THE PRICE OF ICE: ECOLOGICAL CONSEQUENCES OF CHANGING ICE REGIMES FOR LINKED AQUATIC-TERRESTRIAL FOOD WEBS

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A Proposal to the DeVlieg-Taylor Ranch
Graduate Research Assistantship Program at Idaho State University

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Abstract

Winter ice cover and spring 'ice-out' events can be significant ecological disturbances affecting the structure and function of stream-riparian ecosystems. Although limited evidence suggests that increased atmospheric temperatures will reduce the spatial extent and duration of such ice cover, comparatively less is known about the ecological consequences that may accompany these shifts. Reductions in the spatial extent of winter ice cover will likely reduce the frequency and magnitude of these ice disturbances; thus, it suggests a direct pathway for global climate change to alter stream productivity. However, changes in winter ice cover and snow pack may also have more indirect, unforeseen effects on food web linkages. For instance, interactions between wolves and their ungulate prey may be affected, in that decreased snow pack and ice cover might reduce wolf capture efficiency and the abundance of ungulate carcasses. As these ungulate carcasses are frequently deposited into stream channels, this suggests an additional indirect pathway for climate change to alter inputs of high quality resources to stream food webs. Despite these direct and indirect pathways for shifting ice regimes to alter stream ecosystems, there is a paucity of studies addressing these effects, subsequently reducing our ability to adequately predict the net response of streams to climate change.

Here we propose to assess how climate-induced shifts in ice regimes may directly impact stream ecosystems via reductions in the magnitude and frequency of ice scour events, and indirectly via reduced inputs of ungulate carcasses to Big Creek, a 7^{th} order river in central Idaho's Frank Church 'River of No Return' Wilderness. First, utilizing long-term data from the Taylor Wilderness Field Station we will test whether increases in atmospheric temperatures have

decreased the spatial extent and duration of ice cover over time along the mainstem of Big Creek. To increase our understanding of the direct effects of winter ice regimes for stream ecosystems, we will also assess whether prolonged ice cover and 'ice-out' events reduce the standing biomass of streambed periphyton and macroinvertebrates compared to pre-ice conditions. We also predict that increased stream ice cover increases wolf capture efficiency, subsequently increasing inputs of ungulate carcasses to Big Creek; a prediction we will evaluate through a combination of long-term records of wolf predation and repeated surveys during this study. Subsequently, we will assess the effects of these carcass inputs to Big Creek by making comparisons between stream patches with and without ungulate carcasses. Specifically, we will test whether carcass additions increase the biomass of periphyton and macroinvertebrates, and whether fish respond in terms of changes in diet or increased abundance in proximity to carcasses. By comparing these direct and indirect effects, we will assess their relative importance for stream ecosystems and ascertain the net response of Big Creek to changing ice regimes under predicted climate change scenarios.

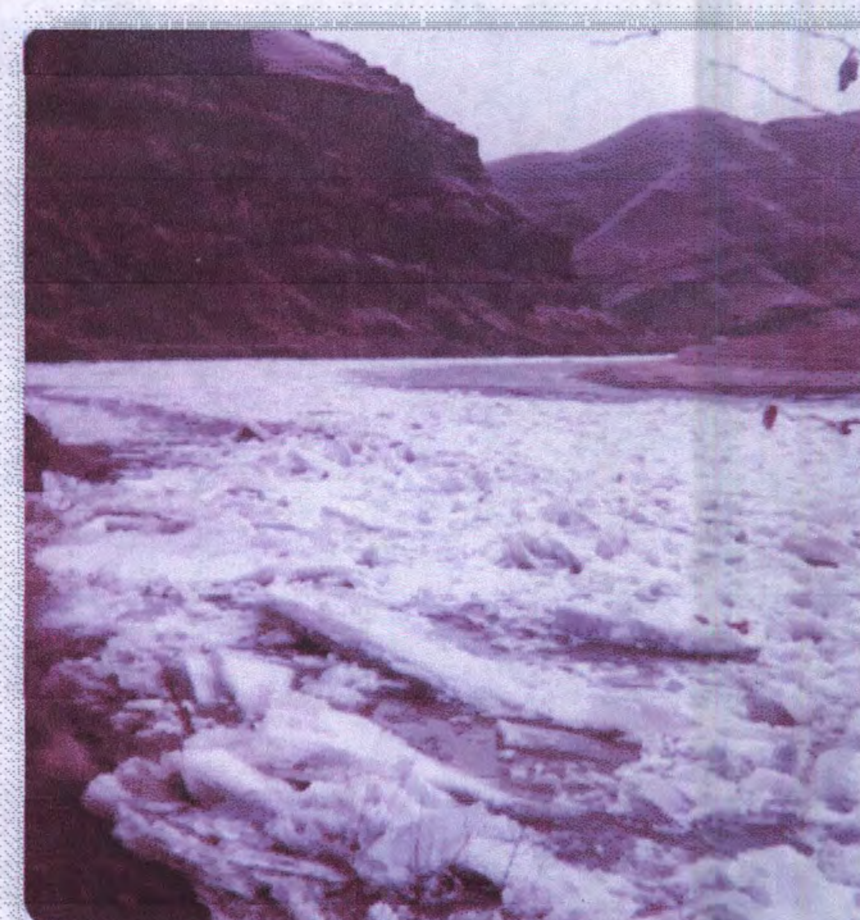
Results from this project will help increase our general understanding of the winter ecology of stream ecosystems, an arena that has been severely understudied, and will link investigations of stream and terrestrial wildlife ecology in unique ways that have not yet been attempted. Results of studies proposed here will also be paired with ongoing research addressing the effects of global climate change on the Salmon River basin. This coupling will increase our understanding of how predicted shifts in stream ice regimes may be affecting the overall Salmon River basin, will help us guide future research projects, and ultimately improve projections to be used in the future adaptive management of natural resources in this region.

