Life after death: the importance of salmon carcasses to watershed function.

by

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Abstract

A model of a British Columbia watershed was constructed using the Atnarko River watershed as a case-study. A new routine in the Ecopath with Ecosim suite of software, Ecotrace, was used to track the flow of marine nitrogen, from returning adult salmon, throughout the aquatic, riparian, and forest regions of the watershed. Although there was no local data available regarding the concentration of marine nitrogen in organisms and secondary data had to be used to parameterize the model, results are consistent with values from other study areas that were derived through stable isotope analysis. The objective of this study was not to predict results for a specific model area but rather a test of the methodology to see if it could be applied to a model area where field data is available. In this respect, the study objective was accomplished. Some possible refinements to the methodology and future uses for the Ecotrace routine are suggested, including using the routine to cross validate diet composition data if used in conjunction with stable isotope data. Also, it is quite clear that salmon managers must consider the importance of marine derived nutrients for all streams and manage salmon harvesting accordingly rather than just focus on the commercially important runs of salmon.

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1. Introduction

1.1 Study objective

The province of British Columbia contains a vast network of lakes, streams, rivers, and ponds. The topography dictates that the majority of freshwater systems flow in a westerly direction, exporting any nutrients contained within the water column away from the interior regions of the province to the Pacific Ocean. Adult salmon are a key link between marine ecosystems and the ones inland as they transport nutrients from the ocean and deposit them in watersheds throughout the province, when they return to spawn. The objective of this study is to construct an ecosystem model that tracks the flow of marine derived nitrogen from spawning salmon carcasses throughout a watershed. This will be accomplished using the Ecopath with Ecosim suite of software (Christensen and Pauly 1992), which includes Ecospace (Walters *et al.* 1998), and a recent addition Ecotrace (C. Walters *pers. comm.*)

1.2 Background information

As returning adult salmon near the streams where they will spawn they cease feeding. Their bodies only contain an insignificant amount (<1%) of residual freshwater derived biomass, i.e., the biomass of developing smolts (Kline *et al.* 1997); thus, the body of an adult salmon is primarily constructed from marine derived nutrients. These marine derived nutrients are released into the freshwater ecosystem before, during, and after spawning through excretion, gametes, and carcass decomposition, respectively (Brickell and Goering 1972). Once released, these marine derived nutrients become available to enter into the food web of both the aquatic and surrounding terrestrial ecosystem. Bilby *et al.* (1996) found that in a small second order stream supporting a population of coho salmon (*Oncorhynchus kisutch*), up to 40% of the nitrogen in some organisms is marine derived from the carcasses of spawning adults. When fewer salmon return back to the spawning grounds, fewer nutrients are supplied to the surrounding ecosystems. Paquet (2000) reports on the findings of Reimchen, who found that salmon carcasses provide the largest single pulse of nitrogen to streamside vegetation. While the aquatic and adjacent terrestrial ecosystems may not specifically require ^{15}N (marine nitrogen), as opposed to ^{14}N (atmospheric nitrogen), but Michael (1998) suggests that watersheds that receive salmon have evolved to capture the annual pulse of nutrients released from carcasses. If spawning stocks decline then there will be less marine derived nitrogen available to supplement atmospheric nitrogen inputs into watersheds, suggesting that the parent generation assist their progeny in their fight for survival long after they are gone themselves. Hence the title of this study.

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1.2.1 Salmon carcasses and the aquatic ecosystem

In order for any organism to increase its weight, it must consume energy. It has been shown that enriched a stream with nitrogen and phosphorus by whole-river fertilization can result in increased juvenile salmonid biomass (Johnston *et al.* 1990). Juvenile fish do not consume fertilizer so the increase in nutrients must indirectly increase the availability of energy to them. The trophic levels below the fish must have a positive response from the increase in nutrients which increases their biomass making more food or higher quality food available for juvenile salmonids. Thus, the addition of nutrients serves to stimulate production in lower trophic levels which can then be transferred up the food web to higher trophic levels.

Salmon die after spawning in the lakes and streams they were born in. Therefore, salmon carcasses have a direct impact on this portion of a watershed as opposed to the terrestrial portion where impacts are less direct. The streams that salmon spawn in flow continuously, thus the nutrients released from carcasses must somehow be retained within the system or else they will be flushed out. One retention mechanism is algal uptake. Algal and biofilm growth were also observed to increase as much as 15 times in streams that were supplemented with salmon carcasses (Fisher Wold and Hershey 1999; Wipfli *et al.* 1998). Since algae are at the bottom of the trophic pyramid, increasing the base of the pyramid may increase the biomasses of higher trophic levels as more energy is available for transfer up the food web.

A group of organisms one level up the trophic pyramid from the primary producers are the macroinvertebrates, which can be classified into four functional feeding groups: shredders, scrapers, collectors, and predators (Cummins 1973). The scrapers feed directly on algae attached to substrates such as logs and rocks while collectors feed on drifting pieces of algae in the water column. Predators, in turn, prey on other invertebrates while shredders feed on vascular plant material. Wipfli *et al.* (1998) found, in the same study that produced a 15 fold increase in biofilm production, that total macroinvertebrate densities increased 25 times in a natural stream that had been carcass-enriched. Kline *et al.* (1990) found that nearly all of the nitrogen found in caddis fly larvae sampled in the spring was marine derived. By increasing the food available to the invertebrates, their biomass can increase which is meaningful to fish since invertebrates are a major food source for them in the stream environment.

Another pathway whereby marine derived nutrients can be passed from adult carcasses to juvenile fish is through direct consumption of flesh and eggs. Using stable isotope analysis, Bilby *et al.* (1998) found that by placing salmon carcasses in a stream, the proportion of marine derived nitrogen in the muscle tissue of juvenile steelhead increased from approximately 34% to

nearly 72%. Gut content analysis revealed that the juveniles had been feeding primarily on carcass flesh and eggs during the period that they were available. Salmon carcasses are available for some time after spawning as carcasses do take some time to fully decompose. Decomposition rates have been shown to vary depending on whether or not the carcass is exposed to air or is submerged (Kline *et al.* 1997), thus making the carcass effects like that of a time release pill. Sterling *et al.* (2000) found that the rate at which slow-release fertilizer pellets dissolved is influenced greatest by the length of exposure to water with pellet size, water temperature, and water flow having a smaller effect. The different salmon species return to spawn at different times of the year, spreading out carcass availability.

The different timing of the spawning runs also results in interactions between salmon species, as the nutrients that are released from the carcasses of one particular species do not benefit their offspring exclusively. For example, in a stream receiving both pink (*O. gorbuscha*) and coho spawners, adult pink salmon carcass biomass had a positive correlation with the coho salmon recruit per spawner ratio (Michael 1995). Pink salmon may be the least economically valuable of the salmon species and receive relatively little management attention compared to others, such as coho and sockeye (*O. nerka*), but the positive impact pink salmon have on the aquatic ecosystem is just as ecologically valuable as any of the other salmon species.

If the nutrients released from salmon carcasses play a vital role in maintaining the health of the aquatic ecosystem, a reduction in the number of adult spawners by humans harvesting them, could lead to a downward spiral situation. A reduction in nutrients could lead to a reduction in primary productivity, which would reduce the amount of energy available to be transferred up to higher trophic level organisms. This downward trend can be reversed through the addition of nutrients to streams (Stockner and MacIsaac 1996).

1.2.2 Manipulation of nutrient levels

The nutrient dynamics of lakes in British Columbia have previously been studied to measure the effect nutrient additions have on juvenile sockeye salmon (Hyatt and Stockner 1985). They found that increasing the amount of zooplankton available for juvenile sockeye impacts the weight they achieve after their first year of growth in the lakes. Data presented in Brocksen *et al.* (1970) also shows a similar trend as sockeye growth rate was seen to increase as zooplankton biomass increased. Ricker (1962) examined the relationship between sockeye smolt size and marine survival and found that larger smolts have higher survival rates. Increasing zooplankton biomass has positive effects on juvenile sockeye salmon but there is still one more step in the food chain from nutrients to juvenile sockeye and that is the phytoplankton. Budy *et al.* (1998)

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found that the addition of nitrogen and phosphorus to a juvenile sockeye rearing lake in Idaho increased phytoplankton production, zooplankton biomass, and fish growth. Nitrogen and phosphorus were added to the North Arm of Kootenay lake in the early 1990s with results indicating that the nutrient additions were successful at increasing the biomass of phytoplankton, zooplankton, and kokanee (Ashley et al. 1997). The addition of nutrients to stimulate primary productivity, with the eventual goal to increase sockeye smolt production, may not always be so simple. Stockner (1987) outlines potential food chains leading from primary producers to juvenile sockeye identifying possible sinks in the transfer of energy up the food chain. These sinks could prevent the effects of nutrient additions to reach the juvenile sockeye.

The addition of nutrients does not exclusively benefit phytoplankton and the organisms that feed on it. Perrin and Richardson (1997) found that adding inorganic nitrogen, by itself and in combination with phosphorus, increased the buildup of periphyton in experimental mesocosms in the Nechako River. They concluded that an increase in insect numbers in the mesocosms was due to the increase in algae and detritus produced from the algae. The increase in insects now provides more food for juvenile salmonids. Johnston et al. (1990) suggests that the increase in fish size seen after fertilization of the Keogh River was due to an increase in periphyton, which led to higher benthic insect production that the juvenile salmonids fed on. Sterling et al (2000) also suggest that autotrophic production may be stimulated by the addition of slow-release fertilizer to streams that are nutrient deficient with the eventual result being the restoration of salmonid production.

1.2.3 Salmon carcasses and the terrestrial ecosystem

The effects of salmon carcasses are not confined to the aquatic ecosystem, as setting ecosystem boundaries are merely an anthropocentric way of compartmentalizing nature. Many bird and mammal species are dependent on the annual flux of spawning salmon and have incorporated this resource in their own yearly migration patterns. Wilson and Halupka (1995) report that over 40 species of mammals and birds in Alaska are known to feed on salmon, carcasses, eggs, and juveniles salmon in freshwater habitats.

Bald eagles (*Haliaeetus leucocephalus*) congregate in areas were the salmon are accessible to them. In some areas numbers of bald eagles can increase from a mere few to thousands due to the arrival of the spawning salmon (Drew 1996). The timing of the spawning salmon gives the eagles an opportunity to accumulate enough energy reserves to survive the winter months. Stalmaster and Kaiser (1997) estimated that chum made up 96% of the eagles

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diet when the salmon were available in the Nisqually River. Chum salmon (*O. keta*) are typically a late spawning species which makes them a vitally important winter food source for these eagles. The eagles' consumption of salmon was once seen as competition to the resource, and between 1917 and 1953, a bounty of 50¢ to two dollars per bald eagle was offered in Alaska (Imler and Kalmbach 1955). Robards and King (1966) report that for years with data available, from 100,000 to 128,000 eagles were recorded in the bounty books.

Bears belong to the many mammals known to depend heavily on spawning salmon as a nutritious food source and can be found congregated along streams feeding on the salmon when available (Hilderbrand *et al.* 1996; Reimchen 1998). Once again, the spawning salmon come at a time when it is most needed as bears feed heavily in the late summer and fall as they prepare for hibernation. During hibernation the bears do not actively feed and need to rely on energy stored within their bodies to maintain basic body processes. In pregnant black bears, the final 6-8 weeks of gestation, birth of the newborn, and the first 10-12 weeks of lactation all occur while the mother is hibernation (Oftedal *et al.* 1993). The mother has to be sure not only to meet her own energy requirements but also those required to produce high quality milk for her offspring. Reproductive success in black bears may be higher for well fed females than for thin ones as Rogers (1976) has shown that a strong positive correlation exists between the fall mass of female bears and reproductive success. Spawning salmon can provide bears the opportunity to accumulate sufficient energy stores to see them through the winter because salmon are one of the most nutrient dense food items for bears in the Pacific Northwest region (Hilderbrand *et al.* 1996).

Grizzly or brown bears have evolved with salmon as a primary food source. Stable isotope analysis of bone samples of grizzly bears known to inhabit the Columbia River drainage around the early 1900s taken from museum specimens revealed that salmon derived nitrogen comprised between 33-90% of the nitrogen assimilated in the bears (Hilderbrand *et al.* 1996). The salmon not only offers the bears a meal that is highly nutritious to get them through hibernation but the salmon diet has also led to some physical differences between coastal and interior bears as Spraker *et al.* (1981), found coastal brown bears to be larger than their interior counterparts and are know to become sexually mature at an earlier age which may be due to their access to spawning salmon.

Mink (*Mustela vision*) are another mammal known to depend on the annual return of salmon for reproduction. It has been shown that mink feed almost exclusively on salmon when they are available in coastal southeast Alaska (Ben-David *et al.* 1997). The salmon have become such an integral part of the minks annual cycle that they may have altered the time of year that

they breed so that the energy intensive activity of lactation can occur when salmon carcasses are available (Ben-David 1997).

1.2.3.1. Salmon carcasses and terrestrial vegetation

Bird and mammal species also play an important role in dispersing salmon carcasses and marine derived nutrients to the surrounding vegetation. For instance, ravens and crows have been observed storing salmon carcass material onto trees, grass, and under rocks (Willson *et al.* 1998). While most of the consumption of carcass material occurs quite close to the stream, the marine derived nutrients may reach well away from the stream into the riparian vegetation by the deposition of fecal matter. Ben-David *et al.* (1998) looked at five species of plants along transects from the stream to the upland forest. The found that the value of $\delta^{15}N$, from salmon carcasses, decreased significantly as distance from the stream increased in three of the five plant species sampled with $\delta^{15}N$ found in vegetation as much as 500 meters away from the stream. The researchers also found that the level of $\delta^{15}N$ in vegetation was generally higher in areas where predator activity was evident than it was in areas where no predator activity could be found.

Hilderbrand *et al.* (1999) investigated specifically the role of brown bears as a major vector of marine nitrogen into the riparian zone. They found that marine nitrogen comprised approximately 15 to 18% of the total nitrogen in spruce foliage within 500 m of the stream. They also estimated that the bears were responsible for distributing 83% of that with the majority being excreted in urine. Reimchen (2000) found that black bears in an old-growth watershed on Haida Gwaii consumed only half of each salmon carcass that they captured and brought into the forest, leaving an average of 1.3 kg of carcass material on the forest floor. In this watershed which receives a relatively small annual spawning run, approximately 5000 salmon, the bears consumed approximately 75% of the spawning run in 1993. He estimated that 70 to 80% of the salmon captured were nearly spawned out or had finished spawning. Reimchen (*pers. comm.*) has further investigated the input of marine nitrogen to the forest by estimating the marine nitrogen content in the growth rings of trees. Paquet (2000) reports on some of his work that shows that the nitrogen input from spawning salmon is the largest single pulse of nitrogen for the forests bordering the streams. Stable isotope analysis has shown that approximately 13% of the nitrogen in the foliage of riparian trees is marine derived and as much as 50% of the nitrogen in individual growth rings comes from the salmon. Results like this and that of Hilderbrand *et al.* (1999) are compelling evidence that resource managers, in both the aquatic and terrestrial settings, must consider the interactions between the two environments rather than only what is happening within the two environments separately.

1.3 Study area

The Atnarko River system has been chosen as the study site. The portion of the watershed that I have chosen to model encompasses an area of 1290 km² (Figure 1). The Atnarko River originates on the interior plateau and flows through the Coast Mountains before joining the Talchako River. The confluence of the Atnarko and Talchako Rivers forms the origin of the Bella Coola River and is located approximately 60 km from the town of Bella Coola.

The valleys in the Atnarko watershed are steep sided as many of the streams that flow into the main channel of the Atnarko originate high in the Coast Mountains. The steep terrain makes many of these streams inaccessible to resident fish and spawning salmon. For this reason I have not included all drainages that lead into the Atnarko River as part of the model area. There are two lakes, Lonesome and Stillwater, within the model area that are accessible to migrating salmonids. Other lakes and streams were not included due to the fact that the steep gradient precludes salmonids from utilizing these areas.

The terrestrial portion of the watershed has been classified as belonging to the Interior Douglas-fir (IDF), Engelmann Spruce – Subalpine Fir (ESSF), Coastal Western Hemlock (CWH) and Alpine Tundra (AT) biogeoclimatic zones according to Meidinger and Pojar (1991). The IDF zone encompasses the majority of the watershed and is found at lower elevations than the ESSF and AT zones. The Atnarko River watershed is the northern and western extent of the IDF zone in British Columbia. The IDF zone has been described as having a continental climate with warm, dry summers and cool winters. The Coast Mountains collects the majority of precipitation creating a rainshadow effect that limits precipitation in the IDF to 300 – 700 mm annually (Meidinger and Pojar 1991).

All five species of Pacific salmon use the Atnarko River for spawning although chum salmon do not do so in any significant numbers, spawning mainly in the Bella Coola River. Almost all of the pink, sockeye, and chinook (*O. tshawytscha*) salmon that enter the mouth of the Bella Coola River will migrate upstream into the Atnarko River to spawn. The Atnarko watershed and the salmon share a symbiotic relationship where the health of one has great impacts on the other.

Figure 1. Map of the Atnarko, Talchako, and Bella Coola Rivers. The dashed line is the approximate boundary for the portion of the Atnarko River watershed that was used in the construction of the Ecopath model.

2. Methods

2.1 Description of model area

The Atnarko River watershed was chosen as the location for this study. As Figure 1 shows, not all parts all the streams were included in the model area. Topography was used as a guide in determining the boundaries of the model area, which made the boundary to the northeast region of the model area difficult to determine. This region is also the transition from the Coast Mountains to the interior plateau so while there is a topographical break, parts of streams that eventually flow into the Atnarko River are east of this break and were left out of the model area. Few of the streams flowing into the Atnarko are used for spawning activities. The total watershed encompasses an area of approximately 1290 km². This was calculated by determining the watershed boundaries and taking subsequent measurements from a topographic map with a scale of 1: 250,000. The model area was then further subdivided into three regions which are described below.

Aquatic zone – This zone includes Lonesome and Stillwater lakes the main channel of the Atnarko River. The lakes above Hunlen Falls were not included in this region due to the fact that Hunlen Falls precludes salmon from entering these lakes. The streams flowing into the Atnarko were also left out of this zone due to the fact that topography also inhibits salmon from migrating up them. Some salmon do use the very lower portions of some of these streams for spawning but the majority of salmon will use the main channel of the Atnarko River. Lonesome and Stillwater Lakes were estimated to have a surface area of 4.5 km² and 0.88 km² respectively. The main channel of the Atnarko was estimated to have a surface area of 0.85 km². This assumed an average stream width of 15 m and a length of 56 km from the confluence of the Atnarko/Talchako to the portion of the river just south of Lonesome Lake where the Atnarko makes an major, almost 90 degrees, turn from flowing west to north. The total surface area of the Atnarko River and Lonesome and Stillwater Lakes was estimated to be approximately 6 km², or approximately 0.5% of the total model area.

Riparian zone – This zone includes the area of forest along the main channel of the Atnarko with a width of 1 km on either side of the river (Figure 2). This boundary was chosen due to the fact that it was reported that redistribution of nitrogen from salmon carcasses by brown bears dropped off greatly beyond 500 m from the stream, with near baseline levels seen beyond 1 km from the stream (Hilderbrand *et al.* 1999). This zone was estimated to be approximately 112 km², or approximately 8.5% of the total model area.

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Figure 2. Cross-section view of model area showing the three sub-model zones used to construct the overall Atnarko watershed model.

Forest zone – This zone comprises the forest area from the boundary of the riparian zone to the model area boundary. This area also includes those streams and lakes that were not included in the aquatic zone. The forest zone was estimated to be approximately 1172 km^2, or approximately 91% of the model area.

2.2 Overview of modeling process

The Ecopath model can be thought of as a model that is comprised of these three sub-models, each forming their own food web. There are, however, several groups that link the three zones as they play a role in each of the three sub-food webs. The Ecopath with Ecosim software package (Christensen and Pauly 1992), which includes Ecosim (Walters 1998), Ecospace (Walters *et al.* 1998), and Ecotrace (C. Walters *pers. comm.*), was used to carry out the objective of this study. The first step in the process was to construct and balance an energy related Ecopath model using wet weight as the currency. This model was then run using the Ecospace routine to verify that the groups could also balance over time and space. Once this was done the next step was to convert the wet weight model into a balanced nitrogen based model so that the flow of marine derived nitrogen from salmon carcasses and eggs could be tracked. This procedure was done using the Ecosim and Ecotrace routines. Below are descriptions of each of these routines. For details on the construction and balancing of wet weight and nitrogen Ecopath models see Appendices 1 and 2, respectively. Table 1 lists the groups used to construct the Ecopath models as well as some of the groups attributes.

Table 1. Groups used to construct Ecopath model.

Ecopath group	Wet weight model function	Nitrogen based model function	Assigned habitat
Forest shrubs	Primary Producer	Consumer	Forest
Forest trees	Primary Producer	Consumer	Forest
Small mammals	Consumer	Consumer	Forest
Predatory terr. insects	Consumer	Consumer	Forest
Herbivorous insects	Consumer	Consumer	Forest
Passerine birds	Consumer	Consumer	Forest
Earthworms	Consumer	Consumer	Forest
Mustelids	Consumer	Consumer	Forest
Riparian shrubs	Primary Producer	Consumer	Riparian
Riparian trees	Primary Producer	Consumer	Riparian
Riparian small mammals	Consumer	Consumer	Riparian
Riparian pred terr ins	Consumer	Consumer	Riparian
Riparian herb ins	Consumer	Consumer	Riparian
Riparian passerine birds	Consumer	Consumer	Riparian
Riparian worms	Consumer	Consumer	Riparian
Riparian mustelids	Consumer	Consumer	Riparian
Herbivorous ducks	Consumer	Consumer	Aquatic, Riparian
Omnivorous ducks	Consumer	Consumer	Aquatic, Riparian
Raptors	Consumer	Consumer	Aquatic, Forest, Riparian
Wolves	Consumer	Consumer	Aquatic, Forest, Riparian
Ungulates	Consumer	Consumer	Aquatic, Forest, Riparian
Black bears	Consumer	Consumer	Aquatic, Forest, Riparian
Grizzly bears	Consumer	Consumer	Aquatic, Forest, Riparian
Demersal fish	Consumer	Consumer	Aquatic
Trout and char	Consumer	Consumer	Aquatic
Periphyton	Primary Producer	Consumer	Aquatic
Biofilm	Primary Producer	Consumer	Aquatic
Macroinvertebrates	Consumer	Consumer	Aquatic
Zooplankton	Consumer	Consumer	Aquatic
Phytoplankton	Primary Producer	Consumer	Aquatic
Macrophytes	Primary Producer	Consumer	Aquatic
Benthos	Consumer	Consumer	Aquatic
Juvenile chinook	Consumer	Consumer	Aquatic
Juvenile coho	Consumer	Consumer	Aquatic
Juvenile sockeye	Consumer	Consumer	Aquatic
Salmon eggs	Primary Producer	Primary Producer	Aquatic
Salmon carcass	Primary Producer	Primary Producer	Aquatic
Riparian detritus	Detritus	Detritus	Riparian
Forest detritus	Detritus	Detritus	Forest
Aquatic detritus	Detritus	Detritus	Aquatic

2.3 Ecosystem modeling using Ecopath

A trend in resource management is to shift from single species to multi-species management. The Ecopath software allows the user to investigate species interactions that may be useful when exploring possible management strategies. The Ecopath approach was initiated by the work of Polovina (1984), and then refined by Christensen and Pauly (1992). Ecopath models are considered mass balanced because whatever biomass is produced in the ecosystem is quantified and assumed to be either consumed or exported out of the system. This relationship can be expressed mathematically by the equation:

$$B_i \cdot (P/B)_i \cdot EE_i = Y_i + \Sigma \, B_j \cdot (Q/B)_j \cdot DC_{ij} \qquad\qquad (1)$$

where B_i is the biomass of i in the system; $(P/B)_i$ is the production per biomass ratio of i in the system which is equal to the total mortality rate of i; EE_i is the ecotrophic efficiency which is the proportion of production that is consumed within the system; Y_i is the yield of i, (i.e. the fishing mortality of i multiplied by the biomass of i). $(Q/B)_j$ is the consumption per biomass for the consumer j; DC_{ij} is the contribution of i in the diet of j. The left side of the equation represents the biomass that is used in the ecosystem while the right side represents the biomass that is consumed or exported out of the ecosystem. A functional group (i) can consist of a single species or a group of species sharing similar characteristics such as prey or predators.

