

Coexistence, Size Overlap and Population Regulation in Tidal vs. Non-Tidal *Palaemon* Prawns

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Summary. The effect of increased habitat heterogeneity in tidal areas on coexistence between *Palaemon* prawns was studied at eight sites along the European Atlantic coast. Two species which are sympatric in non-tidal areas, *Palaemon adspersus* Rathke and *P. squilla* (L.) are largely allopatric in tidal areas, and the sympatric size difference decreases in allopatry. In tidal areas the smaller species, *P. squilla*, is restricted to brown algal belts and rockpools. A third species, *P. serratus* (Pennant), larger than the others, occurs under oceanic salinities in subtidal brown algal belts and there has forced *P. squilla* to restrict its habitat distribution to adjacent intertidal rockpools. At estuarine salinities, however, *P. squilla* also inhabits the brown algal belts. A larger diel variation in stomach fullness index in *P. squilla* than in *P. adspersus* persists in non-tidal areas.

Abiotic factors probably restrict the two largest species, viz. *P. adspersus* and *P. serratus*, to subtidal environments; these species are sensitive to the extremes in salinity, temperature or O₂ levels characteristic of the intertidal zone. Competition and/or predation probably relegates *P. squilla* to the intertidal zone. In non-tidal areas, where this zone is reduced, *P. squilla* increases its niche width and coexists with *P. adspersus*, and the size differentiation associated with sympatry may reduce interspecific competition.

Introduction

Two species of *Palaemon* prawns, *P. adspersus* Rathke and *P. squilla* (L.) (= *P. elegans* Rathke) coexist in non-tidal Swedish *Zostera marina* (L.) meadows. *P. squilla* can also occupy bare sand bottoms, rockpools and brown algal belts (Berglund 1980). However, the latter two habitats are abundant only in tidal areas. As *P. adspersus* cannot occupy intertidal rockpools or brown algal belts, tidal areas provide access for *P. squilla* to extensive habitats of different types.

P. squilla is known to inhabit tidal rockpools (Pyefinch 1943; Rodriguez and Naylor 1972; Daniel and Boyden 1975; Goss-Custard et al. 1979). A third species, *P. serratus* (Pennant), is also found in tidepools but below mean tide levels (Rodriguez and Naylor 1972). Where *P. squilla* and *P. serratus* coexist, *P. squilla* is found in shallower waters (Forster 1951b). However, as far as I know, no quantitative work in order to calculate habitat overlaps or niche sizes has been done, especially comparing tidal vs. non-tidal populations.

Interspecific competition is not considered an important factor in the regulation of non-tidal prawn populations (Berglund and Bengtsson 1981). However, tidal areas offer a very different

environment in that quite different factors may be important in population regulation.

The aim of this study is to outline changes in coexistence in tidal compared to non-tidal areas, starting with the following questions:

1. Will the numerical dominance of *P. adspersus* in tidal *Zostera* meadows increase as a result of the increase in intertidal habitat areas accessible to *P. squilla*?

2. How will the appearance of *P. serratus* in tidal areas affect the pattern of habitat segregation between the other two species?

3. If *P. adspersus* and *P. squilla* do not coexist in tidal areas, will this affect interspecific body size overlap as compared with the case of non-tidal areas? If interspecific competition for limiting resources is of any importance, size differences ought to be larger between coexisting species (Grant 1972), thus presumably reducing competition.

4. In prawn populations in non-tidal areas the lower growth rate of *P. squilla*, compared to *P. adspersus*, was assumed to be due to higher costs for defence mechanisms against temperature/salinity stress and for the higher mobility of the former species (Berglund 1980). If the three prawn species occupy different habitats in tidal areas, will the smallest species occupy the physically harshest habitats, as is the case in non-tidal areas, and thus be more tolerant to varying abiotic factors than the larger species?

Methods

Prawns in deeper (> 1 m) *Zostera* meadows were captured with a small beam trawl (Berglund 1981) with mesh size 2 mm. On shallower *Zostera* and in some *Fucus* belts a push-net (1.5 m wide, 10 mm mesh size) was used. Hand-nets were used in most *Fucus* belts (mesh size 10 mm) and in rockpools (mesh size 2 mm).

