

Biotic and Abiotic Factors Determining the Distribution of Two Prawn Species: *Palaemon adspersus* and *P. squilla*

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Summary. The reasons behind the absence of the prawn *Palaemon adspersus* and the presence of *P. squilla* in rockpools and on bare sand bottoms were studied. Some maximal abundances in different habitats are given. Introduction experiments into natural and artificial rockpools and measurements of tolerance towards low oxygen levels showed that nocturnal hypoxia excluded *P. adspersus* which was significantly more sensitive to oxygen depletion. Respiration rates measured by the closed-bottle method showed no interspecific difference.

On bare sand bottoms *P. adspersus* was probably excluded by predators, since predator exclusion experiments in cages and predator inclusion experiments in containers showed that *P. adspersus* was more vulnerable to predation than *P. squilla*.

The costs for being able to cope with a wide array of habitat in *P. squilla* are probably balanced by the benefits of access to habitats such as intertidal rockpools, very shallow bottoms and deeper sand bottoms. Tolerance towards abiotic factors extends its habitat range upwards into shallower waters, and tolerance towards biotic factors, i.e. predation, extends it downwards.

Introduction

The position of a species on a habitat specialist – generalist gradient is often assumed to be decided by competitive forces: intense competition causing specialization or the relegation of inferior competitors to more stressing habitats. Accordingly a species' habitat range should expand if competition is weak. This "compression hypothesis", stating that specialization is the result of interspecific competition for the same resource, was first clearly enunciated by Svårdson (1949) and has later been elaborated, for example, by MacArthur and Levins (1967), Roughgarden (1972, 1974) and Schoener (1974).

However, this principle does not apply to the habitat distribution pattern of the two prawn species *Palaemon adspersus* Rathke and *P. squilla* (L.) (= *P. elegans* Rathke). Both species are most numerous in *Zostera marina* (L.) beds and eat the same types of food (Berglund 1980), but *P. squilla* also inhabits a wider range of habitats, e.g. rockpools (Pyefinch 1943; Rodriguez and Naylor 1972; Daniel and Boyden 1975; Goss-Custard et al. 1979; Berglund 1980) and bare sand bottoms (Berglund 1980). Thus in addition to the relatively favourable *Zostera* beds, it is also found in several other habitats. These habitats are of distinctly different character. In rockpools abiotic factors such as temperature, oxygen concentration, salinity and pH reach extreme values (Stephenson et al. 1934; Pyefinch 1943; Ganning 1971; Daniel

and Boyden 1975; Goss-Custard et al. 1979; Congleton 1980; Truchot and Duhamel-Jouve 1980). Some authors stress the significance of extremes in oxygen concentrations and temperatures (Ganning 1971; Daniel and Boyden 1975). Furthermore, colonization of rockpools may be difficult. Abiotic factors on very shallow bottoms may also be very stressing; oxygen concentration and temperature values may be extreme (Broekhuysen 1935; Huddart and Arthur 1971; Nixon and Oviatt 1973; Welsh 1975).

On somewhat deeper bare sand bottoms, however, these *Palaemon* prawns never experience difficulties with abiotic factors: ambient levels of temperature and salinity are well within their tolerance limits (Berglund 1980), and hypoxia never occurs. However, predation pressure may be important since there is no vegetation in which to hide and these prawns do not burrow, in contrast, for example, to *Crangon vulgaris* (Fabricius).

The aim of this study was to answer the following two questions:

1. Why is *P. adspersus*, but not *P. squilla* restricted to eelgrass meadows?
2. What are the gains and losses associated with the different distribution patterns of these species?

To answer the first question, survival in natural and artificial rockpools was studied, tolerance to rockpool diet and hypoxic conditions was measured, weight specific respiration was measured and compared interspecifically and, finally, sensitivity to predation was measured by predator exclusion and inclusion experiments on bare sand and *Zostera* substrate.

To answer the second question, some maximal abundances in different habitats are given as an illustration of the value of these habitats.