The model can be used in a wide variety of situations as biomass, carbon, calories, or nutrients can all be used as the unit for the calculations. Equation (1) is applied to all the functional groups that are represented in the model. While equation (1) can appear intimidating, the Ecopath software is set up in a way that is very user friendly. The initial steps in constructing an Ecopath model is to define the ecosystem being modeled and determine the functional groups involved and enter their parameters: B, P/B, Q/B, and the diet composition. The program is set up so that all but one parameter must be entered and the software will estimate this missing parameter. EE is often left as the unknown to be estimated by the program.

After these basic parameters have been entered the next task is to balance equation (1) for each of the functional groups. Since EE is often left to the software to calculate, it is also used to identify the functional groups that are not balanced. For instance if a group has an EE greater than 1.0, it implies that there is too great a demand placed on that group. The input parameters must be adjusted in order for equation (1) to be balanced for that group. Once all the functional groups have been balanced, the software produces various summary statistics on the performance

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of the ecosystem. The trophic interactions can then be expressed as a flow diagram showing the connections that exist within the ecosystem.

It must be kept in mind that a balanced Ecopath model is but one possible representation of the ecosystem. The assumptions and data manipulation used by the model constructor could be manipulated justly by another researcher that would result in a different representation of the same ecosystem.

2.3.1 Biomass

The biomass estimate required for Ecopath as input is the density of the organism in the model area. As I did not conduct any field surveys on any of the organism used in the construction of my model I relied on biomass estimates reported in literature. For Ecopath groups that contained more than one species, biomass estimates were combined for those species to determine an overall biomass for the group.

2.3.2 Production/biomass (P/B)

P/B estimates were not measured directly through conducting field studies but were estimated using several techniques that relied on data found in literature.

A common technique in fisheries science is to estimate P/B using catch curve analysis. Catch curve analysis normally entails plotting the natural logarithm of population numbers against age and then fitting the plot with a linear regression in order to estimate total mortality, where the slope of the line is equal to $-Z$ (Ricker 1975) which is an estimate of P/B under equilibrium (Allen 1971). P/B was also estimated using annual survival rates for various species. Using the equation:

$$N_2 = N_1 \cdot e^{-Z(t2-t1)} \tag{2}$$

where N_1 is the number of organisms alive at time 1 (t1), N_2 is the number alive at time 2 (t2), and Z is the total mortality. An annual survival rate entails a time step of 1 year so equation (2) can be re-expressed as:

$$\ln(N_2/N_1) = -Z \tag{3}$$

where N_2/N_1 is the annual survival rate. As with catch curve analysis, -Z is an estimate of P/B.

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P/B was also calculated by dividing annual production estimates by annual biomass estimates. This was only done were both parameters were reported from the same study area. Dividing a production estimate from one region by a biomass estimate from another region should be avoided. P/B values were also taken directly from Ecopath model previously constructed for other areas in British Columbia and Alaska.

2.3.3 Consumption/biomass (Q/B)

Consumption per biomass estimates were calculated using data available from the literature or previous Ecopath models. One common way to estimate Q/B was to find consumption values reported for a given organism, and divide this by the mean wet weight of that organism.

Another method that was used to estimate this parameter was to use the P/B estimate and an assimilation rate, the proportion of energy that goes into growth and maintenance for that particular species. Dividing the P/B estimate by the assimilation rate gives the P/B ratio.

Q/B estimates were also calculated using equations to estimate an organism's field metabolic rate. Field metabolic rates provide an estimate to the energy demands a particular organism faces. If the energy content of the main food items of the organism is known, it is possible to convert the energy required to the weight of food needed to satisfy metabolic needs. This is done on an annual basis so that the weight of food consumed can be divided by the mean weight of that organism to estimate Q/B.

2.3.4 Diet composition

Diet composition data were taken from studies reported in literature or from previous Ecopath models.

2.3.5 Sensitivity analysis

A sensitivity analysis routine exists in the Ecopath software. The routine varies the basic inputs that the user has used to construct the model in steps from +50% to -50% and measures the effect that the change has on the input parameter estimated by the software. The basic input parameters are:

Biomass;

Production / biomass ratio;

Consumption / biomass ratio;

Ecotrophic efficiency.

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In this case, the ecotrophic efficiencies were left as the unknown to be estimated by the software when constructing the model; therefore, the sensitivity analysis varies the other input parameters one by one and measures the change it has on the ecotrophic efficiency estimate.

2.4 Ecosystem modeling using Ecosim

Thanks to the work of Walters (1998) and Walters *et al.* (1998) an Ecosim application can be used to simulate time-dynamics for the original Ecopath model. The Ecosim program allows the user to impose mortality rates on selected functional groups that are present in the Ecopath model. The relative impact the new mortality regime has on the ecosystem is displayed graphically as the relative biomass of various groups change from their baseline levels entered in the original Ecopath model. The changes occur because the ecosystem must still be in balance after the new mortality regime is imposed. The size and direction of the impact will depend on the connectedness and rates of flows between the functional groups in the Ecopath model. Potential impacts can be predicted by inspecting the trophic impact diagram in Ecopath. Eliminating a prey species 'x' by simulating overfishing or hunting, the predators will shift their diet composition to compensate for the decreased biomass of 'x'.

Ecosim allows the user to explore policy options, and is not intended to be used to determine quota sizes or bag limits for future years. One must also keep in mind that Ecosim operates using an Ecopath model as its baseline; therefore, the assumption made in constructing the balanced model should be kept in mind when using Ecosim.

2.4.1 Ecosim inputs

Ecosim was used to demonstrate the impact salmon carcasses and eggs have on the food web. This was done using a scenario where salmon carcass and egg biomass was doubled and a scenario where carcass and egg biomass was halved. The biomass levels were manipulated using the forcing function in Ecosim. The forcing function allows the user influence the trend that the biomass of a particular group will follow over time. The other groups then react to the changes as the food web tries to reach equilibrium.

There were no changes made to the Ecosim default settings, i.e., no forcing functions, when using Ecosim and Ecotrace to track the flow of marine nitrogen. Since it was not the objective of this study to predict the effects of various management regimes, no attempt was made to vary the baseline mortality rates on any of the Ecopath groups. Therefore, the Ecopath

models were allowed to run at equilibrium so that the Ecotrace routine could track the flow of marine derived nitrogen throughout the food web.

2.5 Ecosystem modeling using Ecotrace

Ecotrace (Walters 1998; Walters *et* al. 1998; Walters *pers. comm.*) is a new routine recently added to the Ecopath software package. This routine allows the user to track the flow of persistent contaminants or isotope tracers within a food web. Tracer dynamics have been well studied and the Ecotrace routine was derived from work on tracer kinetics such as that of Sheppard (1962). Ecotrace works in conjunction with Ecosim to track these flows over time. Tracer materials are able to flow from group to group throughout the ecosystem via:

Uptake from food;

Absorption from the environment;

Concentration in immigrating and emigrating biomass;

Metabolism.

The user must input some initial estimates for tracer parameters in the setup of the routine. The initial inputs for each group may include:

Initial concentration;

Concentration in immigrating biomass;

Direct absorption rate;

Decay rate.

The routine then uses these inputs to compute the concentration of the contaminant or isotope in the biomass of each group as Ecosim runs the Ecopath model over time.

2.5.1 Ecotrace inputs

The Ecotrace routine was used with the nitrogen based Ecopath model so that the flow of marine derived nitrogen could be tracked over time. The first step in setting up the Ecotrace scenario was to determine the amount of marine derived nitrogen entering the system with only salmon carcasses and salmon eggs to produce marine derived nitrogen. The proportion of nitrogen in salmon carcasses and eggs was assumed to be 1 since adult biomass only contains an insignificant amount (<1%) of residual freshwater derived biomass (Kline *et al.* 1997). The input

for the initial concentration in Ecotrace was calculated by multiplying the habitat adjusted biomass by the P/B ratio, the product then being multiplied by the concentration of marine derived nitrogen. For salmon carcasses, the habitat adjusted biomass was 12.994 mg N•m^{-2} which was multiplied with its P/B of 1. Since the concentration of marine derived nitrogen in the nitrogen in a salmon is 100%, 12.994 was also the input for the initial concentration of marine derived nitrogen for salmon carcasses. The same procedure was applied to salmon eggs resulting in an initial concentration of 3.009 mg N•m^{-2}.

The next step was to input the amount of marine derived nitrogen entering the system in immigrating biomass. Salmon carcass and salmon egg biomass were allowed to immigrate into the system by placing a value of 0.1 in the immigrating biomass column on the migrations page in the Ecopath model. The amount of marine derived nitrogen entering the system was calculated by dividing the initial concentration and by the biomass immigrating into the system. This now gives the concentration per immigrating biomass. For salmon carcasses, the initial concentration input was 12.994 mg N•m^{-2} which was divided by an immigrating biomass of 0.1 to produce a value of 129.94 mg N•m^{-2}, which was set as the amount of nitrogen entering the system through immigrating biomass. The same was done for salmon eggs which produced a value of 30.09 mg N•m^{-2}. The Ecotrace routine was run over a time period of 1000 years plotting concentration per biomass over time and it was seen that the concentration per unit of salmon carcasses and salmon egg biomass was constant over time with a value of 1.0 per year.

Converting the wet weight model to a nitrogen based one led to several notable changes in the diet composition matrix of the Ecopath model. These concerned the diets of groups that are considered primary producers in the wet weight model but are considered consumers in the nitrogen model. These groups were the forest and riparian trees and shrubs, periphyton, biofilm, phytoplankton, and macrophytes (Table 1). For the first scenario, the diet composition for these groups was initially set to 100% detritus. The model was then run over a 1000 year time period. After 1000 years the concentration of marine nitrogen in the detritus groups was still increasing; therefore, the concentration of marine nitrogen in groups that fed on detritus also was still increasing. It was felt that imposing a decay rate on the detritus groups would prevent this and cause the concentrations in detritus to approach an asymptote at some level.

The next step in the setup was to determine appropriate decay rates on the detritus groups that would prevent the marine nitrogen concentrations from increasing indefinitely. A base volume exchange loss from environmental concentration was set to 0.1. The Ecotrace routine automatically adds one group, called 'environment', to the model. The environment group derives its concentration level from the detritus groups or the user can set a base inflow rate of

tracer in to it. The base volume exchange loss rate was set by adjusting the value and re-running the model until the concentration level was seen to level off after 1000 years. The detritus groups also needed a decay rate imposed on them so that concentration levels would approach an asymptote and not increase indefinitely. The decay rates were manipulated and the model run until the concentration levels were seen to level off after 1000 years. The corresponding decay rates for the aquatic, forest, and riparian zones are 0.005, 0.050, and 0.005 per year respectively. The forest zone had to have a higher decay rate imposed upon it presumably because there is such a high biomass of groups in the forest zone that a large amount of detritus is produced each year. When plotting concentration per biomass, a higher decay rate is needed to keep the concentration from continually increasing. With the decay rates set for the detritus groups, the model was run for 1000 years and the results recorded.

There were no local data on the concentration of marine nitrogen in the groups that were primary producers in the wet weight model, but consumers in the nitrogen model. Such values were found for riparian trees and shrubs, periphyton, biofilm, and phytoplankton from studies elsewhere (Table 2). The next scenario was to increase the level of marine nitrogen in these groups to approximate those values found in the literature by altering their diet compositions. Rather than allow these wet weight primary producers to only feed on detritus, they were allowed to 'feed' directly on salmon carcasses and salmon eggs. Allowing them to feed directly on carcass and egg biomass increased the levels of marine nitrogen in them and in the detritus groups sufficiently to approximate the literature values for them. Because these wet weight primary producers had relatively high biomass of P/B estimates, they also had high consumption rates.

Table 2. Marine nitrogen as percentage of the total nitrogen content of several groups used in Ecopath model from other study areas.

Group	Marine nitrogen concentration (%)	Midrange	Reference
Riparian foliage	17.5	-	Bilby et al. (1996)
Grizzly bears	33 to 90	61.5	Hilderbrand et al. (1996)
Coastrange sculpin	63 to 69	66.0	Kline et al. (1993)
Age-0, 1, and 2 cutthroat trout	19 to 26	22.5	Bilby et al. (1996)
Epilithic organic matter	20	-	Bilby et al. (1997)
Periphyton	46 to 87	66.5	Kline et al. (1993)
Macroinvertebrates	11 to 25	18.0	Bilby et al. (1996)
Plankton	49 to 73	61.0	Kline et al. (1993)
Age-0 coho	30	-	Bilby et al. (1996)
Sockeye yearlings and smolts	27 to 71	49.0	Kline et al. (1993)

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The high consumption rates placed enormous predation pressure on the salmon carcass and salmon egg groups such that the production values for carcasses and eggs had to be increased significantly in order to satisfy all of the new consumption demands. For example, phytoplankton has a biomass of 285 mg $N \cdot m^{-2}$ and a Q/B of $125.43 \cdot year^{-1}$ resulting in a total consumption value of approximately 32,360 mg $N \cdot m^{-2} \cdot year^{-1}$. If phytoplankton is fed a diet consisting of 10% salmon carcass then the amount of salmon carcass consumed is 3236 mg $N \cdot m^{-2} \cdot year^{-1}$. Since there was an initial biomass estimate for salmon carcasses of approximately 2600 mg $N \cdot m^{-2}$, there is not enough salmon carcass biomass available. Therefore, the production of salmon carcass has to be increased. Decreasing the amount of salmon carcass in the diet composition of phytoplankton was not done because doing so would also reduce the concentration of marine nitrogen. The diet composition level was set so that the concentration of marine nitrogen would approximate the values seen in other studies. While phytoplankton does not actually seek out and prey upon salmon carcasses, they were allowed to do so in this model as it is the most direct way of getting the marine nitrogen into them.

The diet composition and the salmon carcass and salmon egg production values were altered as the model was re-run until the concentration of marine nitrogen in riparian trees and shrubs, periphyton, biofilm, and phytoplankton, after 1000 years of simulation, approximated reported values from studies elsewhere (Table 2). The Ecotrace routine was then run over a time period of 1000 years so that concentrations of marine derived nitrogen had sufficient time to build up and approach an asymptote in the various groups.

An alternative method to increasing the level of marine nitrogen in the wet weight primary producers would be to allow them to absorb the marine nitrogen directly from the environment. The Ecotrace routine does allow the user to set a base inflow rate to, and a direct absorption rate from the environment as an initial input. At this time, the dynamics between the Ecopath groups, the detritus groups, and the environment is not fully captured by Ecotrace so this method was not attempted. One environment group is added to the rest of the Ecopath groups only in the Ecotrace routine. In the case of the Atnarko watershed model, there are three sub-models so there should be three different environments in the Ecotrace routine. The Ecotrace routine was initially constructed for use with marine models where there is only one environment, water. Once the dynamics of the environment group are fully understood it should be possible to increase the levels of marine nitrogen in groups like phytoplankton through direct absorption rather than through direct feeding on salmon carcasses and eggs. This should alleviate the problem of having to increase salmon carcass and egg production in order to meet consumption

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demands, as well as being a more realistic method of getting the marine nitrogen into groups that are primary producers in wet weight models but are consumers in nitrogen based ones.

2.6 Ecosystem modeling using Ecospace

The Ecospace routine developed by Walters *et al.* (1998), builds on Ecopath and Ecosim by allowing the user to run an Ecopath model both over time and space. This is done by assigning various cells in a grid network a particular habitat type (i.e., land, near-shore, and off-shore). The Ecopath groups can then be assigned to the habitat types they prefer and the software will distribute their biomass throughout the grid accordingly. As the program is run, an Ecosim routine is done for each grid cell and groups are allowed to expand or contract their original distribution through movement to adjacent cells. The user can define predation risks and feeding rates for each group if it moves into a grid cell that is non-preferred habitat. These conditions will restrict the flow of biomass form certain cells. This becomes important as organisms that are restricted to utilizing only a small fraction of the total model area must be able to find enough prey groups in that habitat while avoiding being preyed upon too heavily. Even though the Ecopath model may be balanced, once spatial restriction are put in place certain groups may not be able to perpetuate themselves spatially.

The Ecospace routine for this project was used strictly to see if in fact the Ecopath model made sense over space. It was not used to test policy options nor did it have any impact on the Ecotrace routine. While the Ecotrace routine was used with a nitrogen based model, Ecospace requires the base model to be energy related; therefore, the wet weight model was used for this.

2.6.1 Ecospace setup

The first step in setting up the Ecospace scenario was to determine the different habitat types. Three habitat types were chosen corresponding to the aquatic, riparian, and forest region of the model area (Figure 2). A grid size of 32x32 (= 1024 cells^2) was chosen and each habitat type was assigned the appropriate number of cells according to the percentage make-up of the model area. Since the aquatic portion of the model area was estimated to comprise approximately 0.5% of the model area, it was given a total of 5 cells. The riparian and forest regions made up approximately 8.5% and 91% of the model are respectively, so they were assigned 87 and 932 cells each respectively. The cells were assigned so that the aquatic zone cells were surrounded by the riparian cells, which were then surrounded by the forest cells.

The next step in the setup was to assign the groups to their preferred habitat types. Most groups were assigned to their respective habitats (i.e. riparian trees – riparian; zooplankton – aquatic) with the following exceptions. Herbivorous and Omnivorous ducks were both assigned to the aquatic habitat type since most of their time is associated with this zone or very close to it. Raptors, wolves, ungulates, black bears, and grizzly bears were assigned to all habitats. Even though none of these groups spends considerable time in water, they were assigned to all habitat types because some portion of their diet came from groups that do live in the aquatic zone full time. In order for them to feed on the aquatic groups, they have to have access to the aquatic zone.

The final step in the Ecospace setup was to set the dispersal rates and feeding rates for the groups. Neither forest nor riparian trees and shrubs were assumed to be mobile so their base dispersal rates, measured in $km \cdot year^{-1}$, were set to 0. This was also the case for the detritus groups. The model was then allowed to run over a 100 year time period after which several problems were noticed with the dispersal of certain groups. Aquatic groups were seen to disperse into the riparian zone and since organisms such as trout can not live on land, the dispersal rates for aquatic groups had to be changed. This was done by assigning the aquatic groups a high value of 500 for their relative dispersal rate in bad habitat and assigning them a value of 0 for their relative feeding rate in bad habitat. This meant that as the aquatic groups dispersed into the riparian, which is bad habitat, they stopped feeding and quickly moved back into the aquatic zone, or starved. The same procedure was also applied to omnivorous and herbivorous ducks with the exception that the relative dispersal rate in bad habitat was set to 200. This allowed the duck groups to migrate slightly into the riparian zone as ducks do inhabit the regions around lakes and streams. The model was then run again for 100 years.

3. Results

3.1 Ecospace outputs

The Ecospace routine was used to see if the balanced wet weight model was stable over both space and time. The model was run over a 100 year time period so that sufficient time was provided for groups to initialize and stabilize themselves. After the initialization period, the model nearly reached an equilibrium as all but a few groups were neither increasing nor decreasing over time but stable at a particular level. Figure 3 shows the biomass levels of the groups relative to the initial biomass. It can be seen that at the end of 100 years, the biomass of the majority of groups is close to the level they started out at. The fact that no groups increased to extremely high levels or dropped to very low levels, relative to their starting biomass, but instead approached equilibrium at near initial levels implies that the model remained in balance over time and space.

Figure 3. Relative biomass over time as model is simulated over space and time using the Ecospace routine, showing that the underlying Ecopath model leads to a stable Ecospace solution.

3.2 Original nitrogen based Ecopath model

The original nitrogen based Ecopath model refers to the model that was converted from wet weight with the diet composition for the groups: forest and riparian trees and shrubs, periphyton, biofilm, phytoplankton, and macrophytes all set to behave as if consisting of detritus (see below for reason).

3.2.1 Ecopath outputs

The trophic levels along with the pathways leading from primary producer or detritus to consumer groups computed by the software can be seen in Table 3. When examining the trophic levels it must be kept in mind that the model is set up with salmon carcasses and salmon eggs being the only primary producers. Thus, trophic levels do not correspond to values expected from a wet weight model. For instance, ungulates are herbivores and have a trophic level of 2.0

Table 3. Trophic level (TL) and number of pathways leading from primary producers or detritus to consumer groups in the original nitrogen model with unaltered diets.

Ecopath group	TL	# of pathways	mean length of pathway	Ecopath group	TL	# of pathways	mean length of pathway
Aquatic detritus	1.0	-		Zooplankton	3.0	4	1.75
Salmon carcasses	1.0	-		Riparian herb ins	3.0	3	1.67
Salmon eggs	1.0	-		Herbivorous insects	3.0	2	1.50
Riparian detritus	1.0	-		Herbivorous ducks	3.0	8	3.00
Forest detritus	1.0	-		Ungulates	3.0	8	2.00
Periphyton	2.0	2	1.00	Riparian small mamma	3.1	9	2.67
Biofilm	2.0	3	1.00	Small mammals	3.1	6	2.50
Phytoplankton	2.0	3	1.00	Grizzly bears	3.1	13	2.54
Macrophytes	2.0	1	1.00	Black bears	3.2	13	2.54
Riparian shrubs	2.0	3	1.00	Riparian mustelids	3.5	22	3.32
Riparian trees	2.0	2	1.00	Mustelids	3.5	14	3.29
Riparian worms	2.0	1	1.00	Omnivorous ducks	3.5	8	3.00
Forest shrubs	2.0	1	1.00	Trout and char	3.7	18	2.83
Forest trees	2.0	1	1.00	Juvenile coho	3.8	26	3.08
Earthworms	2.0	1	1.00	Riparian pred terr ins	3.8	5	2.00
Macroinvertebrates	2.5	6	1.83	Predatory terr. insects	3.8	3	2.00
Benthos	2.6	7	2.14	Wolves	3.8	45	4.00
Riparian passerine birds	2.9	11	2.45	Raptors	3.9	70	3.89
Passerine birds	2.9	7	2.43	Juvenile chinook	4.0	18	2.83
Demersal fish	3.0	15	2.53	Juvenile sockeye	4.0	10	2.80

in the wet weight model but have a trophic level of 3.0 in the nitrogen based model. This shift in levels occurs due to the fact that plants are no longer producers, with trophic level 1.0, in the nitrogen model but are consumers with a trophic level of 2.0.

The pathways leading from primary producers and detritus to consumer groups is of particular interest in this model since the only primary producers are salmon carcasses and salmon eggs. Groups can accumulate marine nitrogen by either feeding on carcasses and eggs directly or indirectly by feeding on detritus. Thus, the number of pathways leading from primary producers or detritus to consumers represents the number of different ways that a group can accumulate marine nitrogen. It can be seen in Table 3 that, with a few exceptions, the higher a groups trophic level the greater the number of pathways that marine nitrogen can take to get to that group. The mean length of pathway from primary producers or detritus to consumer groups is calculated by dividing the total number of transfers in a pathway by the total number of pathways. For example, if the pathway from primary producer 'p' to consumer 'c' is: p x y z c, then there are a total four transfers in this particular pathway. Groups with a lower mean length of pathway are feeding more directly on the primary producers or detritus than are groups with higher values. Table 3 also shows that, in general, groups with a higher trophic level also have longer pathways.

