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Modelling population effects of juvenile offshore fish displacement towards adult habitat

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ABSTRACT: Recent studies of fish distribution patterns highlight shifts in the spatial distributions of particular life-stages. Focus has thus far been on changes in habitat use and possible drivers for these changes. Yet, small-scale shifts in habitat use of certain life stages may have profound consequences on population dynamics through changes in resource use and competition. To explore this, a conceptual stage-structured model was developed with 3 stages and 2 resources and allowing a move of large juveniles from the shallow to the deep habitat. Large juveniles compete with small juveniles in shallow waters and with adults in deeper waters. Alternative stable states occur, with one state dominated by small juvenile biomass and the other dominated by adult biomass. The model results show for both states that while large juvenile biomass responds to a change in time spent in the deep habitat, the biomass of small juveniles and adults is barely affected. Between the 2 states there is a profoundly different population response to increased fishing mortality. In the adult biomass dominated state, adult biomass is hardly affected while juvenile biomass increases until population collapse, with increased fishing. In the small juvenile dominated state, adult and small juvenile biomass decrease, and large juvenile biomass increases. This state persists at much higher fishing mortality than the adult biomass dominated state. This study highlights that safeguarding nursery functions in a changing environment requires monitoring of juvenile life-stages in a range of habitats and a spatially adaptive management strategy.

KEY WORDS: Stage-structured model · Complex life cycle · Nursery grounds · Spatial distribution · Competition

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INTRODUCTION

Coastal ecosystems are globally among the most productive marine systems, providing habitat in which to feed and grow for many fish species, a large part of which are commercially exploited (Seitz et al. 2014). Increasing anthropogenic pressures have given rise to growing concern for the resilience of these systems and sustainability of their resources (Harley et al. 2006, McClanahan et al. 2015). This concern has highlighted the need for appropriate

integrated management (Hopkins et al. 2011). Coastal habitats are important nurseries for fish, where habitat size and quality strongly influence stock size of commercially important species through growth, survival and connectivity with spawning areas (Gibson 1994). The often complex life cycles require understanding across the entire life cycle in order to anticipate responses of fish populations to external pressures (Petitgas et al. 2013).

In recent decades, considerable changes in the distribution of fish have been reported, and these

changes are increasingly considered as direct or indirect biological responses to the warming of the oceans (Edwards et al. 2002). Distributions of boreal and Lusitanian species move northward, with the Lusitanian species possibly replacing the boreal species in areas of spatial co-occurrence at temperate latitudes (Beare et al. 2004, Rijnsdorp et al. 2009, Petitgas et al. 2013). Besides large-scale shifts of boreal species such as plaice *Pleuronectes platessa* and cod *Gadus morhua* towards northern regions (Rindorf & Lewy 2006), small-scale shifts towards deeper waters where temperatures are lower have been observed in several fish species in European waters and elsewhere (Dulvy et al. 2008).

The change in habitat use from coastal habitat to deeper habitat by a certain life stage implies life stage-dependent shifts in feeding habitats. The consequence of such a shift is that the competitive interactions change when life stages begin or cease to share a habitat. Van Keeken et al. (2007) showed that as a result of the movement of juvenile plaice towards deeper waters, the mean crowding decreased for smaller-sized plaice in the shallows, while it increased for larger-sized plaice in deeper waters. Such a shift in the potential for intra-specific competition between life stages may have consequences at the population level. Additionally, a shift of large juveniles towards deeper areas implies an increase in vulnerability to fisheries as fisheries generally operate more intensely in the deeper areas.

Plaice is the most well studied species within the context of juvenile habitat shifts owing to its commercial importance, but the movement towards deeper areas has been observed for more species such as dab *Limanda limanda* (van Hal et al. in press), megrim *Lepidorhombus whiffiagonis*, grey gurnard *Eutrigla gurnardus*, cod *Gadus morhua*, whiting *Merlangius merlangus*, long rough dab *Hippoglossoides platessoides*, angler *Lophius piscatorius*, lemon sole *Microstomus kitt*, poor cod *Trisopterus minutus* and cuckoo ray *Leucoraja naevus* (Dulvy et al. 2008). Until now, the phenomenon of large juvenile plaice shifting habitat has been studied at the level of individual fish (e.g. Rijnsdorp et al. 2009), from a bycatch perspective (van Keeken et al. 2007) and in relation to possible physiological mechanisms (e.g. Teal et al. 2012). More general studies on the use of shallow habitat by fish have mostly focussed on predicting presence-absence and/or abundance patterns based on habitat suitability (e.g. Vasconcelos et al. 2013). However, to

date, the population dynamic consequences of habitat shifts for juvenile fish towards deeper areas have not been examined. Yet changes in competitive interactions may have profound effects on the biomass distribution along life stages and may give rise to alternative stable states (e.g. Schröder et al. 2005, De Roos et al. 2008). Here, the effects of a habitat shift of juveniles on the population dynamics are explored using a generalized mathematical description of such a system inspired by the observations in the North Sea (Dulvy et al. 2008, Teal et al. 2012, van Hal et al. in press).

