Arch. Hydrobiol. 153 3 503–528 Stuttgart, February 2002

Development and life history of Far Eastern Russian *Pteronarcys* spp. (Plecoptera, Pteronarcyidae)

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With 8 figures and 3 tables

Abstract: Field and laboratory studies of *Pteronarcys reticulata* (BURMEISTER, 1839) and *P. sachalina* KLAPÁLEK, 1908 during several years are combined to elucidate development and life history of these two coexisting Far East Russian stoneflies. They were found to be similar in all studied aspects. Adults fly and oviposit mainly in June. Spontaneous egg development occurs at 16 °C and over; at 12 °C and lower, eggs remain dormant until warming induces development. Speed of development is not distinctly temperature dependent. Ready-to-hatch larvae remain in diapause until warmed again after an exposure to cold, i.e., in the field they apparently hatch the next spring. In the first instar the larva is inactive, its head capsule width (HCW) is 0.4 mm. Qualitative developmental change (gills, pilosity, pronotal corners and abdominal point, antennal and cercal segment numbers, wing pads) is continuous, instars cannot be identified, except the last, mainly by abrupt growth of wing pads. Mode of wing development differs from other Plecoptera studied so far. Larvae in the first two years moult several times per year, larger larvae less; growth is interrupted in winter. In their third summer, larvae enter the penultimate instar and in autumn the last instar which lives for 8–9 months, until adult emergence five years after oviposition. Increment of linear measurements at moults varies individually; average increment is 18 % and little dependent on larval size until specimens prepare visibly for metamorphosis, at HCW > 3 mm. During the last two moults, the increment drops to an average 8 %. Specific or sexual differences in growth rate were not detected. The fundamental unsuitability of the standard approach of size class analyses in random population samples using linearly increasing classes is discussed. An alternative geometrically progressing growth model based on first instar HCW and mean increment at moults recognizes 16 hypothetic instars; last instar males (HCW 3.8–4.7 mm) fall into instar 15, females

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0003-9136/02/0153-0503 $ 6.50

(HCW 4.3–5.6 mm) into instar 16; whether sexes differ by one in actual instar number is uncertain.

Key words: egg incubation, egg dormancy, first instar, larval growth, increment at moult, developmental change, wing development, instar number, Dyar's Rule, life cycle duration.

Introduction

Representatives of the genus *Pteronarcys* are among the largest extant stoneflies and often of great abundance. Larvae occur in a variety of lotic habitats in North America and in parts of the eastern Palearctic region. In view of their size and abundance they must play an important role in these stream systems. *Pteronarcys* larvae are essentially detritivorous shredders but other foods and feeding habitats have also been described (STEWART & HARPER 1996 and references therein). A recent study suggests Nearctic members of the genus may have specific and rather varied trophic relations (PLAGUE et al. 1998). Much published information is available on the eight American species (see references in STEWART & STARK 1988, TOWNSEND & PRITCHARD 1998, 2000) which exhibit a wide variety of life cycle traits. However, little is known of the ecology of the Asian members of the genus, *P. reticulata* (BURMEISTER) and *P. sachalina* KLAPÁLEK which are sibling species (NELSON 1988, STARK & SZCZYTKO 1982). Adults and eggs of both species are well described, but information on their larvae was only recently improved (ZWICK & TESLENKO 2001).

Pteronarcys reticulata and *P. sachalina* are largely allopatric but their distributions overlap in parts of the Russian Far East, mainly under maritime climatic influence. In these areas, the species frequently coexist and fly simultaneously. We were interested in the development, life histories and ecology of the two species on which there is no detailed published information. LEVANIDOVA & ZHILTZOVA (1979) emphasized the broad range of thermal conditions under which *P. reticulata* can occur and indicated that its life cycle extends over several years; ZAPEKINA-DULKEIT (1973) assumed a 4-year life cycle in the Bazaikha River, Yennissei River basin. NIKOLAYEVA (1984) published a regression relating mass to larval body length, and a brief summary on growth, biomass and ecological aspects of *P. sachalina* is also available (TESLENKO 1992).

Our data enable us to describe the temperature dependence of egg development and the morphological change of developing larvae, to interpret population structure in the field in the light of biometric data, and to reconstruct the complete life cycle of the two Far Eastern Russian species. We also provide

information like increase at moults, length of cohort production interval, and other that is needed for an understanding of the ecological role of these common large stream invertebrates.

Material and methods

Insects

Our study integrates results obtained during different study campaigns during several years involving both preserved (I) and live (II) animals.

(I) Preserved material

We used preserved field collections for analyses of population structure and for general biometry. We determined sex and measured head capsule width (HCW) or labrum width (LW) to the nearest 0.02 mm with an eye-piece micrometer at magnifications up to 200 (slide-mounts). Because LW can be directly compared between exuviae and intact larvae, LW was preferred. Antennal and cercal segments of exuviae of many reared specimens and of some field collected large larvae were counted.

In many larvae we recorded also front wing pad length (WL) as the distance between the mesonotal rear margin and the wing tip, parallel to the sagittal axis (Fig. 4). In many specimens whose prospective wing pad tip did not project beyond the rear edge of the mesonotum, we routinely recorded "Zero". Later, we realised the significance of an anterolateral angle on the mesonotal margin. The angle is apparent already in small larvae and shifts backward during development; it finally becomes the tip of the wing pad. To document the shift, we measured the distance of the angle from the mesonotal rear margin behind it precisely in a limited number of larvae and expressed it as a negative value. For comparison of shapes across the larval size range, the wing pad length measured was related to specimen size by calculating a wing index, WI = WL/HCW.

We examined 273 larvae of both species kept in the collections of the Institute of Biology and Soil Sciences, Russian Academy of Sciences, Vladivostok (IBSS). This material was collected by several persons over several years from various streams flowing from the Sikhote Alin Range and the Manchurian Mts. (Russian Far East, the Primorsky and Khabarovsky Regions). Another 150 larvae (in coll. Zwick) were picked from upturned rocks in streams or from random kick-samples taken with a 1 mm mesh-size net in swift current during joint field work in June 1998 in the same region. Some very small larvae were found between pupae of Blephariceridae (Diptera) that had been scratched off rocks in swift current. Because small larvae cannot be identified (ZWICK & TESLENKO 2001), the June 1998 collections are a collective random sample of *P. sachalina* and *P. reticulata*. A series of samples of *P. sachalina* from the Kedrovaya River (43° 01′ N, 131° 24′ E – 43° 09′ N, 131° 36′ E), and one large individual sample from the Narva River (43° 04′ N, 131° 23′ E) (leg. V. Teslenko) consti-

tuted further random samples of population structure at the respective time of collection.

(II) Live material

Work with live material included observations of adults during field work in 1998 (see above), laboratory egg incubation (IIa), rearing of larvae hatching from these eggs (IIb), and field collected larvae caged for a whole year in the field (IIc), or for a short period, until their next moult, in aquaria in the laboratory (IId). Change of size and shape at moults was recorded from comparisons of exuviae with either the corresponding larva which was preserved the next day, or with several successive exuviae of the same laboratory reared specimen. Only apparently healthy specimens were used, asymmetrical individuals and specimens which died shortly after a moult (and had, as a rule, not fully expanded their new cuticle) were excluded.

(IIa) Egg incubation

Dozens of mating pairs of both *Pteronarcys* species were found on grass stems in the partial shade of a bridge on the Komissarovka River, a tributary to Otkosnaya River, near Lesogorye (44° 51′ N, 134° 19′ E), in the Ussuri River Basin on 16 June, 1998. Eight small extruded egg masses of *P. reticulata* (675 eggs) and 2 batches of *P. sachalina* (405 eggs) were obtained and formed the basis for all laboratory rearing.

Egg masses were flushed off the abdominal tip of females and kept in 20 ml polyethylene bottles with little water during ten days of travel; bottles were opened once a day to admit fresh air. During travel, bottles were protected from heat as much as possible and were suspended in a local river at night. Temperature regime during travel was variable, with large daily amplitudes and extreme heat, up to 36.9 °C; however, 30 °C or more occurred only two times, for 1 and 7 hours, respectively (Table 1, from a data logger packed with the samples, 1 reading every 5 minutes).

