Fishing through marine food webs

Timothy E. Essington†, Anne H. Beaudreau, and John Wiedenmann‡

School of Aquatic and Fishery Sciences, University of Washington, Box 355020, Seattle, WA 98195

A recurring pattern of declining mean trophic level of fisheries landings, termed "fishing down the food web," is thought to be indicative of the serial replacement of high-trophic-level fisheries with less valuable, low-trophic-level fisheries as the former become depleted to economic extinction. An alternative to this view, that declining mean trophic levels indicate the serial addition of low-trophic-level fisheries ("fishing through the food web"), may be equally severe because it ultimately leads to conflicting demands for ecosystem services. By analyzing trends in fishery landings in 48 large marine ecosystems worldwide, we find that fishing down the food web was pervasive (present in 30 ecosystems) but that the sequential addition mechanism was by far the most common one underlying declines in the mean trophic level of landings. Specifically, only 9 ecosystems showed declining catches of upper-trophic-level species, compared with 21 ecosystems that exhibited either no significant change ($n = 6$) or significant increases ($n = 15$) in upper-trophic-level catches when fishing down the food web was occurring. Only in the North Atlantic were ecosystems regularly subjected to sequential collapse and replacement of fisheries. We suggest that efforts to promote sustainable use of marine resources will benefit from a fuller consideration of all processes giving rise to fishing down the food web.

ecosystem-based management | fisheries | marine conservation

The status of marine fisheries and their effects on marine ecosystems have become the subjects of intense scrutiny over the past decade (1–5). Arguably, one of the most influential works supporting this movement is that of Pauly *et al.* (6), who documented that the mean trophic level of fisheries landings around the world has been declining since the onset of industrialized fishing. The scientific literature has been nearly unanimous in interpreting this trend, termed "fishing down the food web," as being symptomatic of overfishing, unsustainable harvest, and unintended ecological changes induced by widespread removal of species from high trophic levels. The present study seeks to explore alternative interpretations of fishing down the food web, quantify the commonness of these alternatives, and consider their implications for marine conservation and fisheries management.

There are at least two ways that fishing down the food web could occur. The first is through the sequential replacement of high-value upper-trophic-level species with less valuable lower-trophic-level species as the former are depleted to economic extinction. The second mechanism is through the sequential addition of lower-trophic-level fisheries within an ecosystem. We refer to the latter mode as "fishing through the food web" to emphasize that fisheries for high-trophic-level species are maintained despite a decline in the overall mean trophic level of landings.

The policy implications of the sequential collapse/replacement mode are severe: drastically overfished apex predator guilds (3, 7) with poor prospects for recovery (8, 9) and dramatic restructuring of marine ecosystems with concomitant loss of ecosystem services and biodiversity (1, 10). The sequential addition mode of fishing through the food web appears at first glance to be more benign, because it allows the possibility of sustainable catches of high-trophic-level fishes. Yet, from a policy standpoint, the fishing through the food web process gives rise to potentially untenable conflicts, because developing fisheries that demand different ecosystem services (e.g., productive apex predator stocks vs. productive forage fish stocks) will ultimately force policy makers to make judgments and assign values to these alternative fisheries. History has shown that most policy makers struggle to make effective decisions when facing tradeoffs between user groups (11). Navigating these conflicts is moving to the forefront of contemporary marine fisheries management and conservation (12), and such conflicts have been implicated in the unexpected collapse of capelin in the Barents Sea (13). Moreover, multiple-trophic-level fisheries are rarely an optimal policy on the basis of maximizing yield or economic revenue (14). Finally, if the sequential addition mode is prevalent, then there is a need to develop management plans that explicitly account for interactions among fisheries. These considerations are rarely present in traditional single-species management schemes.

In this study, we evaluated the commonness of each of these alternative mechanisms giving rise to fishing down the food web by examining the temporal dynamics of upper-trophic-level fishery catches when fishing down the food web was occurring. Under the sequential collapse/replacement mode, a decline in the mean trophic level should be accompanied by reduced catches of high-trophic-level species as these species become economically extinct. Under the sequential addition mode, however, we expect catches of upper-trophic-level species to be maintained or even increase.

