

## ABSTRACT

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Modeling the effects of the North American beaver (*Castor canadensis*) on subantarctic stream food webs in the Cape Horn Biosphere Reserve, Chile

Under the Direction of DR. AMY D. ROSEMOND

The North American beaver (*Castor canadensis*) was introduced into southern South America in 1946 and throughout the last half-century has established significant populations throughout the Tierra del Fuego and Cape Horn Archipelagos. Beavers alter both the habitat and resources available to organisms in terrestrial and aquatic ecosystems, potentially affecting community composition, food web dynamics, and entire ecosystem processes. In this context, the goal of this research was to specifically address the influence of the beaver on functional feeding group-level (groupings of taxa based on their feeding mode) and trophic-level food web dynamics of streams. Beaver effects were assessed using data from four catchments in the Cape Horn Biosphere Reserve from two habitat types: natural stream reaches uninfluenced by beaver and beaver ponds created by damming. Previous studies have shown that beavers affect both the flow magnitudes and pathways in aquatic food webs. Using empirical data for basal resources, community composition, macroinvertebrate biomass, and secondary production, we used STELLA™ ecological models to determine whether the alteration of flow magnitudes or the alteration of flow pathways was the dominant controlling mechanism affecting secondary production, our ecosystem response variable. These alternative models, in effect, were used to determine which of the changes wrought by beaver were more important in determining changes in secondary production between natural stream and beaver pond habitats. The results of the ecological model simulations illustrated that the alteration of flow pathways, as opposed to flow

magnitudes, within these systems was the primary driver of total secondary production of the stream consumers. Beaver effects on macroinvertebrate community composition and food web complexity are therefore affecting ecosystem response via reductions in energy flow pathways more than their trophic effect on basal resources. This study adds to the body of knowledge of invasive species effects, and particularly the role of beaver in changing stream food webs in southern South America.

**INDEX WORDS:** Exotic species, Diversity, Ecosystem function, Trophic diversity, Community importance, Aquatic food webs, Trophic modeling, Tierra del Fuego.

MODELING THE EFFECTS OF THE NORTH AMERICAN BEAVER  
(*CASTOR CANADENSIS*) ON SUBANTARCTIC STREAM FOOD WEBS  
IN THE CAPE HORN BIOSPHERE RESERVE, CHILE

by

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## DEDICATION

I would like to dedicate this manuscript to my mother and father who have supported me through the good times as well as the bad. I could not have accomplished this research project without their unconditional support and I am thankful to have such wonderful parents and friends.

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## INTRODUCTION

Population and community changes within an ecosystem can have significant influences on ecosystem function and stability (Hooper *et al.* 2005). Therefore, linking species diversity with ecosystem function, such as primary production, secondary production, nutrient cycling, has become an important way to understand the natural world and occupies a fundamental position in ecology (Aoki and Mizushima 2001). However, within this approach there exists a controversy regarding the ability to link changes in ecosystem function to that of functional substitutions and species richness (Loreau *et al.* 2001). Both experimental and theoretical work on the biodiversity-ecosystem function debate (e.g., Naeem *et al.* 1994, Tilman *et al.* 1996, Grime 1997, Hooper and Vitousek 1997, Naeem and Li 1997) have only begun to determine the role of biotic identity and complexity in overall ecosystem function. It has been suggested that analyzing complexity on multiple scales (i.e. the importance of individual species as compared to functional groups or larger ecosystem indices) may help resolve this controversy (Loreau *et al.* 2001). However, establishing umbrella assumptions across a variety of ecosystems can add difficulty to the debate; it is doubtful that the relationship between diversity and function is universal and the emergent properties of unique systems must be taken into account (Aoki and Mizushima 2001).

The biotic assemblage of an ecosystem, as well as its physical properties, affects ecosystem functions such as nutrient and energy flow (DeAngelis 1975). For example, it is well known that the most abundant species in an ecosystem are important in dictating the rates and directions of many ecosystem level responses (Power *et al.* 1996). However, Paine (1969) demonstrated that even less abundant species could be 'keystone,' having ecosystem level

impacts disproportionately large relative to their abundance. In its original formulation, these keystone species maintained community diversity, but Power *et al.* (1996) have suggested that in some cases the community diversity of an ecosystem may in turn affect the relative importance of certain species. This argument proposes that a loss of species diversity may force more of the remaining species into keystone roles (Lawton and Brown 1993, Tilman and Downing 1994, Chapin *et al.* 1995). Both suggestions have been found to be true in cases where an exotic species is introduced into an ecosystem, and therefore, exotic species are model organisms to study diversity from the perspective of both species and communities.

Invasive exotic species are a global scale ecological and conservation concern, and they can rapidly alter non-native ecosystems, thus affecting diversity and ecosystem function (Vitousek *et al.* 1997). As some invasive exotic species occupy a given ecosystem, they can have pervasive and lasting effects on the structure and function of the system within which they are embedded. Specifically, invasive ecosystem engineers would be expected to be able to change ecosystems disproportionately to their numbers via habitat modification (Crooks 2002). Ecosystem engineers have the ability to influence not just intraspecific interactions, but also abiotic, population, community and ecosystem level aspects of the natural world (Jones *et al.* 1994). For example, beavers, the quintessential ecosystem engineer, alter their surroundings by felling trees and constructing dams. This engineering affects stream hydrology and morphology by sediment deposition and the retention of organic matter, creation of wetlands, modification of nutrient dynamics and decomposition processes, alteration of the riparian zone, and manipulation of the water character, ultimately influencing biotic community composition and diversity (Naiman *et al.* 1986, Naiman *et al.* 1988). Specifically with regards to benthic macroinvertebrates, beavers are known to alter stream macroinvertebrate community

composition by changing functional feeding assemblages (McDowell and Naiman 1986) which in turn affect productivity and food web dynamics (Anderson 2006). Therefore, it is logical that the study of exotic species as well as ecosystem engineers would be useful and important in analyzing the relationship between species diversity and ecosystem function.

The North American beaver (*Castor canadensis*, Kuhl) was brought to southern South America as the result of an unsuccessful endeavor by the Argentine government to establish a fur industry (Lizarralde 1993, Skewes *et al.* 1999). Twenty-five mating pairs of beavers were introduced to Tierra del Fuego Island in 1946, and throughout the last half century beaver have established significant populations and expanded their range into Chile (Lizarralde 1993). Current estimates of beaver populations in the Cape Horn Archipelago exceed 115,000 individuals which are expanding at an estimated rate of 20-23% annually (Skewes *et al.* 1999).

