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Dynamics of fish in Australian desert springs: role of large-mammal disturbance

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ABSTRACT

Human activities affect even the most remote and best preserved places on Earth. One of those places is Dalhousie Springs, Witjira National Park, in the arid centre of Australia. In 2003 we resurveyed the fish communities in springs to document changes since an earlier survey in 1991. Over the 12 years there were 18 population extirpations and only two colonizations, so total occurrences of five native species in 30 springs decreased from 83 to 67 populations. One species, the endemic Dalhousie goby, *Chlamydogobius gloveri*, accounted for 12 of the 18 population extirpations. Each fish species tended to persist in springs larger than some threshold size. Extirpations were related to spring size, with smaller springs more readily loosing populations, and to major habitat changes, which included large increases in the tropical reed *Phragmites* and concomitant decreases in open water, disturbed habitats, and dissolved oxygen. Extirpations of fish populations can be attributed primarily to habitat changes associated with reduced disturbance and herbivory as a result of the removal of feral livestock. These changes highlight the keystone impacts of large mammals on habitats and biotas of desert springs, and should be considered in management practices and policy decisions.

Keywords

Community structure, conservation, desert springs, disturbance, fish.

INTRODUCTION

The environment is constantly changing, but the pace has been accelerated by human activities. Of particular concern is how populations, communities, and ecosystems are affected by different kinds of environmental change. Even in the most remote and best-preserved places on earth, anthropogenic changes in climate and habitats have had large impacts on the abundance, distribution, and diversity of native species. These impacts are obviously relevant for conservation biology, but they are also relevant for understanding the patterns and processes that characterize the long-term dynamics of ecological systems.

To address these issues requires careful monitoring. Experimental studies are valuable, because the controlled manipulation of variables allows the effects of particular factors to be isolated and the mechanisms of their impacts to be inferred. Most experimental studies are not of sufficient temporal and spatial scale, however, to assess many of the potentially important environmental changes in populations and communities. Additionally, the variables that the experimenters choose to manipulate may not be those that are having the greatest ecological impacts. An alternative is to use comparative non-experimental monitoring studies, provided that these have been conducted on sufficiently large temporal and spatial scales so as to allow changes to be documented and their causes to be inferred. Such non-experimental approaches have been standard scientific practice in the Earth sciences, and they are being used with increasing frequency in the ecological sciences.

Surveys of the fish of the Dalhousie Springs in central Australia provide an illuminating case study. Witjira National Park in northernmost South Australia contains approximately 80 artesian springs with associated aquatic and riparian ecosystems and flora and fauna. These springs are exceptionally well conserved due to their spatial isolation, inhospitable desert surroundings, and National Park status protection. Like nearly all aquatic and riparian environments in arid regions throughout the world, the springs have been used by humans, first by aboriginal hunter-gatherers and subsequently by pastoralists and their livestock. Unlike most desert springs elsewhere in the world, however, Dalhousie Springs have experienced minimal human impacts in the form of surface water diversion, groundwater depletion, agricultural development, and introduction of exotic species. They retain an intact assemblage of native freshwater and riparian plant and animal species, many of which are endemic and hence of particular conservation value (Zeidler & Ponder, 1989). This biota includes five species of fish, of which all but one are endemic to the Dalhousie Basin (Wager & Unmack, 2000).

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Despite the extreme isolation and excellent preservation of Dalhousie Springs, repeated surveys of the fish over the last two decades have revealed major changes in the distribution of species and the composition of communities. Surveys by the South Australian Museum in the 1980s (Glover, 1989) provided an incomplete but valuable baseline for two subsequent very thorough surveys: by Kodric-Brown & Brown in 1991, and by the present authors in 2003. The 2003 survey was motivated by evidence that the springs and their biotas are extremely dynamic. Ecological, hydrological, and geological evidence shows that the springs are continually being formed, shifting their outflows, and going extinct – likely on a time scale of decades (Smith, 1989; Zeidler & Ponder, 1989). Additionally, Kodric-Brown & Brown (1993a) documented the complete drying of one spring and the extirpation of its fish population between the 1980s and 1991. So we expected that the 2003 survey would reveal additional changes in the springs, and also in their fish communities due to local colonization and extirpation events. We were surprised, however, by the magnitude of the changes and the fact that extirpations overwhelmingly outnumbered colonizations. Here we document these changes and evaluate explanations for their causes.

METHODS

The system

The Dalhousie Springs comprise approximately 80 active and extinct artesian thermal freshwater springs distributed over an area of 72 km^2 in Witjira National Park, northernmost South Australia. In the 1980s the springs were surveyed and studied by teams from the South Australian Museum. The findings are described in a monograph by Zeidler & Ponder (1989), which should be consulted for additional details. The geology and hydrology are reported by Krieg (1989) and Smith (1989). The springs are very dynamic, forming and going extinct on a timescale of decades to centuries. The smallest springs are fragile, typically consisting of a seep or small pool and a tiny outflow. The larger springs are more permanent, and typically consist of a large source pool, hundreds to thousands of square meters in area, and an outflow stream, sometimes extending for several kilometres into the surrounding desert.

