

Implications of Beaver *Castor canadensis* and Trout Introductions on Native Fish in the Cape Horn Biosphere Reserve, Chile

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Abstract.—Invasive species threaten global biodiversity, but multiple invasions make predicting the impacts difficult because of potential synergistic effects. We examined the impact of introduced beaver *Castor canadensis*, brook trout *Salvelinus fontinalis*, and rainbow trout *Oncorhynchus mykiss* on native stream fishes in the Cape Horn Biosphere Reserve, Chile. The combined effects of introduced species on the structure of the native freshwater fish community were quantified by electrofishing 28 stream reaches within four riparian habitat types (forest, grassland, shrubland, and beaver-affected habitat) in 23 watersheds and by measuring related habitat variables (water velocity, substrate type, depth, and the percentage of pools). Three native stream fish species (puye *Galaxias maculatus* [also known as inanga], *Aplochiton taeniatus*, and *A. zebra*) were found along with brook trout and rainbow trout, but puye was the only native species that was common and widespread. The reaches affected by beaver impoundments had significantly higher puye densities than all other reaches in this study. These results are comparable to those reported for other streams in southern Chile. The presence of trout reduced the abundance of puye, but only in beaver-affected areas; all three natural riparian habitat types had uniformly low puye abundance and were unaffected by the presence or absence of trout. The data suggest that one invasive species, the beaver, enhanced puye habitat and thereby increased the abundance of that species, which, in turn, helped moderate the negative impacts of invasive trout.

The introduction and possible subsequent invasion of nonnative species is a serious threat to ecosystems around the world (Kolar and Lodge 2001; Dunham et al. 2002; Rahel 2002). On a global scale, species invasion reduces biodiversity via extinctions and biotic homogenization, even though introductions may enhance species richness at the regional and local scales

(Sax and Gaines 2003). Invasive species may facilitate the success of other introduced species by modifying the local environment to benefit those species (Simberloff and Von Holle 1999; Bruno et al. 2003; Grosholz 2005). While descriptions of the direct consequences of an individual invasive species can often be shown through experimentation (Lodge 1993), the complex interactions between multiple invasive species are more difficult to quantify, yet are extremely relevant to developing holistic management and restoration plans (Parker et al. 1999).

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Exotic species can become invasive in otherwise remote and pristine areas, such as the subantarctic forest ecoregion of southern South America (Rozzi et al. 2006). In the Cape Horn Biosphere Reserve (CHBR), introduced vertebrates make up one-half of terrestrial mammals and freshwater fish species assemblages (Anderson et al. 2006b). Among the introduced species, beaver *Castor canadensis* (which act as ecosystem engineers) and brown trout *Salmo trutta*, rainbow trout *Oncorhynchus mykiss*, and brook trout *Salvelinus fontinalis*, (which strongly compete with other predators) are expected to have particularly large impacts on streams and their native fish assemblages. Since being introduced to Tierra del Fuego Island in 1946, the initial 25 pairs of beavers have expanded their range across the archipelago and, recently, the Chilean mainland (Godoy 1963; Sielfeld and Venegas 1980; Anderson et al., in press). Beaver densities in southern South America are extremely high and compare to the high densities reported for North America. Their direct and indirect effects on stream ecosystems through riparian foraging and in-stream dam and lodge building are quite dramatic (Naiman et al. 1988; Anderson et al., in press). For example, beaver dams could affect fish communities by providing better habitat for large fish in low-order streams, increasing the number of predators within a system, reducing the number of high or low flows, modifying the temperature regime, shifting the ichthyofaunal assemblage from rapid current dwellers to pond dwellers, and introducing obstructions to upstream migration (Collen and Gibson 2001). Trout are one of the most effective coldwater invaders, capable of out-competing other predators and preying directly on native taxa (Townsend 1996; Glova 2003; McDowall 2003). Brown, rainbow, and brook trout were introduced to southern Chile in the early 1900s as a food and sport fishing resource (Vigliano and Darrigran 2002) and today constitute an important economic resource (Soto et al. 2006).

