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AMPHIPODS ARE A STRONG INTERACTOR IN THE FOODWEB OF A BROWN-WATER SALMON RIVER

By

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Thesis

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Amphipods are Strong-Interactors in the Foodweb of a Brown-Water Salmon River

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ABSTRACT

Marine derived biomass from salmon carcasses is incorporated into coastal Pacific Rim salmon river ecosystems via the organisms and structures of the freshwater foodweb. In brown water rivers of Western Kamchatka, the foodweb is dominated by ubiquitous benthic amphipods (*Anisogammarus kygi)* that consume salmon carcass material. We hypothesized that *A. kygi* are a strong interactor in the feedback loop which links dead spawner biomass to juvenile salmonid growth. We found that *A. kygi* had a complex life cycle with anadromous and resident forms. *A. kygi* dominated the macro-benthos, comprising more than 88.0% (SE=.01, N=7) of invertebrate biomass, and were highly mobile within the system, exhibiting upstream migrations of ovigerous females (23 ind/m3 ± 5), drift of juveniles, and re-distribution during carcass loading. *A. kygi* was observed feeding on 97% of salmon carcasses examined (N=100), making up 98.8% (SE .007) of invertebrate consumers, at densities up to 3,000 carcass^{-1}. Amphipods were an important food item for rearing salmonids, especially during the summer when fish diets reached a peak of 88.7% (SE=6.0%) amphipods in 2005, and 68% (SE=18%) amphipods in 2006. The condition factor of salmonid juveniles (*K*) increased from spring to summer, particularly in juvenile chum, whose spring diet was 76.83% (SE 0.05) amphipods, corroborating the importance of an amphipod based diet for salmonids in this river. We concluded that *A .kygi* is a strong interactor in the Utkholok system. We also observed abundance of *A. kygi* in six other brown water rivers of western Kamchatka which suggests that the amphipod-mediated feedback of marine derived nutrients described for the Utkholok, is typical of brown water systems with salmon.

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I would like to thank my advisor, Dr. Jack A. Stanford for support and the opportunity to work with SaRON and complete Masters research on the Utkholok River. I would also like to thank my committee members Dr. F. Richard Hauer and Dr. Lisa A. Eby for helpful input.

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I dedicate this Masters thesis, as one chapter of my Kamchatka adventure memoirs, to my father and family.

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INTRODUCTION

Annual runs of semelparous salmon occur in most coastal river ecosystems around the north Pacific Rim. Salmon carcasses provide allocthonous nutrient subsidy to aquatic and terrestrial foodwebs. The ecology of salmon around the Pacific Rim varies widely due to the complex physical processes and organismal interactions of salmon rivers. Thus, understanding the role of marine derived nutrients from spawning salmon as a primary driver of riverine productivity and biodiversity is important.

Anisogammarus kygi (Crustacea, Malacostraca, Amphipoda) is a large (adults reach 30mm body length) gammarid amphipod that is widely distributed around the Pacific Rim, inhabiting marine, brackish, and freshwaters (Fig.1). In initial studies (2003-5) *A. kygi* was the dominant (reaching hundreds of individuals per m^2) macro-invertebrate in the riverine food web of the Utkholok River in Western Kamchatka (Russian Federation). Moreover, we observed large numbers of these amphipods feeding on salmon carcasses, apparently playing a primary role in cycling of marine derived nutrients (hereafter MDN) in the Utkholok and the many other tundra-fed (brown-water) rivers of the region. We hypothesized that *Anisogammarus kygi* functioned as a strong interactor (De Ruiter et al., 1995) in the food webs of brown-water salmon rivers in Western Kamchatka and focused study on the Utkholok River as a model. Herein we support this working hypothesis by; 1) documenting abundance and spatial distribution of amphipods in the catchment; 2) describing the life cycle, including ecotypic variation and growth patterns; 3) quantifying *A. kygi* trophic interactions, specifically showing that amphipods catalyze salmon carcass breakdown and nutrient cycling; and 4) demonstrating importance of *A. kygi* as prey for juvenile salmonids and other fishes, thus mediating a key feedback from the carcasses of salmon spawners to the productivity of salmonid juveniles in the river.

Fig. 1. *Anisogammarus kygi* from the Utkholok River, Western Kamchatka. This specimen is a male of the "resident" form; a larger anadromous form also occurs (see text). Note the large secondary gnathopods (circled) characteristic of males, which are used during amplexic reproduction.

BACKGROUND

The Salmonid Rivers Observatory Network[1] (SARON) examines the complexities of salmon river ecosystems using habitat specific cross-site comparisons of salmon rivers in Alaska, British Columbia, and Kamchatka, Russia. The Utkholok River is the only brown water SARON observatory.

In preliminary work conducted in 2003-4, we observed that *A. kygi* was distributed throughout the Utkholok River including the Sea of Okhotsk proper, the large estuary of the Utkholok, the brown-water main channel of the river, its springbrooks, tundra and upland tributaries, and upstream reaches of many of these tributaries. In 2004, amphipods constituted on average 87% (N=7) of the benthic invertebrate biomass, clearly indicating that amphipods dominated the invertebrate community of the river.

Though widespread in the Utkholok and other coastal brown-water rivers, anisogammarids as a group have a very limited freshwater range and represent a very small portion of the gammarid amphipod fauna of the Pacific Rim. Of the 210+ genera and 1350+ species of amphipods described worldwide, ten genera of anisogammarids

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[1] SaRON: www.umt.edu\flbs\Research\SaRON.html

inhabit the North Pacific Basin, of which only three species inhabit the Russian Far East and Kamchatka (Fig. 2) (Barnard and Barnard, 1983).

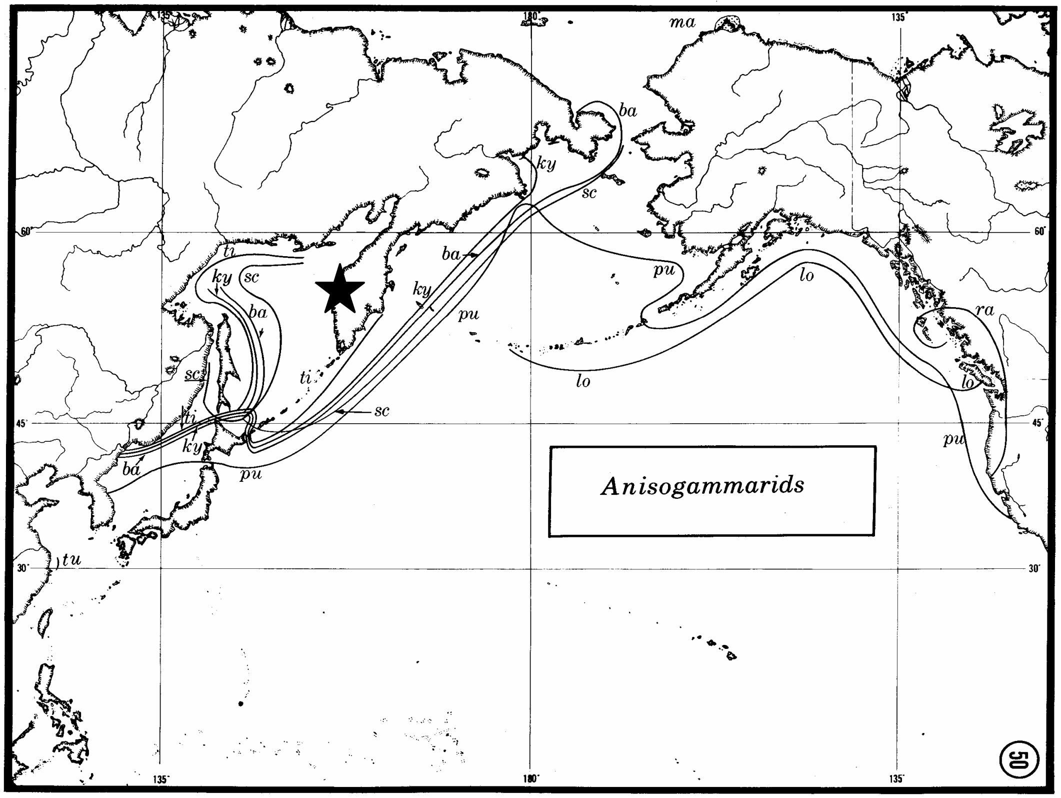


Fig. 2. Geographical range of *A. kygi* (labeled *ky*) after Barnard and Barnard (1983). Black star indicates the position of the Utkholok River.

Because of the relative obscurity of the genus and its remote geographic range, very little is known about the ecology of freshwater anisogammarids in the Russian Far East, though marine species have been studied elsewhere. Ultimately, we found no literature on the freshwater ecology of this amphipod in the context of salmon rivers. One amphipod genus (*Jesogammarus*) was studied relative to salmon carcasses (Kusano and Ito, 2005), but in general, amphipod ecology in salmon rivers is still unexplored.

On the other hand, amphipods as a group are one of the most widespread and diverse of the Crustacea, and ubiquitous in freshwaters world wide. In contrast to *Anisogammarus spp.*, *Gammarus spp.* have been studied extensively in lotic systems and the general ecology of the two groups is probably similar.

Amphipod densities up to 10,000 individuals m^{-1} were reported (Pennak, 1989) around the world with populations occupying a wide range of habitats in lotic and lentic, fresh and brackish waters. Density and spatial distribution of amphipod species were correlated with physical and biotic conditions including temperature and oxygen content (reviewed by Otto, 1998), fish predation pressure (Andersson et al., 1986; González and Burkhart, 2004), food availability (Minkley, 1964), and MDN subsidy (Kusano and Ito, 2005). The same conditions were correlated with distribution of life history attributes within a species' range such as reproductive cycle (Wilhelm and Schindler, 2000), growth rate and maximum size (Panov and McQueen, 1998), and fecundity (Kusano and Ito, 2005).

Amphipods express a range of reproductive strategies and vary in semelparity between and within species (Aljetlawi and Leonardson, 2003). Mating may occur up to several times, either synchronously or not, over the course of one growing season (Pöckl, 2003; Subida et al., 2005).

Amphipods are often assigned a central position in freshwater foodwebs because of their trophic behavior (cf. Otto, 1998). As versatile omnivores, amphipods are capable of dominating macroinvertebrate communities through adaptation to seasonally shifting food sources (Mac Neil et al., 1997; Summers et al., 1997) such as detritus (Summers et al., 1997), algae, salmon roe (Brown and Diamond, 1984), living vegetation (Kelley et al., 2002); captured invertebrates (MacNiel et al., 1997), fish, and carcasses, thus occupying all of the functional feeding groups (FFG) described by Merritt and Cummings (1984).

The idea of interaction strength between species in foodwebs has been widely studied both observationally and empirically (Laska and Wooton, 1998) though there is disagreement about how strength should be measured. In general, interactions are measured per capita for top down effects of a predator's effect on prey, and for per capita bottom up effects of prey on its predator (De Ruiter et al., 1995). In this study, we used the broader community level interaction strength assigned by a relative probability that the foodweb would become unstable due to variation (i.e. removal) of the given foodweb element (De Ruiter et al., 1995) under the assumption that ecosystem stability relies on patterns of interaction between organisms. Stability of ecosystems in this sense refers to the persistence of “states” within the foodweb. Loss of stability results in increased variability in the interactions among organisms which results in either dramatic changes of “state”.

Nutrients from decaying salmon carcasses are thought to be a critical allocthonous subsidy to otherwise intensely oligotrophic lotic systems (Naiman et al., 2002); but the demonstration of mechanisms involved in cycling and quantitative evidence that salmon-derived nutrients actually increase 1^o and 2^o productivity are elusive (Schindler et al 2003). Nonetheless, Kline et al. (1993) and Chaloner et al. (2002) among others have argued that MDN in coastal rivers may sustain sufficient aquatic productivity to support foodwebs and subsequent generations of rearing salmonid juveniles. One way MDN may be assimilated into foodwebs is by direct predation and scavenging on salmon tissues and eggs by invertebrate consumers (Gende et al., 2002; Chaloner and Wipfli, 2002; Schindler et al., 2003). Several studies (Bilby et al., 1996; Ben-David et al., 1998) used Stable Nitrogen (^{15}N) and Carbon (^{13}C) isotope analysis for tracking pathways of MDN transfer between trophic levels in freshwater systems but interpretations have been controversial owing; 1) to differential translocation of the isotopes (Schindler et al. 2003), and 2) to the drawback that MDN permeation of the foodweb does not necessarily imply any ecosystem level effect of the translocated nutrients (Naiman et al., 2002).

Many studies have documented the enriching effects of MDN (and other fertilizer) subsidy on stream invertebrate size and abundance (Peterson et al., 1993b; Wipfli et al., 1998; Chaloner and Wipfli, 2002; Minakawa et al, 2002) and on terrestrial vegetation (Helfield and Naiman, 2001; Mathewson et al., 2003), though fewer studies have investigated the complete feedback from salmon carcasses to salmonid productivity, and literature on MDN cycling in brown water rivers is scarce indeed. In one feedback study, Wipfli et al (2003) found that in small Alaska streams, feedback resulting in the increased growth rate of salmonids occurred via chironomids, mayflies and other aquatic diptera larvae that scavenged on carcasses. Additionally, SaRON research (Morris, Eberle) on the Kol River (a SaRON observatory with an extensive floodplain) demonstrated that MDN were translocated from salmon through riparian soils and vegetation, to terrestrial arthropods which fell on the stream surface and were consumed by salmonid juveniles. Clearly, river geomorphology, invertebrate community structure and nutrient assimilation dynamics, as well as feeding behavior of fish are all important factors in delineating feedback from salmon to their offspring.

In systems where the invertebrate community includes amphipods, fish such as trout (Gonzalez & Burkhart, 2004) and sculpins (Andersson et al., 1986) are amphipod predators, as are other amphipods (Dick, 1999); feeding often is size selective for larger individuals (Newman and Waters, 1984; Wooster, 1998). Predation pressure from fishes can influence the development of nocturnal behavior in amphipods (Andersson et al., 1986), and can affect habitat selection (Mac Neil et al., 2001).

Food quality and quantity lead directly to survival and growth in rearing juvenile fish. High quality foods such as salmon tissue and eggs are enriched with important fatty acids and other nutrients which clearly fosters growth of consumers (Bilby et al., 1998). The idea that invertebrates enriched with salmon derived nutrients increase salmon productivity has been widely postulated but only superficially demonstrated (Bilby et al., 1996; Wipfli et al., 2003). Furthermore, studies on MDN cycling in brown water tundra rivers are lacking. This is a key issue because in the cold rivers of the Pacific Rim, salmonids must survive harsh winter conditions at a small size, undergo the physiological stress of smoltification, migrate long distances to the sea, and avoid predation and competition with larger (body size) cohorts (Kirillov and Kirillova, unpubl.).

Hundreds of brown water rivers exist within the range of Pacific salmon, collectively producing a significant portion of the salmon and salmon-related biodiversity of the Pacific Rim; Kamchatka especially is a key salmon producing region (Augerot, 2005). These rivers are characterized by dark colored water, stained brown by the humic and fulvic acids accumulated as water leeches through the *Sphagnum* tundra mat that overlies the coastal lowlands in much of Western Kamchatka. *A. kygi* appears to be an abundant consumer species in all of the brown rivers we have investigated. Thus, the role of *A. kygi* in the community ecology of brown water rivers, especially in relation to cycling of nutrients from salmon spawners, is an important void in our understanding of salmon river ecology.

STUDY SITE

The Utkholok River is located at 57° North Latitude on the Western Coast of Kamchatka, Russian Federation. The extreme headwaters (elev. 240m) are in coastal hills but tannic tundra tributaries draining the coastal plain dominate the flow. Thus, the Utkholok is low gradient (average Δ elev. = 12m over 50 km), with a constrained channel that meanders through the lowland *Sphagnum* tundra. Braided flood plains are almost completely absent from the river corridor (Fig. 3).

A

B

Fig. 3a. The Utkholok River in fall, 2006, showing the Keislyy tributary, a small tannic stream flowing through the *Sphagnum* tundra that dominates the ancient flood plain of the river and most of the upland areas as well. Scouring flows are limited to the main channel. The upland green areas are dense *Pinus pumila* stands, with old growth birch forest (*Betula ermanii*) occurring on well-drained sandy soils.