The fish fauna of Dalhousie Springs is comprised of five species: goby (*Chlamydogobius gloveri*), gudgeon (*Mogurnda thermophila*), catfish (*Neosilurus gloveri*), perch (*Leiopotherapon unicolor*), and hardyhead (*Craterocephalus dalhousiensis* and *C. gloveri*). The two named species of hardyhead are distinguished by small differences, do not coexist in the same springs, and are treated as a single taxon here. All five species are in different families, and all except perch are endemic to the Dalhousie Basin (Wager & Unmack, 2000). Unlike many desert springs elsewhere in the world, Dalhousie Springs contain no exotic fishes.

The remoteness and harsh surroundings of the springs have contributed to their preservation. Nevertheless, there is a long history of human impact. Stone artefacts, charcoal, and oral history (D. Achee, pers. comm.) attest to the presence of aborigines, who camped, hunted, and fished at the springs. The aborigines were displaced by Europeans in the nineteenth century. From about 1900–25, farmers and pastoralists maintained homesteads, diverted some surface water for agriculture, and introduced exotic date palms. Since the 1870s, however, the most serious impacts were due to livestock, mostly feral donkeys and camels, which watered at the springs and grazed on the emergent vegetation. In 1985, the area was purchased by the South Australian government to create Witjira National Park. Beginning in 1995, a major effort was initiated to remove the feral livestock and control tourist traffic. The central cluster of springs was fenced and tens of thousands of donkeys and camels were killed (G. Axford, pers. comm.). Subsequently, human impacts have consisted largely of tourists swimming and camping at the largest springs. When we revisited the springs in 2003, only small numbers of donkeys and camels were present at a few outlying springs. At most springs, livestock had been absent for many years and both source pools and outflows were heavily vegetated with the native tropical reed, *Phragmites australis*.

Surveys

The present paper is based on comparisons of two surveys of the fish fauna of Dalhousie Springs. In September to October 1991, Kodric-Brown & Brown (1993a,b) intensively surveyed all active springs. They documented 77 populations of fish distributed among 28 isolated springs. They recorded the complete drying of one spring, apparently due to natural successional processes, and the extirpation of its goby population, which must have occurred after the field studies in the 1980s (Glover, 1989). By comparison with earlier aerial photographs, Kodric-Brown and Brown also documented recent changes in several other springs, including joining and separation of outflow streams. For details of methods and results see Kodric-Brown & Brown (1993a,b).

The authors of the present study resurveyed all active springs between 22 August and 10 September 2003. We used essentially identical methods to sample intensively for the presence of each fish species. At each spring we measured depth, temperature, and dissolved oxygen of the water. As reported in Kodric-Brown and Brown (1993a), because each species has a distinctively different ecology, different methods were required to determine its presence or absence. Sampling methods included minnow traps for the larger species (gudgeon, perch, hardyhead) and smaller traps constructed from window screen mesh and dip nets for goby. We did not use seines in the present survey because the outflows were so choked by vegetation that very little open water was available. Since the goal of the resurvey project was to document changes in the fish fauna, we were especially concerned to record any colonizations or extirpations of populations that had occurred since the 1991 survey. Rather than use a fixed collecting protocol, we stopped trapping for a species once its presence was recorded, and devoted increased effort to sampling for the remaining species, especially those that had been collected in that spring in 1991. Effort was unevenly distributed across springs and was affected by spring size as well as the number and identity of species that had been documented in the1991 survey. For example, springs CA5, CD2, and E5 were sampled with 9 to 13 minnow traps/spring. Springs that previously had gobies but had little remaining suitable habitat were sampled intensively with dip nets and small goby traps (e.g. B2, CC4, F2 – 60–70 combined dip net hauls and goby traps). Other springs were repeatedly sampled over 4–5 days and nights with minnow traps, dip nets, and goby traps (e.g. A1 and A2 – 43 minnow traps; CA1– 43 minnow traps; B1 – 40 minnow traps). Approximately 72 person days were expended in the present survey compared to 38 person days during the 1991 survey. The difference in sampling effort was in part because the springs were heavily overgrown with riparian vegetation, which made access to water extremely difficult and open-water habitat hard to find, and in part because we were especially concerned to confirm apparent colonization and extirpation events. Given this intensive sampling effort, we are reasonably confident, but in most cases cannot be absolutely certain, that a species that had been present in 1991 but was not found in 2003 was actually extirpated from that spring. Since the earlier survey was less intensive than in 2003, we also cannot be absolutely certain that the populations that had apparently colonized had not actually been present in 1991.

Data and analysis

We analysed the distribution of the five fish species among springs as follows:

1 Nested subset structure. In 1991, the fish communities comprised almost perfect nested subsets, so we used the program of Atmar and Patterson (http://aics-research.com/nestedness/tempcalc.html) to quantify the degree and compare the patterns of nestedness in 1991 and 2003.

