

Alternative eco-evolutionary stable states hinder recovery in harvested fish populations

Mikael Ohlsson^a, György Barabás^a, Max Lindmark^b, Michele Casini^{b,c}, Viktor Thunell^b, Valerio Bartolino^b, Mattias Sköld^b, and Anna Eklöf^a

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Decades of environmental change and anthropogenic pressures have led to the urgent situation of population collapses of many marine fish species (1, 2). Although some populations can recover if fisheries are well-managed (3, 4), the situation of other populations shows continuous declines despite cessation of fishing (5, 6). The slow or absent recovery for these populations is typically attributed to Allee effects, where a smaller population size interferes with recovery (5). Such explanations are generally only partially sufficient, as with time, populations are expected to recover after fishing stops unless other factors interact (6).

A factor that strongly impacts the dynamic of fish populations is body size (7, 8). Fishing is widely recognized to exert selective pressure on fish populations (9, 10), with fisheries generally targeting larger individuals (10, 11). Body size is heritable, so intense fishing for larger individuals will create an evolutionary advantage for smaller individuals (12, 13). Such changes also change interspecific interactions of the species, which can further influence body size (14). While size dependence is recognized to directly influence dietary preferences (7), this aspect can be further influenced by changes in interspecific competitive relationships (14) and consequently feedbacks between these factors (14).

The Baltic Sea is a semi-enclosed basin that has undergone extensive environmental change in recent decades, particularly a significant expansion of hypoxic and anoxic areas (15). Declining oxygen levels can directly impair fish growth and condition, but in particular also reduce suitable habitat (16–20). At the same time, intense fishing pressure has contributed to the collapse of the cod population (*Gadus morhua*), characterized by sharp declines in abundance, body size, and geographic range (19, 21).

As cod have contracted their range to regions with better oxygen conditions, they increasingly overlap spatially with the flounder species complex (*Platichthys flesus* and *P. solemdali*; hereafter referred to as flounder), which has expanded in both abundance (21, 22) and distribution (19). This spatial overlap may have intensified interspecific competition, particularly for benthic prey. A key prey item historically important for both cod and flounder is the benthic isopod *Saduria entomon* (23). In recent decades, *Saduria* has declined in cod stomach contents (23). This ecological change is accompanied by a notable dietary shift in cod: small individuals have shifted from feeding primarily on benthic invertebrates to more piscivorous diets (23, 24). While the drivers of this shift remain unclear, increased competition with flounder offers a plausible explanation (19, 23).

After decades of intense fishing, cod harvest in the Baltic Sea has declined and was recently halted to support the recovery of weakened populations (21). However, there are still no signs of improvement in cod abundance or condition, with individuals remaining fewer, shorter, and thinner (21). A single explanation for this lack of recovery is unlikely, as cod populations are shaped by multiple factors including fishing pressure, environmental conditions, and species interactions (7). While overfishing initially caused the collapse, continued environmental degradation, altered competition, and dietary changes may together explain the persistence of a small-bodied cod population and its failure to recover.

To explore this complexity, we here present an eco-evolutionary model that tracks a species change in body size

Significance Statement

Understanding why some fish populations fail to recover despite reduced fishing intensity is essential for effective marine management and conservation. This study combines ecological and evolutionary modeling with real-world data to explore how body size changes in Atlantic cod influence competition with flounder in the Baltic Sea. Intense fishing not only reduces cod numbers but also selects for smaller individuals. We show that these smaller cod now compete more directly with flounder for food, creating a feedback loop that prevents cod from regaining larger sizes – even after fishing stops. Our findings reveal how altered species interactions can lock ecosystems into degraded states and highlight the need to consider evolutionary dynamics and interspecific competition in fisheries management.

Author affiliations: ^aBiology, Linköping University, Department of Physics, Chemistry and Biology, Linköping University, 581 83 Linköping, Sweden; ^bDepartment of Aquatic Resources, Institute of Marine Research, Swedish University of Agricultural Sciences, Turistgatan 5, 453 30 Lysekil, Sweden; ^cDepartment of Biological, Geological and Environmental Sciences (BiGeA), University of Bologna, Via Selmi 3, 40126 Bologna, Italy

M.O., G.B., and A.E. designed the study. M.O. and G.B. wrote the code for the eco-evolutionary model. M.L. and M.C. constructed the model for predicting biomass densities. V.T. and M.L. prepared the raw empirical data. M.O. performed the simulations and analyses. M.O., G.B., and A.E. wrote the paper. All authors made significant contributions to the final version of the manuscript.

