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On the ecology of *Heterocypris salinus*, *H. incongruens* and *Cypridopsis aculeata* (Crustacea: Ostracoda) from Baltic brackish-water rockpools

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Abstract

The ostracod fauna of Baltic brackish-water rockpools is made up of two groups: permanent members of the pools, and occasional guests from the littoral zone. The former group consists of *Heterocypris salinus*, *H. incongruens* and *Cypridopsis aculeata*. These species are characterized by rapid development (which starts when the water temperature approaches 15 °C), a short life span, and 2 or 3 separate generations during the summer and autumn. The number of generations is determined by water temperature. Hibernation always takes place as eggs. Hatching and development during the late spring or early summer has been found to be mostly simultaneous. The spawning of the 3 species always starts epidemically. Reproduction is entirely parthenogenetic in the investigated area. Under natural conditions, *C. aculeata* may be found with either *H. salinus* or *H. incongruens*, but these two latter species have never been recorded together. *H. incongruens* is less tolerant to high salinities than the other 2 species and, even after successive adaptation, it does not resist salinities higher than 16 ‰. *H. salinus* has been found in 35.2 ‰ S in the field, and has been kept in 30 ‰ S in the laboratory after successive adaptation. The optimum salinity-temperature range for this species is 5 to 10 ‰ S and 15 °C, when both survival and development are considered. Corresponding figures for *C. aculeata* are 0.5 to 20 ‰ S and 15 °C, although this species, like *H. salinus*, survives longest at 5 °C. The very rapid development, parthenogenetic reproduction and short life span of these species must be considered as favourable adaptations to the variable and unstable environment of the rockpool ecosystems.

Introduction

Rockpool ecosystems are affected by drastic fluctuations of many abiotic parameters such as temperature, oxygen content and pH (GANNING, 1967, 1970). Organic and inorganic chemical agencies are often in large excess, which supports high community metabolism (GANNING and WULFF, 1969, 1970). Few animals and algal species tolerate these unusual environmental and biological conditions in aquatic ecosystems. Only 3 ostracod species are regularly found in the Baltic brackish-water rockpools around the Askö Laboratory, Sweden. These species are easily studied in the pools, where environmental variations may be recorded and the populations dynamics correlated to food supply and predation. Rockpool microcosms are readily simulated in the laboratory, where special dynamic features may be followed closely and in detail.

The population dynamics and ecology of Scandinavian ostracods are poorly known, except for the works of ELOFSON (1941), THEISEN (1966), and HAGERMAN (1969a), who studied benthic, brackish-water, and marine species. The only paper concerning rockpool ostracods is that by PURASJOKI (1948) who, however, only deals with the occurrence and distribution problems of a South African species occasionally found in Finland.

The present investigation is part of a more comprehensive study of the ecosystems of brackish-water rockpools where ecologically important species are presented separately.

Materials and methods

The animals studied are mainly from pools on the island of Vrångskär near the Askö Laboratory. The ostracod populations of 3 pools have been closely followed. Pool 39 has been described earlier (GANNING, 1966); its mean volume is about 1.200 l, salinity varys between 4 and 8‰. The annual fluctuations of the total flora and fauna will be described in a forthcoming paper. This pool has been populated by the ostracod *Heterocypris salinus* (BRADY) every year since the investigation started in 1962. Pool 61 (Fig. 1) has a mean volume of about 900 l, salinity fluctuates between 2 and 8‰. The flora of this pool is dominated by abundant *Enteromorpha intestinalis* L. Other animals occurring in the pool are *Gammarus duebeni* LILLJ., *Nitocra spinipes* BOECK, the water beetles *Helophorus* sp. and *Illybius* sp., and the water bug *Callicorixa producta* REUT. In this pool, *Cypridopsis aculeata* (LILLJ.) has been found every year since 1964. Pool 62 is a very typical biotope for *Heterocypris incongruens* (RAMDOHR). The water is mainly dark brown, which suggests high concentrations of humus, salinity is between 0.5 and 3‰, and the volume may reach about 300 l; however, the pool often dries up completely. *Daphnia magna* STRAUSS,

Fig. 1. Pool 61 in June 1966. This pool is a typical pool for *Cypridopsis aculeata;* note floating *Enteromorpha intestinalis* at the distant end of the pool

Cyclops sp. and chironomid-larvae are the only other inhabitants of the pool. *H. incongruens* has been recorded here in 1968, 1969 and 1970.

The ostracods were collected by methods which provide relative estimates of population densities (SOUTHWOOD, 1966). A net with a mesh size of 160 μ was used, which meant that the first and second larval stages were usually lost. These stages are excluded in the figures showing population variations and age structure.

