

Introduction

Beavers (*Castor canadensis*) build dams on rivers and streams, creating ponds. Waterbird richness and abundance in beaver ponds is much higher than in the adjacent rivers and than expected from habitat availability (Grover and Baldassarre (1995); McCall et al. (1996); McKinstry et al. (2001); Merendino et al. (1995); Rempel et al. (1997)). Furthermore, waterbird presence in beaver ponds is higher than in concurrent lagoons of geological origin (Table 1)(Bulluck and Rowe (2006); Longcore et al. (2006a); Numii and Hahtola (2008); Peterson and Low (1977)). One of the main reasons behind the preference of waterbirds for beaver ponds are trophic cascading effects triggered by river damming by beavers. Damming results in reduced water velocity, which increases sedimentation (McDowell and Naiman (1986); Naiman and Melillo (1984); Naiman et al. (1986)). This, plus the input of allochthonous material to the water body through beaver foraging activities results in accumulation of benthic organic matter (Anderson and Rosemond (2007); Francis et al. (1985); McDowell and Naiman (1986)). As a result, there is a boost in macroinvertebrate biomass and secondary production (Anderson and Rosemond (2007); Margolis et al. (2001); McDowell and Naiman (1986)), thus increasing the availability of food resources for birds that feed on them (Collen and Gibson (2000); Longcore et al. (2006a); Rosell et al. (2005)). Beaver establishment can also have a positive effect on the abundance and density of macrophytes, and therefore also on herbivorous waterbirds, both as a result of increased nutrient availability and of habitat expansion in the flooded areas

Table 1. Waterbird preference of beaver ponds, streams, and lagoons of geological origin in the Northern Hemisphere, according to avian foraging group. A plus/minus sign indicates whether the abundance of that species in that habitat was greater or smaller, respectively, than expected from habitat availability.

	Ponds	Lagoons	Streams
Herbivores			
<i>Aythya collaris</i>	+ ^{2,5}	+ ^{2,5}	- ⁵
<i>Anas discors</i>	+ ⁵	+ ^{3,5}	
<i>Aix sponsa</i>	+ ^{1,2,5}	+ ^{2,5}	- ¹
<i>Anas americana</i>	+ ⁵		
<i>Branta canadensis</i>	+ ^{1,5}	+ ⁵	- ¹
Carnivores			
<i>Lophodytes cucullatus</i>	+ ^{1,2,5}	+ ^{2,5}	- ^{1,5}
<i>Bucephala albeola</i>		+ ⁵	
<i>Podyilymbus podiceps</i>	+ ²		
<i>Bucephala clangula</i>	+ ⁵	+ ^{2,5}	- ⁵
Piscivores			
<i>Gavia inmer</i>	+ ²	+ ^{2,5}	+ ⁵
<i>Mergus merganser</i>	+ ²	+ ^{2,5}	+ ⁵
<i>Ceryle alcyon</i>	+ ^{1,2}	+ ²	- ¹
Omnivores			
<i>Anas platyrhynchos</i>	+ ^{1,5} / - ³	+ ^{3,5}	+ ³ / - ^{1,5}
<i>Anas rubripes</i>	+ ^{2,5} / - ¹	+ ²	+ ¹
<i>Anas crecca</i>	+ ^{2,5}	- ⁵	- ⁴
Shoreline omnivores			
<i>Porzana carolina</i>	+ ^{1,2}		- ¹
Shoreline carnivores			
<i>Botaurus lentiginosus</i>	+ ^{1,2}		- ¹
<i>Ardea herodias</i>	+ ^{1,2}	+ ²	- ¹
<i>Gallinago gallinago</i>	+ ^{1,2}		- ¹
<i>Actitis macularia</i>	+ ^{1,2}	+ ²	- ¹
<i>Rallus limicola</i>	- ¹		+ ¹
<i>Tringa solitaria</i>	+ ¹		- ¹

References: ¹Grover and Baldassarre (1995), ²Longcore et al. (2006), ³Merendino et al. (1995), ⁴Nummi and Pöysä (1997), ⁵Rempel et al. (1997).

Foraging groups were determined according Del Hoyo et al. (1992).

(Naiman et al. (1986); Ray et al. (2001); Rosell et al. (2005)), although this effect has received much less attention in the literature. Beavers have historically been exploited for their fur, and this was the cause both for their near extinction in North America (Rosell et al. (2005)), as well for their introduction to the Tierra del Fuego Archipelago (hereinafter TdF), southernmost Argentina, in 1946. The Fuegian landscape offered a perfect combination of wetlands, woodlands and absence of predators for the establishment of beavers (Anderson et al. (2009); Lizarralde (1993)). Although a fur industry failed to develop in the area, the 25 initial beaver couples successfully spread and established in the Archipelago. A survey carried out over a decade ago estimated over 100,000 individuals and a mean density of 1 beaver colony per km of stream (Skewes et al. (2006)).

The impacts of introduced beavers are better predicted combining knowledge from their impact on their native habitat with that of the recipient ecosystem of TdF (Anderson et al. (2009)). Streams and lagoons of glacial origin are a common feature in the landscape of TdF (Iturraspe and Urciolo (2000)) and, in this context, beaver ponds could be just an extension of an already occurring habitat type (Anderson et al. (2009)). Nonetheless, the oligotrophic nature of Fuegian water bodies could make the impacts of the rapidly eutrophying beaver ponds specially marked in Fuegian streams, and differentiate them from natural lagoons (Collen and Gibson (2000); Iturraspe and Urciolo (2000)). Anderson and Rosemond (2007), studying the impact of beavers in Navarino Island (part of TdF), found that the magnitude of the increase in benthic organic matter in beaver ponds compared to undisturbed streams reached much higher levels than in North America (McDowell and Naiman (1986)), although changes in macroinvertebrate biomass were less extreme.

