

# Adult-larval interactions in the suspension-feeding bivalves *Cerastoderma edule* and *Mya arenaria*

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**ABSTRACT:** The influence of adult density on settlement and recruitment in the suspension-feeding bivalves *Cerastoderma edule* (L.) and *Mya arenaria* L. was investigated in a shallow soft-sediment area on the west coast of Sweden. Quantitative sampling for juvenile bivalves was performed in areas with varying densities of adult *C. edule*. Densities of adult *C. edule* and *M. arenaria* were also manipulated in experimental field plots. In the field study there was a negative relationship between adult density and newly settled bivalve larvae. Four months after peak settlement the density of juvenile bivalves was still 4 times higher in the area with few adult *C. edule*. In the field experiment, adult *C. edule* and *M. arenaria* reduced the settlement of bivalve larvae by up to 40 and 20 % respectively. The significant effect of adult density was, however, leveled out shortly after settlement. We conclude that adult benthic suspension feeders significantly reduce settlement success of bivalve larvae, and hence may limit recruitment of new individuals.

## INTRODUCTION

Recently, the significance of interactions between established adults and settling larvae in structuring soft-bottom suspension-feeding communities (sensu Woodin 1976) has been strongly questioned (Black & Peterson 1988, Ertman & Jumars 1988).

Field studies of suspension-feeding bivalves (e.g. *Cerastoderma edule*) suggest, however, that adult-larval interactions may play an important rôle in population dynamics. In boreal areas, several studies have shown that after severe winters, with few surviving adults, there is an extensive recruitment (Smidt 1944, Kristensen 1957, Hancock 1970, 1973, Beukema 1982, Möller 1986). Likewise, in patches harbouring a large number of adult *C. edule*, a relatively small proportion of newly settled individuals is recorded (Thamdrup 1935, Wohlenberg 1937, Kristensen 1957).

Field experiments designed to test the effects of adult benthic suspension feeders on settling of larvae have yielded variable results: in several cases there were no significant effects on settlement (Groenwold 1986, Commito 1987, Hunt et al. 1987, Black & Peterson 1988, Bingham & Walters 1989, Ólafsson 1989). In part, the lack of effects has been attributed to experimental plot

size (Peterson 1982, Black & Peterson 1988, Ertman & Jumars 1988), and statistical power (Young 1989). Some studies with bivalves, however, have demonstrated a negative effect on settlement: cage experiments by Brock (1980) indicated a negative correlation between adult density and recruitment in *Cerastoderma edule*; Williams (1980) recorded that significantly more spat of *Tapes japonica* settled in areas with no, or moderate, adult clam densities compared to areas with high adult clam densities; Peterson (1982) found a negative correlation between adult density and recruitment in *Protothaca staminea*; in a field experiment in the Danish part of the Wadden Sea, Jensen (1985) noted that adult *C. edule* inhibited recruitment of *Macoma balthica*; in a shallow bay on the Swedish west coast, Möller (1986) showed that treatments with high densities of *Mya arenaria* had fewer settled juveniles of *M. arenaria* and *C. edule* than the control plot with low density of *M. arenaria*. Möller did not, however, use replicate plots.

The mechanism proposed is that adults filter settling larvae out of the water column (Woodin 1976). This has been studied in a few cases: Cowden et al. (1984) showed that *Mytilus edulis* is capable of consuming larvae from several taxonomic groups, and Kristensen

(1957) found that adult *Cerastoderma edule* inhale bivalve larvae up to the size of 900  $\mu\text{m}$ .

In the present study we investigate the influence of adult density of 2 benthic suspension feeders, *Cerastoderma edule* (L.) and *Mya arenaria* L., on bivalve settlement and recruitment, the latter including subsequent juvenile survival for more than 3 mo. We use both a non-manipulative approach, sampling in patches with different densities of adults, and a manipulative method, changing adult density in experimental field plots. The study was carried out in Gullmarsvik, a semi-exposed shallow bay (<1 m water depth) on the west coast of Sweden. The tidal amplitude is <0.2 m, and the sediment is sand (95 % fine and very fine sand, and 5 % silt). The area has been extensively studied since 1977, where population dynamics and production of infauna and epifauna, and their interaction, have been investigated (Möller & Rosenberg 1982, 1983, Pihl 1982, 1985, 1986, Pihl & Rosenberg 1982, 1984, Möller 1985, 1986, Möller et al. 1985). Here, the main spawning in *C. edule* and *M. arenaria* takes place in late May–early June. After a few weeks as plankton the larvae settle on shallow bottoms.