To study the population dynamic effects of larger juveniles shifting habitat and thus shifting the scope for competition between stages within a population, a biomass-based stage-structured model (De Roos et al. 2008, van de Wolfshaar et al. 2011, 2012) was developed. This type of model combines resource-dependent growth and maturation with stage-structure and allows for a mechanistic underpinning of emergent patterns in population dynamics. The model allows for a conceptual exploration of possible population dynamical responses to a habitat shift of large juveniles and changes in intra-specific competition, which may occur for a range of species (Dulvy et al. 2008, van Hal et al. in press). The model results describe the equilibrium population dynamics of a model fish species with 3 life stages foraging in 2 habitats each with 1 resource (Fig. 1). The model results are based on a generalized parameterization for ectothermic species (van de Wolfshaar et al. 2011).

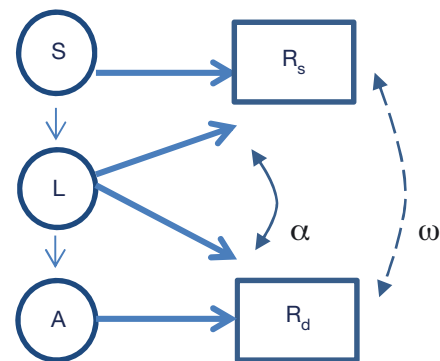


Fig. 1. Model representation of the plaice population. Small juveniles (S) have their resource in the shallow area (R_s), while adults (A) have their resource in the deep areas (R_d). Large juveniles (L) may change from feeding solely on the resource in the shallows (R_s) to feeding solely on the resource in the deep areas (R_d) by changing the value of α . ω scales the carrying capacity of both resources such that their sum always equals K_m . Thin arrows between stages indicate growth

MODEL AND PARAMETER ESTIMATES

Consumer–resource model

To study the effect of changing habitat during ontogeny, a biomass-based stage-structured population model was used (De Roos et al. 2008) and parameterized for ectotherms. Such models are conceptual in the sense that only a limited set of assumptions is considered for exploration; emerging mechanisms may be incorporated in more complex simulation models.

In this type of model, growth and reproduction rates are resource dependent. The stages are based on size, and based on the size limits chosen, a certain amount of growth needs to be realized for each stage. To mature to the next stage (or to reproduce), a certain amount of energy is needed, and with differences in allometry, the resource needs may differ between stages. This implies that there will always be a stage that has the lowest relative growth (or reproduction) rate, and growth (or reproduction) is resource limited (De Roos et al. 2008). Which stage is resource limited is an emergent property of the parameter settings. The key biological features of the stage-structured model are described below, and for a detailed mathematical description, we refer to De Roos et al. (2008).

To model the population, 3 stages and 2 resources are recognized (Fig. 1). The small juveniles (S) only forage on the resource in the shallow area (R_s), and adults (A) only forage on the resource in the deeper area (R_d). Large juveniles (L) may forage on both resources. Therefore, the fraction of time large juveniles spend in the shallow area or the deeper area (α) is varied.

We assume that both resources follow semi-chemostat dynamics, with growth rate r and carrying capacity K . Using logistic growth will not quantitatively change the results (Guill 2009, Nilsson et al. 2010). The maximum equilibrium densities of the resource in the shallow habitat and the resource in the deeper habitat are scaled with fraction ω ($0 \leq \omega \leq 1$) so that:

$$K_s = (1 - \omega)K_m, K_d = \omega K_m \quad (1)$$

When $\omega < 0.5$, the deep habitat is the more productive habitat, and when $\omega > 0.5$, the shallow habitat is the more productive habitat (Fig. 2). For simplicity reasons, differences between resource levels at maximum capacity are scaled solely through K , following van de Wolfshaar et al. (2011). As differences in habitat productivity could have an effect on the population dynamics (van de Wolfshaar et al. 2011),