Fig. 3b. The Utkholok channel at the location of our SaRON camp in early spring. Note the point bar on the right and an eroding tundra bank on the left; alternating point bars of the meandering channel are the primary geomorphic pattern of this river system from headwaters to the Sea of Okhotsk. The river in this view is near base flow, and the water is the tea color (brown-water) characteristic of rivers draining tundra landscapes world wide.

Fig .3 right. Kamchatka Peninsula showing location of the Utkholok River on the Western Coast

The Utkholok flows into the Sea of Okhotsk through a large (0.5km wide, 5km long at high tide) estuary with a strong tide (>4 vertical meters) that flushes to freshwater at low tide. At high tide, river flow is impounded some 5km upstream of the estuary.

The Utkholok River corridor meanders through the coastal tundra landscape (Fig. 3a). Woody vegetation along the very narrow riparian zone of the river was predominantly shrub willows (*Salix spp*), *Chosenia* sp. and alder (*Alnus spp*.) with under story of various grasses (*Poacea spp*.) and herbaceous plants (*Filipendula kamchatica, Senecio spp.).*

The Utkholok hydrograph during the study period increased with snowmelt in May-June and heavy rains in July-October; flow changes are moderated by the extreme storage capacity of the tundra 'sponge'. The tundra *Sphagnum* mat is expansive and is 1-5 m deep throughout the coastal plain of Kamchatka proper. Nonetheless river stage responded to sustained rain events, after tundra saturation (Fig. 4).

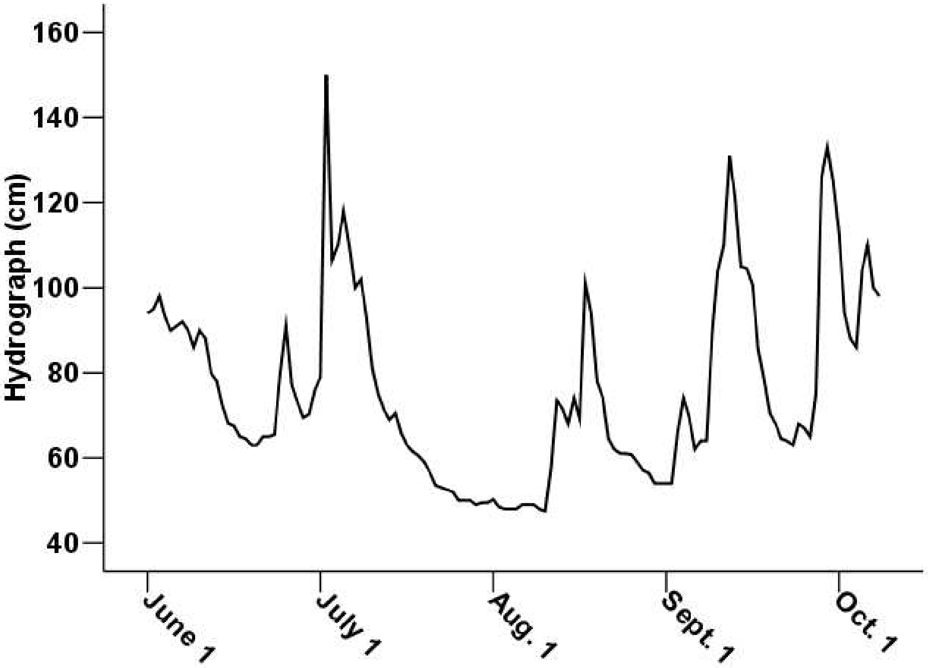


Fig. 4. Daily river stage for Utkholok at Main Camp (Fig. 3). The flow peaks corresponded to major rain events associated with passage of typhoons.

Temperature in the main channel from May to October varied from 2.6^{o}C to 23.5 ^{o}C with a seasonal average of 11.23 ^{o}C (STD=2.79 ^{o}C) (Fig. 5). Upstream of the confluence with Kolkalvayam, the only major tributary, mean temperature was the same though the range was more narrow (4.1 °C to 17.8 °C).

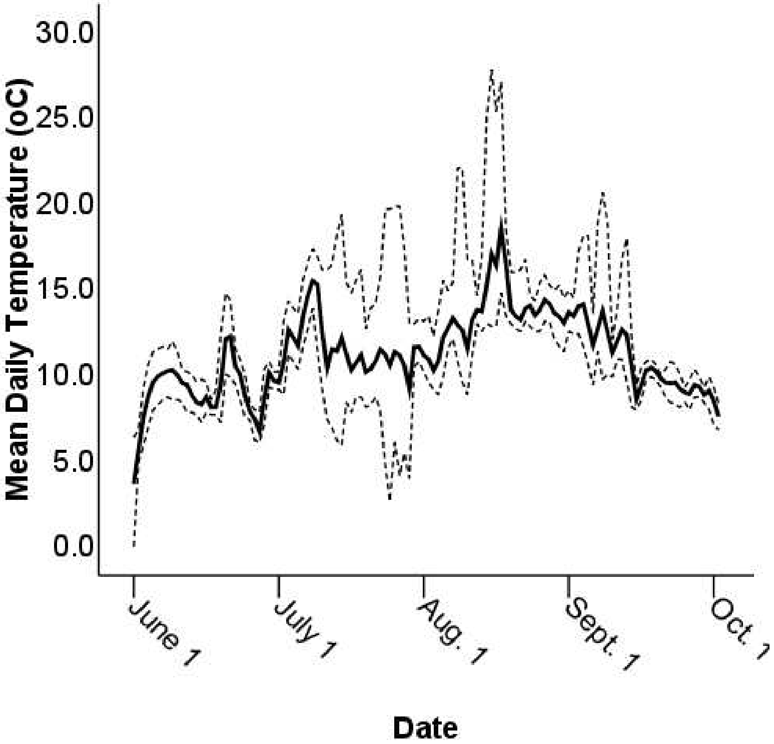


Fig. 5. Daily mean temperature at Utkholok near Main Camp from data loggers. Solid line connects mean daily temperatures for n=24 hourly readings per day. Dotted lines define maximum and minimum values from n=24 hourly reading per day.

From 2003-2006, the Utkholok had a fish assemblage with a range of life history forms including: all five described life history forms (and additional dwarfs) of *Onchorynchus mykiss* (rainbow trout/steelhead), large runs of *Onchorynchus gorbusha* (Pink salmon, even year high), three groups of *Onchorynchus keta* (Chum salmon--spring, summer, and fall), a small spring run of *Onchorynchus masu* (Cherry salmon), and moderate late-fall runs of springbrook spawning *Oncorhynchus kijutsch* (Coho salmon) and *Oncorhynchus nerka* (Riverine Sockeye salmon). Resident (dwarf) and anadromous forms of *Salvelinus malma* (Dolly Varden char) and *Salvelinus kundza* (White Spotted char) were abundant as well. Non-salmonids included four life history forms of *Letentron japonicum* (Pacific lamprey, described by A. Kutcheryavyy, 2007 unpubl.), anadromous three spine sticklebacks (*Gasterosteus aculeatus*), resident nine spine sticklebacks (*Pungitus pungitus*), and starry flounder juveniles (*Platichthys* *stellatus*). Anadromous fishes were present in the river at all times, though spawning of pacific salmon reached peak intensity during late summer (Fig.6).

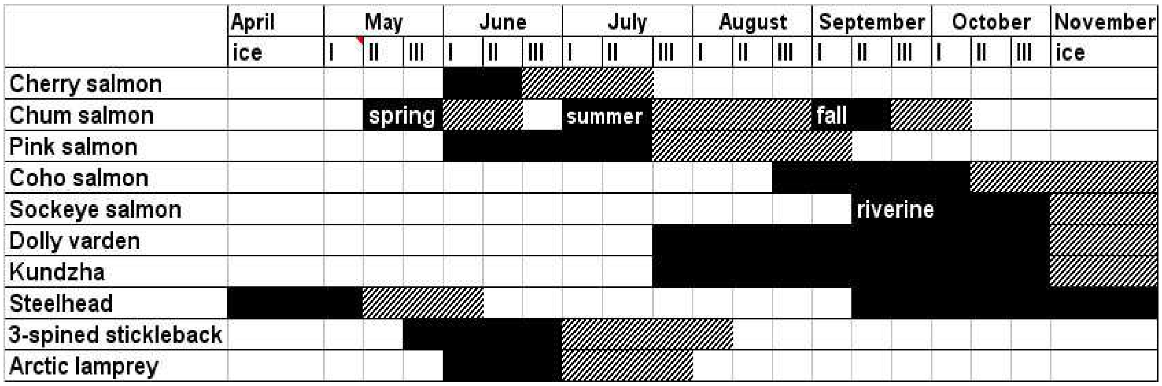


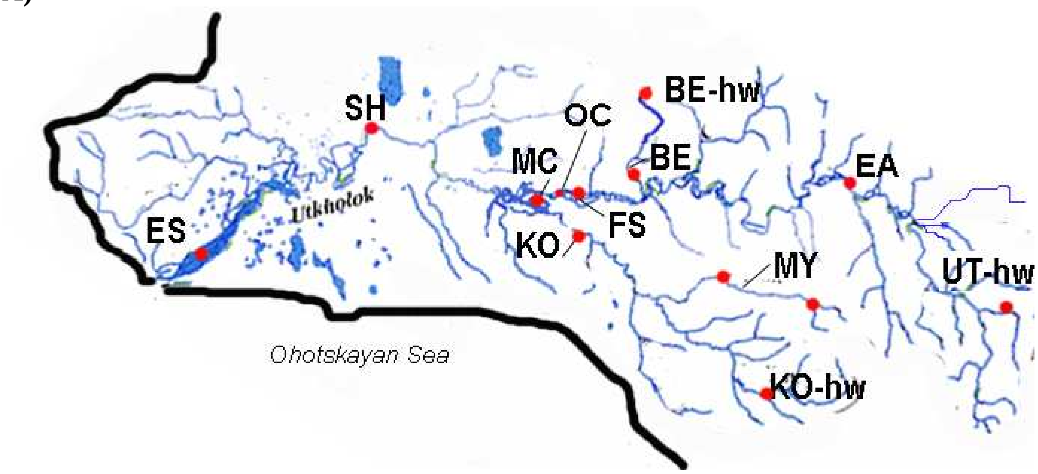
Fig. 6. Run timing of anadromous fishes at Utkholok. Run timing data was derived from 1) bi-monthly index netting near the main camp and 2) daily observations by field scientists working on the Utkholok. Solid bars represent timing of observed runs for 10 day intervals of each month (I, II, III). Shaded bars represent spawning period in the river. Three groups of chum salmon were observed—small individuals in May/June, main channel spawners in the summer, and springbrook spawners in the fall. Steelhead arrived in the fall, but did not spawn until spring. Coho and sockeye spawned in late October and November. Dolly Varden and Kundza (white spotted char) arrived in the river behind the pink and chum salmon, but do not spawn until late-September / October; many of these char were observed to have stomachs full of salmon roe.

Sampling sites

Four focal study sites were selected that represented a wide range of habitat types occupied by *A. kygi* within the SaRON study reach. Focal sites were located in areas also being sampled for SaRON cross site metrics; additional synoptic sites were established in headwater areas of the focal streams, and at the Utkholok estuary (‘ES’ in Fig. 7). The objective in site selection was to sample widely and in diverse habitats such that density and distribution of amphipods could be described relative to environmental conditions of the entire catchment (Fig. 7).

Focal sites included; Main Camp [MC] a main channel shallow shoreline/riffle area (elev. 4m), Kolkalvayam [KO] a large brown tundra tributary (elev. 6m), Byezemanya [*Biz-ee-man-yee*, BE] a small clear upland tributary (elev. 13m), and Fossil Springbrook [FS] a parafluvial spring (elev. 6m) (Tab. 1). This springbrook was one of only two spring channels that occurred in the entire 50km study reach owing to limited floodplain development of the predominately constrained channel of the Utkholok. However, flood plain springbrooks are specific habitat types utilized for SaRON cross site comparison work and FS was included in this study for that reason.

A)



B)

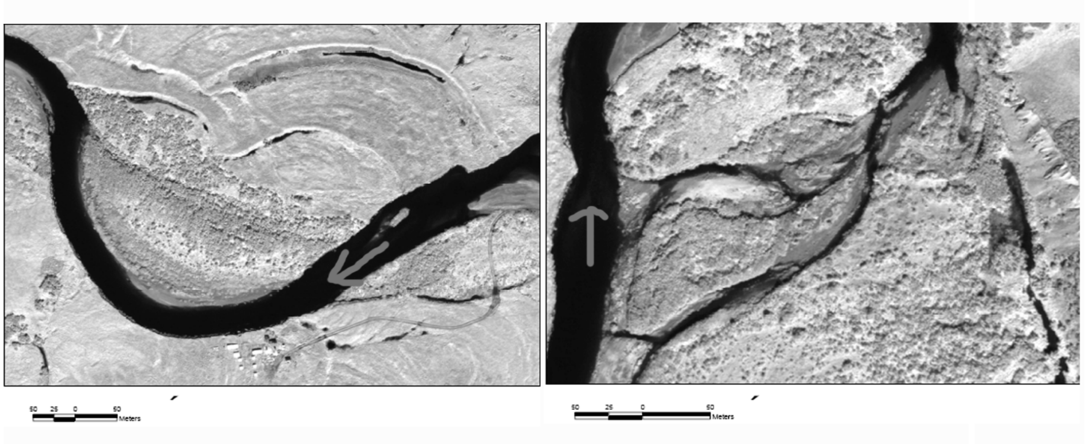


Fig 7a. Utkholok River and tributaries with 2006 sample sites**.** **MC (Main Camp)** is the location of the Utkholok Biostation and river stage staff plate. **UT-hw (Utkholok headwaters)** is a small upland stream at the top of the navigable river; **KO (Kolkalvayam)** is the major tributary to Utkholok; **KO-hw (KO headwaters)** is a small brown water tundra stream. **BE (Byezemanya)** is a small, clear tributary draining the sand slows of the birch-dominated uplands; **BE-hw (BE headwaters)** is an upland spring creek flowing from sandstone bedrock. **FS (Fossil springbrook)** a rare floodplain parafluvial springbrook; **MY (Mysmont)** is a brown water tundra stream at its confluence with KO, and an upland spring creek at its source in the coastal mountains; **SH (Schoolhouse)** is a down river site used for synoptic drift sampling; **ES (UT estuary)** is also shown.

Fig. 7b. Quickbird satellite imagery. **Left)** Utkholok SaRON biostation at main camp**.** The camp is visible at bottom center (vehicle tracks are from modified military tanks that occasionally access the camp; most access is by helicopter only). As the river nears the sea, point bar such as that shown develop as the river deposits gravel and sediment on river left and erodes fresh sediment from the bank on river right. Note limit of leafy vegetation (mostly *Salix spp)* at the point bar. Abandoned river channels form backwaters which fill with sphagnum, limiting tree growth (mostly *Salix spp,* and *Alnus spp)* to the point bar. **Right)** Fossil Springbrook shown flooded over from the Utkholok Main channel. White arrow indicates source of the spring from the alluvial aquifer. Vegetation is *Salix spp* and *Alnus spp*

	Habitat	Stream Width (m) at Base Q	Stream Max Depth (m) at Base Q	2005 Max # Carcass/ 50m	2006 Max# Carcass/ 50m	Substratum
BE	Upland Tributary	2	.60	4	1	cobble on bedrock/sand
FS	Parafluvial Springbrook	1	.20	8	1	gravel on sand/ upwelling
KO	Tannic Tributary	12	.80	16	6	cobble on gravel
UT	Tannic Mainstem	22	.80	40	30	cobble on gravel

Tab. 1. Habitat characteristics and stream size at the main study sites. Stream width and maximum depth were measured at the same location repeatedly for calculation of Q (discharge). Carcass density was measured using a standard point-quarter technique (described below in Methods).

METHODS

Main Camp (MC), Kolkalvayam (KO), Byezemanya (BE), and Fossil Springbrook (FS) were sampled every two weeks, two sites a day, for; flow, temperature and water quality; benthos (3 samples); day-drift (2 samples); and fish diet (10-20 fish).

