

1 Harvesting forage fish can prevent fishing-induced population collapses of large piscivorous 2 fish

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14 **Author Contributions.** All authors contributed to study design and manuscript text. F.H.S. and P.D.v.D. performed data
15 assembly and statistical model analysis. F.H.S. and A.M.d.R. constructed and analyzed the community dynamics model and
16 wrote the manuscript.

17 **Author Declaration.** The authors declare no competing interest.

18 **Keywords.** Fisheries | Predator-prey dynamics | Multiple trophic levels | Size-structured model | Bioenergetics

19 Significance Statement

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

27 Introduction

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

33 The importance of an ecosystem-based, multi-species approach to fisheries management is underscored by potential indirect
34 negative effects of forage-fish fisheries on piscivores (5, 6). Unraveling the effects of multi-species fisheries is a serious challenge
35 due to feedbacks between fisheries, fish populations, and the fishes' food sources (e.g., 7). Understanding these effects is further
36 complicated by nonlinearities in population-level processes (8). The effects of fishing on multiple species at different trophic
37 levels of marine ecosystems are usually assessed using multi-species fisheries models (4, 9). However, it has recently been
38 argued that such models do not contain all necessary processes to predict fish community dynamics (10, 11). Components that
39 are considered essential in models of fish communities are: (1) fish population size structure, (2) consistent accounting of the
40 bioenergetic flows through fish populations and communities, and (3) size-selective predation and harvesting (10, 11).

41 In this study, we investigate the effects of fishing for forage fish on their predators, the piscivorous fish. We do this using a
42 previously published model of the central Baltic Sea community dynamics (12) that was specifically designed to investigate
43 effects of fisheries on fish communities (10, 12). The model incorporates size-structured fish populations, size-dependent feeding
44 interactions, and individual-level energy budgets. In addition, consumption by fish has a direct effect on their food sources,
45 and the flows of energy throughout the system are thus accounted for consistently. Using this model, we explore the effects of
46 fishing for both forage fish and piscivores. We first focus on the Baltic Sea because its food web is relatively simple and the
47 exploited fish species include both piscivores (cod) and forage fish (sprat and herring) (13). Using the global RAM Legacy
48 Stock Assessment Database (14), we then statistically evaluate historical patterns in piscivore biomasses and fishing pressures
49 on forage fish and piscivores. Our dynamic and statistical model analyses agree in demonstrating that harvesting forage fish
50 does not always affect piscivore populations negatively. Instead, such fishing can protect large-piscivore populations from
51 fishing-induced collapses. These results challenge the generally accepted idea that large piscivores always benefit from less
52 fishing of their forage fish (6, 15).

53 Material and Methods

54 Below, we presented the models used for our analyses in general terms. Details are described in the SI Appendix, in Appendix
55 A for the community dynamics model and in Appendix B for the statistical model. Analysis of the community dynamics
56 model is carried out using publicly available C-based simulation programs. The statistical model analysis is based on publicly
57 available data. C-code and R-scripts used for implementation of the community dynamics model and analysis of the statistical
58 model are publicly available (zenodo.org, links available through the journals office).

59 **Community dynamics model of the Baltic Sea.** To analyze the effects of multi-species fishing, we use the stage-structured
60 bioenergetics model of the central Baltic Sea introduced by van Leeuwen et al. (12). The model includes the key ecological
61 interactions between predatory and forage fish and their resources; it is aimed to qualitatively reproduce the dynamics of this
62 system. We improve on the model by van Leeuwen et al. (12) by implementing reproduction as a seasonal process, following
63 Soudijn & de Roos (16). The model structure and size-based, stage-specific parameterization are derived from individual-level
64 data of Baltic cod, sprat, and herring (SI Appendix, Appendix A). Figure 1A shows the interactions between fish populations in
65 the model. Sprat and herring, the prey fish of cod, are assumed to have a similar ecological role. Hence, they are modeled as a
66 clupeid population that uses the same resource (zooplankton) throughout its life. Cod, the piscivore in this community, forages
67 on zooplankton and small fish while juvenile and switches to benthos and larger fish upon maturation (Fig. 1A). Accordingly,
68 there is no direct resource competition between juvenile cod and the clupeids in the model. Using the model, we assess the
69 effects of the instantaneous fishing mortality rates for cod (F_C) and clupeids (F_S) on the community dynamics.

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

82 **Statistical model of interactions between piscivores and their forage fish in ecosystems around the world.** We test how our
83 model predictions generalize across ecosystems using historical patterns of stock biomasses and fishing mortalities from the
84 RAM Legacy Stock Assessment Database (14, version 3.0, publicly accessible at www.ramlegacy.org/database). The stock
85 assessments in the RAM Legacy Stock Assessment Database currently represent the best available syntheses of catch and survey
86 data to derive estimates of stock biomasses and fishing mortalities (SI Appendix, Appendix B). If intermediate harvesting of
87 forage fish can protect piscivores from fishing-induced collapses (Results), an interaction is expected in the effects of forage-fish
88 and piscivore fishing mortalities on changes in piscivore biomass.

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

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

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

110 Some of the assessment models used to generate the time series in the RAM Legacy Stock Assessment Database may provide
111 an estimate of the virgin, pre-harvesting stock biomass prior to periods covered by survey data. Declines in these initial biomass

112 estimates may therefore be model artifacts (SI Appendix, Appendix B). We tested the robustness of our results to the exclusion
113 of four stock combinations exhibiting continuous and long-lasting declines in piscivore biomass from the start of the time series
114 with little spread in the individual data points (SI Appendix, Table S11). In addition, we tested the robustness of our results
115 to the exclusion of three stock combinations exhibiting declines in piscivore biomass starting prior to 1970 (SI Appendix, Table
116 S12).

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

126 Results

127 **Fishing for clupeids can protect cod in the Baltic Sea.** Our community dynamics model of the Baltic Sea demonstrates that
128 fishing for clupeids may prevent a fishing-induced collapse of cod (Fig. 1B). When clupeid harvesting is low, cod is predicted to
129 collapse at high fishing mortality (Fig. 1B). Yet, cod can withstand this high fishing mortality when clupeids are harvested
130 more intensely. In general, cod tolerates much higher fishing mortalities with high harvesting of the clupeids than without
131 (Fig. 2A). The positive effect of clupeid fishing on the resilience of cod remains up to a high clupeid fishing mortality of about
132 $F_S = 1.0 \text{ year}^{-1}$ (Fig. 2A). Further increases of clupeid harvesting decrease the range of fishing mortalities that cod can
133 withstand, and beyond about $F_S = 1.7 \text{ year}^{-1}$ the cod population goes extinct for any level of cod fishing mortality.

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

142 Fishing for clupeids also decreases the range of cod fishing mortalities with bistability in the cod-clupeid population dynamics
143 (Fig. 3). The cod-clupeid system can exhibit two alternative patterns of stable dynamics when cod fishing mortality is low (Fig.
144 3A, $F_C = 0.35$ to 0.5 year^{-1}). In this range, whether cod is present or not depends on the initial conditions, and cod cannot
145 invade the system from low densities. Yet, once cod is present at a sufficiently high density, it persists in the system. The
146 range of cod fishing mortalities leading to such alternative stable states shrinks and is shifted to higher values of cod fishing
147 mortality when clupeid harvesting is intense (Fig. 3B). This means that the conditions under which cod is able to (re)colonize
148 the system become more permissive with intensive clupeid harvesting (Fig. 3).

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

152 Fishing for clupeids decreases the maximum yield that can be harvested from the cod population. The highest maximum
153 yield of cod is found for a low clupeid fishing mortality of $F_S = 0.0$ to 0.05 year^{-1} , where the clupeid yield is low or zero (Figs.
154 2C and D). In addition, with intensifying clupeid harvesting, obtaining the maximum cod yield requires an increasingly high
155 fishing mortality (Fig. 2C). On the other hand, the maximum clupeid yield increases with increasing cod fishing mortality
156 (Figs. 2C and D). The highest maximum yield of the clupeids occurs at values where the cod yield is very low or zero, close to
157 or beyond where cod goes extinct.

158 **Fishing for forage fish can protect piscivores in ecosystems around the world.** Investigating historical piscivore-biomass declines,
159 we find that the statistical model best explaining the declines includes fishing mortalities of both piscivores and forage fish, as
160 well as their interaction (Table 1). The interaction is positive, implying that for high piscivore fishing mortalities, piscivore
161 declines are smaller when the fishing mortalities of forage fish are higher. For low piscivore fishing mortalities, the interaction
162 implies the opposite. This finding, based on piscivore stocks and forage-fish stocks in a wide range of marine ecosystems,
163 corroborates the predictions of the community dynamics model of the Baltic Sea.

164 We considered several alternative definitions for the periods of largest decline in piscivore biomasses (SI Appendix, Appendix
165 B). For all methods considered, the best model is either a model including the interaction term, or a model including only the
166 piscivore fishing mortality. Most often, the model with the interaction term has the lowest AIC score, while explaining 16-39%
167 of the variance (adjusted r^2 , SI Appendix, Tables 1 and S8-S10). When the best model excludes the interaction term, it has
168 poor explanatory power (adjusted $r^2 \leq 0.07$, SI Appendix, Tables S8-S10). When the best model includes the interaction term,
169 the sign of the interaction term is always positive while the signs of the fishing-mortality terms are always negative.

Table 1. Alternative statistical models of the effects of piscivore and forage-fish fishing on piscivore-biomass declines in ecosystems around the world. 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 (Material 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). 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 Δ AIC is the difference in AIC score relative to the model with the minimal AIC score. Δ AIC values in excess of 2 are standardly recognized as characterizing models with substantially less support.

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

170 Our statistical results are robust to changes in the minimum and maximum durations of the considered periods; the model
171 with the interaction term is always selected as the best model (SI Appendix, Table S8). Yet, they are moderately sensitive to
172 processing the raw time series through smoothing or regression; in some cases, the model including only the piscivore fishing
173 mortality is selected as the best model (SI Appendix, Tables S8-S10). The exclusion of the stock combinations for which the
174 forage-fish stock biomass is lower than the piscivore stock biomass (SI Appendix, Fig. S4, Table S6), for which declines start
175 early in the time series (SI Appendix, Table S11), or start prior to 1970 (SI Appendix, Table S12) does not reduce support for
176 the interaction model. The results are sensitive, though, to the inclusion of an influential stock, resulting in three models being
177 similar in their empirical support (SI Appendix, Table S7). Nevertheless, the model including the interaction term still has
178 higher explanatory power.

179 Discussion

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

187 The potential of fishing to alter size distributions of fish is widely recognized (20–22). Here we have shown that, through
188 this secondary effect of fishing, harvesting forage fish may positively affect large piscivores. When, in the community dynamics
189 model, piscivore abundance is low, harvesting forage fish increases the production of small juvenile forage fish. These small fish
190 make up an essential part of the piscivore diet (Fig. 1A). Therefore, the piscivores can benefit from the fishing of their prey.
191 Especially during the onset of piscivory, the availability of small prey items is crucial for piscivore growth, due to the piscivore's
192 body-size constraints (23–25). In the community dynamics model, the production of small forage fish is reduced when the
193 piscivore population shrinks, due to an increase of (adult) forage-fish biomass and competition for food in the forage-fish
194 population. An increase of forage-fish population biomass has often been documented in relation to declines of piscivores
195 (26–28). Signs of competition, such as a reduced growth and body condition, have been observed in forage-fish populations
196 after the declines of cod in the Northwest Atlantic and the Baltic Sea (12, 29, 30). In addition, the estimated total reproductive
197 output of clupeids in the Baltic Sea shows a steep decline during the years leading up to the collapse of cod (12). These
198 examples show that population biomass and competition for food can both increase in forage-fish populations after or during
199 declines of their piscivorous predators. Moreover, piscivores in the Northwest Atlantic and the Baltic Sea appear to suffer from
200 a reduced body condition since their collapse, which may be indicative of a persistent shortage of food (31–34). While the high
201 biomass of forage fish in these ecosystems seems to imply a high food abundance for the piscivores, the signs of food shortage
202 suggest that prey of the right size may in fact be scarce.