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¹To whom correspondence may be addressed. E-mail: anna.eklof@liu.se

under the effect of both environmental and anthropogenic effects, while simultaneously accounting for changes in inter-specific interactions. The model provides a robust theoretical framework for how a changed competitive relationship can lock a species into a less desirable state – even after other selective pressures are removed. We exemplify our theoretical outcome with an empirical data set of cod and flounder in the Baltic Sea, where the cod population has collapsed and undergone rapid evolution towards smaller body sizes. We show that our model is consistent with the observed data and provides a potential explanation for the lack of recovery for Baltic cod.

Results

In our eco-evolutionary modeling approach we make three assumptions; 1) there is variation in some heritable trait z , 2) this trait correlates with diet, and 3) competition increases with more similar diets. The trait z is identified with body size, but only in a relative, prey-determining sense (25). That is, we assume that the body size of the focal species (i.e., cod) and the average size of its prey are sufficiently tightly correlated that z need not refer to the actual cod body size, but instead to the mean body size of its prey. The advantage of this is to simplify our use of language: now we can say “two species of equal size” instead of saying “a size difference between the two species such that their prey are of equal average size”. To simplify the model, we keep the body size distribution of the competitor (i.e., flounder) fixed while it exerts competitive pressure on the focal species to reduce trait similarity, and thus diet overlap. We define μ as the mean of the focal species size distribution $p(z)$ (Fig. 1).

Apart from resource competition, the focal species also has other, intrinsic limits to how large it can grow, e.g. from increased metabolic demands (26). We auxiliary this natural size-dependent mortality with mortality from fishing and hypoxia. Combining all these selective pressures in an eco-evolutionary model results in a simple dynamical equation governing the body size of the focal species, in the form of $d\mu/dt = g(\mu)$. The function g depends only on μ and the parameters describing the above processes (Materials and Methods; Supplement 1). Since we have one equation for one variable, the model can be analyzed qualitatively by solving for equilibria via $g(\mu) = 0$, checking their stability, and looking at their bifurcations as parameters change. In particular, we are interested in the effects of varying fishing pressure.

When cod body sizes are initially large and fishing is absent to moderate, the opposing selective pressures from the environment and from resource competition create an equilibrium for the focal species’ size at point c in Fig. 1AB. The rate of change in body size μ (given by the function g) has one unstable equilibrium b and two stable equilibria at a and c (Fig. 1B). The unstable equilibrium at point b is centered close to the competitor’s mean size μ_F , with environmental factors causing a slight offset. The presence of the competitor keeps the focal species’ size from crossing the unstable point, and so the alternative stable equilibrium at a (where cod body sizes are much smaller) is unattainable.

However, sufficiently intensive fishing will eventually overcome the competitive pressure (Fig. 1D), forcing the focal species’ body size distribution to go below that of its