Methods

Field data were collected from 1978 to 1980 in the Gullmar Fjord on the Swedish west coast (58°15' N, 11°28' E). For capturing and length measurement techniques, see Berglund (1980, 1981). All experiments were made in summer and autumn 1980, except rockpool diet experiments and rockpool introductions which were made during 1978 and starvation experiments which were made during 1979. Prawn abundances were measured in late summer and autumn, when prawns are most numerous (Thorman and Fladvad 1981). On shallow bottoms a drop net (Evans and Tallmark 1979) with a sampling area of 10 m² and a mesh size of 2 mm was used. A deep net with the same sampling area and mesh size as the drop net (Evans and Tallmark in prep.) was used at depths from 1.5 to 3 m. In rockpools prawns on a 0.25 m² area were counted by eye. Introduction experiments of prawns into natural rockpools were made on two occasions in 1978. Recaptures were made with baited prawn traps (5 mm mesh size).

Survival on rockpool diet, i.e. *Enteromorpha intestinalis* L. (verified by stomach analyses on rockpool-living *P. squilla*) was studied by feeding both species with a surplus of this food for three weeks. A starvation experiment with prawns kept apart from each other in separate beakers containing millipore filtered sea water was run for 16 days.

Survival in artificial rockpools was studied in the following way: 4 bowls were filled with 17 l of aerated sea water ($t=18-20^{\circ}\text{C}$, $s=27-30\text{‰}$) and 2 l of *Enteromorpha*, the dominating rockpool alga. One of these bowls was covered with a tight-fitting plastic coated fabric on the water surface, thus preventing oxygen diffusion from the air into the bowl. Another bowl was aerated as control. The prawns were acclimated to experimental conditions for 12 h. Ten specimens of each species were placed in each bowl and survival was recorded after 6, 10 and 14 h. Oxygen concentrations were measured initially and at each survival recording, when dead prawns also were removed.

Tolerance towards low oxygen levels was measured as survival in sea water ($t=20^{\circ}\text{C}$, $s=25-27\text{‰}$), partially deoxygenated with a variable nitrogen flow. Twenty prawns of each species were put in lid-covered 20 l aquaria. The prawns were acclimated to experimental conditions for 12 h. Survival and oxygen concentrations were measured after 6 h.

Respiration was measured by the closed-bottle method (bottle volume 115–130 ml). Two treatments were employed:

a) The bottle was sealed immediately after the introduction of one prawn. The oxygen concentration (related to two control bottles without prawns) was measured after 4 h. Temperature was 15°C , salinity 24‰ and initial oxygen saturation in the millipore-filtered sea water was 100%. 23 prawns of each species were used.

b) The bottle was filled with oxygen saturated millipore filtered sea water and one prawn was introduced. For 2–4 h before the bottle was closed water flowed through it at a rate of $240\text{ ml}\cdot\text{h}^{-1}$, thus allowing the prawn to acclimate. The oxygen concentration after 1 or 2 h was measured and compensated for both oxygen decrease during acclimation and oxygen concentration changes in control bottles without prawns. Temperature was 20°C and salinity $25-29\text{‰}$. Oxygen consumption of 46 *P. adspersus* and 49 *P. squilla* was calculated.

In both treatments the bottles contained carefully washed and sterilized sand as substrate. Prawns were acclimated to the temperature and salinity in question for 12 h. Ashfree dry weight was obtained at 105°C for 24 h and at 600°C for 4 h. Log weight specific respiration was plotted against log weight assuming a straight line relationship (Schindler 1968) and regressions were tested for interspecific differences in slope and elevation (Zar 1974).

All oxygen concentrations were measured by the Winkler method as described by Ahlgren and Ahlgren (1976).

Predator exclusion experiments were made by keeping twenty prawns of each species in three different cages ($1 \times 1 \times 0.5\text{ m}$ aluminium net, mesh size $4 \times 7\text{ mm}$ diagonals). Two cages were placed on a bare sand bottom at 2 m depth and one in a *Zostera* bed at the same depth. The experiment was started on 6 July 1980. Size was measured and survivors counted on 2 and 29 August, 4 September, 13 October and 15 November, when the experiment was terminated. The cages were cleaned on measuring occasions. Individual growth was estimated by comparing changes in length from all measuring occasions, excluding dead prawns. Mean length growth in adjacent natural populations in the *Zostera* bed was measured simultaneously.