The islands included in the territory of Cape Horn, Chile comprise one of the few remaining temperate forests in an almost pristine condition, and they are the earth's southernmost forested ecosystem (Mittermeier *et al.* 2001, Rozzi *et al.* 2006). The area also was recently declared the Cape Horn Biosphere Reserve by the United Nations Educational, Scientific, and Cultural Organization (UNESCO) due to its great natural, cultural, and historical importance (Rozzi *et al.* 2006). Having this status will hopefully promote innovations in land use planning and facilitate the further study of the complexities of these forested ecosystems and the determination of how best to optimally manage the natural resources and exotic species of the area.

Limited research has been conducted to quantify the role that beavers play in the subantarctic ecosystems of southern South America. The studies of beaver to date have focused on population abundance and distribution, habitat preference, geomorphology, nutrient dynamics

and riparian vegetation (Lizarralde 1993, Lizarralde et al. 1996, Coronato *et al.* 2003, Anderson *et al.* 2006a,b). Anderson's (2006) study is the first to analyze the effects of these invasive beavers on stream ecosystem structure and function and is the source of the empirical data used in my analysis. Utilizing techniques of community ecology, network analysis, and ecological modeling, we explicitly modeled the impact that *C. canadensis* have on the aquatic ecosystems of the Cape Horn Biosphere Reserve, Chile. We used data of benthic food webs, which included macroinvertebrate assemblages, trophic basis of production, and the quantification of secondary production to determine the effects of beavers on trophic food web dynamics.

We quantified the impact of beavers on the community importance of functional feeding groups (groupings of taxa based on their feeding mode) and the trophic diversity of the subantarctic stream food webs as they are altered by beaver impacts that affect the species assemblage, richness, and productivity. Furthermore, we constructed dynamic ecological models that allowed us to link changes in ecosystem responses (i.e. secondary production) to two specific beaver impacts on food webs, the alteration of material flow magnitudes vs. the alteration of material flow pathways, found by Anderson (2006). This analysis would allow us to determine which of the changes wrought by beaver were more important in driving differences in ecosystem function. The goal of the ecological models of beaver effects on in-stream food web dynamics is to potentially aide in the research and management agendas of the newly created Cape Horn Biosphere Reserve.

## **METHODS**

### *Study site*

The study was conducted in Cape Horn County, Chile, a part of the Magallanes and Chilean Antarctic Region. The Cape Horn Archipelago is located south of Tierra del Fuego (approximately 55°S) (Figure 1). Data from four catchments on Navarino Island (2,573 km<sup>2</sup>) were utilized in this study: which included Robalo, Faraones, Estrella and Mejillones rivers. All four catchments were located on the northern coast of Navarino Island in watersheds of mixed forest-bog habitats and flowed north draining into the Beagle Channel. Catchments were relatively short (<10 km), and sampling sites were all on the main channels (Anderson 2006). Each stream had two sampling sites that were used as the units of study and are identified as: (1) natural stream reaches uninfluenced by beaver (natural stream) and (2) beaver ponds created by damming (beaver pond).

Macroinvertebrate communities are an important component of southern South America's stream ecosystems and have high degrees of endemism (Illies 1969). Some functional and ecological aspects of rivers have been studied in the Patagonian steppe, located north of Tierra del Fuego Island; however, few studies have been conducted on the functional and ecological aspects of subantarctic streams prior to the empirical study from which the current analysis is derived. Farther north in Patagonia, Miserendino and Pizzolon (1999, 2003) found that anthropogenic land use changes on a large spatial scales could have significant impacts on lotic macroinvertebrate communities. The forests and subantarctic streams of Navarino Island have remained mostly undisturbed, with what little degradation that has occurred originating from

wood collection mainly for fuel as well as introduced animal husbandry and exotic species, such as the beaver.

### *General approach*

Empirical data utilized in this study were taken from a longer-term project involving the effects of the beaver on the subantarctic stream food webs of the Cape Horn Archipelago, Chile (Anderson 2006). Basal resources and community assemblage data were taken from all four catchments. Secondary production and trophic basis of production data were taken from two of the four catchments (Robalo and Mejillones rivers). The empirical data taken from Anderson (2006) were interpreted and incorporated into calculations and food web models depicting the trophic dynamics of the subantarctic stream food webs.

Our approach to quantifying the impact of introduced beavers on trophic food webs included three distinct analyses which describe both community level and ecosystem level dynamics. First, we quantified the community importance of different functional feeding groups as proposed by Power *et al.* (1996) within two of the four catchments' (Robalo and Mejillones Rivers) macroinvertebrate assemblages and compared the results across habitat types to measure how beaver influence the relative importance of the contribution of macroinvertebrate functional feeding group assemblages to total secondary production. Second, we calculated trophic diversity as proposed by Dunne *et al.* (2002) of natural stream and beaver pond food webs in all four catchments to determine the effect of beaver influence on the complexity of the trophic food networks. The taxa resolution for these data included species and morphospecies (Anderson 2006).

Finally, we created systems models of the dynamic food webs within two of the four catchments (Robalo and Mejillones Rivers) to test questions about the relative importance of two

types of beaver impacts to food webs (i.e. alterations on material flow magnitudes vs. alterations on material flow pathways) in determining ecosystem-level responses (i.e. secondary production). Anderson (2006) found that beaver altered stream food web dynamics in two specific ways, and the goal of this study was to determine which of these two alterations was the most important driver of total secondary production.

### *Community analysis*

*Community assemblage:* The macroinvertebrate community assemblage was sampled in all four catchments during three seasons (spring [October], summer [January], and fall [May]) to determine presence/absence of benthic invertebrate taxa, richness, density, biomass, and functional feeding group composition. Three sub-samples were taken at each study site using a core sampler. Collections were transported to the laboratory, where taxa were identified to the lowest possible level (usually family or genus) and functional feeding group (i.e. collector-gatherer [gatherer], collector-filterer [filterer], scraper, shredder and predator) using available keys and references (Merritt and Cummins 1996, Miserendino and Pizzollo 2000, Fernández and Domínguez 2001).

Mean richness, Shannon-Weiner diversity, and density were calculated using EstimateS software (Colwell 1997). During identification, the lengths of specimens were measured to the nearest mm, and biomass was determined for each taxon using length-mass regressions proposed by Benke *et al.* (1999) and Miserendino (2001). Mean annual biomass, expressed as mg of ash-free dry mass (AFDM) m<sup>-2</sup>, was calculated for each taxon and functional feeding group (Anderson 2006). These data were used to determine community importance at the level of functional feeding group.

