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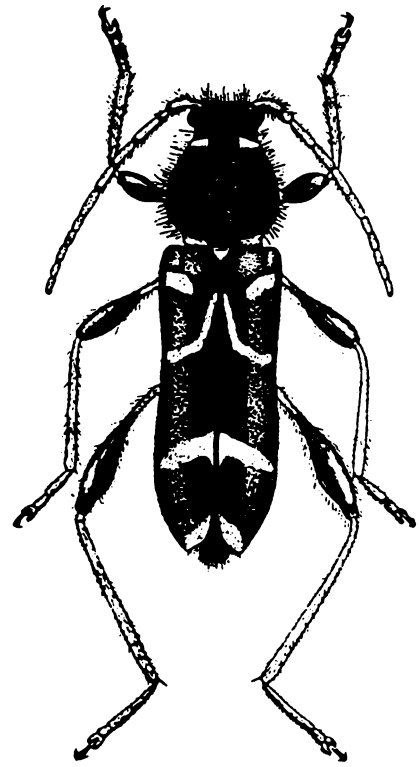

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Molt in Lepidopterans and Tenthredinids and their life strategies in the Arctic

Линька у чешуекрылых и пилильщиков и их жизненные стратегии в Арктике

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КЛЮЧЕВЫЕ СЛОВА: линька, развитие, Lepidoptera, Tenthredinoidea, Арктика.
KEY WORDS: molt, development, Lepidoptera, Tenthredinoidea, Arctic.

ABSTRACT: Growth rate and molting time were estimated in three lepidopterans and four tenthredinids collected in a forest tundra site; data on some other Lepidoptera and Tenthredinoidea species inhabiting the Subarctic and the temperate zone were used as well. In lepidopterans molting was shown to last fairly long (about one day at high temperatures and several days at 10-12°C), and it is quite comparable with biomass doubling time. In sawflies molt lasts only several hours. Thus, molt comprises no less than 25% of the total development in lepidopterans and 3-12% in tenthredinids. Methods of molt estimation are discussed in detail. It was proposed earlier that in some insects molt retardation due to low temperatures is a limiting factor for their northward spread. Shorter molt period in sawflies making them less susceptible to temperature lowering is a useful preadaptation to high latitude conditions.

РЕЗЮМЕ: У трех видов чешуекрылых и четырех пилильщиков, собранных в лесотундре, были определены скорость роста и время линьки; использованы также материалы по некоторым другим видам Lepidoptera и Tenthredinoidea, обитающим в Субарктике и в умеренной зоне. Было показано, что у чешуекрылых линька довольно продолжительная (около суток при высоких температурах и несколько дней при 10-12°C); она вполне сравнима со временем удвоения биомассы. У пилильщиков линька занимает всего несколько часов. Поэтому у чешуекрылых линька составляет не менее 25% от общего времени развития, а у пилильщиков 3-12%. Детально обсуждаются методы оценки времени линьки. Ранее предполагалось, что у некоторых насекомых линька, чрезмерно затянувшаяся при низких температурах, может ограничивать их продвижение на север. Короткая линька пилильщиков, мало чувствительная к понижению температуры, является полезной преадаптацией к существованию в высоких широтах.

Introduction

Most students of larval development in insects commonly identify their rapid development as rapid growth. It is not until recently that molt, as the second component of larval development, has received attention. Time spent on molt has been shown to account for an unexpectedly high proportion of the total time spent on larval development. Through measuring molting times in two subarctic insect species (the leaf beetle, *Galerucella sagittariae*, and the geometrid, *Epirrita autumnata*), Ayres & MacLean [1987] demonstrated that low temperatures retard the development of molting larvae so significantly that the prolonged molting period may constrain the geographic distribution of these species. The third herbivorous species, the sawfly *Dineura virididorsata*, was found to have a shorter molting period under low temperatures [Matsuki, MacLean, 1990]. The relatively rapid molt of *Dineura* was suggested to be an adaptation to the temperature conditions of late summer season when this species is feeding in nature.