Results

We deemed declines in mean trophic level >0.15 to be evidence of ecologically significant fishing down the food web. From an energetic perspective, this decline in trophic level represents an ≈50% decrease in the primary production required to sustain a given amount of catch (15). Of the 48 large marine ecosystems (LMEs) worldwide that had suitable data, 30 showed evidence of substantial fishing down the food web, with an average decline of 0.42 trophic level. These declines were substantially larger than those originally documented in the analysis of more spatially aggregated data (6), consistent with the notion that original estimates from poorer-quality data generally underestimated the magnitude and frequency of fishing down the food web (16).

Visual exploration of catch data revealed evidence for both mechanisms underlying fishing down the food web (Fig. 1). The Scotian Shelf provides a typical example of the sequential collapse/replacement mode (Fig. 1*A*). The mean trophic level in fisheries landings declined markedly beginning in 1987, corresponding with the initial collapse of groundfish stocks. This collapse was succeeded by a decline in herring (*Clupea harengus*) landings, ultimately leading to increased exploitation of northern prawn (*Pandalus borealis*). In contrast, the Patagonian Shelf exhibited a similar decline in mean trophic level between 1980 and 2001, but landings of high-trophic-level species (namely,

ECOLOGY
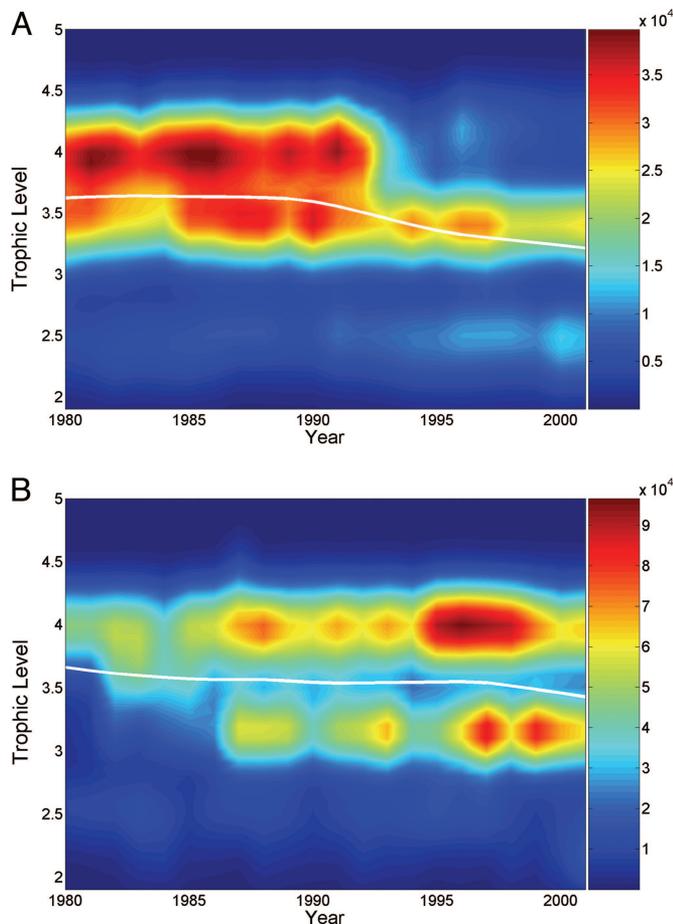
Fig. 1. Illustrative examples of the sequential collapse/replacement (*A*) and sequential addition (*B*) mode of fishing down the food web. Total yearly catch for each 0.1 trophic-level increment is indicated by the color bar on the right (10^4 kg yr^{-1}). The mean trophic level (white line) was smoothed by using a locally weighted regression smoother. (*A*) The Scotian Shelf ecosystem exhibited a sharp decline in mean trophic level from 1990 to 2001 owing to the collapse of the cod fishery followed by a decline in the herring fishery and then the growth of the northern prawn fishery. (*B*) The mean trophic level of the Patagonian Shelf declined from 1980 to 2001, during which time catches for upper-trophic-level species (Argentinean hake) grew substantially while new fisheries for shortfin squid developed.