So far, it has not been assessed whether beaver ponds provide suitable habitat for Fuegian waterbirds, less whether they are preferred to 'natural' water bodies, as it occurs on the native habitat of the beaver. The study of Anderson and Rosemond (2007) in TDF coincide with the scenario described for North America of beaver ponds triggering trophic cascading effects that ultimately lead to increased waterbird richness and abundance in ponds compared to streams and lagoons. In this study we assess the relationship between waterbirds and beaver ponds and compare it to that of 'natural' water bodies. Despite the fact that this relationship is believed to be governed by trophic interactions, studies in North America have not used a trophic-group approach (but see Longcore et al. (2006)). We compare abundance and richness of avian foraging groups in beaver ponds in relation to undisturbed streams and lagoons. If the increased amount of food resources in beaver ponds results in a preference by waterbirds for these habitats in TdF, as it occurs in North America, we should see a greater overall abundance and richness of waterbirds in beaver ponds compared to streams and lagoons. In terms of foraging groups, we expect abundance and richness of herbivores, carnivores and omnivores to be higher in beaver ponds than in streams and natural lagoons. Regarding piscivores, the impact of beaver ponds on fish is highly dependant on the pre-beaver fish conditions (Collen and Gibson (2000)), and knowledge of fish distribution in TDF is very limited. Still, based on that introduced salmonid species are the most abundant in Fuegian streams (Vila et al. (1999)), and that one of them, *Salmo trutta*, appears to be unaffected by ponds (Moorman (2007); Vila et al. (1999)), we expect piscivores not to positively select for beaver ponds, but to be equally distributed along wetland habitats.

Methods

Study site

Tierra del Fuego is an archipelago located at the southernmost tip of South America. This study took place on the Chilean side of the main island, *Isla Grande* (Fig. 1). This Island has a very marked environmental gradient that runs from NE to SW. In the northern part the terrain is flat, precipitations are scarce (250 mm) and vegetation is characterized by grasses, sedges and shrubs forming the Patagonian steppe. To the south, mean altitude increases towards the Darwin Mountain Range, precipitation also increases (400 mm) and becomes more seasonally homogenous, giving way to a forest dominated by trees of the genus *Nothofagus* (Moore (1983)). Permanent and temporary water bodies of glacial origin are a widespread feature throughout the landscape (Iturraspe and Urciolo (2000)).

This study took place in two areas of the forest-steppe ecotone (Figs. 1 & 2), within Karukinka Natural Park, a 300 ha private protected area managed by the Wildlife Conservation Society.

Benthic organic matter and aquatic macroinvertebrates

In order to provide information about the predicted bottom-up increases in trophic resources triggered by beaver activities in the study area, I analyzed a dataset on

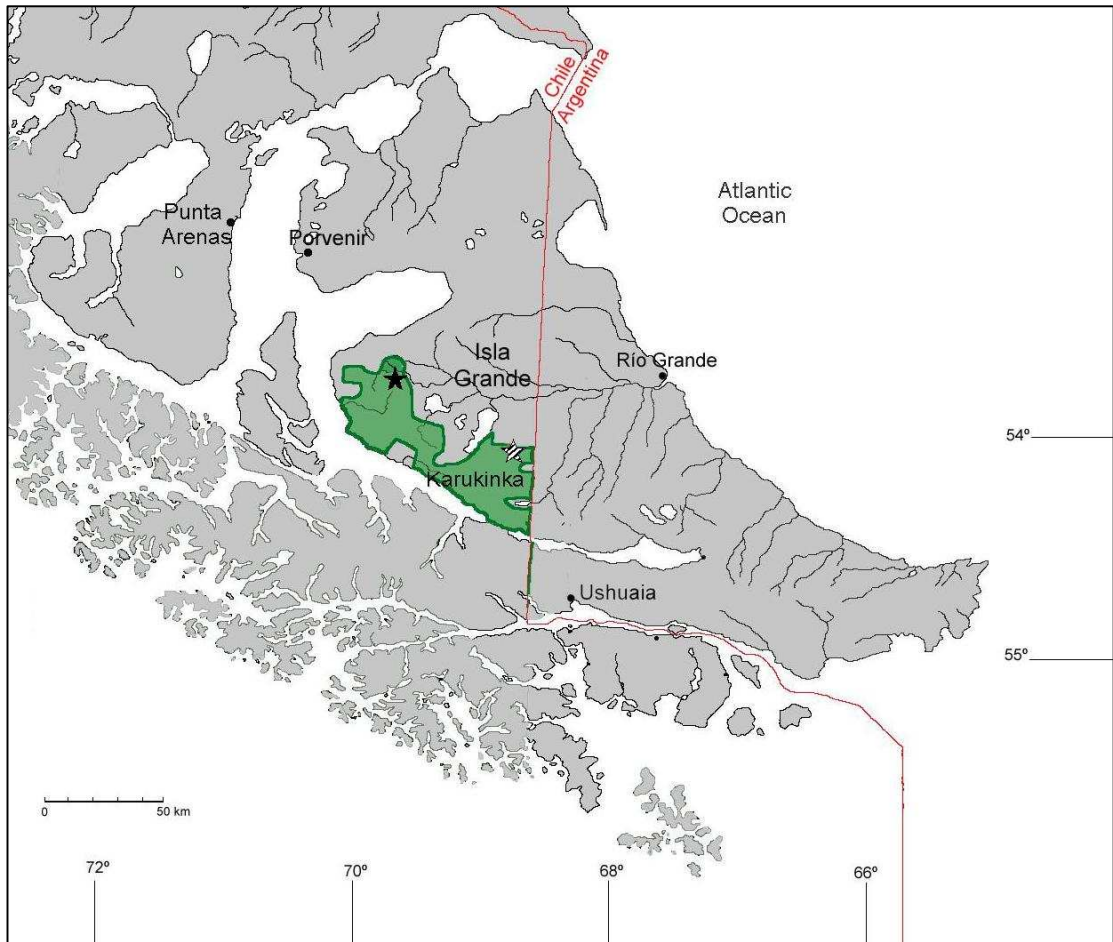


Figure 1. The Tierra del Fuego Archipelago. Main human settlements are identified with their names. Karukinka Natural Park is delimited in green. A black and a striped star indicate each of the two study sites (see Fig. 2 for detailed maps of study sites).

