Processes of tidal transport and accumulation of larval flounder (*Platichthys flesus* L.) in the Ems-Dollard nursery

FLOUNDERING

PROCESSES OF TIDAL TRANSPORT AND ACCUMULATION OF
LARVAL FLOUNDER (*PLATICHTHYS FLESUS* L.) IN THE
EMS-DOLLARD NURSERY

Academisch Proefschrift

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Eb

Ik trek mij terug en wacht.
Dit is de tijd die niet verloren gaat:
iedre minuut zet zich in toekomst om.
Ik ben een oceaan van wachten,
waterdun omhuld door 't ogenblik.
Zuigende eb van het gemoed
dat de minuten trekt en dat de vloed
diep in zijn duisternis bereidt.

Er is geen tijd. Of is er niets dan tijd?

(M. Vasalis)

flounder   flounders, floundering, floundered
1 If something is **floundering**, it has many problems and may soon fail completely.
2 If you say that someone is **floundering**, you are criticizing them for not being decisive or for not knowing what to say or do.
3 If you **flounder** in water or mud, you move in an uncontrolled way, trying not to sink
4 A **flounder** is a flatfish that you can eat. The plural can be either **flounder** or **flounders**.

(Collins Cobuild English dictionary)

CONTENTS

VOORWOORD

Het eiland Terschelling was de bestemming van de zomervakanties gedurende 9 jaar in mijn jeugd. Een hoogtepunt waren de avontuurlijke vistochten die mijn ouders met me ondernamen naar de Boschplaat, waar we in de slenken bot vingen. Ik herinner me het gevoel van platvis die onder mijn blote voeten spartelde op de bodem van de modderige kreek. Met een vangst van meer dan 50 stuks bot keerden we terug naar de tenten.

Een andere herinnering, ergens uit de jaren '70, wordt gevormd door een toevallig bezoek aan Nieuwe Statenzijl, gelegen aan de grens van de Dollard, waar de Westerwoldsche Aa zoet water in dit brakke getijdegebied loost. Destijds was de Westerwoldsche Aa zwaar vervuild met organische afvalstoffen die afkomstig waren van de aardappelmeel- en strokartonindustrie. Wat ik me ervan herinner is een stinkend, inktzwart, dood water. Tegenwoordig is de waterkwaliteit gelukkig drastisch verbeterd.

Nadat ik aan de Landbouw Universiteit Wageningen afstudeerde in de Biologie kreeg ik in dienst van het Rijksinstituut voor Natuurbeheer (RIN, thans IBN-DLO) de kans om de betekenis van de Banc d'Arguin (Mauretanië) voor jonge vis te onderzoeken. Ik was erg onder de indruk van de relatief ongerepte schoonheid en natuurlijke rijkdom van dit gebied dat grenst aan de leegte en woestenij van de Sahara.

Een volgende aanstelling bij het RIN bracht me in Den Oever, waar ik de effecten van zoutgehalteschommelingen door zoetwaterlozingen op de ziekte-ontwikkeling bij bot onderzocht. Door dit werk kwam ik in contact met het Rijksinstituut voor Kust en Zee (RIKZ, toen nog Dienst Getijdewateren), dat dit project financierde, en dat naderhand mijn werkgever werd.

Al deze elementen lijken nu samengekomen te zijn in het onderwerp van de huidige studie: het functioneren van de Eems-Dollard als kinderkamer voor de bot. Het RIKZ (Rijkswaterstaat) gaf opdracht tot het uitvoeren van dit onderzoek. De faciliteiten die tot mijn beschikking stonden, o.a. schepen van de Meetdienst Noord-Nederland van Rijkswaterstaat, maakten de bijzonder intensieve meetcampagnes uitvoerbaar. Franciscus Colijn, toenmalig hoofd van de afdeling Onderzoek Biologie, gaf de aanzet tot dit proefschrift, waarvoor ik hem dankbaar ben.

Niels Daan, in de hoedanigheid van hoogleraar aan de Universiteit van Amsterdam, was zondermeer bereid om op te treden als promotor. Onze discussies in IJmuiden heb ik zeer gewaardeerd, evenals zijn vele bruikbare taalkundige suggesties. Ik herinner me ook de Dollard-excursie van Niels met ons, aan boord van de *Capella* op 3 mei 1994, toen er van alles mis ging terwijl ik juist een goede indruk wilde maken.

Adriaan Rijnsdorp (RIVO-DLO) becommentarieerde als begeleider vele conceptstukken en bemoedigde me door zijn stimulerende opmerkingen en opbouwende kritiek.

Introduction and Synthesis

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Fig. A. *Metamorphic stages of flounder (Platichthys flesus). From top to bottom: stage 4a, stage 4b (3x), stage 4b' and stage 5. Total length 8 to 10 mm.*

INTRODUCTION

Coastal waters and estuaries have a number of functions for the fish fauna (McHugh 1967, Zijlstra 1978, Elliott and Dewailly 1995). They provide living space for adults of some species (migration, spawning) and for juveniles of others (feeding, growth and survival: nursery function). At the same time, man's activities make demands on these waters and may threaten these natural functions. Interference with the nursery function may even affect the potential yield of fish of the North Sea (Zijlstra 1972, Rauck and Zijlstra 1978).

To analyse the processes and factors that determine a nursery, detailed and quantitative information is required which cannot be easily obtained over large areas and for many species at the same time. Therefore, a rather isolated area inside the Wadden Sea - the Ems-Dollard estuary (*fig. b*)- and a single flatfish species - the flounder *Platichthys flesus* (Linnaeus 1758) (**fig. a**) - have been selected to evaluate some of the processes that may be used to define the nursery function.

This choice was partly inspired by a report of Stam (1984), in which he stated that the Dollard probably is important as a nursery for several flatfish species, and that directed investigations would be needed to prove this. One section arousing curiosity concerned flounder. Despite year-round sampling, Stam caught 0-group flounder on the tidal flats only from July onwards, when they had reached an average length of 5 cm.

Another intriguing remark about juvenile flounder by Van der Veer *et al.* (1991) concerned a 'missing month' between the observed arrival of flounder larvae in the planktonic environment and the recruitment to the demersal catches on the tidal flats of the Balgzand (western Wadden Sea). In contrast to plaice (*Pleuronectes platessa* L.), it was suspected that settlement of flounder occurred in other areas, e.g. in the freshwater lake IJsselmeer (the former Zuiderzee).

