Tidal Dispersal of Salt Marsh Insect Larvae within the Westerschelde Estuary
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Tidal dispersal of salt marsh insect larvae within the Westerschelde estuary

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In the Westerschelde estuary, salt marshes are present as isolated patches fringing the estuary. In the present paper tidal transport of stem-boring larvae of *Agapanthia villosoviridescens* (Coleoptera) from salt marshes of the upper reaches of the Westerschelde estuary to marshes of the lower reaches is demonstrated. The evidence for the origin of the larvae is based on comparisons of growth and development characteristics of larvae found in flood debris belts and resident larval populations. These characteristics are different on the various salt marshes along the Westerschelde, probably as a result of estuarine gradients. Additional evidence for the larval origin comes from the plant composition of the flood debris. The occurrence of upward tidal transport is discussed. Considering the comparatively large area of salt marshes in the upper estuary, tidal dispersal of larvae probably will be dominated by transport in seaward direction. So far, very little is known on the role of tidal currents with regard to the exchange between salt marsh populations. The present results suggest that tidal transport may not only be important for dispersal of aquatic organisms in an estuary, but also for organisms inhabiting the semi-terrestrial estuarine salt marshes.

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Introduction

Estuaries are semi-enclosed transitional areas between sea water and fresh water from land drainage. Here the incoming flow of sea water from flood tides and the alternating reverse flow of water during ebb tides are in a constant interaction with the downstream flow of riverine water, resulting in a complex flow pattern. Usually, salt marshes are present in the intertidal zone of the estuary. These may be found as a virtually uninterrupted belt fringing the water body; more often, however, the marshes are found as separate patches within the estuarine area, as a result of varying conditions for salt marsh genesis within the estuary and human activities such as diking for land reclamation and coastal defence. This raises the question if there is exchange between the populations of organisms living on these marshes or that the marshes must be considered as isolated habitats. The dispersal of individuals between populations is an important process in the maintenance of genetic variability and the persistence of local populations (Gaines and McClenaghan 1980, Greenwood and Harvey 1982, Howe and Smallwood 1982). For estuarine organisms living in subtidal areas or on tidal flats, transport with tidal currents is an important means of dispersal and exchange between populations (e.g. Stancyk and Feller 1986). Whether the same applies to the semiterrestrial salt marsh organisms is largely unknown. Seeds of various halophyte species can be trapped in nets on the marsh-tidal flat transition, being transported by ebb and flood currents (Koutstaal et al. unpubl. data, cf. Dalby 1963, Gray 1971). As diaspores of salt marsh plant species may have a floating capacity of weeks or months (Koutstaal et al. 1987), a continuous exchange of gene material of halophytes between estuarine marshes, with the water currents acting as a transport agent, therefore seems plausible. Definite proof of such an exchange, however, has not been given, as the origin of the halophyte seeds carried in the water has not been established so far. To our knowledge

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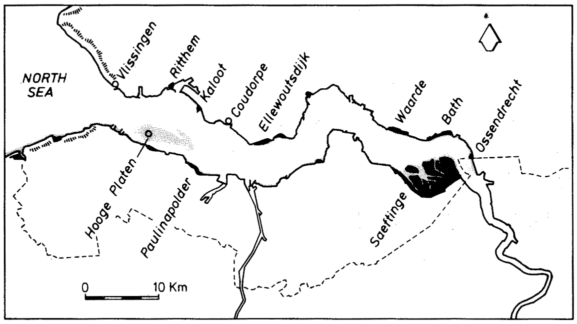

Fig. 1. The Westerschelde estuary with the sampling locations mentioned in this paper. Black areas: salt marshes; grey areas: tidal flats. The open dots indicate dike locations, except Hooge Platen, which marks a low dune formation on a tidal flat. The dotted line is the Dutch-Belgian border.

there are no studies on salt marsh organisms other than halophytes concerning the transport of biota from one estuarine salt marsh to another by means of tidal currents.