benthic organic matter and macroinvertebrates that was collected between October November 2006 by Dr. Christopher Anderson, as part of a private consultancy to WCS. Raw data was provided as a result of this consultancy, but no analysis has so far been conducted on them. The methodology used to collect these data are described below. Benthic organic matter samples were taken with a core-sampler (0.7 m²) from beaver ponds, free-flowing streams (not paired with ponds) and lagoons in the surrounding of Vicuña base camp (marked with a striped star in Fig 1.). Three sub-samples were taken

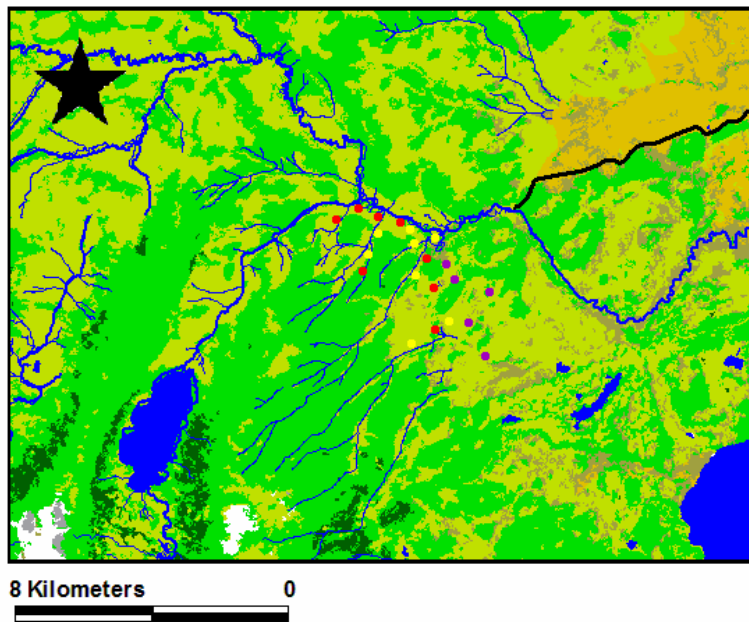
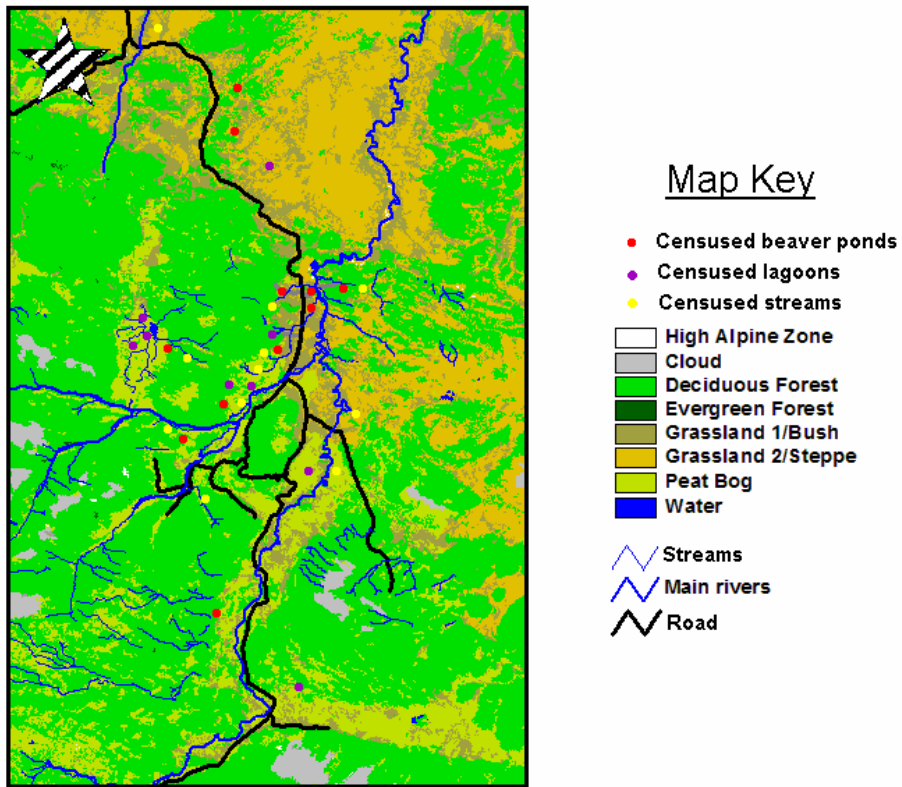


Figure 2. Maps of study sites. Location of bird surveys are indicated with coloured dots (see map key). Striped star: Vicuña base camp and surrounding area. Black star: Lago Escondido base camp and surrounding area. Maps of study sites.

per replicate. Samples were passed first through a sieve of 1mm mesh size to separate coarse benthic organic matter (CBOM) and then through one of 250µm mesh size to separate fine benthic organic matter (FBOM). This separation is done useful because FBOM is a better predictor of macroinvertebrate biomass, since the different macroinvertebrate trophic functional groups feed on different size fractions of benthic organic matter. Samples were dried at 60° and ashed at 500° to determine ash-free dry mass.

Samples of macroinvertebrates were taken with the same core sampler on the same sites for benthic organic matter samples, with three sub-samples on each site. They were passed through a sieve of 250 mesh and stored in ethanol. Macroinvertebrates were separated from detritus under the microscope and identified to the lowest possible taxonomic level according to Fernández and Domínguez (2001) and Anderson (2004).

Bird foraging groups and habitat use

A preliminary list of the waterbirds that occur in our study area was made based on field guides (Couve and Vidal (2003); Venegas (1994)) For the purpose of this study, we considered waterbirds to be those who live and feed associated to inland wetland habitats, as described in Victoriano et al. (2006) and Vilina et al. (2006). Additionally, we also considered for this study those terrestrial birds that do not live in the water, but who are usually found in the surroundings of wetlands and feed on riparian aquatic resources (see Table 2). Birds were classified into foraging groups, according to the diet and feeding behaviour described in Humphrey et al. (1970), Johnson and Goodall (1965) and, secondarily, in Del Hoyo et al. (1992)(Table 2).

Table 2. Waterbirds and terrestrial birds closely associated to wetlands that occur in the study area (see Methods).

