LINKING AN INVASIVE ECOSYSTEM ENGINEER WITH ITS COMMUNITY AND ECOSYSTEM EFFECTS: THE ROLE OF INTRODUCED BEAVERS IN THE CAPE HORN BIOSPHERE RESERVE, CHILE

by

CHRISTOPHER BRIAN ANDERSON

(Under the Direction of AMY D. ROSEMOND)

ABSTRACT

Exotic species are a major component of current, global-scale ecological change. Even otherwise remote and pristine areas, such as the Cape Horn Biosphere Reserve (CHBR), Chile, are replete with introduced species. The North American beaver (*Castor canadensis*), which was introduced to Tierra del Fuego island in 1946, in particular has become highly invasive in the Chilean subantarctic archipelago. Nonetheless, little previous research has addressed its role as an invasive ecosystem engineer. I sought to determine the role of introduced beavers by addressing their impacts on several levels. Nearly all of the CHBR has been colonized by beavers with the only remaining non-invaded areas found in Cape Horn National Park and the far southwestern portion of the archipelago. Furthermore, where it has become established it is found in nearly all watersheds at very high densities. The foraging and dam building activities of beaver have consequently provoked wide-scale deforestation of riparian forests with little regeneration of the two dominant species (*Nothofagus betuloides* and *N. pumilio*). In addition, I found that the beaver meadows that are created by drained ponds provided an avenue for the invasion of exotic plant species into the interior of watersheds. The plant communities created by beaver activities in these meadows were generally more speciose than unimpacted forested reaches. However, the forest understory assemblage was a subset of those found in meadows, rather than each community constituting a unique vegetation community assemblage. In streams, beavers significantly impacted benthic community and ecosystem properties as well. Their effect on benthic macroinvertebrates was to reduce diversity, but increase production in pond sites, while downstream sites were similar to unimpacted reaches. The overall influence of beavers on streams was to make them more retentive of organic matter, which increased the magnitude of terrestrially derived organic matter flows throughout the benthic food web. Overall, I found that beavers have profound effects on both terrestrial and aquatic habitats and the linkages between them. These results highlight the strong need for management of invasive beavers. These findings also provide baseline information for future research in subantarctic streams and investigating the impacts of exotic species in novel ecosystems.

INDEX WORDS: Beaver, Benthic, Cape Horn, *Castor canadensis*, Chile, Exotic, Food web, Invasion, Secondary production, Trophic basis of production

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CHRISTOPHER BRIAN ANDERSON

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CHRISTOPHER BRIAN ANDERSON

Major Professor:	Amy D. Rosemond
Committee:	C. Ronald Carroll J. Bruce Wallace Catherine M. Pringle Aaron T. Fisk

Electronic Version Approved:

Maureen Grasso
Dean of the Graduate School
The University of Georgia
May 2006

Dedicated to my favorite naturalist, who is also my grandmaw Myra McAllister Anderson

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Exotic species in the "pristine" Cape Horn Biosphere Reserve

On a global scale, introduced species cause an overall reduction in biodiversity, but on local and regional levels they may actually enhance species richness (Sax and Gaines 2003). The impacts of non-native species are variable, ranging from no effect to whole ecosystem alteration. For example, in the United States, exotic species are believed to be a major threat to native biodiversity, second only to habitat degradation (Wilcove et al. 1998), but in South America introduced species are implicated in the decline of only 6% of imperiled species (Rodríguez 2001). Regardless, invasive species' cumulative effects presently constitute a principal component of global ecological change (Vitousek et al. 1997). Exotic *ecosystem engineers* in particular have the potential to affect even greater ecological change than other species, since by definition they alter resources and habitat in a manner disproportionate to that which would be expected from their mere abundance (Jones et al. 1996, Crooks 2002). As biological invasions increase around the world, and the consequences of those invasions become greater, studies that quantify the impacts of exotic species on biotic communities and ecosystem processes will be increasingly important.

Species invasions are not only a concern in areas that are heavily impacted by humans. Indeed, even otherwise seemingly remote and pristine areas experience their impacts. For example, the Magellanic Subpolar Forest Ecoregion was recently identified as one of the thirty-seven most pristine remaining wilderness areas in the world (Figure 1.1, Mittermeier et al. 2001), due to its low human population density and its extensive intact native vegetation (Table 1.1). Nonetheless, the southern part of this biome, which corresponds to the Cape Horn Biosphere Reserve, is replete with introduced species (Anderson et al. 2006b, Chapter 2), which in turn constitute a major conservation threat to this area (Rozzi et al. 2004). The archipelago's introduced vertebrate assemblage includes approximately half of terrestrial mammals (12 of 22) and freshwater fish (2 of 5), as well as one exotic invertebrate and two bird species (Chapter 2, Anderson et al. 2006b). Among these exotic species, the North American beaver stands out for the dam building and foraging behaviors that make it an ecosystem engineer, potentially affecting both terrestrial and aquatic ecosystems.

Beavers as ecosystem engineers

The term *ecosystem engineer* describes "organisms that directly or indirectly modulate the availability of resources to other species, by causing physical state changes in biotic or abiotic materials" (sensu Jones et al. 1996). Beaver are the quintessential non-human ecosystem engineer. They affect a wide range of biotic and abiotic environmental variables. For example, in their native habitats they add to a stream as much as one metric ton of woody debris per beaver colony each year during their foraging and building activities (Howard 1982). In the process they alter the light regime, leaf-litter fall, vegetation composition, the partitioning of resources and nutrient cycling of riparian ecosystems (Naiman et al. 1988, 1994). The impact on biota can extend further to fishes, birds, and even humans via ecosystem alterations in decomposition, nutrient cycling and metabolism (Melillo et al. 1984, Naiman et al. 1988). Eventually, beaver impacts can influence economic activities, such as forestry, potable water and infrastructure (Bhat et al. 1993, NCWRC 1997).

In their native range, beaver activities are associated with enhancing diversity of terrestrial and aquatic assemblages via the creation of a more heterogeneous environment (Naiman et al. 1988). They have been shown to increase plant species richness at the landscape scale (Wright et al. 2002), and beaver ponds had higher plant diversity than any other wetland habitat in southeast Alaska (Pollock et al. 1995). In Idaho, Medin and Clary (1991) reported that beavers also enhanced small mammal density and biomass. Hanson and Campbell (1963) also found that beaver ponds had greater fish species richness and standing stock. Finally, Naiman et al. (1988) concluded that in their native range beaver increased ecosystem stability and resilience to disturbance.

Specifically with regard to streams, beavers directly and indirectly alter the physical and biogeochemical conditions of lotic ecosystems (Johnston and Naiman 1987, Naiman et al. 1988). Beaver activity reduces current velocity, thereby inducing sediment deposition, changes in bed-slope and increased retention of organic and sedimentary material (Butler and Malanson 1995). They locally increase detrital standing crop, but at the same time alter the physical conditions of the habitat such that the detritus becomes inaccessible for some macroinvertebrate taxa and functional groups (McDowell and Naiman 1986). Overall, beaver impoundments support more macroinvertebrate biomass, compared to riffles, and they induce significant changes in functional group composition, such as increasing the importance of predators and collector-gatherers (McDowell and Naiman 1986, Rolauffs et al. 2001). Pollack et al. (1995) asserted that invertebrate assemblages from beaver ponds were characteristic of >4th order streams and that such a community may be unique in catchments that do not have higher order segments.

To date, beaver impacts have only been identified in their native range and in Europe, where they have been introduced into the range of their congener *C. fiber*. However, as an exotic species in South America where no ecological equivalent species exists, *C. canadensis* may have effects on ecosystems that are unexpected based on Northern Hemisphere examples. For example, plant and animal communities may not have strategies to take advantage of beaver-associated impacts from flooding and foraging. In addition, in species-poor ecosystems, such as the Tierra del Fuego – Cape Horn Region, there may not be predator or competitive control mechanisms to mitigate the impacts of beaver, causing their effects to become pervasive, instead of patchy and heterogeneous.

Ecology of southern South American temperate forests

South American temperate forests occur between 35° and 56° S latitude and are characterized by relatively low species richness and a high degree of endemism when compared to Northern Hemisphere temperate forests (Armesto et al. 1995, Veblen et al. 1996). Chile hosts the majority of the Southern Hemisphere's temperate forests. Various biogeographic barriers, such as deserts, high mountains and arid pampas, separate these ecosystems from tropical forests to the north, thus isolating the South American temperate forests and making them a biogeographical island for much of their flora and fauna.

This study was conducted in the Magellanic Sub-Antarctic Forest Biome in the Magallanes and Chilean Antarctic Region (Figure 1.2). The Cape Horn Biosphere Reserve is the southernmost part of the continent and the world's southernmost, forested ecosystem (Figure 1.3). It is the Southern Hemisphere latitudinal equivalent of northern British Columbia, Canada and southern Alaska, USA. The Straits of Magellan separate Tierra del Fuego and the austral archipelago from the mainland and numerous channels and fjords divide the area into hundreds of smaller islands.

The biotic communities in the Cape Horn Archipelago region are relatively species poor with regards to most taxa (but non-vascular plants are a notable exception; see below). The forests are dominated by three species of the genus *Nothofagus* (Pisano 1977). Two are deciduous (*N. pumilio* [Poepp. et Endl.] Krasser and *N. antarctica* [Forster f.] Oersted), and one is evergreen (*N. betuloides* [Mirbel] Oersted); all are broad-leaved. In stark contrast to the boreal forests of the Northern Hemisphere, no coniferous trees exist in sub-Antarctic forests. Compared to other taxonomic groups, the described aquatic macroinvertebrate community is comparatively speciose and consists of thirty-five taxa to date (Anderson and Rosemond Chapter 4), but the archipelago's most biological diverse taxa are vascular and nonvascular plant communities, which together have more than 1,500 native species in the Tierra del Fuego-Cape Horn Region (Moore 1983).

Climate

Short, cool summers (mean temperature 9°C) and long, cooler winters (mean average temperature 2°C) characterize the study area, which receives about 500-650 mm of precipitation annually (Tuhkanen et al. 1989) (Figure 1.4). Glaciers covered the entire region until approximately 15,000 years B.P. (McCulloch et al. 1997). Today, there are no extant glaciers on Navarino Island.

The Cape Horn Biosphere Reserve

This study was conducted on Navarino Island, a Chilean island (2,500 km^2) located south of Beagle Channel and north of Cape Horn (approx. 55°S) (see Figure 1.3). Elevations on the island range from 0 to 1000 m.a.s.l. *C. canadensis* arrived to Navarino in the 1960s. Since that time, the beaver has come to occupy most, if not all, watersheds on the islands of the Tierra del Fuego-Cape Horn Region at densities on the high end of the range reported in the Northern Hemisphere literature (Gurnell 1998). While densities described for North America range between 0.08 to 1.4 colonies km^{-1} (Boyce 1983, Beier and Barretto 1987, Howard and Larson 1985 and Robel and Fox 1993), on Tierra del Fuego researchers report between 0.2 to 5.8 colonies km^{-1} (Briones et al. 2001, Lizarralde 1993, Skewes et al. 1999), and the only study on Navarino Island reported 1.1 colony km^{-1} (Skewes et al. 1999).

The present study focused on the north coast of Navarino Island, where forested catchments permit comparisons with mainland habitats and are accessible from Puerto Williams, the only town on the island and the capital of the Chilean Antarctic Province. Beavers also inhabit the southern part of the island, where Magellanic tundra and moorlands dominate with forest patches scattered throughout. However, if the beaver succeeds in colonizing the mainland, its effects will be mainly on the extensive temperate forest habitats between Magallanes and central Chile. As a result, this study concentrated on the beaver's effect on streams in forested habitats.

Dissertation

The goal of this dissertation was to describe and evaluate the impacts of the North American beaver (*Castor canadensis*) on streams and adjacent habitats in the Cape Horn Biosphere Reserve of southern Chile. The beaver came to southern South America in 1946. The Argentine government introduced twenty-five pairs in a failed attempt to create a fur industry (Lizarralde 1993). While the fur industry never succeeded, the habitat of the southern tip of South America proved to be ideal for *C. canadensis*, permitting some of the world's highest reported densities (Gurnell 1998). Many of the ecological consequences of the invasion, however, have never been evaluated. This study addressed several aspects of the effects of invasive beavers in the archipelago, including the general context of exotic vertebrates, riparian community impacts and the their role in engineering stream ecosystems.

General approach

I began my research on exotic species in 2000. Since then, I have participated in expeditions throughout the archipelago to determine the distribution and assemblage of exotic vertebrates in the Cape Horn Biosphere Reserve. For subsequent research on Navarino Island, I chose five streams on the north coast for intensive study. All study sites were at elevations below 100 m in mixed forest-bog watersheds. Study reaches were in the forested portion of catchments with a mix of only two dominant tree species: the broadleaf evergreen *Nothofagus betuloides* and its deciduous congener *N. pumilio*.

The study watersheds were: Robalo (in the Omora Park Experimental Watershed), Mejillones, Estrella (only stream study), Ukika (only riparian study) and Faraones. Study reaches were all on the main stems of the catchments with an average width at natural reaches of 6.6 m (±0.9). Two of these streams (Robalo and Mejillones) were selected for estimates of secondary production and trophic basis of production. Robalo and Mejillones were used because they represented the two major stream types on the island – clear water and dark water (i.e. tannin-enriched streams), respectively. Each stream had three sampling locations that corresponded to: (1) a natural, forested reach never impacted by beavers ('natural'), (2) an active beaver pond ('pond') and (3) a site immediately downstream of the beaver dam ('downstream'). The beaver-impacted sites were previously forested before beaver colonization, as evidenced by the geomorphology of the site and the presence of standing dead tree trunks to the edge of the river.

Chapter 2: Exotic vertebrate fauna in the remote and pristine sub-Antarctic Cape Horn Archipelago region of Chile

Chapter 2 (Anderson et al. 2006b) offers an introduction to the general context of introduced and invasive species in the Cape Horn archipelago. These data represent five years of field work by various investigators and teams, which were synthesized in this publication. The results presented here offer the most detailed survey to date of the assemblage and distribution of exotic vertebrates in the Cape Horn Biosphere Reserve and provide a baseline for future work to quantify their impacts and inform management plans.

Chapter 3: The effects of invasive North American beavers on riparian vegetation communities in Cape Horn, Chile: Do exotic beavers engineer differently in sub-Antarctic ecosystems?

The goal of Chapter 3 (Anderson et al. 2006a) is to address the effects of introduced beavers on riparian plants. This work was inspired by seminal work on the role of beavers as ecosystem engineers in their native habitat (Wright et al. 2002, Wright and Jones 2004, Wright et al. 2004), which found that beaver engineering activities enhance landscape level plant richness and that ensuing changes in habitat productivity by engineers resulted in predictable changes in plant species richness. I quantified beaver effects in a non-native, subantarctic ecosystem to compare with results from previous temperate North American studies to see if “exotic beavers engineer differently?”

Chapter 4: Linking an invasive species with its community and ecosystem impacts: Introduced beavers affect diversity and secondary production of subantarctic stream benthos

Chapter 4 addresses the effects of introduced beavers on subantarctic streams. I analyzed the effect of invasion at two hierarchical ecological scales: community and ecosystem. I then used three habitat types (natural, beaver pond and downstream) to assess the beaver’s impact on assemblage, abundance, richness, diversity and similarity of benthic communities. In addition, we estimated benthic secondary production to get an integrated ecosystem-level response variable. These are the first reported values for secondary production of benthic macroinvertebrates for the temperate forest biome of southern South America.

Chapter 5: Exotic beavers alter the magnitude of terrestrial subsidies and energy flow pathways in subantarctic stream food webs.

Finally, Chapter 5 explores the role of beavers in benthic food webs dynamics by looking at organic matter flow sources and magnitudes. I used stable isotopes and the trophic basis of production as complementary techniques to elucidate food web changes. I also estimated the contribution of individual food categories to production and the magnitude and pathways of organic matter transport in the food web. The trophic basis of production method allowed us to combine individual-based characteristics (such as diet) with ecosystem-level properties (such as material flow) to get a holistic understanding of beaver impacts on subantarctic benthic food webs.

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Table 1.1 Defining the world's pristine wilderness areas. Comparison of the Magellanic Sub-Antarctic Forest Biome with criteria proposed by Mittermeier et al. (2001) for "wilderness" areas.

Criteria	**"Wilderness" defined by Mittermeier et al. 2001**	**Magellanic Sub-Antarctic Forests**
Size	an area greater than 10,000 km^2 (1 million ha)	147,200 km^2 (86% Chilean, 14% Argentine)
Intactness	70% or more of native vegetation cover remaining intact, as well as retaining native fauna, especially large, wide-ranging predators	95% native vegetation cover
Human population density	less than 5 inhabitants km^{-2}	0.14 inhabitants km^{-2}

Figure 1.1. Map illustrating the world’s thirty-seven remaining wilderness areas, including the Magellanic Subpolar Rainforests (Mittermeier et al. 2001).

Source: www.conservation.org/ImageCache/CIWEB/content/library/books/wildernessmap_2ejpg/v1/wildernessmap.jpg

Figure 1.2. Map of southern South America (Rozzi et al. 2004). Tierra del Fuego Island is divided between Chile and Argentina, while the remaining islands south of the Straits of Magellan are under Chilean sovereignty. The darkest shaded portion corresponds to the Magellanic Sub-Antarctic Forest Biome, one of the world's most pristine remaining wilderness areas (Mittermeier et al. 2001).

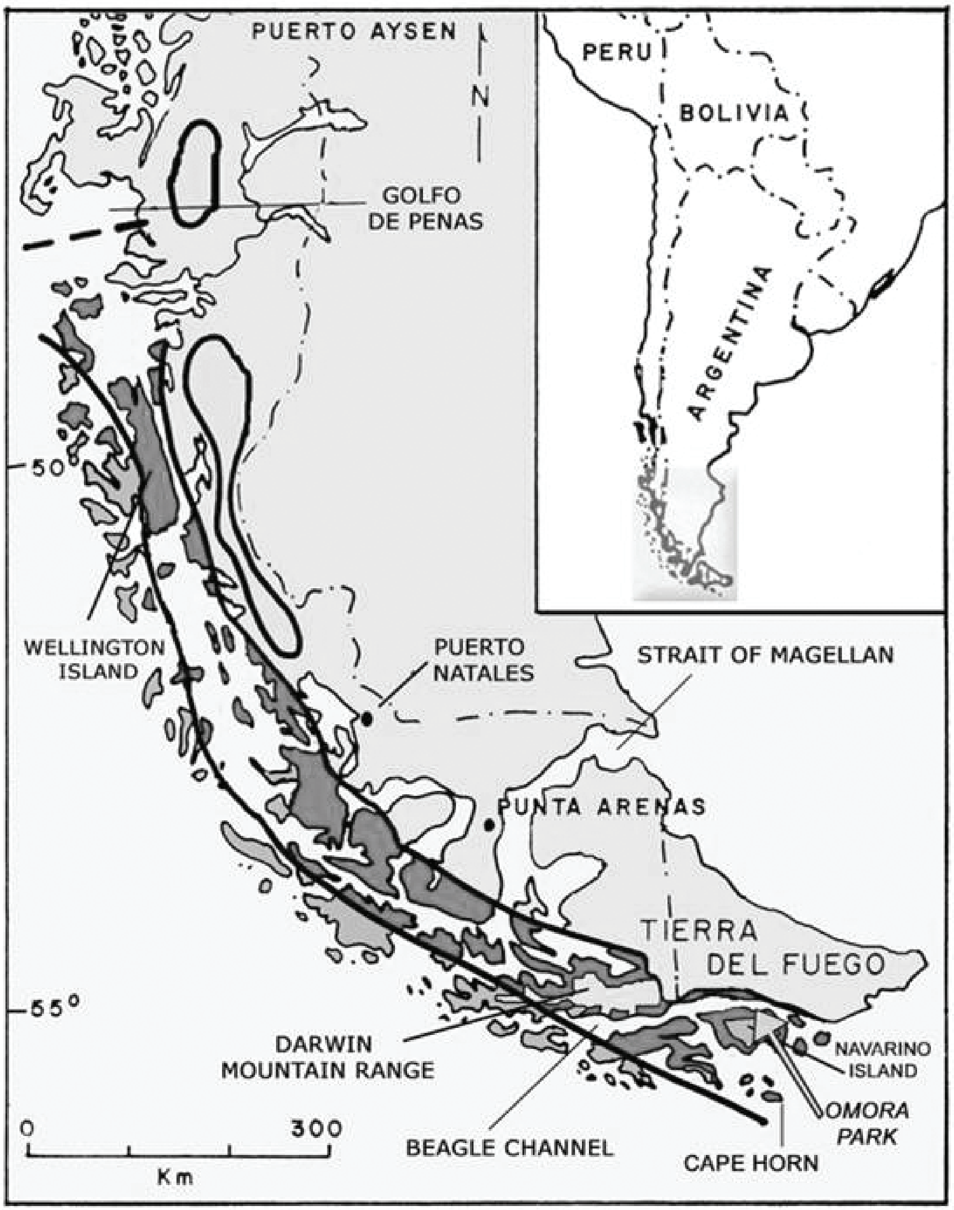
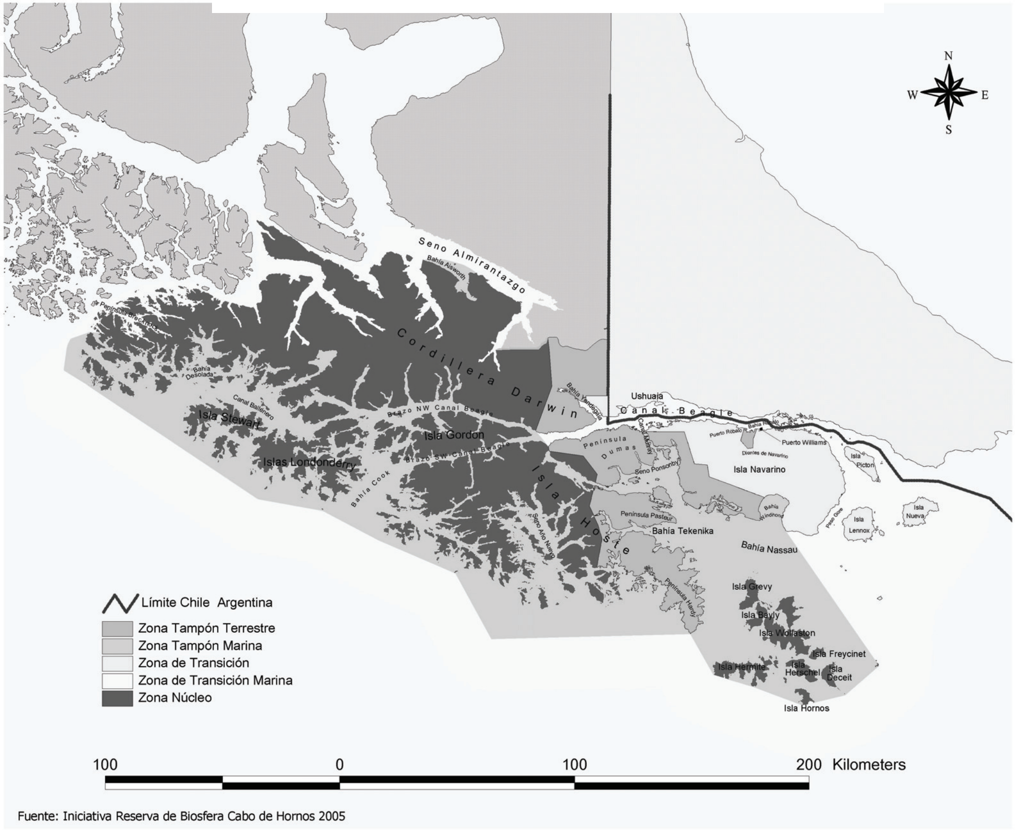

PUERTO AYSEN
N
GOLFO DE PENAS
50
WELLINGTON ISLAND
PUERTO NATALES
STRAIT OF MAGELLAN
PUNTA ARENAS
TIERRA DEL FUEGO
55°
DARWIN MOUNTAIN RANGE
NAVARINO ISLAND
OMORA PARK
BEAGLE CHANNEL
CAPE HORN
0
300
Km
PERU
BOLIVIA
ARGENTINA

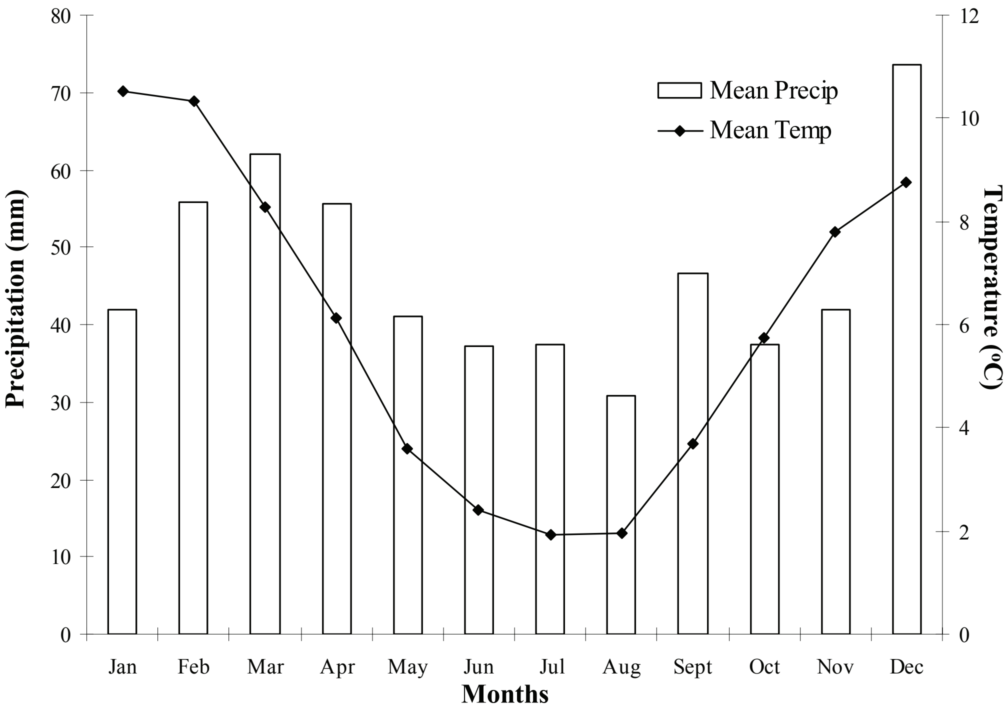
Figure 1.3. Zoning of the Cape Horn Biosphere Reserve, Chile (Rozzi et al. 2006). Darkest shading indicates the core zones that correspond to national parks: Alberto de Agostini and Cape Horn. Intermediate shading on land and shading of sea denote buffer zones, and the lightest contrast signifies transitions zones.

Zoning of the Cape Horn Biosphere Reserve



Fuente: Iniciativa Reserva de Biosfera Cabo de Hornos 2005

Figure 1.4. Mean monthly temperature (^{o}C) and precipitation (mm) for Puerto Williams, Navarino Island, Cape Horn Biosphere Reserve, Chile (approx. 55°S). Data compiled from the Chilean Navy (years 1946, 1947, 1965, 1966, 1970, 1999, 2000).



Precipitation (mm)
80
70
60
50
40
30
20
10
0
Temperature (°C)
12
10
8
6
4
2
0
Mean Precip
Mean Temp
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sept
Oct
Nov
Dec
Months

CHAPTER 2

EXOTIC VERTEBRATE FAUNA IN THE REMOTE AND PRISTINE SUB-ANTARCTIC CAPE HORN ARCHIPELAGO REGION OF CHILE[1]

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[1] Anderson, C. B., R. Rozzi, J. C. Torres-Mura, S. M. McGehee, M. F. Sherriffs, E. Schuettler and A. D. Rosemond. In press. *Biodiversity and Conservation.* Reprinted here with permission of publisher.

Abstract

Pristine wilderness is a scarce global resource, but exotic species are so common that they constitute a principal component of worldwide ecological change. The relationship between these two topics, invasion and remoteness, was the impetus behind five years of fieldwork aimed at identifying the assemblage and range of exotic vertebrates in Cape Horn, Chile, identified as one of the world's most pristine wilderness areas. While the archipelago has extremely low human population density and vast tracts of undisturbed land, we discovered that several terrestrial vertebrate groups were dominated by exotic species. Native birds were diverse (approx. 154 spp), and only 1.3% (or two spp.) were introduced. In contrast, exotic terrestrial mammals (twelve spp.) and freshwater fish (three spp.) outnumbered their native counterparts, constituting 55% and 75% of the assemblages. Using GIS, we found that not all areas were impacted equally, largely due to intensity of human occupation. Human settled islands (Navarino and Tierra del Fuego) hosted the greatest number of exotics, but humans alone did not explain observed patterns. Remote islands also had introduced species. North American beavers (*Castor canadensis*), American minks (*Mustela vison*) and feral domestic dogs and cats were particularly widespread, and their range in isolated parts of the study area raised important ecological and management questions. In conclusion, the Cape Horn Archipelago retained areas free of exotic vertebrates, particularly parts of the Cape Horn and Alberto D'Agostini National Parks, but at many sites introduced species were overwhelming native biota and altering these previously remote natural ecosystems.