203 A positive effect of forage-fish harvesting on piscivores has not been reported in previous model-based studies (e.g., 15, 35).
204 However, it has recently been argued that multi-species fisheries models do not incorporate all relevant biological processes
205 (10, 11). For example, multi-species fisheries models do not always consider size-selective predation and harvesting, as well as
206 the size structures of piscivore and forage-fish populations (10, 11). Moreover, the energy budget of fish is often not accounted
207 for in a consistent way (10), as somatic growth is assumed to be independent of food availability, or costs of maintenance and/or
208 costs and food dependence of reproduction are ignored (10). These factors are all included in the community dynamics model
209 we have used for the present study. Our model predicts a positive effect of clupeid fishing mortality on juvenile clupeid biomass
210 - a phenomenon known as biomass overcompensation, which has been described in both theoretical and experimental studies
211 (17, 36, 37). Crucially, biomass overcompensation does not occur when the size structure of populations is ignored (17, 38). It
212 also does not occur when energy losses through maintenance costs are not explicitly considered (39). Therefore, a consistent
213 treatment of (i) individual energy budgets (in particular, accounting for costs of maintenance), (ii) the size structure of fish
214 populations, and (iii) feedbacks between trophic levels are indispensable for the effects of fishing mortality on the production of
215 juvenile forage fish to become amenable to analysis (10, 17, 37).

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

226 The global RAM Legacy Stock Assessment Database (14), which we have used for our data analysis, is currently the most
227 extensive source of fish-stock assessment data. While the findings from our statistical model support those from our community
228 dynamics model, caution is needed as the former analysis is based on a relatively small number of cases. In addition, the
229 statistical analysis may have biases hindering the detection of effects. For example, no established method is available for

230 choosing the duration of periods of declining piscivore biomass. Furthermore, variability in primary production among the
231 considered fisheries-assessment areas implies that absolute fishing mortalities may not be directly comparable. Moreover, we
232 inferred trophic interactions between forage-fish and piscivorous fish stocks based on spatial overlap and trophic level. This
233 does not necessarily reflect the trophic interactions that occur in the ecosystems. Finally, a global analysis will always remain
234 correlative, rather than establish causation. In-depth studies of prey size distributions in the stomach contents of piscivores
235 could provide more direct evidence of effects of forage-fish fisheries on the feeding conditions of the corresponding piscivores.

236 The RAM Legacy Stock Assessment Database is widely used as the authoritative source of stock-abundance data for
237 fisheries analyses (e.g., 44). The estimates of stock biomass in the database result from single-species stock-assessment models,
238 which typically assume natural mortality to be constant over time. The assumption of constant natural mortality potentially
239 leads to confounding effects of declining predator biomass on the estimates of forage-fish fishing mortality (45). Yet, the
240 forage-fish fishing mortalities used in our analysis seem to fluctuate randomly during the periods of piscivore-biomass decline
241 (SI Appendix, Fig. S2). The assessment methodology may also raise questions about the representativeness of the resultant
242 estimates. Preferably, validation of a hypothesis is based on multiple lines of evidence. A combination of commercial-landings
243 data and biomass estimates is needed to allow for the analysis of trends in biomasses and fishing mortalities. To the best of
244 our knowledge, there are not sufficient trawl-survey-based biomass estimates available to repeat our analysis with alternative
245 data sources (SI Appendix, Figs. S5 and S6, Appendix B). While trawl-survey data may be available for longer periods than
246 shown in the figures, there are no recordings of trawl swept area available, which are needed for the calculation of the catch
247 per unit effort (CPUE) on which biomass estimates are based. The trawl-survey-based biomass estimates that we did find
248 follow the stock-assessment-based estimates relatively closely (SI Appendix, Figs. S5 and S6). Our statistical analysis gives
249 a first indication that the mechanism we discuss here could apply to a range of marine ecosystems. Naturally, additional
250 system-specific empirical and theoretical analyses are needed to determine the mechanisms that locally shape community
251 dynamics.

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

260 The greater part of forage-fish catches is used as feed in aquaculture and terrestrial husbandry (2, 53). The projected
261 increase in global seafood demand (53) and the decrease in trophic levels of fisheries landings (54, but see 55) signal a (future)
262 increase of fishing efforts lower down the food chain. This notion has ignited a debate about the importance of forage fishes
263 for ecosystem functioning and their indirect contributions to the economic value of fisheries (4). It is with good reason that
264 scientists urge caution in the management of forage fish. Yet, our results imply that drastically lowering fishing pressures on
265 forage fishes may have unwanted negative consequences for piscivores that are heavily exploited. In some cases, decreasing the
266 fishing mortality of forage fishes may even cause collapses of the piscivores that depend on them. While we argue that an
267 intermediate fishing pressure on forage fish increases piscivore resilience, forage fishes should obviously not be overfished.

268 section*Acknowledgements We thank the Theoretical Ecology Group at the University of Amsterdam, A. van Leeuwen,
269 and all 2014 YSSP participants for helpful discussions and inspiration. We thank A. Maureaud for cleaning, processing, and
270 standardizing the trawl-survey data used in the SI. This work was partly carried out during the Young Scientists Summer
271 Program (YSSP) at the International Institute for Applied Systems Analysis (IIASA); FHS's participation in the program
272 was financed by the Dutch Research Council (NWO). PDvD received funding from the People Programme (Marie Curie
273 Actions) under Research Executive Agency grant agreement number 609405 (COFUNDPostdocDTU) and conducted the work
274 within the Centre for Ocean Life, a VKR center of excellence supported by the Villum Foundation. MH received funding
275 from the Norwegian Research Council project MESSAGE (255530). FHS, MH, and UD gratefully acknowledge funding from
276 the International Institute for Applied Systems Analysis (IIASA) and the National Member Organizations that support the
277 institute. Jan van Arkel (IBED) designed the illustration displayed in Figure 1A. Portions of the paper were developed from
278 the thesis of FHS.

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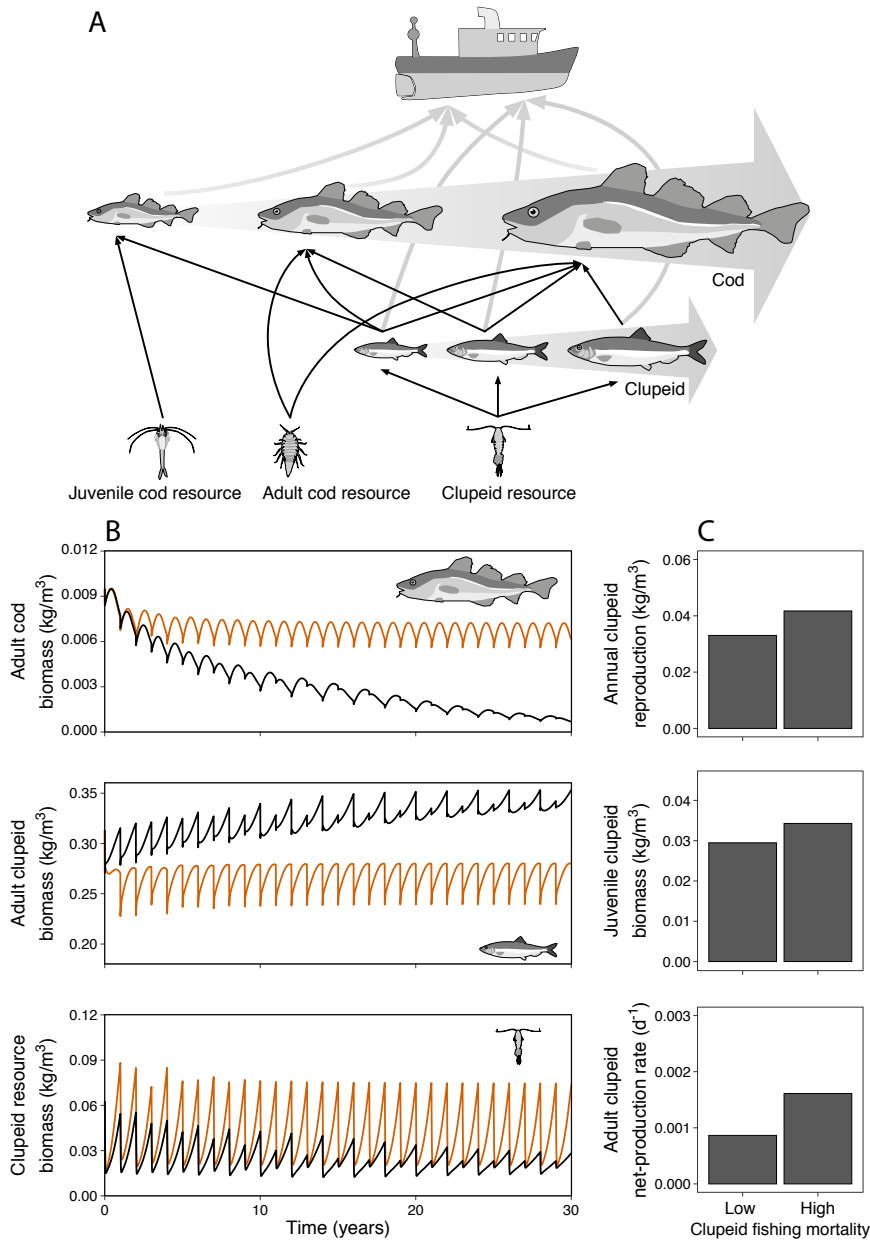


Fig. 1. Interactions between cod and clupeids in the community dynamics model of the Baltic Sea. (A) Trophic interactions among fisheries (narrow grey arrows), cod and clupeid stages, and their resources (black arrows; see SI Appendix, Table S4 for the foraging preferences of the cod stages). Individual fish grow through stages from left to right (broad grey arrows). (B) Time series of adult cod biomass (top), 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, $F_C = 1.0 \text{ year}^{-1}$. The time series start from equilibrium biomass for low cod and clupeid fishing mortalities ($F_C = 0.25 \text{ year}^{-1}$, $F_S = 0.5 \text{ year}^{-1}$). (C) Averages over years 0 to 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).

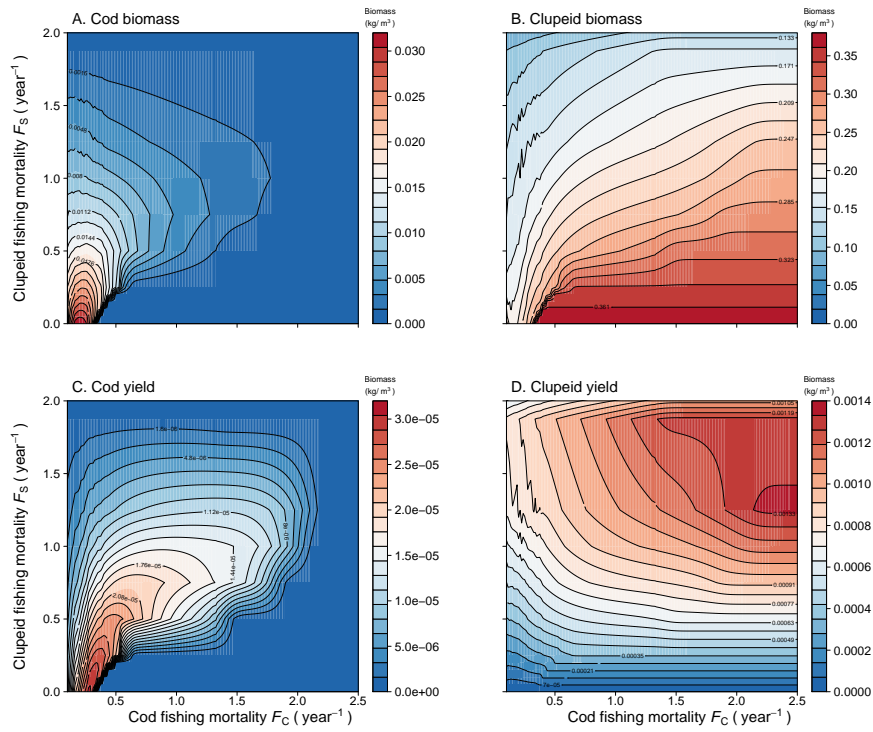


Fig. 2. Effects of fishing on biomasses and yields in the community dynamics model of the Baltic Sea. Biomass of (A) adult cod and (B) adult clupeids, both including reproductive storages, and annual yield of (C) cod and (D) clupeids as a function of cod (F_C , horizontal axes) and clupeid (F_S , vertical 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).