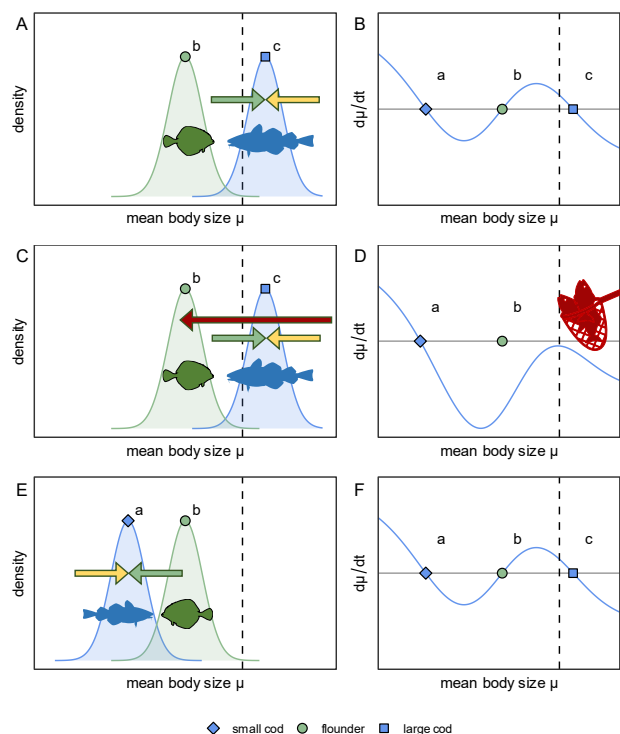


Fig. 1. Conceptual figure of the model. Panels A,C,E: cod (blue) and flounder (green) relative body size distributions. Interspecific competition is assumed to increase as the difference between the body size distributions decreases. Arrows represent different sources of selection on cod: green is the selective pressure from flounder competition, yellow from environmental effects, and red from fishing. The dashed lines show the cod’s “optimal” body size which it would evolve to without competition and fishing. Panels B, D, F: Rate of change of cod mean body size as a function of cod mean body size. Positive (negative) values of $d\mu/dt$ increase (decrease) cod mean body size. For example in panel B, when mean body size is smaller than a , body size increases, while between points a and b body size decreases, making point a a stable equilibrium. Correspondingly, point c is an alternative stable state when cod body size starts larger than b . In panel D the rightmost two equilibria are absent (point b is still shown for reference) due to the presence of active fishing which disproportionately selects large cod, overpowering the counterposing pressure from flounder competition.

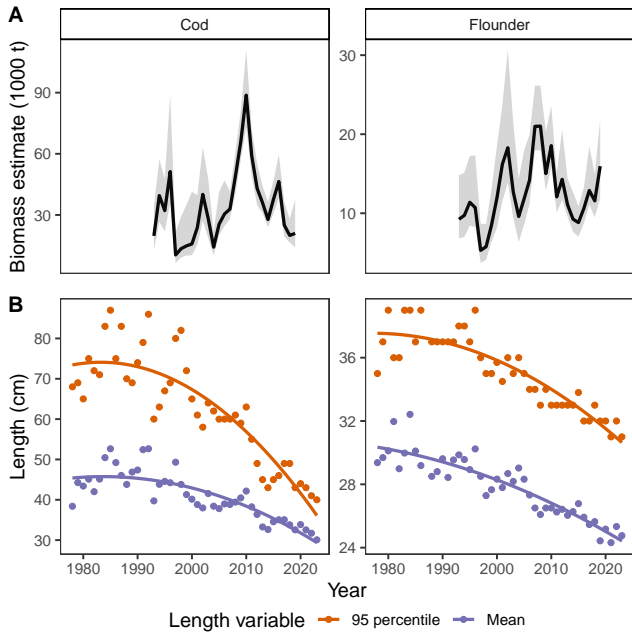


Fig. 2. Panel A shows relative annual biomass estimates in 1000 tonnes of cod and flounder in the Baltic Sea over the years 1993–2019. Panel B shows mean and 95 percentile of cod and flounder body length for the years 1978–2023.

competitor and cross into the alternative, smaller-sized stable state. Now, with the focal species' size distribution in panel E, resource competition pushes the focal species towards smaller body sizes, keeping it locked in its smaller state even after fully relieving the fishing pressure (Fig. 1F, point *a*). The system has thus undergone a critical transition and is now trapped at the undesirable equilibrium point corresponding to small body sizes.

Empirical data on cod and flounder in the Baltic Sea. To illustrate our modelling framework, we use data from Baltic Sea cod and flounder populations. While the cod population has steadily declined since the early 1990s, flounder has increased in recent years (Fig. 2A).

Simultaneously, both cod and flounder have decreased in body size, albeit more extreme for the cod (Fig. 2B). Large individuals in particular are declining, with the 95 percentile of length decreasing from 57 cm in 1993 to 44 cm in 2024. In addition, there has been a clear shift in the cod diet from a largely benthic to a piscivorous diet (Fig. 3). This dietary shift has propagated through all but the smallest length classes of cod.

Historical data on flounder stomach content from the Baltic Sea is not available, limiting dietary comparisons to the flounder diet for years 2015–2020. However, given the relatively limited body size change of flounder (Fig. 2B), and flounder being an obligate benthic feeder, we assume the flounder diet to be constant and compare the historical cod dietary data with the current flounder diet (Fig. 4). Historically, mid-range to larger cod sizes had a more similar diet to flounder. However, in recent years, the larger-sized cod diet has diverged, explained by their change towards a piscivorous diet. In contrast, smaller cod (10–30 cm) now display greater overlap with flounder in their diets.