Key Words: Cape Horn, Chile; exotic species; invasive; global change; Sub-Antarctic Forests; Tierra del Fuego; wilderness

Introduction

The impact and distribution of exotic species is today a major area of scientific interest and conservation concern (Courchamp et al. 2003). Together with habitat fragmentation and global warming, species introductions constitute a principal cause of current global ecological change (Vitousek et al. 1996). As a country, Chile hosts proportionally few exotic vertebrates. Introduced species represent only 3.9% of the Chilean vertebrate assemblage (Jaksic 1998). However, within the Patagonian ecoregion of southern South America, exotics constitute a higher proportion of vertebrate fauna. For example, in the Argentine portion of Tierra del Fuego 67% of mammal species were found to be exotic (Lizarralde and Escobar 2000), and a study of freshwater fish in the Chilean portion of Tierra del Fuego Island described two exotics and only one native species (Vila et al. 1999).

The political unit of Cape Horn County is the world's southernmost forested ecosystem and encompasses all of the islands south of the Beagle Channel, in addition to the Chilean portion of Tierra del Fuego Island located south of the highest peaks in the Darwin Mountain Range (Figure 2.1). The area belongs biogeographically to the Magellanic Biome (Pisano 1981), and more specifically to the Magellanic Sub-Antarctic Forest Ecoregion (Rozzi 2002). It recently has been classified as one of the world's most pristine remaining wilderness areas due to its extensive size, the intact nature of its native vegetation and its low human population density (Mittermeier et al. 2001). Mittermeier et al. (2001) also point out that the Magellanic Sub-Antarctic Forests have a very high percentage of protected area (75% in Cape Horn County and 51% for the whole region), compared to the world's other remaining wilderness areas, and consequently merit special recognition.

Based on these criteria, this region is apparently remote from direct human influence, but in fact the Yahgans first settled the ecosystems of southern Chile 7,500 years ago (Ocampo and Rivas 2000). European explorations began in the 1500s, and colonization commenced in earnest in the late 1800s, provoking the first major landscape changes and introductions of exotic vertebrate fauna, principally associated with livestock grazing (Martinic 1973). The first record of a deliberate introduction of vertebrates to the islands south of the Beagle Channel was in 1867, when goats were brought to Lewaia Bay on Navarino Island by Anglican missionaries (Martinic 1973). During the 20th Century the number of introductions increased and expanded from domestic animals, including invasive species that expanded throughout the archipelago and others that did not become established at all. The realization that non-native biota can reach even the most remote areas left on the planet poses a conservation challenge for southern Chile, particularly given that a large portion is also classified by the Chilean environmental commission (*CONAMA*) as a priority area for national biodiversity conservation (Rozzi and Massardo 2002).

Despite the area's importance, detailed and precise information about exotic species in this area is currently lacking. Effective management of the extant national parks (Cape Horn and Alberto D'Agostini) and the proposed UNESCO Cape Horn Biosphere Reserve requires up-to-date knowledge of the assemblage and distribution of exotics, as well as their associated impacts. In order to achieve this goal, this paper 1) synthesizes existing information of native and non-native vertebrate fauna in the Cape Horn Archipelago, 2) uses five years of monitoring and survey information to describe in greater detail the exotic vertebrate assemblage and distribution patterns and 3) analyzes three taxa identified as particularly harmful or widespread: the North American beaver (*Castor canadensis*), the American mink (*Mustela vison*) and feral domestic predators (dogs and cats). These species further are used to highlight the implications of invasion, demonstrating the effect of ecological barriers, the potential rapidity of establishment and the possibility for changing positive ecosystem feedbacks loops to negative. While providing relevant information for local managers, our information also serves to better comprehend the global context of species invasion dynamics.

Materials and Methods

Study Area

Cape Horn County is located within the administrative district known as the Chilean Antarctic Province, which in turn is itself part of the Magallanes and Chilean Antarctic Region (Figure 2.1). The study area consists of an archipelago with hundreds of islands that cover approximately 15,488 km^2. The political boundaries also correspond largely to biogeographic barriers created by the icecap found towards the north in the Darwin Mountain Range on Tierra del Fuego Island and the sea barriers on all other sides. The area is part of the Magellanic Sub-Antarctic Forest Biome (for a detailed site description see Rozzi et al. 2004a).

Data Collection and Analysis

The data presented here were collected by the authors over five years of fieldwork associated with the Omora Ethnobotanical Park's long-term ecological research efforts in the sub-Antarctic ecoregion. A total of forty sites on nineteen islands were surveyed over the course of five years (Appendix 2.1). Sampling included systematic and opportunistic mistnetting, point-count transects and checklists for birds, which were conducted in alpine, shrub, pasture and forested habitats between January 2000 and January 2005. Avian sampling has been carried out systematically six days per month on Navarino Island since 2000. In addition during January and April 2002; April 2003; January and May 2004; January and May 2005 bird surveys were conducted during boating expeditions throughout the archipelago. Data concerning fish presence and absence were based on at least one day of rod-and-reel fishing per surveyed water body on Navarino, Hoste and Tierra del Fuego Islands, as well as opportunistic observational evidence and interviews with fishermen.

Sherman traps for small mammals were deployed on Navarino Island in quarter hectare grids in shrub, rush wetlands, cushion bog, pasture and evergreen, deciduous and mixed forest habitats. In addition, traps were placed around human settlements. Traps were baited with oats and checked twice daily. In January and May 2004 and January and May 2005 expeditions were conducted by boat through the archipelago in order to access remote and difficult portions of the county, and qualitative Sherman trap sampling for small rodents was conducted from one to two nights per site on Hoste, Herschel and Horn Islands.

Live traps (20 x 20 x 70 cm) were used in April and May 2005 at Pia Sound, Olla Cove and Yendegaia Bay (Tierra del Fuego Island) and on Navarino Island to sample for mink. A total effort of 420 trap nights was carried out on Navarino Island and twenty-five trap nights for TDF. Visual surveys were conducted at each site for a distance of 0.5 to 2 km of stream or coastline and divided into 200 m sections that were classified as positive or negative detection of mink evidence. Detection surveys were made of the places where tracks were likely to be found, such as sandy or muddy ground, and scats were searched for on exposed marking places, such as rocks and fallen trees for territorial scent marking (Dunstone 1993).

At each stop during expeditions, visual transects and surveys were also used to detect evidence (spoor, rooting, disturbance and tracks) of larger exotic species, such as beavers, muskrats and feral domestic animals, throughout the archipelago during stays of one to three days. Locations where observational transects were conducted during expeditions included: London Island; Romanche Bay (Gordon Island); Ventisquero Sound, Pía Sound, Olla Cove and Yendegaia Bay (TDF); Islotes Holger; Parque Omora, Inútil Bay, Wulaia Bay and Douglas Bay (Navarino); Jemmy Button Island; Orange Bay and Ponsonby Sound (Hoste Island); Mascart Island; Kendall Cove (Wollaston Island); Puerto Dillon (Grevy Island); Victoria and Washington Channels (Bayly Island); Puerto Maxwell and Saint Martin Cove (Hermite Island); Martial Cove (Herschel Island); and Cape Horn Island (for details see Appendix 2.1).

All survey and observational information was geo-referenced in order to utilize GIS to produce distribution maps. Maps were then used to identify areas free of exotics and also recognize the species that were particularly wide-spread and independent of human-association. In addition, collected field data were supplemented with a bibliographic review and questionnaires of local residents, sailors, fishermen and scientists. Non-native species under domestic or animal husbandry practices, such as sheep or chickens, were not considered in the analysis because they are kept exclusively in enclosures. On the other hand, pigs, cows, dogs, cats and horses were examined because many also have become feral or are free ranging.

Results

Human Inhabited Islands – Navarino and Tierra del Fuego

We identified a total of seventeen exotic vertebrate species, including mammals, birds and freshwater fish, inhabiting Cape Horn County, Chile (Table 2.1). No native or introduced amphibians or reptiles were discovered in the study area. The twelve recorded exotic mammal species represented a majority (55%) of the total mammalian assemblage (22 total spp.) (Table 2.2). Rodents and carnivores contributed the most introduced species with four non-native species each.

Two typically associated human rodents, *Rattus norvegicus* and *Mus musculus*, were found only in Puerto Williams on Navarino Island. Likewise, the only wild exotic birds detected in the whole stud area were the rock dove (*Columba livia*) and the house sparrow (*Passer domesticus*), which were confined to Puerto Williams. The rock pigeon (*C. livia*) was introduced deliberately by residents of Puerto Williams during the past decade, while *P. domesticus* probably crossed from the Argentine portion of Tierra del Fuego (TDF). These two exotic avifauna made up only 1.3% of the approximately 154 native bird species that inhabit terrestrial and coastal areas of the archipelago (Couve and Vidal 2000). The introduced grey fox (*Pseudalopex griseus*), which is native to the continental mainland of South America, was only found in the study area at Yendegaia Bay on TDF.

Among freshwater fishes, we identified three exotic species, which represented 75% of the archipelago's total assemblage. Only one native species (*Galaxias maculatus*) was confirmed within the county, while three more were described for the adjacent area of Argentina by Cussac et al. (2004). The exotic freshwater fish fauna in the study area were all Northern Hemisphere trout (Salmoniformes), including brown (*Salmo trutta*)*,* rainbow (*Oncorhynchus mykiss*) and reliable fishermen accounts of brook (*Salvelinus fontinalis*) (Table 2.3). No exotic fish were found in the western portion of the county on Hoste or Tierra del Fuego Islands. The only water bodies found to have trout were on Navarino Island and included: 1) Windhond watershed (brown and rainbow), 2) Robalo River below the dam (rainbow), 3) Navarino Lake (brook), 4) Mejillones River (rainbow), 5) Faraónes River (rainbow), 6) Lum River (rainbow), 7) Pilushejan River (rainbow) and 8) Douglas River (brown). In addition, several bog lakes along the north coast of the island, which are unconnected to adjacent water courses, contained brown and rainbow trout.

Feral Animals

While feral domestic animals were most abundant on Navarino and Tierra del Fuego, they were not strictly confined to those human-inhabited islands. We discovered, for example, scat and rooting disturbance from *Sus scrofa* at Romanche Bay on uninhabited Gordon Island in the western portion of the county and on Hoste Island. Pet dogs and cats likewise are being kept at isolated military outposts and ranches throughout the archipelago, such as Hoste, Horn, Lennox, Picton and Wollaston Islands. A similar native terrestrial predator (the Fuegian red fox, *Pseudalopex culpaeus*) only inhabited Hoste and Tierra del Fuego Islands.

On Navarino Island, dogs were found in all types of habitats, ranging from sea-level to above tree line. Cats, likewise, were observed even in remote forests. On several occasions they were seen preying upon songbirds in the Omora Ethnobotanical Park, Puerto Inútil and the small Holger Islands off the northwest coast of Navarino Island. *Sus scrofa*, the feral hog, was detected mostly around the northern and western coastlines of Navarino Island, especially in coastal, shrub and mixed forest habitats. Human-inhabited Navarino and Tierra del Fuego Islands were also the only locations where the European rabbit (*Oryctolagus cuniculus*) was seen. At Yendegaia Bay, they were commonly found along river and coastal shorelines. Rabbits were once common on Navarino Island, as well, but they were virtually eliminated with the viral control program conducted in the 1950s. In 2004, however, we observed rabbits on several occasions on the northwestern tip of the island, and they may be a new introduction from an adjacent ranch.

Mink, Beaver and Muskrat

Based on surveys and mapping, we determined that three of the most widespread or potentially harmful exotic vertebrate species found in the archipelago were the North American beaver (*Castor canadensis*), the American mink (*Mustela vison*) and the muskrat (*Ondatra zibethica*). All three were brought from North America by the Argentine government in the 1940s and 1950s as part of an effort to introduce economically valuable furbearers. Once survey information was geo-referenced and mapped, it was also realized that these species had some the widest distributions of any exotic species in the archipelago and were the least associated with human settlements.

We first confirmed the presence of mink in Cape Horn County in 2001 on Navarino Island (Rozzi and Sherriffs 2003). During transects conducted in the austral summer of 2004 and 2005, we sighted mink or their tracks along the major watercourses of Navarino Island (Figure 2.2). Surveys and trapping also found them in the town of Puerto Williams and Omora Ethnobotanical Park, and one was observed on Hoste Island. On Navarino Island their densities ranged from 0.79 to 1.32 individuals per kilometer along coastal shoreline habitat, which river riparian habitat had a lesser density of 0.26/km. Minks are known also for the Argentine portion of Tierra del Fuego (Massoia and Chebez 1993, Lizarralde and Escobar 2000), but were not detected during our trapping and surveys in the Chilean portion of the island at Pia Sound, Olla Cove and Yendegaia Bay. Residents of the national police outpost at Yendegaia Bay reported never having seen them.

Beaver were detected easily given their dam building and foraging activities. They were found in every watershed on Navarino, Picton, Nueva and Lennox Islands. On Tierra del Fuego and Hoste Islands, their distribution is limited towards the western and southern portions of the study area (Figure 2.3). Overall, their distribution extended in the east from Nueva Island to the western tip of Hoste Island (see eastern and western extremes in Figure 2.3). Parts of the western portion of the Beagle Channel and the extreme, marginal islands along the Pacific Ocean have yet to be invaded. The distribution currently reaches its southern terminus at Orange Bay on Hoste Island, and the Wollaston Island group, which makes up part of Cape Horn National Park, has not yet been colonized.

Burrowing activity by muskrats (*O. zibethica*) and skeletal remains were evident in peat lands (*Sphagnum* spp.) and cushion bogs on Navarino and Hoste Islands. However, muskrats, like beavers, were not found to inhabit the western portion of the survey area, such as the southwestern portion of TDF, or the far southern Cape Horn National Park.

Finally, an important bibliographic review concerning exotic species in Chile reported that reindeer (*Rangifer tarandus*) were brought to Navarino Island in 1972 (Jaksic 1998), but we confirmed that this record was erroneous. A plan did exist to introduce reindeer, but the Chilean navy suspended the project. The individuals remained on the continent, eventually dying there (N. Soto – Wildlife Division Chief, Regional Agriculture and Livestock Service, pers. com.)

Discussion

Lessons and Implications of Invasion

LESSON 1: BARRIERS TO INVASION – Beavers have been able to colonize much of the county and at very high densities (Skewes et al. 1999). The lack of native predators, combined with their relatively high reproductive rates (up to eight offspring per year; Long 2003), allowed beaver populations to grow explosively after initial introduction in the 1940s. In addition, the habitat of the sub-Antarctic forests is very similar to the beaver's native range, and their ability to swim up to 5 miles across water bodies (Long 2003) has facilitated their expansion throughout the archipelago.

In terms of their impacts, "naïve" vegetation in southern Chile lacks a common evolutionary history with the beaver and, therefore, appears be more vulnerable to herbivory and flooding. While in North America some plants, such as the trembling aspen (*Populus tremuloides*), produce defensive chemicals in response to beaver foraging that in turn deters future impacts and allows regeneration (Basey et al. 1988), sub-Antarctic forests are totally suppressed and do not regenerate for at least a couple of decades, if at all (Lencinas et al. 2001). In addition, we have found that the herbaceous community assemblage associated with beaver meadows actually increases the number of exotic plants present in the riparian assemblage, which presents a case of one exotic species facilitating others (C.B. Anderson unpublished data).

The ability of this species to disperse across the Fuegian Archipelago is well documented (Skewes et al. 1999). Therefore, it is informative to note where we did

not find them six decades after the initial introduction. Figure 2.3 showed the sites where we have confirmed the beaver's presence and absence in Cape Horn County. To the west and southwest they have not been successful at colonizing, while farther north in Tierra del Fuego they have been able to travel far greater distances and even arrive to the Brunswick Peninsula on the continental mainland (Skewes et al. 1999). In addition, beaver have not been found in Cape Horn National Park (the Wollaston island group), even though they were present on adjacent Hoste Island and as far east as Nueva Island.

These characteristics of the beaver's geographic distribution indicated that the colonization of certain parts of Cape Horn County is not due to a lack of dispersal ability, but rather intrinsic local conditions that do not permit establishment of viable populations. The uncolonized portion of the county typically receives greater precipitation and has steeper topography. The vegetation community is Magellanic rainforest, typical of the western channels, where the floral assemblage is dominated by *Nothofagus betuloides* and *Drimys winteri* (Rozzi et al. 2004a). Often these forests are also stunted by the strong, constant winds that buffet the seaward side of the county. Physical parameters, such as rainfall and geomorphology, and biological characteristics, such as vegetation assemblage, could act together to create an ecological barrier that would explain why this habitat has not proven suitable for beaver establishment.

LESSON 2: PASSING UNDETECTED – The case of the mink is somewhat different than that which was previously described for beaver, but demonstrates another lesson of species invasions. Mink began to be introduced to Tierra del Fuego in the 1940s (Lizarralde and Escobar 2000), but even as recently as the early 1990s, Massoia and

Chebez (1993) still classified it as a “species of hypothetical or doubtful presence” on Tierra del Fuego Island. Since then, it has not only been confirmed on Tierra del Fuego, but today it is also frequently sighted on adjacent islands in the archipelago (Rozzi and Sherriffs 2003).

Like the beaver, mink have a relatively high fecundity rate (Long 2003). As carnivores introduced onto islands that often lack native predators (only Tierra del Fuego and Hoste Islands have native populations of the fox *Pseudalopex culpaeus* and native otter populations were brought to near extinction due to over-hunting), minks are flourishing in the abundant shoreline and freshwater ecosystems. While *M. vison* is known to utilize aquatic habitats to forage, its dispersal across large, marine water bodies, such as the Beagle Channel (average width approximately 4 km), was an unexpected discovery. We would have predicted that while it may have become an invasive species on Tierra del Fuego, where it was directly introduced, its limited dispersal ability to other islands would have restricted its overall distribution.

The fact that it has been able to establish itself without early detection by scientists and managers and to colonize several islands adjacent to its Tierra del Fuego source population in only a few years, therefore, is quite striking and alarming. This exotic carnivore raises particularly acute conservation concerns. In the Aysén Region of Chile detrimental impacts on bird diversity and abundance have been recorded after the arrival of mink, and consequently it is considered a harmful species (*SAG* 2001). The islands of the Cape Horn area host an abundant and diverse marine, coastal and terrestrial avifauna that evolved without significant terrestrial predators. Many songbird species, such as the austral thrush (*Turdus falcklandii*) and rufous-collared sparrow (*Zonotrichia capensis*), as a result use ground nests in the austral archipelago (S. McGehee unpublished data), while in other parts of Chile the same species nest in trees. Therefore, the impacts of mink on birdlife in Cape Horn County could be even more dramatic, than those experienced in other parts of Chile. Also, mink presence has been shown to affect the distribution of the rare native river otters (*Lontra provocax*) in Argentine lakes (Aued et al. 2003), and Delibes et al. (2004) found that an introduced mink's ecological niche can extend to the intertidal zone, where it would directly compete with sea otters and establish a new top predator throughout the archipelago.

LESSON 3: CONVERTING POSITIVE FEEDBACK LOOPS TO NEGATIVE – In the past, domestic pets have been allowed to be kept by residents stationed in Cape Horn National Park. The fact that we found dogs and cats at many isolated outposts throughout the archipelago is significant. These introduced predators, for example, caused the extermination of Cape Horn Island's colony of Magellanic penguins (*Spheniscus magellanicus*). However more significantly, this impact may not be limited to one population, but rather could extend to an entire community and ecosystem via an intricate feedback system.

The presence of a penguin nesting colony means the accumulation of penguin feces, which in turn elevates levels of nitrogen in the soil. The tundra soils of Cape Horn are naturally nutrient poor, and it is only in these enriched, penguin-modified areas that the grass species *Poa flabellata* are able to exist (Pisano 1982). *P. flabellata* itself further changes soil characteristics and structure, such as organic content and depth, which in turn permits the establishment of Graminae tundra formations (Pisano 1982). The interrelation of these ecosystem components becomes even more complex when we consider that penguin nesting success is also a product of habitat quality, which includes vegetation cover and the height and density of grasses that protect eggs from predation, temperature extremes and wind (Gandini et al. 1997).

This natural positive feedback loop between penguin presence, Graminae vegetation patches and nesting success for the penguin itself in the Cape Horn Archipelago may become a negative feedback that prohibits the recolonization of the island if steps are not taken to remedy this exotic species impact in Cape Horn National Park. The introduction of an exotic species to Cape Horn Island has the potential to alter an entire biotic assemblage and ecosystem, which is consequently a major economic opportunity vis-à-vis ecotourism, and demands prompt action. These results together demonstrate the diverse reasons to better understand and more effectively manage the exotic species in Cape Horn County, Chile.

Conclusions

While Jaksic (1998) found that overall Chile hosts few exotic vertebrates (3.9% of the total), this general trend was not the case in the Cape Horn area, where we discovered seventeen introduced vertebrate species. As a total number, this non-native richness could appear rather minor, when compared to more heavily impacted parts of Chile and the rest of the world. However, when the comparison is made in relation to the quantity of native species richness, the proportional domination of exotic mammals and freshwater fish was striking, 55% and 75% respectively.

Most introduced species were found on human inhabited islands. Those that were associated with human perturbed areas also generally did not appear to greatly affect native populations and ecosystems away from human settlements. On the other hand, several important species did not have distributions closely tied to humans (e.g. beaver, muskrats and mink). Significantly, though, we did find a portion of Cape

Horn County that was still unimpacted by exotics. The unimpacted areas largely corresponded to the Cape Horn and Alberto D'Agostini National Parks, but our further finding that some species' ranges, such as the North American beaver, the mink and feral domestic predators, are increasing into the parks serves to underline the globalized threat of exotic species, even in remote areas, when management and control programs are lacking (Rozzi et al. 2004b and Anderson et al. 2005).

These results present us with lessons on how species become invasive and what their new role becomes within non-native ecosystems. Future work should expand on the information presented here to test the underlying ecological mechanisms for the distributions we have discovered. Finally, we hope that our findings serve to re-enforce the case that management and protection of this area is greatly needed. Care should be taken to prevent future introductions, and controlling the dispersal of those already present must be a priority for local and regional authorities.

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Table 2.1. Summary of introduced vertebrate fauna recorded for Cape Horn County, Chile with their mode of arrival and source of information. 1. Omora database 2. Canclini 1999, 3. Rozzi and Sherriffs 2003, 4. Sielfeld and Venegas 1980, 5. Sielfeld 1977. *indicates reliable fisherman report.

Introduced Vertebrate Species of Cape Horn County, Chile			
Order	***Scientific name***	**Common name**	**Source(s)**
MAMMALS			
Artiodactyla	*Sus scrofa*	Feral pig	1
	Bos tarus	Feral cow	1
Carnivora	*Canis lupus familiaris*	Feral dog	1, 2
	Felis domesticus	Feral cat	1
	Mustela vison	American mink	1, 3
	Pseudalopex griseus	Patagonian grey fox	1
Lagomorpha	*Oryctolagus cuniculus*	European rabbit	1
Perissodactyla	*Equus caballus*	Feral horse	1
Rodentia	*Castor canadensis*	North American beaver	1, 4, 5
	Ondatra zibethica	Muskrat	1, 5
	Mus musculus	House mouse	1
	Rattus norvegicus	Norway rat	1
FRESHWATER FISH			
Salmoniformes	*Salmo trutta*	Brown trout	1
	Oncorhynchus mykiss	Rainbow trout	1
	Salvelinus fontinalis	Brook trout	1*
BIRDS			
Paseriformes	*Passer domesticus*	House sparrow	1
Columbiformes	*Columba livia*	Rock pigeon	1

Table 2.2. Native and exotic mammals of Cape Horn County, Chile. TDF indicates Tierra del Fuego and the other names refer to islands in the archipelago. 1. Omora database, 2. Allen 1905, 3. Cabrera 1961, 4. Milne Edwards 1881, 5. Olrog 1950, 6. Patterson et al. 1984, 7. Peña and Barría 1972, 8. Reise and Venegas 1987, 9. Sielfeld 1977, 10. Sielfeld 1984, 11. Thomas 1916.

Mammals	**Native Species**		**Site**	**Exotic Species**		**Site**
Order	***Scientific name***	**Common name**		***Scientific name***	**Common name**	
Artiodactyla	*Lama guanicoe*	Guanaco	TDF & Navarino[1]	*Sus scrofa*	Feral pig	Navarino, Hoste & Gordon[1]
				Bos tarus	Feral cow	TDF & Navarino
Carnivora	*Lontra provocax*	Large river otter	TDF, Grevy, Picton, Lennox, Wollaston, Hermite[5], Grevy & Gordon[10]	*Canis lupus familiaris*	Feral dog	TDF, Navarino, Hoste & Horn[1]
	Lontra felina	Sea otter	TDF, Hoste, Grevy, Picton, Wollaston[1], Bayly, Hermite, Herschel[5], Grevy & Gordon[10]	*Felis domesticus*	Feral cat	Navarino & Horn[1]
	Pseudalopex culpaeus lycoides	Fuegian red fox	TDF & Hoste[5]	*Mustela vison*	American mink	Navarino, Hoste & Argentine TDF[1]
				Pseudalopex griseus	Grey fox	Yendegaia, TDF[1]
Lagomorpha				*Oryctolagus cuniculus*	European rabbit	Yendegaia, TDF & Navarino[1]
Perissodactyla				*Equus caballus*	Feral horse	TDF & Navarino[1]
Chiroptera	*Histiotus montanus*	Eared bat	TDF, Navarino[5,7] & Wollston[5]			
	Myotis chiloensis	Chiloé bat	TDF, Navarino[5,7] & Grevy[5]			
Rodentia	*Abrothrix xanthorhinus*	Yellow-nosed mouse	TDF, Navarino1 & Hoste[3,9]	*Castor canadensis*	North American beaver	TDF, Navarino, Hoste, Picton, Nueva & Lennox[1]
	Akodon hershkovitzi	Cape Horn mouse	Herschel, Hermite & Horn[1, 6]	*Ondatra zibethica*	Muskrat	TDF, Navarino, Hoste, Picton, Nueva & Lennox[1]
	Euneomys chinchilloides	Fuegian chinchilla mouse	TDF, Wollaston, Hermite & Hoste[1]	*Mus musculus*	House mouse	Puerto Williams, Navarino[1]
	Oligoryzomys longicaudatus	Long-tailed mouse	TDF[8], Wollaston[1], Hermite[3,11] & Hoste[4]	*Rattus norvegicus*	Norway rat	Puerto Williams, Navarino[1]
TOTAL	**10**			**12**		

Table 2.3. Native and exotic freshwater fish fauna found in Cape Horn County Chile. *G. maculatus* is the only native fish confirmed for the study area: 1 = Omora database, 2 = Jenyns (1842), 3 = Vila et al. (1999), *indicates species only cited for areas adjacent to Cape Horn County, Chile in the Argentine portion of Tierra del Fuego (Cussac et al. 2004). When not otherwise noted, sites are located on Navarino Island.

Freshwater Fish	**Native Species**		**Site(s)**	**Exotic Species**		**Site(s)**
Order	***Scientific name***	**Common name**		***Scientific name***	**Common name**	
Osmeriformes	*Galaxias maculatus*	Common galaxia	Navarino I.[1], Hardy Peninsula (Hoste I.)[2] & TDF[3]			
	*Galaxias platei**		Roca, Escondido, Fagnano, Yehuín & Margarita Lakes(Argentine TDF)			
	*Aplochiton taeniatus**		Argentine coast of Beagle Channel on TDF			
	*Aplochiton zebra**		Area near Fagnano Lake (Argentine TDF)			
Salmoniformes				*Salmo trutta*	Brown trout	Pilushejan, Mejillones, Windhond and Douglas Rivers[1]
				Oncorhynchus mykiss	Rainbow trout	Lum, Guanaco, Mejillones, and Róbalo Rivers[1]
				Salvelinus fontinalis	Brook trout	Navarino Lake
TOTAL	**1 (3*)**			**3**		

Appendix 2.1. Sampling for exotic vertebrates was conducted at forty sites on nineteen islands. Here we give the site name, island, coordinates, sampling regime and date surveyed for each study site.

