



How do migratory fish populations respond to barrier removal in spawning and nursery grounds?

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Abstract

Connection between critical habitats is an important consideration in efforts to restore native and socio-economically important fish species or control the spread of invasive species. However, differences in fish life history might influence the effectiveness of restoration and management actions. In addition, the strength of connection among spatially separate subpopulations could affect the response of the overall population to a local environmental change. In this study, we modeled the response of migratory fish populations with different homing rates, straying distances, and reproductive modes (iteroparity and semelparity) to changes in the carrying capacity of spawning/nursery grounds in a lake-stream system. Increasing the carrying capacity of one spawning/nursery ground could increase the abundance of the local subpopulation and overall population, but both short-term (i.e., abundance change in the first 20 years) and long-term (i.e., equilibrium abundance) responses varied with life history traits. Furthermore, the abundance of some subpopulations might decrease because of the movement of straying adults toward more productive spawning/nursery grounds. In general, straying distance influenced the short-term response and spatial pattern of the population while homing rate influenced the equilibrium abundance. This study revealed the effect of life history traits on population response to restoration actions, which may be crucial for managers in charge of multi-species management, such as enhancing native fishes while controlling invasive species.

Keywords Migratory fish · Population dynamics · Barrier removal · Life history · Homing behavior · Straying distance

Introduction

The connection between different habitats plays a key role in population persistence, especially for migratory species (Wilcove and Wikelski 2008). Therefore, the construction or removal of anthropogenic barriers (e.g., dams and fences) to control invasive species and restore native species has been widely applied in natural resource management (Hermoso et al. 2015; McLaughlin et al. 2013). Barriers, such as dams and overhanging culverts, usually decrease the size of available spawning and nursery grounds for migratory species in

riverine ecosystems. Throughout the Laurentian Great Lakes basin, more than 1 billion US dollars has been invested for barrier removal projects to restore the spawning migration of native species, while over 60 barriers have been constructed or modified to suppress the reproduction of invasive sea lamprey (*Petromyzon marinus*; Lavis et al. 2003; Neeson et al. 2015). Barrier removal or modification projects are usually costly, time-consuming, and involve multiple objectives, such as management objectives for native species, invasive species, and other socio-economic interests (McKay et al. 2016; Moody et al. 2017; Zheng and Hobbs 2013). Therefore, it is critical to estimate how different species of interest (both native and invasive) respond to a given management action, such as barrier removal, before implementation (Jensen and Jones 2017; Kočovský et al. 2009; Quiñones et al. 2015).

The distribution of suitable habitats above a barrier for species of interest, derived from historical records, field surveys, and species distribution modeling, can provide an estimate of the effects of barriers on certain species. Habitat distribution data have been used to prioritize barrier removal projects based on the amount of quality habitat above a certain

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barrier (Branco et al. 2014; Kočovský et al. 2009; Quiñones et al. 2015). Nevertheless, changes in the size of suitable habitat might not reflect the changes in population dynamics as species-specific characteristics could modulate population-level responses. Species with different life history traits, such as migration season and timing, reproductive mode, homing rate and straying distance, might respond to the same size of habitat expansion/reduction differently (Pess et al. 2014). For instance, species with low straying rates (e.g., striped bass, *Morone saxatilis*) may have a lower tendency to colonize new habitats, thus, benefiting less from barrier removal compared with species with higher straying rates (e.g., pink salmon, *Oncorhynchus gorbuscha*) in the first few years after barrier removal (Pess et al. 2014).

The most direct way to assess the response of species to barrier removal is to monitor the system before and after the removal (Doyle et al. 2005; Gardner et al. 2013; Shaffer et al. 2017). These types of studies, which typically include monitoring for 5 years or less after barrier removal, suggest that many fish species can occupy newly-opened habitats after removing a barrier (Foley et al. 2017a; Hogg et al. 2015; Pess et al. 2014). However, the long-term trajectories of fish population dynamics after barrier removal are largely unknown because population recovery and recolonization may take decades or centuries, which is beyond the scope of most monitoring plans (Foley et al. 2017a; Pess et al. 2014). Short-term population dynamics may be different from the long-term trajectories (Foley et al. 2017a; Huang and Lewis 2015). In addition, a study on one local subpopulation might neglect the effect on other neighboring subpopulations within the migratory network (Taylor and Norris 2010), which could be crucial if each subpopulation is managed by different authorities.

Population models, which can predict population dynamics under the impact of barriers (or barrier removal), have been built for several well-studied migratory species, such as sea lamprey (Jensen and Jones 2017), walleye (*Sander vitreus*, Cheng et al. 2006; Zheng and Hobbs 2013), and Atlantic salmon (*Salmo salar*, Nieland et al. 2015). Most of these models are fine-tuned for the complexity and parameters specific to their intended species, which limits their application to data-poor species from the same system and their generality across species. A simple and flexible population model that can be applied to species with different life history traits (as discussed in Pess et al. 2014) might be more beneficial for managers in charge of multi-species management.

In this study, we developed a simple population model with a migration component (i.e., separated spawning/nursery and feeding grounds) to simulate population dynamics after barrier removal or construction (i.e., increasing or reducing the carrying capacity in the spawning/nursery ground of a subpopulation) for multiple local subpopulations. The main goal of this study was to compare the short- and long-term responses of

populations with different homing rates, straying distances, and reproductive modes (iteroparity and semelparity). The spatial structure of this model was built to reveal different dynamics among local subpopulations when incorporating the degree of natal homing and straying distance of adult fish.