Given the area of interest of the National Institute for Coastal and Marine Management / *RIKZ*, which is the integrated management of tidal waters, investigating the nursery function of the Ems-Dollard for an estuarine flatfish species, the flounder, seemed particularly appropriate.

In this Chapter, the concept of 'nursery' is introduced and the early life history of flounder is summarised. Following this, the layout of the investigations and of the thesis is exposed and a synthesis of the results is given, including the main conclusions. **Chapter 1** concludes with addressing management implications of the collected knowledge on the nursery function.

NURSERY

The Wadden Sea, stretching along the continental coast from the north of the Netherlands to Denmark, is partly closed off from the open North Sea by a range of sandy islands separated by deep inlets, which are shaped by strong tidal currents. The Wadden Sea appears as an area naturally rich in nutrients, mainly because of large freshwater discharges by rivers. The accumulation of suspended material plays an important role in this coastal water (Postma 1961). The rich evertebrate fauna, serving as a major food resource, sustains a multitude of waders during their migrations (Smit 1980), for which the area is considered one of the most important wetlands on the European continent (Mitsch *et al.* 1994). In addition, the Wadden Sea has been identified as a nursery for a number of species which are of great economic importance to the fisheries in the southern and central North Sea, in particular flatfish and herring (Zijlstra 1972). The Wadden Sea covers about 33% (even nearly 50% for plaice) of the potential nurseries along the continental coasts of the North Sea, the Dutch part being about 12% (Van Beek *et al.* 1989). The Ems-Dollard estuary is an integral part of the Wadden Sea and forms the eastern border of the Dutch Wadden Sea (Fig. 2).

Fig. B. *The Dutch Wadden Sea and the Ems-Dollard estuary.*

A nursery may be defined as a restricted area in which juvenile individuals of a (fish) species spend a defined period of their lifetime, separated from older conspecifics (Bergman *et al.* 1988). The separation may be temporal (juveniles and adults utilising the area in different times of the year) as well as spatial (by using different habitats), but may be incomplete in some species (e.g. flounder *P. flesus* L.). Thus, a single life stage of the fish is concentrated in a relatively small area that meets certain physical-morphological and biological constraints. Many flatfishes have very restricted distributions during their early juvenile phase (Gibson 1994, Beverton 1995).

The nursery provides food, suitable abiotic conditions, and contains relatively few predators or offers the possibility to seek shelter from those. Estuarine conditions may be favourable for juvenile fish, because high turbidity reduces the

encounter rate with visual predators, the habitat structural complexity reduces predator efficiency, and relatively large predators are less common in shallow water (Miller *et al.* 1985).

Nurseries ensure the persistence of populations, but at the same time, owing to their geographical localisation, their limited area and the possible competition between species, they constitute a limitation, and most probably a regulatory mechanism for stocks (Safran 1990, Beverton 1995).

The geographical separation of mutually coherent spawning and nursery grounds must have evolved over long periods of time but requires some mechanism to transport the eggs and larvae from open sea to the coastal areas (Harden Jones 1968). Larval supply depends to some extent on the size of the spawning population and female fecundity, the location of the spawning sites relative to the dominant hydrographic features (Cushing 1990, Sinclair 1988), meteorological conditions at the time of egg- and larval dispersion, which affect residual currents and vertical mixing (Sinclair and Iles 1985, Van der Veer *et al.* 1998), and egg- and larval mortality (Leggett and Deblois 1994). These factors operate outside the nursery. Once the larvae reach the coastal waters, they enter the nurseries.

The traditional approach of the nursery has been from the recruitment point of view, inspired by the commercial interest in the main North Sea fish stocks. Recruitment of juvenile fish to the adult population is the key-issue, and several classical models of fish population dynamics try to describe this stock-recruitment relationship (Ricker 1954, Beverton and Holt 1957, Gulland 1983). The emphasis has been on survival of the larval stages, linked to starvation and predation (see Leggett and Deblois (1994) for a review). However, the success of a particular larval cohort in reaching the nursery grounds will be affected not only by biotic but also by physical processes acting along the transit (Werner *et al.* 1997). Recently, environmental variables have been incorporated in stock-recruitment models, to explain part of the large variability that is inherent in the relationship (Fargo 1994, Iles 1994, Iles and Beverton 1998). However, this remains a 'black box' approach and does not explain the processes and acting mechanisms.

An approach in which the processes and mechanisms that underly variation in recruitment are investigated, taking physical and spatial processes into account (hydrodynamic variability, morpho-dynamics, habitat structure), is gaining attention (Miller 1988, Sinclair 1988, Boehlert and Mundy 1988, Marchand 1991, Gibson 1994, Gibson 1997).

The present study adopted the latter approach and attempts to identify the processes and understand the mechanisms that determine the functioning of a nursery area for flatfish.

Processes that act inside the nursery and determine its functioning are:

Larval input and retention in the area

The nursery receives input of larvae, the magnitude of which is already roughly determined by the factors mentioned above, as well as by the tidal prism and exchange coefficient of the coastal inlet (Bergman *et al.* 1989). Once inside the nursery, the efficiency of transport and synchronisation of migrations with the tidal cycle (Hill 1991) set the premises of retention (*i.e.* the ability to maintain self-sustaining populations within a particular geographic space in the face of dispersal by diffusion; Sinclair 1988) and successful settlement. All flatfish larvae undergo a transformation, called metamorphosis, during which one of the eyes starts migrating to the other side of the head (**fig. a**).

Settlement of flatfish larvae on the tidal flats

At the completion of eye-migration, flatfish larvae are ready to adapt to the bottom dwelling life style that will be a characteristic during the rest of their life. This process, that establishes the spatial distribution of juvenile flatfish on the tidal flats, is called settlement. At settlement, a new potential for feeding and avoiding predators becomes available and gives a boost in growth (Osse and Van den Boogaart 1997). The huge morphological and behavioural transformations that are coupled with the transition from a pelagic to a benthic lifestyle require many adaptations and may make settlement a critical period in flatfish development: vital processes by which recruitment is established occur in a short time window just before and just after metamorphosis (Cushing 1990). Mortality during settlement may dampen variability in abundance if density-dependent processes are operative (Rauck and Zijlstra 1978, Zijlstra *et al.* 1982, Zijlstra and Witte 1985, Van der Veer 1986).