Location	Island	Latitude & Longitude	Type of Sample	Date
Mount Horacio	**London**	54º40’28”S; 71º56’43”W	Transect	Jan and April 2004
Basket Cove	**Basket**	54º41’49”S, 71º35’51”W	Transect	April 2004
Courney Sound	**TDF**	54º37’12”S, 71º20’33”W	Transect	April 2004
Ventisquero Sound	**TDF**	54º46’54”S, 70º19’10”W	Transect	Jan 2004
Pía Sound	**TDF**	54º47’16”S; 69º37’23”W	Transect and mink trapping	Jan 2004 and May 2005
Italy Glacier	**TDF**	54º55’36”S, 69º14’02”W	Transect	April 2004
Olla Cove	**TDF**	54º56’29”S; 69º09’22”W	Transect and mink trapping	Jan 2004 and May 2005
Yendegaia Bay	**TDF**	54°50’S, 68°48’W	Transect, rodent and mink trapping	May 2005
Romanche Bay	**Gordon**	54º57’13”S; 69º29’37”W	Transect	Jan 2004 and May 2005
Group of islets off NE coast of Navarino	**Holger**		Transect	Jan 2004
Piedra Cove	**Picton**		Transect	Oct 2003
	Nueva		Helicopter flyover	May 2003
	Lennox		Helicopter flyover	May 2003
Navarino Lake	**Navarino**		Fishing	2004
Windhond River & Lake	**Navarino**		Transect, rodent trapping, fishing and mistnetting	Mar and Nov 2003
Omora Park, lower elevation areas	**Navarino**	54º57’S; 67º39’W	Transect, rodent and mink trapping, fishing and mistnetting	2000-2005
Omora Park, Bandera Mountain	**Navarino**		Transects, rodent trapping and mistnetting	2000-2005
Omora Park, Róbalo Lake	**Navarino**		Transect, rodent and mink trapping and mistnetting	2000-2005
Guerrico Bay and Hill	**Navarino**	54°54’43”S; 67°51’09”W 54º55’S; 67º54’W	Transect, rodent and mink trapping and mistnetting	2000-2005
Mejillones Bay and River	**Navarino**	54º57’S; 67º39’W	Transect, rodent and mink trapping, fishing and mistnetting	2000-2005
Lum River	**Navarino**		Fishing	2004
Pilushejan River	**Navarino**		Fishing	Mar 2002
Wulaia Bay	**Navarino**	55º03’S; 68º09’W	Transect, rodent trapping and mistnetting	2002 and Jan 2004
Puerto Inútil	**Navarino**	54º58’32”S; 68º12’49”W	Transect, rodent trapping and mistnetting	Jan 2000 and Jan 2004

Appendix 2.1, (cont.)

Douglas Bay	**Navarino**	55º10’28”S; 68º06’18”W	Transect, rodent trapping, fishing and mistnetting	Jan 2000 and Jan and May 2004
14th of July Bay	**Jemmy Button**	55º01’25”S; 68º13’45”W	Transect, rodent trapping and mistnetting	Jan 2004
Isla Grande Bay	**Hoste**		Transect	May 2004
Punta San Bernardo	**Hoste**	55º30’05”S, 68º04’15”W	Transect	May 2004
Misiones Cove	**Hoste**	55º31’18”S, 68º05’49”W	Transect	May 2004
Orange Bay	**Hoste**	55º31’18”S; 68º05’49”W	Transect, rodent trapping and mistnetting	Jan 2004
In Ponsonby Sound	**Mascart**		Transect	May 2004
In Ponsonby Sound	**Quemada**		Transect	May 2004
Kendall Cove	**Wollaston**	55º45’59”S; 67º25’04”W	Transect	Jan 2004
Lientur Cove	**Wollaston**		Transect	May 2004
Washington Channel	**Bayly**	55º40’39”S; 67º35’18”W	Transect	Jan 2004
Victoria Channel	**Bayly**		Transect	Jan 2004
Dillon Port	**Grevy**		Transect	Jan 2004
Martial Cove	**Herschel**	55º49’23”S; 67º18’01”W	Transect and rodent trapping	Jan 2004
Saint Martin Cove	**Hermite**		Transect and rodent trapping	Jan 2004
Maxwell Port	**Hermite**		Transect and rodent trapping	Jan 2004
SE Peninsula	**Cape Horn**	55º57’46”S; 66º13’29”W	Transect and rodent trapping	Jan and May 2004

Figure 2.1. Map of southern South America with inset of the area that includes the Southern Patagonian and Sub-Antarctic Ecoregions. South of the dashed line lies the biogeographic and administrative territory of Cape Horn County, Chile.

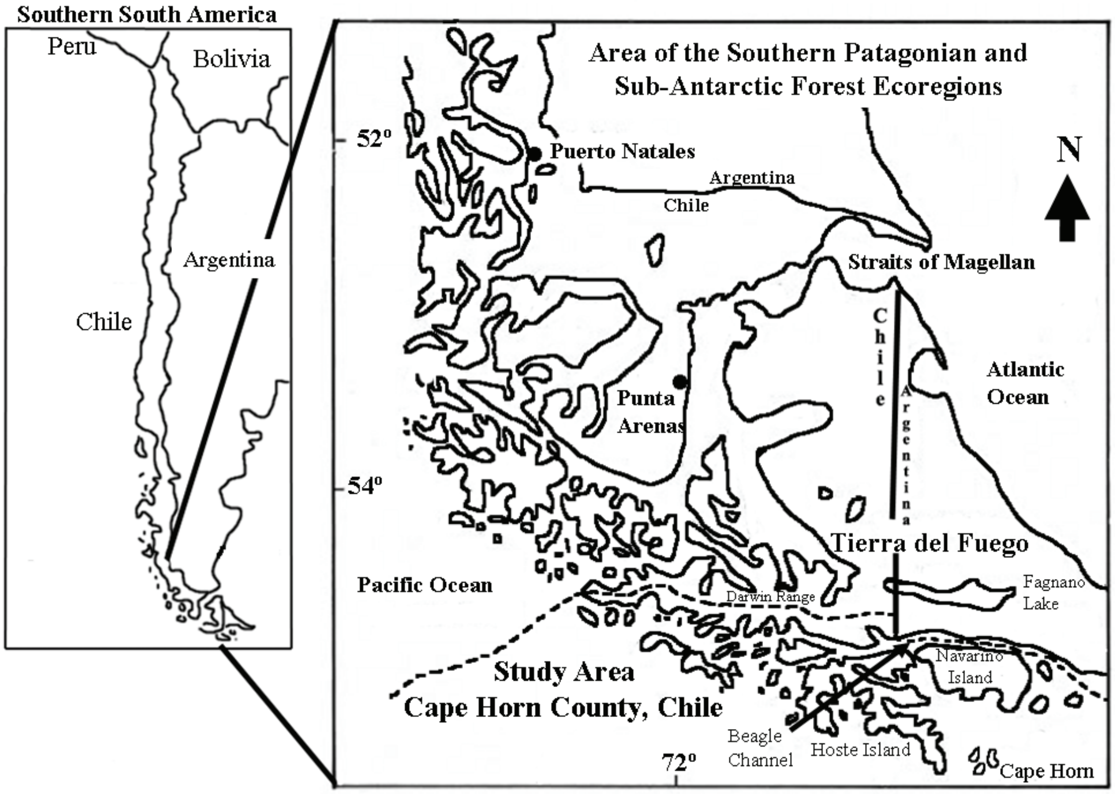

Southern South America
Peru
Bolivia
Argentina
Chile
Area of the Southern Patagonian and Sub-Antarctic Forest Ecoregions
52°
Puerto Natales
Argentina
Chile
N
Straits of Magellan
Chile
Argentina
Atlantic Ocean
Punta Arenas
54°
Tierra del Fuego
Pacific Ocean
Darwin Range
Fagnano Lake
Navarino Island
Study Area
Cape Horn County, Chile
Beagle Channel
Hoste Island
72°
Cape Horn

Figure 2.2. Distribution of American mink (*M. vison*) in Cape Horn County, Chile. The shaded portion shows the county's area. Black dots indicate confirmed mink presence.

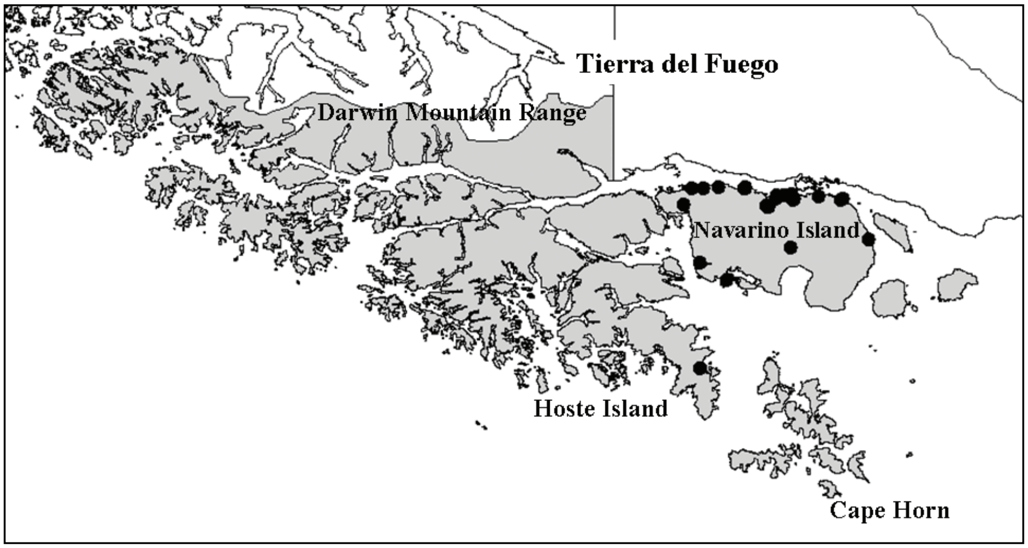
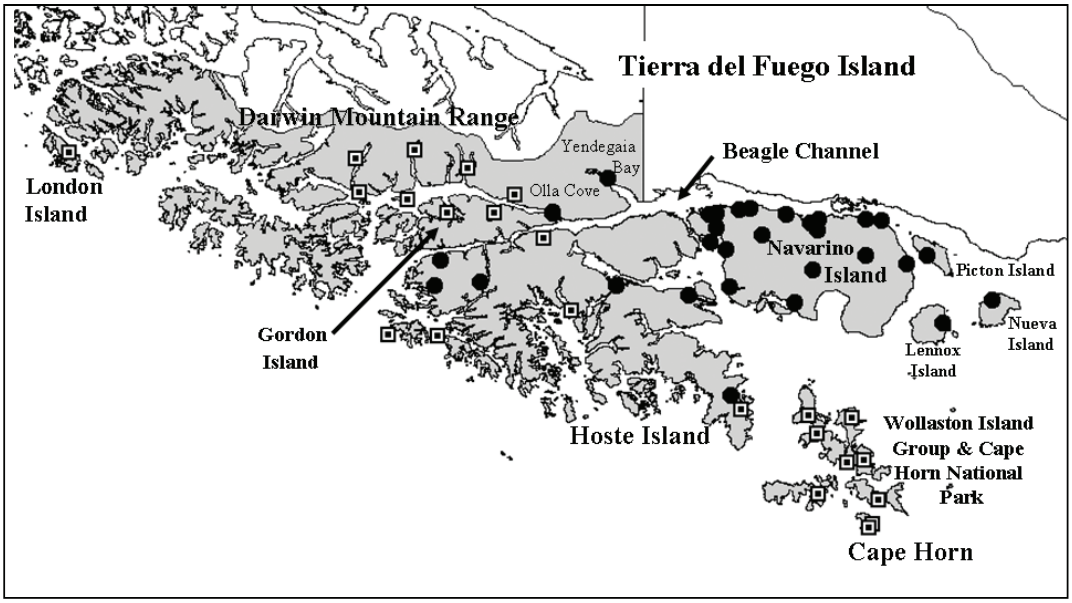

Tierra del Fuego
Darwin Mountain Range
Navarino Island
Hoste Island
Cape Horn

Figure 2.3. Distribution of beaver (*C. canadensis*) in Cape Horn County, Chile. The shaded portion shows the county's area. Black dots indicate confirmed beaver presence; white squares with black dots indicate their confirmed absence.


Tierra del Fuego Island
Darwin Mountain Range
Yendegaia Bay
Olla Cove
Beagle Channel
London Island
Navarino Island
Picton Island
Nueva Island
Lennox Island
Gordon Island
Hoste Island
Wollaston Island Group & Cape Horn National Park
Cape Horn

CHAPTER 3

THE EFFECTS OF INVASIVE NORTH AMERICAN BEAVERS ON RIPARIAN VEGETATION COMMUNITIES IN CAPE HORN, CHILE: DO EXOTIC BEAVERS ENGINEER DIFFERENTLY IN SUB-ANTARCTIC ECOSYSTEMS?[1]

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[1] Anderson, C. B., C. R. Griffith, A. D. Rosemond, R. Rozzi and O. Dollenz. 2006. *Biological Conservation* 128: 467-474. Reprinted here with permission of publisher.

Abstract

Exotic species and their impacts constitute a principal component of global ecological change. A critical question for conservation biology, then, is to define the effects of a species as an exotic, compared to its role in native ecosystems. Even seemingly remote areas do not escape this world-wide invasion phenomenon. For example, North American beavers (*Castor canadensis*) were introduced to southern South America in 1946. Among many other effects, beavers engineer native riparian ecosystems by selectively feeding on particular species, increasing herbaceous richness and creating a distinct plant community. To test their effects as exotic species on sub-Antarctic riparian vegetation, we quantified beaver impacts on tree canopy cover and seedling abundance and composition and herbaceous species richness, abundance and composition on Navarino Island, Cape Horn County, Chile (55ºS). Beavers significantly reduced forest canopy to 30 m away from streams. They nearly eliminated the seedling bank and changed its composition by suppressing *Nothofagus betuloides* and *N. pumilio*, but favoring *N. antarctica*. Herbaceous richness and abundance almost doubled in meadows, due in part to a significant increase in exotic plants. Beaver modifications of meadows, however, did not result in a significantly different community, compared to forests, and 42% of species were shared between both habitat types. Our results indicate that, as predicted from North American studies, beaver-engineering did increase local species richness. However, unlike in their native range, they did not create a unique plant community in this landscape, perhaps since bogs (and thus bog-adapted species) are a natural feature and because beavers do not share a common evolutionary history with these species. Plus, virtual elimination of forests and their seedling bank, which contrasted with expectations from North America, and the creation of invasion pathways for exotic plants together threaten one of the world's most pristine temperate forest ecosystems.

Key Words: *Castor canadensis*, diversity, invasive, global change, *Nothofagus,* pristine, sub-Antarctic, wilderness

Introduction

Exotic species are a primary cause of global ecological change, their effects compounding with habitat and climate alterations (Vitousek et al. 1996). However, not all introduced species have large impacts on ecosystems or their biota. In fact, the majority of introductions fail to become permanently established (Lodge 1993). Therefore, predicting which species will have ecosystem-level impacts requires understanding the mechanisms of invasion and linking species with their ecosystem-level consequences (Jones & Lawton 1994, Courchamp et al. 2002).

In southern Chile's Cape Horn County, which includes the archipelago south of Tierra del Fuego Island, terrestrial mammals and freshwater fish assemblages are dominated by exotics. Greater than 50% of taxa in these groups are introduced (Anderson 2004). One species in particular has received a great deal of attention from scientists, wildlife managers and political authorities: the North American beaver (*Castor canadensis* Kuhl). Beavers were brought to the Argentine portion of Tierra del Fuego Island near Fagnano Lake in 1946 as part of a government effort to economically "enhance" the species-poor Fuegian landscape by introducing exotic furbearers, including beavers, muskrats and minks. Twenty-five mating pairs of *C. canadensis* were released initially. By the 1950s, they had entered into the Chilean portion of the island, and by the 1960s they had succeeded in crossing channels to the adjacent Chilean archipelago, including Navarino and Hoste Islands (Sielfeld & Venegas 1980) (Figure 3.1). Beaver densities rapidly increased to high levels, compared to other reported values in North America (Gurnell 1998), and they now inhabit nearly every available watershed on most of these islands (Sielfeld & Venegas 1980, Lizarralde 1993, Skewes & Olave 1999), except the far southern and western portions of the archipelago (Anderson 2004).

An understanding of the ecological context and natural history of sub-Antarctic broad-leafed *Nothofagus* (Fagaceae) forests is important to predict the effects of beavers in this non-native ecosystem. *Nothofagus* forests on the islands near Cape Horn are embedded is a complex mosaic of habitats that includes several bog types, such as *Sphagnum* peatlands, cushion bogs and rush wetlands (Rozzi et al. 2004*a*). In addition, the forested portions have relatively low native flora and fauna diversity, compared to similar latitudes in the Northern Hemisphere. Many islands completely lack terrestrial mammalian predators (Venegas & Sielfeld 1998), and the regional plant assemblage is very simple (Moore 1983, Martínez-Pastur et al. 2002). In the absence of a common evolutionary history with beaver, *Nothofagus* trees lack the types of defensive mechanisms and reproductive strategies (Rebertus & Veblen 1993 and Cuevas & Arroyo 1999) that we find in North American forests to deal with the impacts caused by beaver foraging and flooding (Basey et al. 1988, Johnston & Naiman 1990). Finally, a more diverse riparian assemblage in North America includes taxa such as conifers, which are not part of the sub-Antarctic assemblage and that are avoided by beaver simply due to their lower nutritional quality and palatability (Jenkins 1980, Johnston & Naiman 1990).

Therefore, beaver herbivory and wetland creation in North America promotes the persistence of an unpalatable stand of riparian trees that remains and regenerates (Naiman et al. 1988 and Müller-Schwarze et al. 1994) and creates a more complex and diverse habitat and herbaceous species assemblage (Pollock et al. 1998 and Wright et al. 2002). In sharp contrast, the forests of the Cape Horn area have only three major tree species, all in the genus *Nothofagus*, which are broad-leafed trees that beavers forage equally (Sielfeld & Venegas 1980). These forests naturally regenerate from sapling banks in a gap dynamic, since seed banks do not persist for long periods in these soils and vegetative reproduction is rare (Cuevas & Arroyo 1999). Also *Nothofagus* forests in general have problems regenerating when under a systematic or permanent disturbance, making them extremely vulnerable to persistent herbivory (Rebertus & Veblen 1993), and only one species (*N. antarctica*) is adapted for boggy soil conditions (Ramírez et al. 1985). Such profound differences in the natural history of sub-Antarctic *Nothofagus* forests leads to the questions: do beavers engineer differently in sub-Antarctic riparian forests and if so, will these differences have implications for the conservation of one of the world's largest and most pristine temperate forests (Mittermeier et al. 2001)?

Here, we first wanted to determine the effect of beavers on riparian forests to see whether tree species would remain or regenerate, either by selective feeding or beaver-adapted defensive and reproductive strategies, as has been seen in North America (Naiman et al. 1988). We also wished to test the hypothesis that beaver activities in this introduced ecosystem would increase riparian plant species richness and diversity and create beaver-specific community assemblages, as expected from studies conducted in its native range (Pollock et al. 1998, Wright et al. 2002, Wright & Jones 2004). Therefore, we compared the impact of *C. canadensis* on canopy cover, tree seedling establishment and herbaceous layer richness, diversity, composition, abundance and similarity in riparian habitats with and without beavers (primary forested stream reaches and beaver-created meadows). The lack of beaver predators and competitors, combined with differences in the regional species pool, defenses, palatability and reproduction for this "naïve" vegetation, led us to predict that the forests will not persist or regrow in beaver-modified areas. Herbaceous species abundance and richness should increase, though, due to the removal of trees and the creation of disturbed areas. However, rather than creating a patchy mosaic, the beaver engineering could decrease overall habitat diversity in the sub-Antarctic ecosystem by eliminating riparian forests. Furthermore, we did not expect to find a beaver-specific meadow vegetation community, since these species lack a common evolutionary history with beaver, and bogs constitute a naturally occurring feature of the landscape. Overall, therefore, we anticipate that beaver impacts will be fundamentally different in sub-Antarctic ecosystems and present specific conservation implications for the region.

Materials and Methods

Study Site Description

This study was carried out on Navarino Island (2,528 km^2) (Figure 3.1), near the town of Puerto Williams, Chile, located south of the Beagle Channel between Tierra del Fuego Island and Cape Horn National Park (approx. 55°S). Cape Horn County, Chile is South

America's (and the world's) southernmost political unit and hosts the world's southernmost forested ecosystems (for a detailed description see Rozzi et al. 2004*a*). These forests are dominated by three broad-leafed species of the genus *Nothofagus* (Pisano 1977). Two of the species are deciduous (*N. pumilio* and *N. antarctica*) and one is evergreen (*N. betuloides*). The natural forest understory has low species richness as well (Moore 1983), but habitat diversity is high, composed of a heterogeneous mosaic of ecosystems compacted over an abrupt topography and complex geography (Pisano 1977 and Rozzi et al. 2004*a*).

Four streams from different watersheds, which were representative of predominantly forested catchments, were chosen for study along 35 km of the north coast of the island. They ranged from 0.5 km to 2 km in distance from the coast and all were below 250 m elevation. In each watershed, two study reaches of at least 100 m were chosen that represented: (1) a natural, primary forest stream with no history of beaver impact either in the stream or in the riparian zone; and (2) a beaver-created meadow along a reach that was previously forested before the beaver's arrival. The study meadows were habitats made by abandoned beaver dams that were less than five years old, which was determined by personal observation. Field work was carried out from February to March 2003 and April 2004, the austral summer months.

Field Methods

To quantify the effect of beaver on tree canopy cover as a function of distance from the stream, ten 1x50 m transects set 10 m apart were run perpendicularly to the stream edge at each study reach. Canopy cover was recorded with a spherical densiometer at 10 m intervals along each transect and averaged for each study stream. Twenty 0.5 m^2 plots also were used per habitat type per stream to survey vegetation in the herbaceous layer (plants < 1 m in height). Plots were surveyed at 10 m intervals along the stream edge of study reaches. Within each plot, herbaceous species were identified and relative percent coverage was estimated. Tree seedlings less than 10 cm tall also were counted and identified in each plot in order to determine the quantity and type of regeneration of forest species in these two different sites. Most specimens were determined to genus and species in the field or placed in a herbarium and returned to the Universidad de Magallanes for later identification using Moore (1983).

Analysis

To analyze the beavers' impacts on the riparian vegetation community, we compared canopy cover, total and per plot species richness, Shannon-Weiner diversity, Morisita-Horn similarity (calculated using EstimateS, Colwell 2004) and *Nothofagus* seedling abundance and composition at primary riparian forest sites and beaver-created meadows. In addition, we quantified the percentage of survey plots containing exotic species and the percent coverage of plant categories (monocots, forbs, bushes, trees, bryophytes and exposed soil/leaf litter) to demonstrate the relative contribution of different groups to community composition.

Using JMP version 5.0.1 (SAS Institute Inc. 1994) significant differences were tested between forest and meadow sites with Student's *t-Test* (richness, diversity and regeneration), a two-way ANOVA with a Tukey-Kramer test for significance (percentage canopy cover as a function of distance from the stream at meadow and forest sites), and a one-way ANOVA with a Tukey-Kramer test for significance (similarity indices between and within habitat types). Community similarity was also visualized with PCOrd version 2.0, using a non-metric multidimensional scaling approach (McCune & Grace 2002).

Results

Riparian Forest Removal and Regrowth

Beavers significantly reduced tree canopy cover to 30 m away from the stream edge in meadow areas (habitat*distance F=57.02, df=5, P<0.0001 with Tukey-Kramer test P<0.05) (Figure 3.2). As a result, beaver foraging converted riparian zones from forested to meadow habitats. The regeneration of the riparian forest likewise was affected by beaver activities. *Nothofagus* seedling abundance in natural riparian forests was significantly greater [7.36 ±2.52 seedlings per plot (mean ± se)] than in meadows, where seedlings were nearly eliminated (0.91 ±0.17 seedlings per plots; *t-Test*=2.55, df=6, P=0.04) (Figure 3.3).

The species composition of the seedling bank was influenced, as well. Natural riparian forests contained exclusively *Nothofagus pumilio* (3.71 ±1.11 per plot) and *N. betuloides* (3.65 ±1.48 per plot) seedlings in the understory. The average number of seedlings for both species was significantly reduced in beaver meadows to near zero (*N. betuloides* = 0.08 ±0.06 and *N. pumilio* = 0.6 ±0.2; *t-Test*=2.791, df=6, P=0.03 and *t-Test*=2.41, df=6, P=0.05, respectively). On the other hand, beaver-impacted riparian zones were the exclusive site of *N. antarctica* seedling establishment, but this was also a very small number (mean seedlings per plot 0.28 ±0.08) (Figure 3.3). Beaver meadows overall had very few *Nothofagus* seedlings, and we observed an assemblage shift from *N. pumilio-N. betuloides* to *N. pumilio-N. antarctica*.

Riparian Vegetation Community Characteristics

Meadows had significantly greater plant species richness and diversity than natural forests. A total of sixty-seven plant taxa were identified in the herbaceous layer for all riparian study sites (Table 3.1). In beaver meadows sixty-three species were found (94% of all surveyed riparian species). Only twenty-eight species (41% of the total riparian assemblage) inhabited forested riparian zones. Herbaceous species richness per survey plot significantly increased in meadows, when compared to forested sites, by nearly doubling from an average of 3.6 ±0.66 species per plot in natural areas to 6.94 ±0.89 in meadows (*t-Test*=-2.99, *df*=6, *P*<0.02; Figure 3.4). The overall diversity calculated for each habitat showed the same result with significantly higher diversity in meadows (H′= 2.42 ±0.07 SD) than forests (H′= 1.89 ±0.16 SD) (*t-Test*=-3.15, *df*=6, *P*=0.02).

The meadows also had a more abundant herbaceous layer with an average of 86.5% total plant coverage per plot, while only 32.2% was recorded in forested sites. The remaining 13.5% and 67.8%, respectively for meadows and forests, was bare ground and leaf litter (Figure 3.5). Meadows specifically were covered by forbs (49.1%), exotics (16%) and native grasses/monocots (14.1%), while forested sites' coverage was dominated by forbs (20.5%), mosses and liverworts (bryophytes: 4.8%), and young shrubs (4.4%) and trees (1.8%) (Figure 3.5).

The comparison of community similarity between the two habitat types (forest-meadow) was not significantly different from comparisons made within habitat types (forest-forest, meadow-meadow) ($F_{2, 25}$=2.064, P=0.14) (Figure 3.6), meaning that beaver-engineered assemblages were not significantly different than naturally occurring communities. The trend in these data showed that forest-forest habitat comparisons were heterogeneous, and that natural riparian zone community composition was variable at the 0.5 m^2 scale. Furthermore, analysis of meadow and forest assemblages revealed substantial overlap between the two habitats (Figure 3.7). Forty-two percent of the total community assemblage was shared between both habitat types. Only four species (or 5.9%) were unique to forested riparian zones. The four forest-obligate species were the perennial herbs *Lagenophora hariotii* (Asteraceae), *Luzula alopecuerius* (Juncaceae), *Macrachaenium gracile* (Compositae) and *Senecio acanthifolius* (Compositae). Those species only found in meadows tended to be grasses, exotic species and the tree *Nothofagus antarctica* (Table 3.1).

Exotic Riparian Plants

We also observed an increase in exotic plant species richness and abundance in beaver meadows, compared to forests. Ten exotic plant species inhabited meadow habitats, but only one species was found in natural, forested riparian zones (Table 3.1). The richness per sample area of exotic plants was significantly greater in meadows as well (*t-Test*=-3.31, *df*=6, *P*=0.02), ranging from an average of 0.03 ±0.01 exotic species per plot in forests to 0.66 ±0.2 in meadow plots. Additionally, introduced species occurred more frequently in meadows. For example, more than half of the eighty beaver meadow survey plots contained at least one exotic species (Table 3.2). Dandelion (*Taraxacum officinale* [Compositae]) and the grass *Cerasticum fontanum* (Caryophyllaceae) were the two most common exotic plants in the herbaceous layer, occurring in 31.3% and 28.8% of meadow plots, respectively (Table 3.2). The remaining introduced species were found in 10% or fewer plots. The forested area only hosted *C. fontanum*, and it was found in just two plots at one stream (2.5% of total).

Discussion

Introduced species are a major constituent of global ecological change. Therefore, quantifying their effects is an especially pressing area of ecological research and management policy. The introduction of North American beavers to southern South America provides a special opportunity to study their role as exotic ecosystem engineers on a relatively simple ecosystem. In this way, the islands of the Cape Horn Archipelago offer a valuable natural laboratory to conduct research on biological invasions and their consequences. In particular, the abundant research done in the native habitat of the beaver provides the context to meaningfully compare its role as both a native and exotic species.

We found that beaver foraging and the creation of meadows in the Cape Horn area did not result in a modified, but persistent riparian forest that regenerates after herbivory, as has been noted in North America (Naiman et al. 1988). Rather, our results indicated a potentially long-term elimination of trees, thus creating an alternative stable state for riparian forests. Considering the *Nothofagus* individuals that did persist, seedlings and adults of the evergreen broadleaf *N. betuloides* were virtually non-existent in meadow riparian sites. In contrast, meadows were the only place that we found the deciduous *N. antarctica*, which otherwise inhabits natural bogs and extreme areas, such as tree line (Moore 1983). Even if forest successional response to beaver in certain places eventually were to produce a new stand of riparian trees, the consequences of such a species assemblage change in the riparian zone would have implications for terrestrial-aquatic linkages via impacts on stream shading and annual leaf litter inputs.

In addition to impacting riparian forests, beavers facilitated the establishment of exotic plant species by creating disturbed streamside corridors. On Navarino Island and in much of the Cape Horn Archipelago, human disturbance is localized around coastal settlements (Rozzi et al. 2004*a* and Rozzi et al. 2004*b*). Consequently, exotic plants associated with livestock and humans, such as grasses, daisies and dandelions, are generally confined to such areas. The beaver-created habitats along these river basins, therefore, are providing early successional, disturbed avenues for the introduction of weedy plant species into the interior of the island and up forested catchments away from the coast. Comparative studies in the United States showed little or no significant increase in exotic species associated with beaver meadows and ponds (Feldman 1995 and McMaster & McMaster 2000). The beaver engineering activities in sub-Antarctic riparian forests appear to be facilitating the establishment and spread of exotics, thereby threatening the region's still highly pristine ecosystems and native biodiversity (Rozzi et al. 2004*b*).

