Essay

Challenges and Opportunities in Implementing Managed Relocation for Conservation of Freshwater Species

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Abstract: *The rapidity of climate change is predicted to exceed the ability of many species to adapt or to disperse to more climatically favorable surroundings. Conservation of these species may require managed relocation (also called assisted migration or assisted colonization) of individuals to locations where the probability of their future persistence may be higher. The history of non-native species throughout the world suggests managed relocation may not be applicable universally. Given the constrained existence of freshwater organisms within highly dendritic networks containing isolated ponds, lakes, and rivers, managed relocation may represent a useful conservation strategy. Yet, these same distinctive properties of freshwater ecosystems may increase the probability of unintended ecological consequences. We explored whether managed relocation is an ecologically sound conservation strategy for freshwater systems and provided guidelines for identifying candidates and localities for managed relocation. A comparison of ecological and life-history traits of freshwater animals associated with high probabilities of extirpation and invasion suggests that it is possible to select species for managed relocation to minimize the likelihood of unintended effects to recipient ecosystems. We recommend that translocations occur within the species' historical range and optimally within the same major river basin and that lacustrine and riverine species be translocated to physically isolated seepage lakes and upstream of natural or artificial barriers, respectively, to lower the risk of secondary spread across the landscape. We provide five core recommendations to enhance the scientific basis of guidelines for managed relocation in freshwater environments: adopt the term* managed translocation *to reflect the fact that individuals will not always be reintroduced within their historical native range; examine the trade-off between facilitation of individual movement and the probability of range expansion of non-native species; determine which species and locations might be immediately considered for managed translocation; adopt a hypothetico-deductive framework by conducting experimental trials to introduce species of conservation concern into new areas within their historical range; build on previous research associated with species reintroductions through communication and synthesis of case studies.*

Keywords: assisted colonization, assisted migration, assisted translocation, climate change, endangered species, landscape connectivity

Retos y Oportunidades para la Implementación de la Reubicación Controlada para la Conservación de Especies Dulceacuícolas

Resumen. *Está pronosticado que la rapidez del cambio climático excederá la habilidad de muchas especies para adaptarse o dispersarse a ambientes más favorables climáticamente. La conservación de estas especies*

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puede requerir la reubicación controlada (también llamada migración asistida o colonización asistida) de individuos hacia localidades en las que puede ser mayor la probabilidad de su persistencia futura. La historia de especies no nativas en todo el mundo sugiere que la reubicación controlada puede no ser aplicable universalmente. Debido a la existencia limitada de organismos acuáticos en redes sumamente dendríticas que contienen charcas aisladas, lagos y ríos, la reubicación controlada puede representar una estrategia de conservación útil. Pero, estas mismas propiedades distintivas de los ecosistemas dulceacuícolas pueden incrementar la probabilidad de consecuencias ecológicas no planeadas. Exploramos sí la reubicación controlada es una estrategia de conservación válida para los sistemas dulceacuícolas y proporciona directrices para la identificación de candidatos y localidades para la reubicación controlada. La comparación de atributos ecológicos y de historia de vida de animales dulceacuícolas asociados con altas probabilidades de extirpación e invasión sugiere que es posible seleccionar especies para la reubicación controlada para minimizar la probabilidad de efectos no planeados en los ecosistemas receptores. Recomendamos que las translocaciones se lleven a cabo dentro del rango de distribución histórica de la especie y, óptimamente, en la misma cuenca hidrológica y que las especies lacustres y de río sean translocadas a lagos aislados físicamente y río arriba de barreras naturales o artificiales, respectivamente, para reducir el riesgo de dispersión secundaria en el paisaje. Proporcionamos 5 recomendaciones clave para incrementar la base científica de las directrices para la reubicación controlada en ambientes dulceacuícolas: adoptar el término translocación controlada para reflejar el hecho de que los individuos no siempre serán reintroducidos en su rango histórico de distribución nativa; examinar los pros y contras de la facilitación del movimiento individual y la probabilidad de la expansión del rango de distribución de especies no nativas; determinar las especies y localidades que pueden ser consideradas inmediatamente para la reubicación controlada; adoptar un marco hipotético-deductivo mediante el desarrollo de pruebas experimentales para introducir especies de interés para la conservación en áreas nuevas en su rango de distribución histórica; basarse en investigaciones previas de reintroducciones de especies mediante la comunicación y síntesis de estudios de caso.