Predator inclusion experiments were made in autumn 1980 using plastic containers measuring $1.9 \times 1.2 \times 0.6\text{ m}$. Cod was chosen as predator because it devours substantial amounts of *Palaemon* prawns under natural conditions (verified by stomach analyses). Two substrates, viz. bare sand and *Zostera* on sand, were used. Sea water was constantly renewed and the temperature range was $4-16^{\circ}\text{C}$ with salinities of $25-27\text{‰}$. Twenty similar-sized prawns of each species were put on each substrate and acclimated to experimental conditions for at least 6 h. One cod was then introduced to each container and survival after a 24 h predation period was measured. At some occasions survival was checked against stomach contents of the cod. The two substrate setups were always run in parallel, with the same temperature in each container. One to three sand containers and one *Zostera* con-

tainer were used simultaneously. Thirteen experiments with sand substrate and seven experiments with *Zostera* on sand substrate were run.

Results

As is evident from Table 1, *Palaemon adspersus* is found in *Zostera* beds, while *P. squilla* thrives in many habitats such as very shallow bottoms, *Zostera* beds and rockpools. It is most numerous in rockpools where, however, specimens are usually very small: average length on 17 November 1980 was only 16.5 (S.D. 3.4) mm ($n=24$) in a rockpool, while average size of the same year class in *Zostera* was 24.1 (S.D. 3.2) mm ($n=106$) nine days earlier. The difference is significant (Student's t -test, $P < 0.01$).

237 specimens of *P. adspersus* were introduced into a rockpool in sympatry with naturally occurring *P. squilla* on 29 August 1978. Ten days later *P. adspersus* was absent. On 31 August 51 specimens of *P. adspersus* and 62 of *P. squilla* were released allopatrically in two rockpools. Nine days later *P. adspersus* was extinct while *P. squilla* was not.

When approximately 100 specimens of each species were fed with a surplus of *Enteromorpha intestinalis* (i.e. rockpool diet) for three weeks, survival of both species was nearly 100%.

In an experiment with twenty specimens of each species, 100% survived after 16 days without food. The experiment was then terminated, as the survival time achieved was longer than that of *P. adspersus* in rockpools.

After 6 h and onwards the survival of *P. squilla* was significantly better than that of *P. adspersus* in artificial rockpools with *Enteromorpha* (Table 2). If air diffusion was prevented survival of both species was equally poor (Table 2). Diffusion from the air was obviously important for the survival of *P. squilla*. When the water was aerated survival was 100% in both species.

When the oxygen concentration was below $2.0\text{ mg O}_2\cdot\text{l}^{-1}$ survival was poor in both species with no statistically significant difference between them (Table 3). In the range $2.0-3.0\text{ mg O}_2\cdot\text{l}^{-1}$ *P. squilla* survived significantly better (Table 3).

Intraspecific comparisons of the regressions from the respiration measurements yielded no significant differences ($P > 0.05$) for neither slopes nor elevations, no matter whether the prawns were acclimated to the Winkler bottles or not. In both treatments, however, *P. squilla* showed a tendency to consume more oxygen per unit weight.

No tendency to reduced survival of *P. adspersus* in the predator exclusion cages on bare sand bottoms can be detected

Table 1. Maximal abundances in different habitats

| Date | Habitat | Depth/m | No. <i>P. adspersus</i> /m ² | No. <i>P. squilla</i> /m ² | Method |
|-------------------------|---------------------------------------|---------|---|---------------------------------------|----------|
| 78. 08. 19 ^a | Mud bottom | 0.5 | 0 | 52.8 | Drop net |
| 78. 09. 04 ^a | Sand bottom | 0.5 | 0 | 1.2 | Drop net |
| 78. 09. 05 ^b | Patchy <i>Ruppia</i> vegetation | 0–0.5 | 3 | 10 | Drop net |
| 78. 09. 05 ^b | <i>Zostera</i> | 0.5–1 | 40 | 60 | Drop net |
| 79. 10. 10 | <i>Zostera</i> | 1.5 | 23.6 | 27.3 | Deep net |
| 79. 10. 10 | <i>Zostera</i> | 3.0 | 11.8 | 17.1 | Deep net |
| 80. 09. 17 | <i>Zostera</i> | 1.8 | 40.9 | 3.2 | Deep net |
| 80. 09. 17 | <i>Zostera</i> | 3.0 | 22.2 | 0.2 | Deep net |
| 80. 07. 31 | Rockpool | 0.1–0.3 | 0 | 80 | Counting |

^a S. Evans and B. Tallmark, pers. comm.