Herbivores	Shoreline carnivores
<i>Anas flavirostris</i> ²	<i>Nycticorax nycticorax</i> ^{1,3}
<i>Anas georgica</i> ¹	<i>Calidris bairdii</i> ³
<i>Anas platalea</i> ¹	<i>Calidris fuscicollis</i> ³
<i>Anas sibilatrix</i> ^{2,3}	<i>Gallinago paraguaiae</i> ^{2*}
<i>Fulica armillata</i> ¹	<i>Vanellus chilensis</i> ^{1*}
	<i>Pardirallus sanguinolentus</i> ¹
Carnivores	<i>Cinclodes fuscus</i> ^{1*}
<i>Lophonetta specularioides</i> ¹	<i>Cinclodes oustaleti</i> ^{1*}
<i>Tachyeres patachonicus</i> ^{1,3}	<i>Cinclodes patagonicus</i> ^{1*}
<i>Phalacrocorax brasilianus</i> ^{1,3}	<i>Cistothorus platensis</i> ^{3*}
<i>Rollandia rolland</i> ³	<i>Lessonia oreas</i> ^{1*}
Piscivores	Omnivores
<i>Podiceps major</i> ^{1,3}	<i>Speculanas specularis</i> ^{1,3}
<i>Ceryle torquata</i> ¹	

References: ¹Johnson and Goodall (1965); ²Humphrey et al. (1970); ³Del Hoyo et al. (1992).

* Terrestrial birds.

Waterbird surveys were conducted on beaver ponds, free-flowing rivers (not paired with ponds) and lagoons from 6.30 to 12.00 a.m. between November 2008 and February 2009. Beaver ponds and lagoons were censused using flush-counts, followed by 10-minutes point-counts with a period of adaptation of 5 minutes. Free-flowing rivers were censused using flush-counts along linear transect counts of 500 m, along the river course (Gregory et al. (2004)) I did not conduct census on days of heavy rain. Sampled sites were selected in a random manner based on maps, aerial photographs and exploratory walks, but also subject to accessibility. In order to avoid species-area effects, I excluded ponds/lagoons that we considered too large for one point-counts. Each site was surveyed only once, and sites were separated from each other by at

least 1 km to prevent double-counting of birds. To make values comparable between habitats, bird richness and abundance were standardized by area of surface water surveyed. Hectares were used as the basic surface unit because it is frequently used for bird surveys on lentic water bodies (e.g. Merendino et al. (1995)). Although it is counterintuitive for streams, it allows comparison between habitat types (for visualization it might help to think that a 500 m stretch of a 20 m wide stream would approx. span 1 hectare of water surface). Area was estimated by assuming an elliptical shape of ponds/lagoons and measuring the transverse and conjugate diameters with a Rangefinder. For rivers, we assumed a rectangular shape and measured average width of the stream using the Rangefinder.

Data analyses

I compared standing crops of total benthic organic matter (BOM), CBOM and FBOM, and macroinvertebrate taxa richness and density according to habitat type. I tested for correlation between standing stocks of organic matter in the different fraction sizes and macroinvertebrate density and richness using Spearman's correlation coefficient. I calculated density and richness all birds and avian foraging groups and the Shannon Diversity Index for the whole bird community, and compared them according to habitat type. Data did not comply with the assumptions of normality and homocedasticity, therefore all differences between habitats were tested using the Kruskal-Wallis one-way analysis of variance by ranks. The Least Significance Difference in ranks was used as a post-hoc test to determine the source of significant differences. Calculations and graphs were carried out in the software MiniTab©. The Shannon Diversity Index was calculated using EstimateS (Colwell (2009)).

Results

Standing stocks of BOM, CBOM and FBOM were all significantly greater (3-6 times) in beaver ponds compared to streams (Table 3). Although stocks of BOM, CBOM and FBOM in lagoons were all lower than in ponds and greater than in streams, these differences were not statistically significant (Table 3).

In total, thirty-six macroinvertebrate taxa were identified (Table 4). Macroinvertebrate density was similar between ponds and lagoons, and lower in streams, but this trend was not significant (Table 3). Macroinvertebrate richness was relatively similar between all habitat types (Table 3).

A significant positive correlation was found between BOM, CBOM and FBOM and macroinvertebrate density. The magnitude of the correlation decreased with decreasing fraction size (Table 5). Macroinvertebrate richness was not correlated to organic matter standing stock in any fraction size (Table 5).

Fourteen species of birds were observed during the surveys (Table 6). Overall density was seven times greater and species richness four times greater in beaver ponds than in streams. Although density and richness values in lagoons were similar to those in ponds, they did not differ significantly from streams (Figs. 3 & 4). Density and richness of herbivorous birds was also greater in ponds as compared to streams, and values in lagoons were low but did not differ significantly from those in either habitat type. Both density and richness of shoreline carnivores were not significantly different between habitats. The carnivore and omnivore foraging groups were very scarce (only one or two sightings per habitat type) so no statistical comparisons could be made among

Table 3. Standing stocks (g ASDM/m²) of BOM, CBOM and FBOM and macroinvertebrate density (n° ind./m²) and richness (n taxa/m²). Median values are given, first and third quartiles are in parenthesis. Differences between habitats were assessed using a Kruskal-Wallis analysis of variance by ranks, followed by a post-hoc LSD test. H Statistic, degrees of freedom (Df) and significance value (*p*) for KW are shown. Different capital letters indicate significant differences between habitats.

	Beaver pond (<i>n</i> =8)	Stream (<i>n</i> =10)	Lagoon (<i>n</i> =3)	H	Df	<i>p</i>
BOM	1.12 (0.93-1.4) A	0.30 (0.24-0.51) B	0.80 (0.49-1.4) AB	12.92	2	0.002
CBOM	0.52 (0.4-0.67) A	0.10 (0.08-0.16) B	0.32 (0.20-1.03) AB	12.00	2	0.002
FBOM	0.64 (0.53-0.77) A	0.20 (0.16-0.36) B	0.39 (0.21-0.40) AB	13.19	2	0.001
Macroinvertebrate density	253.6 (140.0-578.5)	100.5 (21.9-199.0)	279.0 (186.7-422.9)	5	2	0.067
Macroinvertebrate richness	12.6 (12.9-12.9)	10.7 (6.2-13.5)	10.5 (10.5-13.3)	0.75	2	0.721

Table 4. List of the sampled macroinvertebrate taxa and their occurrence in the three different habitat types.

