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DISPERSAL OF INTERTIDAL INVERTEBRATES: A STRATEGY TO REACT TO DISTURBANCES OF DIFFERENT SCALES?*

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ABSTRACT

Investigations on settlement and recruitment of intertidal macrofauna and recolonization experiments shed light on the ability of postlarval stages to disperse, significantly prolonging the dispersal phase of the planktonic stages of macrofauna. Unfortunately, the ecological importance of postlarval dispersal as well as the mobility of adults has been disregarded in the past.

Three types of dispersal are compared in this report: planktonic larvae, postlarvae (temporary meiofauna) and adults of the macrofauna. Data on the permanent meiofauna are also included. Scales of dispersal vary with size and age of the animals involved: (i) large-scale: planktonic larvae, (ii) meso-scale: postlarvae and permanent meiofauna, and (iii) small-scale: adult macrofauna.

Different disturbance scales also exist: large areas (e.g. disturbed by pollutants), zones and patches (e.g. disturbed by feeding of epibenthic predators). It is suggested that all modes of dispersal contribute to the recovery of these areas. Settlement of planktonic larvae predominates if the disturbed areas are large. In smaller affected plots, postlarval transport as well as immigration of adults begin to play a more significant role. It is concluded that the ability of the macrofauna to disperse during their benthic life stage contributes to the elasticity of coastal and intertidal benthic communities.

1. INTRODUCTION

The intertidal soft-bottom habitat of the Wadden Sea consists mainly of unvegetated sand and mudflats which are more or less continuously disturbed by physical and biological forces. There are many examples of disturbances, such as the effects of waves and erosive currents, ice scour, and feeding activities of epibenthic predators and birds. Other types of disturbance can be related to human activities, such as chemical spills (e.g. oil), eutrophication, bait-digging or cockle fisheries. To survive among these predation/disturbance forces, many species have developed strategies with more or less opportunistic characteristics, such as a large population, high reproductive rates and the ability to become widely dispersed (GRASSLE & SANDERS, 1973; GRASSLE & GRASSLE, 1974).

Usually, the planktonic larvae of marine benthic invertebrates are considered as the stage of dispersal (e.g. STRATHMAN, 1974; PALMER & STRATHMAN, 1981; SCHELTEMA, 1986). The type of larvae development (planktotroph vs lecithotroph) in combination with abiotic and biotic conditions determines the duration of the larval stage and thereby the order of magnitude of dispersal. Due to the obvious significance of the planktonic larval stage for the spatial distribution of species and the recovery potential of defaunated

areas, dispersal of postlarvae as well as adults of invertebrate macrofauna was assumed to be negligible. However the results of DAUER & SIMON (1976a, 1976b), SANTOS & SIMON (1980), DAUER (1984) and BONSDORFF (1983), for example, suggested dispersal of benthic stages contributed to the recovery of disturbed areas to a certain degree.

JOHANNESSON (1988) found that transport of these stages can affect the large-scale spatial distribution. She compared the geographical distribution of *Littorina* species with planktonic and nonplanktonic reproductive modes. In the area considered, the spatial distribution of breeding species was more widespread, which could only be explained by transport of postlarval stages.

Several investigations on the emergence of benthic fauna were carried out in tropical and subtropical shallow water systems (e.g. ALDREDGE & KING, 1977, 1980, 1985). These studies imply that dispersal of benthic macrofauna is a common phenomenon in the above-mentioned habitats. Examples of the dispersal of postlarvae or adult stages can also be found for most of the macrofauna species of temperate intertidal areas similar to the Wadden Sea (for references, see Table 1). But due to the classically large mesh sizes (0.5 to 1.0 mm), long time intervals between sampling and lack of combining the methods for studying infauna and hyperbenthos as well as plank-

ton, most data are usually only qualitative. Thus, the estimate of the ecological significance of postlarval and adult dispersal is limited. Nevertheless, more and more evidence suggests that dispersal of benthic stages of macrofauna is not an accidental event but occurs regularly depending on the season and the successional state of the community (ZAJAC & WHITLACH, 1985). Consequently, it may be a structuring force in intertidal areas such as the Wadden Sea (e.g. OHDE, 1981; ARMONIES, 1988a; HEIBER, 1988; GÜNTHER, 1990a, 1990b, 1991).