Our findings that beaver-created habitats increased species richness and abundance only at the habitat scale contrasts with results in the beaver's native range. Wright et al. (2002) reported that beaver activity in the Adirondack Mountains (New York, USA) led to greater plant species richness only at the landscape scale. They showed that on the habitat-scale beavers had no richness effect, but across the landscape they increased the number of species, since very few taxa were shared between natural forests and beaver-engineered plant communities in meadows and alder wetlands. They further found that within the same habitat-type, plant community similarity was high, but the comparison between forested sites and beaver-impacted areas showed significantly different assemblages. In their study, only 17% of 125 species were shared between the two habitats' assemblages and consequently the Morisita-Horn similarity value between beaver impacted and natural plant communities was <0.1 (Wright et al. 2002). In this North American example, the change in plant species composition in beaver-engineered sites led to the conclusion that the beaver wetlands and meadows increased the gamma diversity of plants for the region by creating unique ecological landscape units.

In the Cape Horn Archipelago, we also observed changes in plant richness and abundance between forests and meadows, but while assemblage changes indeed were found, they were not significantly different. These findings are corroborated by another study of beaver impacts on Tierra del Fuego Island with a wider range of meadow ages (0-20 years) that discovered the forested and beaver-impacted habitats shared 73% of their plant species (Lencinas et al. 2001). Here, we found 42% of the species were the same between forest and relatively new beaver meadows. Thus, on a broader scale, our results indicate that beavers do not increase regional diversity or landscape heterogeneity on these sub-Antarctic islands. The ecological context of this area includes a diverse mosaic of bog and forest habitats under natural conditions prior to beaver invasion, which would further signify that the beaver meadows do not represent a unique ecological formation in this area.

Finally, the above conclusions together with preliminary data from the Robalo River watershed show that these impacts are neither patchy, nor localized and could seriously threaten riparian forest conservation. Of the thirty-four km of stream channel in the Robalo drainage network, ranging from sea-level to above tree line, beavers modified the riparian habitat of 40% of the total channel length (M. Cienek-Moorman & C.B. Anderson, unpublished data). Areas free of disturbance were mainly small tributaries in the high alpine zone above tree line, and the forests that remained unimpacted were high gradient slopes, where the river's power was too great for dam construction.

In conclusion, our comparison of riparian plant communities in the Cape Horn area of Chile with studies in North America has shown that the impacts of *C. canadensis* were superficially similar. In both cases, beavers converted forests to early successional gaps and changed plant assemblages to include more species and a more abundant herbaceous layer. However, we also found that beaver activities in Cape Horn are causing long-term alterations by significantly suppressing forest regeneration, which may not permit the re-establishment of *Nothofagus* riparian forests. Additionally, the sub-Antarctic ecosystem appears to be vulnerable to the invasion of introduced plant species with the beaver facilitating the establishment and expansion of exotic plant taxa in an ecosystem that is otherwise largely undisturbed. We did not find that plant communities in beaver habitats were unique assemblages in the sub-Antarctic landscape, and in fact the extensiveness of beaver impacts could homogenize the natural forest-bog mosaic of habitats due to its extensive distribution across the archipelago. Understanding the role of introduced beavers in creating an alternative stable state for riparian ecosystems, therefore, is extremely important for the management and conservation of the Cape Horn

Archipelago, identified as one of the world's largest and most pristine remaining wilderness areas (Mittermeier et al. 2001).

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Table 3.1. Total plant species list for both forested (F) and beaver-impacted riparian zones (M). The last column indicates whether the species is exotic.

Species name	**Forest**	**Meadow**	**Exotic**
Acaena magellanica (Lam.) Vahl	F	M	
Adenocaulon chilense Poepp. ex Less.	F	M	
Agrostis capillaris L.		M	E
Agrostis sp.		M	
Alopecurus magellanicus Lam.		M	
Bellis perennis L.		M	E
Berberis buxifolia Lam.	F	M	
Berberis ilicifolia L.f.	F	M	
Blechnum penna-marina (Poiret) Kuhn	F	M	
Carex banksii Boott		M	
Carex curta Gooden		M	
Carex sp.		M	
Cerastium fontanum Baumg.	F	M	E
Cerastium arvense L.		M	
Chiliotrichum diffusum (Forster f.) O. Kuntze	F	M	
Codonorchis lessonii (D'Urv.) Lindley	F	M	
Cotula scariosa Franch.		M	
Deschampsia antarctica Desv.		M	
Deschampsia kingii (Hooker f.) Desv.		M	
Deschampsia sp.		M	
Dysopsis glechomoides (A. Richard) Muller Arg.	F	M	
Empetrum rubrum Vahl.	F	M	
Epilobium australe Poeppig & Hausskn. ex. Hausskn.		M	
Festuca magellanica Lam.		M	
Festuca sp.		M	
Galium aparine L.		M	
Gamochaeta spiciformis (Sch. Bip) Cabrera		M	
Gaultheria pumila (L. f.) Middleton	F	M	
Gunnera magellanica Lam.	F	M	
Juncus scheuchzerioides Gaudich		M	
Koeleria fueguina Calderón		M	
Lagenophora hariotii Franch.	F		
Luzula alopecurus Desv.	F		
Lycopodium magellanicum (P. Beav.) Swartz		M	
Lichens	F	M	
Liverworts	F	M	
Macrachaenium gracile Hooker f.	F		
Maytenus disticha (Hooker f.) Urban	F	M	

Table 3.1. (cont.)

Mosses	F	M	
Mushrooms	F	M	
Nothofagus antarctica (Forster f.) Oersted		M	
Nothofagus betuloides (Mirbel) Oersted	F	M	
Nothofagus pumilio (Poeppig & Endl.) Krasser	F	M	
Osmorhiza chilensis Hooker & Arn.	F	M	
Pernettya mucronata Gaud.	F	M	
Phleum alpinum L.		M	
Poa fuegiana (Hooker f.) Hackel ex Dusén		M	
Poa pratensis L.		M	E
Poa sp.		M	
Poa trivialis L.		M	E
Primula magellanica Lehm.		M	
Ribes magellanicum Poiret		M	
Rubus geoides Sm.	F	M	
Rumex acetosella L.		M	E
Sagina procumbens L.		M	E
Senecio acanthifolius Hombron & Jacquinot	F		
Senecio sp.		M	
Spergularia marina (L.) Griseb.		M	E
Taraxacum officinale Weber		M	E
Trisetum lechleri (Steud.) Nicora		M	
Trisetum spicatum (L.) K. Richter		M	
Trifolium dubium Sibthorp		M	E
Uncinia lechleriana Steudel		M	
Uncinia sp.		M	
Veronica sp.		M	
Viola magellanica Forster f.	F	M	
Viola sp.	F	M	
TOTAL = 67	**28**	**63**	**10**

Table 3.2. The percentage of survey plots containing exotic plants for each habitat-type. A total of ten exotic plant species were recorded in the forested and beaver meadow riparian zones. All ten were found in meadows, while only one was in forested areas.

Exotic species	**% of Meadow Plots**	**% of Forest Plots**
Agrostis capillaris L.	5	
Bellis perennis L.	5	
Cerastium fontanum Baumg.	28.8	2.5
Poa pratensis L.	10	
Poa trivialis L.	1.3	
Rumex acetosella L.	2.5	
Sagina procumbens L.	1.3	
Spergularia marina (L.) Griseb.	3.8	
Taraxacum officinale Weber	31.3	
Trifolium dubium Sibthorp	1.3	
Total	**53.8%**	**2.5%**

Figure 3.1. Map of southern South America. Dashed line delimits Cape Horn County, Chile, which also corresponds to the sub-Antarctic archipelago area. Study sites on the north coast of Navarino Island are indicated with an arrow.

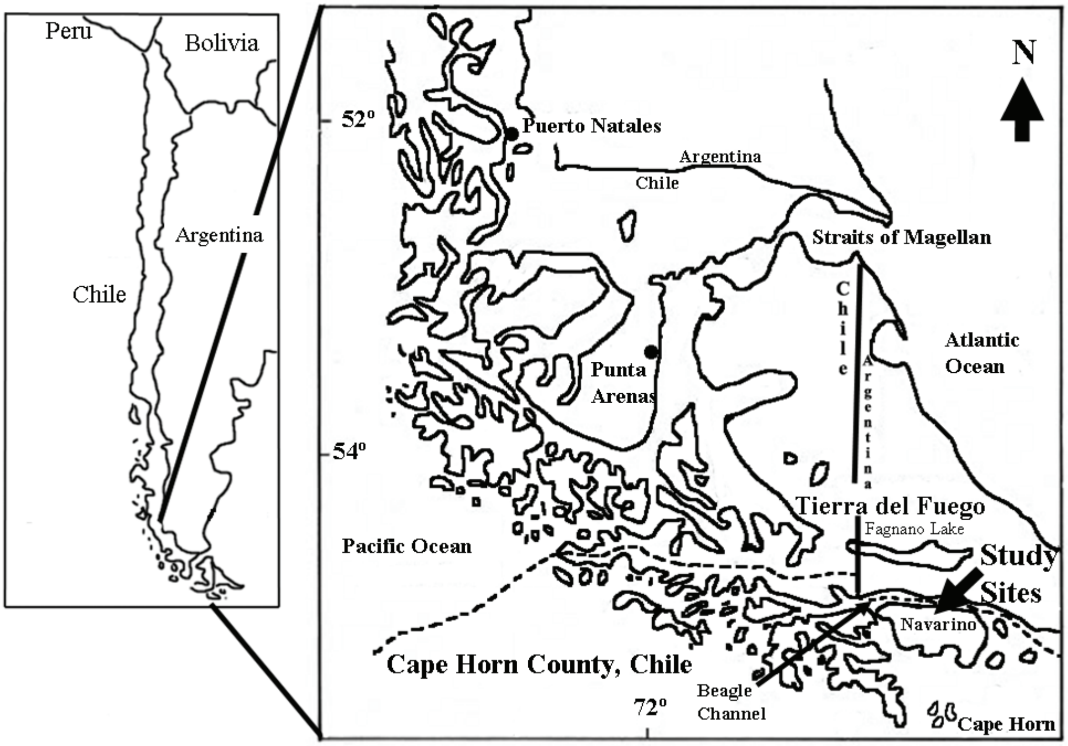

Peru
Bolivia
Argentina
Chile
N
52°
Puerto Natales
Argentina
Chile
Straits of Magellan
Chile
Argentina
Atlantic Ocean
Punta Arenas
54°
Tierra del Fuego
Fagnano Lake
Pacific Ocean
Study Sites
Navarino
Cape Horn County, Chile
Beagle Channel
72°
Cape Horn

Figure 3.2. Canopy cover as a function of distance from the stream and habitat-type. Average percent coverage (± 1 SE) is significantly reduced by beaver foraging to a distance of 30 m away from stream edge (*P*<0.001; asterisks (*) indicate results in beaver-impacted habitat are significantly different from natural sites Tukey-Kramer *P*<0.05). Grey shaded bars designate natural, forested reaches and open, white bars denote beaver meadow sites.

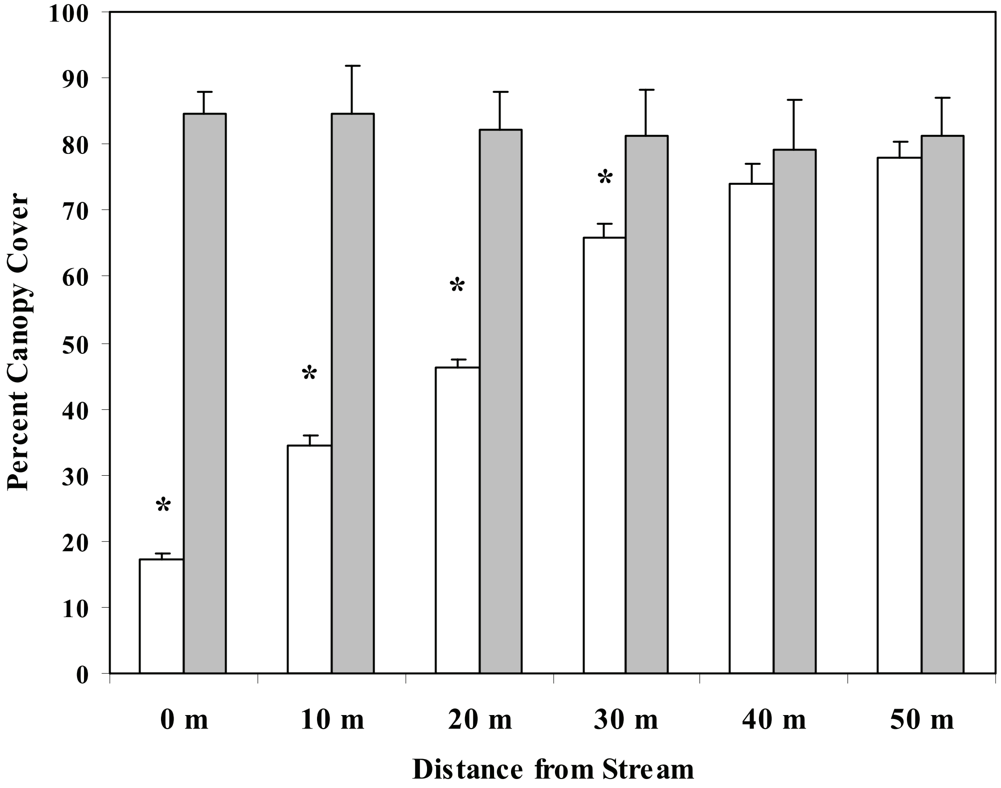

100
90
80
70
60
50
40
30
20
10
0
Percent Canopy Cover
*
*
*
*
0 m
10 m
20 m
30 m
40 m
50 m
Distance from Stream

Figure 3.3. Mean *Nothofagus* seedlings per plot in natural and beaver impacted sites. Beaver meadows showed an overall decrease in the regeneration of *Nothofagus* seedlings (*P*=0.04). A large impact was found on *N. betuloides*, which is virtually eliminated in meadows (*P*=0.05). *N. antarctica*, however, demonstrated an opposite trend, only establishing itself (but in very low numbers) in the riparian area after beaver meadows removed the natural forests.

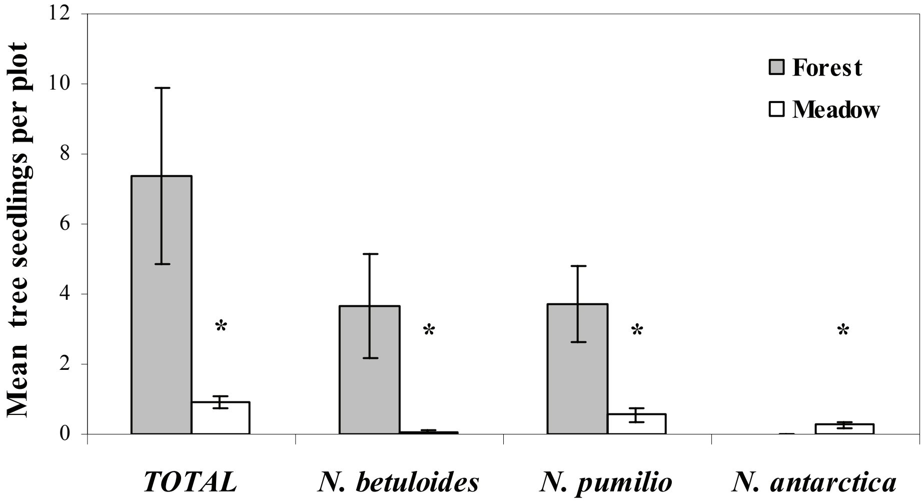

Mean tree seedlings per plot
0
2
4
6
8
10
12
Forest
Meadow
*
*
*
*
TOTAL
N. betuloides
N. pumilio
N. antarctica

Figure 3.4. Herbaceous layer plant species richness in natural and beaver-impacted sites. Average species richness per plot was significantly greater in beaver meadow riparian sites than forested reaches (*P*=0.02). In addition, the number of exotic plants per plot increased in meadows (*P*=0.01). Shading indicates the contribution of exotic species to average richness per habitat type (± 1 SE).

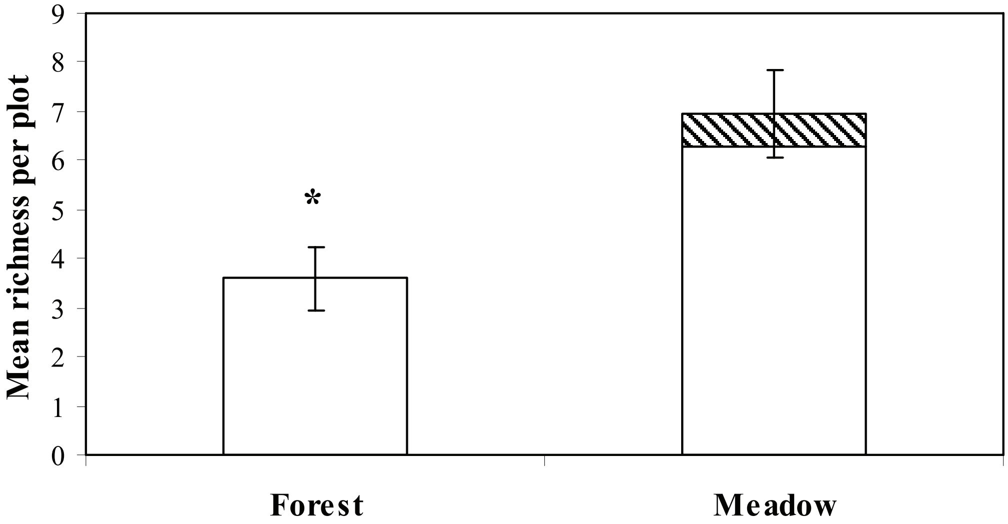
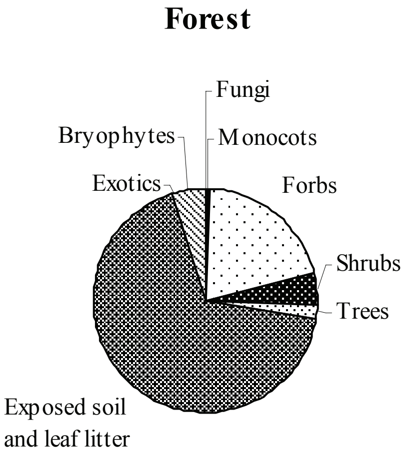

Mean richness per plot
0
1
2
3
4
5
6
7
8
9
*
Forest
Meadow

Figure 3.5. Average percent coverage of different plant types in the herbaceous layer of forests and beaver meadows. The natural forest floor is covered primarily with leaf litter, bryophytes and woody plant seedlings, while meadows are dominated by forbs, monocots (mostly grasses) and exotic species.


Forest
Fungi
Bryophytes
Monocots
Exotics
Forbs
Shrubs
Trees
Exposed soil and leaf litter

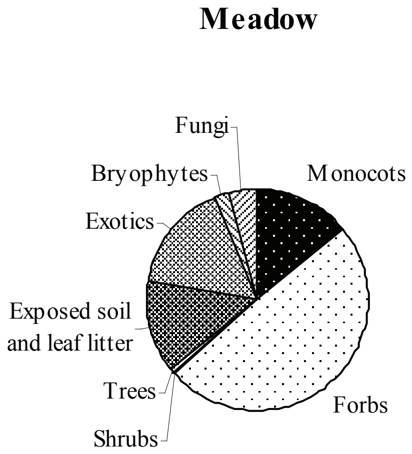

Meadow
Fungi
Bryophytes
Monocots
Exotics
Exposed soil and leaf litter
Trees
Shrubs
Forbs

Figure 3.6. Similarity of riparian plant assemblages in natural and beaver-impacted riparian sites. Average Morisita-Horn Indices (± 1 SE) show no significant differences between community similarity of habitats comparison combinations (forest-forest, meadow-meadow and forest-meadow) (*P*=0.14).

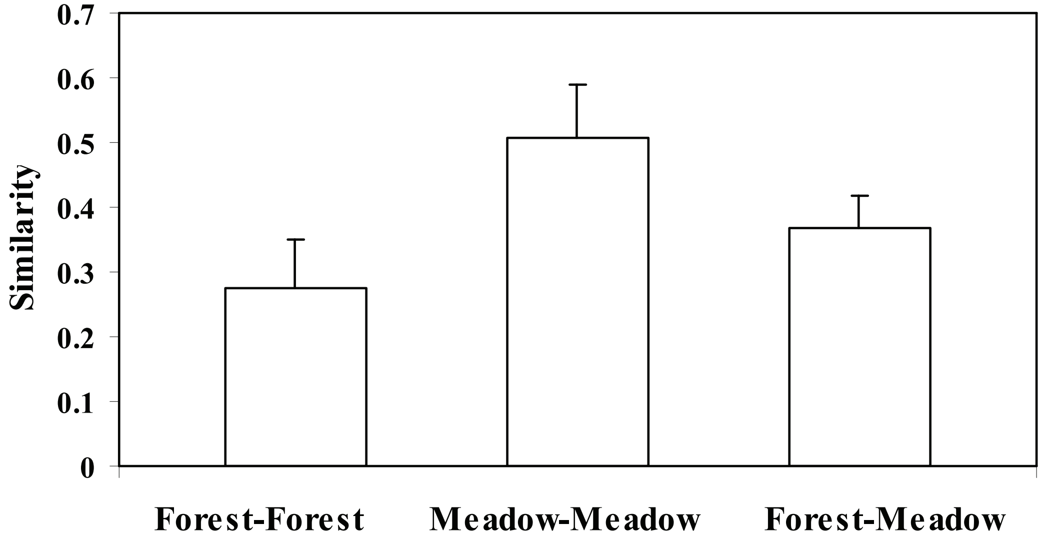
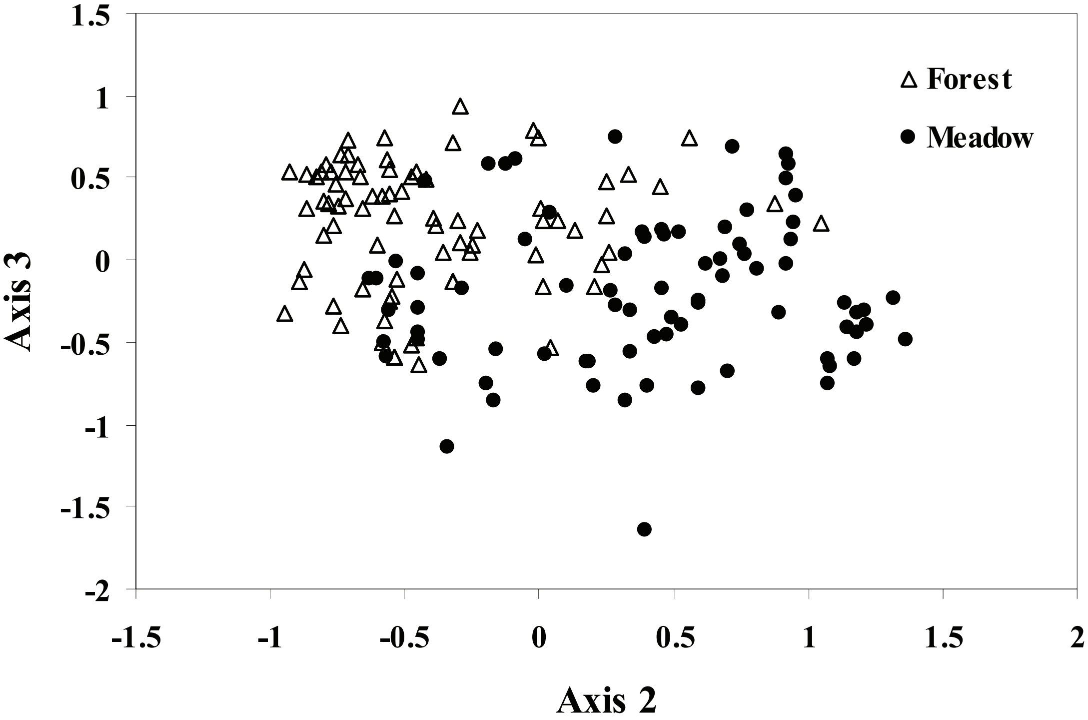

0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Similarity
Forest-Forest
Meadow-Meadow
Forest-Meadow

Figure 3.7. Non-metric multidimensional scaling of survey plots from forested and beaver-impacted riparian zones. The similarity between riparian plant assemblages in natural and beaver-impacted sites is shown by the large degree of overlap of plots from the two habitats.


1.5
1
0.5
0
-0.5
-1
-1.5
-2
Axis 3
-1.5
-1
-0.5
0
0.5
1
1.5
2
Axis 2
△ Forest
● Meadow

CHAPTER 4

LINKING AN INVASIVE SPECIES WITH ITS COMMUNITY AND ECOSYSTEM IMPACTS: INTRODUCED BEAVERS AFFECT DIVERSITY AND SECONDARY PRODUCTION OF SUBANTARCTIC STREAM BENTHOS[1]

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[1] Anderson, C.B. and A.D. Rosemond. To be submitted to *Ecology*.

Abstract

Species invasions are a global phenomenon altering biotic assemblages and ecosystems. Introduced ecosystem engineers, in particular, have the ability to impact not just the structure, but also the function of ecosystems. Here, we link the invasive exotic North American beaver with its community and ecosystem effects on streams in the Cape Horn Biosphere Reserve, Chile. We measured the impact of beavers on habitat variables (physical, chemical and geomorphological), basal resource characteristics (quantity and quality), macroinvertebrate community parameters (density, richness, diversity, similarity and composition) and ecosystem processes (biomass and secondary production) by comparing natural (unimpacted) stream reaches, beaver ponds and sites downstream of beaver dams. Beaver engineering altered stream habitat in ponds, reducing substrate heterogeneity. Basal resource quantity increased, but quality decreased, in ponds compared to the other habitats. The effects on benthos resulted in simplified, but more productive assemblages in ponds, where macroinvertebrate richness, diversity and the number of functional feeding groups decreased by approximately half, while density, biomass and secondary production increased 3-5x compared to natural sites. Evidence indicated that increased benthic organic matter caused decreases in invertebrate richness and diversity via habitat homogenization, while impacts on invertebrate biomass and production were the result of trophic effects by increasing carbon availability. Beaver modifications to invertebrate community structure were largely localized to ponds, but functional increases in benthic production in ponds undoubtedly added to energy production and flow for the entire stream ecosystem. Thus, beaver impacts to species richness may be limited to habitat scales, but changes to production may affect landscape

phenomena. Our findings help elucidate the effects of this invasive ecosystem engineer and provide new information on the ecology of subantarctic lotic ecosystems.

Key Words

Cape Horn, *Castor canadensis*, ecosystem engineer, exotic, invasive, *Nothofagus*, richness, secondary production

Introduction

Species introductions provide an opportunity to investigate general ecological principles concerning the role of species in ecosystems (Elton 1958, Sax et al. 2005). Invasions alter ecosystems via a number of mechanisms such as changing resource availability, energy flow dynamics and disturbance regime (Vitousek 1990). Moreover, an invading ecosystem engineer can influence each of these mechanisms by creating, destroying or modifying habitat (Crooks 2002). Invasive exotic species and their associated impacts constitute a principal part of global environmental change (Vitousek et al. 1996). So, how do introduced species interact with native biotic communities to shape and influence relatively pristine ecosystems?

The Magellanic Sub-Antarctic Forest Ecoregion in southern South America was recently designated as one of the world's last remaining pristine wilderness areas (Mittermeier et al. 2001). However, parts are also replete with exotic species (Anderson et al. 2006). The introduced assemblage in this area includes approximately half of terrestrial mammals (12 of 22 species) and freshwater fish (2 of 5 species) (Anderson et al. 2006, M.C. Moorman unpublished data), as well as two non-native birds and an introduced earthworm (Anderson and Hendrix 2002, Anderson et al. 2006). Among this exotic assemblage, the North American beaver (*Castor canadensis* Kuhl), introduced in 1946, stands out for being an ecosystem engineer.

It is predicted that an invasive ecosystem engineer's affect on species richness is related to its influence on habitat variability with richness increasing or decreasing as an ecosystem engineer creates a greater or less heterogeneous environment, respectively (Crooks 2002). Previous research on beaver engineering has shown that beavers enhance the diversity of terrestrial and aquatic assemblages via the creation of a more patchy mosaic of habitats in their native range (Naiman et al. 1988, Pringle et al. 1988, Wright et al. 2002). The role of an ecosystem engineer in a particular place, however, is a question of scale and context, depending upon the surrounding natural landscape and regional species pool in which the engineering activity is embedded (Crooks 2002, Rosell et al. 2005). Therefore, in a landscape where wetlands occur naturally, we would expect beaver-created habitats to have less influence on enhancing landscape heterogeneity, than compared to where wetlands are absent or less abundant.