Spatial distribution, growth and mortality of settled flatfish

Plaice and flounder settle in the (inter)tidal (Berghahn 1983), where they initially stay in tidal pools on the flats during low water. Some time after settlement, the juveniles evacuate the intertidal area and start to make tidal migrations to populate the flats only during flood (Van der Veer and Bergman 1986). The spatial distribution of 0-group flatfish is generally correlated with sediment composition (Jager *et al.* 1993, Gibson 1994, Moles and Norcross 1995). Food availability and temperature mainly determine growth, and mortality stabilises at reduced levels (Rauck and Zijlstra 1978, Van der Veer and Witte 1993, Jager *et al.* 1995). After a few months, juveniles gradually leave the nursery when temperatures decrease in autumn to remain in deeper waters during the winter months (see Gibson 1997 for a review). During their second year, juvenile flatfish still have a coastal distribution but occupy slightly different habitats than the 0-group (Gibson 1994). Flounder gradually assume a more saline distribution as they grow (Rijnsdorp and Vethaak 1989).

Nursery parameters

Once the specific preferences of a species are defined, suitable nursery habitats can be defined. The area of these habitats may be quantified in a specific estuary. However, not only the quantity of nursery habitat but also its quality is relevant (MacCall 1990, Gibson 1994; **fig. c**). Indices of nursery quality, a.o. abiotic conditions and prey availability, might be derived from the rates of growth and mortality of the juvenile population and condition indices, although these parameters are very difficult to estimate accurately. Moreover, nursery quality and 'carrying capacity' (containing a population size corresponding with zero growth rate (K); MacCall 1990) are likely to vary annually.

Fig. C. Examples of MacCall's (1990) basin model, given by Gibson (1994), applied to two types of habitat. Habitat suitability (solid line) increases downward from 0 and changes horizontally with location. The 'basin' so formed is shown filled with two levels of population density (D_1 and D_2). At the higher density (D_2) the population has to occupy areas of lower suitability. When habitat suitability is 0, the carrying capacity (K) of the habitat is reached. The habitat in A is relatively uniform whereas in B it is complex and areas of high suitability (H) are separated by areas of lower suitability (L). Location X is uninhabitable for any length of time. Locations H are likely nursery areas.

The significance of a nursery becomes clear only by defining its relative contribution of recruits to the adult population compared to other areas (Van Beek *et al*. 1989). This implicitly assumes good knowledge on juvenile and adult population size, and is therefore less suitable for non-commercial species of which stock-assessment data are generally lacking and less is known about the autecology and population dynamics.

The number of species that use the estuary as a nursery may be a useful parameter for habitat conservation purposes, but has less relevance from the species' point of view.

Flounder

The flounder (*Platichthys flesus* L.) is an euryhaline flatfish species of the Pleuronectid family. It has a coastal distribution in the north-eastern Atlantic, ranging from the Mediterranean and Black Sea in the south to the Baltic and White Sea in the north (Whitehead *et al.* 1986). Its ability to live in low-salinity water and its preference for such environments are features that do not occur in other European flatfish species to the same degree. In the Middle Ages flounder was caught in the upper course of the river Rhine (Redeke 1908). At the turn of the century, flounder was fished in the Netherlands in the lower course of the major rivers, the Zuiderzee (July-September), Lauwerszee, Dollard, and the coastal North Sea in winter (Redeke 1908). After the Zuiderzee was closed off by the Afsluitdijk to become the IJsselmeer, catches decreased drastically (Havinga 1954).

Flounder reproduce in the marine environment in the North Sea (Redeke 1908, Ehrenbaum 1911) where the translucent eggs of 1 mm diameter develop in the pelagic. Highest concentrations of eggs were observed in February west and north-west of the Dutch west coast, in the eastern English Channel and the area north-west of Helgoland (Van der Land 1991). The larvae (length 2.25-3.30 mm) hatch after 5 to 7 days, depending on water temperature (Redeke 1908). High concentrations of larvae were found along the west Frisian coast and in the inner German Bight. Stage-specific distributions showed eastward advection of the centre of distribution along the west Frisian coast in late March and April, while the larvae were largely dispersed in the inner German Bight (Campos 1996). Whereas the distribution of early larval stages seems to be mainly determined by processes of advection and diffusion, the older larvae concentrate near the coast in the vicinity of estuaries (Grioche *et al.* 1997). Flounder as small as 10 mm were observed in May near the flat banks of the river Elbe, and free-swimming metamorphosing larvae were caught in the upper water layers of the estuary (Ehrenbaum 1911). Hutchinson and Hawkins (1993) observed metamorphosing larvae in the river Itchen moving upstream with the advancing tide in low-salinity water, where the freshwater layer was in contact with the bottom.

Among the Pleuronectid flatfish, flounder settle at a relatively small size of 8-10 mm (Osse and Van den Boogaart 1997). The first bottom-living stages were caught by the end of April in brackish-water areas near river mouths (Redeke 1908). The juveniles either stay in the brackish environment or migrate further up the rivers. Kerstan (1991) stressed the importance of rivers as nurseries, and concludes that freshwater habitats are preferred by 0-group flounder. In the former Zuiderzee, massive concentrations of juvenile flounder were found near the outflow of the river IJssel, where salinity was lowest (Redeke 1908). The distribution was clearly distinct from juvenile plaice. Redeke raised the question of how the young flounder succeed in their passage from the North Sea to brackish water. Whether it is by attraction to low-salinity waters, the higher temperature of shallow coastal waters in general, or merely instinct: "Of this we still know next to nothing and it is only by continuing meticulous investigations that we may hope to answer these questions in the course of time." ["Wij weten hiervan nog zoo goed als niets en kunnen alleen door voortgezet nauwkeurig onderzoek, hopen wij, mettertijd op al deze vragen een antwoord geven" (Redeke 1908).]