2 Environmental variables. In 1991, species diversity and occurrence of each species were closely correlated with a suite of variables, all related to spring size (Kodric-Brown & Brown, 1993a). So, we used similar, but somewhat more sophisticated methods to quantify these variables. We used the best and most recent available data on source pool size, temperature, and discharge rate (from our measurements in 2003, Kodric-Brown & Brown, 1993a; Smith, 1989). We used aerial photographs taken in 1986 and 2002 to measure changes in outflow streams and area of riparian vegetation. Digital images were obtained from the South Australian Government (http://www.environment.sa.gov.au/mapland/). The images were combined into a single image for each time period and georectified. Subsequently, polygons surrounding each spring were clipped from the image and altered to make the boundary between terrestrial and aquatic habitats more clear. IMAGE ANALYSIS software (ENVI version 4.2, http://www.ittvis.com/envi) was then used to count the number of pixels within the wetland boundary, yielding an estimate of total wetland area. The wetland areas of these springs vary substantially over the course of a year due to changes in flow rate and evapotranspiration. Over the longer term of years to centuries, new springs form, undergo succession, and eventually go extinct due to changes in subsurface water-flow pathways. To capture this variation, we used two types of boundaries for the wetlands, a conservative one defined by living wetland vegetation and a broader one that included dead vegetation, saturated soil areas, and other features indicative of past wetted areas.

3 Effects of habitat variables on species composition. There were a total of 52 covariates available to explain the distribution patterns of the fish assemblage. These fell into three categories: spring size and change in size; aquatic abiotic variables (e.g. temperature, salinity, flow rate, presence of a pool) and biotic variables (presence of fish and crayfish species). Due to the large number of covariates it was necessary to take a selective approach to analyse presence/absence patterns. We did this by first using regression trees, implemented in module Rpart in the R statistical language (http://www.r-project.org/), to determine which variables were important in determining the presence/absence patterns for each species. Trees were pruned according to standard practice, using both the minimal cross-validated error and the 1 standard error rule (Maindonald & Braun, 2003). In all of the trees these two pruning rules yielded the same tree, in part due to the small number of observations available for building the trees. Here we report only the statistically optimal trees, based on the pruning rules above, characterizing the distribution of each species.

4 Modelling extirpation of goby populations. For goby, the large number of springs inhabited in 1991 and the relatively large number of extirpations recorded in 2003 allowed an analysis of environmental variables associated with survival or extirpation. As above, we used a regression tree approach to determine the important variables for goby extirpations. Then, we followed up this analysis with specific logistic regression analyses to investigate the variables of interest. In particular, after accounting for other variables based on the tree analysis, we focused on three classes of explanatory variables that index changes in habitat area between 1986 and 2002: (1) long-term changes in total habitat area; (2) short-term shifts in outflows as indicated by dead vegetation and wet soil; and (3) presence of potential gudgeon, perch, and crayfish predators. We compiled three variables to index net changes in habitat area between the 1986 and 2002 photos: (1) total habitat area: including all living and dead vegetation, open water, and wet soil; (2) area of living vegetation; and (3) openness of habitat: based on variables positively (e.g. living or dead *Phragmites*) or negatively (e.g. open water, wet soil) indicative of vegetation. To index short-term fluctuations (i.e. recent changes in outflows within approximately 1 year prior to the 1986 and 2002 photos, respectively), for each photo we measured the difference between total wetland area (including all living and dead vegetation, open water, and wet soil) and the wet area (including only open water, green vegetation, and wet soil). To assess effects of predation, we used the presence/absence of each predator as a covariate, including gudgeon, perch, and crayfish as potential predators. Since it is recommended that there should be an order of magnitude more data than estimated parameters in a regression analysis, we were constrained to three or fewer explanatory variables (Maindonald & Braun, 2003).

RESULTS

Distribution of populations among springs

Table 1 gives the occurrences of fish species populations in springs in 1991 and 2003. There were 83 total occurrences in 1991, and these had decreased to 67 by 2003. There were 18 extirpations and two colonizations in the 12-year period. From the perspective of the five species, goby populations were extirpated from 12 springs, gudgeon was extirpated from three springs and colonized one, catfish was extirpated from one, hardyhead colonized one, and perch was extirpated from two. From the perspective of the 30 springs, 14 had unchanged species composition, 11 lost one species and three lost two species by local extirpation, one gained one species by colonization, and one lost one species by extirpation and gained another species by colonization. So, instead of extirpations and colonizations being approximately balanced as might be expected from species turnover in response to natural processes, extirpations far outnumbered colonizations (18–2, respectively). In addition, even when populations had persisted from 1991 to 2003, their numbers were often drastically reduced. This is evidenced by the much greater sampling effort required to capture at least one individual and thereby document presence of some species in certain springs in 2003 (see below).

In 1991, species compositions of springs exhibited almost perfect nested subset structure (Patterson, 1987; Table 2). So every spring that contained fish had goby, some subset of these had gudgeon, and so on through catfish, hardyhead, and perch, with one exception (hardyhead absent but perch present in Spring E1). In 2003 the species composition was still statistically significantly nested ($P < 0.0001$), but the quantitative magnitude of nestedness was substantially reduced, and gudgeon occurred in more springs than goby (Table 2). Atmar & Patterson (1993) quantify nestedness in terms of the 'temperature' of the presence–absence matrix of occurrences, which can range from 0°, representing perfect nestedness (by analogy to an ice crystal), to 100°, representing a completely random matrix (by analogy to boiling water). By this measure, the magnitude of disorder or temperature of the matrix increased markedly from 1.9° to 11.9° between in 1991 and 2003 ($P < 0.0001$).

