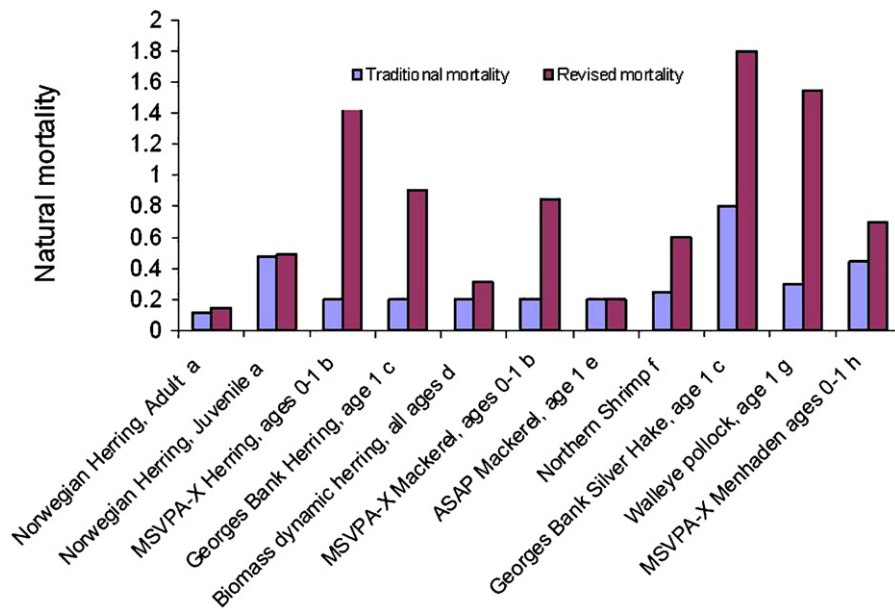


Fig. 1. Comparison of natural mortality rates from traditional stock assessments and models that calculate consumption to more precisely formulate predation mortality (i.e. revised). Source citations for each species that correspond to their superscript for Table 1 are provided.

cally diverse cross-section of forage species' natural mortality rates shows that they can be quite high and in most cases strongly exceed the rates traditionally assumed for these species. For instance, a recent review of the estimated consumptive removals of northern shrimp, *Pandalus borealis*, indicated that a natural mortality rate of 0.6 is more likely than the current value of 0.25 (NEFSC, 2007; Link and Idoine, 2009). When the revised 0.6 value was used to calculate abundance and biomass, an increase of 4–5 times was observed for both biomass and abundance of this species, aligning more closely in magnitude to estimates derived from predatory consumption.

For the majority of the species in Fig. 1, predation mortality forms the bulk of the natural mortality rate. For example, Tsou and Collie (2001a) reported the average annual predation mortality rate over a fourteen year period for age 1 silver hake, *Merluccius bilinearis*, was 1.6. One of the consequences of this chronic underestimation of predation mortality in traditional stock assessments is that the strength of the relationship between prey species population dynamics with that of their predators is underrated.

The importance of incorporating temporally and ontogenetically variable predation mortality has been recognized, especially in the ICES arena, for many years. For instance, although traditional single species methods are still used to calculate BRPs, stock assessments for Baltic herring (*Clupea harengus*), sprat (*Sprattus sprattus*) and cod (*Gadus morhua*) incorporate species interactions such as predation mortality and cannibalism from multispecies models (e.g., ICES, 2008). Similarly for the North Sea, higher natural mortality rates from MSVPA are imported to single species assessments (ICES, 2007). The same has begun in assessments of Atlantic menhaden (*Brevoortia tyrannus*; Garrison and Link, 2004; NEFSC, 2006).

2.3. Effect of accounting for predation on abundance and fishery yield

The revised estimates of natural mortality produced by accounting for predation mortality will also lead to alterations in abundance and fishery yield estimates. For most forage species, the changes in abundance are likely to be particularly dramatic, especially for the youngest age classes. For example, Livingston and Jurado-Molina

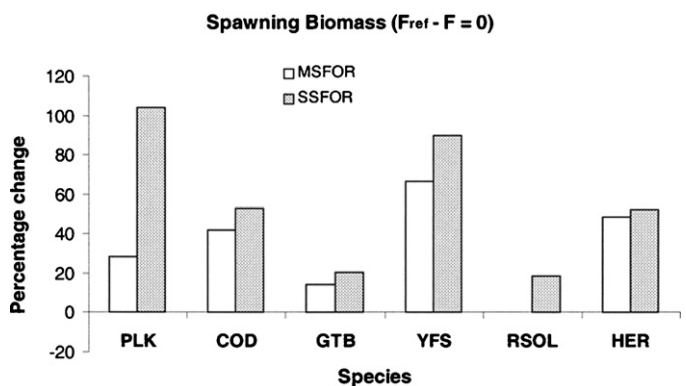


Fig. 2. Percent change in spawning biomass from multispecies and single species forecast models under F_{ref} (average fishing mortality in recent years) vs. a no-fishing scenario. Figure re-printed with permission from Allen Press, North American Journal of Fisheries Management as adapted from Jurado-Molina and Livingston (2002). SSFOR: single species forecasting model, MSFOR: multispecies forecasting model, PLK: walleye pollock, COD: Pacific cod, GTB: Greenland turbot, YFS: yellowfin sole, RSOL: rock sole, HER: Pacific herring.

(2000) found an order of magnitude increase in abundance of age 0 walleye pollock in the Eastern Bering Sea as estimated by MSVPA vs. single species VPA. Similarly, estimates of age 0 menhaden between MSVPA and single species methods differed by approximately 10 billion fish because of the inclusion of predation in the multispecies model (Garrison and Link, 2004). For simulations examining the effect of zero fishing pressure in the eastern Bering Sea ecosystem, MSFOR (multispecies forecast model) produced much smaller increases in spawning biomass than SSFOR (single species forecast model) for 5 of 6 fisheries species (Jurado-Molina and Livingston, 2002, Fig. 2). This is due to multispecies models incorporating the changes in predation mortality that affect commercial species as their predator's populations increase under a no fishing scenario while single species models either ignore or treat this interaction as static. For rock sole, *Lepidopsetta bilineata*, the MSFOR results did not predict an increase in spawning biomass because it was input as a prey item and therefore, increased populations of its predators resulted in higher consumption of rock sole and thus low-

Table 2

Comparison of MSY (maximum sustainable yield) based biological reference points (B_{MSY} : biomass at maximum sustainable yield, SSB_{MSY} : spawning stock biomass at maximum sustainable yield) produced by explicitly incorporating predation (= revised; numerator) and traditional (= fishery; denominator) methods.

Prey species, author	Predators	Revised B_{MSY} or SSB_{MSY} / Traditional B_{MSY} or SSB_{MSY}	Revised MSY/ Traditional MSY
Atlantic herring, Overholtz et al. (2008)	29 species inc. fish, mar mamm, seabirds	1.62	2.39
Atlantic herring, Tyrrell et al. (2008)	11 demersal fish species	1.38	1.25
Atlantic mackerel, Moustahfid et al. (2009a)	13 demersal fish species	2.71	1.83
Atlantic mackerel, Tyrrell et al. (2008)	11 demersal fish species	1.11	1.57
Longfin squid, Moustahfid et al. (2009b)	15 demersal fish species	4.21	3.36

ered its projected spawning biomass estimates. Similar results have also been observed for several species simulated for the southeast Australian fisheries ecosystem (Fulton et al., 2007).

Yield projections for individual species can both increase and decrease when ecological interactions are taken into account, depending on the dynamics between the focal species and whether alternate prey are available. Under the assumption that gray seal, *Halichoerus grypus*, predation on Atlantic cod was additive to other predation mortality, Mohn and Bowen (1996) showed >50% reductions in yield for cod during a time of increased seal abundance. Similarly, in the Northeast US, yields of prey species such as herring will likely decline as their predator stocks recover from decades of overfishing (Overholtz et al., 2008).

For predators with limited foraging areas and little alternate prey, precautionary approaches to calculating fisheries yields are of critical importance. Everson and de la Mare (1996) incorporated the requirements of land based predators (seals, penguins, petrels and other birds) on Antarctic krill, *Euphausia superba*, around South Georgia Island. They suggested a 75% reduction in the precautionary catch limit to allow for acceptable impacts of the krill fishery for these predators with limited foraging ranges.

