



# Harvesting forage fish can prevent fishing-induced population collapses of large piscivorous fish

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**Fisheries have reduced the abundances of large piscivores—such as gadids (cod, pollock, etc.) and tunas—in ecosystems around the world. Fisheries also target smaller species—such as herring, capelin, and sprat—that are important parts of the piscivores’ diets. It has been suggested that harvesting of these so-called forage fish will harm piscivores. Multispecies models used for fisheries assessments typically ignore important facets of fish community dynamics, such as individual-level bioenergetics and/or size structure. We test the effects of fishing for both forage fish and piscivores using a dynamic, multitrophic, size-structured, bioenergetics model of the Baltic Sea. In addition, we analyze historical patterns in piscivore-biomass declines and fishing mortalities of piscivores and forage fish using global fish-stock assessment data. Our community-dynamics model shows that piscivores benefit from harvesting of their forage fish when piscivore fishing mortality is high. With substantial harvesting of forage fish, the piscivores can withstand higher fishing mortality. On the other hand, when piscivore fishing mortality is low, piscivore biomass decreases with more fishing of the forage fish. In accordance with these predictions, our statistical analysis of global fisheries data shows a positive interaction between the fishing mortalities of forage-fish stocks and piscivore stocks on the strength of piscivore-biomass declines. While overfishing of forage fish must be prevented, our study shows that reducing fishing pressures on forage fish may have unwanted negative side effects on piscivores. In some cases, decreasing forage-fish exploitation could cause declines, or even collapses, of piscivore stocks.**

fisheries | predator–prey dynamics | multiple trophic levels | size-structured model | bioenergetics

**F**isheries target both large piscivorous fish—such as gadids (cod, pollock, etc.) and tunas—and small planktivorous fish or forage fish—such as herring, capelin, and sprat (1). Large piscivores are generally more valued for human consumption. Yet, forage fish constitute a substantial 20 to 30% of global fisheries landings (2). Often, both forage fish and large piscivores are fished for in the same ecosystems (3, 4). Forage fish serve as a food source for large piscivores, and it is commonly understood that harvesting of forage fish may indirectly harm the large piscivores that depend on them (3, 4).

The importance of an ecosystem-based, multispecies approach to fisheries management is underscored by potential indirect negative effects of forage-fish fisheries on piscivores (5, 6). Unraveling the effects of multispecies fisheries is a serious challenge due to feedbacks between fisheries, fish populations, and the fishes’ food sources (e.g., ref. 7). Understanding these effects is further complicated by nonlinearities in population-level processes (8). The effects of fishing on multiple species at different trophic levels of marine ecosystems are usually assessed by using multispecies fisheries models (4, 9). However, it has recently been argued that such models do not contain all necessary processes to predict fish-community dynamics (10, 11). Components

that are considered essential in models of fish communities are: 1) fish-population size structure, 2) consistent accounting of the bioenergetic flows through fish populations and communities, and 3) size-selective predation and harvesting (10, 11).

In this study, we investigate the effects of fishing for forage fish on their predators, the piscivorous fish. We do this using a published model of the central Baltic Sea community dynamics (12) that was specifically designed to investigate effects of fisheries on fish communities (10, 12). The model incorporates size-structured fish populations, size-dependent feeding interactions, and individual-level energy budgets. In addition, consumption by fish has a direct effect on their food sources, and the flows of energy throughout the system are thus accounted for consistently. Using this model, we explore the effects of fishing for both forage fish and piscivores. We first focus on the Baltic Sea because its food web is relatively simple and the exploited fish species include both piscivores (cod) and forage fish (sprat and herring) (13). Using the global Ransom A. Myers (RAM) Legacy Stock Assessment Database (14), we then statistically evaluate historical patterns in piscivore biomasses and fishing pressures on forage fish and piscivores. Our dynamic and statistical model analyses agree in demonstrating that harvesting forage fish does not always affect piscivore populations negatively. Instead, such fishing can

## Significance

**In many marine ecosystems, fisheries target predatory fish, known as piscivores, as well as their prey fish, known as forage fish. It is generally thought that harvesting of forage fish negatively affects piscivore population abundance and resilience. Here, we show that, contrary to this widely held belief, piscivorous fish stocks exposed to high fishing mortality benefit from harvesting of their forage fish. On the other hand, piscivorous fish stocks exposed to low fishing mortality are reduced by harvesting of their forage fish. The beneficial effect occurs when the harvesting of forage fish releases density dependence in the forage-fish population. Our findings have implications for policy advice regarding the management of forage-fish fisheries and the protection of piscivorous fish stocks.**

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The authors declare no competing interest.