Most eggs survived. On 4 July, 1998, eggs masses were subdivided and several eggs from each incubated in clean stream water in 15 ml glass vials, under a 14 hr photoperiod, in the laboratory at Schlitz (compare Zwick 1996 for details of procedure). Because of the complex chorion structure, development could first be seen when a large germ band had already formed; details could not be recognized. Only the appearance of eye-spots indicating the completion of embryonic development was noted. Because spontaneous hatching at the various incubation temperatures did not occur during the 21 days after the appearance of eye-spots, only ca. 10 eggs were permanently

Table 1. Temperature exposure of *Pteronarcys*-eggs during 10 days of travel.

Temperatures [°C]	Minimum	Mean	Maximum
Nocturnal exposure in rivers	9.5	15.8	23.0
Transport during the day	12.4	20.5	36.9
Overall mean temperature during travel		19.1	

left at each of the different incubation temperatures, as controls. Most eggs, however, were then cooled to 4 °C for 34 days, and thereafter again warmed to 16 °C. This experimental protocol was followed for eggs incubated at 16, 20 and 22 °C, respectively (Fig. 1).

For eggs incubated at 4, 8, and 12 °C, respectively, the same protocol could not be followed because even after 129 days there was no development. The eggs concerned were then transferred to 16 °C and developed normally but did also not hatch spontaneously. Three weeks after entering the eye-spot stage, the unhatched eggs were cooled to 4 °C for 54 days, and then again warmed to 16 °C. However, only a fraction of the larvae hatched from most egg masses. The remaining eggs were 125 days later again cooled to 4 °C for 41 days, and then returned to 16 °C, which led to additional hatching (Fig. 2) during the next 85 days, until 13 Dec. 1999.

Analysis of hatching performance was then stopped and the remaining eggs transferred to the sprinkler system to rear larvae (see below). Many hatched but their accurate number remains unknown.

(IIb) Rearing of larvae

Like the other Systellognatha, in the first instar, larvae of *Pteronarcys* live on yolk remains in their guts (MILLER 1939) and are inactive. To determine time until first ecdysis, some newly eclosed larvae were kept in loosely capped 15 ml vials with little sand and a little fine detritus, as food after ecdysis. Once in the second instar, larvae survived only briefly in vials and losses were high even if individuals were transferred to running water as soon as ecdysis was noticed. Therefore, the eggs remaining in December 1999 (see IIa) were transferred to the sprinkler rearing system where larvae were kept in small groups until about 5 mm long. Then, they were kept singly or two of different size together.

The rearing system was a recirculating sprinkler system with 25 litres of clean ion-poor circumneutral water from the Breitenbach at Schlitz; water was replaced once a week. An aquarium filter pump passed water from a reservoir into a 2 m long, 15 mm diameter plastic tube with 2 mm holes. From each hole, an individual jet of water was supplied to a cage in a trough underneath. Cages were polyethylene boxes ($5\times5\times5$ or $10\times10\times10$ cm, respectively) with screen windows (mesh size 0.5 mm, except 0.2 mm for eggs and first instars) containing some fine gravel and one larger stone, for cover. Injected water passed through the screen into the trough and circulated back to the reservoir. On average, 30–40 L/h passed through each cage.

Larvae were fed conditioned alder leaves (*Alnus glutinosa*) in excess. Exuviae were collected every 2 or 3 days and cages cleaned once a week; screens were more frequently cleaned with a tooth brush. Although boxes contained only a shallow layer of water far below the upper edge of the box, larvae escaped at night and even 15 mm long individuals travelled through the pump and supply tubes without being harmed; once this was noticed, cages were covered with lids, with inlet screen windows.

Laboratory rearing was in a cellar with a much reduced seasonal temperature regime, without diel pattern. During summer when room temperatures were 12–16 °C an aquarium heater raised temperature to 17 °C for 3 hrs. each early afternoon. After No-

vember, temperature dropped to 8 °C and was further lowered with an immersion cooler to 4 °C ± 0.5 from 12 January to 12 February 2000, and from 10 January to 12 March 2001. Light was from a fluorescent tube 13 hrs every day. When laboratory rearing proved to be successful for longer than initially expected, photoperiod was set parallel to the temperature change and ranged from 7–17 hrs. of light after November, 2000.

(IIc) Field experiment

Fifty-seven larvae of *P. sachalina* from the Narva R. were caged in the Kedrovaya River in the Kedrovaya Pad Reserve, on the west coast of Amur Bay, opposite Vladivostok, from August, 1988 to the end of July, 1989. Larvae were inspected every two weeks during the growth period and once a month during winter; total observation time was 350 days (TESLENKO 1992). Cages were iron cylinders of 0.3, 0.5 and 0.9 litre, respectively; both ends were covered with 1.5 mm plastic mesh screen (TIUNOVA 1991). Each cage was fastened to a string and securely anchored to the bottom. Cages were placed at the downstream end of a small riffle, about 25–30 cm deep. Larvae were fed conditioned leaves (*Alnus, Quercus, Acer, Tilia*) and detritus in excess; there was natural growth of algae on the cage walls.

Although handling of live specimens was difficult, body length (BL) and head capsule width across eyes (HCW) were measured with a ruler or an ocular micrometer, respectively. Wet weight (WW) was determined with torsion balances, to the nearest 0.01, 0.1, and 1.0 mg, respectively, depending on specimen size (TESLENKO 1992).

(IId) Laboratory experiment

Twenty-four larvae from the Narva River réady to moult to the penultimate instar were suspended in cages in an aerated 12 L aquarium in the laboratory at Vladivostok during a short term experiment in May and June, 1999, each larva until it had performed a moult. Cages were thin-walled transparent polyethylene cylinders, 7 cm in diameter, 8 cm deep, with 1.5 mm screen tops and bottoms; they contained one flat light stone. The experiment was at ambient room temperatures (11.2–24.3 °C) under natural photoperiod. Water was from the small clean Shamora River flowing into the Lazurnaya Inlet in suburban Vladivostok. It was replaced once a week, the cages and the aquarium walls were cleaned twice a week. The larvae fed on conditioned alder leaves (*Alnus hirsuta*).

Temperature records

In the Kedrovaya River, water temperatures were measured with a Hg-thermometer at 08 and 20 hrs. and the mean recorded as daily mean temperature, according to regional metereological standard procedures (Fig. 7). During the 1998 field work, stream temperatures at the times of collection or overnight in streams at campsites were recorded at 4-minute intervals with an ORION® Tinytalk data logger. Similar loggers and Dallas Semiconductor I-Buttons recording temperature at 20 min intervals were used during laboratory work at Schlitz. All data are in degree Celsius (°C).

Data analysis

MS EXCEL, version 7, and SPSS for Windows (release 9.0.0), respectively, were used for data analysis.

Results

Habitats and adults

During the June, 1998 collections, larvae of both species were found in a great variety of habitats. *P. sachalina* was sometimes found in very cool streams (for example, Pravaya Poperechka River, 8.0–8.4° between 13:00 and 15:00 hrs.). Both species together were collected from cool mountain forest streams (for example, Upper Nemtu River, late afternoon high 13.1°, nocturnal minimum 9.5°) but also in larger and warmer rivers (for example, Ussuri R. at Kamenka, late afternoon high 17.4°, nocturnal minimum 15.6°). *P. reticulata* alone was found in warm rivers like the Bolshaya Ussurska R. at Dalnerechensk (late afternoon high 23.0°, nocturnal minimum 20.9°).

Mixed groups of exuviae on emergence supports were found several times, and adults of both species were abundant 11–26 June, 1998, repeatedly in mixed groups. Netting of descending specimens from some large swarms observed against the late evening sky over streams showed that swarms were also mixed. Many years of observations by students from IBSS show that both species fly simultaneously, during a single annual flight period (LEVANIDOVA & ZHILTZOVA 1979).