In the present paper, we report on the tidal dispersal of *Agapanthia villosoviridescens* larvae (Coleoptera) in the Westerschelde estuary. These larvae are stemborers of *Aster tripolium,* the sea aster, a dominant halophyte which is found both in the marine and brackish part of the estuary (Beeftink 1957). An account of the growth and development of the *Agapanthia* larvae on the Westerschelde salt marshes is given in Hemminga et al. (1987) and Hemminga and van Soelen (1988). During summer, female *Agapanthia* imagoes pierce the *Aster* flowering stems to deposit a single egg inside the marrow. The larvae which hatch from the eggs remain inside the flowering stems throughout their larval existence; pupation ensues in spring of the following year. The flowering stems gradually die-back in autumn, but they may retain their upright position throughout the winter and spring period. During winter gales, however, a substantial part is washed off the salt marsh or is deposited in debris belts elsewhere on the marsh.

There are three aspects of the *Agapanthia* larval development on estuarine salt marshes which are particularly relevant for the present study: in upstream direction 1) mean larval weights are consistently higher during the entire larval period; 2) the percentage of late instars on a given sampling date generally is higher; 3) the percentage of larvae which undergoes succesful metamorphosis increases. As we have pointed out previously (Hemminga and van Soelen 1988), these phenomena are probably related to the effects of the estuarine salt gradient on the suitability of the host plant, *Aster tripolium.* The differences in larval development on the various salt marshes along the Westerschelde were used as keys in retracing the origin of larvae found in *Aster* stems washed ashore as flood debris in the estuary.

Area investigated

Fig. 1 shows the Westerschelde estuary. The Westerschelde is bordered by sea dikes, but on a number of locations salt marshes are found in front of the dikes. In recent decades, a substantial area of marsh has been lost due to engineering works (Saeijs 1977). The total area of tidal marshes in the estuary presently is c. 3200 ha. Most of these marshes cover only a modest area; generally they are located widely apart. The sites sampled in this investigation cover a c. 50 km stretch of the estuary, from the Dutch-Belgian border to the North Sea. A clear salinity gradient is found in this part of the Westerschelde: chlorinity values range between c. 14.4 g Cl l^{-1} and 6 g Cl l^{-1} (Bokhorst 1988). This gradient coincides with a shift in plant species composition on the tidal marshes along the estuary (Beeftink 1957).

Two tidal marshes received particular attention in connection with the dispersal of *Agapanthia villosoviridescens* by tidal movements: the marshes of Saeftinge and Ellewoutsdijk. The first mentioned is by far the largest tidal marsh in the estuary (2770 ha), and is found in its upper reaches. *Agapanthia* is abundant here: on some locations nearly all *Aster* flowering stems contain larvae. The Ellewoutsdijk salt marsh (71 ha) is located nearer to the estuarine mouth. Although *Aster* is a very common halophyte on this marsh, *Agapanthia* larvae are less abundant here. In seaward direction, the Ellewoutsdijk salt marsh is the last salt marsh where *Agapanthia* can be found in its host plant without large difficulty: although sea asters are found up to the mouth of the estuary, the occurrence of larvae in the lower estuary is rare.

Plant debris originating from the Westerschelde salt marshes, and deposited by the tides in belts on the estuarine shores, is found throughout the year; deposition, however, mainly occurs in winter and early spring, when gales and high floods tear away the dead parts of the vegetation. Depending on the location, the plant debris may be present as a narrow zone of scattered plant remains on exposed sections of the sea dikes, but on the sheltered salt marshes and on the dikes bordering the marshes, the plant debris is often found in wide belts, c. 5–15 cm thick.

Materials and methods

Weight changes of *Agapanthia* larvae were followed in Nov. 1987–March 1988 on the salt marshes of Saeftinge and Ellewoutsdijk. Flowering stems of *Aster tripolium,* which showed circular marks due to ovipository activity of *Agapanthia* females, were collected periodically from the same 100 × 50 m sampling location. Both sites were marsh areas located within 100 m of the marsh edge facing the water front. In the laboratory, the stems were cut open longitudinally and living *Agapanthia* larvae, if present, were frozen on solid carbondioxide, freeze-dried and weighed.

