Spatial variability in the population structure of the shore crab *Carcinus maenas* (Crustacea: Brachyura) in a shallow-water, weakly tidal fjord

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ABSTRACT: The spatial variability in population structure of the shore crab *Carcinus maenas* was studied in a shallow-water fjord in the island of Fyn, Denmark. The fjord comprises an enclosed area which is geomorphologically divided into a shallow cove (mean depth 2 m), known as Kertinge Nor, and a deeper narrow area, closer to the open sea, known as Kerteminde Fjord. Tidal range is small (ca 20 cm). Sex-ratio favoured males at most of the sites sampled with the exception of the inland slope between the shallow Kertinge Nor and the deeper Kerteminde Fjord, which apparently was a spawning site. Crab densities were much higher in Kerteminde Fjord than in the shallower Kertinge Nor. Ventral carapace colour varied between green and orange-red, with the proportion of the green morphotype increasing with increasing distance from the open sea. Analysis of the population size structure identified 3 differentiated areas for both male and female crabs. Sites closer to the mouth of the fjord were characterized by a numerical dominance of small crabs, whereas crabs in Kertinge Nor were clearly of a much larger size. Sites in Kerteminde Fjord were characterized by a wider range of sizes. Some crabs in Kerteminde Fjord carried epibionts on the carapace, but those were absent in crabs from Kertinge Nor, moreover, a few crabs in Kertinge Nor carried *Mytilus edulis* byssus threads indicating that epibionts had fallen from the carapaces. Thus, population structure characteristics, such as colour morphotype proportions, size structure and occurrence of epibionts, are in accordance with the occurrence of a high degree of environmental variability in the area decreasing towards the mouth of the fjord and the open sea.

KEY WORDS: *Carcinus maenas* - Population structure - Crabs - Brachyura

INTRODUCTION

The shore crab *Carcinus maenas* (L.) is a widely distributed species inhabiting European Atlantic coasts and estuaries. It is also present on the North-American Atlantic coasts (Berrill 1982) and has recently colonised some areas in southern Africa, Australia and the Pacific coast of North America (Cohen et al. 1995). Its populations are known to show phenotypic variability which appears to be adaptively adjusted to the high variety of environmental conditions that this species can withstand (Reid et al. 1989). *C. maenas* is known to occur from the high intertidal, where megalopae settle and metamorphose (Zeng et al. 1997), down to a maximum depth of around 60 m, although usually the numbers of crabs are greatly reduced below 20 m (Crothers 1968, Ingle 1980, 1983, Clark 1986). It is also common in estuaries (McVean & Findlay 1979, McGaw & Naylor 1992a). Adult individuals migrate up and down the shore with the tide, whereas juvenile crabs tend to remain in the high intertidal zone (Dare & Edwards 1981, Hunter & Naylor 1993, Warman et al. 1993). The species is therefore exposed to highly variable environmental characteristics, some of which vary cyclically and to which the species has evolved adaptive rhythmic behaviour controlled endogenously (Naylor 1985, 1988).
Variability in population characteristics should therefore reflect the phenotypic adaptive responses shown by individual crabs in relation to their ability to withstand environmental variability. Thus, different physiological and behavioural responses are known to take place in *Carcinus maenas* in relation to sex, size, and time elapsed in intermoult since the last moult (Reid et al. 1989, Kaiser et al. 1990, McGaw & Naylor 1992b, McGaw et al. 1992, Warman et al. 1993, Aagaard et al. 1995). Time since the last moult can be recognised by gradual changes in the ventral colouration of the crab from green in the early intermoult to orange and red forms if intermoult is prolonged (Reid et al. 1989, Kaiser et al. 1990, McGaw et al. 1992). A differential response to changes in salinity, oxygen content, and mating success is known to take place among the different colour phenotypes of the species (Reid et al. 1989, Abelló et al. 1994) and is reflected in different behaviour and distributions on the shore in tidal areas (Hunter & Naylor 1993, Warman et al. 1993). However, not much is known on the ecophysiology and behavioural ecology of *Carcinus* spp. from non-tidal areas, such as the almost tideless Baltic Sea (Rasmussen 1973, Warman et al. 1991, Aagaard et al. 1995).

The study site, Kerteminde Fjord, a shallow-water, weakly tidal Danish fjord, is considered to be an unstable eutrophic ecosystem (Riisgaard et al. 1995). *Carcinus maenas* thrive in this habitat (Aagaard et al. 1995) and considerable variability in the degree of environmental stress experienced by the crabs in this relatively small area, particularly quick salinity and temperature changes, is known to take place (Jørgensen 1995, Petersen & Svane 1995, Riisgaard et al. 1996). The present study therefore set out to analyse variability in population characteristics of *C. maenas* in such a locality, which could be related to the degree of environmental variation to which the population is subjected.