In contrast to the adult macrofauna, the importance of dispersal is better understood for the meiofauna. Meiofauna organisms generally lack planktonic larvae and thus are dependent on dispersal of recruits and adults to colonize new habitats. GERLACH (1977) studied several means of meiofauna dispersal to explain the apparent contradiction between the lack of a pelagic larval stage on the one hand and the wide range of geographical distribution on the other hand. Since then, a variety of approaches have offered a huge amount of data concerning meiofaunal dispersal. The aim of these investigations was to find out:

1. the determining factors of dispersal such as (a) hydrodynamic conditions and behaviour of organisms (BELL & SHERMAN, 1980; PALMER, 1984; ARMONIES, 1988a, 1988b, 1989a); (b) the effects of habitat structure (DEPATRA & LEVIN, 1989n); (c) the availability of food (DECHO, 1986; DECHO & FLEEGER, 1988; KERN, 1990); and (d) density (SERVICE & BELL, 1987);

2. the consequences of dispersal such as (a) the effects on the variability of the spatial distribution (PALMER & BRANDT, 1981; ARMONIES, 1990) and (b) the significance for recolonization (SHERMAN & COULL, 1980; CHANDLER & FLEEGER, 1983; KERN & BELL, 1984; FEGLEY, 1988).

Several recent approaches were reviewed by PALMER (1988a). In conclusion, she proposed a conceptual model in which she used the taxonomic composition, hydrodynamics, above-ground structure and disturbance as factors to distinguish whether active or passive mechanisms of dispersal prevailed in a given habitat.

Assuming that dispersal of benthic stages follows the same ecological patterns, i.e. it occurs under similar selective pressure in the macro- as well as the meiofauna, I intend to show that:

1. postlarvae and adults of intertidal benthic populations have a high potential to disperse; and

2. a relationship exists between dispersal and disturbance which is reflected by analogous spatial scales.

I hypothesize that especially dispersal of benthic stages of intertidal macrofauna contributes substantially to the observed elasticity of intertidal soft-bottom communities.

2. DISPERSAL OF BENTHIC STAGES OF INTERTIDAL MACROFAUNA

Dispersal is any process by which the spatial distribution of an organism is changed. By applying this definition, dispersal is not only a water column phenomenon as stated by BUTMAN (1987), but also includes movement within the sediment or on the sediment surface.

In Table 1, references are listed which cover a wide field of dispersal of intertidal invertebrates (benthic stages; highly mobile epibenthic predators are excluded). Studies are cited where the (a) transport or mode of transport was investigated; (b) transport was indirectly evident from changes in the spatial distribution or dispersion or (c) recolonization experiments gave evidence for immigration of postlarvae or adults. The table concentrates on species which occur in the intertidal Wadden Sea and thus inhabit mainly sheltered sandy or muddy flats. This does not necessarily mean that the references originate from studies carried out in the Wadden Sea. More references can be obtained from SCHELTEMA (1986), BUTMAN (1987) and HEIBER (1988).

Different combinations of causes, seasons and age classes may occur in the process of dispersal. In the following, I compare dispersal occurring in several habitats and for several size categories of the infauna (permanent meiofauna, postlarvae and adults of macrofauna). Data from the Wadden Sea will be used to develop the points, and references from other intertidal areas are included to emphasize that this is not a local phenomenon.

2.1. PASSIVE DISPERSAL: RESUSPENSION

Extremely strong storms can disperse intertidal macrofauna into distant subtidal areas. For example, *Hydrobia ulvae* was resuspended from the tidal flats of the Wadden Sea and transported far into the German Bight, near to Helgoland (REINECK *et al.*, 1968). MEIXNER (1979) observed the rolling of large cockles (*Cerastoderma edule*) on the bottom, which was induced by extreme currents under stormy weather conditions. A high load of suspended macrofauna in the water column was observed by DOBBS & VOZARIK (1983) after a storm in the Long Island Sound. The species composition of the plankton hauls was different to that of the ambient benthic communities; therefore, these animals must have originated from distant benthic habitats. Transport of intertidal macrofauna due to ice scouring is also a cause of dispersal (DIONNE, 1969). Several species of the permanent meiofauna have been found to disperse passively by currents exceeding the friction velocity (BELL & SHERMAN, 1980; PALMER, 1984; PALMER & GUST, 1985).

TABLE 1
References for the dispersal of intertidal invertebrates (benthic stages).