^b Thorman and Fladvad 1981

Table 2. Mortality in experimental rockpools. 10 specimens of each species were used in each experiment

| Treatment | Mean O ₂ -conc./mg O ₂ ·l ⁻¹ (S.D.) | Time/h | Mortality/% (S.D.) | | P (Mann-Whitney U-test) | No. of experiments |
|------------------------------------|--|--------|---------------------|-------------------|-------------------------|--------------------|
| | | | <i>P. adspersus</i> | <i>P. squilla</i> | | |
| 1. Sea water + <i>Enteromorpha</i> | 0.45 (0.23) | 6 | 32 (29) | 11 (14) | <0.05 | 13 |
| | | 10 | 74 (23) | 39 (26) | <0.005 | |
| | | 14 | 91 (12) | 61 (22) | <0.001 | |
| 2. as 1. + cover | 0.31 (0.25) | 6 | 74 (16) | 66 (33) | n.s. | 5 |
| | | 14 | 100 (0) | 100 (0) | n.s. | |
| 3. as 1. + aeration | 10.26 (1.44) | 14 | 0 (0) | 0 (0) | n.s. | 6 |

Table 3. Mortality under hypoxic conditions during 6 h. 20 specimens of each species were used in each experiment. Oxygen levels are given as ranges due to difficulties in keeping the levels constant

| O ₂ -concentration/ mg O ₂ ·l ⁻¹ | Mortality/% (S.D.) | | P (Mann-Whitney U-test) | No. of experiments |
|--|---------------------|-------------------|-------------------------|--------------------|
| | <i>P. adspersus</i> | <i>P. squilla</i> | | |
| <2.0 | 100 (0) | 84 (28) | n.s. | 4 |
| 2.0–3.0 | 32 (28) | 5 (6) | <0.005 | 7 |

Table 4. Mortality (%) in cages between 7 June and 13 October 1980

| | <i>Zostera</i> (20 specimens of each species) | Bare sand (40 specimens of each species) | P (χ ² -test) |
|--------------------------|---|--|--------------------------|
| <i>P. adspersus</i> | 45 | 32 | n.s. |
| <i>P. squilla</i> | 10 | 17 | n.s. |
| P (χ ² -test) | <0.05 | n.s. | — |

Table 5. Length growth in cages/mm increase (S.D.). n=number of prawns

| | <i>Zostera</i> | Bare sand | P (Mann-Whitney U-test) |
|---------------------|-----------------|----------------|-------------------------|
| <i>P. adspersus</i> | | | |
| 7 June– | ♂ 1.0 (1.5) n=7 | 1.8 (1.7) n=16 | n.s. |
| 13 October | ♀ 1.3 (1.5) n=3 | 5.0 (2.5) n=5 | <0.05 |
| 7 June– | ♂ 1.6 (0.9) n=7 | 1.6 (1.6) n=16 | n.s. |
| 15 November | ♀ 3.3 (0.6) n=3 | 4.2 (2.2) n=4 | n.s. |
| <i>P. squilla</i> | | | |
| 7 June– | ♂ 2.1 (0.3) n=7 | 2.6 (0.5) n=19 | <0.05 |
| 13 October | ♀ 2.6 (0.7) n=9 | 3.2 (0.9) n=13 | n.s. |
| 7 June– | ♂ 2.0 (0.6) n=7 | 2.2 (0.6) n=19 | n.s. |
| 15 November | ♀ 2.0 (0.5) n=9 | 3.6 (0.8) n=13 | <0.0002 |

(Table 4). Compared with *P. squilla* survival of *P. adspersus* was lower in *Zostera* but not on bare sand bottoms (Table 4).