An ordinary sensitivity analysis, where only one parameter is changed by a fixed percentage in a single implementation of the model (Majkowski 1982), was performed on the nitrogen based model used to generate the Ecotrace results (Appendix 4). It can be seen that a small change in the input parameters, i.e. +/- 10%, causes a maximum change in ecotrophic efficiency of 11%. As Majkowski (1982) points out, ordinary sensitivity analysis, such as was done here, only provides elementary information on the influence that one parameter has on model predictions due to the fact that the errors associated with input parameter estimation may counteract one another. In this case, a change in the ecotrophic efficiency of a group may result in it becoming unbalanced. For example, if a group 'x' currently has an ecotrophic efficiency of 0.90 and the sensitivity analysis shows that increasing the biomass of group 'y' will increase the ecotrophic efficiency of 'x' by 10%, this will result in an ecotrophic efficiency of 0.99 for 'x' and it will still be in balance. The ordinary sensitivity analysis does not let you know what will happen to the ecotrophic efficiency of group 'x' if the biomass of groups 'y' and 'z' are both increased by 10% at the same time.

3.2.2 Ecotrace outputs

The original nitrogen based model was run over a 1000 year time span so that the concentrations of nitrogen could build up and approach an asymptote. A long time period was needed due to the fact that no groups except salmon carcasses and eggs have any marine nitrogen in them initially at time zero. As time goes on, the nitrogen starts to build relatively quickly in groups that feed directly on salmon carcasses or eggs. Once several groups have accumulated marine nitrogen, the nitrogen concentrations slowly build in the detritus groups as population turnover and biomass goes to detritus. As the concentration of marine nitrogen builds in the detritus groups, groups that do not feed directly on salmon but feed on detritus also accumulate marine nitrogen. In general, the concentration of marine nitrogen in groups that feed directly on salmon carcasses and/or eggs and do not feed heavily on detritus will build and approach an asymptote relatively quickly. Groups that do not feed directly on salmon carcasses or eggs but do feed substantially on detritus will take a longer time for the concentration of marine nitrogen to build and approach an asymptote.

The concentration of marine nitrogen in the groups after 1000 years can be seen in Table 4. Keep in mind that the concentrations do not represent the proportion of marine nitrogen in the

Table 4. Marine nitrogen as percentage of the total amount of nitrogen in each of the Ecopath groups in the original nitrogen based model

Ecopath group	Marine nitrogen concentration (%)	Ecopath group	Marine nitrogen concentration (%)
Forest shrubs	0.1	Ungulates	0.1
Riparian shrubs	0.2	Black bears	10.0
Forest trees	0.0	Grizzly bears	29.0
Riparian trees	0.2	Salmon eggs	100.0
Small mammals	0.0	Demersal fish	9.0
Riparian small mammals	0.4	Trout and char	1.0
Predatory terr. insects	0.0	Periphyton	1.0
Riparian pred terr ins	3.0	Biofilm	1.0
Herbivorous insects	0.0	Macroinvertebrates	1.0
Riparian herb ins	2.0	Zooplankton	1.0
Passerine birds	0.0	Phytoplankton	1.0
Riparian passerine birds	1.0	Macrophytes	1.0
Earthworms	0.0	Benthos	2.0
Riparian worms	2.0	Juvenile chinook	0.8
Mustelids	0.0	Juvenile coho	10.0
Riparian mustelids	3.0	Juvenile sockeye	1.0
Herbivorous ducks	1.0	Salmon carcass	100.0
Omnivorous ducks	2.0	Riparian detritus	0.2
Raptors	5.0	Forest detritus	0.0
Wolves	9.0	Aquatic detritus	1.0

groups wet weight but rather the proportion of marine nitrogen in the groups nitrogen biomass. For example, of the nitrogen in salmon carcasses 100% of it is marine derived. There was no local data to corroborate these results so they were compared to values that were found for studies in other areas (Table 2). It is quite clear that the values predicted by Ecotrace do not approximate values from other study areas, particularly in the lower trophic level groups. Therefore, it was felt that the model needed to be modified in order to better approximate the data from outside the model area.

3.3 Modified nitrogen based Ecopath model

The original nitrogen based Ecopath model was modified by changing only the diet compositions of riparian trees and shrubs, periphyton, biofilm, and phytoplankton since values for marine nitrogen concentration were known for these groups for other study areas. The diet compositions for other groups for which marine nitrogen concentrations were known were not modified from the original nitrogen based model. This is because it was felt that once the marine nitrogen concentrations in the lower trophic levels were increased, the other groups that feed on these groups would also be increased.

3.3.1 Ecopath outputs

The Ecopath outputs described above for the original nitrogen based model still hold true with one exception. Now that riparian trees and shrubs, periphyton, biofilm, and phytoplankton are feeding directly on salmon carcass or salmon eggs, there are more pathways from primary producer or detritus to consumer groups. The increase in number of pathways also affects the mean length of pathways. Figure 4 shows the relationship between the mean lengths of pathways from primary producer or detritus to consumer groups. It is quite clear that marine nitrogen must make more exchanges to reach the top predators. The overall average for mean length of pathways in the aquatic groups is 1.98 and is 2.21 for forest and riparian groups combined. This implies that, as would be expected, consumer groups in the aquatic zone are more closely linked to sources of marine nitrogen than are terrestrial groups.

One major change that occurred when modifying the original model was in the amount of salmon carcass and egg production needed to satisfy all of the new predation on them. As described in the methodology, riparian trees and shrubs, periphyton, biofilm, and phytoplankton have high consumption values so as these groups were given a higher proportion of salmon carcass of egg in their diets, the P/B of salmon carcasses and salmon eggs also had to increase.

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Figure 4. Relationship between the mean length of pathway from primary producers or detritus to consumer groups and trophic level of consumer groups.

By the time that the diet compositions of the selected groups was sufficiently altered so that their concentration of marine nitrogen approximated those values in Table 2, salmon carcass and salmon egg P/B increased from 1.0 to 11.0. The final diet composition matrix can be seen in Appendix 3.

3.3.2 Ecosim outputs

The nitrogen based Ecopath model with the altered diet compositions was used to simulate the impact of increasing and decreasing the biomass of salmon carcasses and eggs on the food web. Figure 5 shows that increasing the biomass of salmon carcasses and eggs impacts the groups differently. The aquatic groups along with the two duck groups, which are associated with the aquatic habitat, respond stronger and quicker than the terrestrial groups. Equilibrium for these groups is reached soon after the carcass and egg biomass is increased. The terrestrial groups also show a positive response although it is less dramatic and slower as many groups have not reached equilibrium after 100 years. All groups end the 100 year simulation with a higher biomass than they started with except forest shrubs, which end near their original level but are still increasing.

The results from the scenario where the biomass of salmon carcasses and eggs was approximately halved can be seen in Figure 6. Again, the aquatic groups are seen to have a much

stronger and quicker response to the decrease in carcass and egg biomass than the terrestrial groups. In this scenario there were no groups that ended the 100 year simulation with a biomass greater than it had at the start. The least impacted groups were those that only occurred in the forest zone, such as mustelids, passerine birds, or small mammals. The riparian groups and groups that occur in both the riparian and forest zones all show a greater response than the forest groups but not nearly as strong as the aquatic groups.

An important point that must be kept in mind when considering the trends seen in Figures 5 and 6 is the fact that the only nitrogen primary producers in the system are salmon carcasses and salmon eggs. Nitrogen fixing bacteria in the forest and nitrogen inputs via rainfall are not in the model. Having these additional nitrogen inputs as part of the model would probably serve to make the impact that increasing or decreasing salmon carcasses and eggs has on the other groups less dramatic. This is because the base of the food web would not be comprised of just two groups so the other primary producer groups would absorb the impact of altering any of the primary producers to some degree. In other words, the base of the food web would be more stable so any perturbations to primary producers would have less dramatic effects on the other groups.

Figure 5. Ecosystem response to an increase in salmon carcass and egg biomass (dashed lines). Relative biomass is the biomass at a particular time divided by the biomass at time 0.

Figure 6. Ecosystem response to a decrease in salmon carcass and egg biomass (dashed lines). Relative biomass is the biomass at a particular time divided by the biomass at time 0.

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3.3.3 Ecotrace outputs

The modified model was again run for 1000 years and the results from the Ecotrace routine can be seen in Table 5. The marine nitrogen concentrations for that riparian trees and shrubs, periphyton, biofilm, and phytoplankton were directly altered via their diet compositions. All other groups kept their original diet composition. The diet compositions of the groups that were modified in order to produce the results are shown in Appendix 3. The values for the above mentioned groups were not matched exactly due to the fact that the known values for these groups came from two different study areas and the inputs for the same groups, used to create the Ecopath model, also came from various study areas.

The results of the Ecotrace routine (Table 5) demonstrate that once the marine nitrogen is input into the system at lower trophic levels, the nitrogen is able to travel up the food web as well as across the food web from the aquatic system to the riparian system. Once the level of marine nitrogen was manipulated so that the Ecotrace results for riparian trees and shrubs, periphyton, biofilm, and phytoplankton approximated levels for the same groups in other study areas, the levels of marine nitrogen in other groups also approached values reported from other areas.

Table 5. Percentage of marine nitrogen of the total nitrogen content of groups in the modified Ecopath model.

Ecopath group	Marine nitrogen concentration (%)		Marine nitrogen concentration (%)
Forest shrubs	0.1	Ungulates	2.0
Riparian shrubs	19.0	Black bears	12.0
Forest trees	0.1	Grizzly bears	31.0
Riparian trees	7.0	Salmon eggs	100.0
Small mammals	0.1	Demersal fish	21.0
Riparian small mammals	7.0	Trout and char	24.0
Predatory terr. insects	0.1	Periphyton	30.0
Riparian pred terr ins	9.0	Biofilm	30.0
Herbivorous insects	0.1	Macroinvertebrates	18.0
Riparian herb ins	7.0	Zooplankton	44.0
Passerine birds	0.1	Phytoplankton	48.0
Riparian passerine birds	8.0	Macrophytes	11.0
Earthworms	0.1	Benthos	13.0
Riparian worms	6.0	Juvenile chinook	10.0
Mustelids	0.1	Juvenile coho	25.0
Riparian mustelids	9.0	Juvenile sockeye	39.0
Herbivorous ducks	11.0	Salmon carcass	100.0
Omnivorous ducks	13.0	Riparian detritus	6.0
Raptors	6.0	Forest detritus	0.1
Wolves	11.0	Aquatic detritus	11.0

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Figure 7 compares the mean values of the ranges of observed concentrations from other study areas (Table 2) and the concentrations estimated by Ecotrace for those same groups. It can be seen that while the absolute value of the concentration estimated by Ecotrace does not precisely match the observed values, altering the diet composition in the underlying Ecopath model can bring the values closer. The diet composition was not altered to precisely match the observed values because the observed values are come from different study areas and the inputs used to construct the model are also from several study areas. What Figure 7 does demonstrate is that if local data is known, the Ecotrace routine can be used to fine tune the diet composition in the underlying Ecopath model.

An ordinary sensitivity analysis was performed to check what effect that the biomass, production per biomass ratio, and consumption per biomass inputs had on the results generated by Ecotrace. These input parameters were altered manually one at a time and the Ecotrace routine implemented for several groups. The amount each parameter was changed was +/-20%. Changing these input parameters had no effect whatsoever on the results generated by Ecotrace. The only input parameter that does affect the results generated by the Ecotrace routine are the diet composition inputs. The changes made to the diet composition table that produced the results seen in Figure 7 are shown in Table 6 below.

Table 6. Changes made to the diet composition used to generate the results seen in Figure 7. The three scenarios (A), (B), and (C) correspond to graphs (A), (B), and (C) in Figure 7.

	A			B			C		
Group	Salmon carcass	Salmon eggs	Detritus	Salmon carcass	Salmon eggs	Detritus	Salmon carcass	Salmon eggs	Detritus
Riparian shrubs	-	-	1.000	0.085	0.050	0.865	0.085	0.050	0.865
Riparian trees	-	-	1.000	0.010	-	0.990	0.010	-	0.990
Periphyton	-	-	1.000	0.200	-	0.800	0.050	0.400	0.550
Biofilm	-	-	1.000	0.100	0.100	0.800	0.100	0.200	0.700
Phytoplankton	-	-	1.000	0.300	0.100	0.600	0.150	0.480	0.370

Figure 7. Comparison of marine nitrogen concentration predicted by Ecotrace and those observed in other study areas. The groups used for comparison were those listed in Table 3. Results from the original diet composition are shown in (A) while (B) and (C) show how the sum of squares (SS) can be reduced by altering the diet composition.

4. Discussion and Conclusions

4.1 Utility of model to resource managers

Willson and Halupka (1995) identified more than 40 species of mammals, birds, and fish that consume salmon eggs, juveniles, or adults in or near freshwater in southeast Alaska. This diversity of organisms utilizing salmon should send a strong signal to fisheries managers that the consequences of management decisions do not stop at the river's edge, but transcend ecosystem boundaries into the forest. Willson *et al.* (1998) suggest that the seasonal occurrence of salmon is responsible for the co-evolution of aquatic and terrestrial organisms in systems where salmon occur. Michael (1998) points out that before the arrival of commercial fish canneries, the majority of salmon biomass harvested by humans and wildlife remained in the watershed. He also suggests that salmon bearing watersheds evolved to capture the yearly input of marine nutrients transported in by spawning salmonids.

If a model can track nitrogen flows and be 'tuned' to a particular system, it could also be developed as a tool to explore policy options as part of a large management scheme, which could address the concerns discussed by Willson *et al.* (1998) and Michael (1998). For instance, in the fall of 1999 several grizzly bears had to be destroyed in the village of Oweekeno, British Columbia. Alex Tizon (Seattle Times; January 30, 2000) reports that the bears were starving due to the lack of returning sockeye salmon and had to be destroyed once they became accustomed to rummaging through the village for food. It was probably not the intention of fisheries managers to starve the grizzly bears. But were the needs of grizzly bears considered when management decisions were made regarding the Rivers Inlet fishery? A model such as the one presented here allows resource managers to anticipate possible impacts to the ecosystem. Figure 6 shows that, in this model, grizzly bears are the most sensitive terrestrial group to a reduction in salmon carcasses. Michael (1998) determined that escapement goals for the Skagit River are only half of the estimated biomass needed to meet the requirements of eagles, nesting birds, and salmonid smolt production. Fisheries managers can not be expected to directly manage all wildlife species present in a watershed where spawning salmon occur but they should be able to anticipate the potential impacts of their decisions. An ecosystem model can serve as a platform to bring resource managers from various disciplines together so that the overall health of a watershed can be managed for, by a process where information is combined to develop an ecosystem framework.

The model discussed in this report can also be of value to projects aimed at rebuilding ecosystems which could be done as part of a larger integrative management process. For example, increasing the number of spawning salmon may not result in a positive ecosystem response seen in Figure 5. Large woody debris inputs into streams in the Pacific Northwest have been reduced in the past due to various logging practices (Cederholm 1972; Bilby and Ward 1991). Placing large woody debris in streams as a technique for rehabilitating streams and increasing juvenile salmonid habitat is described in Cederholm *et al.* (1997) and Slaney *et al.* (1997). In addition, large woody debris and boulders are also known to retain salmon carcasses and increase the ability of the stream to cycle nutrients released from them (Cederholm and Peterson 1985; Fisher Wold and Hershey 1999). While Figure 5 suggests that increasing the amount of salmon carcasses will result in a positive ecosystem response, if there are insufficient physical structures in the stream to retain the additional carcasses, the system may not respond as the model predicts. While an Ecopath model using Ecotrace may not be able to determine the exact effects that placing large woody debris in streams has on a watershed, the model used in conjunction with field data for biomass and stable isotope analysis can give a broad overall picture of the effect that rehabilitation programs could have on watersheds. Stable isotope analysis along with the Ecotrace routine could also help identify possible energy sinks in food chains that may preclude the success of rehabilitation efforts. Stockner (1987) has identified possible energy sinks in the food chain leading from primary production to juvenile sockeye.

If the management goal is to increase the number of spawning salmon to optimize watershed function, an Ecosystem model that tracks the flow of nutrients could be used as a tool for an adaptive management regime. An adaptive management regime is one where management decisions can be viewed as experiments so that the results can be learned from and influence future decisions (Walters 1986). In this case, one experiment could be to increase spawner numbers incrementally over several years, by reducing commercial harvest levels, and measure the biomass and/or ^{15}N response in other aquatic and terrestrial organisms. The model can then be tuned to such time series data so that future policy options can be explored to investigate their possible effectiveness in achieving a pre-defined optimal level of watershed health. While the model itself may not give resource managers all the answers they desire, it can be a valuable tool as part of a watershed management plan, by identifying species of concern, important ecosystem mechanisms and interactions, and species which need more research to better understand the whole ecosystem.

In British Columbia, the Forest Practices Code stipulates that a riparian management area consists of a riparian reserve zone and a riparian management zone, in which the objectives are to

minimize the impacts that forest and range uses have on aquatic ecosystems and the plant and wildlife communities adjacent to them (BCMOF 1995). The minimum riparian management area specified by the Forest Practices Code for fish bearing streams ranges from 30 to 40 m, depending on the width of the channel (BCMOF 1995). There is no mention of the impacts that the aquatic ecosystem has on the forest when considering the width of riparian management areas. Studies have shown that the aquatic ecosystem can impact the adjacent forest ecosystem as much as 1 km away from the stream (Ben-David *et al.* 1998; Hilderbrand *et al.* 1999). If resource managers in British Columbia are going to meet the Forest Practices Code riparian management area objectives, to minimize the impacts that forestry and range use has on the diversity, productivity and sustainability of wildlife habitat and vegetation adjacent to aquatic ecosystems, then they should consider the impacts both ways between the terrestrial and aquatic ecosystems. The Ecotrace routine along with field data could be used to help resource managers determine the extent of inter-ecosystem impacts so that appropriate sizes of riparian management areas could be determined for testing on a site specific basis rather than by a blanket prescription based on stream channel width.

4.2 Ecopath input parameters

While this study claims to model the Atnarko River watershed, very few inputs into the model were actually derived from local data. The model inputs that do reflect local conditions are the model areas, species compositions, salmon escapement, and forest stand composition and density. The model can be thought of as a conceptual watershed model based on the Atnarko River watershed rather than as an explicit model of the Atnarko River watershed. Since the objective of this study was not to predict the marine nitrogen flows in the Atnarko watershed but was more general in trying to determine if a watershed model could be constructed, using the Ecopath and Ecotrace, that could track the flow of marine derived nitrogen from spawning salmon carcasses. Since the flow of marine nitrogen is the focus of the modeling exercise, it is the diet composition data that causes the greatest concern because what the organisms eat determines the pathways for marine nitrogen throughout the food web. Having diet composition consistent from one study area would greatly improve this model as the relationships between the various groups would be consistent. One example that highlights this point is the relationship between black bears and grizzly bears. Jacoby *et al.* (1999) presents diet composition data for black bears and grizzly bears on the Kenai Peninsula, Alaska which shows that when both bear species occur together the black bears do not consume salmon. Where black bears occur

allopatrically, approximately half of their diet consists of salmon. While this relationship was input into the model, there could be similar dynamics among other groups that is not reflected in the diet composition matrix used in the model. This is due to the fact that the diet compositions were taken from various areas where there is a possibility that not all the species present in this model are present in the study area that the diet compositions were taken from or vice versa. The importance of accurate diet composition data for the specific study area data comes to light when using the Ecotrace routine as what a group eats directly affects the flow of marine nitrogen or any other tracer substance in to that group.

4.3 Improvements to the model

There are several aspects of the Ecopath model that could be further investigated to improve the results generated so far. The most obvious challenge is to generate local data to input into the model. As the model stands now, the inputs based directly on local data are biomass estimates for forest trees and salmon carcasses. Another problem area with the nitrogen based Ecopath model is with the primary production of nitrogen. Currently the only primary producers of nitrogen are the salmon carcasses and salmon eggs. These were considered primary producers due to the fact that they accumulate all of their nitrogen during their ocean migrations and do not consume any nitrogen when they enter the river and stop feeding. In this regard the salmon carcasses act as a primary producer of nitrogen

The model is not capturing the nitrogen inputs from the atmosphere in the form of rain and snowfall or through water vapor deposition on trees from clouds and fog which are pathways that nitrogen can take from the atmosphere into vegetation (Perry 1994). True primary producers of nitrogen are confined to certain species of bacteria. cyanobacteria, and actinomycetes as these are able to fix atmospheric nitrogen to a form that can be utilized by other life forms. These missing nitrogen inputs have the greatest effect on the trees, shrubs, aquatic plants and algae, and phytoplankton because in the nitrogen based model they are all direct consumers of nitrogen. Since salmon carcass and eggs are the only nitrogen primary producers in the Ecopath model, the entire system depends on them for nitrogen. Removing the carcasses from the system would imply that there is no longer any input of nitrogen into the system.

4.4 Ecotrace routine

As Figure 7 shows, the values estimated by Ecotrace do not perfectly match the values from other study areas. In order for the values to match two conditions would have to be met.

The first would be that the concentration of marine nitrogen in groups at the base of the food web (i.e. periphyton, phytoplankton) would be the same for both this study area and the areas with known values. The second would be that the diet compositions of the groups would have to be similar since an organisms diet composition will affect the concentration level of marine nitrogen. Since there was no local data available to confirm either, no attempt was made to force the concentrations to match more precisely.

If the Ecotrace routine can estimate reasonable concentrations of marine nitrogen for groups where marine nitrogen concentrations have been estimated using stable isotope analysis, are the concentrations estimated by Ecotrace for the other groups also reasonable? This question brings to light the importance of local data for diet compositions. If the diet compositions were estimated with great confidence, then confidence could also be placed on the Ecotrace estimates for groups where there is no marine nitrogen concentration estimate based on field data. However, in this study, the diet compositions and other Ecopath estimates were taken from several different study areas. As only a few inputs for the Ecopath model were derived from local data, one can see that there is still room for improvement before a great deal of confidence should be placed in the Ecotrace results for estimating the marine nitrogen concentrations of organisms in the Atnarko River watershed. The results may be reasonable for a generalized watershed.

The best case scenario would be to have local data for all of the Ecopath inputs as well as for marine nitrogen concentrations in all of the groups. This would allow for verification of whether or not the Ecotrace routine can accurately capture all of the transfers marine nitrogen makes as it travels throughout a food web. This scenario would be both time consuming and costly so another option would be to only sample for marine nitrogen concentration in organisms at different trophic levels in the aquatic, riparian, and forest regions. Knowing the marine nitrogen levels for several groups at different trophic levels would allow for cross validation of the estimated diet composition. In general, if enough tracer concentrations are known, it may be possible to enter a diet composition for each group and have the software estimate the changes in the diet compositions that would result in Ecotrace estimating tracer concentrations that approximate the known values. For example, if the marine nitrogen concentrations in Table 2 were in fact from the same study area as the Ecopath model, a problem with demersal fish is easily seen. While the estimated diet compositions for the other groups appear reasonable, the diet composition for the demersal fish group needs amending as the Ecotrace routine is only estimating about one-third the amount of marine nitrogen that is actually seen in this group. Altering diet compositions should first be done for lower trophic level groups as bottom–up processes influence how the marine nitrogen is distributed throughout the food web. For

example, raptors have a trophic level 3.9 and there are approximately 70 pathways leading from salmon carcasses and eggs or detritus to them. Altering the marine nitrogen concentrations in lower trophic level groups will undoubtedly impact the concentration level in raptors.

4.5 Improvements to the Ecotrace setup

The most questionable inputs that were used in the Ecotrace routine were the decay rates imposed on the detritus groups. With no decay rate imposed on the detritus groups, the concentration of marine nitrogen in these groups would increase indefinitely. Streams and rivers can transport nitrogen out of a system either in solution (dissolved) or as particulates (undissolved organic or mineral particles) (Perry 1994). Nitrogen can also be lost from the system during forest fires as all of the nitrogen content of organic matter is converted to gas during complete combustion (DeBano, 1990). While nitrogen may not actually decay in the system, the decay rate is assumed to act as the force which exports nitrogen from the system. The level at which the marine nitrogen concentration in the detrital groups reaches can be controlled by altering the decay rates imposed on them. Raising the decay rate results in lower concentration while lowering decay rates increases concentrations. If the concentration is know, then the appropriate decay rate can be set but no such data could be found.

