Common Behavioral Adaptations in Lamprey and Salmonids

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CHAPTER TWENTY THREE

COMMON BEHAVIORAL ADAPTATIONS IN LAMPREY AND SALMONIDS

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Introduction

Quite often among representatives of different taxa which inhabit similar environments, identical adaptations to external conditions in an evolution process are formed. Berg (1935) noted ecological similarity ("ecological parallelism") of lamprey (Petromyzontidae) and salmon fishes (Salmonidae) in a case study of European river lamprey *Lampetra fluviatilis*, bull trout *Salmo trutta* and Atlantic salmon *S. salar*. Subsequently, the ecological similarity was demonstrated in other lampreys and Salmonid species which inhabit the same water bodies including: Arctic lamprey *Lethenteron camtschaticum*, Pacific salmon of the genus *Oncorhynchus*, chars of the genus *Salvelinus*, and Kamchatka rainbow trout *O. mykiss* (Gritsenko 1968; Savvaitova et al. 2007). The similar features between lamprey and salmonid ecology include: the presence of various life forms within particular populations, realization of particular life cycle stages in marine or fresh water and the usage of identical spawning grounds.

Abakumov (1960) suggests that the ecological similarity between lamprey and Salmonids arises because of parasitic lifestyle of the former and the resulting adaptation to the host life cycle. He showed similar dynamics of lamprey and salmonids abundance in particular water bodies as basis of this statement. At the same time, lamprey inhabit some water bodies where they express a resident form only and do not feed after metamorphosis. Gritsenko (1968) further analyzed interrelations between lamprey and salmonids at different life cycle stages: from egg development to feeding and spawning migrations. He concluded that lamprey and salmon do not significantly influence each other. Gross et al. (1988) described another compelling hypothesis of aquatic productivity and the evolution of diadromous fish migration.

Frequently, researchers assign particular phases (spawning and spawning migration) to the life cycle for comparison of ecological and behavioral features of lamprey and salmon. However, it is necessary to note that feeding migrations precede spawning migrations of anadromous species (Schmidt 1946, Hitch et al. 2006). Feeding migrations occur in the form of a downstream migration for anadromous species including lamprey and salmon.

It is known that migrations which takes place in the early phases of development, are a bottle-neck to survival. As abundance is determined during this phase (Nikolsky 1974; Pavlov 1979; Pavlov et al. 2007, 2010, 2011). Change of habitat through migration requires increased energy expenditure by the organism which renders it more vulnerable. Therefore, it is assumed that similar adaptations will result for successful feeding migrations of species which differ taxonomically, but inhabit similar conditions.

Feeding migrations of lamprey and salmon begin in the form of a downstream migration. The downstream migrations occur in juvenile fish and lampreys moving downstream and represent the adaptation directed to dispersion and optimization of usage of trophic resources (Nikolsky 1974; Pavlov et al. 2004, 2007). This might result in dispersion within river systems; moving from river to sea, i.e. to different ecological conditions; or in both of these cases – during different life cycle phases. Lamprey and salmon which make downstream migrations exhibit various morphological and biological characteristics, and can be at different developmental stages or physiological states. Physiological changes (smoltification in salmon, for example) can precede transferring to migratory state.

General patterns have been investigated and some mechanisms of downstream migrations have been revealed in the study of Arctic lamprey *Lethenteron camtschaticum* ammocoetes and salmonid juveniles of the genera *Oncorhynchus* and *Salvelinus* in water bodies of the Kamchatka Peninsula in the Russian Far East. We show that downstream migration represents a common behavioral adaptation for distribution and optimum usage of trophic resources even for such different groups of animals.

Material and Methods

The data for this study were collected from 2004–2007 on the Utkholok and Kalkaveyem Rivers on the Northwest of Kamchatka Peninsula.

Two methods were applied to study Arctic lamprey ammocoetes and Salmonid juvenile downstream migration, and for determining seasonal and diel patterns. A cone net was used for the capture of ammocoetes and salmonid young-of-the-year (YOY). The net was made of 1.41 mm diameter mesh, with inlet area of 0.43 m^2 and length of 2.38 m. The net was set mid-stream in the river at the end of straight section of river channel.