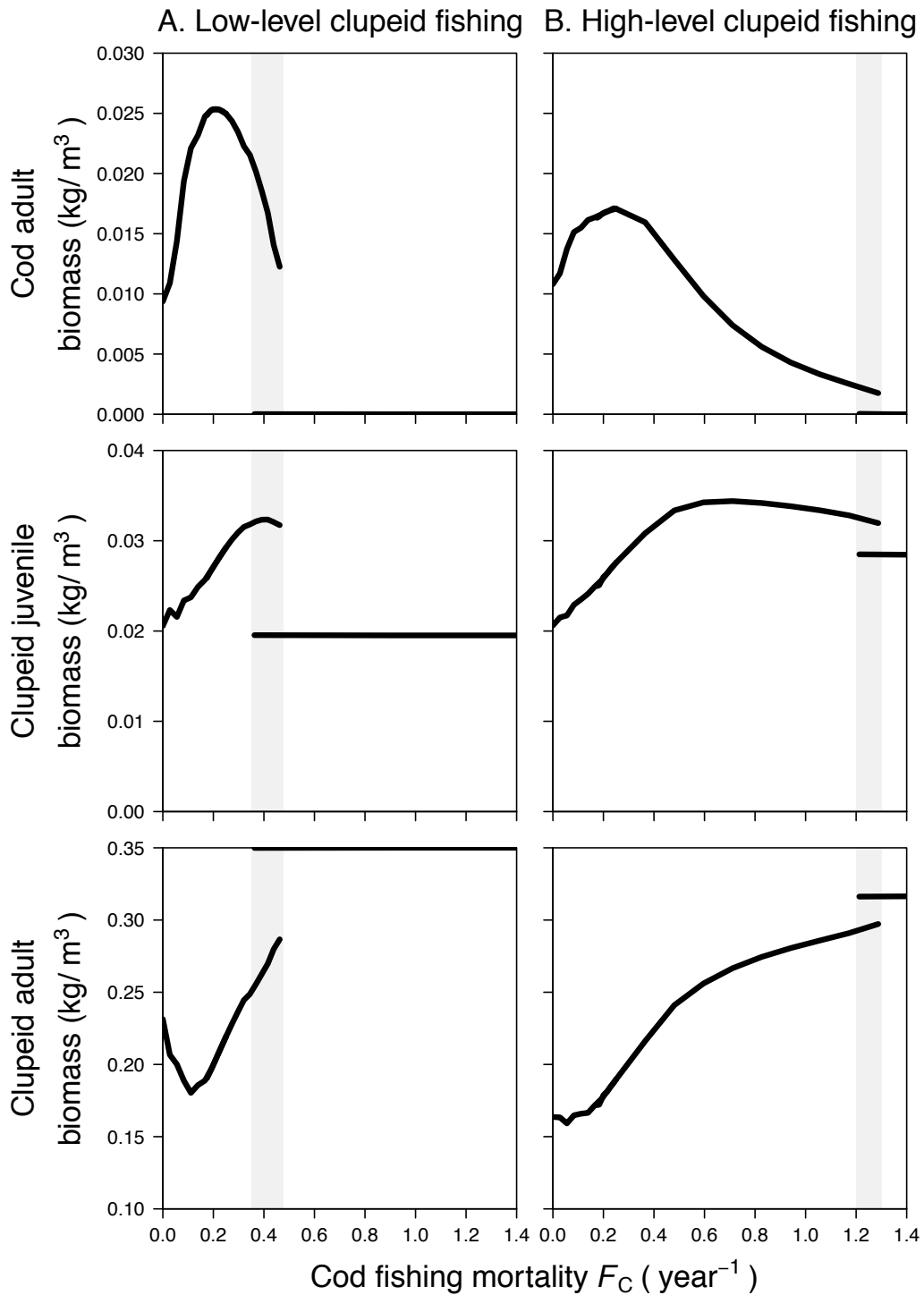


Fig. 3. Effects of fishing on the bistability of cod population dynamics in the community dynamics model of the Baltic Sea. Average adult cod and clupeid biomass (top and bottom panels, respectively, including reproductive storages) and average clupeid juvenile biomass (middle panels) as a function of cod fishing mortality for low (A, $F_S = 0.2$ year⁻¹) and high (B, $F_S = 0.5$ 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).

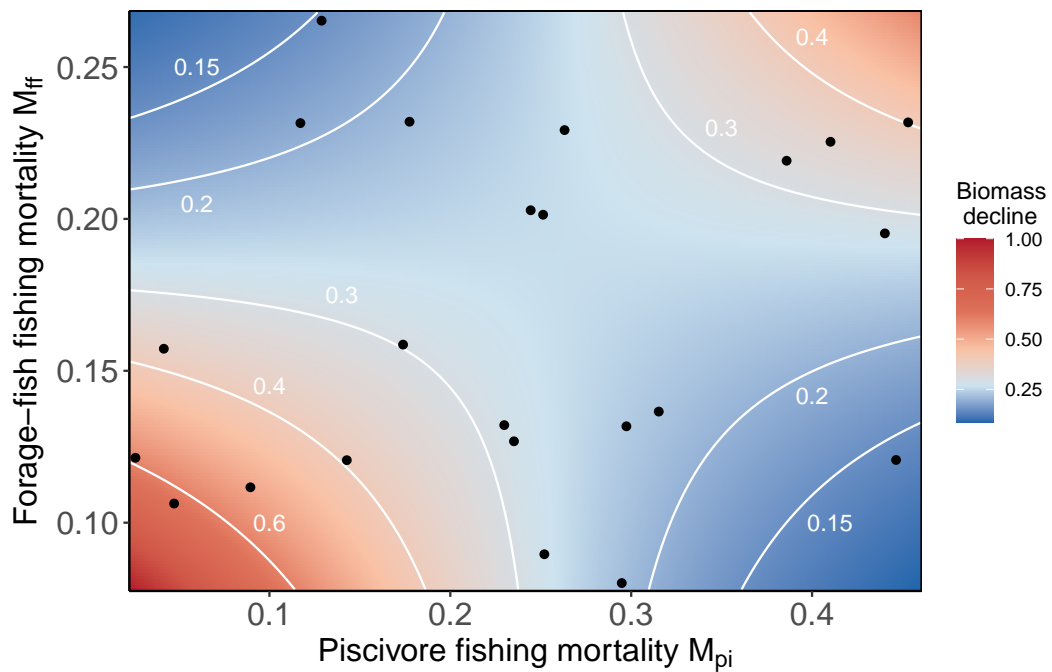


Fig. 4. Effects of fishing on piscivore-biomass declines in the statistical model of piscivore fish stocks and forage-fish stocks in ecosystems around the world. The decline is shown as a function of the average piscivore fishing mortality (horizontal axis) and the average forage-fish fishing mortality (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 (Material 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.

Supplementary Information for

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

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This PDF file includes:

Figs. S1 to S6
Tables S1 to S12
References for SI reference citations

Appendix A. Community-dynamics model

Model description. The community-dynamics model follows the bioenergetics approach introduced by Yodzis & Innes (1), which was extended to a stage-structured version by de Roos et al. (2). The full system of equations can be found at the end of this section, Eq. (6-31). We describe all modeled processes in detail, in terms of mass-specific process rates.

Food ingestion takes place following a Holling Type II functional response as a function of the encountered food density E , and the net-biomass production per unit body mass is

$$\nu(E) = \sigma \frac{I E}{H + E} - T. \quad [1]$$

The food ingestion depends on the maximum ingestion rate I and the half-saturation density H . Ingested food is assimilated with conversion efficiency σ . Subsequently, the energy is used to cover the mass-specific somatic maintenance costs T . The food-encounter rate E is different for all stages of clupeids and cod, as it depends on their feeding preferences for different resources and the resource densities (see below). When the assimilated energy exceeds the somatic maintenance costs, the net-biomass production is invested in somatic growth by juveniles, split between somatic growth and reproduction by small adults, and invested in reproduction by large adults. Under starvation conditions, the net-biomass production rate becomes negative, somatic growth and maturation stops, and no energy is invested in reproduction. The net-biomass production rate restricted to positive values is denoted by

$$\nu^+(E) = \begin{cases} \nu(E), & \text{if } \nu(E) > 0, \\ 0, & \text{otherwise.} \end{cases} \quad [2]$$

The transition rate between stages is based on the derivation described by Soudijn & de Roos (3). It translates individual-level assumptions about energy expenditure into a population-level transition rate per unit biomass,

$$\gamma(\nu, d) = \begin{cases} \frac{\kappa \nu - d}{1 - z^{1 - \frac{d}{\kappa \nu}}}, & \text{if } \nu > 0, \\ 0, & \text{otherwise.} \end{cases} \quad [3]$$

The transition rate from one stage to the next is restricted to positive values of the net-biomass production rate ν and depends on the mortality rate d and the ratio z between the body sizes at the beginning and end of a stage. The transition rate further depends on the fraction κ of energy invested in somatic growth. The energy that is not invested in somatic growth (i.e., the fraction $1 - \kappa$) is allocated to reproduction. Reproductive energy is stored throughout the growing season. For the small-adult stage, the transition rate above also describes the transfer rate of the reproductive storage to the large-adult stage.

Mortality d is comprised of background mortality μ , starvation mortality, fishing mortality F and predation mortality P . Background mortality is size-independent, affecting all individuals equally. Starvation mortality occurs when the food intake is not sufficient to cover the somatic maintenance costs. Fishing mortality and predation mortality are stage- and species-specific. This results in the following general expressions for the mortality rates of cod and clupeids, respectively, d_C and d_S :

$$d_C(E) = \begin{cases} \mu + F - \nu(E), & \text{if } \nu(E) < 0, \\ \mu + F, & \text{otherwise,} \end{cases} \quad [4]$$

$$d_S(E) = \begin{cases} \mu + F + P - \nu(E), & \text{if } \nu(E) < 0, \\ \mu + F + P, & \text{otherwise.} \end{cases} \quad [5]$$

Note that the actual expressions are stage-specific as they depend on stage-specific values of F , P and $\nu(E)$. The adult mortality rate also governs losses of the reproductive-energy storages: when adult individuals die, the energy they have stored for reproduction dies with them.

The model is defined in terms of biomasses per volume and consists of a resource for clupeids (R_S), a resource for cod juveniles (R_J), and a resource for cod adults (R_A), together with size-structured clupeid and cod populations. The clupeid population is divided in one juvenile stage (S_J), two adult stages (S_A and S_B), and their reproductive storages (Sg_A and Sg_B). The cod population is divided in one juvenile stage (C_J), two adult stages (C_A and C_B), and their reproductive storages (Cg_A and Cg_B). Clupeids forage on the clupeid resource throughout their life, and the food-encounter rate is thus equal for all clupeid stages (Table S1). Cod switches diet, and the food-encounter rate in each cod stage depends on the biomass density and stage-specific foraging preference β for the corresponding food source. Predation of clupeids by cod reduces clupeid somatic biomass and the reproductive-energy storages of adult clupeid stages simultaneously. The resource grazing rates G and stage-specific functions for food-encounter rates E and predation rates P are listed in Table S1. Foraging preferences of the cod stages for the different food sources are listed in Table S4.