Species	Direct evidence for dispersal		Indirect evidence for dispersal	
	catches in the water column and in traps, field and laboratory observations		changes in distribution and dispersion	recolonization by juvenile and adults
Polychaeta				
Errantia				
<i>Anatides mucosa</i>	ARMONIES, 1988a; HEIBER, 1988; Haberstroh, pers. comm.			
<i>Eteone longa</i>	ARMONIES, 1988a; HEIBER, 1988; Günther, unpubl. data; Haberstroh, pers. comm.			
<i>Harmothoe sarsi</i>	HARTMANN-SCHRÖDER, 1971; HEIBER, 1988; Haberstroh, pers. comm.			
<i>Nereis diversicolor</i>	ARMONIES, 1988a; HEIBER, 1988; Günther, unpubl. data; Köhler, pers. comm.	EVANS <i>et al.</i> , 1979; REISE, 1979; METTAM, 1981	BONSDORFF, 1983	
<i>Nereis virens</i>	THOMAS & JELLEY, 1972; DEAN, 1978; HEIBER, 1988	MIRON & DESROSIERS, 1990	BLAKE, 1979	
<i>Nereis succinea</i>	THOMAS & JELLEY, 1972; DAUER <i>et al.</i> , 1982			
<i>Nephtys caeca</i>	HEIBER, 1988			
<i>Nephtys hombergii</i>	HEIBER, 1988			
Sedentaria				
<i>Arenicola marina</i>	WERNER, 1956; FARKE & BERGHUIS, 1979a, 1979b; BEUKEMA & DE VLAS, 1979; HEIBER, 1988	BEUKEMA & DE VLAS, 1979; REISE, 1981; POLLACK, 1979	NEWELL, 1948; McLUSKY <i>et al.</i> , 1983; v. d. HEILIGENBERG, 1987	
<i>Heteromastus filiformis</i>	DAUER <i>et al.</i> , 1982; HEIBER, 1988	SHAFFER, 1983	SMITH & BRUMSICKLE, 1989	
<i>Marenzelleria viridis</i>	DAUER <i>et al.</i> , 1980	Essink & Kleef, pers. comm.		
<i>Polydora ligni</i>	DAUER <i>et al.</i> , 1982			
<i>Pygospio elegans</i>	LINKE, 1939; ARMONIES, 1988a; HEIBER, 1988; Köhler, pers. comm.			
<i>Scotoplos armiger</i>	HEIBER, 1988; Köhler, pers. comm.	REISE, 1979	BOSELMANN, 1989; v. d. HEILIGENBERG, 1987	
<i>Tharyx marioni</i>	Günther, unpubl. data			
<i>Oligochaeta</i> spp.	Günther, unpubl. data			
Mollusca				
Gastropoda				
<i>Hydrobia ulvae</i>	HENKING, 1894; ANDERSON, 1971; LITTLE & NIX, 1976; BARNES, 1981; HEIBER, 1988; Günther, unpubl. data	REINECK <i>et al.</i> , 1968	McLUSKY <i>et al.</i> , 1983	
Bivalvia				
<i>Cerastoderma edule</i>	BAGGERMANN, 1953; SCHUIJTEMA, 1970; MEIXNER, 1979; MÖLLER, 1986; ARMONIES, 1988a; HEIBER, 1988; GÜNTHER, 1990b	GÜNTHER, 1990b		
<i>Ensis directus</i>	WILLIAMS & PORTER, 1971; HEIBER, 1988; Günther, unpubl. data			
<i>Macoma balthica</i>	BAGGERMANN, 1953; BEUKEMA, 1973; DE VLAS, 1973; DAUER <i>et al.</i> , 1982; BONSDORFF, 1984; HEIBER, 1988; OLAFSSON, 1988; SÖRLIN, 1988; BEUKEMA & DE VLAS, 1989; GÜNTHER, 1990b; Armonies, pers. comm.	BOYDEN & LITTLE, 1973; MYREN & PELLA, 1977; WOLFF & DE WOLF, 1977; RATCLIFFE <i>et al.</i> , 1981; GÜNTHER, 1990a, 1990b	BONSDORFF, 1983, 1984; McLUSKY <i>et al.</i> , 1983; v. d. HEILIGENBERG, 1987	

TABLE 1 (Continued)
References for the dispersal of intertidal invertebrates (benthic stages).

Species	Direct evidence for dispersal	Indirect evidence for dispersal	
	catches in the water column and in traps, field and laboratory observations	changes in distribution and dispersion	recolonization by juvenile and adults
<i>Mya arenaria</i>	BAGGERMAN, 1953; MÖLLER, 1986; GÜNTHER, 1990b	MATTHIESSEN, 1960	
<i>Mytilus edulis</i>	BAYNE, 1964; DARE, 1976; HEIBER, 1988		
<i>Scrobicularia plana</i>	FRANKIEL & MOUEZA, 1979		
Crustacea			
Amphipoda			
<i>Bathyporeia pilosa</i>	FISH & PREECE, 1970; PREECE, 1971; ELEFTHERIOU, 1979		
<i>Corophium</i> sp.	MEADOWS & REID, 1966; ESSINK <i>et al.</i> , 1989; FLACH, 1992	JENSEN, 1985; HUGHES, 1988; GÜNTHER, 1990a	BONSDORFF, 1983

In conclusion, dispersal due to passive resuspension is often coupled with physical disturbances. The size of the organisms affected and the transported distance will depend on the scale of disturbance. In addition, combinations between passive transport by disturbance and active vertical migrations of the fauna in the bottom can also occur (VADER, 1964; ARMONIES, 1988b).

