RESEARCH ARTICLE

# Impact of species-specific dispersal and regional stochasticity on estimates of population viability in stream metapopulations

**Mark S. Poos · Donald A. Jackson**

**Abstract** Species dispersal is a central component of metapopulation models. Spatially realistic metapopulation models, such as stochastic patch-occupancy models (SPOMs), quantify species dispersal using estimates of colonization potential based on inter-patch distance (distance decay model). In this study we compare the parameterization of SPOMs with dispersal and patch dynamics quantified directly from empirical data. For this purpose we monitored two metapopulations of an endangered minnow, redside dace (*Clinostomus elongatus*), using mark-recapture techniques across 43 patches, re-sampled across a 1 year period. More than 2,000 fish were marked with visible implant elastomer tags coded for patch location and dispersal and patch dynamics were monitored. We found that species-specific dispersal and distance decay models provided qualitatively similar rankings of viable patches; however, there were differences of several orders of magnitude in the estimated intrinsic mean times to extinction, from 24 and 148 years to 362 and >100,000 years, depending on the population. We also found that the rate of regional stochasticity had a dramatic impact for the estimate of species viability, and in one case altered the trajectory of our metapopulation from viable to non-viable. The divergent estimates in time to extinction times were likely due to a combination species-specific behavior, the dendritic nature of stream metapopulations, and the rate of regional stochasticity. We demonstrate the importance of developing comparative analyses using species- and patch-specific data when determining quantitative estimates for mean time to extinction, which in the case of redside dace, were highly sensitive to different estimates of dispersal.

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## Introduction

Species dispersal is a central component in the study of spatially structured populations. At a landscape scale, population viability strongly depends on individual dispersal allowing re-colonisation of empty habitats or patches (Hanski 1999). For this reason, species

dispersal is considered the 'glue' for maintaining local populations within a network of suitable habitats (Hansson 1991). The degree of dispersal has an impact on local population dynamics, on gene flow and on adaptation to local conditions. For example, low dispersal can foster isolation and local adaptations (Resetarits et al. 2005). Alternatively, high species dispersal can have a stabilizing effect on metapopulation dynamics (Hanski 1999).

Many species with spatially structured populations are in decline, and population viability models provide a statistical evaluation of species viability to inform management decisions (Frank and Wissel 1998; Akçakaya 2000). Metapopulation viability analyses provide a spatially realistic evaluation of the local population structure (Hanski 1999; March 2008). By quantifying patch dynamics, metapopulation viability analyses can be used to better understand the importance of ecological processes such as species specific dispersal, patch quality and landscape influences (Moilanen and Hanski 1998), and to inform conservation management through evaluation of minimum amount of habitat or population size needed to maintain viability (Hanski 1999; Robert 2009).

Understanding how species-specific dispersal has the potential to alter metapopulation viability can help inform management decisions. One popular type of metapopulation viability analysis are stochastic patch-occupancy models (i.e. SPOMs), which have been used extensively to model the viability of spatially structured populations (Hanski 1999; Moilanen 1999). SPOMs are comparable to other spatially realistic models (Kindvall 2000; Ovaskainen and Hanski 2004), and have been used in studies of species with conservation concern, such as capercaillie (Grimm and Storch 2000), the American pika and Glanville fritillary and silver spotted skipper butterflies (Hanski 1999). As SPOMs provide a simplification over traditional population-viability analyses (Akçakaya and Sjögren-Gulve 2000), they do not require demographic or stage data, but only occupancy, colonization and extinction rates, which can be easily estimated from empirical data (Hanski 1994; Hanski 1999; Moilanen 1999; Grimm et al. 2004; Moilanen 2004).

The influence of dispersal on metapopulation viability is often analyzed using some approximation of colonization potential (Verboom et al. 1993; Hanski and Gilpin 1997; Frank and Wissel 2002; Heinz et al.

2005). The easiest approach to describe colonization potential (i.e. patch accessibility) is as a function of distance between a starting patch to a target patch and the ability of species to disperse (Hanski 1994; Hanski et al. 1996; Heinz et al. 2005). This relationship can be quantified in several ways; however, most often this estimation is done by assuming that colonization potential declines exponentially with distance (i.e. distance decay; Hanski 1994; Vos et al. 2001; Frank and Wissel 2002). It is uncertain how well the assumption of distance decay can model species-specific dispersal (Heinz et al. 2005). Whether simple formulae are adequate in describing species- and patch-specific movement in metapopulation models remains an open question (Heinz et al. 2005; Marsh 2008).

The objective of this study is to assess the impact of species-specific dispersal on estimates of metapopulation viability. For our assessment, we conducted a detailed mark-recapture survey of metapopulation dynamics of the endangered fish, redside dace (*Clinostomus elongatus*), in the Greater Toronto Area, Ontario, Canada. Redside dace are habitat specialists preferring headwater pool habitats (COSEWIC 2007). Prior to our study, there were no data available for dispersal of redside dace; however, it was commonly believed that due to their habitat preference that movement of redside dace would be highly restricted (COSEWIC 2007). Previous observations of movements by Koster (1939) suggest redside dace disperse to neighboring pools, and to nearby riffles for spawning. Such observations are in agreement with congener species such as the closely related rosyside dace (*C. funduloides*), where dispersal was shown to be limited to between 10–20 m (Hill and Grossman 1987).