Introduction

River ice and changing climate

Ecological disturbance associated with environmental change can be important factors shaping the structure and function of stream ecosystems (Resh et al. 1988). For instance, previous research has largely demonstrated how flooding, drought, and overall changes in the hydrologic flow regime can affect stream productivity and the survival of stream consumers (Poff et al. 1997, Poff and Zimmerman 2009). Moreover, as global climate change is predicted to alter precipitation and flow regimes, there is also considerable evidence showing how increased atmospheric temperature and changing precipitation regimes may alter the structure and function of stream ecosystems via these changes in the hydrologic flow regime (Poff 2002, Gibson et al. 2005). However, prolonged periods of surface ice-cover and associated spring 'ice-out' events can represent an equally important ecological disturbance affecting stream ecosystems (Scrimgeour et al. 1994, Prowse 2001a, b). Despite the relative importance of ice regimes for structuring stream ecosystems during the winter, less is known about how winter ice regimes may shift with future increases in atmospheric temperature. Although increased atmospheric temperatures have been correlated with decreased spatial extent and duration of ice cover within a few ecoregions (Prowse and Beltaos 2002, Prowse and Bonsal 2004), our understanding of how climate-induced shifts may be generally affecting stream ecosystems is limited because of the paucity of studies exploring the winter ecology of stream ecosystems. However, if we are to adequately predict these potential climate-induced shifts, we need to substantially increase our understanding of the winter ecology of stream ecosystems. In particular, studies are needed that address how global climate change may be affecting ice-cover regimes and its subsequent effects on stream structure and function.

Increased atmospheric temperature has lengthened 'ice-free' periods during the winter months when streams would have typically been covered by a thick ice layer (Prowse and Beltaos 2002). Because this reduction in the spatial extent and thickness of stream ice cover also likely reduces the total mass of ice in a stream reach, the amount of ice available for transport during 'ice-out' events may also be declining. As this ice cover is rapidly transported downstream in the form of large ice flows, it can increase bed scour, increase mobility of streambed particles, and decrease periphyton and benthic invertebrate biomass (Scrimgeour et al. 1994, Prowse and Culp 2003). For instance, one-half of annual stream discharge and three-quarters of the sediment load for the Colville River in Alaska occurred during the three to four week period represented by these spring 'ice-out' events



Ice-out on the Grande Ronde River during the winter of 1948-49. Ice cover and ice-out events on rivers like this one may be affected by changing climate (photo from the "Western Memories Project", by Smoke Wade).

(as reported in Prowse 2001a). During these 'ice-out' events, stream temperature can also rapidly change as the temperature regime of the newly exposed stream surface equilibrates with atmospheric temperatures, potentially increasing thermal stress on stream biota. For instance, stream temperature increases of 9°C over 13 hours have been reported during these spring 'ice-out' events, which may decrease the survival of stream organisms because of increased thermal stress (Scrimgeour et al. 1994). Accordingly, this suggests that climate change-induced shifts in spring 'ice-out' events may reduce the frequency and magnitude of these disturbances and may have significant impacts on stream ecosystems.

The effects of ice are not limited to these spring 'ice-out' events because prolonged ice cover itself can also alter abiotic and biotic processes within stream ecosystems (Prowse 2001a, b). Despite significant fluctuations in air temperatures during the winter months, ice cover can insulate stream ecosystems and help to stabilize stream thermal regimes relative to atmospheric temperatures (Gard 1963). Though most concerns regarding temperature alteration expected to accompany climate change have focused on increases in summer water temperatures, major changes in winter thermal regimes could be affected by reductions in ice cover and this has received little investigation. When streams are not insulated by ice cover, rapid fluctuations in temperature can occur that are thought to be linked to increased winter mortality of stream organisms because of the increased thermal stress they incur (Needham and Jones 1959, Schutz et al. 2001, Huusko et al. 2007). Thus, stabilization of stream temperature by ice cover may reduce thermal stress and mortality rates for stream organisms during the winter months. Despite these potentially positive effects of ice cover for stream ecosystems, ice cover may negatively impact stream biota in other ways during the winter months. For instance, snow cover of 0.5 m can attenuate photosynthetically active radiation by as much as 99.5%, subsequently reducing instream autotrophic production (Uehlinger et al. 1998, Schutz et al. 2001). This increased ice cover can also reduce stream oxygen concentrations because of decreases in the air/water interface and decreased photosynthesis by stream autotrophs (Prowse 2001a, b). Thus, climate-induced shifts in stream ice cover dynamics may substantially alter the abiotic habitat template of stream ecosystems.

As habitat conditions strongly influence the distribution and survival of stream organisms, potential shifts in stream ice regimes indicate another pathway through which climate change may be affecting stream organisms. For instance, stream biota have developed mechanisms to persist, and even thrive, during periods of substantial ice cover (Danks 2007, Huusko et al. 2007). Stream fishes and macroinvertebrates will seek out habitat refugia where ice cover is less extensive, such as areas with high influxes of warmer groundwater (Baxter and Hauer 2000, Schutz et al. 2001, Huusko et al. 2007). For those individuals that do not shift their habitat use during prolonged ice cover, they can reduce their

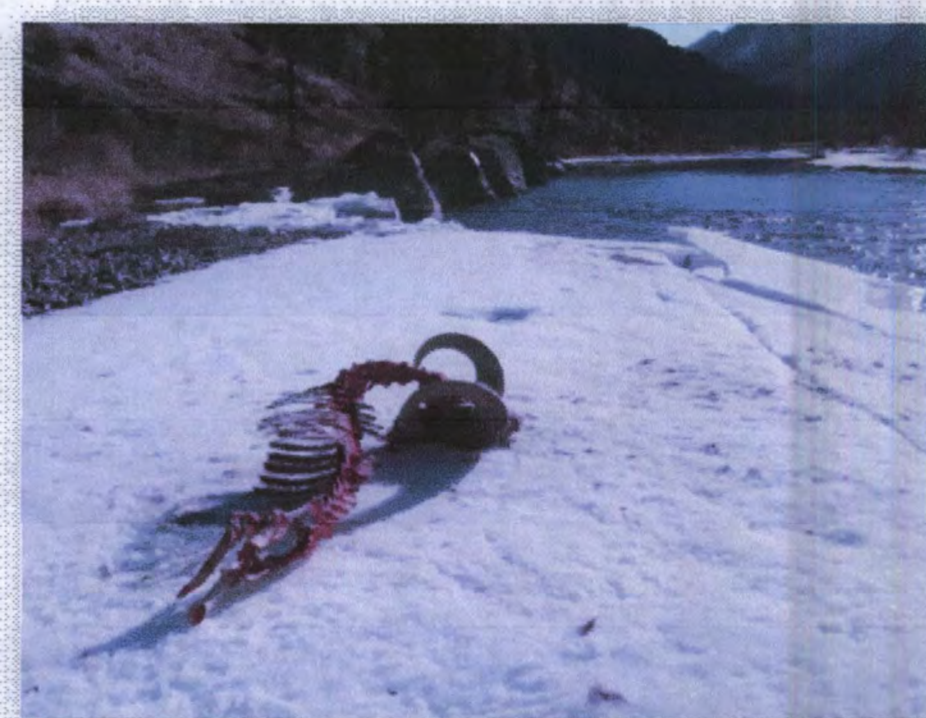
An underwater view beneath the ice taken in the Yankee Fork of the Salmon River, central Idaho. The winter ecology of rivers, and especially life under the ice, is very poorly understood due to the challenges of conducting such studies.

