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RESEARCH ARTICLE

Morphological differences between females of different *Jaera* species (Crustacea: Asellota: Isopoda) in the White Sea: a possible solution to an old problem

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Abstract It is well known that females of "*Jaera albifrons*" species complex cannot be determined on the basis of morphological analysis. In this work, an attempt to separate females of three *Jaera* species on the basis of morphometric characters, the length of so-called "coupling zones" (CZ), was made. Coupling zones are those parts of the partners' bodies that contact during copulation. Female CZ is a region between the posterior edge of the pleotelson and the border between the fourth and the fifth thoracic segments, where openings of dorsal vaginas are situated. Male CZ extends from the anterior edge of the cephalon to the first abdominal segment carrying the copulative organ. Absolute and relative lengths of CZ were used. The latter was calculated as ratio of absolute length of CZ to body length. Two settlements of *Jaera* in the White Sea were studied for 3 years. Species composition of these populations was quite different (the first one was dominated by *J. ischiosetosa* and the second by *J. albifrons* and, 1 year by *J. praehirsuta*). Males of different species were shown to be distinct in terms of absolute and relative length of CZ. Frequency distributions of absolute and relative CZ length of females differed significantly in the two settlements. The experiments based on male choice in mixed samples were organized. They revealed that females chosen by males of different species differ significantly by CZ parameters.

Introduction

It had long been considered that only one species of the isopod genus *Jaera* inhabited northern Atlantic seas: *J. albifrons* Leach 1814 (= *Jaera marina* Fabricius 1780) (Sye 1887; Gaevskaya 1948; Kuznetsov 1964). However, this species was then shown to be subdivided into several races (Forsman 1944, 1949) that, in further investigations, were recognized as independent species (Bocquet 1953). It is now accepted that the so-called "*Jaera albifrons*" complex consists of five distinct species: *J. albifrons* Leach 1814, *J. ischiosetosa* Forsman 1949, *J. praehirsuta* Forsman 1949, *J. posthirsuta* Forsman 1949 and *J. forsmani* Bocquet 1950. The former three species are common in the shallow waters of the White Sea (Kulinich and Frolov 1970; Bek 1988; Kuzmin and Khaitov 2004).

Distinct ecological preferences of different *Jaera* species have been shown in a range of works (Forsman 1949; Bocquet 1953; Naylor and Haahtela 1966; Jones 1972b; De Grave and Holmes 1998). Furthermore, there is some evidence of genetic (Siegismund 2002; Carvalho and Piertney 1997) and karyological (Staiger and Bocquet 1956) distinction between these species.

Clear morphological differences between species of the "*Jaera albifrons*" complex may be found only in males. Species identification of males is based on the secondary sexual characters associated with certain

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parts of certain pereopods that are involved in precopulation overtures (Solignac 1972). Since females lack such characters, confident species identification on the basis of morphological features has been thought impossible (Bocquet 1953). Therefore, investigators either identify *Jaera* females on the basis of genetic markers (Solignac 1978) or simply leave the females out of the research, basing the analysis of species composition on males only (e.g., Jones and Naylor 1971; Sjöberg 1970).

It has been shown that interspecific hybrids in *Jaera* are extremely rare in the nature (Bocquet 1953; Bocquet and Solignac 1969; Solignac 1981). There are only single instances of introgression in very limited areas (Solignac 1969). Solignac (1978) has shown that the choice of a conspecific female by a male is based on genetically determined behavioral patterns, different in different species. Thus, ethological isolation of species may take place.

At the same time, ethological features cannot be used for taxonomic or ecological investigations. Therefore, the necessity of identifying females of different species calls for a search for morphological differences between them. In this work we attempt to solve this problem on the basis of statistical morphometric analysis.

A prerequisite for this analysis is the existence of a typical behavioral pattern demonstrated by all the members of "*Jaera albifrons*" complex during copulation. In the beginning of the coupling, a male climbs up on the dorsal surface of a female and orientates itself in the position "head-to-tail" (Fig. 1). During copulation, certain body areas of the partners are in contact. In case of the male, the contact area extends from the anterior edge of the cephalon to the first abdominal segment carrying the copulative organ, while the female contact area is the part of the dorsal surface between the posterior edge of the pleotelson and the border between the fourth and the fifth thoracic segments, where the openings of dorsal vaginas are situated. Further, we call these body areas "coupling zones" (CZ) (Fig. 1). We assumed that discrepancy in the size of male and female coupling zones should hamper further copulation. Accordingly, our investigation focused on morphometric analysis of these zones.

In the present work we have tested the following hypotheses that follow from our assumption:

1. Males of different species should differ in morphometric parameters of CZ.
2. In settlements with different species composition, a different frequency distribution of female CZ parameters should be observed.