## Methods

We studied the metapopulation dynamics of redside dace by monitoring dispersal of tagged individuals on monthly intervals during a one-year period. For this study, each location was sub-divided into two areas: intensively monitored sites where individuals were tagged and extended sites which were beyond those areas, which were monitored for tagged fish (Fig. 1). As meta-populations can be defined in a number of ways (Hanski 1999), we define a metapopulation as an

**Fig. 1** Study sites on Rouge River, Ontario where redside dace (*Clinostomus elongatus*) dispersal and patch dynamics were monitored. Study locations: (*A*) Leslie Tributary, and (*B*) Berczy Creek, were sub-divided into extensive sites (*black*), where redside dace were tagged with a color-coded visual implant elastomer tag, and extended sites (*grey*), which were monitored for tag movement. *Bottom right* Rouge River, Ontario is shown relative to the Great Lakes, and northeastern United States
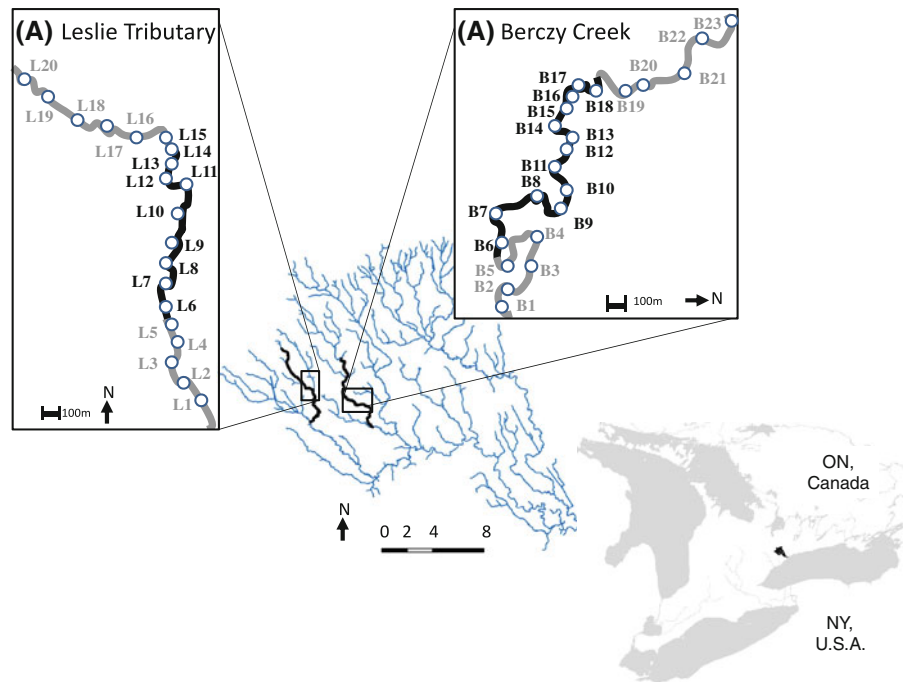
assemblage of local populations inhabiting spatially distinct habitat patches (Moilanen and Hanski 1998). Redside dace live primarily in clear, well-defined pools (COSEWIC 2007); therefore each spatially distinct pool segregated by a well-defined riffle (e.g. a passable, but natural migratory barrier) was selected as a habitat patch.

We studied metapopulation dynamic of redside dace at two locations on the Rouge River, including one location on Leslie Tributary, and the other location on Berczy Creek (Fig. 1). We choose these locations as they were previously shown to have among the highest abundance of redside dace recently sampled across its entire Canadian range (Reid et al. 2008; Poos et al. "In Press"). Leslie Tributary was sub-divided into 20, connected and distinct patches, with 10 intensive sites and five extended sites on both upstream and downstream ends. Similarly, Berczy Tributary was sub-divided into 13 intensive sites with five extended sites on each of the upstream and downstream ends (Fig. 1). The additional three sites in Berczy Creek were included to standardize sample locations by river distance.

Sampling was conducted using multiple-pass depletion surveys at each pool. Using a twenty-foot bag seine (1/4″ mesh) each site was surveyed until depletion of redside dace, with a minimum of three

sampling events conducted at each site per time period. At each pool, redside dace were implanted with visual implant elastomer (VIE) tags color coded for their location (Plates 1, 2). Elastomer tags were chosen because they had good tag retention and negligible effects on survival, growth and behavior when used on other species (Walsh and Winkelman 2004). Tags were injected subcutaneously near the anal fin on the ventral surface (Plates 1, 2). All redside dace were held in well-oxygenated flow-through bins for 2–4 h to monitor for potential physiological stress, and then returned to the river at the captured location. Both intensive and extended sites were re-sampled for redside dace on monthly intervals except under winter-ice conditions (November–March) and when redside dace were spawning (June) so that we did not disrupt this important life stage for an endangered species. All redside dace sampled in a recapture event were examined for the presence of a VIE tag. Redside dace dispersal and metapopulation dynamics were tracked and mark-recapture data were recorded. If redside dace were re-captured at a new location, they were subsequently tagged posterior to the existing tag, with a new color code for the recapture location.