Argentine hake, *Merluccius hubbsi*) generally increased over this period (Fig. 1*B*). Most of the decline in trophic level in this ecosystem was due to the addition of a new fishery targeting the shortfin squid (*Ilex argentinus*).

By fitting statistical models to time series of catches of high-trophic-level species we derived estimates of the mean annual rate of change of high-trophic-level catches (β; yr^{-1}) for each of the 30 ecosystems where fishing down the food web occurred. High-trophic-level catches were calculated in two ways. Apex predators were defined as species with trophic level >4. Upper-trophic-level species were defined within each LME as those species having trophic levels greater than the mean trophic level at the onset of fishing down the food web. We report here only those estimates calculated from apex predator catches, but the results derived from analysis of all upper trophic levels were similar (Table 2, which is published as supporting information on the PNAS web site). Maximum likelihood estimates of β ranged from -12.8% yr^{-1} to 7.0% yr^{-1}, with the two lowest estimates associated with the collapse of Atlantic cod (*Gadus morhua*) stocks in the Scotian Shelf and the Newfoundland–Labrador Shelf. Only nine instances of fishing down the food web
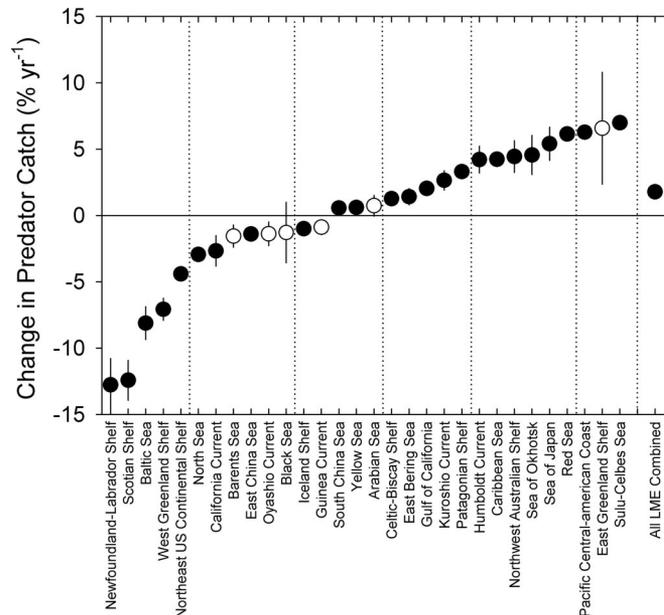
Fig. 2. Estimates of the instantaneous rate of change (% yr^{-1}) in apex predator catches ($\pm$SE) during the time period when the mean trophic level was declining in each ecosystem. Parameter estimates that are statistically different from zero ($P < 0.05$) are indicated by filled circles, and estimates that are not significant are indicated by open circles. Under the sequential collapse/replacement mode ecosystems should show a large decline in apex predator catches, whereas under the sequential addition mode ecosystems should show no change or growth in apex predator catches.

were associated with a statistically significant decline in apex predator catches ($P < 0.05$) (Fig. 2), and only four of these estimates were less than -6.7% yr^{-1} (a rate equivalent to a 50% decline in catches over a 10-year period). In contrast, 6 ecosystems showed no statistically significant change ($P > 0.05$), and 15 showed significant increases in apex predator catches during the period when fishing down the food web was occurring (Fig. 2). Considering catches in all ecosystems worldwide together, the mean trophic level was stable from 1950 to 1956, declined from 3.44 to 3.16 between 1956 and 1986, and has remained stable since 1986. During the time period that the mean trophic level was declining, apex predator catches increased by 1.8% yr^{-1} ($P < 0.001$; Fig. 2). Analyses of lower-trophic-level catches in these ecosystems confirm that declining mean trophic level was associated with rapid increases in lower-trophic-level catches, except for instances in which high-trophic-level catches declined (Table 2). Thus, the data identify the sequential addition mode as the most common process underlying fishing down the food web, representing more than two-thirds of all cases.