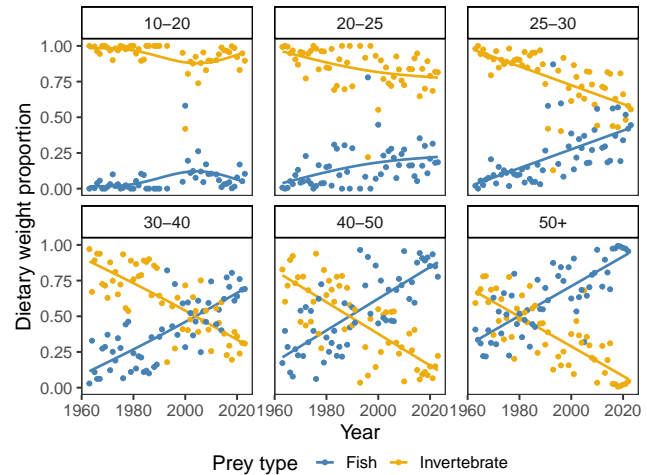


Fig. 3. Cod mean proportional benthic and piscivorous diet, based on stomach content weight for the years 1967–2023 in the Baltic Sea. Facets indicate cod size classes by length (cm).

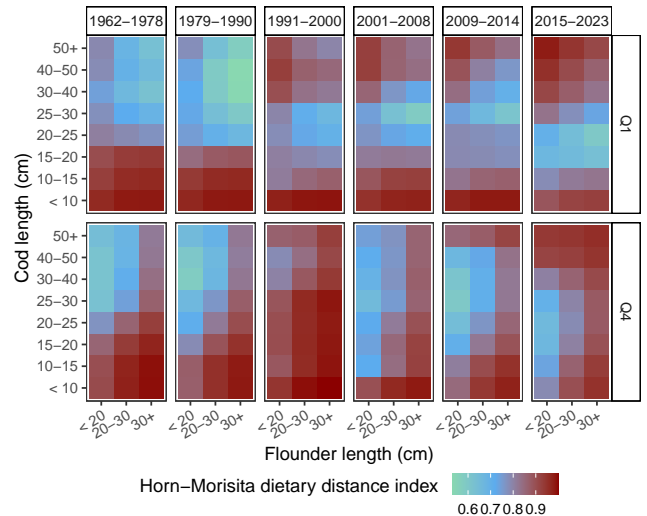


Fig. 4. Dietary distance between cod and flounder of different length classes (cm) using the Horn-Morisita index, where 0 indicates identical diet and 1 indicates no similarity. Data based on individual stomach content weight ratios from cod during 1963–2023 and from flounder during 2015–2022, separated into quarters 1 and 4.

Discussion

In this study, we investigated one potential explanation for the lack of recovery following a double collapse—both in population size and individual body size—of harvested species. These species often fail to recover even after the external pressures that initially caused their collapse have been removed. We focused on how competition combined with eco-evolutionary dynamics plays a key role in locking ecosystems into different, potentially less desirable, stable states. We exemplified this with the pressing issue of the collapsed cod population in the Baltic Sea. The hypothesis is that, following the dramatic reduction in cod body sizes in response to intense fishing (21, 27, 28), competition from flounder is now a strong factor preventing them from growing in body size again, even after fishing pressure is substantially alleviated. The combination of diminished body size and increased competition, due to both increased spatial overlap and increased flounder population, has led to a change in the cod's diet, locking the cod in an alternative stable state. Using an eco-evolutionary model, we demonstrated that this is a robust outcome under a range of plausible assumptions. Long-term empirical data from scientific surveys on cod and flounder stocks from the Baltic Sea support this hypothesis.

