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Population studies on the Amphipoda of Mazoma Lagoon (Greece)

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ABSTRACT: The life cycles of four amphipod species — Gammarus insensibilis, Dexamine spinosa, Microdeutopus gryllotalpa and Corophium insidiosum — were studied in the brackish-water lagoon Mazoma of the Amvrakikos Gulf, Ionian Sea. G. insensibilis has an annual life cycle with limited recruitment over the year and maximum reproductive activity in the winter months. D. spinosa exhibits continuous recruitment in the lagoon with a maximum in summer. Both species produce a single brood per female per year. Continuous recruitment was observed during the summer months for M. gryllotalpa and C. insidiosum, and multiple breeding per female per year. Sex ratios varied considerably over the year, with a persisting preponderance of the females.

INTRODUCTION

The Amphipoda are an important group of Crustacea in benthic ecosystems. They play an important role in sediment stability and in the structure of benthic communities (Mills, 1969). In addition, they represent a significant component in marine benthic food webs, especially in seagrass ecosystems (Fenchel, 1970; Brook, 1977; Robertson & Mann, 1980).

The amphipods studied here, Gammarus insensibilis Stock, Dexamine spinosa Montagu, Microdeutopus gryllotalpa A. Costa and Corophium insidiosum Crawford, are common species occurring in the sublittoral zone of European marine and brackish waters. They extend from the North Atlantic into the Mediterranean and the Black Sea. In addition, C. insidiosum is found in the Pacific, along the west coast of America and in Japan. Details of the distribution of amphipods in the Mediterranean are given by Ruffo (1982).

The biology of several species of Gammarus has been studied in the western Atlantic by, among others, Steele & Steele (1975) and in European waters by Kinne (1959), Stock (1967), Skadsheim (1984) and Leineweber (1985). There is, however, very little information on G. insensibilis in particular. Some aspects of the life cycle are given by Brun (1975) for the Mediterranean and by Grezé (1972) for the Black Sea. Grezé's paper provides information on D. spinosa also. The life cycle of M. gryllotalpa in the Kiel Bight is well described by Anger (1979a), while relatively more work has been done on C. insidiosum

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both in the field (Birklund, 1977; Sheader, 1978; Anger, 1979a) and in the laboratory (Nair & Anger, 1979). For the Mediterranean, the work of Casabianca (1975) is the most significant contribution.

The present paper describes the life cycles of the four dominating amphipod species in Mazoma lagoon (Fig. 1) and provides some information on their reproduction and biology.

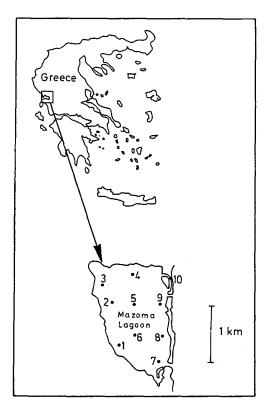


Fig. 1. Sampling area Mazoma lagoon in the Amvrakikos Gulf, Ionian Sea

MATERIAL AND METHODS

Sampling

Samples were taken at ten stations in the brackish-water lagoon Mazoma (3 km² surface area) of the Amvrakikos Gulf, Ionian Sea, at approximately bi-monthly intervals between June 1981 and June 1982. A thin strip of land separates Mazoma from the bay with which it is connected by two narrow openings (approximately 30 m wide). The depth ranges from 1.0 m to 1.4 m except for a "trench" dug in the NE which is 2 m deep.

During the study period, the temperature in the lagoon ranged from 8°C in January to 27°C in June. The salinity ranged from 14 ‰ in January to 37 ‰ in July and September. Dissolved oxygen concentration was lowest (2.11 ml/l) in July and highest

(7.65 ml/l) in January. There were no considerable differences between the stations in the values of the above parameters.

At the period of sampling the bottom was muddy, covered in places by eel-grass Zostera noltii and green alga Chaetomorpha sp. The lagoon is used for the culture of Sparus auratus, various species of Mugil as well as for Anguilla anguilla.

A ponar grab (0.025 m^2) was used from a boat, and four replicates were obtained. The samples were passed through a 0.5 mm mesh sieve, preserved in 4 % Formalin and stained with Rose Bengal.

Laboratory methods

The stretched length of the amphipods was measured under a binocular microscope fitted with a graticule. In order to determine their weight, the animals were rinsed well in distilled water and dried in an oven at 60 °C for 24 h by which time their weight remained constant. The eggs were dissected out from the brood pouch and their longer diameter was measured.

