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Life Cycle of *Gammarus pulex* (L.) in the River Yeşilırmak

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Abstract: Monthly sampling of *Gammarus pulex* for 45 months in the River Yeşilırmak showed that the mean seasonal population density increased to a maximum in summer, and then declined to the lowest level in winter. There was a consistent seasonal pattern of body length distributions, characterised by the arrival of a strong cohort of new juveniles in spring and early summer. The ovigerous adults were few in autumn, peaked around January to March, and were virtually absent from July to October. Estimated sex ratios obtained from the field in general seem to show that females predominated, except in summer.

Key Words: Density, sex ratio, population dynamic, invertebrates, ovigerous female

Gammarus pulex (L.)'in Yeşilırmak Nehri'ndeki Hayat Devri

Özet: *Gammarus pulex*'in Yeşilırmak Nehri'nde 45 ay süresince yapılan örnekleme çalışması sonucunda, mevsimsel ortalama yoğunluk değerleri yaz aylarında maksimum artmış ve sonra kış aylarında bir düşüş göstermiştir. Boy uzunluğu düzenli bir mevsimsel dağılım göstermiş, yeni genç bireyler genelde ilkbaharda ya da yaz başında yoğun olarak görülmektedir. Yumurta taşıyan bireyler sonbaharda az, Ocak ve Mart ayları civarında artmış ve Temmuz ile Ekim ayları arasında ise hiç görülmemiştir. Arazi çalışmaları sonucunda tahmin edilen cinsiyet oranı, genel olarak dişilerin erkeklere oranla yaz ayları hariç neredeyse tüm mevsimlerde baskın olduğu görülmüştür.

Anahtar Sözcükler: Yoğunluk, cinsiyet oranı, populasyon dinamiği, omurgasızlar, yumurtalı dişi

Introduction

Amphipods of the genus *Gammarus* successfully occupy a wide variety of freshwater habitats throughout the northern hemisphere (Karaman and Pinkster, 1977; Barnard and Barnard, 1983). One reason for the success of this genus is its adaptability to various habitats, which differ considerably in characteristics such as light availability, temperature fluctuation, and food resources. Thus, *Gammarus* could play a dominant role in the functioning of the spring and stream communities it inhabits (Glazier, 1991; Crane, 1994).

There are a large number of investigations undertaken on *G. pulex* biology, such as breeding (Mortensen 1982), preference of habitat (Dahl and Greenberg 1996; Elliott, 2002), temperature effect on sex ratio (Lockwood, 1968), light effect on sex ratio (Bulnheim, 1978), feeding behaviour (Kelly et al., 2002), population composition (Kelly et al., 2003), growth rate estimation by model (Duran, 2004), and research of diurnal and noctoral habitat preference (Elliott, 2005).

Still several gaps in the study of life-cycle of *G. pulex* remain, such as sex ratio and new cohort. The purpose of this study was to compare the characteristics of the population structure and life history of populations of this species in the River Yeşilırmak.

Materials and Methods

The total basin of the River Yeşilırmak is 2352.8 km^2 and it is 519 km in length. The study area was a 30-km section of the Yeşilırmak. In this stretch, the Yeşilırmak flows to the city of Tokat and 5 sites were sampled for *G. pulex* monthly from January 1999 to September 2002 (Figure 1). Most of this stretch has a stronger current

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Figure 1. Location of the River Yeşilırmak and stations, G = Gravel, C = Cobble, S = Sandy.

with stony to stony-sandy or (compacted) clay sediments. People have been benefiting from the river by irrigation and fish farming. Riparian vegetation is dominated by trees, mainly *Populus* and *Salix,* and aquatic vegetation, which is not very dense. The densest aquatic filamentous algae are *Spirogyra* sp. and *Ranunculus* sp. and the densest aquatic plant is water milfoil.

The bottom of the river at the stations 1 and 2 is mostly gravely and some cobbly, and the bottom of the stations 3 and 4 is mostly sandy, in places there are plants, some gravely and some silty near the shore and the bottom of the station 5 is mostly sandy, in places there are plants, and silty. A total of 45 monthly samples were taken with a Surber sampler (475 mm mesh, area of base 0.77 m^2) and a bottom kick net (500 mm mesh). Animals were immediately fixed in formaldehyde (4%) in the field and transferred to 70% ethyl alcohol in the laboratory. *G. pulex* was sorted, identified, and counted under a stereomicroscope. The animals were measured from the tip of the rostum to the tip of the third uropod to the nearest millimetre. Minitab 13.2 was used for statistical analysis.