Our estimates of larval growth rate in some subarctic folivorous insects made ten years ago [Bogacheva, 1982, 1985; Bogacheva, Kulakova, 1985] showed that unlike lepidopterans, tenthredinid larvae had very short molting times. We did not measure molting periods then, which was done only in 1991-92 for some Lepidoptera and Tenthredinidae species. This study attempts to demonstrate the systematic relevance of molting time differences within Holometabola. The importance of molt duration for life strategies in two large groups of arctic folivores is discussed.

Material and methods

The study was carried out at the Salekhard research station situated in the lower Ob reaches, in the town of Labytnangi, in the forest tundra zone (66° 40' N, 66° 15' E). Species numerous enough in the current summer season were used in experiments. In 1991 they were *Pieris napi* L. (Pieridae) fed on *Hesperis matronalis*, *Celerio galii* Rott. (Sphingidae) feeding on *Chamaenerium angustifolium*, tenthredinids *Pteronidea polaris* Holm. and *Amauronematus* sp. on *Salix dasyclados* and *Nematus ribesicola* Lqv. on *Ribes nigrum*. In 1992 *Aglais urticae* L. (Nymphalidae) fed on *Urtica dioica* and the sawfly *Loderus eversmanni* Kby. on *Equisetum arvense* were added. The larvae for experiments were collected from field sites, caged and fed with leaves of the same plants as in nature.

All lepidopterans in our experiments were boreal species. *A.urticae* reached Labytnangi only recently, shortly after the colonization of that site by the nettle, its host plant. The study area is the northern edge of the range of *C.galii*. It can be detected only after a sequence of warm growing seasons [Bogacheva, 1990]. *P.napi*, the commonest of the three species, reaches Finnish Lapland and arctic Norway [Pagenstecher, 1901] but at our sites it also becomes rare after the coldest growing seasons [Bogacheva, 1990]. As to sawflies, all the four species used are rather common in the low Ob reaches, though *P.polaris* and possibly *Amauronematus* sp. are distributed farther to the north than *L.eversmanni* ["Key to insects...", 1988] and than *N.ribesicola* connected with *Ribes* which reaches there the northern edge of its range.

Larvae in their penultimate and final instars were kept as singletons in Petri dishes lined with moistened filter paper. Every day at the same time the larvae were weighed to the nearest milligram and provided abundantly with food. The larvae as well as their sloughs (exuviae) were weighed also immediately after ecdysis.

We had no constant temperature chambers at the research station, so cages were kept in the laboratory and outdoors to create contrast temperature conditions. The temperature was recorded around the clock using a thermograph. It fluctuated both within day and between days; all the temperatures mentioned in the paper are mean data of the period in question (growth or molting).

On the assumption that molt in sawflies has to be short and knowing that the method of molting time calculation proposed by Ayres & MacLean [1987] proved to be not quite satisfactory at low temperatures in *Dineura viridiдorsata* with its low growth rate [Matsuki, MacLean 1990], we used our own method to measure molting time. Ayres & MacLean defined the time spent on molt as "the difference between the actual time expended in growing from one instar to the next, and the time that would be required if larvae could skip molt and grow continuously at their nonmolting growth rates" [1987, p. 276]. In our method, molt can be regarded as the period when the larva does not feed. Our definition of molting time does not coincide completely with that by Ayres & MacLean: while after molt the moment of feeding renewal coincides with the onset of growth, there is a period before molt when the larva feeds without any increase in body weight. This period is included in the molting time by Ayres & MacLean, which does not seem correct to me, we hoped, however, that data on molting time obtained by Ayres & MacLean and by our method would not differ significantly.