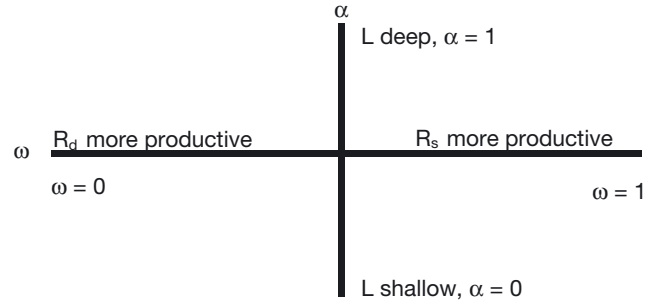


Fig. 2. When $\omega > 0.5$, the shallow juvenile habitat is more productive than the deeper habitat; when $\omega < 0.5$, the deeper habitat is more productive. When α is 1, large juveniles forage only in the deeper habitat, and when α is 0, they forage only in the shallow habitat

the effect of varying relative habitat productivity was included in the study.

All stages forage using a Holling Type II functional response with a half-saturation constant (R_h) and a mass-specific maximum ingestion rate (I_{max}). The total ingested resource (IR_i) by a certain stage i depends on the resource density according to:

$$IR_i = I_{max,i} + 0.1(R_{(i)})(R_h + R_{(i)}) \quad (2)$$

where $R_{(i)}$ can be R_s in case of small juveniles and R_d for adults. The total ingested resource intake of large juveniles depends on both resources and the fraction of time spent in the deeper habitat, α :

$$IR_L = I_{max,L}(\alpha R_s + (1 - \alpha)R_d)/(R_h + \alpha R_s + (1 - \alpha)R_d) \quad (3)$$

When $\alpha = 0$, the large juveniles spend all their time foraging on the resource in the shallow habitat, whereas when $\alpha = 1$, they spend all their time foraging on the resource in the deeper habitat (Fig. 2).

The differential equations describing the dynamics of the resources in shallow and deeper habitat are then as follows:

$$dR_s/dt = r(K_s - R_s) - (S \cdot IR_S + L \cdot IR_{Ls}) \quad (4)$$

$$dR_d/dt = r(K_d - R_d) - (A \cdot IR_A + L \cdot IR_{Ld}) \quad (5)$$

where IR_{Ls} represents the resource consumption of large juveniles in the shallow habitat, and IR_{Ld} represents the resource consumption of large juveniles in the deeper habitat.

The ingested resource is converted with an efficiency δ , and minus the species mass-specific metabolic rate T , this gives the net biomass production for each stage i :

$$v_i(R) = \delta IR_i - T_i \quad (6)$$

The following set of differential equations then describes the dynamics of the 3 stages of the population:

$$dS/dt = v_A^+(R_d)A + v_S(R_s)S - \gamma(v_S^+(R_s))S - \mu_S S \quad (7)$$

$$dL/dt = \gamma(v_S^+(R_s))S + v_L(R_{s,d})L - \gamma(v_L^+(R_{s,d}))L - \mu_L L \quad (8)$$

$$dA/dt = \gamma(v_L^+(R_{s,d}))L + v_A(R_d)A - (v_A^+(R_d))A - \mu_A A \quad (9)$$

where μ_i is the total mortality rate in stage i , $\gamma(v_i^+(R))$ is the rate at which small juveniles and large juveniles mature to the next stage, and $v_A^+(R)$ is the reproduction rate of adults.

The maturation rate depends on the biomass individuals have to accumulate within the stage, the net biomass production of the stage, and mortality:

$$\gamma(v_i^+(R)) = v_i(R) - \mu_i / (1 - z^{(1 - \mu_i/v_i(R_i))}) \quad (10)$$

with z being the ratio between the mass at which an individual enters the stage and the mass at which an individual develops to the next stage. For adults, it is assumed that all surplus energy is converted into offspring. The net biomass production of adults then equals the reproduction rate. To ensure that negative maturation or reproduction does not occur, biomass is only transferred between stages when the net energy intake is positive ($v_i(R) > 0$). If the net biomass production is negative, starvation occurs, and maturation and reproduction do not take place, i.e. $v_A^+(R) = 0$, $\gamma(v_i^+(R)) = 0$.