Because a close examination of the estimates presented in Fig. 2 revealed similarities among ecosystems within similar biogeographic regions, we explored whether there were differences in the mode of fishing down the food web among different ocean regions. Six oceanographic regions had multiple ecosystems exhibiting fishing down the food web: North Pacific, Tropical Pacific, Indian Ocean, North Atlantic, Tropical Atlantic, and South Atlantic. The metaanalysis of β across ecosystems within ocean regions supported the notion that there were region-scale patterns of variation in β. For the apex predator catches, only the North Atlantic region had a mean β that was negative ($P < 0.05$; mean = -4.5% yr^{-1}; Fig. 3). For all other regions, the mean β was positive and was statistically greater than 0 for the Tropical Pacific, Indian Ocean, and the South Atlantic regions ($P < 0.05$; Fig. 3). Contrasts among regions were virtually identical when trends in all upper-trophic-level fisheries were examined: again,

Fig. 3. Comparison of the mean (±SE) instantaneous rate of change in apex predator catches (trophic level > 4; solid bars) and all upper-trophic-level catches (trophic level > mean trophic level; open bars) among ocean regions. An asterisk indicates that the mean is statistically different from zero ($P < 0.05$).

only the North Atlantic region had a mean β that was <0; all others had a mean β that was >0, and these estimates were statistically significant for the Indian Ocean and the South Atlantic region. These results suggest that the North Atlantic is a hotspot for the sequential collapse/replacement mode of fishing down the food web, whereas the sequential addition mode generally describes the process underlying changes in mean trophic level throughout the rest of the world.

Discussion

Our results indicated that fishing down the food web is prevalent among marine ecosystems worldwide and that fishing down the food web was most commonly associated with the sequential addition of new fisheries. In contrast, the sequential collapse/replacement mode of fishing down the food web was common in North Atlantic ecosystems but rare elsewhere. The observed frequencies of these alternative mechanisms may not be accurately reflected in the scientific community's interpretation of fishing down the food web. We analyzed >200 peer-reviewed publications and did not find a single article claiming that fishing down the food web was associated with the sequential addition of new fisheries (Table 1). Instead, our review revealed a scientific community that has embraced the view that fishing down the food web is evidence of unsustainable fishing and human alteration of food web structure and ". . . is clear evidence of ineffective management" (17). This disconnect between perception and reality, which places undue emphasis on the less common sequential collapse/replacement mechanism, is dangerous because it leads us to ignore the policy implications of the more common sequential addition mechanism.

That high-trophic-level fisheries were maintained (or even grew) during most instances of fishing down the food web does not imply that fish stocks are healthy. We emphasize that our results should not be used to make inferences about stock status for at least two reasons. One, we looked at aggregate catches of species that fell within particular trophic levels. Consequently, our analysis cannot address individual stock status or shifts in community structure that might maintain total apex predator productivity despite depletion of individual species (18). Second, increased catches are likely indicative of increased exploitation

Table 1. Interpretations of fishing down the food web as determined through review of scientific literature citing Pauly et al. (6)

Context of citation	No. of citations
Ecosystem effects of fishing	65
Overfishing	52
Replacement of high-trophic-level fisheries with low-trophic-level fisheries	35
Description of phenomenon	26
Method (ecopath)	17
Other	14
Economic value of large fish	6
Need for marine reserves	4
Susceptibility of large fish	4
Thermodynamic basis of fishing down the food web	2
Sequential addition	0

See Table 3, which is published as supporting information on the PNAS web site, for a full listing of all papers and the specific context of each citation.