*Community importance:* The mean annual macroinvertebrate assemblage data were analyzed for two catchments (Robalo and Mejillones rivers) to determine total secondary production values for each taxon and functional feeding group (Anderson 2006). Secondary production values, expressed as g AFDM m<sup>-2</sup> y<sup>-1</sup>, for the two catchment and habitat pairs were determined using the size-frequency method (Hamilton 1969) with the cohort production interval (CPI) correction factor (Benke 1979; Huryn 1996, 1998) and were used to determine community importance at the level of functional feeding group.

Community importance (CI<sub>*i*</sub>) is a measure of the strength of the effect of a species on a quantitative community or ecosystem trait in direct proportion to its biomass (Power *et al.* 1996). Total secondary production values for the macroinvertebrate communities in the two catchments were the ecosystem trait used in this analysis. The CI<sub>*i*</sub> of each functional feeding group in each habitat type was calculated to determine the effect of beaver alterations on community composition (i.e. assemblage) and ecosystem function (i.e. secondary production), thus explicitly linking species to ecosystems. Community importance was calculated as proposed by Power *et al.* (1996) and is represented mathematically as follows:

$$CI_i \text{ of a particular taxon } i = [(t_n - t_d) / (t_n)] \cdot [1 / (p_n)]$$

where  $t_n$  is the ecosystem trait (i.e. secondary production) with the species  $i$  included,  $t_d$  is the ecosystem trait with the species  $i$  deleted, and  $p_n$  is the proportional biomass of the species  $i$ . CI<sub>*i*</sub> values for the functional feeding groups in this study were used to aid in interpreting ecological models to assess the importance of specific functional groups in trophic energy flow and to assess the effect of the beaver on stream community composition.

### *Food web analysis*

*Trophic Diversity:* The trophic diversity of a given ecosystem can be defined as the integration of the number of taxa within each trophic level, the connectance among these trophic levels and taxa, and the strength of the connections of the flow pathways (i.e. energy flows) in the trophic food network. The number of network connections within each of the four catchments were quantified and compared among the two habitat types. Trophic diversity was analyzed by totaling the important taxa (>1% of total secondary production) within a given trophic level and the connectance of trophic interactions within each stream and habitat pair (Loreau 1996, Aoki and Mizushima 2001, Dunne *et al.* 2002). We analyzed four aspects of food web dynamics for both habitat types as proposed by Dunne *et al.* (2002): (1) species richness ( $S$ ), the total number of species in the food web; (2) connectance ( $C$ ), the fraction of all possible trophic links ( $L/S^2$ ); (3) links per species ( $L/S$ ); and (4) average node degree [ $2(L/S)$ ], which is the average number of incoming and outgoing links per species. Results of this analysis were used to determine the network stability and trophic diversity of each habitat type as a way to characterize the role of beaver in altering stream food web dynamics.

*Food web models:* We also constructed dynamic systems models using STELLA<sup>TM</sup> software, a mathematical based modeling program that allows the user to design and simulate complex systems and respective disturbances to these systems. Using system components, such as standing stock compartments, material flow pathways, and information controls, STELLA<sup>TM</sup> allows for an approximation of the complexity of a given system to be represented in a way that research oriented hypotheses can be created and tested. Trophic food web models were conceptualized and created incorporating empirical data from Anderson (2006) for biomass

(standing stock compartments of basal resources) and trophic basis of production (carbon flows to consumers) (Table 1).

The basal resources within the subantarctic streams include biofilm, coarse benthic particulate organic matter (CBOM), fine benthic particulate organic matter (FBOM), suspended particulate organic matter (seston), and woody debris (for details of sampling methods for basal resources see Anderson 2006). Samples were processed to determine  $\text{g AFDM m}^{-2}$ , which is the basic unit of measurement for material flow in the ecological models created. The empirical data of the quantity of basal resources in two of the four catchments (Robalo and Mejillones Rivers) were integrated into STELLA™ modeling software as standing stock compartments of basal resources (Table 1). Only two catchments were used for this parameterization, although all four catchments were quantified, because secondary production and trophic basis of production empirical values were only calculated for two of the four catchments (Robalo and Mejillones Rivers) due to laborious and time consuming methodologies.

Trophic basis of production (Benke and Wallace 1980, 1997) was calculated for eight primary taxa and six predatory taxa in two of the four catchment and habitat pairs (Robalo and Mejillones Rivers). Data were analyzed to determine proportional assimilation values for functional feeding groups within the trophic food networks. In this study, we used appropriate values for amorphous detritus from Anderson (2006), and production supported by these flows was derived predominantly from FBOM. The empirical values of trophic basis of production for the stream macroinvertebrate community were integrated into STELLA™ modeling software as the material flow pathways by which allochthonous and autochthonous resources were integrated into the primary and secondary consumer trophic levels (Table 1).

No values were entered for the standing stock compartments of both primary and secondary benthic macroinvertebrate consumers, as the secondary production values generated from simulations were the ecosystem response variable (output information) of the models (Table 1). These values were graphed and tracked over time as the simulations progressed. Secondary production values from the four model simulations were compared to empirical results found by Anderson (2006). As stated, the standing stock compartments of basal resources and the macroinvertebrate community were connected through a series of material flow pathways representing the transfer of carbon through the ecosystem and the accumulation of this carbon in the macroinvertebrate community was tracked over an arbitrary temporal scale to determine the effect of beaver alteration on this ecosystem level response (secondary production) (Table 1).

Four distinct ecological models were created from the empirical data, which were: (1) a trophic model representing a natural stream, which was used as a template for the three remaining models (Figure 2a); (2) the trophic model template manipulated by altering the quantity of the standing stock compartments of available basal resources to mimic those of a beaver pond, thereby altering the material flow magnitudes (Figure 2b); (3) the trophic model template manipulated by altering the macroinvertebrate community composition to mimic that of a beaver pond, thereby altering the material flow pathways that connect consumers to resources (Figure 2c); and (4) the trophic model template manipulated by altering both the material flow magnitudes and pathways as described in models two and three, thereby representing the dual effects of ecosystem alteration in a beaver pond (Figure 2d). These four distinct trophic models represented the manipulation and control of specific aspects of beaver alterations, which allows

for a sensitivity analysis of the relative importance of each alteration in driving total secondary production.

## RESULTS

### *Community analysis*

*Community assemblage:* A total of thirty-seven benthic invertebrate taxa were identified.

