

## Turnover of postlarval bivalves in sediments of tidal flats in Königshafen (German Wadden Sea)

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**ABSTRACT:** After larval settlement, juvenile bivalves may rapidly re-enter the water column and attain secondary dispersal by byssus-drifting. In order to estimate the quantitative importance of byssus-drifting, the abundance of drifters in the water column, their re-entry into the sediment, and their density in the ambient sediment were measured simultaneously over 3 months on a tidal flat in Königshafen near the Island of Sylt in the North Sea. Turnover of juvenile clams *Macoma balthica* and cockles *Cerastoderma edule* was more than once per week in summer, showing strong short-term variability because of semi-lunar rhythms of drifting activity. While there is currently no evidence for active habitat selection in settling *M. balthica* and *C. edule* larvae, it is suggested that habitat selection occurs following postlarval migrations.

### INTRODUCTION

Individual development of bivalves usually includes a planktonic larva which is often regarded as the major means of dispersal. The current paradigm for settlement of soft-sediment invertebrates invokes passive transport of the larvae in the water column followed by either larval choice of habitat after deposition on or near the sediment (active habitat selection hypothesis; see Woodin, 1991), or larvae sink passively to the sediment according to the hydrographic constraints for sedimentation without active habitat selection (passive deposition hypothesis; Pratt, 1953). However, as Baggerman pointed out as early as 1953, spatfall does not necessarily terminate mobility of the juvenile bivalves. Instead high numbers of juvenile cockles *Cerastoderma edule* were observed drifting in the water column in summer (Baggerman, 1953). During the following decades, many observations on benthic postlarval and adult polychaetes and molluscs accumulated (see review by Butman, 1987), indicating that postlarval drift is not confined to a single species. In juvenile bivalves byssus-drifting seems to be the common mode of transport in the water column. The individuals initiate water column entrance by secretion of a long thread which increases the viscous drag exerted on the young bivalves and enables them to be carried along on relatively weak currents (Sigurdsson et al., 1976). Thus, by byssus-drifting, juvenile bivalves may attain secondary dispersal.

There is a long list of potential benefits from drifting in the water column, including avoidance of habitat deterioration, or selection of another habitat which is more suitable for the next life stage (see Armonies, 1994). On the other hand, traditional benthos ecology does not generally assume that disappearance of individuals from a studied site

has another cause other than mortality. Thus, neglecting the potential for migration may introduce severe bias into almost any benthic field study, provided migrations are quantitatively important in the studied assemblage. Unfortunately, there is a lack of systematic recording of drifting fauna that might enable estimates on the quantitative significance of macrobenthic migrations. In the Wadden Sea, Heiber (1988) studied the drift fauna in a tidal channel. The effects of postlarval migrations in juvenile clams *Macoma balthica* were investigated by Beukema & de Vlas (1989), Günther (1991), and Armonies & Hellwig-Armonies (1992). All abundant bivalves drifting in the tidal waters in Königshafen displayed temporal rhythms of migration, while the direction of transportation depended on the current regime (Armonies, 1992). In mud snails *Hydrobia ulvae*, floating juveniles temporarily use habitats outside the adult range, thus escaping intra-specific competition and enabling genetic exchange between populations (Armonies & Hartke, 1994).

These studies used plankton nets to estimate migratory activity in the water column, and temporal series of sediment samples to estimate the net effect of spatfall, immigration, emigration, and mortality. But it remained unclear whether migrations referred to a small proportion of the total population drifting all of the time, or to nearly all specimens drifting during part of the time. Therefore, traps were sunk into the sediment to record the number of migrating organisms as they return to the sediment. Together with regular sampling of ambient sediment, these data give an estimate of the rates of turnover of these organisms in the sediment. A part of this study, dealing with mud snails *H. ulvae*, has already been published (Armonies & Hartke, 1994). It turned out that, on an average, juvenile mud snails stayed no longer than 1–2 days at the same site in summer. Here, I will concentrate on the dominant bivalves, cockles *C. edule*, and clams *M. balthica*. What evolved is that almost all of the juvenile bivalves migrated during most of the summer, resulting in turnover rates similar to those of mud snails, though the spatial and temporal variability of turnover was more pronounced in bivalves.

#### MATERIAL AND METHODS

The study was conducted at a mid-intertidal site in the Königshafen wadden area near the Island of Sylt in the North Sea (June 4th to August 31st 1992). Bivalves drifting in the water column were recorded using a horizontal plankton net anchored to a vertical pipe. The net (0.5-mm mesh width, 20-cm diameter opening) adjusts itself to the direction of the currents; a complete description is given in Armonies (1992). Abundance in the sediment was estimated by weekly sample collection (20 replicate cores of 5 cm<sup>2</sup> cross-sectional area and 5 cm depth per site and date). Bivalve spat was separated from the sediment using a shaking-decantation procedure (see Armonies & Hellwig, 1986), with subsequent sieving of the decanted water through 0.5-mm mesh.