rates, which can only act to further reduce stock sizes. Moreover, there is little doubt that many predator stocks are overfished and that fisheries preferentially target large, high-trophic-level species (refs. 19 and 20; but see refs. 21–26 for an in-depth discussion on the status of shark and tuna species). Our analyses simply indicate that fishing down the food web was generally not accompanied by declining catches of high-trophic-level species, suggesting that fishing down the food web was not associated with a depletion of these species sufficient to make them economically extinct, i.e., so depleted that the effort required to capture the remaining fish is more costly than the expected profit. We therefore conclude that, in most instances, the standing stock of upper-trophic-level species was sufficiently abundant to support fisheries during the time periods when fishing down the food web occurred. This observation, coupled with our observations that fishing down the food web was accompanied by increased catches of low-trophic-level species, indicates that fishing down the food web is symptomatic of increased direct (harvest) and indirect (harvest of prey) impacts of fisheries on high-trophic-level species. These multiple impacts may be sustainable during the initial phases of fisheries development but can ultimately lead to collapse of high-trophic-level stocks if fisheries develop unchecked and without consideration of these interactions.

The sequential collapse/replacement mode of fishing down the food web was most common and most extreme among ecosystems within the North Atlantic region. The poor status of North Atlantic fisheries and ecosystems has been well documented (27) as groundfish stocks throughout the region have suffered from the combined effects of overcapitalization and climate-induced declines in stock productivity (28). The consistent and large declines in upper-trophic-level landings suggest that there has indeed been a region-wide depletion of upper-trophic-level species so severe as to make directed fisheries for them unprofitable. Yet our results also suggest that the North Atlantic region is an anomaly in this respect, because upper-trophic-level catches generally increased throughout the rest of the world ocean regions.

As with any attempt to explore global patterns and to derive generalizations, several caveats are required. The first issue is the precision and information content in catch data. Fisheries catch data are generally a poor indicator of stock status because catches are dictated by the abundance of targeted species, their availability to the fishing fleet, the capacity of the fleet, and the efficiency of the fleet at capturing them. These all change as

ECOLOGY

fisheries develop, producing ambiguous and sometimes misleading trends in total landings. For example, high catches of Atlantic cod were maintained for several years in the Northwest Atlantic despite the pending collapse in the early 1990s (29). Furthermore, the catch data forming the basis of our analysis originally derived from information reported to the Food and Agriculture Organization (FAO) by individual countries, and these reports may not always be accurate (30). Notably, many of the catch estimates in the FAO database reported by China may be incorrect, although the catch estimates we used attempted to remove this bias through an explicit adjustment of Chinese catches (31). Finally, the partitioning of FAO region-wide catch data into individual LMEs has been conducted with great care (31), but there are limits to the precision of any method that seeks to disaggregate data of this sort. Despite these limitations, which make catch data relatively imprecise, our main conclusion still stands: the best available evidence suggests that fishing down the food web is most commonly caused by the addition of new fisheries, not by the serial replacement of fisheries.

Another possible inaccuracy in our method lies in the fact that we used a single trophic level to describe an entire species. Recent work has indicated that size-selective fishing reduces the average trophic level of fish stocks by removing the largest individuals (32), because trophic level is generally positively correlated with body size (33). However, this process is unlikely to have a large effect on our main conclusions. Most of the cases of fishing down the food web were due to the serial addition of new fisheries with large differences in trophic level (commonly >1.0 trophic level). These contrasts in trophic level greatly exceed the more subtle declines caused by shifts in species' size structures.

We restricted our analyses to marine ecosystems because there exists a large database of fishes catches that permitted this analysis. For this reason, we cannot generalize our conclusions to freshwater ecosystems. Fishing down the food web has been documented in inland freshwater waters (34), and many freshwater ecosystems are severely overfished because of intense recreational fishing pressure (35). Moreover, reduced body sizes resulting from size-selective fishing is a continuing problem facing freshwater fisheries managers. We therefore speculate that the sequential collapse/replacement model may be more prevalent in freshwater ecosystems, but further data analyses are needed to evaluate this claim.

Achieving sustainable use of marine fisheries and ecosystems will not be easy, but it will be enhanced by a better recognition of the scope of the problems facing us. Our analyses indicate that the sequential addition mode is by far the most common explanation for fishing down the food web. Perhaps the most important policy consideration of the sequential addition mode is that, in most ecosystems of the world, several trophic levels are now exploited simultaneously. These diverse fisheries impose conflicting demands on marine ecosystems that are not generally well represented in single-species management plans that do not consider the effects of these alternative fisheries on each other. As the structure of fisheries and the management environment evolve, the scientific community faces a new challenge of conducting broad-scale ecological research to support the development of more holistic, ecologically based approaches to fisheries management.