Statistical analyses such as frequency distributions and correlations were carried out using computing programmes from the Statistical Package for Social Sciences (Nie et al., 1975).

RESULTS

Population structure

Changes in the population structure of the four amphipod species studied are shown in a series of histograms (cf. Figures 2 to 5).

The size frequency histograms for Gammarus insensibilis in Figure 2 show that at the beginning of summer the population consists of approximately equal numbers of small-sized males, females and juveniles from the last brood. From July and during autumn, the individuals of this generation grow in size. An increase in population density occurs in November which does not correspond to recruitment by young individuals as seen by their size-frequency distribution. In January, most of the last year's generation seem to die and is replaced by a large number of juveniles, breeding having taken place between November and January. By May a new generation of young males and females has grown up and in early summer the population consists again mainly of small-sized adults. A number of juveniles can be seen throughout the year implying a continuous recruitment, with a maximum in January.

Figure 3 shows size frequency histograms for *Dexamine spinosa*. It can be seen that in early summer the population comprises small adult animals and juveniles. The population remains relatively constant throughout the autumn and winter with a small increase in individual size. In May the older animals die while more juveniles enter the population to replace them. Recruitment is continuous also in this species. It is noticeable that in each month the number of juveniles is too small to account for the adults of the next month. This may be a sampling deficiency, as mentioned by Anger (1979a) for other small-sized amphipod species. A preponderance of females throughout the year is evident.

In *Microdeutopus gryllotalpa* (Fig. 4), the older generation still exists in June at the beginning of sampling, but it disappears in the next month where there is a remarkable

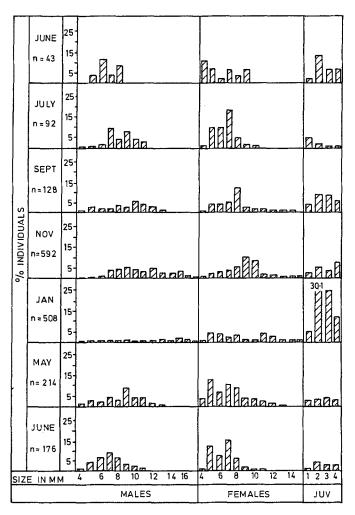


Fig. 2. Size distribution of Gammarus insensibilis

dominance of young females. After a major decrease in density, the population remains low until the end of the sampling period.

From early summer until September a considerable number of mature *Corophium insidiosum* individuals was observed (Fig. 5), with females dominating. The numbers later decline and the species does not appear in the samples after November.

The temporal variation of the sex ratio (number of females/number of males) for the four species is given in Table 1. The females exceeded the males in number in the four species studied. The only exception was C. insidiosum in November, but the numbers sampled were very low (10 ? ?: 17 δ δ). In G. insensibilis the sex ratio ranged from 1.2 in November to 1.7 in May. The range was higher in D. spinosa with a minimum of 2.84 in June 1982 and a maximum of 16.80 in November. A high number of females was also observed in September. The sex ratio in M. gryllotalpa ranged between 1.03 in Novem

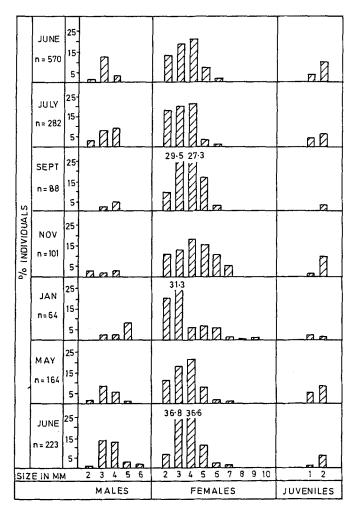


Fig. 3. Size distribution of Dexamine spinosa

ber and 5.75 in January and in C. insidiosum between 0.59 in November and 4.24 in June 1981.

Reproduction

Only size differences were observed between the eggs of the four species. The smaller eggs belonged to the smaller species M. gryllotalpa and C. insidiosum. However, within each species there was neither a significant correlation between the size of the eggs and the size of the females nor any significant correlation between the size and the number of eggs. The number of eggs ranged between 30–60 for G. insensibilis, 25–50 for D. spinosa and 1–8 for M. gryllotalpa and C. insidiosum. Seasonal changes in the mean number of eggs and the percentage of ovigerous females over the total number of females present have been observed. The highest percentage of ovigerous females, suggesting