We compared the dispersal patterns, such as average distance dispersed, and proportion of stationary tags, of our metapopulations using non-parametric

Mann–Whitney $U$-tests and log-linear models ($G$-tests with Yates continuity correction; Zar 1999) respectively, in the R language v2.80 (R Development Team 2008).

### Determining metapopulation viability

SPOMs use a time-continuous Markov-chain model (Hanski 1999; Grimm et al. 2004). Each patch (i) is assumed to be in one of two states, vacant ($X_i = 0$) or occupied ($X_i = 1$). Changes in these states can occur from a patch becoming vacant due to local extinction ($X_i$: $1 \rightarrow 0$) or correlated extinction (i.e. regional stochasticity) from another patch ($X_j$, $X_i$: $1 \rightarrow 0$). Alternatively a vacant patch can become occupied ($X_i$: $0 \rightarrow 1$) via colonization from another patch ($j$). The state of the whole metapopulation ($X_i, \dots X_n$) is given by a vector of states $X_i$ of these individual patches. The models were quantified as follows.

### Colonization rate

We defined colonization between two patches $i$ and $j$ ($b_{ij}$) using an incidence-function model (Hanski 1994): $b_{ij} = y \cdot M_i \cdot \exp(-d_{ij}/d_i)$, where $y$ is a parameter, and $M_i$ is the number of emigrants from pool $i$. We estimated the mean number of emigrants leaving a pool using data from our tagging study. To account for the potential uncertainty with missing emigrants leaving a patch, we quantified the probability of detection at each pool ($PD_i$) of our surveys using maximum likelihood from the $n$-pass depletion surveys with the Bayesian modification (Carle and Strub 1978). These were coded in the R v2.80 (R Development Team 2008) using the fisheries-assessment package FAS (Ogle 2009). We quantified the total number of emigrants leaving each patch ($Mi$) per year as: $M_i = \sum (t_1 \dots t_n) m_i x (1 + (1 - PD_i))$, where $m_i$ is the uncorrected number of emigrants. Similar to most metapopulation models, we used a distance-based dispersal kernel using a negative exponential decay (hereafter distance decay), where $\exp\left(-\frac{d_{ij}}{d_0}\right)$, and $d_{ij}$ is the distance from patch $i$ to patch $j$ and $d_0$ is the mean dispersal ability of redside dace. Distance decay dispersal kernels have been used extensively in metapopulation models and assume that patch accessibility is dependent on distance (Hansson 1991; Hanski et al. 1996; Moilanen 2004). Distance decay
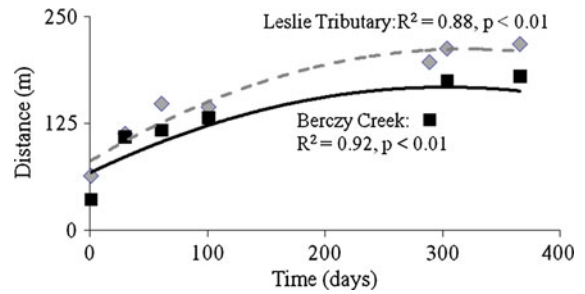


**Fig. 2** Distance decay of redside dace dispersal through time. Shown are mean distance dispersed (m) of recaptured visual implant elastomer tags used to parameterize species specific dispersal

kernels allow researchers to extrapolate relationships in patch occupancy, often by using species life-history characteristics, without the need of labor-intensive field studies (Moilanen 2004; Heinz et al. 2005).

Unfortunately there are no good field estimates of redside dace dispersal ability, and as such we had to define $d_i$ using empirical dispersal data. For example, we used the asymptote of a non-linear (polynomial) regression of mean distance of dispersal of our recaptured tags through time to identify potential dispersal across our patches (Fig. 2). The fit of these non-linear regressions were highly significant (Leslie Tributary; $r^2 = 0.92$, $P < 0.01$, Berczy Creek; $r^2 = 0.88$, $P < 0.01$) and we found that the average distance dispersed ($d_i$) for a one-year period (one time step in final SPOM model) was 210 m for redside dace in Leslie Tributary and 150 m for Berczy Creek (Fig. 2). As we had several consecutive surveys, it was possible to estimate $y$ from the number of transitions (i.e. an empty patch becoming occupied and vice versa; Hanski 1999). We used a GLM procedure which considered multiple snapshots of our sampling events using a binomial distribution and logistic-link function developed in the R programming language v2.80 (R Development Team 2008) using the incidence function (Oksanen 2004). The value of the $y$ parameter for Leslie Tributary was 0.0816 and Berczy Creek was 0.0713. Finally, for $d_{ij}$, we manually created a distance matrix using the river distance between patches as measured using geographic information systems.