Population model

Our population model is derived from a delay-difference model that simulates population abundance over time, based on the number of survivors and recruitment from the previous year (Deriso 1980; Lin et al. 2018). To test the influence of different levels of homing rate and straying distance, we developed a closed system (similar to a stream-lake system for adfluvial fish populations that feed in the same lake but spawn in different streams, such as potamodromous salmonids, trouts, cyprinids, catfish, pikes, and sturgeons) with eight subpopulations, in which most individuals in a subpopulation use one spawning/nursery ground (i.e., individuals in subpopulation j mainly migrate to spawning/nursery ground j , $j = 1-8$, Fig. 1a). The abundance of subpopulation j at time $t + 1$ ($N_{j(t+1)}$) is the sum of post-spawners, P_{jt} , and new recruits, $R_{j(t-lag)}$ (with a time lag that represents the age of maturity), from spawning/nursery ground j (Fig. 1b and Eq. (1)).

$$N_{j(t+1)} = P_{jt} + R_{j(t-lag)} \quad (1)$$

The number of post-spawners, P_{jt} , is

$$P_{jt} = (S_{jt} + S'_t)s_a \quad (2)$$

where S_{jt} is the number of spawners from subpopulation j , S'_t is the number of straying adults from neighboring subpopulations that are within a given straying distance (D , see below), and s_a is the survivorship after spawning. The number of spawners from each subpopulation is the product of subpopulation abundance at time t , N_{jt} , homing rate, h ($0 \leq h \leq 1$), and the survivorship before spawning, s_b

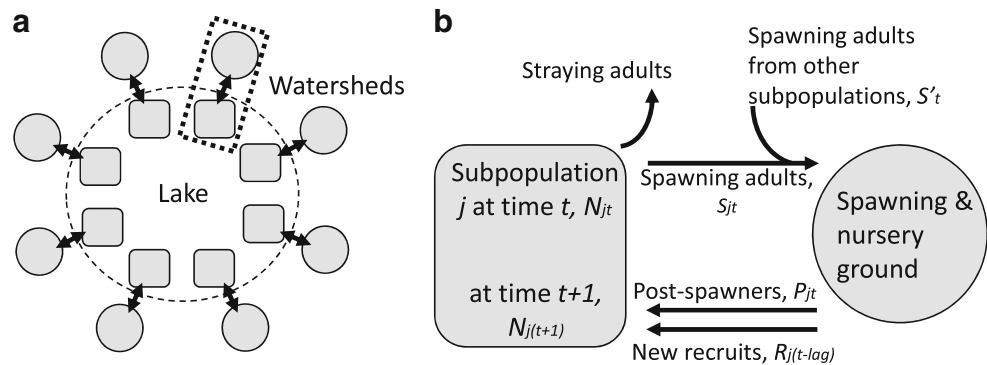
$$S_{jt} = N_{jt}hs_b \quad (3)$$

The number of spawners immigrating from other subpopulations (S'_t) is calculated based on straying distance, the population abundance in neighboring subpopulations, N_{it} ($i \neq j$, $i \in D$), the survivorship before spawning, s_b , homing rate, h , and the relative size of spawning ground j 's carrying capacity among all spawning grounds within the straying distance, D .

$$S'_t = \left(\sum_{i=1}^n N_{it}(1-h)s_b \right) k_j / K_{D-i} \quad (4)$$

In Eq. (4), D represents a set of subpopulations within a given straying distance (n is the number of subpopulations

Fig. 1 The spatial structure of the population model used in this study, which represents a lake-stream system: adult fish use the same water body to feed but migrate to eight separate watersheds to spawn. Panel **b** is the detailed movement between the feeding ground and spawning/nursery ground of a single subpopulation (dotted box in **a**)



except subpopulation j within set D , details in next section), k_j is the carrying capacity in subpopulation j , and K_{D-i} represents the sum of all carrying capacities within set D but without the carrying capacity in spawning/nursery ground i .

The Ricker function (Ricker 1954) was used to model new recruitment from spawning adults,

$$R_{jt} = (S_{jt} + S^t) \left\{ e^{r(1 - ((S_{jt} + S^t)/k_j))} - 1 \right\} \quad (5)$$

where r is intrinsic growth rate and k_j is the carrying capacity of spawning ground j .

Model analysis

First, we modeled species with three levels of straying distance ($D = \text{near, medium, or far}$ in Table 1 and Fig. 2), crossed with three levels of homing rate ($h = 50, 80, \text{ or } 90\%$ in Table 1) to represent a variety of life history combinations. While many wild salmonid populations show homing rates around 80% (e.g., chum *O. keta* and pink salmon) to 90% or more (e.g., Coho *O. kisutch* and Atlantic salmon) and tend to stray to habitats close to their natal streams (Pess et al. 2014), hatchery-origin individuals may have significantly lower homing rates and longer straying distances (Ford et al. 2015; Keefer and Caudill 2014). The estimated homing rate for non-salmonids varies from relatively high in American shad (*Alosa sapidissima*, Pess et al. 2014) and lake sturgeon (*Acipenser fulvescens*, Homola et al. 2012) to relatively low in muskellunge (*Esox masquinongy*, Crossman 1990) and mpasa (*Opsaridium microlepis*, Sungani et al. 2016). However, for most non-salmonid species, there is a lack of direct estimation and systematic review of homing rates. Thus, we used a 50% homing rate to represent a life history between two end points (0 and 100% homing rate). Straying distance “near” means that straying individuals in each subpopulation can migrate to one of the two nearest spawning/nursery grounds ($n = 2$ in Table 1; dark gray circles in Fig. 2a), “medium” means migration to the neighboring four ($n = 4$ in Table 1; dark gray circles in Fig. 2b), and “far” means migration to the

neighboring six spawning/nursery grounds ($n = 6$ in Table 1; dark gray circles in Fig. 2c). Then, two extreme cases were simulated, in which only one type of straying distance was used for each of these two cases: (1) a species that has the ability to explore all spawning/nursery grounds in the system with zero homing behavior ($h = 0\%$ and $D = \text{full}$ in Table 1; i.e., the number of adults migrating to each spawning ground simply is based on the carrying capacity in each spawning ground), similar to sea lamprey (Bergstedt and Seelye 1995; Waldman et al. 2008) and northern pike (*Esox lucius*, Oele et al. 2015) and (2) species with 100% homing rate ($h = 100\%$ and $D = \text{none}$ in Table 1) that represents a species with an extremely low straying rate, such as sockeye salmon (*O. nerka*, Pess et al. 2014). In total, the population dynamics of 11 virtual species were simulated (three levels of straying distance \times three levels of homing rate + two extreme cases).