Annual mean richness in each habitat varied from 15.3 taxa m<sup>-2</sup> in the natural stream habitat to 10 taxa m<sup>-2</sup> in the beaver pond habitat (Table 2). Beaver impacts on community variables in beaver ponds caused significant reductions in mean annual richness ( $p = 0.03$ ) and Shannon-Weiner diversity ( $p = 0.0003$ ) compared to natural stream habitats. Beaver impacts in ponds caused a significant increase in mean annual biomass ( $p = 0.02$ ) compared to natural stream habitats (Table 2). At the functional feeding group level, beaver impacts in ponds caused significant increases in the mean annual biomass of gatherers ( $p = 0.03$ ) and predators ( $p = 0.004$ ) and significant decreases in scrapers ( $p = 0.01$ ) and filterers ( $p = 0.02$ ) (Table 3).

*Community importance:* Overall,  $CI_i$  values showed similar trends in the relative importance of functional feeding groups between natural streams and beaver pond sites (Figure 3). In the natural stream and beaver pond habitats, gatherer and predator functional feeding group  $CI_i$  values are greater than 1. The  $CI_i$  values for all other functional feeding groups in the beaver pond assemblage were similar to those in the natural stream assemblage with scraper, filterer, and shredder functional feeding group  $CI_i$  values less than the relative importance value of 1 (Figure 3). While the mean annual biomass of gatherers and predators are significantly less in natural stream habitats as compared to beaver pond habitats, the  $CI_i$  values of the two functional feeding groups are similar in both habitats.

### *Food web analysis*

*Trophic Diversity:* The food webs of the important taxa (>1% production; Table 4) in natural stream reaches and beaver ponds had significant differences in trophic species ( $p = 0.004$ ), total trophic links ( $p = 0.004$ ), and connectance ( $p = 0.01$ ), illustrating that beavers do affect the trophic diversity of stream macroinvertebrate food webs (Table 5). The average links per species and the average node degrees were constant in natural stream reaches and beaver ponds at 3.8 and 7.6 respectively (Table 5).

*Food web models:* The results of the ecological model simulations were interpreted as a sensitivity analysis of two specific impacts of beaver on stream food web dynamics to determine which type of beaver alteration had a larger impact on the ecosystem level responses of the macroinvertebrate community. Two of the four simulation models (the natural stream template model and the beaver pond model incorporating both food web alterations) were not manipulated and were used to ensure the validity of the trophic structure and ecological model design. The total secondary production values (output information) of these models coincide with findings from the corresponding empirical study (Anderson 2006; Table 4), establishing the reliability of the trophic structure used in all four models, since the natural stream model was used as a template for the two manipulated models and the beaver pond model represents the dual effect of both manipulations which were separated in the two manipulated models (Figure 2a; Figure 2d; Figure 4). The remaining two STELLA™ models created in this study were manipulated to distinguish the dual effect of beaver impacts on (a) organic matter flow magnitudes and (b) organic matter flow pathways in subantarctic stream food webs (Figure 2b; Figure 2c; Figure 5).

Secondary production in the natural stream template model following simulation was  $2.12 \text{ g AFDM m}^{-2} \text{ y}^{-1}$ , which is similar to secondary production values calculated for natural

stream reaches by Anderson (2006) at  $2.4 \text{ g AFDM m}^{-2} \text{ y}^{-1}$  (Figure 4). Modifying the trophic model template to mimic basal resource standing stocks equivalent to those found in beaver ponds increased the material flow magnitudes that connected the sources of productivity with their respective consumers within the stream food web, causing a dramatic increase in secondary production to  $53.88 \text{ g AFDM m}^{-2} \text{ y}^{-1}$ . This value was 5x higher than Anderson's (2006) empirically derived estimates of secondary production ( $10.1 \text{ mg AFDM m}^{-2} \text{ y}^{-1}$ ) (Figure 5). The second manipulation of the trophic model template imposed beaver alterations on the material flow pathways which connect stream benthic consumers to their respective basal resources. Secondary production in this second manipulation was  $9.41 \text{ g AFDM m}^{-2} \text{ y}^{-1}$ , which was similar to the empirical value of  $10.1 \text{ g AFDM m}^{-2} \text{ y}^{-1}$  derived for these ecosystems from Anderson (2006)(Figure 5). Similarly, secondary production in the beaver pond model, which included both beaver alterations on food web dynamics, was  $10.53 \text{ g AFDM m}^{-2} \text{ y}^{-1}$ , which was also similar to secondary production values found by Anderson (2006) for beaver ponds ( $10.1 \text{ g AFDM m}^{-2} \text{ y}^{-1}$ ) (Figure 4).

## DISCUSSION

To understand the relationship between diversity and ecosystem function, depicting the interactions between different trophic levels and larger ecosystem dynamics are of the greatest importance (Naeem *et al.* 2000, Aoki and Mizushima 2001). Therefore, dynamic and holistic approaches to ecosystem complexity are necessary and must encompass the analysis of multiple scale dynamics. The effects of *Castor canadensis* on stream food web dynamics have been shown to be profound in both North America and South America (Naiman *et al.* 1988, Anderson 2006). However, the mechanistic features of these effects have yet to be fully explored. Here, we have used three distinct techniques of analyzing trophic food webs to investigate the effects that the beaver are having on subantarctic benthic macroinvertebrate communities and have found that beaver alterations of material flow pathways was the most important determinant of overall ecosystem function (i.e. secondary production).

If a species has an ecosystem-level effect in direct proportion to its abundance, its  $CI_i$  would be 1 (Power *et al.* 1996). Although community importance values for collectors were reduced by beaver impact in both rivers tested, a larger trend emerged, as the community importance of collectors relative to all other functional feeding groups remained similar in both habitats (natural stream and beaver pond). The relative importance of predators was similar in both habitats as well, and the only two functional groups near or approaching the importance value of one in both habitat types were collectors and predators (Figure 3). There were no functional feeding groups that could be considered keystone (no values significantly larger than 1). The community importance values reported in this study illustrated that although beavers altered species diversity and community composition according to empirical studies (Naiman *et*

*al.* 1988, Anderson 2006) they do not significantly influence the relative importance of functional feeding groups within the subantarctic stream food webs of the Cape Horn Biosphere Reserve.

The validity of the keystone species concept in ecology has been questioned in recent years (Mills *et al.* 1993, Hurlbert 1997), but regardless of potential shortcomings, ecologists have been reluctant to completely dismiss a concept that has proven useful (Kotliar 2000). Comparative studies can overcome many of the limitations of the experimental approach to quantifying the community importance of specific taxa or functional feeding groups (Power *et al.* 1996). For example, the experimental removal of a species is the most convincing way of determining relative community importance values, but requires extensive and laborious analysis. The comparative method has a loss of rigor, given that many factors may differ among contrasting sites (Power *et al.* 1996). In addition, species deletion and comparative experiments may not give a true characterization of ecosystem response because other system components may behave differently in the case of the absence of certain species. For example, although Power *et al.* (1996) discuss redundancy as it relates to the functional roles of species, it is not a part of their definition, and as with overall importance, redundancy can be addressed only within a defined context, adding difficulty to establishing a truly robust definition of community importance (Kotliar 2000).