Flow, Temperature and Water Quality Patterns

Temperature was recorded hourly using Vemco dataloggers deployed at the four focus sites (Fig. 7a). This thermal data is a subset of the multi-year thermal regime analysis in six river systems that is part of the SaRON project. Every day at MC and KO, and during sampling at the other sites, additional physical measurements included point temperature, dissolved oxygen, specific conductance, and pH using an electronic Horiba sonde (pH, was calibrated every two weeks, DO was calibrated in air weekly, and the membrane cleaned every two weeks).

Other measurements, taken during amphipod sampling included point velocity and discharge, measured with a SonTek Flow Tracker. The hydrograph was measured in centimeters daily with a staff gauge installed near the confluence of Kolkalvayam tributary with the Utkholok mainstem (see Fig. 7a. above).

Spatial and Temporal Distribution of A. kygi

A. kygi density in the benthos was measured bi-monthly at the four main study sites (MC, KO, BE, FS). Samples were not collected when flooding prevented access to appropriate riffle habitat. For each site, three repetitions of benthic sampling were performed using standard methods for a Stanford-Hauer kick-net. Amphipods were stored alive in 500ml plastic containers for transport to the laboratory. If samples appeared to contain too few amphipods for analysis of population structure (less than 100), additional amphipods were non-quantitatively collecting using a Kinalyovka net. This net is a trapezoidal frame with parallel sides of lengths .25 and .5m, spaced .25m apart. The frame is covered with 5mm netting, and is operated by holding it in the stream and disturbing the benthos.

In the laboratory at the SaRON camp (MC), samples were transferred in small amounts to a plastic insect sorting tray, and clean river water added. All amphipods were removed from the sample, preserved in 4% formalin and stored in 4 dram glass vials.

Drift of A. kygi

During bi-monthly amphipod sampling at each focus site, drift sampling was completed during the day in two ten minute expositions of a.75m diameter, 250*u*m-mesh plankton net. At the shallow sites (BE, FS, and KO in low water), a .25m diameter 250*u*m plankton net was used instead. Velocity at the mouth of the nets was measured using a SonTek Flow-Tracker, adjusted to the depth of the stream.

Nighttime drift sampling was done weekly in single one minute expositions near the camp at the Main Channel and at Kolkalvayam, and adjusted each week to coincide with the darkest time of the night. Drifting density was calculated as total amphipods/ cubic volume*s^{-1}. All amphipods were preserved in 4% formalin and stored in the laboratory until processing.

Life Cycle and Growth

All amphipods collected during benthos, drift, and synoptic collections were measured with a calibrated ocular micrometer under a stereoscope (5x). Measurement of all amphipods included; body length (L) from base of peduncle (1st antenna) to base of the telson; sex (male/female/immature). For mating pairs collected in amplexus (male grasping the female body segments) additional measurements included; gnathopod size (G1 and G2) as length of 1st and 2nd gnathopods from base of claw to 1st segment of wrist); and head capsule (H) from the peduncle to pereon (Fig. 8).

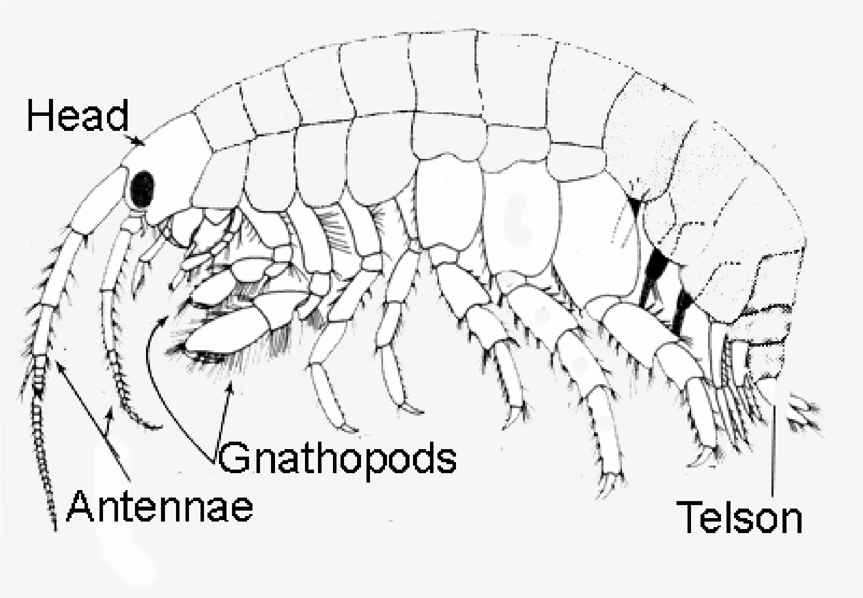


Fig. 8. Diagram of amphipod body sections showing the head, gnathopods, peduncle, pereon and telson, used for morphometric measurements. Males have large 2nd gnathopods as shown here whereas females have 1st and 2nd gnathopods of similar size. The larger gnathopods in males are used during mating, to grasp the body segments of the female. This reproductive position, called "amplexus" may be maintained for some time before sperm is transferred to the female (after Barnard and Karaman, 1991).

Fecundity for all ovigerous females was measured under a stereomicroscope using a dissection needle to pin open the coaxial plates, and a micro-dissection spoon to scoop eggs or neonates out of the brood-space. Neonates typically hatch and are carried in the brood-space until proactively released by the female. The total number of eggs or young recovered was counted and ten individual eggs or young were measured (diameter for eggs on the longest axis, and length for young).

Amphipod body length (L) was used in analysis of growth, and descriptive size distribution statistics. For presentation of general densities, however, all amphipods were assigned to five size bins: 1-3mm, 4-9mm, 10-14mm, 15-19mm, 20-24mm, 25+mm. Binning the data allowed demonstration of life history patterns.

Amphipods were dried after all other meristic measurements were completed. Amphipods were placed in individual wells of a 96 well plastic sorting tray under a 250 watt heat lamp for 10 days, then massed using an analytical balance (AND model HR-60, .0001g). Dry mass was used in calculations of length-weight relationships used in morphometric analysis.

Aquaria were prepared to measure growth of juvenile amphipods and to investigate feeding behavior. Three fifty liter tanks were filled with clean river water, and maintained at cool temperatures in the laboratory with an aquarium chiller and stream-flow filter. Adult females with brooding young were introduced into these aquaria on several occasions but all failed to live longer than 24 hours and a successful brood was never obtained with which to begin growth analysis.

Feeding preferences were investigated qualitatively to explore omnivory by offering food items such as salmon roe, smaller amphipods, juvenile fish, algae, carcass flesh or aquatic invertebrates, to a tank with 50 or 100 like-sized amphipods. Behavioral responses were recorded to examine whether carcasses and juvenile fish would be preferred over algae or plants.

Distribution and Abundance of Salmon Carcasses

Density of carcasses in aquatic and terrestrial habitats was measured in two ways. First, at Old Camp ([OC], see Fig. 7.) in 2005, carcasses were enumerated in fixed rectangular plots (25m x 2m) over time, along two aquatic and two terrestrial habitats including a tundra pool (1.0-2.0m deep), shallow shoreline (.10 to .5m deep), gravel bar, and vegetated river bank. Beginning August 10th, 2005 the total number of carcasses in each plot was tallied every 2-5 days until a large flood on August 27th made counting carcasses in the aquatic habitats impossible. Second, in 2005 and 2006, density of carcasses was measured along 50m transects using a standard point-centered-quarter technique. Transects were 50m long and parallel to the river with enumeration points spaced at 10m intervals. These transects were used for lateral and longitudinal carcass distribution surveys (described below). For each carcass, the distance from the center-point was measured, and species, length, weight, sex and decay were noted. This technique had two applications: 1) Lateral distribution away from the river and 2) Longitudinal distribution along the river corridor.

Lateral distribution was important to quantify because spatial deposition of marine derived nutrients from salmon is a key aspect of SaRON work on foodwebs. Lateral distribution was measured using three 50m transects, parallel to the river at distances of 1m, 3m, and 5m. This was completed at all main *A. kygi* study sites, SaRON protocol sites on the Utkholok main channel, and gravel bars used for longitudinal distribution measurements.

Longitudinal distribution along Utkholok was measured once in 2005 and once in 2006 (including Kolkalvayam) when carcasses were abundant. Beginning as far upstream as possible (Eagle's Nest on Utkholok, and the Mysmont confluence on Kolkalvayam, Fig. 7) three parallel 50m transects, were completed at each of 10 gravel bars, evenly spaced along the length of the river. This application was also used to enumerate carcass density along single gravel bars and pools, whereby transects were completed at the upstream and downstream end of each habitat.

Utilization of Salmon Carcasses by A. kygi

Biota from bears to microbes feed on salmon, alive and dead. We focused on the consumption of carcasses regardless of the source of mortality though most of the carcasses lying on the bed and banks of the river simply resulted from post spawning death. In any case, for each carcass that was sampled we recorded; species, fork length or mandible) in mm; weight (wet biomass) using a 10kg spring-scale with .2kg accuracy or .750g spring-scale with 10g accuracy; sex (based on morphology); and decay index. Observations were made on presence of fungal growth, amphipods, bear chewing, etc.

Consumers of decaying carcasses were sampled in two ways. In 2005, a cage-retention experiment was conducted with methods similar to Chaloner et al. (2002) in which carcasses of like species and size were secured in large mesh envelopes (benthos-side .5mm fiberglass mesh, river side standard steel chicken-wire) anchored in pools, and along shallow shorelines. Cages were removed at regular intervals, all consumers collected, identified, measured for cumulative wet biomass, and sampled for nitrogen and carbon stable isotope analysis.

We attempted to replicate the cage experiment in 2006 with a greater number of cages, however, after cages were placed back into the river, bears removed and destroyed 98 of 100 cages over 24 hours. Thus, a new sampling method was employed whereby carcasses were removed from the stream using a paddle-scoop constructed with .5mm fiberglass mesh stretched over a .5m^2, long handled frame. Collections took place during mid-morning (usually from 10am-1pm). Undisturbed carcasses at rest in aquatic habitats were carefully scooped from the river bed and transferred immediately to a large bucket. All scavengers were picked from the carcass, placed in 500ml whirlpak bags and preserved in 4% formalin until processing in the laboratory. All taxa were sampled for stable isotope analysis as part of the SaRON foodweb analysis.

Samples collected for analysis of δ^{15}N and $\delta\ ^{13}$C in this study were returned to the Flathead Lake Biological Station (FLBS), Polson, Montana for processing

Predation on Amphipods by Fish

The importance of amphipods in the diet of fish was addressed using gastric lavage (for salmonids >50mm) or gut dissection (for salmonids <50mm and sticklebacks of all sizes). A total of 247 and 450 juvenile fish were analyzed in 2005 and 2006, respectively between May and October. Fish were captured during bi-monthly amphipod sampling in the four main study sites (Byezemanya, Fossil Springbrook, Main Camp and Kolkalvayam) using electro-fishing (Smith-Root battery operated backpack electrofishing unit, settings: 760Volts, 60Hz, 12.5% duty cycle), or minnow traps baited with salmon eggs. The first 10-20 fish captured were sampled at each site. SaRON has a protocol for quantitative three-pass electrofishing and growth analysis by site which requires the collection of length weight data of juvenile salmonids. These data were used in this analysis to address change in condition factor over time relative to diet.

Gastric lavage was performed using a 20 ml plastic Nalgene syringe fitted with a 5cm length of flexible plastic tubing with diameter of 2mm (for fish 80-100mm) or 4mm (for fish between 100-250mm). YOY and fish less than 80mm were sampled using a 1.7 ml Samco plastic dropper pipette. Prior to lavage, each fish was measured for species, length and weight. Lavage tube was inserted into the mouth until contact was made with the esophagus. Water was pushed into the stomach until full and then the tube slightly withdrawn and an additional jet of water expelled from the syringe to expel stomach contents. All fish received three consecutive evacuations of water over a plastic insect tray. Regurgitated food items were collected, strained using a 64um brass filter, transferred to 4 dram vials and preserved in 4% formalin.

For analysis, stomach contents were rinsed of formalin and identified to family if possible using Lehmkuhl (1974) and Band (1978). Individual prey items were counted, and the whole sample was dried under a 250 watt heat lamp for ten days, and weighed to .01mg using an AND Hr-60 analytical balance. Dry biomass of the entire stomach was recorded for each fish. For general analysis, prey was divided into five general categories; a) amphipod b) terrestrial invertebrate (any coleopteran, winged dipteran, arachnid, lepidopteron, etc. that was at a terrestrial life history stage), c) aquatic invertebrates (any aquatic stage of diptera larvae, nematoda, water mites, etc. d) roe (eggs of salmon, char, or sticklebacks (rare)), e) YOY (alevin or fry of salmonids).

RESULTS

Flow, Temperature and Water Chemistry Patterns

n=39 for all Mean s (not Q)		**Temp (oC)**	**Sp.Cond (mS/cm)**	**pH**	**DO (mg/l)**	**Base Q (m3/s)**
BE	**Mean**	7.24	.10	7.81	12.23	.1760
	Min.	3.00	.08	7.19	7.39	
	Max.	9.90	.11	8.37	15.80	
FS	**Mean**	8.67	.09	7.77	9.50	.0128
	Min.	4.70	.05	6.94	5.02	
	Max.	12.20	.12	8.43	14.28	
KO	**Mean**	10.41	.07	7.92	11.80	2.1800
	Min.	1.90	.05	7.38	9.37	
	Max.	13.40	.11	8.29	14.90	
UT	**Mean**	10.63	.07	7.39	11.00	3.8100
	Min.	4.90	.05	6.90	6.37	
	Max.	14.90	.09	7.80	14.57	

Tab. 2. Habitat characteristics for 2006 main study sites MC (UT), KO, BE, and FS. Water quality measurements reflect mean values for the period from June 1, 2006 to October 1, 2006 from observations on 39 days. Base Q was measured at the lowest observed water level in 2006.

As noted above the flow in the Utkholok was high in spring due to snowmelt and was very responsive to summer and fall rain events. The Utkholok was frozen from November to mid-May each winter 2004-6. Peak temperatures occurred during mid-summer periods of low water (Fig. 5.) Note that the river warmed rapidly to around 10C in spring owing in part to the high insolation of the brown water; but the river also cooled during rainfall events. Seasonal high occurred in early August, associated with the lowest flow periods (Fig. 5.) Seasonal flow and temperature patterns were similar across sites, though mean temperatures at upstream clear-water sites (i.e., BE and FS were significantly lower than at UT and KO (p = .017 for a mean difference of 3.4^{o}C from an independent samples t-test).

Specific conductance at BE and FS was higher than at UT and KO (p value=.001 for a mean difference of 0.034 *u*S/cm from independent samples t-test). Thus, in general, the brown water sites (UT(MC) and KO) were warmer and had generally lower conductivity than spring/upland sites (FS, BE). The same was observed during synoptic measurements at the brown water headwater sites (KO-hw, MY) compared to the clear water ones (UT-hw, BE, MY-hw).

Finally, carcass deposition following the salmon run in late summer is variable between main sites (see Fig. 7) and did not occur at all in upstream synoptic sites (described below).

Spatial and Temporal Distribution of A. kygi

As anticipated, spatial distribution of amphipods was highly variable over time and at the different sampling sites (Fig. 9). On the first day of sampling, May 28, 2006, amphipod densities at MC (16/m^2 (SE=3.04)), and KO (21.3/m^2 (SE=9.09)) were the lowest recorded for the entire season, including mostly smaller individuals (<14 mm) (*Fig. 11*). Initial densities and size range were greater at BE (196.0/m^2 (SE=80.9)) and FS (243/m^2 (SE=79.3)) than MC and KO, but still low compared to previous years' observations.