Length was measured from the posterior edge of telson to the base of the eyestalks and sex was determined by absence or presence of a process between the third pair of pereopods (Berglund 1981). Only adults, i.e. specimens older than 10 months (estimated from length frequency diagrams), were used when calculating dominance, niche width, habitat diversity and habitat overlaps. Only specimens aged as 1+ were used when calculating size overlaps.

Samples were taken from 24 plots in 8 different areas (Fig. 1, Table 1). The plots were grouped into 12 different habitat types (Table 1). The Swedish samples were collected during July and August 1978–1981, and the other samples were taken during July and August 1981. The dendrogram of the relatedness of

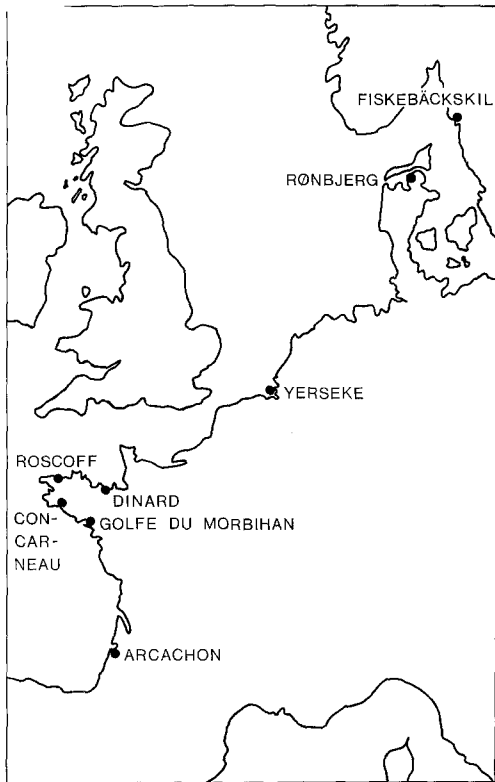


Fig. 1. The main sampling areas

the habitats (Fig. 2) was calculated from habitat overlap values according to Cody (1974). Habitat overlaps were calculated according to Colwell and Futuyama (1971, eq. 3). The allopatry/sympatry length comparisons were made using a large Swedish sample from July 1979 from habitat 8 (Table 1), samples from Golfe du Morbihan taken in July 1981 in habitats 7 and 5, a sample from Arcachon in August 1981 in habitat 3, and a sample from Yerseke taken in August 1981 in habitats 5 and 10. Golfe du Morbihan was regarded as an estuarine environment in spite of the rather high salinity reported in Table 1, as salinity may drop as low as to 22‰ (A. Le Roux, pers. comm.). The same argument applies to Arcachon.

All results from tidal areas are based on samples from a short period during one summer only. By necessity different sites were sampled at different times during summer. Although these circumstances must be kept in mind, sample size generally was so large that the results ought to represent at least summer situations accurately (July and August). From Sweden, a sample from July 1979 was chosen for size overlap calculations because of the particularly large number of individuals involved, but habitat distributions and size differences were similar in 1980 and 1981 as shown by less extensive data from these latter years.

For the calculations of diel variation in stomach fullness index (Berg 1979) prawns were captured in Kilviken Bay, Fiskebäckskil, during July 1979. Samples were taken during four days and nights at 04, 08, 12, 16, 20 and 24 h. Between 90 and 175 specimens of each species from each time were measured, making up a total of 1664 measured prawns. Stomach fullness index (FI) was calculated as (wet weight of stomach contents) \times 100 / (wet body weight). Subjective stomach fullness was also estimated on a 5-point scale (0, 1/4, 1/2, 3/4 and 1).