2.2. ACTIVE DISPERSAL

2.2.1. WINTER MIGRATIONS

Intertidal macrofauna can perform winter migrations from the tidal flats to ambient subtidal areas obviously to avoid freezing. In the Wadden Sea area, this kind of dispersal is known for adults and juveniles of *Arenicola marina* and *Macoma balthica* (BEUKEMA, 1973; BEUKEMA & DE VLAS, 1979; HEIBER, 1988; BEUKEMA & DE VLAS, 1989). BEUKEMA & DE VLAS (1979) estimated that about 30% of the *M. balthica* population carried out winter migrations within the investigated area of the Dutch Wadden Sea. The percentage of the *A. marina* population was assumed to be lower. The selection of currents which flow towards subtidal areas suggests an active dispersal behaviour.

HEIBER (1988) reported that benthic stages of the benthic polychaetes *Harmothoe sarsi*, *Eteone longa*, *Anatides mucosa*, *Nereis virens*, *Scoloplos armiger* and *Heteromastus filiformis* occur in the winter plankton of the Wadden Sea. Some of these species, such as *Nereis virens* are known to leave intertidal habitats under low temperature conditions (DEAN, 1978). Temperature-related emigration of organisms from intertidal habitats can also be found in the group of the epibenthic predators, e.g. *Carcinus maenas*, (KLEIN-BRETELER, 1976; *Crangon crangon*, WOLFF & ZIJLSTRA, 1983). Winter migrations have not yet been described for meiofauna taxa.

It is questionable for most of these species whether the emigrated individuals stay in the subtidal area and contribute to the population there or whether they return to the intertidal zone in the following spring.

In conclusion: low temperatures are assumed to change the behaviour of intertidal infaunal animals, whereby they attempt to disperse actively towards ambient subtidal areas.

2.2.2. SEXUAL REPRODUCTION

Swarming behaviour of adults for sexual reproduction must also be considered here. In the Wadden Sea, this dispersal occurs in the Nereid polychaetes, *Nereis succinea* and *Nereis virens* (HARTMANN-SCHRÖDER, 1971). Both species develop epitok stages in this period to increase the swimming ability. Catches of nereid worms in the water column are reported by EMERY (1968), THOMAS & JELLEY (1972), HOBSON & CHESSE (1976) and DAUER *et al.* (1982). In most cases, these are swarming heteronereid forms which are able to colonize defaunated intertidal areas (SIMON & DAUER, 1977).

Dispersal due to the sexual reproduction process has been observed in harpacticoid copepods inhabiting intertidal salt marshes (BELL *et al.*, 1988, 1989). These authors suggest that dispersal might increase the chance of a male to find a female for mating due to the sex-ratio of copepods in the water column and in the sediment.

2.2.3. SEARCH FOR FOOD OR AVOIDANCE OF COMPETITION/DISTURBANCE

a) Dispersal of postlarvae and adults via the water column

The migratory behaviour of young lugworms (*Arenicola marina*) is a well known example of the dispersal

of postlarval stages. These stages are released from adult burrows in autumn and settle on the border of tidal channels. In spring, the young worms re-migrate into upper parts of the intertidal zone using tidal currents where they can reach densities of more than 200 ind.·m⁻² (pers. obs.), while adults are virtually absent. Dispersal into the adult habitat occurs in autumn of the same year (BEUKEMA & DE VLAS, 1979; FARKE & BERGHUIS, 1979b; REISE, 1981, 1985). This complex migratory behaviour is obviously a strategy of postlarval stages to avoid competition with the adult habitat, where they would be affected strongly by the burrowing and feeding activity of the parental generation (BEUKEMA & DE VLAS, 1979).

The tellinid bivalve *M. balthica* also exhibits extensive dispersal. Settlement of larvae, metamorphosis and postlarval transport can broadly overlap in this species (GÜNTHER, 1990b, 1991). In contrast to the lower parts of the flat where initial settlement of larvae occurred, the upper parts (above mean tide level (MTL)) were mainly colonized by postlarvae which were transported from the place of initial settlement. About 50% of the total 0-group was involved in this dispersal process. Changes in the spatial distribution of *M. balthica* which were attributed to dispersal by benthic stages have been reported by BOYDEN & LITTLE (1973), MYREN & PELLA (1977), WOLFF & DE WOLF (1977), RATCLIFFE *et al.* (1981) and GÜNTHER (1990a, 1990b). Comparable changes in spatial distribution due to dispersal as well as extreme numbers of postlarval recruits in the water column have been observed in *Cerastoderma edule* (BAGGERMANN, 1953; MÖLLER, 1986; HEIBER, 1988; GÜNTHER 1990b), *Mya arenaria* (BAGGERMANN, 1953; MATTHIESSEN, 1960; MÖLLER, 1986), *Mytilus edulis* (BAYNE, 1964; DARE, 1976; DE BLOK & TANMAAS, 1977; HEIBER, 1988), *Hydrobia ulvae* (HENKING, 1894; HEIBER, 1988; Günther, unpubl. data), *Nereis virens* (MIRON & DESROSIERS, 1990) and *Corophium volutator* (JENSEN, 1985; HUGHES, 1988; ESSINK *et al.*, 1989; GÜNTHER, 1990a). The function of these extended dispersal patterns could be to avoid certain habitats (*Arenicola marina*) or to react to changes in the availability of food after settlement, as is assumed for *Macoma balthica* (GÜNTHER, 1990b). Therefore, either avoidance of disturbance or competition would be another reason for dispersal of postlarval stages within a habitat.