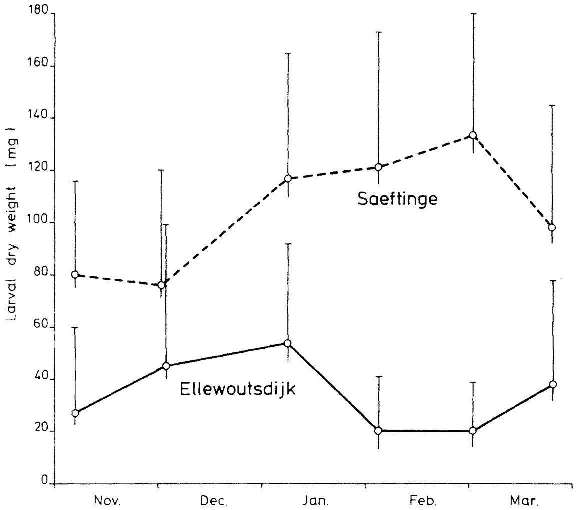

Fig. 2. Time course of *Agapanthia villosoviridescens* larval dry weights. Mean values and S.D. Each point is the mean of 22 observations.

Flowering stems of *Aster tripolium* were collected from debris belts found on salt marshes, dike locations and a low dune formation on a tidal flat on 21–28 April 1987 and on 28–29 March 1988. The *Aster* stems obtained from the salt marshes were collected from debris belts in the 100 m zone near the water front. In addition, standing *Aster* stems were obtained from a number of salt marshes, again collected in the 100 m zones near the water front. *Agapanthia* larvae in the stems were freeze-dried and their head-capsule widths (samples of 1987 and 1988) and weights (samples of 1988) were determined. The number of larvae collected in the samples was generally between 20–30 specimens. In a previous paper (Hemminga and van Soelen 1988), we were able to define early and late instars from the Ellewoutsdijk, Waarde and Bath marshes on basis of the frequency distribution of head-capsule widths measured during larval development in Aug. 1986–May 1987. The size limits dividing the larvae collected from Ellewoutsdijk, Waarde and Bath in early and late instars were also used for the larval samples collected in March 1988 on these marshes. We used the size criterion for Bath also for division of the larval populations of Saeftinge and Ossendrecht. These salt marshes are located near Bath salt marsh (Fig. 1). Furthermore, the head-capsule width range of larvae of Saeftinge and Ossendrecht was comparable to the range measured in the larvae of Bath (March 1988: Saeftinge 1.60–2.32 mm; Ossendrecht 1.51–2.46; Bath 1.44–2.32 mm; compare with: Ellewoutsdijk 1.03–1.95 mm; Waarde: 1.04–2.15 mm). The larvae collected in March 1988 on the Paulinapolder marsh (range 1.01–2.17) were divided using the size limit of Waarde (range in March 1988: 1.04–2.15 mm). The larvae collected from the plant debris belts were considered late instars if their head-capsule widths were >1.45 mm. Although in this case the selection of the size criterion derived from the Bath population was arbitrary, as the origin of the larvae in the plant debris is not obvious a priori, using this 1.45 mm size limit from a marsh of the upper estuary instead of the 1.25 mm limit from a marsh of the middle estuary (Ellewoutsdijk) is potentially more discriminative: in the sampling period (March/April) the percentage late instars in the upper reaches of the estuary already has become very high (approaching 100% on the Bath marsh). Using the low 1.25 mm limit would more easily lead to series of equal (100% late instar) results.

In March 1988, simultaneously with the collection of the *Aster* stems (see above), plant debris samples were collected (c. 125 dm^3) for analysis of plant species composition. Furthermore, on three occasions, 18 Feb., 8 March and 18 April 1988, floating plant debris carried out of the Saeftinge salt marsh with the ebb flow, was collected with landing nets. On each occasion 7 samples were taken during the first two hours after the turn of the tide, in the mouth of two major creeks of the marsh. These samples (each c. 125 dm^3) were also analysed for plant species composition.