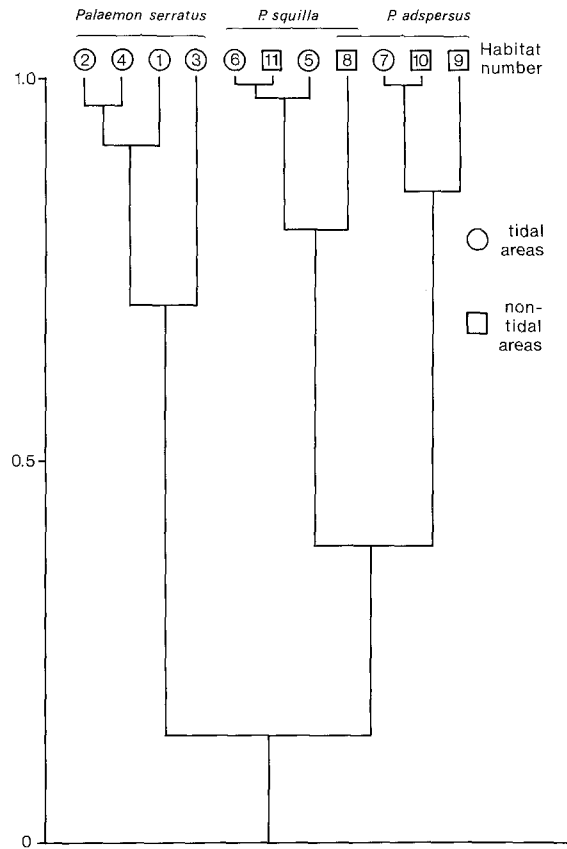


Fig. 2. Dendrogram of the relatedness of the habitats 1-11

The salinity tolerance of *P. serratus* and *P. squilla* was compared at Laboratoire de Biologie Marine de Dinard in July 1981 using salinities of 5 and 15‰. In the 5‰ salinity test 30 prawns of each species were kept in 11 l of continuously aerated sea water ($t=20^\circ\text{C}$) for 24 h. The number of dead specimens was observed after 6, 12, and 24 h, at which times the dead prawns were also removed. No food was given. The same experiment was repeated in 15‰ salinity, but only 15 specimens of each species were used. The number of dead specimens in this case was observed also after 30 h.

A comparison of the tolerance to hypoxic conditions of *P. serratus* and *P. squilla* was also made at the Dinard laboratory. The method used was similar to that described in Berglund and Bengtsson (1981). 30 specimens of each species were put in 15 l of sea water ($t=20^\circ\text{C}$, sal.=35.5‰) together with 3 l of *Enteromorpha intestinalis* (L.). The aquaria were kept in darkness. The experiment was run twice, the results being pooled before calculations. As a control, a similar aquarium with continuous aeration was used. Oxygen levels were measured initially and after 6 h according to Winkler (Ahlgren and Ahlgren 1976). Mortality was recorded after 6 and 12 h, dead prawns being removed at the same time.

Results

Palaemon serratus dominated numerically under oceanic salinities in vegetation on rocks and sandy bottoms, i.e. in habitats 1-4 (Table 2 and Fig. 2). In estuarine environments such as Golfe du Morbihan it is not known to reproduce (A. Le Roux, pers. comm.). *P. serratus* was larger than the other species (Table 3), except in the somewhat estuarine Arcachon bay: the small size

Table 1. The habitats at the sampling plots with approximate temperatures (*t*), salinities (*s*) and tidal range min/max values (*r*)

Habitat number and type	Sampling plot	<i>t</i> (°C)	<i>s</i> (‰)	<i>r</i> (m)
A. Tidal areas				
1. <i>Fucus</i> belt on rocks, oceanic salinity	Pouldohan Bay, Concarneau	15–16	35.5	4–8
	Roscoff	18	35.5	4–10
	Dinard	19	35.5	5–11
2. <i>Zostera</i> on hard sand, oceanic salinity	Roscoff	18	35.5	4–10
	Dinard	19	35.5	5–11
3. <i>Zostera</i> tidepools on mudflats	Ile aux Oiseaux, Arcachon	26	34	1–5
4. <i>Fucus</i> belt on rock, >22° C	Arcachon	22.5	34	1–5
5. <i>Fucus</i> belt on rock, ≤19° C, estuarine salinities	Golfe du Morbihan:			
	Ile Bailleron	19	22–35	2.5–4
	Le Passage St Armel	19	22–35	2.5–4
	Point de Kerners	19	22–35	2.5–4
	Port Blanc	19	22–35	2.5–4
	Yerseke	18	28	2–4
6. Rockpools	Pouldohan Bay, Concarneau	19–20	35.5	4–8
	Roscoff	20	35.5	4–10
	Dinard	19–22	35.5	5–11
7. Estuarine sheltered <i>Zostera</i> on mud bottoms	Golfe du Morbihan:			
	Ile d'Arz west	19	22–35	2.5–4
	Ile d'Arz east	19	22–35	2.5–4
	Ile Tascon	19	22–35	2.5–4
B. Non-tidal areas				
8. Estuarine sheltered <i>Zostera</i> on mud bottoms	Fiskebäckskil:			
	Kilviken Bay north	15–20	15–30	0.5
	Kilviken Bay south	15–20	15–30	0.5
9. Estuarine sheltered <i>Zostera</i> on sand bottoms	Rønbjerg	16	22–23	0.4
	Kvarnbukten Bay, Fiskebäckskil	15–20	15–30	0.5
10. Estuarine polder	Ouwerkerk, Yerseke	21	22	0
11. Non-tidal rockpools	Flatholmen Island, Fiskebäckskil	12–23	4.6–26	0
12. <i>Fucus</i> belt on rock, <19° C, estuarine salinity	Klubban Biological Station, Fiskebäckskil	18	22–23	0.5