Cod diet differs strongly between size classes, whereas flounder is a specialized benthic-feeder with a relatively narrow diet and a limited ontogenetic dietary shift (23). Cod has also historically exhibited considerable individual variation in dietary preferences, suggesting a high degree of feeding adaptability (23). Cod's feeding adaptability, flounder's specialization, and the increase in the flounder population can explain why cod is the species shifting ecological niche. When external pressures (i.e. fishing) give smaller cod individuals an advantage over larger individuals, ultimately causing a genetic shift in the cod's size distribution, the flounder exerts a stronger competitive pressure on the majority of the cod population. The increased spatial overlap between the species further strengthens this pressure. The interspecific competition acts as an effective ecological force for keeping cod locked into smaller sizes. Subsequently, even if the external pressure weakens, it will not necessarily be enough for the cod to recover to the state with a larger body size distribution. Our model effectively demonstrates the plausibility of this mechanism by identifying the equilibrium for cod body size when cod experience competition with flounder and different levels of fishing pressures: as long as cod can keep a mean body size large enough and its ecological niche separated from flounder, that keeps the cod at that large body size. However, when fishing pressure is intense enough and selectively targeting larger individuals, the fishing pressure forces cod to a small enough body size and an increased resource competition with flounder. The only stable equilibrium for cod is now the smaller size one, and even if fishing pressure is removed, cod size stays at that equilibrium due to the competitive pressure from flounder. Consequently, the unstable equilibrium tied to flounder body size acts as a tipping point that cod must surpass to transition between small-bodied and large-bodied population states (29) (see Fig. S2).

But how can we know that competition between the two fish species has been strong enough to affect their ecological niches? A first step is to compare how their diets have changed

over time. Dietary shifts have been observed in the cod populations the Baltic Sea (e.g. 23, 30, 31), where all but the smallest cod has clearly shifted diets from a large proportion being benthic invertebrates towards a piscivorous diet (Fig. 3). Unfortunately, while data on cod diet is available from the 1960's, flounder diet is limited from 2015 onwards. It can however be argued that flounder's diet varies less due to its benthic specialization. With this assumption, comparing the present-day flounder diet and the historical cod diet suggests that larger-sized cod have shifted their dietary preferences, resulting in reduced overlap with flounder (Fig. 4). This is consistent with cod becoming increasingly piscivorous. Although this shift is not necessarily driven by changes in prey availability alone, it is notable that cod have moved away from a historically *Saduria*-rich diet, with *Saduria* now making up a much smaller proportion of their stomach contents. In contrast, flounder continue to utilize *Saduria* to a greater extent, suggesting that cod's dietary changes reflect altered competitive dynamics rather than prey availability alone. The increased dietary overlap observed in smaller cod is likely due to shared consumption of other benthic invertebrates with flounder, pointing to a broader shift in benthic community composition (32). *Saduria* entomon is known to be high in essential fatty acids, and its consumption has been linked to improved cod body condition (20, 33). While this does not directly confirm that flounder are outcompeting cod for specific prey, it remains a plausible contributing mechanism.

Several studies suggest that interspecific competition for food plays an important role when collapsed cod populations fail to recover. For example, Bundy and Fanning (34) showed how small cod of the eastern Scotian Shelf stock appeared, after its collapse in 1993, to face a higher than average level of competition for resources. Walters and Kitchell further suggested that the lack of "cultivation effects", where large-sized adults suppress fishes that are predators or competitors of their juveniles, may be an important factor when populations depleted by fishing fail to recover (35).

In addition, other external factors synergize with the interspecific competition further strengthening the negative effects. For example, hypoxia has detrimental effects on benthic fauna and have caused contraction of distribution of demersal species such as cod and flounder, exacerbating potential interspecific competition between the two species (18). Hypoxia also has direct negative effects via metabolic pathways, and these are predicted to hit larger individuals stronger as they have a smaller aerobic scope (36). Importantly, including hypoxia in our model's current design does not provide any new dynamics, but instead reinforces the same effect that fishing exerts.

Our model shows that a cod population with a smaller body size distribution can recover after removing selection from fishing and with reduced competition from flounder. However, if the shift in body size also has resulted in a genetic shift, the speed of this recovery may be very slow, depending on how strong the selection towards larger body sizes is (7). Larger body size is generally positively influenced by natural selection, e.g. survival from natural predation is often improved with larger body size (37). Further, regarding reproductive output, cod follow a hyper-allometric scaling where larger individuals can produce disproportionately more offspring than multiple smaller individuals of the same total

weight (38). This would also contribute to a natural selection towards bigger individuals if not restricted by other factors. Thus, the negative effects for a population depleted by large individuals will have far-reaching effects on recruitment and population recovery.