The continuous-time dynamics over time t during the growing season ($0 \leq t < Y$, where Y denotes the growing season's duration) are described by the following set of ordinary differential equations:

$$\frac{dR_S}{dt} = \delta(R_{S_{\max}} - R_S) - G_S R_S, \quad [6]$$

$$\frac{dR_J}{dt} = \delta(R_{J_{\max}} - R_J) - G_J R_J, \quad [7]$$

$$\frac{dR_A}{dt} = \delta(R_{A_{\max}} - R_A) - G_A R_A, \quad [8]$$

$$\frac{dS_J}{dt} = \nu_{S_J}^+(E_S) S_J - \gamma_{S_J}(\nu_{S_J}(E_S), d_{S_J}(E_S)) S_J - d_{S_J}(E_S) S_J, \quad [9]$$

$$\begin{aligned} \frac{dS_A}{dt} = & \gamma_{S_J}(\nu_{S_J}(E_S), d_{S_J}(E_S)) S_J + \kappa \nu_{S_A}^+(E_S) S_A - \gamma_{S_A}(\nu_{S_A}(E_S), d_{S_A}(E_S)) S_A \\ & - d_{S_A}(E_S) S_A, \end{aligned} \quad [10]$$

$$\frac{dS_B}{dt} = \gamma_{S_A}(\nu_{S_A}(E_S), d_{S_A}(E_S)) S_A - d_{S_B}(E_S) S_B, \quad [11]$$

$$\begin{aligned} \frac{dSg_A}{dt} = & (1 - \kappa) \nu_{S_A}^+(E_S) S_A - \gamma_{S_A}(\nu_{S_A}(E_S), d_{S_A}(E_S)) Sg_A \\ & - d_{S_A}(E_S) Sg_A, \end{aligned} \quad [12]$$

$$\begin{aligned} \frac{dSg_B}{dt} = & \gamma_{S_A}(\nu_{S_A}(E_S), d_{S_A}(E_S)) Sg_A + \nu_{S_B}^+(E_S) S_B \\ & - d_{S_B}(E_S) Sg_B, \end{aligned} \quad [13]$$

$$\frac{dC_J}{dt} = \nu_{C_J}^+(E_{C_J}) C_J - \gamma_{C_J}(\nu_{C_J}(E_{C_J}), d_{C_J}(E_{C_J})) C_J - d_{C_J}(E_{C_J}) C_J, \quad [14]$$

$$\begin{aligned} \frac{dC_A}{dt} = & \gamma_{C_J}(\nu_{C_J}(E_{C_J}), d_{C_J}(E_{C_J})) C_J + \kappa \nu_{C_A}^+(E_{C_A}) C_A - \gamma_{C_A}(\nu_{C_A}(E_{C_A}), d_{C_A}(E_{C_A})) C_A \\ & - d_{C_A}(E_{C_A}) C_A, \end{aligned} \quad [15]$$

$$\frac{dC_B}{dt} = \gamma_{C_A}(\nu_{C_A}(E_{C_A}), d_{C_A}(E_{C_A})) C_A - d_{C_B}(E_{C_B}) C_B, \quad [16]$$

$$\begin{aligned} \frac{dCg_A}{dt} = & (1 - \kappa) \nu_{C_A}^+(E_{C_A}) C_A - \gamma_{C_A}(\nu_{C_A}(E_{C_A}), d_{C_A}(E_{C_A})) Cg_A \\ & - d_{C_A}(E_{C_A}) Sg_A, \end{aligned} \quad [17]$$

$$\begin{aligned} \frac{dCg_B}{dt} = & \gamma_{C_A}(\nu_{C_A}(E_{C_A}), d_{C_A}(E_{C_A})) Cg_A + \nu_{C_B}^+(E_{C_B}) C_B \\ & - d_{C_B}(E_{C_B}) Sg_B. \end{aligned} \quad [18]$$

When the growing season ends, reproduction takes place instantaneously at times $t_n = nY$ with $n = 1, 2, \dots$. Below, we denote the times just before and just after t_n by, respectively, t_n^- and t_n^+ :

$$R_S(t_n^+) = R_S(t_n^-), \quad [19]$$

$$R_J(t_n^+) = R_J(t_n^-), \quad [20]$$

$$R_A(t_n^+) = R_A(t_n^-), \quad [21]$$

$$S_J(t_n^+) = S_J(t_n^-) + Sg_A(t_n^-) + Sg_B(t_n^-), \quad [22]$$

$$S_A(t_n^+) = S_A(t_n^-), \quad [23]$$

$$S_B(t_n^+) = S_B(t_n^-), \quad [24]$$

$$Sg_A(t_n^+) = 0, \quad [25]$$

$$Sg_B(t_n^+) = 0, \quad [26]$$

$$C_J(t_n^+) = C_J(t_n^-) + Cg_A(t_n^-) + Cg_B(t_n^-), \quad [27]$$

$$C_A(t_n^+) = C_A(t_n^-), \quad [28]$$

$$C_B(t_n^+) = C_B(t_n^-), \quad [29]$$

$$Cg_A(t_n^+) = 0, \quad [30]$$

$$Cg_B(t_n^+) = 0. \quad [31]$$

During a reproductive event, biomass in the reproductive-energy storages is transformed into juveniles, for both clupeids (22) and cod (27). At the same moment, the reproductive-energy storages are thus set to zero (25, 26, 30, 31), while the resource biomasses (19 - 21) and the adult somatic biomasses (23, 24, 28, 29) do not change.

Model parameterization. All parameter values are derived from individual-level data; no population-level data are used for parameterization. Specific parameter values are determined for each fish stage, based on the average body mass in the stage. We test the effects of a range of values for cod and clupeid fishing mortalities on the model dynamics. The model parameterization is based on the study by van Leeuwen et al. (4), except for the parameter values describing seasonal reproduction and fishing of the clupeids. Body sizes, energetic parameters, and mortality parameters for each fish stage can be found in Table S2. Foraging preferences of the cod stages for the different fish and non-fish resources are listed in Table S4. Species-specific and system parameters can be found in Table S3.

Fishing is implemented as a size-dependent process: it affects small individuals less than large individuals. For trawl and gill-net fishing, juvenile-cod fisheries retention (at age 1 year) is estimated to be 2% of adult-cod fisheries retention (at ages 3-7 years) (5). Based on the retention of herring individuals of 3.4 g or about 8 cm (6) in trawling nets with a small mesh size, juvenile-clupeid fisheries retention is estimated at 26.4% (7) of adult-clupeid fisheries retention. Yet, since this estimate increases to 50% for herring individuals that are only 1 cm larger, we use a conservative value of 50%. The fisheries yield for cod is calculated based on the catch of only adult individuals because there is a minimum allowable landing size of 38 cm for cod (8). In contrast, the fisheries yield for clupeids is calculated based on the catch of both juveniles and adults as there are no regulations stipulating a minimum allowable landing size of Baltic sprat and herring.

The length of the growing season is set to $Y = 250$ days. It is assumed that all considered processes (somatic maintenance, food intake, and mortality) decrease to negligible levels during winter. The dynamics are thereby effectively compressed from 365 to 250 days. For the sake of simplicity, the spawning of cod and clupeids are modeled to occur instantaneously and simultaneously at the end of the growing season. The peak-spawning time of clupeids has been relatively constant over the years, occurring at the end of May or the beginning of June (9, 10). The peak-spawning time of cod has been more variable, generally occurring between mid-May and the beginning of July. Both species spawn over a period of about 90 days (9, 10).

The use of a dimensionless constant for the half-saturation density H stems from the argument that both the maximum ingestion rate and the attack rate scale with body size with the same factor (4). Rescaling of the value of H to 1 g/Vol affects the reference volume of all the calculations in the model. Recent studies show that a general value of 3 mg/L can be assumed for H (11). This value of H corresponds to a reference volume of $\text{Vol} = 333$ L for our calculations. We thus transform the values of biomasses per volume predicted by our model in the unit g/Vol to the unit g/L by multiplying them with 0.003 Vol/L.

Model analysis. Model analysis is based on numerical simulations using publicly available C-based simulation programs (model code is publicly accessible at 10.5281/zenodo.3779839). Parameter dependencies are studied by the integrating model dynamics over long time periods of 50,000 days while varying the considered parameter value in small steps (see box 3.5 in 11 for an explanation of this procedure to study parameter dependencies). Time averages of the model variables are calculated over the last 60% of the 50,000 day time periods.

Table S1. Functions describing the encounter rates, predation rates, and grazing rates.

Description	Function
Cod population	
Juvenile food-encounter rate	$E_{C_J} = \beta_{C_J R_J} R_J + \beta_{C_J S_J} S_J$
Small-adult food-encounter rate	$E_{C_A} = \beta_{C_A R_A} R_A + \beta_{C_A S_A} (S_A + S_{gA}) + \beta_{C_A S_B} (S_B + S_{gB})$
Large-adult food-encounter rate	$E_{C_B} = \beta_{C_B R_A} R_A + \beta_{C_B S_A} (S_A + S_{gA}) + \beta_{C_B S_B} (S_B + S_{gB})$
Clupeid population	
Food-encounter-rate	$E_S = R_S$
Predation rate on juveniles	$P_{S_J} = I_{C_J} \frac{\beta_{C_J S_J}}{H + E_{C_J}} C_J + I_{C_A} \frac{\beta_{C_A S_J}}{H + E_{C_A}} C_A + I_{C_B} \frac{\beta_{C_B S_J}}{H + E_{C_B}} C_B$
Predation rate on small adults	$P_{S_A} = I_{C_A} \frac{\beta_{C_A S_A}}{H + E_{C_A}} C_A + I_{C_B} \frac{\beta_{C_B S_A}}{H + E_{C_B}} C_B$
Predation rate on large adults	$P_{S_B} = I_{C_A} \frac{\beta_{C_A S_B}}{H + E_{C_A}} C_A + I_{C_B} \frac{\beta_{C_B S_B}}{H + E_{C_B}} C_B$
Resources	
Grazing rate of clupeid resource	$G_{R_S} = I_{S_J} \frac{1}{H + E_S} S_J + I_{S_A} \frac{1}{H + E_S} S_A + I_{S_B} \frac{1}{H + E_S} S_B$
Grazing rate of juvenile-cod resource	$G_{R_J} = I_{C_J} \frac{\beta_{C_J R_J}}{H + E_{C_J}} C_J$
Grazing rate of adult-cod resource	$G_{R_A} = I_{C_A} \frac{\beta_{C_A R_J}}{H + E_{C_A}} C_A + I_{C_B} \frac{\beta_{C_B R_J}}{H + E_{C_B}} C_B$

Table S2. Default parameter values for all fish stages (from 4). Note that the values for the maximum ingestion rate I and the somatic maintenance costs T are mass-specific. ‘Vol’ indicates that the maximum resource densities are defined per unit of reference volume. Since we have rescaled the model parameters by setting the half-saturation density H to 1 g/Vol, the size of this reference volume is undefined (see SI section ‘Model parameterization’). Values for the fishing mortalities F_C , F_S and the fisheries retentions ρ_C , ρ_S of, respectively, cod and clupeids are shown in table S3.

Description		S_J	S_A	S_B	C_J	C_A	C_B
Initial size (g)	W_b	0.55	10.7	15.0	0.35	104	832
Average size (g)	\bar{W}	3.4	12.7	15.0	18.2	350	832
Maximum ingestion rate (d^{-1})	I	0.23	0.078	0.078	0.08	0.022	0.022
Half-saturation density (g Vol $^{-1}$)	H	1	1	1	1	1	1
Assimilation efficiency	σ	0.3	0.3	0.3	0.3	0.4	0.4
Somatic maintenance costs (d^{-1})	T	0.032	0.02	0.02	0.015	0.006	0.006
Fraction of energy invested in somatic growth	κ	1	0.8	0.0	1	0.8	0.0
Ratio of initial to final body size	z	0.05	0.7	-	0.003	0.125	-
Background mortality rate (d^{-1})	μ	0.001	0.001	0.001	0.001	0.001	0.001
Fishing mortality rate (d^{-1})	F	$\rho_S F_S$	F_S	F_S	$\rho_C F_C$	F_C	F_C

Table S3. Default values of fisheries parameters and system parameters (from 4, unless indicated otherwise). ‘Vol’ indicates that the maximum resource densities are defined per unit of reference volume. Since we have rescaled the model parameters by setting the half-saturation density H to 1 g/Vol, the size of this reference volume is undefined (see SI section ‘Model parameterization’).

Symbol	Value	Unit	Description	Source
F_S	Varied	d^{-1}	Fishing mortality rate of clupeids	
F_C	Varied	d^{-1}	Fishing mortality rate of cod	
ρ_S	0.5	-	Fisheries retention of clupeid juveniles	(6), (7)
ρ_C	0.02	-	Fisheries retention of cod juveniles	(5)
δ	0.1	d^{-1}	Turnover rate of resources	
R_{Smax}	98	g Vol $^{-1}$	Maximum density of clupeid resource	
R_{Jmax}	1	g Vol $^{-1}$	Maximum density of juvenile-cod resource	
R_{Amax}	0.75	g Vol $^{-1}$	Maximum density of adult-cod resource	
Y	250	d	Length of growing season	

Table S4. Foraging preferences of cod stages (from 4).