Salinity determinations were carried out with a Wheatstone bridge, earphone, buzzer and immersion cell (JANSSON, 1962). The accuracy is $\pm 0.5\%$ of recorded resistance value, or $\pm 0.05‰$ S at 7‰ sea-water salinity.

Oxygen consumption was measured polarographically; the oxygen values were recorded in mm Hg. These values were transformed to mg $O_2 \cdot l^{-1}$ by means of a calibration curve; the accuracy of the method is 0.5% of the recorded value. Respiration experiments were carried out at 15 °C.

Test solutions of different salinities were obtained by mixing sea water of 33‰ S and deionized water. Salinities higher than 33‰ were produced by slow dehydration at 60 °C. The laboratory experiments were carried out in darkness. No food was supplied during the tolerance tests.

Results

The ostracod fauna of Baltic brackish-water rockpools may be divided into 2 categories: occasional guests from the littoral zone, and typical, permanent members of the rockpool ecosystems. Of the former group, 7 species have been recorded, especially during spring and autumn, but only for short periods when they have been brought in by waves from the littoral zone during rough weather. The species are:

Leptocythere lacertosa (HIRSCHMANN)
Leptocythere pellucida (BAIRD)
Cytherura gibba (O. F. MÜLLER)
Semicytherura nigrescens (BAIRD)
Elofsonia baltica (HIRSCHMANN)
Hirschmannia viridis (O. F. MÜLLER)
Xestolebris aurantia (BAIRD)

Of these species, *Cytherura gibba* and *Elofsonia baltica* are considered to be true brackish-water species, all the remainder are marine species extending into the Baltic Sea (HAGERMAN, 1967). The group of permanent inhabitants consists of *Heterocypris salinus*, *H. incongruens* and *Cypridopsis aculeata*. The 2 *Heterocypris* species never occur together, but either of them is often found together with *C. aculeata*. The permanent members of the fauna have been considered as belonging to a special group of fresh-water species extending into water of low salinity (HAGERMAN, 1967). They are here presented separately.

Heterocypris salinus

Distribution

Heterocypris salinus is distributed all over Europe, the Azores, North Africa and Western Asia (KLIE, 1938). In Sweden, ALM (1916) has found it in Scania, Bohuslän, Östergötland and on Gothland. Different origins of *H. salinus* are given by these two authors.

ALM suggests that it is a true brackish-water species which only occurs in pools along the coast, KLIE considers *H. salinus* to be a characteristic species of small coastal-water bodies with salt or brackish-water as well as of inland saline waters. FORSMAN (1951) has recorded the ostracod in ephemeral rain-water pools on the Swedish west coast. My own recordings are from rockpools at Halsholmsgrunden and Ören near the Tvärminne Zoological Station (Gulf of Finland) and from many pools on the island of Vrångskär close to the Askö Laboratory (northern Baltic Sea proper). *H. salinus* is also found in great abundance in an eutrophic shallow bay just beside the laboratory building.

Population dynamics

In the investigated area, *Heterocypris salinus* has been found to be strictly parthenogenetic. It passes 8 larval stages before it becomes an adult. The sizes of the different stages of a population in July are shown in Table 1. At this time the mean water temperature was 20 °C.

Table 1. *Heterocypris salinus and Cypridopsis aculeata. Sizes and percentage increase in length of developmental stages*

Developmental stage	*Heterocypris salinus* Size (mm)	Length increase (%)	*Cypridopsis aculeata* Size (mm)	Length increase (%)
Egg	0.160—0.120	—	0.11	—
1	0.176—0.178	11.1	0.13	11.8
2	0.208—0.212	11.9	0.16	12.3
3	0.247—0.253	11.9	0.20	12.5
4	0.315—0.325	12.8	0.24	12.0
5	0.395—0.407	12.5	0.29	12.1
6	0.508—0.522	12.9	0.35	12.1
7	0.680—0.722	13.6	0.44	12.9
8	0.923—0.971	13.6	0.58	12.9
Adult	1.120—1.245	12.4	0.73	12.6

Like some other littoral brackish-water ostracods of the investigated area, e.g. *Elofsonia baltica, Heterocypris salinus* produces more than 1 generation/year. According to the water temperature, 2 or 3 generations are produced from May to November. Hibernation occurs only in the form of eggs, which are deposited in the deep parts of the pools.