During the examination of diel patterns of downstream migration, samples were collected round-the-clock – every two hours, on even hours. To further investigate the seasonality of downstream migrations, night-time collections of ammocoetes were made periodically during collection of icthyoplankton.The net was deployed in the mid-channel flow for 5–30 minutes, with exposure time depending on flow rate and water turbidity. The intensity of ammocoete and YOY salmonids downstream migration was estimated based on migrating individuals number by water volume (ind. / 100 m^3). For this calculation, flow rate was measured at the cone net inlet and in-river at the deployment site. The formula for ammocoete and YOY salmonids concentration (C) in water is as follows:

$$C = \frac{100 \cdot n}{V \cdot k_f},$$

where n is the number of individuals, which have been found in the ichthyoplankton net per exposure time, ind.; $V = t \cdot v_{out} \cdot S$; k_f – filtration factor of ichthyoplankton net; $k_f = \frac{v_{out}}{v_{in}}$; t is ichthyoplankton net exposition value, sec.; v_{out} is flow rate in ichthyoplankton net setting place, m/s; v_{in} is flow rate in ichthyoplankton net opening, m/s; S is area of ichthyoplankton net opening, m^2.

Salmon juveniles of the second and subsequent years of life were captured by a stationary trap, *i.e.* a fyke-net. The diameter of the fyke-net capture hoop was 1 m, length was 4 m, inlet diameter in the hoop was 0.3 m, wings mesh was 10 × 10 mm and of bag 7 × 7 mm, wing-span was 22 m. Fyke-nets were set in the mouth of the Kalkaveyem River and in a side channel of the Utkholok River, upstream of the confluence of Kalkaveyem River.

Both ammocoetes and salmonid juveniles may be divided into three groups based on features of their feeding migrations:

1. Lamprey ammocoetes and YOY salmonids, i.e. individuals which are dispersed from spawning areas to rearing places within the natal river system or which migrate (in salmonid only) to sea soon after emergence from redds;
2. Lamprey ammocoetes and salmon parr of various age groups (1+ and older) which make feeding migrations within the river;
3. Lamprey and salmon smolts 1+ and older which undergo physiological transformations and migrate to sea to forage.

Seasonal patterns of downstream migration in older age classes of juveniles were investigated by regularly sampling with night surveys from 22:00 to 05:00 (concurrent with YOY salmonids and ammocoete sampling). The greatest mass downstream migration of almost all juvenile Salmonid species was observed at this particular time. Round-the-clock sampling data has confirmed that downstream migrations were less intense during the daytime than at dusk-night time. Night surveys were made every other day during the most intense downstream migration season (May–June). The gap between night surveys was been increased to intervals of two, then four days, as downstream migration intensity diminished. Additional night surveys were made when sudden changes of environment abiotic parameters occurred (heavy rain, flood, moonlit or cloudy dark night *etc.*).

Local surveys were made in various river systems with electrofishing (voltage of 600–700 V, frequency of 60–70 Hz), a minnow seine, and dip nets for the assessment of ammocoete and salmonid juvenile distribution within the river basin. Species composition of fishes and lampreys, and also their morphological characteristics were estimated in various habitats.

Results and Discussion

Migrations of Arctic lamprey (ammocoetes of different age groups) and feeding migration of salmonid juveniles took place during the spring–autumn season (from May till October).

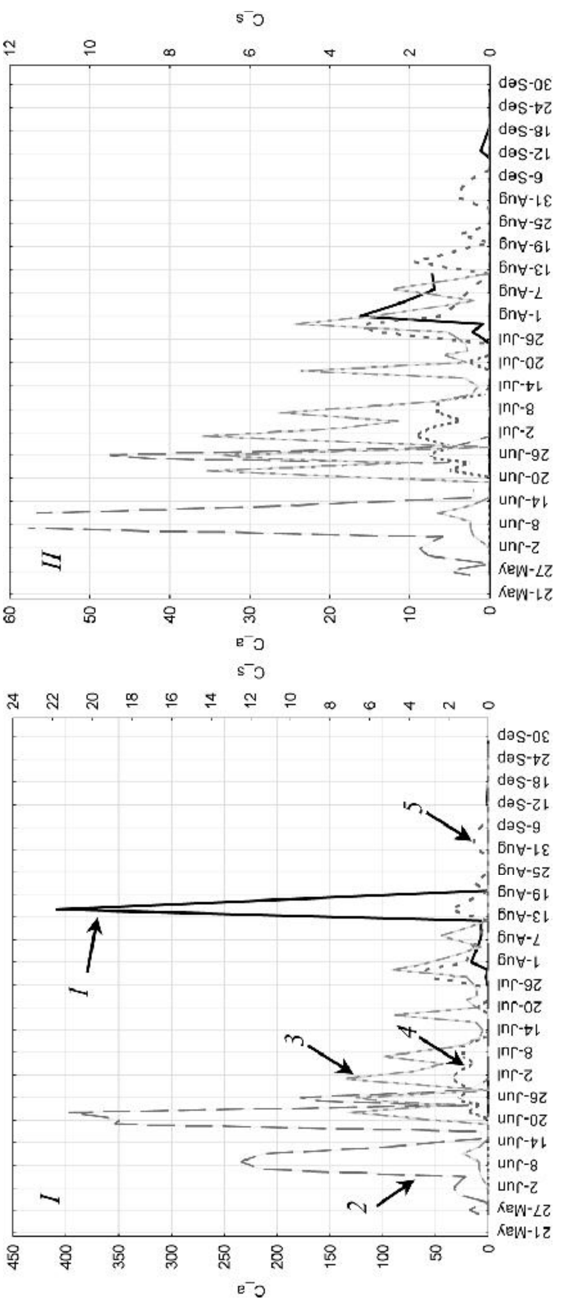
Migration of YOY ammocoetes and salmonids