In order to record the moment when larva stops feeding to molt, or resumes feeding after the molt is over, as accurately as possible, all changes in the larval behavior were observed six times a day, at 4 h. intervals. To the period when new feeding marks on leaves first failed to appear, we added the other four hours because the larva could stop or resume feeding not at the very moment of registration but at any moment between registrations. All data on the seven species investigated, which are represented in Fig. 1, were obtained using our method of observations; we needed the weights of exuvia and of larvae at ecdysis only to compare our results with those obtained using Ayres and MacLean's method. The average gut content was estimated for the same purpose in lepidopterans from a subsample of larvae [Ayres, MacLean, 1987]; in sawflies this amendment was not used at all for reasons which are to be explained later.

Some other parameters of the experiment should be defined more exactly. In every species there were no less than 5-6 replicates (larvae) at two different temperature regimes; every point in Figure 1 represents data on molt or growth for one larva. The data on growth (expressed as biomass doubling time) are given for the final larval instar, from onset to maximal weight. Several food plants, as much as replicates number, were chosen randomly every day to collect leaves for larvae as we intended to escape any pseudoreplication. The significance of differences when necessary was estimated by the t-test. Correlation coefficients were calculated to find a possible relationship between growth rate (or molting time) and body weight.

In August-September of 1991 in Sverdlovsk (56° 50' N, 60° 40' E, south taiga zone), we carried out

