

# Habitat Size, Recruitment, and Longevity as Factors Limiting Population Size in Stage-Structured Species

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**ABSTRACT:** Surprisingly little research has evaluated how habitat size may limit the population size of species that use different habitats at different stages of their lives. Here we develop simple discrete-time models to describe the population dynamics of species that use separate juvenile and adult habitats. Analytic solutions, model simulations, and elasticity and sensitivity analyses show that adult abundance is only limited by the size of the juvenile habitat when both adult habitat size and recruitment are much larger than juvenile habitat size. Juvenile habitat plays a marginally greater role in limiting population size for species with closed populations, where recruitment is proportional to adult abundance, versus open populations. Because adult populations often accumulate pulses of juveniles, adult habitat size can strongly limit population size over a broad range of parameter values, an effect that increases as the longevity of a species increases. Limited empirical research from a range of taxa supports these model predictions, although few studies were designed to actually test the limiting role of juvenile versus adult habitat. Future research must carefully evaluate whether and how processes at the juvenile stage affect adult abundance, and conservation efforts may be able to use this model to evaluate the cost-effectiveness, *vis-à-vis* increasing adult abundance, of time and money allocated to protecting juvenile habitats.

*Keywords:* habitat limitation, juvenile bottleneck, population limitation, longevity, recruitment limitation, amphibians.

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A primary aim in ecology is to identify the processes and factors that limit the local population size of a species. In response, a rich theoretical literature has developed to examine how population dynamics are affected by age or size structure within populations (e.g., Ebenman and Persson 1988; Gurney and Nisbet 1998; Caswell 2001) and by spatial heterogeneity in parameters such as growth and survival (e.g., Kareiva 1990; Tilman and Kareiva 1997). Relatively few studies, however, have examined how spatially explicit population stage structure (i.e., when different life stages exist in different locations) may affect population size and dynamics. Concomitantly, past empirical work evaluating the importance of habitat features in controlling population size has typically focused on the effects of spatial variation in demographic parameters (e.g., growth, mortality) within a single life stage on the abundance of that life stage (reviewed in Wilbur 1980; Beck et al. 2001). It is then typically assumed that the population is limited by the density-dependent mortality in that stage (i.e., the nursery habitat concept when the focus is the juvenile stage) even though the effect of this early-stage mortality on adult abundance is rarely measured.

Similarly, the importance of recruitment, or larval supply, in controlling population dynamics, particularly for marine species, has long been recognized and addressed in ecological research and represents an important focus on species that use distinct habitats (pelagic vs. benthic for marine examples) during a complex life cycle. However, nearly all of this work has focused on the interaction between recruitment rates (the output from the pelagic life stage) and adult-stage processes, with little attention to factors affecting population size of pelagic larvae (e.g., Roughgarden et al. 1985, 1988). This focus is largely due to the difficulties in tracking and measuring these tiny particles in a huge ocean.

Only recently has research begun to address how spatial variation in demographic parameters at one life stage can affect the population sizes of later life stages (e.g., Beebe et al. 1996; Knapp et al. 1998; Dunham and Rieman 1999; Knutson et al. 1999; Hellriegel 2000; Scribner et al. 2001; Halpern 2004a, 2004b; Mumby et al. 2004), and few stud-

ies have compared the relative role of juvenile and adult stage processes in limiting adult populations. Little work has been done to explore how comparable or general the population dynamics of this broad range of species may be, including many amphibians, marine invertebrates, insects, plants, and aquatic and migratory fishes. In particular, very few research efforts have evaluated whether or how adult populations of marine species are limited by the amount of habitat for earlier stages, even though the size of juvenile habitats is often assumed to limit total population size. For example, the assumed importance of nursery habitat drives conservation and management strategies and practices for many stage-structured species. Legislation recently enacted in the United States requires protection of more essential fish habitats, such as nursery habitats (Magnuson-Stevens Act 1996).

Extreme conditions, where a habitat required by a particular life stage is completely absent or in excessive abundance, set clear boundary limits for how habitat availability affects population size (complete limitation vs. no limitation, respectively). However, the response of population size to relatively small amounts of stage-specific habitat may not be straightforward. In particular, because adult abundance typically accumulates over many recruitment events, the effects of juvenile habitat availability on subsequent adult abundances are unlikely to be linear or obvious. Is it possible to predict when juvenile habitat no longer limits adult abundance?

To begin to address this gap in ecological theory, we develop simple discrete-time, stage-structured models that incorporate a carrying capacity for each life stage based on juvenile and adult habitat size. Using these models, we address how the four model parameters (juvenile and adult carrying capacity, recruitment, and longevity) act and interact to limit population size. In particular, under what range of parameter values is adult abundance most sensitive to changes in juvenile carrying capacity compared to changes in the other parameters, and how does residence time (longevity) in the adult habitat influence the effects of habitat availability on population size? Answers to these questions have important applied implications because conservation and management agencies often have limited resources for protecting critical habitat and therefore need to focus their efforts on life stages or processes that are going to affect adult abundance the most.

### Model

We develop a population model based on the life-history characteristics of species that use distinct habitats for discrete amounts of time at different stages of their lives. As a consequence, there is a clear division between juvenile and adult subpopulations, so that processes in the juvenile

habitat affect population sizes in the adult habitat only through the supply of individuals. To model the dynamics of such populations, we describe juvenile and adult abundance according to the following two equations:

$$J_{t+1} = S_j \left[ 1 - \left( \frac{R_t + J_t}{R_t + J_t + K_j} \right) \right] (R_t + J_t), \quad (1)$$

$$\begin{aligned} A_{t+1} &= S_A \left[ 1 - \left( \frac{A_t + J_t}{A_t + J_t + K_A} \right) \right] (A_t + J_t) \\ &= \frac{S_A \times (A_t + J_t) \times K_A}{A_t + J_t + K_A}, \end{aligned} \quad (2)$$

where  $R_t$  is the number of recruits (i.e., settling larvae or eggs laid) entering a population,  $J_t$  is the number of juveniles that survive to move on to the adult population, and  $A_t$  is the adult abundance, all at time  $t$ . The variables  $K_j$  and  $K_A$  are the carrying capacities of the juvenile and adult habitats, respectively, and  $S_A$  and  $S_j$  are the density-independent survival rates for adults and juveniles, respectively. Density-dependent mortality in both stages is a modified form of the logistic equation (see below). For simplicity we focus on a two-patch model (a single juvenile and adult habitat), although some species use more than two habitats.