Ammocoetes disperse within the river system soon after emergence from ground. Among salmon, YOY coho salmon, *Oncorhynchus kisutch,* and rainbow trout *O. mykiss* distribute within riverine habitats (Pavlov et al. 2008; Kirillova et al. 2011); juvenile pink salmon, *O. gorbuscha*, and chum salmon *O. keta*, migrate to the sea. Despite different extension of feeding migration for these species at specific life cycle stage, there are several common patterns.

These feeding migrations have restricted time frames (Figure 23–1) and involve a great amount of individuals. Concentrations of ammocoetes reach thousands of individuals per 100 m^3, while salmon juvenile abundance reaches hundreds individuals per 100 m^3 (Pavlov et al. 2010; Kirillova et al. 2011). Lamprey ammocoetes, coho salmon and rainbow trout disperse within the river system in short time frames from several days up to 2–4 weeks. Pink salmon migration to the sea occurs for longer time up to 1.5 months. Chum salmon juveniles have two strategies of migration – "pink salmon-like" and "coho salmon-like" as described by Gritsenko (1987) and Pavlov et al. (2008). The first ones migrate seaward soon after emergence from redds. They do not feed in the river and most of them have externally visible yolk sack. The second ones spend several weeks in the river until they migrate to sea. They feed intensively and grow significantly. Migrational behavior within the groups is different. Representatives of "pink salmon-like" group avoid light and hide in various shelters during the day time. They migrate downstream in the darkest time of the day, drifting with river flow. "Coho salmon-like" chum salmon are active both in the light and dark time of the day. They gather in the schools and stay in the open water at shallow river curves feeding on insects. Their downstream migration is predominantly active. Only the first group of salmonid migrants demonstrate the special similarity of feeding migration patterns to YOY ammocoetes.

Every year, downstream migrations both in ammocoetes and salmonids begin at a time that varies slightly from year to year, depending on phenological conditions. Migration intensity depends on in-river hydrological conditions such as sudden flooding. Perhaps water temperature does not directly influence the intensity of migration, but does define migration initiation as it is a critical factor in development (Gritsenko, 1987; Pavlov et al., 2008). Here, we illustrate seasonal migration patterns for ammocoetes in the Utkholok and Kalkaveyem Rivers in years with differing hydrological conditions (without separation into age groups) (Figure 23–2).

Figure 23–1 (next page). Seasonal pattern of downstream migration for YOYs of ammocoetes (*1*) and salmons: (*2* – pink salmon, *3* – chum salmon, *4* – coho salmon, *5* – rainbow trout) in Kalkaveyem River (I) and Utkholok River (II), 2006. C_a – ammocoetes concentration in water stream (ind./100 m^3), C_s – concentration of salmon YOYs in water stream (ind./100 m^3).