Feeding was never observed, drumming in the field was occasionally noticed (TESLENKO, unpubl. observations). Females oviposited in flight, during afternoon sunshine as well as at dusk, patrolling over streams and eventually dropping a pea-sized, greenish-grey egg mass into a riffle, from several meters above water. Females then usually landed and extruded a smaller residual egg mass.

Egg development

Eggs developed at 16–22° but not during 4.5 months at 4–12°. The latter eggs were after this time transferred to 16° and then developed. The complex chorion permitted no detailed observation of morphogenesis. Speed of development did not clearly depend on temperature: By 15 August, 1998, no eggs incubated at 16–22° since 4 July had attained the eye-spot stage but at the next inspection, on 3 September when eggs were 10 weeks old, they all had eye-spots (Fig. 1). Most eggs initially incubated at 4–12° were in the eye-spot stage 12 weeks after transfer to 16° (Fig. 2), regardless of the different initial incubation temperatures.

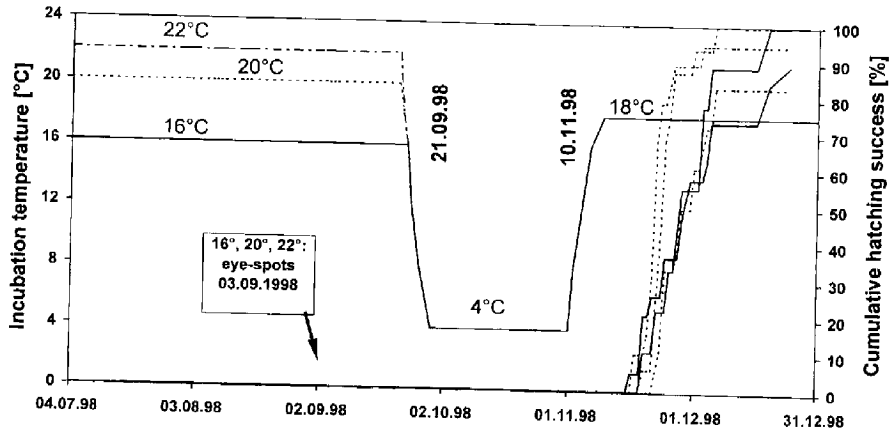

Fig. 1. *Pteronarcys reticulata* and *P. sachalina,* cumulative percentage hatch from eggs. Rising curves show hatching from individual samples, lines showing incubation temperatures labelled. Samples were initially incubated at different constant temperatures (16, 20 and 22 °C, respectively). They attained the eye-spot stage simultaneously and were thereafter all subjected to the same temperature regime.

Dissection of a few eggs in the eye-spot stage showed that the larvae were fully developed but immobile. Because the completely developed embryos left at the incubation temperatures did not hatch within the next 21 days, most were subjected to cooling to 4° for about a month; larvae hatched synchronously three to four weeks after being placed at 18° (Figs. 1, 2). About 30 fully developed embryos that were left permanently at 16, 20 and 22°, respectively, did not hatch; embryos decayed in the eggs, by May, 1999. However, from one of three other samples kept at 16, 20 and 22°, respectively, until early December (three months after eye-spot formation) three individual larvae of *P. reticulata* hatched at 20° after mid November. Together, these three samples contained about 200 ready-to-hatch embryos which were cooled to 4° in December; nine more larvae, a few from each sample, hatched at that temperature. Massive hatching from the same egg masses started 3 weeks after the eggs were returned to 18 °C. The hatching eggs were moved to the sprinkler system to obtain many viable larvae for rearing purposes, so that the accurate number of hatchlings could not be determined.

Hatching success varied between the experiments. In eggs incubated at 16–22° from the start, average success exceeded 90 %. From samples first incubated at 4–12° and then at 16°, 3 to 90 % hatched after eggs had been at 4 °C for 53 days. Hatching success increased to 16–96 % (Fig. 2) after a second cold period of 40 days.

From the beginning, egg masses had fungus infections, initially perhaps mainly supported by organic contaminations in the stream water used for in-

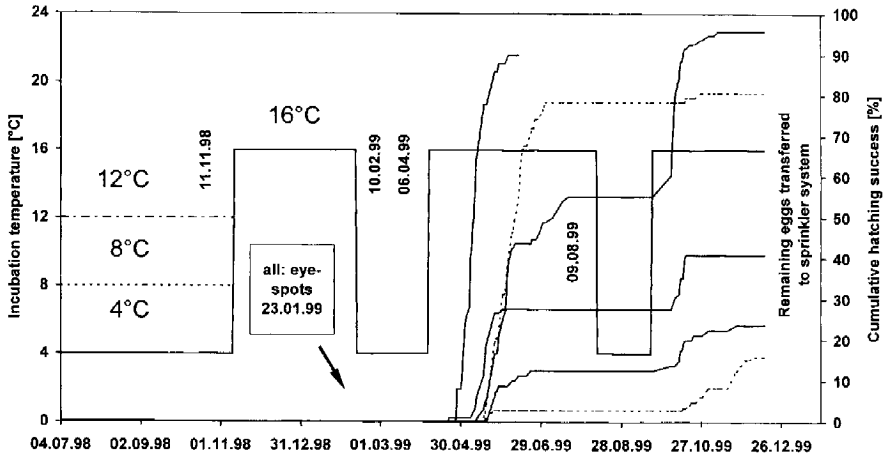

Fig. 2. *Pteronarcys reticulata* and *P. sachalina*, cumulative percentage hatch from eggs. Rising curves show hatching from individual samples, lines showing incubation temperatures labelled. Samples were initially incubated at different constant temperatures (4, 8 and 12 °C, respectively). There was no recognizable development by 11 November, from when on all samples were subjected to the same temperature regime. Hatching from most samples still continued when they were transferred to the running water rearing system where final hatching success could not be determined precisely.

cubation. Massive fungal growth, even if fungal hyphae had penetrated between the layers of the complex chorion, fungi appeared to destroy only eggs that were already dead (see also MILLER 1939, p. 575). Some infected eggs totally lost the complex pillar-shaped outer layers of chorion plus the anchor plate so that only a completely smooth cuticular sphere remained which had visible imprints of fungal hyphae on its surface. From several such eggs larvae hatched when eggs were more than 18 months old.

Hatching, egg burster

Fully developed larvae lie on their side, on the flat bottom of the egg, like *P. dorsata* (SAY) (MILLER 1939). Most larvae opened the complex chorion where their egg burster rested, i.e., at the level of the greatest circumference of the egg; only very few detached the flat anchor pole, as described for *P. dorsata*. In empty glass vials, several larvae failed to exit through the slit in the rigid chorion; this problem was overcome by adding some sand providing a foothold. The egg burster on the embryonal cuticle is a strongly sclerotized crest with 2–4 sharp teeth (Fig. 3 b) on an oval piece of thin cuticle; it remains inside the egg when the larva hatches. Species specific differences were not observed.

Larval growth and development

Instar discrimination

First Instar. Larvae (Fig. 3 a, c) appear milky white, are inactive and move only when disturbed; they survived well in standing water. At 16 °C they lived for about eight days (n = 22; mean = 7.8; range 5–10). First instars of both species have nine-segmented antennae and three-segmented cerci, the last segment only with fine apical sensilla, no setae. Tarsi are three-segmented, the eyes have several ommatidia. Slightly truncate setae occur on the temples and a few short ones across the occiput, longer setae are along the thoracic margins and along the distal margins of the abdominal segments. Thorax and abdomen additionally covered with very fine and slender spindle-shaped hairs. The mouthparts are soft, not functional; teeth and serrations of mandibles and maxillae are barely sclerotised, the maxillary palpus rests in an only three-segmented hull. The yolk-filled middle gut is visible by transparency. Several coniform chloride cells are situated anterolaterally on each thorax segment, and from near each abdominal spiracle ventrally along distal edge of sternite. Short, simple gill stubs occur on abdominal segments one and two, and two postfurcal and two basisternal gills on every thorax segment (Fig. 3 c). The first instar of *P. sachalina* has a highly significantly ($p = 0.003$) narrower labrum (mean = 0.130 mm, ± 0.005 SD; n = 28) than *P. reticulata* (mean = 0.140 mm, ± 0.003 SD; n = 8) (Zwick & Teslenko 2001). Mean HCW is 0.38 and 0.41 mm, respectively.