Length increase was calculated over two periods, one shorter ending on 13 October and one longer ending on 15 November (Table 5). No overall differences in growth can be detected between the two substrates, although both prawn species grew slightly better on bare sand in a few cases. However, length increases in the cages were lower, by 7 to 50%, than in an adjacent natural *Zostera* bed population. Within the cages *P.*

Table 6. Predator inclusion: number of surviving prawns (with S.D. in brackets). Initial number of prawns: 20 for each species. n=number of experiments

| | <i>Zostera</i> (n=7) | Bare sand (n=13) | P (Mann-Whitney U-test) |
|-------------------------|-------------------------|---------------------|-------------------------|
| <i>P. adspersus</i> | 15.1 (4.3) | 5.2 (5.6) | <0.002 |
| <i>P. squilla</i> | 15.0 (2.4) | 9.8 (4.8) | <0.008 |
| P (Mann-Whitney U-test) | n.s. | <0.026 | |

squilla grew significantly better in two cases, in two cases *P. adspersus* did, and in four cases there were no significant differences in growth (Mann-Whitney U-test, level of significance: P<0.05).

The predation inclusion experiments showed that *P. adspersus* was more vulnerable to predation than *P. squilla* on bare sand bottoms (Table 6). In *Zostera*, however, there was no such difference. On bare sand bottoms both species suffered higher predation losses than in *Zostera*, but *P. adspersus* was more heavily affected.

Discussion

There are several possible reasons for the absence of *P. adspersus* in rockpools. One may be an inferior colonization ability compared with *P. squilla*. However, according to Höglund (1943), larvae of both species are found in equal numbers in the uppermost water layers, so both species are probably equally likely to invade a given pool. As *P. adspersus* can metamorphose in aquaria (Makarov and Golodetsky 1980) this should also be possible in rockpools, and thus this factor can be discounted. Moreover, the experiments with rockpool diet and the starvation experiments exclude food as limiting factor. Neither can competition with *P. squilla* explain the rapid extinction of *P. adspersus*, since allopatric introductions of *P. adspersus* into rockpools lead to extinction.

Tolerance towards hypoxic conditions is clearly better in *P. squilla* than in *P. adspersus*. In rockpools with algae oxygen levels may drop to 0.2 mg O₂·l⁻¹ (Ganning 1971) or 1.2 mg O₂·l⁻¹ (Stephenson et al. 1934) during the night. In Bretagne, oxygen levels in rockpools with *Palaemon spp.* dropped to 0.16 mg O₂·l⁻¹ (Truchot and Duhamel-Jouve 1980), and Daniel and Boyden (1975) report from England that *P. squilla* inhabited two pools with minimum oxygen levels of 1.65 and 0.27 mg O₂·l⁻¹, respectively. During such conditions the prawns gathered round the pool edge, presumably utilizing the oxygen gra-

dient resulting from oxygen diffusion. All prawns in the artificial rockpool experiments also behaved in this way, apparently for the same reason. The oxygen concentrations in the artificial rockpools were more than 3 times higher at the surface than at the bottom. The fish species *Clinocottus analis* and *Paraclinus integripinnis* also gathered at the pool edges (Congleton 1980) during hypoxic conditions. If access to the surface was denied to the fishes they died. When oxygen diffusion in our experiments was prevented, all prawns died. Similarly, the copepod *Tigriopus californicus* did not survive when oxygen diffusion was prevented by an oil film (Kontogiannis and Barnett 1973). Toxic substances from the oil played only a secondary role. Thus rockpool populations of *P. squilla* and other animals are presumably sensitive to oil pollution.

Low oxygen levels are also reported from shallow bottoms. Concentrations of $0.5 \text{ mg O}_2 \cdot \text{l}^{-1}$ were recorded in tidal marshes (Nixon and Oviatt 1973, Welsh 1975); in the polluted Thames estuary saturation may be as low as 0.8% (Huddart and Arthur 1971), and in a *Zostera* bed in Holland oxygen concentrations fell to zero (Broekhuysen 1935). Nixon and Oviatt (1973) also pointed out that tidal effects may make oxygen values lower in tidal than in non-tidal areas; normally the water in shallow areas is supersaturated during daytime, but if this water is diluted by water from deeper areas saturated to 100% only, nocturnal oxygen levels will decrease even more.

Thus, temporary oxygen depletion in rockpools is one reason for the absence of *P. adspersus*. Temperature may also be a mortality factor, especially in combination with oxygen stress, and as a matter of fact *P. squilla* tolerates higher temperatures than *P. adspersus* (Berglund 1980). Thus, abiotic factors keep *P. adspersus* out of habitats such as rockpools. The same may apply on very shallow bottom areas.