Here we consider only those species where the juvenile stage is brief relative to the average adult life span and involves little or no overlap between juvenile generations (i.e., the juveniles either migrate to the adult habitat or die at the end of each time step such that  $S_j = 1$  and  $J_t = 0$ ), allowing equation (1) to be simplified to

$$J_{t+1} = R_t \left[ 1 - \left( \frac{R_t}{R_t + K_j} \right) \right] = R_t \left( \frac{K_j}{R_t + K_j} \right). \quad (3)$$

Common species with a relatively short juvenile period include many marine fish and invertebrates with planktonic larvae that settle from the plankton to distinct juvenile habitats before migrating to adult habitats, most amphibians, and many anadromous and catadromous species. We use adult density-independent mortality ( $S_A$ ) to scale the longevity of a species; in the absence of density dependence, adult longevity is simply  $1/(1 - S_A)$  time steps. Using this relationship, we explore how the longevity of a species interacts with habitat availability to affect population size. Plants and insects, which often have long juvenile stages relative to the adult stage, can be modeled by setting  $S_A = 1$  and adjusting the value of  $S_j$ , but we do not explicitly consider these species here.

Since dispersal of juveniles away from their natal site

varies enormously among species (Kinlan and Gaines 2003), we simplify the evaluation of propagule dispersal by considering two extreme cases: open populations, where juveniles recruit from a regional adult population and the rate of recruitment to the local juvenile habitat,  $R_p$ , is assumed to be constant; and closed populations, where all juveniles are assumed to be offspring of local adults and recruitment is defined as  $R_{t+1} = c \times A_t$ . Although fecundity clearly varies with age (size) in most species, we begin with the simplifying assumption of constant birth rates. At the scale of local juvenile and adult habitats, many marine species are thought to have largely open population dynamics (Caley et al. 1996; Cowen 2002; Mora and Sale 2002; but see Jones et al. 1999; Swearer et al. 1999) such that local recruitment is independent of local adult abundance. The closed population model is likely most appropriate for many amphibians and anadromous fish and for marine species whose larvae disperse short distances relative to the habitat scales (direct developers and species with very short planktonic larval durations; see Kinlan and Gaines 2003). Although similar in concept to the models developed by Roughgarden and colleagues (Roughgarden et al. 1985, 1988) and Hellriegel (2000), the model developed here focuses explicitly on density-dependent mortality rates (driven by habitat size) in both the juvenile and adult stages and allows for populations to be open or closed with respect to propagule dispersal.

Density-dependent mortality occurs in each life stage as a function of the carrying capacity of the available habitat at each stage. Carrying capacity is assumed to be directly related to the size of a habitat such that changes in  $K$  equate to changes in habitat size. Carrying capacity could similarly be a function of habitat quality (e.g., food resource availability within a habitat) without changing the results or general conclusions derived from the model. Density-dependent mortality is assumed to occur at the end of each time step so that new recruits to the juvenile habitat and new juveniles entering the adult habitat are counted when calculating the intensity of density-dependent mortality. Equations (1) and (2) reflect this assumption by using the sum of  $R_t$  and  $J_t$  or  $A_t$  and  $J_p$  respectively, as the population size that experiences density-dependent mortality. Carrying capacity ( $K$ ) is reached (asymptotically) only when input rates are extremely large relative to  $K$ , which means that juvenile and adult habitats are rarely filled completely.

### Methods

The population model described above was used to evaluate the consequences of equilibrium adult abundance to changes in juvenile carrying capacity ( $K_j$ ) and adult carrying capacity ( $K_A$ ) across parameter values ranging three

orders of magnitude. We also varied recruitment ( $R_i$ ) across a broad range of values either by directly altering the recruitment rate for open populations or by modifying the reproductive parameter ( $c$ ) for closed populations. The range of model parameter values (three orders of magnitude) used here was chosen to encompass the natural range of variation commonly found in recruitment and habitat availability. To remove a parameter as a potential limiting factor, when needed, we set its value to 5,000 (generally twice as high as the largest value of any other parameter value). Density-independent mortality ( $S_A$ ) can range from 0 to 1, but we focused on values of  $S_A = 0.5$ – $0.98$  such that the average longevity of individuals in the population is two to 50 times (respectively) the duration of the juvenile time step. These values represent reasonable natural extremes.

We also performed a type of elasticity analysis (de Kroon et al. 2000; Link and Doherty 2002) for the three model parameters of most relevance to management ( $K_j$ ,  $K_A$ , and  $R_i$ ) to examine how adult abundance responds to similar percentage changes in the three parameters. We focus on the open population model for these analyses, although simulation results (see below) indicate that the results for closed populations should be very similar. For these analyses, the relative effects of an arbitrary 10% change in  $K_j$ ,  $K_A$ , and  $R_i$  (for the open population) across the entire range of possible values on equilibrium adult abundance were evaluated at three values of  $S_A$  ( $S_A = 0.5, 0.9, \text{ and } 0.98$ ), which represent longevities of two, 10, and 50 times the juvenile time step (i.e., short, medium, and long life spans). Results were then scaled to  $K_j$  for presentation in two dimensions. Because conservation and management efforts to protect habitat in order to enhance declining populations typically must be made with limited budgets (i.e., only small pieces of additional habitat can be set aside), we also conduct sensitivity analyses to test the effect on adult abundance of equivalent absolute changes in  $K_j$  and  $K_A$ .

## Results

### *Analytic Solutions*

At equilibrium, juvenile abundance ( $\hat{J}$ ) for open populations is simply

$$\hat{J} = R \left[ \frac{K_j}{R + K_j} \right], \quad (4)$$

such that changes in  $R$  or  $K_j$  have equivalent effects on the number of juveniles that move on to the adult population. For most open population results below, we present situations where  $R$  was held constant while  $K_j$  varied.

Equivalent results would arise if  $K_j$  were held constant while  $R$  varied. If  $R$  and  $K_j$  differ substantially in magnitude,  $\hat{J}$  converges on whichever parameter is smaller. If  $R \ll K_j$ , then  $\hat{J} = R$ , and if  $R \gg K_j$ , then  $\hat{J} = K_j$ .

Adult abundance at equilibrium ( $\hat{A}$ ) for open populations is

$$\hat{A} = \frac{-\hat{J} + K_A - S_A \times K_A + \sqrt{(\hat{J} + K_A - S_A \times K_A)^2 + 4(S_A \times \hat{J} \times K_A)}}{2}. \quad (5)$$

As described above, changes in the value of  $K_j$  have a large effect on  $\hat{J}$  only when  $K_j$  is small relative to  $R$ , and so  $\hat{A}$  can be limited only by  $K_j$  when  $K_j$  is small relative to  $R$ . This result is intuitively obvious because juvenile habitat will never be saturated if recruitment rates are small. Similarly, we can use boundary conditions to further simplify equation (5). Assuming a long life span ( $S_A \approx 1$ ), recruitment-limited species (i.e.,  $R_t \ll K_j$ ) will have

$$\hat{A} \cong \frac{-R + \sqrt{R^2 + 4(R \times K_A)}}{2}. \quad (6)$$

If  $K_A$ , like  $K_j$ , is large relative to the recruitment rate, the equilibrium adult population size will be approximately

$$\hat{A} \cong \sqrt{R \times K_A}.$$

In this situation, population size scales as the square root of the adult carrying capacity.