LAYOUT

The original plan of the investigation comprised three main aspects of the nursery function:
1. import of flounder larvae in the nursery
2. settlement of larvae on the flats inside the nursery, and habitat use
3. spatial distribution, growth and mortality of settled flatfish.

While proceeding with the investigations, it became clear that each of the three issues might fill a thesis of its own. The decision was therefore made to focus the present work on the larval import, including mechanisms of transport and retention and processes of accumulation in the nursery (**fig. d**).

Recommendations by Weinstein (1988), resulting from the American Fisheries Society Symposium, were taken into account in designing the sampling programme. An approach would be to first develop a model to describe the physical processes, with the assumption that the 'passive' organisms would be transferred entirely by hydrodynamic processes. The second step would be to undertake an intensive sampling program for larvae at a limited number of stations, with greater replication, to address background variability (Weinstein 1988). Data that were collected in the investigation would be a first step to modelling of larval transport in the estuary. The hydrodynamic model of the estuary could be modified to account for larval behaviour, and the adjusted model could be run with and without the presence of interventions (e.g. jetties) to ascertain the impact on the recruitment process (Weinstein 1988).

habitat	nearshore	tidal inlet	estuary	nursery	concepts:
physical process	Ekman transport	alongshore currents	tidal flux	accumulation	carrying capacity
biological process	migration	orientation to estuarine system	tidal migration	retention	recruitment
fishes' activity	larval drift	inshore movement	circatidal rythms	settlement	utilisation of nursery
stimuli	light, temperature, plankton distribution	diel stimuli	tidal stimuli	habitat structure	prey distribution
fishes' behaviour	vertical movement	circadian activity rythms	swimming	habitat selection	feeding, predator avoidance

Fig. D. *Conceptual model of the modulating larval transport process from open sea towards the coastal nursery (adapted after Boehlert and Mundy 1988). Circles with arrows refer to vertical movements of the larvae in the water column. The shaded area represents the focus of the present study.*
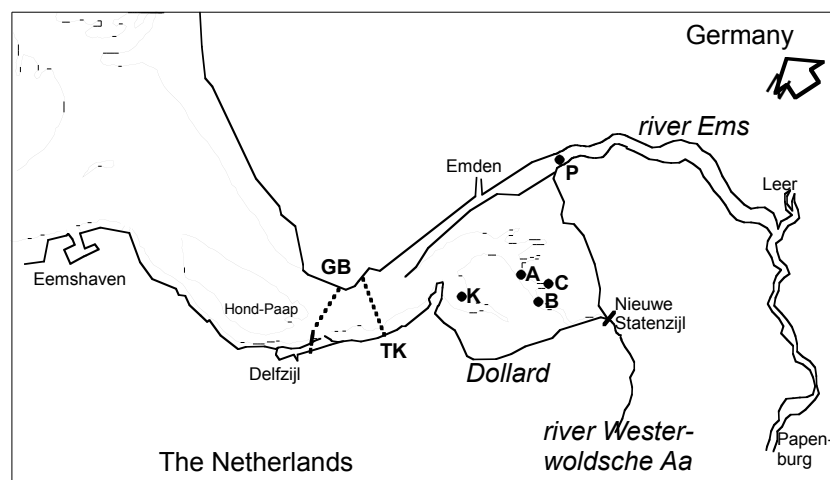
Fig. E. *Map of the Ems-Dollard estuary including the sampling locations (GB, TK, A, B, C, K, P; see Table 1) used in the investigations.*

The extensive knowledge of the physical environment of the Ems-Dollard estuary that already existed (a.o. Stratingh and Venema 1855, Van Voorthuysen and Kuenen 1960, BOEDE 1983, Baretta and Ruardij 1988, Robaczewska 1990, Duits-Nederlandse Eemscommissie 1990, De Jonge 1992), offered a good starting point for the present investigations.

Larval concentrations were measured simultaneous with physical variables in the centre of the main channel in the Dollard (A) during a total of 35 tidal cycles in 1993, 1994 and 1995 (**fig. e**, **table a**). Occasionally, measurements were done in the river Ems near Pogum (P), in a subsidiary channel in the Dollard (K), in two locations near the rims of the Dollard (B and C), and more seaward in the estuary (GB and TK on 26 and 28 April 1994, not in Table 1).

Table A. *Survey plan of flounder larvae investigations in the Ems-Dollard in 1993-1995 at sampling locations A (Groote Gat), B (Schanskerdiep), C (Oostfriesche Gat), K (Kerkeriet) and P (Pogum). A_9 is situated 200 m to the east of A. Sampling methods included double oblique hauls (⊗) or stratified vertical sampling (≡).*

Date **1993**	Location A	K	P	Date **1994**	Location A	B	C	Date **1995**	Location A	A_9
13/04	⊗		⊗	31/03	⊗			30/03	⊗	
15/04	⊗	⊗	⊗	05/04	⊗			06/04	≡ ⊗	
19/04	⊗	⊗	⊗	07/04	⊗			12/04	≡ ⊗	
22/04	⊗	⊗	⊗	11/04	≡ ⊗			18/04	≡ ⊗	
26/04	⊗	⊗	⊗	12/04	≡ ⊗			20/04	≡ ⊗	⊗
29/04	⊗	⊗	⊗	14/04	⊗	⊗	⊗	25/04	≡ ⊗	
03/05	⊗		⊗	18/04	≡ ⊗			27/04	≡ ⊗	⊗
06/05	⊗	⊗		19/04	≡ ⊗			03/05	≡ ⊗	
11/05	⊗	⊗	⊗	21/04	⊗	⊗	⊗	10/05		
13/05	⊗		⊗	26/04	⊗					
18/05	⊗	⊗		28/04	≡ ⊗	⊗	⊗			
				03/05	≡ ⊗					
				10/05	≡ ⊗					
				11/05	≡ ⊗					
				16/05	⊗	⊗	⊗			
				19/05	⊗	⊗	⊗			
				25/05						
TOTAL	11	8	9		8+16	5	5		9+9	2

The main objective in the first year (1993) was to obtain detailed descriptive knowledge of the larval immigration: when does it happen, in which quantities do larvae enter the nursery, and are the Dollard and Ems (which both discharge in the Ems estuary) equally supplied with larvae?