The nested subset structure observed in 1991 was due to the fact that each species tended to occur in all springs larger than some threshold size. Multiple environmental variables, including source pool area, discharge rate, area of riparian vegetation, and length of outflow stream, are all highly intercorrelated as documented in Kodric-Brown & Brown (1993a; for 2003 see regression tree analysis below and Fig. 3). In this paper, we used total area of riparian vegetation, taken from the digitized aerial photographs taken in 1986 and 2002, as a proxy for habitat area in 1991 and 2003, respectively. Presence–absence of each species as a function of these measures of spring size is shown in Fig. 1. Logistic regressions show that four of these relationships are statistically significant at $P < 0.05$, four at $0.05 < P < 0.1$, one at $P = 0.15$ (perch in 2003), and for one no model was possible (goby in 1991, because it was present in all springs).

In both 1991 and 2003 the number of fish species inhabiting each spring was closely correlated with several measures of spring size. Here we show the correlations between number of species and spring size in both 1991 and 2003 as species–area relations, plotted on logarithmic axes and using the same measures of total area of riparian vegetation as above to quantify spring size (Fig. 2). In both years, the relationships were highly significant, with area accounting for approximately 50% of the variation in species richness.

Habitat change and population extirpations

The habitat of the springs, especially the smaller ones, had changed dramatically between 1991 and 2003. These changes were obvious to Kodric-Brown & Brown (1993a), who participated in both surveys, but they were not easy to measure quantitatively. In 1991, grazing and trampling by feral donkeys and camels removed large quantities of riparian vegetation and created substantial areas of open-water habitat along outflows, and disturbance by animals going to water provided ready access to source pools. By contrast, in 2003 there was no sign of feral livestock, except for very light impacts at some outlying springs that were still unfenced (designated with letters E, G, and H in Table 1). All spring source pools (except for CA1 where swimming is allowed and there is substantial human-caused disturbance) and all outflows were overgrown with dense vegetation, dominated by the native tropical reed *P. australis*, and occasionally by the introduced date palm, *Phoenix dactylifera*.

Three additional kinds of information indicate the magnitude of habitat change: (1) It was extremely difficult for us to force our way through the *Phragmites* to gain access to open water and suitable fish habitat. This is best indexed by the fact that nearly twice the total number of person-days was required to determine presence or absence of each fish species: 38 in 1991 and 72 in 2003. This is actually a conservative measure, because in 1991 Kodric-Brown and Brown devoted a substantial proportion of their time learning the spring system at Dalhousie and how to sample for each species, whereas in 2003 the four co-authors used this previous experience and devoted essentially all of their field time to searching for suitable habitat and trapping for fish. (2) In 2003, once we were able to get to water, the living and dead vegetation was often so dense that no light penetrated to the water surface, there were large quantities of decaying biomass in the water, and conditions were anoxic. Because of the high temperatures of the sources of most springs, the water initially contains little dissolved oxygen, and aeration occurs only if there is substantial exposure to light and air in the source pool or outflow. In 2003, it was literally impossible to find water where we could obtain a positive reading on our dissolved oxygen meter in several of the smallest springs. (3) The vast majority of the water discharged from the springs is dissipated by evapotranspiration. This is why the area of riparian vegetation provides a good measure of spring size (high correlation between discharge measured in the 1980s and area of vegetation in the 1986 photo documented in Kodric-Brown & Brown, 1993a). One effect of the increased vegetation and resulting transpiration losses was decreased length of some outflow streams between the two surveys. This is shown by the fact that several springs (CA11, E2, F2, CC4) that had water and fish in 1991 were totally or nearly dry in 2003, and three springs (B1-B2, CC1-CC2, Ga5-Ga6, see Table 1) whose outflows joined in 1991 had shortened outflows and no aquatic connections in 2003.

Table 1 Community dynamics of fishes in Dalhousie Springs, showing changes between 1991 and 2003.

Springs →	CA1	CA5	CD1	CD2	CC3	A1 and 2	E1	A3	CB2	GA123	B1*	GA6*	CC1*	CC2*	CD3	DB3	E5	DA3	DB2	GB2	DA2	A5	H3	DB1	CA11	E2	F2	GA5*	CC4	B2*	Occurrences
Species																															1991→2003
Goby	+	+	+	+	+	+	+	+	+	+	+	+	E	E	+	+	+	E	E	E	E	+	+	+	E	E	E	E	E	E	30→18
Gudgeon	+	+	+	+	+	+	+	+	+	+	+	+	+	+	E	+	+	+	+	E	C									E	21→19
Catfish	+	+	+	+	+	+	+	+	+	+	+	+	+	+	E																15→14
Hardyhead	+	+	+	+	+	+		+	+	C			+	+																	10→11
Perch	+	+	+	+	E	E	+																								7→5
Species no. 1991	5	5	5	5	5	5	4	4	4	3	3	3	4	4	3	2	2	2	2	2	1	1	1	1	1	1	1	1	1	2	83→67
↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓
2003	5	5	5	5	4	4	4	4	4	4	3	3	3	3	1	2	2	1	1	0	1	1	1	1	0	0	0	0	0	0	67

Symbols: + present in both 1991 and 2003; E = extirpation, present in 1991, absent in 2003; C = colonization, absent in 1991, present in 2003.
*Outflows of B1 and B2, CC1 and CC2, and Ga5 and Ga6 were connected in 1991, but no longer connected in 2003.