metabolic rates and overall activity to account for the declines in algal production and oxygen concentrations (Finstad et al. 2004). For instance, fish experiencing conditions similar to those under ice-cover habitat exhibited higher gross growth efficiency because they reduced their metabolic rates and activity levels when compared to fishes in ice-free habitats (Finstad et al. 2004). This suggests that potential shifts in the abiotic conditions related to declines in ice cover may alter stream habitat and the winter survival of stream organisms.

Of ice and wolves…and an unstudied "subsidy" to streams

Shifting ice regimes may not only directly alter the abiotic conditions of stream ecosystems, but reductions in winter ice cover and snow pack have the potential to drive more indirect, unforeseen effects via foodweb pathways that link land and water. Stream ecologists have long recognized and extensively studied flows of materials and organisms such as nutrients, leaves, wood, and invertebrate prey that link streams and their watersheds (Hynes 1975, Baxter et al. 2005, Allan and Castillo 2007) With recent investigations such as those of predators like bears or otters transporting salmon carcasses or fish derived nutrients to terrestrial habitats (Ben-David et al. 1998, Helfield and Naiman 2001, Gende et al. 2002), there is growing appreciation for the role that may be played by vertebrate carcasses as ecosystem subsidies. One such subsidy to streams that has not, to our knowledge, been investigated are inputs of ungulate carcasses that accompany predation by wolves.

In the mountainous regions of the western U.S. where wolves have become reestablished as dominant predators, changes in ice or snow cover might mediate predator-prey dynamics between wolves and ungulates and this, in turn, could affect the delivery of ungulate carcasses to streams. Wolves frequently kill ungulates in and along streams and rivers, and the remains of these animals, though perhaps a small input in terms of biomass, may represent a subsidy to stream food webs of disproportionate quality. Wolf-killed carcasses are most common along river-riparian corridors in winter, when snow pack drives ungulates to lower elevations and snow/ice cover apparently facilitates predation (e.g., Huggard 1993, Ripple and Beschta 2004a). For example, under conditions of moderate snowpack and river ice cover, researchers in central Idaho wilderness have observed up to ~2-3 carcasses per km of river by early spring (J. and H. Akenson, personal communication). During years of reduced snowfall, ungulates move into higher elevation habitat away from stream valleys because lower snow pack can improve their mobility and the availability of forage at higher elevations (Ripple and Beschta 2004a). As ungulates move into these higher elevation habitats, this may reduce carcass inputs to stream ecosystems because wolf-kills likely occur in upslope habitats away from stream riparian areas. Reduced winter snow pack may further reduce ungulate carcass inputs because lower snow pack can reduce wolf capture efficiency as ungulates are better able to escape when snow pack does not impede ungulate movement (Huggard 1993). Wolf capture efficiencies may be further altered by changes in stream ice cover. Specifically, when pursued by predators ungulates will frequently enter rivers where wolves are less likely to follow (J. and H. Akenson, personal communication). However, when rivers are covered by a substantial layer of ice, it can reduce the effectiveness of this anti-predator behavior because wolves are able to pursue and capture ungulates on the ice sheet (J. and H. Akenson, personal communication.). During the spring thaw, those ungulate carcasses that accumulate during the winter months are subsequently deposited into the stream channel where they are available to stream consumers. Thus, if global climate change is reducing winter snow pack and stream ice cover along rivers, this suggests that it may be indirectly reducing inputs of ungulate carcasses to these rivers because of associated changes to ungulate habitat selection and the effectiveness of anti-predator behaviors.



A wolf-killed bighorn sheep carcass on the ice of Big Creek in the central Idaho wilderness, March 2010 (photo courtesy of collaborators Jim and Holly Akenson). Ice cover may influence predation patterns along the river. Carcasses are consumed to varying degrees before being deposited into the river, where they

Previous evidence suggests that the potential reductions in ungulate carcass inputs to stream ecosystems could affect the productivity and distribution of stream consumers, indicating another potential pathway by which changing ice regimes may affect stream ecosystems. In terrestrial ecosystems, ungulate carcasses originating from wolf kills can increase the nutrient content and microbial biomass of soils underlying carcasses (Bump et al. 2009a, Bump et al. 2009b). These nutrient additions can reach such high levels that it can increase the leaf nutrient content of plants growing in these carcass addition areas (Bump et al. 2009a), indicating an important bottom-up pathway through which ungulate carcasses can stimulate higher trophic levels. These ungulate carcasses can also have more direct effects on the distribution and abundance of mesomammals and scavengers, such as coyotes and ravens, that are attracted to ungulate remains (Wilmers et al. 2003a, Wilmers et al. 2003b, Cortes-Avizanda et al. 2009). Thus, even in relatively productive terrestrial ecosystems, ungulate carcass availability can affect the distribution and survival of terrestrial consumers.

This overall importance of ungulate carcasses for terrestrial consumers suggests the potential for similar positive effects on stream ecosystems when such carcasses are made available to stream consumers. This potential is supported by recent evidence from salmon restoration projects that have experimentally increased the availability of salmon carcasses for stream consumers. During spawning, salmon transport large amounts of marine derived nutrients and biomass to upstream habitats (Willson and Halupka 1995). As many of the streams in the Salmon River basin are severely nutrient limited (Thomas et al. 2003), these nutrient and energy subsidies can represent an important resource that can increase stream nutrient content, subsequently stimulating periphyton biomass (Wipfli et al. 1998, Cederholm 1999). This increased basal resource availability can have positive bottom-up effects on stream macroinvertebrate and fish populations (Wipfli et al. 1998, Chaloner and Wipfli 2002). Given the positive effects of salmon carcasses on stream consumer populations, this suggests that influxes of high quality ungulate carcasses to stream ecosystems may have similar positive effects on the distribution and biomass of stream food webs. Moreover, if ice cover is directly related to the availability of such carcasses because of shifts in wolf capture efficiency, it suggests an unrecognized pathway for global climate change to alter stream-riparian resource subsidies and their associated effects on stream productivity.