If recruitment is high relative to the available juvenile habitat (i.e.,  $R_t \gg K_j$ ), then equilibrium adult abundance is

$$\hat{A} \cong \frac{-K_j + \sqrt{K_j^2 + 4(K_j \times K_A)}}{2}. \quad (7)$$

Consequently, if juvenile habitat is rare relative to adult habitat (i.e.,  $K_j \ll K_A$ ),

$$\hat{A} \cong \sqrt{K_j \times K_A}.$$

Adult abundance is approximately the geometric mean of the juvenile and adult carrying capacities, which will change very slowly with increases in  $K_A$  if  $K_j$  is substantially smaller. For example, if  $K_j = 0.1K_A$ , then  $\hat{A} = 0.01K_A$ .

For closed populations, juvenile abundance ( $\hat{J}$ ) is

$$\hat{J} = c \times \hat{A} \left[ \frac{K_j}{c \times \hat{A} + K_j} \right]. \quad (8)$$

The corresponding adult abundance at equilibrium ( $\hat{A}$ ) is

$$\hat{A} = \frac{-y + \sqrt{y^2 + 4(x \times z)}}{2 \times x}, \quad (9)$$

where  $x = c$ ,

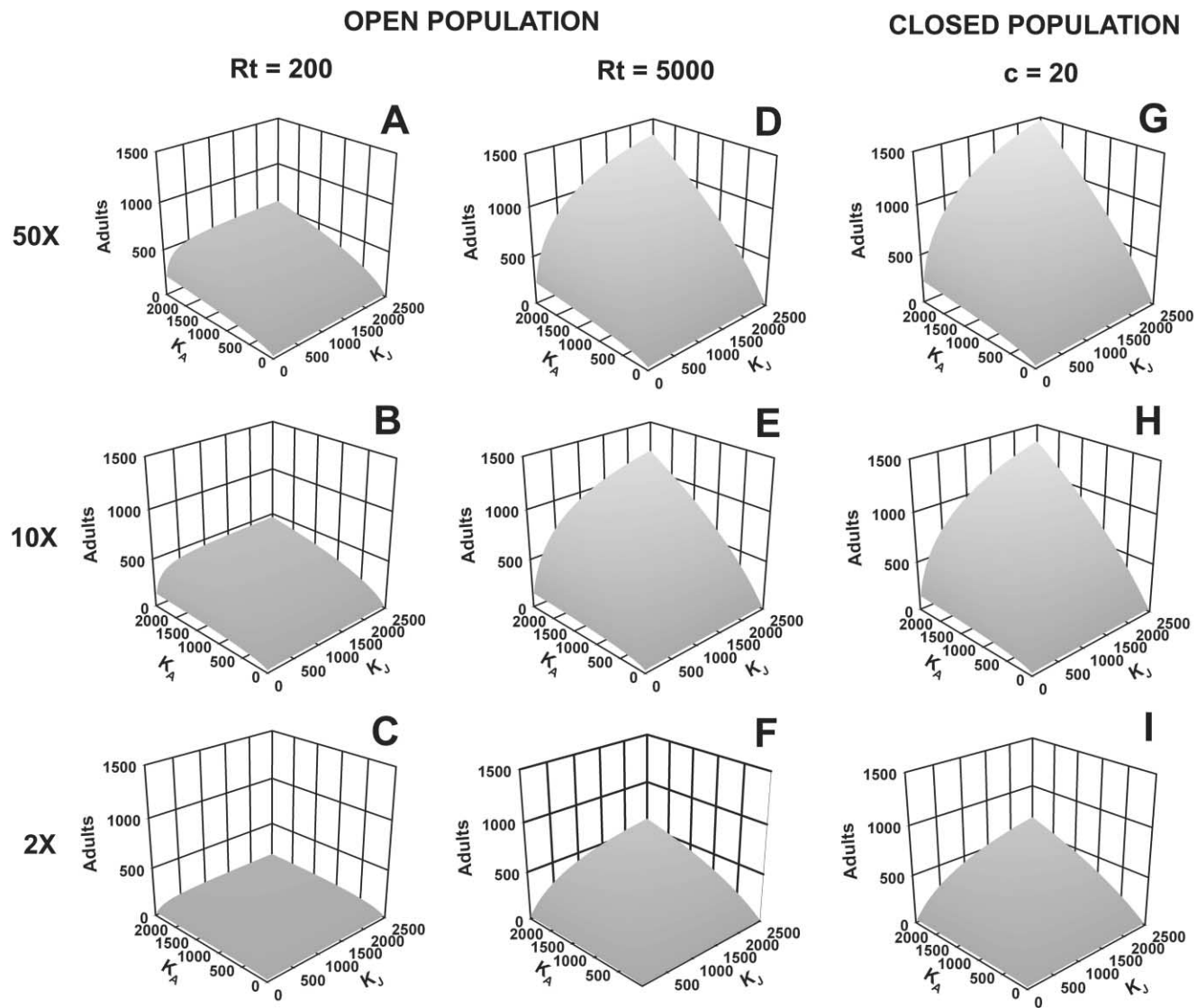
$$y = K_A \times c + K_j \times c + K_j - S_A \times K_A \times c, \quad (10)$$

$$z = K_A \times K_j - S_A \times K_A \times K_j \times c - S_A \times K_A \times K_j. \quad (11)$$

These equations have no simple solution, and so we use model simulations to evaluate how the different parameters affect adult abundance. Model simulations also provide insight into model behavior between these boundary conditions, a primary goal of this article.