To study emergence of *Agapanthia* adults, standing flowering stems of local *Aster tripolium* populations were collected on 21 and 22 March 1988 from the salt marshes of Saeftinge and Ellewoutsdijk, from the same areas as were sampled for the larval growth study (see above). In addition, in this period, a third batch of flowering stems with oviposition marks was collected from plant debris belts deposited on the Ellewoutsdijk marsh; these plant remains were within 100 m from the marsh edge. In the laboratory, each batch of flowering stems was randomly divided in three groups of 25–30 stems. Each group was transferred to a cage. The cages were placed in the open air, sheltered from rain. During the subsequent observation period, until 25 Sept., the cages were regularly checked for imagoes which had emerged. These were freeze-dried and weighed. After the end of the observation period, the initial number of larvae in each cage was determined. To that purpose, the stems were examined for larvae and for exit holes caused by the escaping imagoes. Larvae which were still present in the stems by that time were non-vital and showed signs of desiccation. The total number of larvae calculated to be initially present in the stems, ranged between 70–75 in the three batches.

Results

Growth of larvae and marsh location

Fig. 2 shows the course of the dry weights of the resident *Agapanthia* larvae on the Saeftinge and Ellewoutsdijk salt marshes in the late autumn and winter period of 1987/1988. The results show that during the entire period mean values of the Saeftinge larvae are well above those of the Ellewoutsdijk larvae: mean values of the first mentioned population vary betweeen 86 and

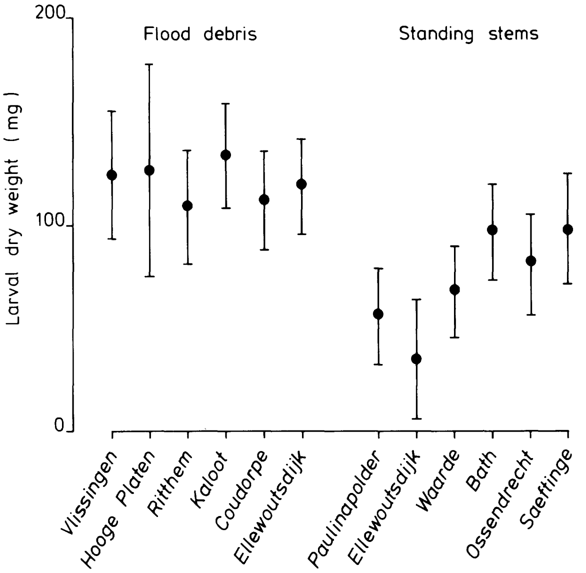

Fig. 3. Dry weights of *Agapanthia villosoviridescens* larvae collected in March 1988 on various locations of the Westerschelde estuary. The flowering stems which contained the larvae were either standing stems from local sea aster populations, or stems collected from flood debris belts. Means and 95% comparison intervals; means with non-overlapping intervals are significantly different. The number of larvae in the samples varied between 20–31, except for the sample of Hooge Platen (n = 6).

134 mg, whereas the mean values of the Ellewoutsdijk larvae vary between 20 and 54 mg. The data demonstrate the differences in larval weights in relation to the salt marsh location within the estuary. Analysis of variance showed that this effect of marsh location on larval dry weight is highly significant ($p<0.001$). Larvae of various size classes, depending on their origin, therefore may be washed off the marshes, as it is during late autumn and winter that dead and withered stems of *Aster* may break and potentially can be carried away with the flood water.