The concentration of nitrogen in the detrital groups plays a key role as the detrital groups are a key pathway that links groups together. As Appendix 3 shows, out of a total of 35 consumer groups, 24 groups directly consume detritus. According to Odum (1969), as an ecosystem matures, the role of detritus in nutrient regeneration becomes more important. He also states that as systems mature, the capacity of the system to entrap and hold nutrients for cycling within the system increases. In mature systems, it can be seen that understanding the nutrient flows in and out of detritus become just as important as knowing any of the other flow in the system.

Another aspect of the model that impacts the results given by Ecotrace is the nutrient cycling within forest and riparian trees. The trees have by far the greatest biomass in the terrestrial portions of the model. This means that the concentration of trees will influence the concentration of the terrestrial detrital groups. Perry (1994) states that the largest input to terrestrial detritus is litter, which is over 80% composed of dead leaves, branches, roots, etc., with leaves and needles comprising the majority of aboveground litter. In a coniferous forest, if it is assumed that it is the older needles that contribute to the aboveground litterfall, then it is the concentration of marine nitrogen in those needles that is important to the concentration of forest

detritus. Trees are able to conserve nitrogen and other nutrients such as phosphorus and potassium by retranslocating them from older to developing foliage. Fife and Nambiar (1982) found that as the age of needles in radiata pine trees (*Pinus radiata*) in increased from 1 to 5 years old, the level of nitrogen, potassium, and phosphorus declined to approximately 40% to 60% of the initial value. No studies could be found to determine if the heavier nitrogen isotope ^{15}N (marine nitrogen) is retranslocated within a tree the same as the lighter isotope, ^{14}N. This has implications for studies such as Bilby *et al.* (1996) or Hilderbrand *et al.* (1999) who both found that approximately 18% of the nitrogen in riparian foliage is marine derived. Sollins *et al.* (1980) reports that 56% of the nitrogen required for the production of new foliage comes from nitrogen that is retranslocated from within the tree. If marine nitrogen is retranslocated along with the other nitrogen then the marine nitrogen content of older foliage will be considerably lower than 18%. If it is the older foliage that comprises the majority of litterfall then the concentration of marine nitrogen in terrestrial detritus will also be considerably lower than the concentration levels seen in new foliage. The amount of nitrogen needed to be taken up by the tree in order to produce the concentration of marine nitrogen seen in Bilby *et al.* (1996) or Hilderbrand *et al.* (1999a) might be overestimated if half of the marine nitrogen in young foliage is provided by retranslocation and not through uptake from the soil.

The most significant improvement that could be made to this model is the method used to allow the concentration of marine nitrogen to build in the riparian trees and shrubs, periphyton, biofilm, and phytoplankton. The method used in this study was to allow these groups to feed directly on salmon carcasses and eggs even though they do not actually do so. The Ecotrace routine creates a group called the environment that accumulates nitrogen from the detritus groups. The user can set direct absorption rates from the environment for any of the groups in the model. This method seems more appropriate for handling groups that do not directly feed on salmon or eggs but absorb the nutrient they release during decomposition. The reason this method was not employed in this study was because it was felt that this model is not the ideal model to be testing such methodology. This model is comprised of 3 different environments, aquatic, riparian, and forest, that are linked by a few of the groups. This creates 3 different detrital pools while only one environment group is created. A better test for this aspect of Ecotrace would be a model with fewer groups where there is only one distinct environment, preferably aquatic as this is the environment that the routine was originally designed for.

4.6 Future work with Ecotrace

Once a credible Ecopath model has been constructed and balanced, Ecotrace could be used to verify diet compositions and possibly consumption rates that were input into the model. What an organism eats, and in what proportion, determines the trophic level of that organisms as well as the transfer of a chemical tracer. Stable isotope analysis allows for biogeochemical problems in ecosystems to be solved by exploiting the fact that the elements C, N, S, H, and O all have more than one isotope (Peterson and Fry 1987). Minagawa and Wada (1984) proposed the potential for nitrogen isotopes to be used as a tracer for dietary analysis and determining the trophic level of organisms. Stable isotope analysis of nitrogen was used to estimate the trophic level of several organisms in Prince William Sound, Alaska which were compared to trophic levels estimated by Ecopath in a model of the same area (Kline and Pauly 1998). An extremely high correlation was found between the trophic levels estimated by the different methodologies. This implies that the diets used in the model are in general congruence with the actual diet composition of the organisms in the ecosystem.

Ecotrace could possibly take this one step further by using the isotope data to trace which specific parts of the diet contribute to the build up of tracer isotope in an organism. Now there would be two ways to verify the validity of the diet composition used in the Ecopath model. First would be to see if the trophic level estimated by Ecopath is similar with an estimate derived through stable isotope analysis. The second way to verify the diet compositions would be to see if the diet composition of an organism allows for sufficient build up of the tracer isotope so that the concentration estimated by Ecotrace for a group is similar to the values seen from field data. Conceivably, the software could be used to estimate a range of diet composition values for a group given the constraints of trophic level and concentration level of a chemical tracer.

The Ecotrace routine might be able to play a role in estimating food consumption rates. Trudel et al. (2000) were able to devise a method for estimating consumption rates of fish based on a mercury mass-balanced model. Inputs required for their model includes the fishes age, size, growth, and the concentration of mercury in the fish and in the fishes food. If the diet and concentration of mercury in the fish and its food is known, then these constraints could be used so that Ecopath estimates the consumption rate required to produce the concentration levels of mercury in the fish using the Ecotrace routine. Mercury concentrations and flows in the food web is of particular concern to the Aboriginal people in the Arctic. Mercury has been identified as a contaminant of fish in the Northwest Territories, Yukon, and northern Quebec which consistently exceeds the guideline limits for subsistence consumption (Braune et al. 1999). Wild (traditional) foods are still an integral part of the northern Aboriginal peoples diets, who were found to be

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exposed to a radiation dose approximately seven times higher than those not eating traditional foods, which was attributed to the bioaccumulation of natural radionuclides in the food chain (Van Oostdam *et al.* 1999). Using field data on the concentration levels of contaminants in various organisms in the food web, it could be possible to construct an Ecopath model where humans would act as consumer group. Using Ecotrace, the contaminants could be traced through the food web so that the impact of changing the diet of humans could be simulated to see what effect it would have on the accumulation of heavy metals or organochlorides in humans.

4.7 Conclusions

Nutrients released by adult salmon as they enter freshwater ecosystems and decompose are able to traverse their way throughout the aquatic and adjacent forest ecosystems. The results of this study show that the Ecotrace routine can be used to track the flow of marine nitrogen, released from salmon carcasses, throughout an ecosystem. The Atnarko River watershed was used as a basic template for the construction of the nitrogen bases Ecopath model. However, the lack of local data on the concentration of marine nitrogen in organisms precludes the conclusion that the results of this study are highly correlated with values actually seen in the study area. The objective of this study was not to accomplish this but rather to test the methodology to see if it could be applied to a model area where field data is available. To this extent, this study can be viewed as a success although there are still aspects of the methodology that could be refined and which would improve the dynamics of the Ecotrace routine. These improvements are sure to come as more experience is gained once the routine is applied to areas where adequate field data exists to properly calibrate the model.

It is quite clear that spawning salmon and the carcasses they produce play a critical role in maintaining ecosystem health and providing links between aquatic and terrestrial ecosystems. The return of anadromous fish to the freshwater ecosystem, including the occurrence of runs in very small streams, has important implications on wildlife biology and conservation of biodiversity (Willson and Halupka 1995). With so many interactions within an ecosystem involving salmon either directly or indirectly, the term keystone species immediately comes to mind. If a keystone species is one that is responsible in maintaining the integrity and health of the ecosystem it interacts in, then salmon certainly fill that role. Power *et al.* (1996) define a keystone species as one whose impact on the system it functions in large and disproportionately large relative to its biomass. In other words, it has a big impact and a small biomass. While

many high trophic level species have been identified as being a keystone species, i.e., sea otters (Estes and Palmisano 1974), Power *et al.* (1996) point out that a high trophic level is not a requirement to be a keystone species as a keystone species can exert its impacts on the system through processes such as competition, dispersal, or habitat modification rather than exclusively through consumption. Shachak *et al.* (1987) describe nitrogen fixing cyanobacteria and lichens in the Negev Desert, Israel, as keystone species. Reimchen (2000) estimated the spawning period for salmon at Bag Harbour to be 45 days, approximately 12% of the year, but impact that these salmon exert on the system goes well beyond this time period. Adult salmon may only be present in coastal watershed for a short time but their impact can be seen at all trophic levels throughout the entire watershed food web. It is quite clear that salmon managers must consider the importance of marine derived nutrients for all streams and manage salmon harvesting accordingly rather than just focus on the commercially important runs of salmon.

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Appendix 1. Wet weight Ecopath model construction and balancing

A1.1 Wet weight model construction

Below is a description each group and how the initial input parameters were derived. The wet weight model was the first model constructed because after it was properly balanced, it served as the basis for the nitrogen based model.

A1.1.1 Terrestrial groups

A1.1.1.1 Forest shrubs

This group contains plant species in the herb and shrub layer in the forest. Meidinger and Pojar (1991) point out, and personal observations confirm, that in the Interior Douglas-fir wet and warm (IDFww) biogeoclimatic zone, which encompasses the majority of the study area, some of the main understory plants include falsebox (*Pachistima myrsinites*), prince's pine (*Chimaphila umbellate*), and twinflower (*Linnaea borealis*). Appendix 5 lists shrub species that occur in the IDFww zone according to Meidinger and Pojar (1991). All of these plants occur on dry soils with prince's pine and falsebox preferring nitrogen-poor soils (Klinka *et al.* 1989). This group is assigned to 91% of the total model habitat area, i.e., forest zone.

Biomass – An estimate for the standing crop of forest shrubs of 44 t•km^{-2} is given in Chapin (1983). This biomass is for the understory shrubs in a black spruce forest in Alaska in which *Vaccinium* and *Ledum* species dominate.

P/B – Chapin (1983) also provides a production estimate of 19 t•km^{-2}•year^{-1} for understory shrubs. This production estimate was then divided by the biomass to produce a P/B estimate of 0.432•year^{-1}.

Detritus fate – 1.0 forest detritus.

A1.1.1.2 Riparian shrubs

This group contains the shrubs that are within the riparian zone. The input parameters are assumed to be the same as the forest shrubs (above). This group is assigned to 8.5% of the total model habitat area, i.e., the riparian zone.

Fate of detritus – 1.0 riparian detritus.

A1.1.1.3 Forest trees

Meidinger and Pojar (1991) characterize the tree layer of the Interior Douglas-fir wet warm biogeoclimatic zone to be dominated by Douglas-fir (*Pseudotsuga menziesii*) and western redcedar (*Thuja plicata*). Personal observations of the study area are consistent with this except that I would also include a small proportion of western hemlock (*Tsuga heterophylla*) in the species composition. Therefore I estimate the species composition to be 60% Douglas-fir, 30% western redcedar, and 10% western hemlock. This group is assigned to 91% of the total model habitat area, i.e., forest zone.

Biomass – A forest stand in the central coast region of British Columbia can have volumes ranging from 200-1500 $m^3 \cdot ha^{-1}$ with typical stands averaging around 500 $m^3 \cdot ha^{-1}$ (P. Lebouder *pers. comm.*). I used this stand volume and the stand composition outlined above to convert stand volume to biomass using wood density estimates for each species. Table 7 summarizes this process which led to an estimate for total tree mass of 197,100 $kg \cdot ha^{-1}$ which converts to 19,710 $t \cdot km^{-2}$.

P/B – A production estimate of 1160 $t \cdot km^{-2} \cdot year^{-1}$ for a Douglas fir dominated stand in the interior of Oregon is given in Law and Waring (1994). This production value was then divided by the biomass estimate of 19,710 $t \cdot km^{-2}$ to give a P/B of 0.059 $\cdot year^{-1}$.

Detritus fate – 1.0 forest detritus.

Table 7. Forest stand volume conversion to biomass. Density estimates taken from Gonzalez (1990).

Tree species	Stand composition	Volume ($m^3 \cdot ha^{-1}$)	Density ($kg \cdot m^{-3}$)	Biomass ($kg \cdot ha^{-1}$)
Douglas-fir	0.60	300	422	126,600
Western redcedar	0.30	150	329	49,350
Western hemlock	0.10	50	423	21,150
Total (mean)	1.00	500	(391)	197,100

A1.1.1.4 Riparian trees

This group contains the trees that are located within the riparian zone. The input parameters are assumed to be the same as the forest trees (above). This group is assigned to 8.5% of the total model habitat area, i.e., the riparian zone.

Fate of detritus – 1.0 riparian detritus.

A1.1.1.5 Small mammals

This group is comprised of mice, voles, shrews, and chipmunks. Appendix 5 lists small mammal species that may occur in the IDFwet zone according to Stevens (1995). This group is assigned to 91% of the total model habitat area, i.e., forest zone.

Biomass – The biomass estimate for this group was derived by obtaining densities for various small mammals from Sullivan *et al.* (1999). These densities were then converted to biomass using body mass estimates in Banfield (1974). Table 8 below shows this conversion. The resulting biomass estimate is 0.054 t•km^{-2}.

P/B – Stoddart (1979) gives a production estimate for several small mammal species. This production estimate of 0.167 t•km^{-2} was divided by the biomass estimate to produce a P/B ratio of 3.087•year^{-1}.

Table 8. Small mammal densities and biomass conversion. Density estimates are from Sullivan *et al.* (1999) and body mass estimates from Banfield (1974).

Species	Density (#•ha^{-1})	Body mass (g)	Biomass (g•ha^{-1})
Clethrionomys gapperi	11.74	25	293.50
Peromyscus maniculatus	9.04	20	180.80
Microtus longicaudus	1.53	35	53.55
Microtus pennsylvanicus	0.05	35	1.75
Tamias amoenus	0.06	50	3.00
Sorex spp.	0.82	10	8.20
Total (mean)	(3.87)	(29)	540.80

Q/B – Drozdz (1968) studied the energy requirements of 2 vole species and 2 mice species and found that individuals had a daily consumption of 12.7 - 16.2 kcal. The caloric value of the food items was also reported to be ranging from 4 to 8 kcal•g^{-1} ash free dry weight. Using a consumption rate of 14.5 kcal • day^{-1} and a conversion ratio of 6 kcal•g^{-1} dry weight I estimated an annual consumption of 882 g dry weight • year^{-1}. Using a wet weight-dry weight conversion ratio of 3.33 g wet weight•g^{-1} dry weight (Nagy *et al.* 1999), the consumption rate is 2937 g. A biomass estimate of 35 g for an individual *Microtus* species was used to derive a Q/B estimate of 83.916•year^{-1}.

Diet composition – Diet compositions vary between shrews, which are primarily insectivores, to voles, which are mainly herbivores. Deer mice have an omnivorous diet where insects comprise the majority of the diet in the spring with a shift towards seeds and plant matter occurring in the summer (Martell and MaCauly 1981). Therefore, I decided to split the diet of this group evenly into insects and detritus. Insects were further broken down assuming that predatory terrestrial insects made up approximately 20% of arthropod biomass. The resulting diet composition used is 0.10 predatory terrestrial insects, 0.40 herbivorous insects, and 0.50 forest detritus.

Detritus fate – 1.0 forest detritus.

A1.1.1.6 Riparian small mammals

This group contains the small mammals that are found in the riparian zone. Input parameters for this group are assumed to be the same as for small mammals (above) with the exception of the diet composition. This group was assigned a diet composition of 0.10-riparian predatory terrestrial insects, 0.40-riparian herbivorous insects, and 0.50-riparian detritus. This group is assigned to 8.5% of the total model habitat area, i.e., the riparian zone.

Fate of detritus – 1.0 riparian detritus.

A1.1.1.7 Predatory terrestrial insects

This group contains arthropods that feed on other arthropods. This group is assigned to 91% of the total model habitat area, i.e., forest zone.

Biomass – A biomass estimate for all arthropods in the canopy of a forest ecosystem was found in Schowalter (1981). An average biomass for the 2 years reported was 0.12 t•km^{-2}. Since Schowalter (1981) presented the biomass estimates by different feeding guilds, I was able to calculate the percent biomass composition of predatory arthropods. Predatory insects comprised 18% of arthropod biomass or 0.025 t•km^{-2}. This estimate was then converted to wet weight using the conversion of 3.33 g wet weight•g^{-1} dry weight (Nagy *et al.* 1999) to produce a biomass estimate of 0.083 t•km^{-2}. These calculations are summed in Table 9 below.

P/B – It is possible to estimate P/B using the Q/B estimate and an assimilation efficiency (i.e., the proportion of food consumed that is converted into biomass). An assimilation rate of 19.4% for herbivorous insects was found by averaging values presented in Hodkinson (1982). This means that 19.4 % of the consumption goes into biomass production. Therefore, I used the Q/B estimate of 23.4•year^{-1} and multiplied it by 0.20 to produce a P/B estimate of 4.68•year^{-1}.

Q/B – A daily consumption rate was obtained from averaging daily consumption rates for 8 insect species in Tanaka (1991). The resulting consumption rate of 13% of body weight•day^{-1} was applied over 180 days yielding a Q/B of 23.4•year^{-1}. The 180 day feeding period was used based on the life cycle of predatory arthropods. Savory (1977) states that the most common life cycle in predatory arthropods, such as arachnids, is one in which the winter months are passed in either the egg stage or as a hibernating nymph. Therefore, no feeding occurs until the spring,.

Diet composition – Since this group contains insects that feed on other insects I assigned the majority of its diet to herbivorous insects. The remaining proportion of the diet I assigned to detritus and salmon carcasses. The resulting diet composition is 0.90-herbivorous insects and 0.10-forest detritus.

Detritus fate – 1.0 forest detritus.

Table 9. Insect biomass and community structure adapted from Schowalter (1981).

Insect type	Dry weight density (kg•ha^{-1})	Proportion of community	Wet weight density (kg•ha^{-1})	Wet weight density (t•km^{-2})
Chewing herbivore	0.85	0.61	2.831	0.283
Sucking herbivore	0.25	0.18	0.833	0.083
Predator	0.25	0.18	0.833	0.083
Other	0.05	0.04	0.167	0.017
Total	1.40	1.00	4.662	0.466

A1.1.1.8 Riparian predatory terrestrial insects

This group contains the predatory terrestrial insects that are found in the riparian zone. The input parameters are assumed to be the same as for predatory terrestrial insects (above) with the exception of the diet composition. The diet composition for this group is 0.90-riparian herbivorous insects, 0.075 riparian detritus, and 0.025 salmon carcass. This group is assigned to 8.5% of the total model habitat area, i.e., the riparian zone.

Fate of detritus – 1.0 riparian detritus.

A1.1.1.9 Herbivorous insects

This group contains chewing, sucking, and other arthropods. This group is assigned to 91% of the total model habitat area, i.e., forest zone.

Biomass – The same total arthropod biomass from Schowalter (1981) that was used for 'predatory insects' was used for herbivorous ones. Once the proportion of predatory insects has been removed, the remaining herbivorous insect biomass is 0.384 t•km^{-2}. See Table 9 for calculations.

P/B – This parameter was calculated using an assimilation efficiency of 0.20 which is the average of values presented in Hodkinson (1982). Using a Q/B of 180•year^{-1} and multiplying it by the assimilation efficiency produces a P/B estimate of 36.0.

Q/B - A daily consumption range of 50 to 150% of the dry body weight•day^{-1} is given in Reichle and Crossley (1967). Other consumption rates reported by Crossley and Howden (1961) and Crossley (1963) put daily consumption at 108 and 136% of dry body weight•day^{-1}. I used a consumption of 100% and assumed a feeding season of 180 days to produce a Q/B of 180•year^{-1}.

Diet composition – The predatory insect biomass was removed from the total arthropod biomass estimate leaving chewing, sucking, and other insect groups. I then calculated the proportion chewing, sucking, and other insect groups contributed to the adjusted biomass estimate. The resulting proportions were 0.75-defoliating herbivores, 0.21-sucking herbivores, and 0.04-other. I combined the proportions for the sucking and chewing insects and assigned them to feed on forest trees. The 'other' group was allowed to feed on detritus since it could not

be determined what type of insects these were. The resulting diet composition is 0.96-forest trees and 0.04-forest detritus.

Detritus fate – 1.0 forest detritus.

A1.1.1.10 Riparian herbivorous insects

This group contains the herbivorous insects that are located in the riparian zone. The input parameters were assumed to be the same as for herbivorous insects (above) with the exception of the diet composition. The diet composition for this group is 0.96-riparian trees and 0.04-riparian detritus. This group is assigned to 8.5% of the total model habitat area, i.e., the riparian zone.

Fate of detritus – 1.0 riparian detritus.

A1.1.1.11 Earthworms

This group contains earthworms that are not native to North America. Earthworms native to North America are believed to have been eliminated from Canada by the Pleistocene glaciation (Reynolds 1973) with the exception of refugia on Vancouver Island and the Queen Charlotte Islands (McKey-Fender and Fender 1982). This group is assigned to 91% of the total model habitat area, i.e., forest zone.

Biomass – No biomass estimate could be found for European earthworms in British Columbia so I used a biomass of $3.624 \text{ t} \cdot \text{km}^{-2}$ for native earthworm. This estimate is the average value for earthworms at various sites on Vancouver Island reported by Marshall and Fender (1998).

P/B – Monthly earthworm surveys were conduced by Rozen (1988) for three sites in the Niepolomicka forest, Poland, over the course of a year. The monthly earthworm abundances, reported as $\text{individuals} \cdot \text{m}^{-2}$, were treated as 'catches' so that a catch curve analysis could be performed in order to estimate P/B. Thus, I plotted the natural logarithm of earthworm numbers against time. I then fit a linear regression through the portion of the plot bounded by the high and low values for the natural logarithm of earthworm numbers. This was done for the data sets for the three sites (Figure 8). The slopes of these lines represented total mortality (-Z), which were then averaged to come up with an estimate for P/B of $4.97 \cdot \text{year}^{-1}$.

Figure 8. Catch curve analysis for earthworms. The three graphs represent the three sites for which monthly earthworm numbers were collected (Rozen 1988).

Q/B - An assimilation efficiency of 0.15 was found in Daniel (1991) who states that the earthworm *Lumbricus rubellus* digested 69-76% of ingested alder leaves. He also states that only 20% of this goes to body tissue and respiration. This results in a conversion efficiency of 15%. The P/B estimate of $4.97 \cdot year^{-1}$ was divided by this estimate in order to calculate the Q/B required to produce this P/B estimate. The result is a Q/B estimate of $33.13 \cdot year^{-1}$.

A daily consumption/biomass rate for a different type of earthworm is given in Kaushal *et al.* (1994). They give a daily Q/B range of .0365 to $0.069 \cdot year^{-1}$. Using the mean of 0.0528, an annual Q/B estimate of $19.25 \cdot year^{-1}$ is calculated. This estimate was then averaged with the estimate above to produce an average Q/B of $26.19 \cdot year^{-1}$ that was used in the model.

Diet composition – The diet composition for this group was entirely forest detritus.

Detritus fate – 1.0 forest detritus.

A1.1.1.12 Riparian earthworms

This group contains the earthworms that are found in the riparian zone. The input parameters are assumed to be the same as earthworms (above) with the exception of the diet composition which is entirely riparian detritus. This group is assigned to 8.5% of the total model habitat area, i.e., the riparian zone.

Fate of detritus – 1.0 riparian detritus.

A1.1.1.13 Passerine birds

Appendix 5 lists the passerine bird species that may occur in the IDFwet zone according to Stevens (1995). This group is assigned to 91% of the total model habitat area, i.e., forest zone.