Parameters

Parameter values for maintenance and ingestion used for the general case were published by van de Wolfshaar et al. (2011). These are based on mass-specific rates proportional to the quarter power of adult body sizes (Yodzis & Innes 1992), and the constants of the power laws are based on ectothermic species (De Roos et al. 2008). van de Wolfshaar et al. (2011) performed a sensitivity analysis on a similar model as used here with 2 resources and 2 stages and confirmed that variation in the other parameter values did not qualitatively change the results regarding general patterns. In contrast to the model used by van de Wolfshaar et al. (2011), 3 stages are used instead of 2. As a result, 1 additional stage boundary is needed. The ratio between size at birth and size at maturation (parameter z) used by van de Wolfshaar et al. (2011) of 1×10^{-5} , an order of magnitude of growth common for fish species, was therefore divided for the 2 juveniles stages used here, 1×10^{-3} and 1×10^{-2} . An increase in background mortality

Table 1. Model variables, parameters and their values for the generalized parameterization (taken from van de Wolfshaar et al. 2011)

Variable	Value	Unit	Description
S		$g\ l^{-1}$	Juvenile biomass
L		$g\ l^{-1}$	Large juvenile biomass
A		$g\ l^{-1}$	Adult biomass
R		$g\ l^{-1}$	Resource biomass
I_{max}	13	$g\ g^{-1}\ d^{-1}$	Maximum intake rate
T	1	$g\ g^{-1}\ d^{-1}$	Maintenance rate
Z_{J-LJ}	0.001		Size ratio small juvenile to large juvenile
Z_{LJ-A}	0.01		Size ratio large juvenile to adult
Δ	0.36		Food conversion factor
μ	0.05	d^{-1}	Background mortality
R_h	0.1	$g\ l^{-1}$	Feeding half saturation constant
r	1	d^{-1}	Resource regrowth rate
K_m	10	$g\ l^{-1}$	Maximum carrying capacity
ω	Varied		Carrying capacity scalar
α	Varied		Partitioning large juveniles shallow-deep habitat
E	Varied	d^{-1}	Fishing intensity
C_A	1		Catchability adult stage
C_L	1		Catchability large juvenile stage in deep habitat

decreases the scope for alternative stable states (results not shown), and juvenile mortality decreases population persistence more than adult mortality does (Nilsson et al. 2010, van de Wolfshaar et al. 2011).

Mortality of all stages is set to $0.05\ d^{-1}$. In addition, adults and large juveniles in the deep habitat may be subjected to fishing mortality, where the realized mortality is a product of fishing intensity and stage-specific catchability. The fishing intensity as used here is a model assumption and does not relate to fishing mortality observed in reality. The use of a single parameter, called fishing intensity, allows simultaneous scaling of additional mortality for adults and large juveniles in the deeper habitat. All parameter values used are listed in Table 1.

RESULTS

Changing relative habitat productivity

The model results display the changes of equilibrium biomass of the different stages as a function of changes in a parameter value. Here, a model with 2 habitats and hence 2 resources is used. The relative difference between the productivity of the 2 habitats