Palabras Clave: cambio climático, colonización asistida, conectividad del paisaje, especies en peligro, migración asistida, translocación asistida

Introduction

Mounting concern regarding the persistence of species in a changing climate has revived interest in the notion of landscape fluidity and the need for organisms to respond to dynamic environmental conditions (Manning et al. 2009). Improved land management and habitat restoration are the current focus of efforts to improve the quality, connectivity, and permeability for dispersal of different species (Mawdsley et al. 2009). Nevertheless, the rapidity of climate change may exceed the ability of some species to adapt or to disperse to more climatically favorable surroundings (Thomas et al. 2004; Parmesan 2006; Loarie et al. 2009). Such findings have resulted in a lively debate among conservation scientists about the merits of translocating individuals to areas where environmental (especially climatic) conditions are likely to be suitable in the foreseeable future. This process is discussed under the rubric of assisted migration, assisted colonization, human-aided translocation, and most recently managed relocation (e.g., Hulme 2005; Hunter 2007; McLachlan et al. 2007; Hoegh-Guldberg et al. 2008).

Managed relocation addresses the detrimental effects of climate change on biological units such as populations, species, or ecosystems (Richardson et al. 2009). It involves the purposeful movement of individuals to locations where the probability of future persistence is likely to be high, but where the species is not known to have occurred previously. Many argue that traditional strategies may no longer ensure population or species persistence given the rapidity of climate change (Harris et al. 2006). Yet, there is good reason to question whether managed relocation is a viable conservation strategy. For example, managed relocation promotes the distributional expansion of species and thus may have undesirable effects on other species or ecological processes (Ricciardi & Simberloff 2009; Seddon et al. 2009). The view that "assisted colonization is tantamount to ecological roulette" (Ricciardi & Simberloff 2009) has been refuted by those who argue that the probability of species' extinctions from climate change is too great to discount managed relocation (e.g., Sax et al. 2009; Schwartz et al. 2009).

Thus far, the discussion of the decision-making process involved in managed relocation has focused primarily on terrestrial organisms. But projected increases in air temperatures and alterations of precipitation and runoff will greatly modify the hydrologic and thermal regimes of riverine ecosystems that directly influence the metabolic rates, physiology, and life histories of aquatic and riparian wetland species (Poff et al. 2002; Dudgeon et al. 2006). Moreover, species endemic to lowland floodplain lakes will be threatened by a combination of sea-level rise and consequent saline intrusions to formerly fresh waters. Climate change will further reduce the area and increase the isolation or fragmentation of aquatic systems, and many species may not be able to disperse to higher latitudes or elevations (Heino et al. 2009). Accordingly, managed relocation may be equally or more useful for increasing the ability of aquatic species to persist than for terrestrial species. We explored whether managed relocation is an ecologically sound conservation strategy for freshwater systems, and if so, whether there are system-specific rules of engagement. We suggest that the distinctive properties of freshwater ecosystems that may make managed relocation a useful conservation strategy for reducing the probability of climate-driven extinctions also may result in unintended ecological consequences.

Applicability of Managed Relocation to Freshwaters

Freshwater ecosystems have properties that violate key assumptions in existing frameworks for assessing the viability of managed relocation. Historically, biogeographic barriers operating at a hierarchy of spatial scales were insurmountable for most freshwater organisms, which typically move by swimming, crawling, or passively drifting through water. The movement of freshwater fishes, for example, is limited by their inability to cross oceans, high mountain ranges or expansive deserts (Rahel 2007). Major catchment divides and coastal saltwater represent barriers to interbasin colonization, and waterfalls and high gradient channels limit intrabasin movement. Movement barriers have isolated river basins and lakes where relatively distinctive species lineages and faunas have been preserved (Olden et al. 2010).

In contrast to many terrestrial species, responses of freshwater fishes and most other obligatory aquatic organisms (with the exception of overland dispersal of adult aquatic insects and some amphibians and water-dependent reptiles) to climate change are constrained because they are limited to dispersal along pathways of connected water. The linear nature of dendritic riverine systems makes them highly prone to fragmentation that can disrupt completion of life cycles for many freshwater organisms (Schlosser 1991; Fausch et al. 2002). Many freshwater systems historically were not geographically continuous. Instead, they were highly insular systems in which dispersal limitation helped shape population dynamics and distributional patterns.

