

Potential of Utilizing Allochthonous Invertebrates by *Gammarus koreanus* Uéno (Amphipoda)

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Received May 16, 2023; revised May 24, 2023; accepted May 26, 2023

Abstract—In an isolating experiment on feeding only on arthropods of terrestrial origin, the potential of their consumption by amphipods from a fishless watercourse has been studied. The data confirm the hypothesis that, on the basis of experiments on feeding exclusively on arthropods, it is possible to determine the maximum proportion of their biomass that the selected consumers are able to utilize. The results of such works can be used for a quantitative assessment of the level of possible losses of allochthonous matter and energy for the communities of recipient water bodies due to the feeding activity of consumers from their tributaries. Assessments of this kind may be relevant when making decisions on the food availability for juvenile Salmonids inhabiting recipient water bodies.

Keywords: allochthonous matter and energy, food base for fish, amphipods

DOI: 10.1134/S1995082923050048

INTRODUCTION

The key factor in the functioning of communities of small watercourses shaded by a coastal plant canopy is the input of terrestrial organic matter (Alimov et al., 2013; Minshall, 1967). Plant litter, processed by hydrobionts-destroyers, is of primary importance among the allochthonous inputs from land (Vannote et al., 1980; Bovill et al., 2020). The consumption of terrestrial heterotrophs is advantageous for hydrobionts of the higher trophic level (Astakhov, 2016). Therefore, in the warm period of the year, terrestrial invertebrates (primarily arthropods) falling from the plants that overhang watercourses can form the basis of the diet of predatory fish (Lotrich, 1973; Nakano and Murakami, 2001). The drift of terrestrial invertebrates getting into fishless headwaters and tributaries increases the productivity of communities in recipient water bodies (Wipfli and Gregovich, 2002; Richardson and Moore, 2010), including spawning rivers and lakes. Naturally, part of the biomass of drifting terrestrial organisms is utilized directly within lotic (flowing) ecosystems, into which they get from land. In fishless streams, they are readily eaten by predatory and omnivorous invertebrates. We consider this feeding activity of these resident consumers as a factor limiting the volumes of allochthonous inputs into recipient water bodies, in other words, as a barrier to the transfer of allochthonous matter and energy in the

form suitable for direct ingestion, e.g., by juvenile Salmonids. In this context, it is relevant to develop approaches to assessing the potential levels of the respective feed losses for consumers from recipient water bodies.

The present study was aimed at experimentally testing one of these approaches. The approach is based on the assumption that a consumer feeding solely on arthropods is able to utilize only a certain (limiting) share of their biomass. The potential of utilization of terrestrial arthropods by freshwater shrimps (Amphipoda), omnivorous hydrobionts usually dominating in small fishless watercourses of mountainous and foothill regions, is considered in this article as a factor limiting the transfer of matter and energy of terrestrial origin.

MATERIALS AND METHODS

The survey was conducted in the summer of 2015 in Yaponsky Brook, a small forest watercourse in the Sea of Japan basin that flows into Kievka Bay in the south of the Russian Far East (42°49' N, 133°41' E). The choice of this brook as a model was primarily due to the fact that it flows into a sea rather than into another fresh water area. Because of the isolating effect of marine environment, the predatory potential of animals in this flowing system is limited to its boundaries,

and the probability of penetration of freshwater predators from the outside is low. These circumstances may provide the higher degree of controllability for the work if further experiments are conducted directly in the brook. The catchment basin of the brook borders on the catchment basins of brooks with similar morphology and riparian vegetation that drain into freshwater bodies, which are used by fish for spawning or feeding. This fact maximizes the adequacy of possible extrapolation of our results to the processes occurring in such watercourses. Finally, the brook flows in a densely forested area not visited by people, which eliminates the possibility of anthropogenic interference during the study.