2.4. Biological reference points are different with ecological considerations

Biological reference points derived with multispecies models differ from their traditional single-species counterparts in that they generally result in more precautionary management advice (Hall, 1999; ICES, 2008). In addition to the studies described in some detail below, many other studies support the finding that BRPs change when predation is explicitly modeled (e.g., ICES, 1997; Collie and DeLong, 1999; Hvingel and Kingsley, 2006). Table 2 summarizes a suite of studies that explicitly compared BRPs from traditional stock assessment model parameterization vs. a situation where consumption on the focal species was calculated and the resulting revised predation mortalities and biomasses were used for BRP estimation.

An important example of changed BRPs from including predation comes from the Baltic Sea ecosystem, where Gislason (1999) reported complex relationships between reference limits for cod and herring and sprat, but with a straightforward overriding conclusion – BRPs of stocks that interact should not be considered in isolation. Similarly, under the adverse recruitment conditions of recent decades, Koster et al. (2009) found that incorporating cannibalism for Eastern Baltic cod lowered the estimated fishing mortality rate that was required to reach B_{pa} . Collie and Gislason (2001) concluded that fishing mortality reference points for prey such as sprat should be conditioned on changes in predator abundance and Jurado-Molina and Livingston (2002) found that their three prey species were also sensitive to the harvest levels of their predators. For Barents Sea capelin Gjøsaeter et al. (2002) advocated stochastic reference points should be developed to account for variable predation by cod and marine mammals. Accurate calculation of reference limits, especially for forage species, requires consid-

eration of the dynamic biomass levels of both predator and prey populations.

Another example of changed BRPs is the northwest Atlantic herring fishery. Overholtz et al. (2008) used a delay difference model to calculate surplus production of age 2+ herring with predatory removals by demersal fishes, marine mammals, large pelagic fishes and seabirds. The B_{MSY} derived from the model with predation explicitly incorporated was higher than the fishery only B_{MSY} by a factor of 1.6. Moustahfid et al. (2009b) incorporated predatory removals of longfin inshore squid, *Loligo pealeii*, using a surplus production model in a similar manner as Overholtz et al. (2008) and found that B_{MUP} (a proxy for B_{MSY} , maximum usable production) increased by more than a factor of three when predation was explicitly accounted for. Similarly, MSY almost doubled and SSB_{MSY} increased by almost three times when predation by 13 demersal fish species was explicitly incorporated into an age-structured assessment model for Atlantic mackerel (*Scomber scombrus*, Moustahfid et al., 2009a). In an MSVPA of 14 predator stocks and 2 age structured prey species (Atlantic herring and Atlantic mackerel) of the Northeast US Continental shelf ecosystem, Tyrrell et al. (2008) found that herring's MSY and B_{MSY} increased in a multispecies vs. single species context, but not to as strongly as reported by Overholtz et al. (2008). For mackerel, the MSVPA biomass estimates also resulted in BRPs that were more conservative than the reference points produced by traditional single-species methods (Tyrrell et al., 2008). Different types of modeling approaches (e.g., age structured vs. non-age structured) and different suites of predators and input parameters have resulted in variable point estimates of BRPs (e.g., Overholtz et al., 2008 vs. Tyrrell et al., 2008). Despite variation in the absolute value of BRPs with and without predation incorporated, B_{MSY} or SSB_{MSY} increased by >10% for all situations where these types of comparisons were made (Table 2). For other reference points such as F_{crash} and $F_{0.1}$ (both based off of stock-recruitment relationships, with $F_{0.1}$ being the fishing mortality rate at 10% of the maximal yield per recruit rate, and F_{crash} being the fishing rate which will produce a long-term spawning biomass per recruit (S/R) equal to the inverse of the instantaneous rate of variation of R with the biomass, at the initial point ($S=0, R=0$)), a similar finding of more conservative reference points being calculated has been reported by other authors. For example, both $F_{0.1}$ and F_{crash} were lower in a multispecies context for MSVPAs of the Barents Sea and the North Sea (ICES, 1997).

As the majority of the aforementioned studies show, inferences from a variety of models for various fisheries species indicate that BRPs for forage species are different and generally point to more conservative harvest rates when ecological considerations are accounted for. To broaden the applicability to EBFM, BRPs can also be calculated for a suite of species in addition to individual values for each species. Mueter and Megrey (2006) aggregated fisheries species into a surplus production model to calculate an ecosystem-level MSY (termed multi-species maximum surplus production) for the Gulf of Alaska and Bering Sea commercially exploited groundfish species. They found that in both ecosystems, this ecosystem-level MSY was smaller than the component sum of single species MSYs (Table 3) and furthermore, that incorporation

Table 3
Comparison of MSY based biological reference points produced by summing single species reference points vs. ecosystem estimated reference points from surplus production models.

Ecosystem, author	Focal species	Ecosystem B_{MSY}/sum of SSB_{MSY}	Ecosystem MSY/sum of $SS\ MSYs$
Northeast US Continental Shelf, NEFSC (2008)	19 groundfish stocks, 2007 assessment	0.89	0.96
Northeast US Continental Shelf, NEFSC (2008)	19 groundfish stocks, previous assessment	0.53	0.63
Gulf of Alaska, Mueter and Megrey (2006)	12 groundfish species	NA	0.61
Bering Sea/Aleutian Islands, Mueter and Megrey (2006)	11 groundfish species	NA	0.72

of environmental variability led to further depressed maximum multi-species surplus production estimates. The authors interpreted these results as indicating that more conservative reference points are the appropriate management targets. Similarly, for the Georges Bank fish community, Collie and DeLong (1999) found that multi-species yield was lower than single species yields when the same combination of harvest rates were used for each calculation. They attribute this result to predators consuming some of the “surplus production”. A similar exercise was undertaken for the Northeast US Continental shelf ecosystem with calculations for all 19 commercially exploited groundfish stocks (NEFSC, 2008). For groundfish, both the most recent and previous assessments indicated that aggregate MSY was lower than the sum of single species MSYs and aggregate B_{MSY} was also lower than the sum of analogous single-species components. However, for the most recent assessment, the difference between the aggregate and summed single species reference points had narrowed, indicating that the current management reference targets were more reasonable (NEFSC, 2008). Overall, most research suggests that current single-species management targets may not be conservative enough to support maximum system-wide production.

2.5. Reevaluating the argument of “increasing uncertainty” by adding in predation mortality

There are several forms of uncertainty in the assessment process (Peterman, 2004; Link et al., 2010) and they all can be important when evaluating the status of fish stocks. We challenge the assertion that precision or estimation uncertainty (i.e., statistical estimation) outweighs other sources of uncertainty such as magnitudinal, process or accuracy uncertainty (i.e., closer to correct order of magnitude of estimates by inclusion of additional factors). These other sources of uncertainty are often downplayed because of concerns regarding adding extra information to these models (Peterman, 2004). The concerns of the precision types of uncertainty largely center about estimation error, particularly of predatory consumption and consumptive removals from food habits data because those data and associated calculations are used to estimate predation mortality. Yet we note that even without requisite food habits data and the ability to model consumption directly, there are other approaches to generically include predation mortality in assessments (see below). For example, M need not be a fixed parameter; in terms of process error, having a time invariant natural mortality for stocks can lead to erroneous projections and estimates, as seen in the shrimp example above (NEFSC, 2007; Link and Idoine, 2009). This process error is magnified when an assessment is using an age or stage-based model, as noted in numerous examples in the previous section as compared to using an age invariant natural mortality (Tables 1 and 2). The simple point we make is that including ecological interactions may in fact increase estimation uncertainty, but may also decrease process uncertainty. Often the two are tradeoffs between better precision in parameter estimates and more accurate magnitudes of those same parameter estimates.

By excluding predation, model results will certainly reflect improved precision uncertainties. But as we have shown, doing so can affect accuracy of the estimates by several orders of magnitude. In such instances we suggest relaxation of variance/confidence interval precision criteria to incorporate predation and to better minimize process, magnitude and accuracy uncertainties.