In this study, we quantitatively evaluated the effects of invasive trout and beavers on the native, subantarctic, freshwater fish assemblage in the CHBR. While little is known about the precise distributions of native and exotic fishes in southern Patagonia (Pascual et al. 2002), four native freshwater fish species were potentially resident in the austral archipelago. All of these species (puye *Galaxias maculatus* [also known as inanga], *G. platei*, *Aplocheilichthys taeniatus*, and *A. zebra*) are members of the family Galaxiidae (Cussac et al. 2004). When brown and rainbow trout are present, galaxiids often occur in reduced abundances and generally inhabit stream shallows (Vila et al. 1999; Glova 2003; Soto et al. 2006). Beavers, however, may

actually create favorable habitat for native species, such as the puye, by constructing barriers to trout invasions, slowing in-stream flow, and creating adequate feeding conditions (Vila et al. 1999). Therefore, the combined effect of beaver and trout invasions on native fishes could be counteractive, and not possible to predict a priori. Given the remoteness of the Cape Horn archipelago and the lack of previous information, we also used this study to document baseline information on stream biodiversity and ecology in southern Chile.

Methods

Study site.—This study was conducted on Navarino and Hoste islands in the eastern portion of the CHBR (approximately 55°S, 67°W; Figure 1). The CHBR is in the most remote part of the Magellanic subantarctic forested ecoregion, which is considered one of the world's most pristine remaining wilderness areas (Mittermeier et al. 2003). These islands have relatively high-gradient catchments that are predominantly forested on the north slope (broad-leaved evergreen and deciduous forests) and consist of Magellanic tundra on the more gently sloping south slope (a mosaic of wetlands including the rush *Marsippospermum grandiflorum* and *Sphagnum* bogs) (Rozzi et al. 2004, 2006).

Habitat characterization.—A total of 28 stream reaches in 22 watersheds and one lake were sampled from mid-January to early March 2006 to characterize riparian habitats and stream fish communities (Figure 1). All reaches were 50 m upstream from the coast to avoid any effects from roads or saltwater. Specific conductance was measured to ensure that the stream reaches were composed of freshwater (i.e., <200 μ S). All sampled reaches covered a distance 20 times the mean channel width, or roughly one meander wavelength, since this distance should adequately represent one riffle–pool–run sequence, or all available geomorphic units in the stream reach (Fitzpatrick et al. 1998). Additional sampling was conducted in a subgroup of streams ($n = 6$) to determine whether fish were present above potential migration barriers (waterfalls and beaver impoundments). At each stream reach, a suite of habitat data were recorded, including (1) stream width, length, and depth (m); (2) percentage of riffle, pool, and run habitat present (%); (3) dominant substrate (e.g., boulder, gravel, sand, silt, or mud); and (4) latitude and longitude using the classification outlined by Fitzpatrick et al. (1998). Average stream depth and width were determined for each stream reach with transects every 20 m (Peterson et al. 2004), and stream area (m^2) was determined from total stream length and average stream width. Dissolved oxygen (mg/L), pH, specific conductance (μ S), ambient

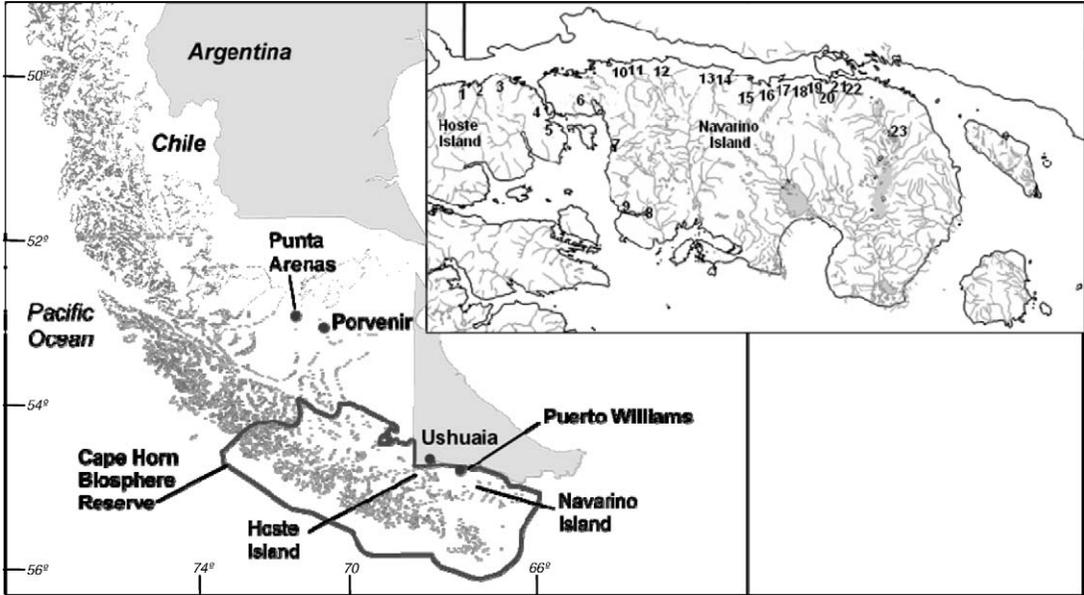


FIGURE 1.—Map of southern South America indicating the location of the study area in the eastern portion of the Cape Horn Biosphere Reserve. The inset shows the study area—Navarino and Hoste islands—in detail, the numbers designating the reaches and watersheds sampled for freshwater fish during January–March 2006.