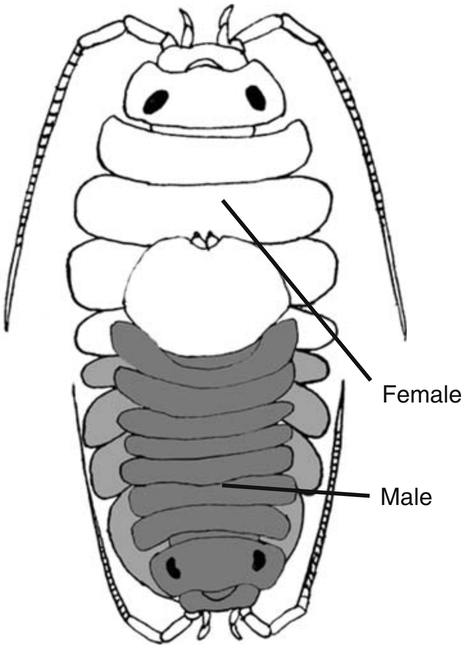

Fig. 1 Position of male and female during copulation. Coupling zones are painted over. Pereopods are not shown

3. CZ of the females chosen as mates by males of different species should have different morphometric parameters.
4. CZ parameters of males of a certain species should correlate with those of females of the same species.

Materials and methods

Samples and experiments

The investigations were carried out in the Kandalaksha Bay of the White Sea (Fig. 2). The samples were taken between late May 2003 to early June 2005 at two stations situated on the intertidal zone of the Youzhnaya Inlet (Ryashkov island, Kandalaksha Nature Reserve). The stations' positions were the same every year.

The first station (St. 1) was situated in the mouth of a small stream in the upper part of the inlet. Submerged stones were sampled there and thoroughly rinsed in a bucket. The second station (St. 2) was in the middle of the eastern shore of the inlet. There, fucoids (*Ascophyllum nodosum* and *Fucus vesiculosus*) were sampled and rinsed. All the samples were taken a few days after the ice had melted. At the time of sampling, water salinity at these two stations was similar (~5‰), though in August it is quite different.

Materials from each station were sorted. In 2003–2004, all animals from different stations were preserved separately in 70% ethanol (a general description of

