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Impacts of estuarine habitat degradation on the modeled life history of marine estuarine–dependent and resident fish species

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Abstract

Shallow coastal and estuarine habitats play an essential role in the life cycles of many fish species, providing spawning, nursery, feeding, and migration areas. However, these ecologically valuable habitats are increasingly threatened by anthropogenic activities, causing substantial changes in both habitat availability and quality. Fish species use these shallow coastal habitats and estuaries during various life stages, leading to their categorization into guilds based on how and when they rely on these areas. This differential functional use of estuaries means that changes to these habitats may affect each guild differently. To understand the impact of estuarine habitat degradation on fish populations, it is therefore necessary to consider the full life cycle of fish and when they rely on these coastal habitats. Here, we use conceptual size-structured population models to study how estuarine habitat degradation affects two functionally different guilds. We use these models to predict how reduced food productivity in the estuary affects the demographic rates and population dynamics of these groups. Specifically, we model estuarine residents, which complete their entire life cycle in estuaries, and marine estuarine–dependent species, which inhabit estuaries during early life before transitioning offshore. We find that total fish biomass for both guilds decreases with decreasing food productivity. However, the density of juveniles of the marine estuarine–dependent guild can, under certain conditions, increase in the estuary. This occurs due to a shift in the population biomass distribution over different life stages and a simultaneous shift in which life stage is most limited by food. At the individual level, somatic growth of juveniles belonging to the estuarine-dependent guild decreased with lower food supply in the estuary, due to increased competition for food. The somatic growth rates of fish belonging to the resident guild were largely unaffected by low food supply, as the total fish density decreased at the same time and therefore the per-capita food availability was similar. These outcomes challenge the assumption that responses to habitat degradation are similar between fish guilds. Our study highlights the need to assess not only fish biomass but also size distributions, survival, and somatic growth rates for a comprehensive understanding of the effects of habitat degradation on fish populations. This understanding is crucial not only for estuary fish communities but also for successful conservation and management of commercially harvested offshore population components.

KEYWORDS
anthropogenic pressure, fish, guilds, habitat degradation, estuary, size-structured population model

1 | INTRODUCTION

Coastal habitats are heavily impacted by a range of anthropogenic activities from both land and sea (Halpern et al., 2008), resulting in significant changes in habitat quantity and quality for fish species (Lotze et al., 2006). These anthropogenic pressures can negatively affect fish population biomass and status (Brown et al., 2018). For example, common sole *Solea solea* L. in the Seine estuary lost 42% in nursery capacity of their estuary since 1850, resulting in an estimated 23% reduction in *S. solea* abundance (Rochette et al., 2010). Eelpout *Zoarces viviparus* L. populations in the German Wadden Sea almost disappeared due to higher water temperatures exceeding their thermal limits (Pörtner & Knust, 2007). This increase in temperature led to oxygen limitation, resulting in reduced somatic growth and increased mortality.

Processes such as reproduction, somatic growth, and mortality are organism-level impacts. However, these impacts scale up to population-level changes, because the population cannot grow if reproduction and somatic growth are limited. For these physiological processes, fish often depend on shallow coastal and estuarine habitats, especially during early life stages. These shallow coastal and estuarine habitats are known to be ecologically important areas due to their role as fish spawning grounds, nursery areas, feeding areas, and migration corridors. Notably, 44% of fish species listed by the International Council for the Exploration of the Sea (ICES) rely on coastal habitats (Seitz et al., 2014). These coastal-zone-dependent stocks play a substantial role in the fishing industry, contributing 77% of commercial landings of species managed by ICES (Seitz et al., 2014).

Different fish species use shallow coastal habitats and estuaries during different stages of their lives. Fish species can therefore be assigned to guilds, which describe how and when they depend on transitional waters such as estuaries (Elliott et al., 2007; Potter et al., 2015). For example, estuarine residents, such as *Z. viviparus*, spend their entire lives in these environments, depending on them throughout all life stages. In contrast, marine estuarine–dependent species, such as cod *Gadus morhua* L., plaice *Pleuronectes platessa* L., and *S. solea*, utilize estuaries primarily during their early life stages before migrating to offshore marine habitats (Tulp et al., 2017). Additionally, marine estuarine–opportunist species, such as European seabass *Dicentrarchus labrax* L. and common dragonet *Callionymus lyra* L., regularly use estuaries, particularly as juveniles, but can also thrive in coastal marine waters as an alternative (Potter et al., 2015). Anadromous species such as trout *Salmo trutta* L. and salmon *Salmo salar* L. rely on these transitional habitats mainly during migration (Elliott et al., 2007). These classifications of fish into guilds are also practical for shallow coastal habitats that may not strictly be defined as estuaries (e.g., Tulp et al., 2017). In this study, we use the term "estuary" in its broadest sense, following Elliott et al. (2007), to include all intermediate habitats influenced by both freshwater and marine water bodies.

Fish community assessments based on functional guilds of estuarine use have been widely applied in estuarine and coastal ecosystems around the world (e.g., Delpech et al., 2010; França et al., 2011; Harrison & Whitfield, 2021). Such analyses provide information on the functioning and structure of fish communities and their ecosystems (Elliott et al., 2007). It is often assumed that estuarine residents, which rely on estuarine habitats throughout their ontogeny, are most sensitive to habitat degradation and that their response to environmental change reflects local conditions (e.g., Harrison & Whitfield, 2021; Teichert et al., 2017). However, the differential use of shallow coastal and estuarine habitats by different guilds means that any changes to these habitats will have different impacts on each guild, resulting in different effects on performance of individual fish and fish population dynamics. For example, increased mortality rates in these shallow areas will affect all life stages of estuarine residents, whereas it will primarily affect the juvenile stage of marine estuarine species. Despite the widespread use of functional guilds to assess estuarine fish assemblages, there are no systematic predictions of how different guilds will respond to environmental change in terms of somatic growth, mortality, and population density.

Although the importance of coastal and estuarine habitats for fish and their vulnerability to anthropogenic pressures are widely recognized (Brown et al., 2018), the consequences of coastal habitat loss or degradation on fish populations are not well understood (Vasconcelos et al., 2014) and from empirical studies difficult to generalize even within guilds. To develop effective conservation and management strategies that can mitigate the ecological and economic consequences of habitat degradation, it is essential to gain a mechanistic insight into how different fish guilds are affected by changes in shallow coastal and estuarine habitats. This study aims to bridge this knowledge gap by systematically analysing the demographic rates and population dynamics of two distinct guilds in a model: estuarine residents and marine estuarine–dependent species. Specifically, we will examine somatic growth, maturation, reproduction, and mortality rate as key demographic factors. In terms of population dynamics, we will investigate resource and fish densities, and the size structure of the fish populations. Our focus is on understanding the impacts of estuarine habitat degradation on these fish populations, defining habitat degradation here by food productivity in the estuary (Gibson, 1994), although acknowledging that other factors such as temperature regime, habitat complexity, fishing mortality, and pollution loads also contribute to habitat quality (Lotze et al., 2006). Diadromous fish, which mainly use estuaries during migration, are excluded from our analysis as they are primarily influenced by estuarine connectivity to fresh water and the ocean rather than estuarine habitat degradation (Isaak et al., 2007).

In this study, we choose a modeling approach that contains organismal detail, although retaining the ability to generalize outcomes. We use a biomass-based, size-structured population model (Soudijn et al., 2021; Soudijn & de Roos, 2017) to investigate the potential responses of individual organisms and overall population dynamics of the two guilds to reduced food productivity of the estuary. Such physiologically structured population models (PSPM, de Roos & Persson, 2001; Metz & Diekmann, 1986) define how an individual's performance—measured by somatic growth, survival (i.e., inverse of mortality), and reproduction—depends on its body mass and the conditions of its environment, which is in our model food availability and mortality risk. All assumptions and parameterizations of these functional relationships are made exclusively at the level of the individual fish. The population model is then derived by systematically accounting for these individual-level processes without making any additional assumptions. Population dynamics are considered over multiple, overlapping generations. Using numerical integration, we explore how reduced food productivity in the estuary affects the life cycles of different fish guilds and how this translates to changes in the composition and density of the fish population. Appendix A shows how habitat-specific mortality (e.g., due to fishing offshore or in the estuary) affects our main results. In Appendix B, we show additional results of a scenario where we decrease habitat availability in the estuary instead of food productivity.

2 | MATERIALS AND METHODS

Classical frameworks often emphasize either population dynamics or physiological details at the individual level. For our analysis of the guild-specific responses to reduced food productivity in the estuary, we need an approach that incorporates the fish life cycle and integrates from individual-level processes to population-level dynamics. Empirical research shows that many fish using estuaries cross over between guilds opportunistically (e.g., Cardoso et al., 2015), which renders generalized insights challenging. To allow generalization over species in a guild, we use an idealized model life-history and guild characterization. For this some details are crucial (i.e., food-dependent somatic growth, condition-dependent reproduction, and ontogenetic habitat shift), whereas others are left out (i.e., stochasticity of processes in the environment, temperature-dependent processes, and evolutionary processes). Given these restrictions, the physiologically structured modeling (PSPM; de Roos & Persson, 2001) framework is precisely suited to include the necessary level of detail and retain the capacity for numerical integration over broad parameter ranges.

2.1 | Model formulation

We formulate and analyse a general PSPM with seasonal reproduction following the framework used in Soudijn and de Roos (2017). We use this model to analyse population dynamics for resident and marine estuarine–dependent fish guilds. The analyses were performed in isolation per guild, meaning that we do not take any competition between the guilds into account. Other trophic interactions and food web components are described later. The model formulation for both guilds follows as much as possible identical definitions, so we can look at the guild characteristic as our factor of analysis. We define the resident guild as species that occupy the same habitat throughout ontogeny, and the marine estuarine–dependent guild is defined as species that migrate offshore upon reaching a threshold body size. We first describe the general life history of the two guilds, followed by the individual-level assumptions and functions. We then describe how we translate the individual-level dynamics to the population level-dynamics and how we generate time series over multiple generations. In addition, we explain how we model the dynamics of the resources. We end this section with an explanation of the parameterization of the model; all parameter values are presented in Table 1.

2.1.1 | Life history

For both guilds, we did not include parameters related to the egg stage, except for assessing egg mortality. We divide the consumers into three life stages: juveniles, subadults, and adults. Most fish species change their diet during ontogeny (Sánchez-Hernández et al., 2019). We therefore assume for both guilds an ontogenetic diet shift, where juveniles initially feed on a juvenile resource and subadults and adults feed on a secondary adult resource. Individuals of both guilds start their lives in the estuary (denoted by the subscript "est") as juveniles with a body mass of $s = Sb$. In the estuary, juveniles feed on a juvenile resource (e.g., zooplankton) with density $R_{1,\text{est}}$. Individuals become subadults when they reach a body mass of $s = Sj$. Individuals of the marine estuarine–dependent guild subsequently migrate offshore (denoted by the subscript "off") where they feed on an adult resource (e.g., small fish) with density $R_{2,\text{off}}$. As oceans and estuaries are generally well connected, we assume that there are no migration costs for marine estuarine–dependent species (see Appendix C for a relaxation of this assumption). Although estuarine residents remain in the estuary throughout their lives, individuals do change their diet during development (Elliott et al., 2007). We therefore assume that subadults of the resident guild also feed on an adult resource (e.g., fish) with density $R_{2,\text{est}}$. When individuals of either guild reach a body mass of $s = Sm$, they are considered adults. Adults continue to feed on the secondary adult resource, but they no longer grow (see Appendix C for a relaxation of this assumption). Instead,

TABLE 1 Model parameters and their default values for marine estuarine–dependent and residents feeding on two resources.

Parameter	Value	Unit	Description
Seasonal dynamics			
Y	250	days	Duration of the growing season
Resource dynamics			
δ	0.1	day^{-1}	Resource turnover rate
$R_{1,\text{est},\max}$	0.1	mg L^{-1}	Maximum density of the first resource in the estuary
$R_{2,\text{est},\max}$	0.05–0.15 (default 0.1)	mg L^{-1}	Maximum density of the second resource in the estuary
$R_{2,\text{off},\max}$	$R_{2,\text{est},\max}$	mg L^{-1}	Maximum density of the second resource offshore
$K_{1,\text{est}}$	Variable	–	Scale parameter for productivity in the estuary
$K_{2,\text{est}}$	$K_{1,\text{est}}$	–	Scale parameter for productivity in the estuary
$K_{2,\text{off}}$	1	–	Scale parameter for productivity offshore
Individual energetics			
T	0.015	$\text{g g}^{-1}\text{ day}^{-1}$	Metabolic rate
a	26.5	$\text{L g}^{-1}\text{ day}^{-1}$	Attack rate
h	12.5	day	Handling time
σ	0.3	g g^{-1}	Efficiency of food assimilation
Mortality			
μ_b	0.001	day^{-1}	Background mortality
μ_egg	0.97	–	Egg mortality
μ_est	0–0.002 (default 0)	day^{-1}	Additional mortality in the estuary
μ_off	0–0.004 (default 0)	day^{-1}	Additional mortality in the offshore habitat
Body sizes			
Sb	0.351	g	Size at birth
Sj	100	g	Size at habitat shift (marine estuarine–dependent guild) or diet shift (resident guild)
Sm	200	g	Size at maturation

they store energy in their reproductive buffer g. Although this assumption is obviously oversimplified given that adult fish do continue to grow, their somatic growth rates are much slower than those of juveniles, and they put the majority of their energy into reproduction (Marshall & White, 2019). In addition, previous work shows that adding an additional growing adult stage often does not qualitatively change the characteristic population dynamics and results (de Roos & Persson, 2013). In our model, reproduction happens once a year at the beginning of the growing season. During the remainder of the growing season, adults store energy into their reproductive buffer.

2.1.2 | Individual dynamics

Individuals in the (sub)adult size classes of the marine estuarine–dependent guild feed on resource $R_{2,\text{off}}$, whereas (sub)adults in the resident guild feed on $R_{2,\text{est}}$. In the remainder of the model description, we will refer to the (sub)adult resource as $R_{2,h}$, where the index h refers to the habitat the resource occurs (either offshore "off" for the estuarine-dependent guild or in the estuary "est" for the resident).

The efficiency of an individual's food consumption depends on its current size s and on the densities of the resources in the habitat (de Roos & Persson, 2013). We assume a Holling type 2 functional response for the mass-specific food intake, $I(s,R_i)$. Mass-specific food intake then equals

$$I(s,R_i) = \begin{cases} \dfrac{aR_{1,\text{est}}}{1+ahR_{1,\text{est}}}, & \text{if } s < Sj, \\ \dfrac{aR_{2,h}}{1+ahR_{2,h}}, & \text{otherwise.} \end{cases} \tag{1}$$

In this equation, parameter a refers to the attack rate and parameter h to the handling time, which is considered constant for both resources and all size classes (de Roos & Persson, 2013).