It became soon obvious that conditions in the Ems river were adverse to the applied sampling method: the quality of the Ems-data was seriously affected by the high current velocities in combination with extremely high turbidities, which caused clogging of the net. Because there was no way to avoid these problems, the Ems location was excluded during the following years, and was not

incorporated in the thesis. The two main channels within the Dollard were initially sampled to estimate their relative importance. Because the 1993-data indicated a relatively small contribution of Kerkeriet to the larval transport, the attention of the investigations was subsequently focused on the Groote Gat. In 1994, the issue of larval input, which had been addressed in 1993, was continued at sample location A. Moreover, the mechanism of larval transport was investigated by testing the premise of passive larvae. The process of accumulation was addressed by sampling over a longitudinal gradient in the Dollard (locations A, B, C). The last year, 1995, was used to obtain additional data on the larval transport processes in the Groote Gat (A). A site (A_9), 200 m east of the regular sampling location, was sampled twice. A total number of 285458 flounder larvae were collected.

The data sets used in the different chapters are summarised in **table b**.

Table B. Overview of data sets used in the different Chapters. Symbols as in Table 1.

Chapter	Location	Sampling Method	Nr of tidal cycles	Year
2	A	$\otimes$	35	1993, 1994, 1995
3	A, B, C	$\otimes$	15 (=3*5)	1994
4	A	$\equiv$	17 (=8+9)	1994, 1995
5	A	$\equiv$	17 (=8+9)	1994, 1995
6	TK, GB, A, A_9	$\otimes$	14 (=2*5+2*2)	1994, 1995
7	A	$\otimes$ $\equiv$	17	1994, 1995

Transport and retention

In **Chapter 2**, the annual input and retention of flounder larvae in the Dollard nursery are quantified by investigating the tidal transport. Immigration of metamorphosing larvae covered a period of about 6 weeks, starting between the end of March or the beginning of April, and reaching its maximum intensity 2 to 3 weeks after observation of the first larvae.

Because the pelagic flounder larvae are known to settle on the tidal flats, net landward larval transport during the tidal cycle was expected. The 1993-data met the expectations, but the high frequency of seaward net larval transport in 1994 and 1995 was an unexpected result.

The general tidal pattern in larval concentrations was that maxima were observed during the first hours of the flood, followed by a rapid decrease. A secondary peak in concentrations was observed during mid-flood. During ebb concentrations were often variable, but a remarkable increase at the end of the ebb period was a recurrent feature. Larval concentrations showed marked tidal variations at all time scales which resulted in very variable tidal transport and retention.

Since the morphology of the Dollard has not changed substantially within the time-span of 3 years (Kiezebrink 1996), other factors must be held responsible for the variability in larval transport and retention. The water circulation and asymmetric features of tidal parameters within a channel, such as current velocity, flood and ebb duration, and salinity, were explored.

The net water transport was positively correlated to larval retention, but not to the net larval transport. A relatively longer flood than ebb duration was positively correlated to both net tidal water transport and larval retention. The wind direction significantly affected the net water transport at the cross-section in the main channel, as well as the net larval transport and retention. Wind conditions during the immigration period may affect transport and settlement of metamorphosing flounder larvae in the nursery.

Because the net transport was so variable between sampling dates, it was not possible to accurately estimate the net larval input in the nursery. The flood transport appeared more reliable, and the estimates of total larval input (flood transport integrated over the immigration period) in the centre of the Dollard ranged between 1 and 7 $.10^9$ individuals during the years of the investigation. The mean larval concentration and the total larval input corresponded to a limited extent with abundance estimates of recently settled flounder in the Ems-Dollard estuary.

Accumulation

The observed tidal concentration pattern of flounder larvae identified in the previous chapter indicated an increasing concentration gradient along the main channel of the Dollard towards the sluice of Nieuwe Statenzijl.

The accumulation of larvae to the rim of the nursery, and the extent of the freshwater influence in this process, was investigated in **Chapter 3**. The hypothesis tested was that flounder larvae accumulate in the part of the nursery area where salinity is lowest because of the regulatory effect of freshwater outflow on transport and retention. The results demonstrated increasing concentrations of flounder larvae towards the fringes of the Dollard compared to the main channel, which coincided with a decrease in mean salinity. The highest larval concentrations were measured around low water (LW) in the channel Schanskerdiep, which is directly connected with the sluice in Nieuwe Statenzijl. The period around LW slack seems to be important, given the high larval concentrations and rapid changes that occur.

The preferential larval transport to the Schanskerdiep could not entirely be explained by the water circulation. This result supports the view that discharge of freshwater affects larval transport of flounder and is responsible for a relatively strong accumulation in the low-salinity area near Nieuwe Statenzijl. The mechanism behind this process remains unknown.

However, the passage to freshwater is obstructed by the sluice which may act as a barrier for the larvae. Since they have limited swimming abilities, the cause of accumulation may simply be a physical one.

Selective tidal stream transport

The spatial separation of adults during spawning and juveniles at settlement implies that larvae must be transported from the spawning areas to the nursery grounds. Migration of flatfish from open sea to the coastal nursery is generally seen as a gradually modulating process (**fig. d**), from entirely passive transport depending on physical factors only to an active participation of the larvae in the form of selective tidal stream transport (STST; Boehlert and Mundy 1988). STST requires directional swimming in the vertical plane in synchrony with the tidal cycle (Hill 1991). Though indications of STST were found in plaice (Creutzberg *et al.* 1978, Rijnsdorp *et al.* 1985), there was no information on flounder, which could elucidate whether this mechanism is a general feature in larval flatfish. The transport mechanism of flounder larvae was therefore investigated during 1994 and 1995 by frequently measuring the vertical distribution of the larvae during the tidal cycle. ANOVA-techniques were used in **Chapter 4** to determine the main factors responsible for variation in larval concentrations.