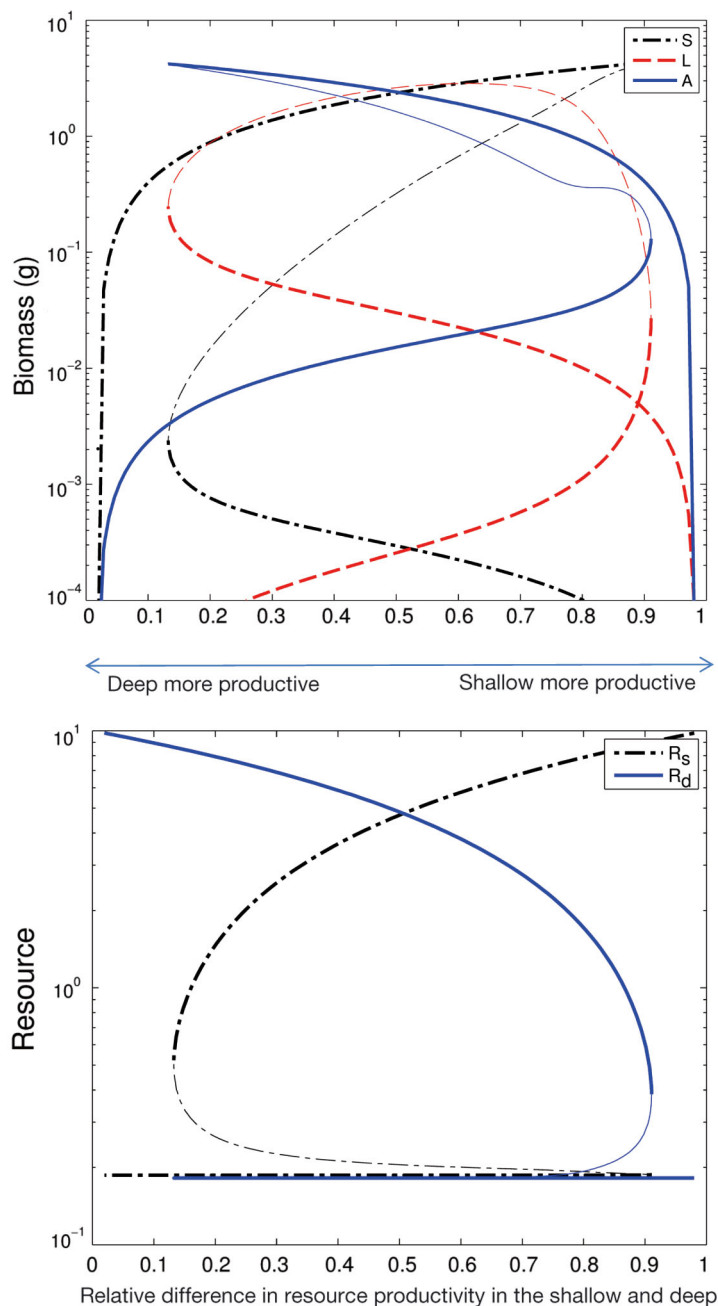


Fig. 3. Biomass of the 3 stages, small juveniles (S), large juveniles (L) and adults (A) (top) and resource densities in the shallow habitat (R_s) and in the deep habitat (R_d ; bottom) as a function of the relative difference in resource productivity in the shallow and deep habitat (ω). Stable states are shown in thick lines, unstable states in thin lines. The fraction of time large juveniles spend in the deeper area: $\alpha = 0.3$

is varied. Large differences in productivity between the deeper (adult) and shallow (juvenile) habitats limit population persistence, as differences that are too large imply that one habitat is not productive enough to support growth or maturation of the stage

present and hence to support the population as a whole (Fig. 3). When the deep habitat is more productive and the shallow habitat is least productive (ω close to zero), most biomass is in the small juvenile stage. The small juveniles are resource limited (ω close to zero) and have little resource for growth and maturation to the next stage. The least biomass is in the large juvenile stage since the influx of small juveniles is hampered by low resource availability and because the large individuals spend time in the deep habitat where they can grow and mature quickly, because the deep habitat is most productive. With increasing ω , total population biomass increases because the productivity of both habitats becomes more equal. When ω reaches 0.9, the stable state collapses to an alternative stable state with most biomass in the adult stage and least biomass in the small juvenile stage. In this state, the adult stage is most resource limited and reproduction is hampered, especially when the deep habitat is the least productive ($\omega > 0.5$). With a decline in ω again, this state returns to the original state if $\omega < 0.13$. The resource follows a similar pattern with low resource density in the shallow habitat and high resource density in the deep habitat in the state with high biomass of the small juveniles (Fig. 3). This means that the individuals in the shallow habitat are resource limited, despite values of ω close to 1. The opposite is the case for the alternative equilibrium with high adult biomass; then, the resource density is low in the deep habitat and high in the shallow habitat. These results indicate that there is scope for alternative stable states when varying the relative habitat productivity (corroborating the results presented for a 2 stage model by van de Wolfshaar et al. 2011). The range of values of ω for which the population can persist is dependent on the total productivity (carrying capacity) of the system and is independent of the time large juveniles spend in the deep habitat (result not shown, but see also van de Wolfshaar et al. 2011).

Changing large juvenile habitat use

When allowing the large juveniles, the intermediate stage, to use the deep habitat more (an increase of α) for a given relative productivity, the biomass of the large juvenile stage decreases while the biomass of the small juveniles remains constant (Fig. 4). Adult biomass shows an initial increase with increasing α but remains constant thereafter. The large juveniles are entering the deep habitat, the habitat with the highest resource density, with rapid growth and mat-