## MATERIAL AND METHODS

**Quantitative field sampling.** In early June 1985, 2 adjacent subareas were selected (Fig. 1), one with a large number of adult *Cerastoderma edule* (Stn 1), and one with very few adults (Stn 2) (see Fig. 2). Samples taken on 25 June 1985 contained no settled larvae. On 4 July, juvenile bivalves first appeared in the benthos, and additional samplings were conducted on 17 July and 28 October. On each occasion we took 8 benthic samples at each station: 5 small cores with a diameter of 44.5 mm to a depth of 30 mm to assess the density of newly settled larvae, and 3 large cores with a diameter of 190 mm to a depth of 100 mm to assess the adult density. All samples were preserved in alcohol. Prior to sorting, individual small core samples were suspended in a glass jar with water. The jar was then shaken by hand 15 times, and the supernatant containing most of the spat decanted through a 160  $\mu\text{m}$  sieve. The material on the sieve was examined under a dissecting microscope at 25 $\times$  magnification; the remaining sediment in the jar was examined at 12 $\times$  magnification. Bivalve juveniles were determined to species, measured in 400  $\mu\text{m}$  intervals and counted. Juveniles of *C. edule* and *Mya arenaria* < 400  $\mu\text{m}$  were often difficult to distinguish from each other, and are referred to as *Bivalvia* sp. Large core samples were washed through a 500  $\mu\text{m}$  sieve. The residue was examined and all macrofauna, including adult *C. edule*, were measured and counted.

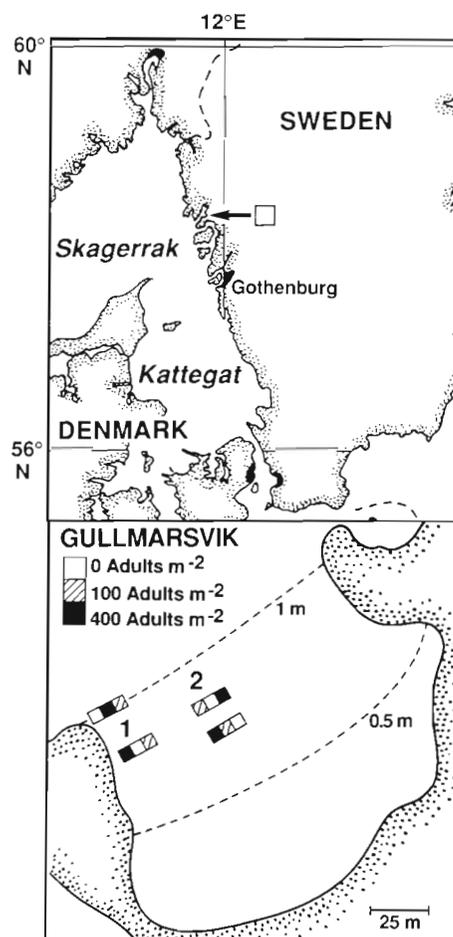


Fig. 1. The study area. Gullmarsvik, with location of sampling stations, 1 and 2, and experimental design. One replicate of each treatment, i.e. 0, 100 and 400 adult *Cerastoderma edule* or *Mya arenaria*  $\text{m}^{-2}$ , is represented in each block

The data were analyzed using *t*-tests, after transformation to  $\ln(1+x)$ .

**Field experiments.** Two manipulative experiments were performed in the same area as the field sampling (Fig. 1). Experimental plots, 70  $\times$  70 cm (= 0.5  $\text{m}^2$ ), were stocked with 0, 50 or 200 *Cerastoderma edule* (3 June 1988) or *Mya arenaria* (3 June 1989). Densities thus correspond to 0, 100 and 400 ind.  $\text{m}^{-2}$ . The plots were first cleared of all adult suspension-feeding bivalves by plowing the sediment by hand to a depth of ca 8 cm. To prevent immigration and emigration by *C. edule* the plots were enclosed by 20  $\times$  20 mm plastic nets, buried to 12 cm, and anchored with wooden bars. Since *M. arenaria* are incapable of migration as adults, and to minimize artifacts, only bars and no net was used in the 1989 experiment. Bivalves used in the manipulation experiments were 30 to 48 mm in length for *C. edule*, and 12 to 37 mm for *M. arenaria*. During the experimental periods the plots were inspected at 5

to 10 d intervals. At each occasion the bivalve siphons were counted, and the plots cleaned of any drifting algae. No marked change in adult densities was noted during the experiments.