The brook bottom is mainly stony, with an increasing proportion of sandy soil in erosion pits and in the area before flowing into the sea. The brook banks are covered with Manchurian alder (*Alnus hirsuta*), Chinese ash (*Fraxinus rhynchophylla*), painted and Korean maple (*Acer mono* and *A. pseudosieboldianum*), slender-leaved mock orange (*Philadelphus tenuifolius*), Maximowicz's spindle tree (*Euonymus maximowiczianus*), scissors-like sedge (*Carex forficula*), tailed-leaf isodon (*Isodon excisus*), Thunberg's smartweed (*Polygonum thunbergii*), goat's beard (*Arunceus dioicus*), false goat's beard (*Astilbe chinensis*), Siberian meadowsweet (*Filipendula palmata*), marsh marigold (*Caltha palustris*), and lady-fern (*Athyrium rubripes*). In the warm season, the channel can be shaded by vegetation up to 100%. The brook is mixed-fed, mainly rain-fed, and therefore has no permanent source; its total length rarely exceeds 900 m in the low-water period. The brook has no fish population. Among representatives of macrozoobenthos, the leading consumers of allochthonous organisms are the dominant amphipod *Gammarus koreanus* Uéno (Gammaridae) and the planaria *Phagocata?* sp. (Planariidae).

In the present study, the quantitative development of the *G. koreanus* population was estimated before counting allochthonous inputs. For this purpose, five benthic stations were placed in the lower third of the watercourse, characterized by different granulometric compositions of sediments and located at a distance of at least 50 m from each other. When the material was collected, the width of the brook at stations varied in the range of 0.6–1.0 m, the depth was 0.05–0.17 m, and the flow rate was 0.1–0.3 m/s. Samples were taken by swabbing from small (0.1–0.2 m) boulders. To avoid the loss of invertebrates when removing the boulders, a washing net was carefully brought to each boulder against the current. The boulder (together with the underlying sediments) was placed into the net and put into a bucket with water, where it was thoroughly washed. Then the stone was outlined on paper in the same position as it was on the bottom in order to determine the projected area of the boulder by the weight method (Zhadin, 1940). The fraction remaining in the bucket was stirred up and filtered through

the washing net. Samples were taken from 5–10 boulders at each station (Bogatov, 1994). The primary results of measuring the number and crude biomass of animals were calculated per 1 m².

Allochthonous inputs were counted in the upper part of the surveyed area (ten 24-hr series: July 19–24 and August 9–14). Terrestrial invertebrates falling into the brook from riparian plants were collected using transparent pan traps randomly placed above the watercourse surface. The water from the brook was poured as a 1.5-cm layer into each trap (12-cm deep, with an area of 0.073 m²) with the addition of ~5 mL of unscented liquid soap (to reduce the surface tension and prevent the loss of captured animals). There were 14 traps exposed simultaneously; thus, the total sampling area was 1 m². Invertebrates caught in the traps at night were collected after sunrise and those caught during the day were collected at sunset.

After the hierarchical structure of catches of the first five 24-hr sampling series had been determined, a two-stage experiment was started to study the potential level of utilization of terrestrial organisms by amphipods. The water from the brook was poured into six flasks, each 11 cm in diameter, with a layer of about 3 cm, where *G. koreanus* adult males ($L = 13\text{--}16$ mm) were placed. At stage I (individual consumption, duration 14 days) one *G. koreanus* was placed into each flask, and at stage II (group consumption, duration 5 days)—two *G. koreanus*. Because Diptera (including Muscomorpha), and Hymenoptera (including Formicoidea) were predominant in the trap collections (see Table 1), uniform-sized ($L = 8\text{--}9$ mm) houseflies *Musca domestica* (Muscidae) and carpenter ants *Camponotus* sp. (Formicidae) were chosen as model prey. Live prey of the Diptera type was placed into half of the flasks (three specimens per flask), and live prey of the Hymenoptera type was placed into the other half of the flasks (three specimens per flask). On a dry basis, the initial biomass of each set of prey of the Diptera type was ~16.6 mg, and that of prey of the Hymenoptera type was ~22.9 mg. It was expected that when forced to feed only one type of prey, amphipods would be able to utilize of the maximum possible amount of it. The appropriate level of consumption was expected to be defined as the difference between the initial biomass of the given type of prey and the mass of their remains at the end of the experiment. The flasks were placed into the brook to maintain the natural temperature regime (Tiunova et al., 2003). On the dates of the experiment, water temperature in the brook varied within a narrow range (16.9–17.2°C). Gas exchange was diffusive (due to the shallow depth and relatively large surface area of water in the flasks). Experimental flasks were covered with a fine-mesh capron net to prevent the intrusion of foreign objects. At the end of experimental stages, the amphipods and the remains of their prey were taken out for further processing.