Table 2. Species distribution (%) in the habitat types. *n*=total numbers of captured prawns

a) Species distribution

Habitat no.	1	2	3	4	5	6	7	8	9	10	11	12
<i>Palaemon serratus</i>	91.8	100	65.2	96.6	2.7	0.8	0.3	0	0	0	0	0
<i>P. squilla</i>	8.2	0	8.4	3.0	97.3	99.2	1.7	39.7	16.1	0.7	100	100
<i>P. adspersus</i>	0	0	26.4	0.4	0	0	98.0	60.3	83.9	99.3	0	0
<i>n</i>	697	30	368	236	670	532	297	5,948	483	135	368	100

Habitat 1–7: tidal areas, habitat 8–12: non-tidal areas

b) Dominating *Palaemon* prawns in different habitats

	Estuaries		Open ocean
	Non-tidal	Tidal	Tidal only
<i>Fucus</i> belt on rock	<i>P. squilla</i>	<i>P. squilla</i>	<i>P. serratus</i>
Rockpools	<i>P. squilla</i>	<i>P. squilla</i>	<i>P. squilla</i>
<i>Zostera</i> on mud bottoms	<i>P. squilla</i> + <i>P. adspersus</i>	<i>P. adspersus</i>	<i>P. serratus</i>

Table 3. Size differences between *Palaemon serratus*, *P. squilla* and *P. adspersus*. Average length in mm \pm S.D., sample size in brackets. All values within any row are significantly different (Student's *t*-test, $P < 0.01$) except the Arcachon *P. serratus* and *P. squilla* male values ($P > 0.1$)

		<i>P. serratus</i>	<i>P. squilla</i>	<i>P. adspersus</i>
Roscoff	♂	38.4 \pm 3.26 (18)	25.4 \pm 3.71 (20)	
	♀	41.5 \pm 6.38 (13)	32.1 \pm 4.64 (46)	
Dinard	♂	42.8 \pm 4.25 (206)	25.4 \pm 2.80 (173)	
	♀	45.9 \pm 5.05 (203)	34.7 \pm 5.17 (169)	
Arcachon, Ile aux Oiseaux	♂	26.7 \pm 2.13 (83)	26.9 \pm 1.80 (12)	28.7 \pm 1.81 (67)
	♀	28.3 \pm 3.82 (157)	36.3 \pm 2.18 (18)	38.9 \pm 2.55 (30)

Table 4. Species proportions, niche widths and species diversity in tidal vs. non-tidal areas, calculated from three comparable habitats from each area

Species proportions (p_j) in	Estuarine rocky <i>Fucus</i> belts	Rock-pools	Estuarine <i>Zostera</i> on mud	Niche width ^a
A. Tidal areas				
<i>Palaemon serratus</i>	0.03	0.008	0.003	1.80
<i>P. squilla</i>	0.97	0.99	0.02	2.04
<i>P. adspersus</i>	0	0	0.98	1
Species diversity ^b	1.13	1.05	1.11	
B. Non-tidal areas				
<i>P. squilla</i>	1	1	0.40	2.66
<i>P. adspersus</i>	0	0	0.60	1
Species diversity ^b	1	1	1.96	

^a Niche width = $1/\sum p_i^2$

i = habitat no.

p_i = species proportion between habitats

^b Species diversity = $e^{H'} = e^{-\sum p_j \cdot \ln p_j}$

j = species no.

p_j = species proportion within a habitat

there may be due to low salinity rather than high temperature, as survival of *P. serratus* was 100% even at 30°C (Richard 1978). *P. squilla*, the smallest species, prevailed in habitats 5, 6, 11 and 12 but also occurred in habitats 8 and 9 together with *P. adspersus*. These habitats all had either a somewhat estuarine character or were rockpools and thus this species spanned the whole salinity range. *P. adspersus*, finally, was the most abundant species in estuarine *Zostera* meadows (habitats 7, 8, 9) and a Dutch polder with estuarine salinity (habitat 10), where the prawns inhabited dense *Chaetomorpha linum* (O.F. Müll.) vegetation.