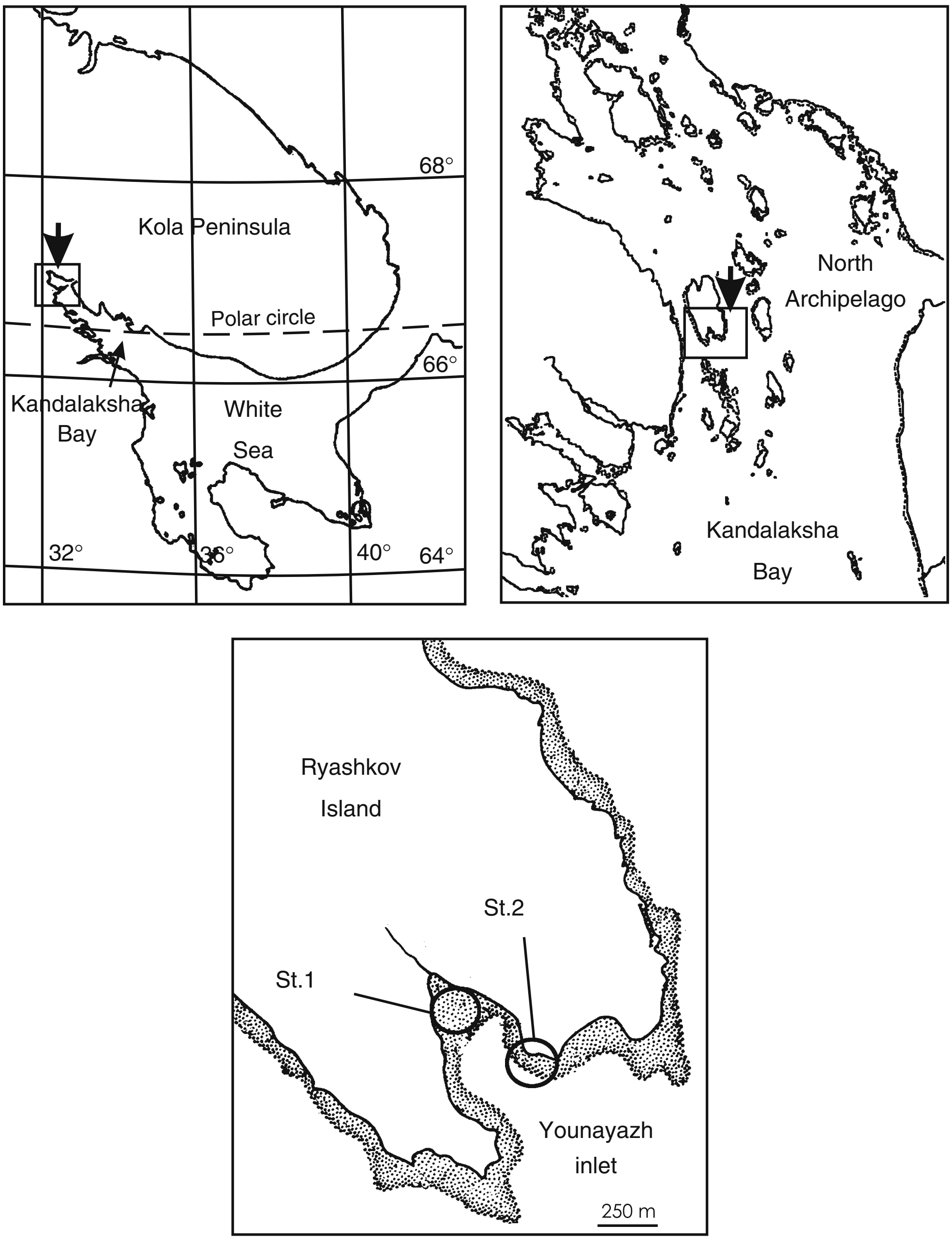

Fig. 2 Sample region and location of stations. Sample stations (Sts. 1 and 2) are *encircled*

material is given in Table 1). In 2005, the scheme of collections was more complicated: two types of samples were taken.

Samples of the first type were the same as in 2003–2004. They were taken on 24 May 2005, 2 and 3 June 2005 (Table 1). However, the isopods sampled on 24 May 2005 were not preserved immediately but placed alive in plastic dishes. After several hours they were dead, although the technique of alive animals' maintenance was fine-tuned in the previous years. The cause of their death is unclear.

According to our previous investigations (unpublished), dead *Jaera* individuals loose natural body proportions. Therefore, dead isopods from the first 2005 batch of samples were not measured, only counted. To correct the failure, new samples were taken (Table 1), where mass *Jaera* mortality was not observed.

Since the sampling period falls on the peak of sexual activity of *Jaera* in the region (our unpublished data), a sufficient number of coupling animals was easy to obtain in a short time. Therefore, in 2005, samples of the second kind were taken that provided material for

Table 1 General characteristics of the material

Sampling date	Station	Total number				Processing of the material
		Females	*J. albifrons* males	*J. ischiosetosa* males	*J. praehirsuta* males	
11.06.03	1	89	2	37	0	Females were measured and males were counted only
11.06.03	2	143	62	6	2	Females were measured and males were counted only
28.05.04	1	401	8	81	0	Females were measured and males were counted only
28.05.04	2	306	85	10	4	Females were measured and males were counted only
24.05.05	1	863	11	155	0	Animals were counted only
03.06.05	1	568	25	108	0	All animals were measured
24.05.05	2	304	102	3	58	Animals were counted only
02.06.05	2	112	0	0	56	All animals were measured
Mixed samples experiments						
27.05.05	1 + 2	604	123 (14)	99 (9)	71 (11)	All paired animals were measured
29.05.05	1 + 2	348	67 (18)	60 (11)	19 (7)	All paired animals were measured
01.06.05	1 + 2	366	56 (28)	63 (38)	31 (17)	All paired animals were measured

Numbers within parenthesis represent number of couples caught

“mixed samples” experiments (Table 1). After the samples from the two stations in a certain day were sorted, all alive animals were placed in one metallic enameled plate with a rugged bottom surface (90 cm^2) filled with fresh seawater. The animals were kept in the laboratory at 7–13°C (water temperature near the shore was 8°C at that time).

In the beginning of the experiment, the plate was shaken in order to mix the isopods. After the water had settled down, we started to catch the animals that demonstrated the “head-to-tail” pattern. Each pair was preserved in separate test tubes with 70% ethanol. Collection was carried out for 40–60 min and after that the plate was shaken again. Catching proceeded as described for 24–48 h in each experiment (3–6 catch periods for each sample). The experiments were repeated three times (Table 1) and their results were pooled for the analysis. The animals that did not demonstrate precopulating behavior were preserved in ethanol and later identified and counted.

The species of each preserved male was determined according to the key given in Kussakin (1988). All animals were pasted on slides with the bakelite–phenolic glue (BF-6) diluted with ethanol (70% of glue, 30% of ethanol and several drops of glycerin per portion). Paired animals were pasted together. For each animal, the body length (L) and the length of CZ (Lczf for females and Lczm for males) were measured, according to the scheme given in Fig. 3. Binocular microscope at 24× magnification with an ocular-micrometer was used. These measurements are further referred to as “absolute measurements”. Besides the absolute value, we used the relative one. The relative CZ length (RLcz) was calculated as a ratio as Lcz to L.

Since the distribution of Lcz and RLcz in most of the samples was different from normal (Kolmogorov–Smirnov test, $P < 0{,}01$), we used nonparametric Mann–Whitney’s U test for statistical comparisons. The rank Spearman coefficient was used for correlation analysis. Standard deviations are given as an estimation of variation in all cases.