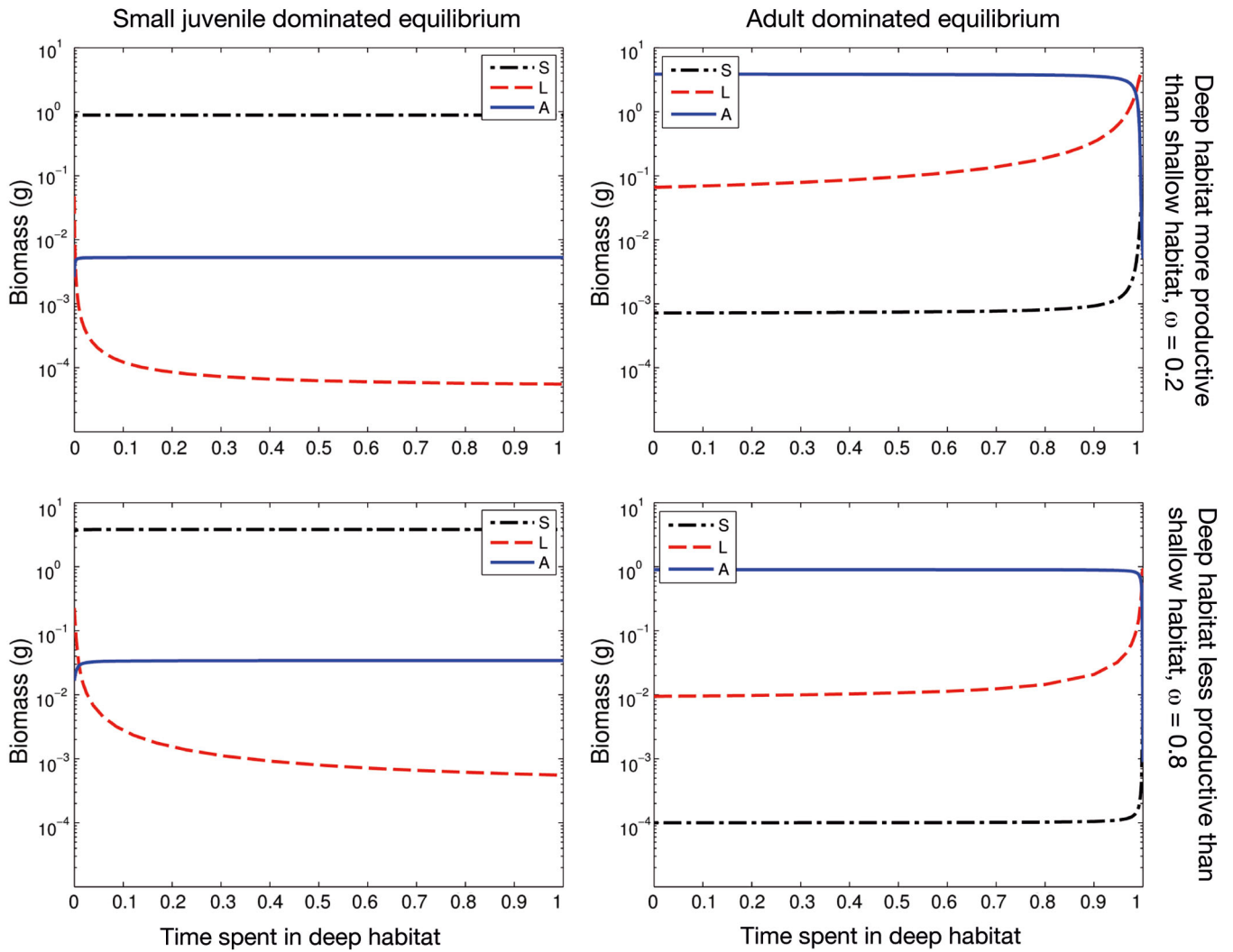


Fig. 4. Change in stage biomass (S: small juveniles; L: large juveniles; A: adults) as function of the time large juveniles spent in the deep habitat (α) for different values of the relative difference in resource productivity in the shallow and deep habitat (ω), and for the 2 different stable states