								Ponds	Streams	Lagoons		
Class	Subclass	Order	Suborder	Sub cohort	Family	Subfamily	Genus					
Arachnida	Acari	Acariformes	Prostigmata	Hydrachnidia				x	x	x		
Bivalvia	Heterodonta	Veneroida			Sphaeriidae		<i>Pisidium</i>	x	x			
Branchiopoda		Diplostraca	Cladocera					x	x	x		
Clitellata	Oligochaeta							x	x	x		
Entognatha	Collembola	Entomobryomorpha							x			
Gastropoda					Lymnaeidae		<i>Lymnaea</i>		x			
Hirudinea								x	x			
Insecta		Coleoptera			Ceratopogonidae			x	x	x		
					Chironomidae	Orthoclaadiinae		x	x	x		
						Podonominae			x			
						Tanypodinae		x	x	x		
						Chironominae	<i>Chironomini</i>	x	x	x		
					Dysticidae				x	x	x	
					Haliplidae							
					Hydrophilidae				x	x		
					Scirtidae						x	
					Simuliidae						x	
					Tabanidae					x		
					Tipulidae					x	x	x
					Ephemeroptera			Baetidae		<i>Andesiops</i>		x
					Leptophlebiae		<i>Massartellopsis</i>		x			

					<i>Meridialaris</i>	x	x	
					<i>Nousia</i>			
		Hemiptera		Corixidae	<i>Corixa</i>			
		Plecoptera		Gryopterygidae	<i>Antarctoperla</i>		x	
					<i>Limnoperla</i>		x	
					<i>Rhithroperla</i>		x	
		Tricoptera		Hydroptilidae			x	
				Limnephilidae		x	x	x
					<i>Monocosmoecus</i>		x	
				Hydrobiosidae	<i>Rheochorema</i>		x	
Malacostraca		Amphipoda		Hyalellidae	<i>Hyalella</i>	x	x	x
Maxillopoda	Copepoda	Calanoida				x		x
		Cyclopoida				x	x	x
		Harpacticoida				x	x	x
Ostracoda						x	x	x

them as most values were zero. No piscivores were observed. Shannon Diversity was higher in streams ($H'=1.79$, $SD=0.03$), followed by lagoons ($H'=1.71$ $SD=0.06$) and by ponds ($H'=1.39$, $SD=0.07$).

Table 5. Correlation between benthic organic matter in its different fraction sizes and macroinvertebrate density and richness.

		Spearman's ρ	T	p
BOM	Density	0.648	3.709	<<0.01
	Richness	0.235	1.052	0.306
CBOM	Density	0.595	3.225	<0.01
	Richness all	0.166	0.074	0.471
FBOM	Density	0.583	3.129	<0.01
	Richness	0.296	1.351	0.193

Table 6. List of birds observed during the surveys and their occurrence the different habitats.

	Pond	Stream	Lagoon
Carnivores			
<i>Lophonetta specularioides</i>		x	x
<i>Nycticorax nycticorax</i>		x	
<i>Phalacrocorax brasilianus</i>	x		
<i>Tchyeres patagonicus</i>	x		
Herbivores			
<i>Anas flavirostris</i>	x	x	x
<i>Anas georgica</i>	x		x
<i>Anas sibilatrix</i>	x		
Omnivores			
<i>Speculanas specularis</i>	x		
Shoreline carnivores			
<i>Calidris fuscicollis</i>			x
<i>Cinclodes fuscus</i>	x	x	x
<i>Cinclodes sp.*</i>		x	
<i>Gallinago paraguaiae</i>		x	
<i>Lessonia rufa</i>	x	x	x
<i>Vanellus chilensis</i>	x	x	x

*It was not possible to differentiate between *C. oustaleti* and *C. patagonicus*, so they were recorded together.

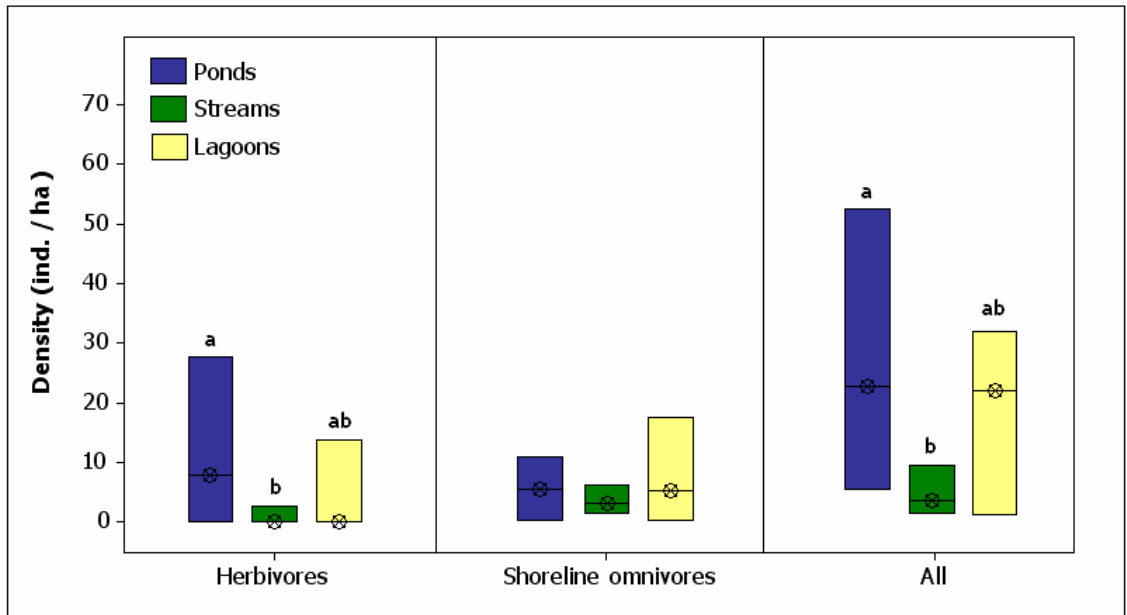


Figure 3. Density of avian foraging groups in relation to habitat type (ponds $n=19$; streams $n=10$; lagoons $n=14$). Bars are range between first and third quartiles and circles mark the median. Different letters indicate significant differences ($p < 0.05$), as tested with Kruskal-Wallis and post-hoc LSD tests. No letters indicate no significant differences.