### Extinction rate

Extinction rates can be quantified in many ways (Hanski 1999). The simplest form of determining

extinction rate ($E_i$) is using the area of the patch ($A_i$), and given by $E_i = e(A_i^x)^{-1}$, where $e$ defines the extinction probability of a patch of unit size, and $x$ defines the scaling of the extinction risk with patch area (Hanski 1998; Moilanen 2004). This model assumes that probability of extinction generally depends on population size, which in turn is usually given the amount of patch area. This relationship has been demonstrated on both empirical and theoretical grounds (Lande 1993; Foley 1994; Hanski 1994; Hanski et al. 1996; Hanski 1999). Here we model extinction rates using patch (i.e. pool) depth ($d$). We measured patch depth by taking the average of 60 equidistant point measurements quantified using the Ontario Stream Assessment Protocol (OMNR 2007). We included patch depth because redside dace are known to be pool-dwelling species (COSEWIC 2007), and therefore depth may be more relevant to model patch dynamics. Indeed, we found that redside dace abundances were more correlated with patch depth ($r = 0.44$, $P = 0.0018$) than patch area ($r = 0.39$, $P = 0.0048$) or volume ($r = 0.40$, $P = 0.0032$; Poos and Jackson "unpublished data"), although we note that the inclusion of patch depth rather than patch area did not alter any of the results. We developed our extinction rate by fitting an incidence function relating species presence in our patches over time and depth. For this modeling we used a GLM procedure which considered multiple snapshots of our sampling events using a binomial distribution and logistic-link function developed in the R programming language v2.80 (R Development Team 2008) using the incidence function (Oksanen 2004). The parameters of the incidence function for Leslie Tributary and Berczy Creek were: $x = 0.4926$, $0.5652$; and $e = 3.685$, $4.187$, respectively.

## Incorporating dispersal directly into the metapopulation model

Recent theoretical studies on the impact of species movement have found that it can alter metapopulation viability (Heinz et al. 2005; 2006; Revilla and Wiegand 2008). As such, we extended the incidence function models by incorporating species dispersal directly into the metapopulation model using empirical data of patch-specific movement. We used a model developed by Frank and Wissel (1998; 2002),

which (in this case) is identical to the incidence function model (outlined above) and allows the incorporation of patch dynamics (Grimm et al. 2004; Heinz et al. 2006). This model took into account three processes; emigration of individuals from occupied patches, dispersal to a target patch, and the establishment of a new subpopulation on the target patch. The rate of colonization, $b_{ij}$, was defined as

$$\begin{cases} \frac{M_i}{n_i} \cdot r_{ij} \cdot \frac{0.5}{I_j} \\ 0 \end{cases}$$

where, $M_i$ was the number of emigrants leaving the occupied patch $i$ per year (previously defined), $n_i$ was the number of connections from patch $i$ to other patches, $r_{ij}$ was the probability of an individual started at patch $i$ successfully dispersing to patch $j$, and $I_j$ was the number of immigrants needed to establish a new subpopulation (Frank and Wissel 1998; 2002). For the probability of dispersal between patches ($r_{ij}$), we developed a patch-colonization matrix using our empirical tagging results for each time period. As our tags were color coded for patch location (at each time period), we defined $r_{ij}$ empirically as the ratio of tags which started at patch $i$ that dispersed to location $j$, across all recaptured tags. In this instance, we did not account for missing tags as we assumed no tag-related behavioral response (i.e. fish that were tagged adequately represented dispersal in general). Finally, to quantify $I_j$ we developed an incidence-function model of probability that a patch persisted (across all time periods) given the starting population size of each patch at the start of our study. For this approach we used the GLM function with binomial distribution and logit link in the R programming language v2.80 (R Development Team 2008). From this model we fitted the equation for the relationships of establishment/persistence at any patch given starting population size (Appendix 1).

## Regional stochasticity

Regional stochasticity refers to the level of correlated extinctions caused by factors influencing a shared geographic location, such as weather or disease (Lande 1993; Foley 1994; Lande et al. 1988). Regional stochasticity has the ability to impact metapopulation viability by incorporating the influence of the fate of proximal patches (Grimm and Wissel 2004). We

considered the influence of regional stochasticity at three levels, 0 (no influence of regional stochasticity), 0.1 (a moderate level of regional stochasticity) and 0.2 (more severe regional stochasticity). Although levels of regional stochasticity are difficult to enumerate in nature, literature values suggest that rates of catastrophes varies among vertebrates from 0 to 0.53 per generation (mean 0.14/generation), with the vast majority (i.e. >83%) representing at least a 50% die-off in species abundances (Reed et al. 2003). Given that the extent of redside dace remains highly fragmented in a largely urbanized landscape (COSE-WIC 2007), it is likely that our levels of regional stochasticity (e.g. 0.1 and 0.2) are low to moderate relative to the highly dynamic stream conditions. For example, rates of small floods have increased by 302% since urbanization in the Don River, a neighboring stream (Poos et al. "In Press").

## Comparing viability of metapopulations using differences in dispersal estimates

The ultimate viability of patch ($i$) was defined using the intrinsic mean time to extinction $T_m = 1/\lambda$, determined using the reciprocal value of the overall extinction rate $\lambda$ calculated using a plot of $-\ln(1 - P_0(t))$, where $P_0$ is the probability of extinction at a given time ($t$) (Verboom et al. 1991; Grimm and Wissel 2004). Intrinsic mean time to extinction has been previously shown to be an adequate currency in assessing the viability of metapopulations and can be easily extracted from simulation data (Frank and Wissel 1998; Grimm and Wissel 2004; Heinz et al. 2006). Transitions in metapopulations were simulated 10,000 times using 'stochastic time steps' (Frank and Wissel 2002; Grimm et al. 2004) of transition probabilities of extinction and colonization rates. For this estimation we used manually created sub-routines in the software program Meta-X (Frank and Wissel 2002; Grimm et al. 2004), a metapopulation program flexible for incorporating behavior into metapopulation-viability analysis (Heinz et al. 2006).