P. squilla, in contrast to *P. adspersus*, increased its niche width in non-tidal areas, compared to tidal conditions (Table 4). Only habitat types resembling one another were used when calculating niches in tidal vs. non-tidal areas. Although *P. serratus* was absent from the non-tidal *Zostera* meadows, species diversity with respect to prawn populations was nevertheless larger than in tidal ones (Table 4). This is due to the increasing proportion of *P. squilla* in non-tidal *Zostera*. The degree of coexistence in tidal *Zostera* meadows was much lower than in non-tidal

Table 5. Numerical dominance comparison in tidal vs. non-tidal estuarine *Zostera* on mud

	No. of specimens of <i>Palaemon adspersus</i>	No. of specimens of other species
Tidal <i>Zostera</i> , Golfe du Morbihan July 1981		
Ile d'Arz west	243	3 ^a
Ile d'Arz east	33	3 ^b
Ile Tascon	15	0
Sum tidal <i>Zostera</i>	291	6
Non-tidal <i>Zostera</i> , Fiskebäckskil July–August		
Kilviken Bay north 1978	453	181 ^a
1979	2,321	1,605 ^a
1980	226	89 ^a
1981	63	4 ^a
Kilviken Bay south 1980	90	375 ^a
1981	985	490 ^a
Sum non-tidal <i>Zostera</i>	4,138	2,744
$\chi^2_{sums} = 171$ $P < 0.001$		

^a *Palaemon squilla*

^b 2 *P. squilla* + 1 *P. serratus*

Table 6. Numbers of *Palaemon serratus* and *P. squilla* in oceanic and estuarine *Fucus* belts

	<i>P. serratus</i>	<i>P. squilla</i>
Oceanic <i>Fucus</i>	640	57
Estuarine <i>Fucus</i>	18	652
$\chi^2 = 1,082$ $P < 0.001$		

meadows (Table 5). This means that *P. squilla* mainly became restricted to adjacent *Fucus* belts in the estuarine tidal areas. In *Fucus* belts under oceanic salinities *P. serratus* dominated significantly (Table 6), and here *P. squilla* was found mainly further up the shore in the rockpools.

When length overlaps between *P. adspersus* and *P. squilla* in sympatry (Kilviken Bay, Fiskebäckskil) and allopatry (Golfe du Morbihan: *Fucus* belts for *P. squilla* and *Zostera* on mud for *P. adspersus*) are compared (Table 7, Fig. 3), we find a more than tenfold increase in average size difference for both sexes as we compare the allopatric situation with the sympatric one. Also, *P. adspersus* increased significantly in length and *P. squilla* decreased significantly in sympatry. Further data on the sympatric size difference is found in Berlund (1981). An allopatric size resemblance was also found in Yerseke (Table 3), but here both species were larger than in sympatry, possibly because the Yerseke sample was taken later in summer. In Arcachon both the degree of numerical dominance (Table 2, habitat 3) and the interspecific size differences (Table 7) were intermediate between Kilviken Bay and the allopatric sites. The high temperature (26°C)

Table 7. Length comparisons in two sympatric (Kilviken Bay, Fiskebäckskil and Arcachon) and two allopatric (Golfe du Morbihan and Yerseke) populations of *Palaemon adspersus* and *P. squilla*. Average lengths in mm \pm S.D. with sample size in brackets. $\Delta\bar{x}$: difference between average lengths. t calculated by Student's t -test