One could argue that the shift in body size distribution towards smaller individuals is due to selective fishing removing old and large individuals, rather than a phenotypic change. However, tracking the body size development shows a decline in growth rate of especially larger individuals (28) and subsequently smaller cod individuals relative to their age (21). This likely also relates to the Baltic cod becoming mature at smaller sizes in recent years (27), indicating that a genetic shift is plausible, and as such the empirical data support our model. In fact, a recent study suggests that intensive fishing has not only driven a steep decline in size and growth potential but also left detectable signatures of directional selection across the genome (39).

There are limitations to our modeling approach, and how we connect its results to empirical data. First, we model one single trait when in fact several traits will be affected simultaneously and those traits may neither evolve in the same direction nor with the same speed. For instance, fishing likely selects for both growth and body size but potentially in different ways, because growth is the net result of multiple processes (40). As such, while body size is both directly targeted by fishing and is important for the presence or absence of species interactions, in particular in aquatic environments (41), we model a much-simplified scenario. Second, we assume that what we see in the dietary data of cod and flounder are effects of competitive interactions that already have taken place and that we now look at a new steady-state of the system. We also assume that those dietary shifts in cod depended on, at least to a large extent, competition from flounder, while they could in theory also be due to changes in prey availability via e.g., changes in spatial overlap or abundance of prey as affected by other drivers (42). We have not included factors such as potential changes in the community of prey species and the potential spatial effects on cod size and prey abundance. Lastly, while our model can produce the demonstrated bistability under a wide range of circumstances, its empirical interpretation critically depends on the fact that in the absence of both fishing pressure and competition from flounder, cod would evolve to occupy the flounder's size niche. Otherwise, cod would evolve towards larger body sizes in Fig. 1AC even without the influence of the flounder. Therefore, the observed pattern that more flounder correlates with a larger dietary distance would lose its connection with competition and would be explained by other mechanisms that are not considered by our model at all.

Conclusions. Fishing directly selects against a large body size in the fished populations, and can therefore cause a forced evolution toward smaller body sizes in the targeted species. Body size is tightly coupled to species-specific factors, but also many ecological features, such as competitive and trophic interactions. Interspecific interactions are strong forces in shaping ecological communities, and body downsizing can therefore reshape natural selection and via eco-evolutionary feedback loops act back on body size of the harvested species (14). Our eco-evolutionary model pinpoints the mechanisms

behind the synergistic effects of external pressures and species competitive interactions on body size. Recognizing these types of competitive traps is critical for understanding why some harvested species fail to recover, and for designing management strategies that account for the interplay between evolution and ecological interactions in the Baltic Sea and elsewhere.

Computer code to implement our model and replicate our results is available at <https://github.com/MikaelOhlsson/CodFleEcoEvo/>.

Materials and Methods

Our eco-evolutionary model tracks the population density and body size distribution of two species through time. Here we focus on cod and flounder as the two species. We assume that the body size z of an individual and the average size of its resources are sufficiently tightly correlated that z need not refer to the actual body size, but instead to the mean body size of its prey (43, 44). Thus, we define $z = \log(B/B_0)$, where B is the average resource size (assumed to be in a quasi-one-to-one relationship with the individual's size) and B_0 is a reference size which can be chosen without loss of generality. Here we set it to be the mean size of the flounder's prey. This choice means that $z = 0$ now corresponds to the point at which the mean prey size of cod and flounder coincide.

We make the important assumption that flounder body sizes do not evolve—this implies that B_0 is constant in the model. To describe the interactions between the two species, we assume that they compete for shared resources. Empirically, it is known that the diets of cod and flounder do overlap, but not completely. To account for the general possibility of incomplete overlap, we model resource consumption in a potentially high-dimensional trait space, the first of which is the body size z . The other traits (which may include preferred depth in the water, swimming speed, coloration, etc.) contribute to resource utilization, but are not under evolutionary influence: since the main driver of trait change is fishing pressure which primarily selects for size, we ignore selection on the other traits.