Some scientists argue that landscape connectivity can be increased by creating new protected lands or altering management practices on relatively unprotected lands along the edges of shifting species distributions (Hannah et al. 2007; Franklin & Lindenmayer 2009). This could be accomplished, for example, by establishing connected reserves that follow longitudinal or elevational gradients (Hannah et al. 2007). Application of this model is more complex in freshwater than terrestrial systems. Many river basins terminate at topographic divides oriented in an east-to-west direction and thus do not provide access to refugia at higher latitudes. For example, fish in prairie river systems of the Great Plains (U.S.A.) are geographically constrained by the prevailing west-to-east direction of the flow of most water in the region (Matthews & Zimmerman 1990). Fishes occupying these drainages (and others with similar orientation) are effectively constrained to a relatively small latitudinal range. The probability of fishes migrating far downstream to the north–south oriented mainsteam Mississippi or Missouri rivers, even over many generations, is low. Even for river basins in which water flows in a north-to-south direction, the quantity of habitat for organisms that must move upstream to access suitable thermal conditions would decrease.

Freshwater organisms will also face numerous and diverse natural and artificial obstacles to latitudinal or elevational movement. Natural barriers include temporary structures such as beaver dams, natural seasonal drying or warming of waterways, and permanent channel characteristics such as high gradient reaches with strong currents, cascades, or waterfalls. Population responses to climate change also will be inhibited by human-engineered structures. Hundreds of thousands of dams, diversions, and impassable road culverts exist globally (Nilsson et al. 2005). In the United States alone, there are over 80,000 large dams and an estimated 2.5 million or more small impoundments (Graf 2006). Mounting evidence shows that culverts at road-stream crossings can limit passage or dispersal of freshwater mussels (Voelz et al. 1998), aquatic insects (Blakely et al. 2006), shrimps (Resh 2005), crayfishes (Kerby et al. 2005), and fishes (Warren & Pardew 1998). Perhaps more so than natural barriers, human-caused habitat fragmentation threatens populations by blocking movement that is essential in the species' life history (e.g., Winston et al. 1991; Vaughn & Taylor 1999).

Increasingly, however, small dams and diversions are being removed for a number of reasons, including the restoration of hydrologic regimes and the enhancement of longitudinal connectivity for fish migration. Similarly, temporary barriers such as impassable culverts under roadways are being modified to allow for easier recolonization and movement of fishes (Roni et al. 2008). The removal of such obstructions, however, can increase the range of non-native species and the spread of diseases and parasites. In recent decades the conversion of culverts into permanent barriers has been a common management approach to protect isolated native populations (e.g., Voelz et al. 1998; Kerby et al. 2005). Given the complexities of invasion–isolation dynamics (Fausch et al. 2009; Jackson & Pringle 2010), it is unlikely that the removal of barriers to enhance habitat connectivity will be a successful adaptation strategy in all areas.

Given the limited mobility of many, if not most, freshwater species and the inability of many species to successfully negotiate natural and artificial barriers, one could argue that managed relocation will be essential. The ability of particular species and populations, especially small-bodied fishes that lack the ability to travel large distances and circumvent barriers (e.g., Schaefer et al. 2003), to migrate to new locations will be severely limited. The majority of globally threatened freshwater fishes are small-bodied species (Olden et al. 2007) that have confined home ranges and poor dispersal abilities. We expect that the thermal requirements of many of these species will not be met as climate changes, especially in flat landscapes at higher latitudes, where the speed of climate change is projected to be the greatest (Loarie et al. 2009). Aquatic insects (larval stages), snails, and crayfish, which move only centimeters to 1 m/day, are especially vulnerable.