Materials and Methods

Data. Our analysis used estimates of yearly catches for each species in each of 62 LMEs worldwide (36) from 1950 to 2001 (31) and estimates of each species' trophic level (37). The catch data derive from an algorithm that spatially disaggregates Food and Agriculture Organization catch statistics into individual LMEs based on regional-scale catch estimates, known international fishing agreements, and species' spatial distributions. These estimates correct for the potential overreporting of

catches from China. The details of this analysis are provided in ref. 31. In our analysis, we considered all fish, echinoderm, cephalopod, and crustacean landings.

We excluded from analysis ecosystems where data were incomplete or insufficiently detailed (14 LMEs), and we did not consider changes in trophic level and fisheries accompanying changes in international fishing rights. To evaluate the precision of each remaining data set, we calculated the percent contribution of overly aggregated catch data (e.g., unspecified marine fishes) for each year, and we did not consider any periods during which unspecified groups contributed >20% of the total landings in any year.

Estimates of trophic level were taken from FISHBASE (37), which calculates trophic level from stomach contents data. When estimates were not available for a species, we used closely related species (same genus). We assumed that, within a population, trophic level was normally distributed with a standard deviation of 0.1, which represents much of the variability in food contents reported by FISHBASE. Also, we adjusted the FISHBASE trophic level estimate of skipjack tuna from 4.3 to 3.8; FISHBASE overestimates this trophic level because larval cannibalism is not separated from cannibalism on fully grown conspecifics. The latter estimate was taken from ref. 38. Although FISHBASE estimates may not be precise for many species, they are demonstrably wrong for skipjack owing to a limitation in the numerical scheme that estimates trophic level based on reported food contents. It was important to adjust skipjack catches because they are comprise one of the world's largest fisheries and because they would erroneously be considered an apex predator without this correction.

Analysis. We identified fishing down the food web as any instance in which mean trophic level exhibited a decline by at least 0.15. The time periods associated with each fishing down the food web event were defined as the year of the highest (start) and lowest (end) observed trophic level. This procedure gave us an estimate of the largest possible decline in mean trophic level of the catch.

To provide a quantitative approach characterizing modes of fishing down the food web, we partitioned the total catches for each ecosystem into upper and lower trophic levels and described the trends in upper-trophic-level catches while fishing down the food web was occurring. This partitioning involved identifying a threshold trophic level and then summing catches for all landings exceeding this threshold. Because any partition of a continuous variable (i.e., trophic level) has the potential to impose artifacts, we used two separate methods to identify the threshold value. The first method used the mean trophic level at the onset of the decline in each ecosystem. We refer to catches calculated in this manner as upper-trophic-level catches. The second method examined the dynamics of apex predators only, which are those species with a trophic level ≥4.0. This threshold value is based on recent interest in the status of large predator species worldwide (3, 7).

We fit an exponential model to the time series of upper-trophic-level and apex predator catches during the time periods when fishing down the food web occurred. This model was of the form $C(t) = C(0)\exp(\beta t)$, where $C(t)$ is the catch rate during year t, $C(0)$ is the catch rate for the initial year, and t is the number of years since the mean trophic level initiated its decline. Estimates of β were made by using robust linear regression of $\log(C(t))$ vs. t (39).

We estimated region-specific estimates of β by using a random-effects metaanalysis that combined estimates of β for all ecosystems in the Indian Ocean, North Pacific, Tropical Pacific, North Atlantic, South Atlantic, and tropical Atlantic. In all instances, tropical regions refer to ecosystems that reside predominantly within 20° N and 20° S (Caribbean Sea, Guinea Current, Sulu-Celbes Sea, South China Sea, and Pacific Central America Coast), and North and South designate ecosystems that reside outside of this region. The random-effects model is described in detail in ref. 40, but we present

a synthesis of these methods here. This method presumes that β is distributed among ecosystems within a region according to a normal distribution with a mean $\bar{\beta}$ and variance σ_β^2. The meta-analysis can therefore be viewed as an attempt to estimate the central tendency of β within a region.