In pool 39, which was studied most thoroughly, the population dynamics were found to differ during the years 1964, 1965 and 1968 (Figs. 2, 3 and 4). During 1964 and 1968, 3 generations were identified, the third one occurring in September (Figs. 2 and 4). The first generation in 1964 started to hatch very successfully in the middle of May. One or two larval stages dominated the population. This simultaneous development coincided with warm and stable weather conditions; water temperature determines whether hatching begins or not. The life cycle comprised about 45 days from hatching until the new eggs were deposited. Great numbers of eggs were found around the 1st of July, but the second generation never developed as simultaneously as the first. At the end of July occurred a sudden decrease in the population after hatching, and it never recovered that year. A third

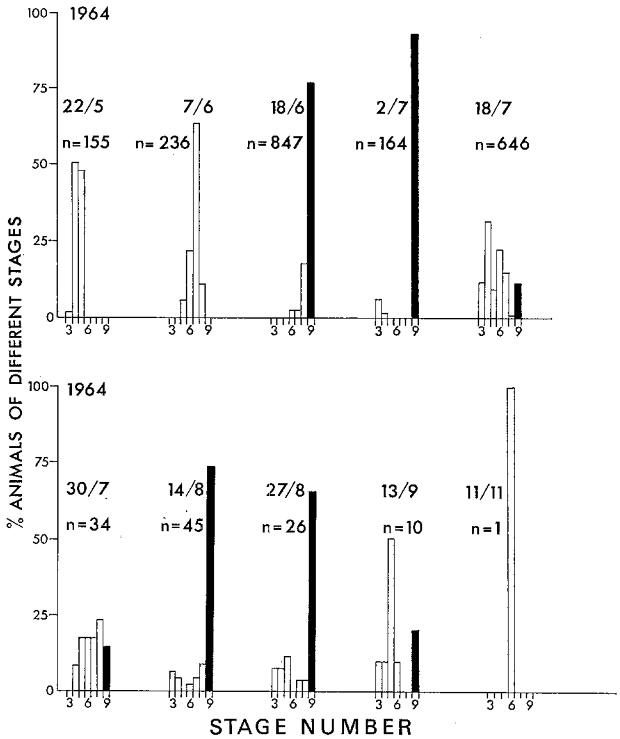

Fig. 2. *Heterocypris salinus.* Abundance of different stages in pool 39 during 1964, n: number of individuals

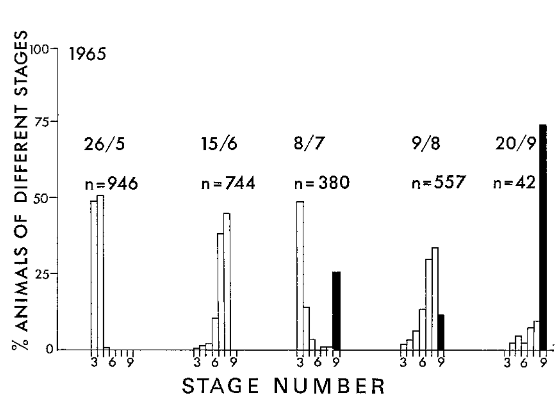

Fig. 3. *Heterocypris salinus.* Abundance of different stages in pool 39 during 1965, n: number of individuals

generation, of low abundance, developed at the end of August. Only 1 animal of larval stage 6 was found in the middle of November of that year. In the following year, 1965, with a fairly cold spring and summer, only 2 generations could be identified, the first from the end of May to the middle of July, immediately succeeded by the second at the end of August (Fig. 3).

Similar temperature conditions prevailed in 1964 and 1968, but population abundances were lower in 1968. The first generation in 1968 showed simultaneous development, the later generations were more mixed.

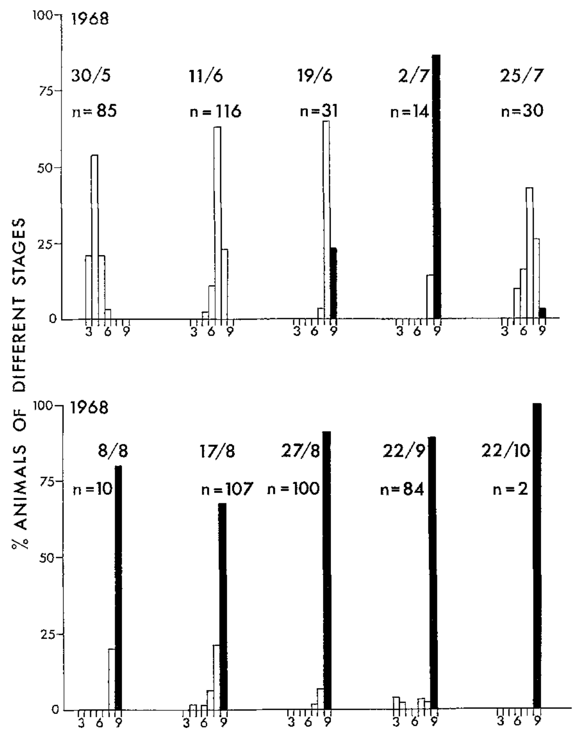

Fig. 4. *Heterocypris salinus*. Abundance of different stages in pool 39 during 1968, n: number of individuals

During the unusually warm May and June of 1968, *Heterocypris salinus* required only about 35 days to complete its life cycle. In laboratory cultures, at constant temperatures, complete development has been found to take 30 days at 25 °C and 40 days at 15 °C. The eggs hatched after 6 days at 25 °C and after 9 days at 15 °C. Deposited eggs never hatched at 5 °C, even after 3 weeks incubation.