Because our main goal was to examine the response of a migratory population to barrier removal/construction based on the differences in homing rates and straying distances, other parameters such as the annual survival rate, intrinsic growth rate, carrying capacity for each spawning/nursery ground before barrier removal/construction, and the starting population abundance were set to be the same for all subpopulations (Table 1).

To simulate the long- and short-term effect of barrier removal/construction on population dynamics, we varied the carrying capacity in one of the spawning/nursery grounds ($k = 250, 2250, 3250, \text{ or } 4250$), while the carrying capacity in other spawning/nursery grounds remained the same ($k = 1250$). Then we ran the population model for 100 years and compared the short- and long-term responses. Short-term response in this study was defined as the percent change in population abundance in the first 20 years (around five generations for a species that matures at 4 years, hereafter, short-term abundance change rate), and long-term response was the average abundance in the last 5 years of simulation (i.e., years 96–100, hereafter, equilibrium abundance). A low number was used as the initial abundance for each subpopulation ($N_0 = 10$) because we wanted to examine the short-term response without the interference of overcompensatory fluctuation introduced

Table 1 Parameter values used in the model

Parameter	Value/level	Description
N_0	10	Subpopulation abundance at time 0
s_b	0.9	Annual survival rate before spawning
s_a	1 (iteroparity), 0 (semelparity)	Annual survival rate after spawning
r	0.5 (iteroparity)	Intrinsic growth rate
k	1250	The carrying capacity of each spawning/nursery ground before barrier removal/construction
lag	4	Age of maturity. We used age 4 to represent a variety of migratory fish species (e.g., salmonids, trouts, walleye, suckers, redhorse, pikes, bass, and lampreys).
h	0, 50, 80, 90, 100%	Percentage of homing adults (homing rate). ^a 0% is comparable to sea lampreys and northern pike; 80% for chum and pink salmon; 90% for Chinook (<i>O. tshawytscha</i>), Coho, and Atlantic salmon; 100% for sockeye salmon
D	None, near, medium, far, full	Straying distance. None: all individuals migrated back to their natal origins; near: straying individuals were able to migrate to one of the two nearest spawning/nursery grounds; medium: to one of the four nearest spawning/nursery grounds; far: to one of the six nearest spawning/nursery grounds; full: to any of the spawning/nursery grounds in the system.
n	0, 2, 4, 6	Number of subpopulations within a given straying distance range. $n = 0$ when D is none, 2 when D is near, 4 when D is medium, and 6 when D is far. A species with straying distance full and 0% homing rate was treated as a single population in the system with no subpopulation structure.

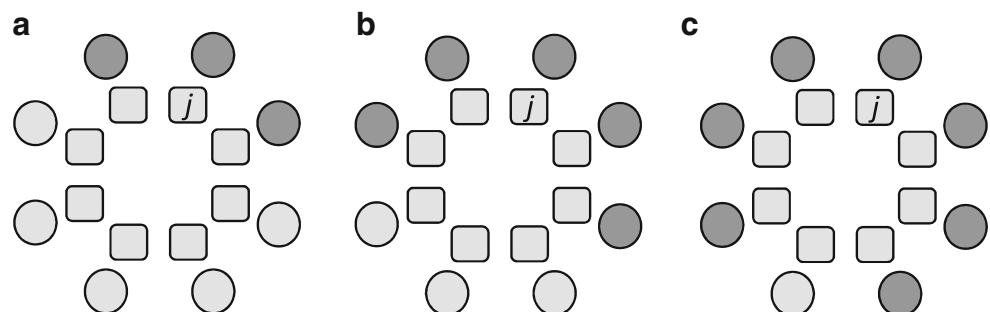
^aWaldman et al. 2008, Pess et al. 2014, Oele et al. 2015

by the Ricker function when the population abundance approaches carrying capacity (Barraquand et al. 2014). We examined responses of (1) the subpopulation that primarily used the reduced or enlarged spawning/nursery ground, and was thus, directly affected by barrier construction or removal (hereafter, target subpopulation), (2) the overall population (the sum of all subpopulations in the system), and (3) the spatial pattern of all subpopulations. For species with no homing behavior, only the responses of the overall population were examined because there is no subpopulation structure for this type of life history. We plotted standardized values as percentage changes in the scenario of interest, relative to the value for the status quo scenario (i.e., when the carrying capacity in every spawning/nursery ground is the same, $k = 1250$ as in Table 1), to examine the difference among subpopulations because we were more interested in relative changes than absolute values.

We varied the post-spawning survivorship to simulate iteroparous ($s_a = 1$) and semelparous ($s_a = 0$) species. While

reducing post-spawning survivorship decreased both the short-term abundance change rate (percent change in population abundance in the first 20 years) and equilibrium abundance (average abundance in years 96–100), similar spatio-temporal patterns were found for both reproductive modes (Figs. 5–10 in the Appendix). Therefore, we only show the results for iteroparous species here. In addition to post-spawning survivorship, we varied the value of other parameters to compare the results. In general, increasing intrinsic growth rate r resulted in a faster short-term abundance change rate and a greater equilibrium abundance (but also increased the annual variation through the Ricker stock-recruitment function). Reducing the age of maturity increased the short-term population abundance change rate, while the equilibrium abundance remained at similar values. However, changing these parameters did not influence the spatial dynamic patterns and relative values among species and subpopulations (Appendix). All simulations and graphs were performed in R (R Core Team 2017).