Objectives of proposed research

Despite the potential effects of changing ice-cover and 'ice-out' events for stream ecosystems, predicting these effects is impeded because there has been so little research on the winter ecology of stream ecosystems compared to their summer ecology; likely because of the logistical challenges associated with conducting winter studies. Previous research has also primarily focused on the direct effects of ice cover and scour on stream structure and function without considering its implications for other ecosystem-level processes (i.e., indirect effects associated with changes in terrestrial subsidies). Given the potential complexities of these direct and indirect effects on stream ecosystems, predicting the net effect of these changes for wilderness stream networks, such as dominates large areas of the mountainous western U.S., is even more challenging.

Here we propose to quantify the direct and indirect effects of ice cover for the structure and function of Big Creek, a mid-sized (7^{th} order) river located in central Idaho's Frank Church 'River of No Return' Wilderness, by using a combination of long-term data and patch-scale experiments to address the hypotheses outlined below. We will assess whether global climate change induced changes in ice cover at Big Creek may be directly impacting stream benthic communities via changes in the spatial extent and duration of ice cover, and through changes in the timing and magnitude of 'ice-out' events. As shifts in the spatial extent and duration of ice cover will likely have direct effects on stream structure and function, we will assess the effects of ice cover and scour on benthic communities. In addition, we will assess whether these shifts in ice regimes are indirectly affecting stream processes by reducing the flux of ungulate carcasses to Big Creek. By contrasting benthic communities at sites with and without ungulate carcasses, we will be able to assess the potential indirect effects of ungulate carcasses on stream ecosystems. The combination of results from this proposed project will help elucidate potential interactions between direct (i.e., ice scour) and indirect (i.e., ungulate carcass subsidies) pathways for winter ice cover to alter stream ecosystems, and assess the net response of streams to climate-induced shifts in stream ice dynamics.

Hypothesis 1: The spatial extent and duration of ice cover on Big Creek has declined over time, likely due to associated increases in atmospheric and stream temperatures. This has likely altered the timing and frequency of large 'ice-out' events.

Methods: We will evaluate Hypothesis #1 by mining long-term data collected at Taylor Wilderness Field Station (TWFS). Using research logs that include description of the timing and frequency of 'ice-out' events over the previous 20 years (available to us through collaboration with long-time field station scientists Jim and Holly Akenson), we will assess whether the frequency and seasonal timing of ice-out events have shifted along the Big Creek mainstem. In addition to direct analysis of data derived from the station records, we will use these data to develop models that allow us to hindcast and forecast ice conditions using meteorological and river discharge data continuously collected at the field station. These modeling efforts, which will involve collaboration with ISU hydrologists and geomorphologists Ben Crosby and Glenn Thackray, will help us determine whether shifts in ice extent and duration, as well 'ice-out' events, have changed over recent decades. Furthermore, it will help evaluate how they might be altered under different climate change scenarios predicted by down-scaled, climate change models for this region (provided to us by the Climate Impacts Group, University of Washington).

Hypothesis 2: Inputs of ungulate carcasses to Big Creek is positively related to the spatial extent and duration of ice cover for a given year.

Methods: To assess Hypothesis #2, we will utilize existing field station data and conduct detailed spatial mapping of carcasses and winter ice cover for a segment of Big Creek over a two year period. Wolves were reintroduced to the Idaho wilderness through several releases in the mid- to late 1990's and quickly colonized the Big Creek area, during which time they were actively studied by field station scientists Jim and Holly Akenson. These studies included locating and identifying wolf-kills along an approximately 20 km segment of Big Creek up and downstream of TWFS. We will collaborate with the Akensons to conduct analyses of these data. During the two years of our study, we will conduct weekly surveys of ice cover and ungulate carcasses within the same study segment. We will continue these surveys during ice-free periods (spring and summer) to assess how these inputs vary when streams are not covered by ice. The detailed data from our two years of study will be coupled with the long-term ice cover (see Hypothesis #1) and ungulate carcass abundance data to assess whether there is a relationship between the abundance of ungulate carcasses and the spatial extent and duration of ice cover on Big Creek.

Hypothesis 3: Periods of prolonged ice cover are associated with reduced periphyton standing crop when compared to pre-ice cover conditions or similar time periods in years with less ice. Similarly, 'ice out' events scour the streambed, driving reductions in periphyton standing crop and the abundance and biomass of benthic macroinvertebrates.

Methods: Hypothesis #3 will be tested via a 'time-for-space' comparative method whereby we will sample and compare periphyton and macroinvertebrate standing biomass in Big Creek during three distinct periods of ice condition: pre-ice cover, sustained ice-cover, post-ice cover (i.e., after the ice-out event). We will conduct a series of repeated sampling within each of these three periods in a study reach encompassing representative habitat upstream of the TWFS. This location corresponds with the site used for annual sampling of the benthos as part of long-term monitoring, and is also positioned upstream of a PIT-tag sensor array located adjacent to TWFS (see particle movement methods below). The pre-ice sampling will provide a 'pretreatment' control that can serve as a baseline to determine what effect ice cover has on benthic communities. Repeated sampling during the ice-cover period will provide a time series to describe how benthic structure changes with prolonged ice cover. In addition, the final ice-cover sample (i.e., taken right before ice-out) will provide us with a baseline to determine what effect ice scour has on benthic communities. By comparing measurements taken immediately preceding the 'ice-out' event with samples taken immediately after ice-out (i.e., when we can safely get back into the stream), we will be able to assess the effects of ice scour on benthic communities. Continued sampling after ice out will determine how quickly the benthic community recovers from this initial scouring event.

Sampling frequency will vary depending on the treatment. We will sample at least 2-3 times pre ice-over to provide an adequate baseline of benthic conditions. We will then sample repeatedly during the winter ice-over period (semi-weekly to monthly, depending on weather and projected duration of ice cover). To increase our likelihood of sampling immediately prior to ice-out, we will increase the frequency of sampling during the time period that will have the highest probability of 'ice-out' (see Hypothesis #1). When ice-out occurs we will repeat the sample as soon as we can safely re-enter the stream, likely within a few days after the 'ice-out' event. To track the recovery of the benthos following ice-out, and because river ice may re-form and go out repeatedly, we will continue to revisit the sites on at least a monthly basis throughout the spring leading up to the high flows of run-off.