### Model Simulations

Both juvenile ( $K_j$ ) and adult ( $K_A$ ) carrying capacity can limit equilibrium adult abundance ( $\hat{A}$ ), although the parameter space in which  $K_j$  limits population size is relatively small (all plots in fig. 1). When recruitment is very high and therefore not a limiting factor (fig. 1D–1F) and where per-adult reproductive output is high enough to remove it as a limiting factor (fig. 1G–1I; see also below), the regions where  $K_A$  or  $K_j$  limit  $\hat{A}$  are clearly defined. For example, when  $K_j$  is high, changes in  $K_A$  lead to proportional changes in the adult abundance (i.e.,  $K_A$  is the limiting factor). Plateaus along only one axis of the surface indicate a strong limiting role of the other parameter; when  $K_A$  is very small, changes in  $K_j$  have little to no effect on equilibrium adult abundance, yet adult abundance scales nearly linearly with  $K_A$  (all cases of fig. 1). A true plateau (across both axes) indicates where recruitment limits population size, as in the back corners of figure 1A–1C. Furthermore, changes in the slope of the surface, as occurs when  $K_A$  is large and  $K_j$  is small but increasing (lower left corner of plots in fig. 1), identify regions of relatively abrupt transition in the cause of population limitation and represent the only parameter space where  $K_j$  limits population size. These shifts in the identity of the limiting factor for population size are quantified in the elasticity analyses described below. For most other parameter values,  $K_A$  is the dominant limiting factor, except when recruitment is very low and  $K_j$  and  $K_A$  are relatively large such that recruitment also limits population size (true plateaus in fig. 1A–1C). These results parallel the analytical solutions above.



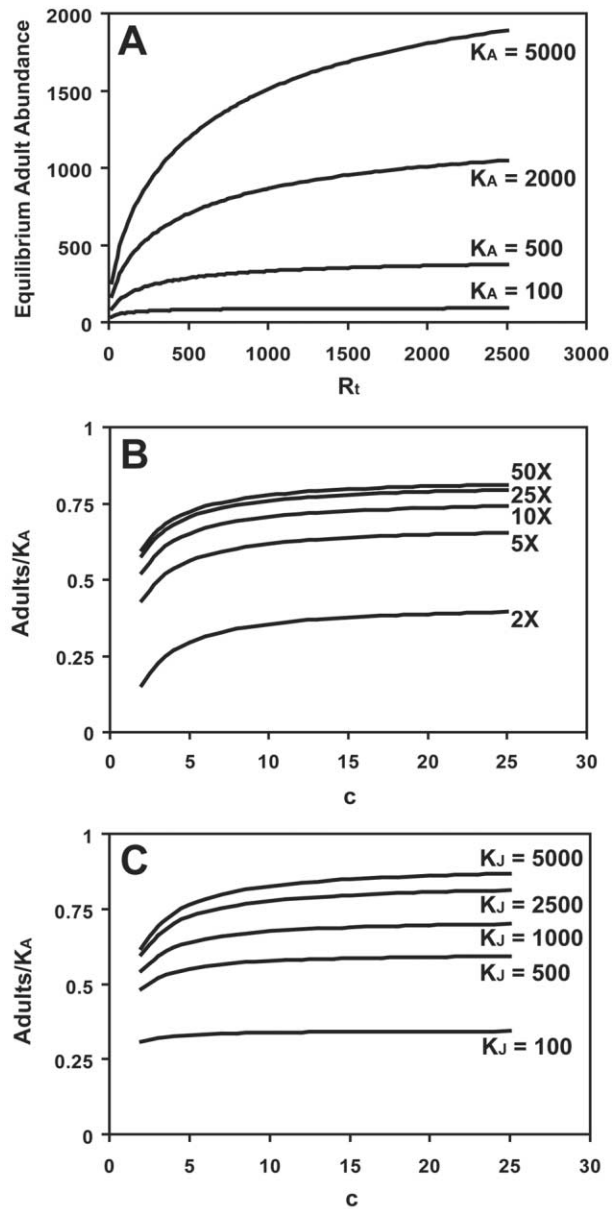
**Figure 1:** Three-dimensional plots of equilibrium adult abundance (*Adults*) as a function of juvenile ( $K_J$ ) and adult ( $K_A$ ) carrying capacity, with different values of longevity (*rows*) and recruitment (*columns*). Closed populations have the reproductive constant ( $c$ ) set at 20 such that it is not a limiting factor.

Interestingly, lowering recruitment rates from high to medium levels had little effect on adult abundance, despite having significant effects on juvenile abundance (see eq. [1]) regardless of the size of the adult habitat ( $K_A$ ; fig. 2A). Only when recruitment is very low did it significantly limit adult abundance (fig. 2A). Similarly, closed populations are limited by per capita reproductive output ( $c$ ) only when it is relatively small ( $c < 10$ ) regardless of the longevity of the species (fig. 2B) or the amount of juvenile habitat (fig. 2C).

Warner and Hughes (1988) have noted that increasing adult longevity increases the number of recruitment pulses that are accumulated in the adult stage, effectively increasing the storage potential of the adult population. Model simulations indicate that the effect of longevity on adult abundance is greatest when species are relatively short-lived; that is, small changes in longevity have a proportionately larger effect on the storage potential regardless of whether the population has open or closed reproduction (fig. 3). If species are long-lived with a high storage potential, increasing the longevity of the species has a relatively small proportional effect on the storage potential of the population and therefore has little effect on  $\hat{A}$  (fig. 3). This relationship between carrying capacity and longevity can also be seen in figure 1. When recruitment is not limiting (fig. 1D–1F), changes in longevity have dramatic effects on adult abundance when  $S_A$  is small and both  $K_J$  and  $K_A$  are relatively large but have little effect when  $K_J$  and  $K_A$  are small regardless of the longevity of the species. Consequently, changes in longevity have a nonlinear effect on the equilibrium adult abundance, with the most dramatic effects on population size occurring when  $S_A$  is small. This result holds whether the population is open or closed and has important implications for conservation and management efforts, as we discuss below.

*Elasticity and Sensitivity Analyses*

Given the strong similarities between simulations of open and closed populations, we focus our elasticity and sensitivity analyses on open populations. There are several key results from elasticity analyses. First, all three parameters are dominant limiting factors in unique regions of parameter space, although juvenile carrying capacity occupies a relatively small portion of the space (fig. 4). However, this small region where juvenile habitat size limits adult abundance could represent a large proportion of real populations if juvenile habitats are commonly quite small relative to adult habitats (see “Discussion” below). This may in fact be the case for many natural populations (table 1). Second, increases in longevity increase the region of



**Figure 2:** Effect of recruitment ( $R_t$ ) on equilibrium adult abundance. In open populations (A), recruitment strongly limits equilibrium adult abundance when  $R_t$  is small, regardless of the size of the adult habitat ( $K_A$ ). In closed populations, equilibrium adult abundance (measured here as a fraction of  $K_A$ ) is limited by the reproductive output per adult ( $c$ ) only when  $c$  is small, regardless of species longevity (B) or the size of the juvenile habitat (C).

parameter space where  $\hat{A}$  is most sensitive to  $K_A$  and decrease the region of sensitivity to  $K_J$  and  $R_t$  (fig. 4) because of its effect on the storage potential of the adult stage. Third, the junction of the isoclines shows where adult abundance is affected similarly by all three parameters (fig.