Ingested food is assimilated with efficiency σ. Assimilated energy is first used to pay the mass-specific maintenance costs, T. The net-energy production per unit of body mass is given by the difference between the energy intake rate and the maintenance costs (de Roos & Persson, 2013), which equals

$$\nu(s,R_i) = \sigma I(s,R_i) - T \tag{2}$$

If the net-energy production is positive $(\nu(s,R_i) > 0)$, juveniles and subadults invest all their net energy in somatic growth, whereas adults invest all their net energy in reproduction. Reproductive energy is stored during the growing season and converted into newborn individuals during reproduction. Adults cannot use their reproductive storage to pay for their maintenance costs under starvation conditions (see Appendix C for a relaxation of this assumption). If an adult dies due to starvation or background mortality, its stored energy (g) is lost.

Individuals can die due to three different sources of mortality: background mortality, starvation mortality, and habitat-specific mortality. In the main text we assume that there is no habitat-specific mortality, but in Appendix A we relax this assumption. All individuals are subject to size-independent background mortality (μ_b), which remains constant throughout the lifetime of fish and across multiple generations. If the assimilated energy is not sufficient to cover maintenance costs ($\nu(s,R_i)<0$), individuals experience an additional starvation mortality equal to $\nu(s,R_i)$. This type of mortality varies over the lifetime of an individual and can fluctuate across generations due to fluctuations in resource availability. Finally, individuals may experience habitat-specific mortality (μ_i, with $i=$"off" for (sub)adults of the marine estuarine–dependent guild or "est" for residents and marine estuarine–dependent juveniles). Habitat-specific mortality can change over an individual's lifetime due to ontogenetic habitat shifts but remains constant across multiple generations of fish. The total per-capita mortality rate equals

$$d(s,R_i)=\begin{cases}\mu_\mathrm{b}+\mu_i-\ \nu(s,R_i), \text{if}\ \nu(s,R_i)<\ 0,\\ \quad\mu_\mathrm{b}+\mu_i, \qquad \text{otherwise.}\end{cases} \tag{3}$$

Whereas residents spend their entire life in the estuary, marine estuarine–dependent species occupy two habitats during their lifetime. Because of these different life histories, habitat-specific mortality will affect the two guilds differently. If mortality in the estuary, μ_est, is increased, for example, due to extreme temperatures or fisheries in the estuary, all life stages of the resident will be affected. For the marine estuarine–dependent guild, however, only juveniles ($s<Sj$) will experience these increased mortality levels. Conversely, increased mortality offshore, μ_off, for example due to offshore fishing mortality, will affect (sub)adults of the marine estuarine–dependent guild only.

2.1.3 | Population dynamics

We model the population dynamics during the growing season with a duration of Y days (Table 1) and ignore conditions during winter. Reproduction occurs once a year at the beginning of the growing season (Soudijn & de Roos, 2017). Because individuals are born with identical size Sb and somatic growth is deterministic, all individuals born at the same time remain identical to each other throughout their lives. Therefore, all individuals born during a reproductive event are grouped into a single cohort. The dynamics of each cohort $k\in\mathbb{N}$ can be described by a set of three ordinary differential equations that track the number of individuals, c_k, their body mass, s_k, and their reproductive buffer, g_k.

During the growing season with duration Y, the dynamics over time τ ($0\le\tau<Y$) are all continuous and can be described by the following set of differential equations.For $Sb\le s_k<Sm$,

$$\begin{cases}\dfrac{\mathrm{d}c_k}{\mathrm{d}\tau}=-d(s_k,R_i)c_k,\\ \dfrac{\mathrm{d}s_k}{\mathrm{d}\tau}=\nu^+(s_k,R_i)s_k,\\ \dfrac{\mathrm{d}g_k}{\mathrm{d}\tau}=0.\end{cases} \tag{4}$$

For $s_k=Sm$,

$$\begin{cases}\dfrac{\mathrm{d}c_k}{\mathrm{d}\tau}=-d(Sm,R_{2,\mathrm{h}})c_k,\\ \dfrac{\mathrm{d}s_k}{\mathrm{d}\tau}=0,\\ \dfrac{\mathrm{d}g_k}{\mathrm{d}\tau}=\nu^+(Sm,R_{2,\mathrm{h}})Sm.\end{cases} \tag{5}$$

In these equations we use the notation $\nu^+(s_k,R_i)$ to indicate the mass-specific net-energy production rates restricted to positive values only. The number of individuals in each cohort, c_k, decreases due to mortality $d(s_k,R_i)$. Juveniles and subadults increase in mass, whereas adults invest their energy in their reproductive buffer g_k.

Reproduction takes place instantaneously at intervals $t_x=xY$. The moment just after a reproductive event t^+, one new cohort is formed from the biomass that was stored up to the point just before reproduction t^-, and the biomass of the reproductive buffer is set to 0. All other cohorts are renumbered. The changes are described by the following sets of equations:

$$\begin{cases}c_0\left(t_x^+\right)=(1-\ \mu_\mathrm{e})\theta\sum\limits_k\dfrac{g_k\left(t_x^-\right)c_k\left(t_x^-\right)}{Sb},\\ s_0\left(t_x^+\right)=Sb,\\ g_0\left(t_x^+\right)=0,\end{cases} \tag{6}$$

$$\begin{cases}c_{k+1}\left(t_x^+\right)=c_k\left(t_x^-\right),\\ s_{k+1}\left(t_x^+\right)=s_k\left(t_x^-\right)\ ,\\ g_{k+1}\left(t_x^+\right)=0.\end{cases} \tag{7}$$

Parameter μ_e indicates the fraction of eggs that die before hatching, and parameter θ represents the efficiency at which gonads are converted into offspring.

2.1.4 | Resource dynamics

Productivity of the resources in both the estuarine and offshore habitats is modeled through the resource dynamics. To allow direct analysis of fish population dynamics based on varying resource productivity, we choose a formulation that is as simple as possible, although explicitly accounting for dynamically changing resource levels due to foraging. Therefore, the dynamics of the resources follow semi-chemostat dynamics (Persson et al., 1998), with turnover rate δ, and will reach a density of $P_{i,\max}$ ($i=$ "1,est" or "2, h") in the absence of consumers.

The productivity of a resource, denoted as $\delta P_{i,\max}$, is the rate at which the resource is generated in grams per liter per day. If the estuary becomes less productive, the productivity of the juvenile resource of both guilds will decrease. The productivity of the adult resource of the resident guild decreases, whereas that of the marine estuarine–dependent guild remains unaffected. Because juveniles and (sub) adults of the resident guild feed on different food sources, changes in habitat productivity may affect these resources differently. To capture these effects, we define $P_{i,\max}$ as $K_i R_{i,\max}$ (with $i=$ "1,est" or "2, h"), where K_i is a scaling parameter that adjusts the productivities of the different resources. For the resident guild, we assume that $K_{2,\text{est}}=K_{1,\text{est}}$, whereas for the marine estuarine–dependent guild, $K_{2,\text{off}}=1$. To compare the two guilds, we assume $R_{2,\text{est},\max}=R_{2,\text{off},\max}$ and vary the scaling parameter $K_{1,\text{est}}$ to study the effect of changes in resource productivity in the estuary. The dynamics of the resources are described by

$$\frac{dR_{1,\text{est}}}{d\tau}=\delta\left(K_{1,\text{est}}R_{1,\text{est},\max}-R_{1,\text{est}}\right)-\frac{aR_{1,\text{est}}}{1+ahR_{1,\text{est}}}\sum_{k|s_k<Sj}c_k s_k,$$

$$\frac{dR_{2,h}}{d\tau}=\delta\left(K_{2,h}R_{2,h,\max}-R_{2,h}\right)-\frac{aR_{2,h}}{1+ahR_{2,h}}\sum_{k|s_k\geq Sj}c_k s_k. \tag{8}$$

Note that the availability of a certain resource depends not only on its productivity but also on the consumption of that resource by fish (the second term in Equation 8). Despite a high productivity, food availability might therefore be low when there are many fish feeding on that particular resource.

During a reproductive event, we assume that the densities of the resources do not change $\left(R_i\left(t_x^+\right)=R_i\left(t_x^-\right)\right)$ (Soudijn & de Roos, 2017).

2.1.5 | Parameterization

As we are interested in understanding how different life histories respond to declining food productivities in the estuary, we keep the parameters for both guilds identical as much as possible. We therefore base the general parameterization loosely on gadiforms in the Baltic Sea, which includes fishes from both the marine estuarine–dependent species (e.g., *G. morhua*) and resident (e.g., five-bearded rockling *Ciliata Mustela* L.) guilds. The parameters are based on those in van Leeuwen et al. (2008) and are presented in Table 1. Note that the aim of this paper is to compare the responses of the two guilds, and our generic model is not intended for species-specific interpretation.

In contrast to van Leeuwen et al. (2008), we keep the parameters for the different size classes the same to ensure that the effects of habitat-specific resource availability and mortality do not interfere with stage-specific parameterization. van Leeuwen et al. (2008) use a value of 0.08 g g^{-1} day^{-1} for the weight-specific maximum ingestion rate M. This corresponds to a handling time h, which is the inverse of the maximum ingestion rate, of 12.5 days. For the half-saturation resource density, S_{half}, we follow de Roos and Persson (2013) and choose a value of 3 mg L^{-1}. The attack rate a, defined as M/S_{half}, is therefore 26.5 L g^{-1} day^{-1}.

Although we ignore the dynamics occurring in the egg and early larval stages, we include a mortality factor of μ_e in the reproduction term (see Equation 6). The egg incubation period in cod is ~20 days, during which the eggs experience a mortality rate of 0.17 per day (Langangen et al., 2013). Therefore, the cumulative egg survival during this period is about 3%, which gives a value of 0.97 for the egg mortality factor μ_e.

We assume that marine estuarine–dependent species migrate offshore at a body length of ~20 cm, whereas residents switch to the secondary resource at this size. We chose this value because at this size *G. morhua* spends approximately 50% of its time feeding on fish and the other 50% feeding on benthic prey species (van Leeuwen et al., 2013). We chose a value of ~25 cm for the body length at maturation (Vainikka et al., 2009), which is smaller than that often reported for *G. morhua*. However, this smaller size makes the dynamics easier to plot, as it avoids a very long time until maturation. This difference will not affect the results qualitatively, only quantitatively. Our aim is to illustrate general patterns rather than species-specific responses. To convert body length to weight, we use the relationship $w=\lambda_1 l^{\lambda_2}$, where w is the body mass (g) and l is the body length (cm). Using a value of 0.013 for λ_1 and a value of 3 for λ_2 (van Leeuwen et al., 2008), the body mass (g) at the diet/habitat shift equals 100 and at maturation 200 g.

All biomass densities are expressed in milligram per liter, and time is expressed in days.

2.2 | Model analysis

The primary focus of this study was to examine the effect of decreased food productivity of the estuary. We model this by decreasing the productivity of this habitat via parameter $K_{1,\text{est}}$. Therefore, we specifically choose not to report on calculations in the opposite direction, that is by increasing $K_{1,\text{est}}$. Appendix D presents for completeness additional results where we increase the parameter $K_{1,\text{est}}$, showing that there is some bistability in the system. This bistability does not qualitatively change the results presented in the main text.

We analysed the population dynamics with numerical simulations using the software package EBTtool (https://staff.fnwi.uva.nl/a.m.deroos/EBT/), and bifurcation analysis was performed using iterative time series with slightly changing bifurcation parameter values. We studied the parameter dependence of the dynamics by integrating over long time periods (100,000 days, i.e., 400 years) while decreasing the value of the focal parameter $K_{1,\text{est}}$ in small steps after each period. In these calculations, we calculated the average, minimum, and maximum values over the last 60% of the 100,000-day period. To test the robustness of our results, we perform these bifurcation calculations for different values of $R_{2,h,\max}$ (main text) and habitat-specific mortality rates (μ_{est} and μ_{off}, Appendix A). Model-specific files are available online.

Additionally, to study the effect of decreased food productivity of the estuary on population dynamics, we show a time series of 80 years (20,000 days) in which we decreased the productivity of the estuary after 40 years (10,000 days) from a high value of 1 to a low value of 0.4.

3 | RESULTS

All life-history processes in our model—somatic growth, survival, and reproduction—depend on food availability. Typically, one of these processes will be more constrained than the others, creating an imbalance or asymmetry (de Roos, 2018; de Roos et al., 2007; Persson & De Roos, 2013). This asymmetry between food-dependent life-history processes leads to different levels of intraspecific competition for food at different life stages (de Roos et al., 2007). When juveniles are more limited by food compared to subadults and adults, juveniles will form the bottleneck in the population. Under such conditions ("maturation controlled," de Roos & Persson, 2013), biomass enters the juvenile stage through reproduction at a faster rate than it leaves this stage via maturation (de Roos et al., 2007), resulting in relatively high juvenile biomass. The low inflow of juveniles into the next size class means that subadults and adults experience minimal competition, allowing individuals in these life stages to grow and reproduce extensively. Conversely, when subadults and adults are more limited by food compared to juveniles ("reproduction controlled," de Roos & Persson, 2013), these life stages will form the bottleneck in the population, leading to a population with relatively high biomasses of these size classes. Under these conditions, adults will reproduce little resulting in a low inflow into the juvenile size class. These juveniles are therefore almost not competing for food and can grow relatively fast. Either decreases in size-specific food availability or increases in size-specific mortality risk may change the life stage that is most limited by food and can therefore result in a change in the size distribution of the population, sometimes even resulting in an increase in biomass of some size classes (Schröder et al., 2014). Note that this phenomenon is not specific to our model but is a general outcome in population models that take juvenile-adult size structure into account (de Roos, 2018).

In our model approach, lowering the productivity of the estuary will decrease food productivity for both resources upon which the resident guild relies, whereas it only lowers food productivity of the resource for the juveniles of the marine estuarine–dependent guild. Due to the feedback between the fish population and the resource dynamics (Equation 8), juveniles of each guild may respond differently to decreases in the productivity of the juvenile food source.

To understand how changes in food productivity of the estuary affect different fish guilds, we first describe how lowering the estuary's food productivity affects resource and population dynamics in both guilds. Next, we explain the changes in somatic growth of individuals when food productivity is reduced. Additionally, we demonstrate how the size distribution of both guilds is impacted. Furthermore, we examine how changes in relative food productivities of the two resources influence our results. We conclude with a brief discussion on the impact of habitat-specific mortality on our results.