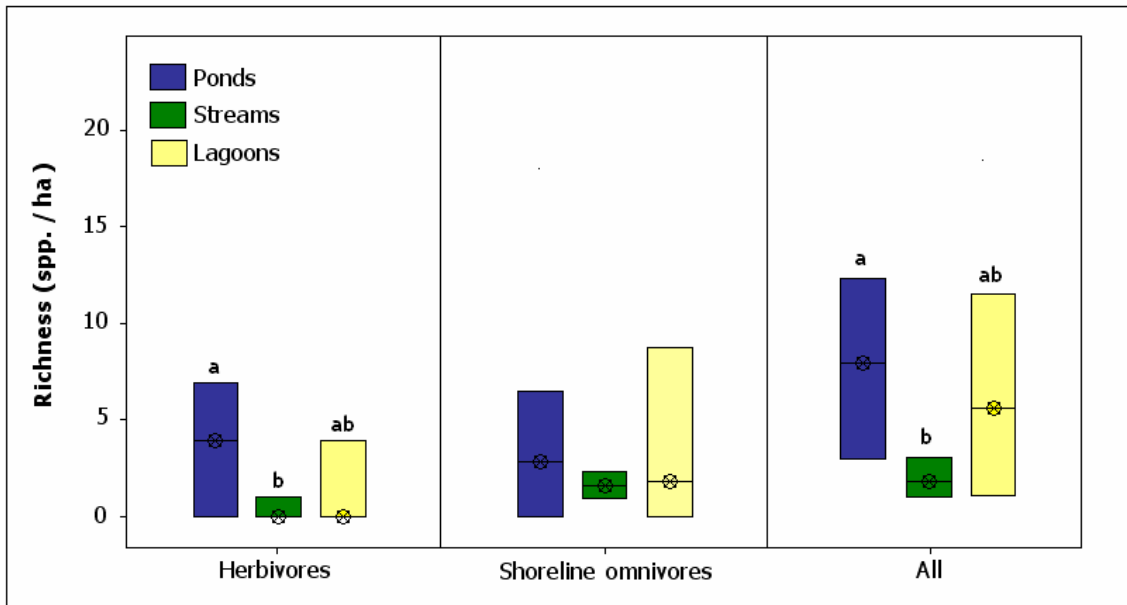


Figure 4. Richness of avian foraging groups in relation to habitat type (ponds $n=19$; streams $n=10$; lagoons $n=14$). Bars are range between first and third quartiles and circles mark the median. Different letters indicate significant differences ($p < 0.05$), as tested with Kruskal-Wallis and post-hoc LSD tests. No letters indicate no significant differences.

Discussion

For BOM, CBOM and FBOM, differences between ponds and streams coincide with previous studies, although the magnitude is not as extreme as observed in other areas of TdF, where increases in ponds in relation to free-flowing systems ranged from 22 to 44 times (Anderson and Rosemond (2007)). This could be a result of the geography of Navarino Island (study site of Anderson and Rosemond (2007)) being more mountainous, making lotic systems shorter and steeper than the transition altitudinal zone of our study site, resulting in greater sediment loads (Iturraspe and Urciolo (2000); Wetzel (2001)). As for lagoons, although not statistically significant, values for benthic organic matter in these habitats were consistently greater than in streams and smaller than in ponds. This is expected since sedimentation is favoured by the slow lentic waters, but they lack the extra input of material contributed by beaver foraging activities (Naiman and Melillo (1984); Wetzel (2001)). The small sample size for lagoon ecosystems is likely to have affected the power of the test to detect significant differences (Motulsky (1999)), so this last result should not be considered conclusive but further investigated.

Despite that benthic organic matter in all its fraction sizes was significantly higher in beaver ponds than streams and that there was a high correlation between this variable and macroinvertebrate density, the latter variable did not differ significantly between habitats. Median values in ponds and lagoons more than doubled that in streams, but there was high within habitat variability in all habitats, so that the bottom part of the range in ponds and lagoons overlapped with the with the top part of the range of values

for streams. A similar result was found in Navarino by Anderson and Rosemond (2007). This suggests that other factors that vary within habitat types and that are not being accounted for could be having an important effect in density of macroinvertebrates. Substrate, and chemical characteristics of the water such as oxygen concentration are important in determining benthic macroinvertebrate communities (Allan (2004); Jonasson (2004); Margolis et al. (2001)). For beaver ponds in particular, age (years since beaver establishment) is an important source of within-habitat variability; as the pond moves from an oligotrophic to an eutrophic state, macroinvertebrate density is expected to increase and oxygen levels to decrease (Collen and Gibson (2000)).

The lack of differences in macroinvertebrate richness between habitats is intriguing. In general, it is expected that species dependant on lotic conditions will disappear from the water body after beaver damming. However, this partial decrease would be compensated by an increase in species better adapted to lentic conditions, such as collector-gatherers, resulting in little or no overall change in richness (Anderson and Rosemond (2007); Margolis et al. (2001); McDowell and Naiman (1986)). However this does not seem to be the case for this study. Most taxa that were present on ponds and lagoons were also present on streams (Table 4), so they were more a subset of stream taxa than a different assemblage. That streams did not show a higher diversity can be explained as follows: streams usually have high microhabitat diversity (e.g. pools vs. riffles; rocky vs. sandy bottoms) allowing coexistence of organisms with different habitat requirements (Closs and Downes (2004)). If sampling on a site does not span two different microhabitats, resulting samples will contain only species from that microhabitat, underestimating total stream richness. To test for this possibility, I calculated the Jaccard Similarity Index for the samples taken on each habitat using EstimateS, and consistently, the index showed that only 33% of the species were

shared between stream samples, while pond samples shared 52% of their species, and lagoon samples shared 67% of their species. Sampling for macroinvertebrates in this study included three sub-samples per site to account for within habitat variability. Based on the results, it is advised that a larger number of sub-samples should be taken on stream habitats.