Earlier studies have shown a decline in settlement of *Cerastoderma edule* and *Mya arenaria* from the outer part of the bay (ca 1 m water depth) towards land (Möller & Rosenberg 1983). To compensate for local variation in settlement, the experimental plots were arranged in a randomized block design, with 1 replicate from each treatment represented in each of 5 blocks (Sokal & Rohlf 1981). In each block the 3 plots were arranged in a row facing the mouth of the bay (Fig. 1)

To detect settlement of bivalve larvae, benthos samples were taken outside the plots at 3 to 5 d intervals, beginning on 11 June both years. On 27 June 1988, settlement of bivalve larvae was first recorded, and 3 cores (40 mm diameter  $\times$  40 mm deep) were randomly taken from within each plot. In addition, 3 cores were taken in unmanipulated bottoms, in the vicinity of each block (in the following referred to as reference samples). The sampling was repeated on 4 July and 3 October.

In the experiment with *Mya arenaria* samples were only taken once, on 19 June 1989, 1 to 5 d after settling, following the same procedure as for *Cerastoderma edule*. Prior to sorting, in 1989, the 3 individual cores taken in each plot were pooled and subsequently sub-sampled, according to Elmgren (1973).

Samples were preserved in formalin buffered with borax in 1988, and in alcohol in 1989. All samples were sorted as described above for the quantitative field study.

The settlement and recruitment data were analyzed using a 2-way ANOVA for randomized blocks, with block and adult density as factors (Sokal & Rohlf 1981). Since the data met the demands for homoscedasticity ( $p > 0.05$ ,  $F$ -max test) they were not transformed. In cases where the ANOVA showed significant treatment effects, means were compared using the SNK-test (Sokal & Rohlf 1981). Data from the individual cores in the *Cerastoderma edule* experiment were pooled prior to statistical treatment. The analysis thus consisted of 5 blocks, each with 1 replicate from each treatment.

## RESULTS

### Quantitative field sampling

Densities of adult *Cerastoderma edule* and bivalve spat at the 2 stations on 4 July are shown in Fig. 2a, b. Adult density was significantly higher at Stn 1,  $1188 \pm 201$  ind.  $m^{-2}$  (mean  $\pm$  SE), compared to Stn 2,

$24 \pm 12$  ind.  $m^{-2}$  ( $p < 0.005$ ). The adult *C. edule* ranged between 18 and 30 mm in length. Significantly more *Bivalvia* sp. were found at the station with low density of adult *C. edule* ( $p < 0.005$ ). Since the taxon *Bivalvia* sp. consists of both *C. edule* and *Mya arenaria* their pooled densities were also estimated. The total density of newly settled Bivalves, i.e. *C. edule*, *M. arenaria* and *Bivalvia* sp., was significantly lower at Stn 1 than at Stn 2 ( $p < 0.01$ ). Densities of juvenile *C. edule* and *M.*

