Habitat structure, population abundance and the opportunity for selection on body weight in the amphipod *Eogammarus oclairi*

Received: 21 November 1995 / Accepted: 24 May 1996

Abstract The importance of oyster-shell habitat-characteristics (depth of the shell layer or degree of fragmentation) to the amphipod *Eogammarus oclairi* were studied in Grays Harbor estuary (Washington, USA) in regard to their effect on local density of *E. oclairi*, the risk of predation by juvenile Dungeness crabs *Cancer magister*, and the opportunity for selection on body weight during pairing. *E. oclairi* was the most abundant macrofaunal species in the intertidal oyster-shell assemblages (density range = 20 to 8500 amphipods m\(^{-2}\)), and its density was positively correlated with the depth of the oyster-shell layer (\(r = 0.85, n = 30, p < 0.005\)). Field experiments showed that amphipod density was much lower when oyster shells were whole (\(x = 340.7 \pm 72.1, n = 10\)) as opposed to fragmented (\(x = 41.4 \pm 9.3, n = 10\); \(t_c\) (Welch's approximate \(t\)-test) = 13.0, \(df = 9.3, p < 0.05\)). Densities of a predator, juvenile *C. magister*, were not affected by depth of the shell layer nor by degree of fragmentation (whole shell, \(x = 14.6 \pm 13.0\) crab; fragmented shell, \(x = 18.7 \pm 2.4\) crab; \(t_c = 0.83, df = 9.7, p > 0.05\)). Predation rate on single amphipods by crabs did not differ between habitat types (whole shells vs fragmented shells), but mating pairs were consumed more often in the whole-shell treatment (whole shell, \(x = 0.9 \pm 0.8\); fragmented shell, \(x = 0.1 \pm 0.3\)). There were no differences in the size of single amphipods (both sexes) consumed between treatments, or in the size of the paired males consumed. Field experiments showed that the opportunity for selection (\(i\)) on male body weight increased with increasing amphipod density which, in turn, increased with increasing degree of shell fragmentation (whole-shell treatment, \(i = 0.0014 \pm 0.0002\); fragmented-shell treatment, \(i = 0.3756 \pm 0.0338\)). Large spatial and temporal fluctuations in population abundance complicate the evaluation of the importance of selection in determining traits such as body weight.

Introduction

Males (Sargent et al. 1986; Thornhill and Gwynne 1986) and females (Sargent and Gebler 1980; Sargent 1982) of several animal species selectively choose their mates according to various traits. If the chosen trait is correlated with reproductive quality, mate choice generates assortative mating based on reproductive quality (Crowley et al. 1991). Several factors may affect mate choice, including operational sex ratio and the size structure of the population (Emlen and Oring 1977). Changes in population density may also affect reproductive behavior and mate choice (Parker 1970; Wells 1977; McLain and Boromisa 1987), suggesting that, ultimately individual reproductive success may also depend on population density.

The factors regulating population density have been the subject of considerable ecological debate (Sinclair 1989). Increased habitat complexity enhances the density and diversity of organisms in a variety of terrestrial (e.g. MacArthur and MacArthur 1961), freshwater (e.g. Gorman and Karr 1978), and marine (e.g. Kohn 1967) environments by providing additional habitat, increasing food availability, and or serving as refuge from predation. Submerged aquatic vegetation in coastal marine and estuarine environments provides substratum for a wide variety of epiphytic flora and fauna (Harlin 1980) and refuge from predators (e.g. Orth et al. 1984). Several studies on the effects of vegetation complexity on abundance and diversity of associated macrofauna and fishes (e.g. Lewis 1987) have generally shown that increasing habitat complexity decreases
predation risk and/or increases food availability by either enhancing prey production or increasing entrapment of organic matter.

Abundance of most epifaunal species, including amphipods living in grassbed habitats, is also correlated with plant biomass (e.g. Lewis 1987). Habitat selection is often the proximate mechanism that produces differences in epifaunal abundance among plant species or between stands of plants at different densities (Lewer 1985; Hacker and Steneck 1990), but predation is likely to be the ultimate selection pressure for choosing safer habitats (Hay et al. 1990). The highest densities of *Gammarus pulex* are in areas of greatest *Spartina* spp. blade density that may aid predator-avoidance (Van Dolah 1978). *Eogammarus confervicolus* is also found associated with vascular plants, benthic algae and detritus (Bousfield 1979), and abundance is directly related to the presence and extent of a sedge-rhizome habitat that provides refuge from predators during low tide (Levings 1973).