Meeting Strict Ecological Criteria for Managed Relocation

We believe that managed relocation efforts are most likely to achieve conservation goals if they meet strict ecological guidelines before they are implemented. In the act of implementing managed relocation, there may be a high probability of establishing populations that ultimately have effects similar to an invasive species (Ricciardi & Simberloff 2009). It is possible that short-distance managed relocations of species with intracontinental origins (i.e., native species introduced to new regions within a continent) will have fewer effects if boundaries of evolutionary significance are not breached. Yet, geographically proximate river basins are often so genetically and ecologically distinct that new colonizations, even from nearby source populations, could have large ecological effects. For example, translocation of monophyletic lineages of a freshwater shrimp (*Paratya australiensis*) from one subcatchment to another within the same drainage system in southeast Queensland, Australia, led to rapid (seven generations) extirpation of the resident genotype (Hughes et al. 2003).

An example of the cascading ecological impacts of species introduced from nearby populations is the rusty crayfish (*Orconectes rusticus*), which is native to the Ohio River of North America and has spread to other watersheds in the same Mississippi River Basin (Hobbs et al. 1989). The highly aggressive and omnivorous feeding behavior of the rusty crayfish has affected entire aquatic food webs, including the displacement of and hybridization with native crayfishes (e.g., Lodge et al. 1994). The smallmouth bass (*Micropterus dolomieu*) is another example of within-basin range expansions resulting in substantial effects on native food webs (e.g., Vander Zanden et al. 1999). The previous two examples are not isolated case studies; regional (or intracontinental) species introductions have effects that are often unexpected.

According to the Non-indigenous Aquatic Species Database (USGS 2009), the number of intracontinental non-native species established in the United States exceeds the number of species of foreign origin (percentage of total number of species in parentheses) for crayfish (92%), turtles (88%), freshwater fishes (72%), frogs (55%), and bivalves (54%). These values far surpass those for terrestrial mammals (16%) and plants (7.5%) (fig. 2 of Mueller & Hellmann 2008). This result, coupled with finding that the effects of non-native species are often independent of the origin of the invader (Ricciardi & Simberloff 2009, implies it is appropriate to examine closely even well-intentioned relocations, whether short or long in distance. It is highly unlikely, however, that non-native species will be candidates for managed relocation (except perhaps those with high economic values).

Reintroduction Biology as a Resource for Informing Managed Relocation

Translocations and reintroductions of threatened species continue to be a popular conservation tool (Seddon et al. 2007), but existing knowledge from these experiences has yet to enter the discussion and design of managed relocation practices. With recent increases in the number of species-reintroduction projects, the opportunity exists to draw on scientifically based protocols for propagation, translocation, reintroduction, and augmentation for managed relocation in freshwaters and elsewhere. We see no difference between the motivations and decade-long practices of species translocation as defined by the International Union for Conservation of Nature (referring to any movement of living organisms from one area to another, including introduction outside its historical native range, reintroduction into its native range, and augmentation of an existing population [IUCN 1987]) and the concept of managed relocation. Perhaps the one exception is that the latter is theoretically more proactive (especially in regard to climate change) compared with the former.

Although the implementation of species reintroductions are biased toward mammals and birds (Seddon et al. 2005) and success rates are historically low or unquantifiable (Fischer & Lindenmayer 2000), lessons from past successes and failures can be applied to managed relocation in freshwaters. Examples of fruitful approaches include experimental studies of the release of captive-bred animals; simulation modeling to identify factors affecting the viability of reintroduced populations; spatially explicit modeling to plan for and evaluate reintroductions; ecological niche modeling to project future climate suitability of targeted localities; and studies that combine experiments, field observations, and modeling to explore the potential effects of translocated species on recipient ecosystems (Seddon et al. 2007; Armstrong & Seddon 2008; Rout et al. 2009).

Relocation of freshwater fishes and mussels (Unionidae) has been occurring in the United States for over 30 years (e.g., Cope & Waller 1995; Minckley 1995; Peck et al. 2007). Results from relocation projects can inform the practice of managed relocation and can even highlight situations in which intentional translocations of species outside their historical range can result in unexpected consequences. For example, the watercress darter (*Etheostoma nuchale*) is listed as endangered under the U.S. Endangered Species Act. It is native to only 4 springs in Alabama that are threatened by watershed development and groundwater pollution (George et al. 2009). In response the USFWS moved 200 individuals in 1988 to establish a new population in Tapawingo Spring, outside the species' native range. The translocation was considered successful because watercress darters now number in the thousands. Nevertheless, the result of translocation was quite different for another threatened fish in Tapawingo Spring, the rush darter (*Etheostoma phytophilum*), which occurs in only three populations and was described as a distinct species in 1999. As the number of watercress darters increased, due to its competitive superiority, the number of rush darters decreased, and by 2001 rush darters had been extirpated from Tapawingo Spring. Thus, translocation of even a seemingly benign endangered species outside of its current range can adversely affect another endangered species.