The resultant material was not fixed. The material from pan traps was rinsed with water; air-dried; and, after taxonomic identification, placed into a drying oven, where the samples reached constant weight at 90°C. The dry weight of experimental material was determined in the same way. The carbon concentration in dry matter was estimated by a dichromate oxidation method modified by A.P. Ostapenya (*Metody ...*, 1968). The nitrogen and phosphorus levels were determined by decomposition of the organic component of dry matter with sulfuric and perchloric acids, followed by the measurement of ammonium and orthophosphate concentrations by colorimetry (Propp et al., 1979).

The intensity of food consumption by one amphipod was taken as the intensity of prey utilization. Therefore, the results of calculations were divided by two when the feeding of two amphipods (group consumption). The calculations were based on the following equation (Agatz and Brown, 2014): feeding rate = consumed food weight/(weight of consumer(s) × numbers of experimental days).

The diagrams were plotted using Microsoft Excel 2003 and STATISTICA 10 StatSoft Inc. For statistical calculations (two-tailed Fisher's exact test and Mann–Whitney test), significance level α was assumed to be equal to 0.05. The mean values are presented as $M \pm SD$.

RESULTS AND DISCUSSION

As expected, amphipods were predominant in the samples from benthic stations, making up 86.3% of the total number of hydrobionts taken into account (5.4 ± 3.1 thous. ind./m²). In second place in terms of representation in samples (13.4% , 0.84 ± 0.4 thous. ind./m²) appeared larvae of amphibiotic insects, namely mayflies of the genera *Ecdyonurus*, *Cinygmula*, *Epeorus* and *Baetis*; caddis flies of the genera *Lepidostoma*, *Neophylax*, *Rhyacophila*, and *Glossosomatidae* sp.; Diptera of the genera *Hexatoma*, *Dicranota*, *Scleroprocta*, and *Pedicia* and of the subfamilies Chironominae and Diamesinae; stoneflies *Nemoura* sp. and Cloroperlidae sp., as well as beetles of the family Elmidae. Among other aquatic animals, the planaria *Phagocata?* sp. (0.22%) and (sporadic) water mites of the Aturidae family were found in benthic samples.

Obviously, the taxonomic diversity of macroinvertebrates in the brook is not confined to the above list. For example, the larvae of the amphibiotic dipterans *Suragina* sp. and *Dixa* sp., as well as oligochaetes and hairworms, had been found here previously in drift samples (Astakhov et al., 2014). It is likely that a special survey throughout different seasons of the year will significantly supplement the data on the brook fauna.

Table 1. Share (%) of the total abundance of terrestrial invertebrates in pan traps

Taxon	Month	
	July	August
Hymenoptera	32.5	20.7
Diptera*	27.0	37.3
Coleoptera	7.9	3.6
Homoptera	7.9	3.4
Aranei	7.1	9.8
Lepidoptera	5.6	2.8
Pulmonata	4.8	1.0
Phalangida	2.4	9.1
Heteroptera	1.6	2.1
Neuroptera	<1	<1
Archaeognata	<1	–
Insecta larv. indet	<1	1.8
Litobiomorpha	<1	1.6
Oniscidea	<1	<1
Collembola	–	3.1
Psocoptera	–	<1
Mecoptera	–	<1
Acariformes	–	<1
Mermithida	–	<1

* Excluding ones with immature aquatic stage; a dash indicates not detected.

Benthic biomass at the stations varied within a range of 25.5–101 g/m²; the average biomass of *Gammarus koreanus* was 52.6 ± 30.8 g/m².

In the Far East, such watercourses are characterized by the overwhelming dominance of the *Gammarus* with low numbers of other typical brook inhabitants. This type of brook community is recognized as the main one in the region (Chertoprud et al., 2020). However, in the Yaponsky Brook it is possible to obtain material with the higher share of planaria. This opinion is based on the fact that these animals are found here quite often during the prolonged periods of cool weather in summer. Their low representation in our samples may be a result of relatively high (~17°C) water temperature during the period of survey. As is known, when water temperature rises to 12°C, brook planaria begin to migrate to the colder headwaters (Beauchamp, 1937). Consequently, most planaria were probably distributed upstream of the surveyed area at the time of sampling. It is also important that, “due to the difficulty of adequate selection” of planaria by the standard methods of quantification of benthic communities (Reynoldson, 1983), special approaches are required to assess the development of populations of these animals (Reynoldson, 1966; Young and Reynoldson, 1999). This circumstance