The trophic diversity of an ecosystem is a descriptive analysis of the complexity of the food web through which carbon and energy flows. Evaluations of trophic diversity vary widely across aquatic ecosystems, influenced by numerous factors, including the number of trophic species, the number of trophic levels, and levels of omnivory (Dunne *et al.* 2002). Beaver alteration of the subantarctic stream benthic food webs caused significant differences in the

number of trophic species ( $S$ ), total links ( $L$ ), and connectance values ( $C$ ) for the natural stream and the beaver pond sites (Table 5). Recent studies on the trophic diversity of macroinvertebrate food webs have varied significantly in methodologies, using multiple indices to describe particular aspects of unique food webs (e.g., Dauby *et al.* 2001, Correia 2002), thus making it difficult to find species, community, and ecosystem level generalizations across a variety of ecosystems. Therefore, measurements of trophic diversity at present can only be understood on a case by case basis. However, comparisons can be made with studies using similar techniques, and this analysis of the trophic diversity of stream macroinvertebrate food webs coincides with trophic diversity values for lakes in findings from Dunne *et al.* (2002). My results illustrate that not only do beaver alter the diversity and composition of subantarctic stream food webs as found by Anderson (2006), they also have a significant impact on the trophic diversity of the macroinvertebrate food webs.

Beaver have been shown to affect both the flow magnitudes and pathways in the aquatic food webs of the Cape Horn Archipelago, Chile (Anderson 2006). The goal of the models used in this study was to determine the individual impact, independent of one another, of each of these food web alterations caused by beaver. The trophic food web simulations used in this study specifically addressed two influences that beaver have on sub-Antarctic stream food webs, and the results show that the alteration of flow pathways, as opposed to flow magnitudes, within these systems is the primary driver of total secondary production of the stream consumers (Figure 5). Beaver alter in-stream food web dynamics and ecosystem level responses in multiple ways; however, specific alterations within the trophic networks act more strongly than others in influencing the community and ecosystem as a whole, based on my analysis.

Using the three techniques described and reported above, we have specifically linked changes in ecosystem function caused by an exotic ecosystem engineer to that of functional substitutions and species richness, thereby analyzing ecosystem complexity on multiple scales. By quantifying species effects on ecosystem functioning, our results contribute to the issues dealing with the role of species in ecosystems and the diversity-ecosystem function debate.

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Table 1. Parameterization used in the STELLA™ ecological models. Model components used and not used are listed. Those model components included in the models are detailed by how they were parameterized as well as any assumptions that were made and components not incorporated into the ecological models are listed with their respective assumptions.

<b>Model Component/Interaction</b>	<b>Parameterization</b>
Inflows to Basal Resources	Created to hold constant the standing stocks of basal resources; donor controlled.
Standing Stocks of Basal Resources	Data from Anderson (2006); see also Appendix 2.
Standing Stocks of Benthic Invertebrates	No initial values. Results from simulations were the output information.
Material Flows to Consumers	Data from Anderson (2006); see also Appendix 4.
Respiration Outflows	Data from Beche et al. (2006).
Unit of Time	Arbitrary. One simulation cycle was equivalent to one year.
Cycling of Egested Material	No parameterization; outside of the defined boundary of interest.
Omnivory	No parameterization; outside of the defined boundary of interest.
Decomposition	No parameterization; outside of the defined boundary of interest.
Nutrient Cycling	No parameterization; outside of the defined boundary of interest.

Table 2. Benthic invertebrate community variables for natural and beaver pond sites. Annual means ( $\pm$ SE) are based on seasonal replicates for each of four sites for each habitat (n=8). Values within each category with different letters were significantly different with a Tukey HSD test ( $p < 0.05$ ). Data from Anderson (2006).

<b>Category</b>	<b>Natural</b>	<b>Beaver Pond</b>	<b>F</b>	<b>p</b>
Richness (taxa m <sup>-2</sup> )	15.3(1.8) <sup>A</sup>	10 (0.9) <sup>B</sup>	5.7	<b>0.03</b>
Diversity (H')	2 (0.1) <sup>A</sup>	1.4 (0.1) <sup>B</sup>	22.79	<b>0.0003</b>
Density (individuals m <sup>-2</sup> )	2,611.5 (504.9) <sup>A</sup>	14,350 (10,381) <sup>A</sup>	2.6	0.13
Biomass (mg AFDM m <sup>-2</sup> )	257.9 (89.4) <sup>A</sup>	864.1 (179.8) <sup>B</sup>	6.47	<b>0.02</b>

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

Tables 3. Benthic invertebrate biomass. Mean annual values ( $\pm$ SE) in mg ash-free dry mass  $m^{-2}$  for each functional feeding group in two habitat types (natural reaches and beaver ponds). Annual means ( $\pm$ SE) are based on seasonal replicates for each of four sites for each habitat (n=8). Values within each category with different letters were significantly different with a Tukey HSD test ( $p < 0.05$ ). Data from Anderson (2006).

<b>Mean Annual Biomass</b>	<b>Natural</b>	<b>Beaver Pond</b>	<b>F</b>	<b>p</b>
Gatherer	149.8 (71.9) <sup>A</sup>	708 (180) <sup>B</sup>	5.4	<b>0.03</b>
Scraper	35.7 (12.1) <sup>A</sup>	3 (3) <sup>B</sup>	10.2	<b>0.005</b>
Shredder	15 (4) <sup>A</sup>	2.8 (1.7) <sup>A</sup>	3.91	0.06
Filterer	52.2 (16.8) <sup>A</sup>	5.3 (4.1) <sup>B</sup>	6.74	<b>0.02</b>
Predator	5.2 (1.3) <sup>A</sup>	144.3 (43.4) <sup>B</sup>	10.96	<b>0.004</b>

Table 4. Mean secondary production of benthic invertebrate consumers. Values from the Robalo and Mejillones Rivers are shown for taxa that had a relative contribution (%) of >1% at two habitat-types (natural reaches and beaver ponds). Biomass (B) and secondary production (P) are in units of mg ash-free dry mass [AFDM] m<sup>-2</sup> and mg AFDM m<sup>-2</sup> y<sup>-1</sup>, respectively. Data from Anderson (2006).