conductance (μS), temperature ($^{\circ}\text{C}$), nitrate (mg/L), nitrite (mg/L), and phosphate (mg/L) were measured at each reach.

Riparian habitats along the sampled reaches were categorized according to the general vegetation classifications outlined by Moore (1983), with the addition of a category to represent habitats affected by beaver impoundments. These habitat categories included (1) forest, (2) scrubland, and (3) meadow. Forests were composed primarily of mature evergreen or deciduous *Nothofagus* species and were the dominant habitat on the north slope of the islands. Scrublands were a transitional habitat between meadow and forest when the meadow began to be recolonized by larger plants and small trees. Scrub habitats represented transitional zones between the forests, and bog or meadow communities. Meadows were dominated by native and nonnative grasses and coincided with areas deforested in the past by beavers or loggers (Anderson et al. 2006a; Martínez Pastur et al. 2006). In addition, the presence of a beaver impoundment directly

upstream from the sampled reach was noted and used to define reaches directly affected by the presence of beavers. A separate habitat class was added for reaches located directly downstream from beaver impoundments. An unbalanced sampling design with respect to riparian habitat type and the presence of beaver impoundments was used because of the difficulty in accessing all watersheds (Table 1). Only the north coast of Navarino Island has a road; the southern portion of the island and all of Hoste Island is only accessible by boat.

Fish sampling.—Backpack electrofishing was considered the most effective method of determining fish community structure (Lyons and Kanehl 1993; Moulton et al. 2002) based on the depth (wadeable, $<1\text{ m}$) and width (1–10 m) of these streams as well as their average ambient conductivity ($<100\ \mu\text{S}$; Moorman et al. 2006). All watersheds were sampled for fish using double-pass electrofishing techniques with a Smith-Root LR-24 backpack electrofisher. Block nets of 0.5-cm knotless mesh, measuring 2 m deep \times 15 m long,

TABLE 1.—Mean abundance (number of fish/ m^2 ; SEs in parentheses) of freshwater fish species by riparian habitat type in the Cape Horn Biosphere Reserve, Chile.

Riparian vegetation	Puye	Rainbow trout	Brook trout	<i>n</i>
Forest	0.02 (0.01)	0.002 (0.001)	0.06 (0.03)	10
Beaver disturbed	0.38 (0.2)	0.00	0.02 (0.01)	4
Herbaceous	0.06 (0.04)	0.001 (0.001)	0.05 (0.02)	5
Shrubland	0.04 (0.02)	0.01 (0.01)	0.02 (0.01)	3

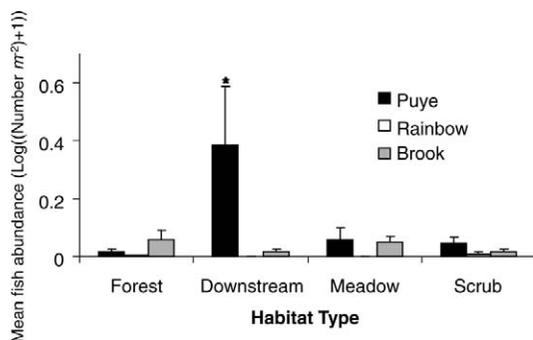


FIGURE 2.—Mean (+SE) abundance of puye, brook trout, and rainbow trout in the four habitat types studied (forest, downstream from a beaver impoundment, meadow, and shrubland). The asterisk indicates a significant ($P < 0.05$) difference from the other values according to a one-way ANOVA.

enclosed the upstream and downstream ends of the reach during electrofishing. Voltage settings for the backpack electrofisher ranged from 200 to 600 V, and frequency settings ranged from 20 to 70 Hz. Owing to the remoteness of the study area and the lack of previous field studies in the region, we chose to use double-pass removal to sample more streams during the 2-month field season than would be possible with multipass sampling. We did, however, conduct multipass removals at a subset of streams to aid in the validation of demographic estimates from the double-pass removal method (Moorman 2007).