Comparison of larvae from salt marsh populations and from flood debris

In April 1987 and March 1988 *Agapanthia* larvae were collected from standing *Aster* flowering stems on various marshes and from *Aster* stems found in flood debris deposited on salt marshes, dike locations and a low dune formation on a tidal flat in the estuary (Hooge Platen). The larvae found in the *Aster* stems of the plant debris samples were almost without exception alive and vital. The stem cavity which housed the animals generally was dry. In many cases the animals had locked up their living space on either end of the stem cavity by masses of scrapings from the wood cylinder and faeces. Presumably, this helped to keep out water and to keep the stem cavity dry. For measurements on the larvae only the living specimens were used. Fig. 3 shows the mean dry weight of the larvae in the 1988 samples. After analysis of variance, which showed that there were significant differences between the groups, 95% comparison intervals were calculated using a GT2 a posteriori test (Sokal and Rohlf 1981). The mean weights of the resident larvae collected from standing flowering stems is highest in the upper reaches of the Westerschelde and decreases towards the mouth of the estuary, reaching its lowest value on the Ellewoutsdijk marsh. The mean weights of the larvae from the plant debris samples are all of the same magnitude; these values are not significantly different from weights of larvae in standing *Asters* of the upper estuarine marshes, as can be concluded from the overlapping comparison intervals, but they differ significantly, almost without exception, from the weights of larvae in standing *Asters* of lower estuarine marshes (Ellewoutsdijk and Paulinapolder). The results therefore suggest that the *Aster* stems in the plant debris found in the lower reaches of the estuary originate from tidal marshes of the upper reaches. This suggestion is corroborated by the data on percentage late instars found in the samples (Tab. 1). These data were analysed with an unplanned test of homogeneity of replicates (Sokal and Rohlf 1981). The analyses showed that both in 1987 and in 1988 the division between early and late instars in the various samples of larvae was not homogeneous. Furthermore, the analyses showed that, with regard to the 1987 data, the maximal non-significant set of samples (in terms of homogeneity) excluded Waarde and Ellewoutsdijk (standing stems); with regard to the 1988 samples, the maximal non-significant set excluded Waarde, Ellewoutsdijk (standing stems) and Paulinapolder. These results thus indicate that the instars found in the plant debris samples of the lower half of the

Tab. 1. Percentage late instars of *Agapanthia villosoviridescens* in *Aster tripolium* flowering stems collected in April 1987 and in March 1988 on various locations in the Westerschelde estuary. The flowering stems were either standing stems from local sea aster populations or stems collected from flood debris belts. The number of larvae in each sample is indicated between brackets.

	1987	1988
Standing stems		
Saeftinge	100 (26)	100 (22)
Ossendrecht	–	100 (29)
Bath	94 (32)	93 (30)
Waarde	76 (25)	87 (31)
Ellewoutsdijk	25 (12)	66 (21)
Paulinapolder	–	81 (31)
Flood debris stems		
Ellewoutsdijk	96 (23)	90 (29)
Coudorpe	100 (22)	100 (28)
Kaloot	96 (25)	100 (30)
Ritthem	100 (14)	100 (25)
Hooge Platen	100 (7)	100 (6)
Vlissingen	100 (18)	100 (20)

Tab. 2. Major plant species and their volume percentage in samples (c. 125 dm^3 each) of (A) flood debris collected from various locations in the Westerschelde estuary, March 1988, and (B) floating plant debris carried with ebb tides from the Saeftinge marsh; means of 7 samples taken during the first two h after the turn of the tide.

	E. dijk	Coudorpe	Kaloot	Ritthem	Hooge Pl.	Vliss
(A)						
Scirpus maritimus	25	45	20	15	25	15
Elymus pycnanthus	65	35	45	60	5	30
Aster tripolium	4	14	10	1	3	8
Spartina anglica	1	1	7	20	5	8
Phragmites australis	1	1	1	1	0	0
Aquatic macrophytes (mainly *Fucus* spp.)	1	2	15	1	60	35
remaining spp.	3	2	2	2	2	4
(B)	18 Feb		8 March		18 April	
Scirpus maritimus	32		35		45	
Elymus pycnanthus	60		60		30	
Aster tripolium	4		2		20	
Spartina anglica	1		1		1	
Phragmites australis	1		1		2	
remaining spp.	2		1		2	

estuary, are in a comparable stage of their development as the instars from standing stems of the upper estuary.

Plant species composition of flood debris

The species composition of the plant debris samples collected in March 1988 in the lower reaches of the estuary is given in Tab. 2A. A number of halophyte species, including *Aster tripolium,* can be found in the samples. The contribution of each species to the total sample volume is rather variable; two species, however, consistently are of major importance: *Elymus pycnanthus* and *Scirpus maritimus.* The first species is common throughout the investigated part of the estuary. *Scirpus maritimus,* however, is limited to the upper reaches, i.e. the more brackish part of the estuary; this plant species is particularly common on the marshes of Saeftinge, Ossendrecht and Bath (Beeftink 1957, De Kogel 1979). Except for a very small patch (<100 m^2) on the Ellewoutsdijk salt marsh, this plant species is absent from the lower half of the estuary.