♂	<i>P. adspersus</i>	<i>P. squilla</i>	$\Delta\bar{x}$	t	$P <$
Sympatry Kilviken Bay	31.8 \pm 3.91 (1,139)	25.0 \pm 2.28 (1,069)	6.8	49.3	0.001
Sympatry Arcachon	28.7 \pm 1.81 (67)	26.9 \pm 1.18 (12)	1.8	3.13	0.005
Allopatry Golfe du Morbihan	28.3 \pm 2.71 (235)	27.7 \pm 3.24 (284)	0.6	2.62	0.01
Allopatry Yerseke	33.0 \pm 3.84 (49)	32.9 \pm 3.70 (17)	0.1	0.1	n.s.
♀	<i>P. adspersus</i>	<i>P. squilla</i>	$\Delta\bar{x}$	t	$P <$
Sympatry Kilviken Bay	38.7 \pm 4.95 (695)	31.1 \pm 2.01 (300)	7.6	25.9	0.001
Sympatry Arcachon	38.9 \pm 2.55 (30)	36.3 \pm 2.18 (18)	2.6	3.53	0.001
Allopatry Golfe du Morbihan	33.8 \pm 4.82 (57)	35.7 \pm 3.49 (339)	-1.9	3.59	0.001
Allopatry Yerseke	42.9 \pm 5.46 (85)	41.4 \pm 4.35 (23)	1.5	1.21	n.s.

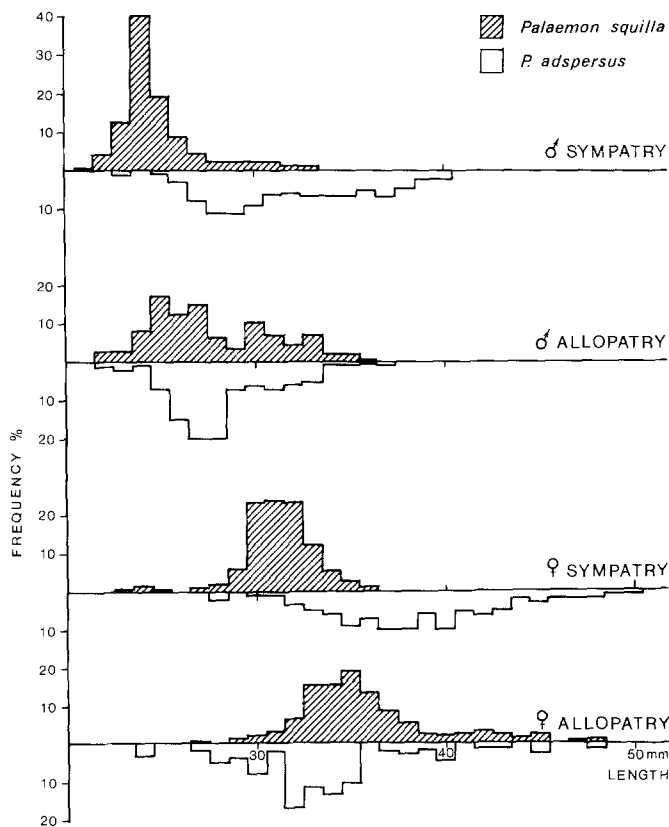


Fig. 3. Length frequency distributions of *Palaemon adspersus* and *P. squilla* in sympatry (Kilviken Bay) and allopatry (Golfe du Morbihan)

in Arcachon complicates the situation: it probably decreases the abundance of *P. squilla* and *P. adspersus*. Furthermore, the low salinity may decrease the size of *P. serratus* as mentioned.

Length overlap between *P. serratus* and the other species was usually small (Table 3), since on one hand the *P. serratus* 0-group was smaller (*P. serratus* reproduces during winter and the other species during summer) and, on the other hand, the *P. serratus* 1-group was larger than adults of *P. adspersus* or *P. squilla*.

The diel variation in stomach fullness index (Fig. 4) in the prawn samples from Kilviken Bay, Fiskebäckskil, shows that the stomachs of both species present were significantly fuller