I
II
C_a
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1
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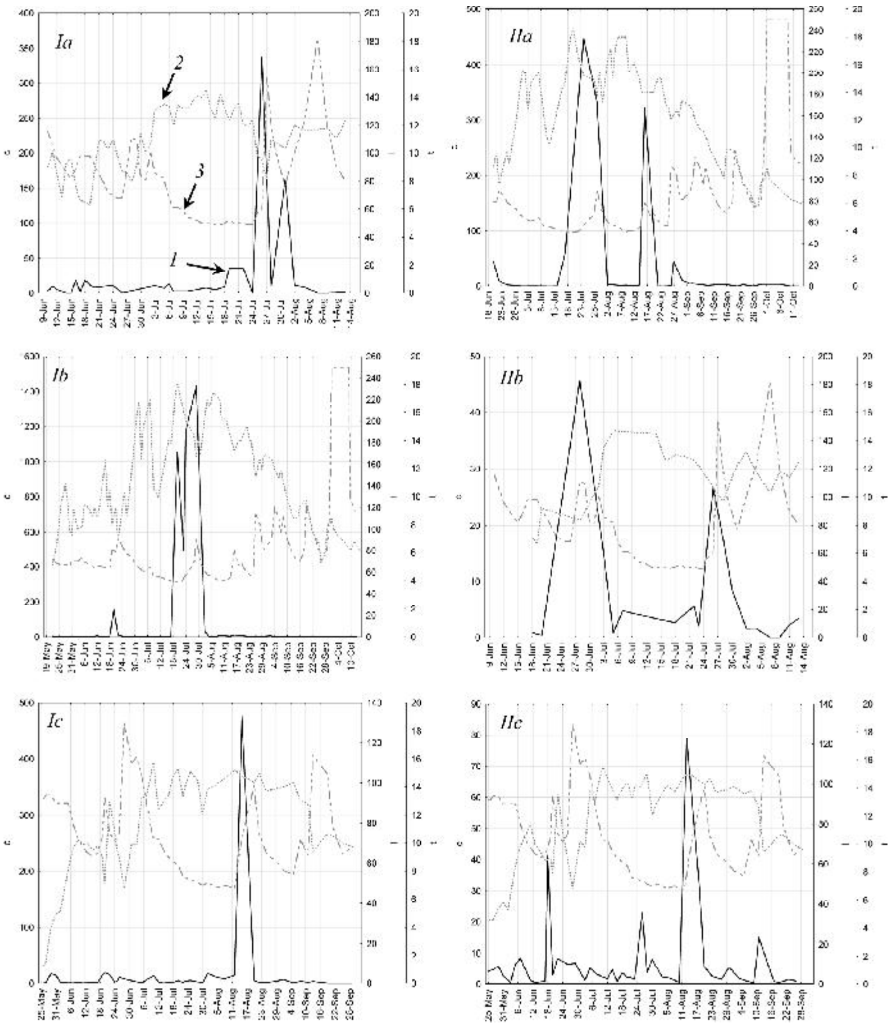

Figure 23–2. Seasonal pattern for ammocoetes downstream migration - c, ind./100 m^3 (*1*), for temperature - t, ˚C (*2*), for water line - l, sm (*3*), in Kalkaveyem river (*I*) and Utkholok River (*II*). *a* – 2004, *b* – 2005, *c* – 2006.

Migration of ammocoetes and salmon YOY primarily takes place during the night-time at illuminance of less than 1 Lx: beginning at twilight and ending at dawn (Figure 23–3). Diel downstream migration is demonstrated only in chum salmon juveniles belonging to the "coho salmon-