In Tab. 2B the plant species composition of plant debris washed off the Saeftinge salt marsh during three ebb tides in Feb.—April 1988 is given. The data show that *Scirpus maritimus* is a major component of the material that leaves this marsh after high tides. The combined results of these observations on plant debris composition therefore also point to transport of material from the tidal marshes of the upper estuary to the shores of the lower estuary.

Adult emergence and weight

To obtain further evidence regarding the origin of the *Agapanthia* larvae in flood debris belts of the lower half of the estuary, emergence of adults was investigated from local (standing) *Aster* stems collected on the Ellewoutsdijk and Saeftinge marshes and from stems found in flood debris belts on the Ellewoutsdijk marsh. The cumulative emergence curves are shown in Fig. 4. There is a clear difference between the groups of larvae with respect to the final percentage of successful metamorphis. From 58% of the larvae of the Ellewoutsdijk population living adults arise. This proportion is 87% for the Saeftinge larvae. Although the larvae in the plant debris belts have been washed away within the flowering stems from their original habitat, the larvae are still vital: from 83% of the larvae imagoes arise. Emergence of imagoes from Saeftinge and from the flood debris starts before emergence of imagoes from the resident Ellewoutsdijk population. Statistical analysis of the emergence dates using a nested anova showed that within each experimental group the replicate subgroups did not differ significantly, but that there was a significant difference ($p<0.001$) between the three experimental groups (Tab. 3A). Further statistical analysis, using a linear orthogonal contrast a priori test, showed that emergence dates of the Saeftinge larvae

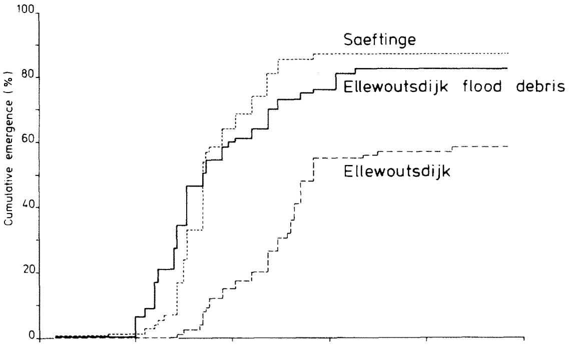

Fig. 4. Cumulative emergence of *Agapanthia villosoviridescens* imagoes.

Tab. 3. Two-level nested analysis of variance of (A) emergence dates and (B) dry weights of *Agapanthia villosoviridescens* imagoes. The between groups sum of squares was divided into two single degree of freedom linear orthogonal comparisons: Ellewoutsdijk, flood debris larvae (Efd) vs. Saeftinge, larvae from standing stems (Sss); and: Ellewoutsdijk larvae from standing stems (Ess) vs. Efd and Sss.

Level	SS	DF	MS	F	p
(A)					
Between groups	12657.00	2	6328.50	12.98	p<0.001
Efd – Sss	3.17	1	3.17	0.01	ns
Ess – (Efd + Sss)	12653.84	1	12653.84	25.95	p<0.001
Between replicate groups	2925.75	6	487.62	2.03	ns
Error	37919.74	158	239.99		
(B)					
Between groups	3951.23	2	1975.62	32.07	p<0.001
Efd – Sss	232.30	1	232.30	3.77	ns
Ess – (Efd + Sss)	3718.94	1	3718.94	60.37	p<0.001
Between replicate groups	369.57	6	61.59	1.26	ns
Error	6503.16	133	48.90		

were not significantly different from those of the plant debris larvae, but that the difference between these two groups on the one hand and the Ellewoutsdijk larvae collected from the standing stems on the other hand was highly significant (p<0.001). Mean dry weights of the imagoes which had emerged were 16.0 mg (Ellewoutsdijk, from standing stems), 26.2 (Ellewoutsdijk, from plant debris), and 29.2 (Saeftinge, from standing stems). A similar statistical procedure as used for the emergence data was carried out on the dry weight measurements of the imagoes. Identical statistical results were obtained (Tab. 3B), including the final result that there was no difference between the dry weights of the Saeftinge and plant debris imagoes, but a highly significant difference (p<0.001) between these groups and the Ellewoutsdijk imagoes emerged from the local *Aster* flowering stems. In conclusion, the observations clearly show the similarity between the emergence characteristics and weights of *Agapanthia* from the plant debris belts on the Ellewoutsdijk salt marsh and the characteristics of the resident Saeftinge population. Again the findings suggest that *Aster* stems are washed from the upper estuarine marshes such as Saeftinge, and are deposited after high tides on salt marshes in the lower part of the estuary.