Biomass – A total passerine bird density estimate of 122 males•ha^{-1} (Folkard and Smith 1995) was converted to biomass. Table 10 shows how the biomass estimate was calculated using the breakdown of bird species which comprised this total biomass and bird body mass found in Dunning (1993). The resulting biomass estimate of 0.209 t•km^{-2} was then doubled to compensate for the fact that no females were included in the density reported by Folkard and Smith (1995). Since passerine birds are migratory, flying south for the winter, the biomass estimate was also divided by 2 to reflect that migratory birds only spend half a year in the study area. Therefore, the final biomass adjusted for sex ratio and seasonality is 0.209 t•km^{-2}.

P/B – This parameter was estimated using an annual survival rate of 0.50, based on annual survival rates for blue tits (*Parus caeruleus*) of 0.57 (Blondel and Pradel 1990) and 0.40 (Hilden 1990). Using the annual survival rate of 0.50 with equation (3), a total mortality estimate of –0.693 is obtained and since –Z is an estimate of P/B, the P/B input for the model was 0.693•year^{-1}.

Q/B – Smaller birds are known to consume more food per body weight than birds of larger size. A blue tit is reported to eat around 30% of its body weight•day^{-1} (Welty 1982). Since a blue tit is a small bird weighing approximately 13 g (Dunning 1993), this consumption estimate

Table 10. Passerine bird density and biomass estimate. Densities were adapted from Folkard and Smith (1995) and body masses were taken from Dunning (1993).

Species	Species density (# males•ha^{-1})	Body mass (g)	Species density (g•ha^{-1})
Dendroica coronata	61.0	11.94	728.34
Junco hyemalis	24.4	19.50	475.80
Parus hudsonicus	24.4	9.80	239.12
Catharus ustulatus	3.1	32.80	100.04
Perisoreus canadensis	3.1	73.00	222.65
Zonotrichia leucophrys	3.1	29.40	89.67
Turdus migratorius	3.1	77.30	235.77
Total (mean)	122.0	(36.25)	2091.39

should be generous enough to cover the food requirements of most passerine birds. A bird population in Czechoslovakia was reported to have consumed approximately 25% of its weight daily (Turcek 1952). I used the consumption value of 30% body weight•day^{-1} which produces an annual Q/B of 110.

Diet composition – The diet composition for passerine birds was assumed to be comprised of seeds and insects. I also added a small proportion of salmon eggs to the diet since some birds such as the American dipper (*Cinclus mexicanus*) are known to feed on salmon eggs (Obermeyer *et al.* 1999) as well as a small proportion of earthworms. Since the predatory insects made up approximately 20% of the total insect biomass, I further divided the diet composition to reflect this (i.e., 48% of the diet was assumed to be insects and 20% of that was predatory insects and the remainder herbivorous insects). Therefore, I used a diet composition of 0.51-forest detritus which represents seeds, 0.384-herbivorous insects, 0.096-predatory insects, and 0.01-earthworms.

Detritus fate – 1.0 forest detritus.

A1.1.1.14 Riparian passerine birds

This group contains passerine birds that are in the riparian zone. The input parameters are assumed to be the same as those for passerine birds (above) with the exception of the diet composition. The diet composition for this group is 0.50-riparian detritus, 0.384-riparian herbivorous insects, 0.096-riparian predatory terrestrial insects, 0.01-riparian earthworms, and 0.01-salmon eggs. This group is assigned to 8.5% of the total model habitat area, i.e., the riparian zone.

Fate of detritus – 1.0 riparian detritus.

A1.1.1.15 Mustelids

This group consists of small mammalian predators belonging to the family Mustelidae. Appendix 5 lists mustelid species that may occur in the IDFwet zone according to Stevens (1995). This group is assigned to 91% of the total model habitat area, i.e., forest zone.

Biomass – Using density estimates and body masses for several mustelid species a total biomass estimate of 0.005 t•km^{-2} was calculated. These calculations are summarized in Table 11.

Table 11. Mustelid species density and biomass estimates.

Species	Density ($\#\cdot km^{-2}$)	Body mass (kg)	Biomass ($kg\cdot km^{-2}$)	Source (density; body mass)
Long-tailed weasel	1.840	0.102	0.188	Jedrzejewski *et al.* (1995); Banfield (1974)
Ermine spp	6.100	0.055	0.336	Robitaille and Raymond (1995); Banfield (1974)
Marten	1.000	1.360	1.360	Thompson (1994); Cowan and Guiguet (1965)
Fisher	0.875	3.350	2.931	Banci (1990); Banci (1990)
Total (mean)	(2.454)	(1.217)	4.814	-

P/B – This parameter was estimated using the annual survival rate of 0.54 for fishers (Kohn 1993) and equation (3). The resulting P/B is $0.616\cdot year^{-1}$.

Q/B – The consumption rate for this group was estimated using a field metabolic rate for carnivores in Nagy *et al.* (1999). The equation given for estimating FMR for carnivores is:

$$FMR = 1.67 \, (body \, mass)^{0.918} \qquad (5)$$

where the body mass is in g and FMR is in $kJ\cdot day^{-1}$. Nagy *et al.* (1999) also gives a dry weight-wet weight relationship for animal matter stating that fresh matter is usually around 70% water. This relationship was used to convert dry matter consumption to wet matter consumption. The average annual consumption for several mustelids was calculated, and then divided by the average body mass to produce a Q/B estimate of $44.50\cdot year^{-1}$ (Table 12).

Diet composition – The diet composition of 0.61-small mammals, 0.11 passerine birds, and 0.28-forest detritus are averaged values for various species (Table 13). Food categories

Table 12. Annual consumption estimates for various mustelid species. Equation for calculating FMR and dry weight-wet weight conversion from Nagy *et al.* 1999.

Species	Body mass (kg)	FMR ($kJ\cdot day^{-1}$)	Daily intake (kg dry matter)	Yearly intake (kg dry matter)	Yearly intake (kg wet matter)
Long-tailed weasel	0.102	92.94	0.006	2.02	6.72
Ermine spp	0.055	54.34	0.003	1.18	3.93
Marten	1.360	882.60	0.053	19.18	63.85
Fisher	3.350	1931.88	0.115	41.97	139.77
Mean	1.217	740.44	0.044	16.09	53.57

Table 13. Diet composition of mustelid species.

Species	salmon	rodents	birds	berries	deer carcass	Other	Adapted from
	Proportion of food items in diet		
Fisher	0.00	0.30	0.06	0.29	0.15	0.20	Arthur *et al.* (1989)
Marten	0.07	0.54	0.11	0.15	0.10	0.03	Ben-David *et al.* (1997)
Weasel	0.00	0.71	0.16	0.00	0.00	0.13	Moors (1975)
Ermine	0.00	0.90	0.10	0.00	0.00	0.00	Raymond *et al.* (1984)
Average	0.02	0.61	0.11	0.11	0.06	0.09	-

berry, deer carcass, and other were combined into detritus. The salmon carcass portion of the diet was omitted as this group is assumed not to feed on salmon carcasses.

Detritus fate – 1.0 forest detritus.

A1.1.1.16 Riparian mustelids

This group contains the mustelids that are found in the riparian zone. The input parameters are assumed to be the same as for mustelids (above) with the exception of the diet composition. The diet composition for this group is 0.61-riparian small mammals, 0.11-riparian passerine birds, 0.26-riparian detritus, and 0.02-salmon carcasses. This group is assigned to 8.5% of the total model habitat area, i.e., the riparian zone.

Fate of detritus – 1.0 riparian detritus.

A1.1.1.17 Herbivorous ducks

This group contains ducks that feed on aquatic vegetation. Appendix 5 lists duck species that may occur in the IDFwet zone according to Stevens (1995). This group is assigned to 9% of the total model habitat area, i.e., the aquatic and riparian zones.

Biomass – A biomass estimate of 0.005 t•km^{-2} for sea ducks in Prince William Sound (Esler 1998). This estimate took into consideration the seasonal occurrence of migrating ducks when it was originally derived. I split this biomass in half to represent herbivorous ducks and omnivorous ducks. Therefore, a biomass estimate of 0.002 t•km^{-2} was used in this model.

P/B – The P/B estimate of 0.20•year^{-1} used in this model was also taken from Esler (1998).

Q/B – The consumption estimate was calculated using body masses for various herbivorous duck species and an equation to estimate field metabolic rate (FMR) for seabirds using flapping flight (Nagy *et al.* 1999), which is estimated using the equation:

$$FMR = 10.3 \; (body \; mass)^{0.726} \qquad\qquad (3)$$

where the body mass is in grams and FMR is in kJ•day^{-1}. The daily energy requirements for the herbivorous duck species was calculated, then converted into the amount of food required to satisfy this need based a food energy content estimate of 10 kJ•g^{-1} dry matter (Nagy *et al.* 1999). This daily consumption was then extended over 365 days and converted to wet weight assuming that plants are 85% water (Jørgensen 1979). The average yearly consumption was then divided by the average biomass of the ducks used in the calculations to come up with a Q/B estimate of 400•year^{-1} (Table 14).

Table 14. Herbivorous duck species yearly consumption estimates based on field metabolic rate. Energy content of food used in calculations was 10 kJ•g^{-1} dry matter.

Duck species	Body mass (g)	FMR (kJ•day^{-1})	Daily food intake (g dry weight)	Yearly intake (kg wet weight)
Wood duck	658	1145	115	279
Green-winged teal	341	711	71	173
Mallard	1082	1643	164	400
Northern pintail	1010	1563	156	381
Blue-winged teal	386	777	78	189
Cinnamon teal	386	777	78	189
Gadwall	920	1461	146	356
Eurasian wigeon	771	1285	128	313
American wigeon	755	1265	127	308
Canvasback	1219	1792	179	436
redhead	1045	1602	160	390
Ring-necked duck	705	1204	120	293
Mean	773	1269	127	309

Diet composition – I used the diet information for canvasback ducks in Hohman (19900 as a guideline for generating the diet composition for this group. I set the diet composition at 0.95-macrophytes and 0.05 benthos.

Detritus fate – 0.94 riparian detritus; 0.06 aquatic detritus.

A1.1.1.18 Omnivorous ducks

This group contains ducks that feed primarily on benthic organisms. Appendix 5 lists duck species that may occur in the IDFwet zone according to Stevens (1995). This group is assigned to 9% of the total model habitat area, i.e., the aquatic and riparian zones.

Biomass - A biomass estimate of 0.005 $t \cdot km^{-2}$ for sea ducks in Prince William Sound (Esler 1998). This estimate took into consideration the seasonal occurrence of migrating ducks when it was originally derived. I split this biomass in half to represent herbivorous ducks and omnivorous ducks. Therefore, a biomass estimate of 0.002 $t \cdot km^{-2}$ was used in this model.

P/B – The P/B estimate of $0.20 \cdot year^{-1}$ used in this model was also taken from Esler (1998).

Q/B – The Q/B for this group was derived in the same manner as for herbivorous ducks with the exception that omnivorous species were used in the calculations and the energy content of the food differed (Table 15). I used the food energy content of 1.65 $kJ \cdot g^{-1}$ for a mussel (Esler 1998) since the majority of the diet for this group is benthos.

Diet composition – The diet composition was derived from averaging the values for the diets of bufflehead, lesser scaup, goldeneye, and harlequin ducks (Table 16). The resulting diet composition was 0.83-benthos and 0.17-macrophytes.

Detritus fate – 0.94 riparian detritus; 0.06 aquatic detritus.

Table 15. Omnivorous duck species yearly consumption estimates based on field metabolic rate. Energy content of food used in calculations was 1.65 kJ•g^{-1} wet mass

	Body mass (g)	FMR (kJ•day-1)	Daily food intake (g wet mass)	Yearly intake (kg wet weight)
Greater scaup	945	1489	903	329
Harlequin duck	623	1101	667	243
Northern shoveler	613	1088	659	241
Lesser scaup	720	1223	741	270
Oldsquaw	873	1406	852	311
Black scoter	950	1495	906	331
Surf scoter	950	1495	906	331
White-winged scoter	1757	2336	1416	517
Common goldeneye	900	1438	871	318
Barrow's goldeneye	910	1449	878	321
Bufflehead	404	804	487	178
Hooded merganser	610	1084	657	240
Red-breasted merganse	1022	1577	955	349
Ruddy duck	545	999	605	221
Mean	844	1356	822	300

Table 16. Omnivorous duck diet composition used in model.

Duck species	Proportion of food in diet		Source
	Benthos	Macrophyte	
Bufflehead	58	42	Gammonley and Heitmeyer (1990)
Lesser Scaup	72	28	Gammonley and Heitmeyer (1991)
Goldeneye	100	0	Winfield and Winfield (1994)
Harlequin	100	0	Rodway (1998)
Mean	82.5	17.5	-

A1.1.1.19 Raptors

This group contains hawks, eagles, and falcons. Appendix 5 lists raptors species that may occur in the IDFwet zone according to Stevens (1995). This group is assigned to 99.5% of the total model habitat area, i.e., the riparian and forest zones.

Biomass – Biomass was calculated using density estimates for various raptors found in Kruger (2000) and Newton (1979). The density estimates for the raptor species were then multiplied by their respective body mass taken from Dunning (1993). Table 17 summarizes these calculations which result in a biomass of 0.003 t•km^{-2}.

P/B – This estimate was derived by calculating the average annual survival for the raptor species. Mortality estimates were taken from Newton (1979) for the raptor species listed in Table 17 with the exception of the mortality estimate for bald eagles which was taken from Bowman *et al.* (1995). The average annual mortality rate came out to be 0.307. This gives an annual survival rate of 0.693, which produces a P/B estimate of 0.367•year^{-1} when used with equation (3).

Q/B – A daily consumption rate estimate of 2.5% of body weight for the red-tailed hawk (Tabaka *et al.* 1996) was used to estimate consumption for this group. This daily consumption rate produces an annual Q/B of 9.125.

Diet composition – The diet composition was averaged for several raptors (Table 18) with the resulting diet composition being 0.52-passerine birds, 0.40-small mammals, 0.05-salmon carcasses, and 0.03-mustelids. This was broken down further to 0.473-passerine birds, 0.047-riparian passerine birds, 0.364-small mammals, 0.036-riparian small mammals, 0.027-mustelids, 0.003-riparian mustelids, and 0.05-salmon carcasses.

Detritus fate – 0.91 forest detritus; 0.09 riparian detritus.

Table 17. Raptor body masses and densities used to estimate biomass.

Bird species	Body mass (g)	Density (birds·km^{-2})	Density (g·km^{-2})	Density source
Red-tailed hawk	1125	0.578	650	Kruger (2000)
Rough-legged hawk	955	0.578	552	Kruger (2000)
Cooper's hawk	440	0.141	62	Kruger (2000)
Sharp-shinned hawk	135	0.141	19	Kruger (2000)
Northern goshawk	1025	0.141	145	Kruger (2000)
Bald eagle	4740	0.064	303	Kruger (2000)
Northern harrier	420	0.236	99	Kruger (2000)
American kestrel	115	0.500	58	Newton (1979)
Merlin	190	0.500	95	Newton (1979)
Osprey	1485	0.400	594	Newton (1979)
Total (mean)	(1063)	3.279	2577	-

Table 18. Raptor diet composition.

Species	Proportion of food items in diet				Source
	Birds	Mammals	Fish	Other	
Red-tailed hawk	0.24	0.74	0.00	0.02	Bosakowski and Smith (1992)
Northern goshawk	0.66	0.34	0.00	0.00	Bosakowski and Smith (1992)
Cooper's hawk	0.84	0.16	0.00	0.00	Bosakowski and Smith (1992)
Sharp-shinned hawk	0.91	0.09	0.00	0.00	Joy et al. (1994)
Rough-legged hawk	0.15	0.85	0.00	0.00	Springer (1975)
Bald eagle	0.53	0.09	0.34	0.04	Knight et al. (1990)
American kestrel	0.24	0.74	0.00	0.02	Hiraldo et al. (1991)
Mean	0.51	0.43	0.05	0.01	.

A1.1.1.20 Wolves (*Canus lupus*)

This group is assigned to 99.5% of the total model habitat area, i.e., the riparian and forest zones.

Biomass – Wolf density estimates of 0.014 individuals·km^{-2} and 0.0027-0.0044 individuals·km^{-2} are given in Boertje et al. (1996) and Ballard et al. (1997) respectively. Therefore, I used a density of 0.010 individuals·km^{-2} and a body mass of 63.5 kg (Cowan and Guiguet 1965) to calculate a biomass estimate of 0.001 t·km^{-2}.

P/B – An average annual survival rate of 0.552 is given by Ballard *et al.* (1997). Applying this survival rate to equation (3) produces a P/B estimate of 0.594•year^{-1}.

Q/B – A daily consumption rate of 2.5-3.6 kg•wolf^{-1} (Weise *et al.* 1979) was used to calculate this parameter. I used a daily consumption rate of 3 kg•wolf^{-1} and extended this over a year to get an annual consumption of 1095 kg•wolf^{-1}. This estimate was then divided by a body mass of 63.5 kg (Cowan and Guiguet 1965) to produce a Q/B of 17.244•year^{-1}.

Diet composition – The diet composition consisted of 0.09-salmon carcasses (Szepanski 1999) and 0.85-ungulates, 0.005-riparian mustelids, and 0.055-mustelids (Forbes and Theberge 1996).

Detritus fate – 0.91 forest detritus; 0.09 riparian detritus.

A1.1.1.21 Ungulates

This group contains moose (*Alces alces*) and deer (*Odocoileus hemionus*). This group is assigned to 99.5% of the total model habitat area, i.e., the riparian and forest zones.

Biomass – A biomass for deer was derived using a density estimate of 14 deer•km^{-2} (Klinger *et al.* 1989) and a body mass of 84.15 kg (Shackleton 1999) to produce a biomass of 1.178 t•km^{-2}.

A moose biomass was calculated using a density estimate of 0.40 moose•km^{-2}. This density falls within the range of estimates of 0.005-0.417 moose•km^{-2} that is presented in Gasaway *et al.* (1983) and 0.183-1.020 moose•km^{-2} presented by Boertje (1996). A body mass of 375 kg (Shackleton 1999) was used to calculate a biomass estimate of 0.150 t•km^{-2}. This estimate was then combined with the one for deer to get an overall biomass estimate for ungulates of 1.329 t•km^{-2}.

P/B – An average annual survival rate for ungulates was adapted from Kunkel and Pletscher (1999) who report a survival rate of 0.74 for deer and 0.88 for moose. The average value, 0.81, was then applied to equation (3) to produce a P/B estimate of 0.211•year^{-1}.

Q/B – A consumption rate of 10 kg•day^{-1}•moose^{-1} was used for moose. This estimate was adapted from Gasaway and Coady (1974) who reports a range of 1.7-19 kg•day^{-1}•moose^{-1}.

Extending this consumption rate over a year and then dividing it by a body mass of 375 kg leads to a Q/B of 9.733•year^{-1} for moose.

A consumption rate range for deer was found to be 0.95-1.7 kg•day^{-1}•deer^{-1} (Brown *et al.* 1985). Using a value of 1.35 kg•day^{-1}•deer^{-1} and extending this over a year and dividing by the body mass of 84 kg for deer produces a Q/B estimate of 5.866•year^{-1}. The average of the Q/B estimates of 7.80•year^{-1} for deer and moose was used in the model.

Diet composition – Ungulates are herbivores feeding on a variety of trees and shrubs. In addition to trees and shrubs, moose are known to feed on aquatic plants (Cowan and Guiguet 1965). Therefore, I approximated ungulate diet as 0.18-forest trees, 0.02-riparian trees, 0.10-macrophytes, 0.65-forest shrubs, and 0.05-riparian shrubs.

Detritus fate – 0.91 forest detritus; 0.09 riparian detritus.

A1.1.1.22 Black bears (*Ursus americanus*)

Biomass – A black bear density estimate of 0.35 bears•km^{-2} (Doan-Crider and Hellgren 1996) was converted into biomass using a body mass of 90.7 kg for black bears (Erickson 1965). The resulting biomass is 0.032 t•km^{-2}. This group is assigned to 99.5% of the total model habitat area, i.e., the riparian and forest zones.

P/B – An annual survival rate of 0.755 for male and female black bears (Kasbohm *et al.* 1996) was used to estimate P/B using equation (3). The resulting P/B is 0.281•year^{-1}.

Q/B – A consumption value similar to grizzly bears was assumed since an estimate for black bears could not be found.

Diet composition – The diet composition was adapted from data presented in Jacoby *et al.* (1999). Black bears are known not to eat as much salmon when feeding in areas where grizzly bears are also present. The diet composition entered was 0.55-forest shrubs, 0.05-riparian shrubs, 0.30 ungulates, and 0.10-salmon carcasses.

Detritus fate – 0.91 forest detritus; 0.09 riparian detritus.

A1.1.1.23 Grizzly bears (*Ursus arctos*)

Biomass – A density of 0.250 bears•km^{-2} (Miller 1997) along with a body mass of 175 kg (Hilderbrand *et al.* 1999b) was used to calculate a biomass of 0.044 t•km^{-2}. This group is assigned to 99.5% of the total model habitat area, i.e., the riparian and forest zones.

P/B – An annual survival rate of 0.916 (Hovey and McLellan 1996) was used to calculate an annual P/B of 0.088 using equation (3).

Q/B – A spring consumption value of 541 kg of meat and a fall consumption value of 1003 kg of meat (Hilderbrand *et al.* 1999b) were combined for a total consumption of 1544 kg of meat. Using the body mass of 175 kg, a Q/B estimate of 8.823•year^{-1} was calculated.

Diet composition – Seasonal data from *et al.* (1999b) was adapted to produce a diet composition of 0.205-forest shrubs, 0.02-riparian shrubs, 0.487-ungulates, and 0.288-salmon carcasses.

Detritus fate – 0.91 forest detritus; 0.09 riparian detritus.

A1.1.2 Aquatic groups

A1.1.2.1 Salmon eggs

This group contains the egg biomass deposited in the Atnarko River by chinook, coho, pink, and sockeye salmon. This group is assigned to 0.5% of the total model habitat area, i.e., the aquatic zone.

Biomass – A biomass estimate of approximately 157 tonnes (Table19) was derived for this group. This estimate was calculated by using the average number of spawners from 1950 to 1998 for chinook, sockeye, and pink and 1950 to 1994 for coho since escapement data could not be found for the same period as other salmon species. An even sex ratio was assumed so the average escapement divided in half to estimate the number of females which was then multiplied by species fecundity in Groot *et al.* (1995). The number of eggs for each species was then

Table 19. Biomass of eggs deposited in the Atnarko Watershed each year.

Species	Average escapement	# Females	Fecundity (eggs/female)	Total eggs (x10^6)	Egg mass (g)	Total egg mass (tonnes)
Sockeye	43,546	21,773	3000	65.32	0.145	9.47
Coho	30,519	15,260	3500	53.41	0.168	8.97
Pink	832,776	416,388	1600	666.22	0.188	125.25
Chinook	17,881	8,941	5000	44.70	0.300	13.41
Total (mean)	924,722	462,361	(3275)	829.65	(0.200)	157.10

multiplied by the mass of its eggs. Egg masses were taken from: chinook - Rombough (1985), coho - Flemming and Ng (1987), sockeye - Groot and Margolis (1991), and pink - Beacham *et al.* (1998). The total biomass estimate of 157 tonnes was then assumed to be present in the ecosystem for 6 months (laying time and incubation time) so it was divided in half. The new estimate was assumed to be distributed throughout the aquatic portion of the ecosystem, approximately 6 km^2, and was adjusted accordingly to produce a biomass estimate of 13.083 t•km^{-2}.

P/B – No salmon eggs survive more than a year as they hatch, are eaten, or decompose. Therefore the P/B ratio was set at 1 so that the product of the biomass estimate and the P/B ratio equaled the estimated number of eggs deposited in the system per year.

Fate of detritus – 0.995 aquatic detritus; 0.005 riparian detritus. A small portion of the detritus from this group is portioned to riparian detritus. This is because most of the egg biomass that is brought into the riparian zone via birds and bears will be consumed leaving a small amount which becomes riparian detritus.