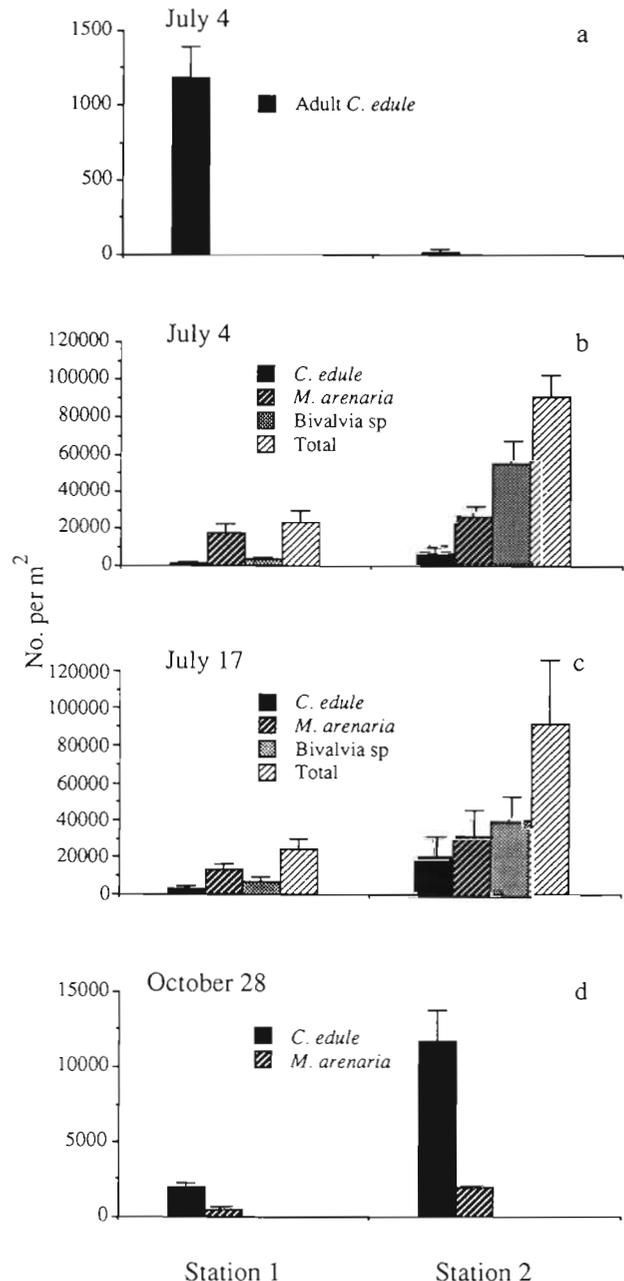


Fig. 2. Mean densities ( $\pm$  SE) of (a) adult *Cerastoderma edule* and (b, c and d) juvenile *C. edule*, *Mya arenaria*, *Bivalvia* sp. and total juvenile bivalves at Stns 1 and 2 on 3 subsequent sampling occasions during 1985

*arenaria* tested separately, however, did not differ significantly between stations ( $p > 0.05$ ). On 17 July the density of *Cerastoderma edule* spat differed significantly between stations ( $p < 0.05$ ), whereas the differences in densities of *M. arenaria*, *Bivalvia* sp. and all taxa combined were not significant ( $p > 0.05$ ) (Fig. 2c). A third sampling was performed on 28 October to examine if recruitment was affected. The number of juvenile bivalves had declined at both stations (Fig. 2d). There were significantly less juvenile *C. edule* ( $p < 0.0005$ ) and *M. arenaria* ( $p < 0.005$ ) at the station having a high density of adult *C. edule*. The length-frequency distributions of recruited *C. edule* and *M. arenaria* at the 2 stations are shown in Fig. 3. In the area with a high density of adult *C. edule* (Stn 1) very few specimens of *C. edule* and *M. arenaria* exceeded 3 mm in length. At Stn 2 both species had peak densities for individuals  $< 3$  mm. Beyond this size, juveniles of *C. edule* were rather evenly distributed.

#### Field experiments

At the first sampling occasion, on 27 June 1988, the density of newly settled *Cerastoderma edule* was significantly reduced in the treatment with 400 adult *C.*