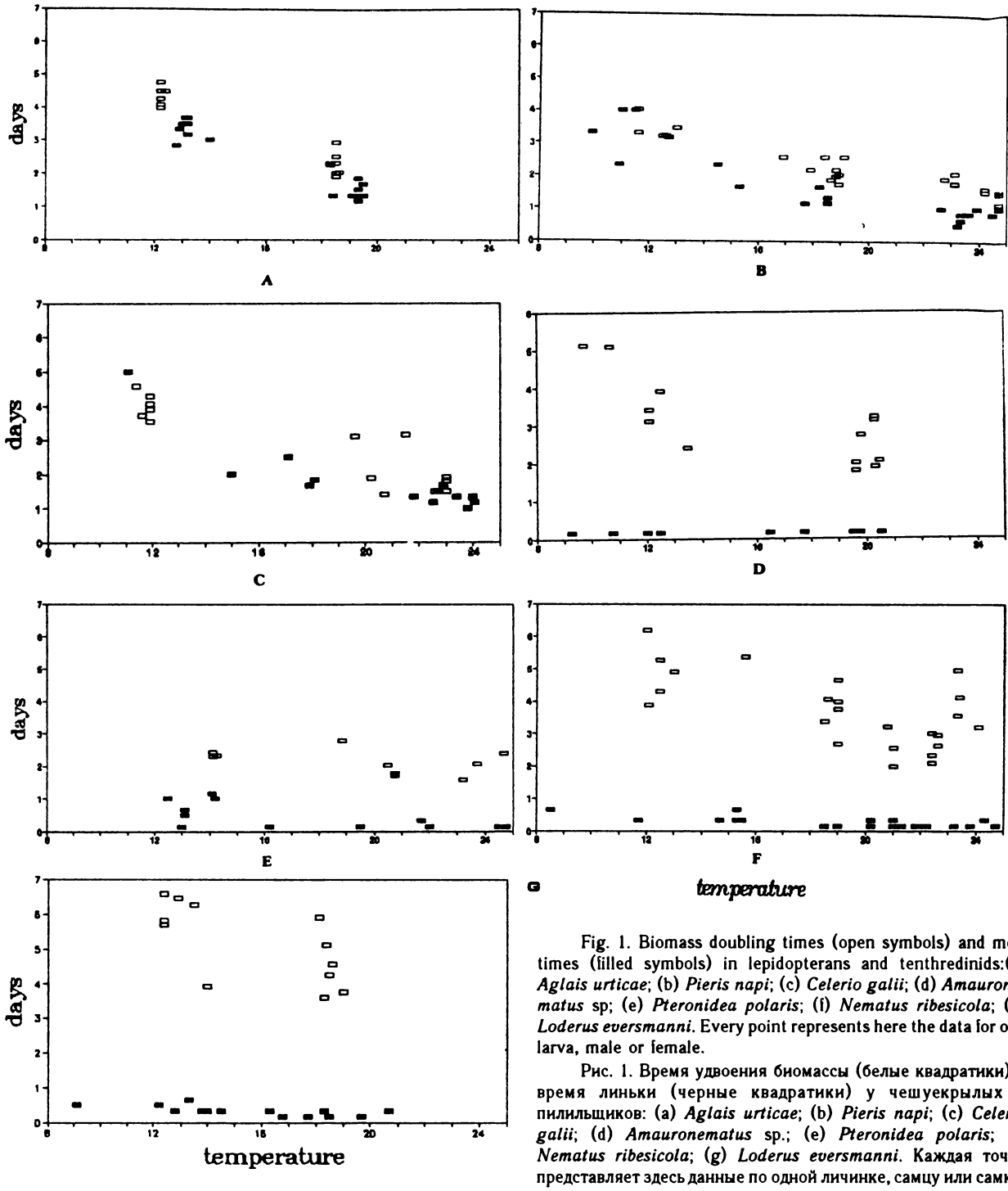


Fig. 1. Biomass doubling times (open symbols) and molt times (filled symbols) in lepidopterans and tenthredinids:(a) *Aglais urticae*; (b) *Pieris napi*; (c) *Celerio galii*; (d) *Amauronematus* sp; (e) *Pteronidea polaris*; (f) *Nematus ribesicola*; (g) *Loderus eversmanni*. Every point represents here the data for one larva, male or female.

Рис. 1. Время удвоения биомассы (белые квадратики) и время линьки (черные квадратики) у чешуекрылых и пилильщиков: (a) *Aglais urticae*; (b) *Pieris napi*; (c) *Celerio galii*; (d) *Amauronematus* sp.; (e) *Pteronidea polaris*; (f) *Nematus ribesicola*; (g) *Loderus eversmanni*. Каждая точка представляет здесь данные по одной личинке, самцу или самке.

the experiments with two sawfly species: *Croesus* sp., feeding on *Betula pubescens*, and *Nematus* sp. on *Populus balsamifera*. The only difference between this experiment and those described above consistent in the constant temperatures used in Sverdlovsk. In addition, we used the data on lepidopterans and symphytans obtained in 1978-1981 in Labytnangi [Bogacheva, 1982, 1985; Bogacheva; Kulakova, 1985] and in Sverdlovsk. Though only larval growth was studied that time and molt time was not measured, the general design of experiments was the same, except for the 24 h. intervals of observations. We do not intend to demonstrate here all these materials but shall refer to them when necessary; the data on geometrid *Epirrita autumnata* Bkh., a species dealt with in the

paper by Ayres & MacLean [1987], and those on sawfly *Pamphilius* sp. are of considerable interest for our task. Both species were fed on birch leaves. Nine lepidopterans belonging to seven families and nine sawfly species of 2 families were used.

Results

Molting time in lepidopterans and symphytans.

All the three lepidopteran species studied in Labytnangi in 1991-1992 demonstrated similar patterns (Fig. 1a-c) resembling that of *E.autumnata* obtained by Ayres & Maclean [1987]: time spent on molt is in them almost as long as biomass doubling time. On the other hand, the patterns for four sawfly species were quite similar as well, being characterized by a very short molting time; doubling time exceeds it by an order of magnitude (Fig. 1d-g). Only some *Pteronidea* specimens at 12-14°C molted for over one day. As a rule, the molting period was much shorter, and above 18°C larvae began and completed molting within one period between our registrations, i.e.molt lasted less than 4 hours. Molting times were equally short in two sawfly species studied in Sverdlovsk in 1991. In *Amauronematus* sp. (Fig. 1d) we did not observe molting lasting longer than four hours at all the temperatures used.

True, my method of molting time estimation is too rough for short molting periods in sawflies: we ought to do more frequent registrations. But our attempts to estimate sawflies molting times according to formulae by Ayres a. MacLean also failed, as negative values were yielded.