The ensemble of traits can be denoted with the vector \mathbf{x} , the first component of which is the body size z by convention. Our goal is to derive a form for the per capita growth rate $r(\mathbf{x})$ of individuals with phenotype \mathbf{x} . The processes determining this growth rate are (1) growth due to consumption of resources, (2) natural mortality, (3) mortality due to size-dependent fishing pressure, (4) mortality from oxygen-deprived regions which affect bigger individuals more due to different food-seeking behaviour, and (5) competition from individuals with trait vector \mathbf{x}' (irrespective of which species that phenotype belongs to). We can write this as follows:

$$r(\mathbf{x}) = \int u(\mathbf{x}, \mathbf{y}) R(\mathbf{y}) d\mathbf{y} - m(z) - f(z) - H(z), \quad [1]$$

where the first term describes growth on (as well as competition for) shared resources, the second term $m(z)$ is natural mortality, the third $f(z)$ is mortality due to fishing, and the fourth $H(z)$ is mortality due to hypoxia. In the first term, $R(\mathbf{y})$ is the availability of resources of type \mathbf{y} , $u(\mathbf{x}, \mathbf{y})$ is the utilization of resource type \mathbf{y} by an individual of phenotype \mathbf{x} , and the integration is understood to apply separately for each component of \mathbf{y} .

In turn, resource availability is given as the maximum (saturation) resource levels, minus what is currently being consumed by the cod and flounder populations. We make the assumption of time scale separation, with the resource dynamics being faster than the consumer dynamics (45–47). Resource competition is moderated by the overlap of the resource utilization curves,

$$a(\mathbf{x}, \mathbf{x}') = \int u(\mathbf{x}, \mathbf{y}) u(\mathbf{x}', \mathbf{y}) d\mathbf{y}, \quad [2]$$

determining the competition coefficient between phenotypes \mathbf{x} and \mathbf{x}' . Here we choose $u(\mathbf{x}, \mathbf{y})$ to be multivariate Gaussian.

For the natural mortality $m(z)$, we assume that too large or too small body sizes lead to increasing mortality due to physiological limits. That is, we assume that the mortality $m(z)$ is smallest

at some optimal body size z^* , and increases from there in both directions. Making this increase quadratic, we write

$$m(z) = \varrho \frac{(z - z^*)^2}{\theta^2}, \quad [3]$$

where ϱ is the maximum intrinsic growth rate based on the phenotype's resource utilization and θ is the width of the body size region where positive growth is possible.

Size-dependent fishing often saturates for large body sizes (48), and we thus describe mortality from fishing $f(z)$ as low to high values of the sigmoid curve. Similarly, reduction in growth caused by hypoxia, $H(z)$ is also described as a sigmoid curve, with smaller phenotypes affected less than larger phenotypes.

Eco-evolutionary dynamics. In case body size variation is influenced by very many loci where each locus has a small additive effect, the infinitesimal model of quantitative genetics (49) is suitable to model the eco-evolutionary dynamics of the population densities N_i and mean body sizes μ_i (where in our case $i = C$ or $i = F$). The governing equations (47) are

$$\frac{dN_i}{dt} = N_i \int r(z) p_i(z) dz, \quad [4]$$

$$\frac{d\mu_i}{dt} = h_i^2 \int (z - \mu_i) r(z) p_i(z) dz. \quad [5]$$

Here $p_i(z)$ is the phenotype distribution of species i (which is normal with mean μ_i in the quantitative genetic limit), h_i^2 is its heritability, and $r(z)$ is the per capita growth rate of individuals with size z . In our model, this growth rate is given by a combination of resource consumption and -competition, size-dependent natural mortality, fishing-induced mortality, and hypoxia-induced mortality (Supplement, Eq. 1).

One further simplification to the model is to assume that the flounder population density N_F is constant, being at an equilibrium value that is unaffected by cod. This allows one to reason about body size evolution much more simply, because the equations decouple between cod and flounder as well as between population densities and body sizes (Supplement 1). That is, Eq. 5 for cod reduces to the simple one-dimensional dynamical system $d\mu/dt = g(\mu)$, where $\mu = \mu_C$ is the cod mean size and $g(\mu)$ is a function depending only on μ itself and model parameters. In particular:

$$\begin{aligned} \frac{d\mu}{dt} = h_C^2 \left[\frac{2\varrho\sigma_C^2}{\theta^2} (z^* - \mu) - \frac{\eta\sigma_C^2}{\sqrt{\pi(2\sigma_C^2 + \tau^2)}} e^{-\frac{(\mu - \varphi)^2}{2\sigma_C^2 + \tau^2}} \right. \\ \left. - \frac{\kappa\sigma_C^2}{\sqrt{\pi(2\sigma_C^2 + \nu^2)}} e^{-\frac{(\mu - \zeta)^2}{2\sigma_C^2 + \nu^2}} \right. \\ \left. + \frac{\mu\sigma_C^2 N_F \alpha_0 \alpha_I}{\sqrt{2\pi(\sigma_C^2 + \sigma_F^2 + \omega^2)^3}} e^{-\frac{\mu^2}{2(\sigma_C^2 + \sigma_F^2 + \omega^2)}} \right] \quad [6] \end{aligned}$$

(Supplement, Eq. 37). The curves in the right column of Fig. 1 were plotted using this function. It turns out that the predicted body size dynamics from this decoupled and simplified model are qualitatively the same as those from the full model. The details of the model and its parameters are described in Supplement 1.