Second instar. LW and HCW of the two species overlap completely, means are 0.17 and 0.49 mm, respectively. *P. sachalina* has 3 cercus segments, but the first with a supernumerary hair ring (Fig. 3 d), *P. reticulata* has 4 cercus segments. Number of antennal segments is 9–11, mostly 10. Larvae that had entered second instar survived at most a day or two in standing water but were easily raised in running water. They immediately ate fine detritus.

Subsequent instars. Attempts to identify instars by size, meristic characters (numbers of cercal and antennal segments) or size or combinations thereof failed. Distinction of sexes was first possible in larvae >15 mm long by a gap in the setal fringe at the rear of sternite 8. In larger larvae the scar of the developing female genital opening also appears and shifts backwards at moults until it reaches the rear margin of the sternite; however, it takes no specific shape (compare Folsom & Manuel 1983). Males show no particulars of their own until when the epiproct hull appears. It acquires its species specific definite form only in the last instar (Zwick & Teslenko 2001).

The last instar is easily recognized by its large freely projecting wing pads (Fig. 4, last), see below. HCW is 3.8–5.6 mm, numbers of cercus and antennal segments are 25–34 and 63–75, respectively.

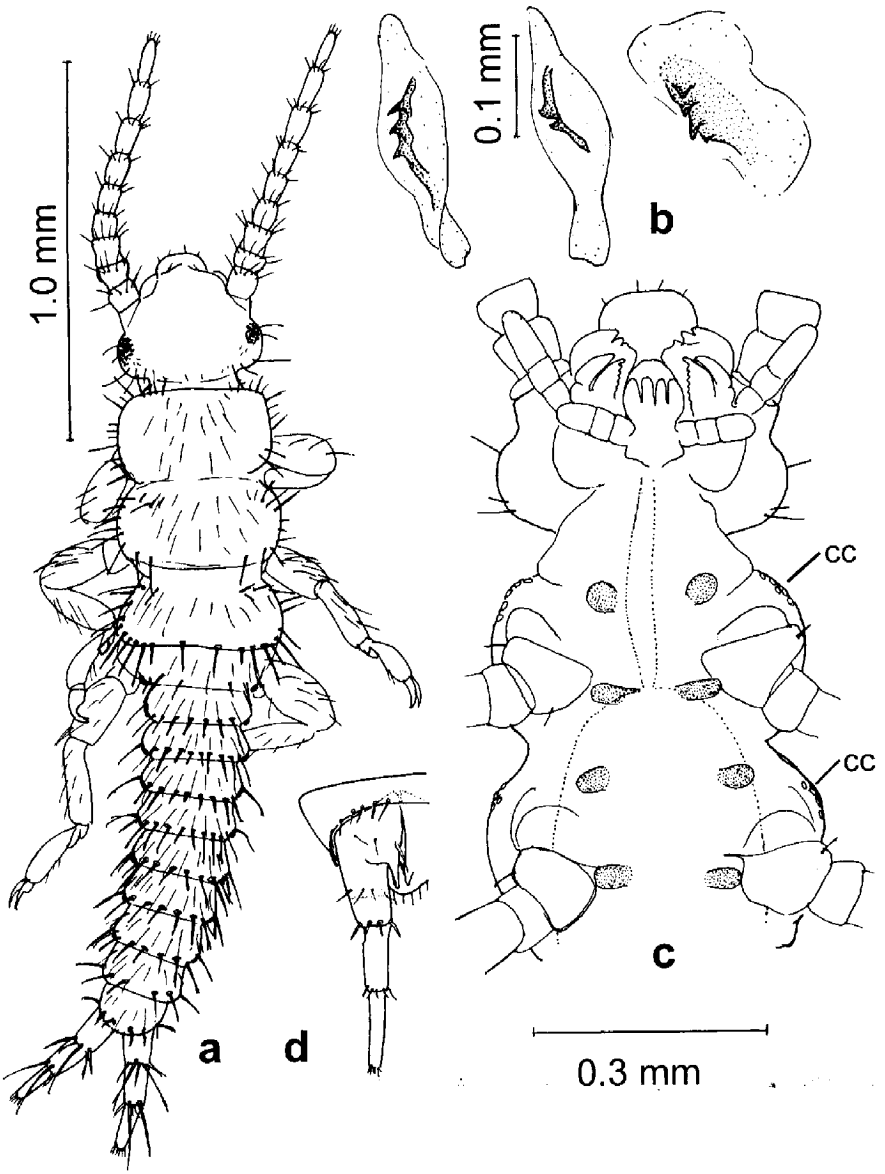

Fig. 3. *Pteronarcys sachalina*: **a)** larva in the first instar, habitus; **b)** egg bursters; **c)** ventral view of fore body, showing gills stubs (stippled) and chloride cells (cc); **d)** paraproct and cercus of second instar (same scale as in c).

Morphological change

We describe morphological change from observations on differently sized preserved larvae and from observations on individual live specimens that we