	β_{C_J}	β_{C_A}	β_{C_B}
R_S	0.0	0.0	0.0
R_J	0.8	0.0	0.0
R_A	0.0	0.5	0.2
S_J	0.2	0.3	0.25
S_A	0.0	0.1	0.3
S_B	0.0	0.1	0.25

Appendix B. Statistical model

Choice of data source. The stock assessments in the RAM Legacy Stock Assessment Database currently represent the best available syntheses of catch data and trawl-survey data that exist to derive estimates of biomasses and fishing mortalities. Commercial catch data tend to go back furthest in time, but typically suffer from sampling bias (as fishermen do not ‘sample’ in a scientific manner). Scientific trawl-survey data, on the other hand, ideally are less biased, but tend to be noisy and have shorter time horizons. Stock assessments have two advantages: they are normally conducted by local experts, who are best positioned to select and process the available data, and they combine both data sources in a way that takes best advantage of the differential strengths of each data source. We acknowledge that stock assessments are not perfect, but using raw data in the form of commercial catches and/or trawl-survey data is unlikely to mitigate the underlying uncertainties and would likely compound other problems. Below we describe in more detail the (limited) possibilities for deducing biomass estimates from trawl-survey data in more detail (‘Alternative data sources’ section, Figs. S5 and S6).

Statistical analysis. We examined whether there is a statistical interaction between the effects of forage-fish fishing mortality and piscivore fishing mortality on the decline of piscivore stock biomass through time. We defined fish stocks in the RAM Legacy Stock Assessment Database (12, version 3.0, publicly accessible at www.ramlegacy.org/database) as forage-fish stocks based on the list provided by Essington et al. (13). We extracted information on the trophic level of all fish stocks from FishBase using `rfishbase` (14). We defined fish stocks as piscivorous when their trophic level exceeds 4.0. All piscivores that are classified as highly migratory species by the United Nations (15) were excluded from the analysis. Highly migratory species are expected to depend on several forage-fish stocks along their migration route, and may be fished at different locations along their migration route. From the remaining piscivores, we selected the fish stocks for which the data spans at least 20 years.

For each piscivore, we selected the period, between 5 and 15 years long, of largest decline in piscivore biomass in the time series (Fig. S1). For each selected period, we calculated the average fishing exploitation rates of the piscivore and the forage fish. For both forage fish and piscivores, we used only fish stocks with data on the fishing exploitation rate (annual catch/biomass) since this information was available for most of the stock pairs and we did not want to mix different measures of fishing mortality. When multiple forage-fish stocks overlap with a single piscivore, aggregate forage-fish fishing exploitation rates were calculated as biomass-weighted averages in each year of the decline period (when the total stock biomasses of the forage fish were not available, their spawning stock biomasses were used instead).

We performed ordinary least-squares multiple regression analyses to evaluate how the piscivore-biomass declines depend on the exploitation rates of piscivores and forage fish. Based on the inspection of model fits, we used the natural logarithm of the biomass ratios. We compared models with and without an interaction term between piscivore and forage-fish fishing mortalities and with only piscivore fishing mortality. We determined the explanatory power of the models based on AIC (Akaike information criterion) scores for model fit. When the AIC scores of models differed by less than 2 AIC units, we selected the model with the fewest parameters as the ‘best’ model.

Excluded data and robustness tests. We excluded the stocks of North East Atlantic Blue whiting and South Africa kingklip as their biomasses predominantly increased over the time series (Fig. S1, Table S5). One forage fish, Iceland capelin, has extremely high exploitation rates (in some years exceeding 3) that are considered unrealistic; this stock was thus removed from the analysis. The combinations of piscivore stocks and forage-fish stocks used for the analysis are listed in Table S5.

We analyzed all data without the combination of the Southern Blue whiting piscivore stock and the Chilean jack mackerel forage-fish stock. This combination has the highest average fishing exploitation rates for the forage fish and the lowest for the piscivore stock in the dataset. Since it has a particularly strong influence on the interaction model (according to its Cook’s distance, Fig. S3), we decided to exclude it from our analysis. The inclusion of this stock combination considerably reduces the statistical support for the interaction model (Table S7).

For four stock combinations (piscivore stocks: Spotted spiny dogfish Pacific Coast, Pacific hake Pacific Coast, Atlantic cod Iceland, and Arrowtooth flounder Pacific Coast), the biomass of the forage-fish stock is lower than that of the piscivore stock (Fig. S4). Since this might indicate that the forage-fish stock is not large enough to singly support the piscivore stock, we tested the robustness of our results to the exclusion of these stock combinations (Fig. S4 and Table S6). The exclusion of these stock combinations does not reduce the statistical support for the interaction model, and in the main text we therefore show results with these stock combinations included.

Biomass declines at the start of time series can, when predicted by assessment models that estimate virgin biomass, be artifacts of the assessment-model assumptions. This is especially relevant when predicted declines occur prior to periods that

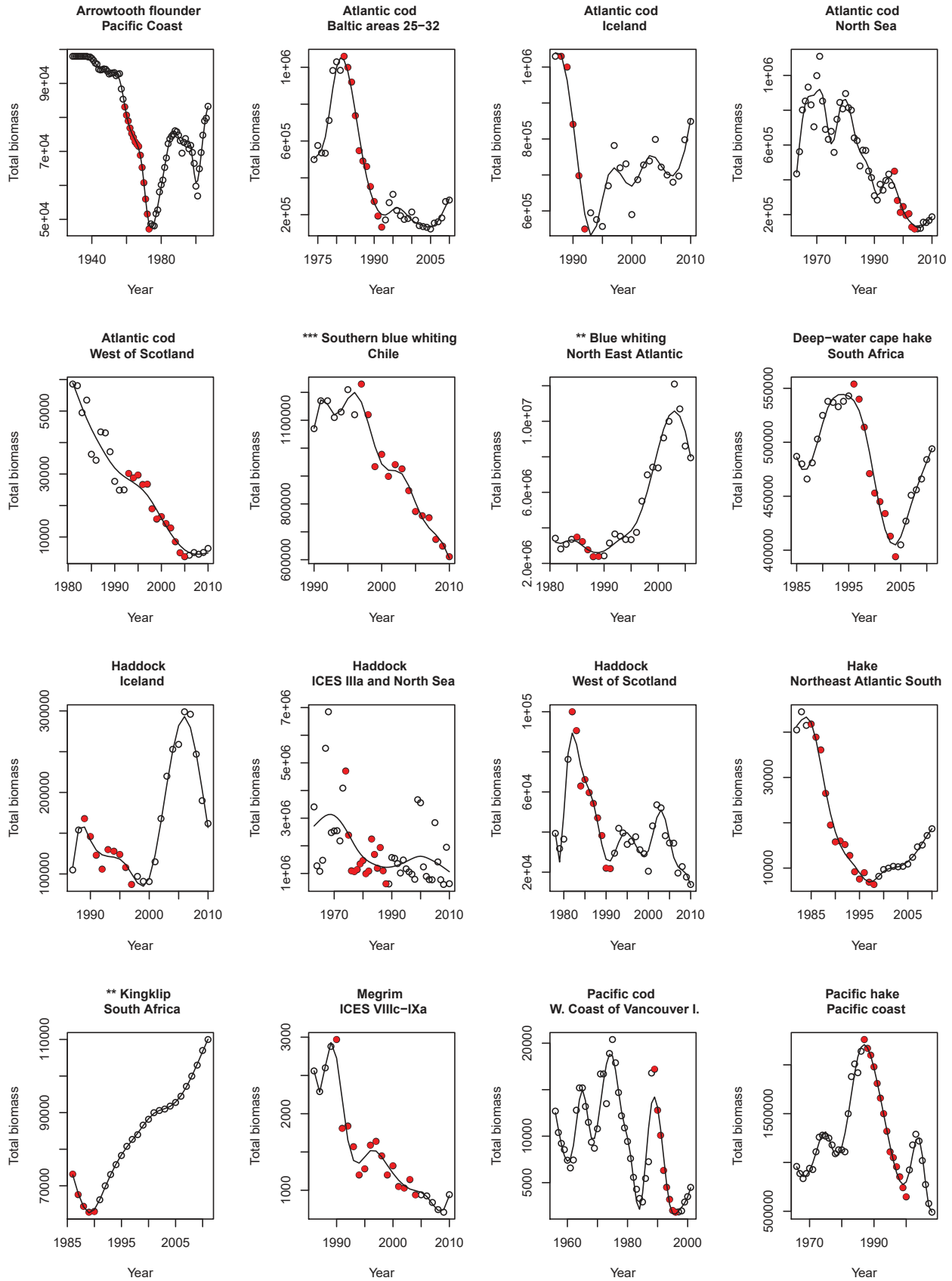
are covered by catch data and/or survey data. These problems are likely to be most prevalent before 1970. We therefore tested the robustness of our results to the exclusion of four stock combinations with continuous and long-lasting declines in piscivore biomass occurring from the start of the time series with little spread in the individual data points (piscivore stocks: Arrowtooth flounder Pacific Coast, South hake Chile, Petrale sole Pacific Coast, and Yelloweye rockfish Pacific Coast); the results are shown in Table S11. In addition, we tested the robustness of our results to the exclusion of three stock combinations with declines in piscivore biomass starting prior to 1970 (piscivore stocks: Arrowtooth flounder Pacific Coast, Petrale sole Pacific Coast, and Spotted spiny dogfish Pacific Coast); the results are shown in Table S12. In both cases, the exclusion of these stock combinations does not reduce the statistical support for the interaction model, and in the main text we therefore show results with these stock combinations included.

Selection of period with strongest piscivore biomass decline. The length of periods with declining piscivore biomass varies among stocks (Fig. S1). Therefore, we allowed the selected period to vary between 5 and 15 years and tested for the robustness of our results against variation in the minimum and maximum length of this period (Tables S8-S10).

To determine the time periods over which the decline in piscivore biomass is the largest, we used three different methods. For the first two methods, we defined a decline in biomass as the ratio between the piscivore biomasses at the end and at the beginning of the period. The period with the strongest biomass decline in a time series is then taken as the period for which this ratio is the smallest. For the first method, the biomass ratio is calculated based on raw data of piscivore biomass. For the second method, the biomass ratio is calculated based on a smoothing spline fitted to the piscivore biomass data. The number of free knots used to derive the smoothing spline is 1/3 of the total number of years per stock (Fig. S1). For the third method, we fitted linear regression models to subranges of the piscivore biomass data. A decline in biomass is then defined as a negative regression slope, and the period of strongest biomass decline is taken as the period with the most negative regression slope. The main results (Fig. 4, Table 1 and S5) are based on the first method, i.e., on biomass ratios of raw piscivore biomass data.

Alternative data sources. The newest version of the RAM Legacy Stock Assessment Database (16) contains data on catch per unit effort (CPUE) from trawl surveys for two of the piscivore stocks in our analysis (Fig. S5). In addition, we derived CPUE information from eight bottom-trawl surveys for some other, European, piscivore stocks (Fig. S6). The data were taken from the ICES DATRAS (17) and processed following the methodology described by Maureaud et al. (18). Specifically, we used trawl-survey data from the North Sea International Bottom Trawl Survey, the Scottish West Coast International Bottom Trawl Survey, the French Southern Atlantic Bottom Trawl Survey, the Irish International Groundfish Survey, the French Channel Groundfish Survey, the Northern Ireland Groundfish Survey, the Portuguese International Bottom Trawl Survey, and the Baltic International Trawl Survey.

Several steps were needed to estimate relative changes in CPUE from the ICES trawl-survey data over time. First, the assessment region was selected for each piscivore stock by overlapping the bounding regions of the fisheries-assessment areas (19) with a 1-degree grid to obtain gridded assessment regions. Second, the trawl-survey coordinates were linked to the grid cells. Third, grid cells that contain one or more survey samples per year across the time series were selected, and grid cells that were infrequently sampled (<3 times since 1980) were removed. Fourth, the average CPUE was calculated over cells per year by averaging over all sampling locations in each grid cell and then across the grid over cells. Some fisheries-assessment areas overlapped with multiple surveys, in which case the average CPUE was estimated for the entire region. The averaging resulted in an estimate of how the CPUE changes over time, which was compared to the stock-assessment data. For some stocks, trawl-survey data was available for longer periods, but no CPUE could be calculated. This occurred because the swept area (defined by the trawl's wing spread or door spread multiplied by the sampled distance) could not be estimated from the available data or because estimates of the weight of caught fish were not reported. For three other stocks, no CPUE data was available, and we instead show time series of average trawl-survey-based catches (Fig. S6). All trawl-survey-based estimates were manually rescaled to overlap with the stock-assessment-based values in the same time periods (this rescaling is immaterial for our analyses as only relative changes in biomass over time are used in our analysis).