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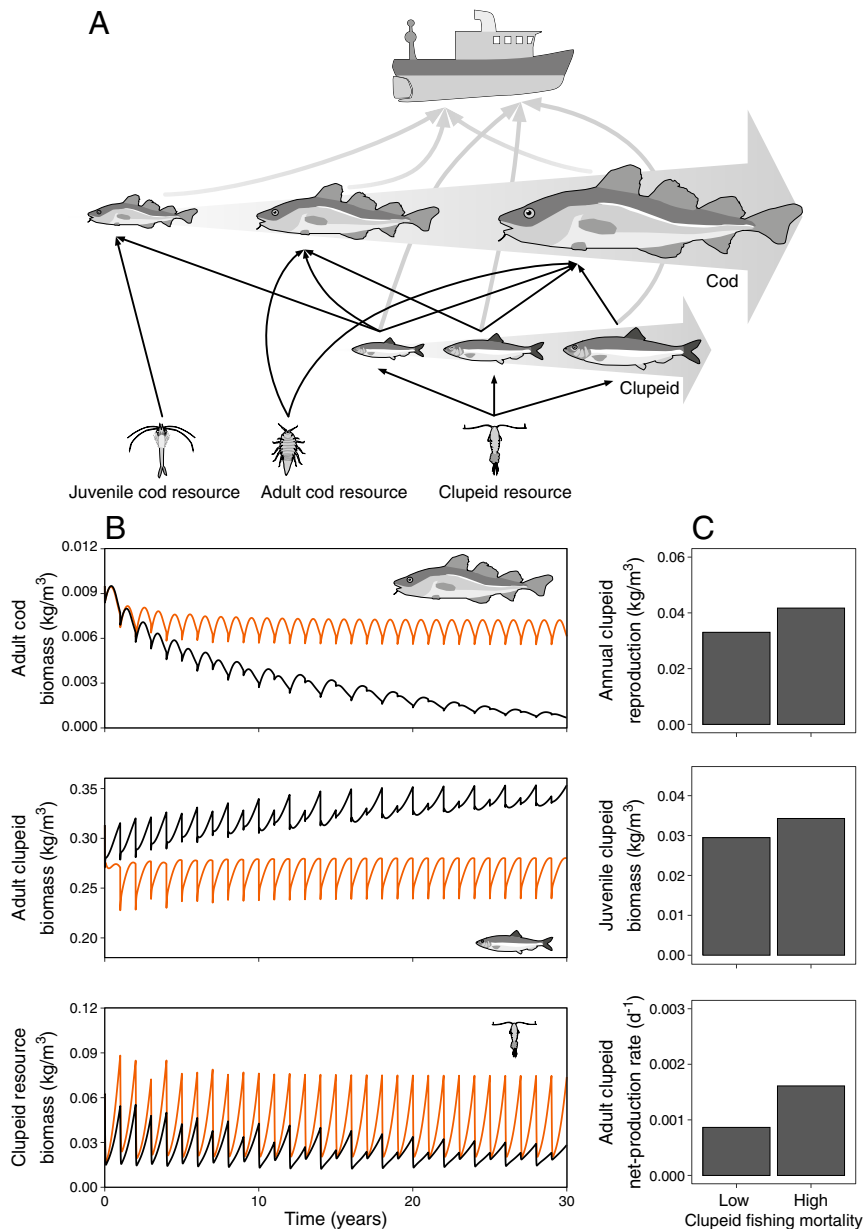
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protect large-piscivore populations from fishing-induced collapses. These results challenge the generally accepted idea that large piscivores always benefit from less fishing of their forage fish (6, 15).

### Materials and Methods

Below, we present the models used for our analyses in general terms. Details are described in *SI Appendix*, in *Appendix A* for the community-dynamics model and in *Appendix B* for the statistical model. Analysis of the community-dynamics model was carried out by using publicly available C-based simulation programs. The statistical model analysis is based on publicly available data.

**Community-Dynamics Model of the Baltic Sea.** To analyze the effects of multispecies fishing, we used the stage-structured bioenergetics model of the central Baltic Sea introduced by van Leeuwen et al. (12). The model includes the key ecological interactions between predatory and forage fish and their resources; it is aimed to qualitatively reproduce the dynamics of this system. We improve on the model by van Leeuwen et al. (12) by implementing reproduction as a seasonal process, following Soudijn and de Roos (16). The model structure and size-based, stage-specific parameterization are derived from individual-level data of Baltic cod, sprat, and herring (*SI Appendix, Appendix A*). Fig. 1A shows the interactions between fish populations in the model. Sprat and herring, the prey fish of cod, are assumed to have a similar ecological role. Hence, they are modeled as a clupeid population that



**Fig. 1.** Interactions between cod and clupeids in the community-dynamics model of the Baltic Sea. (A) Trophic interactions among fisheries (narrow gray arrows), cod and clupeid stages, and their resources (black arrows; see *SI Appendix, Table S4* for the foraging preferences of the cod stages). Individual fish grow through stages from left to right (broad gray arrows). (B) Time series of adult cod biomass (*Top*) and adult clupeid biomass (*Middle*), both including reproductive storages; and biomass of the clupeid resource (*Bottom*) for low (black lines;  $F_S = 0.2 \text{ year}^{-1}$ ) and high (red lines;  $F_S = 0.5 \text{ year}^{-1}$ ) clupeid fishing mortality. The cod fishing mortality is high,  $F_C = 0.75 \text{ year}^{-1}$ . The time series start from equilibrium biomasses for low cod and clupeid fishing mortalities ( $F_C = 0.5 \text{ year}^{-1}$ ,  $F_S = 0.2 \text{ year}^{-1}$ ). (C) Averages over years 0–10 of the biomass of annual clupeid reproduction (*Top*), clupeid juvenile biomass (*Middle*), and the mass-specific net-biomass-production rate of adult clupeids (*Bottom*) for low (left bars:  $F_S = 0.2 \text{ year}^{-1}$ ) and high (right bars:  $F_S = 0.5 \text{ year}^{-1}$ ) clupeid fishing mortality. Fishing mortality is here measured by the instantaneous fishing mortality rate. All other parameters are set to default values (*SI Appendix, Tables S2–S4*).

uses the same resource (zooplankton) throughout its life. Cod, the piscivore in this community, forages on zooplankton and small fish while juvenile and switches to benthos and larger fish upon maturation (Fig. 1A). Accordingly, there is no direct resource competition between juvenile cod and the clupeids in the model. Using the model, we assess the effects of the instantaneous fishing mortality rates for cod ( $F_C$ ) and clupeids ( $F_S$ ) on the community dynamics.