The total variance of β for each ecosystem ($v_i{}^*$) reflects both the variance associated with measurement uncertainty (i.e., the square of the standard error = v_i) and the variance of each ecosystem β around the population mean $\bar{\beta}$ (σ_β^2).

$$v_i{}^* = v_i + \sigma_\beta^2 \qquad [1]$$

The population variance of β is calculated from the k independent measurements of β and their associated estimation variances (v_i).

$$Q = \sum_{i=1}^{k}\frac{\beta_i^2}{v_i} - \frac{\left(\sum_{i=1}^{k}\frac{\beta_i}{v_i}\right)^2}{\sum_{i=1}^{k}\frac{1}{v_i}} \qquad [2]$$

$$\sigma_\beta^2 = \frac{Q - (k-1)}{\sum_{i=1}^{k}1/v_i - \frac{\sum_{i=1}^{k}(1/v_i)^2}{\sum_{i=1}^{k}1/v_i}} \qquad [3]$$

$\bar{\beta}$ is calculated as a weighted average of the sample estimates:

$$\bar{\beta} = \frac{\sum_{i=1}^{k}\frac{\beta_i}{v_i{}^*}}{\sum_{i=1}^{k}\frac{1}{v_i{}^*}}, \qquad [4]$$

where the variance of this estimate equals

$$\sum_{i=1}^{k}\frac{1}{v_i{}^*}.$$

Statistical significance is based on the ratio of $\bar{\beta}/\mathrm{var}(\bar{\beta})^{0.5}$, which, under the central limit theorem and null hypothesis of no change in catches, is normally distributed with a mean of 0 and a standard deviation of 1. Significance is therefore judged from critical values of the Z statistic (1.96 for $\alpha = 0.05$).