Once collected, each fish was identified, weighed, and measured. Both standard length (SL; the distance from the tip of the closed mouth to the estimated posterior end of the caudal peduncle) and total length (TL; the distance from the closed mouth to the extreme tip of the caudal fin when the lobes of the caudal fin are squeezed together) were recorded to the nearest millimeter. Weight was measured to the nearest 0.1 g with an Aculab portable electronic scale. Representative specimens of each species were preserved in 10% solutions of formalin to create a reference collection and to confirm proper identification. Voucher specimens were incorporated into the Chilean Museum of Natural History and the North Carolina Museum of Natural Science permanent collections.

Data and statistical analysis.—Fish abundance and capture probability were computed from the double-pass electrofishing data using a constant capture probability estimator (Zippin 1956; model M_b) in the program CAPTURE (Rexstad and Burnham 1991). Abundance values were then normalized by area, dividing estimated abundance by estimated area for each sampled reach. All abundance data were log

transformed to achieve normality. The response variables evaluated in this study were (1) the abundance of native puye and (2) the abundance of introduced trout. Using SAS (SAS Institute, Cary, North Carolina), we conducted separate one-way analyses of variance (ANOVA; $P < 0.05$) to test the effect of riparian habitat type (forest, scrubland, meadow, or beaver impoundment) on fish abundances (puye, rainbow trout, and brook trout). A two-way ANOVA was used to evaluate the relationship between native puye and introduced trout and beavers using (1) trout presence or absence and (2) the presence of beaver impoundments directly upstream and adjacent to the sampled reach as independent variables. If ANOVA tests were significant, the Student–Newman–Keuls multiple comparisons test was used to determine significant relationships. Regressions were also used to measure the response of puye abundance to abiotic factors, including (1) percent soft substrate, (2) percent pool, (3) measured stream velocity, and (4) stream depth. Finally, Akaike's information criterion (AIC; Akaike 1973) was used to fit the best overall model to explain puye abundance.

Results

Freshwater Fish Assemblages

During the sampling period, we recorded three native freshwater fish species in the CHBR (puye, *Aplochiton zebra*, and *A. taeniatus*) and two species of introduced fish (rainbow and brook trout). The presence of brown trout on Navarino Island that was reported by local recreational fishers (cited in Anderson et al. 2006b) was not confirmed despite sampling 16,397 m² of streams.

The puye was the only native species sampled in substantial numbers and with a wide distribution, being found in 18 of the 22 sampled reaches on both islands. *Aplochiton zebra* was only found in Navarino Lake (Figure 1, site 23), and *A. taeniatus* was surveyed once in a small stream at Wulaia Bay (Figure 1, site 7). Therefore, we could not compute abundances for the other native fish species and only considered puye and trout in all further analyses. Overall, puye was the most abundant taxon in the study area with brook trout intermediate and rainbow trout the lowest (Figure 2). Both puye and rainbow trout were found above beaver dams, but low sample size prevented statistical analysis of these data. In contrast, no native or introduced fishes were found above the four waterfalls sampled.

Comparison of Double-Pass and Multipass Electrofishing Methods

Our multipass depletion sampling in a subset of the study streams suggested that fish abundances estimated

TABLE 2.—Mean puye abundance (number/m²; SEs in parentheses) as affected by introduced beavers and trout.

Beaver impact	Trout	Puye	n
Disturbed	Present	0.62 (0.49)	2
	Absent	0.13 (0.16)	3
Undisturbed	Present	0.03 (0.06)	13
	Absent	0.01 (0.02)	4

from double-pass electrofishing were similar to those obtained from multipass electrofishing in all reaches, except reaches downstream from beaver dams (Moorman 2007). Multipass depletion estimates indicated that our method for beaver-affected areas underestimated puye abundances, which would make our subsequent tests of beaver effects based on the double-pass method actually conservative and therefore strengthen inferences regarding their impacts.

Effects of Riparian Habitat on Fish Abundance

Mean puye density varied significantly by riparian habitat type, whereas the density of trout did not (puye: $F_{3, 18} = 4.66, P = 0.01$; brook trout: $F_{3, 18} = 0.36, P = 0.78$; rainbow trout: $F_{3, 18} = 1.74, P = 0.19$; Table 1). Puye were significantly more abundant in reaches directly downstream of beaver impoundments than in other habitat types (Student–Newman–Keuls test: $P = 0.05$; Figure 2).