Beginning in early June, however, we observed a large scale upstream migration of thousands of large ovigerous female amphipods swimming upstream from sites as far downstream as school Schoolhouse ([SH], Fig.7). This migration occurred continuously during the first two weeks of June, and individuals were observed passing BE in large numbers (more than 15km from Schoolhouse). Individuals sampled from the migrating group were all large ovigerous females with a mean length of 22.0mm (SE= 0.13). Females swam along shallow shorelines in low velocity water, and in deeper water along tundra pools (23 ind/m^3 +/- 5). The rate of upstream travel was measured at 12.85cm/s (SE= 1.87, n=10), demonstrating a travel potential of approximately 70km/wk, which, given the low gradient, meandering character of the Utkholok, is unimpeded by any physical boundary (see http://www.umt.edu/flbs/People/AThompson/default.htm to view video clip). These highly mobile individuals were very fecund (~70eggs/female, data presented below), and following the release of their brooding juvenile cohort (1-3mm) in mid/late June, density of amphipods in the benthos at MC increased an average of 600 amphipods/ m^2 (Fig. 9). KO density likewise increased though not until early July.

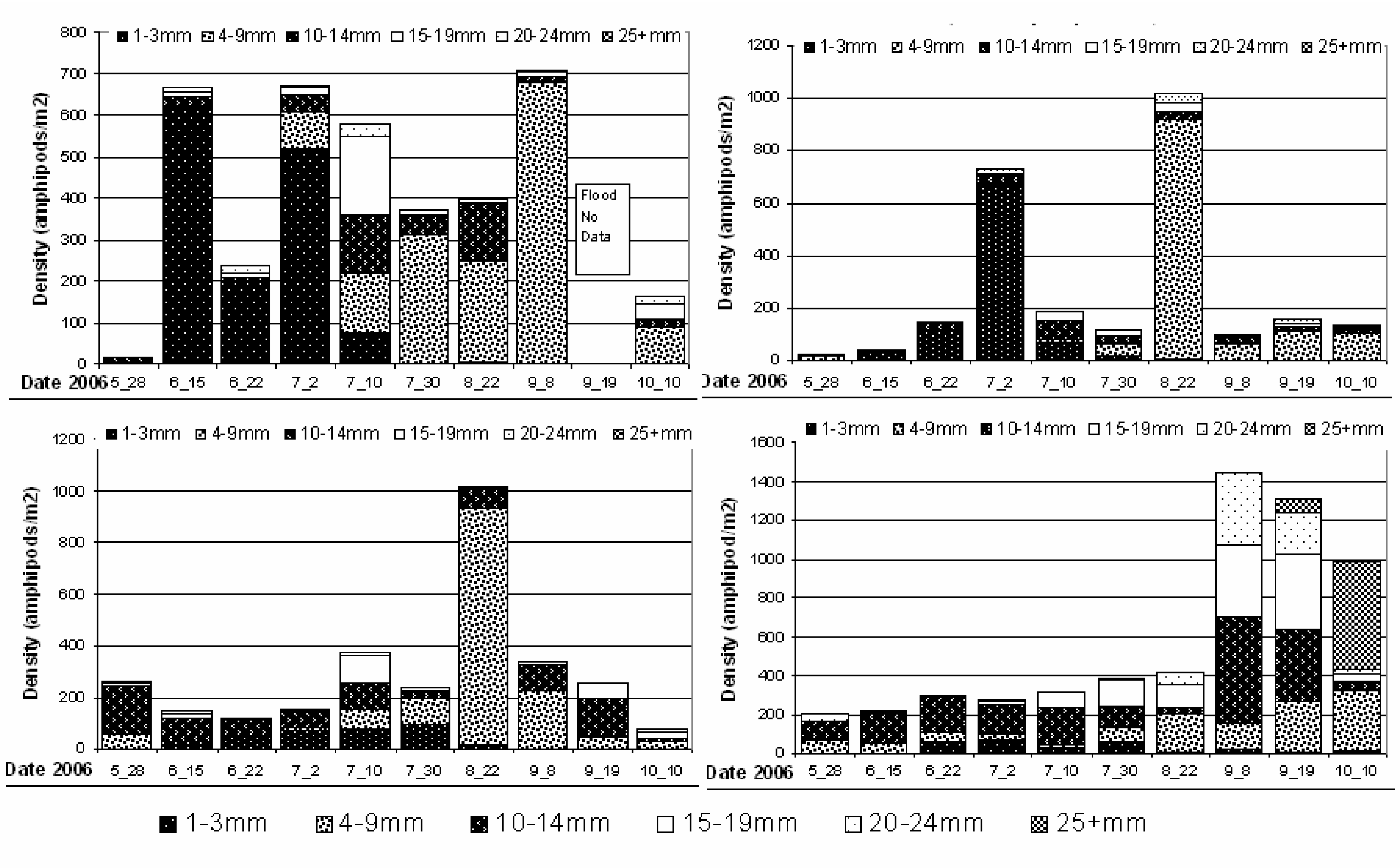


Fig. 9 2006 Seasonal benthic density for all sites stacked by size class. May- October 2006. MC (top left): Main Camp density shows a peak in early June of 1-3mm individuals. Subsequently, a large portion of overall seasonal density is attributable to amphipods of size class 1-3mm, and 4-9mm. A similar, though later peak in density (also from 1-3mm juveniles) was evident at KO (top right). Kolkalvayam. KO and FS (bottom left). Fossil Springbrook share a peak in 4-9mm density in late august. KO, FS, and

Migrant females did not enter FS or BE in great numbers, and consequently the benthos at these sites did not contain as many 1-3mm amphipods in early spring as the other sites (Fig. 9), perhaps due to different thermal conditions at those sites. However, both of these sites contained a larger and more consistent number of 10-19mm amphipods throughout the season than MC and KO. A second much smaller group of 1-3mm amphipods appeared at BE and FS in July, in the absence of migratory females, suggesting a two-period production of young (see below).

The large increase in densities at all sites between August 22nd and September 8th was concurrent with the first major summer rise in the hydrograph (increase of 50cm), as well as the first appearance of salmon spawners in the river. At this time, average density increased at MC by 400 amphipods/m^2, at FS by 800 amphipods/m^2, and at KO and BE density increased by 1000amphipods/m^2. The peaks at MC, KO, and FS were almost entirely 4-9mm amphipods, while at BE, the newcomers consisted of mostly very large (>20mm) amphipods, not previously observed to be so abundant at this site.

The abundance of juvenile amphipods in the river (following brood release from migratory females) coupled with synchronous density increases over time covering two orders of magnitude, reinforced how abundant and mobile these organisms were.

Drift of A. kygi

Given the spatial and temporal variability in amphipod abundance observed, we expected corresponding high levels of drift activity in the water column. As expected, drift, especially of small cohorts, was observed, with greater intensity during the night than during the day. Diel drift dynamics were measured at all four sites at 12 hour intervals (1400hr and 0200hr) on July 11, 2006. Mean amphipod density per unit discharge increased at all sites by a factor of 4-10X between light and dark samples, though size distribution was unchanged.

Seasonally, in weekly 1 minute night drift samples at Utkholok and Kolkalvayam, amphipod density averaged about 5 individuals/m3*s^{-1} with two major peaks of intensity on Utkholok, and one on Kolkalvayam (Fig.10). The Utkholok peak observed on 6/13 included 4,500 individuals of sizes 1-3 and 4-9mm. This abundance of small sizes correlates exactly with the timing both of brood release by ovigerous females, and appearance in the benthos of abundant juvenile amphipods at Utkholok. The subsequent peak on both Utkholok (7/20 with 2,200 amphipods/min) and Kolkalvayam (7/20 with 3,200amphipods/min) also consisted of small size classes (1-3, 4-9mm) *A .kygi* and correlated exactly with the arrival of 1-3mm amphipods in the benthos at KO. After 8/29, drifting amphipods were of much larger size (15-30mm) and drift was relatively less intense, but still between 200 and 1,000 adult amphipods/min.

A least squares multiple regression was performed to test the hypothesis that temperature or changing hydrograph may explain some variance in seasonal drift intensity however no reasonable model using temperature or hydrograph could be adequately fit to drift intensity. We concluded simply that the amphipods were constantly moving about, perhaps in search of food.

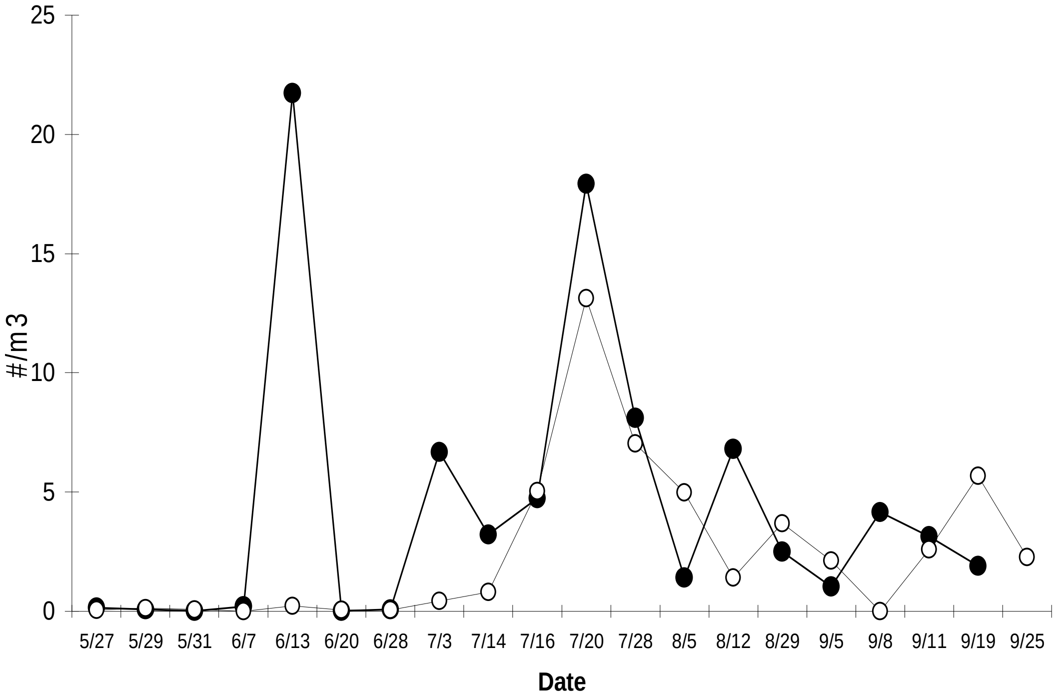


Fig. 10 Drift of *A. kygi* based on two successive night-time expositions (1 minute duration) at Utkholok near camp (shaded circles), and at Kolkalvayam (open circles) 1 km upstream from the confluence with Utkholok. Peaks on June 13 and July 20 were small cohorts of *A. kygi* while drifting activity later in the season was predominantly larger cohorts.

Indeed, the large movement downstream of small amphipods observed in the July 22, 2006 drift sample at the main stem site was unexplained but interesting since brood release occurred several weeks earlier. So, to determine the downstream extent of juvenile travel associated with this event, we completed a synoptic drift sampling at “Schoolhouse” (SH, see Fig.7). This site is approximately 12km downstream from Main Camp, and less than 5km upstream from the estuary. At SH, tidal impoundment caused a >1.2 vertical meter increase in river stage; and flow shifted upstream at a velocity of 30cm/s. One minute samples were collected during the night at low tide, high tide, and falling tide (Fig. 11).

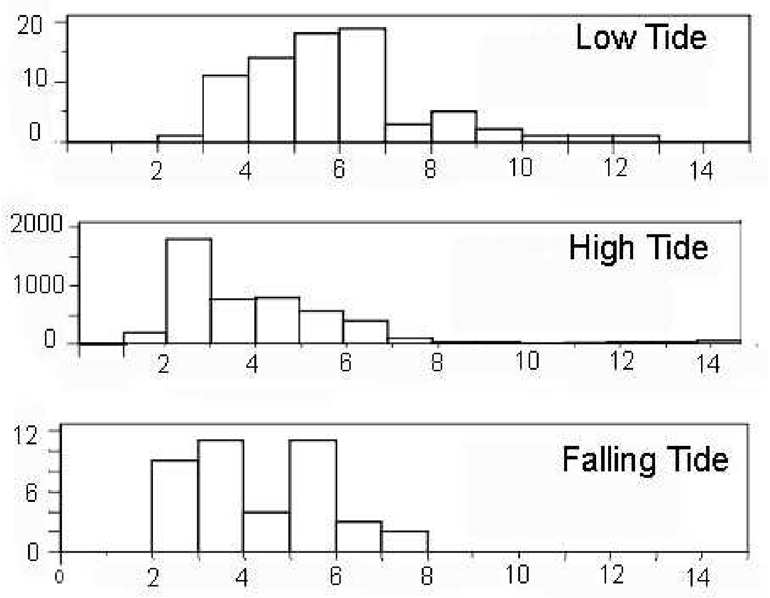


Fig. 11 *A. kygi* drift at Schoolhouse during a dark- time tidal cycle. July 22, 2006. Frequency (y axis) of 1mm size classes of *A. kygi* collected in a one minute samples (x-axis) are shown for Low Tide (top), High Tide (middle), and Falling Tide (bottom). Density and size distribution were relatively similar for Low Tide (76 amphipods /min) and Falling tide (40 amphipods/min), but significantly different for the sample of impounded tidal water, flowing upstream in which amphipod size distribution was skewed toward smaller individuals, with a total density of 4,837 individuals/min.

At high tide, drift was collected in an upstream direction and included not only juvenile amphipods, but Mysid shrimp and flounder alevin as well (estuarine species). Thus, we concluded that juvenile amphipods were conveyed downstream to the estuary or out to sea when the tide ebbed strongly. This implied that either juvenile abundance in the river was greater than the carrying capacity of the benthos, prompting the juveniles to relocate, or that there was a physiological reason or life history strategy that motivated movement to saline/marine conditions. In either case, the presence of juvenile amphipods in such abundance at a distance so great from where they were released from brooding females further supported our strong notion of amphipods as abundant, ubiquitous, and highly mobile within the Utkholok River system.

Life Cycle and Growth of A. kygi

In addition to the considerable variability in amphipod densities at the main sampling sites, we also observed considerable variation in body sizes, maturity stages, and sex ratio within samples collected at individual sites over time. This observation, coupled with the identification of a migratory female group, a two-period production of juveniles, and intense juveniles drifting into tidal waters, suggested that the population is characterized by significant life history variability. In 2006, enumeration of female fecundity and observations on timing of reproduction and brood release suggested that that *A. kygi* on the Utkholok may have two distinct life history types or that two species were present. This was indeed clarified by further morphometric analysis (Fig. 12). Two life history forms: “Anadromous” (A-form, migratory) and “Resident” (B-form, non-migratory) were distinctively clear (see summary Tab. 3). We concluded that there was only one species of amphipod because 1) SaRON benthos analysis has identified only one species in 7 samples from MC, FS, and KO, and 2) there were no identifiable morphometric differences other than size at maturity.

In temporal context, A and B form *A. kygi* had different life history patterns over the season. Due to high variability and high mobility of amphipods between main sites, comparisons of growth rate at the different main study sites was not attempted. However, the general growth trends for A and B amphipods were identified from analysis of changes in length frequencies over time at Byezemanya [BE] (Fig. 12). Differences in female fecundity were significant between the female size-classes in Fig 12. (Fig 13) Interpretation of length frequency patterns in the data from Main Camp [MC] and Fossil Springbrook [FS] (data not shown) was more difficult because there were no clear patterns, probably as a result of high mobility within the Main Camp site, and flood induced changes in amphipod assemblages at Fossil.