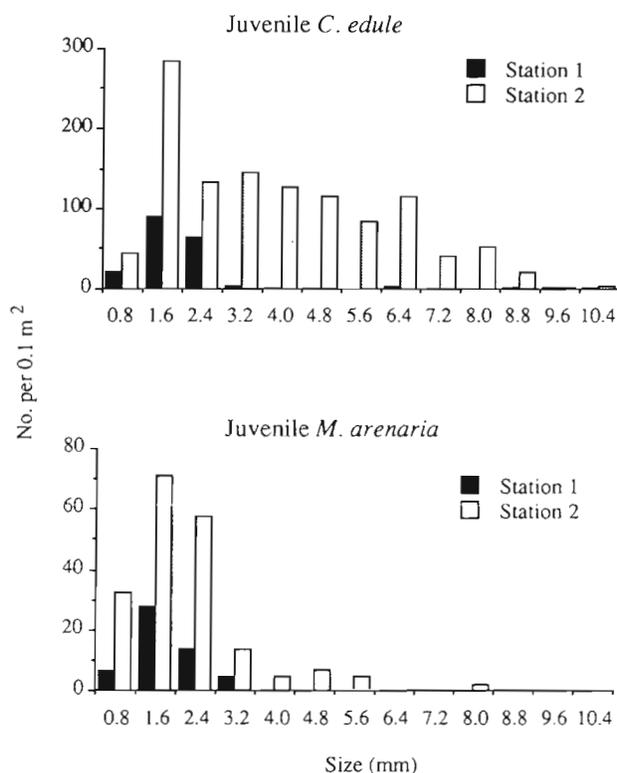


Fig. 3. *Cerastoderma edule* and *Mya arenaria*. Length-frequency distributions of juveniles at Stn 1 (1188 adult *C. edule*  $m^{-2}$ ) and Stn 2 (24 adult *C. edule*  $m^{-2}$ ) on 28 Oct 1985. Class width 0.8 mm

*edule*  $m^{-2}$  compared to the treatments with 0 and 100 adults  $m^{-2}$  ( $p < 0.05$ ), whereas densities of newly settled *Mya arenaria* and *Bivalvia* sp. were independent of the density of adult *C. edule* (Fig. 4). The p-values from the main ANOVA tests are presented in the figures. The total density of juvenile bivalves, *C. edule*, *M. arenaria* and *Bivalvia* sp. was significantly lower in the treatment with 400 adults  $m^{-2}$  than in the treatment with 100 adults  $m^{-2}$  ( $p < 0.05$ ) (Fig. 4). One week later, on 4 July, no effects of adult density on numbers of juvenile bivalves could be found (Fig. 5). On 10 October the density of the juvenile bivalves was  $< 10\%$  of the initial density. Most individuals were  $< 1$  mm in length which indicates that the bivalves had settled quite recently. There was no difference among treatments (Fig. 6).

In the manipulative experiment with adult *Mya arenaria* the parametric ANOVA procedure did not reveal any differences among treatments (Fig. 7). At all 5 blocks there were, however, fewer settled *Bivalvia* sp. and total bivalve spat in the treatment with 400 adult *M. arenaria* compared to the control with no adults. Therefore we reanalyzed the 1989 data employing the non-parametric 'Friedmans method for randomized block', based on ranks (Sokal & Rohlf 1981). Using the non-parametric method the total number of settled bivalve spat was significantly affected by adult density ( $p < 0.025$ ).

During 1988, average densities of adult *Cerastoderma*

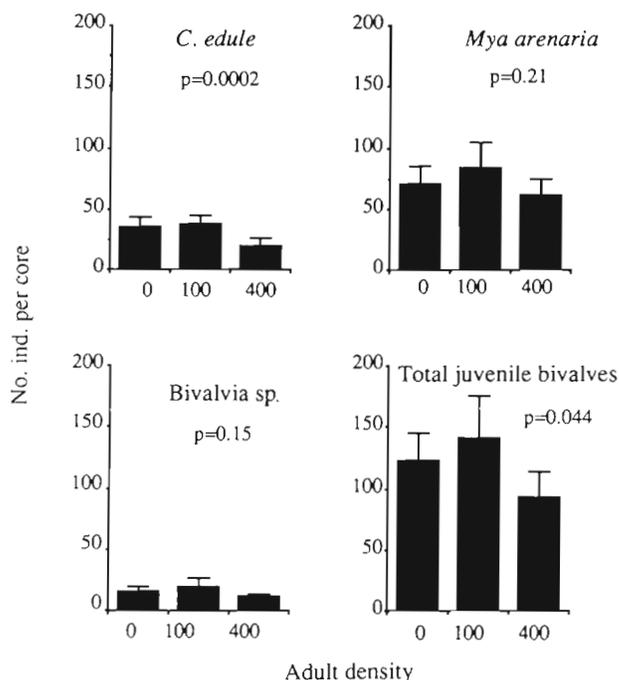


Fig. 4. Mean densities ( $\pm$  SE) of newly settled bivalves in experimental plots with 0, 100 and 400 adult *Cerastoderma edule*  $m^{-2}$  on 27 June 1988; p-values indicate the probability for no difference among treatments