D.viridi dorsata [Matsuki, MacLean, 1990] resembles our sawfly species in the pattern of its molt: the molting time at all temperatures was shorter than the doubling time. On the other hand, the actual molt duration in *D.viridi dorsata* was an order of magnitude higher than in the other species studied, ranging from 3.80 d at 6°C to 1.74 d at 24°C. This fact called for interpretation. We had first to make sure that these differences in the results were not caused by the differences in the methods of experiments. There were two features distinguishing our experiments from those of Ayres & MacLean [1987]: (1) the use of variable temperatures instead of constant ones; (2) the different methods to measure molting time.

(1) It is well known that development rates of invertebrates at variable and at constant temperatures are different [Galkovskaja, Sutschenja, 1978]; as a rule, variable temperatures accelerate development. The only species kept at both temperature regimes was the geometrid *E.autumnata* [Ayres, MacLean, 1987 vs. Bogacheva, Kulakova, 1985]. Using our data and the formulae by Ayres and MacLean [1987] to estimate the molting time in this species, we failed to record any significant differences between our data and those of Ayres and MacLean. In other words, the molt of this species was not affected by the temperature regime. Further, two sawfly species kept in Sverdlovsk at constant temperatures demonstrated the same very short molting times as northern species at variable temperatures. Though both these arguments are indirect and each species might have its own response to variable temperatures [Hagstrum & Hagstrum, 1970, as reported in Galkovskaja, Sutschenja,1978], we do not believe that variable temperatures might be the reason for the profound differences between *D.viridi dorsata* and our northern species.

(2) Defining molt as a period when the molting larva does not feed, I could expect to obtain somewhat shorter molting periods than the values calculated after Ayres and MacLean. To verify this assumption, I have made these calculations for two lepidopteran species (Tab. 1). No signiicant differences between the data obtained by two different methods were found; hence the period before the molt when larvae are still feeding but already do not increase their weight would be very short. Thus, I have every reason to believe that the observation method yields the actual values of molting periods.

It is possible to estimate roughly whether molt-

Table 1.
Comparison of molt time (x + SE) in two lepidopteran species obtained by calculation according to Ayres & MacLean [1987] and by observations

Species	Aglais urticae		Pieris napi	
Temperature	13.1°C	19.2°C	12.5°C	22.0°C
By observations	3.33+0.10	1.14+0.08	2.66+0.31	1.00+0.06
By calculations	3.58+0.13	1.53+0.11	2.49+0.31	0.96+0.09

ing period is much longer or shorter than 24 hours, using the plot of larval growth. In lepidopterans growth is interrupted by molting periods (Fig. 2a). Growth line in sawflies has no gaps (Fig. 2b,c); it is not uncommon that on the day of molt growth rate would not even decrease (Fig. 2b). Those plots without gaps in larval growth testify that molt takes much less than 24 hours, and it was the only pattern of growth in all sawfly species which we had dealt with.

Our nine sawfly species were not uniform taxonomically or ecologically. Among them there were representatives of the Nematinae subfamily, including seven species, one species belonging to Dolerinae subfamily (*L.eversmanni*) and *Pamphilius* sp., representing the other family of Symphyta (Fig. 2c). Most sawflies feed on trees and shrubs, though one species feeding on *Equisetum*. This heterogeneous group of sawflies is however quite uniform as regards the molting pattern; all of them are "short-molting" species. On the other hand, *D.viridididorsata*, quite similar to most our sawfly species in all other respects, proved to be "long-molting". No reasons having been found for the differences between *D.viridididorsata* and our sawfly species, my conclusion is that these differences are partly an artifact created by the calculation method in this species with very low growth rate [Matsuki, MacLean, 1990]: the actual values of its molting time might be somewhat lower. Anyhow, these "long-molting" sawfly species have to be rather uncommon since I have failed to find another "long-molting" sawfly among our casual set of species.

The effect of some factors on the molting time and on its proportion in the total time of larval development.