Discussion

In this study we present evidence for tidal transport of stem-boring insect larvae from salt marshes in the upper reaches of an estuary to isolated marshes in the lower reaches. This evidence comprises several elements: (1) larvae found in flood debris *Aster tripolium* stems on salt marshes and dike locations in the lower reaches of the estuary have a similar mean weight as resident larvae found on marshes of the upper estuary; (2) the similarity also holds for their developmental stage (percentage late instars); furthermore, (3) the emergence characteristics and weights of *Agapanthia* imagoes from flood debris *Aster* stems collected on a marsh of the lower half of the estuary (Ellewoutsdijk) are identical with those of the *Agapanthia* population of an upper estuarine marsh (Saeftinge); finally (4), the flood debris belts of the lower reaches of the estuary contain *Scirpus maritimus,* a plant species limited to the tidal marshes of the upper estuary, as a major component.

The tide must be considered as an essential part of the dispersal mechanism: only if a flooding tide covers the marsh, particularly in the winter period, the dead and withered *Aster* stems will be taken up from the marsh surface, and may float on the water to be deposited elsewhere on the estuarine shores. The present results demonstrate a flow of biological material from the salt marshes of the upper reaches of the estuary in a seaward direction. As Saeftinge is by far the largest salt marsh of the Westerschelde, it is reasonable to assume that this marsh contributes the major part of the salt marsh plant debris to the estuary. Together with the nearby marshes of Ossendrecht and Bath, the sheer mass of plant material transported from these wetlands apparently is such that mixing with the modest amounts of plant debris from the small marshes in the lower reaches of the Westerschelde hardly affects the "upstream" character of the *Agapanthia* population in the flood debris belts found in the lower reaches of the estuary. Given the distribution of salt marsh areas in the Westerschelde, it will be much more difficult to demonstrate transport of organisms from the marine towards the brackish part of the estuary. Tidal dispersal in both directions, however, seems plausible. Experiments with batches of floating sunflower seeds which were shed on the water of the Oosterschelde, a large sea inlet near the Westerschelde, showed that transport of the seeds could take place in all directions, and was dependent on tidal water movements, wind direction and wind speed (Koutstaal et al. 1987). De Pauw (1975) calculated that it takes a theoretical upstream "water particle" in the Westerschelde on average about 60 tidal cycles (30 d) to cover the distance from Zandvliet (near Saefinge) to the North Sea. There is a gradual shift of the water particle towards the sea, but at each flood tide it is pushed back in the reverse direction by the sea water front. In this respect, it is interesting that studies with floating transmitting buoys showed that these were transported over 20 km upwards into the Westerschelde during one flood tide (Huiskes pers. comm.). In an experiment carried out in an outdoor basin with continuous wave generation, we found that the majority of *Aster* flowering stems (with larvae) remained afloat for a period of at least 4 wk (data not shown). Presumably also *Aster* debris, once drifting in the estuary, will move up and down the Westerschelde during a number of tidal cycles, before it is deposited on its shores or enters the North Sea. Therefore, both tidal transport of larvae from salt marshes of the upper reaches of the estuary to salt marshes of the lower reaches and transport in the reverse direction is expected to occur; for reasons mentioned above, however, the larvae transported with tidal water from the extensive marshes in the upper part of the Westerschelde most probably will greatly outnumber the larvae carried away from the marshes of the lower estuarine marshes.