Larval concentrations decreased after the LW slack and increased again at the end of the ebb in both the midwater and surface layer, but surface concentrations were significantly higher. Near-bottom concentrations showed a relatively strong increase during the ebb. No day-night differences could be detected. Because of the high surface concentrations and the varying vertical distribution of flounder larvae during the tidal cycle, the hypothesis of an entirely passive transport mechanism had to be rejected, and at least during flood there were strong indications of STST. During ebb, larvae concentrated not only in the near-bottom layer but also in the surface layer, which was not in accordance with predictions by the STST hypothesis. The larvae that concentrate in the surface layer during ebb may have been flushed back from the flats after an unsuccessful settlement attempt. The next flood tide will provide them with a new opportunity to colonise the tidal flats.

Transport velocity

Even though the STST mechanism was likely to occur in flounder larvae, the unresolved question was to what extent the larvae, when subjected to strong tidal currents and turbulence, might influence their transport by using STST. This question was addressed in **Chapter 5**, where the concept of 'larval velocity' (Rowe and Epifanio 1994) was applied to flounder larvae. In order to make comparisons with other substances in the water column, the concept was broadened to a more generally applicable 'transport velocity' concept that could

be used to calculate displacements of suspended matter (as passive particles) and salinity (as a dissolved substance and tracer of water masses). The transport velocity of a substance can be expressed relative to the mean tidal current velocity. Differences between the two are caused by variations in the temporal or vertical distribution of the substance, or a combination of both. Contributions of vertical and temporal concentration variations to the transport velocity were calculated separately.

Theoretical knowledge about the influence of underlying physical processes on the concentration distribution, and hence transport velocity, was applied to get more insight in the estuarine transport processes. The relative transport velocity of flounder larvae, suspended matter and salinity showed different tidal patterns. In salinity, temporal variation was dominant over vertical variation, indicating that longitudinal advection was important. Contributions of temporal and vertical variation were equally important to the transport velocity of suspended matter, but of opposite signs. Erosion-deposition appears to be the dominant process. In flounder larvae, the vertical concentration variation was most important during flood, while the contribution of temporal variation dominated during ebb. This is a strong indication that larval activity (i.e. swimming) affects the transport process during flood, but less so during ebb.

Swimming increases the larval transport velocity during flood by 6%. Although this may seem a small percentage in the absolute sense, one has to bear in mind that this contribution operates repeatedly during every tidal cycle and eventually leads to a cumulative effect on the residual displacement of flounder larvae in the Dollard. Moreover, the pattern that is observed with the larvae is remarkably different from the (negative) contribution of vertical variation which was observed in suspended matter. Thus, the 6% contribution of swimming is a resultant, which includes overcoming the negative contributions of physical processes to the transport velocity. The temporal variation during ebb is probably linked to the accumulation process, but the variability of the data hampers firm conclusions on the dominant processes during this tidal phase.

Across-channel distribution

The investigations described in the previous chapters were all based on measurements in the deepest point in a cross-section of the main channel in the centre of the Dollard, on the underlying assumption in the transport calculations that larval concentrations were homogeneous. This assumption is quite critical for the results and therefore needed foundation by investigating the larval distribution across the width of the channel (**Chapter 6)**. Ideally, the investigation would result in correction factors which could be applied in case one sampling position is chosen as representative of a cross-section of the

channel. Such investigations are costly because they require simultaneous measurements with multiple vessels. Therefore, the issue could only be explored to a limited extent by using ships of opportunity which were actually involved in a different project in the more seaward section of the estuary, where channel width is more extensive than in the central Dollard.

The results convincingly showed that the assumption of homogeneous larval concentrations over the width of the cross-section was not justified. Moreover, tidal concentration variations differed between sampling positions. The largest transport was realised in the deeper, middle part of the cross-sections. Due to the high variability in concentrations and the limitations of the number of measurements it was not possible to derive correction factors.

The larval transport on 28 April 1994 was considerably higher in the middle part of the estuary (1459 10^6 - flood, 547 10^6 - ebb) than in the Dollard (39 10^6 - flood, 84 10^6 - ebb) on the same date, which is largely caused by the larger water transport through the former cross-section.

Methodical evaluation

The larval (flood, ebb, residual) transport estimates, presented in Chapters 2 and 3, are biased by several sources of error. For practical reasons, sampling took place from one ship on a cross-section in the Groote Gat, which served as a platform to measure larval concentrations and current velocity. Water flow and larval concentrations were extrapolated to the entire cross-section. A brief consideration of the applied methodology is due here, in an attempt to rate the larval transport estimates at their true value.

Several sources of bias were identified in the different Chapters:

1. The larval flux through the cross-section was derived by multiplying the local depth-averaged concentration by the water flow through the cross-section. Extrapolation of water flow was done by regression of the current velocity at the sampling position on that of the cross-section. Although the correlation coefficient of this regression equation was high (0.98), variation of unknown magnitude may occur due to the spring/neap cycle or wind conditions.
   Some other important assumptions underly the method:

   * *larval concentrations are homogeneous over the depth of the water column.* Chapters 4 and 5 showed that this is not the case. Ignoring the vertical stratification gives a 5% bias in the larval transport estimates.

   * *larval concentrations are homogeneous over the width of the cross-section.* This assumption does not hold either (Chapter 6), and may cause serious (up to 50%) under- or overestimation of the larval transport depending on the sampling position within the cross-section.

2. The Eulerian approach was taken in the investigations. This means that sampling was done at a fixed position and that during the tidal cycle different

water masses were sampled. By sampling at one position in a cross-section, part of the water transport is missed in the measurements and the net (residual) transport becomes unreliable (Chapter 5).

3. Type of net. The large-opening net that was used is sensitive to clogging which may have reduced fishing efficiency. The small-opening plankton net, equipped with a conus, was less sensitive to clogging but may have been more sensitive to net avoidance by the larvae, although these effects could not be demonstrated in the investigations. The mean concentrations obtained by both nets did not statistically differ, but when looking at the raw data, it appears that concentrations obtained by the large net tend to be slightly higher than those by the small nets (see Chapter 7). The patchy distribution of the larvae may have had a larger effect in sampling with the large net, whereas patchiness was leveled down by sampling with the small nets (sampling duration 20-30 min). The larval transport estimates by both methods differed up to 50% and were highest with the large net. Very high concentrations around LW slack, which were included or just missed, are mainly responsible for these differences.

4. The calculations in Chapters 2 and 3 disregarded the slack periods because sampling was not possible during these time-intervals. Another option would have been to interpolate larval fluxes over slack periods. Including slack tides would lead to 5% (flood) to 10% (ebb) higher transport estimates, but does not significantly affect the estimated net transport.