A1.1.2.2 Demersal fish

This group contains bottom dwelling fish such as whitefish (*Prosopium williamsoni*) and sculpins, family Cottidae. This group is assigned to 0.5% of the total model habitat area, i.e., the aquatic zone.

Biomass – A biomass estimate of 0.757 t•km^{-2} for mottled sculpins (*Cottus bairdi*) was used for this group (Neves and Pardue 1983).

P/B – A P/B of 1.1•year^{-1} for mottled sculpins was also taken from Neves and Pardue (1983).

Q/B – The estimate of 10.80•year^{-1} was taken from Becharof Lake, Alaska (Mathisen and Sands 1999).

Diet composition – The diet composition was taken from the demersal fish group in a model of Becharof Lake (Mathisen and Sands 1999) and is 0.02-salmon eggs, 0.06-demersal fish, 0.05-zooplankton, 0.17-macrophytes, 0.40-benthos, 0.02-salmon carcasses, and 0.28-aquatic detritus.

Fate of detritus – 1.0 aquatic detritus.

A1.1.2.3 Trout and char

This group contains rainbow trout (*Oncorhynchus mykiss*), cutthroat trout (*Oncorhynchus clarki*), and dolly varden char (*Salvelinus malma*). This group is assigned to 0.5% of the total model habitat area, i.e., the aquatic zone.

Biomass – A biomass of 0.193 t•km^{-2} for rainbow trout in Kootenay Lake (Thompson 1999) and an estimate of 0.86 t•km^{-2} for brook trout (Neves and Pardue 1983) were used to generate the biomass for this group. Since both estimates are for single species I combined the two to get an overall biomass for trout and char of 1.053 t•km^{-2}.

P/B – The P/B estimate of 1.6•year^{-1} used is for brook trout (Neves and Pardue 1983).

Q/B – This estimate was made by averaging the Q/B values for rainbow trout in Kootenay Lake (Thompson 1999) and for apex predators in Becharof Lake (Mathisen and Sands 1999). The resulting Q/B is 4.45•year^{-1}.

Diet composition – The diet composition was estimated using seasonal diet data for cutthroat and rainbow trout (Baldwin *et al.* 2000) and diet data for dolly varden char (Nakano *et al.* 1999). Table 20 summarizes the data that produced the diet composition used in this model. The resulting diet composition is 0.024-predatory insects, 0.097-herbivorous insects, 0.023-trout and char, 0.595-macroinvertebrates, and 0.261-zooplankton. The proportion of terrestrial insects

Table 20. Diet composition for trout and char species.

| Species | Proportion of food items in diet | | | | | Adapted from |
	Cutthroat	Cyprinids	Daphnia	Macroinverts	Terrestrial insects	
Rainbow	0.027	0.003	0.184	0.787	0.000	Baldwin *et al.* (2000)
Cutthroat	0.042	0.000	0.596	0.362	0.000	Baldwin *et al.* (2000)
Dolly varden	0.000	0.000	0.000	0.638	0.363	Nakano *et al.* (1999)
Mean	0.023	0.001	0.260	0.595	0.121	

in Table 20 was broken down into herbivorous and predatory insects assuming that predatory insects comprised approximately 20% of terrestrial insect (see above for notes on predatory insect biomass for details).

Fate of detritus – 1.0 aquatic detritus.

A1.1.2.4 Periphyton

This group is assigned to 0.5% of the total model habitat area, i.e., the aquatic zone. While this group has been entered into the model separate from the biofilm group (below), it is realized that periphyton and biofilm are difficult to separate in reality as they are both components of the aufwuchs community in lakes and streams. The two groups have been modeled separately but they could have been combined to form just one group because they behave similarly. The overall performance of the model would not have changed much had the two groups been combined compared to the current setup with the two groups separated.

Biomass – A biomass estimate of 14.462 t•km^{-2} was attained by averaging values for periphyton for the Thompson River (Langer and Nassichuk 1975).

P/B – A daily P/B ratio for periphyton of 0.04 for a small stream in Alaska (Murphy 1984) was used as the basis to estimate this parameter. A growing season of 180 days for periphyton was assumed which produces an annual P/B estimate of 7.20.

Fate of detritus – 1.0 aquatic detritus.

A1.1.2.5 Biofilm

Biofilms have been described as an accumulation of living matter which may contain microscopic bacteria, fungi, or algae (Bott 1999). This group is assigned to 0.5% of the total model habitat area, i.e., the aquatic zone.

Biomass – A biofilm estimate of 15 t•km^{-2} for a stream in southeastern Alaska (Wipfli *et al.* 1998) was used in this model.

P/B – A production estimate of 0.01-22.0 mg C•m^{-2}•hour^{-1} for benthic bacteria is given in Findlay *et al.* (1986). I used an estimate of 11.0 mg C•m^{-2}•hour^{-1} and extended it over a day and then over a year to produce an annual production estimate of 96.36 t C•km^{-2}. Findlay *et al.* (1986) also report a biomass of 0.75 t C•km^{-2} which was used to calculate a P/B ratio of 128.48.

This value is within the range of P/B values given in Jørgensen (1979) who gives a daily P/B range of 0.3-0.6 which works out to be 110-219 annually. Wetzel (1983) also reports an annual P/B for bacteria of 141.0.

Fate of detritus – 1.0 aquatic detritus.

A1.1.2.6 Macroinvertebrates

This group contains the aquatic insects. This group is assigned to 0.5% of the total model habitat area, i.e., the aquatic zone.

Biomass – A biomass of 1.758 t•km^{-2} was taken by averaging values for macroinvertebrates in the Thompson River (Langer and Nassichuk 1975). This estimate is close to one given by Robinson and Minshall (1998) who report a biomass of 1.069 t•km^{-2} for macroinvertebrates.

P/B – Robinson and Minshall (1998) report annual P/B estimates for several taxa of macroinvertebrates. I averaged these values to produce a P/B ratio of 16.353•year^{-1}.

Q/B – A daily consumption rate of 4-46% body weight for macroinvertebrate shredders is given in Arsuffi and Suberkropp (1989). I used a consumption rate of 20% body weight per day which produces an annual Q/B estimate of 73.

Diet composition – The diet composition is a reflection of the functional feeding community structure. I estimated the percent composition of the different feeding groups for a 3rd-4th order stream according to the river continuum concept (Vannote *et al.* 1980). I then took this composition to be the diet composition for the entire group based on the types of food the different groups rely upon according to Cummins and Klug (1979). The community structure along with major food item in parenthesis is 45% collectors (detritus), 35% grazers (algae), 10% predators (macroinvertebrates), and 10% shredders (detritus). It was unclear to what extent biofilm was fed upon so a minor portion of the diet was given to biofilm resulting in a diet composition for the entire group of 0.30-periphyton, 0.05-biofilm, 0.10-macroinvertebrates, and 0.55-aquatic detritus.

Fate of detritus – 1.0 aquatic detritus.

A1.1.2.7 Zooplankton

The zooplankton of Lonesome and Stillwater Lakes does not appear to have been studied, hence the study of Thompson (1999) on Kootenay Lake was used as the key reference. This group is assigned to 0.5% of the total model habitat area, i.e., the aquatic zone.

Biomass – The biomasses of zooplankton groups in Kootenay Lake (Thompson 1999) were summed to produce a total biomass of 19.88 t•km^{-2} and was applied to Lonesome and Stillwater Lakes.

P/B – The annual production for each of the zooplankton groups in Kootenay Lake (Thompson 1999) was calculated by multiplying the P/B estimate by its biomass (Table 21). The production estimates for each zooplankton group were then summed and divided by the total biomass to produce a P/B estimate of 10.40•year^{-1}.

Table 21. Zooplankton diet from Kootenay Lake (Thompson 1999).

Zooplankton type	Proportion of food items in diet					
	Copepod	Cladoceran	Daphnia	Rotifers	Phytoplankton	Detritus
Copepod	0.05	0.03	0.05	0.05	0.83	0.00
Cladoceran	0.00	0.03	0.03	0.03	0.93	0.00
Daphnia	0.00	0.00	0.00	0.00	1.00	0.00
Rotifers	0.00	0.00	0.00	0.01	0.61	0.39
Mean	0.01	0.01	0.02	0.02	0.84	0.10

Table 22. Zooplankton diet from Kootenay Lake (Thompson 1999).

Zooplankton type	Copepod	Cladoceran	Daphnia	Rotifers	Phytoplankton	Detritus
	Proportion of food items in diet					
Copepod	0.05	0.03	0.05	0.05	0.83	0.00
Cladoceran	0.00	0.03	0.03	0.03	0.93	0.00
Daphnia	0.00	0.00	0.00	0.00	1.00	0.00
Rotifers	0.00	0.00	0.00	0.01	0.61	0.39
Mean	0.01	0.01	0.02	0.02	0.84	0.10

Q/B – The same procedure used to estimate P/B was also used to estimate Q/B (Table 21). The resulting Q/B is 81.59•year^{-1}.

Diet composition – The diet composition is an average of the diet compositions of the zooplankton groups in Kootenay Lake (Thompson 1999). Table 22 summarizes this data that led to a diet composition for zooplankton of 0.84-phytoplankton, 0.06-zooplankton, and 0.10-aquatic detritus.

Fate of detritus – 1.0 aquatic detritus.

A1.1.2.8 Phytoplankton

This group is assigned to 0.5% of the total model habitat area, i.e., the aquatic zone.

Biomass – The biomass estimate of 15 t•km^{-2} came from Kootenay Lake (Thompson 1999).

P/B – A P/B value of 113.0•year^{-1} for phytoplankton is given in Wetzel (1983).

Fate of detritus – 1.0 aquatic detritus.

A1.1.2.9 Macrophytes

This group contains aquatic plants. This group is assigned to 0.5% of the total model habitat area, i.e., the aquatic zone.

Biomass – The biomass estimate of 600 t•km^{-2} for this group comes from Lawrence Lake, Michigan (Rich *et al.* 1971).

P/B – The P/B estimate of 2.0•year^{-1} comes from Wetzel (1983). He states that a relatively constant biomass of perennial macrophytes is a common characteristic of lakes and that turnover rates of perennial plant populations are approximately 1.5 to 5.0 times maximum biomass. He also states that annual plant population turnover rates are relatively low at 1.02-1.2 times max. biomass. Therefore, I used a P/B of 2.0•year^{-1}.

Fate of detritus – 1.0 aquatic detritus.

A1.1.2.10 Benthos

This group contains mollusks, worms, and other organisms associated with the benthic habitat. This group is assigned to 0.5% of the total model habitat area, i.e., the aquatic zone.

Biomass - This biomass estimate comes from the estimate for benthos in Lake Ontario, i.e., 0.206 t dry weight•km^{-2} (Halfon *et al.* 1996). They also provided a conversion factor of wet weight = dry weight•0.15^{-1} which results in a biomass of 1.373 t•km^{-2}.

P/B - A daily production value for macrobenthos in Lake Ontario is 0.012 kcal•m^{-2}•day^{-1} (Halfon *et al.* 1996). They also presented a conversion factor for macrobenthos of 3558 J•gram wet weight^{-1}. This estimate was converted from kcal to J and then from J to grams wet weight resulting in an annual production estimate of 5.154 t•km^{-2}. P/B was then calculated by dividing 5.154 t•km^{-2}•year^{-1} by the biomass estimate of 1.373 t•km^{-2} to get a P/B of 3.751•year^{-1}.

Q/B – A Q/B estimate of 23.0•year^{-1} was taken from the Becharof Lake model (Mathisen and Sands 1999).

Diet composition – The diet composition for this group was adapted from Becharof Lake (Mathisen and Sands 1999) and is 0.03-zooplankton, 0.549-macrophytes, 0.001-salmon carcasses, and 0.42-aquatic detritus.

Fate of detritus – 1.0 aquatic detritus.

A1.1.2.11 Juvenile chinook (*Oncorhynchus tshawytscha*)

This group is assigned to 0.5% of the total model habitat area, i.e., the aquatic zone.

Table 23. Juvenile salmon biomass estimates. Smolt per spawner ratio taken from Johnson and Cooper (1993) and body masses taken from Groot *et al.* 1995.

Species	Average escapement	Smolt per spawner	# of smolts	Body mass (g)	Total mass (t)
Sockeye	43,546	15.2	661,899	5	3.31
Coho	30,519	15.2	463,889	7	3.25
Chinook	17,881	15.2	271,791	9	2.45

Biomass – The biomass for this group was calculated by using escapement data for the Atnarko River and a ratio of 15.2 smolts•spawner^{-1} that was found for coho salmon in Snow Creek, Washington (Johnson and Cooper 1993). Table 23 shows how the juvenile chinook biomass of 2.45 tonnes was derived. This biomass was then divided by the area of the aquatic portion of the model area, approximately 6 km^2, to reach a biomass estimate of 0.408 t•km^{-2}.

P/B – An egg-fry survival rate of 2.2 % for chinook in the Cowichan River (Nagtegaal and Carter 2000) was used in equation (3) to produce a P/B estimate of 3.817•year^{-1}.

Q/B – A daily ration for juvenile coho and chinook was estimated to be between 2.4-3.7% body weight•day^{-1} (Brodeur 1991). I used an estimate of 3% which works out to be an annual Q/B of 10.95.

Diet composition – The diet composition was adapted from data presented in Rondorf *et al.* (1990) and Becker (1972). In both cases I had to divide the data on insects into terrestrial and aquatic components based on the life stage. Adult life stages were presumed to be terrestrial insects while larval stages were presumed to be macroinvertebrates. The total terrestrial insect portion of the diet was further subdivided in to herbivorous and predatory terrestrial insect by assuming that herbivorous insects comprised approximately 80% of terrestrial insects (see biomass notes for predatory terrestrial insects for details). The resulting diet composition used was 0.158-predatory terrestrial insects, 0.633-herbivorous terrestrial insects, 0.204-macroinvertebrates, and 0.005-zooplankton

Fate of detritus – 1.0 aquatic detritus.

A1.1.2.12 Juvenile coho (*O. kisutch*)

This group is assigned to 0.5% of the total model habitat area, i.e., the aquatic zone.

Biomass – Juvenile coho biomass was estimated the using the same procedure that was used to calculate juvenile chinook biomass using escapement data and a 15.2 smolt•spawner^{-1} ratio (Johnson and Cooper 1993). A biomass of 3.25 tonnes was calculated (Table 23) which was then divided by the area of the aquatic portion of the model area, approximately 6 km^2, to reach a biomass estimate of 0.524 t•km^{-2}.

P/B – The P/B estimate of 3.60•year^{-1} came from Becharof Lake (Mathisen and Sands 1999) who calculated it based on growth curve data.

Q/B – The Q/B was calculated the same way as for juvenile chinook Q/B using a daily ration estimate between 2.4-3.7% body weight•day^{-1} (Brodeur 1991). I used an estimate of 3% which works out to be an annual Q/B of 10.95.

Diet composition – Diet composition data was adapted from Johnson and Ringler (1980) who present data on summer diet, Bilby *et al.* (1998) who present fall and winter diet observation, and from Mathisen and Sands (1999) who present data from Becharof Lake, Alaska. I used these observations and data to estimate a yearly diet composition of 0.41-maroinvertebrates, 0.34-terrestrial insects, 0.15-juvenile sockeye, 0.05-salmon eggs, and 0.04-salmon carcasses.

Fate of detritus – 1.0 aquatic detritus.

A1.1.2.13 Juvenile sockeye (*O. nerka*)

This group is assigned to 0.5% of the total model habitat area, i.e., the aquatic zone.

Biomass - Juvenile sockeye biomass was estimated the using the same procedure that was used to calculate juvenile chinook and juvenile coho biomass using escapement data and a 15.2 smolt•spawner^{-1} ratio (Johnson and Cooper 1993). The biomass of 3.31 tonnes (Table 23) was only averaged over the lake portion of the area, approximately 5.375 km^2, to produce a biomass estimate of 0.523 t•km^{-2}.

P/B – McGurk (1999) reports mean egg-smolt survival estimates for several lakes in British Columbia and Alaska. The average survival rate of 0.024 was used in equation (3) to produce a P/B estimate of 3.719•year^{-1}.

Q/B – A Q/B estimate for age 0+ and 1+ kokanee in Kootenay Lake is 5.4•year^{-1} and 9.0•year^{-1} respectively (Thompson 1999). The average of these two values is 7.2•year^{-1}. Juvenile sockeye in Becharof Lake were estimated to have a Q/B of 7.3•year^{-1} based on a daily consumption rate of 2% body weight•day^{-1} (Mathisen and Sands 1999). Therefore, I used a Q/B of 7.25•year^{-1} in this model.

Diet composition - Barraclough and Robinson (1972) report monthly data on juvenile sockeye diet which was used to produce a diet composition of 0.214-macroinvertebrates and 0.786-zooplankton.

Fate of detritus – 1.0 aquatic detritus.

A1.1.2.14 Salmon carcasses

This group contains the carcasses of chinook, coho, sockeye, and pink salmon which all spawn in the Atnarko system. This group is assigned to 0.5% of the total model habitat area, i.e., the aquatic zone.

Biomass - The biomass estimate came from multiplying the average escapement for each species by the species weight. Escapement was averaged from 1950 to 1998 for chinook, pink, and sockeye and 1950 to 1994 for coho as these were the years for which data was available. The totals were then summed producing a biomass estimate of 2079 tonnes. The biomass estimate was then divided by 4 since I assumed that the main spawning occurred over 3 months. This produces a biomass of 519.75 tonnes. This was assumed to be distributed over the aquatic portion of the model area, approximately 6 km^2. This resulted in a biomass estimate of 86.625 t•km^{-2} (Table24).

Table 24. Salmon carcass biomass estimated from average annual escapement and body masses. Body mass estimates from Groot *et al.* (1995).

Species	Average escapement	Body mass (kg)	Total mass (t)
Sockeye	43,546	3	131
Pink	832,776	2	1,666
Coho	30,519	4	122
Chinook	17,881	9	161
Total (mean)	924,722	(5)	2,079

P/B – No salmon carcasses survive more than a year as they decompose. Therefore the P/B ratio was set at $1 \cdot \text{year}^{-1}$ so that the product of the biomass estimate and the P/B ratio equaled the estimated number of carcasses deposited in the system per year.

Fate of detritus – 0.95 aquatic detritus; 0.05 riparian detritus. Some of the detritus was portioned to the riparian detritus group due to the fact that terrestrial wildlife will bring carcasses into the riparian zone before eating them. The parts of the carcass that are not eaten will become part of the riparian detritus group.

A1.2 Wet weight model balancing

Once all of the parameters were input into Ecopath there were 4 groups that were not in balance. Ungulates, predatory terrestrial insects, riparian predatory terrestrial insects, and benthos all had an ecotrophic efficiency (EE) greater than 1, implying there was not enough of these groups to satisfy the amount of predation on them. In order to balance a group with an EE greater than 1.0, several options are available, i.e., (a) their biomass can be increased, (b) P/B can be raised, (c) Q/B of predators can be adjusted, or (d) diet composition of their predators can be changed. The option that is used to balance a group depends upon the reliability of the original parameters. For instance, if one is confident in diet composition data but not so in biomass estimates then options (a) and (b) may be implemented, and vice versa. Below is an overview of how I dealt with the groups whose inputs needed to be modified for the model to balance. A summary of the biomass, P/B, and Q/B inputs for the wet weight model after the model was balanced can be seen in Table 25

A1.2.1 Ungulates

Ungulates had an EE of 1.029 after the first attempt to balance the model was made. Predation mortalities indicated that the grizzly bear group was exerting the highest predation mortality on ungulates. Therefore, I adjusted the diet composition of the grizzly bear group from 0.205-forest shrubs, 0.020-riparian shrubs, 0.487-ungulates, and 0.288-salmon carcasses to 0.25-forest shrubs, 0.025-riparian shrubs, 0.437-ungulates, and 0.288-salmon carcasses.

This change in the diet composition balanced the ungulate group as the EE for ungulates dropped from 1.029 to 0.96.

A1.2.2 Predatory terrestrial insects

This group had an EE of 4.021 after the initial balancing attempt. The major source of predation mortality on this group came from the passerine bird group. Therefore, the parts of the diet composition of passerine birds that were modified are predatory terrestrial insects from 0.096 to 0.050 and forest detritus from 0.51 to 0.556. This change did not fully resolve the problem, as the model was still unbalanced with predatory terrestrial insects having an EE of 2.653.

Since reducing predation mortality did not balance this group, the next attempt was to alter P/B and Q/B estimates since confidence in these parameters are less than the biomass parameter. In order to balance this group the annual P/B estimate had to be increased from 4.68 to 12.5; consequently, the EE estimate dropped to 0.993. I then used the new P/B value along

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Table 25. Wet-weight biomass, habitat adjusted biomass, P/B, and Q/B inputs for balanced wet weight based model

Ecopath group	Fraction of habitat area	Wet-weight biomass (t•km⁻²)	Habitat adjusted biomass (t•km⁻²)	Nitrogen P/B (•year⁻¹)	Nitrogen Q/B (•year⁻¹)
Forest shrubs	0.910	44.000	40.040	0.432	-
Riparian shrubs	0.085	44.000	3.740	0.432	-
Forest trees	0.910	19,710.000	17,936.100	0.059	-
Riparian trees	0.085	19,710.000	1,675.350	0.059	-
Small mammals	0.910	0.054	0.049	3.074	83.916
Riparian small mammals	0.085	0.054	0.005	3.074	83.916
Predatory terr. Insects	0.910	0.083	0.076	12.500	62.500
Riparian pred. terr. insects	0.085	0.083	0.007	13.500	67.000
Herb. insects	0.910	0.384	0.349	36.000	180.000
Riparian herb. insects	0.085	0.384	0.033	36.000	180.000
Earthworms	0.910	0.105	0.096	0.693	110.000
Riparian earthworms	0.085	0.105	0.009	0.693	110.000
Passerine birds	0.910	3.624	3.298	4.970	26.190
Riparian pass. birds	0.085	3.624	0.308	4.970	26.190
Mustelids	0.910	0.005	0.005	0.616	44.027
Riparian mustelids	0.085	0.005	0.000	0.616	44.027
Herbivourous ducks	0.090	0.002	0.000	0.200	400.000
Omnivorous ducks	0.090	0.002	0.000	0.200	355.000
Raptors	0.995	0.003	0.003	0.367	9.125
Wolves	0.995	0.001	0.001	0.594	17.244
Ungulates	0.995	1.328	1.321	0.211	7.800
Black bears	0.995	0.032	0.032	0.281	8.823
Grizzly bears	0.995	0.044	0.044	0.088	8.823
Salmon eggs	0.005	13.083	0.065	1.000	-
Demersal fish	0.005	0.757	0.004	1.100	10.800
Trout and char	0.005	1.053	0.005	1.600	4.450
Periphyton	0.005	14.462	0.072	7.200	-
Biofilm	0.005	15.000	0.075	128.480	-
Macroinvertebrates	0.005	1.758	0.009	16.353	73.000
Zooplankton	0.005	19.880	0.099	10.400	81.590
Phytoplankton	0.005	15.000	0.075	113.000	-
Macrophytes	0.005	600.000	3.000	2.000	-
Benthos	0.005	1.373	0.007	10.500	23.000
Juvenile chinook	0.005	0.408	0.002	3.817	10.950
Juvenile coho	0.005	0.542	0.003	3.600	10.950
Juvenile sockeye	0.005	0.552	0.003	3.719	9.000
Salmon carcasses	0.005	86.625	0.433	1.000	-

with an assimilation rate of 0.20 (see above for notes on herbivorous insect P/B for details) to estimate a new Q/B. The annual Q/B estimate was increased from the original value of 23.4 to 62.5.