Implementing Managed Relocation in Freshwater Systems

The effects of introducing a freshwater species to a new location are uncertain (Leprieur et al. 2009) and we believe they must be balanced against the probability of species loss associated with doing nothing. We offer some general guidelines for deciding whether to consider managed relocation in freshwater systems and where these relocations should occur. We do not address the ecological and social criteria in the evaluation of managed relocation (see Hoegh-Guldberg et al. 2008; Richardson et al. 2009) or discuss broader ethical issues (Sandler 2010). Richardson et al. (2009) devised a decision-making framework for individual cases of managed relocation that is multidimensional and informed by differences in social values. We believe their perspective is equally valid for freshwater, marine, and terrestrial species. Here, we focused on species for which the risks of managed relocation might be minimal and on recipient locations that may reduce the probability of undesirable effects.

Determining Candidacy for Managed Relocation

It first needs to be determined on the basis of ecological data and causal mechanisms of climate change whether the species of concern is declining and whether it can move or adapt in response to climate changes. Next, an assessment of the trade-offs between the probability of extirpation in the target region versus the probability of causing declines of native species or loss of ecosystem function in the recipient region is required. Direct estimates of probabilities of extirpation and invasion are lacking for most species. But, ecological theory and empirical data can be used to identify suites of species' traits, such as life history, trophic status, and dispersal ability, that are associated with the risk of extirpation (e.g., Olden et al. 2008; Sodhi et al. 2008; Larson & Olden 2010) and invasion (e.g., Ricciardi & Rasmussen 1998; García-Berthou 2007; Larson & Olden 2010).

We found few common ecological and life-history traits of freshwater animals that were associated with probabilities of extirpation and invasion (Table 1). Species with large body size, long life, delayed maturity, minimal parental care to offspring, and specialized feeding behaviors typically have greater probability of extirpation and tend to be less invasive. These species have low maximum rates of population growth and thus seem to be strong candidates for managed relocation in terms of minimizing the probability of unintended effects on recipient ecosystems. Nevertheless, species' traits related to invasion success are not always the opposite of those related to extinction probability (Table 1; Blackburn & Jeschke 2009). This result emphasizes that care must be practiced when considering even an imperiled species for managed relocation.

Identifying Suitable Localities for Managed Relocation

Three core criteria may assist in the determination of where to relocate freshwater organisms with the goal of minimizing the potential effects on recipient ecosystems. First, we suggest translocations occur within the species' historical range and optimally within the same major river basin so that boundaries of evolutionary significance are maintained. Multiple ecologically significant units can occur in a single drainage, however, and hybridization with a refugial population can lead to extirpation of the native lineage (e.g., Hughes et al. 2003).

Second, for lacustrine species, relocation to physically isolated lakes (e.g., seepage lakes with no inlets or outlets) rather than drainage lakes will lower the probability of secondary spread across the landscape from the relocation site. For riverine species, relocating populations upstream of natural or artificial barriers (e.g., waterfalls and large dams, respectively) helps prevent individuals from moving downstream (e.g., Rood et al. 2010). Nevertheless, a trade-off exists between maximizing the geographic extent of the receiving area and minimizing the potential undesirable ecological impacts at greater spatial extents. Moreover, this strategy also may result in greater effects at the relocation site. For example, seepage lakes often have endemic faunas because they lack predatory fish and have been geographically isolated for long

Table 1. General characteristics of freshwater animal species associated with probabilities of extinction and invasion and our assessment of their utility in identifying candidate species for managed relocation.*

Characteristic	*Likely to be extirpated*	*Likely to be invasive*	*Informative for managed relocation*
Abundance and distribution in native range	low and limited	high and extensive	√
Environmental tolerance	narrow	wide	√
Genetic variation	low	high	√
Body size	small or large	small or large	
Life span	short or long	short or long	
Growth rate	low	high	√
Maturation	delayed	early	√
Fecundity	low	high	√
Diet breadth	narrow	wide	√
Parental care	low or high	low	
Gregariousness	no	yes	√
Mobility	limited or wide	wide	