Taxa (Functional Feeding Group)	Natural			Beaver Pond		
	B	P	% P	B	P	% P
<b>Non-Insects</b>						
Amphipoda						
<i>Hyalella simplex</i> (Gatherer)	103.6	1,180.3	50	451.6	4,188.7	41
Oligochaeta (Gatherer)	17.1	120.4	5	402.5	2,381.9	24
<b>Insects</b>						
Diptera						
<i>Gigantodax spp.</i> (Filterer)	44	85	4			
Non-Tanypodinae (Gatherer)	44.4	493	21	203.8	2,892.2	29
Tanypodinae (Predator)				209	412.7	4
Tipulidae (Gatherer)	11.5	41.2	2			
Ephemeroptera						
<i>Andesiopsis spp.</i> (Gatherer)	20.7	70.7	3			
<i>Meridialaris</i> (Gatherer)	14.6	176.4	8			
Plecoptera						
Gripopterygidae (Shredder)	10.1	37.7	2			
<b>Sub-Total</b>	<b>265.9</b>	<b>2,204.6</b>	<b>93</b>	<b>1267</b>	<b>9875.5</b>	<b>98</b>
<b>Grand Total</b>	<b>281.2</b>	<b>2359.1</b>		<b>1447</b>	<b>10,144.4</b>	
<b>Richness (&gt;1%)</b>	<b>8</b>			<b>4</b>		

Table 5. Trophic diversity of the food web networks. Annual means ( $\pm$ SE) are based on seasonal replicates for each of four sites for each habitat (n=8). Total number of trophic species ( $S$ ) and total links ( $L$ ) in the food webs were significantly reduced in beaver pond sites, while total food web connectance ( $C$ ) was significantly increased in beaver pond sites.

<b>Index</b>	<b>Natural</b>	<b>Beaver Pond</b>	<b><i>F</i></b>	<b><i>p</i></b>
<b>Species</b>	9.5 (2.1) <sup>A</sup>	4.8 (0.5) <sup>B</sup>	19.7	<b>0.004</b>
<b>Links</b>	36 (7.2) <sup>A</sup>	18 (2.3) <sup>B</sup>	21.6	<b>0.004</b>
<b>Links/Species</b>	3.8 (0.09) <sup>A</sup>	3.8 (0.4) <sup>A</sup>	0	1
<b>Connectance</b>	0.42 (0.1) <sup>A</sup>	0.81 (0.15) <sup>B</sup>	19.3	<b>0.01</b>
<b>Node Degree</b>	7.6 (0.2) <sup>A</sup>	7.6 (0.8) <sup>A</sup>	0	1

$S$  = Total trophic species in the food web,  $L$  = Total flow pathways (links) in the food web,  $L/S$  = Mean flow pathways (links) per species,  $(L/S^2)$  = Connectance of the trophic network,  $(2(L/S))$  = Average node degree in the trophic network.

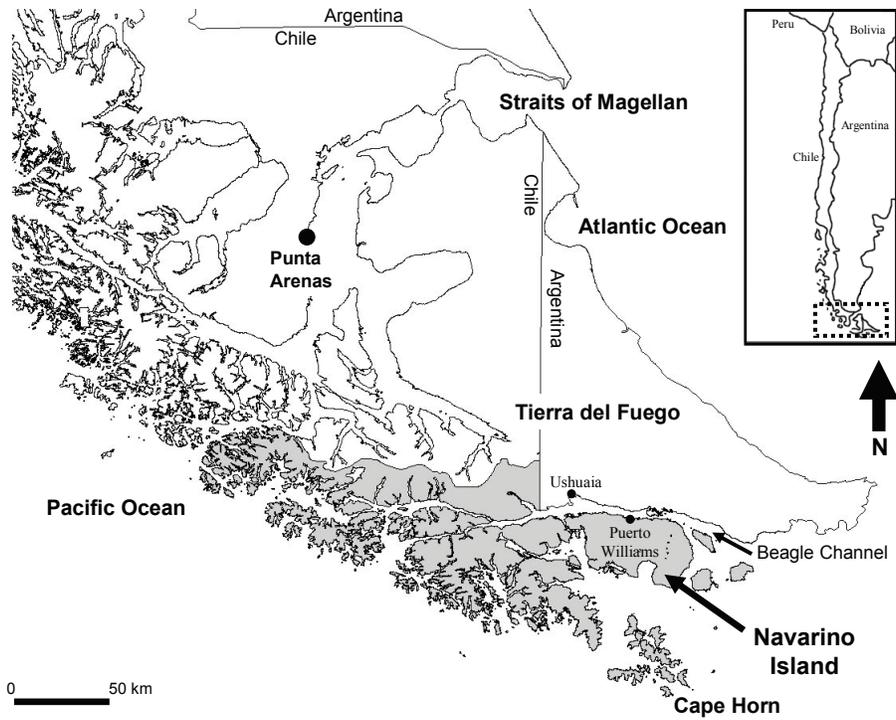


Figure 1. . Cape Horn County, Chile. The Cape Horn Archipelago, a part of the Magallanes and Chilean Antarctic Region, is located south of Tierra del Fuego (approximately 55°S) (Figure 1). Data from four catchments on Navarino Island (2,573 km<sup>2</sup>) were utilized in this study: which included Robalo, Faraones, Estrella and Mejillones Rivers. All four catchments were located on the northern coast of Navarino Island in watersheds of mixed forest-bog habitats and flowed north draining into the Beagle Channel.

Figure 2.