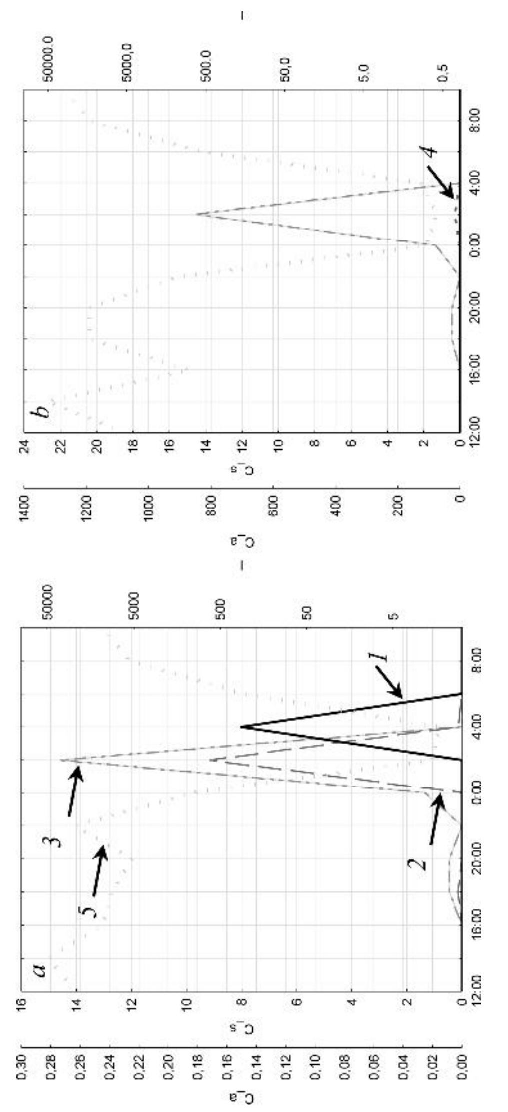

Figure 23–3. Downstream migration diel pattern of ammocoetes (*1*) and salmon YOYs– pink salmon (*2*), chum salmon (*3*), rainbow trout (*4*) YOYs in connection with illuminance (*5*) in Kalkaveyem River, June, 13 (*a*) and July, 23 (*b*) 2005. C_a – ammocoetes concentration in water stream, ind./100 m^3, C_s – concentration of salmon YOYs in water stream, ind./100 m^3, I – illuminance, Lx.

like" group which stay in the river for a while before their seaward migration. This mechanism of downstream migration is typical for early ontogenetic stages of juvenile fish of various species (alevins and fry) for which the vision is the leading mechanism for orientation in the river (Hoar 1958; Ali & Hoar 1959; Pavlov, 1970a, 1979; Pavlov et al. 1999).

As soon as ambient illuminance drops below threshold values for optomotor reaction, juvenile fishes lose visual reference points and are carried instead by instream flow. This downstream migration mechanism provides protection for juveniles against predatation (mainly by larger salmon juveniles) (Hoar 1958; Pavlov, 1970a). Chum salmon have a more complex mechanism of downstream migration initialization. Chum salmon fry ("pink salmon-like" type) emerge into the instream flow under conditions of visual orientation loss when illuminance drops below threshold value (Hoar 1958; Ali & Hoar, 1959 etc.). Illuminance threshold values for optomotor reaction increase concurrently with juvenile growth. Additionally, the older juveniles orient themselves in the instream flow not only by use of eyesight, but also at the by use of other sense organs including touch, lateral line, and equilibrium (Dijgkraaf 1962; Pavlov 1970b; Harden & Jones 1968; Pavlov & Tyuryukov 1986, 1988, 1993).

Chum salmon orientation during night-time hours improves as juveniles grow and results in an intensity decrease for nighttime downstream migrations (Pavlov et al. 2010). The increased intensity of diel migrations is associated with exhibition of other downstream migration mechanisms. In fact, downstream migration of grown in the river chum salmon from "coho salmon-like" group is initiated by mechanisms which are inherent for older juveniles start to predominate (Pavlov et al. 2010). Reduction of feeding areas at summer mean water and interspecific competition for food make chum salmon migrating seaward.

YOY ammocoete eyes are underdeveloped relative to salmonid species, though they are capable of discriminating changes in illuminance. Therefore, their mechanism of downstream migration initiation differs from that of salmonid juveniles. As it gets dark, ammocoetes make bursting movements to the water surface. This movement gets them away from the ground and involve in the current (Kirillova et al. 2011).

Clearly, migration of this group of ammocoetes and Salmonid YOY (except for "coho salmon-like" chum salmon) is passive. This allows them to preserve their small energy reserves that are critical for as-yet non–feeding young fishes (Kanidiev & Levanidov 1968).

Migrations of older age groups within the river basin

Lamprey ammocoetes of various age groups and salmon parr of 1+ and older age groups that make feeding migrations within the river, are very diverse in biological characteristics and age composition. These organisms make repeated migrations within the river system to disperse within water body for optimal exploitation of food resources. These migrations take place from early spring to late fall. These migrations are distinct from that of younger juveniles in that they are observed in both upstream and downstream directions.

This group of salmon juveniles includes parr (juveniles in the river phase of life) of coho salmon, cherry salmon, rainbow trout, Dolly Varden char and white-spotted char (Pavlov et al. 2008, Pavlov et al. 2011). Ammocoetes are represented by various-aged individuals – both pre- and post- metamorphosis (Kirillova et al. 2011).

Comparison of downstream migration intensity is improper due to variation in capture methods for ammocoetes and larger salmon juveniles. Also it is impossible to estimate the scale of upstream migrations. However, available data does allow us to present qualitative characteristics of the upstream migration process.