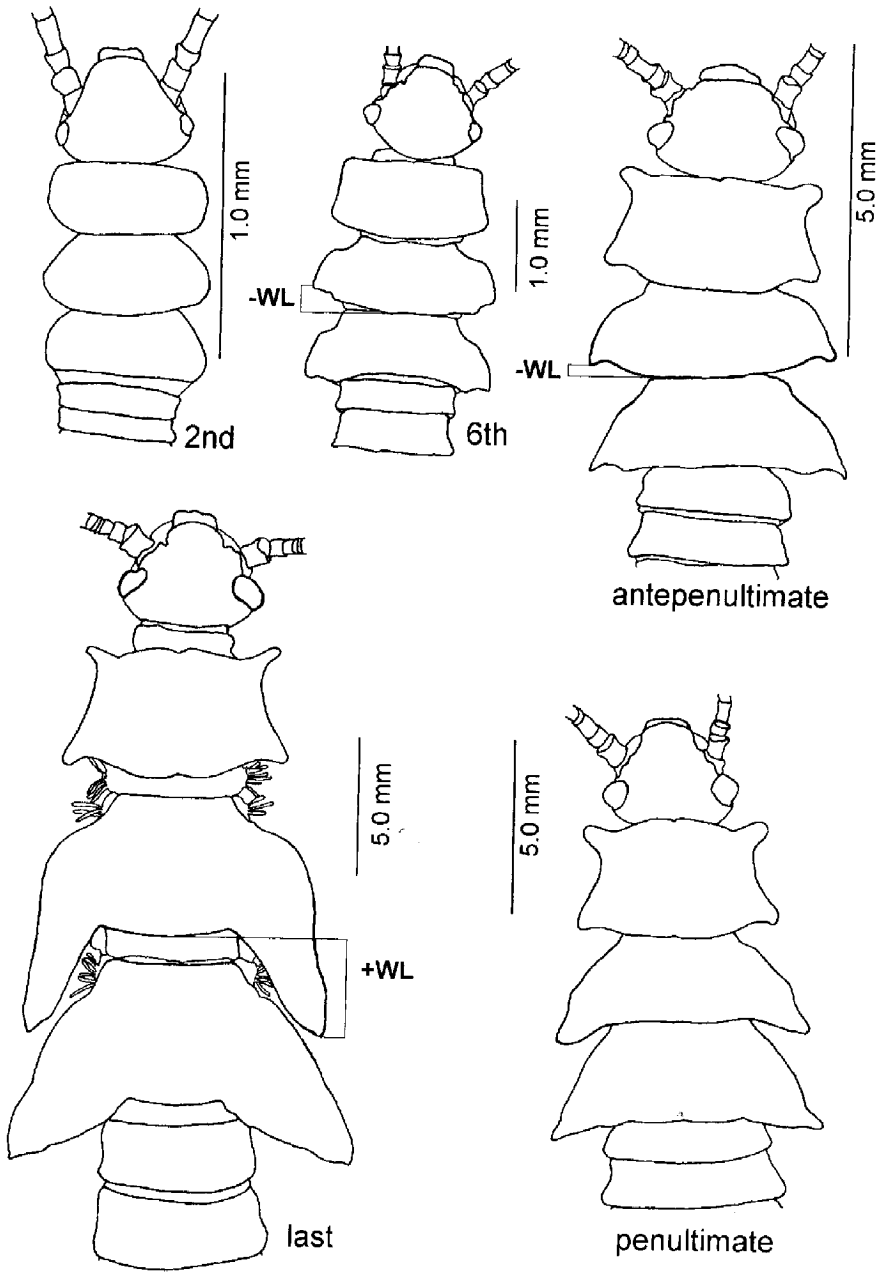

Fig. 4. *Pteronarcys sachalina,* habitus of larval fore body. Actual instar numbers known from individual life histories. The lateral mesonotal projection of early instars becomes the wing pad tip in older specimens. Negative and positive wing lengths, respectively, were defined as the distance of the lateral mesonotal projection to or from, respectively, the mesonotal rear margin.

reared from eggs and kept singly. Several of them attained the last instar in September, 2000. They were of normal size and attempted to moult to adults in April, 2001 but because this was noticed late the animals drowned in the small rearing containers.

Gills. The first instar (Fig. 3 d) possesses most of the gills that occur in the last instar (see figures in STEWART & STARK 1988), only the prothoracic basisternal gills (often called cervical gills) increase in number in later instars. Initially, gills are simple, unbranched stubs or rods in the immediate vicinity of chloride cells. The first apical branching of filaments is noticed in larvae about 3.5 mm long and probably in the 4th instar. Branching of the two existing cervical gills could not be distinguished from doubling of the cervical gills. Successive increase of gill size, increasing numbers of secondary gill filaments on each gill axis, and appearance of chloride cells on gills are the changes during development.

Pilosity and surface sculpture, pigmentation. Small larvae have long, simple, pointed setae; these become numerous but relatively shorter and increasingly blunt as the larvae grow. Already 8 mm long specimens have many short, truncate setae along the notal edges, the abdominal setal fringes are shorter than the intersegmental membranes. Large larvae are without obvious hairs, even the cercal setae are short and closely appressed; the body surface is matt and rough because of a dense cover of very short setae. Most setae are truncate, only about 2–3 times longer than wide; those along the notal margins, especially on the pronotal horns, are also flattened, spatulate. Species specific differences were not found.

Wing development. Large larvae of *P. reticulata* and *sachalina* have bizarre, horn-like corners of the pronotum and angular sides of the meso- and metathorax (Fig. 4, last). These projections, and the spine at the apex of abdominal segment 10 develop gradually and become increasingly distinct. An angle on the mesonotum appearing already in small larvae becomes very distinct when HCW is near 0.5 mm (Fig. 4, 6th instar) and eventually turns into the wing pad tip. In small larvae the angular projection lies in front of the mesonotal rear margin, i.e., the distance is negative and increases (i.e., the angle seems to shift forward) for some time as larvae grow. Later, the angle shifts distinctly backward and eventually the tip of the wing pad extends far beyond the mesonotum (Fig. 5 A).

A positive wing index is attained when HCW is between 3 and 4 mm. A plot of the abundance of linear 0.05 mm classes of wing length permits no distinction of instars, except the last which is widely separate from the others. At the last moult, the wing index rises abruptly from about 0.4 to at least 0.6 but may reach 1.15 in individual specimens (Fig. 5 B). In the field, the sudden appearance of long wing pads is striking; it occurs mainly in September.

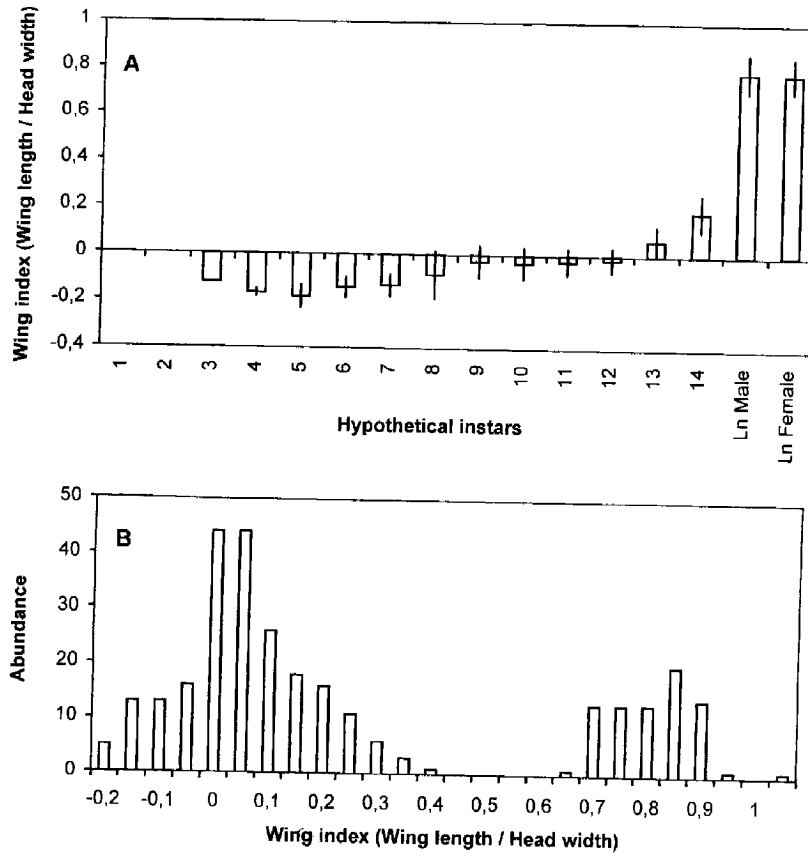

Fig. 5. *Pteronarcys reticulata* and *P. sachalina*, development of larval wing pads. **A:** Wing index during the first 14 hypothetic instars and in last instar males and females, respectively; means ± 1 SD. **B:** Frequency distribution of wing indices, linear 0.05 mm classes. The large gap around WI = 0.5 separates the penultimate from the last; however, the peak around WI = 0 is an artifact resulting from different availability of specimens; see text for details.

During laboratory rearing, many larvae in some late instar were examined once or twice a week, for months. The shape attained at a given moult was maintained until the next moult, there was no change in the intermoult period.

Body shape, size and biomass. We noticed no other change of shape than mentioned above, overall proportions remain the same throughout larval development. The relation of some measures and of body length with wet weight are described by the following equations (Table 2).