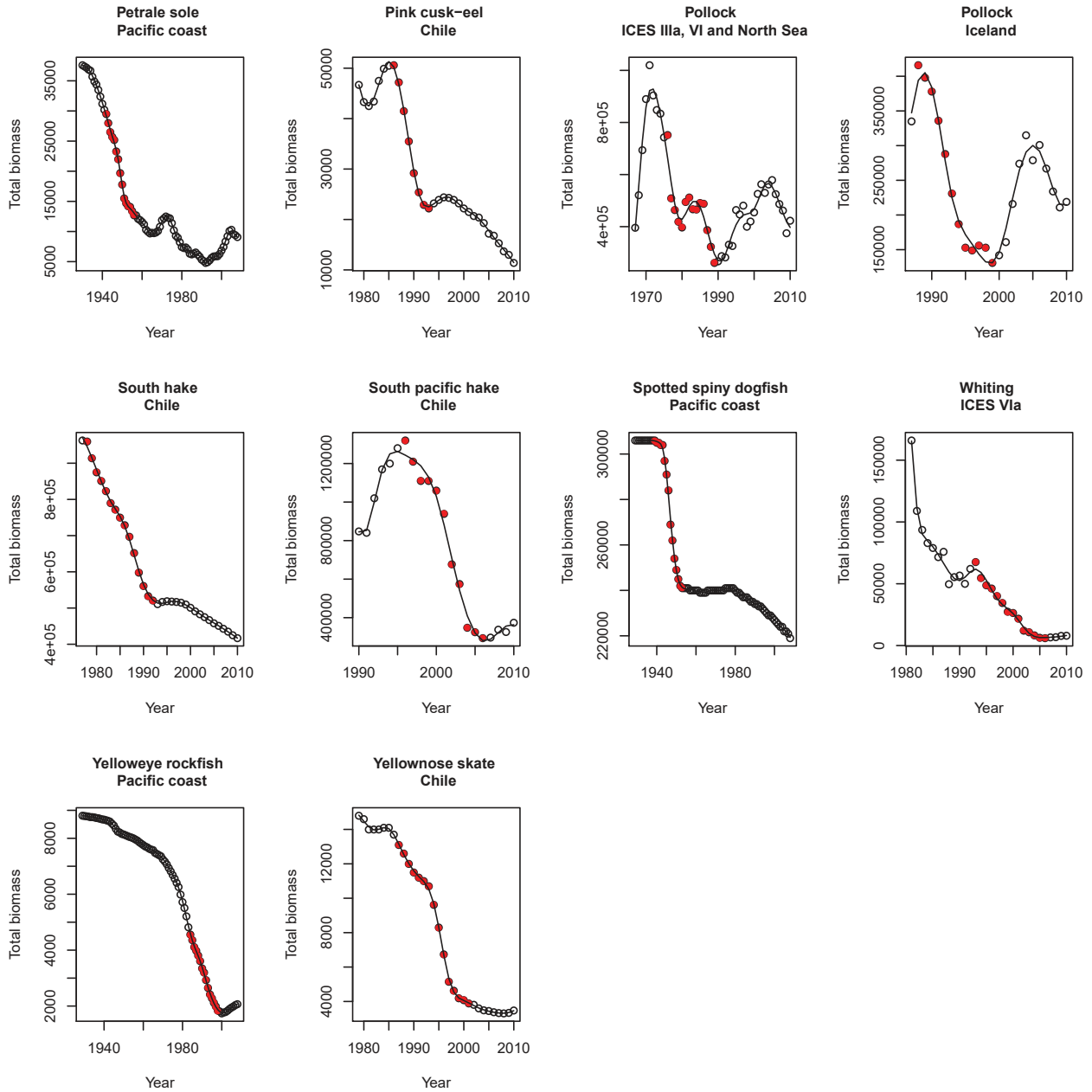


Fig. S1. Biomass time series of all piscivore stocks (open circles; in metric tons) and periods with strongest piscivore-biomass decline (red dots; the periods are allowed to vary between 5 and 15 years). This data is used to produce Figure 4 and Tables 1 and S5. The black lines represent the smoothing splines used to determine the periods with strongest piscivore-biomass decline as shown in Table S9. We excluded four piscivore stocks marked with ** because their biomass was predominantly increasing, as well as the single piscivore stock marked with *** because it had a strong influence on the interaction model (Fig. S3, Table S7).

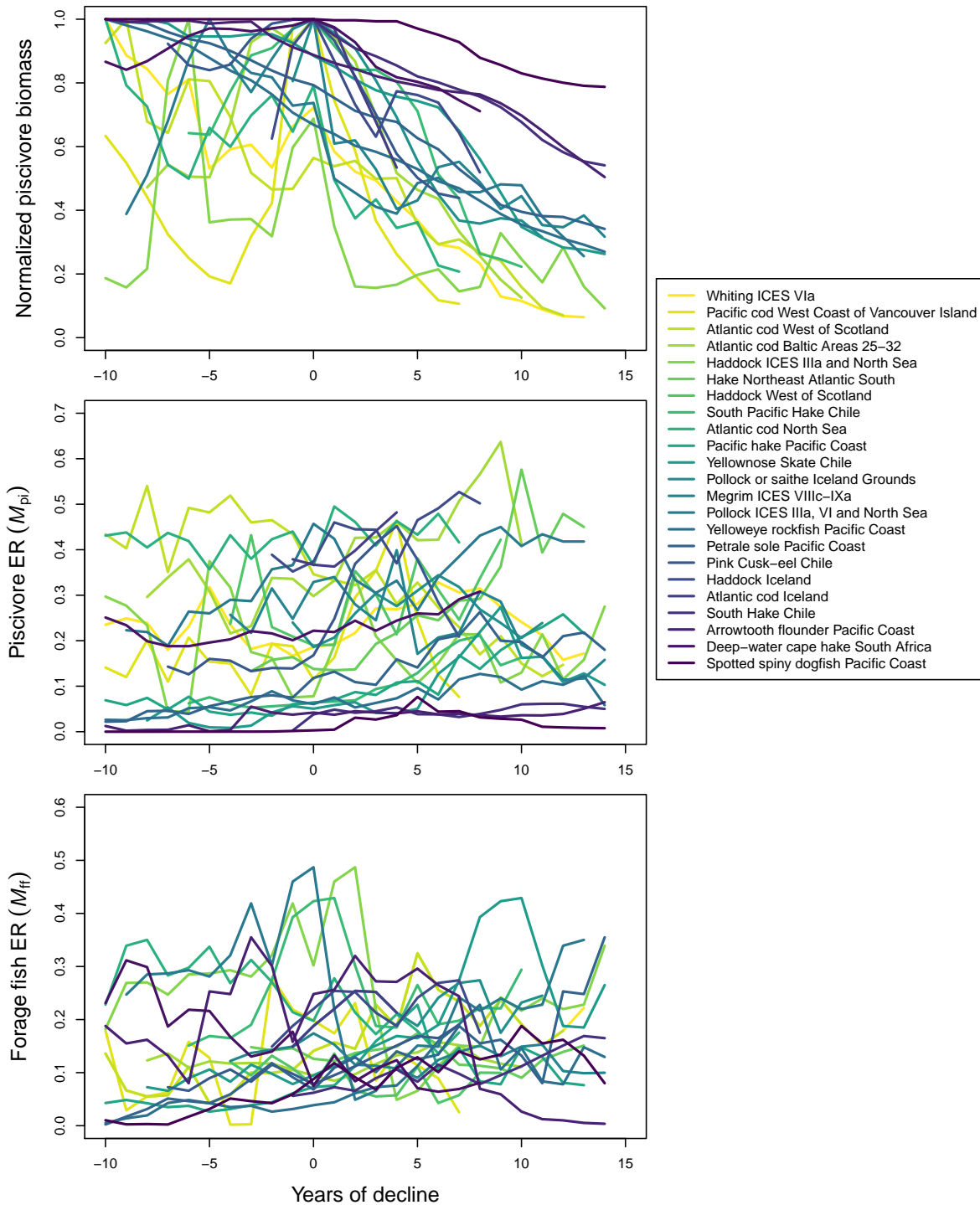


Fig. S2. Trends in piscivore biomass and fishing mortality of piscivore and forage-fish stocks that were linked to the piscivore stocks, during the 10 years prior to the selected period of strongest piscivore-biomass decline. Piscivore biomass is normalized by dividing by the maximum biomass in each time series. Fishing mortality is measured by the exploitation rate (annual catch/stock biomass), abbreviated by ER and denoted by M_{pi} for piscivores and M_{ff} for forage fish.

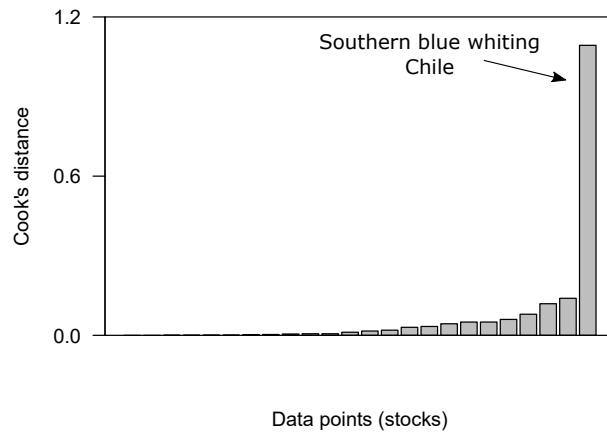


Fig. S3. Cook's distances for all considered stock combinations, which measure the effect of deleting an observation. The stock combination with the piscivore stock 'Southern Blue whiting Chile' has a much larger Cook's distance than all other stock combinations, and therefore all analyses were done without this stock combination.

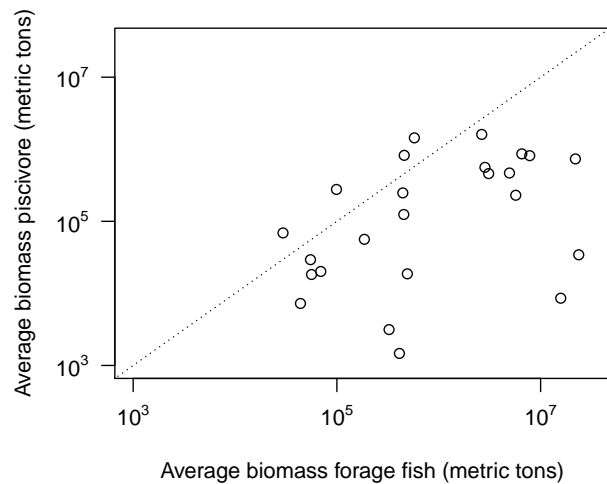


Fig. S4. Average biomass of piscivore and forage-fish stocks for the selected periods of strongest piscivore-biomass decline. The diagonal represents the line along which piscivore biomass and forage-fish biomass are equal. For the four stock combinations (piscivore stocks: Spotted spiny dogfish Pacific Coast, Pacific hake Pacific Coast, Atlantic cod Iceland, and Arrowtooth flounder Pacific Coast) above the diagonal, the piscivore biomass exceeds the forage-fish biomass.