Table 2 Maximally nested presence–absence matrices for Dalhousie Spring fish communities in 1991 and 2003; Note the decrease in nestedness in the 12-year period.

1991

Spring →	CA1	CA5	CD1	CD2	CC3	A1 and 2	E1	A3	CB2	C1 and 2	GA123	B1 and 2	CD3	GA6	DA3	DB2	DB3	E5	GB2	A5	CA11	CC4	DA2	DB1	E2	F2	GA5	H3
Species ↓																												
Goby	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Gudgeon	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X									
Catfish	X	X	X	X	X	X	X	X	X	X	X	X	X	X														
Hardyhead	X	X	X	X	X	X		X	X	X																		
Perch	X	X	X	X	X	X	X																					

2003

Spring →	CA1	CA5	CD1	CD2	CC3	A1 and 2	E1	A3	CB2	GA123	GA6	B1	CC1	CC2	DB3	E5	DA3	DB2	DA2	CD3	A5	DB1	H3
Species ↓																							
Gudgeon	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X				
Goby	X	X	X	X	X	X	X	X	X	X	X	X			X	X				X	X	X	X
Catfish	X	X	X	X	X	X	X	X	X	X	X	X	X	X									
Hardyhead	X	X	X	X	X	X		X	X	X			X	X									
Perch	X	X	X	X			X																

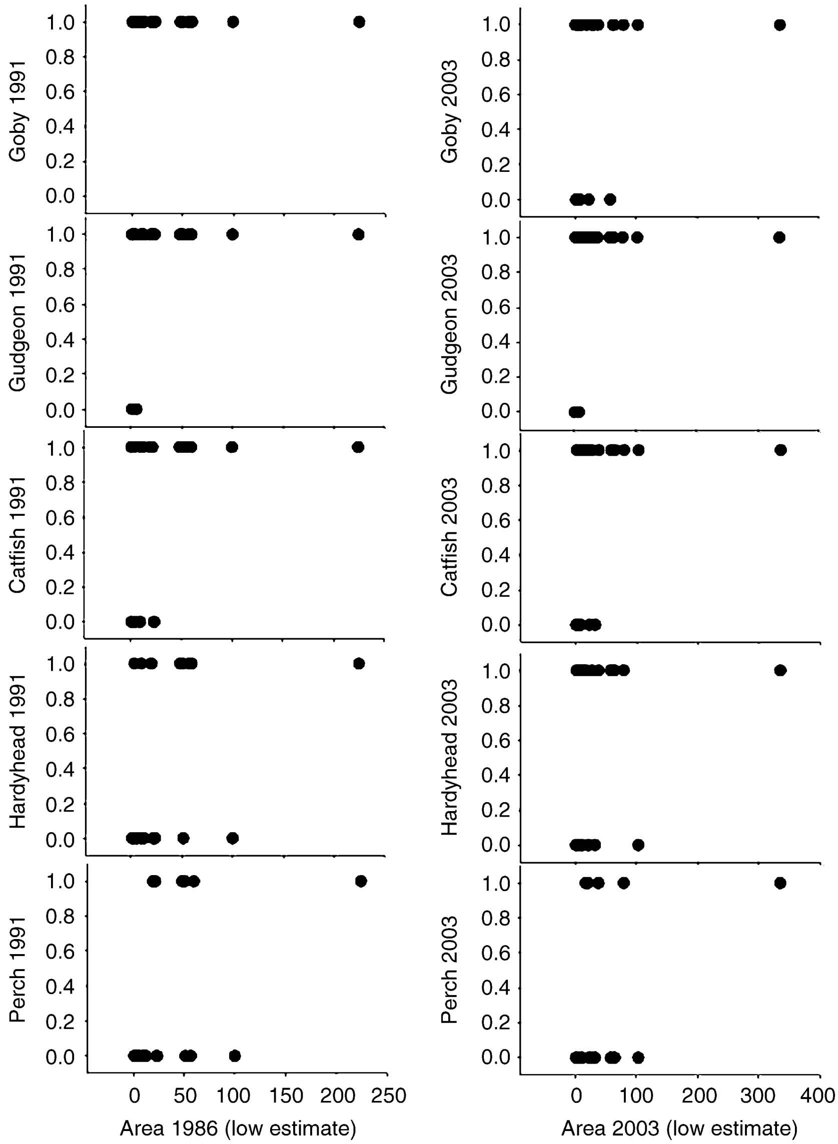

Figure 1 Presence (1) or absence (0) of each species in 1991 and 2003 as a function of spring size. Spring sizes in 1991 and 2003 were estimated as the total area of riparian vegetation, using the digitized aerial photographs taken in 1986 and 2002.

These changes since 1991 were more pronounced in the smaller springs, where most fish population extirpations had occurred. Fourteen of the 18 documented extirpations occurred in small springs that contained three or fewer fish species in 1991 (Table 1). Large increases in vegetation around source pools and along outflows were also obvious, however, even in the largest springs. Although most of these still retained most of their fish populations in 2003, two of seven populations of perch, a top predator of open-water habitats, were extirpated from large springs in the 12-year period.