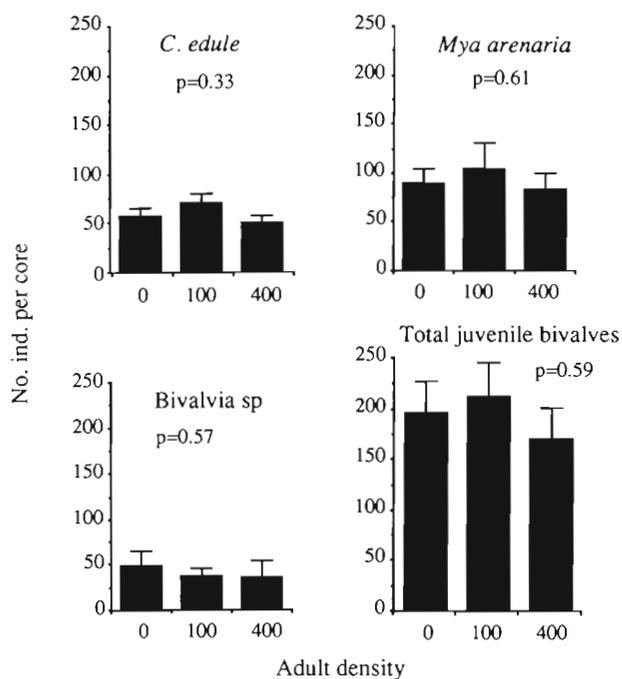


Fig. 5. Mean densities ( $\pm$  SE) of newly settled bivalves in experimental plots with 0, 100 and 400 adult *Cerastoderma edule*  $m^{-2}$  on 4 July 1988; p-values indicate the probability for no difference among treatments

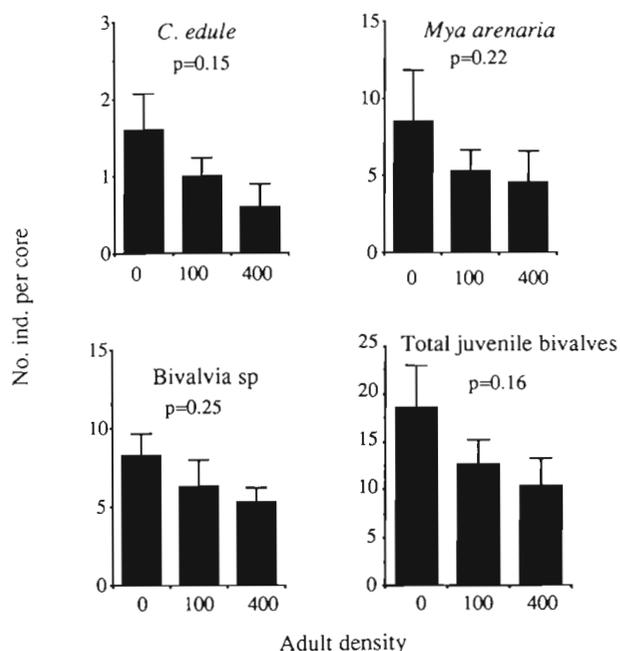


Fig. 6. Mean densities ( $\pm$  SE) of newly settled bivalves in experimental plots with 0, 100 and 400 adult *Cerastoderma edule*  $m^{-2}$  on 3 October 1988; p-values indicate the probability for no difference among treatments