Assemblages of bivalve shells (the soft-shell clam *Mya arenaria*, and cultivated oyster *Crassostrea gigas*) deposited in the intertidal zone of Grays Harbor estuary (Washington, USA) are also an important habitat for several invertebrate and fish species (Iribarne et al. 1992). Juvenile Dungeness crabs, *Cancer magister*, shore crabs, *Hemigrapsus oregonensis*, juvenile hermit crabs, *Pagurus hirsutiusculus* (mostly without shells), isopods *Iodothea* spp., and gunnels *Pholis ornatus* are all found almost exclusively in shell habitats (Armstrong et al. 1992). Shell habitats support higher density and diversity of epifauna by supplying shelter, higher food density, or by increasing survival rate (Fernandez et al. 1993). The relationship between assemblages of epifaunal animals and intertidal shells shows a close parallel to the epifauna–aquatic plant relationship. Both habitat types are temporally and spatially variable. Plant species differ in longevity, and thus habitat stability, shelter availability (Hacker and Steneck 1990), and protection from predators also fluctuate over time (e.g. Hay et al. 1990). A shell habitat may also vary in density, structure, quality, and spatial distribution (Dumbauld et al. 1993) due to sedimentation caused by bedload transport or by burrowing shrimp (Armstrong et al. 1992).

The amphipod *Eogammarus oclairi* is found both in eelgrass (Bousfield 1979) and shell habitats (Armstrong et al. 1992; Iribarne et al. 1992). In intertidal shell habitats, amphipod abundance is habitat-dependent (Armstrong et al. 1992); spatial and temporal variations of these habitats may generate variability in the local abundance of populations. Since laboratory experiments have shown that mating behavior in *E. oclairi* is density-dependent (Iribarne et al. 1995b), differences in mating behavior may vary between shell habitats as a reflection of differences in population size structure and abundance. In addition, habitat characteristics may also affect the mating system by exposing individuals of different sizes or sexes to different risks of predation. Under laboratory conditions, paired *Gammarus pulex* males were eaten more often than unpaired males (Ward 1986). Furthermore, differences in growth rate, age at maturity, and precopulatory behavior between populations of *Hyalella azteca* have been related to differences in fish predation pressure (Strong 1973). Thus, it is likely that the intensity of selection, or the opportunity for selection, will differ either between habitats or within a single habitat over time.

Differences in selective pressure between or within habitats over time have not been experimentally tested, mainly due to lack of agreement on how to approach the problem. A technique to estimate the potential intensity of selection episodes was developed by Arnold and Wade (1984a), who showed that selection can be measured in phenotypic terms without knowledge of character inheritance. Their technique allows partitioning of directional selection into stanzas corresponding to segments of the subject's life cycle. This approach permits quantification of the opportunity for selection; i.e. the maximum amount by which the mean of any characteristic can be shifted by directional selection. The estimation of selection intensity is useful for comparing selective pressures in different populations (Falconer 1981), since it measures the shift in the mean of a characteristic caused by directional selection in units of phenotypic standard deviations (Arnold and Wade 1984b). The method proposed by Arnold and Wade (1984a) offers a solution to the problem of analyzing multiple selection-episodes, such as episodes of natural or sexual selection. While the distinction between sexual selection and natural selection is useful, the difference is not critical to the analysis. The significant point is that the recognition of selection-episodes permits analysis of selection that may change in importance and direction during the life cycle (Arnold and Wade 1984a).

One episode of selection identified in amphipods (Ward 1988) occurs during pairing. This episode generates two groups of males and females with discrete fitness success, those that pair and those that do not. Several amphipod species (e.g. *Gammarus pulex*, Ward 1988 and *Eogammarus oclairi*, Iribarne et al. 1995b) show male competition for access to females. In most cases, larger males win by either entering amplexus faster or by taking over females from smaller males (Ward 1983; Elwood et al. 1987; Iribarne 1994). Since male competition is evoked to account for the outcome, this episode can be considered an episode of sexual selection (Darwin 1871; Arnold 1983). Since pairing in *E. oclairi* depends mainly on the male's behavior, and male behavior is affected by density (Iribarne et al. 1995b), this selection episode should be density-dependent. Thus, changes in habitat structure may also affect the opportunity for selection on certain traits by affecting local population density of *E. oclairi*.