Results

Species composition

Males of three *Jaera* species were present at the two stations (Table 2). The settlement at St. 1 was mostly formed by *J. ischiosetosa*; *J. albifrons* males were not numerous and *J. praehirsuta* males were not observed at all. This pattern of species composition was stable during the 3 years of investigation. Species composition at St. 2 changed from year to year. In 2003–2004, the population was dominated by *J. albifrons*; males of *J. ischiosetosa* and *J. praehirsuta* were rare. In 2005, a dramatic increase in the proportion of *J. praehirsuta* males was observed (Table 2). Samples that were taken

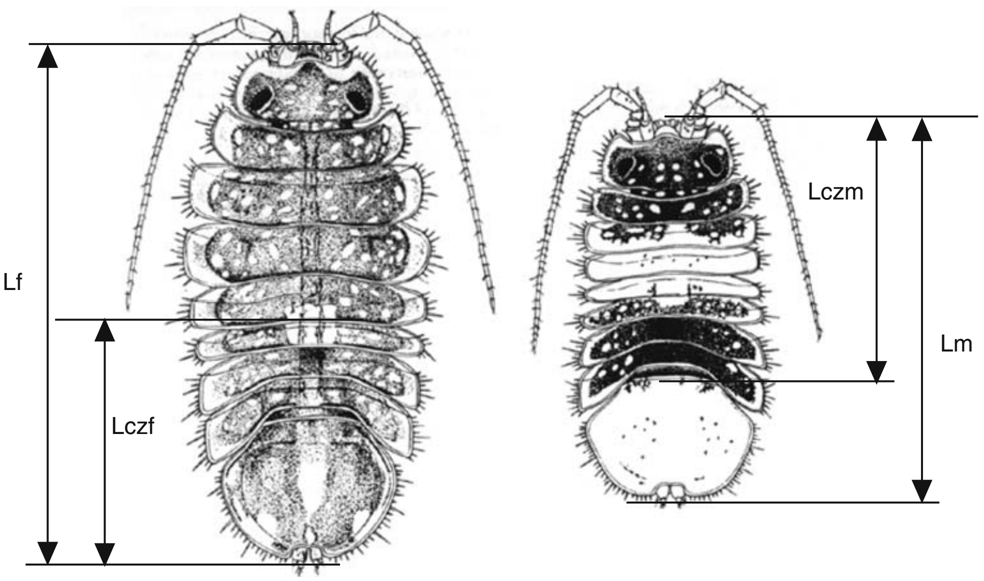

Fig. 3 A scheme of animals measurements. *Lm* and *Lf* body lengths of male and female, respectively. *Lczm* and *Lzcf* absolute lengths of coupling zone of male and female, respectively

Table 2 Proportion (%) of males of different species at the two stations in different years

Station	Year	*J. albifrons*	*J. ischiosetosa*	*J. praehirsuta*
St. 1	2003	5.1	94.9	0.0
St. 2	2003	88.6	8.6	2.8
St. 1	2004	9.0	91.0	0.0
St. 2	2004	85.9	10.1	4.0
St. 1	2005	12.0	88.0	0.0
St. 2	2005	46.6	1.4	52.0

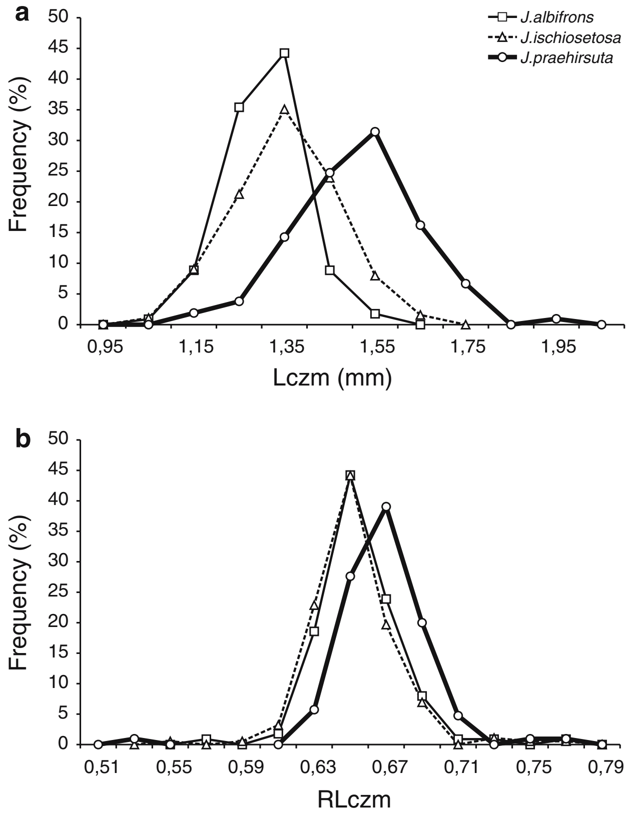

Fig. 4 Frequency distribution of absolute (**a**) and relative (**b**) length of CZ of males belonged to different species

on 2 July 2005 at St. 2 included only *J. praehirsuta* males (Table 1), but materials collected earlier (taken on 24 May 2005) showed the presence of all three species at this station.

Body parameters of males

Since the sampling size for males of all three species was large enough only in 2005, only this material was used for comparisons of male body parameters.

Frequency distributions of Lczm (Fig. 4a) and RLczm (Fig. 4b) were quite different in males of the three species. Mean values of Lczm and RLczm and the results of statistical testing are given in Tables 3 and 4.