To provide quantitative insight, we performed exploratory regression tree analyses of spring characteristics associated with presence or absence of each fish species. The outcome shows that somewhat different environmental factors were selected to explain presence/absence of each of the five species (Fig. 3). For example, temperature was selected for goby and hardyhead and dissolved oxygen for gudgeon. Nevertheless, the primary factors selected for all species were variables correlated with each other and with overall spring size: i.e. presence/absence of source pool for goby, habitat area for gudgeon, discharge flow rate for catfish and hardyhead, and source pool depth for perch. The importance of spring size matches the patterns shown in Fig. 1. This reinforces the interpretation that in 1991 the smallest springs inhabited by each species were near the threshold size required for persistence. However, the difference in the explanatory variables suggests that somewhat different proximate factors may operate for each species.

Goby was the species by far most seriously impacted by the habitat changes. Between 1991 and 2003, 12 of 30 populations were extirpated and goby was replaced by gudgeon as the most widely distributed species. Only goby had a sufficient number of population extirpations for quantitative analysis of the variables associated with extirpation or persistence, so we performed a separate regression tree analysis just on goby. We found that extirpations between 1991 and 2003 occurred differentially in springs without source pools and with shallow average depths, characteristics associated with small spring size (Fig. 4). Goby

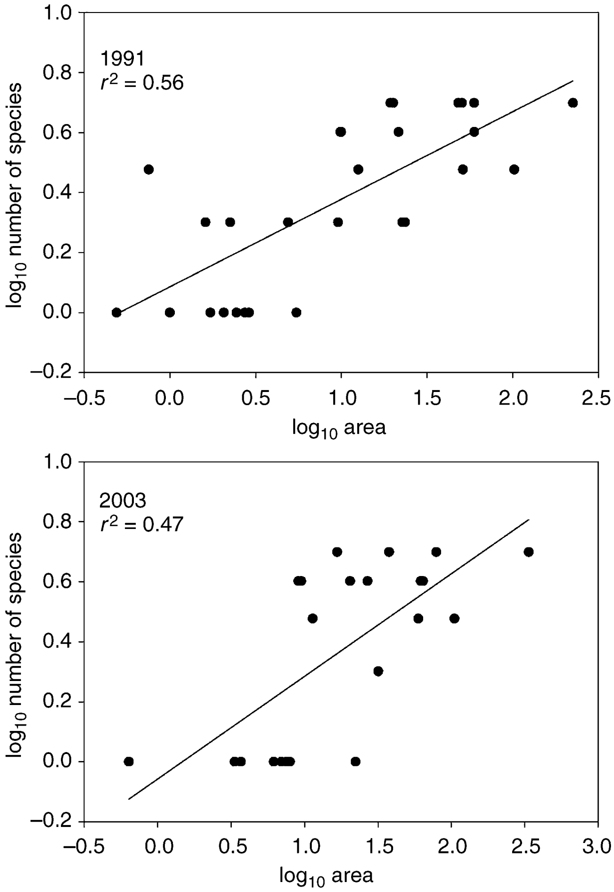

Figure 2 Number of species as a function of spring size in 1991 and 2003, plotted as species–area relations on logarithmic axes. Spring sizes were estimated as the total area of riparian vegetation, using the digitized aerial photographs taken in 1986 and 2002.

populations also were extirpated, however, from two relatively large springs (CC2 and DB2). So we explored more detailed logistic regression models, which incorporated additional variables, including measures of spring area, variation in spring size, and impact of gudgeon, perch, and crayfish predators. Some of these models gave slightly better likelihoods than the base model, but they could not meet the criteria of preferred models due to the Akaike Information Criteria penalty for parsimony. Therefore, the best single predictor of goby extirpation remains small spring size (Fig. 4).

DISCUSSION

Fish communities of Dalhousie Springs are dynamic. Fish were resurveyed in 2003 because of indications that extirpation and colonization events may be fairly frequent (Kodric-Brown & Brown, 1993a,b). Information in the literature and obtained in conjunction with the 1991 survey suggested that each mound spring undergoes a cycle of formation, succession, and extinction (Boyd, 1990). The rate of this process appears to be size-dependent: more rapid in small springs than large ones. Kodric-Brown & Brown (1993a,b) attributed the original nested subset structure of fish communities in 1991 to the fact that both colonization and extirpation rates are high, so that all species have the opportunity to colonize all springs – apparently during extreme flood events – and subsequent extirpations occur differentially among species as a function of spring size. Similar colonization–extirpation dynamics apparently occur in hydrobiid snails, which show high levels of gene flow (Colgan & Ponder, 1994). Kodric-Brown & Brown (1993a) attributed colonization and extirpation events and resulting changes in species composition to natural processes of spring succession. The one documented extirpation prior to 1991 appeared to be due to the natural drying of a small spring.

Results of our resurvey in 2003 stand in marked contrast to this scenario of natural succession, which would predict an approximately equal number of extirpations and colonizations and approximately constant overall species richness. Instead, extirpations far outnumbered colonizations (18–2). The extirpations differentially impacted goby populations and the smaller springs. Not only did overall species richness decrease, but also species composition and the degree of nestedness changed substantially. These changes in fish assemblages point to changes in habitat that caused extirpation of many goby populations, and resulted in gudgeon replacing goby as the most widely distributed species. We conclude that the large increase in emergent vegetation was largely responsible. Goby extirpations occurred in two circumstances: (1) in 10 of the 13 smallest springs, some of which had completely dried and the others had become densely overgrown; and (2) in two large springs, which experienced large reductions of shallow open-water habitat around the margins of spring pools and along the outflows where the feral livestock had grazed and watered (note that this was prime goby habitat, whereas gudgeon preferred the somewhat deeper and more vegetated parts of outflows; Kodric-Brown & Brown, 1993a).