3.1 | Fish biomass decreases in all size classes of the resident guild, whereas only subadult and adult biomass decreases in the marine estuarine–dependent guild

With high estuarine resource productivity, both guilds experience the same environmental conditions ($K_{2,\text{est}}R_{2,\text{est,max}} = K_{2,\text{off}}R_{2,\text{off,max}} = 0.1$); therefore, the individual- and population dynamics for both guilds are the same. Under these conditions, population cycles occur in both guilds with a periodicity of ~17 years (Figure 1a). During these dynamics, there are always relatively many subadults and adults present (Figure 1a) that deplete the secondary adult resource (Figure 1b) to low levels. The density of this resource regularly decreases below the minimum level required for somatic growth and reproduction, resulting in starvation mortality among subadults and adults. These starvation events relax competition among the remaining individuals, resulting in periods of fast somatic growth and high reproduction. The newly produced offspring have large quantities of food available (Figure 1b) and therefore become subadults quickly. These subadults now deplete the secondary adult resource to low levels, resulting in starvation among themselves and in the remaining adults. Due to these fluctuations in resource availability, the number of offspring produced by adults varies considerably over the 17-year period, sometimes even resulting in total recruitment failure.

When the productivity of both the juvenile and adult resources is high, intraspecific competition for both guilds is primarily limited to the subadult and adult life stages due to (i) the relatively high egg mortality, which reduces competition among juveniles, and (ii) long life span of the adult life stage, which increases competition among subadults and adults. This strong intraspecific competition for food results in subadults that have trouble growing up due to food limitation, whereas adults cannot always reproduce maximally due to a lack of food. Juveniles, on the contrary, have most of the time large quantities of food available (Figure 1b) and therefore grow quickly.

When the productivity of the estuary decreases, the population dynamics of the resident guild remain qualitatively similar (Figure 1). Although the overall biomass of all size classes is reduced with lower productivity, the population dynamics still exhibit large-amplitude fluctuations with a period of ~17 years. This results in periods where the secondary adult resource decreases below the starvation threshold, whereas the juvenile resource remains relatively abundant. Consequently, there are still relatively many subadults and adults compared to juveniles, indicating that the pattern and type of fluctuations remain consistent despite the lower densities.

For the marine estuarine–dependent guild, a decrease in estuarine food productivity results in low-amplitude fluctuations in population dynamics (Figure 1). A decrease in the productivity of the estuary reduces juvenile food availability (Figure 1b). Juvenile food density

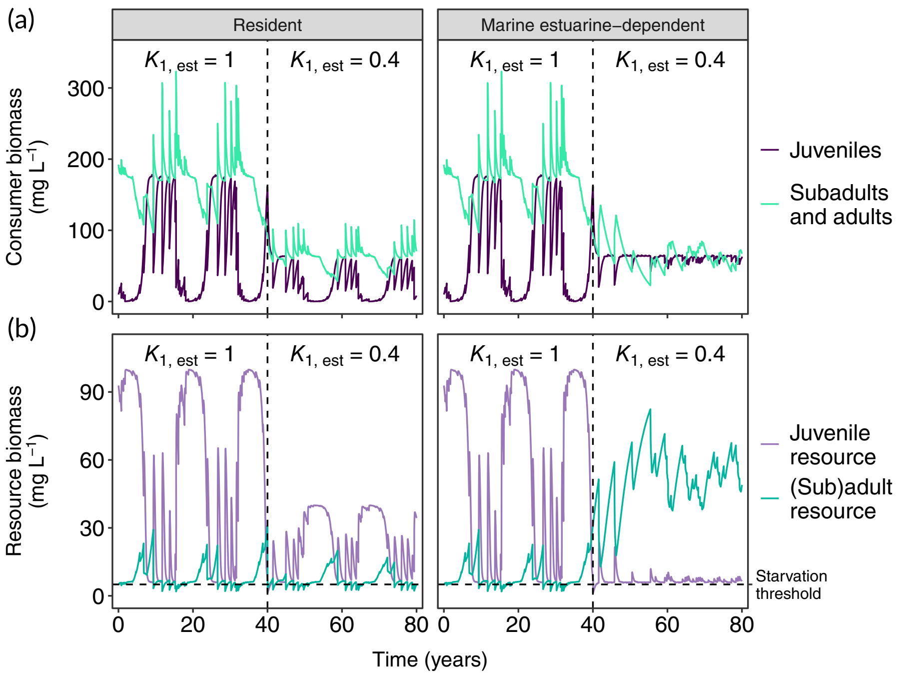

FIGURE 1 Response of the consumer population to decreased productivity of the estuarine habitat. At 40 years (dashed vertical lines) the productivity is decreased by lowering parameter $K_{1,\mathrm{est}}$. Panels on the left show the response of the resident guild, and panels on the right show the response of the marine estuarine–dependent guild. (a) The densities (in mg L^{-1}) of juveniles (dark purple) and (sub)adults (light green); (b) the densities (in mg L^{-1}) of the juvenile resource $R_{1,\mathrm{est}}$ (lilac) and the (sub)adult resource $R_{2,h}$ (dark green). The horizontal dashed lines in panel (b) indicate the minimum resource density required for somatic growth and reproduction. Below this critical resource level, individuals stop growing and reproducing and experience starvation mortality (see Equation 3). We set $R_{1,\mathrm{est,max}} = R_{2,\mathrm{est,max}} = R_{2,\mathrm{off,max}} = 0.1$; other parameters have default values as presented in Table 1.

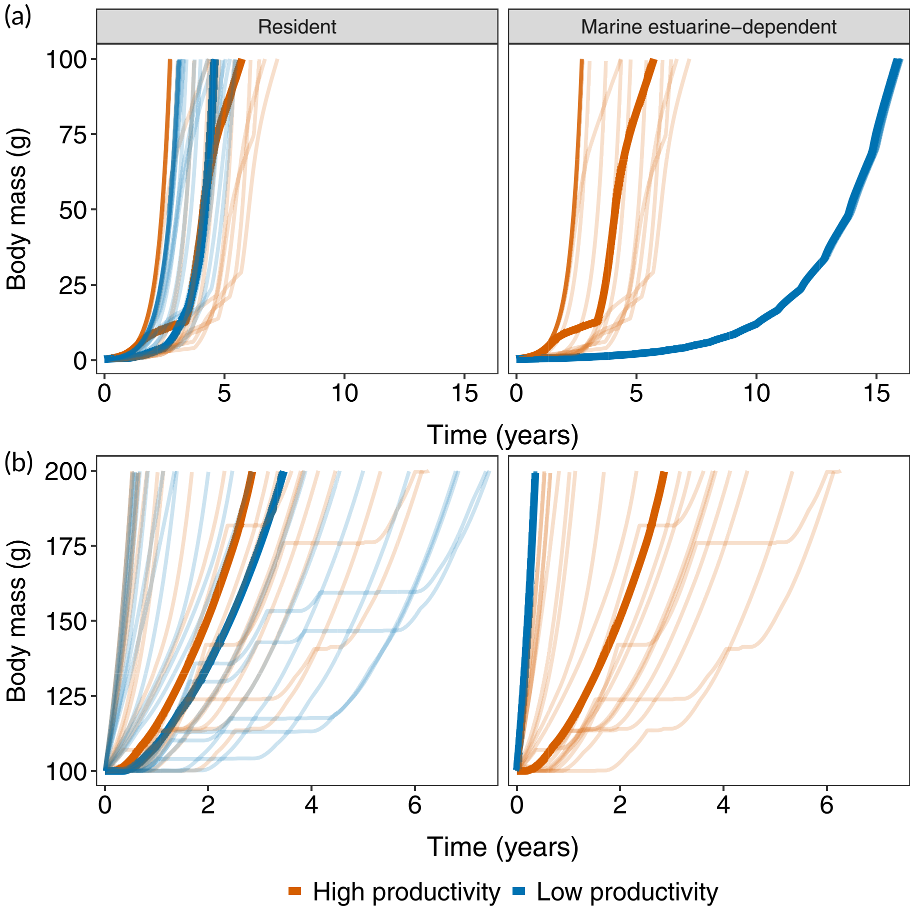

FIGURE 2 Declining productivity of the estuary hardly affects the somatic growth rate of residents, whereas it decreases the somatic growth rate of (a) juveniles and increases the somatic growth rate of (b) subadults of the marine estuarine–dependent guild. Somatic growth curves of the juvenile phase ($s < Sj$, panel a) and subadult phase ($s \geq Sj$, panel b) of the resident guild (left) and marine estuarine–dependent guild (right) for high ($K_{1,\mathrm{est}} = 1$, orange) and low ($K_{1,\mathrm{est}} = 0.4$, blue) levels of productivity in the estuary. Thin lines show the potential somatic growth trajectories throughout the time series, alongside the somatic growth curves of an average grower (thick lines). We use time on the horizontal axis instead of age to clearly show the somatic growth patterns for both juveniles and subadults, as subadults reach this stage at different ages depending on productivity. $R_{1,\mathrm{est,max}} = R_{2,\mathrm{est,max}} = R_{2,\mathrm{off,max}} = 0.1$; other parameters have default values as presented in Table 1.

becomes much lower and is close to the minimum level required for somatic growth. Competition is now primarily confined to the juvenile size class, reducing recruitment to the offshore population and resulting in lower subadult and adult biomass (Figure 1a). Due to the reduced inflow into the subadult size class, there is less competition for food among the subadult and adult size classes, resulting in an increase in the secondary adult resource (Figure 1b). The lower food supply for juveniles creates a bottleneck at this life stage, resulting in slower somatic growth of juveniles and a longer retention time. Consequently, the average juvenile biomass remains similar to that under high food productivity due to this longer retention time, but it becomes almost constant over time.

3.2 | Somatic growth rates decline in juveniles of the marine estuarine–dependent guild, not in juveniles of the resident guild

In addition to the population dynamics described earlier, we studied how the decrease in the food productivity of the estuary affects the somatic growth of individuals of both guilds (Figure 2). Due to fluctuations in the resource densities (see Figure 1b), somatic growth (which depends on food availability, Equation 2) varies within the lifetime of an individual but also across generations. Figure 2 therefore shows different somatic growth curves for different years of birth within a full period, capturing all possible growth trajectories that can be observed in the population over multiple years. In case the productivity of the estuary is high, juveniles of both guilds grow quickly (Figure 2a). Most of the time, large quantities of food are available for juveniles (Figure 1b), resulting in fast somatic growth. When a new cohort is born, the primary juvenile food source is temporarily depleted to low levels. These low food levels result in slower somatic growth of older cohorts that have not yet reached the subadult size class. The somatic growth of subadult individuals (bottom panels) varies over time but is generally slow due to the low food availability for this size class (Figure 1b).

Even though a lower productivity of the estuary decreases total food densities for the resident guild population (Figure 1b), juveniles of this guild still grow fast (Figure 2a), and somatic growth is similar as for high-productivity levels. Because both food sources are affected similarly when the productivity of the estuary decreases, all life stages are equally affected, and intraspecific competition is still primarily limited to the subadult and adult life stages. Although there is, in absolute terms, less food available, due to the lower density of fish in all size classes (Figure 1a), the fish that are there have, per capita, the same amount of food available compared to the situation at high food productivities. Due to the lower productivity, the amplitude of the resource dynamics is lower compared to a situation with a high productivity (Figure 1b). Therefore, there is less variation in the somatic growth curves among young individuals (Figure 2a).

Individuals of the marine estuarine–dependent guild grow much slower in the juvenile phase when the productivity in the estuary is low (Figure 2a). Individuals now take a long time (15 instead of 5 years) to reach the body mass necessary to migrate offshore. Decreases in the productivity of the estuary reduce the productivity of the juvenile resource, but not that of the offshore secondary adult resource. This asymmetric change in resource productivity levels alters the relative levels of competition within different size classes. The lower juvenile food density (Figure 1b) increases competition for food among juveniles, resulting in slower somatic growth of this size class (Figure 2). Because the juvenile resource is almost constant over time (Figure 1b), there is little variation among individuals in this scenario; they all grow slow (there is a single somatic growth curve for juveniles of the marine estuarine–dependent guild in this scenario). Subadults, however, now grow much faster compared to the situation where the productivity in the estuary was high. Large quantities of food are available for this life stage (Figure 1b), enhancing their somatic growth rates.

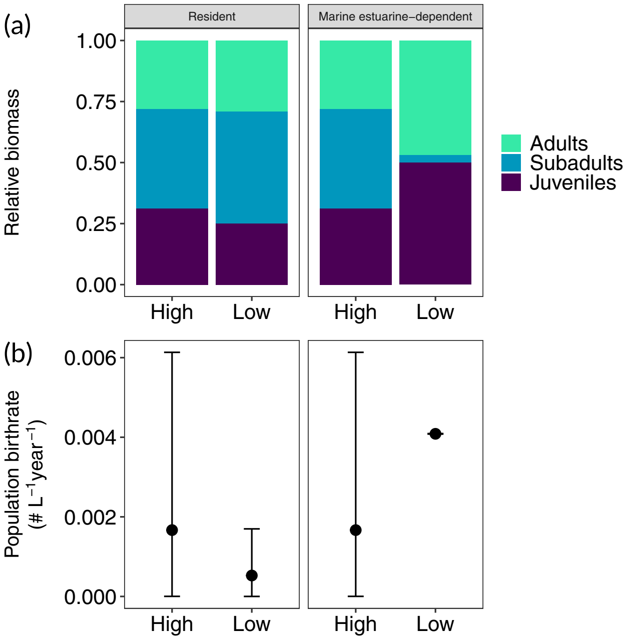

FIGURE 3 Decreasing productivity of the estuary hardly changes the size distribution of residents (top left, a), whereas it results in relatively more juveniles in the marine estuarine–dependent guild (top right, b), due to the increase in birth rate (bottom right) and the slower somatic growth rate of juveniles (Figure 2a) relative to high productivity. (a) Mean relative biomass of the three size classes for the two guilds for high ($K_{1,\text{est}} = 1$) and low ($K_{1,\text{est}} = 0.4$) productivities of the estuary area. (b) Mean, minimum, and maximum values of the population birth rate for the two guilds for high ($K_{1,\text{est}} = 1$) and low ($K_{1,\text{est}} = 0.4$) productivities of the estuary area. $R_{1,\text{est,max}} = R_{2,\text{est,max}} = R_{2,\text{off,max}} = 0.1$, whereas other parameters have default values as presented in Table 1.

3.3 | Size-frequency distribution of the marine estuarine-dependent guild shifts to dominance of juveniles

Lower estuarine productivity affects both food sources of the resident guild in the same way. Therefore, all size classes respond similarly, and the size distribution remains the same as for high productivity (Figure 3a). Due to the lower food availability (Figure 1b), the population birth rate decreases (Figure 3b), which decreases the biomass of all size classes (Figure 1a).