A1.2.3 Riparian predatory terrestrial insects

This group had an EE of 4.232 after the initial balancing attempt. The major source of predation mortality on this group came from the riparian passerine bird group. Therefore, the parts of the diet composition of passerine birds that were modified are riparian predatory terrestrial insects from 0.096 to 0.050 and riparian detritus from 0.50 to 0.546. This change did not fully resolve the problem, as the model was still unbalanced with predatory terrestrial insects having an EE of 2.864.

Since reducing predation mortality did not balance this group, the next attempt was to alter P/B and Q/B estimates. In order to balance this group the annual P/B estimate had to be increased from 4.68 to 13.5; consequently, the EE estimate dropped to 0.993. I then used the new P/B value along with an assimilation rate of 0.20 (see above for notes on herbivorous insect P/B for details) to estimate a new Q/B. The annual Q/B estimate was increased from the original value of 23.4 to 67.

A1.2.4 Benthos

The EE for this group was 2.834 after the initial balancing attempt. Omnivorous ducks were seen to be exerting the most predation mortality on benthos. Altering the diet composition of omnivorous ducks was seen to have little effect in lowering benthos EE. In order to balance the benthos group, the omnivorous duck diet would have to be changed so that benthos is reduced from 0.83 to 0.15 in order to bring the EE for benthos below 1. Therefore, I left the omnivorous ducks diet composition at 0.8-benthos and 0.2-macrophytes and decided to alter the P/B ratio of benthos. The annual P/B ratio was increased from 3.751 to 10.5 which resulted in the EE dropping to 0.986.

Appendix 2. Nitrogen based Ecopath model construction and balancing

A2.1 Conversion from wet weight to nitrogen based model

After the wet weight model was balanced, the next step was to convert the balanced wet weight input parameters to nitrogen based ones. Below is a description of the process used to perform this conversion.

A2.1.1 Biomass conversion

The first procedure in converting a wet weight Ecopath model into a model that can track the flow of marine derived nitrogen is to convert the input parameters to total nitrogen content. Biomass for each group was converted to total nitrogen using either a direct nitrogen content estimate or by estimating the protein content of the organisms and then applying a protein to nitrogen ratio.

A2.1.1.1 Forest and riparian shrubs

Data presented in Chapin (1983) was used to calculate the nitrogen content for forest shrubs. A shrub biomass of 44 g•m^{-2} was also reported to be 0.41 g N•m^{-2} which works out to be approximately 0.9% nitrogen. The wet weight biomass of 44.0 t•km^{-2} was then converted to 396.0 mg N•m^{-2}.

A2.1.1.2 Forest and riparian trees

A nitrogen content estimate came from Larsen *et al.* (1976) who calculated the nitrogen content of young loblolly pine (*Pinus* taeda) trees in Alabama. The resulting nitrogen content was estimated to be approximately 5.4% of total biomass. The wet weight biomass for forest trees is 19719.0 t•km^{-2} which converts to 106434.0 mg N•m^{-2}.

A2.1.1.3 Small mammals and riparian small mammals

Nitrogen content for mammalia, 12.8% of dry weight, is presented in Jørgensen (1979). This was converted to percent of wet weight using a wet weight-dry weight conversion ratio of 3.33 g wet weight•g^{-1} dry weight found in Nagy *et al.* (1999). This resulted in a nitrogen content of 3.8% of wet weight. The wet weight biomass of 0.054 t•km^{-2} was then converted to 1.756 mg N•m^{-2} using this nitrogen conversion factor.

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A2.1.1.4 Predatory terrestrial insects and riparian predatory insects

A nitrogen content of 12.3% of dry weight for arthropods was found in Jørgensen (1979). This was converted to a nitrogen content of 3.7% of wet weight using the conversion factor from Nagy *et al.* (1999) outlined above. The nitrogen conversion factor was applied to the wet weight biomass of 0.083 t•km^{-2} to produce a nitrogen biomass estimate of 3.32 mg N•m^{-2}.

A2.1.1.5 Herbivorous insects and riparian herbivorous insects

The same procedure was used to estimate nitrogen content that was used for predatory terrestrial insects above. The nitrogen conversion factor was applied to the wet weight biomass of 0.384 t•km^{-2} to produce a nitrogen biomass estimate of 14.0 mg N•m^{-2}.

A2.1.1.6 Earthworms and riparian earthworms

A nitrogen content estimate of approximately 10% of dry weight is presented for Annelida in Jørgensen (1979). This was also converted to percent of wet weight using the conversion factor of 3.33 (Nagy *et al.* 1999). The resulting nitrogen content of 3% of wet weight was used to convert the wet weight biomass of 3.624 t•km^{-2} to a nitrogen biomass of 108.72 mg N•m^{-2}.

A2.1.1.7 Passerine birds and riparian passerine birds

No direct nitrogen conversion factor could be found for passerine birds so the protein content for birds was estimated by averaging the protein content for a roasting chicken and an adult turkey (Munchen 1981) which was estimated to be 20.4%. A nitrogen to protein conversion factor for chicken was found to be 5.82 (Sosulski and Imafidon 1990) which produces a nitrogen content estimate of 3.5%. This estimate was used to convert the wet weight biomass of 0.105 t•km^{-2} to a nitrogen biomass of 3.68 mg N•m^{-2}.

A2.1.1.8 Mustelids and riparian mustelids

The nitrogen content for mustelids was estimated using the same values that were used to estimate the nitrogen content of wolves. The nitrogen content of 3.3% (see section 2.4.1.11 above for details) converts a wet weight biomass estimate of 0.005 t•km^{-2} to a nitrogen biomass estimate of 0.163 mg N•m^{-2}.

A2.1.1.9 Herbivorous ducks

Herbivorous ducks were estimated to have a protein content of 18.1% using a value for ducks from a food nutrition table (Munchen 1981). A nitrogen to protein conversion factor of 5.82 for chicken (Sosulski and Imafidon 1990) was used to convert the protein content to a nitrogen content of 3.1%. The wet weight biomass estimate was 0.002 t•km^{-2} which converts to 0.062 mg N•m^{-2}.

A2.1.1.10 Omnivorous ducks

The nitrogen content for omnivorous ducks was estimated the same way as for herbivorous ducks. The nitrogen content of 3.1% resulted in a nitrogen biomass of 0.062 mg N•m^{-2} when applied to the wet weight biomass estimate of 0.002 t•km^{-2}.

A2.1.1.11 Raptors

Raptor nitrogen content was also estimated by using a protein content estimate. The protein content estimate of 20.4% also came from estimates for a roasting chicken and an adult turkey (Munchen 1981). The nitrogen to protein conversion factor of 5.82 for chicken (Sosulski and Imafidon 1990) produces a nitrogen content estimate of 3.5%. This nitrogen content results in a nitrogen biomass estimate of 0.105 mg N•m^{-2}.

A2.1.1.12 Wolves

The protein content of 18.6% for wolves was estimated by averaging values for horse meat, sheep meat, goat, rabbit, pork, beef, and veal (Munchen 1981). A nitrogen to protein ratio of 5.72 for beef (Sosulski and Imafidon 1990) was used to convert the protein estimate to a nitrogen content estimate of 3.3%. This nitrogen content was used to convert the wet weight biomass estimate of 0.001 t•km^{-2} to a nitrogen biomass of 0.033 mg N•m^{-2}.

A2.1.1.13 Ungulates

A protein content estimate of 21.5% for venison (Munchen 1981) was used along with a nitrogen to protein ratio of 5.72 for beef to convert the wet weight biomass of 1.328 t•km^{-2} to nitrogen biomass. The resulting nitrogen content for ungulates is 3.8% which produces a nitrogen biomass estimate of 49.916 mg N•m^{-2}.

A2.1.1.14 Black bears

Black bear nitrogen content was also estimated using the same values as for wolves (see section 2.4.1.11). The nitrogen content of 3.3% was used to convert the wet weight biomass estimate of 0.032 t•km^{-2} to a nitrogen biomass estimate of 1.041 mg N•m^{-2}.

A2.1.1.15 Grizzly bears

The nitrogen content for grizzly bears was also estimated using the same values as for wolves (see section 2.4.1.11). The nitrogen content of 3.3% was used to convert the wet weight biomass estimate of 0.044 t•km^{-2} to a nitrogen biomass estimate of 1.431 mg N•m^{-2}.

A2.1.1.16 Salmon eggs

The protein content of salmon eggs was estimated using values for herring roe and caviar (Munchen 1981). The protein content of 26.1% was then converted to nitrogen using a nitrogen to protein conversion factor of 5.73 for eggs (Sosulski and Imafidon 1990). The resulting nitrogen content of 4.6% was used to convert the wet weight biomass of 13.729 t•km^{-2} to a nitrogen biomass estimate of 625.352 mg N•m^{-2}.

A2.1.1.17 Demersal fish

The protein content was estimated using the protein content of 19.5% for brown trout (*Salmo trutta*) (Munchen 1981). A nitrogen to protein conversion factor of 5.82 for fish (Sosulski and Imafidon 1990) was used to calculate a nitrogen content of 3.4%. This nitrogen content converts the wet weight biomass estimate of 0.757 t•km^{-2} to a nitrogen biomass of 25.363 mg N•m^{-2}.

A2.1.1.18 Trout and char

The same nitrogen content for trout and char was used that was calculated for demersal fish above. The nitrogen content of 3.4% was used to convert the wet weight biomass of 1.053 t•km^{-2} to a nitrogen biomass of 35.281 mg N•m^{-2}.

A2.1.1.19 Periphyton

A nitrogen content of approximately 4% of dry weight (Lester *et al.* 1994) was converted to a wet weight estimate using the conversion factor of 3.33 (Nagy *et al.* 1999). The resulting nitrogen content of 1.2% of wet weight converted the wet weight biomass of 14.462 t•km^{-2} to a nitrogen biomass estimate of 173.544 mg N•m^{-2}.

A2.1.1.20 Biofilm

No nitrogen or protein content estimates could be found for biofilm so the nitrogen content was assumed to be the same as periphyton. The resulting nitrogen biomass is 180.0 mg $N \cdot m^{-2}$.

A2.1.1.21 Macroinvertebrates

A nitrogen content of approximately 9% of dry weight for chironomid spp. (Jørgensen 1979) was converted to wet weight content using the wet to dry conversion factor of 3.33 (Nagy et al. 1999). The resulting nitrogen content of 2.7% of wet weight was used to calculate the nitrogen biomass of 47.466 mg $N \cdot m^{-2}$.

A2.1.1.22 Zooplankton

Lindley (1998) presents nitrogen content values for several species of zooplankton. I took the average value of 9.3% of dry weight and converted this to wet weight using the conversion factor of 3.33 (Nagy et al. 1999). The resulting nitrogen content of 2.8% of wet weight was used to convert the wet weight biomass estimate of 19.88 $t \cdot km^{-2}$ to a nitrogen biomass estimate of 556.64 mg $N \cdot m^{-2}$.

A2.1.1.23 Phytoplankton

Behrendt (1990) reports a nitrogen content for phytoplankton of 6.3% of dry weight. This was then converted to a wet weight estimate by the conversion factor of 3.33 (Nagy et al. 1999) to get a nitrogen content estimate of 1.9% of wet weight. This was then used to convert the wet weight biomass of 15.0 $t \cdot km^{-2}$ to a nitrogen biomass of 285.0 mg $N \cdot m^{-2}$.

A2.1.1.24 Macrophytes

A nitrogen content estimate for macrophytes came from Lodge (1991) who estimated nitrogen content as approximately 3% of dry weight. Macrophyte dry weight is approximately 20% of its wet weight (Jørgensen 1979) so the nitrogen content is approximately 0.6% of wet weight. This estimate was used to convert the wet weight biomass to a nitrogen biomass of 183.6 mg $N \cdot m^{-2}$.

A2.1.1.25 Benthos

A nitrogen content of 8.5% of dry weight for mollusks (Jørgensen 1979) was converted to a wet weight estimate by dividing by the conversion factor 3.33 (Nagy et al. 1999) to produce a

nitrogen content estimate of 2.5% of wet weight. This nitrogen content produces a nitrogen biomass estimate of 34.325 mg N•m^{-2}.

A2.1.1.26 Juvenile chinook

The nitrogen content of 3.4% of wet weight was calculated the same as for demersal fish (see section 2.4.1.17 above). This conversion factor produced a nitrogen biomass estimate of 20.103 mg N•m^{-2}.

A2.1.1.27 Juvenile coho

The nitrogen content of 3.4% of wet weight was calculated the same as for demersal fish (see section 2.4.1.17 above). This conversion factor produced a nitrogen biomass estimate of 10.956 mg N•m^{-2}.

A2.1.1.28 Juvenile sockeye

The nitrogen content of 3.4% of wet weight was calculated the same as for demersal fish (see section 2.4.1.17 above). This conversion factor produced a nitrogen biomass estimate of 17.523 mg N•m^{-2}.

A2.1.1.29 Salmon carcasses

An average nitrogen content for adult salmon species of 3% (Larkin and Slaney 1997) was used to convert carcass wet weight biomass to a nitrogen biomass of 2713.74 mg N•m^{-2}.

A2.2 P/B conversion

Production per biomass ratios do not change when converted from wet weight to nitrogen based. This is because the same conversion factor is applied to both the production estimate and the biomass estimate. Since both parts of the P/B ratio gets adjusted by the same nitrogen conversion factor, the ratio does not change.

A2.3 Q/B conversion

The Q/B estimate for each group was converted to a nitrogen based Q/B estimate by calculating the amount of nitrogen that each group consumed by examining the total consumption, diet composition, and nitrogen content of prey items. The total nitrogen consumption was then divided by that group's nitrogen biomass. Below is an example of how this was done for the juvenile sockeye group.

For groups that are primary producers in the wet weight model, this technique is not possible since they lack Q/B and diet composition estimates. The nitrogen based Q/B estimates for these groups are discussed below.

A2.3.1 Q/B calculation for juvenile sockeye

The first step in calculating the nitrogen Q/B is to determine the amount of wet weight consumption for each prey item. Total wet weight consumption, 4.707 t•year^{-1}, was found by multiplying biomass by Q/B. The diet composition for juvenile sockeye is 21.4% macroinvertebrates and 78.6% zooplankton which leads to a total consumption for each prey item of 1.007 t•year^{-1} and 3.70 t•year^{-1} respectively. These prey consumption values were then converted into nitrogen consumption based on the nitrogen content for each prey item. Macroinvertebrates were estimated to be 2.7% nitrogen and zooplankton 2.8%. That leads to a nitrogen consumption of 0.027 t N•year^{-1} and 0.104 t N•year^{-1} respectively. The nitrogen consumption was then summed and divided by the nitrogen biomass of 0.018 t N•km^{-2} to produce a nitrogen based Q/B estimate of 7.266•year^{-1}.

A2.3.2 Q/B calculations for primary producers

Primary producers in the wet weight model include: forest trees and shrubs, periphyton, biofilm, phytoplankton, and macrophytes. Lightfoot *et al.* (1993) presents nitrogen production and consumption values for several primary producers in a wetland ricefield ecosystem. The nitrogen consumption estimates for these organisms were all approximately 1.11 times higher

than the production estimates. Therefore, I increased the P/B values for the groups listed above by a factor of 1.11 to estimate the Q/B values.

A2.4 Balancing the nitrogen model

Converting the model from a wet weight to a nitrogen based model caused 3 groups to become unbalanced as they had an ecotrophic efficiency greater than 1. These 4 groups were the predatory terrestrial insects, riparian predatory terrestrial insects, and periphyton. The methods used to balance them are described below. A summary of the biomass, P/B, and Q/B for the balanced nitrogen based model can be seen in Table 26

A2.4.1 Predatory terrestrial insects

After the nitrogen conversion process, this group to had an EE of 1.06. In order to balance the model I did not alter the diet composition in order to keep it consistent with the one used in the wet weight model. Therefore, the P/B value was increased from $12.5 \cdot year^{-1}$ to $13.5 \cdot year^{-1}$. This increase resulted in an EE of 0.981.

A2.4.2 Riparian predatory terrestrial insects

After the nitrogen conversion process, this group to had an EE of 1.036. In order to balance the model I did not alter the diet composition in order to keep it consistent with the one used in the wet weight model. Therefore, the P/B value was increased from $13.5 \cdot year^{-1}$ to $14.5 \cdot year^{-1}$. This increase resulted in an EE of 0.973.

A2.4.3 Periphyton

The EE for this group increased to 1.139 after the model was converted to nitrogen. In order to balance it the P/B was increased from $7.2 \cdot year^{-1}$ to $9.0 \cdot year^{-1}$. This increase resulted in an EE of 0.911. In order to maintain a Q/B to P/B ratio of 1.11 the Q/B estimate was increased to $9.99 \cdot year^{-1}$.

A2.5 Biomass immigrations

To simulate time-dynamics with the nitrogen based model, both salmon carcasses and salmon eggs had to have an annual immigrating biomass. This is to simulate the fact that salmon return annually to spawn in the system. An annual biomass immigration of 0.10 mg $N \cdot m^{-2} \cdot year^{-1}$ was set for both groups.

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Table 26. Nitrogen based biomass, habitat adjusted biomass, P/B, and Q/B inputs for balanced nitrogen based model.

Ecopath group	Fraction of habitat area	Nitrogen biomass (mg N•m^{-2})	Habitat adjusted biomass (mg N•m^{-2})	Nitrogen P/B (•year^{-1})	Nitrogen Q/B (•year^{-1})
Forest shrubs	0.910	396.000	360.360	0.432	0.480
Riparian shrubs	0.085	396.000	33.660	0.432	0.480
Forest trees	0.910	1,064,340.000	968,549.438	0.059	0.065
Riparian trees	0.085	1,064,340.000	90,468.898	0.059	0.065
Small mammals	0.910	1.756	1.598	3.074	106.479
Riparian small mammals	0.085	1.756	0.149	3.074	106.479
Predatory terr. Insects	0.910	3.320	3.021	13.500	145.636
Riparian pred. terr. insects	0.085	3.320	0.282	14.500	145.636
Herb. insects	0.910	14.000	12.740	36.000	441.994
Riparian herb. insects	0.085	14.000	1.190	36.000	441.994
Earthworms	0.910	108.720	3.349	4.970	17.415
Riparian earthworms	0.085	108.720	0.313	4.970	17.415
Passerine birds	0.910	3.680	98.935	0.693	137.457
Riparian pass. birds	0.085	3.680	9.241	0.693	137.457
Mustelids	0.910	0.163	0.148	0.616	41.703
Riparian mustelids	0.085	0.163	0.014	0.616	41.703
Herbivourous ducks	0.090	0.062	0.006	0.200	89.390
Omnivorous ducks	0.090	0.062	0.006	0.200	248.503
Raptors	0.995	0.105	0.104	0.367	8.702
Wolves	0.995	0.033	0.033	0.594	17.111
Ungulates	0.995	49.916	49.666	0.211	3.605
Black bears	0.995	1.041	1.036	0.281	5.584
Grizzly bears	0.995	1.431	1.424	0.088	9.309
Salmon eggs	0.005	601.818	3.009	1.000	-
Demersal fish	0.005	25.363	0.127	1.100	7.973
Trout and char	0.005	35.281	0.176	1.600	2.027
Periphyton	0.005	173.544	0.868	9.000	7.992
Biofilm	0.005	180.000	0.900	128.480	142.613
Macroinvertebrates	0.005	47.466	0.237	16.353	99.937
Zooplankton	0.005	556.640	2.783	10.400	58.649
Phytoplankton	0.005	285.000	1.425	113.000	125.430
Macrophytes	0.005	3,600.000	18.000	2.000	2.220
Benthos	0.005	34.325	0.172	10.500	13.620
Juvenile chinook	0.005	0.168	0.068	3.817	12.036
Juvenile coho	0.005	0.168	0.091	3.600	10.927
Juvenile sockeye	0.005	0.168	0.092	3.719	7.266
Salmon carcasses	0.005	2,598.750	12.994	1.000	-

Appendix 3. Diet composition used in Ecotrace routine

Prey \ Predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1 Forest shrubs																		
2 Riparian shrubs																		
3 Forest trees																		
4 Riparian trees																		
5 Small mammals		0.050							0.960						0.610			
6 Riparian small mammals										0.960						0.610		
7 Predator terr. insects					0.100						0.050							
8 Riparian pred. terr. ins.						0.100						0.050						
9 Herb. insects					0.400		0.900				0.384							
10 Riparian herb. insects						0.400		0.900				0.384						
11 Passerine birds															0.110			
12 Riparian pass. birds																0.110		
13 Earthworms											0.010							
14 Riparian earthworms												0.010						
15 Mustelids																		
16 Riparian mustelids																		
17 Herbivorous ducks																		
18 Omnivorous ducks																		
19 Raptors																		
20 Wolves																		
21 Ungulates																		
22 Black bears																		
23 Grizzly bears																		
24 Salmon eggs																		
25 Demersal fish																		
26 Trout and char																		
27 Periphyton																		
28 Biofilm																		
29 Macroinvertebrates												0.010						
30 Zooplankton																		
31 Phytoplankton																		
32 Macrophytes																	0.950	0.200
33 Benthos																	0.050	0.800
34 Juvenile chinook																		
35 Juvenile coho																		
36 Juvenile sockeye																		
37 Salmon carcasses				0.010				0.025	0.040	0.040	0.556	0.546	1.000					
38 Riparian detritus	1.000	0.085		0.990	0.500	0.500	0.100	0.075						1.000		0.020		
39 Forest detritus		0.865	1.000												0.280	0.260		
40 Aquatic detritus																		
Import																		
Sum	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000

Appendix 3. continued

Prey \ Predator	19	20	21	22	23	25	26	27	28	29	30	31	32	33	34	35	36
1 Forest shrubs			0.650	0.550	0.250												
2 Riparian shrubs			0.050	0.050	0.025												
3 Forest trees			0.180														
4 Riparian trees			0.020														
5 Small mammals	0.364																
6 Riparian small mammals	0.036																
7 Predator terr. insects																	
8 Riparian pred. terr. ins.							0.024								0.158		
9 Herb. insects																0.068	
10 Riparian herb. insects							0.097								0.633	0.274	
11 Passerine birds	0.473																
12 Riparian pass. birds	0.047																
13 Earthworms																	
14 Riparian earthworms																	
15 Mustelids	0.027	0.055															
16 Riparian mustelids	0.003	0.005															
17 Herbivorous ducks																	
18 Omnivorous ducks																	
19 Raptors																	
20 Wolves																	
21 Ungulates		0.850		0.300	0.437												
22 Black bears																	
23 Grizzly bears																	
24 Salmon eggs						0.020			0.100			0.100				0.050	
25 Demersal fish						0.060											
26 Trout and char							0.023										
27 Periphyton										0.300				0.030			
28 Biofilm										0.050	0.060						
29 Macroinvertebrates						0.050	0.595			0.100					0.204	0.418	0.214
30 Zooplankton							0.261								0.005		0.786
31 Phytoplankton											0.840						
32 Macrophytes			0.100			0.170											
33 Benthos						0.400											
34 Juvenile chinook																	
35 Juvenile coho																	
36 Juvenile sockeye																	
37 Salmon carcasses	0.050	0.090		0.100	0.288	0.050		0.200	0.100			0.300		0.550		0.150	
38 Riparian detritus																0.040	
39 Forest detritus																	
40 Aquatic detritus														0.010			
Import						0.250		0.800	0.800	0.550	0.100	0.600	1.000	0.410			
Sum	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000

Appendix 4. Results from sensitivity analysis of nitrogen based Ecopath model.