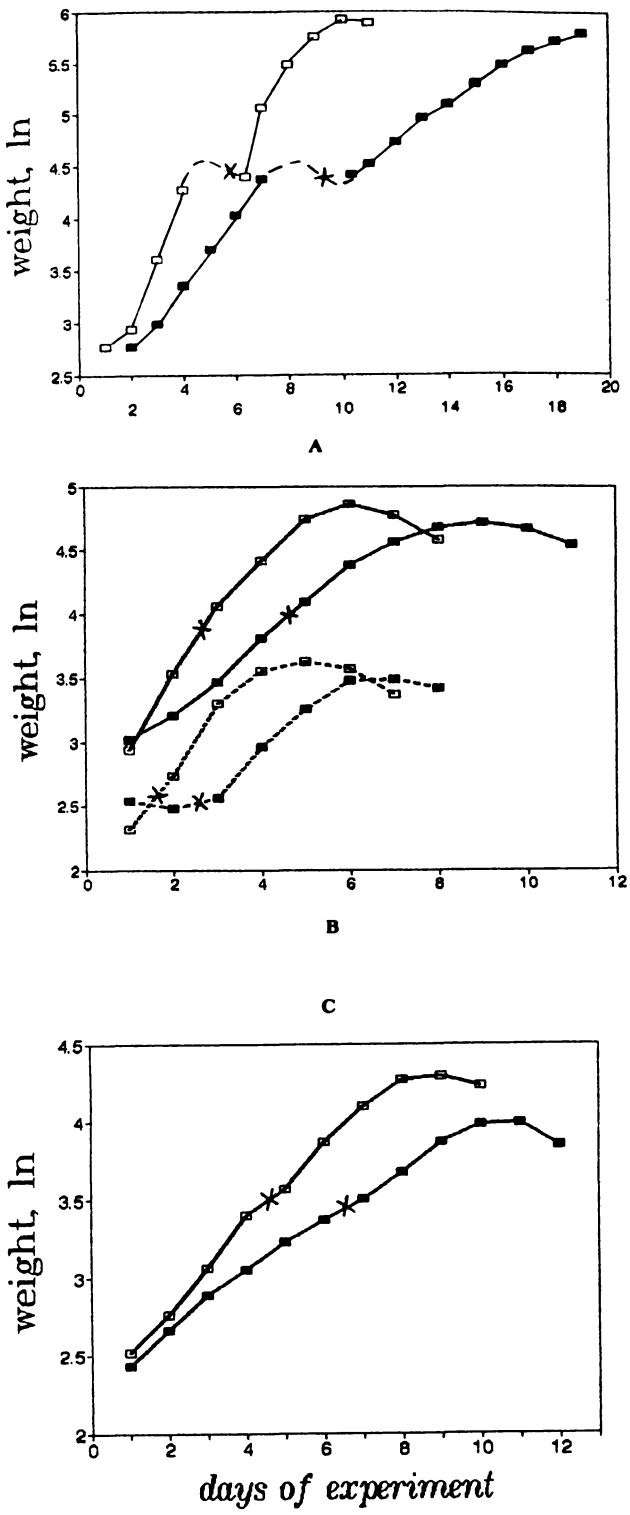
Due to the long molt in lepidopterans, they spend a significant part of their development in molt. Ayres & MacLean [1987] found that molt in *Epirrita comprises* 43% of the total time of developing from the onset of penultimate instar to the onset of the final instar. For the lepidopterans investigated here I obtained somewhat lower proportions of molting time (Tab. 2). In our four tenthredinid species molt comprises only 3.5-12.6% of the total development at different temperatures. The concrete values of molting proportions are however modified by many factors.

Temperature exerts the ultimate effect both on growth and on the molt (Fig. 1). It was shown for *Epirrita* that molt is more sensitive to temperature than growth [Ayres, MacLean, 1987]. The lepidopterans confirm this tendency (Fig. 1b, c). The opposite trend was found in *Dineura* [Matsuki, MacLean, 1990]. It is difficult to discuss our data in tenthredinids, because our estimation of their molting times was not sufficiently precise for this end.