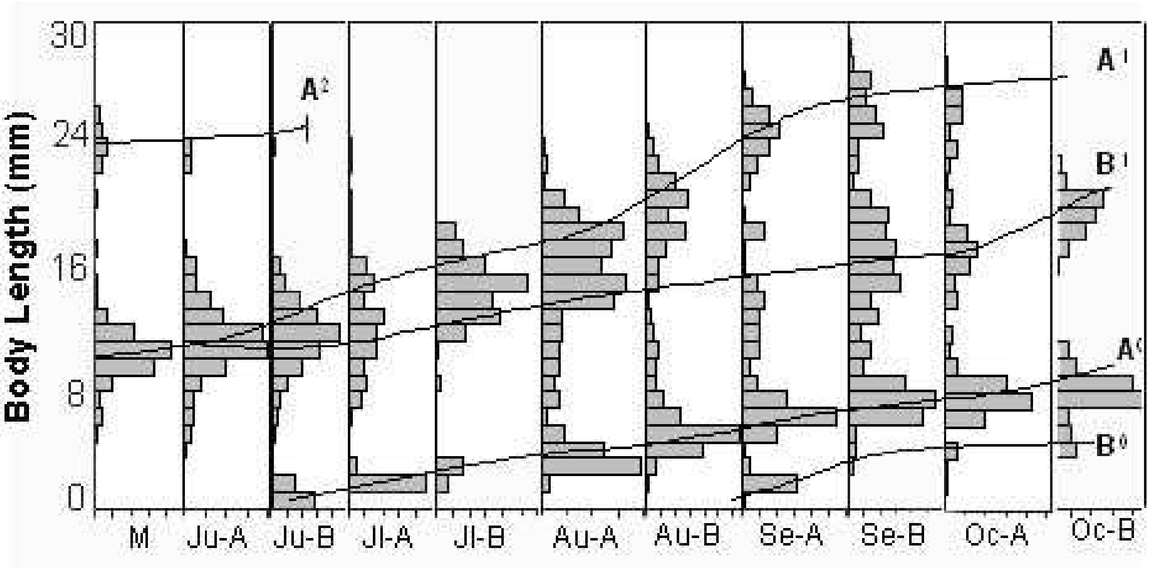


Fig. 12. Life history trajectory of *A. kygi* at Byezemanya Creek (BE) over time. Data are size frequencies (bins) of body length for each sampling date, two per month labeled with the two first letters of the month, and A or B (e.g. Ju-A is the first sampling of June). Two life histories (A - anadromous and B - resident) were apparent, based on characteristics given in Tab. 3. The anadromous form required 2 years to complete the life cycle while the resident form required 1. Young of the year cohorts are indicated by A^o and B^o. The reproductive B cohort and immature (1 yr. old) A cohort are indicated by A^1 and B^1. Ovigerous anadromous females are indicated by A^2. Curves were eye-fit to correspond with Tab 3. .

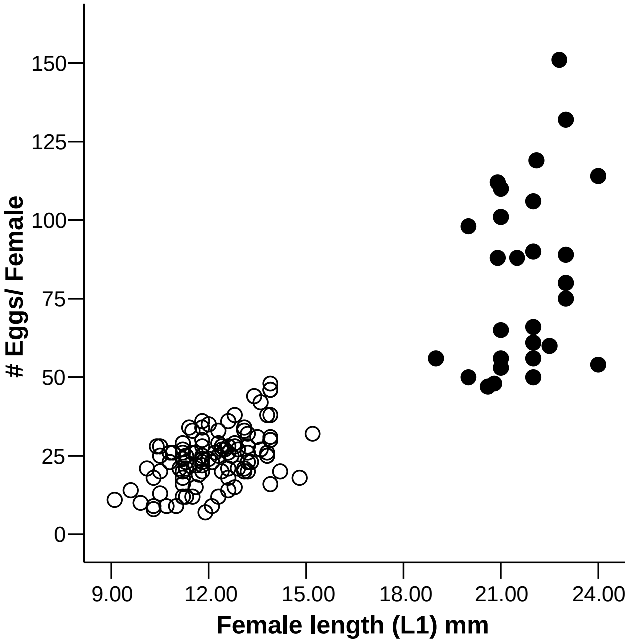
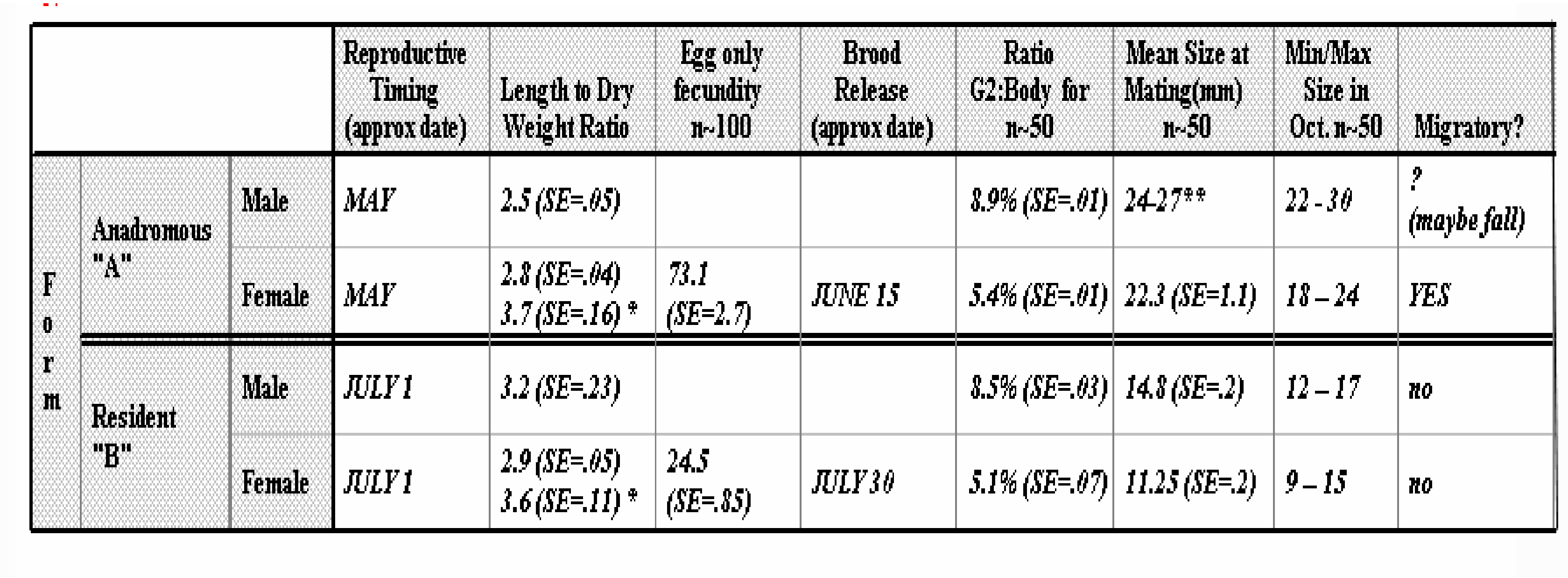


Fig. 13 Fecundity of ovigerous females, 2006. Ovigerous females (n=130) formed two clusters; Large anadromous individuals (shaded circles) with mean length 22.1mm (SE= 0.13) and max fecundity 151eggs; and small resident (open circles) individuals with mean length 11.25mm (SE= 0.1) and max fecundity 48 eggs. Mean egg size was not significantly different between the two groups.

Two distinct groups were present in May, followed by release of the brooding juvenile A^o cohort (<3mm) beginning June 15. The larger initial group (20.8mm ± 2) was predominantly large ovigerous A^2 females that diminished in number to zero with time. The smaller initial group (10.68mm ± 2) was immature A^1 individuals and mature B^1 males and B^1 females. This group diverged beginning in July into faster growing A^1 adults (>20mm) and slower growing B^1 adults (~15mm). B^1 adult females mated in July and produced a new B^o cohort (most obvious in BE). By late fall, there was clear distinction between; 1) Two unsexed juvenile cohorts; B^o of mean length ~5mm, and A^o of mean length ~7mm; 2) a mature B^1 group of mean length ~18mm (♀<♂); and 3) an A^1 group of mean length >22mm (♀<♂).

A-form amphipods appeared to live a full two years, reproducing once in the river. It seemed that A-form females either died or left the system after releasing their broods since they were not subsequently found in the benthos. B form amphipods were brooded and released in late July/early August and appeared to reproduce the following year, however, following B from mating and brood release, mature adults persisted in the system suggesting they may live for some time after mating.

The two life history patterns indicated in Fig 12 suggested ecotypic variation in the population as we could find no evidence that two species were present. Male and female *A. kygi* of the resident form mated during the summer (July). Ovigerous females of the A-form were captured in June, though A-form males of the appropriate size to be partners were found very rarely and A-form mating pairs were observed on only one occasion in freshwater, and otherwise only in the estuary and Sea of Okhotsk. For breeding pairs of resident *A. kygi*, collected in amplexus, male amphipods were an average of 30% larger than their female mates (95% C.I. = 26% to 38% larger). Sexual dimorphism within pairs existed also in a significantly greater ratio of 2nd gnathopod length to body length in males (8.5%, SE=0.3%) than in females (5.1%, SE=.07%) (two-sided p-value=.001 for ANOVA) (Tab. 3).



Form			Reproductive Timing (approx date)	Length to Dry Weight Ratio	Egg only fecundity n~100	Brood Release (approx date)	Ratio G2:Body for n~50	Mean Size at Mating(mm) n~50	Min/Max Size in Oct. n~50	Migratory?
Form	Anadromous "A"	Male	*MAY*	*2.5 (SE=.05)*			*8.9% (SE=.01)*	*24-27***	*22 - 30*	*?* *(maybe fall)*
		Female	*MAY*	*2.8 (SE=.04)* *3.7 (SE=.16) **	*73.1* *(SE=2.7)*	*JUNE 15*	*5.4% (SE=.01)*	*22.3 (SE=1.1)*	*18 – 24*	*YES*
	Resident "B"	Male	*JULY 1*	*3.2 (SE=.23)*			*8.5% (SE=.03)*	*14.8 (SE=.2)*	*12 – 17*	*no*
		Female	*JULY 1*	*2.9 (SE=.05)* *3.6 (SE=.11) **	*24.5* *(SE=.85)*	*JULY 30*	*5.1% (SE=.07)*	*11.25 (SE=.2)*	*9 – 15*	*no*

Tab. 3. Life history summary characteristics of male and female *A. kygi* of "Anadromous" and "Resident" forms based on 2006 morphometric data and field observations of reproductive timing. * indicates ovigerous females. ** indicates that the average size of Anadromous males is an estimate based on the male to female length differences observed in Resident males and females during amplexus. All lengths are in millimeters. Reproductive timing in Anadromous *A. kygi* is supposed since copulation among large individuals was not observed in the river.

Spatial distribution of anadromous and resident *A. kygi* life history forms had distinct trends. The ratio of anadromous to resident amphipods tended to decrease in upstream areas of the river system. Life history ratio surveys for 3 replicate benthos samples collected in three of the four main study sites (with the exception of Fossil Springbrook), and their upstream reaches (see map, Fig.7), indicated that the two forms are almost isolated from each other in the extreme end-points of the range. Amphipods at the upstream end of the range in small headwater streams are almost all resident, while amphipods in the meandering lower river and estuary are on average greater than 80% anadromous.

As was demonstrated for density patterns in benthos and drift, the ratio of anadromous to resident amphipods varied by season at all sites with the exception of the Utkholok headwaters where anadromous amphipods were never captured. Main sampling sites showed an influx of anadromous *A. kygi* in the fall, as did one headwater site: MY-hw (up from 0 % to about 20% anadromous). This variability in life history ratios over such a large spatial scale indicates that anadromous amphipods, if not both forms, were moving around in the system at different times of the season. Since we observed in 2004-5 that amphipods were extremely abundant on decomposing carcasses, we conjectured that redistribution and increased fall amphipod density at main sites may be driven by the need to find carcasses.

Deposition of Salmon Carcasses

The main spawning run of salmon began in late July in 2005, and in mid-August in 2006, though small numbers of spring chum and cherry salmon had already spawned in upstream reaches in June of both years (above, Fig. 6). Pink and chum runs began slowly for the first few weeks as fish were observed holding but not spawning in the lower river. In early August however, the water was low and clear, and both species were observed spawning throughout the main channel. As a result of redd construction by so many fish (estimated at half a million fish, Morris and Stanford, unpubl. data), the entire gravel bed of the river was turned over by the end of the summer.

In 2005 and 2006, spawning salmon, char, and steelhead, utilized all areas of the Utkholok system. The main channel and lower parts of Kolkalvayam including MC and

KO were used heavily by pink, summer chum, and some coho. Clear springbrooks, including FS were used by small numbers of fall chum and coho, mostly in late September and October when the river stage was high enough to allow access. Finally, semelparous salmon in the upper reaches of smaller tributaries including BE-hw, MY-hw, KO-hw, MY-hw, were almost exclusively coho, though non-semelparous char were also abundant. In the extreme upland source streams, Dolly Varden were the only spawners, and Dolly Varden juveniles and dwarf residents were the only fish species observed at these sites.

The distributions of semelparous salmon and the distribution of amphipod life history and density in the Utkholok were highly correlated (Fig. 14). Extreme upland source streams where salmon carcasses were absent were also void of amphipods. Upstream headwater sites (Be-hw, UT-hw, MY-hw, KO-hw) where carcasses were present but scarce, had fewer amphipods, mostly of the resident form, as well as other benthic invertebrates (ephemetroptera, plecoptera, tricoptera, gastropoda, etc). Main channel sites where carcasses were.

At Old Camp in 2005, carcasses in both the terrestrial and aquatic habitats persisted about 45 days. In the 50m^2 gravel bar plot, the density trend over the 45 day period was bell-shaped; the first fish carcasses appeared August 11th, density peaked on September 2nd at 0.8 fish/m2 and carcasses had disappeared by September 26th. Data for the aquatic habitats were incomplete because a flood event (August 26th, stage increase ~40cm) deposited enough fine sediment to bury carcasses in the river, however, we determined that burying of carcasses had implications for consumers such as lampreys. relatively abundant (MC, KO), had little benthos other than anadromous amphipods.

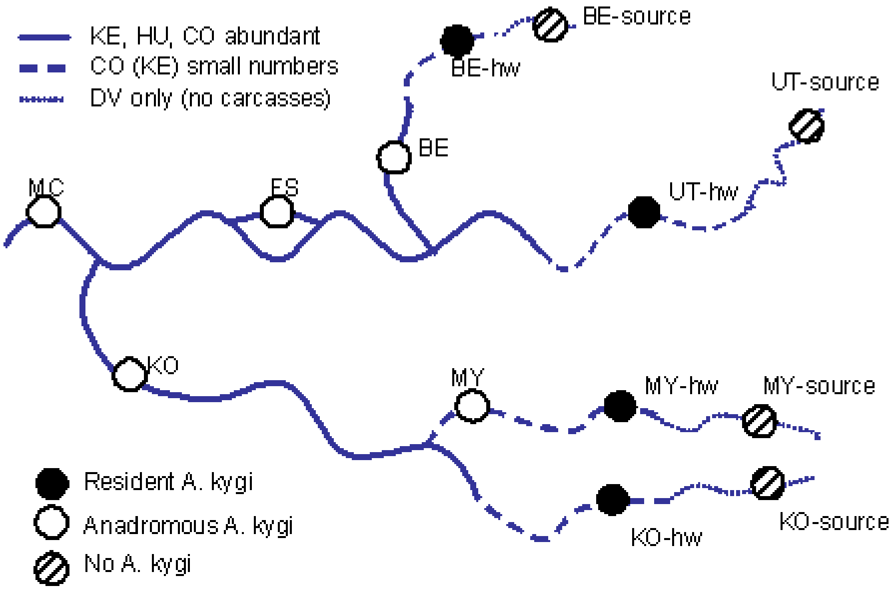


Fig. 14. Spatial distribution of spawner density on the Utkholok River relative to distribution of *A. kygi* life history forms. The Utkholok River (not to scale) main sample sites (MC, FS, KO, BE), headwater sites (UT-hw, BE-hw, MY-hw, KO-hw), and the upland source of each stream. The dominant life history of *A. kygi* was the anadromous form (open circles) in the lower river where semelparous spawner density was the greatest (solid blue line). B-form *A. kygi* were dominant in the upper sites (shaded circles) where spawning was limited to coho and rare chum (dashed line). Finally, in source streams where only Dolly Varden spawn (dotted line), *A. kygi* were absent entirely (hashed circles).

Prior to the flood, carcass density in aquatic habitats (pool and shallow shoreline) was greater than that in terrestrial habitats (gravel bar and river bank) (Fig. 15). The percent of carcasses in aquatic biotopes ranged from 13.6% on August 11th, 2005 (n=31) to 93.9% on August 25th, 2005 (n=114) as the total number of carcasses in the area increased. As the August 26th flood receded many carcasses were deposited on the gravel bar, reflected in our August 30th observation of higher terrestrial carcass density (75% of total carcasses) than aquatic.