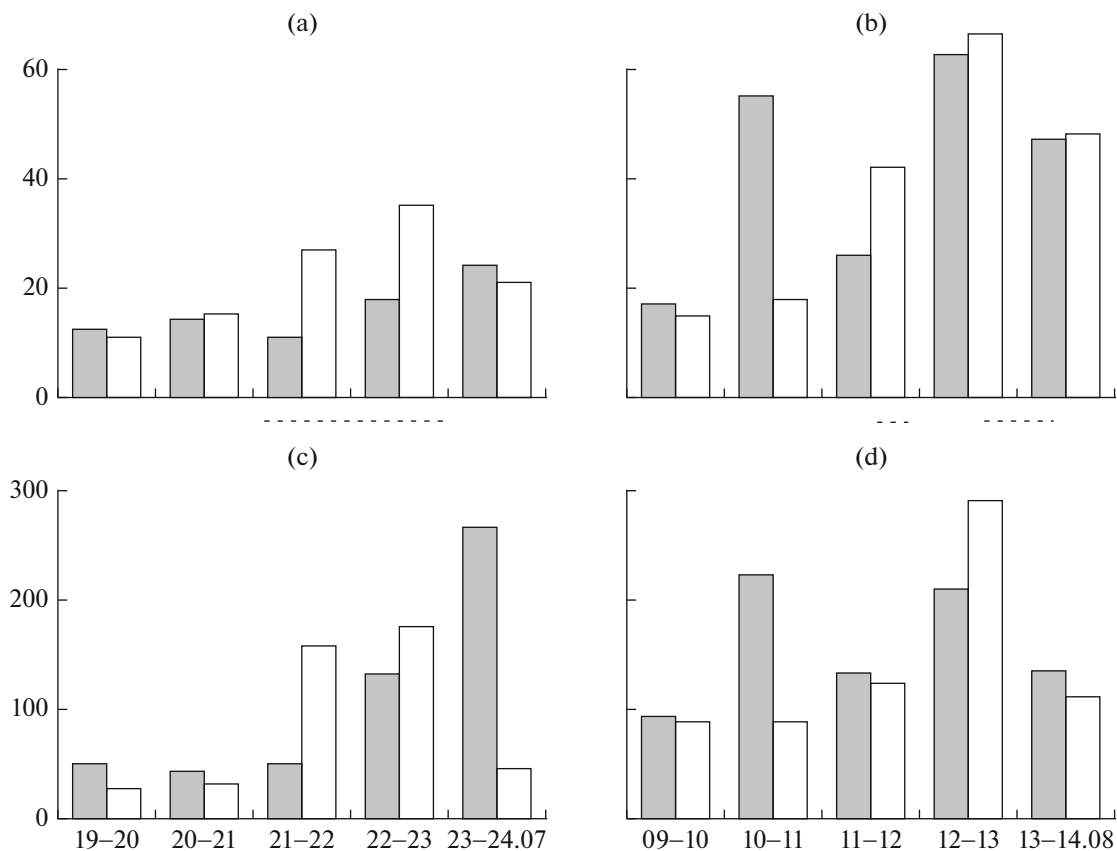


Fig. 1. Inputs of terrestrial invertebrates in the Yaponsky Brook: dates are on the X axis; the Y axis shows the intensity of inputs ((a, b) in number ($\text{ind./m}^2 \times \text{day}^{-1}$) and (c, d) in weight of dry matter ($\text{mg/m}^2 \times \text{day}^{-1}$)). The night results are shown by dark columns. Dashed lines indicate the periods with predominantly cloudless weather.

should be taken into account in further studies of the *Gammarus*' consumption of terrestrial organisms, which are also eaten by planaria (Reynoldson, 1966; personal observations) and, hence, compete with amphipods for this matter and energy source.

Representatives of 18 groups of invertebrates were found in pan traps in the period of survey. The maximum diversity at the level of higher taxa was observed in August: 17 groups (see Table 1), probably due to the specific phenological development of animals taken into account.

The variability of qualitative composition of the samples increased in clear or partly cloudy weather. This is probably due to the fact that such weather is characterized by more marked intraday fluctuations in air temperature and humidity, as well as illumination, which are the main factors influencing the activity of terrestrial invertebrates (Beklemishev, 1934).