Growth rates are also influenced by food quality. Though the latter has no effect on molting time, proportion of molting in the total development time changes [Ayres, MacLean, 1987]: molting duration

Table 2.
Size and some characteristics of larval development in final instars at 12°C (m - males, f - females).

Species	Sex	n	Fresh body weight, mg	Biomass doubling time, days	Molting time days	%
A.urticae	m f	9	376.1	4.45	3.83	28.1
P.napi	m f	25	181.6	3.65	2.77	26.9
C.galii	m f	11	4225.4	3.95	3.47	24.6
P.polaris	m	10	36.2	3.94	0.57	9.0
	f	6	119.7	3.94	0.57	12.6
N.ribesicola	m	8	22.4	4.86	0.43	5.9
	f	16	76.9	4.86	0.43	6.2
Amaurone-matus sp.	m	8	15.5	3.86	0.16	5.1
	f	8	29.9	3.86	0.16	4.2
L.eversmanni	m	12	27.3	5.87	0.42	9.1
	f	4	72.3	5.87	0.42	6.1



is proportionally longer in fast growing species (or specimens).

Growth rates must depend on larval body weight, but despite the immense range of variability in body weights, from *Amauronematus* to Celerio (Tab. 2), we failed to record this dependence for a set of species, particularly because of differences in food quality. This factor does not alter molting rates, but any connection between molting rate and body weight was not found either; lepidopterans of different body weights have similar molting times.

Sexual dimorphism in molting times and growth rates might be surmised, especially in sawflies. But despite clear sexual differences in body weight (Tab. 2), we have found no significant differences in growth and molt between males and females in sawflies (Fig. 2b); Matsuki & MacLean [1990] in *Dineura* have not found them either. Hence all the data on males and females were pooled to calculate doubling time and molting periods in every species (Fig.1d-g).

Structure of molting time

Matsuki & MacLean [1990] discerned four stages in the molting time: evacuation of gut content, apolysis, ecdysis, and hardening of the new exoskeleton. As to the evacuation of gut content, I am afraid it is hardly correct to consider it as an independent component of molting time. When the larva stops feeding with the onset of molt, the passage of food through the alimentary canal continues. Gut clearing requires 4-6 hours in lepidopterans [Stewart, Nelson, 1977; Peterson, 1987] while the duration of apolysis is much longer; this appears to indicate that the evacuation of gut content is the first stage of molting followed by apolysis. Meanwhile our sawfly species in the course of their short molting usually have no time to clear the gut; the gut content is well detectable through semitransparent cuticle in *Amauronematus* sp. and *N.ribesicola* larvae up to the end of their molting. Hence, the evacuation of gut content is neither an independent component of molting time nor a necessary one though the process of gut clearing is undoubtedly associated intimately with weight loss during molting.

Fig. 2. Growth of some species in their penultimate and final larval instars. The mean temperatures were: in *Aglais urticae* (a) 12.2° and 18.4°C; in *Nematus ribesicola* (b) 13° and 21.2°C ; in *Pamphilius* sp. (c) 16° and 21.8°C . Filled symbols indicate the growth at the lower temperature. Males (dashed lines) and females (solid lines) were separated in (b) and pooled in (a) and (c). The moments of ecdysis are marked by crosses.

Рис. 2. Рост личинок некоторых видов в предпоследнем и последнем возрастах. Средние температуры: у *Aglais urticae* (a) 12,2° и 18,4°C; у *Nematus ribesicola* (b) 13° и 21,2°C ; у *Pamphilius* sp. (c) 16° и 21,8°C. Для обозначения роста при более низкой температуре использованы черные квадратики. Самцы (обозначены прерывистыми линиями) и самки разделены на рис. 2b и объединены на рис. 2a и 2c. Крестиками показан момент экдизиса.