In seasonal patterns of ammocoetes downstream migration, it is possible to distinguish three phases of different migratory activity which correspond to habitat redistribution (Kirillova et. al 2011): spring (May–June), summer (July) and autumn (August–September). In the spring phase, migrants are predominantly one- and two-year olds; in the summer phase, a massive migration of new-generation ammocoetes takes place; subsequently in the autumn phase, four- and five-year old individuals (including metamorphic ones) migrate most intensely.

The concentration of older ammocoetes migrating downstream is generally insignificant in comparison with the concentration of young-of-the-year ammocoetes at during the preliminary migration phase (Figure 23–2, 23–4); their concentration did not exceed 10 ind./100 m^3.

As mentioned previously, salmon juveniles migrate within the river system from early spring through late fall, i.e. the entire phase when water temperature allows fish juveniles to feed (above 2–3 ˚C) (Chebanova 2002). Water level fluctuations indirectly influence parr migration intensity: feeding habitat decreases as secondary channels and creeks dry up. Because of this, fish juveniles are forced to leave secondary habitats (side channels, brooks, abandoned channels) and move to large tributaries and main channel. It appears that these changes trigger parr migrations. In addition, both ammocoetes and salmon juveniles leave those parts of rivers where spawning areas are located in season of mass spawning of Pacific salmon *Oncorhynchus* (in July–September) when there is intensive benthic disturbance.

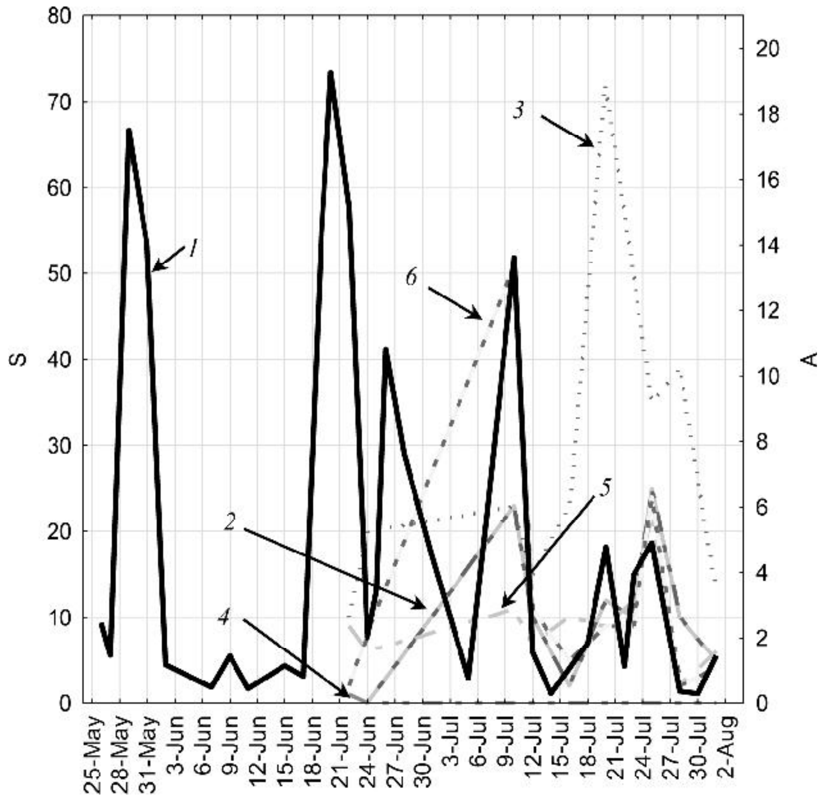

Figure 23–4. Downstream migration seasonal pattern of ammocoetes (1) and parrs of salmon old ages groups (rainbow trout – 2, coho salmon – 3, cherry salmons – 4, white-spotted char – 5, Dolly Varden – 6) age groups 1 + and older. S – downstream migration intensity of salmon juveniles, spec. / night, A – downstream migration intensity of ammocoetes, ind. / 100 m3.