Several explanations to the absence of *P. adspersus* on deeper bare sand bottoms can be refuted. Differences in colonization ability is unlikely, as *Zostera* beds and bare sand bottoms often are adjacent habitats. Abiotic factors obviously do not exclude *P. adspersus* from bare sand bottoms, since *P. adspersus* in the caging experiments managed as well on bare sand as in the preferred habitat, viz. *Zostera* beds. Food depletion was obviously a cage effect, resulting in low growth rate. This ought to intensify food competition, and yet none of the species was excluded or showed a lower overall growth rate than the other. Thus competition for food does not exclude *P. adspersus*. Differences in the degree of parasitism has not been observed between the cages; in fact no parasites were detected.

Differences in sensitivity to predation remains as explanation, and this is consistent with the predator inclusion experiments; nearly twice as many *P. squilla* as *P. adspersus* survived on bare sand substrate. In the *Zostera* habitat no difference in predation vulnerability is evident. The reason behind the different sensitivity to predation remains obscure. However, *P. squilla* is more active than *P. adspersus* (Berglund 1980) and may thus be able to escape from predators.

High activity of course costs energy. Tolerance towards oxygen depletion also implies costs. As no difference in respiration rates was found between the two species, the difference in tolerance towards hypoxic conditions may be due to a respiratory pigment more efficient at low oxygen tensions in *P. squilla* than in *P. adspersus*. Such a pigment is less efficient at high oxygen levels (Brafeld 1978). Costs for high activity and a less efficient respiratory pigment may be reflected in the lower growth rate of *P. squilla*, which is less than half of that of *P. adspersus* (Berglund 1980, 1981). Egg numbers may also be lower in *P. squilla* due to its smaller size.

Thus, the wide habitat range of *P. squilla* has a price. Why does it pay this price rather than specializing on the more productive and abiotically less severe and less predator-infested eelgrass beds? In other words, why does it not adopt the strategy of *P. adspersus*?

Swedish rockpools are habitats of limited extent due to the lack of tidal effects, but the large continental tidepool areas should contribute substantially to prawn stocks. Is adaptation to the conditions on the Swedish west coast then prevented by a gene flow from tidal areas? This is unlikely, since the Swedish variety of *P. squilla* (var. *typica* de Man) is found only in Denmark and northwards, and thus the gene flow from tidal areas is not large enough to prevent the Swedish prawns to adapt to non-tidal conditions. Probably access to very shallow bottoms with occasional oxygen depletion is of importance for Scandinavian prawns because of their rich food supply, and increased reproductive success in these habitats may balance the cost of high tolerance towards abiotic extremes. Access to deeper bare sand bottoms may be beneficial during winter when both prawn species migrate to deeper waters.

If competition is supposed to determine the abundance and distribution of the two prawn species, *P. squilla* is a generalist and should thus be excluded from the eelgrass beds due to unsuccessful interactions with the superior competitor *P. adspersus*. However, they do coexist in the *Zostera* beds. The high production in *Zostera* meadows (Adams 1976) makes the explanation of food as a limiting resource less probable, and moreover, during food scarcity (cf. the cage experiments) the prawns grew equally well. *P. squilla* also found food items faster than *P. adspersus* did in feeding experiments (Berglund 1980), and aggressive encounters did not occur. Therefore, *P. squilla* is not an inferior competitor, and competition does probably not limit the populations nor regulate the distributions of *P. adspersus* and *P. squilla*.

Connell (1961 a, b) showed that the upper limit of intertidal barnacles was set by abiotic factors, whereas biotic factors determined the lower range. The same regulation pattern is found in the prawn species, where a high tolerance in *P. squilla* towards abiotic factors and predation extends its upper and lower range respectively. The relative importance of these factors obviously varies between different habitats and species; in rockpools and on very shallow bottoms abiotic factors, i.e. oxygen and temperature, keep *P. adspersus* out, on bare sand bottoms biotic factors, i.e. predation, restricts its range.

Acknowledgements. We thank T. Fagerström, S. Nilsson and S. Ulfstrand for valuable comments on the manuscript. The study is part of a project supported by the Swedish Natural Science Research Council.

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Received April 10, 1981