Reproductive behaviour

The bright, red to orange coloured, oval eggs of *Heterocypris salinus* are generally attached to some substratum such as a rough rocky bottom or *Enteromorpha* thalli. When the eggs are deposited upon algae, the thallus must have a fold or a hole to which the animals can cling. Breeding seems to occur simultaneously or epidemically. As soon as one female starts to breed, the other animals become restless until they too begin breeding. The second antenna is used for testing the substratum before the eggs are cemented on the substratum. The female often clings to its own or to foreign eggs, and eggs are arranged in several layers. Thirty to 40 eggs are commonly deposited by each female. The animals of the third generation deposit their eggs more randomly than the 2 earlier generations. The eggs of the last generation each year are, therefore, found in the bottom sediments where they are protected against ice during the winter.

Diel activity and feeding

Heterocypris salinus feeds during the daytime. During the night most individuals are found inactive near the water surface. A negative phototactic reaction to light values as low as 900 lux has been observed (GANNING, 1967), and this dim light initiates activities such as swimming and creeping towards deeper parts of the pool. No resting period has been recorded during the daytime. Laboratory studies conducted in petri dishes under a stereomicroscope show that the animals actively search in the bottom substratum for green algae, e.g. the desmids *Scenedesmus* sp. and *Pediastrum* sp. as well as *Chlorella*-like algae. Analyses show that these algae constitute 50 to 90% of the stomach contents of *H. salinus* in June, July and August.

Salinity-temperature tolerance

The ecological effects of temperature and salinity are closely related (cf. KINNE, 1964, 1970). Therefore, salinity tolerances have been studied at different temperatures (Fig. 5). At all salinities, except 5‰ S, *Heterocypris salinus* died most rapidly at 25 °C and lived longest at 5 °C. The salinity concentrations 0.5 to 15‰ had comparable LD_{50} values for respective temperatures. The absolute optimum was found at 10‰ S – 5 °C, with LD_{50}, after 22 days. However, it should be remembered that development is retarded at this low temperature. Optimum combinations occurred at 15 °C and 5 to 10‰ S, according to both survival and development with LD_{50} values after 15 days, and hatching after 9 days. When transferred to salinities of 15‰ or higher, no hatching took place. When salinity increased above 15‰, survival time also decreased rapidly. At 30‰ S and 15 °C, LD_{50} is already reached after 4 days. A few experiments have been carried out at 30 °C, but no animals survived longer than 3 days in any salinity. In the field, *H. salinus* has been found in pools at 32 °C and 8‰ S, but the high temperature figures only persist for a few

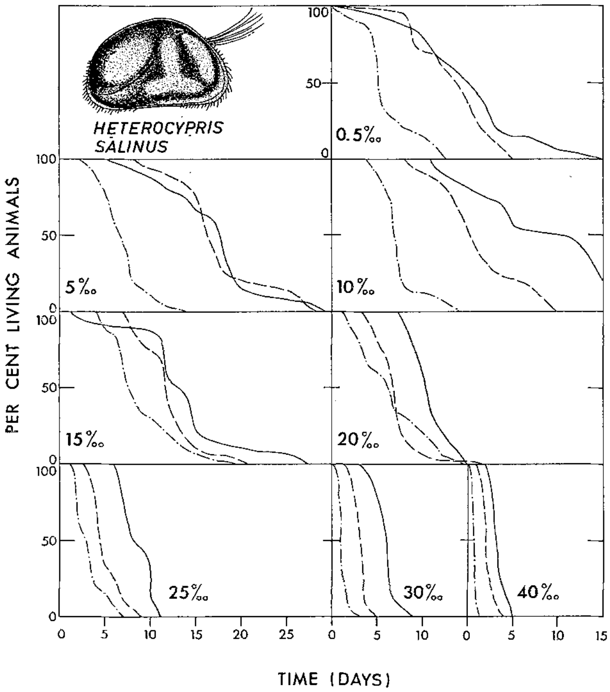

Fig. 5. *Heterocypris salinus*. Tolerance to different salinity-temperature combinations, 6 July to 5 August, 1966. ——— 5 °C, ----- 15 °C, —·—·—·— 25 °C, n = 30