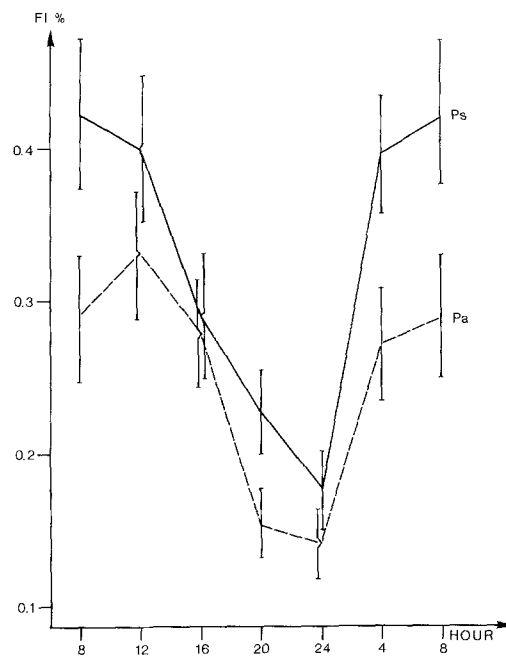


Fig. 4. Diel variation in stomach fullness index (FI) in *Palaemon adspersus* (Pa) and *P. squilla* (Ps) with S.E.

at 8 h than at midnight. Thus both species showed a diel pattern of food intake with mainly nocturnal eating habits. However, as the stomach fullness index of *P. squilla* was significantly higher than that of *P. adspersus* at 4, 8 and 20 h but not at 12, 16 and 24 h, diel variation was larger in *P. squilla* (all tests Student's t -test, $P < 0.05$). The subjective fullness estimate yielded similar results. Average size differences between the prawn species or between sampling times do not affect these results as no correlation between weight of prawn and stomach fullness index was found (average $r = 0.158$, range = -0.093 to 0.426).

The salinity tolerance tests show that *P. serratus*, in contrast to *P. squilla*, was unable to survive in 5‰ sea water. Both species survived equally well when salinity was increased to 15‰, however (Table 8).

The same difference in tolerance was found during low oxygen stress: *P. serratus* showed a higher mortality rate than did *P. squilla* (Table 9).

Table 8. Salinity tolerance in *Palaemon serratus* and *P. squilla*

Time/h	Number of dead		χ^2	<i>P</i> <
	<i>P. serratus</i>	<i>P. squilla</i>		
a) 5‰ salinity. 30 specimens of each species were used				
0	0	0		
6	3	3		
12	25	3	20.3	0.001
24	29	6	33.2	0.001
b) 15‰ salinity. 15 specimens of each species were used				
0	0	0		
12	0	0		
24	1	1		
30	1	1		n.s.

Table 9. Tolerance to oxygen depletion in *Palaemon serratus* and *P. squilla*

Time/h	O ₂ conc./ mg O ₂ ·l ⁻¹	No. dead <i>P. serratus</i>	No. dead <i>P. squilla</i>	χ^2	<i>P</i> <
a) Experiment: 60 specimens of each species were used					
0	4.26	0	0		
6	0.45	51	15	41.2	0.001
10		60	27	42.8	0.001
b) Control with aeration: 30 specimens of each species were used					
0	3.91	0	0		
6	5.18	0	0		
10		0	0		n.s.

Discussion

In general *P. squilla* is common both in tidal and non-tidal areas, where it occurs in many habitats. *P. adspersus* is common in non-tidal areas, where it is found in estuarine *Zostera* meadows. In tidal oceanic *Fucus* belts a third species, *P. serratus*, replaces *P. squilla* (Table 6). Here, *P. squilla* occurs mainly in marginal habitats, i.e. rockpools. At high tide the two species may overlap somewhat more, but *P. squilla* still prefers more shallow waters (Forester 1951a, b; Rodriguez and Naylor 1972). The disappearance of *P. squilla* from the *Fucus* belt may be due to competition with *P. serratus*, since the abundance of the latter in the *Fucus* belt increases as it migrates downward when the water level sinks. Abundances may be very high, and at low tide it is fished for consumption in, for instance, Dinard. Alternatively, predation by large *P. serratus* on *P. squilla* may restrict the habitat distribution of the latter species.

The fact that *P. squilla* is not displaced from the rockpool environment is probably due to the inability of *P. serratus* to cope with such an abiotically variable environment: the poor survival of *P. serratus* at low salinity (Table 8) and during hypoxia (Table 9) may be responsible for its absence from this habitat. Note the absence of *P. adspersus* from non-tidal rockpools, where its sensitivity to high temperatures and low oxygen levels is believed to be the reason for its absence (Berglund and Bengtsson 1981).