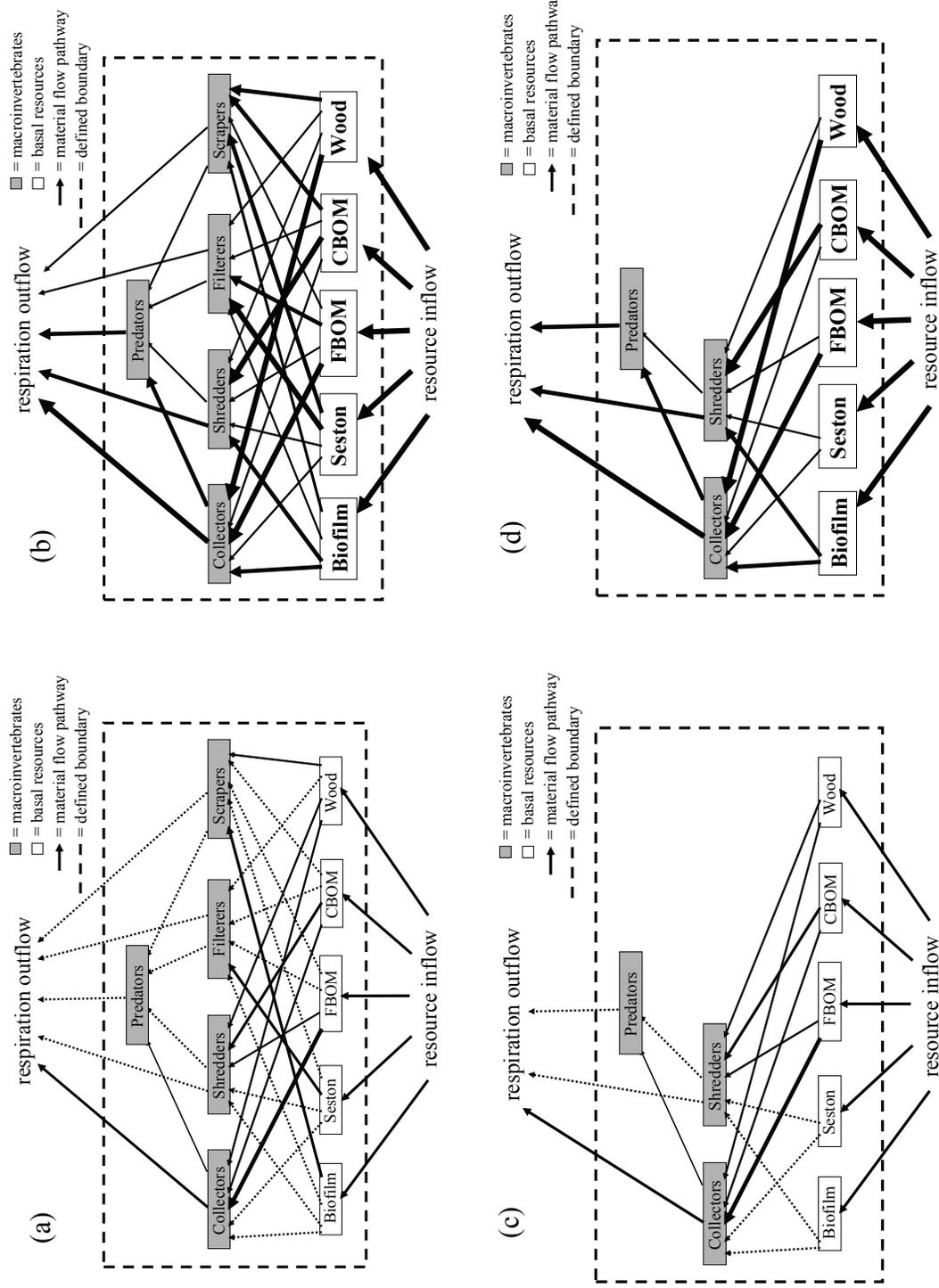


Figure 2. Structural framework of the trophic food webs. The trophic network is donor controlled, ultimately regulated by inputs into basal resource standing stocks. From the primary producers, assimilated carbon flows through a series of pathways varying in magnitude to primary consumer functional feeding groups. Carbon flow is then lost to primary consumer respiration or assimilated by secondary predators in the trophic network. (a) the natural stream habitat model, (b) the ecological model with manipulated flow magnitudes, (c) the ecological model with manipulated flow pathways, (d) the beaver pond model

Figure 3.

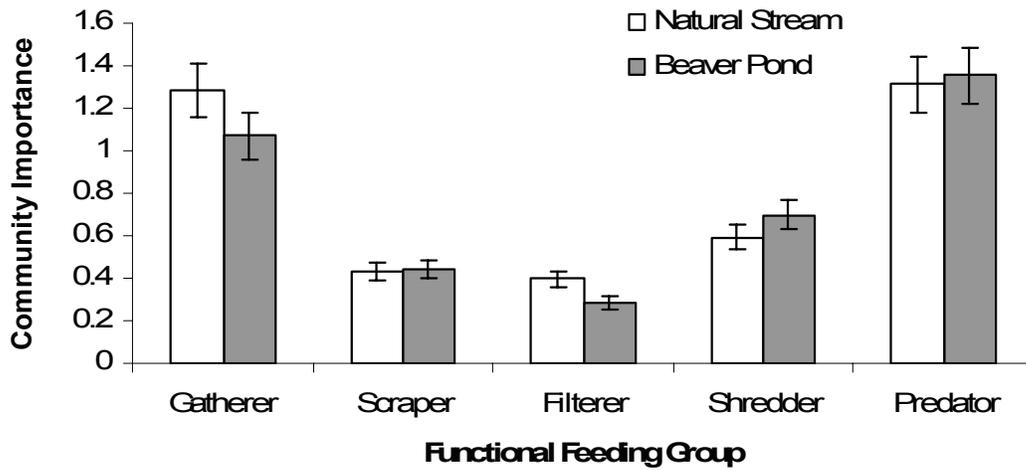


Figure 3. Mean community importance.  $CI_i$  values are for functional feeding groups in the Robalo and Mejillones food webs. White bars represent the natural stream habitat and grey bars represent the beaver pond habitat. Analysis is kept at the functional feeding group-level to analyze large shifts in community composition.

Figure 4.