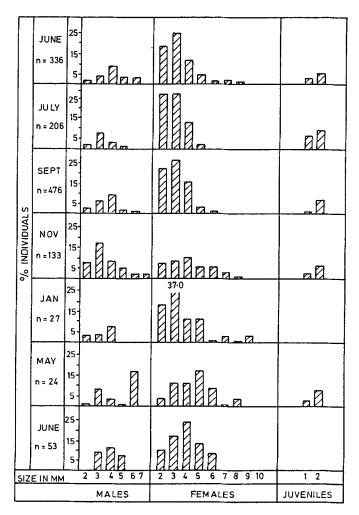


Fig. 4. Size distribution of Microdeutopus gryllotalpa

increased reproductive activity, occurs for *G. insensibilis* in November and for *D. spinosa* in the summer months. In the other two species, the highest percentage of egg-carrying females is found in September.

Length/weight ratios

The correlations between stretched body length and dry weight (transformed into logarithmic data) are shown in Figures 6 to 8. They were significant at the P=0.0001 level for G. insensibilis and D. spinosa and at P=0.001 level for M. gryllotalpa.

Table 1. Temporal variation of sex ratio (number of females/number of males) in the four amphipods
studied. n: number of individuals examined

Species	Sampling date						
	6/81	7/81	9/81	11/81	1/82	5/81	7/82
Gammarus insensibilis	1.31	1.48	1.50	1.20	1.60	1.70	1.51
n	30	82	85	491	130	186	163
Dexamine spinosa	3.18	2.90	11.14	16.80	5.56	4.35	2.84
n	477	269	85	89	59	139	211
Microdeutopus gryllotalpa	2.35	5.03	3.24	1.03	5.75	2.00	2.33
n	305	175	411	120	27	21	53
Corophium insidiosum	4.24	2.11	2.13	0.59			
n	236	112	247	27			

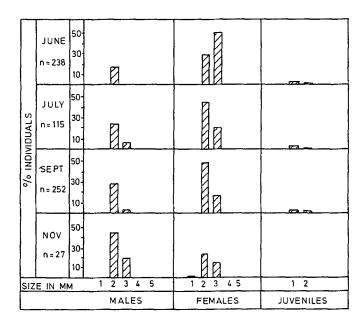


Fig. 5. Size distribution of Corophium insidiosum

DISCUSSION

Gammarus insensibilis in the Mazoma lagoon seems to have an annual life cycle, although limited recruitment takes place throughout the year. The main reproductive period is in December–January, after which the adults die. The new generation appears in spring, grows during the warmer summer months and reaches its highest reproductive activity in late autumn, as revealed by the percentage of ovigerous females found in the samples taken. This means that the juveniles grow to maturity within four to five months. Because of its winter reproduction, G. insensibilis, should be characterized as a psychrophilous species. Other species of Gammarus, G. oceanicus and G. salinus, are known to

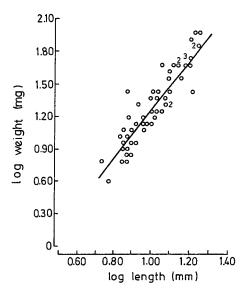


Fig. 6. Correlation between dry weight and stretched body length of Gammarus insensibilis (log $W = -1.07108 + 2.39542 \log L$)

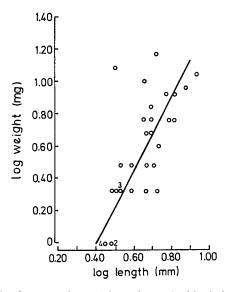


Fig. 7. Correlation between dry weight and stretched body length of Dexamine spinosa (log W = -0.83533 + 2.13822 log L)

have their major reproductive activity in late winter and spring (Skadsheim, 1984), while continuous reproduction occurs in *G. insensibilis* from the Black Sea (Grezé, 1972) and the Mediterranean (Brun, 1975). Kolding & Fenchel (1981), examining the patterns of reproduction in different populations of five *Gammarus*, species concluded that the

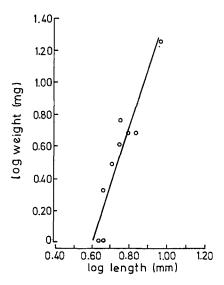


Fig. 8. Correlation between dry weight and streched body length of *Microdeutopus gryllotalpa* (log W = -2.30402 + 3.83690 log L)

geographical variation in breeding periods within each species, may be due, apart from temperature, to interspecific relationships. The timing of reproduction of *Gammarus* in Mazoma may be a result of resource partitioning between this species and *Dexamine spinosa*. Of special interest is a sudden increase in the adult population in November, the period of highest reproductive activity. Migrations of adults between different habitat types related to the breeding periods are mentioned for three species of *Gammarus* (Kolding, 1981). It is possible that some migration may take place from the area outside the lagoon but this should be investigated by simultaneous studies of the species inside and outside the lagoon.