Thus both biotic (*P. squilla*) and abiotic (*P. serratus*) factors may explain prawn distribution. *P. squilla* seems well adapted to shallow tidal environments with large diel variations in water level, temperature, salinity and oxygen level. This may be re-

flected also in non-tidal prawn populations: *P. squilla* was found to have a more marked diel locomotory activity than did *P. adspersus* (Berglund 1980), and diel variation in stomach fullness was also larger than in *P. adspersus* (Fig. 4).

Obviously *P. adspersus* and *P. squilla* are sympatric in non-tidal estuarine *Zostera*-on-mud habitats and mainly allopatric in the corresponding tidal habitats. The comparison between Kilviken Bay and Golfe du Morbihan seems relevant as differences in salinities and temperatures were rather small and habitat types were similar. The pattern emerging from this comparison is interesting: *P. squilla* inhabits *Zostera* to a higher degree in non-tidal areas (Table 5), its niche widens, and the species diversity in *Zostera* beds with respect to prawns increases (Table 4). In the non-tidal sympatric case, size overlap between *P. adspersus* and *P. squilla* decreases remarkably compared to the tidal situation (Fig. 3, Table 7). This can be interpreted as an effect of competition in sympatry (Grant 1972). However, as I have no idea of the effect of other selective forces operating on size, neither in allopatric nor in sympatric habitats, no certain conclusions about the possible role of competitive interactions and character displacement can be made (Connell 1980). Thus, for example, size differences may also be a result of sexual character displacement if recognition of conspecifics is based on size.

As mentioned earlier, intertidal and slightly subtidal algae such as *Fucus* species occupy larger areas in tidal than in non-tidal waters (Doty 1957), thus providing additional habitats for *P. squilla* in tidal areas. Still, this does not explain why *P. squilla* is absent in *Zostera* beds in tidal areas. As it obviously can inhabit such sites in non-tidal areas, coexisting with *P. adspersus*, *P. squilla* should spread to tidal *Zostera* meadows from the adjacent *Fucus* belts if intraspecific competition in the *Fucus* belts exceeds interspecific competition in the *Zostera* meadows. This, however, requires a *P. squilla* population large enough to spill over to the *Zostera*. As winter mortality probably is high (as is the case in Sweden, where numbers of prawns in my catches drop by 93–98% per catch effort from autumn till next summer), there may simply not be prawns enough to inhabit the *Zostera* meadows as well as the *Fucus* belts. In Sweden, however, the *Fucus* belt is so narrow that *Zostera* becomes the major habitat for *P. squilla*.

To sum up, two prawn species being sympatric in nontidal areas by and large become allopatric when new habitats become accessible in tidal areas, to which especially one of the species is well adapted. Thus, with increased spatial and temporal habitat heterogeneity in tidal areas the prawn species segregate their habitats. At the same time the sympatric size difference becomes an allopatric size resemblance.

Although one more species appears in tidal areas the degree of habitat segregation is still very high, and each species greatly prevails in one habitat. Species distributions are probably explained by abiotic factors relegating the largest two species to their specific habitats while biotic factors (i.e. competition or predation) may relegate the smallest species to physically somewhat harsher habitats.

The smallest species lives in the intertidal zone. In such an environment tolerance to physical stress must be important, and accordingly the intertidal species shows higher tolerance to temperature, salinity and oxygen fluctuations than do the subtidal species. Similar patterns were observed in *Conus* gastropods on intertidal reef rock benches (Leviten and Kohn 1980) and on subtidal reefs (Kohn and Nybakken 1975), where tolerance to abiotic factors characterized the intertidal *Conus* species, while habitat and food segregation was important for the subtidal ones.

Under severe abiotic conditions or at the edge of a species' geographical distribution range, density-independent population-limiting factors may dominate and coexistence between the prawn species will be possible, as in Arcachon (high temperatures) and at the Swedish west coast (fewer habitats). One may therefore predict an increase in coexistence during autumn and winter in tidal areas, which also has been observed in Golfe du Morbihan (A. Le Roux, pers. comm.).

Thus, whether two or more species can or cannot coexist may be primarily due to physical factors, in this case tide fluctuations. If adult prawn populations are limited mainly by high winter mortality (predation, food scarcity) there seems to be little need to invoke competition in summer habitats to explain the distribution patterns, except in a few cases when *P. squilla* may become displaced by larger species.

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