By influencing resource availability and productivity, ecosystem engineers can also have trophic and species richness effects that are unrelated to their actual membership in the food web (Jones et al. 1994, Wright and Jones 2004). For example, invasive species can modify food web dynamics by introducing novel traits that affect resource flow and availability (e.g., Vitousek et al. 1987). They may also dominate ecosystem function due to their sheer numbers (e.g., Strayer et al. 1999). The engineering activities of beavers in their native range have been shown to make stream ecosystems more retentive by impounding organic material (Naiman et al. 1986), nitrogen (Naiman and Melillo 1984), sediment (Butler and Malanson 1995) and water (Burns and McDonnell 1998). As a consequence of this increased retention, it has been proposed that beaver engineering increases stream stability and resilience to disturbance (Naiman et al. 1988). The trophic effect of such habitat and resource alteration is increased total biomass of benthos, especially predatory and collector-gatherer taxa (McDowell and Naiman 1986) and shifts in the invertebrate assemblage structure toward taxa typical of higher order streams. Such effects potentially make beaver pond invertebrate communities unique in headwater streams (Pollock et al. 1995).

Very little is known about the ecology of streams or the role of beavers in modifying lotic ecosystems in southern Chile (but see Lizarralde et al. 1996). Understanding the impact of introduced beavers is important for informing management and conservation initiatives in the Cape Horn Biosphere Reserve (Rozzi et al. 2006) and will provide new information of the structure and function of subantarctic lotic ecosystems. Furthermore, the study of introduced beavers can help answer basic questions of the underlying ecological mechanisms by which invasive ecosystem engineers "engineer ecosystems." To determine the role of beavers as exotic ecosystem engineers, we addressed their effects on stream habitat (physical, chemical and geomorphological), basal resources (quantity and quality), benthic invertebrate communities (richness, diversity, similarity, density and community assemblage) and ecosystem functional response variables (biomass and secondary production of stream benthos). We tested the impacts of beavers by comparing these parameters at three habitat types: (a) natural, forested stream sections that were never affected by beavers, (b) beaver ponds and (c) reaches downstream of ponds.

Methods

Site description

Chile's temperate forests are the most extensive in the Southern Hemisphere, occurring between 35-56°S latitude, and are characterized by a high degree of endemism, when compared to temperate forests in the Northern Hemisphere (Armesto et al. 1995, Veblen et al. 1996). The austral limit of this biome is found in the Cape Horn Archipelago, which is also the world's southernmost forested ecosystem. This study was conducted at the southern tip of these temperate forests on Navarino Island at approximately 55°S (Figure 4.1) and has elevations that range from 0 to 1000 m.a.s.l. with tree line at approximately 450 m. Short, cool summers (mean temperature 9°C) and long, cooler winters (mean temperature 2°C) characterize the study site, which receives about 500-650 mm of precipitation annually (Tuhkanen et al. 1989).

Four streams were studied on the island's north coast at elevations below 100 m in mixed forest-bog watersheds. Catchments are relatively short (<10 km), and study reaches were established on the main channels. Average width of natural reaches was 6.6 m (±0.9). The study watersheds were Robalo (in the Omora Park Experimental Watershed), Mejillones, Estrella and Faraones, all located within 30 km of each other on the north coast of the island. Each stream had three sampling locations that represented: (1) a natural, forested reach never impacted by beavers (natural), (2) an active beaver pond (pond) and (3) a site downstream of the beaver dam, whose riparian zone was foraged by beaver (downstream). The beaver-impacted sites were previously forested before beaver colonization, as evidenced by the geomorphology of the site and the presence of standing dead tree trunks to the edge of the river. Most variables were collected monthly, bimonthly or seasonally (spring [October], summer [January] and fall [May]) from January to December 2003.

Habitat characterization

Physical – Riparian forest canopy cover was estimated seasonally at 10 m intervals along each study reach with a spherical densiometer. Stream temperature was recorded with Hobo™ dataloggers every 15 minutes for 1 year in three streams (Robalo, Mejillones and Farellones). Degree days were calculated as the sum of daily averages over 0°C for a year for the Robalo River, due to missing data at the other sites.

Chemical – Stream water samples were taken bimonthly at each site using a syringe mounted membrane filter (Millipore 0.45 µm pore size). Samples were frozen and transported to the Analytical Chemistry Lab at the Institute of Ecology, University of Georgia (UGA), Athens, Georgia, USA. Nitrate and soluble reactive phosphorus (SRP) were measured using an Alpkem RFA 300 automated analyzer. Dissolved organic carbon concentrations were measured with a Shimadzu TOC-5000A Total Organic Carbon Analyzer with ASI-5000A Auto Sampler. We used an YSI 85D meter to measure dissolved oxygen and specific conductance, and a Beckman 250 probe was used to determine pH once at each site.

Substrate –Substrate characteristics were determined at each site using Wolman pebble counts to quantify particle size distribution (Harrelson et al. 1994). One hundred points were chosen randomly along each study reach, and the diameter of the first object encountered in the substrate was measured. These values were then used to determine substrate diversity by applying a Shannon-Weiner Diversity Index to the abundance of particular size classes of substrate found during the pebble counts.

Basal resources

Quantity: The standing crops of basal resources were measured during spring (October), summer (January) and fall (May) in 2003. At each site, we collected coarse benthic organic matter (CBOM), fine benthic organic matter (FBOM), very fine benthic organic matter (VFBOM) and rock biofilm. Seston and wood standing crops were measured once in spring 2005. CBOM, FBOM and VFBOM were collected using a core sampler (0.07 m^{-2}), and the number of sub-samples was determined by the size of the stream with three stream width transects and one sample per meter in natural and downstream sites (usually 9-12) and ten replicates in ponds. Contents of the sampler were removed to a depth of 10 cm and passed through two sieves: 1mm and 250 µm. The total >1mm portion was collected and constituted the CBOM; FBOM was the fraction of the sample collected by the 250 µm sieve. VFBOM was collected in a bucket under the sieve, a sub-sample of which was passed through pre-ashed filter (0.7 µm, Whatman GF/F). All samples were frozen until they could be transported to the laboratory at the University of Magallanes (UMAG), Punta Arenas, Chile, where they were dried at 60°C, weighed, ashed at 500°C and reweighed to determine g ash-free dry mass (AFDM) m^{-2}. Biofilm was collected during each season from three to five rocks (sub-samples) in downstream and natural sites using a stiff brush to scrub the interior area of a core sampler. The slurry was removed and pipetted through a pre-ashed filter (0.7 µm, Whatman GF/F). Filters were frozen and processed for AFDM as above.

Seston (suspended organic material > 0.7 µm) was collected once in spring 2005. Stream water was passed through a pre-ashed filter (0.7 µm, Whatman GF/F), which was stored, dried, ashed and weighed as above. Estimates of wood biomass were also made at each stream and habitat type in austral spring 2005 using the method of Wallace and Benke (1984) to determine wood volume, which was then converted to biomass based on specific weight values for these tree species (CONAF 1988).

*Quality: S*amples of all resources were also collected at each collection period for C:N analysis. Wood, CBOM and FBOM were collected in 20 ml scintillation vials, and VFBOM, seston and biofilm were collected on pre-ashed filters. All were dried at UMAG and transported to UGA for C:N analysis using a Costech elemental analyzer (CHN).

Community analysis

Benthic macroinvertebrates were sampled seasonally to determine richness, diversity, similarity, density, biomass and functional feeding group structure. Three sub-samples were taken at each study reach with a core sampler. The contents were passed through a 250 µm sieve, and collections were transported in jars of ethanol to the laboratory, where invertebrates were separated from detritus under a dissecting microscope (7x) and stored in 70% ethanol. Taxa were identified to the lowest possible level (usually family or genus), and functional feeding groups (FFGs), i.e. collector-gatherer [gatherer], collector-filterer [filterer], scraper, shredder and predator, were determined using Merritt and Cummins (1996), Miserendino and Pizzollo (2000), Fernández and Domínguez (2001) and by other experts for particular taxa (see Acknowledgments).

Mean richness, Shannon-Weiner diversity and Bray-Curtis community similarity were calculated using EstimateS (Colwell 1997). During identification of seasonal invertebrate samples, the lengths of specimens were measured to the nearest mm under a dissecting scope, and biomass was determined for each taxon using length-mass regressions developed by Benke et al. (1999) and Miserendino (2001). Mean annual biomass, expressed as mg AFDM m^{-2}, was calculated for each taxon and functional feeding group.

Ecosystem function

Due to its time- and labor-intensive nature, our analysis of secondary production was limited to two of the four study streams: Robalo and Mejillones. These two streams were chosen because they reflected the archipelago's two principal stream types: clear water and tannin-enriched water, respectively. These streams capture the range in natural DOC variation, thus enabling us to interpret variation in food web dynamics across for the typical lotic ecosystem types in the Cape Horn area. Samples for secondary production were taken separately from those for community analysis (above). Four sub-samples were taken on a monthly basis from the two streams from January to December 2003; samples were not taken in August 2003 due to deep snow. Macroinvertebrates were collected, identified, and measured for biomass as described above. We used the size-frequency method (Hamilton 1969) with the cohort production interval (CPI) correction factor (Benke 1979) to calculate secondary production. Size distributions, graphed using each sample date, showed that cohorts were asynchronous, and we used CPIs derived for similar taxa from biogeographically related streams in New Zealand (Huryn 1996, 1998).

For a few taxa we used an estimated CPI based on reported values or general life history information (Amphipoda: Pickard and Benke 1996, Bivalva: Winterbourn 1973, Copepoda, Gastropoda and Ostracoda: Thorp and Covich 1991, Simuliidae: M. Mercado [Laboratorio Benthos, Chile, pers. comm.]).

Statistical analyses

Streams were used as replicates to determine variation in parameters among habitat types. Canopy cover, temperature, nitrate, dissolved organic carbon, total benthic organic matter, substrate particle size, conductivity and dissolved oxygen were compared between habitat types with one-way ANOVAs. pH was expressed as the median value for each habitat. Differences in mean standing crops of organic matter and C:N were analyzed with a two-way ANOVA model testing for habitat type (natural, pond and downstream) and season (spring, summer and fall) effects using streams as replicates. Significant main effects were followed by a Tukey HSD test of significance.

Macroinvertebrate community data (density, richness, diversity and biomass) were log transformed to achieve normality, and mean annual values based on seasonal samples were compared as above. Secondary production was compared qualitatively between the two streams and with other published values, as the time- and labor-intensive nature of obtaining these estimates does not allow sufficient replicates for statistical analyses.

To examine the relationship between beaver alterations and the richness and production of benthos, we examined the relationship of beaver-mediated substrate diversity (H' of pebble counts) and benthic invertebrate richness. Additionally, we regressed resource quantity (g AFDM m^{-2}) and quality (g N m^{-2}) to benthic invertebrate biomass (mg AFDM m^{-2}). All statistical analyses were performed with JMP 5.0.1 (SAS Institute, Cary, NC, USA).

Results

Habitat characterization

Natural study reaches were heavily shaded, and as expected, beavers significantly reduced canopy cover at ponds and downstream sites (Table 4.1). Temperature did not differ significantly among habitat types, but daily temperate range and degree days showed an increasing trend from natural to downstream to beaver pond sites (Table 4.1).

Water chemistry did not differ among habitat types (Table 4.1). Nitrate concentrations were low and unaffected by beaver modifications; soluble reactive phosphorus (SRP) was undetectable; dissolved organic carbon was uniformly high; and median pH was circumneutral in all habitat types (Table 4.1). Specific conductance values were uniformly low, while dissolved oxygen was supersaturated (Table 4.1).

Stream bed substrate differed in ponds compared to the other habitats (Table 4.1). The substrate profile of pond sites contained almost exclusively organic material and lacked natural rocky substrate, while the downstream site retained the same substrate particle size profile as natural reaches. Consequently, pond sites had a significantly less diverse substrate index than both natural and downstream reaches (Table 4.1).

Basal resources

Quantity: The quantity of several resource categories varied with habitat type. In ponds, standing crop of wood was significantly higher by 6x, CBOM by 4x, FBOM by 44x and VFBOM by 22x compared to natural reaches, but organic matter standing crop at sites downstream of beaver ponds was similar to natural reaches (Table 4.2). Seston and DOC did not vary among habitat types (Table 4.2). The quantity of no basal resource varied seasonally ($p>0.05$), even though these streams pass through deciduous forests and receive autumnal leaf litter inputs.

Quality: Beaver habitat modification also influenced the quality of benthic organic matter, but only in ponds, where FBOM and VFBOM had lower quality (i.e. higher C:N) compared to downstream and natural sites (Table 4.3). The quality of all other basal resources remained consistent throughout the three habitats (Table 4.3), and season did not affect basal resource C:N ($p>0.05$).

Benthic invertebrate assemblage

We identified a total of thirty-five benthic invertebrate taxa representing all functional feeding groups. Natural sites had the greatest total taxa richness (33) with ponds being the lowest (28) and downstream reaches intermediate between the other two (31) (Appendix 4.1). Ten species and fourteen genera could be determined. The eleven remaining taxa were identified to family or order. The assemblage included a total of fifteen orders from five classes (Annelida, Arthropoda, Crustacea, Insecta and Mollusca), and most taxa were insects (74%) with Diptera being the most diverse order (13 morpho-species).

Beaver ponds had significantly lower richness and diversity, compared to natural and downstream sites (Table 4.4). Community similarity indices showed a significant difference between ponds and natural sites, while the downstream reach was intermediate between the two (Down-Down=0.46^{A}, Natural-Down=0.43^{A}, Pond-Pond=0.43^{A}, Natural-Natural=0.42^{A}, Down-Pond=0.35^{AB}, Natural-Pond=0.22^{B}; $F_{5,65}$=6.26, p<0.001; values separated by different letters were significantly different with a post-hoc Tukey HSD test, p<0.05).

Invertebrate density was 2-5x higher in downstream and pond sites than natural reaches, but this trend was not statistically significant (Table 4.4). Total biomass of benthic invertebrates was higher in beaver ponds (5x) compared to natural sites, and downstream sections were again intermediate between the two (approximately 2x the biomass of natural sites) (Table 4.4). Gatherers were the dominant functional feeding group by biomass in all three habitat types, but ponds had the highest biomass of gatherers from all three habitats (Table 4.5A). In ponds, predator and gatherer biomasses were significantly higher by 8-20x, and scraper, shredder and filterer were statistically significantly lower by 5-10x, compared to the other two habitats (Table 4.5A). Downstream sites exhibited an increase in total biomass (Table 4.4), as well as the biomass of every FFG, on the order of 1.5x, compared to natural sites, but these increases were not significant (Table 4.5A). The relative contribution of scrapers, shredders and filterers was significantly decreased in ponds, while the proportion of predators increased, compared to natural and downstream sites (Table 4.5B).

Secondary production

In both Robalo and Mejillones streams, secondary production was highest in ponds and lowest in natural sites (Tables 4.6A, B). The values for natural sites were similar in both streams. Secondary production at the Mejillones beaver pond was higher than at Robalo, and the Robalo downstream was higher than at Mejillones (Figure 4.2).

In all habitat types, gatherer *Hyalella simplex* and non-Tanypodinae chironomids were the dominant taxa with regards to secondary production. The number of taxa that contributed >1% of the total secondary production was reduced in ponds relative to the other habitats. In downstream and natural sites, we found from 7 to 9 taxa at each site constituted >1% of production (Table 4.6A, B). Whereas, in beaver ponds, only 4 taxa (*Hyalella simplex*, Oligochaeta, Tanypodinae and non-Tanypodinae chironomids) contributed similarly.

Natural and downstream sites had few predatory taxa; only the Mejillones downstream reach had predatory Tanypodinae chironomids that made up >1% of production (Table 4.6B). In general, a more speciose and productive assemblage of scrapers (Ephemeroptera: Baetidae and Leptophlebiidae), filterers (Diptera: Simuliidae) and gatherers (Plecoptera: Gripopterygidae, Diptera: Tipulidae and non-Tanypodinae, Oligochaeta, and Amphipoda: *H. simplex*) inhabited downstream and natural sites, compared to ponds (Tables 4.6A, B).

The relationship of beaver alterations to benthic richness and production

Invertebrate richness significantly decreased as a function of decreasing habitat heterogeneity of benthic substrate, caused by beavers in pond habitats (Figure 4.3). In contrast, benthic invertebrates biomass significantly increased in ponds as a function of the carbon standing crop (g AFDM m^{-2}) of total BOM and total FBOM, but not CBOM (Figures 4.4A, C, E). Standing crop of nitrogen, however, was not found to be significantly related to invertebrate biomass (Figures 4.4B, D, F).

Discussion

Beaver invasion of subantarctic ecosystems

We found that beavers had profound effects on the community and ecosystem properties of subantarctic streams. Beavers presently inhabit nearly all of the streams and watersheds of the Cape Horn Biosphere Reserve with major impacts on riparian vegetation (Anderson et al. 2006a, Martínez Pastur et al. in press) and attaining densities of approximately 1.1 colony km^{-1} (Skewes et al. 1999, Anderson et al. 2006b). Our own calculations of beaver impact in the Robalo Experimental Watershed found that 20% of the forested portion (which is 1/3 of the total watershed) was beaver-impacted (M.C. Moorman and C.B. Anderson, unpublished data). Since their establishment in 1946 on Tierra del Fuego Island, beavers have continuously expanded their range (Lizarralde 1993, Skewes et al. 1999), even recently being reported on the continental mainland (N. Soto, Director of Wildlife, Regional Agriculture and Livestock Service, Punta Arenas, Chile, pers. comm.). The land area that is potentially habitable by beaver includes at least the entire temperate forest biome found in Argentina and Chile from 35° to 56° S. This entire region, as with the subantarctic islands, has evolved in the absence of an organism that is functionally equivalent to the beaver.

Beaver effects on benthic invertebrate richness and diversity

The thirty-five invertebrate taxa we found in the study streams on Navarino Island (Appendix 4.1) is less than values reported for more northern sites in Chile and Argentina, where from seventy-seven and ninety-five were reported, respectively (Miserendino 2001, Figueroa et al. 2003). Beaver activities reduced both richness and diversity of invertebrates in beaver ponds relative to unimpacted sections and reaches downstream of ponds. General ecological theory predicts that species richness increases with habitat heterogeneity, which has been supported by studies for multiple taxa and ecosystems (e.g., Kerr and Packer 1997, Downes et al. 1998, Guegan et al. 1998, Kerr et al. 2001). Crooks (2002) extended this concept to ecosystem engineers, asserting that the influence of engineering activity on affecting species richness should be related to whether or not the engineer increases or decreases habitat diversity. Evidence from our study supports the assertion that beaver engineering activities in ponds decrease species richness as a function of decreasing habitat heterogeneity (Figure 4.5). By burying substrate under a layer of organic matter, beavers reduced the complexity of benthic habitat in ponds, in contrast to unimpacted or downstream sites, where there were a variety of substrates present (Table 4.1). Benthic taxa richness and diversity were negatively related to these beaver-induced changes in substrate heterogeneity.

Landscape-scale impacts of beavers on benthic species richness and diversity may not be as strong, however. In contrast to local effects on substrate, beaver modifications enhanced heterogeneity along forested reaches of these streams by introducing two new habitat types (beaver ponds and deforested downstream reaches). Aggregating all three habitat types, beaver habitats increased benthic macroinvertebrate richness, given the presence of water boatmen (*Corixa* sp.) and bivalves (*Pisidium magellanicum* Dall) that were not found in the natural forested stream sections (Appendix 4.1). However, if we consider only dominant taxa (>1% of biomass) in each habitat, the beaver ponds' invertebrate community represented only a subset of those inhabiting unimpacted sections, while the community at downstream sites was similar to natural conditions. Taking a step further out to the landscape, the Cape Horn archipelago contains a mosaic of forests interspersed among natural lentic habitats such as glacial lakes and peat bogs (Rozzi et al. 2006). In this case, beaver ponds may not be distinct from other lentic habitats found in this forest-bog mosaic, and even the enhancement of taxa richness along forested reaches was slight. Thus, beaver modifications of community structure appeared to be largely restricted to pond habitats, coinciding with broader scale predictions of weaker ecosystem engineer effects in landscapes in which their impacts are not unique (Wright et al. 2002, Rosell et al. 2005).

Beaver effects on benthic invertebrate biomass and production

The measures of ecosystem function that we made in this study consisted of quantifying benthic macroinvertebrate biomass and production. In contrast to the generally negative relationship between taxa richness and the quality of organic matter, total benthic organic matter standing crop was positively related to invertebrate biomass in these systems. Increased retention of organic matter in ponds enhanced this ecosystem function. The opposing trends observed for richness (–) and production (+) in relation to organic matter standing crop in ponds appeared to derive from the fact that their drivers, while originating from the same source, operated along different pathways (Figure 4.5).

Specifically, both processes showed evidence of occurring due to beaver-mediated enhancement of the quantity of terrestrially-derived benthic organic matter in streams. This increased benthic organic matter then had two types of impacts: Whereas negative effects on species richness may have occurred via a habitat pathway (reductions in benthic substrate heterogeneity associated with increased quantity of organic matter), increased biomass and secondary production of invertebrates apparently resulted from a resource availability pathway (increased quantity of benthic food resource availability associated with increased organic matter retention). Both of these mechanisms are consistent with general predictions set out for the effects of invasive ecosystem engineers whose habitat modifications can influence novel ecosystems via the pathways of resources availability, trophic dynamics and disturbance regime (Vitousek 1990, Crooks 2002). In our study, changes in invertebrate species richness and biomass were apparently associated with alterations in physical and trophic resources, respectively, resulting in simultaneous reductions in invertebrate richness and increases in production.

Comparison of the structure and function of benthic assemblages to streams worldwide

Gatherers were the principal functional feeding group at all sites, which also agrees with the community structure found in New Zealand streams, which have a similar biogeographical and evolutionary history (Winterbourn and Ryan 1994). Our results also showed that unimpacted sites corresponded with expectations for mid-order streams (approx. 5th order), based on the River Continuum Concept (RCC: Vannote et al. 1980). The RCC predicts that intermediate order streams would have co-dominant scrapers and collectors with less shredders and predators. In contrast, higher order streams would be expected to be dominated by collectors and predators. The functional feeding groups found in beaver ponds indicated that the benthic assemblage shifted to reflect conditions of larger order streams, as proposed by Pollock et al. (1995). Furthermore, the increase in invertebrate predators in ponds, and their virtual absence in natural and downstream sites, indicated enhanced trophic diversity due to the added importance of the secondary consumer trophic level. Thus, effects of beavers were propagated through at least three trophic levels: basal carbon, primary consumers and secondary consumers. Also, increased trophic diversity in ponds occurred concurrently with decreased taxonomic diversity.

Our estimates for secondary production are the first such values for aquatic invertebrates in temperate forests of South America. Furthermore, these are the most southern representatives of many freshwater benthic invertebrate taxa (Ashworth et al. 2000). Secondary production at natural sites in our study was lower than 97% of the 58 reported estimates summarized by Benke (1993) for world-wide streams. However, they fit with expectations for cold, nutrient-poor sites (Huryn and Wallace 2000), and comparison of subantarctic Chilean streams with other high latitude sites from the Northern and Southern Hemispheres showed similar relationships (Table 4.5). The effect of beavers on secondary production is to move them into the median range of values for world sites – in essence changing high latitude sites to characteristics of more temperature values.

In conclusion, we found that introduced beavers had major impacts on community and ecosystem properties of the pond habitats they create. Their landscape effects on the benthic invertebrate community may be less since the Cape Horn Biosphere Reserve has natural lentic habitats in its watersheds, which has major implications for the maintenance of native biodiversity in the face of this invasion. The question, then, for managers is to what extent and density are beaver ponds being constructed across the landscape and to what degree are beavers dominating these watersheds rather than creating a patchy mosaic. Furthermore, beaver enhancement of benthic secondary production adds to overall consumer production and energy retention in subantarctic stream ecosystems. Therefore, determining the fate of this increased invertebrate production and its potential links with riparian ecosystems will be an important future area of work in determining the role of this exotic ecosystem engineer in the subantarctic landscape. These results provide new information on the ecology of subantarctic streams and serve to highlight the importance of context in determining an invasive species' role in affecting community structure and ecosystem processes.

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Table 4.1. Description of physical and chemical habitat variables from four study streams on Navarino Island, Cape Horn Biosphere Reserve, Chile (55°S). Means (±SE) were compared with a one-way ANOVA for habitat effects, except for temperature range, annual degree days above °C and median pH. Values within each category with different letters were significantly different with a Tukey HSD test ($p<0.05$).

Characteristic	Natural	Pond	Downstream	*F*	*p*
Canopy Cover (%)	85.2 ±2.7^{A}	18.2 ±5.3^{B}	28.7 ±2.9^{B}	88.23	**<0.0001**
Mean Daily Temperature (°C)	4.5 ±0.1^{A}	4.8 ±0.4^{A}	4.8 ±0.2^{A}	0.3	0.8
Yearly Temperature Range (°C)	-0.6 to 16	-2 to 20	-0.6 to 18		--
Annual Degree Days (> 0°C)	1781	1853	1830		--
N-NO$_3$ (ppm)	0.05 ±0.01^{A}	0.04 ± 0.01^{A}	0.05 ± 0.01^{A}	0.29	0.8
SRP (ppm)	undetectable	undetectable	undetectable		--
DOC (ppm)	13.5 ±5.3^{A}	12.2 ±5.4^{A}	13.1 ±5.5^{A}	0.02	0.97
Conductivity (µS cm^{-1})	118.2 ±25.9^{A}	103.5 ±15.8^{A}	77.2 ±14.9^{A}	1.14	0.4
DO (mg L^{-1})	9.6 ±0.6^{A}	8.3 ±1.5^{A}	10.8 ±0.3^{A}	1.68	0.3
pH	7.5	7.1	7.6		--
Substrate diversity (H')	0.81 ±0.08^{A}	0.14 ±0.14^{B}	0.85 ±0.05^{A}	16.8	**0.001**
Substratum					
Organic (%)	0.5 ±0.3^{A}	88.8 ±13^{B}	5.3 ±3.3^{A}	54.8	**<0.001**
Sand (%)	11 ±5.4^{A}	8 ±9.2^{A}	11.3 ±6.6^{A}	0.08	0.9
Gravel (%)	37 ±8.1^{A}	2.8 ±3.2^{B}	46.8 ±6^{A}	19.3	**0.001**
Cobble (%)	45.3 ±17.2^{A}	0.5 ±0.6^{B}	22 ±6.8^{AB}	5.8	**0.02**
Boulder (%)	0.3 ±0.3^{A}	0.0^{A}	0.8 ±0.9^{A}	0.7	0.5
Bedrock (%)	6 ±4.1^{A}	0.0^{A}	14 ±6.7^{A}	3.2	0.09

N-NO$_3$ = nitrate, SRP = soluble reactive phosphorus, DOC = dissolved organic carbon, DO = dissolved oxygen, Total BOM = total benthic organic matter.

Table 4.2. Mean basal resource standing crops (g AFDM m^{-2}) at natural reaches, beaver ponds and downstream sites (±SE). ANOVA results are only for habitat main effects, since season and season*habitat interaction effects were never significant. Values within the same row with different letters indicate a significant different with Tukey HSD test ($p<0.05$).

Quantity	**Natural**	**Beaver Pond**	**Downstream**	$F_{habitat}$	***p***
Wood	558.4 (37.7)^{A}	3,561.7 (232.8)^{B}	662.9 (245.2)^{A}	22.25	**0.002**
CBOM	10.6 (3)^{A}	438.2 (134.4)^{B}	15.4 (6.7)^{A}	154.52	**<0.0001**
FBOM	18 (1.3)^{A}	786.8 (63.4)^{B}	66 (7.5)^{A}	112.57	**<0.0001**
VFBOM	26 (6.1)^{A}	574 (139)^{B}	34.6 (6)^{A}	73.64	**<0.0001**
Biofilm	5.6 (2)^{A}	NA	7.4 (1.8)^{A}	2.25	0.15
Seston	0.002 (0.0004)^{A}	0.003 (0.001)^{A}	0.003 (0.001)^{A}	0.16	0.86

CBOM: coarse benthic organic matter, FBOM: fine benthic organic matter; VFBOM: very fine benthic organic matter.

Table 4.3. The mean of basal resource quality (C:N) at natural reaches, beaver ponds and downstream sites (±SE). ANOVA results are as in Table 4.2.

Quality	**Natural**	**Beaver Pond**	**Downstream**	$F_{habitat}$	***p***
CBOM	41.5 (6.3)^{A}	41.2 (7.7)^{A}	39.8 (12.8)^{A}	1.14	0.34
FBOM	21.7 (1.4)^{A}	26.7 (1.7)^{B}	20.5 (0.7)^{A}	6.48	**0.003**
VFBOM	14.5 (0.9)^{A}	18.7 (1.1)^{B}	14 (0.8)^{A}	4.21	**0.01**
Biofilm	9.5 (0.4)^{A}	NA	9.8 (0.2)^{A}	0.38	0.57
Seston	12.8 (1.6)^{A}	9.4 (0.8)^{A}	11.7 (0.4)^{A}	2.69	0.15

CBOM: coarse benthic organic matter, FBOM: fine benthic organic matter; VFBOM: very fine benthic organic matter.

Table 4.4. Benthic invertebrate community variables for natural, beaver pond and downstream sites. Annual means (±SE) of bare based on seasonal replicates for each of four sites for each habitat (n=12). Values within each category with different letters were significantly different with a Tukey HSD test (p<0.05).