We recognize that even if predation is suspected to be important and should be considered, not all ecosystems or regions have the extant data to estimate a long time series of consumption (e.g., Overholtz et al., 2008), to validate various functional forms of predation (Moustahfid et al., 2010), or to estimate predation mortality directly and thus address the process uncertainty concern. However, we note even in instances where there are no food habits data, there are models and general principles very much extant (e.g., ICES, 1997; Collie and DeLong, 1999; *sensu* Moustahfid et al., 2010) that can relate predator and prey abundance to inform predation parameters used in calculating predation and revised BRPs. Usually, at least in most fisheries contexts, there are some set of surveys that can estimate the abundances or biomasses of both predators and prey in a given ecosystem, which can then be statistically linked (e.g., GLMs relating abundance to % BW consumed or to other consumption values; *sensu* Overholtz et al., 2008) or linked via process modeling (e.g., various functional response forms; *sensu* Moustahfid et al., 2010). Certainly using such an indirect approach may initially only provide contextual information in stock assessments, perhaps only informing suggested revisions to M or Z (e.g., the *Pandalus* example above; NEFSC, 2007; Link and Idoine, 2009). And certainly the sensitivities to the parameters and functional forms will need to be examined and presented in full sensitivity or risk analysis contexts (Punt and Butterworth, 1995; Peterman, 2004; Kinzey and Punt, 2009). Clearly not all instances will resolve concerns over uncertainty to the point of being useful, and certainly such approaches will need to be evaluated with and compared to best practices and results from similar situations in comparable ecosystems. And certainly these indirect approaches should be considered with all the appropriate caveats. Yet what we have noted here is at least one way to initially scope out the possible effects of predation on stocks when doing so is germane and where highly resolved data may not be available. This highlights that there are theoretical and empirical approaches readily available to begin to elucidate the magnitude of these ecological interactions in instances where there is a real or perceived limited set of data.

2.6. Effect of rebuilding or recovery of marine predators

In the US as in many other areas around the world, fisheries managers are attempting to rebuild severely depleted stocks. As the abundance of high trophic level demersal fish increases, the importance of their predation on forage stocks will likewise be enhanced. For instance, the abundance of marine mammals along the US east coast has generally increased over the past two decades (Waring et al., 2002) and these escalating marine mammal populations are expected to have a negative influence on the abundance of forage

stocks (Bogstad et al., 1997; Overholtz and Link, 2007). This is also the case for seals in Atlantic Canada (Bowen et al., 2008, 2009), such that concerns over seal predation on fish stocks have led to calls for seal culls to allow various fish species to escape from a “predator pit” that may be regulating the abundance of these stocks. In the North Sea, herring are recovering from overfishing in the late 1960s and their consumption of sandeel, *Ammodytes marinus*, larvae may have led to food shortages for breeding seabirds (ICES, 2007). Rebuilding predator populations, whether they are fisheries species; or protected, endangered or threatened marine mammals; or other consumers such as seabirds, will affect the abundance of their prey (e.g., Punt and Butterworth, 1995; Constable, 2001; ICES, 2008). Failing to account for these types of predatory interactions in estimating the stock recovery trajectory of prey species will lead to poor management advice such as overly optimistic recovery times (ICES, 1997; Bjørnsson and Sigurdsson, 2003; Moustahfid et al., 2009b). As an example, Harvey et al. (2008) found that by incorporating predation by Pacific hake, *Merluccius productus*, on widow rockfish, *Sebastes entomelas*, there were significant increases in the median time to rebuild widow rockfish populations.

3. Conclusions

We assert that the need to consider species interactions in fisheries management has been reasonably documented here and elsewhere (e.g., Hollowed et al., 2000; Jurado-Molina and Livingston, 2002). We recognize that the influence of predation mortality for estimating abundance is more important for some fish species than others. But we trust that the exemplary case studies we have shown highlight the importance of considering predation for at least some marine fish species. The methods to incorporate predation mortality into quantitative determinations of BRPs exist across a wide range of applications. The concerns over increasing precision uncertainty by including predatory considerations are largely offset by improvements such inclusions provide to process and accuracy uncertainties. None of what we point out is singularly novel, but what we have collectively documented is how important including M_2 can be, especially for forage species.

An ecosystem based approach to fisheries management calls for, among other things, a “best practice” approach for BRP calculations. Population dynamics models that explicitly include predation mortality indicate that BRPs that treat overall natural mortality as low and constant through time result in management advice that is overly optimistic. We show that a wide variety of modeling approaches have produced BRPs that are more conservative when predation mortality is explicitly incorporated in prey abundance calculations. For a strongly interacting predator prey complex (e.g., cod, herring and sprat in the Baltic) simultaneously achieving MSY as determined by single-species methods has been deemed impossible (ICES, 2008; *sensu* NEFSC, 2008; *sensu* Worm et al., 2009). Explicitly adopting the more conservative reference points will not insure sustainability of the fisheries for forage species in and of itself. Nevertheless, we recommend that these revised reference points be presented as part of the package of management informing advice because they represent an easily implemented component of EBFM, account for more factors that can affect a stock, and represent a precautionary approach. More so, we conclude by noting that the need to do them is apparent, the tools to do so are extant, and the consequences of continuing to ignore these considerations could be problematic.

Acknowledgments

We extend our appreciation to the present and past members of the Food Web Dynamics Program for their maintenance of a

large food habits database that in many respects allowed us to do these calculations and think more broadly about these types of approaches. Those efforts made the explicit incorporation of predation for models of the northeast US ecosystems possible. The content of this paper benefited from comments provided by two anonymous reviewers. This work was supported by Lenfest Ocean Program Grant Number 2004-001492-105.

References

- Bjørnsson, H., Sigurdsson, T., 2003. Assessment of golden redfish (*Sebastes marinus* L.) in Icelandic waters. *Sci. Mar.* 67 (1), 301–314.
- Begley, J., Howell, D., 2004. An overview of GADGET, Globally applicable Area-Disaggregated General Ecosystem Toolbox. ICES CM 2004/FF:13, p. 16.
- Bogstad, B., Hauge, K.H., Ulltang, Ø., 1997. MULTISPEC - A multi-species model for fish and marine mammals in the Barents Sea. *J. Northwest Atl. Fish. Sci.* 22, 317–341.
- Botsford, L.W., Castilla, J.C., Peterson, J.H., 1997. The management of fisheries and marine ecosystems. *Nature* 277, 509–515.
- Proceedings of the National Workshop on the Impacts of Seals on Fish Populations in Eastern Canada. 12–16 November (Part 1) Bowen, W.D., Hammill, M.O., Koen-Alonso, M., Stenson, G., Swain, D.P., Trzcinski, K. (Eds.), 2008. DFO Canadian Science Advisory Secretariat Proceedings Series 2008, p. 021.
- Proceedings of the National Workshop on the Impacts of Seals on Fish Populations in Eastern Canada. Fisheries and Oceans Canada, Halifax, November 24–28 (Part 2) Bowen, W.D., Hammill, M.O., Koen-Alonso, M., Stenson, G., Swain, D.P., Trzcinski, K. (Eds.), 2009. DFO Canadian Science Advisory Secretariat Proceedings Series 2009, p. 020.
- Brodziak, J., Cadrin, S.X., Legault, C.M., Murawski, S.A., 2008. Goals and strategies for rebuilding New England groundfish stocks. *Fish. Res.* 94, 355–366.
- Browman, H.I., Stergiou, K.I., 2004. Perspectives on ecosystem based approaches to the management of marine resources. *Mar. Ecol. Prog. Ser.* 274, 269–303.
- Collie, J.S., DeLong, A.K., 1999. Multispecies interactions in the Georges Bank fish community. *Ecosystem Approaches for Fisheries Management*, Alaska Sea Grant College Symposium, AK-SG-99-01.
- Collie, J.S., Gislason, H., 2001. Biological reference points for fish stocks in a multi-species context. *Can. J. Fish. Aquat. Sci.* 58, 2167–2176.
- Constable, A.J., 2001. The ecosystem approach to managing fisheries: achieving conservation objectives for predators of fished species. *CCAMLR (Commission for the Conservation of Antarctic Marine Living Resources)*. *Science* 8, 37–64.
- Constable, A.J., de la Mare, W.K., Agnew, D.J., Everson, I., Miller, D., 2000. Managing fisheries to conserve the Antarctic marine ecosystem: practical implementation of the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR). *ICES J. Mar. Sci.* 57, 778–791.
- Everson, I., de la Mare, W.K., 1996. Some thoughts on precautionary measures for the krill fishery. *CCAMLR Sci.* 3, 1–11.
- Fulton, E.A., Smith, A.D.M., Smith, D.C., 2007. Alternative Management Strategies for Southeast Australian Commonwealth Fisheries: Stage 2: Quantitative Management Strategy Evaluation. Australian Fisheries Management Authority Report, Canberra, Australia.
- Gamble, R.J., Link, J.S., 2009. Analyzing the tradeoffs among ecological and fishing effects on an example fish community: a multispecies (fisheries) production model. *Ecol. Model.* 220, 2570–2582.
- Garcia S.M., Zerbi A., Aliaume C., Do Chi T., Lasserre G., 2003. The ecosystem approach to fisheries. Issues, terminology, principles, institutional foundations, implementation and outlook. FAO Fisheries Technical Paper. No. 443. Rome, FAO.
- Garrison, L.P., Link, J.S., 2004. An expanded multispecies virtual population analysis (MSVPA-X) to evaluate predator-prey interactions in exploited fish ecosystems. In: User's Manual and Model Description, Version 1.1. Atlantic States Marine Fisheries Commission (accessed November 2008) www.asmfc.org/researchStatistics/msvpa-X.DocumentationJune03.pdf.
- Garrison, L.P., Link, J.S., Cieri, M., Kilduff, P., Sharov, A., Vaughan, D., Muffley, B., Mahmoudi, B., Latour, R., 2010. An Expansion of the MSVPA Approach for Quantifying Predator-Prey Interactions In Exploited Fish Communities. *ICES J. Mar. Sci.* 67, 856–870.
- Gislason, H., 1999. Single and multispecies reference points for Baltic fish stocks. *ICES J. Mar. Sci.* 56, 571–583.
- Gislason, H., Helgason, T., 1985. Species interaction in assessment of fish stocks with special application to the North Sea. *Dana* 5, 1–44.
- Gjøsaeter, H., Bogstad, B., Tjelmeland, S., 2002. Assessment methodology for Barents Sea capelin, *Mallotus villosus* (Müller). *ICES J. Mar. Sci.* 59, 1086–1095.
- Hall, S.J., 1999. Managing fisheries within ecosystems: can the role of reference points be expanded? *Aquat. Conserv.* 9 (6), 579–583.
- Harvey, C.J., Gross, K., Simon, V.H., Hastie, J., 2008. Trophic and fishery interactions between Pacific hake and rockfish: effect on rockfish population rebuilding times. *Mar. Ecol. Prog. Ser.* 365, 165–176.
- Hilborn, R., 2006. Faith-based fisheries. *Fisheries* 31, 554–555.
- Hjermann, D.Ø., Ottersen, G., Stenseth, N.C., 2004. Competition among fishermen and fish causes the collapse of Barents Sea capelin. *Proc. Natl. Acad. Sci. U.S.A.* 101 (32), 11679–11684.
- Hollowed, A.B., Ianelli, J.N., Livingston, P.A., 2000. Including predation mortality in stock assessments: a case study for Gulf of Alaska walleye pollock. *ICES J. Mar. Sci.* 57, 279–293.