Ecopath groups					
1	For. shrubs	9	Herb. insects	17	Herb. ducks
2	Rip. shrubs	10	Rip. herb. ins.	18	Omn. ducks
3	For. trees	11	Pass. birds	19	Raptors
4	Rip. trees	12	Rip. pass. birds	20	Wolves
5	Sm. mamm's	13	Rip. earthworms	21	Ungulates
6	Rip. sm mamm's	14	Earthworms	22	Black bears
7	Pred terr. Ins.	15	Mustelids	23	Grizzly bears
8	Rip pred. terr. ins.	16	Rip. mustelids	24	Salmon eggs

25	Demersal fish	33	Benthos
26	Trout and char	34	Juv. chinook
27	Periphyton	35	Juv. coho
28	Biofilm	36	Juv. sockeye
29	Macroinverts.	37	Salmon carcasses
30	Zooplankton		
31	Phytoplankton		
32	Macrophytes		

Impacting group	Altered parameter	Impacted group	Impacted parameter	Change to altered parameter										
				-50%	-40%	-30%	-20%	-10%	0%	10%	20%	30%	40%	50%
1	B	1	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
1	P/B	1	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
2	B	2	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
2	P/B	2	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
3	B	3	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
3	P/B	3	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
4	B	4	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
4	P/B	4	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
5	B	5	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
5	B	7	EE	-0.21	-0.17	-0.13	-0.09	-0.04	0.00	0.04	0.09	0.13	0.17	0.21
5	B	9	EE	-0.08	-0.06	-0.05	-0.03	-0.02	0.00	0.02	0.03	0.05	0.06	0.08
5	P/B	5	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
5	Q/B	7	EE	-0.21	-0.17	-0.13	-0.09	-0.04	0.00	0.04	0.09	0.13	0.17	0.21
5	Q/B	9	EE	-0.08	-0.06	-0.05	-0.03	-0.02	0.00	0.02	0.03	0.05	0.06	0.08

Appendix 4. Cont'd

				Change to altered parameter										
Impacting group	Altered parameter group	Impacted group	Impacted parameter	-50%	-40%	-30%	-20%	-10%	0%	10%	20%	30%	40%	50%
6	B	6	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
6	B	8	EE	-0.20	-0.16	-0.12	-0.08	-0.04	0.00	0.04	0.08	0.12	0.16	0.20
6	B	10	EE	-0.08	-0.06	-0.05	-0.03	-0.02	0.00	0.02	0.03	0.05	0.06	0.08
6	P/B	6	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
6	Q/B	8	EE	-0.20	-0.16	-0.12	-0.08	-0.04	0.00	0.04	0.08	0.12	0.16	0.20
6	Q/B	10	EE	-0.08	-0.06	-0.05	-0.03	-0.02	0.00	0.02	0.03	0.05	0.06	0.08
7	B	7	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
7	B	9	EE	-0.22	-0.17	-0.13	-0.09	-0.04	0.00	0.04	0.09	0.13	0.17	0.22
7	P/B	7	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
7	Q/B	9	EE	-0.22	-0.17	-0.13	-0.09	-0.04	0.00	0.04	0.09	0.13	0.17	0.22
8	B	8	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
8	B	10	EE	-0.21	-0.17	-0.13	-0.09	-0.04	0.00	0.04	0.09	0.13	0.17	0.21
8	P/B	8	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
8	Q/B	10	EE	-0.21	-0.17	-0.13	-0.09	-0.04	0.00	0.04	0.09	0.13	0.17	0.21
9	B	3	EE	-0.49	-0.39	-0.29	-0.20	-0.10	0.00	0.10	0.20	0.29	0.39	0.49
9	B	9	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
9	P/B	9	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
9	Q/B	3	EE	-0.49	-0.39	-0.29	-0.20	-0.10	0.00	0.10	0.20	0.29	0.39	0.49
10	B	4	EE	-0.49	-0.39	-0.29	-0.19	-0.10	0.00	0.10	0.19	0.29	0.39	0.49
10	B	10	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
10	P/B	10	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
10	Q/B	4	EE	-0.49	-0.39	-0.29	-0.19	-0.10	0.00	0.10	0.19	0.29	0.39	0.49
11	B	7	EE	-0.29	-0.23	-0.17	-0.12	-0.06	0.00	0.06	0.12	0.17	0.23	0.29
11	B	9	EE	-0.21	-0.16	-0.12	-0.08	-0.04	0.00	0.04	0.08	0.12	0.16	0.21
11	B	11	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
11	B	13	EE	-0.50	-0.40	-0.30	-0.20	-0.10	0.00	0.10	0.20	0.30	0.40	0.50
11	P/B	11	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
11	Q/B	7	EE	-0.29	-0.23	-0.17	-0.12	-0.06	0.00	0.06	0.12	0.17	0.23	0.29
11	Q/B	9	EE	-0.21	-0.16	-0.12	-0.08	-0.04	0.00	0.04	0.08	0.12	0.16	0.21
11	Q/B	13	EE	-0.50	-0.40	-0.30	-0.20	-0.10	0.00	0.10	0.20	0.30	0.40	0.50

Appendix 4. Cont'd

Impacting group	Altered parameter	Impacted group	Impacted parameter	Change to altered parameter										
				-50%	-40%	-30%	-20%	-10%	0%	10%	20%	30%	40%	50%
12	B	10	EE	-0.20	-0.16	-0.12	-0.08	-0.04	0.00	0.04	0.08	0.12	0.16	0.20
12	B	12	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
12	B	14	EE	-0.50	-0.40	-0.30	-0.20	-0.10	0.00	0.10	0.20	0.30	0.40	0.50
12	P/B	12	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
12	Q/B	8	EE	-0.27	-0.22	-0.16	-0.11	-0.05	0.00	0.05	0.11	0.16	0.22	0.27
12	Q/B	10	EE	-0.20	-0.16	-0.12	-0.08	-0.04	0.00	0.04	0.08	0.12	0.16	0.20
12	Q/B	14	EE	-0.50	-0.40	-0.30	-0.20	-0.10	0.00	0.10	0.20	0.30	0.40	0.50
13	B	13	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
13	P/B	13	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
14	B	14	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
14	P/B	14	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
15	B	5	EE	-0.46	-0.37	-0.28	-0.18	-0.09	0.00	0.09	0.18	0.28	0.37	0.46
15	B	11	EE	-0.31	-0.25	-0.18	-0.12	-0.06	0.00	0.06	0.12	0.18	0.25	0.31
15	B	15	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
15	P/B	15	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
15	Q/B	5	EE	-0.46	-0.37	-0.28	-0.18	-0.09	0.00	0.09	0.18	0.28	0.37	0.46
15	Q/B	11	EE	-0.31	-0.25	-0.18	-0.12	-0.06	0.00	0.06	0.12	0.18	0.25	0.31
16	B	6	EE	-0.46	-0.37	-0.28	-0.18	-0.09	0.00	0.09	0.18	0.28	0.37	0.46
16	B	12	EE	-0.30	-0.24	-0.18	-0.12	-0.06	0.00	0.06	0.12	0.18	0.24	0.30
16	B	16	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
16	P/B	16	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
16	Q/B	6	EE	-0.46	-0.37	-0.28	-0.18	-0.09	0.00	0.09	0.18	0.28	0.37	0.46
16	Q/B	12	EE	-0.30	-0.24	-0.18	-0.12	-0.06	0.00	0.06	0.12	0.18	0.24	0.30
18	B	33	EE	-0.36	-0.29	-0.22	-0.14	-0.07	0.00	0.07	0.14	0.22	0.29	0.36
18	Q/B	33	EE	-0.36	-0.29	-0.22	-0.14	-0.07	0.00	0.07	0.14	0.22	0.29	0.36
19	B	5	EE	-0.04	-0.03	-0.02	-0.02	-0.01	0.00	0.01	0.02	0.02	0.03	0.04
19	B	6	EE	-0.04	-0.03	-0.03	-0.02	-0.01	0.00	0.01	0.02	0.03	0.03	0.04
19	B	11	EE	-0.19	-0.16	-0.12	-0.08	-0.04	0.00	0.04	0.08	0.12	0.16	0.19

Appendix 4. Cont'd

Impacting group	Altered parameter	Impacted group	Impacted parameter	-50%	-40%	-30%	-20%	-10%	0%	10%	20%	30%	40%	50%
														Change to altered parameter
19	B	12	EE	-0.20	-0.16	-0.12	-0.08	-0.04	0.00	0.04	0.08	0.12	0.16	0.20
19	B	15	EE	-0.22	-0.18	-0.13	-0.09	-0.04	0.00	0.04	0.09	0.13	0.18	0.22
19	B	16	EE	-0.25	-0.20	-0.15	-0.10	-0.05	0.00	0.05	0.10	0.15	0.20	0.25
19	Q/B	5	EE	-0.04	-0.03	-0.02	-0.02	-0.01	0.00	0.01	0.02	0.02	0.03	0.04
19	Q/B	6	EE	-0.04	-0.03	-0.03	-0.02	-0.01	0.00	0.01	0.02	0.03	0.03	0.04
19	Q/B	11	EE	-0.19	-0.16	-0.12	-0.08	-0.04	0.00	0.04	0.08	0.12	0.16	0.19
19	Q/B	12	EE	-0.20	-0.16	-0.12	-0.08	-0.04	0.00	0.04	0.08	0.12	0.16	0.20
19	Q/B	15	EE	-0.22	-0.18	-0.13	-0.09	-0.04	0.00	0.04	0.09	0.13	0.18	0.22
19	Q/B	16	EE	-0.25	-0.20	-0.15	-0.10	-0.05	0.00	0.05	0.10	0.15	0.20	0.25
20	B	15	EE	-0.28	-0.22	-0.17	-0.11	-0.06	0.00	0.06	0.11	0.17	0.22	0.28
20	B	16	EE	-0.25	-0.20	-0.15	-0.10	-0.05	0.00	0.05	0.10	0.15	0.20	0.25
20	Q/B	15	EE	-0.28	-0.22	-0.17	-0.11	-0.06	0.00	0.06	0.11	0.17	0.22	0.28
20	Q/B	16	EE	-0.25	-0.20	-0.15	-0.10	-0.05	0.00	0.05	0.10	0.15	0.20	0.25
21	B	1	EE	-0.47	-0.38	-0.28	-0.19	-0.10	0.00	0.10	0.19	0.28	0.38	0.47
21	B	2	EE	-0.47	-0.37	-0.28	-0.19	-0.09	0.00	0.09	0.19	0.28	0.37	0.47
21	B	21	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
21	B	32	EE	-0.45	-0.36	-0.27	-0.18	-0.09	0.00	0.09	0.18	0.27	0.36	0.45
21	P/B	21	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
21	Q/B	1	EE	-0.47	-0.38	-0.28	-0.19	-0.10	0.00	0.10	0.19	0.28	0.38	0.47
21	Q/B	2	EE	-0.47	-0.37	-0.28	-0.19	-0.09	0.00	0.09	0.19	0.28	0.37	0.47
21	Q/B	32	EE	-0.45	-0.36	-0.27	-0.18	-0.09	0.00	0.09	0.18	0.27	0.36	0.45
22	B	21	EE	-0.11	-0.09	-0.07	-0.04	-0.02	0.00	0.02	0.04	0.07	0.09	0.11
22	Q/B	21	EE	-0.11	-0.09	-0.07	-0.04	-0.02	0.00	0.02	0.04	0.07	0.09	0.11
23	B	21	EE	-0.36	-0.29	-0.22	-0.15	-0.07	0.00	0.07	0.15	0.22	0.29	0.36
23	Q/B	21	EE	-0.36	-0.29	-0.22	-0.15	-0.07	0.00	0.07	0.15	0.22	0.29	0.36
25	B	33	EE	-0.13	-0.11	-0.08	-0.05	-0.03	0.00	0.03	0.05	0.08	0.11	0.13
25	P/B	25	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
25	Q/B	25	EE	-0.50	-0.40	-0.30	-0.20	-0.10	0.00	0.10	0.20	0.30	0.40	0.50
25	Q/B	33	EE	-0.13	-0.11	-0.08	-0.05	-0.03	0.00	0.03	0.05	0.08	0.11	0.13

Appendix 4. Cont'd

Impacting group	Altered parameter	Impacted group	Impacted parameter	Change to altered parameter										
				-50%	-40%	-30%	-20%	-10%	0%	10%	20%	30%	40%	50%
26	P/B	26	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
26	Q/B	26	EE	-0.50	-0.40	-0.30	-0.20	-0.10	0.00	0.10	0.20	0.30	0.40	0.50
27	B	27	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.23	-0.33
27	P/B	27	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
28	B	28	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
28	P/B	28	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
29	B	27	EE	-0.50	-0.40	-0.30	-0.20	-0.10	0.00	0.10	0.20	0.30	0.40	0.50
29	B	28	EE	-0.50	-0.40	-0.30	-0.20	-0.10	0.00	0.10	0.20	0.30	0.40	0.50
29	B	29	EE	0.28	0.19	0.12	0.07	0.03	0.00	-0.03	-0.05	-0.07	-0.08	-0.10
29	P/B	29	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
29	Q/B	27	EE	-0.50	-0.40	-0.30	-0.20	-0.10	0.00	0.10	0.20	0.30	0.40	0.50
29	Q/B	28	EE	-0.50	-0.40	-0.30	-0.20	-0.10	0.00	0.10	0.20	0.30	0.40	0.50
29	Q/B	29	EE	-0.36	-0.29	-0.22	-0.14	-0.07	0.00	0.07	0.14	0.22	0.29	0.36
30	B	30	EE	0.07	0.05	0.03	0.02	0.01	0.00	-0.01	-0.01	-0.02	-0.02	-0.02
30	B	31	EE	-0.50	-0.40	-0.30	-0.20	-0.10	0.00	0.10	0.20	0.30	0.40	0.50
30	P/B	30	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
30	Q/B	30	EE	-0.47	-0.37	-0.28	-0.19	-0.09	0.00	0.09	0.19	0.28	0.37	0.47
30	Q/B	31	EE	-0.50	-0.40	-0.30	-0.20	-0.10	0.00	0.10	0.20	0.30	0.40	0.50
31	B	31	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
31	P/B	31	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
32	B	32	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
32	P/B	32	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
33	B	33	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
33	P/B	33	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
35	B	29	EE	-0.06	-0.05	-0.04	-0.03	-0.01	0.00	0.01	0.03	0.04	0.05	0.06
35	B	36	EE	-0.50	-0.40	-0.30	-0.20	-0.10	0.00	0.10	0.20	0.30	0.40	0.50
35	Q/B	29	EE	-0.06	-0.05	-0.04	-0.03	-0.01	0.00	0.01	0.03	0.04	0.05	0.06
35	Q/B	36	EE	-0.50	-0.40	-0.30	-0.20	-0.10	0.00	0.10	0.20	0.30	0.40	0.50
36	B	36	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33
36	P/B	36	EE	1.00	0.67	0.43	0.25	0.11	0.00	-0.09	-0.17	-0.23	-0.29	-0.33

Appendix 5. List of species corresponding to Ecopath groups used in Atnarko Watershed model. Based on Stevens (1995) for species listed in the IDF wet zone.

Ecopath group	Common name	Scientific name
Forest shrubs	Pinegrass	*Calamagrostis rubescens*
	Saskatoon berry	*Amelanchier alnifolia*
	Red-stemmed feathermoss	*Pleurozium schrebeeri*
	Soapberry	*Shepherdia canadensis*
	Birch-leaved spirea	*Spirea betulifolia*
	Falsebox	*Paxistima myrsinites*
	Twinflower	*Linnaea orealis*
	Step moss	*Hylocomium splendens*
	Prince's pine	*Chimaphila umbellata*
	Thimbleberry	*Rubus parviflorus*
	Black huckleberry	*Vaccinium membranaceum*
	Tall Oregon-grape	*Mahonia aquifolium*
		Cladonia spp.
		Peltigera spp
Small mammals	Common shrew	*Sorex cinereus*
	Dusky shrew	*Sorex monticolus*
	Vagrant shrew	*Sorex vagrans*
	Pacific water shrew	*Sorex bendirii*
	Snowshoe hare subsp.	*Lepus americanus washingtonii*
	Southern red-backed vole subsp.	*Clethrionomys gapperi occidentalis*
	Northern flying squirrel	*Glaucomys sabrinus*
	Columbian ground squirrel	*Spermophilus columbianus columbianus*
	Douglas squirrel	*Tamiasciurus douglasii*
	Red squirrel	*Tamiasciurus hudsonicus*
	Yellow-pine chipmunk	*Tamias amoenus*
	Least chipmunk	*Tamias minimus*
	Townsend's chipmunk	*Eutamias townsendi*
	Common pika	*Ochotona princeps*
	Meadow vole	*Microtus pennsylvanicus*
	Heather vole	*Phenacomys intermedius*
	Bushy-tailed woodrat	*Neotoma cinerea*
	Deer mouse	*Peromyscus maniculatus*
	House mouse	*Mus musculus domesticus*
	Western jumping mouse	*Zapus princeps*

Appendix 5. Cont'd

Ecopath group	Common name	Scientific name
Mustelids	Marten	*Martes americana*
	Fisher	*Martes pennanti*
	Long-tailed weasel	*Mustela frenata*
	Mink	*Mustela vision*
	Striped skunk	*Mephitis mephitis*
	River otter	*Lutra canadensis*
	Wolverine	*Gulo luscus*
	Ermine	*Mustela erminea*
Herbivorous ducks	Wood duck	*Aix sponsa*
	Green-winged teal	*Anas crecca*
	Mallard	*Anas platyrhynchos*
	Northern pintail	*Anas acuta*
	Blue-winged teal	*Anas discors*
	Cinnamon teal	*Anas cyanoptera*
	Canvasback	*Aythya valisineria*
	Gadwall	*Anas strepera*
	Eurasian wigeon	*Anas penelope*
	American wigeon	*Anas americana*
	Redhead	*Aythya americana*
	Ring-necked duck	*Aythya collaris*
Omnivorous ducks	Northern shoveler	*Anas clypeata*
	Greater scaup	*Aythya marila*
	Lesser scaup	*Aythya affinis*
	Harlequin duck	*Histrionicus histrionicus*
	Oldsquaw	*Clangula hyemalis*
	Surf scoter	*Melanitta perspicillata*
	White-winged scoter	*Melanitta fusca*
	Common goldeneye	*Bucephala clangula*
	Barrow's goldeneye	*Bucephala islandica*
	Bufflehead	*Bucephala albeola*
	Hooded merganser	*Lophodytes cucullatus*
	Common merganser	*Mergus merganser*
	Red-breasted merganser	*Mergus serrator*
	Ruddy duck	*Oxyura jamaicensis*

Appendix 5. Cont'd

Ecopath group	Common name	Scientific name
Raptors	Osprey	*Pandion haliaetus*
	Bald eagle	*Haliaeetus leucocephalus*
	Northern harrier	*Circus cyaneus*
	Sharp-shinned hawk	*Accipiter striatus*
	Cooper's hawk	*Accipiter cooperii*
	Northern goshawk subspp.	*Accipiter gentilis*
	Red-tailed hawk	*Buteo jamaicensis*
	Rough-legged hawk	*Buteo lagopus*
	American kestrel	*Falco sparverius*
	Merllin	*Falco columbarius*
Passerine birds	Ash-throated flycatcher	*Myiarchus tuberculifer*
	Olive-sided flycatcher	*Contopus pertinax*
	Alder flycatcher	*Empidonax alnorum*
	Willow flycathcer	*Empidonax traillii*
	Least flycatcher	*Empidonax minimus*
	Hammond's flycatcher	*Empidonax hammondii*
	Dusky flycatcher	*Empidonax oberholseri*
	Pacific-slope flycatcher	*Empidonax difficilis*
	Cordilleran flycatcher	*Empidonax occidentalis*
	Say's phoebe	*Sayornis saya*
	Western wood-pewee	*Contopus sordidulus*
	Eastern kingbird	*Tyrannus tyrannus*
	Horned lark	*Eremophila alpestris*
	Tree swallow	*Tachycineta bicolor*
	Violet-green swallow	*Tachycineta thalassina*
	Northern rough-winged swallow	*Stelgidoptryx serripennis*
	Bank swallow	*Riparia riparia*
	Cliff swallow	*Hirundo pyrrhonota*
	Barn swallow	*Hirundo rustica*
	Gray jay	*Perisoreus canadensis*
	Steller's jay	*Cyanocitta stelleri*
	Clark's nutcracker	*Nucifraga columbiana*
	Black-billed magpie	*Pica pica*
	American crow	*Corvus brachyrhynchos*
	Northwestern crow	*Corvus caurinus*

Appendix 5. Cont'd

Ecopath group	Common name	Scientific name
Passerine birds cont'd	Common raven	*Corvus corax*
	Black-capped chickadee	*Parus atricapillus*
	Mountain chickadee	*Parus gambeli*
	Boreal chickadee	*Parus hudsonicus*
	Red-breasted nuthatch	*Sitta canadensis*
	Brown creeper	*Certhia americana*
	Winter wren	*Troglodytes troglodytes*
	Marsh wren	*Cistothorus palustris*
	American dipper	*Cinclus mexicanus*
	Golden-crowned kinglet	*Regulus satrapa*
	Ruby-crowned kinglet	*Regulus calendula*
	Mountain bluebird	*Sialia currucoides*
	Townsend's solitaire	*Myadestes townsendi*
	Veery	*Catharus fuscescens*
	Swainson's thrush	*Catharus ustulatus*
	Hermit thrush	*Catharus guttatus*
	American robin	*Turdus migratorius*
	Varied thrush	*ixoreus naevius*
	Northern mockingbird	*Mimus polyglottos*
	American pipit	*Anthus rubescens*
	Bohemian waxwing	*Bombycilla garrulus*
	Cedar waxwing	*Bombycilla cedrorum*
	Northern shrike	*Lanius excubitor*
	European starling	*Sturnus vulgaris*
	Solitary vireo	*Vireo solitarius*
	Warbling vireo	*Vireo gilvus*
	Red-eyed vireo	*Vireo olivaceus*
	Tennessee warbler	*Vermivora peregrina*
	Orange-crowned warbler	*Vermivora celata*
	Nashville warbler	*Vermivora ruficapilla*
	Yellow warbler	*Dendroica petechia*
	Yellow-rumped warbler	*Dendroica coronata*
	Black-throated gray warbler	*Dendroica nigrescens*
	Townsend's warbler	*Dendroica townsendi*
	Blackpoll warbler	*Mniotilia varia*
	American redstart	*Setophaga ruticilla*
	Northern waterthrush	*Seiurus noveboracensis*

Appendix 5. Cont'd

Ecopath group	Common name	Scientific name
Passerine birds cont'd	MacGillivray's warbler	*Oporornis philadelphia*
	Common yellowthroat	*Geothlypis trichas*
	Wilson's warbler	*Wilsonia pusilla*
	Western tanager	*Piranga ludoviciana*
	Lazuli bunting	*Passerina amoena*
	Rufous-sided towhee	*Pipilo erthrophthalmus*
	Chipping sparrow	*Spizella passerina*
	Vesper sparrow subspp.	*Pooecetes gramineus*
	Savannah sparrow	*Passerculus sandwichensis*
	Fox sparrow	*Passerella iliaca*
	Song sparrow	*Melospiza melodia*
	Lincoln's sparrow	*Melospiza lincolnii*
	Golden-crowned sparrow	*Zonotrichia atricapilla*
	White-crowned sparrow	*Zonotrichia Leucophrys*
	Harris' sparrow	*Zonotrichia querula*
	Dark-eyed junco	*Junco hyemalis*
	Snow bunting	*Plectrophenax nivalis*
	Red-winged blackbird	*Agelaius phoeniceus*
	Western meadowlark	*Sturnella neglecta*
	Rusty blackbird	*Euphagus carolinus*
	Brewer's blackbird	*Euphagus cyanocephalus*
	Brown-headed cowbird	*Molothrus ater*
	Rosy finch	*Leucosticte arctoa*
	Pine grosbeak subpp.	*Pinicola enucleator*
	Purple finch	*Carpodacus purpureus*
	Cassin's finch	*Carpodacus cassinii*
	House finch	*Carpodacus mexicanus*
	Red crossbill	*Loxia curvirostra*
	White-winged crossbill	*Loxia leucoptera*
	Common redpoll	*Carduelis flammea*
	American goldfinch	*Carduelis tristis*
	Evening grosbeak	*Coccothraustes vespertina*
	House sparrow	*Passer domesticus*