Increment at moults. Increment of linear body dimensions at moults varied much but not consistently between species or sexes. The largest increments at

Table 2. Regressions between various body dimensions and measurements of larval *P. sachalina* and *P. reticulata*. BL = body length [mm]; HCW = head capsule width [mm]; LW = labrum width [mm]; N = number studied; WW = wet weight [mg]

[1]	$HCW = 2.975 \times LW + 0.002$;	$r^2 = 0.995$; N = 102
[2]	$WW = 2.668 \times HCW^{3.664}$;	$r^2 = 0.997$; N = 32 (TESLENKO 1992)
[3]	$WW = 0.0297 \times BL^{2.794}$;	$r^2 = 0.995$; N = 246 (NIKOLAYEVA 1984)

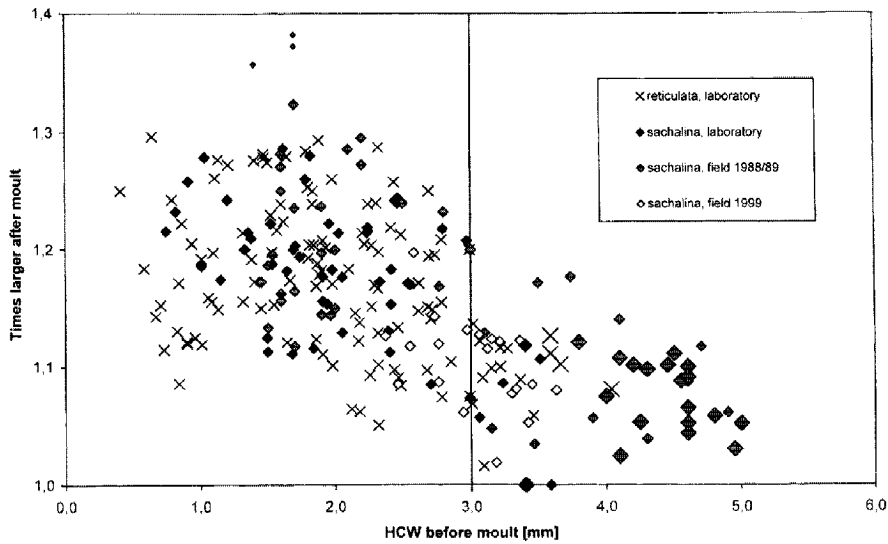

Fig. 6. *Pteronarcys reticulata* (ret) and *P. sachalina* (sa) larvae, increase of linear measurements at a moult plotted against head capsule width (HCW) before the moult. The vertical line separates early instars from the last two instars. Specimens that actually attained the adult stage at the next moult (1988/89 field experiment and laboratory rearing, respectively) identified by large symbols. Small symbols identify three presumably unreliable readings, compare text.

moult were recorded in the 1988/89 field experiment, while the 1998 data for field collected specimens moulting in captivity agreed with data of laboratory-reared larvae. Data for small larvae are from laboratory rearing (Fig. 6).

Larger specimens grow highly significantly less than small ones, especially during the last two moults (Fig. 6). Among juvenile larvae not yet visibly preparing for metamorphosis (WI = 0), size and increment are significantly but weakly negatively correlated ($r = -0.213$) (Table 3).

Seasonal growth pattern and intermoult intervals

Larvae caged in the Kedrovaya River for 12 months moulted soon after they had been collected in September, at mean water temperatures >10 °C, and a

Table 3. *Pteronarcys reticulata* and *P. sachalina* larvae, increment of HCW at each of the last two moults and during all earlier moults; means and standard deviation (SD). **: highly significantly different from the other two means.

Instar or size group	Mean increment	SD
Last instar	1.0780	0.0399
Penultimate instar (larvae HCW > 2.99 mm, except last instar)	1.0952	0.0445
Larvae except last and penultimate instars (HCW ≤ 2.99 mm) **	1.1864	0.0632

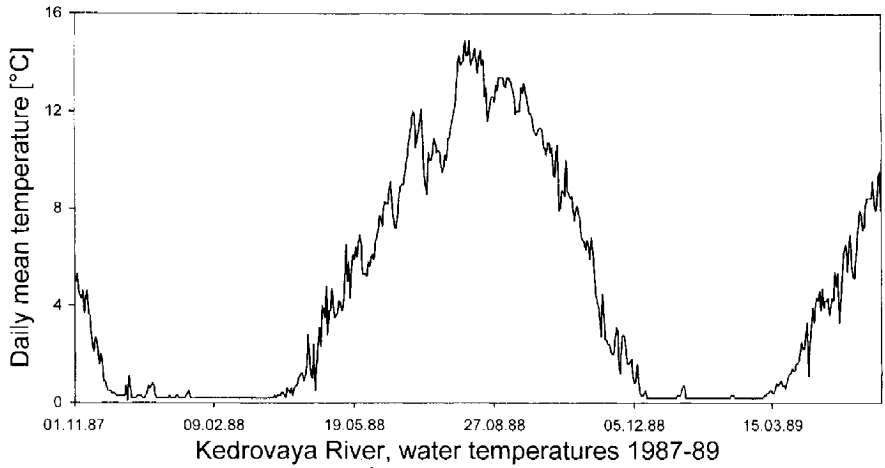

Fig. 7. Daily mean water temperatures in the Kedrovaya River in 1987–89; data courtesy of Mr ZAYEV. Mean daily temperature was estimated as the mean of the 08:00 and 20:00 hour readings, in conformity with the practice of the meteorological service in the Russian Far East. The annual temperature sum in the river is 2790 degree-days above 0 °C (LEVANIDOVA 1982).

12 hr.-photoperiod (Fig. 7); there were no moults during the winter months. Moulting was resumed in the middle of April, under a 12 hr.-photoperiod which was rapidly increasing, at mean water temperatures only near 4 °C (Fig. 7).

Larvae belonged to three size groups which differed in the number of moults and in the temporal pattern of moulting during the one year of observation. Twenty-nine large larvae (HCW 3.8–5.0 mm) entered the final instar in autumn and 23 of them survived to adult emergence, early in June the next year. Six slightly smaller larvae (HCW 3.0–3.6 mm) moulted in autumn and at least one more time between April and August the following year; whether any of them then entered the last instar was not recorded. Among the much smaller larvae (HCW 1.5–2.0 mm) losses were high but the few survivors to the end of the field experiment moulted up to 5 times during one year.

Under the 1999 laboratory conditions, there was a loose correlation (r = 0.55) between HCW and intermoult period. Data points were scattered between a minimum rising from 10 days (HCW = 0.5 mm) to around 40 days (HCW = 2.8) and a maximum from 32 to about 150 days, respectively.

Population structure in random field samples

The June 1998 fieldwork was during the flight period. The last larval instar was represented only by numerous exuviae which were not generally larger than some of the live larvae, However, even the largest live larvae had poorly developed wing pads. HCW of live larvae ranged from 0.6 to 5.8 mm HCW. Last instar exuvial HCW ranged over one third of the total size range, and over one quarter of the range for individual sexes (Fig. 8 a).

Larval HCW in the pooled June 1998 sample was classified in two ways (Figs. 8 a, b). Linear 0.2 mm classes produced a plurimodal distribution, with 3 or more groups of larvae. A classification by hypothetic instars (ZWICK & TESLENKO, submitted) distinguished three groups, placed actual last instar exuviae in the last two hypothetical instars, and separated them by sex, with two exceptions.

Discussion

Adults

The overall recorded flight period of *P. reticulata* and *P. sachalina* extended from May to July or even August, at the northern distributional limit, in Yakutiya (ZAPEKINA-DULKEIT 1958, LEVANIDOVA & ZHILTZOVA 1979, ZAPEKINA-DULKEIT & DULKEIT 1980, POTIKHA & ZHILTZOVA 1996, TESLENKO, unpubl. data). In 1998, we collected numerous adults and found many last instar exuviae between 11 and 26 June, but benthos samples contained not a single live last instar. This suggests that in a given area emergence is actually short and synchronous. Very short synchronous pulses of adult emergence have been recorded for North American *Pteronarcys* species (DEWALT & STEWART 1995, TOWNSEND & PRITCHARD 1998, SHELDON 1999) but there are no published records of mixed flights of American species, although B. KONDRATIEFF (pers. comm.) observed mixed flights of *P. biloba* NEWMAN, *P. comstocki* SMITH, and *P. dorsata*. In regions where *P. californica* NEWPORT and *P. dorsata* co-occur in the Yukon, the two species have never been found to inhabit the same section of any stream (STEWART & RICKER 1999).