- Hvingel, C., Kingsley, M.C.S., 2006. A framework to model shrimp (*Pandalus borealis*) stock dynamics and to quantify the risk associated with alternative management options, using Bayesian methods. *ICES J. Mar. Sci.* 63, 68–82.
- ICES, 1997. Report of the multispecies assessment working group. ICES Headquarters, Copenhagen, Denmark, 11–19 August 1997. ICES Ciencia Marina 1997/Assess:16.
- ICES, 1998. Report of the study group on the precautionary approach to fisheries management, February 1998. ICES Ciencia Marina 1998/ACFM:10.
- ICES, 2001. Report of the study group on multispecies predictions in the Baltic. ICES Ciencia Marina 2001:H04, Charlottenlund, Denmark.
- ICES, 2007. Report of the Working Group on Multispecies Assessment Methods (WGSAM), 15–19 October 2007, San Sebastian, Spain. ICES Ciencia Marina 2007/RMC:08.
- ICES, 2008. Report of the Workshop on Reference Points in the Baltic Sea (WKREF-BAS), 12–14 February 2008, ICES Headquarters, Copenhagen. ICES Ciencia Marina 2008/ACOM:28. Ref: AMAWGC.
- Jackson, J.B.C., Kirby, M.X., Berger, W.H., Bjørndal, K.A., Botsford, L.W., Bourque, B.J., Bradbury, R.H., Cooke, R., Erlandson, J., Estes, J.A., Hughes, T.P., Kidwell, S., Lange, C.B., Lenihan, H.S., Pandolfi, J.M., Peterson, C.H., Steneck, R.S., Tegner, M.J., Warner, R.R., 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293, 629–638.
- Jennings, S., 2004. The ecosystem approach to fisheries management: a significant step towards sustainable use of the marine environment? *Mar. Ecol. Prog. Ser.* 274, 269–303.
- Jurado-Molina, J., Livingston, P., 2002. Multispecies perspectives on the Bering Sea groundfish fisheries management regime. *N. Am. J. Fish. Manage.* 22, 1164–1175.
- Jurado-Molina, J., Livingston, P.A., Ianelli, J.N., 2005. Incorporating predation interactions in a statistical catch-at-age model for a predator-prey system in the Eastern Bering Sea. *Can. J. Fish. Aquat. Sci.* 62, 1865–1873.
- Kinzey, D., Punt, A.E., 2009. Multispecies and single-species models of fish population dynamics: comparing parameter estimates. *Nat. Res. Model.* 22 (1), 67–104.
- Koster, F., Vinther, M., MacKenzie, B., Plikshs, M., Eero, M., 2009. Environmental effects on recruitment and implications for biological reference points of Eastern Baltic cod. *J. Northwest Atl. Fish. Sci.* 41, 205–220.
- Larkin, P.A., 1996. Concepts and issues in marine ecosystems management. *Rev. Fish. Biol. Fish.* 6, 139–164.
- Link, J.S., 2002. Ecological considerations in fisheries management: when does it matter? *Fisheries* 27 (4), 10–17.
- Link, J.S., 2010. *Ecosystem-Based Fisheries Management: Confronting Tradeoffs*. Cambridge Univ. Press, Cambridge, UK.
- Link, J.S., Idoine, J.S., 2009. Estimates of predator consumption of the northern shrimp *Pandalus borealis* with implications for estimates of population biomass in the Gulf of Maine. *N. Am. J. Fish. Manage.* 29 (6), 1567–1583.
- Link, J.S., Ihde, T.F., Townsend, H.M., Osgood, K.E., Schirripa, M.J., Kobayashi, D.R., Gaichas, S., Field, J.C., Levin, P.S., Aydin, K.Y., Harvey, C.J. (Eds.), 2010. Report of the Second National Ecosystem Modeling Workshop (NEMoW II): Bridging the Credibility Gap—Dealing with Uncertainty in Ecosystem Models. U.S. Dep. Commerce, NOAA Tech. Memo. NMFS-F/SPO-102, p. 72.
- Livingston, P.A., Methot, R.D., 1998. Incorporation of predation into a population assessment model of eastern Bering Sea walleye pollock. In: *Fishery Stock Assessment Models*. Alaska Sea Grant College Program Publication, AK-SG-98-01.
- Livingston, P.A., Jurado-Molina, J., 2000. A multispecies virtual population analysis of the eastern Bering Sea. *ICES J. Mar. Sci.* 57, 294–299.
- Mace, P.M., 2001. A new role for MSY in single-species and ecosystem approaches to fisheries stock assessment and management. *Fish. Fish.* 2, 2–32.
- May, R.M., Beddington, J.R., Clark, C.W., Holt, S.J., Laws, R.M., 1979. Management of multispecies fisheries. *Science* 205 (4403), 267–277.
- Micheli, F., 1999. Eutrophication, fisheries and consumer–resource dynamics in marine pelagic ecosystems. *Science* 285 (5432), 1396–1398.
- Mohn, R., Bowen, W.D., 1996. Gray seal predation on the Eastern Scotian Shelf: modelling the impact on Atlantic cod. *Can. J. Fish. Aquat. Sci.* 53, 2722–2738.
- Moustahfid, H., Overholtz, W.J., Link, J.S., Tyrrell, M.C., 2009a. The advantage of explicitly incorporating predation mortality into age-structured stock assessment models: an application for Northwest Atlantic mackerel. *ICES J. Mar. Sci.* 66 (3), 445–454.
- Moustahfid, H., Tyrrell, M.C., Link, J.S., 2009b. Accounting explicitly for predation mortality in surplus production models: an application to longfin squid (*Loligo pealeii*). *N. Am. J. Fish. Manage.* 29, 1555–1566.
- Moustahfid, H., Tyrrell, M.C., Link, J.S., Nye, J.A., Smith, B.E., Gamble, R.J., 2010. Functional feeding responses of piscivorous fishes from the Northeast US continental shelf. *Oecologia* 163 (4), 1059–1067.
- Mueter, F.J., Megrey, B.A., 2006. Using multi-species surplus production models to estimate ecosystem-level maximum sustainable yields. *Fish. Res.* 81, 189–201.
- Myers, R.A., Worm, B., 2003. Rapid worldwide depletion of predatory fish communities. *Nature* 423, 280–283.
- Northeast Fisheries Science Center (NEFSC), 2006. 42nd Northeast Regional Stock Assessment Workshop (42nd SAW): 4th SAW assessment report. Part B. US Department of Commerce, Northeast Fish Science Center Reference Document 06-09b.
- Northeast Fisheries Science Center (NEFSC), 2007. 45th Northeast Regional Stock Assessment Workshop (45th SAW): 45th SAW assessment US Department of Commerce, Northeast Fish Science Center Reference Document 07-16.
- Northeast Fisheries Science Center (NEFSC), 2008. Assessment of 19 Northeast Groundfish Stocks through 2007 Report of the 3rd Groundfish Assessment Review Meeting (GARM III), Northeast Fisheries Science Center, Woods Hole, Massachusetts, August 4–8, 2008. Section 2.1. US Department of Commerce, Northeast Fisheries Science Center Reference Document, 08-15.
- Overholtz, W.J., Link, J.S., Suslowicz, L.E., 2000. Consumption of important pelagic fish and squid by predatory fish in the Northeastern USA shelf ecosystem with some fishery comparisons. *ICES J. Mar. Sci.* 57, 1147–1159.
- Overholtz, W.J., Link, J.S., 2007. Consumption impacts by marine mammals, fish, and seabirds on the Gulf of Maine–Georges Bank Atlantic Herring (*Clupea harengus*) complex during 1977–2002. *ICES J. Mar. Sci.* 64, 83–96.
- Overholtz, W.J., Jacobson, L.D., Link, J.S., 2008. An ecosystem approach for assessment advice and biological reference points for the Gulf of Maine–Georges Bank herring complex. *N. Am. J. Fish. Manage.* 28, 247–257.
- Pauly, D., Christensen, V., Guenette, S., Pitcher, T.J., Sumaila, U.R., Walters, C.J., Watson, R., Zeller, D., 2002. Towards sustainability in world fisheries. *Nature* 418, 689–695.
- Peterman, R.M., 2004. Possible solutions to some challenges facing fisheries scientists and managers. *ICES J. Mar. Sci.* 61, 1331–1343.
- Pikitch, E.K., Santora, C., Babcock, E.A., Bakun, A., Bonfil, R., Conover, D.O., Dayton, P., Doukakis, P., Fluharty, D., Heneman, B., Houde, E.D., Link, J., Livingston, P., Mangel, M., McAllister, M., Pope, J., Sainsbury, K.J., 2004. Ecosystem-based fishery management. *Science* 305 (5682), 346–347.
- Plaganyi, E.E., 2007. Models for an ecosystem approach to fisheries. *FAO Fisheries Technical Paper No. 477*. Rome, FAO, p. 108.
- Punt, A.E., Butterworth, D.S., 1995. The effects of future consumption by the Cape fur seal on catches and catch rates of the Cape hakes. 4. Modelling the biological interaction between Cape fur seals *Arctocephalus pusillus pusillus* and the Cape hakes *Merluccius capensis* and *M. paradoxus*. *S. Afr. J. Mar. Sci.* 16, 255–285.
- Restrepo, V.R. (Ed.), 1999. Proceedings of the 5th National NMFS Stock Assessment Workshop: Providing Scientific Advice to Implement the Precautionary Approach Under the Magnuson-Stevens Fishery Conservation and Management Act. U.S. Dep. Commer., National Oceanic and Atmospheric Administration Technical Memorandum NMFS-F/SPO-40.
- Restrepo, V.R., Thompson, G.G., Mace, P.M., et al., 1998. Technical Guidance on the Use of Precautionary Approaches to Implementing National Standard 1 of the Magnuson-Stevens Fishery Conservation and Management Act. National Oceanic and Atmospheric Administration Technical Memorandum NMFS-F/SPO 31.
- Townsend, H.M., Link, J.S., Osgood, K.E., Gedamke, T., Watters, G.M., Polovina, J.J., Levin, P.S., Cyr, N., Aydin, K. (Eds.), 2008. Report of the National Ecosystem Modeling Workshop (NEMoW). National Marine Fisheries Service, National Oceanic and Atmospheric Administration Technical Memorandum NMFS-F/SPO-87, p. 93.
- Tsou, T.S., Collie, J.S., 2001a. Predation-mediated recruitment in the Georges Bank fish community. *ICES J. Mar. Sci.* 58, 994–1001.
- Tsou, T.S., Collie, J.S., 2001b. Estimating predation mortality in the Georges Bank fish community. *Can. J. Fish. Aquat. Sci.* 58, 908–922.
- Tyrrell, M.C., Moustahfid, H., Link, J.S., Overholtz, W.J., 2008. Evaluating the effect of predation mortality on forage species population dynamics in the Northeast US continental shelf ecosystem: an application using multispecies virtual population analysis. *ICES J. Mar. Sci.* 65, 1689–1700.
- Walters, C.J., Christensen, V., Martell, S.J., Kitchell, J.F., 2005. Possible ecosystem impacts of applying MSY policies from single-species assessment. *ICES J. Mar. Sci.* 62, 558–568.
- Waring, G.T., Quintal, J.M., Fairfield, C.P. (Eds.), 2002. U.S. Atlantic and Gulf of Mexico marine mammal stock assessments – 2002. National Oceanic and Atmospheric Administration Technical Memorandum NMFS-NE-169.
- Whipple, S.J., Link, J.S., Garrison, L.P., Fogarty, M.J., 2000. Models of predation and fishing mortality in aquatic ecosystems. *Fish. Fish.* 1 (1), 22–40.
- Worm, B., Hilborn, R., Baum, J.K., Branch, T.A., Collie, J.S., Costello, C., Fogarty, M.J., Fulton, E.A., Hutchings, J.A., Jennings, S., Jensen, O.P., Lotze, H.K., Mace, P.M., McClanahan, T.R., Minto, C., Palumbi, S.R., Parma, A.M., Ricard, D., Rosenberg, A.A., Watson, R., Zeller, D., 2009. Rebuilding global fisheries. *Science* 325, 578–585.