Drifting organisms returning to the sediment were recorded using a trap sunk into the sediment. It consisted of two concentric plastic pipes, 15 and 12 cm in diameter, respectively. The outer pipe prevented collapse of the ambient sediment when the inner pipe (the trap *sensu stricto*) was removed. A funnel mounted in the inner pipe reduced the chance of escape, once an individual had sunk to the bottom of the trap. The lower end of the inner pipe was sealed by a removable lid composed of a narrow plastic ring covered with gauze of 0.063-mm mesh. The trap protruded above the sediment by about

2 cm. Both pipes were covered by a piece of wire mesh (5-mm mesh width) to prevent entrance of larger epifauna such as shrimps and shore crabs. For further details of the trap construction, see Armonies & Hartke (1994).

The sediment trap and plankton net were emptied once per day, i.e. after two tidal cycles. In the laboratory, the contents of the sediment trap were sieved through 0.5-mm mesh. This was done to restrict the estimate of sediment re-entry to the same size classes of organisms as those caught by the plankton nets. Thus, settling larvae and postlarvae < 0.7 mm were excluded and the calculations of turnover may be too conservative.

Turnover was calculated as the ratio between the number of organisms caught per m<sup>2</sup> of sediment trap opening during one week, and the average abundance per m<sup>2</sup> of ambient sediment (the mean of abundance from sediment samples collected at the beginning and the end of the respective week). Thus, turnover has the unit individuals m<sup>-2</sup> week<sup>-1</sup>/individuals m<sup>-2</sup> = week<sup>-1</sup>.

## RESULTS

Abundance of drifting *Macoma balthica* in the water column and numbers entering the sediment ran roughly parallel (Fig. 1). Spearman's rank correlation coefficient of the weekly numbers collected by either device revealed a positive correlation ( $r_s = 0.935$ ,  $n = 13$ ,  $p < 0.001$ ) which was mainly due to the common seasonal decrease in abundance of juveniles. However, rank correlations calculated for the daily numbers of specimens caught by the trap and plankton net within a week yielded a significant positive correlation only once in 8 weeks (June and July data; August data excluded because of low abundance). This indicates that short-term hydrographic conditions for transport in the water column may differ from the conditions for sediment re-entry.

A comparison of the numbers of organisms caught by the sediment trap with the ambient sediment densities revealed that the entire population of 0-group specimens was exchanged at least once a week, in June and July. In late July and August, estimates of turnover rates became unreliable because of low abundance in the sediment.

In juvenile cockles *Cerastoderma edule*, the situation was similar to that of the clams (Fig. 2). Abundance of drifters and of immigrants to the sediment correlated seasonally ( $r_s = 0.687$ ,  $n = 13$ ,  $p < 0.01$ ) but only occasionally, on a weekly basis. Turnover of specimens in the sediment was higher than in *M. balthica*. This means that, on the average, juveniles of these two species will reside for only a few days at the same site during the summer months.

## DISCUSSION

The current paradigm for recruitment of soft-sediment invertebrates suggests passive transport of the larvae in the water column, followed by larval choice of habitat after deposition on or near the sediment (Woodin, 1991). An alternative is the passive deposition hypothesis (Baggerman, 1953; Pratt, 1953). As Butman (1987) pointed out, the two hypotheses are not mutually exclusive but may coexist within different spatial and temporal scales. In the intertidal zone of the Wadden Sea, spat of the bivalves *Macoma balthica* and *Mya arenaria* seems to be passively deposited on the sediment according to the hydrographic conditions for sedimentation (Günther, 1991, 1992; Armonies & Hellwig-Armonies, 1992). Subsequently, the juveniles may change their intertidal position by