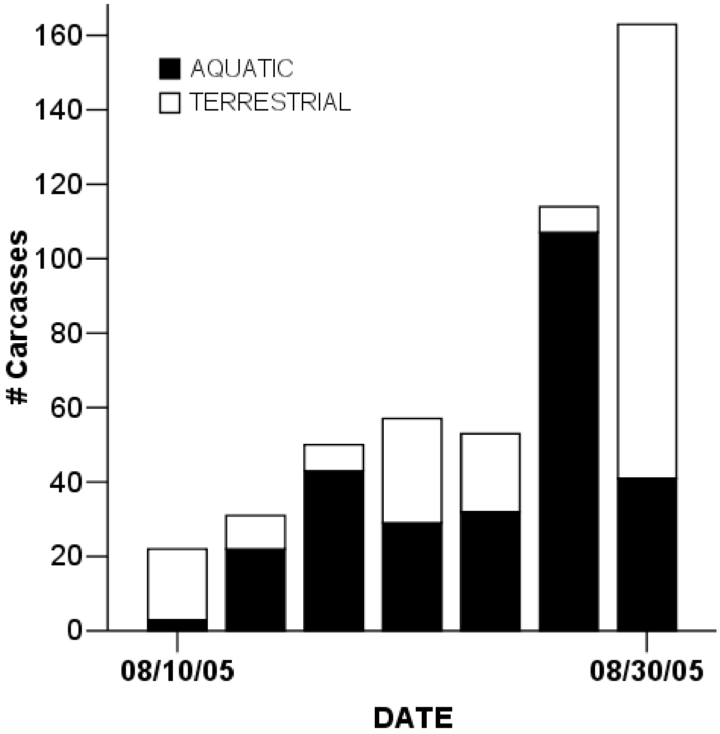


Fig. 15. Carcass density in aquatic and terrestrial biotopes, Old Camp 2005**.** Cumulative number of carcasses (y-axis) counted in two aquatic biotopes (black bars=tundra pool + shallow shoreline) and two terrestrial biotopes (white bars = gravel bar+ river bank). Survey area in each of the 4 biotopes was a 25m x 2m band (total $50m^2$). Density of carcasses was greater in aquatic habitats until a flood August 25th which relocated many carcasses to the gravel bar as the water receded, resulting in higher observed terrestrial densities.

In 2006, carcass densities calculated from all point quarter transects at 3m from the river were significantly lower than for transects 1m from the river (p-values between 0.001 and 0.005 for all two sample t-tests), and transects 5m from the river usually had insufficient carcasses for density calculation. The differences in carcass density along 1m vs. 3m transects, however were less significant at upstream sites. For example, At Old Camp and Carcass Bar (within 2km of Main Camp), carcasses along 3m transects were 2.1m (95% CI =3.0 to 1.7), and 2.61m (95% CI= 3.8 to 1.6) farther from enumeration points than on 1m transects, whereas at Eagle's Nest (EA, >40km upstream, Fig.7), carcasses on 3m transects were only .7m further (95% CI= 1.3 to 0.3) from enumeration points than on 1m transects. Of note is that carcasses in the upper part of the river appeared to be predated on more by bears. Near MC, the percentage of carcasses with evidence of bear chewing (i.e. the brain, or brain and head was missing) was 30.8% (SE=

3.4%, N=5 transects) while at upstream sites bear evidence was 61.7% (SE= 2.8%, N=5 transects).

During lateral transect sampling in early September, 2006 there were no major changes in river stage or re-distribution of carcasses, thus based on observed ratios of carcass density in aquatic and terrestrial habitats from 2005 (see Fig. 15.) we believe that the majority of dead spawners in 2006 remained in aquatic habitats or on gravel bars close to the river.

Longitudinal density distribution along Utkholok gravel bars was variable in 2005 and 2006, but not between years. Density of carcasses in 2005 ranged from 0.06fish/m2 to 0.81fish/m2 (mean=.48fish/m2, std= .32), and in 2006 ranged from .02fish/m2 to 1.4fish/m2 (mean=.40fish/m2, std=.30). There did not appear to be a density pattern along the river section surveyed in either year. Along Kolkalvayam however, density at the KO site was .12fish/m2 while no site further upstream had sufficient carcasses for transect sampling.

Though longitudinal density along the river did not demonstrate a pattern, on upstream and downstream areas of an individual gravel bar, distribution of carcasses differed significantly. At the Old Camp gravel bar, a 1m transect at the top of the bar had 2.4 fish/m2 (SE= .7, N=6) while a similar transect at the bottom had significantly less with only 1.2 fish/m2 (SE=.24, N=6, p-value =.01 for two samples t-test). The reciprocal pattern was observed for the pool on the opposite side of river. This pattern of carcass deposition may contribute to the uneven distribution of MDN in aquatic biotopes, leading to uneven distribution of scavengers such as amphipods.

Utilization of Salmon Carcasses by A. kygi

During spawning, salmon were either killed or scavenged by other vertebrates such as brown bears, red foxes, seagulls, Stellar’s eagles, and sea lions (in the estuary); and their eggs were consumed by juvenile fish of all species. The remaining salmon in both terrestrial and aquatic habitats were colonized and scavenged primarily by invertebrates. The scavenger guild on carcasses was variable between aquatic and terrestrial habitats, and among aquatic habitats. Terrestrially deposited carcasses were colonized by up to three species of terrestrial diptera and hymenoptera. These invertebrates laid large numbers of eggs (max # eggs =13,126) in moist areas of the mouth, under the operculum, and near eyes. Once hatched, larvae rapidly consumed the carcass, reducing it to bones and fecal matter in days.

In 2005, decomposition in aquatic habitats was investigated using fixed carcasses in retention cages. The consumer guild was dominated by *A. kygi* and pacific lamprey ammocoetes (*Letentron japonicum*), but included other groups such as caddisflies, and juvenile salmonids (*O. coho, O. mykiss)* as well (Fig. 16).

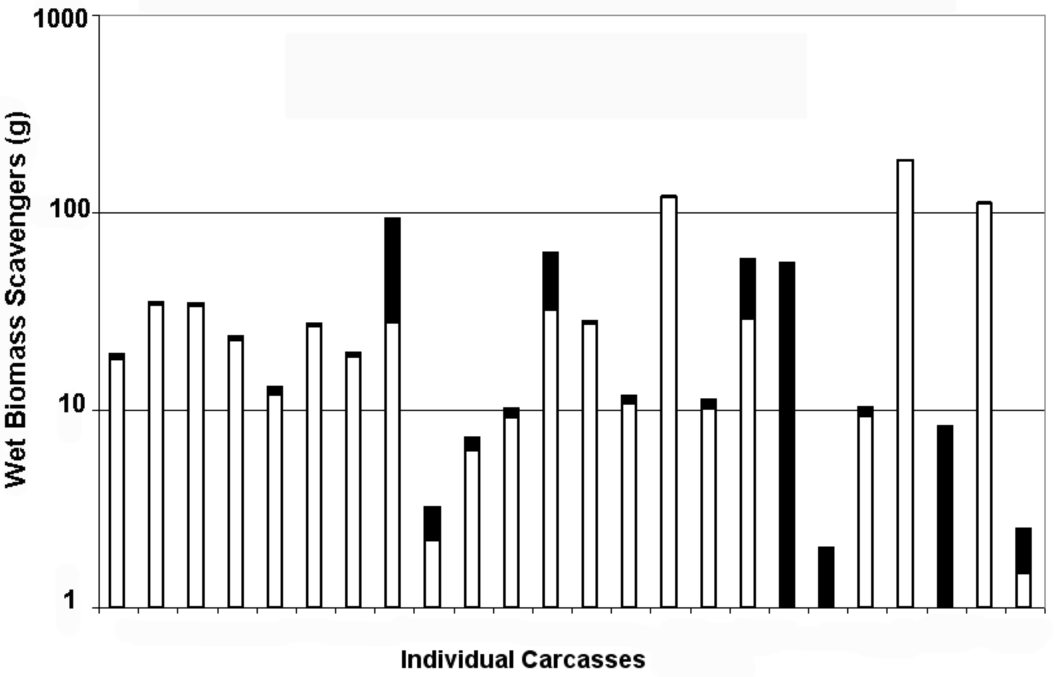


Fig. 16 2005 aquatic carcass scavengers**.** Scavenger guild is shown for each carcass (x-axis, n=24 carcasses) as the total wet biomass of scavengers (g). *A. kygi* (open bars) was the only dominant invertebrate, and Pacific lamprey ammocoetes (shaded bars) was the only dominant vertebrate. Wet biomass of *A. kygi* reached a maximum of 220g (>3,000 individuals), while that of lamprey reached 81g (~100 individual ammocoetes).

Variation in the number of amphipods was not related to the habitat (pool, shallow shoreline) or to decay index of the carcass. The proportion of amphipod to lamprey biomass, however, was dependent on whether the carcass was buried in fine sediment or not. 95% of exposed carcasses (n=19) were colonized by only amphipods, and 5% by amphipods and lampreys, while 80% of buried carcasses (n=4) were colonized by only lampreys, and 20% were colonized by both species. The sedimentation of these cages occurred during the same flood (~August 27th, 2005) which buried other carcasses in aquatic habitats, preventing further enumeration. The opportunity for observation of scavenger guilds in buried carcasses provided an important insight into the river's potential for entrainment of carcasses in the bed sediment during floods. All of the carcasses retrieved from the sediment were at advanced, liquefied stages of decomposition, with lamprey abundance up to 120 ammocoetes per carcass.

In 2006, scavenger community on carcasses was explored for a greater number of carcasses and the scavenger guild was more diverse, including more tricoptera genera (lymniphellid, apataniidae, glossosomatidae). As in 2005, amphipods were ubiquitous, being present on 99% of the carcasses surveyed, and accounting for 98.8% (SE=.007) of scavenger abundance (Fig. 17). As in 2005, the proportion of amphipods relative to caddisflies was independent of biotope (pool vs. shallow shoreline), carcass species, or decay index (insignificant two sided p-values for all tests).

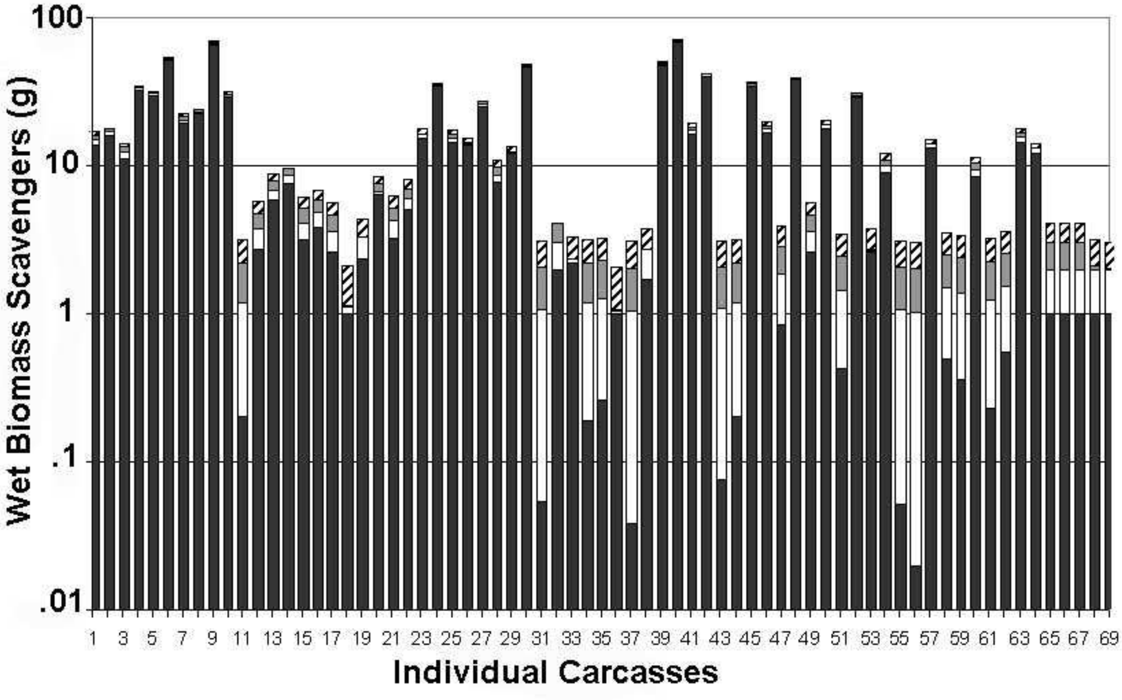


Fig. 17 2006 Main stem Utkholok carcass scavenger biomass. *A. kygi* (black bars) accounted for significantly more of the total scavenger biomass (y axis, log scale) than did lymniphellid (white bars), apataniidae (gray bars), or glossosomatidae (hashed bars) for carcasses surveyed in near shore habitats (n=70), reaching a maximum biomass of 67g (1,050 individuals) per carcass.

The size distribution of *A. kygi* on carcasses did not reflect size distributions in the benthos at the same sites. Amphipod assemblages on carcasses did not include any individuals less than 11mm though larger size groups were generally well represented. Overall, we determined that amphipods were not only the dominant scavenger on carcasses in aquatic habitats, but that amphipods probably traveled from habitats with low or no carcass densities to areas of higher density to feed on the MDN rich tissue.

Clearly, carcasses were a highly important and possibly essential aspect of the diet of amphipods on the Utkholok, though during times when carcasses were not present, amphipods were ubiquitous, observed consuming a wide variety of other foods. Indeed in qualitative feeding experiments *in aquaria*, *A. kygi* were voracious feeders, and preyed enthusiastically on algae, detritus, invertebrates such as stoneflies, caddisflies, and chironomids, juvenile fish, un-hardened salmon roe, smaller amphipods, and carcasses of pacific salmon and other fishes. These observations merely supported the general notion (Pennak, 1989) that amphipods are versatile omnivores, and adaptable to whatever happens to be available as a food source, including their own kind. These observations are coherent with the observed delta 15N and delta 13C levels for Utkholok amphipods collected in spring, summer, and fall for the SaRON Cross-site comparison protocol in 2004 (Fig 18b). Amphipods from MC have elevated δ15N which indicates that they consume organisms in trophic positions including herbivore, and primary consumers.

Stable isotope data were used in this study to corroborate two major observations; first, that anadromous amphipods migrated from the estuary where they had been feeding, and second, that amphipods were consumers of carcass tissue (Fig 18a), and thus were assimilating MDN and fatty acids from salmon carcass which resulted in their own enrichment as a potential food item for juvenile fishes.

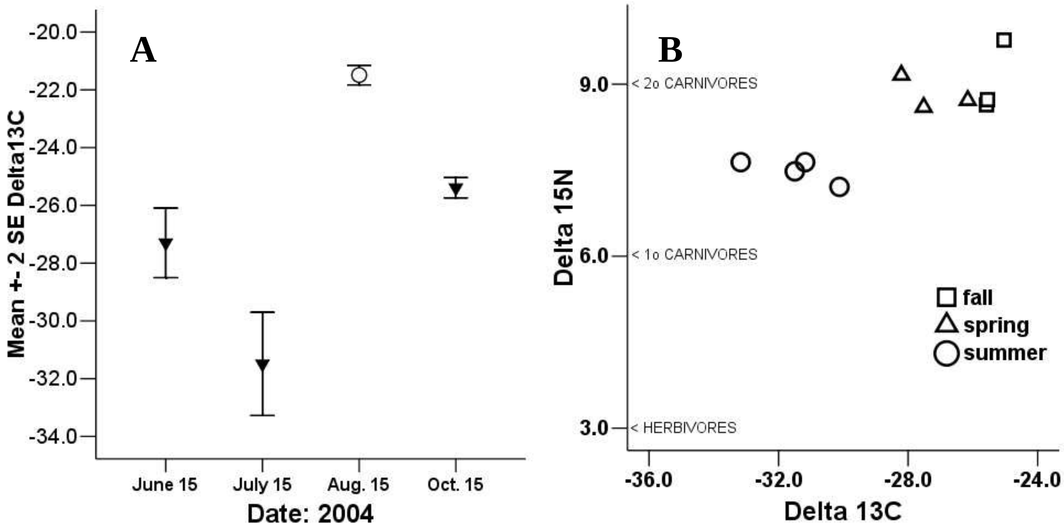


Fig. 18.a. δ^{13}C for *A. kygi* and Carcass at Main Camp 2004.Each data point represents three samples, each of which is a mean signal from n=10-20amphipods. Large *A. kygi* (shaded triangles) collected for SaRON protocol work in 2004 had elevated δ^{13}C level of -27.3 (SE=0.6, n=3) on the spring sampling date, followed by a period of more negative δ^{13}C in the summer (-31.5, SE=0.89, n=3), and a return to elevated levels in the fall (-25.4, SE= 0.17, n=3). For reference, pacific Salmon carcass (open circle, n=6), abundant in the river in August, have a strongly marine δ^{13}C signature (-21.5, SE=.17)
Fig. 18.b. Dual isotope plot of δ15N against δ^{13}C for Utkholok main camp amphipods in the spring, summer, and fall showing the trend in marine signal (less negative carbon) in addition to the change in trophic position as indicated by δ15N.