creasing demands of supporting and moving greater weight on land and the benefits of having more upright toe bones but directing some loads away from the toes with the predigits and fat pad, which resulted in the peculiar compromise that persists in the feet of extant elephants.

The recognition of elephant predigits as enlarged sesamoids that perform digit-like functions fuels inspiration for examining the evolution of foot function, terrestriality, and gigantism in other lineages. Sauropod dinosaurs had expansive foot pads, particularly in their pedes (24); however, no evidence of predigits has been found. Considering that the predigits form on the medial border of the feet, they would tend to be lost if digit I is lost or reduced, as it was in early perisodactyls and artiodactyls. This loss might limit foot pad expansion and thereby explain why rhinos and hippos seem to lack predigits [but see (18) for a possible rudimentary pollex in hippos] and have less expanded foot pads than elephants do (8). Regardless, the previously misunderstood and neglected predigits of elephants now deserve recognition as a remarkable case of evolutionary exaptation (4), revealing how elephants evolved their specialized foot form and function.

References and Notes

1. D. D. Davis, *Feldiana* 3, 1 (1964).
2. H. Endo *et al.*, *J. Anat.* **195**, 295 (1999).
3. S. J. Gould, *Nat. Hist.* **87**, 20 (1978).
4. S. J. Gould, E. S. Vrba, *Paleobiology* **8**, 4 (1982).
5. M. Fabrezi, *Zool. J. Linn. Soc.* **131**, 227 (2001).
6. M. R. Sánchez-Villagra, P. R. Menke, *Zoology* **108**, 3 (2005).
7. P. Blair, *Philos. Trans.* **27**, 53 (1710).
8. H. Neuville, *Arch. Mus. Natl. Hist. Nat. Paris* **13**, 6e Serie, 111 (1935).
9. K. von Bardeleben, *Proc. Zool. Soc.* **1894**, 354 (1894).
10. C. Mitgutsch *et al. Biol. Lett.*, 10.1098/rsbl.2011.0494 (2011).
11. Materials and methods are available as supporting material on Science Online.
12. G. E. Weissenburger *et al.*, *J. Anat.* **209**, 781 (2006).
13. F. Galis, J. J. M. van Alphen, J. A. J. Metz, *Trends Ecol. Evol.* **16**, 637 (2001).
14. J. Prochel, P. Vogel, M. R. Sánchez-Villagra, *J. Anat.* **205**, 99 (2004).
15. J. R. Hutchinson, C. E. Miller, G. Fritsch, T. Hildebrandt, in *Anatomical Imaging: Towards a New Morphology*, R. Frey, H. Endo, Eds. (Springer, Berlin, 2009), pp. 23–38.
16. C. E. Miller, C. Basu, G. Fritsch, T. Hildebrandt, J. R. Hutchinson, *J. R. Soc. Interface* **5**, 465 (2008).
17. D. R. Carrier, N. C. Heglund, K. D. Earls, *Science* **265**, 651 (1994).
18. A. B. Clifford, *J. Vertebr. Paleontol.* **30**, 1827 (2010).
19. N. Court, *Palaontogr. Abt. A* **226**, 125 (1993).
20. D. E. Lieberman *et al.*, *Nature* **463**, 531 (2010).
21. F. Michilsen, P. Aerts, R. Van Damme, K. D'Août, *J. Zool. (London)* **279**, 236 (2009).
22. A. A. Biewener, *Science* **250**, 1097 (1990).
23. M. N. Scholz, M. F. Bobbert, A. J. van Soest, J. R. Clark, J. van Heerden, *J. Exp. Biol.* **211**, 3266 (2008).
24. M. F. Bonnan, in *Thunder-Lizards: the Sauropodomorph Dinosaurs*, K. Carpenter, V. Tidwell, Eds. (Indiana Univ. Press, Bloomington, IN, 2005), pp. 346–380.
25. M. M. Smuts, A. J. Bezuidenhout, *Onderstepoort J. Vet. Res.* **69**, 1 (1993).