**MATERIALS AND METHODS**

Sampling was carried out in Kerteminde Fjord (Fig. 1), a shallow water fjord located in the northern part of Fyn, near Odense, in Denmark (55°26' N, 10°37' E). Two geomorphologically different subareas can be identified: the one nearest to the open sea, the actual Kerteminde Fjord, is narrow and relatively deep (4 to 7 m), whereas that farthest from the open sea, known as Kertinge Nor, is a shallow cove of less than 3 m depth. Salinity varies typically between 14 and 27% over the year (Riisgaard et al. 1995, 1996), and tidal range varies between 10 and 30 cm (Aagaard et al. 1995, Petersen & Svane 1995).

A total of 12 sampling stations were distributed in a sea-to-land gradient (Fig. 1). All stations were located at a depth of approximately 2 m, where crabs were known to be abundant. Crab sampling took place using unbaited fixed eel-nets (fyke nets; Nedelec 1975) consisting of 2 funnel conical nets linked by a 70 cm high vertical net which intercepted the movements of the crabs. Each net cone was 3.5 m long with an entrance diameter of 70 cm, narrowing down to 30 cm and with 3 built-in funnels to prevent crabs from escaping the net. The nets were left overnight, the period of highest activity for the species in the study area (Aagaard et al. 1995). Sampling was performed on 4 consecutive days in April 1993. All crabs caught were counted and examined for sex, size (carapace width, CW, to the nearest mm), reproductive condition (occurrence of ovigerous females), colour morphotype ('green' and 'red'; according to McGaw et al. 1992), oc-
currence and type of epibionts, and chela loss. A total of 3915 crabs (2036 males and 1879 females) were examined.

The significance of deviations between observed and expected (1:1) sex-ratio was tested with a G-test (Sokal & Rohlf 1981). Cluster analysis based on the resemblance between size frequency distributions by site was applied to male and female crabs by using Czekanowski’s percentage similarity index (Goodall 1978) as the similarity index and the UPGMA (Un-weighted Pair Group Method using Arithmetic Averages) as the aggregation algorithm. Czekanowski’s percentage similarity index \( PS = 2 \cdot \frac{\sum \min(x_i, y_i)}{\sum (x_i + y_i)} \) is a measure of the intersection surface in relation to the reunion surface of 2 equal area frequency distributions. LAW1 software (J. Lleonart unpubl.) was used to perform the analysis.

RESULTS

Patterns of abundance

The overall and per sex catch per unit effort (CPUE, expressed as number of crabs caught per eel-net per night) per sampling site (Fig. 2) shows that the highest densities, of over 100 crabs, were found throughout Kerteminde Fjord to the mouth of Kertinge Nor, i.e. between Sites 2 and 7 to 8. Densities were much lower throughout the shallow Kertinge Nor, between Sites 8, 9 and 12.

Densities of male crabs were generally much higher than those of female crabs, with the exception of Sites 4, 5 and 12. Female densities were highest at Site 5.

The highest relative proportions of male crabs were found in Kertinge Nor. Sex-ratio significantly favoured males at Sites 1, 3, 7, 8, 9, and 11, and significantly favoured females at Sites 4 and 5 (Fig. 3).

Colour morphotype variability

The proportion of green crabs clearly increased from the sites located near the mouth of Kerteminde Fjord, which had the lowest proportion of green crabs, to those in Kertinge Nor (Table 1). Thus the male population varied between 46.3% green crabs at Site 1 and 88.6% at Site 11. A similar pattern was also exhibited by female crabs, with the proportion of the green morphotype ranging from 20.7% at Site 1 (that nearest to the open sea) to 68.8% at Sites 8 and 10, in Kertinge Nor.

Population size structure

Figs. 4 & 5 show the size frequency distributions obtained for males and females, respectively, differentiating between green and red colour morphotypes, in 3 mm CW size classes. There was a clear tendency for size to increase from Kerteminde Fjord to Kertinge Nor in both male and female crabs. Thus, mean male size increased from 40.5 mm CW at Site 1 near the mouth of Kerteminde Fjord to 61.3 mm CW at Site 12 at the farthest end of Kertinge Nor (Table 1), whereas in females, mean size increased from 37.0 mm CW at Site 1 to 53.1 mm CW at Site 10 or 52.5 mm CW at Site 12 in Kertinge Nor. Other descriptors of the distributions, as

![Fig. 2. Carcinus maenas. Catch per unit effort (CPUE, expressed as number of crabs caught per eel-net per night) per sampling site, as total number and number of male and female crabs caught per eel-net per night.](image2.png)

![Fig. 3. Carcinus maenas. Sex-ratio, as percentage male crabs, at each sampling station, with indication (stars) of those samples which showed a significantly different proportion from a theoretical 1:1 sex-ratio.](image3.png)
Table 1. *Carcinus maenas*. Characteristics of the population sampled in Kerteminde Fjord per sampling site in April 1993. CPUE: catch per unit effort, in number of individuals caught by eel-net per night; size: carapace width, in mm; SD: standard deviation; byssus: *Mytilus edulis* byssus threads on the carapace.