## Results

In total, we tagged 2,141 redside dace and monitored their movement across 43 patches during seven recapture events in a one-year period from 2007 to 2008. Due to logistical issues, we were unable to sample our stream systems during winter-ice conditions (November–March) and due to ethical concerns when redside dace were spawning in June given the potential to disrupt spawning activities. Recapture rates for redside dace—calculated as the proportion of fish marked during the preceding marking period/s that were recaptured—were generally high (>25%) during our initial four monitoring events, ending in October 2007. These numbers were greatly reduced by the following spring, with recapture rates <10% likely due to high over-winter mortality. In addition, our capture efficiency—as determined by probability of detection using our $n$-pass depletion surveys (Zippin 1958; Carle and Strub 1978)—was also very high for both study systems: Leslie Tributary (mean 71%) and Berczy Creek (mean 65.6%; Appendix 1).

## Metapopulation dynamics

Metapopulation dynamics of redside dace was characterized by: (1) large number of stationary individuals, and (2) high level of localized, short distance movements to adjacent pools. Across our eight sampling events, 41% (Berczy Creek) and 31% (Leslie Tributary) of individuals were recaptured at the same location in as where they were tagged. The remaining movement (88% for Berczy Creek, 61% for Leslie Tributary) could be classified as localized dispersal, occurring at <100 m, with 3.8% of individuals dispersing beyond 300 m (1.5% Berczy Creek, and 8.5% Leslie Tributary). In all cases, dispersal was higher in Leslie Tributary as compared with the Berczy Creek. The difference in dispersal was not due to more tags dispersing as there was no significant difference in the proportion of stationary tags. More likely, the increase in dispersal was due to larger average dispersal per individual, as indicated by mean and maximum dispersal through time (Fig. 2).

## Metapopulation and patch viability

Metapopulation viability, as indicated by both probability of extinction through time and the intrinsic mean time to extinction, were orders of magnitude different depending on whether the patch-occupancy model was parameterized using distance decay or directly using observed colonization (Fig. 3; Table 1). For example, when the patch-occupancy models were
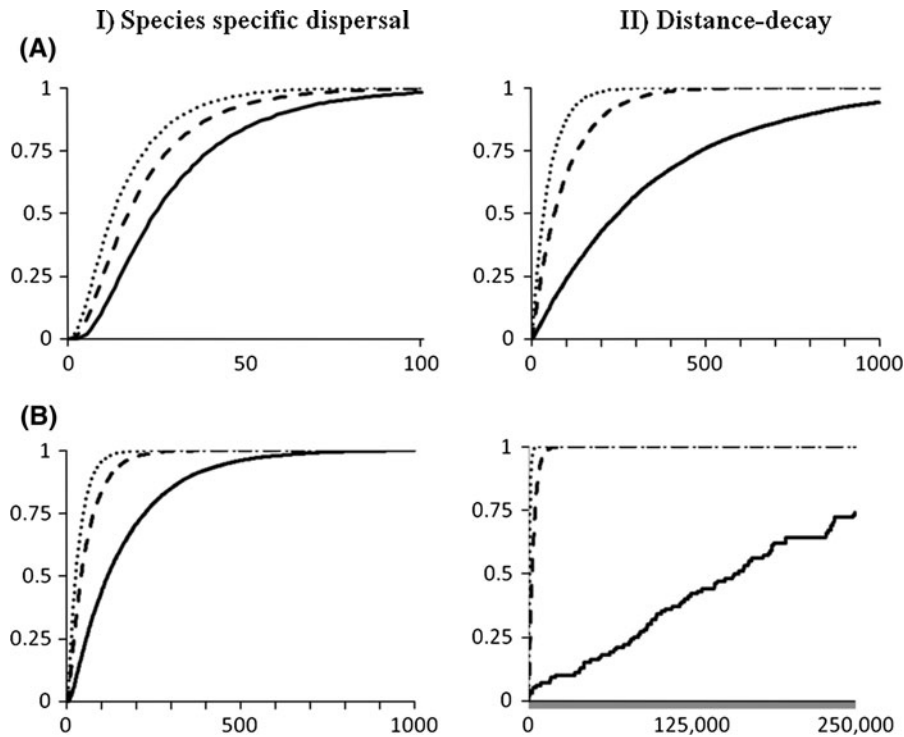
**Fig. 3** Metapopulation viability of the endangered species the redside dace (*Clinostomus elongatus*) in two stream metapopulations: **a** Leslie Tributary, and **b** Berczy Creek. Shown are the probabilities of extinction (*Y*-axis) in time (*X*-axis) of a stochastic patch-based metapopulation (SPOM) model. SPOM models were parameterized using: (I) dispersal based on distance decay of colonization via patch distance, (II) direct parameterization of colonization using species specific estimates of dispersal from a mark-recapture study. Note: *Vertical hashes* represent a time interval of 100 years, *solid lines* indicate population trajectories where regional stochasicity was set to 0, *dashed lines* set to 0.1 and *dotted lines* set at 0.2