The effect of lowering productivity on the marine estuarine–dependent guild is vastly different. A lower estuarine productivity

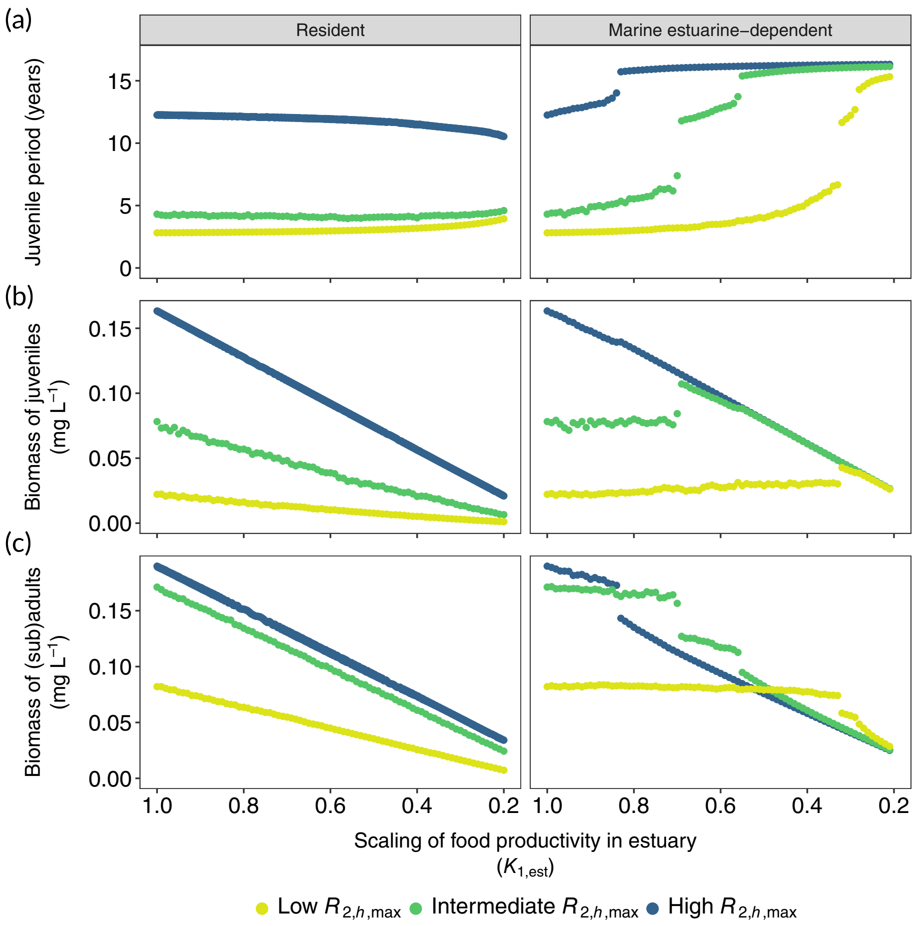

FIGURE 4 Equilibrium dynamics of both the resident and marine estuarine–dependent guilds are qualitatively equivalent for different levels of the relative food productivity of the juvenile versus the food productivity of the adult resource. Because the somatic growth rate of juveniles varies over the lifetime of individuals, we plot in panel (a) the juvenile period (in years), which is the time taken by juveniles to mature and is inversely proportional to the average somatic growth rates experienced by individuals. For decreasing productivities in the estuary, somatic growth of the resident guild is hardly affected because per-capita food availability does not change (a, left), whereas somatic growth of juveniles of the marine estuarine–dependent guild decreases, resulting in a longer juvenile period (a, right). The biomass of all size classes of the resident guild decreases for lower productivity (b, left; and c, left), whereas for the marine estuarine–dependent guild the (sub)adults decrease (or stay constant) and the juveniles can even increase in biomass for lower food productivity (b, right). To change the relative amount of food productivity of the two resources, we varied $R_{2,h,\max}$ (0.05 [yellow], 0.1 [green], or 0.15 [dark blue] mg L^{-1}), keeping $R_{1,\text{est},\max}$ constant at 0.1 mg L^{-1}. All other parameters have default values as presented in Table 1.

affects the food source of only the juveniles. Due to the lower food availability, juveniles grow much slower than with high productivity (Figure 2a), which results in a longer period before migration to the offshore habitat. Because individuals take a longer time to mature, fewer individuals survive the juvenile period, resulting in lower recruitment to the subadult population. The biomass of the subadults and adults therefore decreases for lower productivities of the estuarine habitat (Figure 1a). Competition in these size classes is then decreased, resulting in faster somatic growth (Figure 2b) and high reproduction (Figure 3b). The increased birth rate in combination with the longer juvenile period results in a size distribution where juveniles become the dominant size class in the marine estuarine–dependent guild population (Figure 3a). For this guild, the relative biomass of subadults decreases for lower productivity of the estuary area (Figure 3a). This is caused by the fast somatic growth in this size class. Subadults mature quickly into the adult size class where they start to reproduce.

3.4 | The relative levels of food productivity for juveniles and (sub)adults do not affect the results qualitatively

In the aforementioned results, we discussed a situation where both resources initially had an equal productivity, resulting in a situation where competition was strongest among the (sub)adult size classes. Here, we show that our results are qualitatively similar in case we start with a situation where the productivity of the secondary adult resource is initially lower (yellow lines in Figure 4) or higher (dark-blue lines in Figure 4) compared to the productivity of the juvenile resource. In the following section, we describe how decreasing the productivity of the estuary (by decreasing parameter $K_{1,\text{est}}$) affects the average juvenile period (Figure 4a), and the average densities of juveniles (Figure 4b) and (sub)adults (Figure 4c). The juvenile period is the time taken by individuals to recruit to the subadult size class, which is inversely proportional to somatic growth rate.

For the resident guild, a decrease in the productivity of the estuary always results in lower biomass of juveniles and (sub)adults while the juvenile period remains relatively constant (Figure 4a). This finding is independent of the value of $R_{2,\text{est,max}}$. The reason for this finding is that for the resident guild, both the juvenile and the adult resources are affected by reduced productivity of the estuary. Therefore, changes in estuary productivity will not change which size class is most limited by food. Lowering the productivity will, in this situation, decrease the biomass of all size classes but not affect somatic growth rates or the size structure of the population.

Independent of the productivity of the offshore resource, $R_{2,\text{off}}$, the juvenile period of the marine estuarine–dependent guild will increase with decreasing estuary productivity (Figure 4a). This response is most pronounced for intermediate values of the offshore resource productivity, $R_{2,\text{off}}$. The reason the response is less extreme in case the productivity of the offshore adult resource, $R_{2,\text{off}}$, is low is that, in this scenario, a small quantity of food is available for subadults and adults resulting in strong competition for food. Consequently, there is little somatic growth and reproduction in these size classes. Due to the low birth rate, there are only a few juveniles in the population. Therefore, these juveniles experience little competition, resulting in fast somatic growth and a short juvenile period (Figure 4a). A reduction in the productivity of the estuarine habitat initially has a negligible impact on the population, as the decline in food availability for juveniles does not result in an increase in competition for food. Only when the productivity of the estuarine habitat is very low will juveniles grow slowly, which initially results in an increase in the biomass of this size class (Figure 4b) due to the longer juvenile period in combination with the increase in the reproduction rate of adults (not shown).

The increase in the juvenile period is relatively small when the productivity of the offshore adult resource, $R_{2,\text{off}}$, is high (Figure 4a). In this case, juveniles have little food available, whereas (sub)adults have plenty of food, resulting in a strong competitive bottleneck early in life. Juvenile somatic growth is in this situation therefore already extremely slow. Decreasing the productivity of the estuary will initially increase the juvenile period slightly (Figure 4a), but for lower values of the parameter $K_{1,\text{est}}$, the effect is minimal and the response is mostly observed in the decrease in juvenile biomass (Figure 4b) and (sub)adults (Figure 4c). Note that in this situation, the biomass of all size classes decreases considerably with lower productivity in the estuary (Figure 4).

3.5 | The results are robust under conditions of high mortality in either the estuary or the offshore habitat

Appendix A shows that for high mortality in the estuary (Figure A1) or in the offshore habitat (marine estuarine–dependent only, Figure A2), the results remain qualitatively similar. Mortality in the estuary area affects all life stages of the resident guild, whereas only juveniles ($s < Sj$) of the marine estuarine–dependent guild are affected. For high mortality rates, there are therefore fewer juvenile individuals in the population of the marine estuarine–dependent guild (Figure A1b). Therefore, these individuals experience low competition for food, and a decrease in the productivity of the estuary initially almost does not affect them. Only for very low productivity values does competition become intense among juveniles, resulting in a longer juvenile period (Figure A1a).

4 | DISCUSSION

This study showed how lowering food availability in the estuary impacts the demographic rates and population dynamics of resident and marine estuarine–dependent fish species, which use these habitats at different life stages. Our results showed different responses of the two functional guilds studied. With decreasing estuarine productivity, the estuarine guild, although decreasing in biomass, did not show changes in individual somatic growth rate or size structure of the population. All life stages within this guild were equally affected by declines in estuarine food productivity. Consequently, the relative food availability between size classes remained unchanged and thereby also the strength of intraspecific competition the different size classes experienced. The decrease in food productivity resulted in a lower population birth rate of the resident guild, leading to a smaller overall population size. On a per-capita basis, however, there was little change in food availability, resulting in minimal changes in individual somatic growth rates. For marine estuarine–dependent species, on the contrary, only the juvenile resource was affected by reductions in estuarine food productivity. Reduced food availability for small individuals resulted in slower somatic growth rates early in life and a change in the size structure of the population. Reductions in food productivity of the estuary may therefore change the dynamics of marine estuarine–dependent guild from a situation where the population is mostly limited late in life, in the offshore habitat ("reproduction controlled," de Roos & Persson, 2013), to a situation where the population is mostly limited early in life, within the coastal, estuarine zone ("development controlled," de Roos & Persson, 2013).

The majority of studies investigating the effects of habitat degradation on fish populations focus on habitat-specific biomass densities (Vasconcelos et al., 2014), as it is often assumed that a relatively high density of a species equates to high habitat value (Beck et al., 2001). We show that focusing on biomass alone may give a false impression of habitat quality for the marine estuarine–dependent guild. Due to a change in the size distribution of the population, decreasing food productivity in the estuary does not necessarily translate into lower local biomass densities. Under some conditions, we even found an increase in the average biomass density of juveniles in the marine estuarine–dependent guild with decreasing food productivities. This increase in biomass occurs as a result of a change in the size distribution of the population. As food productivity in the estuary decreases, recruitment to the larger size classes decreases as well. This results in a lower biomass of large individuals and therefore a higher per-capita somatic growth rate and reproduction rate of these larger fish. The higher reproductive rate results in a higher influx of offspring into the estuarine habitat, leading to an increase in local biomass. This finding is consistent with the study by Schreiber and Rudolf (2008), who also showed in a stage-structured consumer-resource model that a decrease in the productivity of the juvenile habitat can lead to a regime shift where the abundance of juveniles increases.

Individual somatic fish growth is another common method used to study habitat quality (Vasconcelos et al., 2014), although this metric may lead to incorrect conclusions if underlying factors, such as size-selective mortality, are unknown (Le Pape et al., 2003; Le Pape & Bonhommeau, 2015; Searcy et al., 2007). Our study also showed that somatic growth rates should be interpreted with caution. Although we found that somatic growth rates declined with deteriorating food conditions for juveniles of the marine estuarine–dependent guild, high mortality in either the estuary or adult habitat increased somatic growth rates due to reduced density dependence (see Appendix A). In addition, somatic growth rates of individuals of the resident guild showed no clear response to reductions in food productivity of the estuary, as per-capita food availability remained unchanged. This model result is consistent with empirical findings for resident fish species in the western Wadden Sea, a coastal region bordering the Netherlands and southern North Sea. Despite lower nutrient levels, recent somatic growth rates of resident fish exceed historical somatic growth rates, probably influenced by higher temperatures, and show no response to de-eutrophication (Bolle et al., 2021).

Resident fish are often used in studies on the effects of environmental change in estuaries because their responses at the juvenile and adult stages are assumed to reflect local conditions (e.g., Bolle et al., 2021; Harrison & Kelly, 2013; Teichert et al., 2017; Tulp et al., 2017). However, our study shows that observations in the resident guild do not necessarily lead to a similar response in the marine estuarine–dependent guild. To gain a comprehensive understanding of how estuarine habitat degradation affects fish dynamics and the ecosystem, it is necessary to explicitly include the marine estuarine–dependent guild. Although studying this guild can improve our understanding of the effects of estuarine change, caution must be exercised in interpretation, as changes outside the juvenile habitat will also affect the response of this guild. For example, increased mortality at sea may mitigate the effect of reduced food productivity on early-life somatic growth rates (see Figure A2), leading to the erroneous conclusion that estuary quality is high when it is not.

Our study focused on food productivity as a key factor influencing estuarine habitat quality and its impact on fish populations. This choice was based on the fact that many energetically expensive processes, such as somatic growth and reproduction, are directly dependent on food availability. Although we acknowledge that anthropogenic activities can have various effects beyond reducing food productivity—such as higher nutrient input, contaminant loads, increased temperatures, or reduced habitat complexity and availability—many of these secondary effects are likely to influence food availability for fish as well. For example, higher nutrient input can alter the composition of the benthic community (Philippart et al., 2007), affecting benthic feeders. Increasing temperatures can lead to the disappearance of certain prey species, impacting food availability for piscivores. To ensure the robustness of our findings, we also examined the effects of estuarine habitat loss in Appendix B. Our results showed similar patterns to those we present in the main text, reinforcing the consistency of our conclusions under a scenario of direct habitat loss. Future studies should build on this work by exploring the effects of compounding stressors, such as reduced food availability coupled with pollution, warming, and hypoxia.

Our study suggests that the biomass of the resident guild declines with reductions in food productivity of the estuary, whereas populations of the marine estuarine–dependent guild may not always decline locally in the estuary (Figure 4; Figures A1 and A2). This finding contrasts with observations in the Wadden Sea, a heavily anthropogenically modified coastal region along the North Sea coast of Denmark, Germany, and the Netherlands (Lotze et al., 2005). The Wadden Sea supports more than 140 different fish species, including fish from the estuarine resident and marine estuarine–dependent guilds. Total fish biomass in the Dutch Wadden Sea has declined sharply since the 1980s (Tulp et al., 2008; van der Veer et al., 2015), with the most dramatic declines observed for fish belonging to the marine estuarine–dependent guild (Tulp et al., 2017). Although our model analysis showed that reductions in food productivity in the estuary will also affect populations of this guild, we predict a stronger and earlier response in population biomass of the resident guild. This discrepancy between model results and observations may be caused by factors outside the Wadden Sea that affect marine estuarine–dependent populations, such as higher mortality in the adult habitat or the loss of connectivity to the estuary area (Sterl et al., n.d. [personal communication]). Here, we outline several other possible reasons for the observed disparities between observations and model predictions. Although we discuss these mainly with regard to observations in the Dutch Wadden Sea, these insights have broader implications for understanding the dynamics of coastal ecosystems undergoing habitat degradation.