Category	**Natural**	**Beaver Pond**	**Downstream**	***F***	***p***
Richness (taxa m^{-2})	15.3(1.8)^{A}	10 (0.9)^{B}	15.8 (1.2)^{A}	5.7	**0.03**
Diversity (H')	2 (0.1)^{A}	1.4 (0.1)^{B}	1.9 (0.1)^{A}	22.79	**0.0003**
Density (individuals m^{-2})	2,611.5 (504.9)^{A}	14,350 (10,381)^{A}	5,086.2 (1029.8)^{A}	2.6	0.13
Biomass (mg AFDM m^{-2})	257.9 (89.4)^{A}	864.1 (179.8)^{B}	443.3 (68.2)^{AB}	6.47	**0.02**

H' = Shannon-Weiner Diversity Index, AFDM = ash-free dry mass.

Tables 4.5. Mean annual values (±SE) of benthic invertebrate biomass (mg ash-free dry mass m^{-2}) for each functional feeding group in three habitat types (natural reaches, beaver ponds and downstream sites); and 3B. The relative annual biomass (%) of benthic invertebrates (±SE) for each functional feeding group as well. ANOVAs are presented as in Table 4.4.

A) Mean Annual Biomass	**Natural**	**Beaver Pond**	**Downstream**	***F***	***p***
Gatherer	149.8 (71.9)^{A}	708 (180)^{B}	258 (70.2)^{AB}	5.4	**0.03**
Scraper	35.7 (12.1)^{A}	3 (3)^{B}	45.8 (23)^{A}	10.2	**0.005**
Shredder	15 (4)^{A}	2.8 (1.7)^{A}	37.5 (20.8)^{A}	3.91	0.06
Filterer	52.2 (16.8)^{A}	5.3 (4.1)^{B}	84.8 (40.8)^{A}	6.74	**0.02**
Predator	5.2 (1.3)^{A}	144.3 (43.4)^{B}	17.2 (7.5)^{A}	10.96	**0.004**

B) Relative Annual Biomass	**Natural**	**Beaver Pond**	**Downstream**	***F***	***p***
Gatherer	51.4 (13.5)^{A}	79.1 (7.5)^{A}	55.6 (6)^{A}	2.45	0.14
Scraper	14.4 (3.8)^{A}	0.4 (0.4)^{B}	11.1 (6.3)^{A}	15.07	**0.001**
Shredder	6.2 (0.3)^{A}	0.3 (0.1)^{B}	7.3 (3.3)^{A}	8.66	**0.01**
Filterer	25.7 (12.7)^{A}	0.7 (0.6)^{B}	21.9 (11)^{A}	8.12	**0.01**
Predator	2.3 (0.6)^{A}	19.5 (8.1)^{A}	4.2 (2.2)^{A}	4.27	0.05

Table 4.6A. Secondary production of benthic invertebrate consumers in the Robalo River is shown for taxa that had a relative contribution (%) of >1% at three habitat-types (natural, beaver pond and downstream). Biomass (B) and secondary production (P) are in units of mg ash-free dry mass [AFDM] m^{-2} and mg AFDM m^{-2} y^{-1}, respectively.

Robalo	**Natural**			**Beaver Pond**			**Downstream**		
Taxa	**B**	**P**	**%**	**B**	**P**	**%**	**B**	**P**	**%**
Non-Insects									
Amphipoda									
Hyalellidae									
Hyalella simplex	128.8	1188.6	52.5	654.8	5495.2	73.0	428.5	3510.0	62.4
Gastropoda									
Lymneidae									
Lymnea sp.	15.6	33.0	1.5						
Oligochaeta	12.4	59.3	2.6	67.2	383.3	5.1	9.7	86.3	1.5
Insects									
Diptera									
Simuliidae									
Gigantodax spp.	22.3	113.7	5.0						
Chironomidae									
Tanypodinae				13.5	113.7	1.5			
Non-Tanypodinae	33.5	377.5	16.7	113.8	1283.1	17.0	46.7	609.2	10.8
Ephemeroptera									
Baetidae									
Andesiops torrens	30.9	97.4	4.3				109.8	500.0	8.9
Leptophlebiidae									
Massarotellopsis spp.	22.4	280.6	12.4				42.0	455.0	8.1
Plecoptera									
Gripopterygidae	7.9	32.5	1.4				46.8	251.5	4.5
Miscellaneous	29.9	80.2	3.5	172.4	254.5	3.3	87.0	215.3	3.8
Total	303.6	2262.6		967.7	7529.5		770.5	5627.4	
# of Taxa >1%	9			4				7	
% of Production			96.5			96.6			96.2

Table 4.6B. Secondary production of benthic invertebrate consumers in the Mejillones River is shown for taxa that had a relative contribution (%) of >1% at three habitat-types (natural, beaver pond and downstream). Biomass (B) and secondary production (P) are reported in units of mg ash-free dry mass [AFDM] m^{-2} and mg AFDM m^{-2} y^{-1}, respectively.

Mejillones	**Natural**			**Beaver Pond**			**Downstream**		
Taxa	**B**	**P**	**%**	**B**	**P**	**%**	**B**	**P**	**%**
Non-Insects									
Amphipoda									
Hyalellidae									
Hyalella simplex	78.3	1172.0	47.7	248.5	2882.2	22.9	81.1	1138.2	42.1
Oligochaeta	21.8	181.5	7.4	737.7	4380.5	34.7	30.3	193.1	7.1
Insects									
Diptera									
Simuliidae									
Gigantodax spp.	39.7	165.3	6.7				106.3	338.1	12.5
Chironomidae									
Tanypodinae				404.6	711.8	5.6	6.3	58.5	2.2
Non-Tanypodinae	60.8	641.5	26.1	293.9	4501.4	35.7	61.8	667.1	24.7
Tipulidae	7.3	39.6	1.6						
Ephemeroptera									
Baetidae									
Andesiops torrens	10.4	44.0	1.8				7.7	30.7	1.1
Leptophlebiidae									
Massarotellopsis spp.	6.9	72.3	2.9				20.0	197.1	7.3
Plecoptera									
Gripopterygidae	12.4	42.8	1.7				12.0	49.5	1.8
Miscellaneous	21.2	96.7	4.0	66	112.7	1.0	9.3	32.0	1.2
Total	258.8	2455.7		1750.7	12588.6		334.8	2704.3	
# of Taxa >1%	8			4			9		
% of Production			96			99			98.8

Table 4.7. Comparison of secondary production values from high latitude sites in the Northern and Southern Hemispheres.

Name, Location (Country)	Lat. (°)	Temp. (°C)	Habitat type	2° Production (mg AFDM m^{-2})	Comments	Reference
Northern Hemisphere						
Esko River (Norway)	60°N	3	Mixed forest	2,344 - 3,838	regulated weir sites	Baekken et al. 1984
				2,068 - 8,227		Fjellheim et al. 1989
Laxá River, North-Iceland (Iceland)	65°N	$0.3\text{-}2.3^a$ $9.5\text{-}13^b$	Subarctic tundra	32,000 - 352,000	• only quantifies blackflies at lake outflow • sheep farming and volcanic activity in vicinity	Gíslason and Gardarsson 1988
Kuparuk River, Alaska (USA)	68°N	0^a $8\text{-}10^b$	Subarctic tundra	6,000 - 12,000	• control • 4 dominant taxa	Petersen et al. 1993
				14,000 - 19,000	• nutrient addition • 4 dominant taxa	
Oksrukuyik Creek, Alaska (USA)	68°N	0^a $10\text{-}13^b$	Subarctic tundra	1,500 - 2,200	• pre-fertilization experiment • 3 dominant taxa	Harvey et al. 1998
				2,300 - 4,400	• 1-4 yr nutrient addition • 3 dominant taxa	
Southern Hemisphere						
Hinau Stream, North Island (New Zealand)	40°S	11	*Nothofagus* forest with limited intervention	8,400	forested	Hopkins 1976
				32,530	open canopy	
				73,690	organically enriched	
Horokiwi Stream, North Island (New Zealand)	41°S	13.5	*Nothofagus* forest heavily intervened by agriculture	24,630	forested	
				56,450	open canopy	
				43,550	open canopy	
Sutton & Stony Creeks, South Island (New Zealand)	45°S	5.6 to 6	Grasslands	8,503 - 13,352	exotic pasture and native tussock grassland	Huryn 1998
Robalo & Mejillones Streams, Cape Horn Biosphere Reserve (Chile)	55°S	4.5	Subantarctic *Nothofagus* forest-bog mosaic	2,263 - 2,456	forested	this study
		4.8		7,530 - 12,589	beaver pond	
		4.8		5,627 - 2,704	downstream of beaver pond	

Lat. refers to ° latitude north (N) or south (S). Temperature values are presented as yearly means, except when noted as ranges for [a]winter and [b]summer. AFDM = ash-free dry mass.

Figure 4.1. Map of southern South America, including the subantarctic Cape Horn Archipelago. Tierra del Fuego Island is divided between Chile and Argentina, while the remaining portion of the archipelago to the south of the Straits of Magellan is under Chilean sovereignty. Study sites were located on the north coast of Navarino Island, which is in the Cape Horn Biosphere Reserve (shaded area).

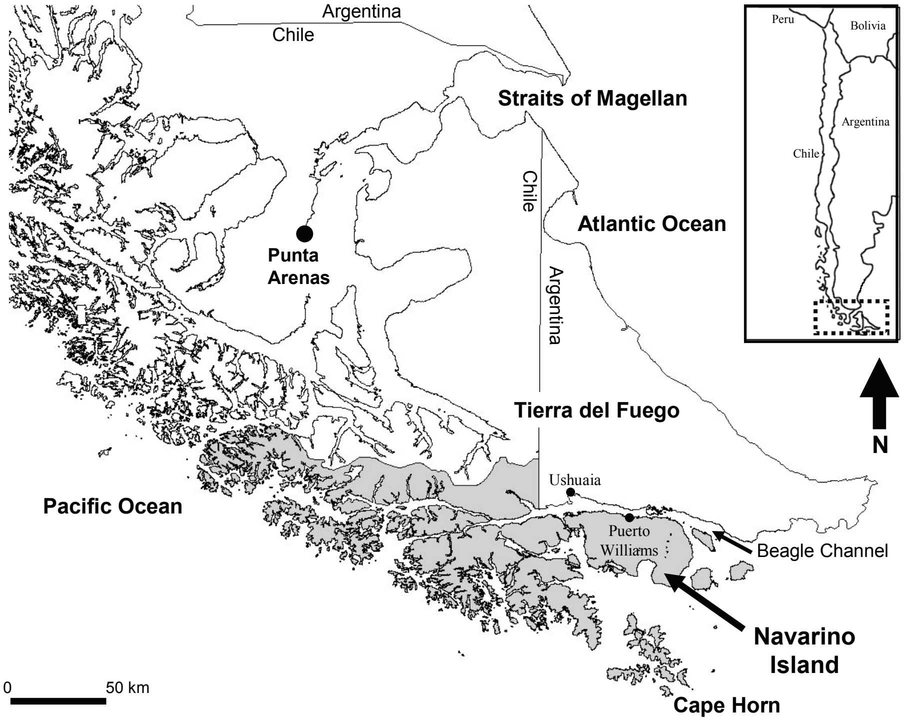

Argentina
Chile
Straits of Magellan
Punta Arenas
Chile
Argentina
Atlantic Ocean
Tierra del Fuego
Ushuaia
Pacific Ocean
Puerto Williams
Beagle Channel
Navarino Island
Cape Horn
0
50 km
N
Peru
Bolivia
Argentina
Chile

Figure 4.2. Secondary production and proportional representation of functional feeding groups for the Robalo and Mejillones Rivers. Total secondary production (mg ash-free dry mass m^{-2}) and the number of taxa that constituted >1% of production are presented for each habitat type (natural, beaver pond and downstream). Size of pie chart is proportional to its total secondary production, and relative contribution of functional feeding groups is shown for each habitat.

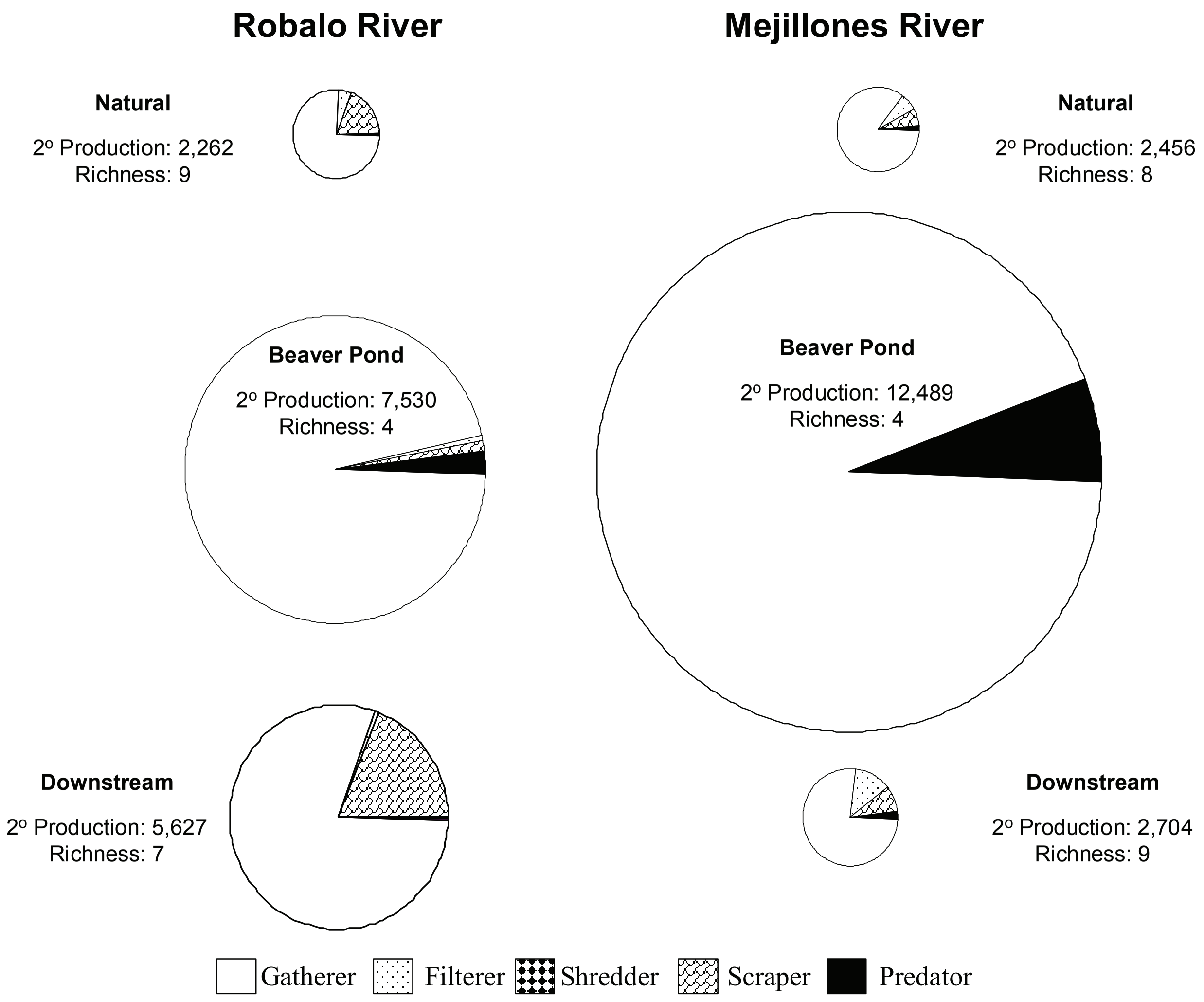

Robalo River
Mejillones River
Natural
2º Production: 2,262
Richness: 9
Natural
2º Production: 2,456
Richness: 8
Beaver Pond
2º Production: 7,530
Richness: 4
Beaver Pond
2º Production: 12,489
Richness: 4
Downstream
2º Production: 5,627
Richness: 7
Downstream
2º Production: 2,704
Richness: 9
Gatherer
Filterer
Shredder
Scraper
Predator

Figure 4.3. Benthic substrate diversity (measured with a Shannon-Weiner Diversity Index, H') was regressed with mean benthic invertebrate richness per site. Note that x-axis is reversed to demonstrate that benthic invertebrate richness decreases with decreasing substrate diversity caused by beaver impacts. Habitat is indicated by N (natural), P (beaver pond) and D (downstream of pond).

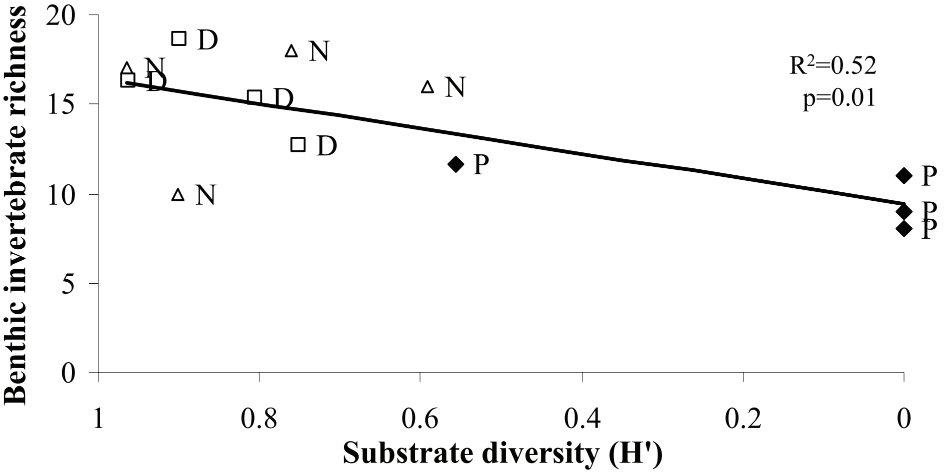

Benthic invertebrate richness
Substrate diversity (H')
20
15
10
5
0
1
0.8
0.6
0.4
0.2
0
D
D
D
D
N
N
N
N
P
P
P
P
R²=0.52
p=0.01

Figure 4.4. The mean annual biomass of invertebrates (mg AFDM m^{-2}) of invertebrates was regressed against categories of carbon (g AFDM m^{-2}) and nitrogen (g N m^{-2}) in total benthic organic matter (BOM), coarse benthic organic matter (CBOM) and total fine benthic organic matter (FBOM + VFBOM).

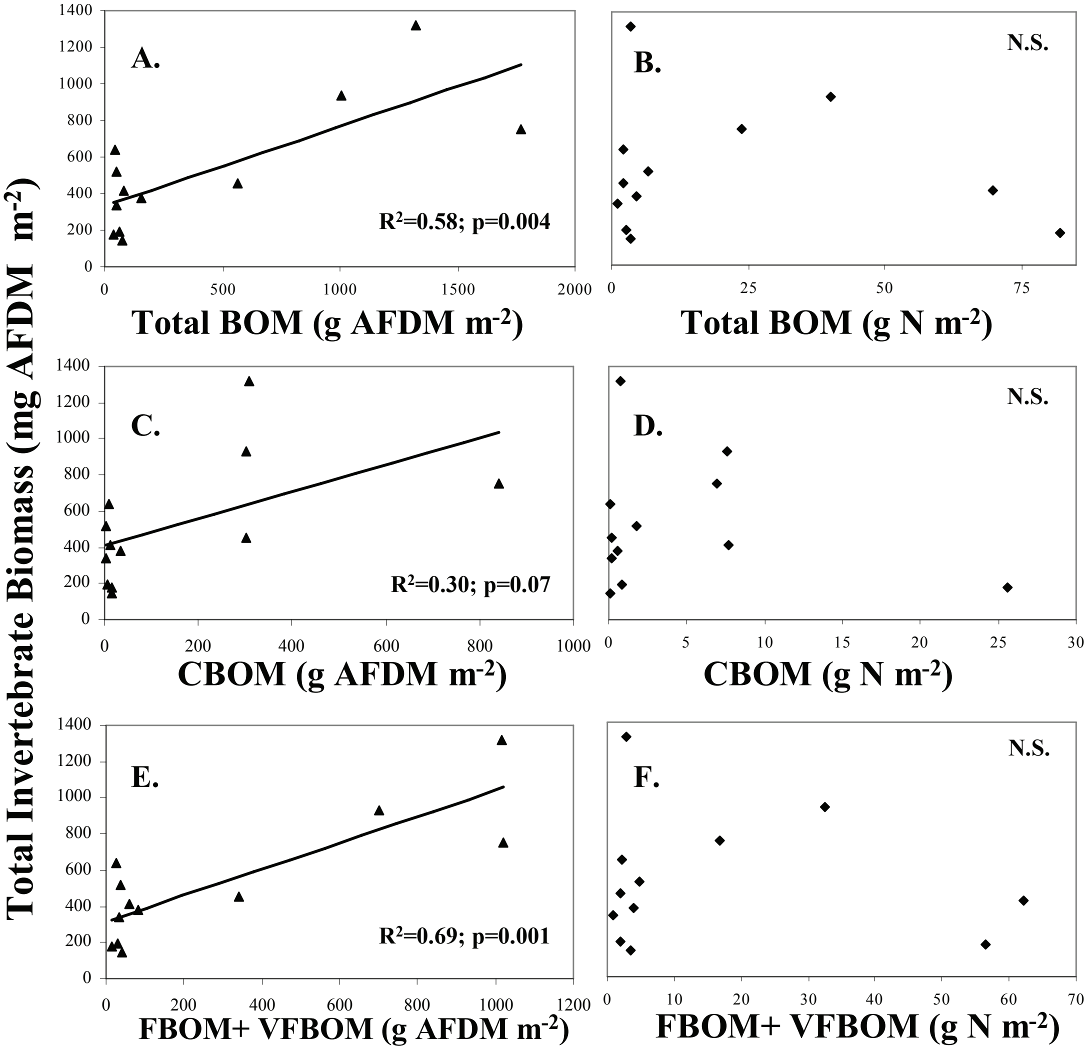
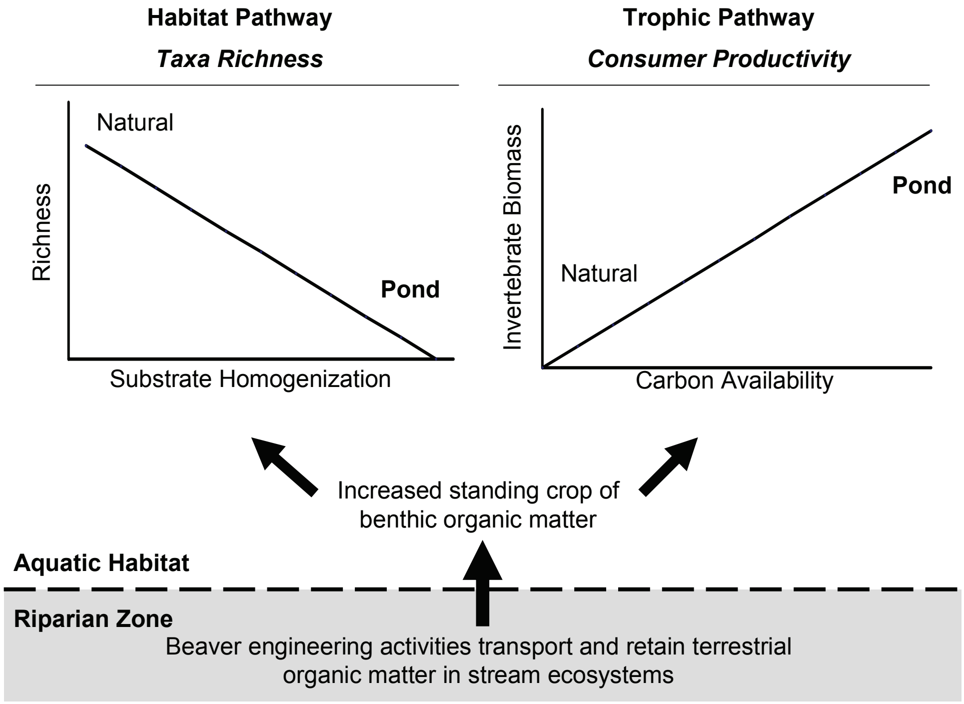

Total Invertebrate Biomass (mg AFDM m-2)
A.
R2=0.58; p=0.004
Total BOM (g AFDM m-2)
B.
N.S.
Total BOM (g N m-2)
C.
R2=0.30; p=0.07
CBOM (g AFDM m-2)
D.
N.S.
CBOM (g N m-2)
E.
R2=0.69; p=0.001
FBOM+ VFBOM (g AFDM m-2)
F.
N.S.
FBOM+ VFBOM (g N m-2)
0
200
400
600
800
1000
1200
1400
0
500
1000
1500
2000
25
50
75
600
800
1000
5
10
15
20
30
40
50
60
70

Figure 4.5. Mechanistic explanation of observed beaver-induced changes to taxa richness and secondary production following proposed pathways for the general effect of invasive ecosystem engineers on community and ecosystem properties (Crooks 2002). Benthic invertebrate richness was lowest in beaver ponds, where substrate heterogeneity was reduced due to organic matter cover. In contrast, consumer biomass increased in beaver ponds as a function of increased benthic organic matter retention.


Habitat Pathway
Taxa Richness
Natural
Richness
Pond
Substrate Homogenization
Trophic Pathway
Consumer Productivity
Invertebrate Biomass
Pond
Natural
Carbon Availability
Increased standing crop of benthic organic matter
Aquatic Habitat
Riparian Zone
Beaver engineering activities transport and retain terrestrial organic matter in stream ecosystems

Appendix 4.1. Total list of all taxa described during the course of the study in natural (N), beaver pond (P) and downstream (D) sites. FFG refers to functional feeding group: par = parasite, pred = predator, gath = collector-gather, fil = collector-filterer, sc = scraper and sh = shredder.

Class/Order	**Family**	**Sub-Family**	***Genus***	***Species***	**FFG**	**N**	**P**	**D**
Annelida/ Hirudinae					par-pred	X	X	X
Oligochaete					gath, pred	X	X	X
Arthropoda/ Collembola	Entomobryomorpha				gath, pred	X	X	X
Hydracarina					par-pred	X	X	X
Crustacea/ Amphipoda	Hyalellidae		*Hyalella*	*simplex* Schellenberg	gath	X	X	X
Copepoda					gath	X	X	X
Ostracoda					gath	X	X	X
Insecta/ Coleoptera	Dytiscidae		*Lancetes*	sp.	pred	X	X	
	Elmidae		*Luchoelmis*	sp.	sc	X		X
Diptera	Blephariceridae		*Edwarsina*	sp.	sc	X		
	Ceratopogoniidae				pred	X	X	X
	Chironomidae	Aphroteniinae	*Aphroteniella*	sp.	gath	X		X
		Chironominae	*Chironomini*	sp.	gath	X	X	X
		Orthocladiinae	Multiple genera		gath	X	X	X
		Podonominae	*Podonomus*	sp.	gath	X	X	X
		Tanypodinae	Multiple genera		pred	X	X	X
	Empididae		*Hemerodromia*	sp.	pred	X	X	X
	Ephydridae					X		
	Muscidae					X		
	Simuliidae		*Gigantodax*	Bryophii complex (*rufescens* Edwards & *antarcticus* Bigot)	fil	X	X	X
	Tipulidae		*Hexatoma*	sp.	gath, pred	X	X	X

Appendix 4.1. (cont.)

			Tipula	sp.	gath	X	X	X
Ephemeroptera	Baetidae		*Andesiops*	*torrens* Lugo-Ortiz & McCafferty	sc	X	X	X
	Leptophlebiidae		*Meridialaris*	spp.	sc	X	X	X
			Massartellopsis	*irarrazavali* Demoulin	sc	X	X	X
Hemiptera	Corixidae		*Corixa*	sp.	pred		X	X
Plecoptera	Gripopterygidae		*Antarctoperla*	*michaelseni* Klapálek	gath, sh	X		X
			Limnoperla	*jaffueli* Navás	gath	X	X	X
			Rhithroperla	*rossi* Froehlich	gath	X	X	X
			Pelurgoperla	sp.	gath	X	X	X
Trichoptera	Glossosomatidae		*Matigoptila*	*brevicornuta* Schmid	sc	X		X
	Hydrobiosidae		*Rheochorema*	*magellanicum* Flint	pred	X	X	X
	Limnephilidae		*Monocosmoecus*	*hyadesi* Mabille	sh	X	X	X
Mollusca/ Bivalva	Sphaeriidae		*Pisidium*	*magellanicum* Dall	fil		X	X
Gastropoda	Lymnaeidae		*Lymnaea*	sp.	sc	X	X	X
				35 Taxa Total		**33**	**28**	**31**

CHAPTER 5

EXOTIC BEAVERS ALTER THE MAGNITUDE OF TERRESTRIAL SUBSIDIES AND ENERGY FLOW PATHWAYS IN SUBANTARCTIC STREAM FOOD WEBS[1]

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[1] Anderson, C.B. and A.D. Rosemond. To be submitted to *Oikos*.

Abstract

Exotic species alter biotic assemblages and ecosystems worldwide. Invasive ecosystem engineers have the ability to affect interactions even across ecosystem boundaries, due to their ability to influence entire landscapes. To address the impact of invasive exotic North American beavers on streams in the Cape Horn Biosphere Reserve, Chile, we studied beaver-related habitat types that included 1) unimpacted, forested stream reaches, 2) beaver ponds and 3) stream sections downstream of the pond. We assessed the effects of beaver modifications to stream food webs by quantifying the magnitude and sources of organic matter flow using stable isotope and trophic basis of production techniques. Isotopic signatures of resource types did not differ significantly among habitat types, but there was a trend for invertebrate consumers to have more negative $\delta^{13}C$ signatures downstream of beaver ponds. Invertebrate diet composition did not differ among habitat types, and amorphous detritus was the most important food type for all taxa at all sites. Beaver modifications caused an increase in organic matter flow to consumers in pond habitats by an order of magnitude, but also decreased the number of flow pathways by reducing taxonomic richness of invertebrates and the number of functional feeding groups found in ponds. Downstream food webs were largely similar to natural reaches, despite our prediction that canopy removal would increase dependence on primary production. Our findings show that subantarctic streams are driven by allochthonous energy sources and that an invasive ecosystem engineer, the North American beaver, impacts these stream food webs via enhancement of cross-boundary organic matter subsidies.