Mobility of streambed particles— In order to evaluate stream bed mobility and scour associated with ice-out events, we will follow the movements of individual stream particles of various sizes using techniques being utilized by Drs. Crosby and Baxter as part of studies throughout the Salmon Basin. These techniques involve measurement and analysis of substrate size distributions at a location, followed by the collection of stones representative of the size distribution of the streambed materials present. In the same reach within which ecological sampling is conducted, ca. 30 stones will be removed. The stones will be transported back to TWFS where their dimensions will be measured, and each will be drilled and passive integrated transponder (PIT) tags will be installed. PIT tags will be inserted into the hole and epoxy will be applied to seal them in. Studies have shown that recovery rates of individual pit tagged particles is much higher (up to 90% annually) than in cases where particles are simply painted (5% and 50%; Lamarre et al. 2005). Moreover, this technique allows particles to be followed without creating any visual artifact of the study, an important consideration for work in this sensitive wilderness setting. Following the PIT tagging, stones will be reintroduced to the streams from which they were removed. An initial datum point will be recorded for each of the particles at the time of reintroduction. Particles will be relocated following an ice-out event using a portable pit tag reading device. PIT tags will be used that can also be detected by NOAA stationary receivers positioned above and below the Big Creek pack bridge. Information collected by these techniques will allow us to estimate the average distance traveled by particles of different sizes in association with ice-out events.

Periphyton – On each sampling occasion, periphyton will be sampled at 4 locations at each site. Rocks will be chosen haphazardly at each location, placed in tubs holding small amounts of stream water, and then scrubbed with a wire brush to remove all attached periphyton.

The resulting periphyton slurry will be subsampled, filtered onto GF/F filters, and transported back to the lab on ice. Standing crop of periphyton on the filters will be estimated by using standard methods to quantify chlorophyll-*a* concentrations and ash-free dry mass (AFDM). Rock area will be estimated by tracing the planar area of the rock onto paper and then weighing these paper cutouts.

Sampling stream invertebrates from the beneath the ice in the Yankee Fork of the Salmon River. Similar techniques would be used in this study.

Benthic macroinvertebrates – Using a surber sampler (0.3 x 0.3m frame, 250μm mesh net) benthic macroinvertebrates will be sampled at three haphazardly locations at each sampling location on each sampling date. Samples will be preserved in ethanol and transported back to the lab. Macroinvertebrates will be separated from detritus, and identified to genus, then dried and weighed to obtain a mean biomass for each taxon.

We acknowledge that our sampling design will likely confound ice cover and seasonal effects. Specifically, because we will not have a section of stream that remains 'ice-free' during this same time period, we won't be able to isolate the effects of ice cover on benthic communities. However, because it is logistically impossible to directly manipulate ice cover or scour in such a large river, three factors will help us indirectly separate the direct effects of ice. First, as we will be sampling immediately before and after ice-over, this frequent resampling will likely help us assess the immediate effect of ice-cover on benthic communities. Temporal changes will be minimal under such a short-duration resampling regime. A similar sampling regime immediately prior to and following 'ice-out' will allow us to similarly assess the immediate effects of scour on benthic communities. Second, scouring of the stream benthos is relatively heterogeneous. This suggests that some of our 'ice-cover' sample plots will not be directly scoured during the ice-out events. We will be quantifying bed scour during these 'ice-out' events; thus, we will be able to identify those sites that did not scour. By selectively processing a subset of those sites within areas that were either scoured or not scoured during the ice-out event, we will be able to determine the relative effect of ice scour on ice-covered benthos. Third, opportunistic interannual variation in the distribution of ice cover may provide us with additional information to isolate ice-cover effects. We will revisit our sampling sites over a two year period. If ice coverage varies for a site between years, it will serve as 'control' and allow us to assess the relative importance of ice-cover vs. ice-free conditions. Despite these inherent difficulties associated with maintaining an 'ice-free' control, data collected with this 'time-for-space' method will provide invaluable data detailing benthic responses of a large river during the winter months, a severely underrepresented data set for stream ecosystems.

Hypothesis 4: Ungulate carcasses represent an important localized subsidy that increases stream productivity at the 'patch-scale.' Specifically, stream nutrient concentrations,

periphyton biomass, and macroinvertebrate biomass will be higher at those sites receiving ungulate carcasses than at random sites without such carcasses. This increased benthic production will increase fish abundance and the relative contribution of carcass-derived macroinvertebrates to fish diets in those patches receiving ungulate carcasses.

Methods: To assess Hypothesis #4, we will sample periphyton, macroinvertebrates, and the fish communities at sampling points along Big Creek with and without ungulate carcasses. Ungulate carcass locations will be determined based on our weekly winter surveys of ungulate carcasses (see Hypothesis #2). Sampling of the benthos will commence immediately after spring thaw when carcasses are deposited onto the stream bed (likely starting in late February or early March). Sampling points without ungulate carcasses will be randomly selected locations that exhibit similar substrate composition, stream flow, and stream depth. If an insufficient number of ungulate carcasses are located in a given year, carcasses found in terrestrial areas may be transported and deposited along the ice-covered stream. These 'additional' treatments will not be considered in the testing of Hypothesis #2. Stream biota will be sampled at least semi-weekly for the period during which a given carcass persists in a streambed patch to assess how carcass effects on stream productivity vary over time.

Nutrients— During each sampling event, stream water will be collected immediately up and downstream of each of the sites with and without carcasses for analysis of nutrient concentrations . Water samples will be analyzed according to standard methods for concentrations of NH_4, NO_3, and soluble reactive phosphorus (APHA 1998).

Periphyton – On each sampling occasion, periphyton will be sampled at 3 locations surrounding a specific sampling location (either carcass or no-carcass treatment type). Rocks will be chosen haphazardly at each location, placed in tubs holding small amounts of stream water, and then scrubbed with a wire brush to remove all attached periphyton. The resulting periphyton slurry will be subsampled, filtered onto two GF/F filters, transported back to TWFS on ice, and frozen for transport to the lab. Standing crop of periphyton on the first filter will be estimated by using standard methods to quantify chlorophyll-*a* concentrations and ash-free dry mass (AFDM). After drying, the second filter will be analyzed for elemental composition using standard methods (i.e., % carbon, % nitrogen, and % phosphorus). Rock area will be estimated by tracing the planar area of the rock onto paper and then weighing these paper cutouts. Repeating this sampling regime on at least a semiweekly basis will allow us to see how quickly periphyton standing crop responds to ungulate carcass additions and to determine the temporal extent of these effects.