1. Jackson, J. B. C., Kirby, M. X., Berger, W. H., Bjorndal, K. A., Botsford, L. W., Bourque, B. J., Bradbury, R. H., Cooke, R., Erlandson, J., Estes, J. A., *et al.* (2001) *Science* **293,** 629–638.
2. Botsford, L. W., Castilla, J. C. & Peterson, C. H. (1997) *Science* **277,** 509–515.
3. Myers, R. A. & Worm, B. (2003) *Nature* **423,** 280–283.
4. Baum, J. K., Myers, R. A., Kehler, D. G., Worm, B., Harley, S. J. & Doherty, P. A. (2003) *Science* **299,** 389–392.
5. Hilborn, R., Branch, T. A., Ernst, B., Magnusson, A., Minte-Vera, C. V., Scheuerell, M. D. & Valero, J. L. (2003) *Annu. Rev. Environ. Resour.* **28,** 359–399.
6. Pauly, D., Christensen, V., Dalsgaard, J., Froese, R. & Torres, F. (1998) *Science* **279,** 860–863.
7. Baum, J. K. & Myers, R. A. (2004) *Ecol. Lett.* **7,** 135–145.
8. Hutchings, J. A. (2000) *Nature* **406,** 882–885.
9. Myers, R. A. & Worm, B. (2005) *Philos. Trans. R. Soc. London B* **360,** 13–20.
10. Lotze, K. K. & Milewski, I. (2004) *Ecol. Appl.* **14,** 1428–1447.
11. Kindler, J. (1999) *Ecol. Appl.* **8,** 591–600.
12. Walters, C. & Martell, S. J. D. (2004) *Fisheries Ecology and Management* (Princeton Univ. Press, Princeton).
13. Hjermann, D. Ø., Ottersen, G. & Stenseth, N. C. (2004) *Proc. Natl. Acad. Sci. USA* **101,** 11679–11684.
14. Clark, C. W. (1990) *Mathematical Bioeconomics* (Wiley, New York).
15. Pauly, D. & Christensen, V. (1995) *Nature* **374,** 255–257.
16. Pauly, D., Watson, R. & Alder, J. (2005) *Philos. Trans. R. Soc. London B* **360,** 5–12.
17. Steneck, R. S. (1998) *Trends Ecol. Evol.* **13,** 429–430.
18. Dulvy, N. K., Metcalfe, J. D., Glainville, J., Pawson, M. G. & Reynolds, J. D. (2000) *Conserv. Biol.* **14,** 283–293.
19. Friedlander, A. M. & DeMartini, E. E. (2002) *Mar. Ecol. Prog. Ser.* **230,** 253–264.
20. Russ, G. R. & Alcala, A. C. (2004) *Oecologia* **138,** 622–627.
21. Polacheck, T. (2006) *Mar. Policy*, in press.
22. Burgess, G. H., Beerkircher, L. R., Cailliet, G. M., Carlson, J. K., Cortés, E., Goldman, K. J., Grubbs, R. D., Musick, J. A., Musyl, M. K. & Simpfendorfer, C. A. (2005) *Fisheries* **30,** 30–31.
23. Burgess, G. H., Beerkircher, L. R., Cailliet, G. M., Carlson, J. K., Cortés, E., Goldman, K. J., Grubbs, R. D., Musick, J. A., Musyl, M. K. & Simpfendorfer, C. A. (2005) *Fisheries* **30,** 19–26.
24. Hampton, J., Sibert, J. R., Kleiber, P., Maunder, M. N. & Harley, S. J. (2005) *Nature* **434,** E1–E2.
25. Baum, J. K., Kehler, D. & Myers, R. A. (2005) *Fisheries* **30,** 27–29.
26. Walters, C. (2003) *Can. J. Fish. Aquat. Sci.* **60,** 1433–1436.
27. Pauly, D. & Maclean, J. (2002) *In a Perfect Ocean* (Island, Washington, DC).
28. Beaugrand, G., Brander, K. M., Alistair Lindley, J., Souissi, S. & Reid, P. C. (2003) *Nature* **426,** 661–664.
29. Hutchings, J. A. (1997) *Can. J. Fish. Aquat. Sci.* **53,** 943–962.
30. Watson, R. & Pauly, D. (2001) *Nature* **414,** 534–536.
31. Watson, R., Kitchingman, A., Gelchu, A. & Pauly, D. (2004) *Fish Fish.* **5,** 168–177.
32. Badalamenti, F., D'Anna, G., Pinnegar, J. K. & Polunin, N. V. C. (2002) *Mar. Biol.* **141,** 561–570.
33. Jennings, S., Greenstreet, S. P. R., Hill, L., Piet, G. J., Pinnegar, J. K. & Warr, K. J. (2002) *Mar. Biol.* **141,** 1085–1097.
34. Pauly, D., Palomares, M. L., Froese, R., Sa-a, P., Vakily, M., Preikshot, D. & Wallace, S. (2001) *Can. J. Fish. Aquat. Sci.* **58,** 51–62.
35. Post, J. R., Sullivan, M., Cox, S. P., Lester, N. P., Walters, C. J., Parkinson, E. A., Paul, A. J., Jackson, L. & Shuter, B. J. (2002) *Fisheries* **27,** 6–17.
36. Sherman, K. (1991) *Ecol. Appl.* **1,** 349–360.
37. Froese, R. & Pauly, D. (2000) *FishBase 2000: Concepts, Design and Data Sources* (International Center for Living Aquatic Resources Management, Los Baños, Laguna, Phillipines).
38. Cox, S. P., Essington, T. E., Kitchell, J. F., Martell, S. J. D., Walters, C. J., Boggs, C. & Kaplan, I. (2002) *Can. J. Fish. Aquat. Sci.* **59,** 1736–1747.
39. Holland, P. W. & Welsch, R. E. (1977) *Commun. Stat. Theory Methods* **A6,** 813–827.
40. Cooper, H. & Hedges, L. V., eds. (1994) *Handbook of Research Synthesis* (Russell Sage Foundation, New York).

ECOLOGY