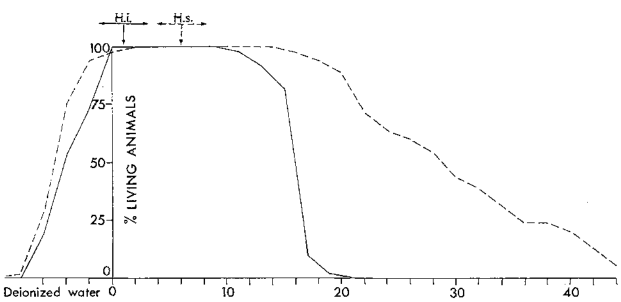

Fig. 6. Successive adaptation of *Heterocypris salinus* and *H. incongruens* to increasing and decreasing salinity (2‰ S every 24 h). To the left of the ordinate, de-ionized water was changed once a day. The original salinities for the two species are indicated on the top of the curves ——— *Heterocypris salinus* n = 50, ——— *Heterocypris incongruens*, n = 50

Table 2. *Heterocypris salinus. Respiratory rate at different salinities*

Salinity (‰)	1	10	20
Mean oxygen consumption (mg · 24 h^{-1} · individual^{-1})	2.68	2.91	3.90
Standard deviation	0.77	1.09	1.17
Number of individuals	25	20	24

hours. The tolerance tests are well in accordance with the preference experiments carried out earlier (GANNING, 1967). In these experiments, 6‰ S (common biotope salinity) was preferred to higher or lower salinities at 20 °C.

All the described tolerance experiments were carried out without pre-adaptation to the different salinities. In order to investigate the effects of slow increase or decrease of salinity, an experiment with successive changes of 2‰ S per day was maintained (Fig. 6). During this test, some individuals were still alive in 44‰ S after 19 days. Fifty percent of the animals survived to 30‰ S 12 days after the start of the experiment. Decrease of salinity from biotope water of 6‰ S showed that even 2‰ S was lethal to some animals. De-ionized water rapidly killed all the animals in 4 days. In field studies, *Heterocypris salinus* has been recorded alive in 35.2‰ S in a small pool, with rapid salinity increase due to evaporation.

Oxygen consumption is considered to be a useful index of adaptation to, or stress caused by, unsuitable conditions (HAGERMAN, 1969b). *Heterocypris salinus* was tested in 1, 10 and 20‰ S at 15 °C. As can be seen from Table 2, there was a slight increase in oxygen consumption with increasing salinity. The difference between 1 and 10‰ S is not statistically significant, between 10 and 20‰ S it is significant at the 5% level.

Heterocypris incongruens

Heterocypris incongruens has been well known ecologically for a long time (WOHLGEMUTH, 1914). Only a few remarks will, therefore, be included for comparison with features of the related *H. salinus*.

Heterocypris incongruens is a cosmopolitan species found in all types of fresh water. It is known from many places in Sweden (ALM, 1916). This species prefers brown-water pools without macroscopic vegetation (see description of pool 62, p. 271). I have recorded *H. incongruens* in several pools at Halsholmsgrunden in the Gulf of Finland, and in pool 62 on Vrångskär in the neighbourhood of the Askö Laboratory. This species also begins a simultaneous development but, in pools which do not dry out, this parallelism soon disappears. Egg laying behaviour is very much the same as that described for *H. salinus*. However, a greater number of eggs are released separately in the bottom substratum. This may result from difficulties in finding a hard, rough surface in these pools. Suitable conditions are always preferred when offered.

Heterocypris incongruens is at least facultatively carnivorous (LIPEROWSKAJA, 1948; BARTHELMES, 1965). In the pools investigated, the ostracod often attacks *Daphnia magna* and *Cyclops* sp. Many ostracods may be found clinging to the same living specimen of *D. magna*; when the latter is dead, still more *H. incongruens* cover the body. However, microscopic algae have also been found in the stomachs of this species.

Salinity tolerance is low in *Heterocypris incongruens*. Only 1 to 5‰ S is tolerated by 50% of the animals for 20 days or more (Fig. 7). At 10‰, LD_{50} values are already reached within 3 days. Compared with salinities of 15‰ or higher, even deionized water offers better conditions and longer survival times. However, during successive adaptation to higher salinities, most ostracods survived up to 16‰ S, at which salinity they all suddenly died. Deionized water is somewhat better tolerated by *H. incongruens* than by *H. salinus* (Fig. 6).