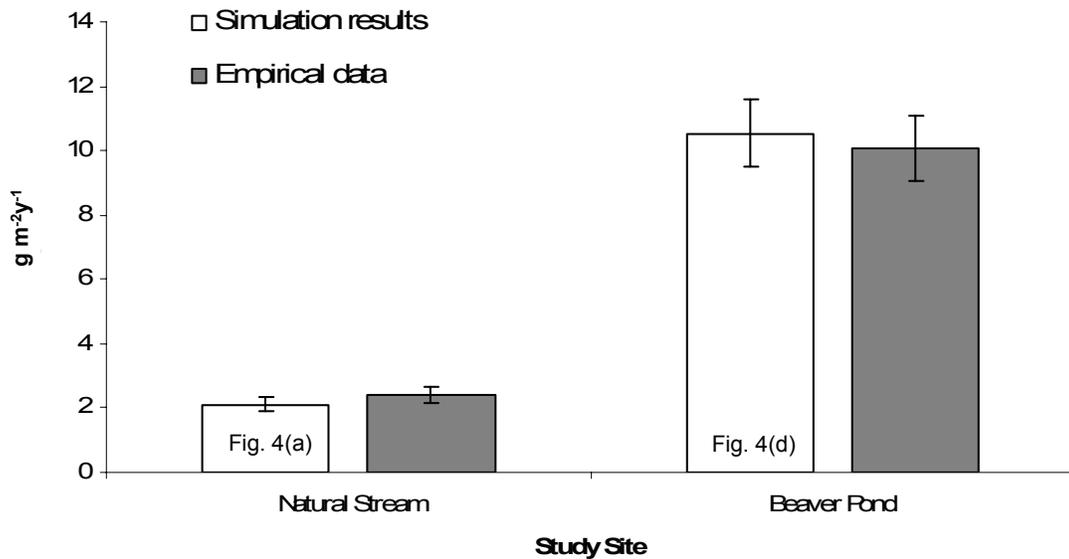


Figure 4. Secondary production of reference models. Total secondary production of consumers for the two ecological models created with STELLA™ software that were not manipulated and total secondary production values from Anderson's (2006) empirical study. Secondary production values after simulation were reported as 2.12 g AFDM m<sup>-2</sup>y<sup>-1</sup> in the natural stream model and 10.53 g AFDM m<sup>-2</sup>y<sup>-1</sup> in the beaver pond model. Empirical secondary production values were reported as 2.4 g AFDM m<sup>-2</sup>y<sup>-1</sup> in the natural stream habitat and 10.1 g AFDM m<sup>-2</sup>y<sup>-1</sup> in the beaver pond habitat.

Figure 5.

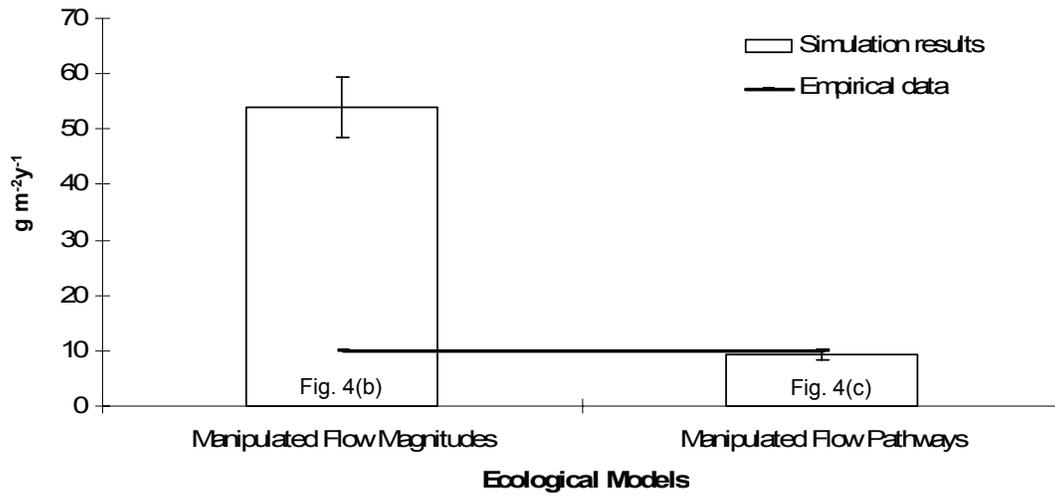


Figure 5. Secondary production of manipulated models. Total secondary production of consumers for the two ecological models created with STELLA™ software that were manipulated graphed with the empirical secondary production value for beaver pond habitats found by Anderson (2006) to be 10.1 g AFDM m<sup>-2</sup>y<sup>-1</sup>. Secondary production values after the model simulations were reported as 53.88 g AFDM m<sup>-2</sup>y<sup>-1</sup> in the ecological model with manipulated flow magnitudes and 10.53 g AFDM m<sup>-2</sup>y<sup>-1</sup> in the ecological model with manipulated flow pathways.

## APPENDICES

Appendix 1. Quantity of basal resources. These were used in STELLA™ models to represent the standing stocks of basal resources and were taken from Anderson (2006).

Quantities are reported in g AFDM m<sup>-2</sup> y<sup>-1</sup>.

<i>Quantity</i>	<b>Natural</b>	<b>Beaver Pond</b>
Wood	558.4	3,561.7
CBOM	10.6	438.2
FBOM	18	1,360.8
Biofilm	5.6	0
Seston	0.002	0.003

Appendix 2. Trophic basis of production values. These were input into STELLA™ models to represent flow magnitudes and pathways of resources to consumers.

Quantities are reported in g AFDM m<sup>-2</sup> y<sup>-1</sup>.

<b>Functional Feeding Group</b>	<b>Food type</b>	<b>Average</b>	
		<b>Natural</b>	<b>Pond</b>
<b>Collector-gatherer</b>	Amorphous	1.18	7.485
	Diatom	0.15	0.765
	Leaf	0.385	0.92
	Wood	0.07	0.17
	Animal	0.025	0.12
	Total	1.81	9.46
<b>Collector-filterer</b>	Amorphous	0.07	0
	Diatom	0.065	0
	Leaf	0.007	0
	Wood	0.00025	0
	Animal	0	0
	Total	0.14225	0
<b>Predator</b>	Amorphous	0	0
	Diatom	0	0
	Leaf	0	0
	Wood	0	0
	Animal	0.025	0.49
	Total	0.025	0.49
<b>Scraper</b>	Amorphous	0.12	0
	Diatom	0.05	0
	Leaf	0.001	0
	Wood	0	0
	Animal	0	0
	Total	0.176135	0
<b>Shredder</b>	Amorphous	0.0025	0.005
	Diatom	0.0005	0.0005
	Leaf	0.0065	0.004
	Wood	0.001	0.005
	Animal	0	0
	Total	0.0085	0.0125

### Appendix 3. Glossary of terminology.

<b>Term</b>	<b>Definition</b>
Species Richness	The number of species within a defined area. (A term commonly used as a measure of species diversity, but technically is only one aspect of diversity).
Shannon-Weiner Diversity	An index of species diversity that is affected by both the number of species and their evenness.
Density	A measure of a population of a species per unit area.
Biomass	The mass of biological organisms expressed per unit area.
Secondary Production	The mass of biological organisms expressed per unit area and per unit time.
Functional Feeding Group	Groupings of taxa based on their feeding mode (collector-gatherers [gatherers], scrapers, collector-filterers [filters], shredders, and predators).
Community Importance	A measure of the strength of the effect of a species on a quantitative community or ecosystem trait in direct proportion to its biomass.
Trophic Diversity	A measure of the integration of the number of taxa within each trophic level, the connectance among these trophic levels and taxa, and the strength of the connections of the flow pathways (i.e. energy flows) in the trophic food network
Links ( <i>L</i> )	Material flow pathways in trophic food webs that connect a given species to its respective source of energy and/or productivity.
Links per Species ( <i>L/S</i> )	A measure of the number of links per species in a trophic food web.

Connectance ( $L/S^2$ )

A measure of the fraction of all possible trophic links.

Average Node Degree  $2(L/S)$

A measure of the average number of incoming and outgoing links per species.