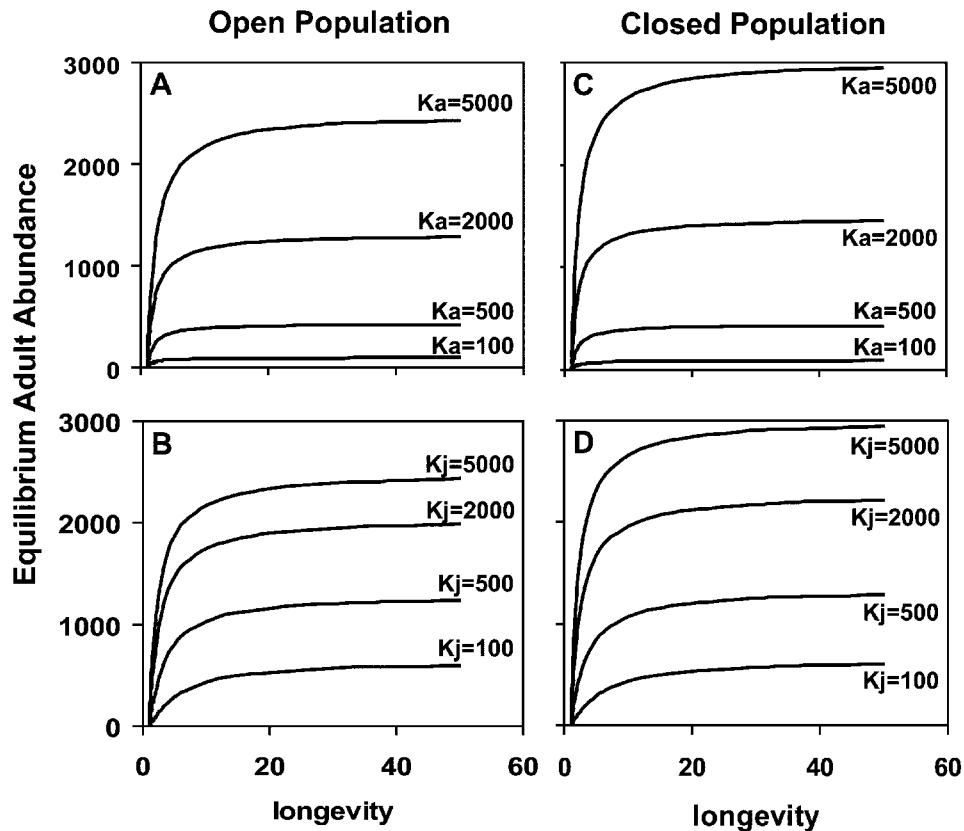


Figure 3: Effect on adult abundance of interactions between carrying capacity ( $K_j$  and  $K_a$ ) and longevity in open (A, B) and closed (C, D) populations. Variable  $K_j$  is removed as a limiting factor ( $K_j = 5,000$ ) in A and C;  $K_a$  is removed as a limiting factor ( $K_a = 5,000$ ) in B and D.

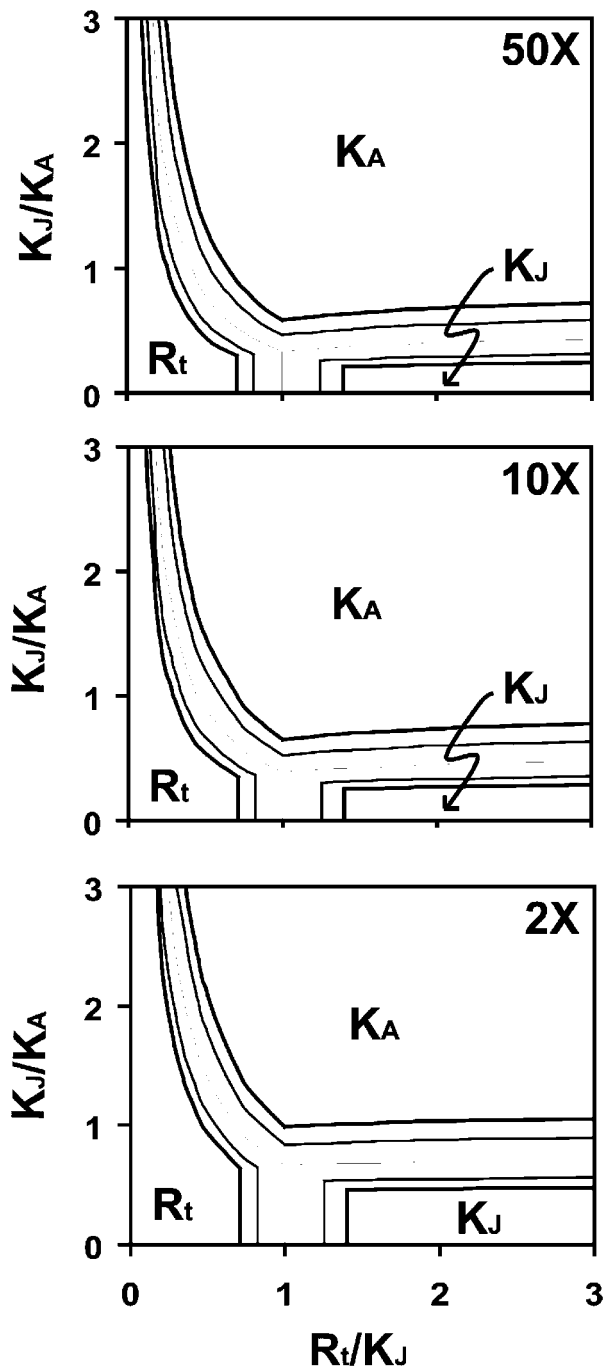
4). In this region of parameter space, all three factors limit population size. Manipulations of any single parameter would lead to significant changes in population size, and as a consequence, experiments that only focus on the effects of a single parameter on  $\hat{A}$  could be easily misinterpreted.

Sensitivity analyses show the effect on adult abundance of equivalent absolute (rather than relative) changes in  $K_j$  or  $K_a$ . Such analyses approximate management scenarios when there are sufficient resources to protect or restore only a given amount of habitat area, requiring that a choice be made between juvenile and adult habitats (or small amounts of both). We simulated the addition of 100 units (e.g.,  $m^2$ , hectares,  $km^2$ ) of either juvenile or adult habitat and found that only when  $K_a$  is relatively small does adult abundance respond significantly to increases in either  $K_j$  or  $K_a$ , with the greatest response when  $K_j$  is large and  $K_a$  is small (fig. 5). Increasing longevity decreases the effect on  $\hat{A}$  of changing  $K_j$  but does not affect how  $K_a$  interacts with changes in  $K_j$  to increase adult abundance.