In our modeling approach, we assumed that the guilds differ in their use of the estuaries, while keeping the individual-level parameters of both guilds the same. Although this approach makes it possible to compare the responses of each guild, it is a simplification of reality. Different guilds are often associated with particular life histories. For example, many estuarine residents produce relatively large demersal eggs to prevent seaward flushing, whereas marine estuarine–dependent species primarily produce many small pelagic eggs adapted for dispersal to nursery grounds (Franco et al., 2008; Teichert et al., 2017). Furthermore, marine estuarine–dependent species are more frequently associated with a large body size and longer life spans compared to estuarine residents (Teichert et al., 2017). Life-history traits, such as maximum body size and parental care, strongly impact population dynamics (Savage et al., 2004) and therefore the guild-specific responses to environmental change. In addition to a decline in total biomass, mean individual biomass has decreased significantly in the Dutch Wadden Sea (van der Veer et al., 2015). This decline may indicate that larger-bodied species are more vulnerable to environmental change, possibly affecting populations of marine estuarine–dependent species more than estuarine residents. An interesting next step is to investigate how guild-specific responses to environmental change are influenced by life-history traits such as maximum body mass, parental care, and generation time.

Although our study improves our understanding of guild-specific responses to environmental change, it does not provide insight into how specific species will respond. Our conceptual study examines the impact of general factors such as food and mortality on population dynamics, but species differ in their food and habitat requirements, thermal tolerances, susceptibility to predation, vulnerability to fishing pressure, and so on. For example, increasing water temperatures in the Wadden Sea make this habitat less suitable for cold-affinity species such as *P. platessa*, dab *Limanda limanda* L., and *Z. viviparus* (Pörtner & Knust, 2007; van der Veer et al., 2022). Conversely, warm-affinity species, such as *D. labrax*, benefit from the temperature increase, resulting in increased abundance in the Wadden Sea (Cardoso et al., 2015). Changes in productivity, for example, due to eutrophication, can influence the composition of the prey community (Philippart et al., 2007), which will affect species in different ways. In the Wadden Sea, the trophic niche space of estuarine-dependent fish species is smaller than that of residents (Poiesz et al., 2021). It is possible that changes in the prey community due to changes in eutrophication levels have affected the marine estuarine–dependent guild more than the resident guild. To understand how a particular species responds to environmental change, a species-specific approach is essential, where knowledge of habitat and food requirements is crucial.

Finally, each modeling framework needs to find a balance between generality and specificity. Here, we choose a generic framework that does not represent a specific species. Although some assumptions are clearly not realistic for most fish species, the benefit of this generic framework is its relative simplicity, making it easier to understand the underlying mechanisms that lead to our results. Note, however, that due to the relatively simple structure of the model, the results of our analysis show how lowering the productivity of the estuary changes individual- and population-level responses of the two guilds and should not be interpreted as quantitative findings. To test the robustness of our results, we also analysed a detailed, more realistic, species-specific model in Appendix C. This model distinguishes between the different types of tissue individuals have and takes into account that many fish species have more than one ontogenetic diet shift. Despite large differences in model structure, our results remain qualitatively similar.

Some other model assumptions could be addressed in future research. For example, we assumed that declines in resource productivity affected all life stages of the resident equally. This is clearly not realistic as many estuarine residents change their diet during ontogeny (Elliott et al., 2007). It is likely that changes in primary production will affect higher trophic levels differently (e.g., Philippart et al., 2007), thereby altering the relative food availability between life stages. In addition, although we included habitat-specific mortality in our analysis, we did not include size-specific mortality. Mortality can be highly variable among life stages, for example, due to size-specific predation by seal (Aarts et al., 2019) or shrimp (van der Veer et al., 1991). Finally, for both guilds we assumed that individuals move to another resource (and habitat in the case of the marine estuarine–dependent guild) at a fixed body size. However, fish species show high plasticity in the size and age of such ontogenetic habitat shifts. For example, *P. platessa* now migrates offshore at a much smaller size due to declining growth conditions in the Wadden Sea. Such plastic responses to changing conditions will likely affect the responses to environmental change (see, e.g., Van De Wolfshaar et al., 2015) and should be taken into account in future research.

In conclusion, our study highlights the importance of considering not only biomass but also size distribution, survival, and somatic growth rates to gain an in-depth understanding of how stressors affect fish populations. Our results challenge the assumption that responses observed in the resident guild translate into parallel responses in marine estuarine–dependent guild. The differences we found highlight the complexity of estuarine ecosystems and emphasize the importance of considering different life stages and functional guilds. In a rapidly changing world where systems are under high anthropogenic pressure, understanding the diversity of responses of estuarine fishes is crucial for effective conservation and management strategies.

AUTHOR CONTRIBUTIONS

Hanna ten Brink: conceptualization, analysis, and writing (original draft and editing). **Anieke van Leeuwen:** conceptualization and writing (editing).

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DATA AVAILABILITY STATEMENT

All model-specific files and scripts for running the model are available online at https://bitbucket.org/HannatB/compareguilds.

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APPENDIX A: EFFECTS OF HABITAT-SPECIFIC MORTALITY A

Here we show that increased mortality in either the estuary or offshore habitat does not qualitatively change the model results we present in the main text. We repeated the analysis of reduced food productivity, here including three different levels of mortality (Figure A1). Mortality in the estuarine habitat affects all individuals of the resident guild, whereas it affects only juveniles of the marine estuarine–dependent guild. This results in different responses to mortality of the two guilds.

Independent of the level of mortality, the biomass of all size classes decreases with decreasing productivity levels in the resident guild. As before, somatic growth of individuals is hardly affected by decreasing productivity levels, resulting in little change in the juvenile period (Figure A1a). Because all size classes are equally affected by mortality, mortality does not change which life stages experience the strongest competition for food and lowers only total biomass.

In the marine estuarine–dependent guild, we find, independent of the mortality level, similar responses of the population to decreasing levels of food productivity in the estuary. As before, the juvenile period increases, and the biomass of juveniles sometimes increases, whereas the biomass of (sub)adults decreases with decreasing productivity levels. The strength of the response, however, is strongly affected by mortality in the estuary. For high mortality rates, there are fewer juvenile individuals in the population of the marine estuarine–dependent guild (Figure A1b). Therefore, these remaining individuals experience low competition for food and have a short juvenile period. A decrease in estuary productivity initially has therefore little effect on juveniles, because competition is mostly among (sub)adults. Only at very low productivities does competition among juveniles intensify, resulting in a longer juvenile period (Figure A1a). Although the estuary mortality leads to lower juvenile biomass (Figure A1b), it hardly affects the biomass of (sub)adults, as long as the productivity of the estuary is high.

Figure A2 shows the effect of increased mortality in the offshore area. As residents never move offshore, we only show results for the marine estuarine–dependent guild. Figure A2a shows that for all mortality rates the juvenile period increases as the productivity of the estuary decreases. This longer juvenile period leads to a decrease in (sub)adult biomass due to less recruitment in the subadult size class. Although the biomass of juveniles will eventually decrease at low productivities, the biomass of this size class may initially increase due to the slower somatic growth rate.

The response of marine estuarine–dependent species to offshore mortality is not linear. Although the biomass of both size classes decreases considerably for high mortality rates (dark-blue lines in Figure A2), the response is different at intermediate mortality rates (green lines in Figure A2). When the productivity of the estuarine

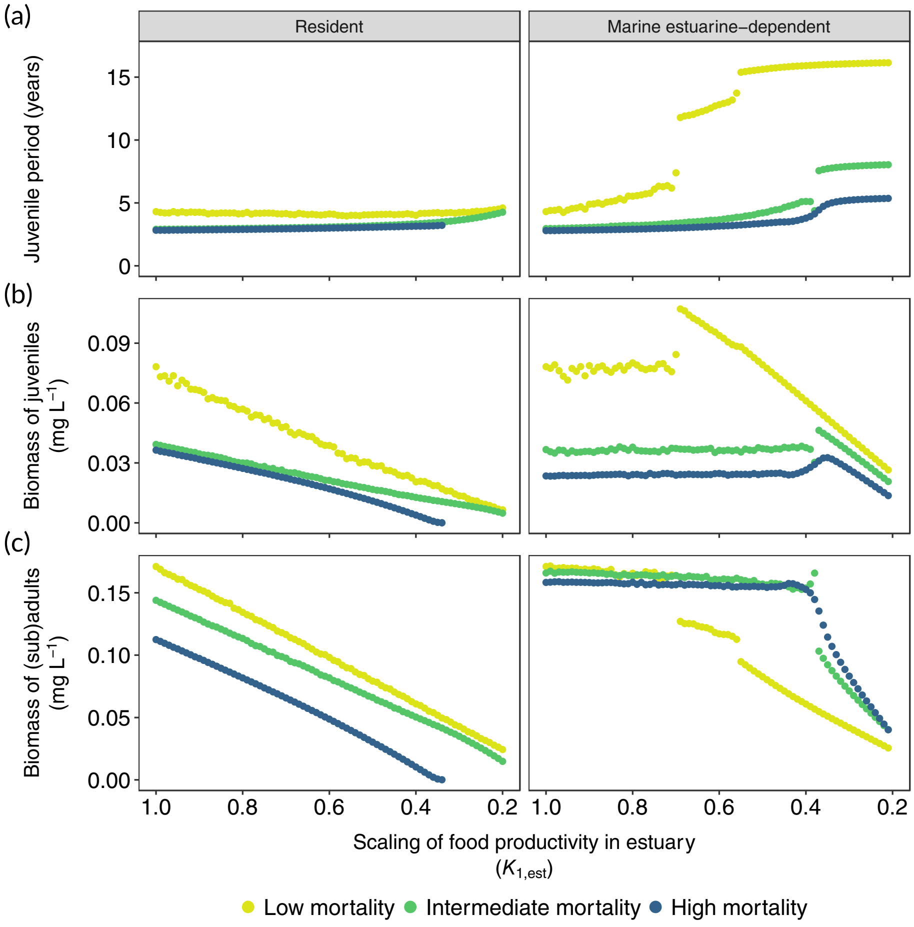

FIGURE A1 Mortality in the estuarine habitat does not affect the results qualitatively. For decreasing productivities in the estuary, growth of the resident guild is hardly affected, whereas growth of juveniles in the marine estuarine–dependent guild decreases, resulting in a longer juvenile period (a, right panel). The biomass of all size classes of the resident guild decreases for lower productivity (b and c, left panels), and for the marine estuarine–dependent guild, the (sub)adults decrease (or stay constant), whereas the juveniles can even increase in biomass for lower food productivity (b, right panel). Note that mortality in the estuarine habitat affects all size classes of the resident guild, whereas it affects only juveniles of the marine estuarine–dependent guild. The mortality rate in the estuary equals 0.001 (yellow), 0.002 (green), or 0.003 (blue) per day. We set $R_{1,\mathrm{est,max}} = R_{2,\mathrm{est,max}} = R_{2,\mathrm{off,max}} = 0.1$; other parameters have default values as presented in Table 1.

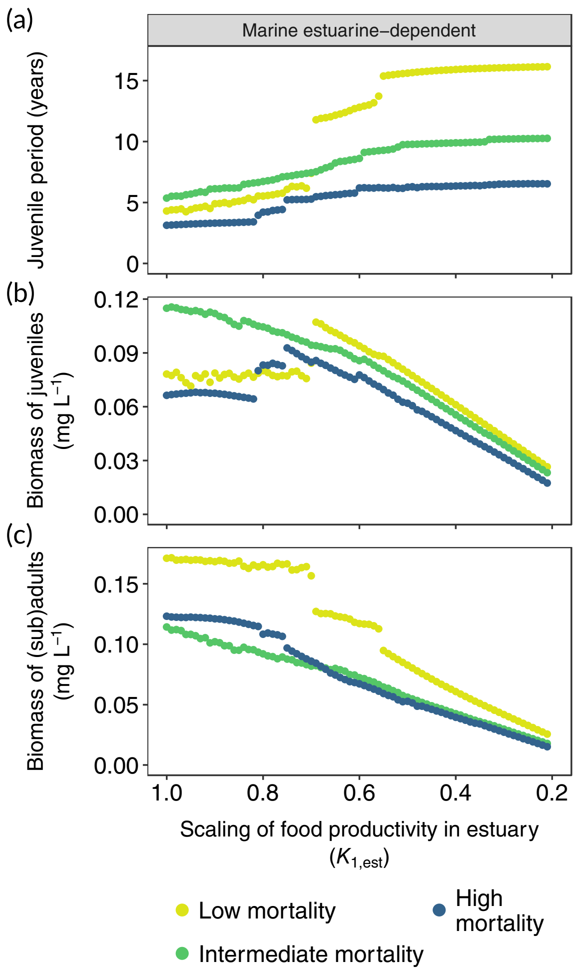

FIGURE A2 Mortality in the offshore habitat does not affect the results qualitatively. Because residents never move offshore, we show results only for the marine estuarine–dependent guild. For this guild juvenile period increases with lower productivity (panel a). The (sub) adults decrease (or stay constant) (panel c), whereas the juveniles can even increase in biomass for lower food productivity (panel b). The mortality rate (background plus habitat specific) in the adult habitat equals 0.001 (yellow), 0.003 (green), or 0.005 (blue) per day. We set $R_{1,\mathrm{est,max}} = R_{2,\mathrm{est,max}} = R_{2,\mathrm{off,max}} = 0.1$; other parameters have default values as presented in Table 1.

habitat is high, the population is mostly regulated in the (sub)adult size classes. Increasing mortality of this size class results in less competition, which translates to a higher per-capita birth rate of the adults. At intermediate mortality rates, this higher per-capita birth rate compensates for the loss of biomass due to mortality. Therefore, mortality leads to an increase in the juvenile size class, a phenomenon known as biomass overcompensation (De Roos et al., 2007).

APPENDIX B: EFFECTS OF DECREASING HABITAT AVAILABILITY B

In main text, we study the effects of reduced food productivity in the estuary. However, the quality of the estuary could also change due to reduced habitat availability, for example, due to dredging, salt- or gas extraction, or construction activities. Here we show that the model results remain qualitatively equivalent to the effects of reduced food productivity when the habitat availability of the estuary decreases (compare Figure 4 with Figure B1).