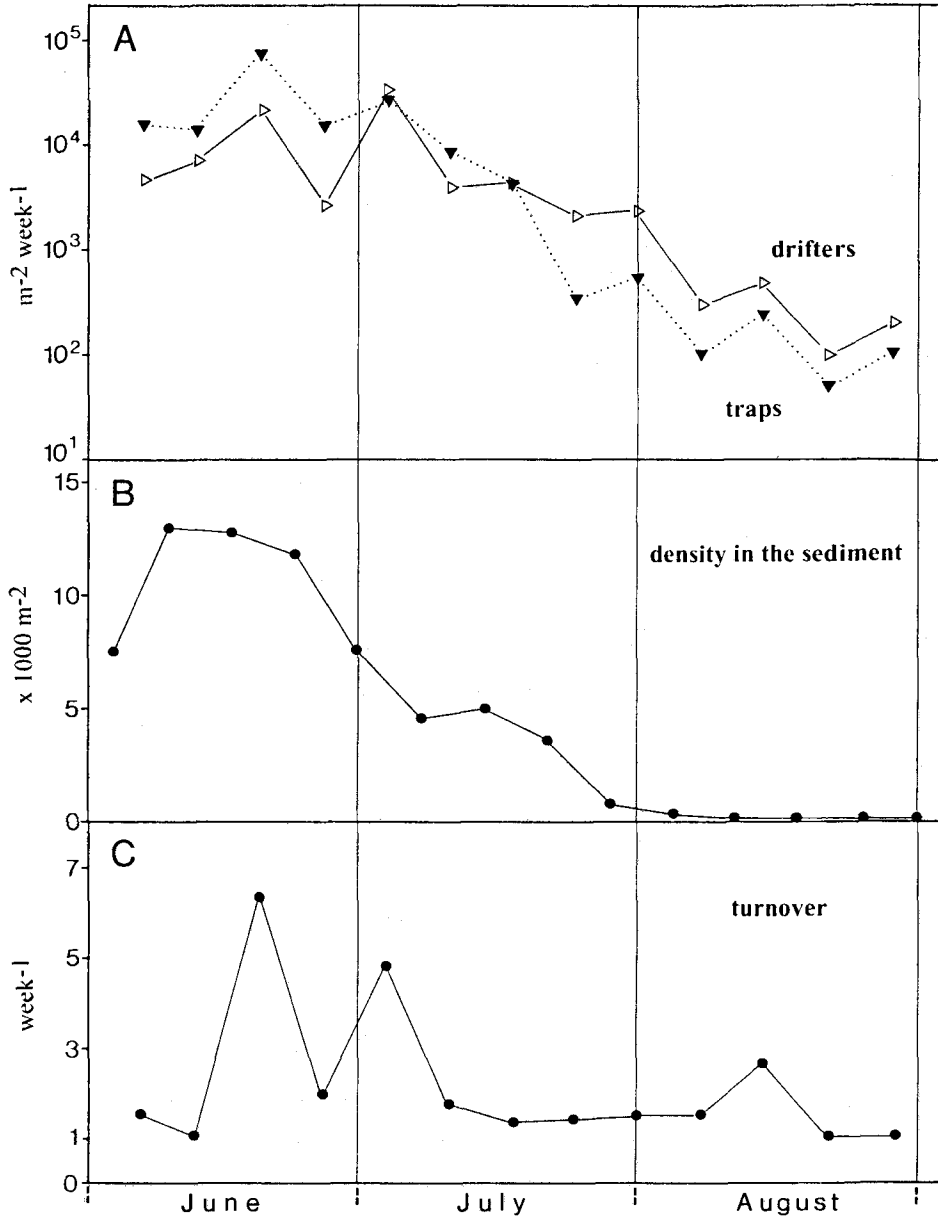


Fig. 1. Seasonal variability of turnover in *Macoma balthica*. A: Abundance of drifters (open triangles, plankton nets) and in sediment traps (closed triangles) per m<sup>2</sup> of opening, per week. B: Abundance of juveniles in the ambient sediment (10<sup>3</sup> m<sup>-2</sup>, weekly estimates). C: Weekly turnover of juveniles in the sediment (= ratio of no. of individuals collected by the sediment trap per week per m<sup>2</sup> of trap opening/average abundance per m<sup>2</sup> in the sediment during that week)