Results

The mean lengths of *G. pulex* samples collected from the river each month show consistent decreases in summer (June-July) (Figure 2) due to a substantial increase in the numbers of small *Gammarus* (<3 mm) in the samples from May to July. In addition, Figure 2 clearly shows that the large *Gammarus* (13-15 mm) disappeared from July to October. The monthly pattern of *G. pulex* size distributions indicates regular patterns from 1999 to 2002 since the Kruskal-Wallis test revealed no significant value between their size classes and the years they were found (Kruskal-Wallis test, $P < 0.46$). The proportion of 7-9 mm and 10-12 mm sizes of *G. pulex* was found more abundant than other size categories each year (Figure 3). The arrival of a new cohort of juveniles was observed in winter and from spring through early summer, from January to February, and from May to June depending on the date of sampling and sampling conditions. The progressive increase in body size of this cohort through the succeeding summer months as the *Gammarus* grow is also clearly discernible (Figure 3).

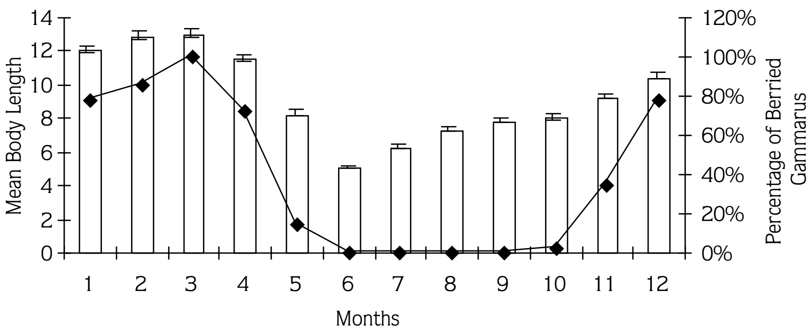

Figure 2. The average mean body length (mm) for 49 months (Y1 axis) and percentage of ovigerous *Gammarus* (Y2 axis). X axis; months (i.e. 1 = January, 2 = February), bar; mean body length, and line; percentage of ovigerous *Gammarus.*

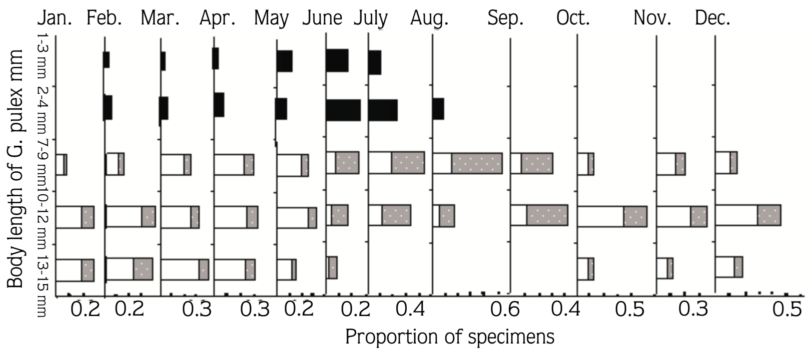

Figure 3. Average monthly size frequency distribution of *Gammarus pulex* from the Yeşilırmak from 1999 to 2002. Grey bars show males, white bars show female, and black bars show indeterminate sex.

A total of 30,785 individuals were collected from the 5 stations. The average density decreased to a minimum in January (38 indv. m^{-2}) and then slowly built up until March, after which there was a rapid increase in May (361 indv m^{-2}) (Table). The mean density of *Gammarus* significantly differed among stations (Student's t test, $P < 0.000$ among all stations, $P < 0.001$ between S1 and S2, $P < 0.000$ between S2 and S3, $P < 0.000$ between S3 and S4, and $P < 0.000$ between S4 and S5), among months (one-way ANOVA, $P < 0.000$) and among seasons (one-way ANOVA, $P < 0.014$). However, the density of the 5 stations did not differ among the years from 1999 to 2002 (one-way ANOVA, $P < 0.752$).