5. Day-to-day variation. Especially the 1994-data demonstrated that it can be considerable. It makes interpolation between sampling dates a tricky exercise. The magnitude of the error can not be estimated.

The above summing up of sources of bias does not intend to be complete, but nevertheless leads to the conclusion that quantitative estimates of larval transport have a large intrinsic inaccuracy. The error that is introduced by ignoring the vertical distribution (by depth-averaged sampling) is small compared to the others and may be neglected. The sampling method, using the large net, seems most effective for the purpose of obtaining larval transport estimates. The largest error seems to be caused by the use of only one sampling position in a cross-section. A high number of replications may, however, reduce the error and eventually result in a figure which is at least correct in estimating the order of magnitude of the larval input and in establishing the direction (landward or seaward) of the residual transport.

SYNTHESIS

Larval transport is facilitated by using selective tidal transport during flood, a process which is concisely and adequately seized by 'floundering': to move

around in an uncontrolled way, trying not to sink. During ebb, physical processes take over. All stages of metamorphosis are represented but the relative composition among flounder larvae varies during the tidal cycle as well as within the water column (**fig. f**).

During LW slack waters, larvae rest on the channel bed. As soon as the current starts running, which is somehow perceived by the larvae, they rise upward in the water column and form dense pelagic concentrations (-6). Flood water enters, and brings in a fresh supply of larvae from the outer part of the estuary. These are generally in early stages of metamorphosis, and are less concentrated than the larvae that had accumulated on the channel bottom during previous tides. It causes an apparent dilution in larval concentrations during the early phase of the flood (-5). The water level rises continuously and water starts to spill over the tidal flats (-4). Larvae that are aggregated in the surface layer are carried along on its tidal excursion. The metamorphic stages 4b' and 5 gradually disappear from the channel, and larval concentrations drop, especially in the surface layer (-3). The flood proceeds, still carrying on larvae (-2), but at this time only a relatively small proportion of water is contained within the tidal channels.

The turn of the tide is preceded by a falling water level (-1,1). During HW slack, current velocity falling to zero, larvae sink out again (1). They either settle on the substratum of the flats where they will remain in the intertidal during ebb, or rest on the channel bed, where they will have to face the strong ebb current. In the case of unsuccessful settlement, due to an unknown variety of causes, the larvae will be carried back with the outflowing ebb water, and finally collect in the main channel where they form increasing concentrations during the later phase of the ebb.

At the time of maximum current velocity (2) part of the larvae are swirled up from the channel bottom, unable to resist the vigorous turbulence. After the flats emerge (3), the tidal violence calms down and larvae sink again (4). The last unsettled larvae are flushed from the flats into the surface layer (5), and water containing near-bottom larval accumulations passes the cross-section at its return from nearshore parts of the Dollard. Midwater concentrations are relatively low. Finally, the current falls to zero and the flounder larvae present settle on the channel bed (6) for a short interlude during LW slack, preparing for another forward leap when the new flood tide comes in.

Because of the combination of tidal processes, determining the water circulation, and larval behaviour, the larvae are carried back over less distance during ebb than they make progress during flood.
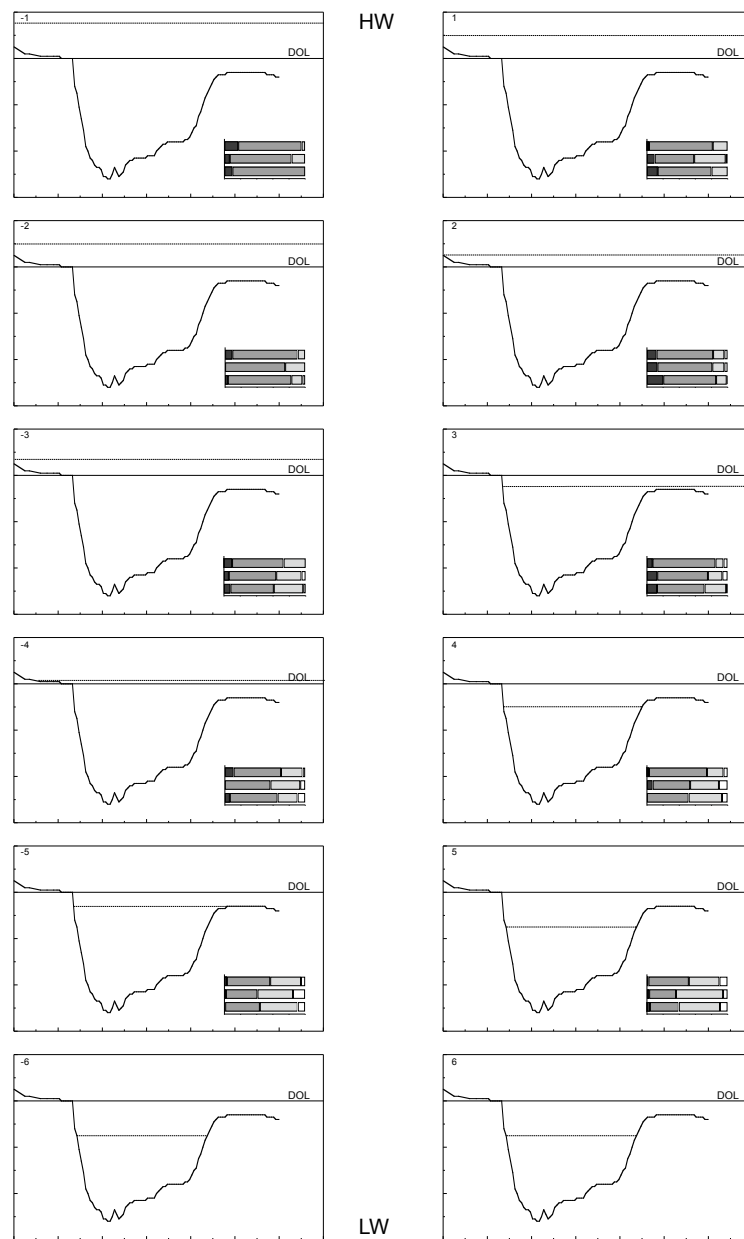
Fig. F. *Conceptual model of the larval transport process inside the nursery area. Reading clockwise from bottom left to bottom right, the different stages of the tidal cycle are indicated by numbers that refer to the time (h) relative to the moment of HW slack. The cross-section of the sample location (A) is used as an example. The water level (....) and D.O.L.(—) are indicated. Larval concentrations in the water column are indicated by dots. The relative stage composition of the flounder larvae is shown by histograms in the bottom right corner of each figure. The vertical scale represents 3 water layers (from top to bottom: surface, midwater and near-bottom), the horizontal scale ranges from 0-100%. The metamorphic stages are indicated by shades of grey (4a=darkest grey, 4b=middle gray, 4b'=light grey, 5=white). At stage 5, the metamorphosis is completed.*