D. spinosa displays continuous reproduction in the lagoon, reaching its peak in the summer months, as can be concluded by the population increase in number and the highest percentage of ovigerous females in the samples of June 1981 and June 1982. Dexamine should be considered a thermophilous species. Continuous reproduction for D. spinosa was also observed in the Black Sea by Grezé (1972).

In the Mazoma lagoon, *Microdeutopus gryllotalpa* displays continuous reproduction in the summer months with a peak in June and an even higher one in September, when a maximum percentage of egg-carrying females is observed. After that, the number of ovigerous females remains low and the population declines in number. There might be several broods per female as already described for this species (Bousfield, 1973).

Continuous recruitment in the summer months is also true for *Corophium insidiosum*, but its population declines more drastically in November and disappears completely thereafter. A "resting stage" in *C. insidiosum* between November and December has been observed by Sheader (1978) on the east coast of England. Some migration in and out of the lagoon may be possible for this species too, as migration into deeper water and overwintering has also been mentioned for *C. insidiosum* by Bousfield (1973).

The fact that the populations of all four amphipod species are composed predominantly of young stages throughout the year may be attributed to considerable predation (Grassle & Sanders, 1973). According to Richards (1963) and Nelson (1979a), predation by fish and large invertebrates is the main factor controlling the amphipod population structure in eelgrass communities. In Mazoma, predation by fish is more intensive in summer months since stocking of the lagoon with fry takes place in spring, and harvesting between October and December. In G. insensibilis the highest densities of individuals are found in the late autumn and winter months when fish predators are supposed to be at their minimum. This however is not true for D. spinosa and the other two species. It has been observed (Nelson, 1979b) that removal of predatory fish from an eelgrass community resulted in an increase of predatory decapods; thus the amphipod abundances were still kept down. In Mazoma, there were high abundances of the decapod Carcinus mediterraneus, which also may have contributed to the predation on amphipods. However, an estimation of the abundance of the Carcinus population was not possible using the sampling method described here. Prey-predator relations need further study in the lagoon. However, if predation is continuous, then the abundance of the amphipods considered appears to be governed by the reproductive patterns of the different species.

Changes in the abundance of populations inhabiting eel-grass ecosystems may also be associated with the die-back of eel-grass (Nelson, 1979a). In the present case, *Zostera* was mixed with *Chaetomorpha* at many stations; thus, the changes in vegetation were not significant. Some changes did occur at individual stations, but as the populations were studied over the whole lagoon, such differences should be alleviated.

In all four species studied, the sex ratio varied considerably over the year, exhibiting a preponderance of the females. Gammarus showed the lowest variation and the ratio was closest to unity (1.2) in November, coinciding with the maximum reproductive activity of the species. Grezé (1972) also observed a dominance of the females but the number of males and females was almost equal in the period previous to breeding in Black Sea amphipods including G. insensibilis and D. spinosa. Conversely, Brun (1975) occasionally found more males than females in some Mediterranean lagoons. High variability has been observed in the ranges of sex ratio. For example, the range of sex ratio (number of females/number of males) for C. insidiosum on the northeast coast of England (Sheader, 1978) was 1.10 to 10.00, in Kiel Bight (Anger, 1979b) 1.49 to 25.00 and off Helgoland (Nair & Anger, 1979) 3.03 to 4.00. In Mazoma, the values ranged from 0.59 to 4.24. Difference in longevity between sexes may offer some explanation. Nair & Anger (1979), who observed a dominance of females in C. insidiosum, also found that the females generally had a longer life span than the males. Finally, some differences observed may be an artifact caused by different habits of the sexes and various sampling methods. For example, Brun (1975) mentions that the males of G. insensibilis often tend to accumulate on the surface of vegetation debris under conditions of low oxygenation while the females remain in the centre of the debris mass. Our measurements do not offer conclusive evidence in support of any of the possible explanations. There is some evidence that sex ratio variability is widespread in amphipods, among which Gammarus species have been studied in more detail (Bulnheim, 1972, 1978).

It was noticed that the larger species, G. insensibilis and D. spinosa which have a single brood per female per year had a much higher number of eggs than the smaller

species *M. gryllotalpa* and *C. insidiosum* known to have multiple broods per female per year. This fact was also noted for other species of amphipods (Nelson, 1980).

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