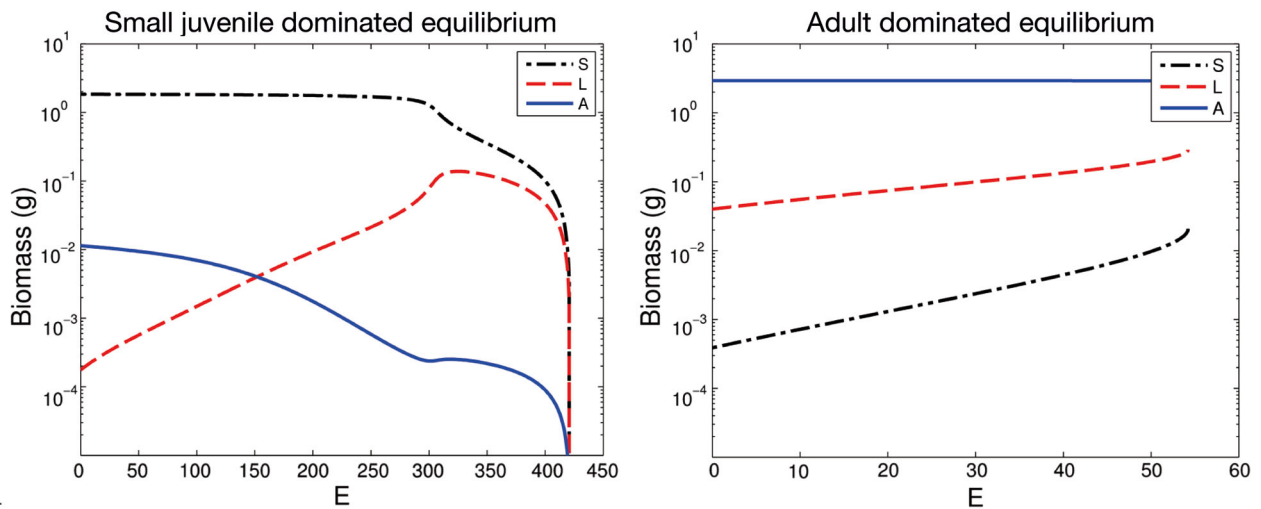


Fig. 5. Change in stage biomass (S: small juveniles; L: large juveniles; A: adults) as function of fishing intensity E for the 2 different stable states ($\omega = 0.4$ and $\alpha = 0.3$)

uration to the adult stage. The adults are reproducing at maximum capacity, and the low resource density in the shallow habitat limits maturation of the small juveniles. This is the case irrespective of the value of ω , the relative habitat productivity. A change in relative habitat productivity increases the total biomass in the system but not the qualitative patterns in biomass. However, when in the alternative stable state, dominated by adult biomass, an increase in α results in an increase in large juvenile biomass. For values of α close to 1, small juvenile biomass increases and adult biomass decreases. The biomass of large juveniles increases because they are spending more time in the deep habitat, which has low resource densities. Here, resource competition hampers growth and maturation, and biomass builds up. Again, the pattern is stable for different values of relative habitat productivity (ω).

Changing fishing intensity

When introducing fishing mortality for adults and large juveniles in the deep habitat, the dynamics respond differently between the 2 alternative stable states (Fig. 5). When the population is in the state with most biomass in the small juvenile stage, the population can endure high values of fishing intensity before collapse. With increasing fishing intensity, adult biomass decreases while large juvenile biomass increases. The increase in large juvenile biomass is an indirect result from the fishing mortality. The decrease in adult biomass results in a decrease in reproduction. The decrease in reproduction reduces the competition in the small juvenile stage, which in turn allows for an increase in maturation to the large adult stage. At a fishing intensity around 300, the reduction in adult biomass is such that it leads to a profound reduction in small juvenile biomass after which they are no longer resource limited and mature at maximum rate. The large juvenile biomass is then at its peak because now juveniles become resource limited, which delays maturation to the adult stage. With an even further increase in fishing intensity, the biomass removal from the system can no longer be compensated, and the biomass of all stages decreases.

When the population is in the adult biomass dominated state, the increase of fishing intensity leads to an increase of juvenile biomass in both stages, while adult biomass is hardly affected (Fig. 5, right panel). The adult biomass removal by fishing is compensated through increased reproduction. Both juvenile stages mature at maximum rate, except for those

large juveniles that are in the deep habitat. They suffer from the low resource availability and fishing mortality. With even higher fishing intensity, the population becomes extinct.

DISCUSSION

Changes in ontogenetic habitat shifts may cause changes in intraspecific competition affecting population dynamics. This study, based on a life-stage structured population model, demonstrated that differences in productivity of the shallow and deep habitat influence the population response to a stage-specific change in habitat use in a quantitative manner. The model is especially applicable for species, such as flatfish, with a strong dependence on coastal areas as nursery grounds (Able & Fodrie 2015), but may also apply to other species (Seitz et al. 2014). For a given productivity, adult biomass increases with increasing time large juveniles spend in the deep habitat. The results described here illustrate general concepts concerning habitat productivity and habitat use. Changes in habitat use by life stages can influence population dynamics, which may have implications for the way fisheries and habitats should be managed.