It is necessary to note the importance of salmonid spawning season in relation to the migration initiation in salmon parr and ammocoetes. During this time, the salmon juveniles stay close to spawning areas since they feed on eggs which have been washed out of redds (Pavlov et al. 2011). Ammocoetes, by contrast, feed on the decaying tissue of salmon that die after spawning (Kucheryavy 2010). At this period salmon parrs migrate – both downstream and upstream from various rearing areas of the river to spawning grounds to feed on eggs. It might be supposed that ammocoetes also concentrate at salmon spawning grounds at this time. Salmonid eggs and carcasses due to their high nutrition (Bogatov, 1994) support salmonid juveniles and ammocoetes with energy that is important for further survival in winter (Lund et al., 2003) and might play an important role in choice of life strategy (Kucheryavy et al., 2010). Various aged ammocoetes, as well as salmon parr can move both downstream and upstream. It proves to be true that large ammocoetes (body length of 87–216 mm that corresponds to age 2 + and older, up to metamorphic individuals) are found in Mysmont river middle course (second order tributary of Utkholok River), considerably (5–10 km) upstream of previously documented spawning areas (Kirillova et al. 2011). Results of examinations on other species confirm the possibility of additional lamprey upstream dispersion (Sugiyama & Goto 2002; Quintella et al. 2003, 2005)

Despite the similarity in seasonal downstream migration pattern in ammocoetes and salmon parr, their diel migration patterns differ. Salmon parr migrate both at night and during the day, while ammocoetes migrate only at night. Depending on the species, salmon juvenile migration can be most intense in the evening or morning twilight (rainbow trout, coho salmon), or in the afternoon (cherry salmon). Migration intensity and confinement to a certain time of day in salmonids is defined by feeding and defensive behavior (Pavlov et al. 2011).

Seaward migration

Lamprey and salmon smolts of 1+ and older age groups is the special group for which migration is directed to habitat change from freshwater to marine, which includes significant morphological and physiological transformations (i.e. smoltification). In outward appearance the smoltification process manifests as a change to a silvery pelagic coloration both for salmonid fish and for lampreys. External changes are accompanied by a physiological transformation which allows the organism to survive in sea water.

The migration patterns of salmonid smolts of various species has been well studied, and numerous studies have been devoted to various aspects of this phenomenon (Quinn 2005; Pavlov et al. 2008, Shuntov & Temnykh 2008; Pavlov et al. 2011). Downstream migration of smolt to the sea takes place in the season when conditions for this are optimal, both in a river and in the sea (Saunders & Bailey 1980). It is well demonstrated that this statement also is true of lamprey. Therefore, seaward migration is strictly time-limited and is generally invariable from year to year. Some insignificant variations are associated with discrete phenological features of a specific year.

In a case study of salmon smolts in the Utkholok River, we elucidate specific terms of seaward migration in a variety of species: firstly, Dolly Varden migrate downstream to the sea, followed closely, if not simultaneously by coho salmon. Unlike Dolly Varden, coho salmon downstream migration is longer. Corresponding with the end of the coho salmon downstream migration, the white-spotted char presence in the migratory group increases. The white-spotted char abundance is then replaced by rainbow trout and cherry salmon. In the Utkholok River, coho salmon migration duration is approximately 2.5 months, rainbow trout migration lasts 2 months, cherry salmon migration lasts 1 month; Dolly Varden char and white-spotted char downstream migration usually does not last longer than than 1.5 months (Figures 23–5 and 23–6).

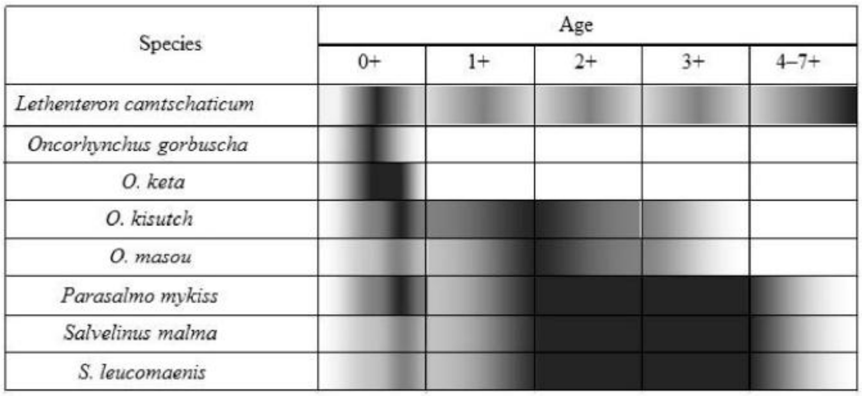

Figure 23–5. Downstream migration intensity of salmon juveniles and ammocoetes at various stages of life cycle.