It is obvious that *J. praehirsuta* males are slightly larger than males of the other two species. Moreover, they have different body proportions, which is expressed in a relatively longer CZ. Body proportions of *J. albifrons* and *J. ischiosetosa* seem to be indistinguishable. However, absolute measurements are slightly larger in *J. ischiosetosa* than in *J. albifrons*.

Table 3 Mean values (±SD) of absolute CZ length (mm) in males of different species and the results of interspecific comparisons by Mann–Whitney's test

	J. albifrons 1.29 ± 0.08	*J. ischiosetosa* 1.34 ± 0.11	*J. praehirsuta* 1.50 ± 0.13
J. albifrons	–		
J. ischiosetosa	***	–	
J. praehirsuta	***	***	–

***Differences significant at $P < 0.01$

Table 4 Mean values (±SD) of relative CZ length in males of different species and results of interspecific comparisons by Mann–Whitney's test

	J. albifrons 0.65 ± 0.023	*J. ischiosetosa* 0.65 ± 0.024	*J. praehirsuta* 0.67 ± 0.026
J. albifrons	–		
J. ischiosetosa	NS	–	
J. praehirsuta	***	***	–

NS Difference is not significant

***Differences significant at $P < 0.01$

Body proportions of females from populations with different species composition

Frequency distributions of RLczf (Fig. 5) across populations were significantly different every year (U test, $P < 0.01$ in all comparisons). On average, females from St. 1 have a larger relative CZ than females from St. 2. This pattern was stable throughout the investigation period. However, frequency distributions of absolute CZ length demonstrate certain changes from year to year (Fig. 6). At the same time, the differences in frequency distributions of Lcz across stations were also significant every year. In 2003–2004, the females from St. 2 had a significantly shorter CZ than those from St. 1. In 2005, a contrary pattern was observed: coupling zones of females from St. 2 were larger than those of females from St. 1.

Body parameters of paired animals in "mixed samples" experiments

In "mixed samples" experiments, males could choose partners from females of all the species present at the two stations. Noteworthy, according to the data presented in Table 2, *J. praehirsuta* and *J. albifrons* males used in these experiments are likely to come mostly from St. 2, while *J. ischiosetosa* males mostly come from St. 1.

Comparisons of absolute CZ length (Fig. 7a) display an obvious separation of Lczf-distribution of females from pairs with *J. albifrons* males. These females have a significantly shorter CZ than females from pairs with males of other species (Table 5). At the same time, the differences in absolute CZ length of females from pairs with *J. ischiosetosa* and *J. praehirsuta* males were not significant.

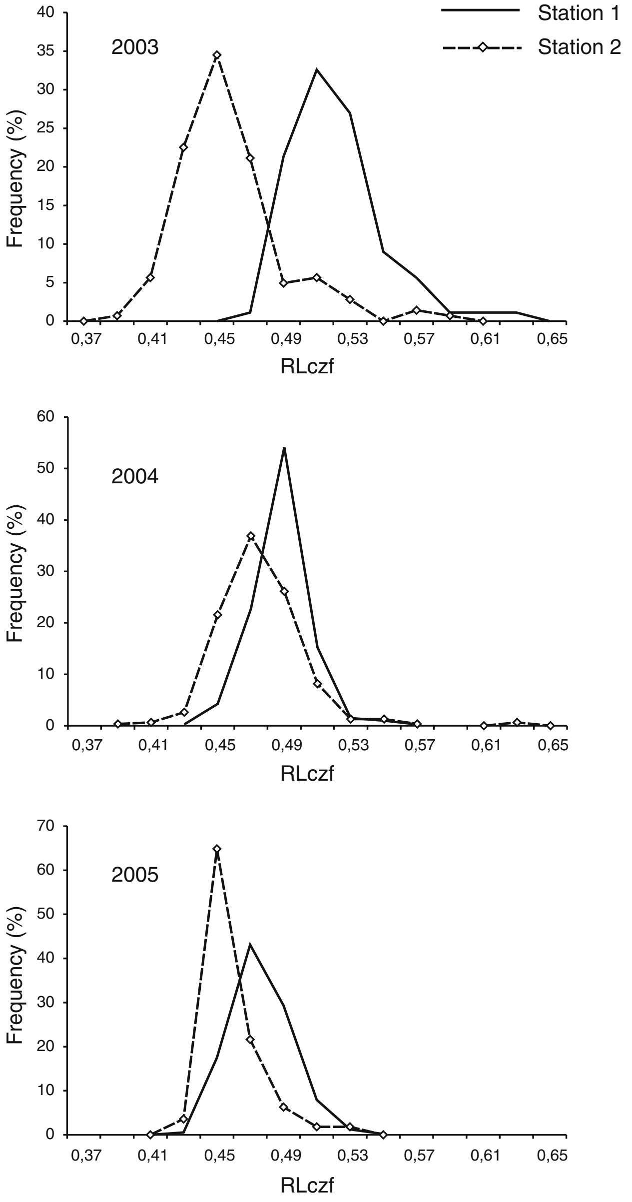

Fig. 5 Frequency distribution of relative length of coupling zone of females(*RLczf*) on two stations in different years

Females from pairs with *J. ischiosetosa* males have a significantly longer CZ in terms of relative length than females from pairs with *J. albifrons* and *J. praehirsuta* males (Table 6; Fig. 7b). The differences between RLczf of the latter two species were not significant.