**Table 1** Estimates of intrinsic mean time to extinctions of two metapopulations of the endangered fish the redside dace (*Clinostomus elongatus*) quantified using: (1) species-specific dispersal and (2) distance–decay

| | (A) Leslie Tributary | | | (B) Berczy Creek | | |
|---|---|---|---|---|---|---|
| Regional Stochasicity | 0 | 0.1 | 0.2 | 0 | 0.1 | 0.2 |
| (I) Intrinsic mean time to extinction (in years) parameterized with species-specific dispersal | 362 | 95 | 48 | 109,594 | 3,417 | 764 |
| (II) Intrinsic mean time to extinction (in years) parameterized with distance–decay | 24 | 17 | 12 | 148 | 54 | 32 |

parameterized directly using observed colonization, the Leslie Tributary population was unviable long-term and the Berczy Creek showed much longer viability. The intrinsic mean time to extinction for Leslie Tributary was 24 years, and occurred in as little as 12 years (regional stochasicity set at 0, 0.2 respectively). When we plotted the probability of extinction over time, 95% of the simulations went extinct in less than 100 years. Similarly, the intrinsic mean time to

extinction for Berczy Creek was 148 years and occurred in as little as 32 years (regional stochasticity = 0, 0.2 respectively), with 95% of simulations showing metapopulation extinction in under 1,000 years (Fig. 3; Table 1).

When the patch-occupancy models were parameterized using distance decay, one population (Berczy Creek) was deemed as viable and quasi-stationary (regional stochasticity = 0; Table 1), with 95% of

simulations showing viability beyond 250,000 years (Fig. 3). The remaining population estimates varied considerably in their viability, ranging in intrinsic mean times to extinction from 48 to 348 years in Leslie Tributary and from 764 to >109,000 in Berczy Creek (regional stochasticity 0.2, 0, respectively). Specific-patch viability mirrored overall metapopulation viability, with all patches showing reduced viability when parameterized directly from species specific data (Fig. 4). In all cases (except L12) patch viability was over-estimated with the distance decay (Fig. 3). Mean patch viability was significantly higher with the use of distance decay relative to species specific data in all SPOMs for both Leslie Tributary (mean patch viability using distance decay = 0.51 ± 0.10, mean patch viability using species specific dispersal = 0.35 ± 0.08; Welch's $t$-test; $t = 26.85$, $P$ value $\ll 0.0001$) and Berczy Creek (mean patch viability using distance decay = 0.69 ± 0.09, mean patch viability using species specific dispersal = 0.39 ± 0.08; Welch's $t$-test; $t = 11.204$, $P$ value $\ll 0.0001$).

Interestingly, the rankings of patch viability did not markedly differ based on the parameterization of the SPOM. For example, SPOMs using both distance decay and species specific dispersal identified the same
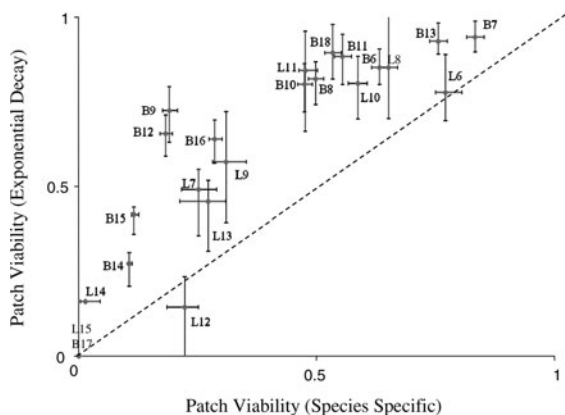


**Fig. 4** Differences in patch viability using dispersal parameterized using distance decay (Y-axis) and species specific data (X-axis) of the endangered species the redside dace (*Clinostomus elongatus*). Patches are shown from intensively monitored sites from two stream metapopulations: A) Leslie Tributary (L6-L15), and B) Berczy Creek (B6-B18). Shown are the mean probabilities of persistence of a given patch across 10,000 simulations with 25% quantiles shown on the negative axes and 75% quantiles shown on positive axes. A *1:1 line* is superimposed to demonstrate agreement between patch viabilities

five most-viable patches per population (overall) as: L6, L8, L10, L11, L9 and B7, B13, B6, B11, B18. One notable difference in patch viability was that several patches that were in close proximity to good-quality patches had significantly lower viability when parameterized using species specific dispersal (Fig. 4). Specifically, patches L9, L11, B6 and B9 had reduced viabilities when parameterized using species specific data relative to distance decay (mean patch viability using distance decay = 0.57, 0.84, 0.86, 0.90, respectively; mean patch viability using species specific dispersal = 0.28, 0.46, 0.63, 0.17; Fig. 4).