In the main text, our model is formulated in densities per liter. To study the effect of changing habitat availability, we need to formulate the model in densities per habitat. To do this, we reformulate the equations for the resource dynamics (Equation 8) as follows:

$$\frac{dR_{1,\mathrm{est}}}{d\tau} = \delta\left(K_{1,\mathrm{est}} R_{1,\mathrm{est,max}} - R_{1,\mathrm{est}}\right) - \frac{1}{V_{\mathrm{est}}} \frac{aR_{1,\mathrm{est}}}{1 + ahR_{1,\mathrm{est}}} \sum_{k|s_k < Sj} c_k s_k,$$

$$\frac{dR_{2,h}}{d\tau} = \delta\left(K_{2,h} R_{2,h,\mathrm{max}} - R_{2,h}\right) - \frac{1}{V_h} \frac{aR_{2,h}}{1 + ahR_{2,h}} \sum_{k|s_k \geq Sj} c_k s_k. \qquad \text{(B1)}$$

In these equations, the intake of the consumers is scaled by the volume of the habitat in which they forage. For residents, who remain in the same habitat, we assume $V_h = V_{\mathrm{est}}$. Individuals in the marine estuarine–dependent guild, on the contrary, migrate offshore and therefore $V_h = V_{\mathrm{off}}$. To study the effect of habitat loss, we set $V_{\mathrm{off}} = 1000\,\mathrm{m}^3$ and then decrease habitat availability in the estuary by decreasing parameter V_{est}. Note that the dynamics of the guilds are determined by the ratio of V_{off} to V_{est}. The absolute size of the two habitats does not qualitatively affect the results because it is the relative availability of the two habitats that drives competition and resource dynamics.

Figure B1 shows the results of reduced habitat availability. As before, we find that the juvenile period of marine estuarine–dependent individuals increases with decreasing habitat availability, whereas the juvenile period of resident juveniles is unaffected. Whereas the biomass of both guilds will eventually decrease with habitat loss, the densities of juveniles from the marine estuarine–dependent guild initially increase with decreasing habitat availability at low offshore resource productivities.

APPENDIX C: GENERALITY OF RESULTS C

In the main text, we demonstrated using a basic size-structured consumer-resource model that responses to estuarine habitat degradation differ notably between marine estuarine–dependent species and residents. Despite a decrease in total biomass with declining habitat quality for both guilds, the somatic growth rate of the resident guild remains largely unaffected at the individual level, whereas that of marine estuarine–dependent juveniles is reduced early in life. Appendix C shows that these results are robust to a structurally different model formulation (with higher physiological resolution) and different parameter choices.

We study the dynamics of both guilds using a detailed and more realistic species-specific model based on the interaction between a size-structured predator, cod *G. morhua* L, feeding on three different resources: zooplankton, benthos, and prey fish. The model

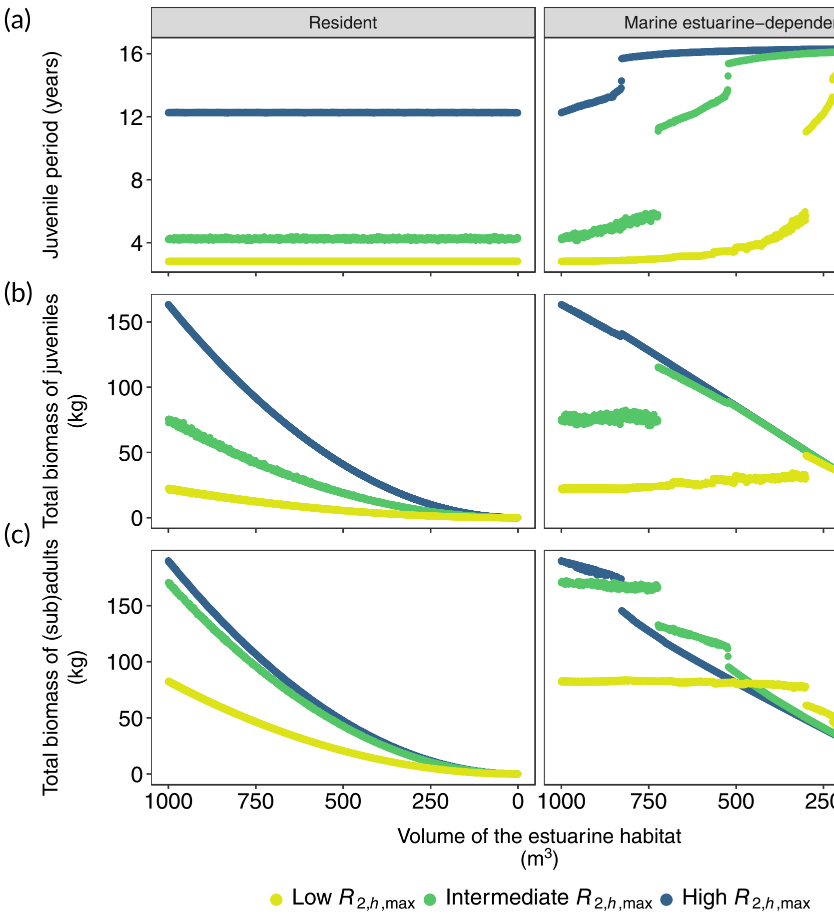

FIGURE B1 Juvenile period (panel a) and stage-specific biomasses (juveniles—b; adults—c) in the stable attractor dynamics as a function of decreasing estuarine habitat. For decreasing habitat availability of the estuary, growth of the resident guild is hardly affected (a, left), whereas growth of juveniles of the marine estuarine–dependent guild decreases, resulting in a longer juvenile period (a, right). The biomass of all size classes of the resident guild decreases for lower habitat availability (b, left; and c, left), whereas for the marine estuarine–dependent guild, the (sub)adults decrease (or stay constant) and the juveniles increase in biomass for lower habitat availability (b, right). The relative amount of food productivity of the two resources does not affect the results qualitatively. To change the relative amount of food productivity of the two resources, we varied $R_{2,h,\max}$ (0.05 [yellow], 0.1 [green], or 0.15 [dark blue] mg L^{-1}), keeping $R_{1,\text{est},\max}$ constant at a value of 0.1 mg L^{-1}. The volume of the offshore habitat is set at $V_{\text{off}} = 1000\,\text{m}^3$. All other parameters have default values as presented in Table 1.

formulation and parameterization are generally equivalent to those of van Leeuwen et al. (2013) (also see Persson et al., 1998, for the original definition of consumer physiology in this framework). In contrast to van Leeuwen et al. (2013), we ignore the size structure of the prey fish. The full model description is provided at the end of Appendix C. The main model components and the differences from the basic model in the main text are summarized here.

In contrast to the basic model, individuals are now characterized by both structural mass (bones and organs) and energy reserves (fat and gonads). The structural mass is directly linked to the length of an individual and represents essential body mass that cannot be lost through starvation. Energy reserves represent the nonessential part of the body that can be used and replenished. When maintenance costs exceed the energy gained from feeding, individuals will use these reserves to cover their maintenance costs. Starvation mortality occurs only when individuals are in poor condition, determined by the ratio of reserves to structural mass. In addition to background and starvation mortality, this model includes a size-dependent mortality that decreases exponentially with increasing body mass. Mortality during the egg and larval stages is equal to the mortality of a newborn individual.

Eggs hatch after 15 days, and larvae begin exogenous feeding at 22 days old. Initially, individuals are obligatory zooplanktivores until they reach a length of 5 cm, after which they gradually shift to the demersal zone and start benthic feeding. This diet shift is modeled as a continuous transition, following a sigmoid-shaped function (Table C2, Equation C28). At a length of 15 cm, individuals stop foraging on zooplankton entirely and feed only on benthos. At a length of 20 cm, individuals undergo a second diet shift to exclusively feed on fish (Table C2, Equation C3). In contrast to van Leeuwen et al. (2013), we model this diet shift as an abrupt transition to also allow for a habitat shift to the offshore habitat for the marine estuarine–dependent guild. This habitat shift may incur migration costs, which we model as reduced survival during the transition and additional energetic costs in the form of fat reserve loss. We study the dynamics of the marine estuarine–dependent guild in both the absence and presence of these migration costs. When fish reach a length of 30 cm, they begin to allocate energy to the buildup of gonadal mass. In this model, we assume that growth is indeterminate, implying that adults will continue to invest energy into growth (Table C2, Equations C15 and C16). We refer to individuals feeding on zooplankton and benthos as juveniles (l < 20 cm), immature individuals that feed on fish as subadults ($20 \leq l < 30$ cm), and mature individuals ($l \geq 30$ cm) as adults. We make this distinction of three size classes to facilitate the comparison with the basic model in the main text.

Because we want to compare the response of two guilds (with stereotypical life histories), the marine estuarine–dependent and resident guilds differ in the habitat they occupy as subadults and adults

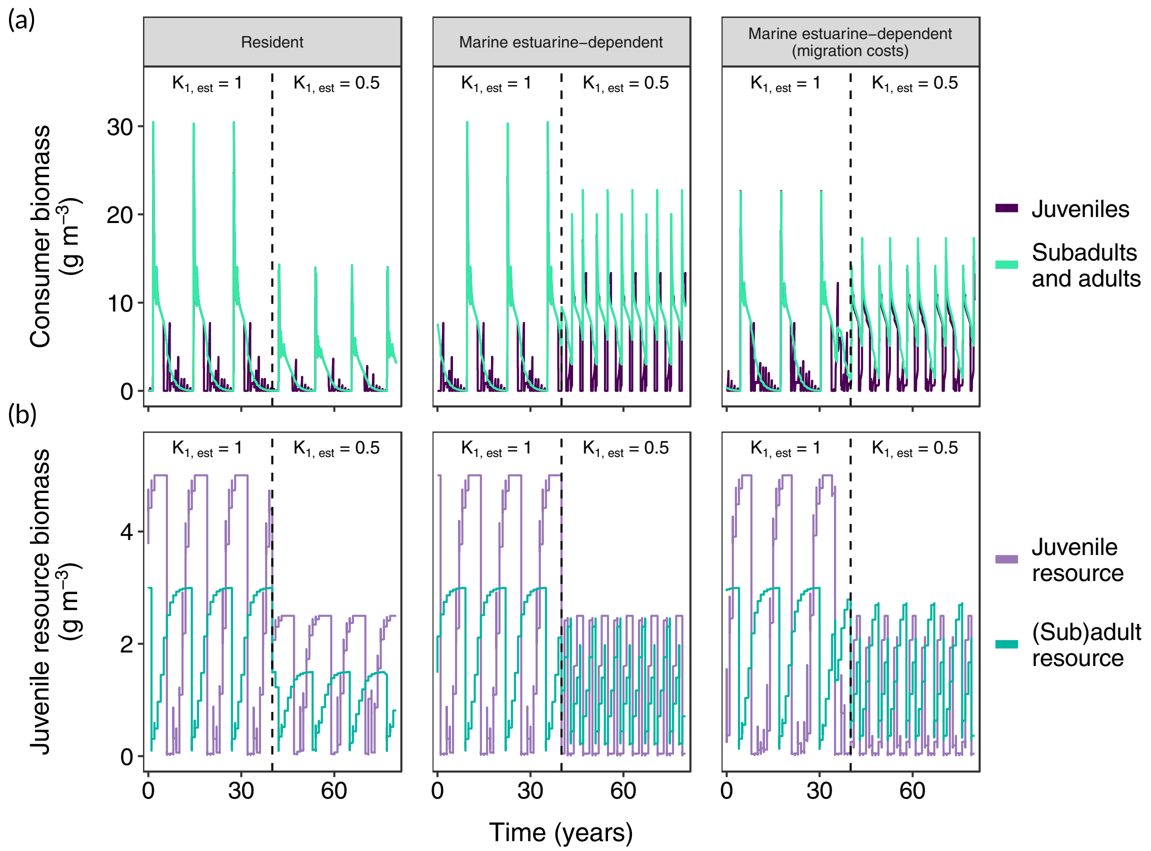

FIGURE C1 Response of the consumer population to decreased productivity of the estuarine habitat. At 40 years (dashed vertical lines) the productivity is decreased by lowering parameter $K_{1,\mathrm{est}}$. Panels on the left show the response of the resident guild, and other panels show the response of the marine estuarine–dependent guild in the absence (middle) and presence (right) of migration costs. Top panels (a) show the densities (in g m^{-3}) of juveniles (dark purple) and (sub)adults (light green), and bottom panels (b) show the densities (in g m^{-3}) of the juvenile resource $R_{z,\mathrm{est}}$ (lilac) and the (sub)adult resource $R_{f,h}$ (dark green). For clarity, we have not plotted the density of the benthic resource ($R_{b,\mathrm{est}}$). Migration costs in the right panel equal $\mu_{\mathrm{mig}} = 0.2$ and $c_{\mathrm{mig}} = 0.3$. All other parameters have default values as presented in Table C3.

only. All other factors in the model, including parameter values and general model structure, are identical between the two guilds.

C.1. | Results

When the productivity in the estuary is high, we observe population cycles of ~13 years in both guilds. There is plenty of food for small juveniles (Figure C1b), resulting in fast growth of this size class. After ~2 years, these individuals transition to the subadult stage (Figure C2a). These recruitment events lead to peaks in the (sub)adult population, consequently causing dips in resource densities (Figure C1b). As a result, the growth of subadults is relatively slow, taking an additional 3 years to reach maturation size (30 cm).

Due to fluctuating food densities (Figure C1b), (sub)adults often face periods of low food availability where they must rely on their fat reserves. This leads to high variability in the condition of the (sub) adults (Figure C3c), and their condition sometimes drops below the minimum required for survival, resulting in starvation. Note that because the condition of adults varies much due to reproduction, we do not show adult condition as this variable is too complex to interpret straightforwardly.

The results for marine estuarine–dependent species paying migration costs are comparable to the situation where no costs are paid. Due to mortality during migration, the population of (sub)adults is slightly lower, resulting in less competition for food and slightly faster growth in the subadult size class (now taking an average of 2.75 years instead of 2.9 years to reach maturity).

When the productivity of the estuary is low, we continue to observe population cycles of ~13 years for the resident population. Due to the lower productivity, the birth rate of the population is reduced (Figure C3b), resulting in a smaller population size (Figures C1a and C4). Individual growth during the juvenile stage is minimally affected (Figures C2a and C4a), whereas growth of the subadults is somewhat slower (Figure C2b). The size distribution of the resident population is hardly affected (Figure C2a), with relatively fewer adults due to the slower growth of the subadults.