Ovipositing behaviour has not been previously described in the family. Dropping an egg mass in flight high above water, instead of fluttering down to the river surface and washing eggs directly into the water, was described only

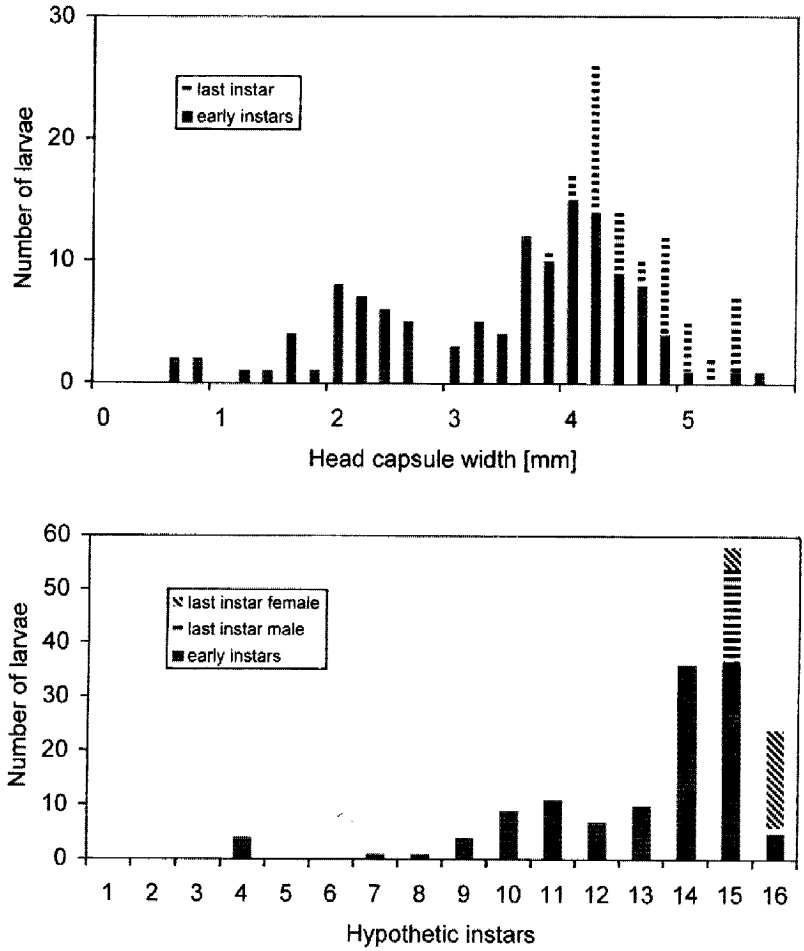

Fig. 8. *Pteronarcys* spp., larval size distribution in collections made in the Russian Far East in June, 1998. Data are grouped in linear 0.2 mm size classes **(a)** and alternatively in geometrically progressing size classes using actual first instar head width as the starting point and mean increment at moults as the progression factor **(b)**; compare text for details. "Early instars" corresponds to all larvae except the last instar specimens which in this particular case were exuviae picked from emergence supports.

for relatively few Plecoptera, in particular *Leuctra* spp. (Leuctridae) and *Leptoperla* sp. (Gripopterygidae) (references in ZWICK 1980).

Egg development, hatching, egg burster

In the laboratory, spontaneous development occurred between 16 and 22° and was completed within 10–12 weeks, without clear dependence of speed of de-

velopment on actual temperatures. The fully developed embryos hatched only after they experienced a cold period. This knowledge permits inferences on egg development and hatching in Primorye and the southern part of the Khabarovsky Region. We observed oviposition in the field, in June when temperatures in most streams where we collected *Pteronarcys* spp. (see habitats, above) were in the range supporting spontaneous development. The same is true of the 1987–89 summer temperatures in the Kedrovaya River (Fig. 7). Almost certainly, eggs in streams in Primorye are fully developed at the end of summer, embryos remain dormant throughout the winter and hatch when water temperatures increase again, the following spring. In a given stream, larval growth probably begins synchronously, and at similar times in different streams. Differences between the two taxa were not noted.

Egg development of *P. proteus* NEWMAN seems to be similar to the Far Eastern Russian species; its fully developed larvae spend winter in the egg and hatch only in spring, or when warmed experimentally (MILLER 1939). *P. californica* also has an almost year-long egg development (DEWALT & STEWART 1995), but there seems to be an early diapause before active development begins (TOWNSEND & PRITCHARD 2000). In contrast, *P. dorsata* exhibits direct egg development and spontaneous hatching after about one month in a warm-water river (LECHLEITNER & KONDRATIEFF 1983).

Egg bursters of Pteronarcyidae have so far not been precisely described but that of *P. proteus* seems to be not very different from those of the present two species. To hatch, larvae of *P. proteus* would normally detach the flat bottom of egg with the anchor plate (MILLER 1939), which was observed in only two specimens of the present two species.

Larval growth and development

Larval identification is only possible in specimens over 15 mm body length and is most reliable in late instars, especially last instar males (ZWICK & TESLENKO 2001). Data from field samples of the two species had to be treated together which is not much of a problem in view of the simultaneous adult emergence, the complete agreement in egg development, in larval shape (as also evidenced by Regression [1], Table 2), and similar increment at moults. We cannot confirm species specific differences in larval shape described and illustrated by NELSON (1988); both his habitus figures, especially the one of *P. sachalinensis,* show unnaturally plump and wide body shapes.

The inactive first instar digesting yolk is typical of Systellognatha. Numbers of cercal and antennal segments are standard for first instars of macropterous representatives of the order (references in ZWICK 1980, STEWART & STARK 1988). Differences in LW and HCW between the two species disappear by the 2nd instar. These differences probably indicate a different shape of the

post-embryonic stage instead of a real size difference between the species; however, the egg of *P. sachalina* is slightly smaller than that of *P. reticulata* (NELSON 1988). HCW of the present first instar agrees with the smallest field collected larvae of *P. californica* (TOWNSEND & PRITCHARD 1998), but is less than of laboratory hatched *P. proteus* (0.45–0.46 mm; MILLER 1939).

Wing development in Plecoptera differs among families. Most families, including Pteronarcyidae, have freely projecting wing pads that are separate from the thoracic notum. Wing development through three morphologically distinct late instars was described for Leuctridae and Nemouridae (ZWICK 1991, BEER-STILLER & ZWICK 1995), but appears to be common (from personal observations of most stonefly families). There is no study of Peltoperlidae, Perlidae or Chloroperlidae whose wing pads are fused to the notum and together with it form a dorsal shield, much like in certain mayflies (the Pannota; MCCAFFERTY & EDMUNDS 1979, MCCAFFERTY 1991).

Pteronarcyidae are exceptional among families with free wing pads in that wing development is continuous and gradual. Only the last instar is morphologically distinct (Fig. 5 A, B), our data agree with findings on *P. californica* (TOWNSEND & PRITCHARD 1998). In Figure 5 B, the peak around WL = 0 and the decline towards both sides are artifacts: we simply had available and measured many more middle-sized than large and very small larvae, respectively. However, no specimens at all had wing indices between 0.4 and 0.65, the large gap in the frequency distribution is real.

HOLDSWORTH (1942) stated increased wing growth in the last two instars of *P. proteus* which is correct in that the wing pad tip begins to extend rearward beyond the mesonotal edge. TOWNSEND & PRITCHARD (1998) measured overall thorax length, including the wing pad, and could therefore not notice the shift of the anterolateral angle of the mesonotum which eventually becomes the tip of the wing pad. This long-continued change documents that larvae prepare for wing development even when real wing pads are still missing. During our months long observations of individual larvae (several of which eventually attained the last instar after several moults) shape changed exclusively at moults. Growth between moults as suggested by TOWNSEND & PRITCHARD (1998) did not occur.

Increment at moults varies among specimens (Fig. 6) but there is no evidence of species-specific or sex-related differences. Data for specimens reared in the laboratory overlap completely with data for specimens collected in the field shortly before a moult which they then performed in the laboratory; apparently, artifacts play no significant role in our laboratory data. Data from the long-term field experiment in the Kedrovaya River are more variable than the other and include the highest increments recorded in this study. However, these may be unreliable because of the difficult handling of live specimens. In fact, several successive measurements of the same specimen gave slightly dif-

ferent results and increment at moults had to be calculated from means of pre- and post-moult data.