So these changes in the fish communities were due not to natural cycles of spring hydrology and ecological succession, but to large, long-term, unidirectional changes in the aquatic and riparian habitat. The changes in the fish fauna and the spring environments coincided with a major change in management – the implementation of a program to remove all feral livestock from Dalhousie National Park. Effects of livestock removal, and the resulting reduction in disturbance and herbivory on spring environments were dramatic. The large increase in *Phragmites*, and consequent reductions in open-water habitats, decreases in dissolved oxygen, and increases in evapotranspiration-reduced habitat for all fish species. Effects were especially severe in the smallest springs, some of which literally dried up as a result of increased transpiration from the vegetation.

The detrimental effects of livestock removal on spring environments and the persistence of native fish species point to an important role of physical disturbance by large mammals in the ecology of these springs (Kodric-Brown & Brown, in press). We hypothesize that for tens of thousands of years the Dalhousie Springs experienced virtually continuous disturbance: first by native marsupial megafauna, then by aboriginal people, and most recently by domestic and feral livestock (Cohen, 1989; Harris, 1989; Flannery, 1994). Activities of these large mammals

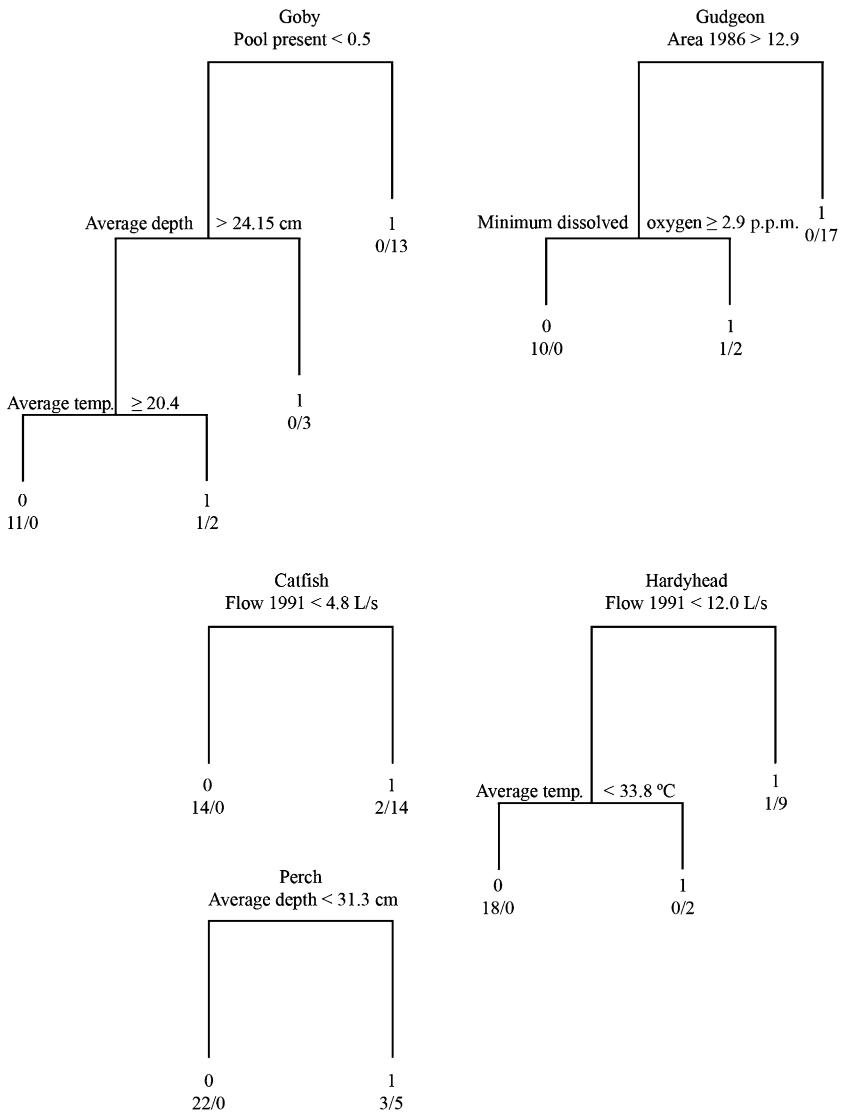

Figure 3 Results of regression tree analysis describing the characteristics of springs associated with the presence or absence of each fish species. The trees are pruned to their statistically optimal size (see details in Methods). Height of a vertical line gives the relative separation at each node. Criteria at each node are for taking the left branch. The upper number at the terminal end of each branch indicates presence (1) or absence (0) of the species, and the lower pair of numbers gives the number of absences/presences in that terminal branch.