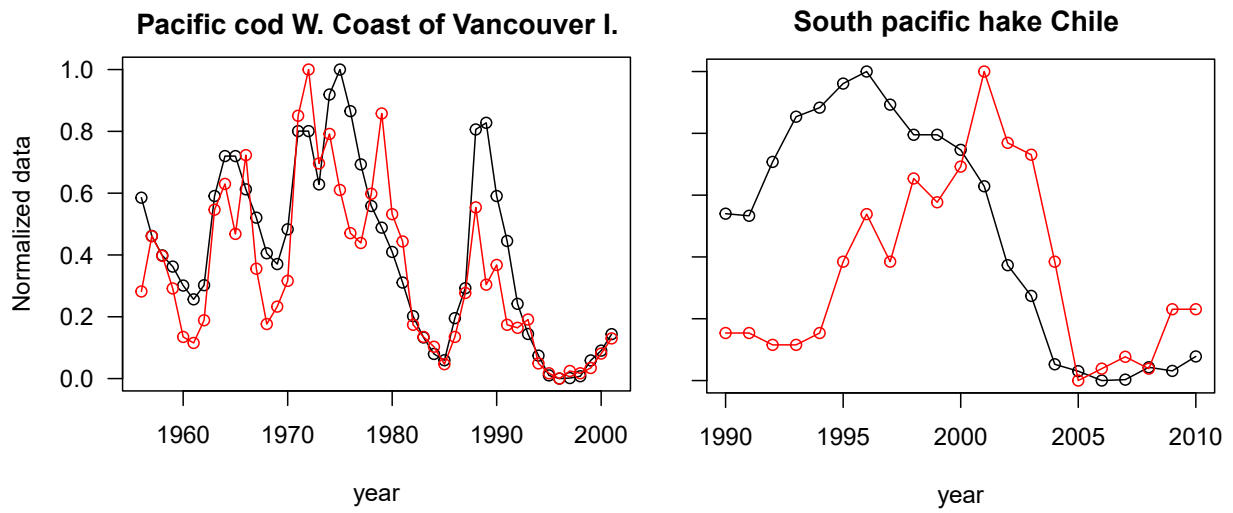


Fig. S5. Comparison of trawl-survey-based (red) and stock-assessment-based (black) stock-biomass estimates for two of the piscivore stocks included in our analysis, from the RAM Legacy Stock Assessment Database (16). Both time series are normalized to the unit interval according to their minimum and maximum values.

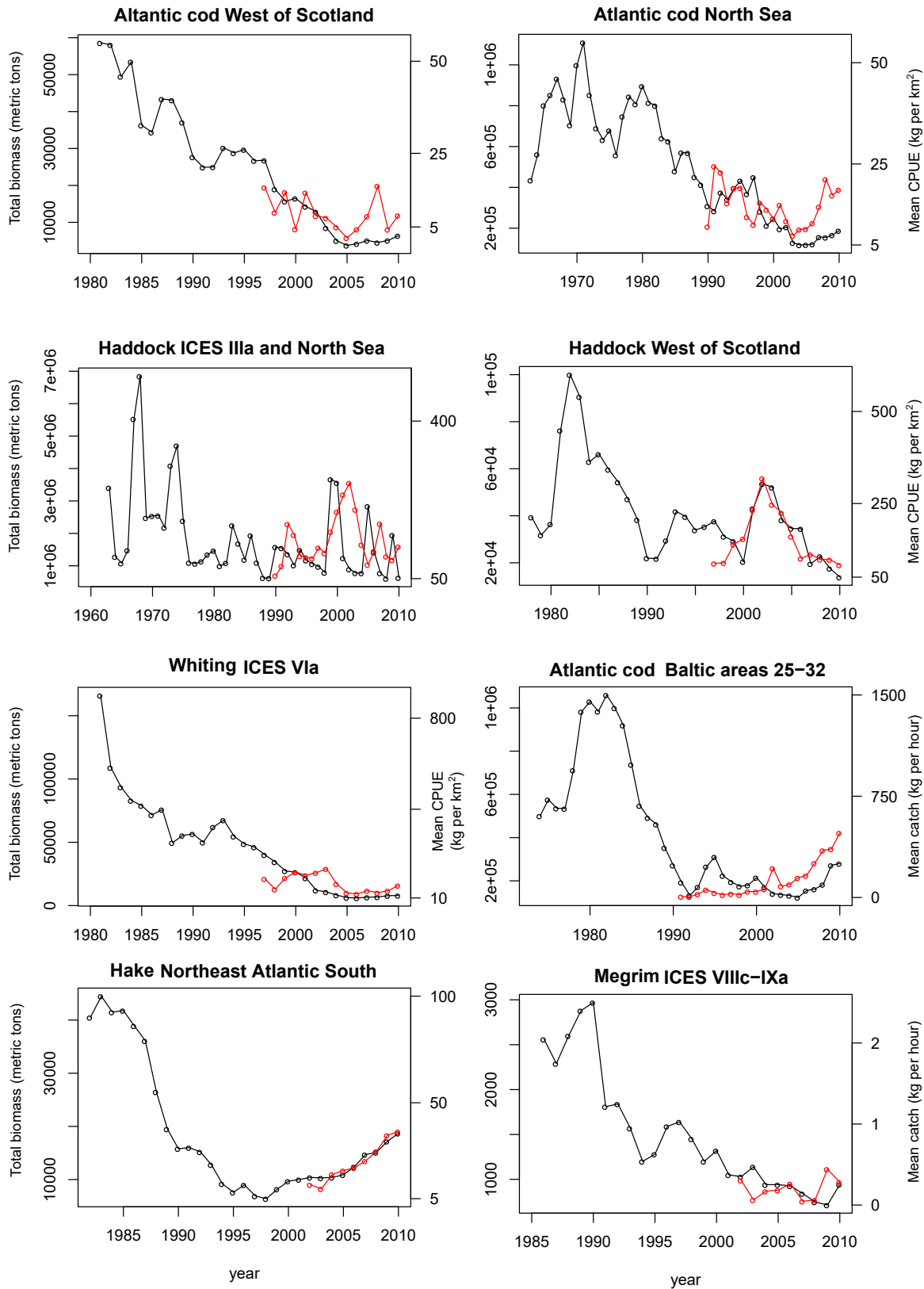


Fig. S6. Comparison of trawl-survey-based (red) and stock-assessment-based (black) stock-biomass estimates. The trawl-survey-based estimates are available only for a small part of the time series and were determined either according to catch per unit effort based on the area swept (CPUE; for the first five stocks) or according to catch per hour (for the last three stocks). Note that the two estimates are shown on different scales: the trawl-survey-based estimates were manually rescaled to overlap with the stock-assessment-based estimates in the same time period (this rescaling is immaterial for our analyses as only relative changes in biomass over time are used in our analysis).

Table S5. Overview of the combinations of piscivore stocks and forage-fish stocks used for the statistical model. The piscivore-biomass decline B_{pi} is measured as the ratio of piscivore biomasses at the end and at the beginning of the selected decline period (Fig. S1). Fishing mortalities M_{pi} and M_{ff} for, respectively, piscivores and forage fish are averaged over these decline periods. When multiple forage-fish stocks overlap with a single piscivore stock, aggregate forage-fish fishing mortalities were calculated as biomass-weighted averages. Fishing mortality is measured by the exploitation rate (annual catch/stock biomass). We excluded the forage-fish stock marked with * because it was doubly represented, four piscivore stocks marked with ** because their biomass was predominantly increasing, and the piscivore stock marked with * because it had a particularly strong influence on the interaction model (Fig. S3 and Table S7).**

Piscivore stocks						Forage-fish stocks			
Common name	Stock location	Start	Period (yr)	B_{pi}	M_{pi}	Common name	Stock location	M_{ff}	Stocks
Arrowtooth flounder	Pacific Coast	1959	15	0.57	0.04	Pacific chub mackerel	Pacific Coast	0.16	2
Atlantic cod	ICES Baltic Areas 25-32	1982	11	0.13	0.45	Pacific sardine	Pacific Coast		
						Sprat	ICES Baltic Areas 22-32	0.12	2
						Herring	ICES Baltic Areas 25-32		
Atlantic cod	Iceland	1988	5	0.53	0.41	Herring (summer spawners)	Iceland	0.23	1
Atlantic cod	North Sea	1997	8	0.26	0.44	Sandeel	North Sea Area 1	0.2	4
						Sandeel	North Sea Area 2		
						Sandeel	North Sea Area 3		
						Herring	North Sea		
Atlantic cod	West of Scotland	1993	13	0.12	0.25	Herring*	ICES Area VIa	0.16	2
						Herring	ICES Areas VIa-VIIb-VIIc		
Southern Blue whiting***	Chile	1997	14	0.5	0.04	Chilean jack mackerel	Chilean EEZ and offshore	0.28	1
Blue whiting**	North East Atlantic	1985	5	0.7	0.24	Mackerel	North East Atlantic	0.19	1
Deep-water cape hake	South Africa	1996	9	0.71	0.25	Sardine	South Africa	0.09	2
						Anchovy	South Africa		
Haddock	Iceland	1989	9	0.52	0.45	Herring (summer spawners)	Iceland	0.23	1
Haddock	ICES Area IIIa and North Sea	1974	15	0.13	0.18	Sandeel	North Sea Area 1	0.23	4
						Sandeel	North Sea Area 2		
						Sandeel	North Sea Area 3		
						Herring	North Sea		
Haddock	West of Scotland	1982	10	0.22	0.29	Herring*	ICES Area VIa	0.11	2
						Herring	ICES Areas VIa-VIIb-VIIc		
Hake	Northeast Atlantic South	1985	14	0.15	0.3	European pilchard	ICES Areas VIIIc-IXa	0.13	1
Kingklip**	South Africa	1986	5	0.86	0.11	Sardine	South Africa	0.25	2
						Anchovy	South Africa		
Megrim	ICES Areas VIIIc-IXa	1990	15	0.32	0.24	European pilchard	ICES Areas VIIIc-IXa	0.13	1
Pacific cod	West Coast of Vancouver Island	1989	8	0.11	0.23	Pacific herring	West Coast of Vancouver Island	0.13	1
Pacific hake	Pacific Coast	1987	14	0.29	0.14	Pacific chub mackerel	Pacific Coast	0.12	2

Table S5. Continued.

Piscivore stocks						Forage-fish stocks			
Common name	Stock location	Start	Period (yr)	B_{pi}	M_{pi}	Common name	Stock location	M_{ff}	Stocks
Petrale sole	Pacific Coast	1942	15	0.43	0.17	Pacific sardine	Pacific Coast		
						Pacific chub mackerel	Pacific Coast	0.16	2
Pink cusk-eel	Chile	1986	8	0.44	0.32	Pacific sardine	Pacific Coast		
						Chilean jack mackerel	Chilean EEZ and offshore	0.14	1
Pollock	ICES Areas IIIa, VI and North Sea	1976	14	0.35	0.39	Sandeel	North Sea Area 1	0.22	4
						Sandeel	North Sea Area 2		
						Sandeel	North Sea Area 3		
						Herring	North Sea		
Pollock	Iceland	1988	12	0.31	0.26	Herring (summer spawners)	Iceland	0.23	1
South hake	Chile	1978	15	0.54	0.05	Chilean jack mackerel	Chilean EEZ and offshore	0.11	1
South Pacific hake	Chile	1996	11	0.22	0.13	Chilean jack mackerel	Chilean EEZ and offshore	0.27	1
Spotted spiny dogfish	Pacific Coast	1939	15	0.79	0.03	Pacific chub mackerel	Pacific Coast	0.12	2
						Pacific sardine	Pacific Coast		
Whiting	ICES Area VIa	1993	14	0.09	0.24	Herring*	ICES Area VIa	0.17	2
						Herring	ICES Areas VIa-VIIb-VIIc		
Yelloweye rockfish	Pacific Coast	1984	15	0.4	0.09	Pacific chub mackerel	Pacific Coast	0.11	2
						Pacific sardine	Pacific Coast		
Yellownose skate	Chile	1987	15	0.3	0.12	Chilean jack mackerel	Chilean EEZ and offshore	0.23	1

Table S6. Effects of the exclusion of four stock combinations (piscivore stocks: Spotted spiny dogfish Pacific Coast, Pacific hake Pacific Coast, Atlantic cod Iceland, and Arrowtooth flounder Pacific Coast) with low forage-fish biomasses (compared to Table 1) on alternative statistical models of the effects of piscivore and forage-fish fishing on piscivore-biomass declines. The piscivore-biomass decline B_{pi} is measured as the ratio of piscivore biomasses at the end and at the beginning of the selected decline periods (Fig. S1). The models describe the logarithmic decline as a function of the average piscivore fishing mortality M_{pi} and the average forage-fish fishing mortality M_{ff} during the decline period. Fishing mortality is measured by the exploitation rate (annual catch/stock biomass). 19 combinations of piscivore stocks and forage-fish stocks were included in this 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 Δ AIC is the difference in AIC score relative to the model with the minimal AIC score.