The role of tides in the dispersal of salt marsh insects is little known. It has been demonstrated that tide-mediated transport probably is an important dispersal mechanism for *Pemphigus trehernei;* first instar larvae of this root aphid are released from the salt marsh soil during tidal coverage and float on the water surface for some time; in this way they may reach other host plant locations on the salt marsh (Foster and Treherne 1978, Foster 1978). It is also known that salt marsh Collembola frequently are washed away from their habitat during tidal coverage; due to their unwettable integument these apterygote insects may drift on the water surface for a considerable period (van der Kraan 1973, Joosse 1976). The potential importance of tidal transport for exchange between salt marsh populations is quite conceivable in view of the observation that seashore inhabiting Collembola belonged to the first colonizers of new born volcanic islands (Lindroth et al. 1973). The findings described in this paper demonstrate that tidal transport may connect insect populations from salt marshes which are located widely apart, such as is the case in the Westerschelde estuary. For *Agapanthia villosoviridescens* tidal transport may represent the major link between the populations of these marshes. The imagoes only very rarely seem to fly: during our investigations on these animals we observed this only on one occasion for a single specimen.

There are clear differences in emergence characteristics and weights between imagoes originating from a brackish and a more saline marsh (Fig. 4). This complicates the question of the significance of arrival of specimens from another tidal marsh for the local *Agapanthia* population. The *Agapanthia* imagoes show a clear preference for the largest flowering stems of an *Aster* population for ovipository activity (Hemminga et al., 1987). Several eggs may be deposited in suitable stems during the summer. In November, however, the vast majority of the infected stems contains only one larva (Hemminga et al. 1987); as laboratory observations show that the larvae are highly aggressive towards each other – a phenomenon also observed with other stem-boring larvae (Stiling and Strong 1983) – the most likely explanation for this finding is that it is the result of direct intraspecific aggression and killing. If we now consider the case of transport of larvae from Saeftinge to Ellewoutsdijk, we may assume that the imagoes originating from these Saeftinge larvae will, on average, deposit their eggs in the *Aster* stems before the resident female adults, which emerge later on in the summer. This will give the resulting larvae from the immigrant imagoes the advantage of a larger size due to a longer growth period when violent interactions in the stems occur; probably, this larger size is decisive for the outcome of these encounters (cf. Stiling and Strong 1983). The larger weight of the immigrant imagoes may also have consequences for their reproductive potential, although this remains to be investigated. In conclusion, the significance of tidal transport of larvae obviously cannot only be derived a priori from the number of immigrants that arrive on a particular marsh. In the Westerschelde estuary, where in view of the large total area of the Saeftinge marsh tidal dispersal of *Agapanthia* larvae will be dominated by transport from this marsh in a seaward direction, the impact of immigrant larvae on local *Agapanthia* populations of the lower estuary probably is greater than their numbers suggest.

Computer simulations have shown that population stability, measured as persistence in time, is greatly enhanced by the introduction of dispersal between populations, even at low intensity (Roff 1974, van der Eijk 1987). With respect to the *Agapanthia* populations in the Westerschelde, tidal dispersal may be particularly relevant for the persistence of populations in the lower estuary. The salt marshes in the Westerschelde present a set of habitats of variable quality for *Agapanthia:* probably as a result of the changing host plant quality along the estuary (Hemminga and van Soelen 1988), these animals become rare near the mouth of the estuary; moreover, the reproductive success of the resident population on the saline marshes of the lower estuary presumably is limited. As it is well known that the risk of extinction of animal populations decreases with the average population size (e.g. Pimm et al. 1988), the year to year persistence of *Agapanthia* on these marginal habitats may well depend on the annual influx of immigrant larvae.

It is unlikely that the connections between insect populations of isolated estuarine salt marshes by the mechanism of tidal transport, as described in this paper, are restricted to *Agapanthia villosoviridescens* only. Stem-borers and other endophagous species may well be especially amenable to drift transport with plant remains (cf. Heatwole and Levins 1972), but the endophagous habit is relatively often found among salt marsh insects during the pre-adult part of their life cycle; this can be considered as an adaptation protecting them from the direct impact of the tidal water (Heydemann 1979, Tischler 1981). Furthermore, we found several non-endophagous insect species associated with *Aster* flowering stems which were transported with ebb tides from the salt marsh of Saeftinge (data not shown). Presumably, these animals had entered the dead, hollow stems through small crevices and holes. The observations described in this paper therefore lead us to the conclusion that tidal transport of insects between isolated estuarine salt marshes is an actual process and probably is more common than is apparent until now. The existence of this phenomenon will contribute to the persistence of local salt marsh insect populations and therefore to the stability of species on the larger scale of the estuary.

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