Fig. 2 Straying distance **a** near, **b** medium, and **c** far for subpopulation j

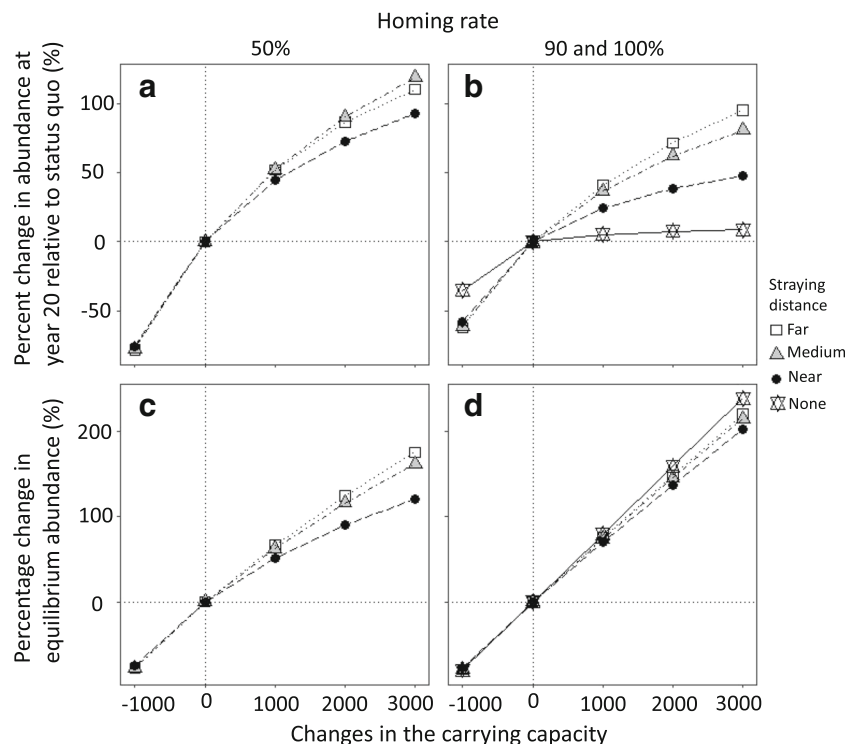


Results

The dynamics of the target subpopulation

For the target subpopulation, both short-term abundance change rate (percent change in population abundance in the first 20 years) and equilibrium abundance increased with increases in carrying capacity in the spawning/nursery ground, but the patterns among species were different (Figs. 3 and 4; the results of 80% homing rate can be found in Appendix Figs. 1 and 2). The short-term abundance change rate of species with lower homing rates and medium to far straying distances were more sensitive to changes in carrying capacity (Figs. 3a and 4a, b). For short-term abundance change rate, species with 50% homing rate and medium straying distance exhibited the greatest rate of change with changing carrying capacity (Figs. 3a and 4a, b). In all other instances, as straying distance and homing rate increased, the percent change in population abundance at year 20 declined (Figs. 3b and 4a, b). In contrast, species that all migrated to their natal origin ($h = 100\%$, $D = \text{none}$) reached the greatest equilibrium abundance when carrying capacity increased, followed by species with 90 and 80% homing rate (Figs. 3d and 4d). The smallest change was found in species with 50% homing rate and short straying distance (Fig. 3c). In general, we found that as straying distance increased, short-term and equilibrium abundances of the target subpopulation increased, but that species with greater homing rates experienced slower initial subpopulation growth, but larger equilibrium abundances.

Fig. 3 The percent change in abundance at year 20 relative to status quo (a, b) and equilibrium abundance (c, d) of the target subpopulation (j) when carrying capacity was reduced (-1000 on the x axis, barrier construction) or increased ($1000\text{--}3000$, barrier removal) in the corresponding spawning/nursery ground. Three levels of straying distance (far, medium, near) were assigned to species with partial homing behavior (50 and 90%), while species with 100% homing rate did not stray (straying distance = none). The horizontal and vertical dotted lines represent status quo (the carrying capacity in every spawning/nursery ground is the same, $k = 1250$ as in Table 1)



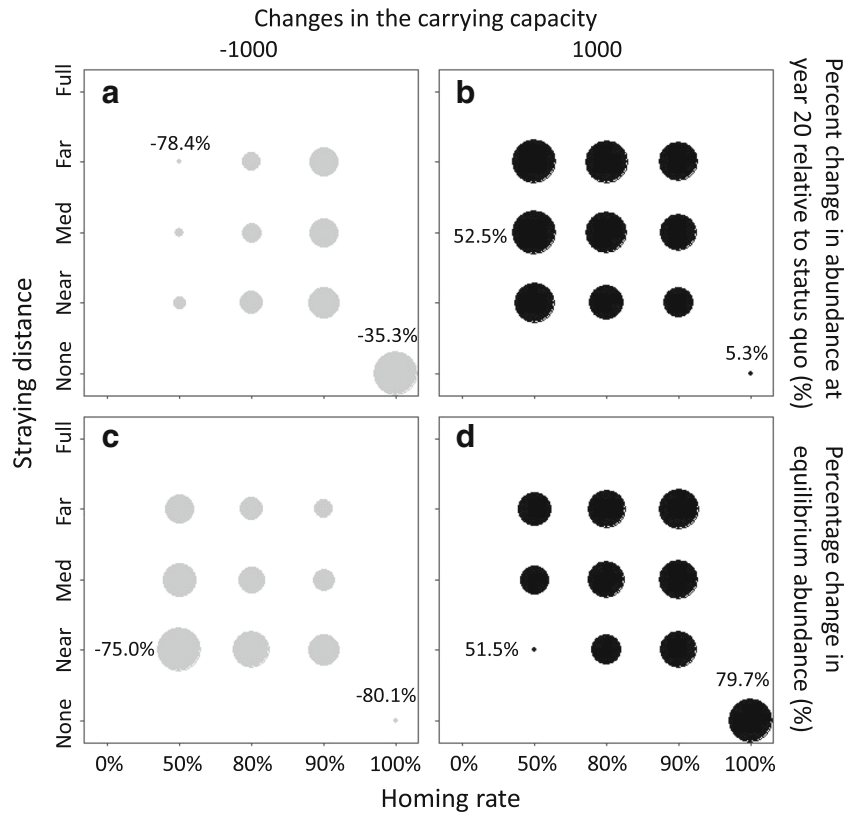
The dynamics of the overall population

For most species, the short-term abundance change rate and equilibrium abundance increased with increased carrying capacity in the target spawning/nursery ground (Figs. 5 and 6). The species with zero homing behavior and the ability to explore every spawning ground in the system showed the highest values in short-term abundance change rate and equilibrium abundance at all levels of carrying capacity (Figs. 5a, c and 6). For the short-term abundance change rate, higher values were observed in species with medium straying distance, closely followed by species with near straying distance, and species with far straying distance (Figs. 5a, b and 6a, b). In contrast, species with higher homing rates (100 and 90%) showed higher equilibrium abundance than species with lower homing rates (80 and 50%, Figs. 5c, d and 6c, d).