26. M. M. Smuts, A. J. Bezuidenhout, *Onderstepoort J. Vet. Res.* **61**, 51 (1994).
27. A. Boyde, R. Travers, F. H. Glorieux, S. J. Jones, *Calcif. Tissue Int.* **64**, 185 (1999).
28. C. Delmer, *Acta Palaeontol. Pol.* **54**, 561 (2009).
29. E. Gheerbrant, *Proc. Natl. Acad. Sci. U.S.A.* **106**, 10717 (2009).
30. E. Gheerbrant, P. Tassy, *C. R. Palevol.* **8**, 281 (2009).

Acknowledgments: We thank the staff of the Structure and Motion Laboratory of the Royal Veterinary College for assistance and three anonymous reviewers for constructive criticism. Many individuals assisted with the collection of the cadaveric data; we particularly thank the European-based zoos that provided the specimens and G. Fritsch for CT scans done in Germany. O. Cosar, R. Weller, A. Wilson, and K. Jespers assisted with the ex vivo loading experiments. J. Molnar assisted with Figs. 1 to 4 and the movies. This project was funded by the Biotechnology and Biological Sciences Research Council (BBSRC) (grants BB/C51684/1 and BB/H002782/1 to J.R.H.). Additionally, A.A.P. appreciates funding from Arthritis Research UK and the BBSRC, and A.B. was supported by the Veterinary Advisory Committee of the UK Horserace Betting Levy Board. The data reported in this paper are tabulated in the SOM. The authors declare no conflicts of interest.

Supporting Online Material

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20 July 2011; accepted 8 November 2011

10.1126/science.1211437

Global Seabird Response to Forage Fish Depletion—One-Third for the Birds

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Determining the form of key predator-prey relationships is critical for understanding marine ecosystem dynamics. Using a comprehensive global database, we quantified the effect of fluctuations in food abundance on seabird breeding success. We identified a threshold in prey (fish and krill, termed “forage fish”) abundance below which seabirds experience consistently reduced and more variable productivity. This response was common to all seven ecosystems and 14 bird species examined within the Atlantic, Pacific, and Southern Oceans. The threshold approximated one-third of the maximum prey biomass observed in long-term studies. This provides an indicator of the minimal forage fish biomass needed to sustain seabird productivity over the long term.

Public and scientific appreciation for the role of top predators in marine ecosystems has grown considerably, yet many upper trophic level (UTL) species, including seabirds, marine mammals, and large predatory fish, remain depleted owing to human activities (1–4). Fisheries impacts include direct mortality of exploited species and the more subtle effects of altering trophic pathways and the functioning of marine ecosystems (5). Specifically, fisheries for lower trophic level (LTL) species, primarily small

coastal pelagic fish (e.g., anchovies and sardines), euphausiid crustaceans (krill), and squid (hereafter referred to as “forage fish”), threaten the future sustainability of UTL predators in marine ecosystems (6, 7). An increasing global demand for protein and marine oils contributes pressure to catch more LTL species (8). Thus, fisheries for LTL species are likely to increase even though the consequences of such activity remain largely unknown at the ecosystem level. It remains challenging, however, to assess fishing

impacts on food webs because numerical relationships between predators and prey are often unknown, even for commercially valuable fish (9, 10). Ecosystem models and ecosystem-based fisheries management, for which maintaining

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predator populations is an objective (2, 11, 12), will remain controversial until these relationships are more fully quantified.

To improve our understanding of the effects of LTL fisheries on marine ecosystems, more information on predator-prey relationships across a range of species and ecosystems is required (6). Seabirds are conspicuous members of marine ecosystems globally. Many aspects of seabird ecology have been measured consistently for decades, encompassing ecosystem change at multiple scales (13). Substantial long-term data sets on seabird breeding success have been compiled for many taxa in several marine ecosystems around the world (14–16), but for relatively few has independent information on prey availability been obtained concurrently. For those where prey data are available, temporal covariance in predators and their prey suggests that seabirds can be used as indicators of forage fish population fluctuations (7, 16, 17). Here, we used data collected contemporaneously over multiple decades from seabirds and forage fish to test the hypothesis that the form of the numerical response between seabird breeding success and forage fish abundance is consistent across species and ecosystems. We used data from seabird species that have strong dietary dependencies on forage fish prey and where the time series for both the predator and the prey have high spatial and temporal congruence. We compiled data from 19 time series covering seven marine ecosystems, nine sites, and 14 seabird species and their major prey (Fig. 1 and table S1). The data set included 438 data points spanning 15 to 47 colony-years per breeding site (table S1). The abundance of principal prey for each seabird species was estimated independently of the data collected from the birds, usually as part of population assessments conducted in support of fisheries management (table S1).

To examine empirical relationships between seabird breeding success and prey abundance, we used nonparametric statistical methods that facilitate nonlinear modeling by making no a priori assumptions about the form of the relationships (generalized additive models, or GAMs). Initially, each time series (seabird breeding success and prey abundance) was normalized by expressing the measurements as the number of standard deviations from the mean; this enables robust comparisons across species and ecosystems. Once the numerical relationship was established, we used a change-point analysis (sequential *t* tests that find the most likely point at which the slope of breeding success changes in relation to prey abundance) to identify thresholds within nonlinear relationships (18) (Fig. 2A). A bootstrap analysis was used to calculate confidence intervals of the threshold, and the variance in seabird breeding success was calculated for each prey abundance class. Last, a selection of a priori parametric models ranging from linear, sigmoid, asymptotic, to hierarchical (table S2) was fitted to the general relationship. The most parsimonious

model was then used to fit the relationship between seabird breeding success and forage fish population size for each ecosystem (pooling all species) and each seabird species (pooling all ecosystems).

Seabird breeding success showed a nonlinear response to changes in prey abundance (Fig. 2A). The threshold at which breeding success began to decline from the asymptote was not significantly different from the long-term mean of prey abundance (range -0.30 and $+0.13$, standard deviation of the mean, Fig. 2A). The threshold was 34.6% (95% confidence interval 31 to 39%), or approximately one-third of the maximum observed prey abundance. The coefficient of variation between the different thresholds among species and ecosystems was 28% (table S1). All time series were of sufficient duration to identify the threshold (detection is possible after 13 years of observation, fig. S1) and the maximum biomass (detection is possible after 11 years, fig. S2). Variance in breeding success increased significantly (*F* test, $P < 10^{-4}$) below the threshold of prey abundance (Fig. 2B). Fitting parametric models to individual responses showed a similar inflection point and similar asymptotic values across ecosystems and species (Figs. 2, C and D, and 3), indicating that the functional form was a general feature of the seabird–forage fish relationship.

The asymptotic form of the relationship between seabird breeding success and forage

fish abundance has been reported previously (15, 16, 19–24), but the common scaling across species and ecosystems and the consistency of threshold values are new observations. The global pattern shows a threshold below which the numerical response declines strongly as food abundance decreases and above which it reaches a plateau and does not change even as food abundance increases. This pattern is apparently robust to the varying life-history strategies, habitat preferences, and population sizes of the seabird species considered. Nonetheless, we acknowledge that a range of factors may interact to weaken or possibly accentuate the relationship between seabird breeding performance and prey species abundance. Alternative drivers of change in breeding success include changes in habitat characteristics or predation pressures, or complex intercolony dynamics. Predators may also show more or less capacity to switch to alternative prey items, which may buffer productivity against declines in any single prey species (25).