Benthic Macroinvertebrates –Benthic macroinvertebrates will be sampled using a surber sampler (0.3 x 0.3m frame, 250µm mesh net) at both carcass and no-carcass sites. On each sampling date, three samples will be collected at each site. Samples will distributed haphazardly and, at sites with carcasses, within the patch (< ca. 5m) immediately downstream of the carcass. In addition, small samples will be taken directly from carcass to determine abundance and biomass of invertebrates that colonize the carcass. Samples will be preserved in ethanol and transported back to the lab. Macroinvertebrates will be separated from detritus, and identified to genus, then dried and weighed to obtain a mean biomass for each taxon.

Fish— We will assess fish responses to carcass additions via two different methods. Fish assemblage and abundance responses will be assessed by nighttime snorkel surveys at the same time interval as above. At both the carcass and no-carcass sampling locations, fishes will be identified to species and enumerated. To assess shifts in fish dietary reliance on carcass-derived macroinvertebrates, fish will be collected via angling and night-time dip-netting of individuals.

Electrofishing for fish diet sampling will not be possible because of concerns over possible negative effects on endangered Chinook salmon (*Oncorhynchus tshawystcha*), steelhead (*O. mykiss*), and bull trout (*Salvelinus confluentus*)—all of which are to be found in Big Creek, and because of the need to adhere to wilderness standards for research activity. However, previous research in this area has shown that nighttime dip-netting of fishes in combination with angling are equally reliable methods for capturing fish. Once captured, we will quickly process fish onsite and use non-lethal methods to collect contents from fish stomachs. This involves brief anesthesia and use of a pipette to flush prey items from the stomach (Giles 1980), and has been performed by the principal investigator on thousands of fish (including endangered species, with appropriate permits) with little to no observed mortality. Gut contents will be preserved in ethanol and transported back to the lab. Gut contents will be identified to the lowest taxonomic resolution, enumerated, then dried and weighed to obtain mean biomass for each taxon.

Hypothesis 5: These potentially negative direct (Hypothesis #3) and positive indirect (Hypothesis #4) effects of ice cover interact to alter periphyton standing crop, macroinvertebrate biomass, and fish abundance. However, the net effects of changing ice regimes for stream ecosystems are difficult to predict because they largely depend on the relative magnitude of these direct and indirect effects.

Methods: Despite the uncertainty associated with Hypothesis #5, we will use results from this study to assess any potential interactions between direct and indirect of changing ice regimes, and to ascertain the net response of stream ecosystems to changing ice regimes. We will assess the net effect of changing ice regime on stream benthic communities by combining our results from Hypotheses #3 and #4. Specifically, we will scale our estimates of the effects of ice regime and carcasses by extrapolating measurements made at patch-scales, using our river segment-scale maps of ice cover and ungulate carcasses. This scaling up to the river segment will allow us to calculate to what extent the benthic community (e.g., standing biomass of periphyton and macroinvertebrates) would be impacted by reductions in ice cover, scour, and/or ungulate carcass availability. Comparing these segment-scale calculations will allow us to assess the relative magnitude of direct and indirect impacts of ice regime change on benthic communities. Moreover, we will be able to ascertain the net response of streams to changing ice dynamics (i.e., the "price of ice") via these two potentially interacting pathways.

Significance of results and broader impacts

The results from this proposed research will have direct implications for ecological research within the Big Creek watershed and more broadly to our understanding of the winter ecology of stream ecosystems. This project will provide funding for a graduate student to help synthesize and organize an existing long-term data set describing the frequency and duration of 'ice-out' events within the Big Creek watershed. These data are not readily accessible in their current form, (e.g., entries as journal logs); thus, the testing of Hypothesis #1 will synthesize these data into a form that will help inform us about potential shifts in ice regimes associated with global climate change. As we will also be pairing these long-term data with more-detailed surveys of ice coverage and ungulate carcass abundance, it will allow us to broaden the impact of our shorter-duration 'patch-scale' manipulations (ice/no-ice and carcass/no-carcass) and to put these shorter-term effects in 'deep' time context. Our lab is also currently involved with a large collaborative project assessing global climate change effects on the Salmon River basin; thus, this proposed project will inform this larger collaborative project and help guide future climate change research in the Salmon River. Similarly, we will also couple our proposed Big Creek sampling with Dr. Minshall's annual sampling of tributaries throughout the Big Creek watershed. This long-term monitoring has continued under Dr. Baxter, but for most years until recently the Big Creek mainstem has not been sampled. These proposed sampling locations along the mainstem of Big Creek will continue to be sampled as part of this longer-term study; thus, it will help us assess whether patterns we have previously observed in the upstream tributaries can be scaled up to explain patterns in the Big Creek mainstem.

The majority of the sampling will occur during the winter months; thus, this proposed project will also provide us with excellent data detailing the winter ecology of stream organisms in a wilderness area. Our understanding of the winter ecology of stream ecosystems is not only deficient in the Big Creek watershed, but for global aquatic ecosystems as a whole. The winter ecology data collected during this project will provide us with invaluable data that will be of interest beyond Big Creek. These two winter field seasons will provide capstone data for more targeted sampling of Big Creek during the spring and summer months. Because spring/summer samples are less challenging and cheaper to collect, these additional samples could be collected at little additional cost. As part of a value-added component to this project, we will conduct lower intensity sampling of sites along the Big Creek mainstem during the intervening spring and summer months. This will provide us with a full-year of macroinvertebrate data that could be used to calculate macroinvertebrate secondary production for Big Creek. In other ecoregions, secondary production has helped interpret the response of macroinvertebrate food webs to environmental change; effects that are not necessarily apparent when assessed with simple metrics of community abundance and biomass (e.g., Wallace et al. 1997, Davis et al. 2010). There are no comparable secondary production estimates for Big Creek and few examples from large western rivers. Thus, the coupling of these secondary production estimates with future sampling in the Big Creek basin would provide us with a unique data set that could be used for other studies throughout the Salmon River basin. For instance, production to biomass ratios calculated from this proposed Big Creek project could then be used to estimate secondary production at other sites where only average annual biomass was measured. Given the few examples of secondary production estimates in the western U.S., these data from a large wilderness river would provide an invaluable tool for a number of ecological comparisons in the western U.S.