The spatial pattern of non-target subpopulations

Among all non-target subpopulations, the short-term abundance change rate (percent change in population abundance in the first 20 years) only showed positive correlation with changes in the carrying capacity in the target spawning/nursery ground for subpopulations that were located closer to the target subpopulation (Figs. 7 and 8, and Appendix Fig. 3). The two subpopulations immediately adjacent to the target subpopulation increased for species with a short straying distance and all

Fig. 4 The percent change in abundance at year 20 relative to status quo (a, b) and equilibrium abundance (c, d) of the target subpopulation (*j*) when carrying capacity was reduced (−1000: a, c) or increased (1000: b, d) in the corresponding spawning/nursery ground. The size of dots represents the relative value within each panel (i.e., larger dots mean higher values) and the color indicates whether the value is larger (black) or smaller (gray) than status quo (0%). Numbers within each panel correspond to the largest and smallest values



levels of homing, as well as species with medium straying distance and a 50% homing rate (Fig. 7a, b). The species with medium straying distance and 50% homing rate also showed positive correlation with carrying capacity in the

next two subpopulations (Appendix Fig. 3a, b). Declining short-term abundance change rate with increasing carrying capacity was found for subpopulations farthest from the target subpopulation, while the level of change varied

Fig. 5 The percent change in abundance at year 20 relative to status quo (a, b) and equilibrium abundance (c, d) of the overall population when carrying capacity was reduced (−1000 on the x axis, barrier construction) or increased (1000–3000, barrier removal) in the target spawning/nursery ground. Three levels of straying distance (far, medium, near) were assigned to species with partial homing behavior (50 and 90%), while species with 100% homing rate did not stray (straying distance = none) and species without homing behavior could explore all spawning grounds in the system (straying distance = full). The horizontal and vertical dotted lines represent status quo (the carrying capacity in every spawning/nursery ground is the same, $k = 1250$ as in Table 1)

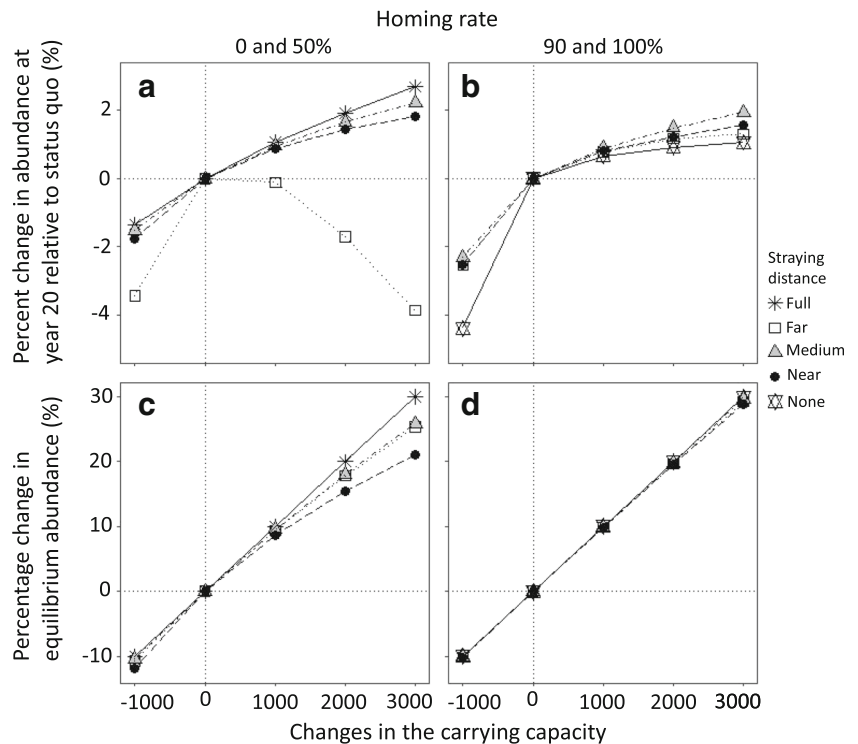
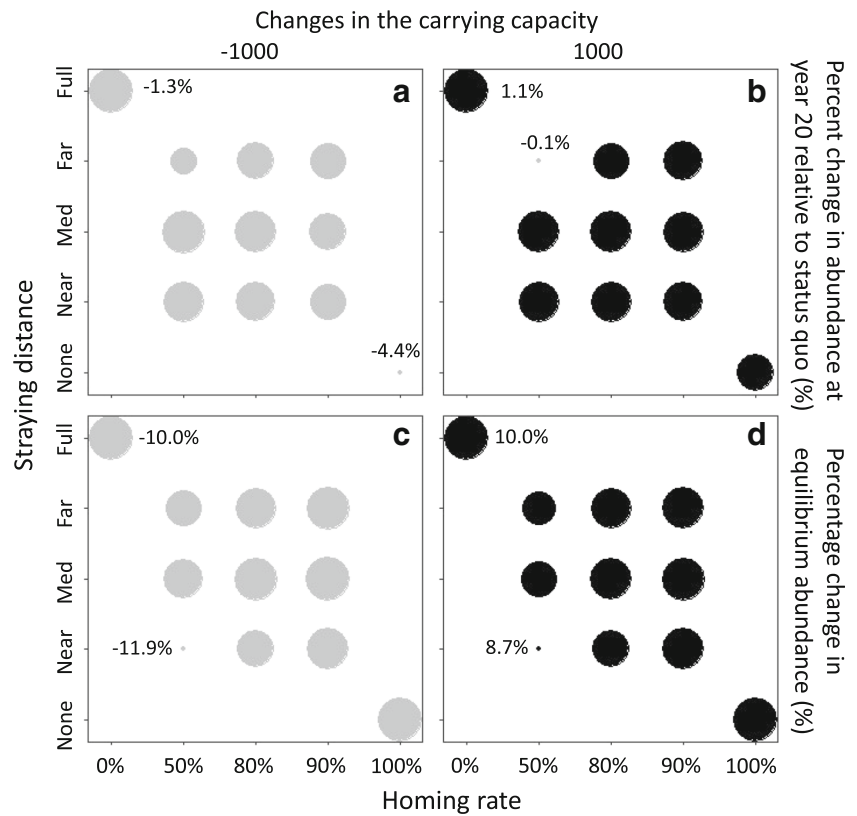