Predation on amphipods by fishes

Diet of juvenile salmonids was dominated by amphipods, (Fig. 19.), although terrestrial invertebrates were important for coho and rainbow/steelhead. *A .kygi* (black bars) was found in all diets. KZ and DV (char) consumed the greatest proportion with 29.51% (SE=.05) and 46.51% (SE=.07) of total diet being amphipods, respectively. Other salmonids CO, MY and MA consumed fewer amphipods with diets 16.1% (SE=.03), 13.5% (SE=.04), and 0% amphipods respectively. Chum salmon fry (young of the year, YOY, *O. keta*) had a diet 80% (SE=.05) amphipods. Non-salmonid fishes; sticklebacks (GA, PP) and flounder (FL), preyed the most on amphipods with 95.8% (SE=.04), 59.2% (SE=.17), and 83.1% (SE=.01) of diet being *A. kygi*, respectively. All of the fishes consumed salmon roe preferentially when it was available.

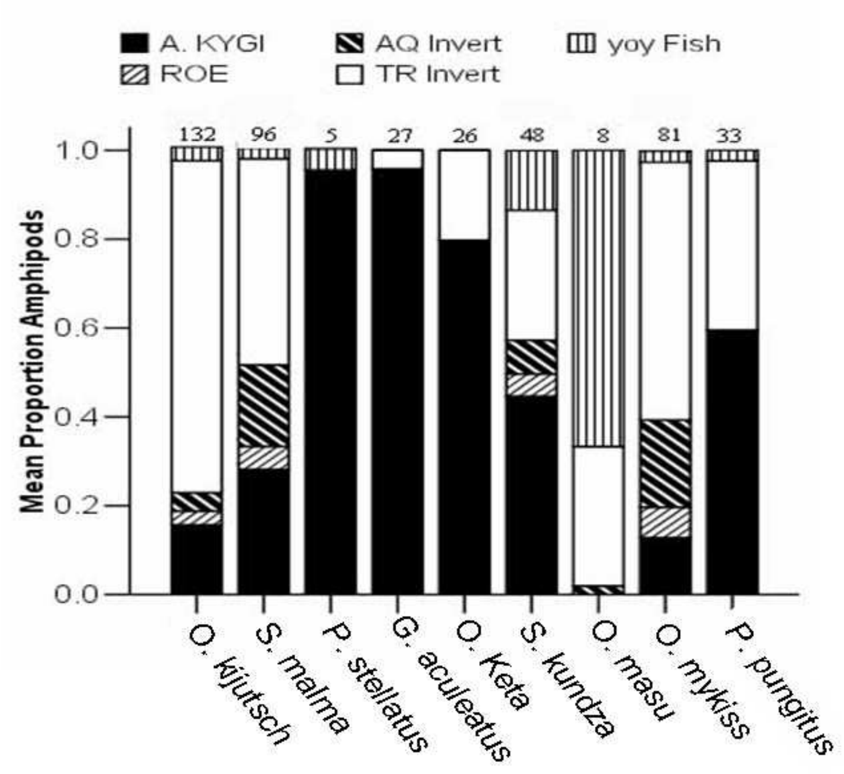


Fig. 19. Proportion of amphipods in the diet of juvenile fish, with all samples pooled May-October, 2006. Bars represent amphipods (black bars, *A. kygi),* aquatic invertebrates (AQ Invert), terrestrial invertebrates (TR Invert), salmon roe (ROE), and salmon fry (YOY fish).

In some cases, certain species fed differently in the different sites. In the char group for example (DV and KZ), in the main channel (MC), these fish consumed almost 100% amphipods, while at BE, the same species consumed relatively few amphipods. This is due, no doubt to habitat differences, and corresponded to a greater range of available terrestrial invertebrates at BE compared with MC and KO.

In 2005 and 2006, the presence of *A. kygi* in the diet of fishes was variable seasonally Fish consumed large numbers amphipods in the spring (after *A. kygi* A^{o} brood release), exhibited a seasonal peak in predation on *A. kygi* in the summer, and consumed very few during the fall (Fig. 20). For the diet of all fishes sampled, percent *A. kygi* reached 40% in June, followed by a decrease to less than 10% in early July. In summer (mid-July to mid-August), predation on amphipods reached a seasonal peak on 7/22/06 with greater than 70% of all diets being amphipods. This peak was mirrored by a dramatic drop in terrestrial invertebrate consumption (down to 20% from 66%) as well as a decrease in consumption of aquatic invertebrate prey (down to 10% from >30%), both prey items reaching seasonal lows on 7/22/06. Predation on *A. kygi* declined significantly in fall, correlated with the arrival of salmon, and the availability of salmon roe as a food source, reflected by the dramatic peak in roe to near 100% of diets in late September.

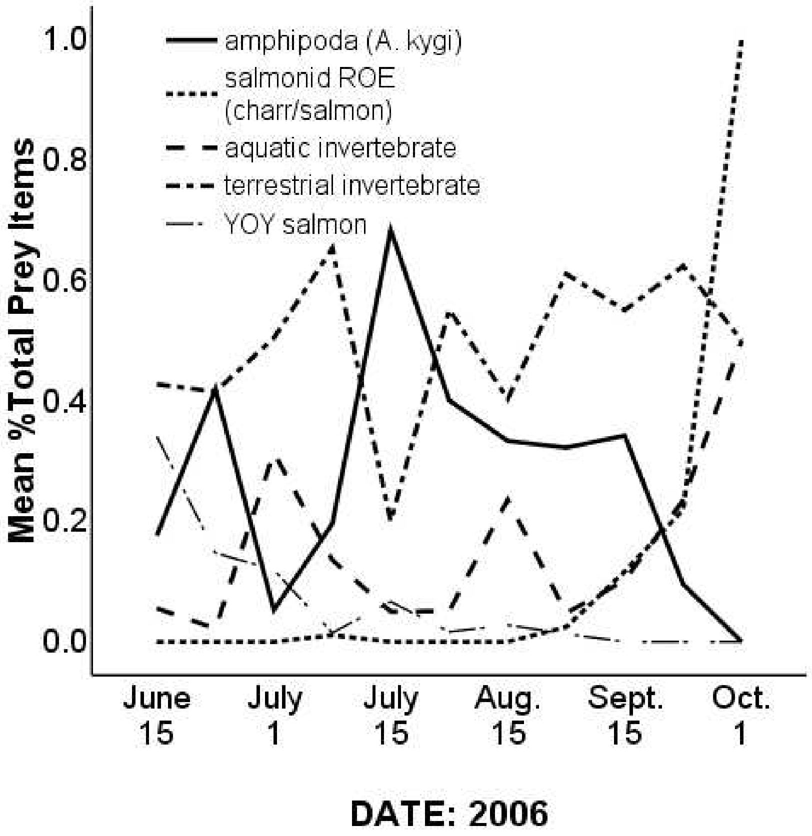


Fig. 20. 2006 Seasonal trends in prey consumption by all fish species.

The trends in fish predation on *A. kygi* in 2006 were similar to those observed in 2005, with two exceptions. First, terrestrial invertebrates in general were less frequently consumed by fish in 2006, with spring (6/15/05) and fall (9/21/05) peaks each around 40%, but were almost nonexistent in summer diets. For aquatic invertebrates the same trend as in 2006 was observed, but this group was a consistently a greater proportion of prey items in 2005 (~40%) than in 2006(~20%). Second, while the percentage of *A. kygi* in diets was greatest in the summer, the magnitude of this peak reached more than 90% in 2005, about 15% greater than the 2006 peak.

Predation on *A. kygi* was size selective within and between seasons. In 2006, all salmonids (CO, DV, KE, KZ, MY) ate a large number of juvenile amphipods (size classes 1-3mm and 4-9mm) in the spring, with DV and KZ also consuming large individuals (>16mm). In the summer, the mean amphipod size consumed shifted to the 16-19mm group, again with DV and KZ exerting the most predation pressure. In the fall, mean size consumed shifted in a reverse direction, being concentrated in the 10-15mm size group, while the number of amphipods consumed was (as shown above) lower than in both spring and summer.

This feeding analysis identified two fishes whose diet was almost entirely amphipods at all times and across all sites. First, in 2006, young of the year chum (*O. keta)* rearing in off channel habitats (FS) preyed heavily on *A. kygi* in June and exclusively on *A. kygi* in August before migrating downstream. In June, diet of n=23 chum salmon with mean fork length 42.8mm (SE=.58) consisted of 74.4% (SE=.057) amphipods (of size 1-3mm) with the remaining 25.6% divided evenly between adult Culcidae (mosquitoes), Chironomids (midges) and unidentified terrestrial dipterans. In August, diet of n=9 chum with mean fork length 46.0mm (SE=.86) consisted of 100% (SE=0) *A. kygi* of sizes ranging from 4-9mm.

Second, in 2005, the diet of sticklebacks (9-spine: PP, and 3-spine: GA) was consistently very high in, or exclusively amphipods, most often supplemented by stickleback roe, or aquatic larvae (chironomids, tipulids) (Fig. 21).

Predator avoidance behavior was observed in *A. kygi* during the period of carcass persistence in 2005. Amphipods were found to be significantly less abundant in minnow traps baited with carcass during light conditions than during dark conditions, a pattern opposite to that of visual predators (sticklebacks) which had greater abundance in traps during light conditions (Fig. 22).

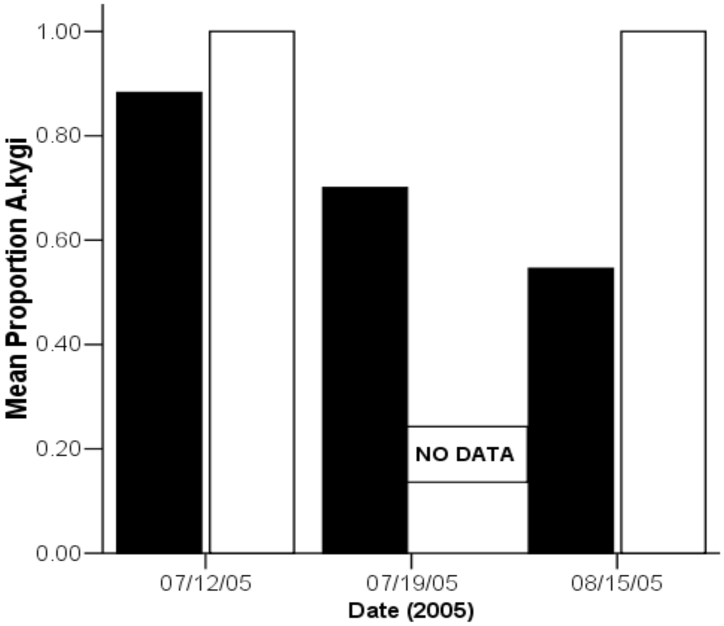


Fig. 21. *A. kygi* in the diet of sticklebacks (GA and PP). In 2005, stickleback diet, for both 9-spine (PP, white bars) and 3-spine (GA, black bars) consisted predominantly of *A. kygi*. In early July, the diet of GA was 88.3% (SE=.06), and that of PP was 100% (SE=0). In fall, GA consumption of *A. kygi* declined to 54.6% (SE=.019), replacing this food source with salmon roe (not shown), while PP diet remained at 100% (SE=0) *A. kygi* as prey.

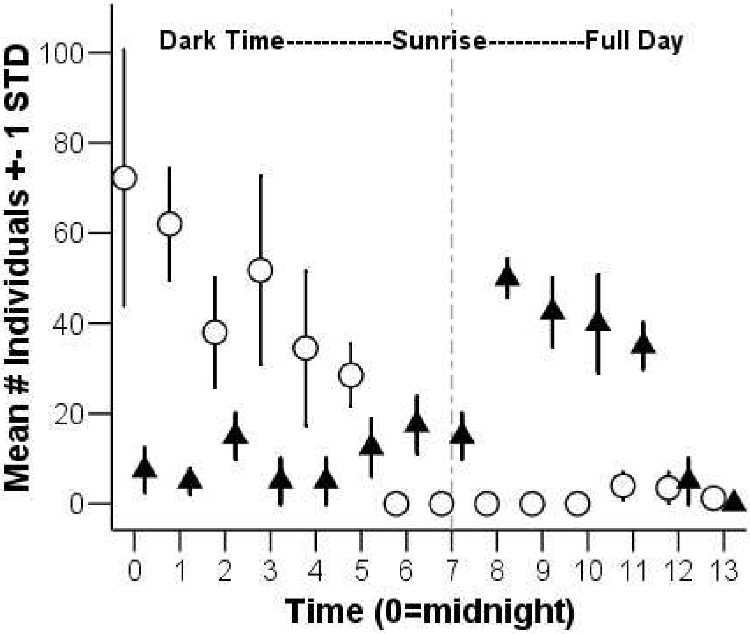


Fig. 22. Diel change in *A .kygi* and fish abundance**.** *A. kygi* (open circles) present in carcass-baited minnow traps (n=4) declined in mean abundance toward sunrise, while visual predators such as fish (GA, CO, shaded triangles) increased in abundance after sunrise. Stomach analysis of visual predators show 100% presence of amphipods (motivation for entering the trap) and 0% presence of bait (carcass).

Following the observation that fish predation on amphipods is most intense in the beginning of August (i.e. the proportion of amphipods in diets peaked), we used SaRON data for length and weight of fish species in the different habitats, combined with our own length weight data for fish used in the stomach content analysis, to calculate change in condition factor (K) from early spring (June-July) to late summer (Aug). *K* was calculated using: $K = W(100)/L^{-3}$ (Moyle and Cech, pg 132) as a basic indicator of the trend is robustness (rotundity) in the juvenile fish population. The greatest changes in mean condition were observed at KO (all species), and at BE (KZ and DV). At FS, mean KE fry and CO *K* increased while other species declined. At the main channel, with the exception of MY, mean condition increased modestly. This apparent decrease in MY condition may represent a loss of pre-migrating smolts from the populations which generally were more robust than the resident fish that remained in the river (Fig. 23).