For the marine estuarine–dependent guild, lower productivity in the estuary leads to a decrease in juvenile resources. The reduced food availability results in slower growth, with juveniles now taking

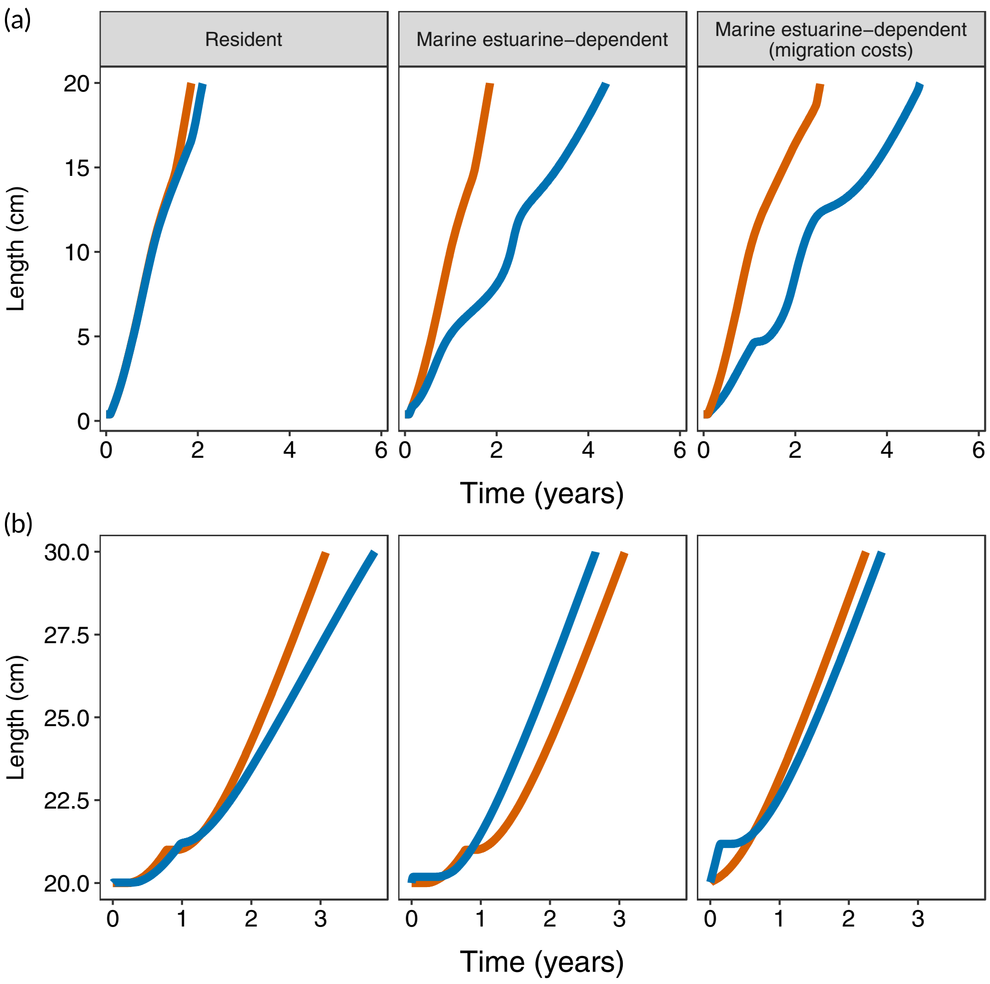

FIGURE C2 Declining productivity of the estuary hardly affects the growth of residents, whereas it decreases the growth rate of juveniles of the marine estuarine–dependent guild and increases the growth rate of subadults of the marine juvenile guild. Growth curves of the juvenile phase ($l < 20$, a) and subadult phase ($20 \leq l < 30$, b) of the resident guild (left) and marine estuarine–dependent guild (middle and right) for high ($K_{1,\text{est}} = 1$, orange) and low ($K_{1,\text{est}} = 0.5$, blue) levels of productivity in the estuarine habitat. Lines show the growth curves of an average grower. We use time on the horizontal axis instead of age to clearly show the growth patterns for both juveniles and subadults, as subadults reach this stage at different ages depending on productivity. Migration costs in the right panel equal $\mu_{\text{mig}} = 0.2$ and $c_{\text{mig}} = 0.3$. All other parameters have default values as presented in Table C3.

~4.5 years to recruit to the subadult population (Figures C2a and C4a). Due to the lower inflow into the subadult population, these large individuals have more food available (Figure C1b, with lower peaks in the resource density) and are consequently in better condition (Figure C3c). During periods of low food densities, subadults have sufficient reserves to deal with low food availability, and their condition never drops below the minimum level for survival. This improved situation results in a higher population birth rate (Figure C2b) and consequently stronger competition among juveniles.

Although the basic model showed a relative increase in the density of juveniles with lower productivity (Figure 4b), we now observe a relative and sometimes absolute increase in the subadult and adult size classes (Figures C3a and C4). This difference is partly due to the distinction between reversible and irreversible masses. The increase in biomass is caused by individuals being in better condition. This improved condition not only directly increases biomass but also ensures that individuals have enough reserves to survive periods of low food availability, leading to much higher overall survival rates for individuals in the larger size classes and therefore higher densities than in the model without explicit reserve biomass.

With migration costs, the main difference is that subadults grow slightly faster under lower-productivity conditions (Figure C2b). In this scenario, competition is even lower compared to when there are no migration costs, as some of the migrating individuals die.

C.2. | Detailed model formulation

All individual-level equations (in this appendix referred to with an equation number) are presented in Table C2. Parameter definitions and values are presented in Table C3.

Individuals of the size-structured consumer population are characterized by their physiological state (i-state). The i-state is defined by age, body size (x, structural mass), and energy reserves (y, subdivided into fat and gonads). These i-states influence individual feeding, growth, development, reproduction, and survival (Table C1). In addition, we model the environmental conditions, or e-state, which includes all factors that determine the changes in the i-state and individual survival, that is, resource densities and time in the season. The dynamic energy budget model, capturing the energetic flow at the individual level, forms the core of the population model (as in Persson et al., 1998). The energy budget is a balance (Table C2, Equation C14) describing the difference between assimilated energy (food intake, scaled by a conversion factor; Table C2, Equation C13) and the daily energy costs needed for maintenance (Table C2,

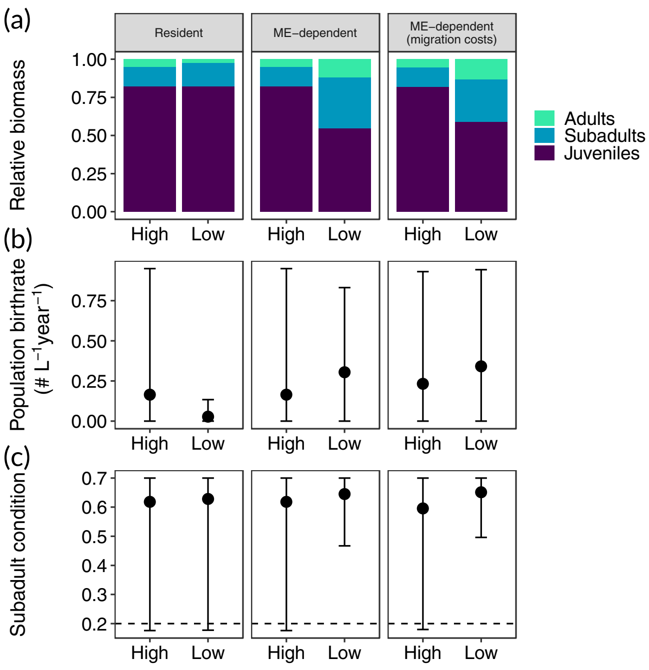

FIGURE C3 Decreasing productivity of the estuary hardly changes the size distribution of residents (a, left panel), whereas it results in relatively higher biomass densities of subadults and adults in the marine estuarine–dependent guild (abbreviated as ME-dependent in panel titles; a, middle and right panels). (a) Mean relative biomass of the three size classes for the two guilds for high ($K_{1,\mathrm{est}} = 1$) and low ($K_{1,\mathrm{est}} = 0.5$) productivities of the estuarine habitat. (b) Mean, minimum, and maximum values of the population birth rate for the two guilds for high ($K_{1,\mathrm{est}} = 1$) and low ($K_{1,\mathrm{est}} = 0.5$) productivities of the estuarine habitat. (c) Mean, minimum, and maximum conditions (measured as y/x) of the subadults ($20 \leq l < 30$) for high and low productivities of the estuarine habitat. Migration costs in the right panel equal $\mu_{\mathrm{mig}} = 0.2$, and $c_{\mathrm{mig}} = 0.3$. All other parameters have default values as presented in Table C3.

Equation C8). The net energy (Table C2, Equation C14) is used for growth and reproduction (Table C2, Equations C15–C17) if it is positive and results in starvation (reducing fat and gonadal mass) if it is negative (eventually leading to an increase in mortality; Table C2, Equation C19). Reproduction is seasonal and happens at the start of the year. The dynamics at the population level are an emergent result from integration of the processes as defined at the individual level. Food availability and seasonal timing (i.e., spawning period) determine the potential for growth, survival, and reproduction of individuals.

C.2.1. | Life history

Eggs hatch after 15 days, and at age 22 days larvae start to feed on zooplankton (Table C2, Equation C2). From a length of 5 cm onward, fish start benthic feeding for an increasing part of its foraging time (Table C2, Equations C1 and C28). When fish reach a size of 15 cm, they have completely switched to the benthic resource. When individuals reach a size of 20 cm, they abruptly switch to a diet of fish (Table C2, Equation C3). Individuals of the resident guild remain in the estuary, whereas individuals of the marine estuarine–dependent guild move offshore. During this transition, individuals have a probability of μ_{mig} to die. Additionally, they lose $c_{\mathrm{mig}} y_f$ gram fat.

Attack rates of the predator on zooplankton, benthos, and fish follow power functions with individual length (Table C2, Equations C4–C6). Food intake is described by a type II functional response (Table C2, Equations C9–C11), where the digestion time is length based and independent of resource type (Table C2, Equation C7).

C.2.2. | Energy allocation

The energy budget is modeled using a net production model (as in Persson et al., 1998), giving maintenance priority over growth and reproduction in the allocation of net energy (Table C2, Equation C14). If subtraction of maintenance costs yields a positive balance, the net energy is invested in the buildup of the irreversible mass and reversible mass (Table C2, Equations C16 and C17). The fraction of net energy allocated to irreversible mass follows a saturating function that depends on the condition of the individual (Table C2, Equation C15), where condition is defined as the ratio of reversible to irreversible mass. When individuals are in bad condition (i.e., below the target condition that is set separately for juvenile and adult individuals; Table C3, q_J and q_A, respectively), the buildup of reserves is prioritized over growth in irreversible mass (i.e., length). This reflects the assumption that the organism needs to be in sufficient condition to start investing energy in length growth and structural mass. If maintenance costs exceed the energy gains from feeding, the individual starves and regains biomass from its gonads and fat reserves to cover its energy demands. Fat reserves are at first instance used to cover costs of starvation. In fish, it is a well-known phenomenon that previously built-up reproductive tissue may be reclaimed to survive periods of low energy intake (atresia); therefore, the costs of starvation can additionally be covered by an individual's gonadal mass when fat reserves are low. If all reserves are very low, the individual experiences increased starvation-induced mortality (Table C2, Equation C19), which occurs below the starvation condition threshold (Table C3, q_s).

C.2.3. | Spawning and reproduction

We use a 250-day period (Table C3, year) for the annual growth season, assuming that during winter growth and other dynamic processes can be ignored. Reproduction occurs at the start of the growing season (i.e., on day 0). The decision for adult individuals to allocate energy sources to reproduction is made late in the growing season (Table C3, σ). The outcome of this decision depends on both body size (maturation length; Table C3, l_m: this is the starting size for allocation of biomass to gonads) and body condition (minimum threshold for

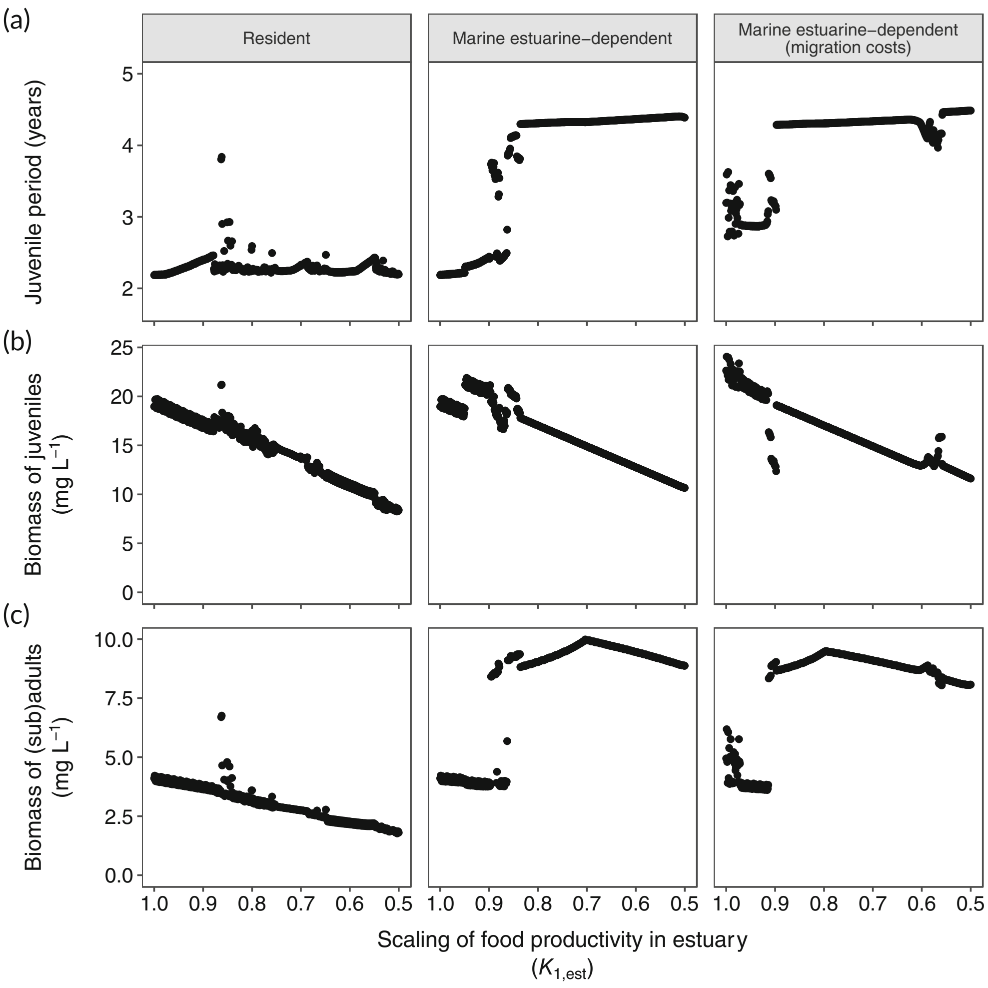

FIGURE C4 For decreasing productivities in the estuary, growth of the resident guild is hardly affected (a, left), whereas growth of juveniles of the marine estuarine–dependent guild decreases, resulting in a longer juvenile period (a, middle and right panels). The biomass of all size classes of the resident guild decreases with lower productivity (b, left; and c, left), whereas for the marine estuarine–dependent guild the juveniles decrease and the (sub)adults can even increase in biomass for lower food productivity (c, middle and right panels). Migration costs in the right panel equal $\mu_{\mathrm{mig}} = 0.2$ and $c_{\mathrm{mig}} = 0.3$. All other parameters have default values as presented in Table C3.

TABLE C1 System variables, i-state variables, and derived variables.