The records of river temperature, pH, dissolved oxygen, and *Gammarus* density were taken at each season and a correlation matrix was calculated. There was a significant correlation between density and temperature ($r^2 = 0.976$, $P < 0.019$). However, there was no significant correlation between density and pH ($r^2 = 0.578$, $P < 0.422$), or density and O_2 ($r^2 = -0.355$, $P < 0.645$).

The proportion of ovigerous adult *Gammarus* increases from autumn through spring, peaking up to 100% until about March (Figure 2). After this, the proportion of egg-bearing falls until July and during October. Ovigerous females were essentially absent from the populations. There was a consistent hiatus in the number of egg-bearing females in each summer and early autumn. The first eggs appear in October or November and the number of females carrying eggs increases to a peak in March and April, and then falls to virtually zero from July to October, and so eggs are carried in the river for about 8 months of the year.

Table. The records of monthly abundance of *Gammarus pulex* taken at the stations.

Stations	January	February	March	April	May	June	July	August	September	October	November	December
S1												
1999	38	42	110	142	223	200	217	89	87	62	35	29
2000	36	53	126	137	249	197	221	88	85	64	38	32
2001	29	40	114	151	232	203	229	96	80	60	42	33
2002	32	45	117	139	226	207	219	89	82	65	39	28
Total	135 ± 3.35	180 ± 3.87	467 ±	569 ± 3.6	910 ± 5.02	807 ± 4.73	886 ± 4.96	365 ± 3.18	334 ± 3	251 ± 2.46	154 ± 2.06	122 ± 1.84
S2												
1999	40	53	132	157	232	212	225	92	92	69	42	35
2000	42	58	136	162	238	219	229	87	94	72	45	30
2001	35	47	142	169	243	215	233	83	89	67	49	33
2002	39	60	147	163	237	217	227	89	91	71	46	31
Total	156 ± 2.08	218 ± 2.46	557 ± 3.93	651 ± 4.25	950 ± 5.13	863 ± 4.89	914 ± 5.03	351 ± 3.12	366 ± 3.18	279 ± 2.78	182 ± 2.24	129 ± 1.89
S3												
1999	43	85	155	163	242	223	231	99	97	78	48	41
2000	40	79	164	171	247	228	241	102	95	82	52	39
2001	42	82	144	174	257	224	247	119	92	81	56	42
2002	47	83	178	179	243	226	251	105	99	87	53	39
Total	172 ± 2.18	329 ± 3.02	641 ± 4.21	687 ± 4.36	989 ± 5.24	901 ± 5	970 ± 5.19	425 ± 3.43	383 ± 3.26	328 ± 3	209 ± 2.4	161 ± 2.11
S4												
1999	48	90	182	182	275	240	273	139	116	91	62	49
2000	49	87	197	175	272	246	277	135	114	95	67	45
2001	57	83	191	179	278	243	281	137	109	92	71	46
2002	50	95	189	182	269	239	288	127	119	93	65	44
Total	204 ± 2.38	395 ± 3.31	759 ± 4.59	718 ± 4.46	1094 ± 5.51	968 ± 5.18	1119 ± 5.57	538 ± 3.86	458 ± 3.56	371 ± 3.21	265 ± 2.71	184 ± 2.26
S5												
1999	45	89	163	177	263	236	278	116	102	88	56	46
2000	43	83	182	174	273	242	271	120	110	91	53	42
2001	49	73	182	167	273	239	274	119	100	93	62	43
2002	42	89	178	177	270	236	281	110	103	79	58	41
Total	179 ± 2.22	334 ± 3	705 ± 4.42	665 ± 4.29	1079 ± 5.47	953 ± 5.14	1104 ± 5.53	465 ± 3.59	415 ± 3.39	351 ± 3.12	229 ± 2.52	172 ± 2.18
Total average	169 ± 1.45	291 ± 1.9	625 ± 2.79	658 ± 2.86	1004 ± 3.54	898 ± 3.35	999 ± 3.53	429 ± 2.31	391 ± 2.21	316 ± 1.98	208 ± 1.61	154 ± 1.38

The sex ratio (female/male) changed during the year. The average ratio was 1.9:1 in winter, 3.28:1 in spring, 0.72:1 in summer, and 1.3:1 in autumn. Estimated sex ratios obtained from the field samplings of the river in general seem to reflect that females predominated, except in summer (Figure 3).