Dispersal of postlarval and/or adult stages via the water column has been concluded from studies carried out in North Sea intertidal areas (MCLUSKY *et al.*, 1983; VAN DEN HEILIGENBERG, 1987; FRID, 1989), the Baltic Sea (BONSDORFF, 1983) and in other soft-bottom communities (DAUER & SIMON, 1976a; McCALL, 1977; SANTOS & SIMON, 1980; BHAUD *et al.*, 1981; BELL & DEVLIN, 1983; DIAZ-CASTANEDA & SAFRAN, 1986). Comparable to the dispersal of meiofauna (DECHO, 1986; DECHO & FLEEGER, 1988; KERN, 1990), the emergence of macro-

fauna may be related to the search for food (GRANT, 1980; BARNES, 1981; DE WIT, 1979).

b) Dispersal due to crawling and burrowing

Small-scale movements of macrofauna organisms (either within the sediment or at the surface), such as crawling and burrowing, are mainly due to feeding activity. These movements result in continuously changing patterns of spatial configurations, modified by interactions between species and individuals such as the territorial behaviour of sponidids (LEVIN, 1980), nereid worms (REISE, 1979) and amphipods (for example, *Corophium volutator*). SCHUITEMA (1970) assumes that small-scale dispersal of *C. edule* which is in the order of magnitude of 10 cm may be directed by gradients in the availability of food.

In conclusion, causes for dispersal include disturbances, changes in behaviour due to changes in the temperature, reproductive behaviour and local food limitations. Some of these may be only the triggering factors for endogenous migratory rhythms.

The frequency of occurrence of the different kinds of dispersal varies with the cause. In the the Wadden Sea, strong storms may occur in spring and autumn; extreme storms occur on the average of one per decade. Winter migrations as well as the swarming behaviour of adults are assumed to occur once a year under ice conditions. It is assumed that the dispersal of postlarvae, if not part of a very specialized life-history strategy as in, e.g. *Arenicola marina*, occurs several times a year. GÜNTHER (1990b) concludes from fluctuations in abundance and length-frequency distributions that dispersal within the higher eulittoral of postlarval *M. balthica* is possibly governed by cyclic rhythms during summer. The transport frequency may be related to the size of the organisms, as was obvious for recruits of *H. ulvae*. High transport rates were found as long as most of the recruits were smaller than 1 mm (HEIBER, 1988). As the animals grew larger, the proportion of transported individuals decreased. BAGGERMANN (1953) also reports that tidal-current transport of *C. edule* is dependent on the size of the postlarvae. Individuals larger than 2 mm are assumed to be more or less stationary.

There is a lack of good data on the dispersal of postlarval and adult stages, especially when studies are carried out in tidal channels, but dispersal may occur only within the eulittoral or in an on-shore direction (e.g. *M. balthica*). Investigations on dispersal of intertidal bivalves in different parts of the intertidal habitat have been carried out by BAGGERMANN (1953, intertidal near tidal channels), HEIBER (1988, sublittoral) and GÜNTHER (1990b, above MTL). The results vary with the distance to the areas from where the dispersing organisms originate (e.g. cockle bed), the size (weight) of the individuals as well as their behav-

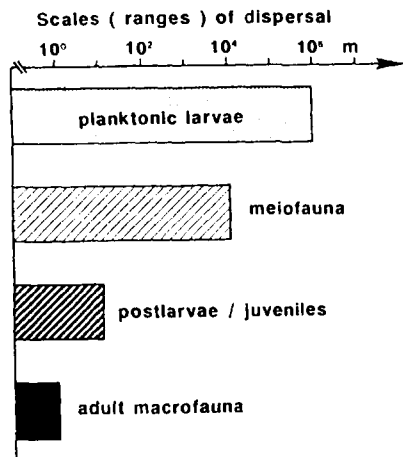


Fig. 1. Scales of larval, meiofauna, postlarval and adult dispersal in a logarithmic representation. All scales have to be considered as species specific ranges. The order of magnitude was estimated according to SCHELTEMA (1971, planktonic larvae), HAGERMAN & RIEGER (1981, meiofauna), GÜNTHER (1990b, postlarvae) and e.g. BELL & DEVLIN (1983, adult macrofauna). For further explanations, see text.

our (directed transport, possibility to anchor by byssus-threads, use of these threads to facilitate tidal current transport, changes in burrowing depth). Similar conclusions were drawn by WILLIAMS & PORTER (1971), who compared the postlarval transport of bivalves obtained from three different sampling stations.