Periods of consistently high or low breeding success, or occasional complete breeding failures, are normal in seabirds, and most species are adapted to fleeting anomalous environmental conditions. However, chronic food scarcity, as potentially defined by prey abundance below the threshold described here for seabirds, will compromise long-term breeding success, and this may affect the trajectory of their populations.

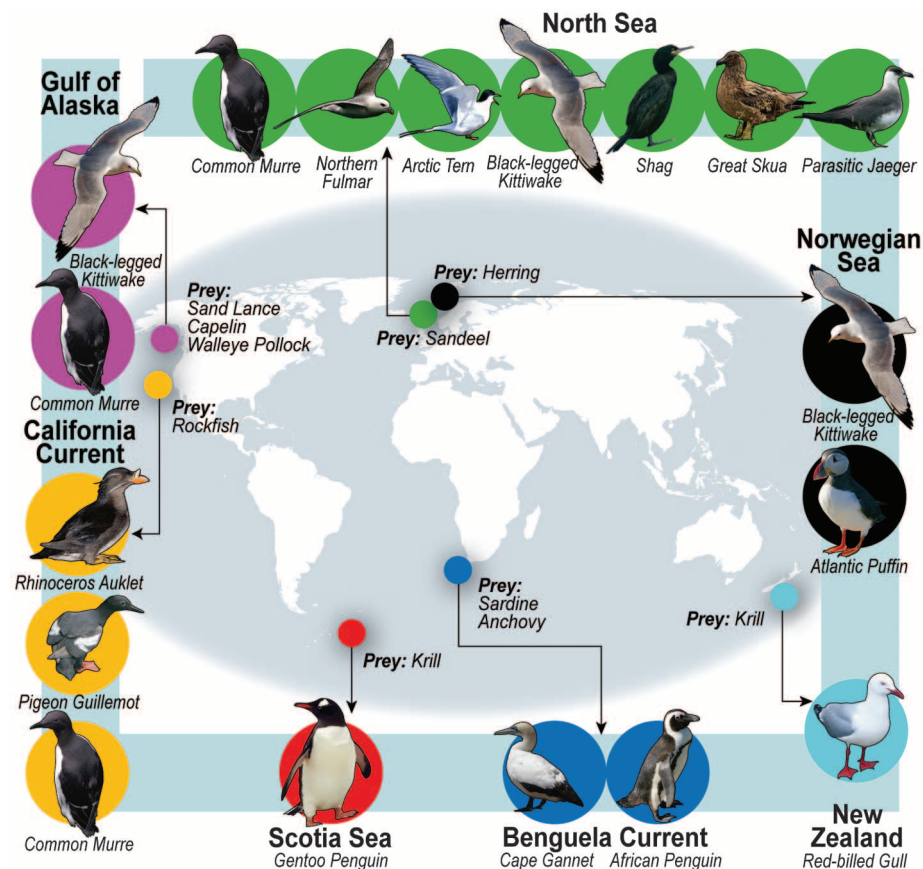


Fig. 1. Map of the distribution of seabird and prey species considered in our analysis.

Fig. 2. (A) Relationship between normalized annual breeding success of seabirds and normalized prey abundance. Each data point from all the time series was plotted with the predictions of a generalized additive model (GAM) (solid line). The gray area represents the 95% confidence interval of the fitted GAM. The threshold in the nonlinear relationship (black solid vertical line) and its 95% confidence interval (black dashed vertical lines) were detected from a change-point analysis. (B) Change in variance across the range of normalized food abundance ranging from -1.5 to 2 standard deviations in eight classes. Variance below the threshold was 1.8 times higher than above it. (C and D) Similar relationships were present when data were pooled (C) for species within ecosystems and (D) for species pooled among ecosystems using the best-fitting asymptotic model (table S2). The Arctic Tern (not shown) model fit was not significant (table S1). The colors in (A) and (C) represent the data set for each ecosystem and in (D) for each seabird species.

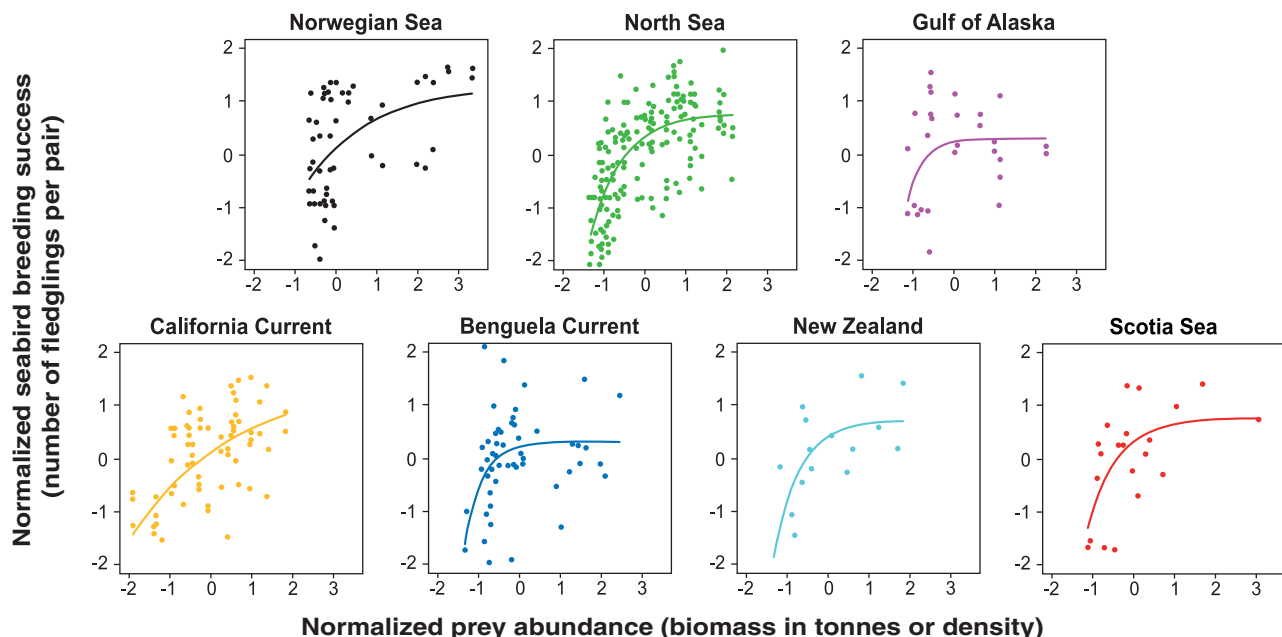
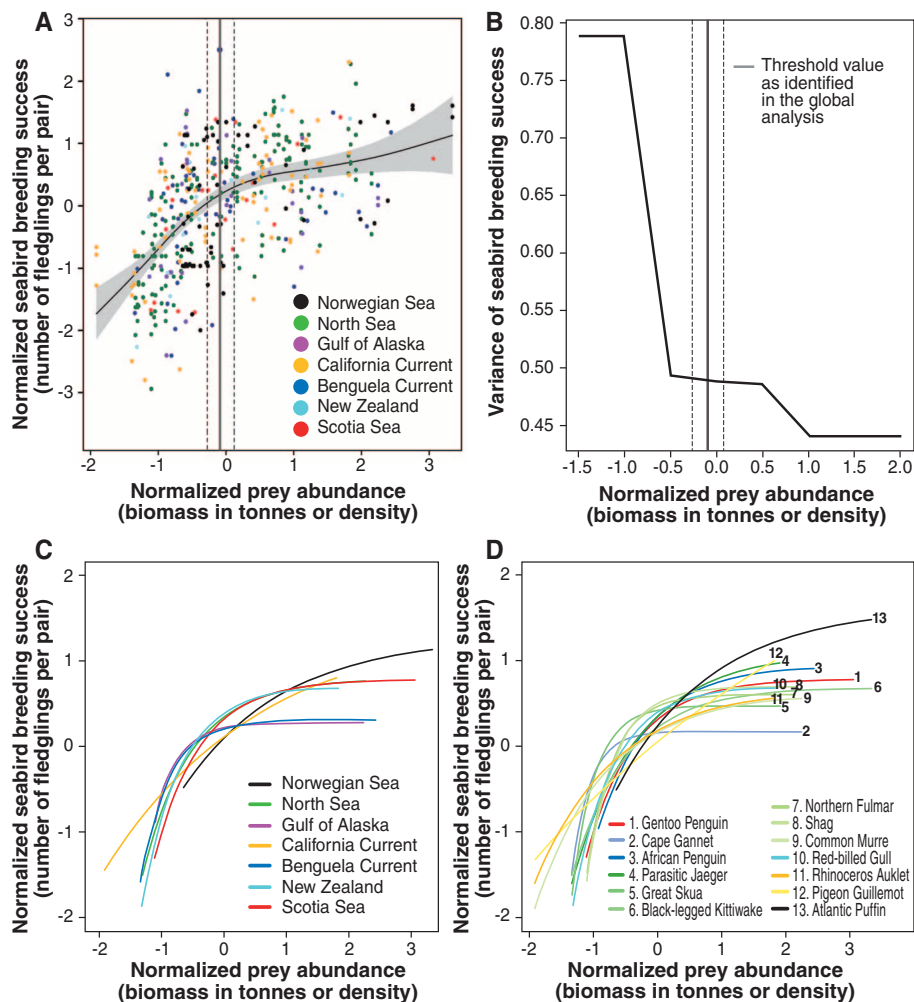


Fig. 3. Relationship between normalized annual breeding success of pooled seabird species and normalized prey abundance for the seven different ecosystems using the most parsimonious asymptotic model (table S2).