More broadly, our results will also help increase our understanding of how wolf reintroduction may be altering stream ecosystems. Recent data from the greater Yellowstone ecosystem has indicated the importance of wolves for structuring ecosystem processes via 'the ecology of fear' that alters prey behavior and spatial distributions (Ripple and Beschta 2004a). These relationships have apparently led to trophic cascades in terrestrial ecosystems and shifts in stream geomorphology due to changing riparian vegetation (Ripple and Beschta 2004b, Beschta and Ripple 2006, 2009). Assuming that our predictions based on Hypothesis #5 are correct, then it suggests another pathway by which wolf predation and their 'ecology of fear' may be altering stream processes through changes in cross-boundary resource subsidies.

Research Timeline:

Spring / Summer 2010: Advance study design and select study sites via discussions with Ben Crosby, Glenn Thackray, Jim and Holly Akenson
Fall 2010: Collect pre-ice cover 'reference' benthic samples
Winter 2010: Collect prolonged ice-cover benthic samples, map ice cover, and survey ungulate carcass distributions
Spring 2011: Collect post-ice cover benthic samples, collect 'patch-scale' ungulate benthic samples
Summer 2011: Continue to collect targeted benthic samples for secondary production estimates, process winter and spring samples
Fall 2011: Continue to collect targeted benthic samples for secondary production estimates and process samples
Winter 2011: Process samples, map ice cover, survey ungulate carcass distributions, and conduct targeted ice cover benthic sampling to assess interannual variation
Spring 2012: Data analysis
Summer 2012: Finish data analysis
Fall 2012: Manuscript preparation and M.Sc. defense
Summer 2013 and Beyond: Continue to sample Big Creek mainstem to be incorporated into the Minshall-Baxter long-term monitoring of the Big Creek watershed

Budget Justification

To conduct the proposed study, funding is required for masters-level graduate student stipend and fees (2 years), transportation, food and lodging, lab sample analyses, misc. field supplies, and equipment. The DeVlieg-Taylor Ranch Graduate Research Assistantship would cover the graduate student stipend and fees. As the DeVlieg Foundation does not pay institutional overhead, such funds have not been included in the budget below. As these research goals overlap with our current NSF EPSCoR grant assessing the effects of global climate change on the Salmon River Basin, we will use parts of those funds to pay for a field assistant (including fringe benefits), and all operational expenses such as travel and field equipment needed for this study. The ISU Stream Ecology Center is fully equipped for processing the study samples, performing data analysis, and publishing our findings. As noted above, our intent will be to use the data derived from this proposed project to inform our research goals for future proposals and projects that will assess the long-term effects of climate change on the Salmon River basin.

Research Budget

		Year 1	Year 2	Summary
Salaries				
	MSc. Student	14400	14400	28800
	Field Assistant	3000	3000	6000
Fringe		1550	1550	3100
Sal & Fringe		18950	18950	37900
Fees/Tuition	Grad Student Fees	5400	5778	11178
Oper. Expenses				
	Field supplies	500	500	1000
	Elemental Analysis	2000	2000	4000
	Travel (auto/plane)	1000	1000	2000
	Food & Lodging	1000	1000	2000
Total		28850	29228	58078

<u>Funding request:</u>
DeVlieg-Taylor Ranch Graduate Fellowship ($18,500/year @2 yrs) $37,000

<u>Other funding support obtained:</u>
NSF EPSCoR $21,078

<u>Total project funds:</u> $58,078

Literature Cited:

Allan, J. D. and M. M. Castillo. 2007. Stream Ecology: Structure and Function of Running Waters. 2nd edition. Springer.

APHA. 1998. Standard methods for the examination of water and wastewater. 20th edition. American Public Health Association, Washington, D.C., USA.

Baxter, C. V., K. D. Fausch, and W. C. Saunders. 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zone. Freshwater Biology **50**:201-220.

Baxter, C. V. and F. R. Hauer. 2000. Geomorphology, hyporheic exchange, and selection of spawning habitat by bull trout (Salvelinus confluentus). Canadian Journal of Fisheries and Aquatic Sciences **57**:1470-1481.

Ben-David, M., T. A. Hanley, and D. M. Schell. 1998. Fertilization of terrestrial vegetation by spawning Pacific salmon: the role of flooding and predator activity. Oikos **83**:47-55.

Beschta, R. L. and W. J. Ripple. 2006. River channel dynamics following extirpation of wolves in northwestern Yellowstone National Park, USA. Earth Surface Processes and Landforms **31**:1525-1539.

Beschta, R. L. and W. J. Ripple. 2009. Large predators and trophic cascades in terrestrial ecosystems of the western United States. Biological Conservation **142**:2401-2414.

Bump, J. K., R. O. Peterson, and J. A. Vucetich. 2009a. Wolves modulate soil nutrient heterogeneity and foliar nitrogen by configuring the distribution of ungulate carcasses. Ecology **90**:3159-3167.

Bump, J. K., K. B. Tischler, A. J. Schrank, R. O. Peterson, and J. A. Vucetich. 2009b. Large herbivores and aquatic-terrestrial links in southern boreal forests. Journal of Animal Ecology **78**:338-345.

Cederholm, C. J., M. D. Kunze, T. Murota, and A. Sibatani. 1999. Pacific Salmon carcasses: essential contributions of nutrients and energy for aquatic and terrestrial ecosystems. Fisheries **24**:6-15.

Chaloner, D. T. and M. S. Wipfli. 2002. Influence of decomposing Pacific salmon carcasses on macroinvertebrate growth and standing stock in southeastern Alaska streams. Journal of North American Benthological Society **21**:430-442.

Cortes-Avizanda, A., N. Selva, M. Carrete, and J. A. Donazar. 2009. Effects of carrion resources on herbivore spatial distribution are mediated by facultative scavengers. Basic and Applied Ecology **10**:265-272.

Danks, H. V. 2007. How aquatic insects live in cold climates. Canadian Entomologist **139**:443-471.