From the perspective of changes in trophic resources for waterbirds, biomass would have been the most indicative value. Although one might intuitively use density or richness as a proxy for changes in biomass, Anderson and Rosemond (2007) found a positive linear correlation between macroinvertebrate biomass and BOM/FBOM, while no correlation was found between species richness and biomass, and abundance did not differ significantly between habitats. CBOM was not a good predictor of biomass, and this is believed to be related to shredders, which feed on CBOM, not being able to survive in the substrate and water velocity conditions of beaver ponds (Collen and Gibson (2000); McDowell and Naiman (1986)). Based on the relationship between BOM/FBOM and biomass, it is reasonable to hypothesize that macroinvertebrate biomass would also have been greater in beaver ponds in relation to streams, but this remains in the realm of speculation.

The number of bird species detected during the surveys was low*. Nonetheless, the values for bird richness presented here are similar to those of other waterbird surveys in Patagonia (e.g. Garay et al. (1991); Lancelotti et al. (2009)). Certain species cited for the study area are particularly rare or hard to see (e.g. *Anas platalea*, *Cistothorus platensis*; Couve and Vidal (2003)). Grebes, such as *Rollandia rolland* and *Podiceps major*, are good divers and might prefer deep lakes instead of the shallower beaver ponds and

* Species accumulation curves were calculated to assess adequacy of sampling size and are included in Appendix 1.

lagoons (Fjeldsa (2004)). It would have been particularly interesting to detect piscivores, such as *Ceryle torquata*, to gain better understanding on how dams might affect fish distribution and this bird foraging group. Given their rather low density on the study area, a study targeting exclusively those species is recommended.

Our results show that waterbird species in our study area have a greater density and richness in beaver ponds in relation to free flowing streams. This is consistent with what is known about the effects of beaver dams in North America (Grover and Baldassarre (1995); McCall et al. (1996); McKinstry et al. (2001b)). In most cases, this effect has been related to trophic cascading effects of beaver resulting in increased macroinvertebrate density (Longcore et al. (2006b); McDowell and Naiman (1986); Numii and Hahtola (2008)) triggered by beaver establishment. However, invertebrate consumers (carnivores) in this study were too scarce to detect any preferences between habitat types, and thus we cannot tell whether this trophic group is responding to the alleged increase in food availability. Herbivorous birds did show a significant preference for beaver ponds, but unfortunately the effect of beaver on macrophytes has not been as well studied as that on macroinvertebrates, either in TdF or in North America, where I only found one study (Ray et al. (2001)). On the other hand, many of the species here classified as herbivorous switch to a carnivore diet during the breeding season (Del Hoyo et al. (1992)), so they could also respond to changes in invertebrates. Regarding shoreline carnivores, which are mainly terrestrial species the lack of response to the different habitats could owe both to the fact that they are less dependant on water bodies for feeding and to beavers having no significant effect on the portion on invertebrates within their reach. These birds will also be less affected by other, non-trophic characteristics of the water body that can influence use by birds, such as water velocity. Interestingly, although beaver ponds had higher bird density and

richness than streams, they had the lowest diversity, as measured by the Shannon Index. This is likely to result from a low equity between species, as 50% of the individuals observed in beaver ponds corresponded to one species, *Anas flavirostris*, and no other species exceeded 20% of the individuals observed. On the other hand, while *Anas flavirostris* also dominated the observations in the other habitat types with 37% and 23% in lagoons and streams respectively, other species were equally or more represented (e.g. *Cinclodes fuscus* and *Lessonia rufa* respectively)(data not shown).

Whether focusing on the two avian foraging groups or on all birds values of density and richness had a high variability in ponds and lagoons, while the range of values for this variables in streams was consistently narrower. This higher variability in the lentic habitats indicates that suitability of these habitats for waterbirds, although in general higher than in streams, is far from a stable, fixed characteristic, urging to include other factors in the determination of their adequacy for waterbirds. Besides food resources, birds need adequate protection from predators and territory isolation for breeding. Both terrestrial (riparian) and aquatic vegetation can contribute to this by providing cover and habitat heterogeneity, and they have been shown to affect density and richness of waterbirds (Cooke and Zack (2008); Edwards and Otis (1999); Found et al. (2008)).

Conclusion

This study shows that the ponds created by an invasive species, the North American beaver, can constitute suitable habitat for waterbirds and terrestrial birds associated to water courses in the Tierra del Fuego Archipelago. In general terms, beaver ponds are preferred by these birds before free-flowing streams, but there it is not clear that they are favoured in relation to naturally occurring lagoons, as it occurs in the beaver's native habitat. Furthermore, there is high variability in the use of both these habitats by birds, indicating that other factors other than those analyzed here affect selection by birds.

As for waterbirds, the impact of beaver introduction to TdF does not seem to have had such a strong impact as on other components of the ecosystem (e.g. Anderson et al. 2006, Silva & Saavedra 2008). This could be explained by the lack of a common evolutionary history of between the elements of Fuegian limnic ecosystems and beavers, resulting in a lesser capacity of native species to adapt and take full advantage of the conditions offered by beaver engineering, thus ponds not being able to become the favourable habitat for waterbirds they are in their range of origin.

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Appendix 1

Curvas de acumulación de especies por tipo de hábitat. La línea punteada indica el número de sitios recomendado por Oosting (1956), basado en que un nuevo sitio no aportaría más del 10% de las especies ya encontradas.