Fig. 6 The percent change in abundance at year 20 relative to status quo (**a, b**) and equilibrium abundance (**c, d**) of the overall population when carrying capacity was reduced (−1000: **a, c**) or increased (1000: **b, d**) in the target spawning/nursery ground. The size of dots represents the relative value within each panel (i.e., larger dots mean higher values), and the color indicates whether the value is larger (black) or smaller (gray) than status quo (0%). Numbers within each panel correspond to the largest and smallest values



with homing rate and straying distance (Fig. 8a, b). Species with 100% homing rate (straying distance: none) showed no change in other subpopulations because there was no interaction between the target and non-target subpopulations (Fig. 8b, d and Appendix Fig. 3c, f).

The correlation between the equilibrium abundance in each non-target subpopulation and the carrying capacity in the spawning/nursery ground of the target subpopulation also varied with the relative location among subpopulations (Figs. 7 and 8 and Appendix Fig. 4). For subpopulations that were closest to the target subpopulation, increasing abundances were observed for all species when carrying capacity increased (Fig. 7c, d). On the contrary, the equilibrium abundance in the farthest subpopulation of all species showed negative correlations with carrying capacity (Fig. 8c, d). For the other subpopulations, the correlation between equilibrium abundance and carrying capacity varied with homing rate and straying distance (Appendix Fig. 4). In general, the straying distance of a species could determine the correlation between each subpopulation and the target subpopulation and homing rate influenced the level of changes. The number of non-target subpopulations that were positively correlated with the target subpopulation increased with the straying distance of a species. For species with higher homing rates, the differences in the equilibrium abundance among non-target subpopulations were lesser than the species with lower homing rates.

Discussion

Our study provides a quantitative method to assess the effect of barrier removal or construction on migratory fish populations, which is comparable to the conceptual model and discussions in Pess et al. (2014). Specifically, our results revealed the population dynamics of species with different life history combinations when one subpopulation experienced a decrease or increase in the size of available spawning/nursery habitat. This model could be used to inform management planning and monitoring projects that include barrier construction or removal to control or restore fish populations.

Implications for management

A careful consideration of the different responses among species of interest (native and invasive) under a particular management action is crucial for multi-species management. Our results suggest that species with lower homing rates might respond to changes in the amount of available spawning/nursery habitat faster than species with higher homing fidelity at both global (Figs. 5 and 6) and local scales (Figs. 3 and 4). The effect of barrier removal on species/populations that lack homing behavior (e.g., sea lamprey and northern pike) could outweigh the benefit of restoring species/populations with strict natal homing (Jensen and Jones 2017). For species with a high homing rate and short straying distance, such as

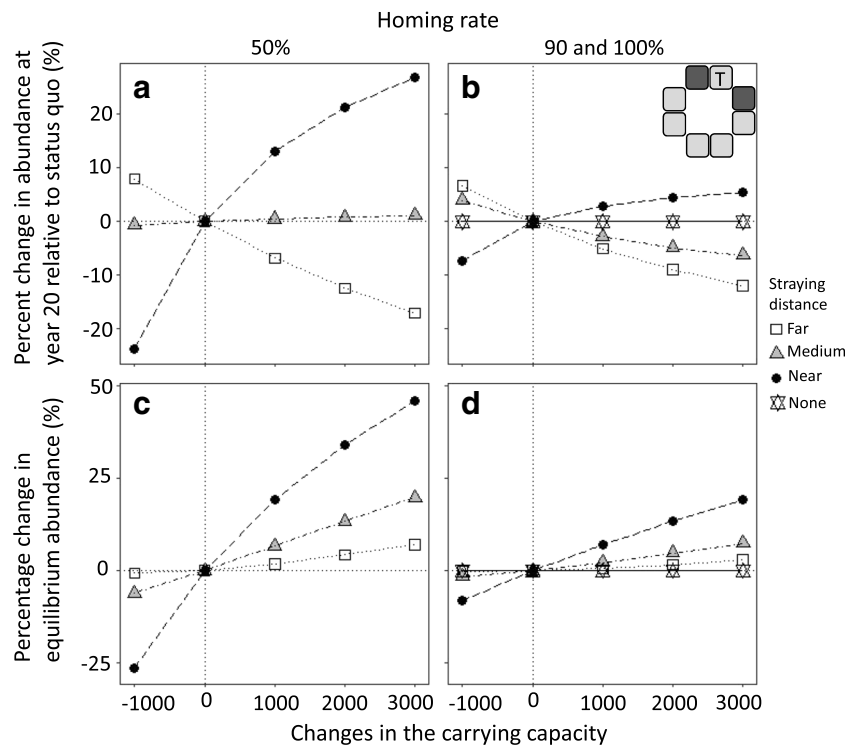


Fig. 7 The percent change in abundance at year 20 relative to status quo (**a, b**) and equilibrium abundance (**c, d**) of the two subpopulations that were immediately adjacent to the target subpopulation when carrying capacity was reduced (−1000 on the x axis, barrier construction) or increased (1000–3000, barrier removal) in the target spawning/nursery ground. Three levels of straying distance (far, medium, near) were assigned to species with partial homing behavior (50 and 90%), while

only one level straying distance (none) was assigned to species with 100% homing rate. The horizontal and vertical dotted lines represent status quo (the carrying capacity in every spawning/nursery ground is the same, $k = 1250$ as in Table 1). The eight boxes on the top of **b** indicate the spatial location of these subpopulations (dark gray boxes) and target subpopulation (*T*)