<table>
<thead>
<tr>
<th>Site</th>
<th>Samples taken</th>
<th>Total number</th>
<th>Number of males</th>
<th>Number of females</th>
<th>% males</th>
<th>Males</th>
<th>Females</th>
<th>% green males</th>
<th>% green females</th>
<th>% ovigerous females</th>
<th>% with epibions</th>
<th>% with barnacles</th>
<th>% with algae</th>
<th>% with hydrozoans</th>
<th>% with mussels</th>
<th>% with byssus</th>
<th>% males with chela loss</th>
<th>% females with chela loss</th>
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Median and modal values, also showed this tendency to increase with increasing distance from the mouth of the fjord (Table 1). Large crabs, as shown by the maximum sizes found at each site, occurred at most stations from Site 3 onwards, but the minimum size clearly increased following the same tendency as mean size (Table 1).

To compare and establish similarities among the samples based on the resemblance in shape of size frequency distributions, samples were compared by means of the percentage similarity index to create a similarity matrix among all of the samples. Samples were accordingly grouped to build a graphic dendrogram (Fig. 6). This descriptive technique allowed the identification of discrete areas in the fjord which showed a high degree of similarity in the size structure of the crab population sampled. Cluster analysis showed a high degree of classification, with a high cophenetic correlation (0.678 for males, 0.829 for females) and a low degree of enchainment (0.218 for males, 0.127 for females). Thus, 3 main groups of samples were identified for both male and female crabs according to their size frequency distribution resemblance. The first dichotomy of the 2 dendograms clearly separated the samples from Kertinge Nor (Sites 7 to 12) from those in Kerteminde Fjord (Sites 1 to 6). Within the samples from Kerteminde Fjord, those nearest to the mouth of the fjord formed a distinct group (Sites 1 and 2 in males, Sites 1 to 3 in females).

**Epibionts**

A few crabs were found carrying marine macroepibionts, especially barnacles algae, mussels and hydrozoans, on their carapaces (Table 1). However, only the crabs in Kerteminde Fjord (at Sites 1 to 5) were found to carry epibionts on their carapaces, whereas none of those collected in Kertinge Nor were. Furthermore, a few crabs were found with *Mytilus edulis* byssus threads attached to their carapaces, indicating that those crabs had previously carried mussels, but that they had fallen off.
Fig. 4. *Carcinus maenas*. Size frequency distribution of males at each sampling station in 3 mm carapace width size classes, showing red (shaded) and green (clear) colour morphotypes.

Fig. 5. *Carcinus maenas*. Size frequency distribution of females at each sampling station in 3 mm carapace width size classes, showing red (shaded) and green (clear) colour morphotypes.

Chela loss

The proportion of male crabs with chela loss ranged between 2.7% at Site 1 and 17.2% at Site 12. The proportion was clearly higher in Kertinge Nor than in Kerteminde Fjord (Table 1). In females, however, this tendency was not as marked, probably due to the small number of female crabs captured at Sites 10 to 12.

DISCUSSION

Kerteminde Fjord is a eutrophic ecosystem with high physical and biological variability in which the biological structure is controlled by the interactions between primary producers (phytoplankton, macroalgae and seagrass *Zostera marina*), suspension feeders (especially the ascidian *Ciona intestinalis*) (Petersen & Riss-
Increasing proportion of green crabs in the fjord is consistent with the occurrence of environmental variability in conditions. Thus, the pattern observed in the present field study is consistent with the ecological and physiological differences reported in the literature between the 2 colour morphotypes.

Differences in the crab population size structure observed within the fjord allowed the detection of 3 well-differentiated, and rather internally homogeneous, areas in the fjord. Although large crabs can be found throughout the fjord, it is the smaller crabs which appear to be most affected by the environmental conditions in Kertinge Nor, since they seem to avoid the area.

The strongly biased sex-ratio towards the females at the inland slope between the shallow Kertinge Nor and the deeper Kerteminde Fjord (Sites 4 to 5) and the fact that most of them were found to be spawning or ready to spawn, indicates that the area was apparently a spawning site.

The absence of epibionts on the carapaces of crabs from Kertinge Nor, and in particular the occurrence of mussel byssus threads, further support the view of the occurrence of strong environmental variability in Kertinge Nor. This suggests that marine epibiont organisms could not tolerate the environmental conditions found in the shallow area, as indicated by mussels, which apparently could no longer adhere to crab carapaces. In fact, only small individuals of Mytilus edulis have been reported in Kertinge Nor, as epibionts on Zostera marina (Petersen & Svane 1995).

Chela loss was also higher in Kertinge Nor than in Kerteminde Fjord. The most important factors affecting the degree of chela loss in crabs are predation and intraspecific conflicts (McVean & Findley 1979, Smith & Hines 1991, Abello et al. 1994). Since there is no evidence to suggest that predation on crabs may be higher in Kertinge Nor, the higher degree of chela loss in Kertinge Nor is probably due to a size effect, since chela loss is higher in larger-sized crabs, especially in males (Abelló et al. 1994), which have a larger foraging range than juveniles.

In conclusion, the present study revealed the occurrence of strong internal variability in the population characteristics of the crabs inhabiting a shallow-water fjord which is consistent with the occurrence of a gradient of environmental variability along the studied area.

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