The Effects of Beavers and Trout on Puye

The mean abundance of puye varied significantly according to both main and interaction effects between

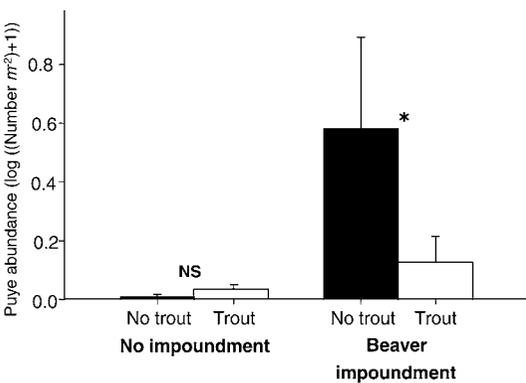


FIGURE 3.—Mean (+SE) puye abundance with respect to introduced beavers and trout. The asterisk indicates a significant ($P < 0.05$) difference between impounded and unimpounded stream reaches with an interaction effect of trout on puye abundance in the impounded areas according to a two-way ANOVA using the Student–Newman–Keuls test to determine differences between groups; NS = no significant difference.

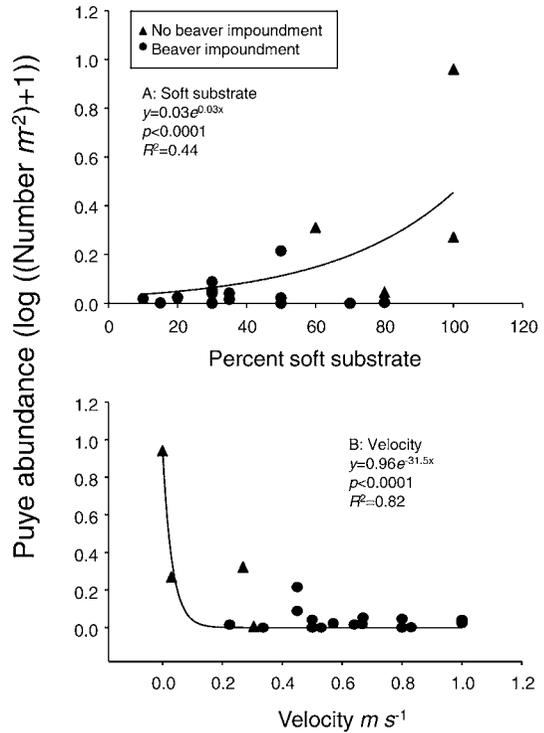


FIGURE 4.—Estimated relationships between puye abundance and the abiotic factors percent soft substrate and stream velocity.

the presence of trout and beavers (trout: $F_{3, 18} = 10.02, P = 0.0054$; beavers: $F_{3, 18} = 15.69, P = 0.0009$; interaction: $F_{3, 18} = 12.65, P = 0.0023$; Table 2; Figure 3). The interaction effect was due to the fact that puye displayed significantly higher abundance in the absence of trout in beaver impoundments (Student–Newman–Keuls test: $P < 0.05$; Figure 3). Conversely, in the absence of beaver impoundments, average puye abundance was uniformly low and did not vary with the presence of trout.

Effects of Habitat Variables on Puye

There was a positive and statistically significant relationship between puye abundance and percent soft substrate. Conversely, a negative trend was observed between puye abundance and stream velocity during the summer (Figure 4). Based on the AIC, these two relationships are best described by an exponential growth and decay model (Table 3). Mean puye abundances did not vary significantly with any other environmental gradients measured in this study (percent pool: $R^2 = 0.02, P = 0.07$; mean depth: $R^2 = 0.05, P = 0.51$; stream visual assessment protocol score: $R^2 = 0.09, P = 0.17$).

TABLE 3.—Estimated models of puye abundance as functions of the percentage of soft substrate and stream flow. Abbreviations are as follows: RSS = the residual sum of squares; AIC_c = the Akaike information criterion with a second-order correction for small sample size; ΔAIC_c = the difference between AIC_c value of interest and the lowest such value among the different models; $\exp(-1/2\Delta AIC_c)$ = an intermediate calculation for the model probability estimate; and W_i = the model probability estimate. Asterisks denote the best model for each habitat variable.