In *Pteronarcys,* the negative correlation between specimen size and increment at moults is highly significant, mainly because the increment drops notably during the last two instars when the tip of the wing pad starts extending beyond the rear margin of the mesonotum and animals visibly prepare for metamorphosis. However, over the greater part of the animal's life, during approximately 3 out of 4 years of larval life, differences in percentage increment at moults are very small (Table 3) and little different from a constant increase of 1.18. Dyar's (or Brooks') Rule (DYAR 1890, CROSBY 1973; we use the widely known name) which states that linear measures of insects increase by a constant proportion at moults approximately describes the situation, except during the last phase of life.

This notion forms the basis of our new, different way to classify specimen size (ZWICK & TESLENKO, submitted) by hypothetical model instars; class width of the size-distribution is geometrically progressing. We start from the mean HCW of *P. sachalina* first instar larvae and use the mean increase by 1.18 at moults (except the last two) as the progression factor (Table 3, Fig. 8 b). Because specimens in the ante-penultimate and penultimate actual instars cannot be recognized by size or morphology the lower increase at the last two moults known from individually reared specimens was not applied to the field sample. This imprecision affects only the last two hypothetical instars which cover a wider size range than actual instars. Details of the procedure and our rebuttal of objections raised in the literature against Dyar's Rule as well as our fundamental critique of attempts to recognize instars from linear size classifications are discussed elsewhere (ZWICK & TESLENKO, submitted).

Instar number

Failure to recognize instars (except first and last) from linear size distributions is common (FINK 1980, 1982, 1984). Size alone is not normally sufficient to identify **actual** instars, also not in the present material. We tried several class widths in linear classifications and also ordered larval sizes in field samples and among reared specimens by size. The plotted curves rose continuously, without discontinuities, also when sexes were examined separately. The same was true of the more than 4000 readings of *P. californica* (TOWNSEND & PRITCHARD 1998; courtesy G. PRITCHARD). Sexual, individual and perhaps also seasonal size differences between specimens of similar age or in the same actual instar complicate matters further (STEWART & STARK 1988). If discontinuous size distributions in individual samples actually occur they probably reflect sampling error and variation between individuals, or indicate presence of several different cohorts (ZWICK & TESLENKO, submitted).

The easily identified and biologically homogenous last instar is in linear classifications spread over a number of classes, also in the present material (Fig. 8 a). In contrast, the geometrically progressing classification assigns actual last instar specimens (either exuviae or specimens with fully developed wing pads) to the last two hypothetical instars, with sexes largely separate (Fig. 8 b). The same happened with *P. californica* (TESLENKO & ZWICK, submitted; data from TOWNSEND & PRITCHARD 1998). A few direct observations (KHOO 1964 a, b, OBERNDORFER & STEWART 1977) showed males pass through less instars than females. Our model seems to support this but provides no proof for a real sexual difference in actual instar number. Instead, growth rate might differ between sexes, as recorded for *P. californica* (TOWNSEND & PRITCHARD 1998); we have no evidence in the present species.

Our model indicated a total of 16 **hypothetical** instars in all three *Pteronarcys*-species considered which is probably very close to the number of actual instars. The present number is also similar to instar numbers recognized in several other Plecoptera. However, instar number may not to be rigidly fixed, even in a given species (references in STEWART & STARK 1988). Our estimate is in conflict with results by HOLDSWORTH who counted 11 and 12 actual instars, respectively (1941 a, b) in *Pteronarcys*. Like ourselves, he stated conformity with Dyar's Rule. However, he actually only justified some a priori grouping of specimens by the statement that size differences between group modes conformed with the rule.

Population structure in the field

Sampling with a 1 mm net almost certainly missed many very small larvae but even specimens about 10 mm long were rarely caught. Their microhabitat may differ from that of larger larvae. Some may also have been overlooked during sorting of samples in the field, because young larvae tend to roll up and remain motionless for some time. However, small larvae were also not found in samples from the Narva River which were preserved in the field and sorted in the laboratory.

We analysed the size distribution in our large June 1998 field sample in the two ways explained above, comparing linear and geometrically progressing size classes. For linear classifications, we tried several class widths and always obtained plurimodal distributions without ever being certain of the number of cohorts involved. Figure 8 a shows a linear classification based on narrow class limits which we chose to attain a high resolution. It is doubtful if the nodes in the smaller part of the size distribution separate up to three different groups of larvae, or if we are instead dealing with a single, incompletely collected cohort. In contrast, the distinctly larger specimens in the right half of Figure 8 a include the largest live larvae and the exuviae. They all seem to be-

long to one single cohort which is, however, not the case. By their wing pads, the largest live larvae were at best in the antepenultimate instar and would have required several more months of growth and another moult before adults could eventually have emerged from them. They were definitely not of the same generation as the numerous exuviae that we found and whose corresponding adults were still abundant at the time of collection.

The modes and nodes in the geometrically progressing classification by hypothetic instars are less obvious, but permit only one interpretation: there were three cohorts of live larvae plus the exuviae with the corresponding adults.

Seasonal change of population structure

Sufficiently many samples to consider seasonal change of population structure from field data are available only from the Kedrovaya River, even though size of several individual samples is not really satisfactory. Small larvae are obviously underrepresented. From this limited data base, the observed seasonal change agrees with the structure of the June, 1998, samples, and also with the lifespan and the time of moult of larvae in the penultimate and last instars kept in cages in that same river. The last instar appears in autumn and overwinters. After adult emergence in May–June, three distinct larval year classes but no last instars remain, i.e., population structure agrees well with observations in 1998. All other individual field samples from various localities are fully compatible with this interpretation.

Synopsis of life cycle, and related taxa

A conspectus of population structure in the field, egg development, longevity of the last few instars, and seasonal growth pattern, mainly the cessation of growth in winter, suggests the total life cycle of *P. reticulata* and *P. sachalina* extends over 5 years: adults collected in June 1998 developed from eggs that were laid in 1993. This differs from ZAPEKINA-DULKEIT (1973) who hypothesised a 4-year life cycle of *P. reticulata* in the Yennissei River basin, without adequate supporting data.

Egg development and life cycle lengths apparently differ greatly among species of the genus *Pteronarcys* (see also references in STEWART & STARK 1988, DEWALT & STEWART 1995), and there is evidence of regional variation. *Pteronarcys* species occur over a large geographical area; even individual species inhabit areas between approximately 35 °N and the Polar Circle; life histories are certainly influenced by the regional climatic conditions. In Alberta the total life cycle of *P. californica* NEWPORT lasts 5 years (TOWNSEND & PRITCHARD 1998, 2000); application of our geometrical classification to the original

data supports the authors' interpretation. Even in more benign environments the larval life of *P. californica* requires no less than 3 years (DEWALT & STEWART 1995). Larval growth of *P. scotti* (RICKER) continues for 24 months, from May of the first to April of the third year; there is no information on egg development (FOLSOM & MANUEL 1983). *Pteronarcys dorsata* is clearly univoltine in a warm-water river (LECHLEITNER & KONDRATIEFF 1983) but has an at least three year cycle in Saskatchewan (DOSDALL & LEHMKUHL 1979).

Acknowledgements

Our work was in part supported by the Russian Fund of the Thorough Investigation (Grant Number 96-04-50388, Iya M. LEVANIDOVA, Principal Investigator), the Deutsche Forschungsgemeinschaft (travel aid 436 RUS 18/28/97, P. Zwick) and the Max-Planck-Gesellschaft zur Förderung der Wissenschaften, which is gratefully acknowledged. We are very grateful to T. AREFINA, Dr M. TIUNOV, Dr T. TIUNOVA and V. LYUBORETS (IBSS, Vladivostok) for help during our field work. We would like to thank Dr G. PRITCHARD (Calgary), Dr C. R. NELSON (Provo) and Dr K. W. STEWART (Denton) for helpful comments on a draft of this paper.

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Submitted: 4 October 2000; accepted: 6 July 2001.