The stage-structured biomass model (17) is based on the bioenergetics approach originally introduced by Yodzis and Innes (18). Following their approach, assimilated energy is first used to cover maintenance costs. If maintenance costs exceed the assimilated energy, biomass is lost due to starvation mortality, and no growth or reproduction occurs (12, 17). If energy is left after covering maintenance costs, biomass is invested in growth and/or reproduction. Both cod and clupeids consist of a juvenile, small-adult, and large-adult stage (12). Juveniles use all net-energy production for somatic growth. Small adults allocate part of their energy to somatic growth and the remainder to reproduction. Large adults invest all energy in reproduction. The transition rates from the juvenile to the small-adult stage and from the small-adult to the large-adult stage depend on net-energy production and mortality (16). For all adult fish stages, energy allocated to reproduction is stored in reproductive storages until the reproductive season. The reproductive storages are part of the adult body and are thus affected by the same processes as the adults. Biomass in the reproductive storages is converted to juvenile biomass at the start of each reproductive season. The three unstructured resources in the model are assumed to have a constant productivity and turnover rate and, hence, follow semichemostat growth in the absence of foraging and decline through ingestion by fish.

**Statistical Model of Interactions between Piscivores and their Forage Fish in Ecosystems around the World.** We test how our model predictions generalize across ecosystems using historical patterns of stock biomasses and fishing mortalities from the RAM Legacy Stock Assessment Database (ref. 14; version 3.0; publicly accessible at <https://www.ramlegacy.org/database/>). The stock assessments in the RAM Legacy Stock Assessment Database currently represent the best available syntheses of catch and survey data to derive estimates of stock biomasses and fishing mortalities (SI Appendix, Appendix B). If intermediate harvesting of forage fish can protect piscivores from fishing-induced collapses (Results), an interaction is expected in the effects of forage-fish and piscivore fishing mortalities on changes in piscivore biomass.

We selected time periods with a strong decline of piscivore biomass in the considered fisheries-assessment areas (SI Appendix, Figs. S1 and S2). We used three different methods to derive periods of greatest decline in piscivore biomass (SI Appendix, Appendix B). In addition, we varied the minimum (5 to 14 years) and maximum (8 to 19 years) durations of the periods that could thus be selected (SI Appendix, Tables S8–S10 and Appendix B). In Results, we show results based on a minimum duration of 5 years and a maximum duration of 15 years. The piscivore-biomass decline was measured as the ratio of piscivore biomasses at the end and at the beginning of the decline period.

We determined the degree of spatial overlap for each combination of forage-fish stock and piscivore stock based on the geographical coordinates of the bounding regions of their fisheries-assessment areas (19). We found 23 combinations of forage-fish and piscivore stocks with a spatial overlap in excess of 95% between them. We assumed these stocks to interact trophically. For three other stock combinations, we found spatial overlaps of 50 to 95%. We included these stocks in the analysis, but verified the robustness of results to their inclusion. Stock combinations with spatial overlaps of less than 50% were not included in our analysis. The resultant list of stocks is shown in SI Appendix, Fig. S1 and Table S5. We excluded one stock based on Cook's distance and two stocks that only increased through time (SI Appendix, Appendix B, Fig. S3, and Table S7). In total, 23 stock combinations were used for the analysis.

For four stock combinations, the biomass of the forage-fish stock was lower than that of the piscivore stock (SI Appendix, Fig. S4). This might suggest that the forage-fish biomass was not sufficient to singly support the piscivore stock. However, forage-fish stock biomass is jointly determined by the forage-fish biomass-production and forage-fish biomass-depletion rates. Without knowledge of these forage-fish stock turnover rates, forage-fish stock biomass cannot easily function as an indicator of the importance of the forage-fish stock for piscivore persistence. We tested the robustness of our results to the exclusion of these stock combinations (SI Appendix, Fig. S4 and Table S6). In Results, we show results with these stock combinations included.

Some of the assessment models used to generate the time series in the RAM Legacy Stock Assessment Database may provide an estimate of the virgin, preharvesting stock biomass prior to periods covered by survey data. Declines in these initial biomass estimates may therefore be model artifacts (SI Appendix, Appendix B). We tested the robustness of our results to the exclusion of four stock combinations exhibiting continuous and long-lasting declines in piscivore biomass from the start of the time series, with little spread in the individual data points (SI Appendix, Table S11). In addition, we tested the robustness of our results to the exclusion of three stock combinations exhibiting declines in piscivore biomass starting prior to 1970 (SI Appendix, Table S12).