## Discussion

Not surprisingly, we have shown that all three key parameters—recruitment, juvenile carrying capacity, and adult carrying capacity—can play a critical role in limiting adult abundance, depending on the relative values of these parameters. In particular, factors affecting early life stages, such as juvenile habitat availability, can limit adult abundance regardless of the life span of the species, but only within a limited parameter space.

This result has broad consequences for efforts to understand the population dynamics of stage-structured species and is particularly important for spatially oriented conservation and resource management efforts. A long history of debate exists about the potential role of recruitment in limiting population sizes of marine species (reviewed in Chesson 1998; Doherty 2002), but researchers and policy practitioners have generally assumed, with little theoretical or experimental confirmation, that factors affecting the juvenile stages of a species' life history (e.g., nursery habitats, essential fish habitats, etc.) limit adult or



**Figure 4:** Contour plots for elasticity analyses of the effect of 10% changes in recruitment ( $R_t$ ), juvenile carrying capacity ( $K_J$ ), and adult carrying capacity ( $K_A$ ) on equilibrium adult abundance ( $\hat{A}$ ). Each plot is for a specific value of longevity (50X, 10X, and 2X), but all plots are independent of absolute values of  $R_t$ ,  $K_J$ , or  $K_A$  because axes are presented as ratios. Contour lines show where parameter values have an equal (light lines), 1.5:1 (medium-weight lines), and 2:1 (bold lines) effect on  $\hat{A}$  relative to the adjacent parameter. Regions where single parameters play a dominant role in limiting  $\hat{A}$  are labeled on the plots.

overall population size (although a few notable exceptions exist; see table 1). At the boundary (no juvenile habitat), this must be true. But what is the proper ratio of juvenile to adult habitat to maximize production?

For research and conservation efforts aimed at anadromous fish and amphibians, where there is a fairly long history of recognizing the importance of juvenile habitat in regulating population size, surprisingly little work has actually tested the effect on adult abundances of changing the relative size of the juvenile habitat, and even fewer studies have compared the relative effect of juvenile versus adult habitat on limiting population size (table 1). We show here that juvenile habitat availability limits adult abundance in a relatively small region of parameter space compared with the regions where recruitment and adult carrying capacity are limiting. Importantly, the model can be used to predict under what relative parameter values any particular parameter will no longer limit population size (i.e., where thresholds exist). For example, when recruitment is relatively small, as may be true if many species are recruitment limited, juvenile habitat availability may not affect adult abundance unless such habitat is extremely scarce.

Although not exhaustive in its review, table 1 and the studies presented there offer several other important tests of model predictions. For species with open population dynamics and a long life span (e.g., marine fishes), adult populations appear to be limited by juvenile habitat size only when that habitat was extremely scarce relative to the amount of adult habitat available, as predicted by the model. For species with open population dynamics but a short adult life span (e.g., hermit crabs), adult habitat size played a key role in limiting adult abundance, again as predicted by the model. Results were similar for closed populations (e.g., amphibians and salmonids). When  $K_J$  was very small relative to  $K_A$  (two salmonids and several amphibians in table 1), populations were limited by  $K_J$ . As  $K_J$  increased and  $K_A$  varied in size (e.g., several amphibians in table 1), populations were instead limited by  $K_A$ . However, in only a few cases did the research involve experimental manipulations of habitat size, and only one study (based on correlations; Halpern 2004b) has explicitly tried to determine the size at which juvenile habitat no longer limits population size.

Results from our model simulations highlight the importance of measuring changes in adult abundance when assessing the limiting role of various population parameters. Increases in recruitment or juvenile carrying capacity always translated into proportionate increases in the number of juveniles at a given time step (via eq. [1]) but had a significant effect on adult abundance much less frequently. Most studies attempting to document the importance of juvenile habitats in limiting overall population

**Table 1:** Species with spatially discrete, stage-structured population dynamics, life-history traits, and evidence for where limitation occurs