Symbol	Unit	Expression	Description
System variables			
C_j	no. m^{-3}		Number of individuals in cohort j
R_z	g m^{-3}		Zooplankton density
R_b	g m^{-2}		Benthos density
R_f	g m^{-3}		Density of prey fish
i-State variables			
a	days		Age
x	g		Irreversible mass
y_f	g		Fat reserves
y_g	g		Gonadal mass
Derived variables			
y	g	$y_f + y_g$	Total reversible mass
w	g	$x + y$	Total body weight
l	cm	$\left[\frac{x(1+q_J)}{\lambda_1}\right]^{\frac{1}{\lambda_2}}$	Total body length

spawning, taken equal to the condition target of juveniles; Table C3, q_g). From the reversible mass, the surplus over $q_J x$ is then allocated to gonads, which ensures that after reproductive allocation the individual has at least the juvenile target condition, disregarding the gonads. Therefore, at the time of reproductive allocation the reversible mass values are reset to

TABLE C2 Functions related to individual-level processes.

Function	Equation	Number
Benthos foraging time	$t_b(l_j) = \begin{cases} 0, & l_p \le l_j < l_b, \\ Q(l_j, l_b, l_{\mathrm{bhalf}}), & \text{otherwise.} \end{cases}$	C1
Zooplankton foraging time	$t_z(l_j) = \begin{cases} 0, & l_j \ge l_p, \\ 1 - Q(l_j, l_b, l_{\mathrm{bhalf}}), & \text{otherwise.} \end{cases}$	C2
Fish foraging time	$t_f(l_j) = \begin{cases} 0, & l_j < l_p, \\ 1, & \text{otherwise.} \end{cases}$	C3
Zooplankton attack rate	$a_z(l_j) = \chi_1 l_j^{\chi_2}$	C4
Benthos attack rate	$a_b(l_j) = \psi_1 l_j^{\psi_2}$	C5
Piscivory attack rate	$a_f(l_j) = \gamma_1 l_j^{\gamma_2}$	C6
Digestion time	$h(l_j) = \zeta_1 l_j^{\zeta_2}$	C7
Maintenance requirements	$m(w) = p_1 w_j^{p_2}$	C8
Zooplankton intake	$I_z(l_j) = t_z(l_j) \frac{a_z(l_j) R_z}{1 + h(l_j) a_z(l_j) R_z}$	C9
Benthos intake	$I_b(l_j) = t_b(l_j) \frac{a_b(l_j) R_b}{1 + h(l_j) a_b(l_j) R_b}$	C10
Fish intake	$I_f(l_j) = t_f(l_j) \frac{a_f(l_j) R_f}{1 + h(l_j) a_f(l_j) R_f}$	C11
Total food intake	$I_t(l_j) = I_z(l_j) + I_b(l_j) + I_f(l_j)$	C12
Acquired energy	$\theta_A I_t(l_j)$	C13
Net-energy production	$E_t(l_j, w_j) = \theta_A I_t(l_j) - m(w_j)$	C14
Allocation factor	$\kappa(x_j, y_j) = \begin{cases} \frac{1}{q+1}, \text{if } \frac{y_j}{x_j} > q, \\ \left(\frac{y_j}{x_j}\right)^2 \frac{1}{(1+q)q^2}, \text{otherwise,} \end{cases}$ with $q = q_J$ if $l < l_m$ and $q = q_A$, otherwise.	C15
Fraction of energy allocated to *x*	$N_x(l_j, w_j) = \begin{cases} \kappa(x_j, y_j) E_t(l_j, w_j), \text{if } E_t(l_j, w_j) > 0, \\ 0, \text{otherwise.} \end{cases}$	C16
Fraction of energy allocated to *y*	$N_y(l_j, w_j) = \begin{cases} (1 - \kappa(x_j, y_j)) E_t(l_j, w_j), \text{if } E_t(l_j, w_j) > 0, \\ 0, \text{otherwise.} \end{cases}$	C17
Fecundity	$F(y_g) = \begin{cases} \frac{\theta_f y_g}{\lambda_1 l_0^{\lambda_2}}, & l_j > l_m, \\ 0, & \text{otherwise.} \end{cases}$	C18
Starvation mortality	$d_s(x_j, y_j) = \begin{cases} 0, & \frac{y_j}{x_j} > q_s, \\ \mu_s\left(q_s \frac{y_j}{x_j} - 1\right), & \text{otherwise.} \end{cases}$	C19
Size-dependent mortality	$d_l(l_j) = \mu_J e^{-(l_j/l_d)^{\lambda_2}}$	C20
Total mortality	$d_t = \begin{cases} \mu_e e^{-(l_0/l_d)^{\lambda_2}}, \text{if } a < a_J, \\ \mu_b + d_s(x_j, y_j) + d_l(l_j), \text{otherwise.} \end{cases}$	C21
Growth of zooplankton	$P_z = \beta(K_{1,\mathrm{est}} R_{z,\mathrm{est,max}} - R_z)$	C22
Growth of benthos	$P_b = \beta(K_{1,\mathrm{est}} R_{b,\mathrm{est,max}} - R_b)$	C23
Growth of prey fish	$P_f = \beta(K_{1,h} R_{f,\mathrm{ht,max}} - R_f)$	C24
Grazing on zooplankton	$G_z = \sum_j I_z(l_j) C_j$	C25
Grazing on benthos	$G_b = \sum_j I_b(l_j) C_j U$	C26
Predation on fish	$G_f = \sum_j I_f(l_j) C_j$	C27
Continuous, piecewise-differentiable, bounded sigmoid function (C28)		

(Continues)

TABLE C2 (Continued)

Function	Equation	Number
$Q(n,n_s,n_h)=\begin{cases} 0, & \text{for } f(n,n_s,n_h) \leq 0 \\ \frac{1}{6}f(n,n_s,n_h)^3, & \text{for } f(n,n_s,n_h) \leq 1 \\ -\frac{3}{2}f(n,n_s,n_h)+\frac{3}{2}f(n,n_s,n_h)^2-\frac{1}{3}f(n,n_s,n_h)^3+\frac{1}{2}, & \text{for } f(n,n_s,n_h) \leq 2 \\ \frac{9}{2}f(n,n_s,n_h)-\frac{3}{2}f(n,n_s,n_h)^2+\frac{1}{6}f(n,n_s,n_h)^3-\frac{7}{3}, & \text{for } f(n,n_s,n_h) \leq 3 \\ 1 & \text{otherwise,} \end{cases}$		
with $f(n,n_s,n_h)=\frac{3}{2}\frac{n-n_s}{n_h-n_s}$		

TABLE C3 Parameter symbols, description, and values.

Symbol	Value	Unit	Description
U	5	m	Ratio of volume to surface, that is, average depth
Seasonal dynamics			
Year	250	Day	Duration of the season
σ	200	–	Spawning decision date
Resource dynamics			
β	0.1	day^{-1}	Resource growth rate
$R_{z,\mathrm{est,max}}$	5	g m^{-3}	Maximum density of zooplankton resource
$R_{b,\mathrm{est,max}}$	50	g m^{-2}	Maximum density of benthic resource
$R_{f,\mathrm{est,max}}$	3	g m^{-3}	Maximum density of fish resource in estuary
$R_{f,\mathrm{off,max}}$	3	g m^{-3}	Maximum density of fish resource offshore
$K_{1,\mathrm{est}}$	Variable	–	Scale parameter for productivity in the estuary
$K_{2,\mathrm{est}}$	$K_{1,\mathrm{est}}$	–	Scale parameter for productivity in the estuary
$K_{2,\mathrm{off}}$	1	–	Scale parameter for productivity offshore
Length–weight			
λ_1	0.01	g cm$^{-\lambda_2}$	Length–weight conversion constant
λ_2	3		Length–weight conversion exponent
Ontogeny			
q_J	0.7	–	Juvenile condition target
q_A	1.4	–	Adult condition target
q_g	0.7	–	Minimum spawning condition
θ_f	0.5	–	Gonad–offspring conversion
l_0	0.39	cm	Size at birth
l_d	3.68	cm	Characteristic size in size-dependent mortality rate
l_m	30	cm	Length at maturation
l_b	5	cm	Length at start benthivory
l_{bhalf}	10	cm	Length at 50% switch to benthivory
l_p	20	cm	Length at start piscivory/habitat shift
a_J	22	days	Age at first feeding
Attack rates and handling			
ζ_1	364.1	day^{-1} g cm$^{-\zeta_2}$	Allometric scalar for digestion time
ζ_2	-2.34	–	Allometric exponent for digestion time
χ_1	0.3	m^3 day^{-1} cm$^{-\chi_2}$	Zooplankton attack rate scaling constant
χ_2	1.8	–	Zooplankton attack rate scaling exponent
ψ_1	0.4	m^2 day^{-1} cm$^{-\psi_2}$	Benthic attack rate scaling constant
ψ_2	0.6	–	Benthic attack rate scaling exponent

TABLE C3 (Continued)

Symbol	Value	Unit	Description
γ_1	1.6	$\mathrm{m}^3\ \mathrm{day}^{-1}\ \mathrm{cm}^{-\gamma_2}$	Piscivory attack rate scaling constant
γ_2	0.6	–	Piscivory attack rate scaling exponent
Metabolism			
p_1	0.03	$\mathrm{g}^{1-p2}\ \mathrm{day}^{-1}$	Allometric scalar for maintenance rate
p_2	0.8	–	Allometric exponent for maintenance rate
θ_A	0.5	–	Food assimilation efficiency
Mortality			
μ_e	0.03	day^{-1}	Egg and yolk-sac mortality
μ_J	0.03	day^{-1}	Size-dependent mortality scaling constant
μ_b	0.003	day^{-1}	Background mortality
μ_s	0.2	day^{-1}	Starvation mortality scaling constant
q_s	0.2	–	Minimum/starvation condition
Migration			
μ_{mig}	0–0.2	–	Probability of dying during migration
c_{mig}	0–0.3	–	Fraction of fat loss during migration

$$y_g = \begin{cases} 0 & \text{if } y_f < q_J x, \\ y_f - q_J x & \text{otherwise,} \end{cases}$$

and

$$y_f = \begin{cases} y_f & \text{if } y_f < q_J x, \\ q_J x & \text{otherwise.} \end{cases}$$

For the remainder of the year, if an individual's net-energy production is positive, its fraction invested into buildup of reversible mass (Table C2, Equation C17) is used to increase the gonads as opposed to the fat reserves. Similarly, if net-energy production is negative, fat reserves are reclaimed first to cover maintenance requirements, whereas gonadal mass is used only after the fat reserves have been starved away down to the starvation condition. At the start of the following year, the total biomass invested in gonadal mass (or what is left of it if starvation has occurred) is converted to eggs (Table C2, Equation C18). The conversion coefficient θ_f (Table C3) involves losses to males, conversion from somatic to gonadal tissue, and the energy content of the yolk sac.

APPENDIX D: ECOLOGICAL BISTABILITY D

Bistability is a common feature in models where individuals undergo ontogenetic diet shifts (e.g., Guill, 2009; de Roos & Persson, 2013; Schreiber & Rudolf, 2008; Sun & de Roos, 2015). It is therefore not surprising that we find some bistability in our system, especially for the marine estuarine–dependent guild (Figure D1, right panels). Depending on the initial conditions, two ecological equilibria are possible. In one equilibrium, there are relatively many small juveniles, resulting in strong competition among them and therefore a long juvenile period. In the other equilibrium, the biomass of small juveniles is a bit lower, resulting in less competition and thus a shorter juvenile period.

The consequence of this bistability is that small changes in the productivity of the estuary habitat can lead to sudden changes in the population dynamics of the fish in case the system switches to the other equilibrium. It also implies that there is hysteresis in the system, so that after a change in the productivity of the estuary, it may be difficult to reverse the system to its previous state, even if the productivity is restored to its original value (Figure D1).

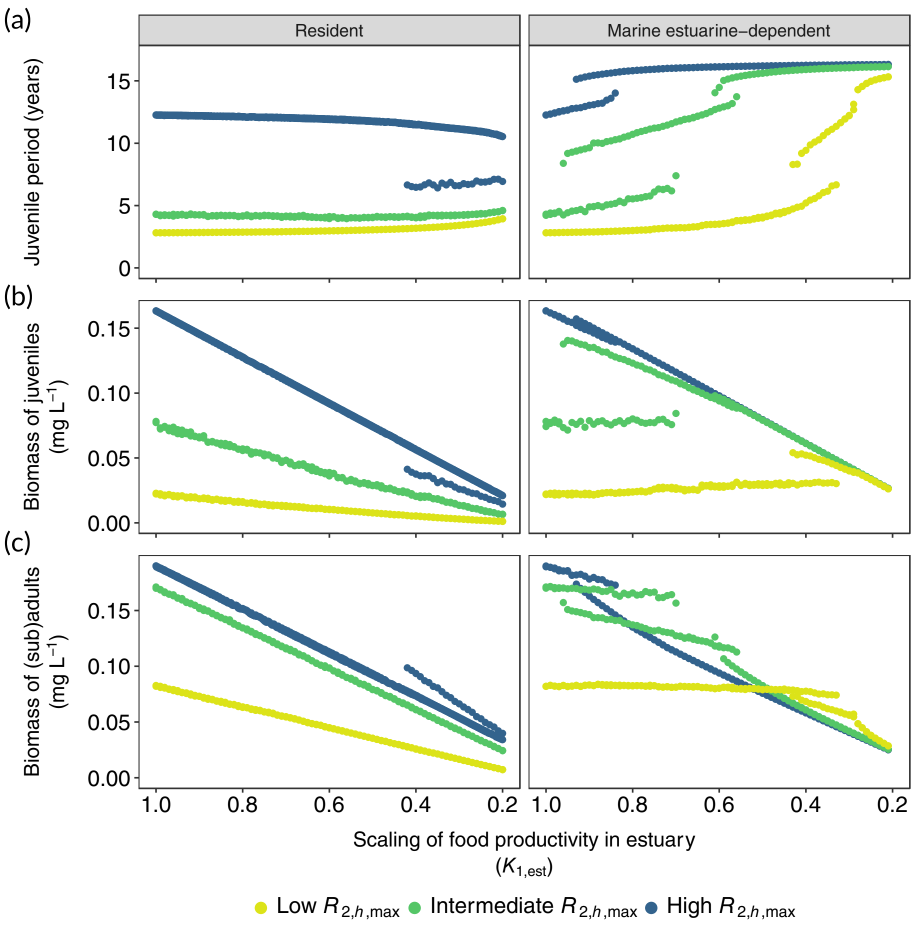

FIGURE D1 (a) Average juvenile period, (b) average density of juveniles, and (c) subadults and adults as a function of parameter $K_{1,\mathrm{est}}$. In the calculations we both increased and decreased this parameter to capture the potential bistability. To change the relative amount of food productivity of the two resources, we varied $R_{2,h,\max}$ (0.05 [yellow], 0.1 [green], or 0.15 [dark blue] mg L^{-1}), keeping $R_{1,\mathrm{est},\max}$ constant at a value of0.1 mg L^{-1}. All other parameters have default values as presented in Table 1.