3. RELATIONSHIP BETWEEN DISPERSAL AND DISTURBANCE

From conclusions drawn above, physical disturbances may cause passive resuspension of organisms (erosive currents, storms, ice scour, disturbance by epibenthic predators). From long-distance transports of juvenile and adult macrofauna due to resuspension under stormy weather conditions (REINECK *et al.*, 1968; DOBBS & VOSZARIK, 1983), it can be concluded that the scale of this dispersal is related to the scale of the causing disturbance.

Chemical disturbances due to e.g. oil and oil/dispersant mixtures (FARKE *et al.*, 1992), organic waste

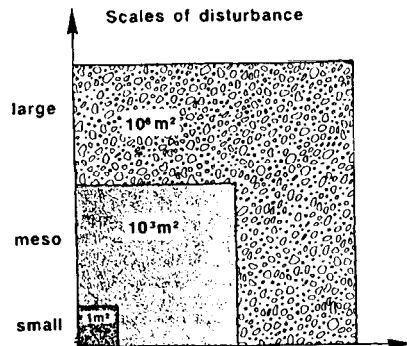


Fig. 2. Scales of disturbance estimated according to GRASSLE & GRASSLE (1974, large-scale) and personal observations (meso- and small-scale).

(ESSINK, 1978) or oxygen deficiency (e.g. caused by algal blooms (CADÉE, 1990)) will also affect the organisms. To compensate their inability to adapt, the macrofauna will appear at the sediment surface and this may be interpreted as emigration from an unfavourable area.

From the organisms' viewpoint, dispersal predisposes them to colonize disturbed and partly or totally defaunated areas. If parts of a population (either larvae, postlarvae or adults) disperse during most of the year, additional resources will become available. According to theoretical explanations of GADGIL (1971), this dispersal results in emigration from less suitable habitats and an uneven distribution within an area. Enhanced mortality as well as transport into areas of low carrying capacity are the risk of dispersal. But in general, this strategy is advantageous for the population because an extended area of distribution increases the chance of a species' survival within systems characterized by strongly fluctuating environmental conditions and competition (CHESSON & HUNTLEY, 1988).

If dispersal is a strategy to find free resources (space, food) within an unpredictable and disturbed habitat then the frequency and/or scale of dispersal and of disturbance should be analogous. Due to the availability of information, the spatial scales will be taken into consideration in the following.

In Fig. 1, the scales of dispersal of planktonic larvae, meiofauna, postlarvae and adults of the macrofauna are compared. These scales have to be regarded as landmarks within a continuum. They cover wide ranges of transport distances: planktonic

larvae may be transported as little as a few metres (if the larvae become competent within minutes after release) or as much as thousands of kilometres (teleplanic larvae e.g. SCHELTEMA, 1971). Meiofauna can be transported as far as 10 km by erosive tidal currents (HAGERMAN & RIEGER, 1981), but some taxa (e.g. nematodes) may be more or less sessile due to vertical downward migrations at high tide (PALMER & MALLOY, 1986). Postlarvae of *Macoma balthica* were observed to migrate 16 m per tide (GÜNTHER, 1990b). Postlarvae of *Arenicola marina* migrate from the border of tidal channels to the upper parts of flats. To avoid the intermediate areas inhabited by adults, the transported distance ranges around 1 km. Both meiofauna and postlarval transport are summarized as meso-scale dispersal.

Small-scale dispersal due to burrowing activity and water transport of adult macrofauna was assumed to be less than one metre per tide (SCHUITEMA, 1970; BELL & DEVLIN, 1983; BONSDORFF, 1984; SMITH & BRUMSICKLE, 1989).

Scales of dispersal vary with size and age of the animals involved:

- (i) large-scale - planktonic larvae,
- (ii) meso-scale - postlarvae and permanent meiofauna, and
- (iii) small-scale - adult macrofauna.

Firstly, it is generally assumed that dispersal of planktonic larvae is bound up with genetic exchange (STRATHMAN, 1974, 1986). Secondly, the distribution of species on a geographical scale is another aspect to be considered (MILEIKOVSKY, 1971; SCHELTEMA, 1986; JABLONSKI, 1986). While larvae can reach new intertidal systems, the transport distance of postlarvae

and adults reflects more the potential of exchange within a system.

Comparable scales to those of dispersal can be found in disturbance (Fig. 2). Large-scale disturbances (in the order of several km²) occur if tidal flats are affected in total, by e.g. chemical pollution (GRASSLE & GRASSLE, 1974) or red tides (SIMON & DAUER, 1977). Meso-scale disturbances such as ice scour which can result in sediment erosion at the border of a tidal channel may affect areas between 100 and 1000 m². But most of the disturbances influence very small areas (defaecation mounds of sediment-dwelling polychaetes (FLACH, 1992), the feeding of epibenthic predators, migrating ripple marks, feeding pits of birds or rays). In contrast to large- or meso-scale disturbances, the frequency is much higher and may be related to the tidal elevation.