Thus, in our experiments with "mixed samples", males of *J. ischiosetosa* preferably formed pairs with females that had larger relative coupling zones. Males

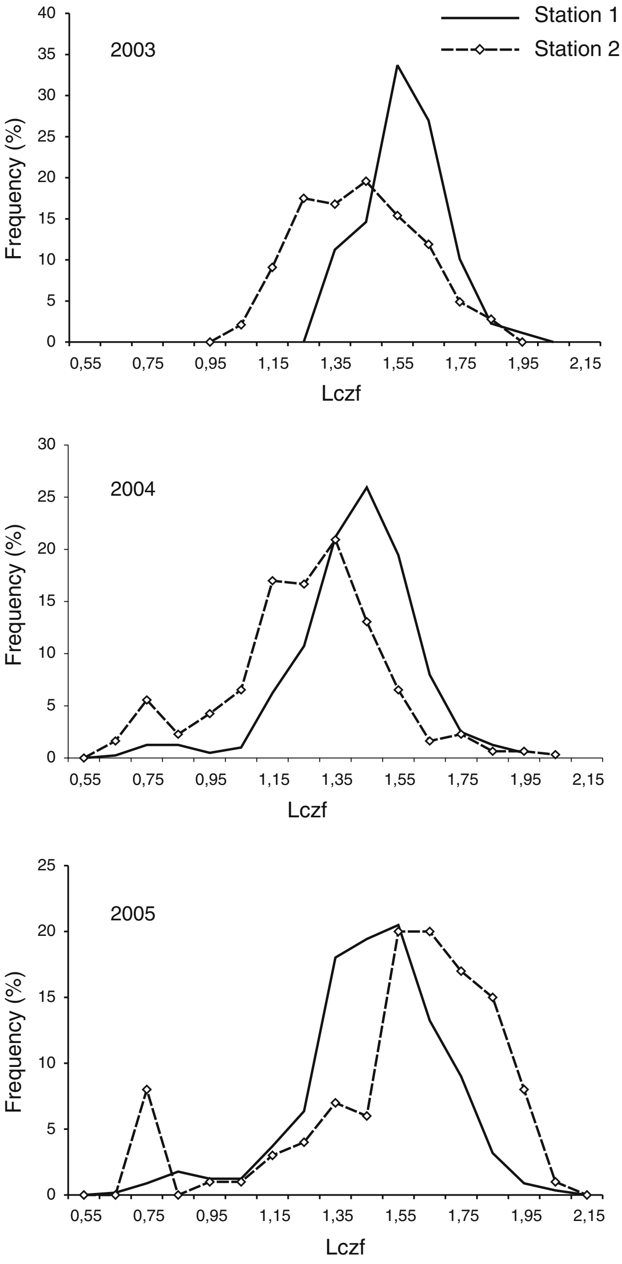

Fig. 6 Frequency distribution of absolute length of coupling zone of females (*Lczf*) on two stations in different years

of *J. praehirsuta* chose females with the largest absolute CZ size. Males of *J. albifrons* preferred females with the shortest CZ in terms of both absolute and relative length.

Correlation of body parameters of males and females

The materials of "mixed samples" experiments were used for analysis of correlations between parameters of males and females in pairs (Table 7). Rank Spearman coefficients were not significant for all the species taken separately. However, analysis of all pairs (without separation according to the species of the male) displays a significant correlation between the absolute size of both the body and the CZ of paired males and females.

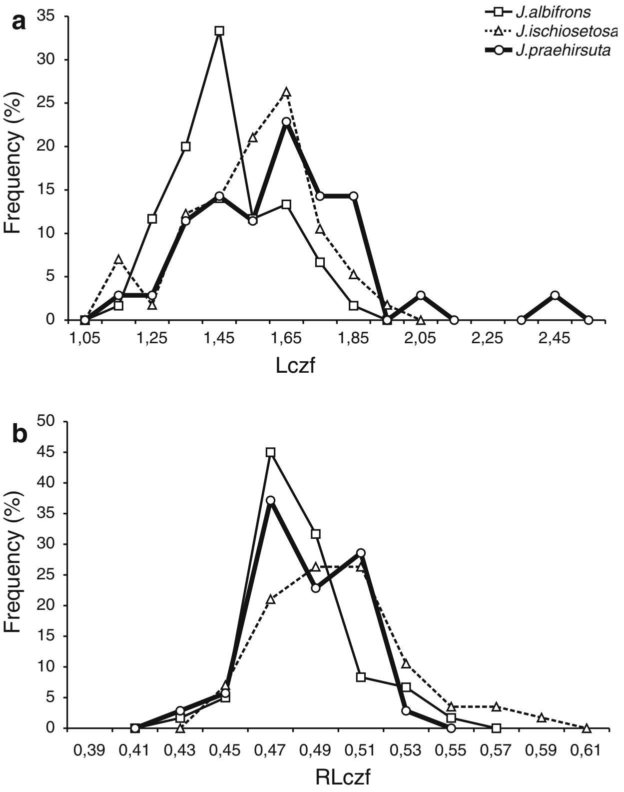

Fig. 7 Frequency distributions of absolute (**a**) and relative (**b**) length of coupling zone of females (*Lczf* and *RLczf*, respectively) from pairs with males of different species