Two alternative stable states exist: one dominated by small juvenile biomass and one by adult biomass. Alternative stable states may arise in models of species with complex life cycles and differences in habitat productivity between adult and juvenile resources (van de Wolfshaar et al. 2011). Assumptions on resource dynamics do not affect the occurrence of alternative stable states (Guill 2009). Increased (fishing) mortality reduces the scope for alternative stable states (corroborating van de Wolfshaar et al. 2011). The state dominated by adult biomass collapses at lower fishing intensity than the state dominated by small juvenile biomass. This collapse occurs after only a minor change in adult biomass, while juvenile biomass showed a large increase. This illustrates that stock indicators need to consider the whole population and should not be limited to the adult stage.

When including fishing mortality in the deeper habitat, the effects of increased competition between adults and large juveniles, resulting from the habitat shift of larger juveniles, are reduced by the removal of biomass through harvest. As a result of fishing mortality and the subsequent changes in resource competition, overcompensation of large juvenile biomass occurs (De Roos et al. 2007, van de Wolfshaar et al. 2011). Increasing juvenile mortality will affect the

population dynamics depending on the state the population is in (De Roos et al. 2007, van de Wolfshaar et al. 2011). When resource competition is most severe among juveniles, increased juvenile mortality reduces the competition in the shallow habitat and hence will promote maturation to the next stage and promote biomass in the forthcoming stages. When resource competition is most severe among adults, increased juvenile mortality will have little effect on the population dynamics but will reduce the total biomass. Increased juvenile mortality will reduce the scope for alternative stable states and will more negatively affect population persistence than corresponding levels of adult mortality (Nilsson et al. 2010, van de Wolfshaar et al. 2011).

Understanding the mechanism driving changes in habitat use may guide management to anticipate these changes. Recent studies on North Sea plaice, a boreal flatfish species common in the North Sea, showed an increase in mean depth of ~3.6 m per decade (Dulvy et al. 2008) as well as a change in the mean geographical distribution (Engelhard et al. 2011). North Sea plaice age 1+ currently no longer occur in the shallow coastal zone, and findings in recent literature show more juveniles, especially large juveniles, present in deeper waters (van Keeken et al. 2007, Beare et al. 2010, Teal et al. 2012, van Hal et al. in press), while the North Sea stock and spawning biomass has increased over the past 10 yr (ICES 2014). The absence of large plaice juveniles in coastal nurseries has been attributed to temperature (van Keeken et al. 2007, van der Veer et al. 2011, Teal et al. 2012, van Hal et al. in press). It was suggested that higher temperatures increase energy demands in juvenile plaice, and the resulting reduction in the scope for growth causes an earlier offshore movement (Teal et al. 2012). van Hal et al. (in press) compared the change in depth distribution of several flatfish species and found that only the distribution of the boreal species has shifted towards deeper parts thereby maintaining a constant temperature, while the distribution of Lusitanian species did not change. Although we acknowledge that temperature affects physiological rates, it was not considered in the model presented here.

An important issue implied by large juveniles switching habitats is the management of marine protected areas. These areas are typically established at fixed locations, but a change of habitat use by the protected species or life-stage might call for relocation of the protected area. With the intense use and planning of marine areas by humans, with fishing, shipping, pipelines, etc., relocation of protected areas may be hard to accomplish. The 'plaice box' in

the German Bight of the North Sea may serve as an illustrative example. After establishment of the protected area, called the 'plaice box', the size classes of plaice that were supposed to profit from the measure moved out of the area, most likely due to increasing sea water temperatures that occurred almost simultaneously with the area closure (Beare et al. 2010). Shifts in habitat have potential consequences for habitat protection programs or no-take zones when the target individuals move out of the protected area. Furthermore, shifts in habitat use may have consequences for harvesting and bycatch. By-catches of plaice with sizes below the legal landing size have increased from 18 to 30% during 1970 to 1990, and up to 50% in 2003 (van Keeken et al. 2007). Large juveniles moving into potentially fished areas result in higher bycatch mortality from the fisheries. However, the adults in the deeper habitat are also affected by juvenile migration. Increased crowding in deeper areas has already been observed (Van Keeken et al. 2004) and would potentially increase with increasing offshore migration. In conclusion, from a management perspective, a shift of juveniles towards deeper habitats needs to be addressed, and an understanding of the mechanisms causing and following these changes will aid in designing marine protected areas, resolving bycatch issues and understanding changes in adult growth and reproduction. Safeguarding nursery functions in a changing environment requires monitoring of the juvenile life stages in a range of habitats, a better understanding of how changes in nursery habitat quality and quantity translate into changes in growth and mortality, and an adaptive management strategy.

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