Key words: Cape Horn Biosphere Reserve, *Castor canadensis*, invasion, resource subsidies, terrestrial-aquatic linkages

Introduction

Exotic species are a major contributor to the rapid, global-scale alteration observed in aquatic biotic assemblages (Allan and Flecker 1993). Impacts of exotic species, combined with human-mediated climate and habitat alterations, are also identified as a principal cause of global ecological change (Vitousek et al. 1996), and invasive species have been shown to dramatically affect ecosystem level processes (e.g., Strayer et al. 1999, Simon et al. 2004). The mechanisms by which invasion can alter ecosystems include changes in resource availability, food web dynamics and disturbance regimes (Vitousek 1990). In particular, ecosystem engineers can be especially influential in affecting resource subsidies and food webs, due to their ability to modify habitats and entire landscapes (Crooks 2002).

It has long been recognized that the structure and function of fluvial ecosystems are a complex interaction of landscape level processes taking place between fluvial and terrestrial habitats (Likens and Bormann 1974, Hynes 1975, Vannote et al. 1980). While streams draining many forested biomes depend heavily on energy subsidies from the terrestrial landscape (Fisher and Likens 1973, Wallace et al. 1997, 1999), fluvial ecosystems in other ecoregions have important autochthonous energy sources (Minshall 1978, Minshall et al. 1992). Today, various aspects of global change associated with human impacts, such as riparian habitat degradation and nutrient enrichment, influence these terrestrial-aquatic linkages (Naiman and Décamps 1997, Cross 2004). However, it has also been shown recently that species invasions of stream ecosystems can even affect the transboundary flow of subsidies between streams and adjacent riparian zones (Baxter et al. 2004).

The extent of species invasions is not only a problem in areas of high human impact or colonization; even in otherwise remote areas, introduced species are able to arrive, naturalize and sometimes become invasive. Overall, the Magellanic Sub-Antarctic Forest Biome of southern South America is generally considered to be highly pristine with an exceptionally large percentage of state protected wilderness areas (Mittermeier et al. 2001, Rozzi et al. 2006). However, the Cape Horn Biosphere Reserve portion of this biome is also replete with introduced species (Anderson et al. 2006b). Among this exotic assemblage, the beaver merits particular attention from ecologists and managers for being an ecosystem engineer, potentially affecting both terrestrial and aquatic ecosystems.

In North America, it has been shown that beavers can have ecosystem impacts ranging from abiotic changes that alter basal resource type and standing crop (Naiman et al. 1986), stream geomorphology (Meetenmeyer and Butler 1999), and water and soil chemistry (Naiman et al. 1994, Margolis et al. 2001) to impacts on habitat that consequently shift stream benthic invertebrate communities from lotic to lentic taxa (Pollock et al. 1995). Generally, beaver modifications favor collector-gatherer and predatory functional feeding groups (McDowell and Naiman 1986), and the overall impact of beaver engineering is to make streams more retentive and thus potentially more productive (Naiman et al. 1984, Chapter 4) and resilient to disturbance (Naiman et al. 1988). However, to date, no studies have attempted to quantitatively measure food webs dynamics of material flows and pathways in either the beaver's native or introduced range.

A number of methods have been developed to generate quantitative food webs. Stable isotope analysis has become one of the most common food web analysis techniques because it integrates changes in diet and trophic status over time. However, it is based on expectations that isotopic signatures of dietary assimilation and trophic position occur in a predictable manner (Petersen and Fry 1987). This assumption, however, can be tenuous since elimination rates after dietary change can be variable for different parts of the same individual (Hamilton et al. 2004, Logan et al. 2006, MacNeil et al. 2006) and trophic fractionation, particularly for insects, may not correspond to generally used estimates (Cattaneo et al. 2004). Another useful method, known as the trophic basis of production (Benke and Wallace 1980), has also been used effectively to determine quantitative food web dynamics along a stream continuum (Hall et al. 2001, Rosi-Marshall and Wallace 2002), under an increased nutrient regime (Cross 2004), with a reduced resource base (Hall et al. 2000, Eggert 2003) and due to impacts caused by pollution and metal contamination (Shieh et al. 2002, Carlisle and Clements 2003). This procedure relies on estimates of assimilation efficiencies, when directly measured values are not available. It also cannot usually quantify microbial contents in guts (but see Hall et al. 2000 and Cross 2004). Here, we used both approaches to strengthen our ability to achieve the most complete quantification possible of food web dynamics.

We examined how invasive exotic beavers impacted benthic food webs dynamics by focusing on (a) alteration of the energy base and (b) modification of organic matter flow dynamics in subantarctic streams. To evaluate these factors, we determined the relative contribution of basal resource components to consumers using stable isotope techniques and the trophic basis of production method. Our study is designed to evaluate how introduced beavers influence transboundary dynamics of subantarctic streams and also to provide new information on the structure and function of lotic ecosystems at the far southern tip of the American Continent.

Materials and Methods

Study site

This study was conducted on Navarino Island (2,528 km^2) in the Cape Horn Biosphere Reserve, south of the Beagle Channel and north of Cape Horn Island, Chile (approx. 55°S) (Figure 5.1). Elevations on the island range from 0-1000 m.a.s.l. with tree line at approximately 450 m. Short, cool summers (mean temperature 9^{o}C) and long, cooler winters (mean temperature 2^{o}C) characterize the study area, which receives about 500-650 mm of precipitation annually (Tuhkanen et al. 1989). Average stream water temperature was 4.5^{o}C and degree days above 0^{o}C ranged from 1781 in natural sites to 1853 in beaver ponds (Chapter 4). This area is the world's southernmost forested ecosystem, known as the Magellanic Sub-Antarctic Forest Biome and is part of the South American temperate forests that occur between 35^{o} and 56^{o} S latitude (Armesto et al. 1995, Veblen et al. 1996). Twenty-five mating pairs of *C. canadensis* were introduced to Tierra del Fuego Island in 1946, and they now have colonized most of the archipelago, and possibly the mainland (Lizarralde 1993, Skewes et al. 1999, Anderson et al. 2006b).

Four streams were studied on the north coast of Navarino Island at elevations below 100 m in mixed forest-bog watersheds. Study reaches were in the forested portion of catchments with a mix of only two dominant tree species: the broadleaf evergreen *Nothofagus betuloides* (Mirbel) Oersted and its deciduous congener *N. pumilio* (Poepp. et Endl.) Krasser. The study watersheds were: Robalo (in the Omora Park Experimental Watershed), Mejillones, Estrella and Faraones. They displayed similar physico-chemical characteristics with the exception of dissolved organic carbon (DOC), which was higher in two streams (Table 5.1, data from Chapter 4). Two of these streams (Robalo and Mejillones) were selected for estimates of secondary production and trophic basis of production. Robalo and Mejillones were used because they represented the two major stream types on the island: clear water and tannin-enriched, respectively. Each stream had three sampling locations that corresponded to: (1) a natural, forested reach never impacted by beavers ('natural'), (2) an active beaver pond ('pond') and (3) a site immediately downstream of the beaver dam ('downstream'). The beaver-impacted sites were previously forested before beaver colonization, as evidenced by the geomorphology of the site and the presence of standing dead tree trunks to the edge of the river.

Resource base and energy flows

Stable isotopes: Basal resources and major invertebrate taxa were collected from each site in the three seasons and analyzed for their stable isotopic signatures ($\delta^{13}C$ and $\delta^{15}N$). VFBOM, biofilm and seston were collected on pre-ashed filters (0.7 μm, Whatman GF/F), and all other samples were collected in 20 ml scintillation vials. The guts of invertebrates were removed before freezing. They were then dried at 70^{o}C at UMAG and transported to UGA, where they were homogenized with a ball mill (CertiPred 8000-D

Mixer Mill), weighed on a micro-balance (Sartorius M2P) and analyzed using a mass-spectrometer (Finnigan Delta Plus).

Diet analysis: To determine the diet of primary consumers, we collected dominant benthic taxa in the Robalo and Mejillones Rivers during the three seasons. Specimens were collected and preserved in Kahle's solution each season. In the laboratory, gut contents were dissected from four individuals per taxon per season under a dissecting microscope. The contents were sonicated and then fixed onto microscope slides. Using ImagePro® 5.1.1 image analysis software, slides were digitized and categorized under a phase contrast microscope (Olympus® BX40) as i) amorphous detritus (i.e. without cellular structure), ii) leaf, iii) wood, iv) diatom, v) fungi or vi) animal material. Filamentous algae were never found in guts. Predators were assumed to consume only animal material.

Trophic basis of production: We used the trophic basis of production method to quantify the resource base and organic matter flow in the food webs of the Robalo and Mejillones study sites (Benke and Wallace 1980, 1997). The secondary production values for each taxon were obtained from Anderson and Rosemond (Chapter 4). Assimilation efficiencies (AE) were based on published values: 10% for leaves, wood and amorphous detritus, 30% for diatoms, 50% for fungi, and 80% for animal material, and the net production efficiency (NPE) was estimated to be 0.4 (Benke and Wallace 1980).

The fraction of invertebrate production derived from a food type was calculated by multiplying its proportional area in the gut by the assimilation efficiency for that food type and again multiplying by the net production efficiency: $F_i = (G_i \times AE_i \times NPE)$, where F_i = fraction of production from food type i, G_i = percent of food type i in gut contents (mean annual percent), AE_i = assimilation efficiency for food type i, and NPE = net production efficiency. This was then converted to a relative proportion compared to all food types (PF_i) by simply dividing the fraction of production of food type i by the sum of all food types ($PF_i = F_i/\sum F_{(i\ldots n)}$). Finally, organic matter flows to and between consumers were estimated as the consumption of each food type required to support the calculated values of production: $C_i = (PF_i \text{ x } P) / (AE_i \text{ x } NPE)$, where C_i = the amount consumed of food type i, and P = secondary production of the consumer. Values for the trophic basis of production are reported as g AFDM m^{-2} y^{-1}. From these data, energy flow pathways and magnitude were compared between habitat types, accounting for the flow from specific basal resource categories to particular taxa and functional feeding groups. We also determined the proportional contribution of terrestrial versus autochthonous resources to total community secondary production.

Statistical analyses

Consumer $\delta^{13}C$ values were corrected by 0.4‰ fractionation for each trophic level before analysis (Post 2002). A two-way ANOVA was used to detect differences in the stable carbon isotopic signatures as described above. Mixing models could not be used to determine the amount of production supported by particular food sources because basal resources could not be significantly distinguished (see Results). Mean $\delta^{13}C$ and $\delta^{15}N$ (±SE) were calculated and graphed in a scatter plot to assess qualitative differences between resources and consumers at different habitat types.

Gut contents were quantified as the mean percentage area of particles from each category, and the relative proportion of each diet category for each functional feeding group was then compared between habitat types within each stream using non-parametric Kruskal-Wallis ranked-sum tests.

To test the effect of basal resource modifications as a driver of benthic invertebrate production, we regressed basal resource standing crop (g AFDM m^{-2}) and nutrient availability (g N m^{-2}) with estimates of invertebrate biomass from sites at all four study streams. Biomass data for benthos were taken from Anderson and Rosemond (Chapter 4) and were derived from seasonal samples from the three habitat types in our four study streams (n=36) that estimated mean annual biomass based on length-mass regressions developed by Benke et al. (1999) and Miserendino (2001).

Results

Invertebrate diet

Stable isotopes: For all basal resources at all sites, isotopic analysis found that the origin of organic matter was primarily terrestrial ($\delta^{13}C$ = approximately -28‰) (Table 5.2), and we were therefore not able to differentiate the signature basal resources with stable carbon isotope signatures. CBOM $\delta^{13}C$ was significantly affected by a habitat*season interaction effect ($F_{season*habitat}$=13.45, d.f. 4, p<0.0001) whereby at natural sites it was significantly more negative in fall (-30.6 ±0.2). The depletion of $\delta^{13}C$ of CBOM in natural streams in May (fall) coincided with the signature of fresh autumnal leaf litter [mean *Nothofagus* leaf $\delta^{13}C$ = -30.4‰ (±0.4)]. FBOM, VFBOM, biofilm and seston showed no habitat or season effects (p>0.05).

Stable isotope values of consumers and basal resources in each habitat type were compared in scatter plots (Figure 5.2). Values for $\delta^{15}N$ generally showed that predatory taxa, such as leeches, the caddisfly *Rheochorema magellanicum* Flint and the diving beetle *Lancetes* sp., had the highest trophic positions. The graphs also showed that the assemblage in downstream and natural sites had more depleted values of $\delta^{13}C$ than ponds (Table 5.2). Since basal resources could not be differentiated, we could not use stable isotope mixing models for subsequent analyses of contribution of particular basal resources to consumers. We also were not able to detect in the basal resources we collected any values that were as negative as some consumers found in downstream habitats.

Gut analysis: The six major taxa whose gut contents we examined constituted >75% of the annual secondary production in each habitat type in both the Mejillones and Robalo Rivers (Chapter 4). Diet did not significantly vary between habitats within a stream for a particular taxon or functional feeding group (Figure 5.3, $p>0.05$). At all sites in both rivers, all functional feeding groups' guts contained predominantly amorphous detritus, being greater than 50% of stomach contents of scrapers, filterers and collector-gatherers and between 38-42% in shredders (Figure 5.3A-D). The only two taxa that were abundant in all three habitat types were collector-gatherer amphipods (*Hyalella simplex* Schellenberg) and non-Tanypodinae chironomids; neither of these showed a shift in diet as a function of beaver modifications associated with habitat types (Figure 5.3, $p>0.05$). Filterers had the greatest amount of diatoms in their guts with 22-26% in natural sites and 22-35% at downstream reaches (Figure 5.3B). Scrapers, on the other hand, had comparatively low diatom content with only 7-14% in natural sites and 3-24%

in downstream sections, depending instead on amorphous detritus (75-82% in natural and 92-97% in downstream sites) (Figure 5.3C). For shredders, leaf material constituted between 36-77% of contents (Figure 5.3D).

Energy flow magnitudes and pathways

The amount of secondary production supported by individual food types differed from their contribution to diet as a result of differential assimilation efficiencies for resources, as well as differing contribution of individual taxa to overall production. Similar to results for diet composition, the most important energy source contributing to secondary production was amorphous detritus, which was the source of more than 50% of primary consumer production (Figure 5.4). For gatherers and scrapers at both rivers (53-81% for gatherers and 50-92% for scrapers) amorphous detritus constituted their principle energy source. Filterers had the largest amount of production based on diatoms (as much as 51%) of any functional feeding group. The trophic basis of production of shredders was divided between amorphous detritus (9-55%), leaves (26-77%) and the downstream site on the Robalo River shredders also had a high percentage of production derived from diatoms (36%). Both natural and downstream sites had an overall larger portion of secondary production based on autochthonous energy sources (i.e. diatoms = 13-27%), compared to ponds (6-9%), but this effect was reduced in the Mejillones River, whose water was darkened by tannins from wetlands in the upper part of its watershed (Figure 5.4).

The number of energy pathways decreased in ponds, due to the overall reduction in taxa and functional feeding groups (Figures 5.5A and B), compared to the other two sites. The only two functional feeding groups and energy pathways that constituted more than 1% of the energy flow in ponds were collector-gatherers and predators, while downstream and natural sites had a complete assemblage of functional feeding groups. In contrast, the total amount of matter flow increased in ponds and was intermediate in downstream sites (Table 5.3). Total organic matter flow from consumption to invertebrates increased from 3.8-5x in ponds, while downstream sites had 1.1-2.1x enhanced flows compared to natural sites (Table 5.4). The food type that had the greatest increase in flow magnitude was amorphous detritus, which was enhanced by 4.9-5.8x in ponds relative to natural sites (Table 5.4). Increases in basal resource standing crop and consumption showed similar patterns in terms of the magnitude of increase, but were less for consumption (Table 5.4).

Discussion

Beaver-mediated habitat modifications have been shown to increase the retentiveness of streams (Naiman et al. 1986) and to alter the land/water interface (Johnston and Naiman 1987) in their native habitat. Our work shows that beaver invasion of subantarctic watersheds has had especially strong effects on resource subsidies and energy flow dynamics in streams. Information from stable isotopes, invertebrate gut contents, and the trophic basis of production all indicated that these subantarctic streams depend predominantly on terrestrially-derived organic matter as the energy base of their food webs, like forested streams in other biomes (Fisher and Likens 1972, Vannote et al. 1980, Wallace et al. 1997, 1999). Beavers' engineering in this non-native habitat caused an increase in the magnitudes of terrestrially-derived resources flowing through benthic food webs compared to unaffected streams.

While beaver modifications led to an order of magnitude increase in energy flows in the benthic food webs of pond habitats, they also reduced the number of flow pathways. Although beavers strongly changed benthic communities in ponds, the impact was quickly mitigated downstream; reaches below the dam demonstrated basal resource and energy flow characteristics that were similar to unimpacted sites. The majority of organic matter passed through collector-gatherers at all sites, and amorphous detritus was the principal basal resource for primary consumers in all habitat types. However, as a proportion of energy flow, amorphous detritus was a greater percent of consumption in ponds compared to natural and downstream habitats.

An increased proportion of amorphous detritus in the trophic basis of production has also been found along a downstream gradient, shifting from dependence on leaf material at low order sites, to diatoms at intermediate sites and finally to amorphous detritus at higher stream orders (Rosi-Marshall and Wallace 2002) in agreement with River Continuum Concept (RCC) predictions of changes in energy base and fauna along a stream continua (Vannote et al. 1980). Here, we likewise saw that beaver activities enhanced the importance of amorphous detritus to the trophic basis of production in ponds, which coincides with the assertion that pond benthic assemblages are representative of higher order streams (Pollock et al. 1995). This impact was not observed at downstream sites. However, Rosi-Marshall and Wallace (2002) also found that energy flow increased along a stream continuum from 5th to 7th order streams by about 20x, while the changes wrought by beaver in our study ponds only increased consumptive flows by 3-5x.

An additional comparison of our results with biogeographically similar streams in New Zealand showed that both benthic invertebrate communities were dominated by generalist taxa that depend predominantly on fine benthic organic matter and biofilm basal resources (Winterbourn and Ryan 1994). Like subantarctic streams, the river systems in the southern part of New Zealand arise above tree line in steep, alpine catchments that are relatively short and dominated by southern beech (*Nothofagus* Blume) forests. New Zealand's biogeography, evolutionary history, geomorphology and biotic assemblage all are very similar to southern Chile, and these results demonstrated that further ecological comparison of streams should be explored in future work.

The trophic transfer of primary consumer production to invertebrate predators increased by an order of magnitude in ponds relative to unimpacted sites (Table 5.3). However, as an overall percentage of organic matter flow and secondary production, benthic predatory taxa were always a very small fraction. These findings contrast with other studies that quantified flow in benthic invertebrate food webs and found that predators consumed nearly 100% of invertebrate production (Wallace et al. 1997, Hall et al. 2000, Cross 2004). The other potentially significant predators of benthic invertebrates in the Cape Horn archipelago that were not accounted for here include a few native (*Galaxias maculatus* Jenyns, *Aplochiton taeniatus* Jenyns, *Aplochiton zebra* Jenyns) and exotic (*S. fontinalis* and *O. mykiss*) freshwater fish species, but these do not occur in all streams in this area (Anderson et al. 2006b).

While the fate of some invertebrate production undoubtedly goes to these vertebrate predators, we know that insect emergence is also a significant link between aquatic and riparian ecosystems in the form of an aquatic prey subsidy to riparian consumers (Sabo and Power 2002, Sanzone et al. 2003). It has been found that from 2-29% of instream production ultimately results in emergence (Jackson and Fisher 1986), and a study of *Baetis* spp. (Ephemeroptera) reported that up to 98% of adult emergence was consumed in the adjacent terrestrial zone, rather than returning to the stream (Werneke and Zwick 1992). It is unclear whether or not beaver modifications would increase insect emergence, and thus enhance aquatic-terrestrial linkages in the same way that they enhanced the flow of terrestrially-derived organic matter to benthic food webs. Two of the most productive taxa found in ponds in our study do not leave the water as adults (*H. simplex* and Oligochaeta), like many insects. Naiman et al. (1984) also found no consistent pattern of insect emergence as either abundance or biomass from beaver ponds compared to adjacent riffles, but Roulaffs et al. (2001) reported that beaver dams had 5x greater emergence than adjacent riffles and 5.4x greater than the pond itself. Determining the fate of benthic secondary production will be key in further elucidating the potential instream and transboundary effects of beaver in subantarctic ecosystems.

The trophic basis of production method proved to be a useful tool to integrate disparate aspects of food webs by combining estimates of secondary production, diet and assimilation to determine material flows and pathways in this study. Since the technique was first developed (Benke and Wallace 1980), it has been employed to test the effects of different kinds of environmental change in streams (Hall et al. 2000, Rosi-Marshall and Wallace 2002, Shieh et al. 2002, Carlisle and Clements 2003, Eggert 2003, Cross 2004).

This approach allowed us to estimate energy flows from particular food resources that would not have been possible using stable isotopes, since we were unable to differentiate basal resources. Nonetheless, the trophic basis of production method had the disadvantage of not assessing the microbial contribution to dietary components (but see Hall et al. 2000 and Cross 2004). Using complementary stable isotopes analyses, we were able to detect highly depleted carbon signatures of consumers in downstream sites. Methanotrophic bacteria from anoxic habitats, such as *Sphagnum* bogs, have previously been shown to produce benthic invertebrate $\delta^{13}C$ values as low as -54‰ (Kohzu et al. 2004). On the other hand, these values could simply be the result of changes in the $\delta^{13}C$ of periphyton, which is known to respond to changing habitat conditions, such as flow and dissolved carbon (Findlay 2004). At this time we are unable to determine the source of this negative signature using either of our analyses.

In conclusion, energy flow modification via the alteration of food web dynamics and resource subsidies is an important way that exotic species can affect the ecosystems they invade (Vitousek 1990, Baxter et al. 2004). North American beavers have inhabited the extreme southern tip of Chile and Argentina for over fifty years, and in that time they have colonized most of the archipelago and become a major structuring influence on biota and ecosystems. Their impacts have caused extensive deforestation with limited regeneration, while at the same time permitting the establishment of exotic plants in riparian zones (Martínez Pastur et al. 2006, Anderson et al. 2006a). Here, we have shown that the introduced North American beaver's engineering impacts also affect terrestrial-aquatic linkages that ultimately influence benthic food web dynamics. Future work will determine whether or not there is also a reciprocal subsidy to adjacent riparian zones associated with beaver ponds in the form of insect emergence.

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Table 5.1. Physical and chemical characterization of the four study streams. Yearly means (n=6) are presented with (±1 SE); all other values are from one sample period. Data was missing from Estella Stream for some variables (---).

Characteristic	**Robalo**	**Estrella**	**Mejillones**	**Faraones**
Latitude	54°57”15.0’ S	54°55”34.8’ S	54°54”33.7’ S	54°54”20.0’ S
Longitude	67°38”70.5’ W	67°45”18.2’ W	67°59”97.8’ W	68°04”96.7’ W
% Canopy cover	56.3 (9.3)	80.5 (2.6)	68.2 (7.2)	72.8 (11.3)
Slope (m m^{-1})	0.02	0.04	0.02	0.05
Temperature (°C)	4.4 (2)	---	4.8 (2.2)	4.5 (2.2)
Conductivity (µS cm^{-1})	68.7	---	130	156
pH	7.71	---	7.48	7.03
DO (mg L^{-1})	10.3	---	10.1	8.3
N-NO$_3$ (ppm)	0.06 (0.02)	0.03 (0.01)	0.04 (0.01)	0.06 (0.02)
DOC (ppm)	5.0 (1.5)	3.9 (1.1)	24.2 (8.1)	23.9 (6.9)
Substrate	s,g,c	s,g,c	s,g,c	g,c

DO = dissolved oxygen, N- NO$_3$ = nitrate, DOC = dissolved organic carbon, s = sand, g = gravel and c = cobble.

Table 5.2. The mean $\delta^{13}C$ (‰) at natural, pond and downstream sites (±SE). ANOVA results are as in Table 5.2.

Category	**Natural**	**Beaver Pond**	**Downstream**	$F_{habitat}$	p
CBOM	-29.1 (0.53)^{A}	-28.4 (0.2)^{B}	-28.3 (0.13)^{B}	11.72	**0.006**
FBOM	-27.4 (0.1)^{A}	-27.7 (0.3)^{A}	-27.6 (0.2)^{A}	1.2	0.32
VFBOM	-26.9 (0.4)^{A}	-27.5 (0.2)^{A}	-26.9 (0.5)^{A}	0.282	0.76
Biofilm	-28 (0.6)^{A}	NA	-27.3 (0.9)^{A}	0.018	0.9
Seston	-27.0 (0.9)^{A}	-27.1 (0.7)^{A}	-26.6(1.1)^{A}	0.11	0.9
Lancetes sp.	NA	-29.6 (1.1)	NA	---	---
H. simplex	-27.44 (0.74)^{A}	-28.29 (1.14)^{AB}	-29.73 (1.1)^{B}	5.4139	**0.01**
Gigantodax spp.	-30.38 (0.46)^{A}		-32.43 (2.05)^{A}	2.87	0.12
Massartellopsis spp.	-30.69 (1.56)^{A}		-33.53 (1.06)^{B}	12.39	**0.004**
R. magellanicum	-29.88 (0.9)^{A}		-31.45 (0.09)^{A}	2.0	0.2

CBOM: coarse benthic organic matter, FBOM: fine benthic organic matter; VFBOM: very fine benthic organic matter.

Table 5.3. Organic matter flow (consumption: g AFDM m^{-2} y^{-1}) from food categories to invertebrate consumers in natural, beaver pond and downstream sites from the Robalo and Mejillones Rivers.

Consumption flows						
	Robalo			**Mejillones**		
Food category	**Natural**	**Pond**	**Down**	**Natural**	**Pond**	**Down**
Amorphous detritus	27.94	137.31	62.08	40.43	237.11	44.46
Diatom	2.80	3.78	9.05	1.69	9.01	2.78
Leaf	12.11	24.91	23.58	8.00	21.32	9.84
Wood	2.18	5.46	4.56	1.19	3.13	0.52
Animal	0.03	0.56	0.07	0.30	3.24	0.23
Total Organic Flow	45.06	172.03	99.34	51.60	273.82	57.82
% Allochthonous	0.94	0.98	0.91	0.97	0.97	0.96
% Autochthonous	0.06	0.02	0.09	0.03	0.03	0.04

Table 5.4. Magnitude of change observed for beaver ponds (Pond) and downstream sites (Down) compared to natural reaches. Comparison was made for basal resource standing crop (g ash-free dry mass [AFDM] m^{-2}) and consumption flows (g AFDM m^{-2} y^{-1}).

	Robalo		**Mejillones**	
Standing crop	**Pond**	**Down**	**Pond**	**Down**
Wood	5.7	0.9	8.0	2.3
CBOM	32.9	2.7	84.0	3.5
FBOM	33.9	4.2	16.1	2.9
VFBOM	28.1	2.1	25.4	1.1
Biofilm	--	1.3	--	2.2
Invertebrate	19.8	0.09	18.4	0.08
Total	7.5	1.0	9.2	2.1
Consumption	**Pond**	**Down**	**Pond**	**Down**
Wood	2.5	2.1	2.6	0.4
Leaf	2.1	1.9	2.7	1.2
Amorphous	4.9	2.2	5.9	1.1
Diatom	1.4	3.2	5.3	1.6
Animal	18.7	2.3	10.8	0.8
Total	3.8	2.2	5.3	1.1

Figure 5.1. Map of southern South America, including the subantarctic Cape Horn Archipelago. Tierra del Fuego Island is divided between Chile and Argentina, but the remaining portion of the archipelago to the south of the Straits of Magellan is under Chilean sovereignty. Study sites were located on the north coast of Navarino Island, which is in the Cape Horn Biosphere Reserve (shaded area).