Due to their longer transport distance, it has to be assumed that larvae can occupy large defaunated areas faster and in higher numbers than postlarval or adult forms. This presupposes that competent larvae are available which in turn depends upon the season when the disturbance occurs. Studies on large-scale disturbed communities show that, in spite of adult immigration, larval settlement is the predominant mode of recolonization (GRASSLE & GRASSLE, 1974; SIMON & DAUER, 1977; McCALL, 1977; SANTOS & SIMON, 1980). Small-scale experiments on recolonization show that the recovery depends on the fast immigration of benthic stages of macrofauna (BELL & DEVLIN, 1983; FRID, 1989; SMITH & BRUMSICKLE, 1989). Control levels are reached within several days (BELL & DEVLIN, 1983; FRID, 1989), as was seen in experiments with permanent meiofauna. The relationship between the recoloniza-

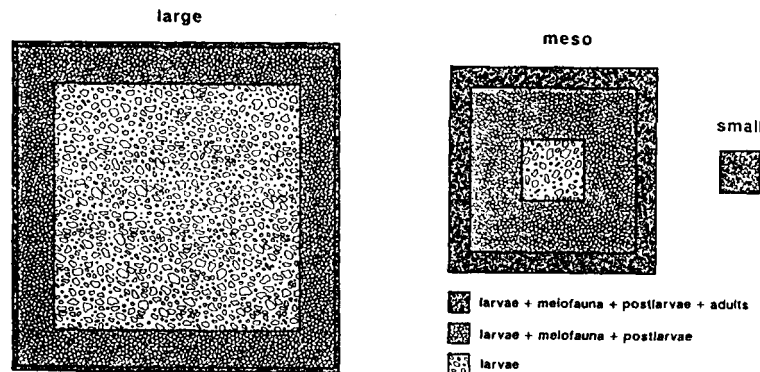


Fig. 3. A modified version of the SMITH & BRUMSICKLE (1989) model of the interrelationship between the scale of a disturbed area and the mode of recolonization (for explanation, see text).

tion mode and recovery rate to the patch size on the other was demonstrated by SMITH & BRUMSICKLE (1989). These authors investigated the recolonization of two disturbed patches of different sizes and found that the recovery rate and mode were size-dependent. Based upon this result, they developed a conceptual model on the relationship between scales of disturbance and the mode of recolonization. A modified version of this model is given in Fig. 3. At time t_1 after a disturbing event, an affected large-scale area is colonized at the boundaries by all means of dispersal (Fig. 3a). But the largest part of the area will be mainly colonized by settling larvae. The smaller the affected area the more the immigration of adults, postlarvae and meiofauna increases in importance (Fig. 3b, 3c). Very small disturbed areas recover by way of the colonization potential of organisms inhabiting the ambient area.

In this model, the shape and frequency of the disturbed area, the changes in transport direction and the possibility of transport series (successive transports over several tides) within an intertidal zone were not considered. If transport series occur, the importance of postlarval and adult dispersal may be underestimated.

It must also be assumed that an interrelation exists between the frequency of disturbance and dispersal. Unfortunately, there are few investigations similar to that described by HALL *et al.* (1991) in which the numbers of disturbing events have been recorded.

4. CONCLUSIONS

There are two relationships between dispersal and disturbance:

1. disturbance is the cause of dispersal; and
2. dispersal is related to the availability of resources which in turn are continuously redistributed by disturbances in intertidal areas.

Although more information concerning adult and postlarval dispersal is warranted, there is evidence that this dispersal is a reaction to and compensation for disturbances in intertidal areas.

As with permanent meiofauna (SHERMAN & COULL, 1980; ARMONIES, 1988a), dispersal of benthic stages of macrofauna obviously increases the elasticity of species (definition according to SANTOS & BLOOM, 1980; elasticity ORIANI, 1974, resiliency BOESCH, 1974) to react to local disturbances and competition. The possibility of redistribution can make species relatively independent of the timing of reproduction, the need for a planktonic larval stage and the availability of suitable space and conditions for settlement. According to BEUKEMA *et al.* (1983), *Arenicola marina* exhibits one of the most stable populations in the Dutch Wadden Sea. Factors contributing to this stability may include its relative longevity, and its potential to dis-

perse, thus avoiding competition and disturbance interference with adults (BEUKEMA & DE VLAS, 1979) as well as predation by epibenthic predators (REISE, 1985).

If life-history aspects of intertidal species are transferred to the community level, as done by GRASSLE & GRASSLE (1974) or McCALL (1977), the dispersal potential of several species (Table 1) increases the elasticity of the community. How strong this influence may be depends on the season and is also related to the successional stage of the community (ZAJAC & WHITLICH, 1985).

The mobility of organisms was rarely included in models for the macrofauna on the community level. POSEY (1987) considers mobility in context to community structuring species interactions. In several examples, mobile organisms excluded small sedentary species.