Interestingly, the number of invertebrates trapped in daylight hours increased only in the absence of cloud cover. In the case of cloudy weather, the total number of trapped animals was approximately the same both in the daytime and at night (Figs. 1a, 1b). The exception to this situation was the 24-hr series of

August 10–11, when the intensity of allochthonous inputs in the dark period drastically increased because of cold wind and significantly exceeded the analogous daytime parameter. In general, the dry matter inputs of terrestrial invertebrates (Figs. 1c, 1d) were within the published range: $2.4\text{--}450 \text{ mg/m}^2 \times \text{day}^{-1}$ (Baxter et al., 2005; Zhang and Richardson, 2011).

As has been mentioned in Materials and Methods, Diptera and Hymenoptera were predominant in pan traps with respect to abundance (see Table 1). The model prey representing these two groups of insects in our experiment were actively eaten by amphipods. Observations showed that the latter not only utilized the already drowned terrestrial invertebrates but also predated on live invertebrates that had just fallen into water, capturing them from the surface.

G. koreanus more readily ate dipterans. The intensity of feeding on this type of prey was much higher in case of individual consumption than in case of group consumption per one amphipod (Fig. 2). This is consistent with the well-known rule that the average rate of food intake by each specimen decreases in the presence of other consumers (Bigon et al., 1989). At the same time, the intensity of feeding on hymenopterans

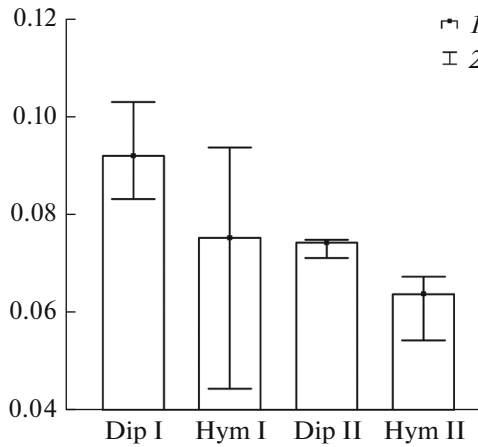


Fig. 2. Utilization rates of model prey: the X axis shows experimental stages (Dip I/Dip II and Hym I/Hym II are the individual and group consumption of Diptera and Hymenoptera, respectively); the Y axis gives indicators of the utilization (feeding) rate. (1) median; (2) minimum and the maximum.

actually was not different for individual and group consumption (Fig. 2).

Curiously, the level of individual consumption of dipterans (per the initial biomass of dry matter; see Materials and Methods) could be more than 93%, while the maximum individual consumption of hymenopterans was only 71% (Fig. 3). The null hypothesis that the final utilization rate does not depend on the type of prey proved to be inadequate (Fisher’s exact test, $p < 0.001$ for individual consumption, $p = 0.012$ for group consumption).

However, the hypothesis that the final level of utilization of the same type of prey does not depend on the number of consumers (individual vs. group consumption) proved to be correct ($p = 0.999$ for Diptera, $p = 0.156$ for Hymenoptera). These results are most likely due to the fact that the bodies of Hymenoptera insects, owing to their stronger integuments, may contain more nonedible components than the bodies of Diptera insects of the same size.

When analyzing the information on the group consumption of hymenopterans, we had to operate with two incidents of cannibalism. Nevertheless, regardless of the fact that the proportions of utilized biomass of conspecifics noticeably varied between experimental flasks (78 and 97%), the values of consumed Hymenoptera biomass remained at a level of ~70%. The same level of hymenopteran utilization was recorded in the absence of cannibalism (Fig. 3). As is known, Gammaridae of different species tend to eat conspecifics under conditions of food deficiency (Bogatov, 1994; Dick, 1995; Ironside, 2019). The fact that we have observed cannibalism solely in the cases of group feeding on hymenopterans suggests that the “utilization limit” of the latter (~70% of dry weight) could be