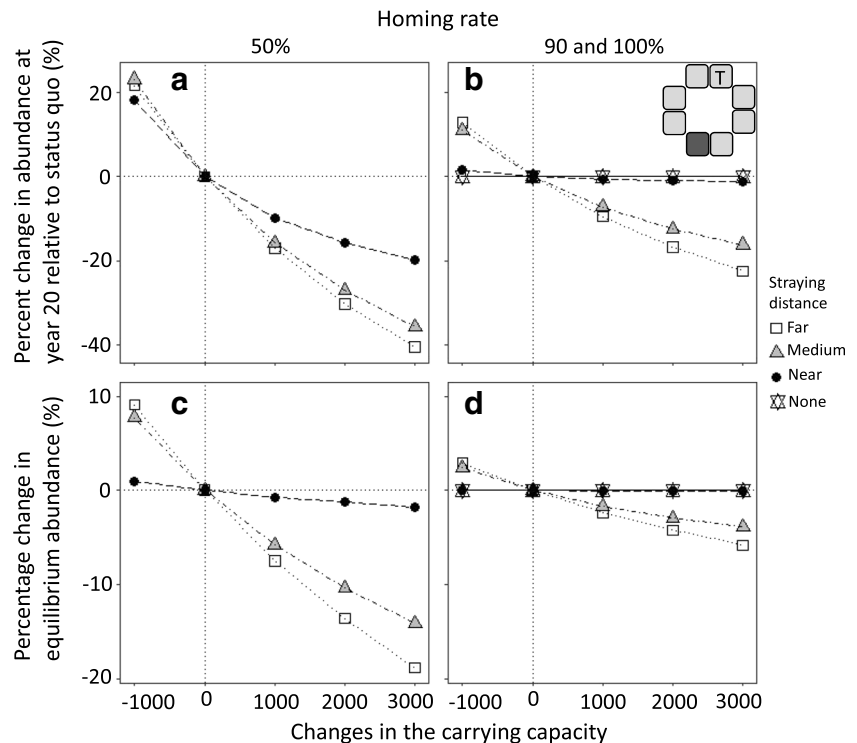
American shad and Coho salmon, reintroduction may be required to accelerate the pace of restoration of the local subpopulation (Figs. 3b and 4b and Pess et al. 2014). The rate of change in short-term population abundance could be validated by empirical monitoring data. For example, the changes in fish communities have been studied by Hogg et al. (2015) and Poulos et al. (2014) for 2 and 3 years, respectively, after the dam was removed. However, these responses might be influenced by other temporal factors, such as the temporary habitat disruption, water temperature change, sedimentation, and contamination during and after dam removal (Foley et al. 2017a). Therefore, it is crucial to apply long-term monitoring to assess the response of fish populations until the habitats stabilize (Brewitt 2016; Foley et al. 2017a, b; McHenry and Pess 2008).

While we acknowledge the importance of collecting long-term monitoring data, our model could be used to predict some possible trajectories of populations with different life history traits. In general, our results indicated that species with higher homing rates might maintain a higher abundance than species with a higher percentage of straying adults in the long run (Figs. 3d, 4d, 5d, and 6d). Interestingly, species with either no homing behavior or complete homing behavior could also reach a high population abundance (Figs. 5c, d and 6c, d). Species that either home completely to their natal habitat or that explore all

spawning grounds in the system likely are able to occupy the newly-opened spawning/nursery habitat at a level closer to the new carrying capacity, relative to species with many straying individuals. For salmonids, a higher homing rate might be a better strategy for species that spawn in rivers with stable environmental conditions among years (Pess et al. 2014). However, long-term fish abundance data from systems in which a barrier has been removed will be needed to confirm this phenomenon.

Besides the temporal scales, simulations showed different responses between the target subpopulation and the overall population, especially for species that have the ability to use distant spawning/nursery grounds. While most studies focus on the response of the local subpopulation to barrier removal (exceptions: Jensen and Jones 2017; Zheng and Hobbs 2013), the strength of connection among spatially separate subpopulations, such as the propensity of adults to stray, could influence how the overall population responds to a local environmental change. Two main differences were identified in our simulations. First, for species that can move to distant spawning grounds, the short-term population abundance change was relatively fast at a local scale but could be slower than status quo at the global scale (e.g., straying distance “far” in Figs. 3 and 4 versus in Figs. 5 and 6). Second, while straying distance and homing rate influenced the sensitivity

Fig. 8 The percent change in abundance at year 20 relative to status quo (**a, b**) and equilibrium abundance (**c, d**) of the subpopulation that is the farthest from the target subpopulation when carrying capacity was reduced (-1000 on the x axis, barrier construction) or increased (1000 – 3000 , barrier removal) in the target spawning/nursery ground. Three levels of straying distance (far, medium, near) were assigned to species with partial homing behavior (50 and 90%), while only one level of straying distance (none) was assigned to species with 100% homing rate. The horizontal and vertical dotted lines represent status quo (the carrying capacity in every spawning/nursery ground is the same, $k = 1250$ as in Table 1). The eight boxes on the top of **b** indicate the spatial location of this subpopulation (dark gray box) and target subpopulation (T)



of target subpopulation response to changes in carrying capacity (e.g., the subpopulation that increased the most with increasing carrying capacity decreased the most with reduced carrying capacity, and vice versa), the relative values of short-term percent change in population abundance and equilibrium abundances were similar among overall populations (e.g., species with higher short-term abundance change rate or equilibrium abundance remained higher among all species regardless of increasing or decreasing carrying capacity, and vice versa). Species-specific modeling and monitoring projects are recommended to further elucidate these differences because the response of the overall population (rather than the dynamic of a local subpopulation) is crucial for controlling invasive species and conserving threatened species (Jensen and Jones 2017; Zheng and Hobbs 2013).