Habitat variable	Model	Number of parameters	RSS	AIC_c	ΔAIC_c	$\exp(-1/2\Delta AIC_c)$	W_i
Soft substrate	Linear	2	0.619	-73.92	3.18	0.204	0.117
	Quadratic	3	0.5008	-75.88	1.22	0.545	0.311
	Exponential*	2	0.5358	-77.10	0.00	1.000	0.572
Flow	Linear	2	0.61	-74.25	29.48	0.000	0.000
	Quadratic	3	0.3656	-82.81	20.92	0.000	0.000
	Exponential*	2	0.1597	103.73	0.00	1.000	1.000

Discussion

Freshwater Fish Assemblages of the Cape Horn Biosphere Reserve

Our surveys confirmed the presence of two rare native freshwater fish species in the Cape Horn Biosphere Reserve, *A. taeniatus* and *A. zebra* (Cussac et al. 2004; Anderson et al. 2006b). We provide new information on the distribution and assemblage of introduced trout, documenting presence of brook and rainbow trout, but not brown trout on Navarino and Hoste islands. The latter finding corrects a previous citation by Anderson et al. (2006b) in which brook trout were evidently misidentified as brown trout. It was surprising that brown trout were not found on Navarino and Hoste islands given that they are well established on nearby Tierra del Fuego Island (Vila et al. 1999; Cussac et al. 2004) and are widely anadromous at cold latitudes. The absence of brown trout on Navarino and Hoste islands, both of which are located south of the Beagle Channel, suggests that the Beagle Channel, or environmental and ecological conditions south of the channel, may form a biogeographic barrier to brown trout. Future studies should identify the mechanisms precluding brown trout invasion south of the Beagle Channel.

Implications of Introduced Beavers and Trout on Native Puye

The interacting effects of multiple introduced species on native species or ecosystems are seldom known, even though ecosystem-based management is inherently based on the knowledge of such interactions (Simberloff 2006). In this study, we found correlational evidence that one invasive species, the beaver, enhanced the native puye's habitat, thereby increasing its abundance which, in turn, helped moderate the negative effects of invasive trout. In the presence of beaver impoundments, puye abundances were four times higher than in a range of streams studied in others parts of southern Chile (Soto et al. 2006). The presence

of brook trout reduced puye abundances in beaver impoundments, but puye were still greater than two times more abundant in these areas than in other habitat types sampled in this study or in other streams in southern Chile (Vila et al. 1999). The values we found for puye abundance in the other habitat types (forest, meadow, and shrublands) were similar to those reported for streams further north in the Magallanes region of Chile (Soto et al. 2006). All studies were conducted during the summer season. The two abiotic habitat variables linked to puye abundance, percent soft substrate and water velocity, also corresponded to two of the major habitat features affected by beaver impoundments (Butler and Malanson 1995). Similarly, studies of puye ecology in New Zealand have demonstrated that puye prefer habitats downstream from flow constrictions, where food is concentrated and velocities are slow enough for them to hold a feeding position (Jowett 2002).

The overall effect of beavers on ichthyofaunal assemblages in Chile were similar to those in North American streams, shifting fish assemblages from rapid current dwellers to lentic pond dwellers (Schofield 1994; Collen and Gibson 2001). In North American streams, beaver impoundments have been described as a favorable habitat for brook trout by providing refugia for larger fish in small streams during periods of low flow (Collen and Gibson 2001). In this study, there was no increase in brook trout abundance downstream from beaver impoundments when compared with trout abundances in the other reach habitats sampled. The fact that trout abundance did not increase may be attributed to increased siltation downstream from beaver impoundments, which may be unfavorable for trout (Snodgrass and Meffe 1998; Collen and Gibson 2001).

One mechanism previously hypothesized for the increased puye abundance associated with beaver impoundments is that the impoundments serve as a barrier to upstream trout movement, thereby concen-

trating these predators below impoundments (Vila et al. 1999). Yet puye are poor climbers, tend to be lowland pool and run dwellers, are diadromous, and normally have a life span of 1 year (McDowall 1968). Our data suggest that both puye and trout can migrate above beaver impoundments (as evidenced by their presence above such impoundments) but not above large waterfalls (as evidenced by their absence in such areas) (Moorman 2007). Studies using mark–recapture methods, passive integrated transponder (PIT) tagging, or radio telemetry would be necessary to better understand the movement capabilities of native puye and introduced trout as a function of stream elevation, beaver impoundments, and waterfalls.

The ecological consequence of invasive species is an important conservation and management topic in the austral archipelago. Current eradication plans for the beaver (Anderson et al., in press) and other control efforts for exotic species in general are being designed. This makes the CHBR an ideal laboratory for understanding how the removal of invasive species may subsequently alter ecological interactions. Specifically, managers and scientists should pay attention to the effects of beaver removal on native puye and introduced trout, which could provide further insight into the counteractive effects of multiple invasive species.

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