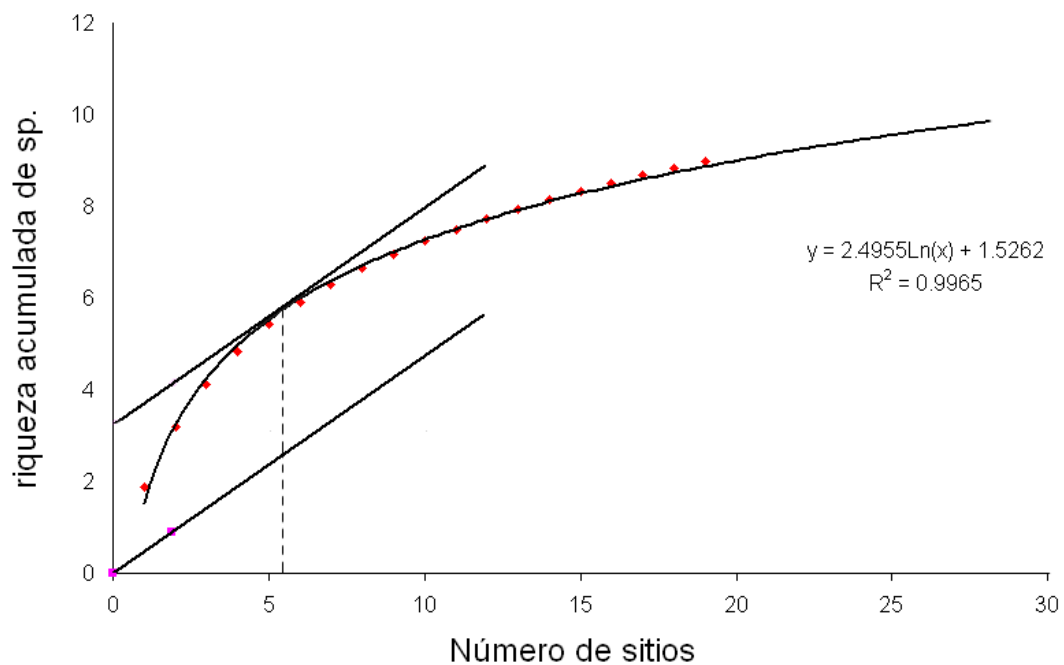


Fig. 1. Curva de acumulación de especies en castoreras (n=19)

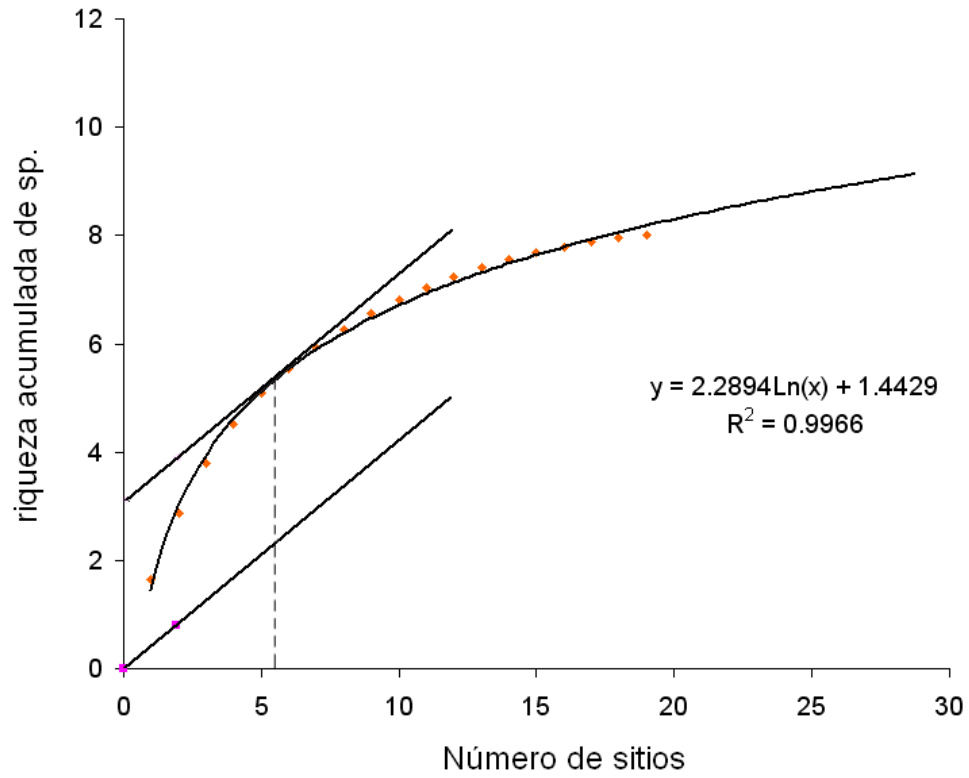


Fig. 2. Curva de acumulación de especies en ríos (n=19).

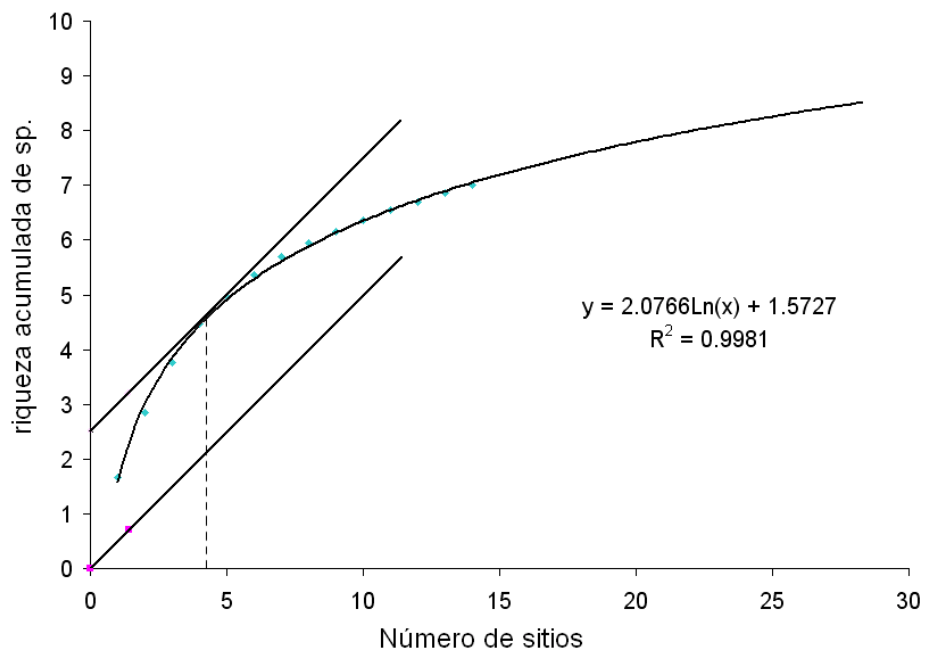


Fig. 3. Curva de acumulación de especies en lagunas (n=14).

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