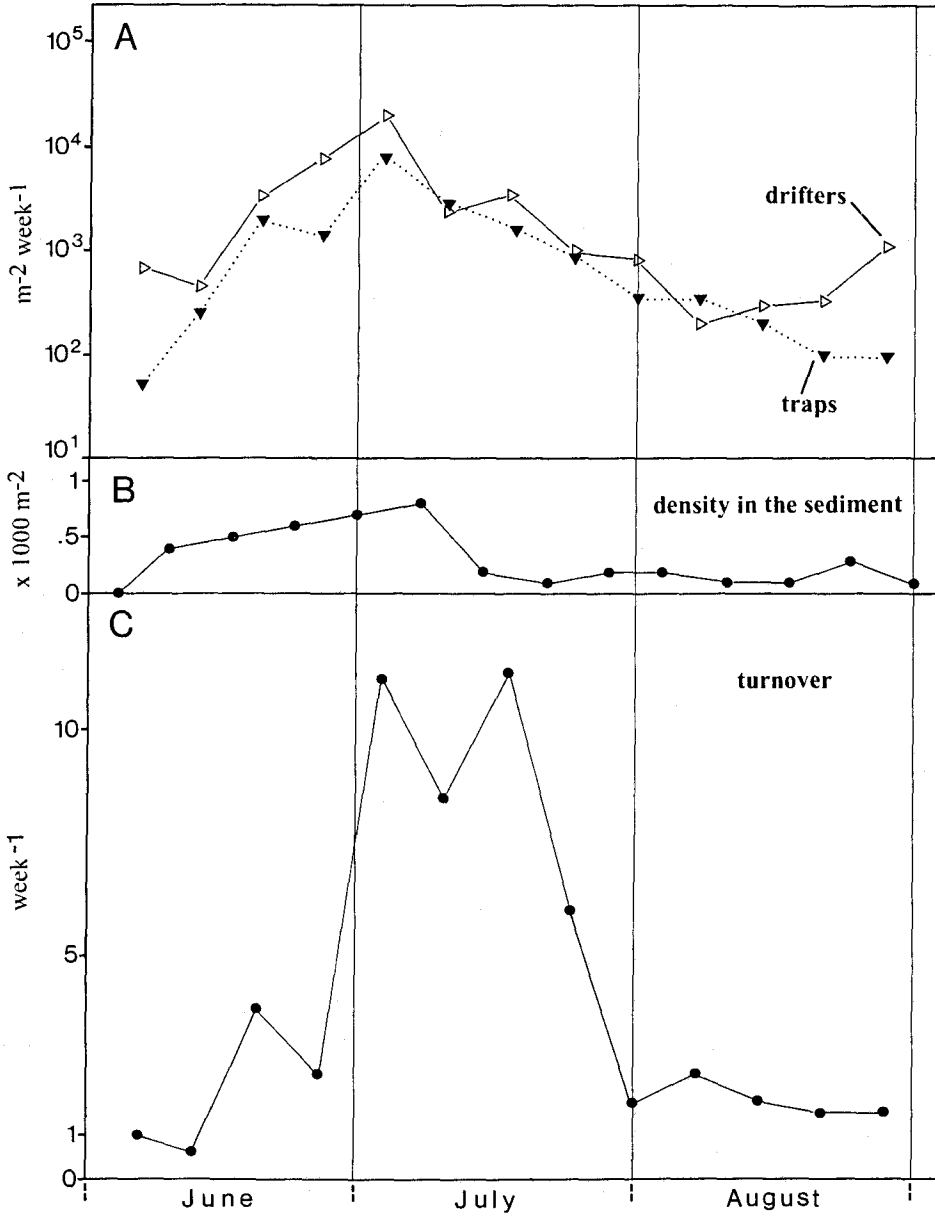


Fig. 2. Seasonal variability of turnover in *Cerastoderma edule*. A, B, and C as in Figure 1.

byssus-drifting. The high rates of turnover of juvenile cockles and tellinid clams found during this study suggest that redistribution by byssus-drifting juveniles in summer is not an exception only occurring in a minor part of the population. Particularly in cockles, the turnover exceeded  $7 \text{ week}^{-1}$  in July (Fig. 2) which means that the entire population may

be exchanged every night, statistically. In fact, juvenile cockles show a lunar periodicity in migratory activity with peak abundance in the water column during spring tides (Armonies, 1992). Although turnover in the present study was estimated from data integrated over one week, these peaks in migratory activity still show up in the integrated turnover rates of June and July (weekly alterations of a higher and a lower turnover rate; Fig. 2). Thus, on a temporal scale of days a period with a greatly increased turnover is followed by a period with less turnover of specimens in the sediment. As a consequence, mean turnover cannot be properly estimated from a temporal scale of a few days.

Although drifting specimens depend on the hydrographic conditions (with respect to water column entrance, direction of transport, and re-entry into the sediment), choice of habitat during this phase of secondary dispersal may overcompensate the constraints of hydrography and result in a net transport of specimens into other areas than those where spatfall occurred (Günther, 1991; Armonies & Hellwig-Armonies, 1992).

Postlarval migrations may be beneficial for various reasons: (1) juveniles are less time-limited than larvae when searching for a favourable habitat; (2) postlarval migrations may compensate for local losses of spat, e.g. from predation (Reise, 1985), and (3) juveniles might even use additional resources while drifting around, thus escaping intraspecific competition. In the clam *M. balthica* there are two periods of migration, during their first summer and first winter. From site-specific growth and survival rates, Beukema (1993) concludes that timely migration to areas more suitable for the next life stage can be regarded as an adaptive strategy explaining the relatively low interannual variability of recruitment success noted in this species (Beukema, 1982). Postlarval migrations may thus increase the temporal stability of populations.

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