Davis, J. M., A. D. Rosemond, S. L. Eggert, W. F. Cross, and J. B. Wallace. 2010. Long-term nutrient enrichment decouples predator and prey production. Proceedings of the National Academy of Sciences of the United States of America **107**:121-126.

Finstad, A. G., T. Forseth, T. F. Faenstad, and O. Ugedal. 2004. The importance of ice cover for energy turnover in juvenile Atlantic salmon. Journal of Animal Ecology **73**:959-966.

Gard, R. 1963. Insulation of a sierra stream by snow cover. Ecology **44**:194-&.

Gende, S. M., R. T. Edwards, M. F. Willson, and M. S. Wipfli. 2002. Pacific salmon in aquatic and terrestrial ecosystems. Bioscience **52**:917-928.

Gibson, C. A., J. L. Meyer, N. L. Poff, L. E. Hay, and A. Georgakakos. 2005. Flow regime alterations under changing climate in two river basins: Implications for freshwater ecosystems. River Research and Applications **21**:849-864.

Giles, N. 1980. A stomach sampler for use on live fish. Journal of Fish Biology **16**:441-444.

Helfield, J. M. and R. J. Naiman. 2001. Effects of salmon-derived nitrogen on riparian forest growth and implications for stream productivity. Ecology **82**:2403-2409.

Huggard, D. J. 1993. Effect of snow depth on predation and scavenging by gray wolves. Journal of Wildlife Management **57**:382-388.

Huusko, A., L. Greenberg, M. Stickler, T. Linnansaari, M. Nykanen, T. Vehanen, S. Koljonen, P. Louhi, and K. Alfredsen. 2007. Life in the ice lane: The winter ecology of stream salmonids. River Research and Applications **23**:469-491.

Hynes, H. B. N. 1975. The stream and its valley. Verh. Internat. Verein. Limnol. **19**:1-15.

Lamarre, H., B. MacVicar, and A. G. Roy. 2005. Using passive integrated transponder (PIT) tags to investigate sediment transport in gravel-bed rivers. Journal of Sedimentary Research **75**:736-741.

Needham, P. R. and A. C. Jones. 1959. Flow, temperature, solar radiation, and ice in relation to activities of fishes in Sagehan Creek, California. Ecology **40**:465-474.

Poff, N. L. 2002. Ecological response to and management of increased flooding caused by climate change. Philosophical Transactions of the Royal Society of London Series a-Mathematical Physical and Engineering Sciences **360**:1497-1510.

Poff, N. L., J. D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegaard, B. D. Richter, R. E. Sparks, and J. C. Stromberg. 1997. The natural flow regime. Bioscience **47**:769-784.

Poff, N. L. and J. K. H. Zimmerman. 2009. Ecological responses to altered flow regimes: a literature review to inform the science and management of environmental flows. Freshwater Biology **55**:194-205.

Prowse, T. D. 2001a. River-ice ecology. I: Hydrologic, geomorphic, and water-quality aspects. Journal of Cold Regions Engineering **15**:1-16.

Prowse, T. D. 2001b. River-ice ecology. II: Biological aspects. Journal of Cold Regions Engineering **15**:17-33.

Prowse, T. D. and S. Beltaos. 2002. Climatic control of river-ice hydrology: a review. Hydrological Processes **16**:805-822.

Prowse, T. D. and B. R. Bonsal. 2004. Historical trends in river-ice break-up: a review. Nordic Hydrology **35**:281-293.

Prowse, T. D. and J. M. Culp. 2003. Ice breakup: a neglected factor in river ecology. Canadian Journal of Civil Engineering **30**:128-144.

Resh, V. H., A. V. Brown, A. P. Covich, M. E. Gurtz, H. W. Li, G. W. Minshall, S. R. Reice, A. L. Sheldon, J. B. Wallace, and R. C. Wissmar. 1988. The role of disturbance in stream ecology. Journal of the North American Benthological Society **7**:433-455.

Ripple, W. J. and R. L. Beschta. 2004a. Wolves and the ecology of fear: Can predation risk structure ecosystems? Bioscience **54**:755-766.

Ripple, W. J. and R. L. Beschta. 2004b. Wolves, elk, willows, and trophic cascades in the upper Gallatin Range of Southwestern Montana, USA. Forest Ecology and Management **200**:161-181.

Schutz, C., M. Wallinger, R. Burger, and L. Fureder. 2001. Effects of snow cover on the benthic fauna in a glacier-fed stream. Freshwater Biology **46**:1691-1704.

Scrimgeour, G. J., T. D. Prowse, J. M. Culp, and P. A. Chambers. 1994. Ecological effects of river ice break-up: A review and perspective. Freshwater Biology **32**:261-275.

Thomas, S. A., T. V. Royer, G. W. Minshall, and E. Snyder. 2003. Assessing the historic contribution of marine-derived nutrients to Idaho streams. American Fisheries Society Annual Meeting **34**:41-55.

Uehlinger, U., R. Zah, and H. Burgi. 1998. The Val Roseg project: temporal and spatial patterns of benthic algae in an alpine stream ecosystem influenced by glacier runoff. Pages 419-425 *in* K. Kovar, U. Teppeiner, N. E. Peters, and R. G. Craig, editors. Hydrology, water resources, and ecology in headwaters. IAHS Press, Wallingford, UK.

Wallace, J. B., S. L. Eggert, J. L. Meyer, and J. R. Webster. 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. Science **277**:102-104.

Willson, M. F. and K. C. Halupka. 1995. Anadromous fish as keystone species in vertebrate communities. Conservation Biology **9**:489-497.

Wilmers, C. C., R. L. Crabtree, D. W. Smith, K. M. Murphy, and W. M. Getz. 2003a. Trophic facilitation by introduced top predators: grey wolf subsidies to scavengers in Yellowstone National Park. Journal of Animal Ecology **72**:909-916.

Wilmers, C. C., D. R. Stahler, R. L. Crabtree, D. W. Smith, and W. M. Getz. 2003b. Resource dispersion and consumer dominance: scavenging at wolf- and hunter-killed carcasses in Greater Yellowstone, USA. Ecology Letters **6**:996-1003.

Wipfli, M. S., J. Hudson, and J. Caouette. 1998. Influence of salmon carcasses on stream productivity: response of biofilm and benthic macroinvertebrates in southeastern Alaska, U.S.A. Canadian Journal of Fisheries and Aquatic Sciences **55**:1053-1511.