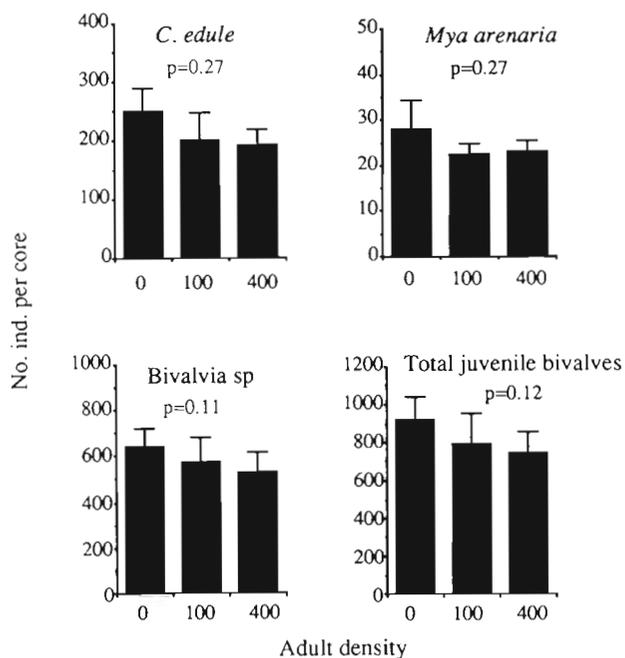


Fig. 7. Mean densities ( $\pm$  SE) of newly settled bivalves in experimental plots with 0, 100 and 400 adult *Mya arenaria*  $m^{-2}$  on 19 June 1989; p-values indicate the probability for no difference among treatments

*edule* and *Mya arenaria* in the reference area, outside plots, were 160 and 77 ind.  $m^{-2}$  respectively. In June 1989 there were 212 adult *C. edule*  $m^{-2}$ ; no adult *M. arenaria* was found in the outer part of the bay. On 27 June 1988 there were significantly fewer juvenile *C. edule* in the treatment with 400 adult *C. edule*  $m^{-2}$  than in the reference area ( $p < 0.05$ ; 2-way ANOVA). On all other sampling occasions in 1988 and 1989 no difference in densities of juvenile bivalves between experimental plots and unmanipulated bottoms could be found.

## DISCUSSION

The quantitative study in 1985 indicates a negative relationship between densities of the adult suspension feeder *Cerastoderma edule* and newly settled bivalve larvae. Four months after peak settlement densities of 0-groups of *C. edule* and *Mya arenaria* were still 5 and 4 times higher, respectively, in the area with few adults compared to the area harbouring a large number of adults; thus, recruitment of *C. edule* and *M. arenaria* was also negatively correlated with adult density. Length-frequency distributions of *C. edule* and *M. arenaria* on 28 October 1985 (Fig. 3) showed peak densities in the size range 1 to 2.5 mm at both stations, probably due to a recent settlement event. At Stn 2, *C. edule*  $> 2.5$  mm were evenly distributed in size, indicating that mortality may be size-independent beyond a critical size. This could be due to decreased predation

by epibenthic predators (Reise 1985). *Crangon crangon* (L.), one of the main predators on juvenile bivalves in the area, have been shown to mainly feed on *C. edule* and *M. arenaria* < 2 mm in length (Möller & Rosenberg 1983; Pihl & Rosenberg 1984).

Manipulation of adult *Cerastoderma edule* showed that adult density had a significant influence on the density of newly settled juveniles of *C. edule* in 1988. On 27 June 1988, mean density of *C. edule* spat was 43% lower in the treatment with 400 adults  $m^{-2}$  compared to the control treatment. On subsequent sampling occasions, 1 wk and 3 mo after peak settlement respectively, we found no significant differences among treatments. The field experiment with *C. edule* thus did not reveal any influence of adult density on recruitment. On 19 June 1989, all 3 categories of larvae, *C. edule*, *Mya arenaria* and *Bivalvia* sp., had a 20% lower mean density in the treatment with 400 adult *M. arenaria*  $m^{-2}$  compared to the control treatment. Our results thus support the suggestion by Möller (1986) that high densities of adult *C. edule* and *M. arenaria* reduce successful settlement of bivalve larvae.

Predation on settling larvae is the major mechanism invoked to explain inhibition of settlement by established adult suspension feeders (Thorson 1950, Woodin 1976). Using a video technique, André & Jonsson (pers. obs.) observed that swimming larvae of *Cerastoderma edule* suspended in aquaria with adult cockles had no possibility of avoiding the inhalant water currents, and were sequentially ingested; gut analysis of adult *C. edule* placed in a laboratory flume with drifting competent *C. edule* larvae indicates that adults readily consume larvae (André & Jonsson pers. obs.). These findings together with evidence from experiments with other suspension feeders (review in Young & Chia 1987) suggest that a great potential exists for direct predation by adult suspension feeders on settling larvae.