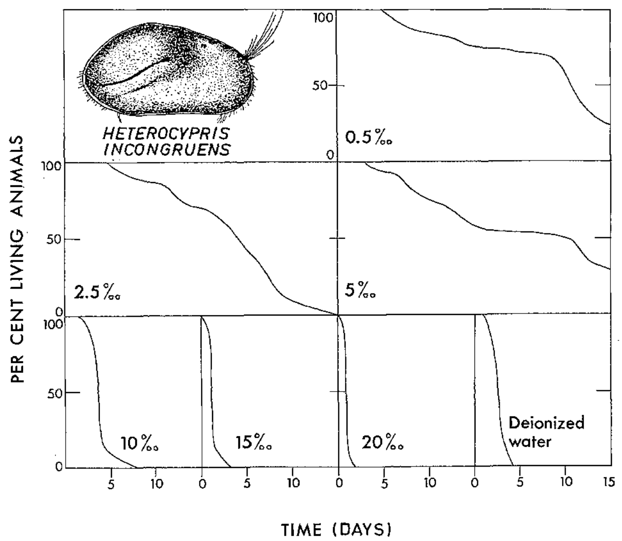

Fig. 7. *Heterocypris incongruens*. Tolerance to different salinities, 9 August to 8 November, 1963. n: 25

FOX and TAYLOR (1955) demonstrated that *Heterocypris incongruens* prefers water with low oxygen concentration to aerated water. In oxygen-consuming, closed systems, 50% of 50 experimental specimens died at 0.4 mg $O_2 \cdot l^{-1}$ (4.4% saturation), when salinity was optimum or 0.5‰, and temperature was 20 °C. These figures should be compared with those found for *H. salinus* where saturations between 18 to 31% are lethal after a comparable time (GANNING, 1967).

Cypridopsis aculeata

Distribution

Like *Heterocypris incongruens*, *Cypridopsis aculeata* is cosmopolitan. It mainly occurs in brackish water, but has occasionally been found in pure fresh water (KLIE, 1938). In Sweden, *Cypridopsis aculeata* is found in Scania, Bohuslän and Östergötland (ALM, 1916). I have recorded this species in many pools at Vrångskär, but also at Halsholmsgrunden and Ören in the Gulf of Finland. According to KLIE (1938) *C. aculeata* avoids waters with dense vegetation, but this observation does not agree with my own. I have found it mainly in pools with abundant *Enteromorpha intestinalis*, but also in waters coloured green by flagellates.

Population dynamics

Like the former two species, *Cypridopsis aculeata* is entirely parthenogenetic in the investigated area. The different stages are separated in size without

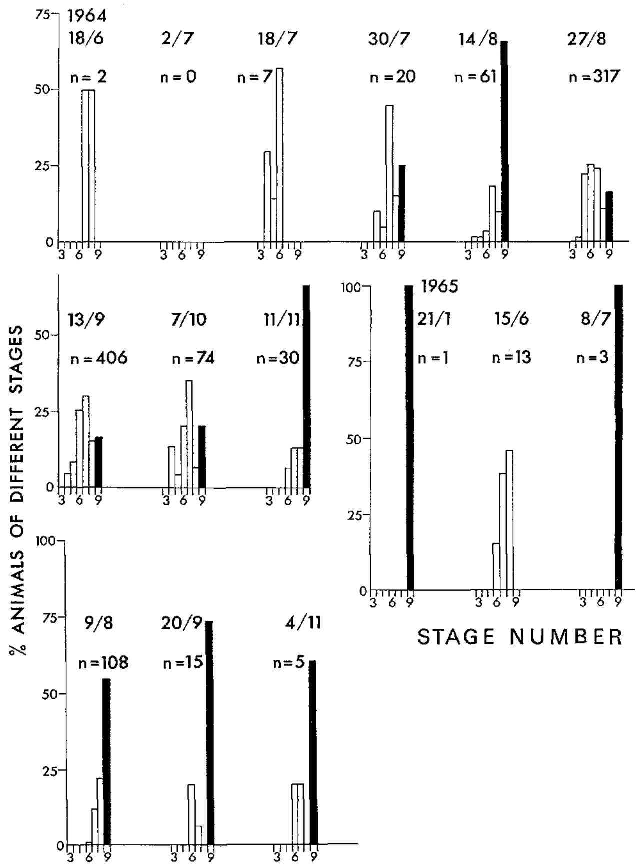

Fig. 8. *Cypridopsis aculeata*. Abundance of different stages in pool 61 during 1964 and 1965, n: number of individuals

overlapping (Table 1). There are 8 larval stages. During the 2 years of more continuous study, 1964 to 1965, development of *C. aculeata* began in mid-June (Fig. 8). Contrary to my findings for *Heterocypris salinus*, no hatched specimens were observed during May or at the beginning of June, although several samplings were made. The first generation in 1964 was low in abundance, and not until mid-August did the population increase, when the second generation developed. It was not possible to detect a separate third generation that year. An autumn decrease occurred in November. In January, just before freezing of the water began, 1 adult specimen was found. In 1965 also, the population was fairly low in abundance but, that year, a third generation was identified. In the field, full development was found to take about 30 days in 1965 at a mean temperature of 15 °C. At 20 °C, under laboratory conditions, the entire cycle from egg to egg was completed in 17 days. The first 2 larval stages were passed in less than 48 h. Stage 1 lasted only about 12 h. Stage 8 lasted for 7 to 9 days before moulting to adult.