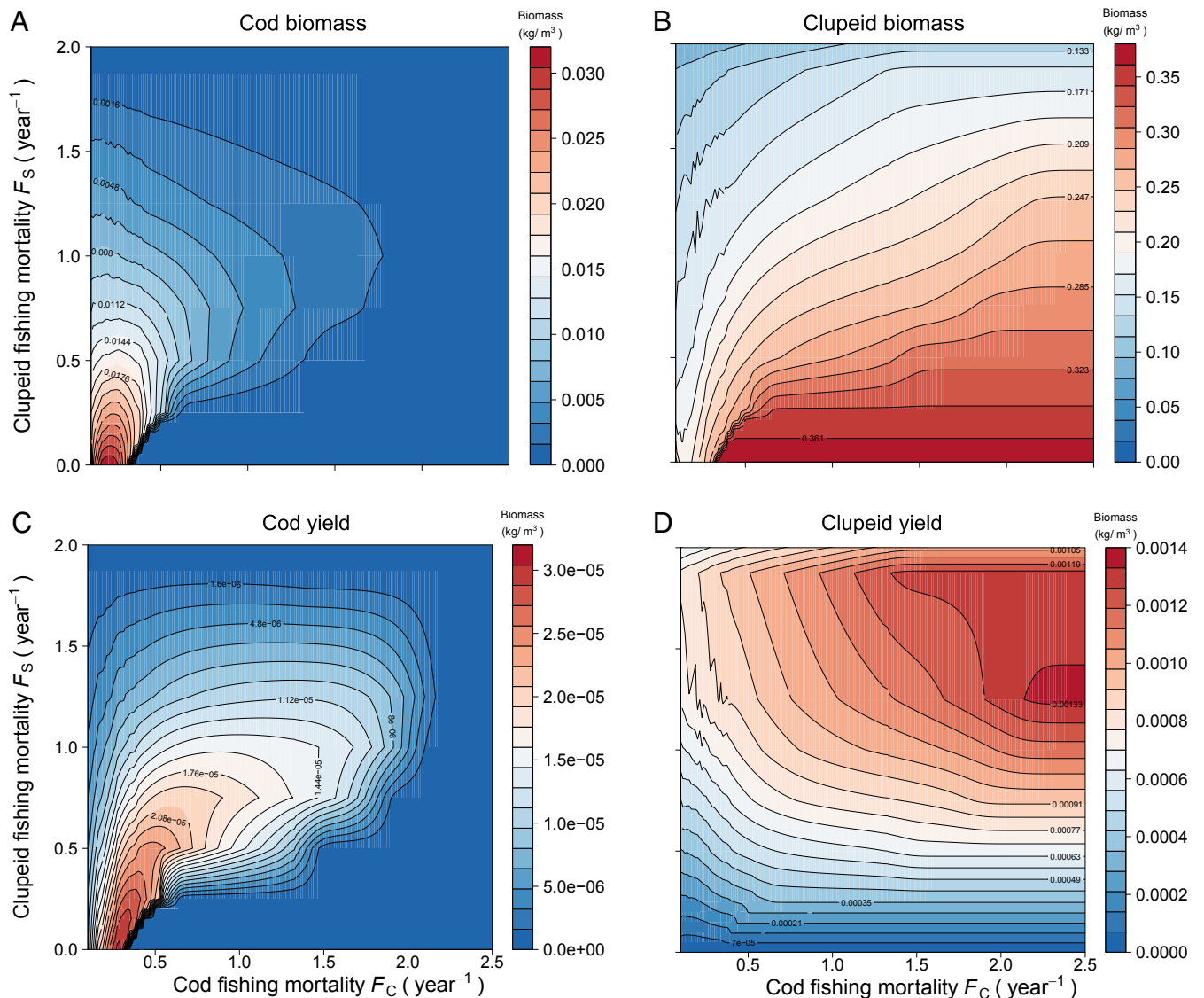
We defined the response variable in our statistical analysis as the natural logarithm of the aforementioned piscivore-biomass declines. We defined the corresponding predictor variables as the average annual fishing mortalities of piscivores and forage fish during these periods. For fishing mortality, we used the exploitation rate, as this is the quantity most commonly available in the database (annual catch/stock biomass). In some cases, multiple forage-fish stocks overlapped with a single piscivore. If so, forage-fish exploitation rates were, in each year of the decline period, calculated as biomass-weighted averages (when total biomass was not available, spawning-stock biomass was used). We performed a linear ordinary least-squares multiple-regression analysis of the logarithmic biomass ratios on these average fishing mortalities. Based on Akaike information criterion (AIC) scores for model fit, we tested models with and without an interaction term between piscivore and forage-fish fishing mortalities and with and without the forage-fish fishing mortality.

## Results

**Fishing for Clupeids Can Protect Cod in the Baltic Sea.** Our community-dynamics model of the Baltic Sea demonstrates that fishing for clupeids may prevent a fishing-induced collapse of cod (Fig. 1B). When clupeid harvesting is low, cod is predicted to collapse at high fishing mortality (Fig. 1B). Yet, cod can withstand this high fishing mortality when clupeids are harvested more intensely. In general, cod tolerates much higher fishing mortalities with high harvesting of the clupeids than without (Fig. 2A). The positive effect of clupeid fishing on the resilience of cod remains up to a high clupeid fishing mortality of about  $F_S = 1.0 \text{ year}^{-1}$  (Fig. 2A). Further increases of clupeid harvesting decrease the range of fishing mortalities that cod can withstand, and beyond about  $F_S = 1.7 \text{ year}^{-1}$ , the cod population goes extinct for any level of cod fishing mortality.