Model	p-value	SE	r^2	AIC	Δ AIC
$\ln(B_{pi}) = 0.8 - 7.9 M_{pi} - 11.8 M_{ff} + 42.6 M_{pi}M_{ff}$	$p_1 = 0.05$	1.0	0.11	38.5	0
	$p_2 = 0.04$	3.7			
	$p_3 = 0.05$	5.3			
		20.4			
$\ln(B_{pi}) = -0.9 - 0.5 M_{pi} - 1.9 M_{ff}$	$p_1 = 0.69$	0.5	-0.05	41.3	2.8
	$p_2 = 0.47$	1.3			
		2.6			
$\ln(B_{pi}) = -1.2 - 0.6 M_{pi}$	$p_1 = 0.65$	0.3	-0.08	39.9	1.6
		1.2			

Table S7. Effects of the inclusion of Blue whiting Chile (compared to Table 1) on alternative statistical models of the effects of piscivore and forage-fish fishing on piscivore-biomass declines. The piscivore-biomass decline B_{pi} is measured as the ratio of piscivore biomasses at the end and at the beginning of the selected decline periods (Fig. S1). The models describe the logarithmic decline as a function of the average piscivore fishing mortality M_{pi} and the average forage-fish fishing mortality M_{ff} during the decline period. Fishing mortality is measured by the exploitation rate (annual catch/stock biomass). 24 combinations of piscivore stocks and forage-fish stocks were included in this 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 Δ AIC is the difference in AIC score relative to the model with the minimal AIC score.

Model	p-value	SE	r^2	AIC	Δ AIC
$\ln(B_{pi}) = 0.3 - 6.6 M_{pi} - 6.6 M_{ff} + 29.8 M_{pi}M_{ff}$	$p_1 = 0.04$	0.7	0.09	49.1	0.1
	$p_2 = 0.10$	3.1			
	$p_3 = 0.08$	3.8			
		16.1			
$\ln(B_{pi}) = -0.8 - 1.2 M_{pi} - 0.8 M_{ff}$	$p_1 = 0.22$	0.5	-0.01	51.0	1.9
	$p_2 = 0.73$	1.0			
		2.2			
$\ln(B_{pi}) = -0.9 - 1.2 M_{pi}$	$p_1 = 0.20$	0.3	0.03	49.0	0
		1.0			

Table S8. Effects of different minimum and maximum durations of the periods of strongest piscivore-biomass decline (compared to Table 1) on model selection for the effects of piscivore and forage-fish fishing on piscivore-biomass declines. The piscivore-biomass decline B_{pi} is measured as the ratio of piscivore biomasses at the end and at the beginning of the selected decline periods (Fig. S1). The models describe the logarithmic decline as a function of the average piscivore fishing mortality M_{pi} and the average forage-fish fishing mortality M_{ff} during the decline period. Fishing mortality is measured by the exploitation rate (annual catch/stock biomass). The best model is selected on the basis of AIC scores; the model with the fewest degrees of freedom is selected when the differences in AIC scores are < 2 . 23 combinations of piscivore stocks and forage-fish stocks were included in this analysis. F indicates that a full model, $\ln(B_{pi}) = a + bM_{pi} + cM_{ff} + dM_{pi}M_{ff}$, has the minimal AIC score. The coefficient of determination is shown in parentheses (adjusted r^2); best models with an r^2 below 0.05 are not shown (indicated by '-').

		Maximum length (yr)											
		8	9	10	11	12	13	14	15	16	17	18	19
Minimum length (yr)	5	-	F (0.29)	F (0.32)	F (0.32)	F (0.35)	F (0.31)	F (0.28)	F (0.26)	F (0.29)	F (0.17)	-	F (0.18)
	6	F (0.19)	F (0.29)	F (0.32)	F (0.32)	F (0.34)	F (0.30)	F (0.26)	F (0.25)	F (0.27)	-	-	-
	7	F (0.23)	F (0.30)	F (0.33)	F (0.33)	F (0.35)	F (0.31)	F (0.27)	F (0.25)	F (0.29)	-	-	-
	8		F (0.29)	F (0.33)	F (0.33)	F (0.35)	F (0.31)	F (0.27)	F (0.25)	F (0.29)	-	-	-
	9			F (0.32)	F (0.32)	F (0.33)	F (0.30)	F (0.26)	F (0.27)	F (0.27)	-	-	-
	10				F (0.33)	F (0.35)	F (0.32)	F (0.28)	F (0.28)	F (0.28)	-	-	F (0.18)
	11					F (0.34)	F (0.29)	F (0.28)	F (0.26)	F (0.26)	-	-	F (0.18)
	12						F (0.21)	F (0.28)	F (0.27)	F (0.28)	-	F (0.18)	F (0.20)
	13							F (0.29)	F (0.27)	F (0.26)	-	-	F (0.19)
	14								F (0.23)	F (0.25)	-	-	F (0.17)

Table S9. Effects of processing the raw time series through smoothing (compared to Table S8) on model selection for the effects of piscivore and forage-fish fishing on piscivore-biomass declines. The piscivore-biomass decline B_{pi} is measured as the ratio of biomasses at the end and at the beginning of the selected decline periods based on a smoothing spline fitted to the piscivore-biomass data (Fig. S1). The minimum and maximum durations of the period of strongest piscivore-biomass decline were varied. The models describe the logarithmic decline as a function of the average piscivore fishing mortality M_{pi} and the average forage-fish fishing mortality M_{ff} during the decline period. Fishing mortality is measured by the exploitation rate (annual catch/stock biomass). The best model is selected on the basis of AIC scores; the model with the fewest degrees of freedom is selected when the differences in AIC scores are < 2 . 23 combinations of piscivore stocks and forage-fish stocks were included in this analysis. F indicates that a full model, $\ln(B_{pi}) = a + bM_{pi} + cM_{ff} + dM_{pi}M_{ff}$, has the minimal AIC score, whereas S indicates that a simple model, $\ln(B_{pi}) = a + bM_{pi}$, has the minimal AIC score. The coefficient of determination is shown in parentheses (adjusted r^2); best models with an r^2 below 0.05 are not shown (indicated by '-').

		Maximum length (yr)											
		8	9	10	11	12	13	14	15	16	17	18	19
Minimum length (yr)	5	S (0.06)	-	F (0.20)	S (0.07)	-	-	-	-	-	-	-	-
	6	-	-	F (0.18)	F (0.26)	-	-	-	-	F (0.18)	-	-	-
	7	-	-	F (0.30)	F (0.26)	-	-	-	-	F (0.18)	-	-	-
	8		F (0.22)	F (0.30)	F (0.26)	-	-	-	-	F (0.18)	-	-	-
	9			F (0.39)	F (0.33)	S (0.06)	-	-	F (0.19)	F (0.22)	-	-	-
	10				F (0.32)	S (0.05)	-	-	F (0.21)	F (0.22)	-	-	-
	11					-	-	-	F (0.19)	F (0.20)	-	-	-
	12					-	-	-	F (0.20)	F (0.21)	-	-	-
	13							F (0.17)	F (0.19)	F (0.20)	-	-	-
	14								F (0.20)	F (0.16)	-	-	-

Table S10. Effects of processing the raw time series through regression (compared to Table S8) on model selection for the effects of piscivore and forage-fish fishing on piscivore-biomass declines. The piscivore-biomass decline B_{pi} is measured as the ratio of biomasses at the end and at the beginning of the selected decline periods based on a linear regression fitted to the piscivore-biomass data. The minimum and maximum durations of the period of strongest piscivore-biomass decline were varied. The models describe the logarithmic decline as a function of the average piscivore fishing mortality M_{pi} and the average forage-fish fishing mortality M_{ff} during the decline period. Fishing mortality is measured by the exploitation rate (annual catch/stock biomass). The best model is selected on the basis of AIC scores; the model with the fewest degrees of freedom is selected when differences in AIC scores are < 2 . 23 combinations of piscivore stocks and forage-fish stocks were included in this analysis. F indicates that a full model, $\ln(B_{pi}) = a + b M_{pi} + c M_{ff} + d M_{pi} M_{ff}$, has the minimal AIC score, whereas S indicates that a simple model, $\ln(B_{pi}) = a + b M_{pi}$, has the minimal AIC score. The coefficient of determination is shown in parentheses (adjusted r^2); best models with an r^2 below 0.05 are not shown (indicated by '-').

		Maximum length (yr)											
		8	9	10	11	12	13	14	15	16	17	18	19
Minimum length (yr)	5	S (0.07)	S (0.07)	S (0.07)	S (0.07)	S (0.07)	S (0.07)	S (0.07)	S (0.07)	S (0.07)	S (0.07)	S (0.07)	S (0.07)
	6	-	-	-	-	-	-	-	-	-	-	-	-
	7	-	-	-	-	-	-	-	-	-	-	-	-
	8	-	-	-	-	-	-	-	-	-	-	-	-
	9	-	-	-	-	-	-	-	-	-	-	-	-
	10				F (0.20)	F (0.20)	F (0.20)	F (0.20)	F (0.20)	F (0.20)	F (0.20)	F (0.20)	F (0.20)
	11					F (0.25)	F (0.25)	F (0.25)	F (0.25)	F (0.25)	F (0.25)	F (0.25)	F (0.25)
	12						F (0.22)	F (0.22)	F (0.22)	F (0.22)	F (0.22)	F (0.22)	F (0.22)
	13							F (0.17)	F (0.17)	F (0.17)	F (0.17)	F (0.17)	F (0.17)
	14								F (0.18)	F (0.18)	F (0.18)	F (0.18)	F (0.18)

Table S11. Effects of the exclusion of four stock combinations (piscivore stocks: Arrowtooth flounder Pacific Coast, South hake Chile, Petrale sole Pacific Coast, and Yelloweye rockfish Pacific Coast) with declines early in the time series (compared to Table 1) on alternative statistical models of the effects of piscivore and forage-fish fishing on piscivore-biomass declines. The piscivore-biomass decline B_{pi} is measured as the ratio of piscivore biomasses at the end and at the beginning of the selected decline periods (Fig. S1). The models describe the logarithmic decline as a function of the average piscivore fishing mortality M_{pi} and the average forage-fish fishing mortality M_{ff} during the decline period. Fishing mortality is measured by the exploitation rate (annual catch/stock biomass). 19 combinations of piscivore stocks and forage-fish stocks were included in this 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 Δ AIC is the difference in AIC score relative to the model with the minimal AIC score.

Model	p-value	SE	r^2	AIC	Δ AIC
$\ln(B_{pi}) = 1.3 - 10.0 M_{pi} - 14.4 M_{ff} + 54.4 M_{pi} M_{ff}$	$p_1 = 0.03$	1.1	0.16	39.4	0
	$p_2 = 0.03$	4.1			
	$p_3 = 0.02$	5.9			
		21.5			
$\ln(B_{pi}) = -1.2 - 0.1 M_{pi} - 1.0 M_{ff}$	$p_1 = 0.95$	0.6	-0.12	44.1	4.7
	$p_2 = 0.74$	1.3			
		2.8			
$\ln(B_{pi}) = -1.3 - 0.1 M_{pi}$	$p_1 = 0.93$	0.4	-0.06	42.2	2.9
		1.3			

Table S12. Effects of the exclusion of three stock combinations (piscivore stocks: Petrale sole Pacific Coast, Arrowtooth flounder, Pacific Coast, and Spotted spiny dogfish Pacific Coast) with declines starting prior to 1970 (compared to Table 1) on alternative statistical models of the effects of piscivore and forage-fish fishing on piscivore-biomass declines. The piscivore-biomass decline B_{pi} is measured as the ratio of piscivore biomasses at the end and at the beginning of the selected decline periods (Fig. S1). The models describe the logarithmic decline as a function of the average piscivore fishing mortality M_{pi} and the average forage-fish fishing mortality M_{ff} during the decline period. Fishing mortality is measured by the exploitation rate (annual catch/stock biomass). 20 combinations of piscivore stocks and forage-fish stocks were included in this 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 Δ AIC is the difference in AIC score relative to the model with the minimal AIC score.

Model	<i>p</i> -value	SE	r^2	AIC	Δ AIC
$\ln(B_{pi}) = 0.7 - 8.0 M_{pi} - 12.1 M_{ff} + 46.1 M_{pi}M_{ff}$	$p_1 = 0.03$ $p_2 = 0.03$ $p_3 = 0.03$	0.9 3.5 5.0 18.8	0.15	39.1	0
$\ln(B_{pi}) = -1.2 - 0.1 M_{pi} - 1.2 M_{ff}$	$p_1 = 0.95$ $p_2 = 0.64$	0.5 1.2 2.5	-0.10	43.5	4.4
$\ln(B_{pi}) = -1.3 - 0.01 M_{pi}$	$p_1 = 0.99$	0.3 1.0	-0.06	41.7	2.6

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