Discussion

A consistent seasonal pattern of abundance at the stations was found over the 4 years surveyed; it starts with low numbers in winter, and then *Gammarus* numbers build up during spring into autumn before dropping again in winter. The results of mean lengths show consistent decreases in summer (June or July), agreeing with Welton's (1979) findings that the largest mature females died around the end of July and the largest mature males died in September. This means that there might be insignificant breeding taking place at this time. The new spring cohort showed increasing body length through the summer months until December. In addition, decreases in summer could be explained with Allan and Malmqvist's (1989) results that trout consumed disproportionately more of the larger sizes of *G. pulex* in comparison to the sizes available in either the drift or the benthos. Somewhat more of the larger amphipods were consumed by trout presumed to have been feeding during the night, and this may reflect the greater availability of larger amphipods in the drift. Sculpin diet also reflected a bias toward larger prey relative to size classes present, although this trend appears less distinct than that of trout.

The distinctiveness of the new cohort from May to June (< 3 mm) through to December implies some degree of synchronicity in the production of juveniles and no substantial further production in summer, whose presence would have obscured the clear modal progression through the summer and autumn months. Animals released from brood pouches earlier in the year were nearly all sexually mature (> 7-9 mm) by about 10 or 11 months from January to October, and about 8 or 9 months from May to December or January.

G. pulex may breed throughout the year (Welton, 1979) or may not (Hynes, 1955; Macan and Mackereth, 1957; Hultin, 1971). However, either breeding did not take place or it was insignificant during winter (Mortensen, 1982), and probably the same is true for the population in the Yeşilırmak. The details of the timing of breeding varied somewhat from year to year, but the overall pattern of one major breeding period remained the same in the study. The absence of *Gammarus* eggs in summer and early autumn suggests that high quality food is necessary for the growth and maturation of the eggs and for the continued survival of females who carry the eggs and develop their young, until the young are sufficiently developed to survive on their own. The incubation of egg periods is related to the temperature. Some studies (Havinga, 1930; Wear, 1974; Boddeke, 1982; Henderson and Holmes, 1987) observed a strong relationship between water temperature and the duration of embryonic development. Adults may spawn once or twice during the year. In general, older females start egg laying earlier in the year than smaller and younger females. Those producing eggs in November or December will have spawned by January or February, and it is likely that these individuals will produce another clutch of eggs and spawn a second time in May or June. Some young females (> 7–9 mm) entering the population for the first time in their first spring will produce eggs and spawn in that spring but are unlikely to have the time or bodily resources to spawn a second time (in autumn) in that year. This is in complete agreement with Welton and Clarke (1980) in a Danish spring and Hynes (1955) and Welton (1979) in an English chalk stream.

In the Yeşilırmak, sex ratios seem to show that females predominated, except in summer. This contrasts with Welton (1979), who reported that from April to June there were slightly more males than females, but during the period from July to September this was reversed. Furthermore, the results in general seemed to conflict with Locwood's (1968) results that *G. duebeni* mature adults kept above 8 °C produced female offspring only. In that case, temperature might not be the only factor affecting the sex ratio. The dominance of males in summers could be explained by the finding that longer day length leads to the development of more males in a brood (Bulnheim, 1978). Moreover, this could be the result of increases in numbers of indeterminate *Gammarus* or females (presumably males too) that were washed out after birth during the summer.

Consequently, the following is a likely scenario for the *G. pulex* life-cycle in the Yeşilırmak; the first eggs seen on adults at the beginning of October hatch by January or February (depending on temperature) and the ensuing juveniles develop by the beginning of April. Consequently, the first adults develop from these by December in the same year as reported previously by Duran (2004); the growth rate of *Gammarus* was estimated 12 months for the Duran model and 12-13 months for the field growth rate. The range of times for each growth period reflects the various river temperatures taken at different times of year. The proportion of ovigerous adults with eggs was initially low and so these first juvenile recruits were small in numbers. The number of ovigerous females increased through the winter leading to most eggs occurring in the periods from January to March. These went through egg and juvenile stages increasingly quickly and gave rise to the main recruitment of juveniles in May and June and the first adults from the spring cohort to develop by December or January. The declining number of animals greater than 8 mm long implies that most of the generation released in the previous spring probably died during the summer.

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