Fishing for clupeids affects cod positively through a change in the clupeid size distribution. When the cod population decreases, the adult clupeid biomass increases as the predation pressure from cod is lessened (Figs. 1B, 2B, and 3). This increase in adult clupeid biomass becomes less pronounced at higher clupeid fishing mortalities. Surprisingly, juvenile clupeid biomass increases with clupeid fishing mortality (Figs. 1C and 3). Harvesting clupeids reduces the adult clupeid biomass, thereby reducing intraspecific competition for food and increasing the density of the resource of the clupeids (Fig. 1B). This enables a higher net-energy production by adult clupeids and, consequently, a higher reproduction and production of juvenile clupeids (Fig. 1C). Finally, the higher production of juvenile clupeids benefits cod, since cod depend strongly on juvenile clupeids in their diet (Fig. 1A and SI Appendix, Table S4).

Fishing for clupeids also decreases the range of cod fishing mortalities with bistability in the cod-clupeid population dynamics (Fig. 3). The cod-clupeid system can exhibit two alternative patterns of stable dynamics when cod fishing mortality is low (Fig. 3A;  $F_C = 0.35$  to  $0.5 \text{ year}^{-1}$ ). In this range, whether cod is present or not depends on the initial conditions, and cod cannot invade the system from low densities. Yet, once cod is present at a sufficiently high density, it persists in the system. The range of cod fishing mortalities leading to such alternative stable states shrinks and is shifted to higher values of cod fishing mortality when clupeid harvesting is intense (Fig. 3B). This



**Fig. 2.** Effects of fishing on biomasses and yields in the community-dynamics model of the Baltic Sea. Biomass of adult cod (A) and adult clupeids (B), both including reproductive storages, and annual yield of cod (C) and clupeids (D) as a function of cod ( $F_C$ ; horizontal axes) and clupeid ( $F_S$ ; vertical axes) fishing mortalities. All other parameters are set to default values (SI Appendix, Tables S2–S4). Fishing mortality is here measured by the instantaneous fishing mortality rate. Yield is measured by the annual catch of, for cod, adults only and, for clupeids, adults and juveniles together (SI Appendix, Appendix A).

means that the conditions under which cod is able to (re)colonize the system become more permissive with intensive clupeid harvesting (Fig. 3).

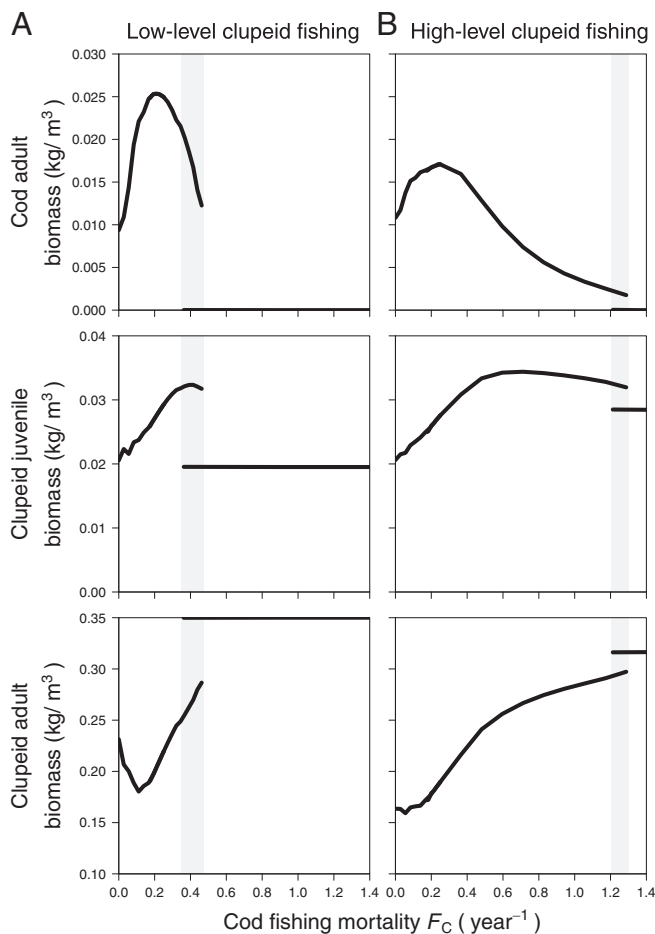
At low cod fishing mortalities, however, fishing for clupeids decreases cod biomass (Fig. 2A). This happens because when cod is present at high density, cod predation keeps the clupeid population at a low level (Figs. 1B and C and 3). Consequently, competition for food in the clupeid population is weak, even without clupeid harvesting.