Survey data. We relate the mechanisms of our eco-evolutionary model to cod and flounder populations in the Baltic Sea. Using available survey data for both species, we compare model expectations with observed biological data to support the model's conclusions.

We used data from the Baltic International Trawl Survey (BITS) to evaluate relative biomasses and diets of cod and flounder in the southern Baltic Sea. BITS is a bi-annual bottom trawl survey, conducted during quarters one and four. Data on catch per unit effort can be downloaded from the ICES DATRAS database (<https://datras.ices.dk/>). We standardized these data for differences in gear following (20, 50), to acquire survey catches in density per area (kg/km^2). We fit these data with a geostatistical generalized linear mixed-effects model, using a

Tweedie distribution (51–53) and a log-link function, due to the presence of zeros and continuous densities.

For details about the biomass model, we refer to Supplement 2 and (20). We used this model to predict the biomass density of cod and flounder over a regular grid of 4×4 km squares with covariates to calculate indices of relative biomass based on a random-field model (54, 55) over the spatial domain. While the model was fit to data from years 1993–2020 in ICES subdivisions 24–28, we only make predictions for subdivisions 25–28 to match where we have the most diet data (Supplementary Fig. S2), while excluding subdivision 24 where mixing with the western cod population occurs more frequently. Cod and flounder body sizes were also extracted from the DATRAS database, including catch per unit effort of length, weight and age. As finding individuals of older ages is increasingly rare in recent years, a minimum of five individuals was required to include the mean length of a specific year and age-class.

The stomach content data for cod and flounder were compiled from different sources. The majority of the cod stomach data have been collated in EU funded projects (56, 57) and are available at the International Council for the Exploration of the Sea (ICES) stomach content database (<https://www.ices.dk/data/data-portals/Pages/Stomach-content.aspx>). In addition, we used recent cod stomach data collated in (58). Flounder stomach data are from (59). This compiled data set comprised of cod stomach data between 1963 and 2023 and flounder stomach data between 2015 and 2022. For both species, data collected from 1993 and onwards were mainly collected on the bi-annual Baltic International Trawl Survey (BITS) conducted in the first and fourth quarter of the year, but also from other cruises conducted in other times of the year (see (56), (57), and (58, 59) for a detailed description of the data sources). The stomach samples included data for individuals larger than 6 cm, and separated into quarters one and quarter four. Whenever possible, one flounder and one cod stomach were collected for each cm class of fish length and trawl haul. Prey items was grouped into 15 taxonmical groups based on (23).

We used the stomach content data to calculate the dietary distance, and thus possible interspecific competition, between cod and flounder. The dietary distance was used to estimate interspecific competition for the same prey items. We aggregated cod and flounder data into arbitrary length classes (Cod < 20 cm, 20–30 cm, 30–40 cm and > 50 cm, flounder < 20 cm, 20–30 cm, and > 30 cm). Stomach content weight was used for calculating dietary and proportions and dietary distances. For each individual sample, prey proportions based on the respective prey species weights was calculated. This was then used to obtain the average dietary proportions for the respective time periods and size classes. The proportions were then used to calculate the dietary distances using the Horn-Morisita index with the abdiv package (version 0.2.0, 60) in R, where the dissimilarity between two vectors x and y consisting of, in our case, the dietary proportion elements i is described as

$$d(x, y) = 1 - \frac{2 \sum_i x_i y_i}{(\lambda_x + \lambda_y) N_x N_y}, \quad [7]$$

and

$$\lambda_x = \frac{\sum_i x_i^2}{N_x^2}, \quad [8]$$

where $N_x = \sum_i x_i$. The resulting distance index has a value of 0 if the diets are identical and 1 if the diets have nothing in common.

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