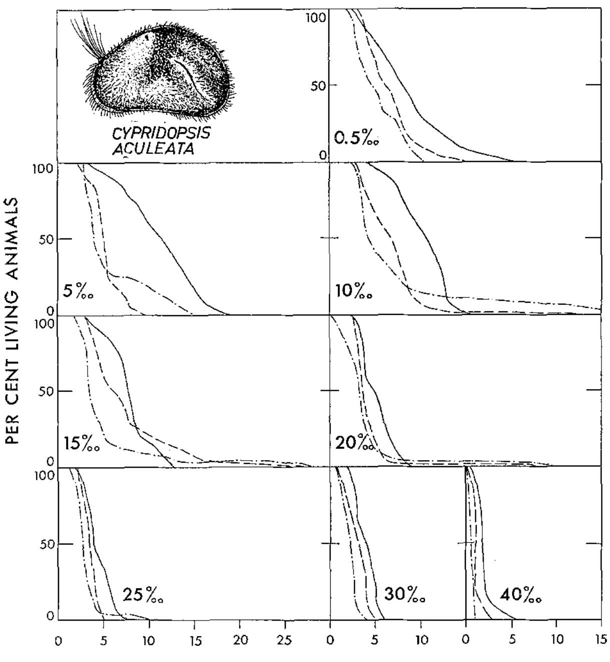

Fig. 9. *Cypridopsis aculeata*. Tolerance to different salinity-temperature combinations, 31 March to 30 April, 1966. ——— 5 °C, ----- 15 °C, —·—·—·— 25 °C. n: 30

Reproductive behaviour

The bright orange eggs are attached to a substratum such as rough rock or folded *Enteromorpha* thalli, but empty shells of dead ostracods may often be found filled with eggs. One female of 15 studied produced 36 eggs, but the normal figure is 20 to 30. Under laboratory conditions, at 20 °C and normal daylight, 80% of the eggs hatched. The epidemic breeding observed in *Heterocypris salinus* was also recognized for this species, but development was not as simultaneous for *Cypridopsis aculeata* as for *H. salinus*. The behaviour before and during egg-laying is very much the same for the two species.

Salinity-temperature tolerance

Cypridopsis aculeata survived longest at 5 °C and at 0.5 to 15‰ S. Optimum survival occurred in 5 and 10‰ S, where LD_{50} was 11 days (Fig. 9). Survival times at 15° and 25 °C were almost the same for equal salinities. The differences in tolerance at these temperatures were small, within the salinity range 0.5 to 20‰. Even at 30‰ S, 50% of the animals were alive after 3 to 4 days. Only in 40‰ S did the ostracods die almost immediately. In the field, this species has been found in salinities up to 17.2‰. This salinity was recorded in a pool of about 200 l.

Discussion and conclusions

Of the 3 permanent rockpool ostracods described, *Heterocypris salinus* and *H. incongruens* are to be considered as seasonal forms restricted to the "summer" in the sense of ALM (1916). They do not appear in the pools until the mean water temperature approaches about 10 °C, and they disappear in October to November when the temperature decreases below 5° to 10 °C. *Cypridopsis aculeata*, on the other hand, is more temperature-tolerant in the autumn, and may still be found when the pool water starts to freeze. However, also this species hibernates as egg, but it needs higher hatching temperatures than the other 2 species. *C. aculeata* may, therefore, be considered as a summer to winter seasonal form. In regard to the annual cycle, the rockpool ostracods resemble most fresh-water species, but also some littoral, brackish-water species such as *Cytherura gibba* and *Elofsonia baltica* behave in the same way. The latter species requires a cold period before its eggs can hatch (THEISEN, 1966), which is not true for the 3 species studied here. Eggs from these species are easily hatched all the year round, regardless of how long or at which temperature they have been maintained. In this respect they are similar to fresh-water ostracods as well as to many brackish-water ones.

Development of rockpool ostracods is highly dependent upon temperature. The eggs do not start hatching until water temperatures exceed certain minimum values, but it has not been possible to correlate egg formation within the females of the last generation each year with the temperature, and no retardation in egg formation has been found even at very low temperatures.

Hatching times are very short for the rockpool ostracods. ELOFSON (1941) has provided some of the very sparse notes on hatching times for littoral forms. He found for example that it takes 40 days for eggs of *Xestolebris aurantia* to hatch in the spring, and 30 to 35 days in the summer. The temperatures were not recorded, but were probably 14° to 20 °C in the summer. These values should be compared with 6 and 9 days for *Heterocypris salinus* at 25° and 15 °C, respectively. This is even faster than the values for *H. incongruens*, which needed 3 to 6 days at 28° to 30 °C and 7 to 9 days at 17° to 19 °C (WOHLGEMUTH, 1914).