**Characteristics are based on McKinney (1997) and Kolar and Lodge (2001), and values refer to "typical" values that are derived from current scientific understanding (notable exceptions exist for all). Challenges of identifying traits associated with extinction and invasion were not considered (García-Berthou 2007; Olden et al. 2008).*

periods. Thus, candidate relocation sites must be evaluated not only on the basis of successful establishment and long-term maintenance of the threatened species but also on the basis of minimizing collateral damage of the translocation event.

Third, current ecological integrity and future threats to candidate geographical areas for managed relocations must be evaluated carefully. A relocation is more likely to be successful in areas that have not been highly affected by human activities or non-native species. This site characteristic is relatively easy to quantify, but less certain are future changes in land tenure and continued effects of climate change. Hoegh-Guldberg et al. (2008) state that determining whether a species faces a high probability of decline or extinction as climate changes requires in-depth knowledge of the species' biology and the changes occurring within its environment. We suggest that the current state of knowledge and capacity to reliably predict how freshwater systems and biota will be affected by climate change remains limited (Heino et al. 2009). Even in recipient areas unlikely to change much in response to climate change, long-term efficacy of managed relocation requires an ongoing commitment to mitigate potential threats. It may be possible to establish new freshwater protected areas that are strategically located to support future populations.

Conclusion

There are those who believe managed relocation goes too far (Ricciardi & Simberloff 2009; Seddon et al. 2009) and those who believe it is a necessary consideration as climate changes (McLachlan et al. 2007; Sax et al. 2009). Decision-making frameworks that incorporate ecological and social values may minimize the possibility of inadvertent undesirable effects of managed location (Richardson et al. 2009). Although conservation of narrowly endemic freshwater species may require managed relocation, the risks associated with translocations will, in some cases, be substantial. Given that watercourses with natural or artificial barriers could limit, or even preclude, the ability of fish and other water-dependent biota to move in response to climate change, it may be worthwhile to consider removing these barriers or, alternatively, managed relocation. Assisted short-distance translocations to overcome natural and artificial barriers will, in many cases, be less risky than moving species across major topological divides or large distances. Nevertheless, these approaches increase probabilities of species invasions (Fausch et al. 2009; Jackson & Pringle 2010).

Given the many uncertainties, we recommend the establishment of an interagency commission of scientists and policy makers from academia, non-governmental organizations and state and federal agencies to develop clear guidelines for managed relocation in freshwater environments. We offer five recommendations to enhance the scientific basis of such guidelines.

1. Adopt the term *managed translocation* instead of managed relocation to reflect the fact that individuals will not always be reintroduced within their historical native range. Specifically, we recommend that *managed introduction* be used to describe the intentional movement of an organism outside its historical native range and *managed reintroduction* be used to describe the intentional movement of an organism into part of its former native range.
2. Use a systematic planning and prioritization process to examine the trade-off between facilitation of individual movement in response to climate change (e.g., removal of small barriers) and the probability of range expansion of non-native species currently in a system.

3. Determine which species and locations might be immediately considered for managed translocation by linking the current status of species with recent estimates of the rate at which local climate is projected to change. In mountainous regions, the rate of temperature change may be as low as 0.8 km/year, whereas in grassland and desert biomes it may approach 1.3 km/year (Loarie et al. 2009). Thus, species with slow generation times and limited dispersal ability that occurs in low-gradient rivers with many dams may be good candidates.
4. Adopt a hypothetico-deductive framework by conducting experimental trials to introduce species of conservation concern into new areas within their historical range.
5. Build on previous research through continued communication and synthesis of case studies (i.e., meta-analysis). Inevitably, the process of managed translocation, much like the history of species reintroductions, will rely heavily on evidence from case studies. Thus, creation of integrated monitoring and information systems will help establish a reliable database to guide future research and implementation of managed relocation.

Advances in these areas, when coupled with the legal reality of species translocations (Joly & Fuller 2009; Shirey & Lamberti 2010) will help ensure that the best available science informs decisions about managed relocation for conservation of freshwater organisms.

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