## Discussion

Metapopulation-viability models have a long history of use (Hanski 1999) and provide advantages over traditional population-viability analyses (PVAs). One clear advantage of using stochastic patch-occupancy metapopulation models (SPOMs) over traditional PVAs (e.g. structured models, demographic models; Akçakaya, Sjögren-Gulve 2000; Morris and Doak 2002) is that they require the parameterization of fewer variables (Ovaskainen and Hanski 2004). This reduction is especially advantageous for modeling endangered species, where enumeration is complicated by rarity and where greater uncertainty exists (Akçakaya 2000). As incorporating species-specific or demographic data into ecological studies can be difficult, time consuming, or not economically possible; simplification is often needed. SPOMs allow for simplification of metapopulations, as only patch occupancy, colonization and extinction rates are needed, even within a single snapshot (Moilanen 2004; Marsh 2008).

There is a tradeoff between simplification of PVAs by using less parameters and with the added value and information that those parameters may have. In this study, we show that differences in species dispersal patterns, a key component of metapopulation models such as SPOMs, have the ability to dramatically impact estimates of metapopulation viability. Species-specific dispersal reduced estimates of viability of redside dace metapopulations by several orders of magnitude over estimates using distance–decay models. In one case, in Berczy Creek, the distance decay model suggested that redside dace were viable, while the same model estimated using species specific data

suggested that the populations were not viable (regional stochasticity = 0; Fig. 3). These results demonstrate the importance of dispersal in SPOMs, as others have noted previously (Verboom et al. 1991; Heinz et al. 2005; Schtickzelle et al. 2006). Perhaps more importantly these results should emphasize caution with the use of naive dispersal estimates, such as distance decay models, which may not account for species specific differences. These conclusions are in agreement with others who suggest that better integration of species-specific behaviour is needed into the analyses of metapopulations (Tischendorf 2001; Vos et al. 2001; Heinz et al. 2005, 2006; Baguette and vanDyck 2007; Marsh 2008).

Developing robust estimates of species specific dispersal is important to allow for accurate metapopulation viability models and to ensure appropriate management action. Although in all cases our species-specific estimates of dispersal (e.g. 150–210 m) produced metapopulation projections moving towards extinction, it appears our estimates of mean time to extinction may, if anything, be conservative. Prior to our study, little was known about the dispersal of redside dace. Generally, it was accepted that as redside dace were habitat specialists and dispersal would be limited to adjacent pools, with slightly larger dispersal towards riffles during spawning (Koster 1939; COSE-WIC 2007). Therefore our estimates of dispersal of redside dace are higher than previously shown, as well as higher for many of its congeners (Hill and Grossman 1987). For example, dispersal estimates can be estimated using well known correlations with body size allometry (sensu Minns 1995). Given average adult (i.e. reproductive) length of redside dace ranges between 48 (age 2+ individuals) to 78 m (McKee and Parker 1982); dispersal of redside dace based on body size is estimated between 32–72 m (Poos "unpublished data"). Additionally, previous estimates of a close conger the rosyside dace, suggest dispersal limited to 10–20 m, with site fidelity close to 80% (Hill and Grossman 1987). These data suggest that our species specific estimates of dispersal, if anything were high, and that the estimated mean time to extinction may actually be lower. Nonetheless, it appears that the redside dace is a species moving towards extinction and not—as the case in one metapopulation viability model based on distance decay—a species with high likelihood of long term persistence.

There are many species specific behaviors which may account for the divergent dispersal estimates between species specific dispersal and the distance decay model (Roitberg and Mangel 1997; Heinz et al. 2006; Baguette and vanDyck 2007). First, many small-bodied fishes often school with a mixture of other species to reduce predation pressure. Redside dace are known to school with other more common minnow species such blacknose dace (*Rhinichthys atratulus*), creek chub (*Semotilus atromaculatus*), and common shiner (*Luxilus cornutus;* COSEWIC 2007). Given that densities of redside dace remain below more common species, ecological theory suggests that the advantage of this indirect trait mediated interaction is to enhance prey coexistence and mutualism (Bolker et al. 2003). Second, many fishes utilize reproductive tactics that require trait mediated interactions that may further alter rates of species specific dispersal. For example, many fishes parasitize nests built by congeners. This reproductive strategy has not only energetic benefits but is also thought to help reduce predation pressure of juveniles (Novinger and Coon 2000). Theoretical examples of simple communities (e.g. one predator, two prey systems) suggest that these types of indirect trait mediated interactions can act as both a stabilizing and de-stabilizing pressures for ecological communities (see Bolker et al. 2003 for review). Therefore, dispersal of redside dace may be due to a combination of predator avoidance and reproductive strategy; which may act differently than the distance decay model, or optimal foraging theory suggest (Pierce and Ollason 1987).

Accounting for regional and stochastic processes are important considerations for the management of endangered species. In this study, regional stochasticity had a strong influence on intrinsic mean time to extinction. For example, when we altered the rate of regional stochasticity, the intrinsic mean time to extinction quickly decreased (Table 1). In cases where populations were already considered to be unviable (e.g. Leslie Tributary with 0 stochasicity), the impact of regional stochasticity was small; in comparison to when populations were viable or quasi-stationary (e.g. Berczy Creek with 0 stochasicity), where it had an enormous impact (Fig. 3). For example, in one case, when regional stochasicity was ignored, Berczy Creek was considered to be viable (Table 1). Altering rates of regional stochasticity from 0 to 0.1 and 0.2 caused the populations to quickly go to extinction (intrinsic

mean time to extinction dropped from >109,000 to 54 and 32 years, respectively). Although the rates of environmental stochasticity are difficult to enumerate, previous attempts to quantify both the frequency and severity of stochastic events were both within our low and high we used here (Reed et al. 2003). Our results suggest that regional stochastic factors (e.g. weather, drought) which may alter patch dynamics, can have undue influence on metapopulation viability (Lande 1993; Foley 1994; Robert 2009).