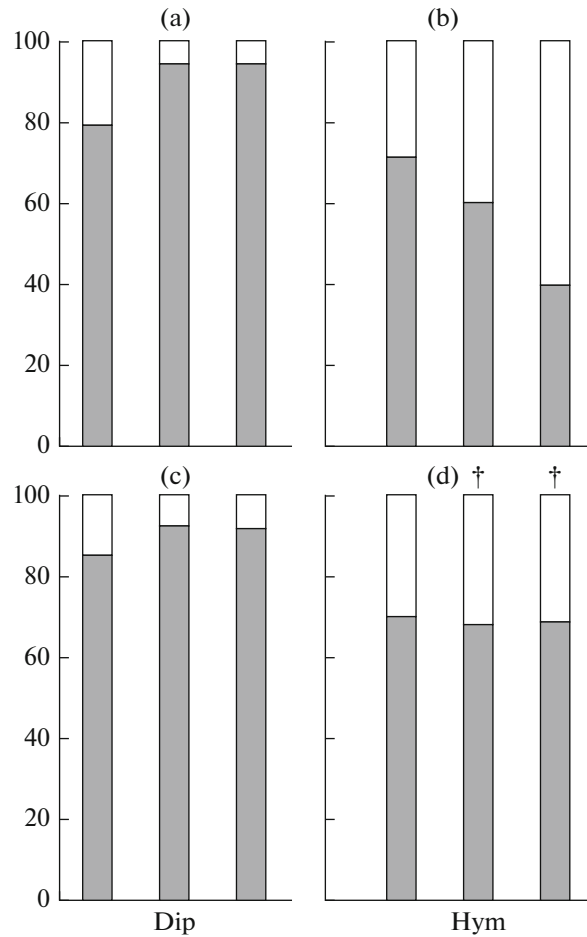


Fig. 3. Utilization level of model prey: (a, b) individual and (c, d) group consumption. The X axis gives the type of prey (Dip, Diptera; Hym, Hymenoptera); the Y axis gives the biomass of prey expressed in dry weight, %. Each column characterizes a separate experimental microcosm (the consumed portions of prey biomass are highlighted with dark filling; cases of cannibalism are marked with crosses).

exhausted within 5 days (duration of stage II of the experiment) and, therefore, the amphipods began to starve.

In the same time period, the maximum group consumption of dipteran matter reached 93%. There were no incidents of cannibalism and, hence, it can be assumed that this level of utilization is not ultimate for this type of prey. However, we assume that cannibalism would have been observed in the flasks with dipterans as consumption objects, if the duration of step II had been longer.

The time factor undoubtedly plays an important role in reaching the maximum level in utilization of prey of terrestrial origin. In watercourses, the time of availability of terrestrial invertebrates for freshwater predators and euryphagous animals is obviously determined by the flow rate and cross section of the stream. The higher the flow rate is, the faster allochthonous

food objects are transported out of the lotic ecosystem. The lifestyle of a consumer hydrobiont (daily or nocturnal) and, accordingly, the time of day when this or that number of prey of a given type entered the watercourse, may be of some importance. Naturally, the degree of “processing” of allochthonous food items by different aquatic consumers will depend on the local density and individual sizes of the latter, as well as on the structural peculiarities of their mouthparts.

In the case of amphipods, it is important that in the presence of sufficient amount of such a common feed resource for them as leaf litter, they may tend primarily to consume animal objects, which are more nutritionally valuable (Chambord et al., 2017). This statement has been convincingly supported by the experimental results of D. Kelly et al. (Kelly et al., 2002). In their experiment, amphipods of the genus *Gammarus* were simultaneously offered animals (mayfly larvae) and leaves (beech and maple) as food objects. However, the predatory tendencies of amphipods did not significantly decrease even with an excess of leaf material. This means that the leaf litter per se does not fully satisfy the nutritional needs of gammarids. The satisfaction of nutritional requirements is closely associated with the biological value of food. It is believed (Bigon et al., 1989; Frost and Elser, 2002; Lau et al., 2008) that the molar ratios of biogenic elements (carbon (C), nitrogen (N), and phosphorus (P)) contained in a food object are the reliable indicators of its quality. The lower are the C : N and C : P ratios in a food, the higher is its value. Due to the high level of carbon in plant cell walls, the C : N ratio in plant material is up to 20–40, while in animals it is no more than 10 (Bigon et al., 1989). Even in alder leaves, which are most rapidly processed by macroinvertebrates, the average C : N ratio is close to 16. This ratio remains unchanged for about a month after alder leaves enter a watercourse; it decreases to 11.8–9.2 only after 3.5-month “conditioning” by aquatic bacteria and fungi (Groom and Hildrew, 1989). Since there are literature data on the feedback between the molar ratios of biogens in food and the intensity of its consumption (Gergs and Rothhaupt, 2008; Agatz and Brown, 2014), we have calculated the C : N and C : P ratios for the model prey used in our experiment. The C : N and C : P ratios were in the following ranges: 6.5–6.9 and 167–279 for Hymenoptera and 6.7–6.8 and 119–257 for Diptera, respectively. Such a considerable overlap of the above ranges is determined by the absence of significant differences between carbon, nitrogen, and phosphorus concentrations in the dry matter of these insects (Mann–Whitney test, all $p > 0.100$). Consequently, the fact that the *G. koreanus* in our experiment ate hymenopteran insects less intensively is most likely associated not with the biogenic composition of the latter, but with their greater mechanical strength (compared to dipteran insects).