Arctic lamprey metamorphosed juveniles preparing for or migrating to the sea which we label as smolts (after Sidorov & Pichugin 2005), are captured in samples beginning in the final third of June and persist until the middle of October. However, it is impossible to discuss concrete features of downstream migration of arctic lamprey since the available data is based on a collection method that the juveniles can avoid due their

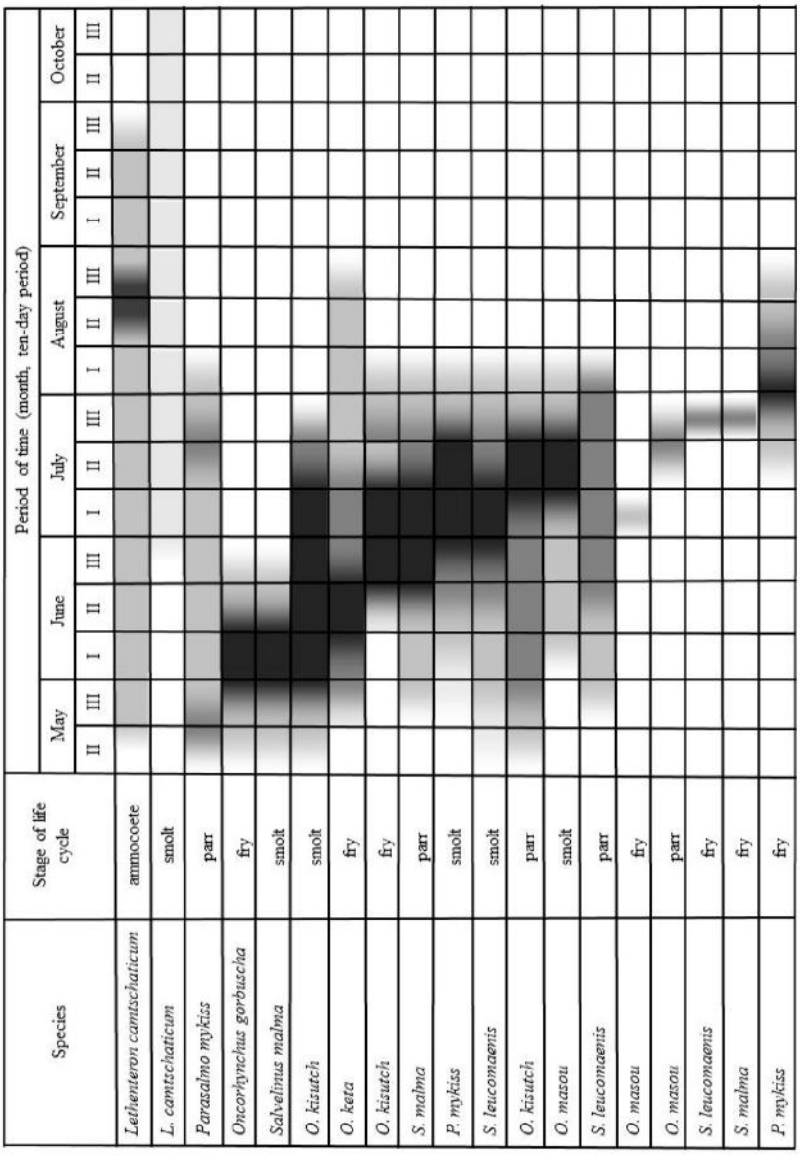

Figure 23–6. Seasonal (spring to autumn) patterns of intensity of salmon juveniles and ammocoetes downstream migration at different stages of life cycle.

ability to swim upstream against strong currents. Therefore, the collected data are rather qualitative. Quite often lamprey smolts were captured during electrofishing samples at eroding riverbanks, among exposed roots and other vegetation. It is possible to deduce that lamprey smolts select these habitats during the day time where the soft substrate and overhanging banks protect them from bright light.

Comparison of downstream migration patterns for foraging, has shown that salmon juveniles and Arctic lamprey ammocoetes have a series of analogous patterns. The preliminary migration of YOY fishes, dispersion of older age individuals within the river system, and seaward run of smolts all occur as downstream migrations (Savvaitova et al. 2007; Pavlov et al. 2008, 2010, 2011). All these movements previously described, represent an adaptation to foraging resources and optimum usage of habitats. The scale of feeding migration vary among species and years. From year to year, the triggers for the beginning, duration and downstream migration intensity are defined by ecological factors such as water temperature and water level. Ammocoetes and salmonids that make downstream migration, form the “migratory” part of the aquatic vertebrate community in the river (Pavlov et. al. 2008). Numerous similarities in pattern and mechanism of the initialization of downstream migrations are a clear example of behavioral adaptations for phylogenetically distinct groups of organisms which inhabit similar environments.

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