Studies have been conducted to understand the response of target subpopulations and the connections among subpopulations to the removal of barriers (Pess et al. 2014; Schick and Lindley 2007). For example, the proportion of straying adults and the distance from source subpopulations can influence the rate of recolonization in a newly opened habitat (Pess et al. 2012; Schtickzelle and Quinn 2007). However, the dynamics of other subpopulations that are not directly affected by barriers receive less attention (exception see Schick and Lindley 2007). In our study, lower (than status quo) short-term population abundance change rates and long-term equilibrium abundances were predicted, especially in subpopulations beyond the straying range of the target subpopulation (Fig. 8, Appendix Figs. 3 and 4), regardless of the expected benefit to

the target subpopulation and overall population. Our results suggested that the spillover effect (i.e., more straying adults move from the target subpopulation to other subpopulations after barrier removal) might be limited by the straying range of the species. Overall, there might be more fish straying from non-target subpopulations toward the target subpopulation in searching for larger spawning/nursery grounds in a closed system. While we call for more monitoring and modeling research on the dynamics of non-target subpopulations, this effect should be taken into consideration if every subpopulation is managed by different management authorities.

Model generalizations and assumptions

Because our main goal was to assess the influence of homing rates, straying distances, and reproductive modes on population dynamics, we simplified the model by assuming all other life history and habitat related parameters were the same. While these assumptions helped us identify the influence of several key life history traits, it is well-recognized that there are correlations and trade-offs in life history traits. For example, species with lower homing rates may be less specialized for riverine spawning/nursery habitats and have low variation in age of maturity (e.g., pink salmon), while species with higher homing rates are more specialized for spawning grounds and have larger variation in age at maturity (e.g., Chinook salmon; Pess et al. 2014). Furthermore, populations residing in different environments may exhibit different life history traits due to local adaptation. Higher rates of

iteroparity, serial spawning, and batch fecundity are found in northern populations of American shad (Pess et al. 2014). While sea lamprey has a low tendency to colonize new habitats in their native range (Pess et al. 2014), invasive populations in the Laurentian Great Lakes appear to lack homing behavior and are able to quickly occupy new habitats in the system (Jensen and Jones 2017). The potential for among-population differences in life history traits emphasizes the need to obtain species- or population-specific parameter estimates when applying this model to a particular system.

We assumed that the proportion of straying adults moving to adjacent spawning grounds within a given straying range was simply based on the carrying capacity in those spawning grounds. However, if the spatial scale of the system is relatively large and/or the swimming ability of the species is poor, using dispersal kernels to incorporate the gradual effect of distance, such as travel cost, may be more reasonable. Intermediate/mixed patterns between results with different straying distances (between near and medium or medium and far) might be observed under this situation. While in general, most salmonids stray to habitats close to their natal stream, the relation with straying distance among populations is largely unknown, especially for wild populations (Schtickzelle and Quinn 2007). In this study, a fixed homing rate was applied for each species through time, however, the straying rate might vary when population abundance changes if density-dependent dispersal occurs (Haugen et al. 2007; Pess et al. 2012). However, density-dependent dispersal is rarely studied in fish (Amarasekare 2004) and its influence on the homing tendency of migratory fish is seldom addressed.

The spatial structure among subpopulations is more complex in the real world than the circular structure we modeled. While our model could be used as a case study for a lake-stream system, other model structures may be more suitable for other systems, where some subpopulations have more connections and some are more isolated. For example, a linear structure could be used to represent the north-south latitudinal distribution of American shad along the coast. In contrast, network structures are more similar to the subpopulations of pink salmon in Alaska or Chinook salmon in California watersheds. Nevertheless, the simple structure of this model is flexible and could be modified to simulate other types of systems. Finally, the differences in the carrying capacity and asynchronous stochastic variation of each spawning and nursery ground in the real world might weaken the spatial patterns observed in this study.

Future perspective and conclusions

For managing migratory species, it is critical to consider the interaction among local subpopulations, such as straying and metapopulation dynamics, because it could attenuate the link between local abundance and local demographic characteristics (Schtickzelle and Quinn 2007). The differences between spatial

(local and global) and temporal (short-term abundance change rate and equilibrium abundance) scales found in this study highlight the need for monitoring projects that have a broader scope beyond the scale of most existing studies (as discussed in Brewitt 2016; Foley et al. 2017a, b; McHenry and Pess 2008). In addition, further studies on species (or populations) and system-specific parameters (e.g., homing rate, straying distance, post-spawning mortality, stock-recruitment relationship, fishing mortality, subpopulation structure) are required to improve the accuracy of the model and make it more suitable for other species (native and invasive) or systems of interest. The comparison among multiple species might become more important as management and restoration plans move from targeting a single species/subpopulation to multiple species/subpopulations (Hermoso et al. 2015; McKay et al. 2016).

In conclusion, this study demonstrates a way to examine possible population dynamics for migratory species after barrier removal/construction. Our model could be used to assess both short-term and long-term responses of local subpopulations or the overall population, but the results should be compared with monitoring data when available. The results suggested different responses of local subpopulations and the overall population after a change in local carrying capacity. Interestingly, for subpopulations within the same system but beyond the straying distance of the target subpopulation, a lower increase rate and equilibrium abundance might be observed. This information could be critical for prioritizing barrier removal or construction projects when managing multiple species.

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