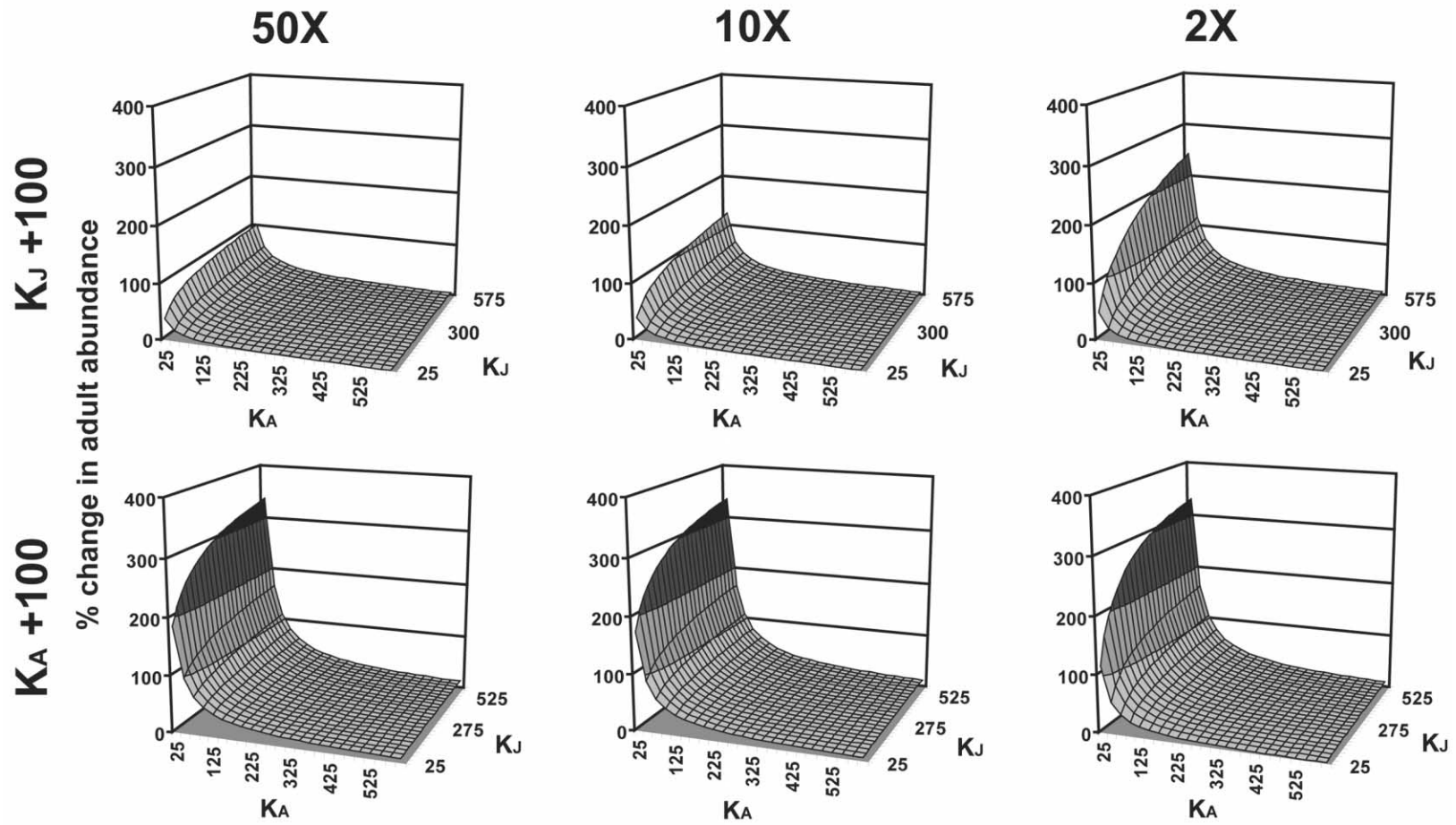
Taxa	Juvenile residence time	Recruitment frequency	Maximum life span	$K_j$	$K_A$	Limiting stage	Both habitats evaluated?	Method	Reference
Marine species:									
Fish:									
<i>Lutjanus apodus</i>	1–2 months	Monthly	>10 years	Varied	Large	$K_j, K_A?$	N	Correlations	Halpern 2004b
<i>Gerres cinereus</i>	1–2 months	Monthly	>5 years	Varied	Large	$K_j, K_A?$	N	Correlations	Halpern 2004b
<i>Scarus guacamaia</i>	?	?	Long	Varied	Medium	$K_j$	N	Correlations	Mumby et al. 2004
<i>Totoaba macdonaldi</i>	2–3 months	4–6 times/year	~25 years	Varied	Medium	$K_j?$	N	“Natural” experiment	Cisneros-Mata et al. 1995
Crabs:									
<i>Pagurus samuelis/hirsutisculus</i>	2–3 months	4–6 times/year	1–2 years	Varied	Varied	$K_A, R$	Y	Experiments	Halpern 2004a
<i>Menippe mercenaria/adina</i>	?	?	~10 years	Varied	Varied	$K_A$	Y	Experiments	Beck 1995
Salmonids:									
Anadromous:									
<i>Salmo trutta</i>	2–3 years	1/year	4–5 years	Varied	Large	$K_j$	N	Natural experiment	Elliott 1985
Freshwater:									
<i>Oncorhynchus mykiss aguabonita</i>	~1 month	1/year	~6 years	Varied	Medium	$K_j$	N	Correlations	Knapp et al. 1998
<i>Salvelinus confluentus</i>	2–3 years	1/year	~8 years	Small	Medium	$K_A$	N	Correlations	Dunham and Rieman 1999
Amphibians:									
<i>Bufo calamita</i>	<40 days <sup>a</sup>	Several/year <sup>a</sup>	10–12 years <sup>b</sup>	Varied	Medium	$K_j$	Y	Correlations/experiments	Beebee et al. 1996
<i>Bufo calamita</i>	<40 days <sup>a</sup>	Several/year <sup>a</sup>	10–12 years <sup>b</sup>	Small?	Varied	$K_A, K_j?$	N	Experiments	Golay 1996
<i>Bufo bufo</i>	<40 days <sup>a</sup>	1/year	>10 years	Varied	Medium	$K_A, K_j?$	Y	Correlations	Scribner et al. 2001
<i>Rana sylvatica</i>	~2.5 months	1/year	~3 years	Varied	Large	$K_j$	N	Correlations	Berven 1990
<i>Rana sylvatica</i>	~2.5 months	1/year	~3 years	Varied	Large	$K_j$	N	Correlations	Berven and Grudzien 1990
<i>Rana sylvatica</i>	~2.5 months	1/year	~3 years	Medium?	Varied	$K_A$	N	Correlations	Gibbs 1998
<i>Rana lessonae</i>	1–4 months	1/year	?	Varied	Large	$K_j, K_A?$	Y	Experiments	Altwegg 2003
<i>Physalaemus pustulosus</i>	3–5 weeks	5–12/year	1 year	Varied	Medium	$K_j, K_A?$	N	Experiments	Marsh 2001
<i>Dendrobates pumilio</i>	~3 weeks <sup>c</sup>	1–3/year <sup>c</sup>	~16 years <sup>c</sup>	Varied	Large	$K_j$	N	Experiments	Donnelly 1989
<i>Notophthalmus v. viridescens</i>	3–4 months <sup>c</sup>	1/year <sup>c</sup>	12–15 years <sup>c</sup>	Medium?	Varied	$K_A$	N	Correlations	Gibbs 1998
<i>Gastrophryne carolinensis</i>	3–9 weeks	1/year	6 years	Small?	Varied	$K_A, K_j?$	N	Experiments	Golay 1996
<i>Ambystoma opacum</i>	3–6 months	1/year	>6 years	Varied	Large?	$K_j$ (weak)	N	Experiments	Scott 1994
<i>Ambystoma maculatum</i>	~3 months <sup>d</sup>	1/year <sup>d</sup>	~25 years <sup>d</sup>	Medium?	Varied	$K_A$	N	Correlations	Gibbs 1998
Mix of eight spp.	Variable	1/year	Variable	Varied	Varied	$K_A, K_j$	Y	Correlations	Knutson et al. 1999

<sup>a</sup> Banks and Beebee 1988.

<sup>b</sup> <http://www.offwell.free-online.co.uk/toads2.htm#Lifespan>.

<sup>c</sup> [http://animaldiversity.ummz.umich.edu/site/accounts/information/Dendrobates\\_pumilio.html](http://animaldiversity.ummz.umich.edu/site/accounts/information/Dendrobates_pumilio.html).

<sup>d</sup> Silver et al. 1999.



**Figure 5:** Percent change in equilibrium adult abundance as a result of equivalent absolute changes in  $K_J$  or  $K_A$  at three values of longevity. Recruitment,  $R_i = 5,000$  for all cases. In the top three panels,  $K_J$  is increased by 100 across a range of values of  $K_J$  and  $K_A$ . In the bottom three panels,  $K_A$  is increased by 100 at across a range of values of  $K_J$  and  $K_A$ .

size have focused only on juvenile abundance without monitoring how adult populations were affected by the quality and size of the juvenile habitat (reviewed in Beck et al. 2001).