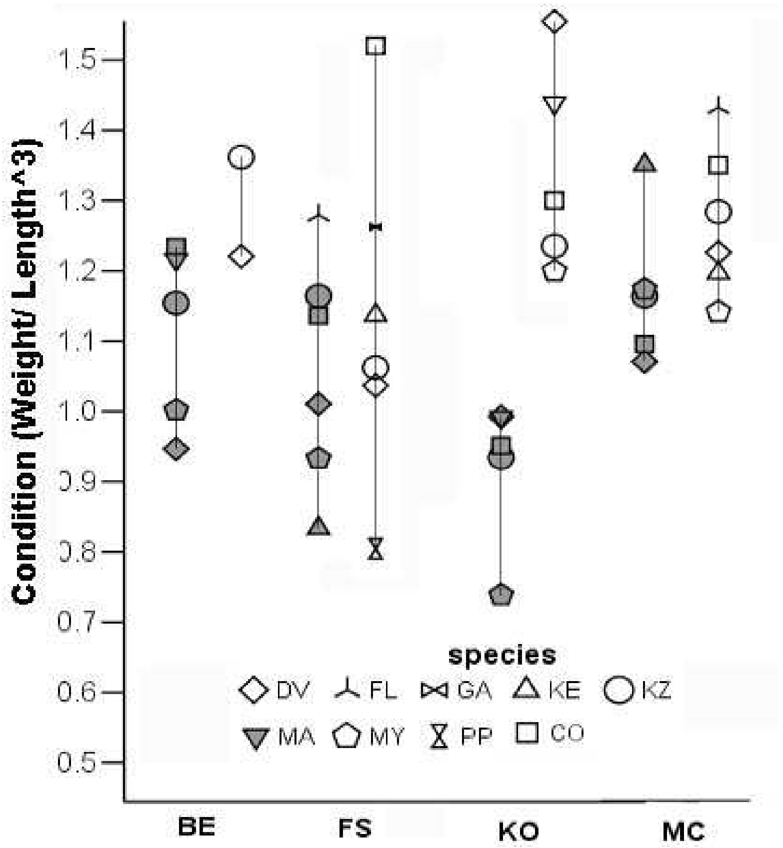


Fig. 23. Condition factor (K) for rearing juvenile fishes at four main study sites on the Utkholok River. K (y-axis) for fishes is the mean $W(100)/L^{-3}$ for each species (W=weight (g), L=length (cm). Spring values (shaded shapes) were generally lower than summer values (open shapes) when species were captured in both seasons.

DISCUSSION

Flow, Temperature and Water Chemistry Patterns

Tundra fed rivers like the Utkholok drain much of the Western coast of Kamchatka and the Russian Far East. These rivers are fed primarily by humic rich water leeching through the *Sphagnum* tundra mat of the surrounding landscape and therefore the river water is stained brown by humic and fulvic acids (Clifford et al., 1969). Brown water tundra rivers typically are oligotrophic compared to rivers fed by upland clear water streams because most of the nutrient load is tied up in the *Sphagnum* mat. Primary productivity in brown water rivers therefore responds quickly to allocthonous nutrient subsidy (particularly phosphorous) based on fertilizer experiments (Peterson et al., 1993a; Peterson et al., 1993b). Nutrient poverty was telltale on the Utkholok in the lack of abundant algae and primary consumers like snails, planaria, mayflies and other shredders identified by SaRON foodweb analysis on the richer, clear water rivers around the Pacific Rim. Our thesis is that *A. kygi* was the primary processor of salmon carcasses in the Utkholok and thereby mediated enrichment of the foodweb that subsequently had the feed back effect of rearing more robust salmon. These salmon then return as spawners thus creating a MDN legacy effect. A kygi is abundant in other Kamchatka brown water rivers with robust salmon runs: Kvachina, Xavrahn, Snatylvayam, Sopachanaya, Kehkta, and Saichek Rivers. Thus, amphipod ecology in the Utkholok likely can be broadly interpreted as a condition of brown water rivers, at least in Kamchatka.

Spatial and Temporal Distribution of A. kygi

It is generally understood that density of benthos in streams is patchy and difficult to estimate. As expected, our results reflected that paradigm, though over the time scale studied, we also documented variability in the proportions of life history form, which we would expect to be more stable within a habitat. The density of amphipods at all study sites in the lower river (MC, KO, BE, FS) reached peak levels during carcass loading in late August. The density of *A. kygi* on carcasses reflected this general spike in abundance. Increased amphipod density was likely the result of relocation from areas with few or no salmon, to areas of the main stem river and lower tributaries with greater densities of carcasses. This relocation demonstrates the importance of amphipod mobility to the ecology of *A. kygi* on the Utkholok.

Mobility is important in an ecosystem where food availability is often low, and highly variable seasonally and spatially. Omnivory allows organisms to adapt to seasonal changes in food type, but mobility within a system further allows omnivores to relocate to areas with optimal foraging conditions (Otto 1998). We found *A. kygi* to be highly mobile as demonstrated by intense drifting activity, large scale changes in benthic density and life history ratios over time, and in the ultimate example of mobility: group migration of reproducing adults.

Drifting activity during the growing season distributed thousands of juvenile *A. kygi* throughout the river and into the tidal zone. We found *A. kygi* activity in the water column and on carcass bait in minnow traps was most intense during the dark time of night which has been documented for other Gammarid species (Otto, 1998) and is probably a strategy of predator avoidance (Andersson et al., 1986). Several studies have described patterns of drift in stream invertebrates as being either a re-distribution to more favorable food or temperature conditions (Minkley, 1964), a result of production in excess of benthic carrying capacity (Waters, 1965), or a function of intense flooding (Hughes, 1970).

Mobility was further demonstrated by the upstream migration documented during the two week period prior to brood release. Given the lack of physical boundaries such as velocity, gradient, or predation (on this size class), an amphipod traveling ~70 km/wk could reach any point on the low gradient Utkholok and its lower tributaries. The colonization cycle of winged invertebrates was described by Muller (1974) as an upstream flight to re-establish densities in depleted upstream reaches. For invertebrates that are always aquatic, such as *A. kygi* colonization of upstream reaches must be accomplished in different way, such as upstream migration, observed here. Based on work primarily on estuarine species of amphipods, upstream migration has additionally been correlated with environmental factors such as food availability (Hughes, 1970), temperature and salinity, in addition to reproductive events (Hough and Naylor, 1992).

For anadromous *A. kygi*, brood release, as a reproductive event, was probably a key factor in migration.

This migration provided further information regarding the life history trajectory of some anadromous amphipods. Since copulation occurred in early spring, we assumed that large anadromous (A-form) males must have been at the downstream end of the female migration range. Since some A-form *A. kygi* were observed in amplexus at the estuary and in the Sea of Okhotsk, we concluded that the spatial range in which A-form *A kygi* reproduce might include these saline locations.

Life Cycle and Growth of A. kygi

We documented what appears to be a rather unique case of phenotypic variation in *A. kygi* wherein a single amphipod species has developed a resident and an anadromous life history, though phenotypic variation has been observed in other amphipods. Wilhelm and Schindler (2000) described phenotypic plasticity along a latitudinal and thermal gradient for *Gammarus lacustris*. Traits which exhibited plasticity across environmental gradients included female size, fecundity, egg size, and egg biomass. They concluded that such a high degree of phenotypic plasticity in reproductive traits contributed to the success of *G. lacustris* in a wide range of aquatic habitats within the system. This finding is coherent with observations made about resident and anadromous *A. kygi* on the Utkholok which inhabited and dominated benthic invertebrate assemblages in most of the river system across a range of habitat types.

Kusano and Ito (2005) also studied phenotypic plasticity in female *Jesogammarus spp* (Amphipoda) on Hokkaido in relation to influence of Pacific salmon carcasses. They found carcass input to be highly influential on total female size, which was correlated with egg production. Furthermore, they suggested that higher fecundity is the result of the gradual development of greater size, achieved by female amphipods that foraged on carcasses and carcass enriched food (Kusano and Ito, 2005).

Life history variation on the Utkholok, and the achievement of large size and high fecundity in the anadromous females may be related to spatial distribution of A and B forms across gradients of carcass input and thermal regime. Spatial variation in carcass loading and temperature patterns on Utkholok correlated precisely with the spatial distribution of resident and anadromous amphipods. We observed that these forms, as expected, diverged in body size, fecundity, and abundance, and were distributed differently spatially.

Anisogammarids are primarily a marine genus of amphipods with a movement of into freshwater that is relatively recent (Barnard and Barnard, 1983). Thus, it is possible that persistence of a semi-marine (anadromous) form, and the ability of both forms to tolerate a wide range of salinity, may be relict characteristics of prior marine ancestors. Furthermore, the development of a resident form may simply be the phenotype that results from a strictly freshwater existence. Finally, the fact that anadromous *A. kygi* are capable of utilizing the river, estuary, and the sea to maximize their survival and productivity is demonstrative of their adaptability as a species. In turn, the productivity, especially of anadromous amphipods and their abundant juvenile cohorts, is critical to the river ecosystem in the pivotal role this multitudinous population plays in the processing of MDN.

Deposition of Salmon Carcasses and Use by A. kygi

Every year, with the coming of the salmon, the brown water rivers of Kamchatka receive a large nutrient subsidy in the form of semelparous salmon carcasses. Due to the landscape of the tundra, and the constrained nature the river channels that divide it, the majority of salmon nutrient deposition occurred in aquatic habitats; lateral distribution was very limited except during rare extreme over-bank flooding (2004). Many vertebrate and some invertebrate consumers utilize the limited numbers of terrestrially deposited carcasses including bears, foxes, seagulls, eagles, and fly larvae. These terrestrial groups however do not appear to contribute on a large scale to the assimilation of these carcass nutrients into the aquatic foodweb.

Scavenger colonization of carcasses in the aquatic habitats however appeared to function strongly in MDN cycling. *A. kygi* and other less abundant species (lamprey ammocoetes and caddisflies) colonized carcasses, but *A. kygi* aggregates reaching maxima > 3,270 amphipods/carcass were by far the dominant scavenger, and the only aquatic invertebrate to contain elevated 13C ratios (Ellis, SaRON, 2004 unpubl.)

Like other omnivorous crustaceans, *A .kygi* appeared to depend heavily on carcass tissue (animal protein) for their growth, but survived during periods in the river without carcasses by consuming a wide range of invertebrates, algae and plants, adapting feeding habits to the available food source (Stenroth and Nystrom, 2003). This versatility makes amphipods as a group especially important in large oligotrophic rivers because food variability can be high, and being omnivorous allows amphipods to shift seasonally between different food items, maintaining robust populations (Summers et al., 1997). Additionally, amphipods in this system were highly mobile, and thus capable not only of adapting to changing food conditions, but capable of relocating in search of more favorable food conditions, a capability documented in other gammarid species as well (Hughes, 1970, Hough and Naylor, 1992)

Our analysis of stable carbon and nitrogen isotopes in amphipods provided support both for the omnivory of this species, and demonstrated *A. kygi* preference for carcasses tissue. The rise in late-season invertebrate $\delta^{13}C$, after the arrival of salmon carcasses, has been demonstrated by many studies (Naiman et al., 2002), though not specifically for natural populations of amphipods. The high spring $\delta^{13}C$ could have resulted either from release of ^{13}C stored in groundwater or terrestrial soil during the large scale flood which occurred in the spring of 2004, or because anadromous females feed in the estuary and the sea and would glean high N and C values from marine foraging. Finally, high fall δ13C levels are a good indication of the important role these amphipods played in transferring MDN from carcasses to their fish predators.

In 2005, however, we determined that aquatic carcasses are not universally available to amphipods. In the main channel, amphipods and lampreys were observed colonizing nearly exclusive groups of carcasses—lampreys being abundant on carcasses buried in sediment, while amphipods were abundant on exposed carcasses. The reason for this difference is probably simply a difference in niche preference for the two species. Lamprey ammocoetes colonized low turbulent areas with organic rich fine sediments, while amphipods were more abundant in riffles and gravel shorelines. However, in years with more intense flooding, and fine sediment transport, a greater proportion of carcasses may become buried leading to a greater emphasis on lampreys as scavengers.

Many studies have addressed the enriching effect that carcass biomass input has on stream invertebrates. Wipfli et al (1998) found increased production and fitness in invertebrates correlated with carcass input as well as significant increases in density of invertebrates in experimental streams following carcass input. Similarly, Ito (2003) demonstrated increased mean size and fecundity of amphipod populations reared in situ with carcasses leachate, leading to the increased productivity of subsequent generations. Given these findings, consumption of carcasses by *A. kygi* on the Utkholok may be a key factor in maintaining the observed high density and sustaining a large body size, especially for the larger anadromous (A-form).

Given the dramatic increase in ^{15}N and ^{13}C in fall amphipods (post carcass) discussed above, we can extrapolate that amphipods as a highly abundant foodweb taxa become significantly enriched with marine nutrients following the carcass season, a condition not observed for non-amphipod invertebrates on Utkholok, Thus, *A. kygi* was extremely valuable to predators going into the late fall, and winter months after the completion of salmon spawning.

Predation on Amphipods by Fishes

SaRON cross site comparisons have indicated that rearing juvenile fish populations in 2004-2006 on the Utkholok River were small compared to clear water floodplain rivers like the Kol (southern Kamchatka) (This does not apply to pink, sockeye and some chum which out-migrated to the sea immediately). This difference is probably based in the lower primary productivity of the system resulting from the brown water conditions, which limit the productivity of higher trophic levels (Peterson et al., 1993). These rearing fish populations, despite their small size, were probably challenged to find enough food given the low observed productivity of lower trophic levels. We determined that amphipods, though not optimal prey, nonetheless alleviated predation pressure on juvenile fishes.

We found that *A. kygi* were a significant seasonal food item for juvenile salmonids and other fish, particularly during the summer interval after the few aquatic diptera larvae hatched, and before salmon roe was available (which was the preferred food of all fish capable of consuming it). Spring size-selective predation on amphipod juveniles (1-3mm) was intense following brood release, and peaked in summer such that some juveniles' diets were 100% amphipods. Though no data on winter feeding was collected to support the idea, amphipods may be an exceptionally important prey item in the winter when food availability likely decreases even further.

Fish condition factor (K) analysis indicates that between spring and late summer, most fish species increased in condition, or rotundity at all study sites. This may be a direct result of predation on amphipods for species such as chum that consumed little else. Overall, whether the fish condition is directly a result of *A. kygi* consumption or not, clearly amphipods are an important food item for rearing juvenile salmonids and other fishes, especially in the summer when they became enriched with MDN (the heavier 15N and 13C) following carcass scavenging. We do not believe that amphipods are preferentially selected over other food items. Kirillov and Kirillova (2006, unpubl.) found in feeding experiments, that *A. kygi* was invariably the last item to be eaten when several invertebrates were offered, and in some cases, even ignored for many days before consumption. That we found so many fish eating amphipods suggests that those fish probably did not have other food options and that amphipods, if not preferred, were probably essential to these fish for survival in a river that might not otherwise be able to support them between periods of caviar availability and limited summer terrestrial invertebrate input.

Based on the observation of the important community-scale interactions amphipods had which directly and singularly linked the most important nutrient resource (salmon carcasses) to salmonid juveniles, we suggest that amphipods are indeed a strong interactor (De Ruiter et al., 1995). We concluded that the probability that the Utkholok ecosystem could maintain as it is, and that the foodweb could maintain its structure in the absence of amphipods is extremely low.

CONCLUSION

Amphipods are a versatile and abundant omnivorous crustacean that dominated the benthic community of the Utkholok River and other brown water rivers of Kamchatka. Because of life history variation and adaptability to changes in food availability and environmental condition, amphipods have become established as the dominant macroinvertebrate a range of aquatic niches from the headwaters to the Sea.

Anadromous ovigerous females (*A. kygi*) migrated upstream from the sea in early spring to release their broods in freshwater, increasing the already high benthic amphipod abundance—effectively filling the riverine benthos with eager consumers. We determined that this multitude of voracious amphipods played two critical ecosystem roles.

First, amphipods were the primary consumers of carcasses in the river, thus mediating the assimilation of MDN into the foodweb. This assimilation was critical because salmon carcasses (a form of nutrient fertilizer) are an essential allocthonous nutrient subsidy to low productivity tundra-fed rivers. The Utkholok main channel, like other tundra rivers, is constrained by the tundra landscape and thus, when spawning salmon die, carcass biomass distribution is limited to aquatic habitats where amphipod abundance translates into MDN assimilation efficiency. Dead spawner tissue is so valuable to consumers like amphipods that scavenging aggregates on carcasses are multitudinous, and consumption is both rapid and complete.

Second, rearing juvenile fishes prey heavily on amphipods in spring and in some cases exclusively on amphipods in summer. This predation contributes to the sustenance and survival of these fishes as they grow in the river, and prepare for migration to the sea, from whence they will return, spawn, and die, re-initiating the cycle.

We conclude that *A. kygi* is a strong interactor, and critical ecosystem component in the ubiquitous brown water rivers of Western Kamchatka, mediating and catalyzing a direct feedback loop of MDN from spawning salmon to the sustenance of juvenile salmonids.

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