Fishing for clupeids decreases the maximum yield that can be harvested from the cod population. The highest maximum yield of cod is found for a low clupeid fishing mortality of  $F_S = 0.0$  to  $0.05 \text{ year}^{-1}$ , where the clupeid yield is low or zero (Fig. 2C and D). In addition, with intensifying clupeid harvesting, obtaining the maximum cod yield requires an increasingly high fishing mortality (Fig. 2C). On the other hand, the maximum clupeid yield increases with increasing cod fishing mortality (Fig. 2C and D). The highest maximum yield of the clupeids occurs at values

where the cod yield is very low or zero, close to or beyond where cod goes extinct.

**Fishing for Forage Fish Can Protect Piscivores in Ecosystems around the World.** Investigating historical piscivore-biomass declines, we find that the statistical model best explaining the declines includes fishing mortalities of both piscivores and forage fish, as well as their interaction (Table 1, Fig. 4). The interaction is positive, implying that for high piscivore fishing mortalities, piscivore declines are smaller when the fishing mortalities of forage fish are higher. For low piscivore fishing mortalities, the interaction implies the opposite. This finding, based on piscivore stocks and forage-fish stocks in a wide range of marine ecosystems, corroborates the predictions of the community-dynamics model of the Baltic Sea.

We considered several alternative definitions for the periods of largest decline in piscivore biomasses (SI Appendix, Appendix B). For all methods considered, the best model was either a



**Fig. 3.** Effects of fishing on the bistability of cod population dynamics in the community-dynamics model of the Baltic Sea. Average adult cod and clupeid biomass (Top and Bottom, respectively, including reproductive storages) and average clupeid juvenile biomass (Middle) as a function of cod fishing mortality for low (A;  $F_S = 0.2 \text{ year}^{-1}$ ) and high (B;  $F_S = 0.5 \text{ year}^{-1}$ ) clupeid fishing mortality. Fishing mortality is here measured by the instantaneous fishing-mortality rate. All other parameters are set to default values (SI Appendix, Tables S2–S4).

model including the interaction term or a model including only the piscivore fishing mortality. Most often, the model with the interaction term has the lowest AIC score, while explaining 16 to 39% of the variance (adjusted  $r^2$ ; Table 1 and SI Appendix, Tables S8–S10). When the best model excludes the interaction term, it has poor explanatory power (adjusted  $r^2 \leq 0.07$ ; SI Appendix, Tables S8–S10). When the best model includes the interaction term, the sign of the interaction term is always positive, while the signs of the fishing-mortality terms are always negative.

Our statistical results are robust to changes in the minimum and maximum durations of the considered periods; the model with the interaction term is always selected as the best model (SI Appendix, Table S8). Yet, they are moderately sensitive to processing the raw time series through smoothing or regression; in some cases, the model including only the piscivore fishing mortality is selected as the best model (SI Appendix, Tables S8–S10). The exclusion of the stock combinations for which the forage-fish stock biomass is lower than the piscivore stock biomass (SI Appendix, Fig. S4, Table S6) or for which declines start early in the time series (SI Appendix, Table S11) or start prior to 1970 (SI Appendix, Table S12) does not reduce support for the interaction model. The results are sensitive, though, to the inclusion

of an influential stock, resulting in three models being similar in their empirical support (SI Appendix, Table S7). Nevertheless, the model including the interaction term still has higher explanatory power.

**Discussion**

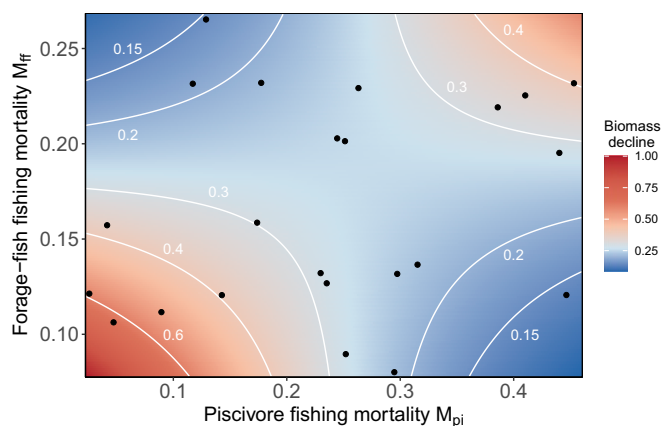
Our findings challenge the paradigm that the fishing of forage fish is always harmful for large piscivores (6, 15). In line with this paradigm, our community-dynamics model of the Baltic Sea predicts a decrease of cod biomass with increasing clupeid harvesting at low piscivore fishing mortality. Yet, contrary to what the paradigm suggests, intermediate harvesting of clupeids prevents cod population collapses at high piscivore fishing mortality. In accordance with these theoretical predictions, our statistical model shows a positive interaction between fishing mortalities of piscivores and their forage fish on the magnitude of piscivore-biomass declines. These latter results are not completely robust to some details of the statistical methods, but nevertheless support the hypothesis that fishing for forage fish can benefit large piscivores.