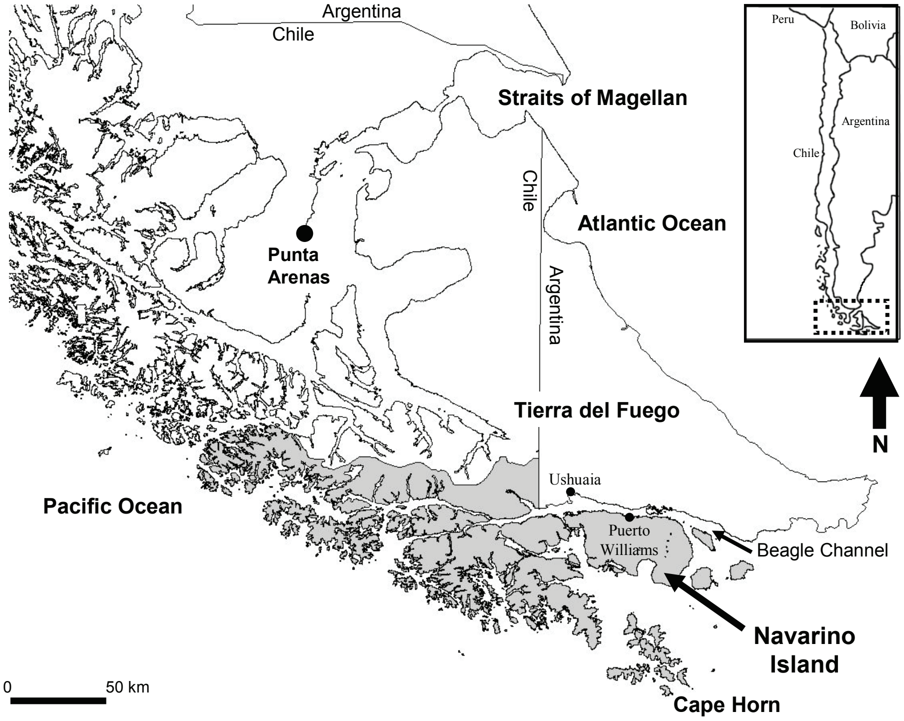

Argentina
Chile
Straits of Magellan
Chile
Argentina
Atlantic Ocean
Punta Arenas
Tierra del Fuego
Ushuaia
Pacific Ocean
Puerto Williams
Beagle Channel
Navarino Island
Cape Horn
0
50 km
Peru
Bolivia
Argentina
Chile
N

Figure 5.2. Scatter plots of $\delta^{13}C$ and $\delta^{15}N$ for three natural, pond and downstream sites (±SE). Square boxes represent benthic organic matter (CB: coarse benthic organic matter, FB: fine benthic organic matter, VF: very fine benthic organic matter); triangles are seston (Se); diamonds are biofilm (Bf); and circles indicate dominant taxa for each functional feeding group (Hs: *Hyalella simplex* [collector-gatherer], Le: leech [predator], Gi: *Gigantodax* spp. [filterer], Rm: *Rheochorema magellanicum* [predator], Da: Dytiscidae adult, *Lancetes* sp. [predator], Ma: *Massartellopsis* spp. [scraper], Mh: *Monocosmoecus hyadesi* [shredder]). $\delta^{13}C$ were corrected by 0.4‰ at each trophic level for trophic fractionation.

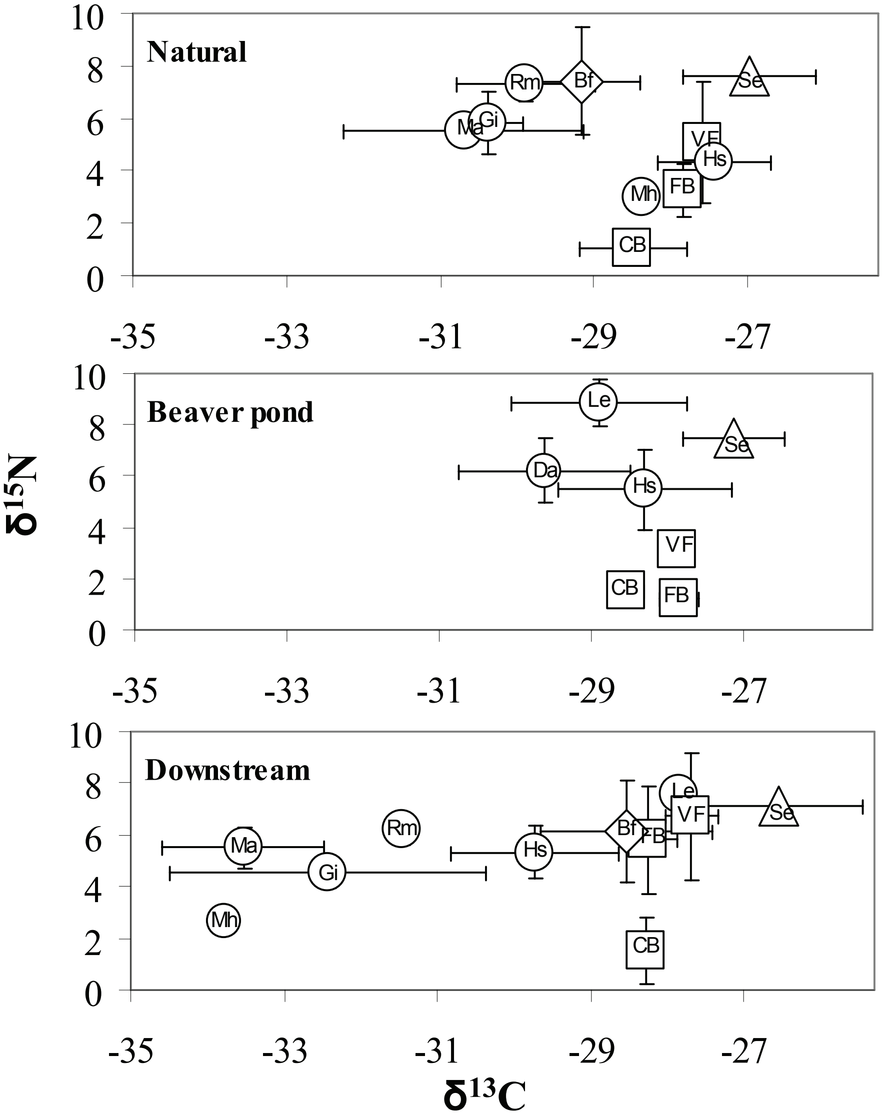

Natural
Beaver pond
Downstream
δ15N
δ13C
10
8
6
4
2
0
-35
-33
-31
-29
-27
Rm
Bf
Se
Ma
Gi
VF
Hs
FB
Mh
CB
Le
Da

Figure 5.3. The mean percent of gut contents for each food category for collector-gatherer, collector-filterer, scraper and shredder functional feeding groups from natural, pond and downstream sites Robalo and Mejillones Rivers.

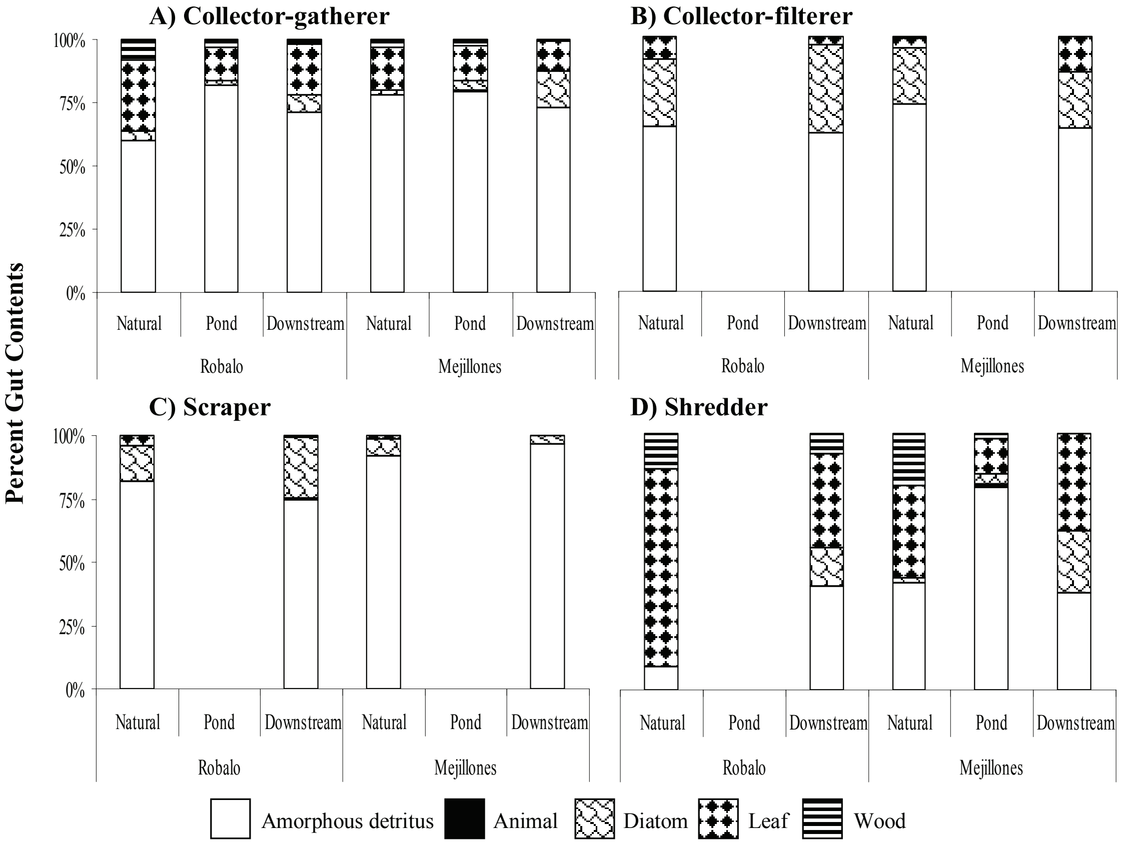

A) Collector-gatherer
B) Collector-filterer
C) Scraper
D) Shredder
Percent Gut Contents
100%
75%
50%
25%
0%
Natural
Pond
Downstream
Robalo
Mejillones
Amorphous detritus
Animal
Diatom
Leaf
Wood

Figure 5.4. The proportion of primary consumer production derived from basal resource food categories in natural, beaver pond and downstream sites at the Robalo and Mejillones Rivers.

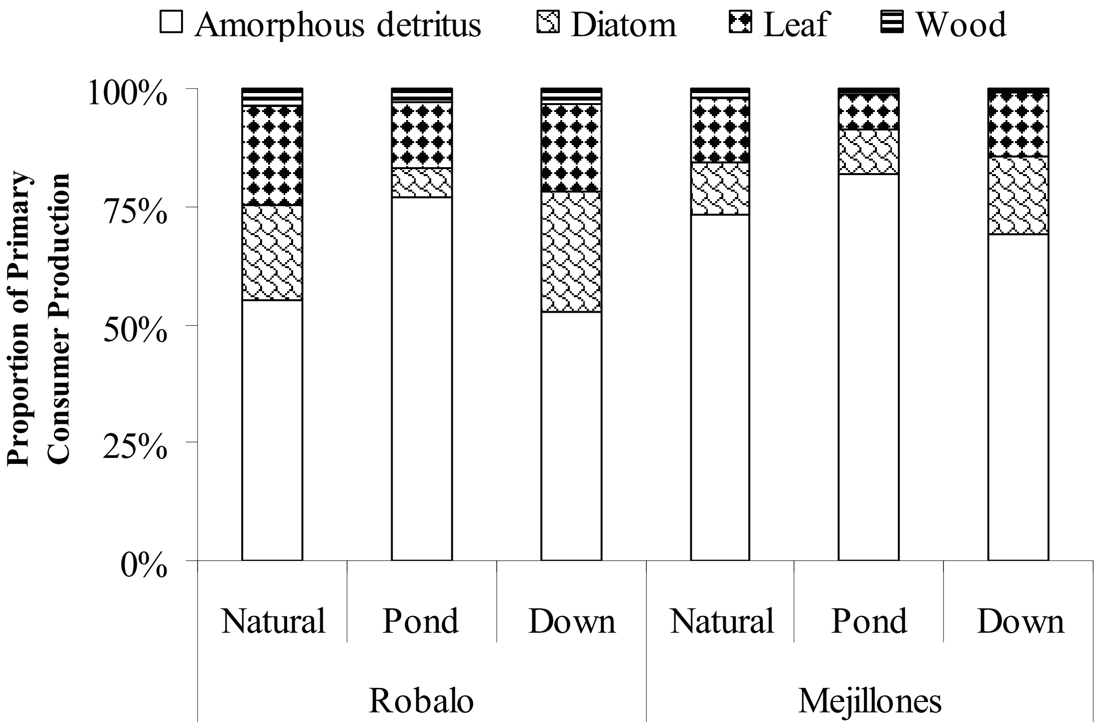

☐ Amorphous detritus
▨ Diatom
Leaf
Wood
Proportion of Primary Consumer Production
100%
75%
50%
25%
0%
Natural
Pond
Down
Natural
Pond
Down
Robalo
Mejillones

Figure 5.5A. Organic matter flows from basal resource food categories and secondary production of functional feeding groups (g AFDM m^{-2} y^{-1}) in natural, beaver pond and downstream sites for the Robalo River. Size of arrow indicates size of flow.

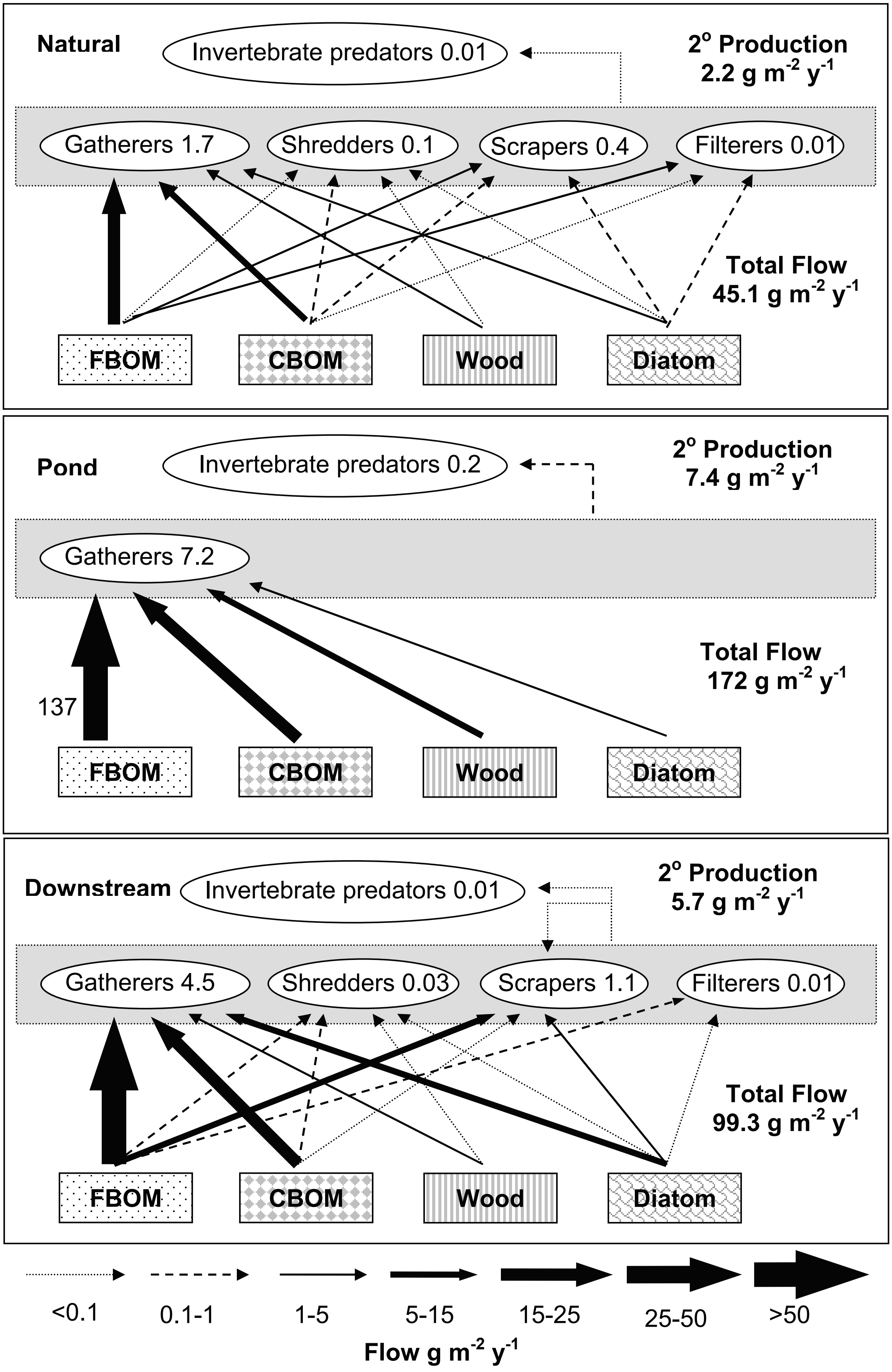
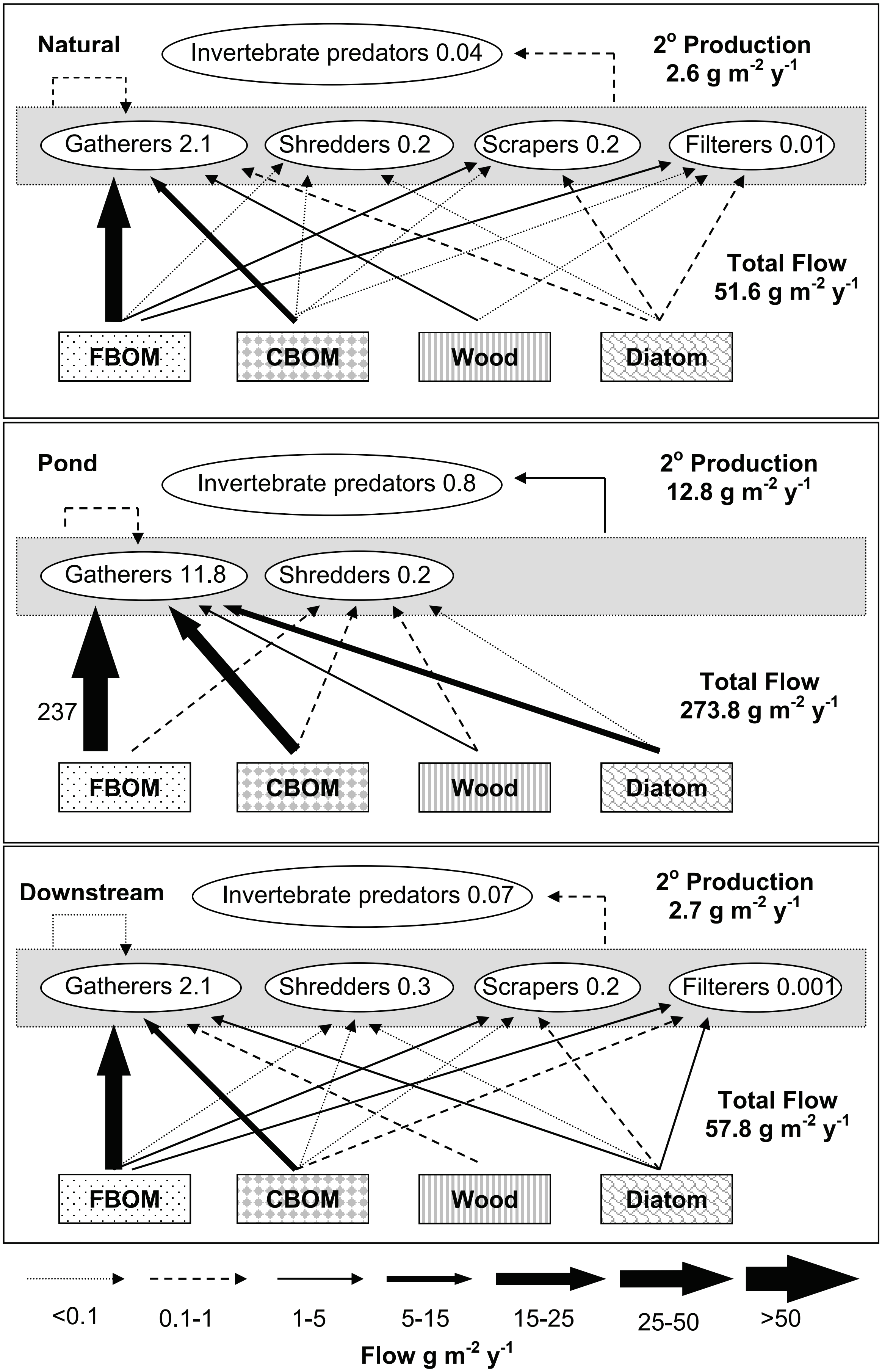

Natural
Invertebrate predators 0.01
2° Production
2.2 g m-2 y-1
Gatherers 1.7
Shredders 0.1
Scrapers 0.4
Filterers 0.01
Total Flow
45.1 g m-2 y-1
FBOM
CBOM
Wood
Diatom
Pond
Invertebrate predators 0.2
2° Production
7.4 g m-2 y-1
Gatherers 7.2
Total Flow
172 g m-2 y-1
137
FBOM
CBOM
Wood
Diatom
Downstream
Invertebrate predators 0.01
2° Production
5.7 g m-2 y-1
Gatherers 4.5
Shredders 0.03
Scrapers 1.1
Filterers 0.01
Total Flow
99.3 g m-2 y-1
FBOM
CBOM
Wood
Diatom
<0.1
0.1-1
1-5
5-15
15-25
25-50
>50
Flow g m-2 y-1

Figure 5.5B. Organic matter flows from basal resource food categories and secondary production of functional feeding groups (g AFDM m^{-2} y^{-1}) in natural, beaver pond and downstream sites for the Mejillones River. Size of arrow indicates flow quantity.


Natural
Invertebrate predators 0.04
2° Production
2.6 g m-2 y-1
Gatherers 2.1
Shredders 0.2
Scrapers 0.2
Filterers 0.01
Total Flow
51.6 g m-2 y-1
FBOM
CBOM
Wood
Diatom
Pond
Invertebrate predators 0.8
2° Production
12.8 g m-2 y-1
Gatherers 11.8
Shredders 0.2
237
Total Flow
273.8 g m-2 y-1
FBOM
CBOM
Wood
Diatom
Downstream
Invertebrate predators 0.07
2° Production
2.7 g m-2 y-1
Gatherers 2.1
Shredders 0.3
Scrapers 0.2
Filterers 0.001
Total Flow
57.8 g m-2 y-1
FBOM
CBOM
Wood
Diatom
<0.1
0.1-1
1-5
5-15
15-25
25-50
>50
Flow g m-2 y-1

CHAPTER 6

GENERAL CONCLUSIONS

Significance of this research

While much of the austral archipelago is uninhabited by humans, large parts are nonetheless used for forestry, ranching, fishing and tourism; all of these human activities influence the ecology and conservation of the area (Rozzi et al. 2004). Furthermore, the southern tip of Chile and Argentina is the only human populated area outside of Antarctica to receive the direct impact of the Antarctic Ozone Hole (Kirchhoff et al. 1997). In addition, the archipelago is replete with introduced species (Anderson et al. 2006). These threats highlight the global nature of today's ecological challenges, even in otherwise remote and "pristine" wilderness areas.

Exotic species invasion is a major driver of current global environmental change (Vitousek et al. 1996) and is particularly relevant to the Cape Horn Biosphere Reserve (Anderson et al. 2006b). However, not all introduced species cause significant impacts. Indeed most introductions actually fail to establish permanent populations (Lawton and Brown 1986). However, the impact of an invasive ecosystem engineer has the potential to be pervasive, affecting a large spatial extent and number of ecological characteristics of an area. Exotic ecosystem engineers, such as the beaver, potentially modify not just local biotic communities, but also entire ecosystems (Crooks 2002). Therefore, our understanding of the role of beavers in the context of global biological invasions can help understand broader global processes, vis-à-vis the global effects of invasive species in an age of change. Plus, the study of beaver invasion in subantarctic watersheds is important not only for testing general principles, but also providing new information for management and policy making in a little-studied part of the globe.

While the beaver has inhabited the austral archipelago for more than fifty years, relatively little work had previously been conducted on its influence as an ecosystem engineer of streams and entire watersheds. The goal of this dissertation was to link the role of beavers as non-native ecosystem engineers in the subantarctic watersheds of the Cape Horn Biosphere Reserve, Chile. To do that, we addressed its effects at several hierarchical levels, including the general context of invasion in Cape Horn (Chapter 2), the effect of beavers on riparian plant communities (Chapter 3) and the community and ecosystem level changes to streams caused by beaver engineering (Chapters 4 and 5).

Our analysis of the assemblage and distribution of exotic vertebrate fauna (Anderson et al. 2006b) demonstrated that in several cases exotic species richness outnumbers the corresponding native taxa for several groups, and the islands that were most heavily impacted were also those that were human inhabited. However, our results also highlight the threat to even otherwise remote areas in the southwestern portion of the archipelago, where mink, beaver, muskrat and fox have been able to colonize. Furthermore, our findings showed that the introduction of domestic predators as pets (i.e. dogs and cats) by the Chilean Navy to such places as Horn Island can have major implications for conservation even in national parks.

Chapter 3 assessed the influence of beavers on riparian ecosystems (Anderson et al. 2006a). We found that in the early stages of succession and conversion to a beaver meadow, *Nothofagus* seedling regeneration was severely virtually eliminated. In addition, the only riparian sites where we found *N. antarctica* was in beaver meadows. Plus, meadow sites permitted the establishment of significantly more exotic plants, compared to natural forested riparian zones. Overall, as a result of beaver activity, meadows had greater herbaceous species richness and higher percent coverage, but were not significantly different than the communities of forested riparian understory plants, which were a subset of the larger species pool, rather than a unique and distinct assemblage. These results draw attention to the need to restore riparian habitats, which have been dramatically altered by beaver invasion.

The final two research chapters of the dissertation (Chapters 4 and 5) both relate to the influence of beavers on in-stream community and ecosystem characteristics. These are the first studies to address the role of beavers on stream ecology in subantarctic watersheds, and also one of the few to investigate the ecology of subantarctic streams. Results showed that changes caused by beaver activities were largely localized to pond habitats, but since these watersheds are highly colonized with beaver ponds, cumulative effects result in potentially major changes to the subantarctic landscape. These impacts included decreasing taxa richness and increasing secondary production. Furthermore, we found that the assemblage of benthic fauna in beaver ponds represented a subset of the larger species pool, rather than a unique beaver associated community, which is predicted based on the landscape context of subantarctic watersheds (Rosell et al. 2005). Future work should seek to determine the fate of increased benthic production and whether or not it is transferred to fish or adjacent riparian ecosystems in the form of insect emergence. Also, subsequent research should address the landscape context of beaver impacts more fully by also making comparisons between beaver ponds and other natural lentic habitats such as lakes and bogs.

In conclusion, this body of work represents the most comprehensive assessment to date of introduced beaver impacts in the subantarctic biome of southern South America. It is my hope that these findings will provide a baseline and impetus for future and long-term work that investigates broader and more detailed questions. The approach taken here prioritized characterizing subantarctic stream ecology. It is my hope that future work will focus on using this information to explicitly addressing these larger scales in order to place the beaver's impact into a broader context and make for more powerful comparisons with its impact in a novel landscape.

Promoting the interface of science with education and conservation

Research has broader meaning, utility, and perhaps is even improved by feeding back into the social context from which it springs. Ecological knowledge of specific systems can be a powerful vehicle for making good conservation and management decisions, and science-based education programs are important ways to insert ecological research into socially- and environmentally-relevant decision-making and problem solving initiatives.

This dissertation was conducted in collaboration with the Omora Foundation, which in turn allowed for further partnerships with the Puerto Williams Elementary School and the University of Magallanes to help train both school children and university students in ecology in general and aquatic ecology, specifically. Tangible products of this integration of science and education were the publication of an environmental education workbook (Rozzi and Anderson 2005) and poster on aquatic biodiversity (Anderson

2004), which dealt with aquatic ecosystems and exotic species. Furthermore, a number of undergraduate students at the University of Magallanes and the University of Georgia were able to participate in this research as interns, field assistants and conducting independent research projects, and I published a summary insert box on invasive beavers in the preeminent conservation biology textbook (Anderson 2005).

In addition, through the Omora Foundation, this research became part of a larger decision-making conservation initiative in conjunction with the *Servicio Agrícola y Ganadero* (*SAG*: the Chilean Agriculture and Livestock Service), which has jurisdiction over exotic species in Chile, and the Chilean Antarctic Provincial Government to prepare and evaluate a regional program of control of exotic species in the Magallanes Region. Furthermore, this study was developed as part of a broader research and survey program on a national level in Chile to help the *Comisión Nacional del Medio Ambiente* (*CONAMA*: the Chilean Environment Ministry) catalog regional biodiversity and prioritize conservation sites, which culminated in the Cape Horn Archipelago being prioritized as a national priority for biodiversity by the Council of Ministers. Finally, the culmination of the integration of this work into conservation and planning in the Cape Horn area came through participation in the steering committee of the Cape Horn Biosphere Reserve Initiative helping co-author the application to UNESCO, which was successful in having the Cape Horn Biosphere Reserve declared on June 24, 2005 (Rozzi et al. 2006b).

Finally, an outgrowth of this involvement with conservation became a natural link with sustainable development. To this end, the investigators of the Omora Foundation have prioritized the transfer of their information to outreach efforts and/or ecotourism materials. In this way, I have helped co-author and produce a number of books and audio-visual materials associated with aquatic ecology and the Cape Horn Biosphere Reserve (Anderson 2006, Rozzi et al. 2003, Rozzi et al. 2004 and Rozzi et al. 2006a). While I recognize that my situation was uniquely positioned by working with an organization actively involved in "socially-relevant" science, I firmly believe that at differing levels and scales, all research projects can also be integrated into the social process of which they are a part, thus strengthening both science and society.

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