The findings generally support the hypothesis that the experiments on the forced feeding exclusively by

arthropods make it possible to determine the maximum share of their biomass that can be utilized by the selected consumers. For example, according to our results, two adult *G. koreanus* needed only 5 days to reach the limit of consumption of hymenopterans’ substance with an initial mass of ~22.9 mg (dry weight). As a rough approximation, this utilization rate can be taken as approximate for the group with any number of *G. koreanus* individuals. Then, the groups of 10 and 240 amphipods can process the specified amount of hymenopteran biomass within 24-hrs and in an hour, respectively. In the brook, the average number of *G. koreanus* individuals of the same size as in the experiment ($L \geq 13$ mm) was about 216 ind./m². However, smaller individuals may also take part in the consumption of allochthonous organisms. As it has been reported (Berezina and Maximov, 2016), most amphipod species act as predators when they become 7 mm in length. In this regard, it should be noted that individuals of ≥ 7 mm were predominant in the population of *G. koreanus* in Yaponsky Brook in the period of the survey (52.7% of the total number). The mean daily inputs of dry matter of Hymenoptera and Diptera insects per 1 m² of surface of the brook were as follows: 32.7 ± 30.2 and 16.6 ± 16.2 mg/m² day⁻¹ in July and 42.3 ± 16.9 and 92.8 ± 56.2 mg/m² day⁻¹ in August, respectively. In view of the above, it should be concluded that amphipods from 1 m² of the brook bottom may need no more than a few hours for the maximum utilization of any of these amounts.

CONCLUSIONS

The possible development of research in this area implies that the following provisions (partially stated above) should be taken into consideration:

Predators and euryphages of a fishless tributary utilize terrestrial invertebrates falling into water until the moment they are carried away to the recipient water body, and thereby reduce the amount of entering there allochthonous sources of matter and energy. The respective feeding activity of such resident heterotrophs should be considered as a limiting factor.

The potential impact of this factor should be studied under the conditions of isolation experiments with the forced feeding on model terrestrial prey. Thus, it will be possible to quantitatively assess the share of bodies of a certain type of prey that can be taken up by a particular consumer within a given period of availability. Under natural conditions, the period of availability of allochthonous food objects is determined by the time of their stay within the watercourse.

The bodies of allochthonous invertebrates can be retained in the calm water zones for an indefinite period of time; however, when flow rate increases (e.g., during a flood), uneaten allochthonous organics are transported into the recipient water area. Thus, experiments of different duration will contribute to the

specification of the ultimate levels of utilization of model prey of a given type by a particular consumer. In the future, the total dry biomass of organisms with morphology allowing them to be combined into a group of prey of a particular type, which enter the watercourse within the period of accounting, can be used to calculate the total probable value of their consumption during the time of availability for a particular consumer. Summing up the relevant indicators for different types of prey will allow a quantitative assessment of the degree of possible losses of allochthonous matter and energy for the recipient community.

At first, the inaccuracy of the approach under consideration may be high, but the level of errors should decrease due to the accumulation of the initial data. This opinion is based on the wide use of diet and production calculations, though the error in determining these parameters reaches 50% and the error in calculating abundance or biomass can be 100% or more (Reshetnikov and Tereshchenko, 2017). Obviously, the efficiency of research aimed at assessing the effectiveness of the approach proposed will be higher in small watercourses with species-poor communities, where it is easier to distinguish the impact of separate consumers. In the future, the accumulated information may provide an opportunity of substantiated work in larger lotic systems.

COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interests. The authors declare that they have no conflicts of interest.

Statement on the welfare of animals. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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Translated by E. V. Makeeva