Indeed, food scarcity can also reduce adult survival in seabirds (26), with immediate population-level impacts. Whether caused by persistent overfishing, or directional or stochastic environmental change that reduces ecosystem carrying capacity, recruitment and survival will probably have thresholds of prey abundance shifted to the left of that for breeding success (15, 16). Consequently, the threshold for breeding success is likely to provide a precautionary guideline to what level of food reduction might seriously impact seabird populations.

The threshold defined by our study suggests that if management objectives include balancing predator-prey interactions to sustain healthy UTL predator populations and ecosystem functions (2), a practical indicator would be to maintain forage fish biomass above one-third of the maximum observed long-term biomass. The application of such a management guideline will depend upon local circumstances, such as the need to implement spatial management around breeding colonies or the conservation status of species (27). Although we cannot assume similarity between all taxa in the value of the predator-prey threshold, our study demonstrates consistency among a broad range of seabirds. There is also evidence that some marine mammals and predatory fish share the general form of the relationship (17, 19, 25, 28).

Tuning management goals to ensure sufficient biomass of forage fish for seabird reproduction may be a useful step toward ensuring sustainability of predator-prey interactions for other, less well-studied predators in marine ecosystems. Even for predators not showing high dependency on exploited species, this is likely to provide a precautionary step. The “one-third for the birds” guiding principle could be applied widely to help

manage forage fisheries to benefit ecosystem resilience. Indeed, predator responses of this type are already included in some specific management systems (29). Although such a guideline might be difficult to consider for new fisheries, where there are few data to determine the maximum biomass, most of the economically important coastal pelagic fish populations have sufficient data to define the threshold in many ecosystems (e.g., in the Benguela, California, and Humboldt Currents) (figs. S1 and S2).

The generality of the asymptotic form of the predator-prey relationship suggests that it is rooted in fundamental life history and ecological theory (e.g., demographic trade-offs and functional responses). In a practical context, “one-third for the birds” is a simple, empirically derived guiding principle that embraces the ecosystem approach to management aimed at sustaining the integrity of predator-prey interactions and marine food webs for the benefit of both natural predators and humans.

References and Notes

1. J. B. C. Jackson *et al.*, *Science* **293**, 629 (2001).
2. E. K. Pikitch *et al.*, *Science* **305**, 346 (2004).
3. H. K. Lotze, B. Worm, *Trends Ecol. Evol.* **24**, 254 (2009).
4. M. Hoffmann *et al.*, *Science* **330**, 1503 (2010).
5. M. Coll, S. Libralato, S. Tudela, I. Palomera, F. Pranovi, *PLoS ONE* **3**, e3881 (2008).
6. A. D. M. Smith *et al.*, *Science* **333**, 1147 (2011).
7. P. Cury *et al.*, *ICES J. Mar. Sci.* **57**, 603 (2000).
8. R. L. Naylor *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **106**, 15103 (2009).
9. P. A. Abrams, L. R. Ginzburg, *Trends Ecol. Evol.* **15**, 337 (2000).
10. L. C. Stige *et al.*, *Proc. R. Soc. Lond.* **277**, 3411 (2010).
11. H. M. Pereira *et al.*, *Science* **330**, 1496 (2010).
12. T. P. Dawson, S. T. Jackson, J. I. House, I. C. Prentice, G. M. Mace, *Science* **332**, 53 (2011).

13. R. D. Wooller, J. S. Bradley, J. P. Croxall, *Trends Ecol. Evol.* **7**, 111 (1992).
14. R. W. Furness, K. Camphuysen, *ICES J. Mar. Sci.* **54**, 726 (1997).
15. D. K. Cairns, *Biol. Oceanogr.* **5**, 261 (1987).
16. J. F. Piatt *et al.*, *Mar. Ecol. Prog. Ser.* **352**, 221 (2007).
17. I. L. Boyd, *Aquat. Conserv.* **12**, 119 (2002).
18. T. Andersen, J. Carstensen, E. Hernández-García, C. M. Duarte, *Trends Ecol. Evol.* **24**, 49 (2009).
19. I. L. Boyd, A. W. A. Murray, *J. Anim. Ecol.* **70**, 747 (2001).
20. J. M. Durant, T. Anker-Nilssen, N. C. Stenseth, *Proc. Biol. Sci.* **270**, 1461 (2003).
21. K. Reid, J. Croxall, D. Briggs, E. Murphy, *ICES J. Mar. Sci.* **62**, 366 (2005).
22. R. W. Furness, *J. Ornithol.* **148** (suppl. 2), 247 (2007).
23. J. A. Mills *et al.*, *J. Anim. Ecol.* **77**, 1129 (2008).
24. J. C. Field, A. D. MacCall, R. W. Bradley, W. J. Sydeman, *Ecol. Appl.* **20**, 2223 (2010).
25. M. E. Hunsicker *et al.*, *Ecol. Lett.* **14**, 1288 (2011).
26. A. S. Kitaysky *et al.*, *Funct. Ecol.* **24**, 625 (2010).
27. L. Pichegru, D. Grémillet, R. J. Crawford, P. G. Ryan, *Biol. Lett.* **6**, 498 (2010).
28. J. F. Piatt, D. A. Methven, *Mar. Ecol. Prog. Ser.* **84**, 205 (1992).
29. D. J. Agnew, *Antarct. Sci.* **9**, 235 (1997).

Acknowledgments: This work was partly funded by Eur-Oceans Consortium, the Institut de Recherche pour le Développement (IRD), the Lenfest Forage Fish Task Force, Mistra, the Sea Around Us Project, and the South African Research Chair Initiative. Disclaimers and acknowledgment of institutes and collaborators are provided in the SOM. Data, methods, and codes are available in the SOM.

Supporting Online Material

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19 August 2011; accepted 8 November 2011
10.1126/science.1212928

Mouse B-Type Lamins Are Required for Proper Organogenesis But Not by Embryonic Stem Cells

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B-type lamins, the major components of the nuclear lamina, are believed to be essential for cell proliferation and survival. We found that mouse embryonic stem cells (ESCs) do not need any lamins for self-renewal and pluripotency. Although genome-wide lamin-B binding profiles correlate with reduced gene expression, such binding is not directly required for gene silencing in ESCs or trophoblast cells. However, B-type lamins are required for proper organogenesis. Defects in spindle orientation in neural progenitor cells and migration of neurons probably cause brain disorganizations found in lamin-B null mice. Thus, our studies not only disprove several prevailing views of lamin-Bs but also establish a foundation for redefining the function of the nuclear lamina in the context of tissue building and homeostasis.

The major structural components of the nuclear lamina found underneath the inner nuclear membrane in metazoan nuclei are type V intermediate filament proteins called

lamins (1). Mammals express both A- and B-type lamins encoded by three genes, *Lmna*, *Lmnb1*, and *Lmnb2*. *Lmnb1* and *Lmnb2* express lamin-B1 and -B2, respectively. *Lmnb2* also expresses

lamin-B3 through alternative splicing in testes. Mutations in lamins have been linked to a number of human diseases referred to as laminopathies (2), although the disease mechanism remains unclear. A-type lamins are expressed only in a subset of differentiated cells and are not essential for basic cell functions (3, 4). By contrast, at least one B-type lamin is found in any given cell type. Because numerous functions, including transcriptional regulation, DNA replication, and regulation of mitotic spindles, have been assigned to B-type lamins, they are thought to be essential for basic cell proliferation and survival (1, 5–8).

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