The potential of fishing to alter size distributions of fish is widely recognized (20–22). Here, we have shown that, through this secondary effect of fishing, harvesting forage fish may positively affect large piscivores. When, in the community-dynamics model, piscivore abundance is low, harvesting forage fish increases the production of small juvenile forage fish. These small fish make up an essential part of the piscivore diet (Fig. 1A). Therefore, the piscivores can benefit from the fishing of their prey. Especially during the onset of piscivory, the availability of small prey items is crucial for piscivore growth, due to the piscivore’s body-size constraints (23–25). In the community-dynamics model, the production of small forage fish is reduced when the piscivore population shrinks, due to an increase of (adult) forage-fish biomass and competition for food in the

**Table 1. Alternative statistical models of the effects of piscivore and forage-fish fishing on piscivore-biomass declines in ecosystems around the world**

Model	SE	$r^2$	AIC	$\Delta$ AIC
$\ln(B_{pi}) = 1.2 - 9.6 M_{pi} - 13.4 M_{ff} + 51.1 M_{pi} M_{ff}$				
$p_1 = 0.005$	0.8	0.26	43.0	0
$p_2 = 0.009$	3.1			
$p_3 = 0.009$	4.6			
	17.5			
$\ln(B_{pi}) = -0.8 - 1.0 M_{pi} - 1.5 M_{ff}$				
$p_1 = 0.37$	0.5	-0.02	49.6	6.6
$p_2 = 0.54$	1.1			
	2.5			
$\ln(B_{pi}) = -1.0 - 1.1 M_{pi}$				
$p_1 = 0.29$	0.3	0.01	48.0	5.0
	1.0			

The three models describe the logarithmic decline  $\ln(B_{pi})$  as a function of the average piscivore fishing mortality  $M_{pi}$  and the average forage-fish fishing mortality  $M_{ff}$  during the decline period. The piscivore-biomass decline  $B_{pi}$  is measured by the ratio of piscivore biomasses at the end and at the beginning of the decline period (Materials and Methods and SI Appendix, Fig. S1). The duration of the decline period is allowed to vary between 5 and 15 years. Fishing mortality is here measured by the exploitation rate (annual catch/stock biomass). A total of 23 combinations of piscivores and forage fish were used for the analysis.  $p_1$ ,  $p_2$ , and  $p_3$  show the P values for the regression coefficients of, respectively, the model terms  $M_{pi}$ ,  $M_{ff}$ , and  $M_{pi} M_{ff}$ .  $r^2$  is the coefficient of determination (adjusted  $r^2$ ), SE is the standard error of the intercept and the regression coefficients, AIC is the AIC score, and  $\Delta$ AIC is the difference in AIC score relative to the model with the minimal AIC score.  $\Delta$ AIC values in excess of two are standardly recognized as characterizing models with substantially less support.



**Fig. 4.** Effects of fishing on piscivore-biomass declines in the statistical model of piscivore fish stocks and forage-fish stocks in ecosystems around the world. The decline is shown as a function of the average piscivore fishing mortality (horizontal axis) and the average forage-fish fishing mortality (vertical axis). The piscivore-biomass decline is measured by the ratio of piscivore biomasses at the end and at the beginning of the decline period (*Materials and Methods* and *SI Appendix, Fig. S1*). Fishing mortality is here measured by the exploitation rate (annual catch/stock biomass). The dots represent the 23 combinations of piscivores and forage-fish stocks used for the analysis. The estimated model shows that piscivore biomasses decline more strongly for higher piscivore and forage-fish fishing mortalities, with a positive interaction.

forage-fish population. An increase of forage-fish population biomass has often been documented in relation to declines of piscivores (26–28). Signs of competition, such as a reduced growth and body condition, have been observed in forage-fish populations after the declines of cod in the Northwest Atlantic and the Baltic Sea (12, 29, 30). In addition, the estimated total reproductive output of clupeids in the Baltic Sea shows a steep decline during the years leading up to the collapse of cod (12). These examples show that population biomass and competition for food can both increase in forage-fish populations after or during declines of their piscivorous predators. Moreover, piscivores in the Northwest Atlantic and the Baltic Sea appear to suffer from a reduced body condition since their collapse, which may be indicative of a persistent shortage of food (31–34). While the high biomass of forage fish in these ecosystems seems to imply a high food abundance for the piscivores, the signs of food shortage suggest that prey of the right size may, in fact, be scarce.

A positive effect of forage-fish harvesting on piscivores has not been reported in previous model-based studies (e.g., refs. 15 and 35). However, it has recently been argued that multispecies fisheries models do not incorporate all relevant biological processes (10, 11). For example, multispecies fisheries models do not always consider size-selective predation and harvesting, as well as the size structures of piscivore and forage-fish populations (10, 11). Moreover, the energy budget of fish is often not accounted for in a consistent way (10), as somatic growth is assumed to be independent of food availability, or costs of maintenance and/or costs and food dependence of reproduction are ignored (10). These factors are all included in the community-dynamics model we have used for the present study. Our model predicts a positive effect of clupeid fishing mortality on juvenile clupeid biomass—a phenomenon known as biomass overcompensation, which has been described in both theoretical and experimental studies (17, 36, 37). Crucially, biomass overcompensation does not occur when the size structure of populations is ignored (17, 38). It also does not occur when energy losses through maintenance costs are not explicitly considered (39). Therefore, a consistent treatment of 1) individual energy budgets (in partic-

ular, accounting for costs of maintenance), 2) the size structure of fish populations, and 3) feedbacks between trophic levels are indispensable for the effects of fishing mortality on the production of juvenile forage fish to become amenable to analysis (10, 17, 37).