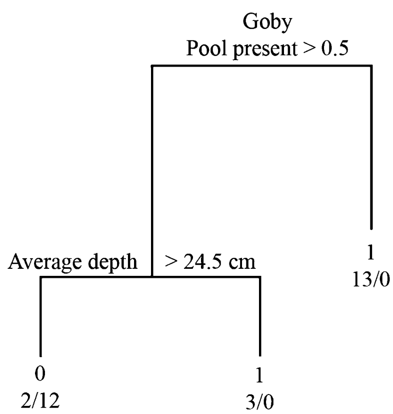

Figure 4 Optimally pruned regression tree selecting characteristics of springs in which goby populations were extirpated or persisted. Height of vertical lines gives the relative separation at each node. Criteria at each node are for taking the left branch. The upper number at the terminal end of each branch indicates extirpation (0) or persistence (1), and the lower pair of numbers is the number of persistences/extirpations in that terminal branch.

removed emergent vegetation and created open-water and disturbed shallow-water habitats around both spring pools and outflows. By 2003, in the absence of large mammals, the springs had become densely vegetated. The only large-scale disturbances that removed vegetation were infrequent lightning-caused fires and date palm removal by park personnel, and these occurred at just a few springs between 1991 and 2003 (G. Axford, pers. comm.).

At present it is difficult to evaluate the seriousness and long-term consequences of the habitat changes and losses of native fish populations that have occurred at Dalhousie Springs. For one thing, it is difficult to know whether prolonged absence of large mammals occurred in the past, and whether compensatory management practices will be employed in the future. For another, it is difficult to evaluate the effects of population extirpations that have occurred in the last several years on the genetic structure and the long-term distribution and survival of the fish species. The changes have been particularly severe for goby, where 12 of 30 populations were extirpated, and for perch, where two of seven populations were lost. None of the species appears critically threatened with global extinction at present, but impacts of local extirpations and population reductions on genetic diversity and long-term persistence should be cause for concern.

Changes in habitat and fish communities at Dalhousie point to the difficulties of conserving the ecology of desert springs. Throughout the arid regions of the world, natural springs provide a scarce, localized source of water and lush green vegetation that attracts and concentrates impacts of large herbivorous mammals and humans. Activities of these mammals create disturbances and remove vegetation. Ecological changes similar to those reported here for Dalhousie Springs also have occurred in North American deserts (Kodric-Brown & Brown, in press; Williams *et al*., 1985; Miller *et al*., 1989; Minckley & Deacon, 1991). On both continents, drastic reductions of native fish populations, sometimes to the point of local extirpation, have occurred when springs have become densely overgrown with vegetation following removal of feral or domestic livestock and cessation of aboriginal burning. On both continents it appears that there was a sequence of near-continuous disturbance due to native megafauna, aboriginal humans, and livestock. Large mammal disturbance was virtually eliminated following incorporation of the springs into parks or reserves. Studies on the effects of grazing and disturbance on riparian plant communities often show beneficial effects in maintaining plant species diversity and reducing herbaceous cover (e.g. Allen-Diaz & Jackson, 2000; Jackson & Allen-Diaz, 2006).

Similar changes due to new management practices have occurred at other desert springs in Australia and North America. Fatchen (2001) documents drastic changes in the vegetation of Hermit Hill Springs in South Australia after the removal of livestock. *Phragmites* was either absent or present at low density at mound springs. After the removal of livestock in 1984, *Phragmites* had completely dominated the plant community by 2000. Fatchen & Fatchen (1993) suggested that disturbance by trampling and grazing of livestock, as well fires, suppressed the growth of *Phragmites*. The role of fire as a management tool in controlling the growth of riparian vegetation and restoring fish habitat has yet to be assessed in a systematic way. Natural burns of springs and outflows due to lighting fires on both continents reduced vegetation density and restored aquatic habitat, at least temporarily (Kodric-Brown, Unmack, pers. obs.). The effects of a lighting-caused fire at one of the Hermit Hill Springs in 1994 on the growth of *Phragmites* were still evident in 2000, suggesting that controlled fires could be used as a management tool to reduce biomass, restore open water, and increase plant diversity on mound springs (Fatchen, 2001).

In recent decades, desert springs have become a major target of conservation efforts, because they not only support unique ecosystems but also contain rare and endangered animal and plant species (Williams *et al*., 1985; Jensen *et al*., 1998; Fatchen, 2000; Sada *et al*., 2001; Harris, 2002; Thompson *et al*., 2002; Ponder, 2004). It is becoming increasingly clear, however, that active management practices are required to maintain spring environments and biotas. Mechanical removal of salt cedar from a spring outflow in Nevada increased populations of two endangered species of fish (Kennedy *et al*., 2005). Efforts to conserve and restore desert springs typically include fencing, removal of invasive species, and reduction of human impacts. In order to conserve small springs, which often contain endemic and endangered populations, it is especially important to maintain open water and disturbed habitats. In many cases, this 'ecological service' was performed free of charge by large mammals and aboriginal humans. To conserve spring habitats and native biota, conservationists are confronted with the challenge of understanding and recreating an appropriate, sustained regime of disturbance and vegetation removal. Possible alternative management practices include some combination of manual or mechanized vegetation removal, controlled burning, and reintroduction of native or exotic large herbivorous mammals. The last alternative, which might often be cheapest and most effective, is almost never considered, let alone tested as an adaptive management experiment.

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