FRID & TOWNSEND (1989) apply patch dynamic models on stream and intertidal benthos to describe communities with mobile faunal members affected by disturbance. It seems questionable how far this approach can be applied to soft-bottom communities, because it is based on experience from hard-substratum where species compete for space (DOWNS, 1990).

5. RECOMMENDATIONS

1. More quantitative studies are necessary concerning dispersal processes such as numbers of transported organisms per unit area, transport distances, frequencies, directions and causes in intertidal infauna, especially postlarval stages of the macrofauna.
2. The different scales of dispersal should be included in the evaluation of life histories on a species level.
3. Similar information is needed in the cases of disturbance: size of affected area, strength of the effect on the macrofauna community, frequency of disturbance.
4. The relationship between size of disturbed area, mode of colonization and recovery rate should be assessed.
5. A dynamical approach to the structure and function of intertidal benthic communities should be developed in which all scales of dispersal related to scales and frequencies of disturbance are included.

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DRIFTING ALGAE AND ZOOBENTHOS - EFFECTS ON SETTLING AND COMMUNITY STRUCTURE

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ABSTRACT

Shallow (5 to 10 m) sandy bottoms in the Baltic Sea are important areas for zoobenthic production. The infaunal communities are generally governed by the hydrographical conditions and transport of the sediment through wind effects. With increasing eutrophication in the Baltic Sea, drifting mats of annual algae (*Cladophora*, *Stictyosiphon*, *Polysiphonia*, *Rhodomeia*, *Sphacelaria*, *Pilayella*, *Furcellaria*, *Ceramium*, etc) have become increasingly common, adding to the structuring and regulating factors for the infauna. In 1990 and 91, a field-study (SCUBA diving; zoobenthos and algae sampling) was carried out in the Åland archipelago, in the northern Baltic Sea, to quantify the amount of drift-algae and their structuring effect on the zoobenthos. Algal biomass increased from 150 ± 19 g DW·m⁻² in 1990 to 832 ± 60 g DW·m⁻² in 1991, having no effect on oxygen saturation in 1990, but showing signs of reduced oxygen saturation in 1991. Organic content of the sediment remained stable (0.60 to 0.74%) during the entire study period. The zoobenthic community showed significant responses to the drifting algae at population level and in terms of community structure (by 1991: significantly reduced species number; low similarity values (40 to 65%) between bare sand and under the algae). The main species affected were the dominating bivalve *Macoma balthica*, the polychaetes *Pygospio elegans* and *Manayunkia aestuarina*, and the amphipod *Corophium volutator*. The settlement of *M. balthica* spat was significantly reduced by the algae (>70% in 1990/91), and no individuals of the dominating polychaetes were recorded under the mat. *C. volutator*, however, benefited from the algae, and greatly increased in numbers. The results clearly demonstrate the types of physical effects drift-algae will have on sandy-bottom benthos, and show that significant changes in the communities over large areas can be expected with increasing eutrophication.

1. INTRODUCTION

In the northern Baltic Sea, sandy bottoms are relatively sparse (BLOMQUIST & BONSDORFF, 1986), but are highly diverse and productive (LAPPALAINEN & KANGAS, 1975; LAPPALAINEN *et al.*, 1977; PERSSON, 1983; PERSSON & OLAFSSON, 1986). Such shallow (5 to 10 m) areas are also important nursery grounds for fish and shrimp (PHIL, 1982; PHIL & ROSENBERG, 1984; MATTILA *et al.*, 1990). In these sandy biotopes, the main factors regulating the zoobenthos are the annual changes in hydrography (mainly steep temperature gradients) and wave-induced sediment transport which forms local microscale gradients within the habitat (BLOMQUIST & BONSDORFF, 1986). With increasing eutrophication of the northern Baltic Sea (ELMGREN, 1989; CEDERWALL & ELMGREN, 1990; BONSDORFF *et al.*, 1991), primary production and the subsequent degradation of annual algae have increased, manifesting as large mats of drifting algae on beaches and sandy bottoms during late summer and early fall (July to

September). However, the possible effects of the drift-algae on the zoobenthos of the sandy, low-organic sediments are poorly known. In the Baltic Sea, no field studies to date have quantified both the drifting algae and the underlying fauna, although OLAFSSON (1988) experimentally tested the effects of the algae on the settling process and population dynamics of the sandy-bottom infauna. The algae may exhibit both promotive and repressive influences on the underlying infauna by changing the hydrography, light conditions, shelter, food supply to filter-feeders, refuge from predation *etc*. The recruits of the zoobenthos can undergo filtering (*i.e.* preventing the larvae from reaching the sediment) which will also affect the underlying filter-feeders. It is evident that the success of the settling stages of the benthic infauna are of crucial importance in determining the structure and functioning of the entire community (WILSON, 1983; ROUGHGARDEN *et al.*, 1985), while migrations and redistribution of settled juveniles, within or on the sediment surface, may be of importance at the local level (ZAJAC