Egg-deposition behaviour in rockpool ostracods very much resembles that of many fresh-water species in the deposition of distinct egg clusters. The egg-laying behaviour patterns common to marine ostracods (i.e. separately deposited eggs in the bottom substratum, KLIE, 1938) is only observed in the last generation of each year. Great similarities are found during the periods of hatching and development for the rockpool species studied and littoral forms such as *Cytherura gibba* and *Elofsonia baltica* (THEISEN, 1966). The fact that development is retarded as the animals grow older (ELOFSON, 1941) is well in accordance with my own findings. In the number of generations each year, the rockpool ostracods also resemble fresh- or brackish-water species more than marine ones. According to climatic conditions, 2 or 3 generations occur annually. As hibernation occurs at egg stage, and specific temperatures are needed for the commencement of hatching, *Heterocypris salinus* and *Cypridopsis aculeata* exhibit a more or less pronounced simultaneous development of all successive generations.

Very little has been written about the food and feeding of ostracods. Stomach analyses have been made, and it is known that suspension feeders, deposit feeders, herbivores and carnivores occur (ELOFSON, 1941). LIPEROWSKAJA (1948) found that *Cyprideis littoralis* consumes only diatoms; and *Heterocypris incongruens* is a facultative carnivore. I have found that the latter species often attacks *Daphnia magna* or *Cyclops* sp., which agrees with the observations of LIPEROWSKAJA. On the other hand, *H. salinus* and *Cypridopsis aculeata* are strictly confined to the small, green algae of the pools such as the desmids. The extent to which bacteria living in the bottom substratum or on the algae serve as food is not, however, known. Neither of these 2 species have ever been known to attack other rockpool inhabitants, nor have any pieces of other animals been found in the stomach contents of *H. salinus* or *C. aculeata*.

Temperature-salinity relations are extremely important to the distribution of most aquatic organisms. This is true also of the brackish-water rockpool ostracods studied. The important relationship of hatching and development has already been discussed. The tolerance of adult specimens is large. KORNICKER and WISE (1960) demonstrated that the marine ostracod *Hemicythere conradi* HOWE and MCGUIRT had wider tolerance limits in the laboratory than in nature, but that these limits were always much wider than for rockpool species, 6 to 65‰/6° to 36 °C and 8 to 51‰/2° to 35 °C, respectively. The limits for rockpool species are still wide compared with the limits of littoral species: 0.5 to 25‰/5° to 25 °C for *Heterocypris salinus* and 0.5 to 15‰/5° to 25 °C for *Cypridopsis aculeata*. It must be kept in mind that, within these well-tolerated values, ostracods die of old age more than of true physiological stress. Also, rockpool ostracods tolerate more extreme temperature-salinity combinations in the pools than in the laboratory, at least for short periods of time.

The 3 ostracods discussed have a high biological potential, as most other successful rockpool organisms. Their rapid development and short generation time are successful adaptations to life in ephemeral or semi-ephemeral ecosystems such as rockpools. Despite similarities with fresh-water relatives, these ostracods are considered to be well adapted, brackish-water organisms, surviving under severe conditions. GREEN (1959) for example, found that *Heterocypris incongruens* is well adapted to anaerobic conditions. This ostracod produces a yellow pigment, pteridine, which is useful for metabolic purposes when the animal lives under low oxygen tension. The other 2 rockpool ostracods, which are almost as resistant to anaerobic conditions as *H. incongruens*, possibly solve their oxygen tolerance problems in a similar way.

Summary

1. Rockpool ostracods can be divided into 2 groups: permanent pool members, and occasional guests from the littoral zone. In the Baltic Sea area, *Heterocypris salinus*, *H. incongruens* and *Cypridopsis aculeata* comprise the first group.

2. The rockpool ostracods have 2 or 3 generations during each summer-autumn period, determined by water temperature. Hatching and spawning are simultaneous, spawning is epidemically initiated.

3. Reproductive behaviour, diel activity and feeding of the rockpool ostracods have been studied.

4. The salinity — temperature optimum of *H. salinus* occurs at 5 to 10‰ S and 15 °C in the laboratory. In the field it occurs at 2 to 35‰ S and 5° to 32 °C.

5. The salinity — temperature optimum of *C. aculeata* occurs at 0.5 to 20‰ S and 15 °C in laboratory experiments, while it has been recorded at 0.5 to 17‰ S, and 5° to 28 °C in the field.

6. Despite high salinity tolerance, the permanent rockpool ostracods have more in common with fresh-water ostracods than with marine species, e.g. hibernation as eggs, more than 1 annual generation, rapid development, adaptations useful for survival in unstable rockpool ecosystems.

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