Table 5 Mean values (±SD) of absolute CZ length (mm) of females from pairs with males of different species and results of interspecific comparisons by Mann–Whitney's test (significance levels are given)

	J. albifrons 1.46 ± 0.150	*J. ischiosetosa* 1.53 ± 0.178	*J. praehirsuta* 1.61 ± 0.247
J. albifrons	–		
J. ischiosetosa	0.010	–	
J. praehirsuta	0.001	NS	–

NS Difference is not significant

Discussion

The search for specific differences between females of "*J. albifrons*" complex has a long tradition. It was accepted that *Jaera* females had no unique morphological characters allowing species distinction (Forsman 1944; Bocquet 1953). At the same time, Solignac (1972) found significant ethological differences between species.

Table 6 Mean values (±SD) of relative CZ length of females from pairs with males of different species and results of interspecific comparisons by Mann–Whitney's test (significance levels are given)

	J. albifrons 0.48 ± 0.021	*J. ischiosetosa* 0.50 ± 0.030	*J. praehirsuta* 0.49 ± 0.021
J. albifrons	–		
J. ischiosetosa	0.001	–	
J. praehirsuta	NS	0.040	–

NS Difference is not significant

However, the above ethological differences do not have much value for female identification in most kinds of investigations. Therefore, several attempts to find structural characters that could be used for female identification were made. For example, Solignac (1978, 1981) tried to apply specific markers (color variations). However, this character is unsuitable for pilot investigations, when the researcher knows nothing about phenetic structure of populations in a certain area. Moreover, markers like these could not be found in several populations of the White and Barents seas (our unpublished data). All phenetic characters that were at first hypothesized to be specific were later encountered in populations with a different species composition. Molecular and cytogenetic methods are also useless for female identification because they only work *post factum*, even though they provide sound evidence of morphological or ecological variety at a species level. Thus, only morphological features of females may be applicable to identification.

It is well known that males of different species are fairly different as to parameters of allometric growth (Bocquet 1953; Solignac et al. 1990). An analogous analysis for females shows only slight differences that are impossible to use (Boitard et al. 1982; Solignac et al. 1990). In a work of Boitard et al. (1982), analysis of principal components was based on the width of segments and length of some parts of pereopods, cephalon and pleotelson. Females of different species were shown to be separate from each other at the level of the third component. These differences were not as obvious as those of males because of greater variability in females (Boitard et al. 1982).

Our analysis of body parameters shows that males of different species have both different CZ size and different body proportions in relation to the CZ. It means that secondary sexual characters of males (upon which species diagnoses are based) are not the only ones that can be used for species separation. Absolute CZ length in males (in 2005) increases in the following series: *J. albifrons*–*J. ischiosetosa*–*J. praehirsuta*. An analogous pattern of male CZ length distribution across the species was shown in 2003 (Kuzmin and Khaitov 2004).

Presence of differences in absolute and relative CZ length between males leads us to expect differences like these between females. If this hypothesis is correct, a significant difference in female body parameters between groups of individuals of various species should be observed. We used two criteria for separation of females into groups with presumptively different species composition: ecological differences between populations and male choice experiments.

The pattern of species distribution observed in this investigation (in analysis of males) agrees with the results presented by Jones (1972a) who showed that *J. ischiosetosa* was the most euryhaline form of the "*J. albifrons*" complex. It may live on stones in freshwater streams crossing the intertidal zone at low tide, whereas the other species tend to inhabit more saline areas (Naylor and Haahtela 1966). In the investigation area, the majority of *J. ischiosetosa* individuals were found in the mouth of a stream, while individuals of other species are far from the stream's influence.

Species composition at St. 1 was relatively stable from year to year. However, a dramatic increase in *J. praehirsuta* proportion was observed at St. 2 in 2005. This was probably associated with an unusually strong gale that destroyed the fucoid belt in the investigation area in the end of August 2004. Sampling at St. 2 in 2005 was much more difficult than in the previous years. The isopods were by far less numerous, so we

Table 7 Spearman correlations between body parameters of mates in pairs with males of different species

Body parameters	Species of males in pairs			All pairs
	J. albifrons	*J. ischiosetosa*	*J. praehirsuta*	
Lm versus Lf	0.04	0.24	0.15	0.28***
Lczm versus Lczf	0.15	0.13	0.21	0.31***
RLczm versus RLczf	−0.10	0.13	0.13	−0.05

Significant correlations are marked with asterisks

Lm and *Lf* body lengths of male and female, *Lczm* and *Lzcf* absolute lengths of coupling zone of male and female, *RLczm* and *RLczf* relative lengths of coupling zone of male and female respectively had to process huge amounts of fucoids to procure the necessary material. It is possible that *J. praehirsuta* that partly replaced *J. albifrons* at this site arrived there from the low intertidal or the upper subtidal zone.