Previous studies have ascribed reduced growth of piscivore populations after a decline in their population to cultivation-dependence mechanisms (40–42). After a piscivore decline, increased forage-fish biomass may, for example, lead to increased competition between juvenile piscivores and forage fish and/or predation of forage fish on eggs and larvae of piscivores (40, 41). These mechanisms could lead to the same net positive effect of harvesting forage fish on piscivore persistence as biomass overcompensation, the mechanism explained above. To determine the importance of the different mechanisms, detailed data on the interaction between forage fish and piscivores are required. Such data are not generally available. For the central Baltic Sea, detailed analyses of available data have shown that biomass overcompensation could explain the lack of recovery of cod in this ecosystem (43), while no sufficient data are available to test whether predatory cultivation-dependence could explain the lack of cod recovery. For this reason, we did not include cultivation-dependence mechanisms in our community-dynamics model. The inclusion of these mechanisms in the model would likely strengthen the observed effect.

The global RAM Legacy Stock Assessment Database (14), which we have used for our data analysis, is currently the most extensive source of fish-stock assessment data. While the findings from our statistical model support those from our community-dynamics model, caution is needed, as the former analysis is based on a relatively small number of cases. In addition, the statistical analysis may have biases hindering the detection of effects. For example, no established method is available for choosing the duration of periods of declining piscivore biomass. Furthermore, variability in primary production among the considered fisheries-assessment areas implies that absolute fishing mortalities may not be directly comparable. Moreover, we inferred trophic interactions between forage-fish and piscivorous-fish stocks based on spatial overlap and trophic level. This does not necessarily reflect the trophic interactions that occur in the ecosystems. Finally, a global analysis will always remain correlative, rather than establish causation. In-depth studies of prey size distributions in the stomach contents of piscivores could provide more direct evidence of effects of forage-fish fisheries on the feeding conditions of the corresponding piscivores.

The RAM Legacy Stock Assessment Database is widely used as the authoritative source of stock-abundance data for fisheries analyses (e.g., ref. 44). The estimates of stock biomass in the database result from single-species stock-assessment models, which typically assume natural mortality to be constant over time. The assumption of constant natural mortality potentially leads to confounding effects of declining predator biomass on the estimates of forage-fish fishing mortality (45). Yet, the forage-fish fishing mortalities used in our analysis seem to fluctuate randomly during the periods of piscivore biomass decline (*SI Appendix, Fig. S2*). The assessment methodology may also raise questions about the representativeness of the resultant estimates. Preferably, validation of a hypothesis is based on multiple lines of evidence. A combination of commercial-landings data and biomass estimates is needed to allow for the analysis of trends in biomasses and fishing mortalities. To the best of our knowledge, there are not sufficient trawl-survey-based biomass estimates available to repeat our analysis with alternative data sources (*SI Appendix, Figs. S5 and S6 and Appendix B*). While trawl-survey data may be available for longer periods than shown in the figures, there are no recordings of

trawl-swept area available, which are needed for the calculation of the catch-per-unit effort, on which biomass estimates are based. The trawl-survey-based biomass estimates that we did find follow the stock-assessment-based estimates relatively closely (*SI Appendix*, Figs. S5 and S6). Our statistical analysis gives a first indication that the mechanism we discuss here could apply to a range of marine ecosystems. Naturally, additional system-specific empirical and theoretical analyses are needed to determine the mechanisms that locally shape community dynamics.

Forage fish form an essential link in many food webs for the transfer of energy from lower to higher trophic levels and are often strongly affected by fisheries (4, 46, 47). Forage-fish stocks show a tendency to fluctuate widely in biomass, but recover relatively easily after a decline (48). It has been argued that collapses of forage fish stem from overfishing in combination with temporal fluctuations in primary productivity (49, 50). Forage-fish declines may lead to harmful jellyfish blooms (27, 51) and negatively affect abundances of predatory seabirds (9, 52). Moreover, collapses of forage fish have been linked to collapses of piscivores (46). These examples underscore the negative effects that forage-fish fisheries can have on piscivores and marine ecosystems. On the other hand, benefits to piscivores by forage-fish fisheries have so far been reported only rarely (e.g., ref. 7 reports a piscivore-biomass decline after a reduction of forage-fish harvesting in the North Sea).

The greater part of forage-fish catches is used as feed in aquaculture and terrestrial husbandry (2, 53). The projected increase in global seafood demand (53) and the decrease in trophic levels of fisheries landings (ref. 54, but see ref. 55) signal a (future) increase of fishing efforts lower down the food chain. This notion has ignited a debate about the importance of

forage fishes for ecosystem functioning and their indirect contributions to the economic value of fisheries (4). It is with good reason that scientists urge caution in the management of forage fish. Yet, our results imply that drastically lowering fishing pressures on forage fishes may have unwanted negative consequences for piscivores that are heavily exploited. In some cases, decreasing the fishing mortality of forage fishes may even cause collapses of the piscivores that depend on them. While we argue that an intermediate fishing pressure on forage fish increases piscivore resilience, forage fishes should obviously not be overfished.

**Data Availability.** C code and R scripts used for implementation of the community-dynamics model and analysis of the statistical model have been deposited at <https://zenodo.org/10.5281/zenodo.3779839>. The RAM Legacy Stock Assessment Database used for the statistical model analysis is publicly accessible (ref. 14; version 3.0; <https://www.ramlegacy.org/database/>).

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