Longevity can also directly and indirectly affect population size. By modifying the storage potential of the adult habitat, increasing longevity directly affects population size by allowing populations to accumulate longer-lived individuals across many pulses of juveniles. Longevity can also affect population size indirectly by causing the limiting factor for population size to shift between  $K_A$  and  $K_J$ . For example, if longevity decreases (e.g., under heavy fishing pressure), adult abundance becomes limited more by juvenile carrying capacity (or recruitment) than by adult carrying capacity (fig. 3). This is an important lesson for efforts to manage populations and species.

It may be possible to predict which species are likely to be limited by adult versus juvenile carrying capacity based in part on their average life span. Longer-lived species ( $S_A > 0.9$ ), such as most predatory reef fish, are likely to be limited by the amount of available adult habitat unless juvenile habitat is extremely limited. In contrast, species with high mortality (either natural or due to harvesting) may be more limited by juvenile habitat availability (or recruitment) than by adult habitat availability such that short-lived species may be more susceptible to the loss of juvenile habitat than long-lived species. These "rules of thumb" will of course depend on the actual amount of juvenile and adult habitat available, but they indicate that habitat-based management and conservation efforts may well be different for short-lived versus long-lived species.

Importantly, factors that change longevity are likely to have nonlinear effects on population size. For long-lived species, initial reductions in longevity will have small and linear effects on the size of a population; however, further reductions in longevity may cause population size to decrease nonlinearly (fig. 3). Fishing and hunting, which tend to take the oldest and largest individuals of a population (Pauly et al. 1998; Myers and Worm 2003), may result in sudden decreases in population size as smaller and smaller individuals are sequentially removed, while efforts to protect heavily exploited populations (e.g., through marine reserves) might work in the reverse. Consequently, increased harvesting pressure may make juvenile habitats even more important for supporting adult abundance, whereas efforts to reduce harvest pressure may decrease the relative importance of juvenile habitats. The interaction of these parameters creates unique challenges in designing reserves and refuges intended to protect the appropriate amount of each type of habitat required by different life-history stages of a given species.

Results from sensitivity analyses also demonstrate how longevity can interact with changing amounts of juvenile

or adult habitat to affect adult abundance. When species are short-lived and juvenile habitat strongly limits adult abundance (2X in fig. 5), increasing  $K_J$  has a large impact on adult abundance when  $K_A$  is small; there is a much weaker effect of increasing  $K_J$  when species are long-lived (50X in fig. 5). In contrast, changes in  $K_A$  have consistently larger effects on adult abundance than changes in  $K_J$ , regardless of a species' longevity, because increases in adult habitat capitalize on the storage effect. A species can take advantage of larger juvenile habitat only for the period of time it is present in that habitat whereas it can take advantage of larger adult habitat for a minimum of two time steps (as modeled here). Longevity matters only when both  $K_A$  and  $K_J$  are very small relative to the amount of adult habitat being added, a situation that is not likely to be typical for most conservation and restoration efforts. In particular, these results highlight that one should avoid broad generalizations about maximizing the areas of protected habitat for particular life-history stages.

In the population model developed here, we have focused primarily on habitat size and life span as key limiting factors for stage-structured populations because these factors are likely to be important for regulating population size and have typically been overlooked in past theoretical and empirical work. However, there are key parameters that were not modeled here that also may play important roles in limiting population size. For example, the level of connectedness between juvenile and adult habitats may modify the importance of the juvenile habitat; well-connected, small juvenile habitats may be less limiting than large, poorly connected juvenile habitats. Distance and barriers between juvenile and adult habitats can play important roles in the population dynamics of many amphibians (e.g., Lehtinen et al. 1999; Marsh and Trenham 2001), and in an analogous manner, recruitment can play a key role in controlling population size of many marine species (Roughgarden et al. 1985, 1988). The level of connection between juvenile and adult habitats is likely to be a complex function of distance between habitats, modes of dispersal between the habitats, and the behavior and mobility of the juveniles of a given species. Furthermore, interactions with other species may modify the form of density-dependent mortality in juvenile or adult habitats, altering the importance of either habitat in regulating population size of the focal species. Such community-level interactions are likely to be habitat- and location-specific.

Surprisingly, the effect of habitat size and longevity on adult abundance differed little between open and closed populations. These similarities may not be as strong for natural populations, since open populations are likely to have highly variable recruitment (rather than the constant recruitment modeled here), while closed populations should have less variable reproduction (but see Eckert

2003). In closed populations, more adults ultimately beget more adults, whereas there is no guarantee of this for open populations. In fact, many marine species with open population dynamics can suffer periods of zero recruitment such that the population becomes highly dependent on recruitment (i.e., recruitment limited). In these cases, shifts in either juvenile or adult habitat would have little effect on adult abundance unless habitat size were altered on a scale equivalent to an entire population's range.

It is important to note that many of the species addressed in this article have three distinct phases that use three different habitats. For example, marine species have pelagic larvae, juveniles that reside in nursery habitats, and adults that live in adult habitat. Little is known about density-dependent processes in the pelagic phase of marine species. If they exist, then the larval habitat may also play a key role in limiting the adult abundance of many species, ultimately decreasing the overall role of adult habitat in limiting population size because fewer individuals would survive to that stage. For amphibian species with closed population dynamics, theoretical research suggests that egg mortality does not significantly affect adult abundance (Vonesh and de la Cruz 2002). However, for species with open populations (e.g., marine species), recruitment is often a key limiting factor, and so density-dependent mortality during the larval stage may be more important than the mortality during the egg stage for closed populations. Interestingly, for marine species that have a larval phase but do not use distinct juvenile habitats, as is the case for many species, our model can provide heuristic predictions about how density-dependent processes in the larval phase can affect the population dynamics of these species. For example, because the pelagic habitat is generally quite large relative to potential adult habitat and the amount of larvae exported to this habitat, these species are not likely to be limited by density-dependence in the pelagic stage.

In summary, juvenile habitat can act as a primary limiting factor for adult abundance, but recruitment and adult carrying capacity play a much greater role in limiting population size throughout a much larger portion of parameter space. Limited empirical evidence, however, suggests that many populations may be currently limited by juvenile habitat. Thus, natural populations may commonly fall within the parameter space where the size of juvenile habitat limits population size. Model results also show the role that a species' life span plays in limiting population size through interactions with adult carrying capacity. Further empirical work is needed to verify these conclusions, but at a minimum, the results suggest that future ecological research and conservation decisions must carefully evaluate the degree to which juvenile habitat limits adult abundance in order to properly identify limiting stages to population size.

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