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Shoaling preferences in decapod crustacea

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The aggregation behaviour of fish has been extensively studied, but little is known about the shoaling of marine invertebrates. We investigated aggregation behaviour in two species of a decapod crustacean: the brown shrimp, *Crangon crangon*, a cryptic species that should not rely on aggregations to avoid predation, and the rockpool prawn, *Palaemon elegans*, a species that lives in areas without shelter and we expect to aggregate. A field survey revealed that prawns had a strongly clumped distribution, whereas shrimps only showed a tendency towards aggregating. However, size segregation was found to be strong in both species. Choice experiments in the laboratory confirmed the field results on the differences in the aggregative tendencies for the two species, as prawns showed a strong preference for shoaling with a group of five conspecifics versus a single conspecific, while shrimps only showed a trend in that direction. Surprisingly, we found no evidence for a size-assortative preference in prawns, suggesting that size segregation in the field might be a consequence of indirect or passive factors rather than individual preferences.

Keywords: *Crangon*; grouping; *Palaemon*; prawn; shoaling; shrimp; size assortativeness; sociality

Aggregation, the grouping of conspecific individuals, may be the result of density-independent responses to local cues or of the response of individuals to other members of the population. It is important to distinguish between these two types of aggregation as this difference reflects on the ecology and evolution of the species involved. Much of the research effort on grouping in the aquatic environment has focused on fish models, and this has provided the basis for our current understanding of grouping behaviour (Krause & Ruxton 2003). Such studies have shown that aggregations of some fish species can be attributed to the independent response of individuals to a common external stimulus, such as a gradient of light, temperature, water currents or food (Shaw 1978). In contrast, social groups are formed through the mutual attraction of conspecifics, with individuals having an innate gregariousness that has evolved in response to some selective advantage of grouping. Thus, to assess the extent to which a species is socialwe must examine the behaviour of the individual (Hamner 1985).

The extent to which size assortment occurs within social groups is also of interest to behavioural ecologists. Shoals of many fish species, as well as aggregations of tadpoles and invertebrates, are noted to be remarkably uniform in terms of the size of member individuals, both in the laboratory (Pitcher et al. 1986; Ranta & Lindström 1990) and in the wild (Ritz 1994; Krause et al. 1996; Peuhkuri et al. 1997). Size segregation within a group, like grouping itself, could conceivably result from various external factors or biological constraints (e.g. swimming speed: Watkins et al. 1992). Alternatively, it could be generated by behavioural preferences of component individuals, if size assortativeness is selected (e.g. to minimize competition with superior individuals, or to avoid being targeted by predators as the 'odd' individual in the group; Landeau & Terbough 1986; Krause & Ruxton 2003). Laboratory choice experiments show that individual fish will preferentially associate with conspecifics of similar body size (Ranta & Lindström 1990; Krause & Godin 1994), suggesting that at least some fish are able to assess their own body size relative to that of their neighbours and use the information this provides to assort themselves by size within and between shoals.

Whilst the shoaling tendencies of fish have received widespread attention, little empirical work has addressed the decisions faced by aquatic invertebrates, despite many

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reports of marine invertebrate aggregations (e.g. Hardy 1936; Catteral & Poiner 1983; Watkins 1986; Goswami 1994; Hunt & Seibel 2000). Many of these groups appear to behave in a remarkably similar way to fish, leading Ritz (1994) to suggest that in the case of krill (order: Euphausiacea), they are best considered 'small sardines'. We attempted to address this deficit of knowledge by examining the social tendencies of small decapod crustacea, adopting an approach similar to the one used in the early work on fish models. We selected two crustacean species with different ecologies, the brown shrimp, *Crangon crangon* and the rockpool prawn, *Palaemon elegans*, allowing us to test predictions on the strength of sociality. The brown shrimp is found in shallow waters with a sedimentary substrate (Tiews 1970) and remains buried during the day, emerging at night to hunt. Shrimps are mottled grey or brown in colour (Smaldon 1979) and when viewed against a background of sand this appearance is highly cryptic (S. R. Evans & M. Finnie, personal observations). Other Crangonids are known to rely on burrowing into the sediment to evade predators (Lloyd & Yonge 1947) and it seems reasonable to suppose that this is true of the brown shrimp. Aggregation may be deleterious to a cryptic species (Harvey & Greenwood 1978; Butler et al. 1999) if it increases conspicuousness; the best predator defence for shrimps may therefore be to limit movement and rely on camouflage. We therefore predict that they will show low levels of sociality. In contrast, prawns are found in midtidal rockpools and along harbour walls (Smaldon 1979), where sediment is not available as a concealing medium. Landeau & Terbough (1986) point out that intraspecific gregariousness is most common amongst species occupying open habitats that offer little opportunity for concealment. Assuming that in their natural habitat they are unable to hide themselves as individuals, we thus predict that prawns will actively aggregate with conspecifics, reducing their personal predation risk through the dilution effect. In this way, the differences in the ecology of the two crustacean species are perhaps analogous to contrasts between different piscine taxa. For example, as with the shrimp, flatfish have a highly cryptic appearance and rely upon immobility, burial and crypsis as antipredatory defence mechanisms (Ryer et al. 2004). Indeed, the common sole, *Solea vulgaria*, like the brown shrimp, is a nocturnal species that remains buried and motionless during the day (Kruuk 1963). On the other hand, the high sociality of conspicuous species such as sticklebacks, *Gasterosteus aculeatus*, has made them popular models for studies of grouping behaviour (Krause & Ruxton 2003).