The dendritic nature of stream systems provides unique characteristics from which to study metapopulation dynamics. Unlike most terrestrial systems, stream metapopulations act in a linear, stepping stone fashion, where species must disperse through one patch in order to reach another. This linear spatial arrangement is advantageous for monitoring colonization and extinction in a metapopulation framework, as we were able to monitor of all patches (i.e. pools) and their connections; however, it may also hinder long distance dispersal. Individuals who disperse must decide between staying at a current habitat patch or expend energy to move further upstream or downstream. In this study, we found that stream metapopulations were best described by dispersal of short to intermediate distances. We found that regardless of time period, of the tags we recaptured, between 75 and 90% of tags were recaptured within 350 m of their starting pool (Appendix 1). Although it is possible that in some cases, patch colonization may be underestimated in our empirical model because of the potential for long-distance dispersal, our monitoring of patches beyond our study areas demonstrated that this is likely not the case here. In addition, dendritic stream networks can provide additional rescue potential not considered in terrestrial systems (Fagan 2002), which may reduce the requirement for long distance dispersal. For example, increased genetic variation can occur due to the existence of additional isolation in dendritic networks and downstream propagule rain of novel alleles (Gotelli 1991; Morrissey and de Kerckhove 2009). Although we rarely found asynchrony in dispersal (i.e. Fall, Berczy Creek, $G$-test, $P < 0.05$; Fig. 2), recent theoretical studies suggest that genetic variation may be enhanced in stream metapopulation with even small levels of asynchrony (i.e. propagule rain) or across short time periods (Morrissey and de Kerckhove 2009). As such, one hypothesis regarding the differences between our empirical dispersal

estimates and distance decay, may be due to the behavior of individuals within a linear stream network. Understanding how a linear spatial arrangement may alter metapopulation dynamics remains an important challenge for future research in landscape ecology.

It remains an open question on how best to treat stream fishes in a metapopulation framework. Stream fish do not likely fit classic Levin's type metapopulation models due to asyncrony in movement (Gotelli and Taylor 1999; Morrissey and de Kerckhove 2009) and/or linear spatial arrangement of stream networks. In some cases, these may cause problems with in the performance of metapopulation models (Gotelli and Taylor 1999). However, recent advancements suggest that metapopulation models, such as SPOMs, are robust to the assumptions of a classic metapopulation models, and that they can handle a range of spatially structured populations: from classic metapopulations to species found in fragmented landscapes with patchy distributions (Ovaskainen and Hanski 2004). Our study demonstrates that this may be true in a qualitative sense only. For example, despite finding large differences in the prediction of intrinsic mean time to extinction (Table 1), we also found that regardless of how the SPOMs were parameterized, there were minimal qualitative differences between the use of traditional metapopulation models (e.g. using distance–decay) and those modeled with empirical data collected from stream fish metapopulations (Fig. 3). However, our results should cast doubt on whether intrinsic mean times to extinction can be reliably estimated in stream metapopulations. As others empirical studies have noted, large temporal variation in patch dynamics (i.e. colonization and extinction rates) can lead to sensitivity in SPOMs (Ovaskainen 2004; Heinz et al. 2005); and these in turn can lead to drastic differences in the estimated mean time to extinctions. As Revilla and Wiegand (2008) suggest; it is likely that the best way to improve conservation and management of stream metapopulations, is through improved understanding in the processes behind the variability shown between (and within) patch dynamics, rather than attempt to see how those may be used to estimate quantitative extinction times.

Incorporating species-specific dispersal into metapopulation models may help inform management decisions. In this study, we show that empirical estimation of patch viability may be qualitatively

similar when parameterizing SPOMs, but that esti-
mates of metapopulation viability can be altered by
orders of magnitude. By incorporating species- and
patch-specific data directly into metapopulation mod-
els, managers may be better at determining the relative
importance of spatial and temporal factors (McCoy
and Mushinsky 2007). Additionally, quantifying spe-
cies- and patch-specific dispersal, as done here, may
be expensive both in time and money, and superfluous
if they provide similar responses to distance–decay
dispersal kernels. Unfortunately, we demonstrate that
not to be the case as species-specific behavior may
provide alternative dispersal patterns. We also dem-
onstrate the potential impact of regional processes (i.e.
regional stochasticity); which can drastically reduce
estimates of mean times to extinction. Overall this
study demonstrates that care is needed in ensuring
that even simplified metapopulation models, such as
SPOMs, reflect biological data. Comparisons of how
species- and patch-specific data directly impact meta-
population models may be one way to help ensure
appropriate management actions for endangered spe-
cies (Dreschler et al. 2003; Grimm et al. 2004). Future
research on how to parameterize species and patch-
specific dispersal will only help aid in developing
robust tools for conservation management (Heinz et al.
2006; Baguette and vanDyck 2007; McCoy and
Mushinsky 2007).

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