As to three other stages discerned generally in the molt, apolysis is the longest of them. In lepidopterans it comprises 70-90% of the total molting time. Ecdysis is a short stage; some observations on ecdysis in our species have shown that it lasts 20-30 min. The hardening of new exoskeleton account for 9-21% of the total molting time (from 7 h in *Pieris* to 12.7 h in *Celerio*) at 12-16°C and 16-27% (from 4.5 h in *Pieris* to 8.4 h in *Celerio*) at 18-23°C. Thus, it can be concluded that apolysis is the stage extremely susceptible to temperature.

Discussion

Lepidopterans belonging to several families and several sawflies were used to measure molting times. It was shown for species studied that lepidopterans had rather long molting times while sawflies had very short ones. Ayres & MacLean [1987] hypothesized systematic differences in molting times between holometabolous and hemimetabolous insects; those differences appeared to also exist within Holometabola. Some physiological and biochemical traits undoubtedly underlie these differences in molting times.

Though I believe that lepidopterans differ from sawflies in their molting times, some lepidopteran species (maybe even families) with short molting times and, conversely, some "long-molting" sawfly species may exist. One such species, *D.viridi dorsata*, has possibly been found already [Matsuki, MacLean, 1990]. The relatively rapid molt demonstrated in this species at 6°C in contrast to *Epirrita* is caused surely by taxonomic but not ecologic reasons. This is clear from the comparison of *D.viridi dorsata* with "short-molting" subarctic sawflies which develop in July , at the highest temperatures of summer season (*N.ribesicola*, *Amauronematus* sp.). Thus, we believe that ecological differences among species should be studied using taxonomically uniform material.

Ayres and MacLean did well to attract the attention of researchers to molting of subarctic species, as that component of larval development was underestimated earlier. They have shown that molt may comprise high percentage of the total development, which would increase with decreasing temperature. It was found that some insects are unable to molt at 6°C, therefore their distribution to the north may be constrained by molt retardation at low temperatures.

I believe, though, that the impact of molt retardation on insect distribution should not be overestimated. Firstly, all three lepidopteran species studied by us do live on the southern edge of the Subarctic, but at low temperatures (7-8°C) feeding in their larvae was not observed. Therefore, not only molting time but also growth may be dangerously retarded by low temperature. Secondly, insects in nature actively use basking to increase body temperature [Strelnikov, 1940; Downes, 1964; Danks, 1986]. Larval behavior directed to body warming, especially after night fall of air temperature, is almost the same in any region where this fall takes place, from deserts [Casey, 1976] to the mountains [Strelnikov,1940] and the Arctic [Kevan et al., 1982]. As a result, body temperature of larvae feeding or basking on a sun-lit substrate is much higher than the temperature of air [Kevan et al., 1982; Grossmueller, Lederhouse, 1985]. This is true also for molting larvae, as larvae certainly choose sun-lit microsites for their molting. We have observed that in *Celerio* caterpillars which molt in fireweed inflorescences sun-lit from early morning. I think that only where or when larvae cannot use radiative warming because of cloudy weather the molting retardation by low temperatures might prove really adverse to them.

The short and cold summer season is the main obstacle to the distribution of phyllophagous insects in the Subarctic [Chernov, 1974, 1978]. In lepidopteran larvae feeding in summer and autumn their growth (because of low temperatures and of low food quality, especially in dendrophages) and molting may be retarded. Large insects might not succeed in reaching the stage at which these species hibernate; we have observed such failure in *Nymphalis antiopae* L. and in the coldest growing seasons in P. napi [Bogacheva 1990]. This situation is followed by an abrupt decrease of density in these species. The alternative life strategy, when larvae can hibernate and continue their development in the next year, would be more successful at high latitudes [Chernov, 1974, 1978]. In some cases, as in *Gynaephora*, larva can hibernate many times [Kevan et al., 1982; Kukal a. Dawson, 1989].

Sawflies, with their summer and autumnal phenology of larval feeding, often have rather low growth rates. Meanwhile they hibernate, as a rule, at the stage of prepupa (or pupa), so they have to accomplish their larval development by the end of current growing season. Small body weight and short molting, less susceptible to temperature decrease, allow them to spread in the Subarctic without changing the life strategy peculiar to this group in the temperate zone.

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