The contrasting ecology of the two species leads us to predict that whilst prawns will express sociality at the individual level in the laboratory this will be absent in the shrimps. The consequences of Landeau & Terbough's (1986) 'oddity effect' lead us to make an additional prediction concerning the behaviour of prawns: that the prawn population in the field will be sorted with respect to size, and that in a binary choice test in the laboratory, individual prawns will associate with similarly sized conspecifics. Size assortativeness should be absent in shrimps, given that they appear to rely on crypsis rather than group defence to evade predators.

METHODS

Study Site and Species

We carried out the study in August 2004 at the town of Wells-next-the-sea, Norfolk. A preliminary survey with a sweep net indicated that there were large populations of both prawns and shrimps at the study site and suggested that they were segregated by habitat type. Using Smaldon (1979), the prawns were identified as *P. elegans* (Palaemonidae), and the shrimps as *C. crangon* (Crangonidae).

Field Survey of Shoaling Patterns

We sampled two 245 m transects: at Wells Harbour wall (grid reference, GR: TF918438) and Stonemeal Creek (GR: TF926438). Using a square-framed pond dipping net with 250 mm sides, we took 61 sweeps at approximately 4 m intervals at each site. A previous pilot study at the two locations had shown that body size in both species followed a discrete, multimodal distribution (a common occurrence in decapod crustacea; Lloyd & Yonge 1947; Forster 1959), which allowed separation into three size classes (defined by the distance between the tip of the rostrum and the end of the telson): small (10–30 mm), medium (30–40 mm) and large (>40 mm). For each sweep, the number of individuals of each species and size class was recorded, before the catch was returned to the water. Surveys were carried out by moving upstream to minimize the disturbance of areas yet to be sampled, and we consider it unlikely that single individuals would have been sampled more than once. For the subsequent analyses, the two survey sites (Wells Harbour and Stonemeal Creek) were treated as exclusive habitats for prawns and shrimps, respectively. This was justified by the absence of shrimps at the Wells Harbour site and the near-absence of prawns at the Stonemeal Creek site (a single prawn was recorded).

To characterize the distribution pattern of the two populations, Fisher's dispersion index (DI; Fisher 1950) was calculated for each transect, pooling all the individuals caught in each sweep irrespective of their body size. A distribution can be classed as random ($\mathrm{DI} = 1$), clumped ($\mathrm{DI} > 1$) or uniform ($\mathrm{DI} < 1$). Departure from randomness was formally tested by comparing the observed distribution of frequencies with the expected Poisson distribution fitted to the data (using a chi-square test).

The survey data also allowed us to examine whether size assortment occurred in the natural environment. Under the assumption that the distribution of individuals with respect to size was random, the expected probability of a sweep catching individuals all belonging to the same size class could be calculated as:

$$\begin{aligned}&\mathrm{Prob}(\text{fully size-assorted group of size } n)\\&\quad = P(s)^n + P(m)^n + P(l)^n\end{aligned}$$

where $P(s)$ represents the proportion of individuals in the whole population belonging to the small size class, $P(m)$ to the medium size class and $P(l)$ to the large class. The number of expected size-assorted groups (E) was compared