Jaera is known to form local assemblages (Piertney and Carvalho 1995a, b; Bek 1988). This may account for the fact that in one of the samples at St. 2 (2 June 2005, Table 1) males of *J. praehirsuta* were exclusively found, although samples were made at the same place by the same methods. Local assemblages of *J. praehirsuta* had never been found during previous investigations. However, the partial replacement of *J. albifrons* by *J. praehirsuta* in 2005 provided an additional possibility to test female population structure because changes in the number of males of a certain species should probably be accompanied by changes in the number of its females.

Results of female body parameters analysis confirm that the difference in distribution of males and temporary changes in species composition correlate with size-frequency distributions of females. Thus, at Sts. 1 and 2 both the size and the body proportions of females were significantly different. In 2003–2004, females demonstrated lesser values of absolute and relative CZ length at St. 2, where *J. albifrons* males were numerous, than at St. 1, where *J. ischiosetosa* males dominated.

In 2005, when *J. praehirsuta* expansion was observed, frequency distribution of absolute female CZ length at St. 2 shifted to the region of larger values. As follows from frequency distribution of absolute female CZ length (Fig. 6) in 2005, *Jaera* population at St. 2 was dominated by larger females than in previous years. At the same time, values of *relative* CZ length of females were smaller at St. 2 than at St. 1. Thus, in terms of RLcz, females in the population dominated by *J. praehirsuta* males differ from females in the population dominated by *J. ischiosetosa* males in the same way as the latter differ from females in the population dominated by *J. albifrons* males.

To sum up, *Jaera* females, on average, have a larger relative CZ length in populations where *J. ischiosetosa* males are numerous than in populations where *J. albifrons* or *J. praehirsuta* males are numerous. Values of absolute CZ length in females are lower in populations dominated by *J. albifrons* males than in populations dominated by *J. praehirsuta* males.

However, ecological separation of males does not necessarily mean that females are ecologically separated in the same way. Moreover, the differences observed between frequency distributions of body parameters may be explained otherwise (e.g., growth pattern may change under different conditions). To avoid this uncertainty, male choice experiments were performed.

In experiments with crossbred males (hybrids of *J. albifrons* and *J. ischiosetosa*), males that “contain” more “*albifrons* genes” chose more willingly *J. albifrons* females (Solignac 1978). Thus, male choice experiments may allow us to divide females into species groups, although this grouping will certainly have probabilistic nature because confuses in male choice are quite frequent (Solignac 1978).

Since in our “mixed samples” experiments significant differences were found between females chosen by males of different species, we may conclude that males of different species formed pairs non-randomly. Thus, values of relative CZ length of females chosen by *J. albifrons* and *J. praehirsuta* males were less than those of female chosen by *J. ischiosetosa* males. These results agree with those of RLczf frequency distribution analysis of females collected at different stations (see Fig. 5 and the above discussion). The values of absolute CZ length of females chosen by *J. praehirsuta* males were the largest. This fact corresponds with the results of frequency distribution analysis at two stations in 2005 (Fig. 6) and with the values of males’ body parameters (Table 3; Fig. 4). Analogously, females with a short CZ are chosen by *J. albifrons* males with the shortest CZ.

Summing up all the results, we may propose the following draft scheme of species differentiation for females. Individuals with a large relative CZ length (more than 0.49–0.50 or, in usual terms, more than a half of body length) may be considered as females of *J. ischiosetosa*. It should be noted that an experienced researcher can easily evaluate this ratio without measuring. Females with a short relative CZ (less than a half of the body length) may be identified as *J. albifrons* or *J. praehirsuta*. Separation of females of these species may be based on the absolute CZ length: females of *J. praehirsuta* are larger then those of *J. albifrons* (concrete values of CZ length may probably differ in different areas). The proposed scheme of female identification should be confirmed by an analysis of male species composition and verified further by molecular, genetic and karyological methods.

The last question to be discussed in the context of identification of *Jaera* females concerns sympatric coexistence of three species that are able to produce hybrids. Possible mechanisms of this coexistence were studied and reviewed by Solignac (1972, 1978, 1981). Ecological and ethological differences were shown to be pre-copulation factors, and hybrid inferiorities, a post-fertilization factor (Solignac 1981). Our results suggest one more pre-copulative isolation mechanism based on size incompatibility of coupling zones of males and females of different species. We found a certain correlation between absolute length of coupling zones of partners. It was negligible within one species but quite significant for all sets of pairs (Table 7). It means that males of different species tend to choose females of their own size class. This mechanism is certainly statistical and effective only in combination with other isolation forces.

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