As pointed out by Black & Peterson (1988), the spatial scale at which field experiments on adult-larval interactions in benthic suspension feeders are conducted sets limits to the generality of such experiments. Provided that settling larvae inhaled by adult suspension feeders do not survive, the strength of the adult impact on settling larvae is determined by the probability of settling larvae to encounter feeding adults. The encounter rate between settling larvae and suspension feeding benthic predators will vary with patch size (Peterson 1982, Ertman & Jumars 1988), adult density, and movements (active or passive) of the larvae (Butman 1987). In shallow areas horizontal flow velocities often exceed larval swimming speeds (Butman 1986). Site selection under such circumstances is thus limited to crawling on the sediment surface or swimming near the bottom, where flow speeds are lower, or repeated vertical upward transport, followed by horizontal

advection. Both crawling, near bottom swimming/drift-ing and repeated upward and downward transport have been observed in a laboratory flume for larvae of *Cerastoderma edule* (André & Jonsson pers. obs.). In high flow velocities and turbulent water resuspension of already metamorphosed animals could occur (Möller 1986, Butman 1987). Baggerman (1953) reports that *C. edule* can be resuspended into the water column up to a size of 1800 to 2000  $\mu m$ . In large patches of suspension feeders each larvae has the possibility of encountering adults several times before final settlement (as in the quantitative study); in small patches larvae may encounter adults fewer times, and the risk of being inhaled is lower (as in the manipulative experiments). Further studies on the interaction between larval behaviour and hydrodynamic processes during the settlement phase are warranted to better understand spatial scales of adult-larval interactions.

Reise (1985) proposes an alternative hypothesis to account for enhanced recruitment after severe winters. This hypothesis predicts high survival of juvenile cockles in the absence of surface-feeding omnivores and small epibenthic predators. Predator enclosure experiment (Reise 1978, 1979, 1981), laboratory experiment (Jensen & Jensen 1985) and stomach analysis (Pihl & Rosenberg 1984, Pihl 1985) have shown that a guild of mobile epibenthic predators, mainly juveniles of *Carcinus maenas* (L.), *Crangon crangon* and *Pleuronectes platessa* L., prey heavily on newly settled larvae and juveniles of *Cerastoderma edule*. Peak immigration of 0-group *C. maenas* and *C. crangon* in the study area usually occurs in late July. After strong winters immigration was delayed by 1 to 2 mo (Pihl & Rosenberg 1982). Recruitment of bivalves is not, however, delayed to the same extent by preceding severe winters (Möller & Rosenberg 1983, pers. obs.). In years when epibenthic predators arrive late in the shallow areas a great proportion of juvenile bivalves may have reached an invulnerable size (Reise 1981, Pihl & Rosenberg 1984, Jensen & Jensen 1985). The population dynamics of *C. edule* and *Mya arenaria* in shallow areas is thus to a considerable extent controlled also by the timing of reproduction of these bivalves and their predators. Nevertheless, by reducing the number of successfully settled larvae, adult suspension feeders also strongly influence the recruitment of benthic invertebrates with planktonic life stages.

In order to explain variations in distribution of sessile adult organisms it is important to distinguish between planktonic events, settlement success and subsequent mortality (Keough & Downes 1982). Variation in number of settling larvae (Connell 1985, Underwood & Fairweather 1989) is beyond the scope of this paper. Settlement of bivalve larvae was reduced by up to 40% in the presence of adult *Cerastoderma edule*, and by

20% by *Mya arenaria*. Post-settlement mortality was substantial for both *C. edule* and *M. arenaria*. Although we found no experimental evidence for influence of adult bivalves on recruitment, the correlative data in the quantitative field study indicates that a reduced settlement limits the establishment of new benthic animals.

**Acknowledgements.** We thank Anette Asp, Anna Bisther, Lars-Johan Hansson, Birthe Hellman, Gisela Holm, Gustaf Hulthe, Per Jonsson, Birgitta Larsson, Erland Lettewall, Susanne Liljenström, Mats Lindegarh, Lars-Ove Loo, Anders Modig, Ingrid Möllmark, Marianne Saur and Anna Thessing for technical assistance. Per Jonsson and Linda Schaffner made valuable comments on the manuscript. Tjrnö Marine Biology Laboratory and Kristineberg Marine Biological Station provided working facilities. This study was supported by the Swedish National Research Council, the Royal Academy of Science, and the Helge Ax:son Johnsson, Colliander and Lundgren Foundations.

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*This article was submitted to the editor*

*Manuscript first received: October 12, 1990*

*Revised version accepted: February 7, 1991*