This process is repeated during every tide and eventually leads to larval accumulation at the rims of the nursery, until larval input gradually comes to an end (by the end of May) and settlement is completed. The freshwater discharges in the area are correlated with larval accumulation, but a causal relationship could not be demonstrated because fluctuations in both larval concentrations and salinity were highly correlated with the tidal cycle.

Interfering processes of transport and accumulation hamper accurate assessment of larval input in the nursery. De Haas and Eisma (1993) described the suspended sediment transport in the Dollard. During flood they observed a primary and secondary maximum in concentrations. The first peak is explained by resuspension by turbulence of mainly freshly deposited sediment. The second is caused by the increased, strong, current velocity which erodes the more consolidated bottom sediments. De Haas and Eisma propose that the actual concentration curve is composed of two different curves. In analogy, this idea can be applied to the measured larval concentration curves. In contrast to suspended sediment, processes of accumulation and tidal advection are proposed as the main components that shape the resultant larval concentration curve. The two curves (**fig. g**) are superimposed to form the resultant tidal concentration pattern that was observed in the main channel of the Dollard.
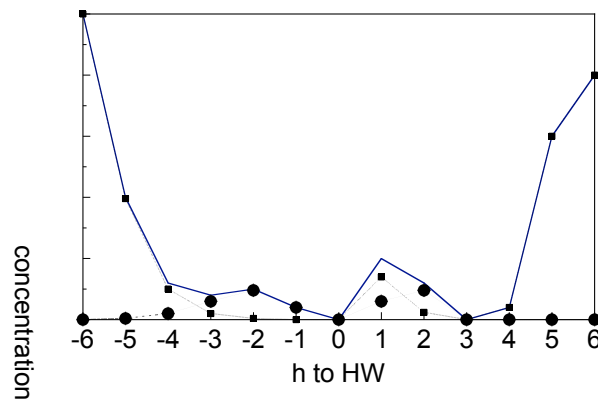
Fig. G. *Resultant curve (thick drawn line) of tidal variations in larval concentrations, obtained by superimposing the curve reflecting tidal transport (striped line, black dots) on that reflecting accumulation (dotted line, square markers).*

The morphology of the Dollard is such that the main gullies branch off the Groote Gat in eastward direction (**fig. e**). Also, the easterly border of the Groote Gat is at a less high level than the west side (**fig. f**). At rising water levels during flood, the water will first spill over the east side and some time later over the west side. This implicates that the first larvae carried with the flood will mainly move eastward, and populate the tidal flats east of the channel. Only later during the flood, larvae may move also in westward direction.

For the Dollard, it means that the tidal flats of Hoogzand, Maanplaat and Oostfriesche Plaat (see Fig. 1 in Chapter 2) can only be supplied with larvae from the Groote Gat, whereas the Heringsplaat will be mainly supplied from the Kerkeriet and only in a later tidal phase by the Groote Gat. Because the larval input via Kerkeriet is lower than that via Groote Gat, this may implicate that the abundance of settled flounder is higher in the eastern part of the Dollard with the Groote Gat as a metaphorical watershed.

The extremely high larval concentrations observed during this study (up to 1000 m^{-3}) and the estimates of overall larval input during the whole immigration period (in the order of 10^9 individuals) suggest that the Dollard is a very important nursery for flounder. Beside the Dollard, the adjacent river Ems receives a substantial input of flounder larvae, which may be of the same magnitude. However, the relative importance of Ems and Dollard, taking quantity and quality of the nursery into account, as well as the mutual coherence of both ecosystems, remain the subject of further study.

MANAGEMENT IMPLICATIONS

Threats

Because estuaries are the interface of fresh water and the marine ecosystem, they are the focus of a wide range of human activities that may conflict with natural functions, such as the nursery function (see *fig. h*).

Fig. H. Human activities in the Ems-Dollard estuary which may interfere with the nursery function for flounder.

Closing off the Rhine delta (Haringvliet), Zuiderzee (3200 km^2) and Lauwerszee (94 km^2) resulted in considerable loss of flounder nursery habitat in the (recent) past. The Dollard was successively reclaimed after it was formed in the Middle Ages (see Fig. 2 in Chapter 2). All ancient transitions from saline to fresh water in the Dutch Wadden Sea have been closed off by sluices, dams or dikes. The sluice at Nieuwe Statenzijl is one example of a physical barrier for fish migrations to fresh water.

The river Ems, although no longer in a pristine condition due to canalisations in the past, still has a relatively undisturbed estuarine gradient up to Herbrum. However, this situation is at present endangered by concrete plans to construct a storm surge barrier in the river Ems (Bezirksregierung Weser-Ems 1997) for coastal protection, as well as in the interest of a Papenburg shipyard, which depends on and is restricted by this shallow waterway to transport its products (cruise ships of gigantic dimensions) to the open sea. The planned construction of the 'Sperrwerk Ems' may form a threat to the rare undisturbed estuarine transitions that remain on the European continent. Closure, even of short duration, of the 'Sperrwerk' during the larval immigration period (April/May for flounder) may disturb the tidal transport process with unpredictable results for the nursery function of the Ems.

The river Ems is an important shipping route from the harbours of Eemshaven, Delfzijl and Emden to the North Sea. Dredging activities are needed to keep the Ems at sufficient depth to sustain this function. The quantity of dredged material was on average 1.6 10^6 m^3 annually between 1950 and 1965, and subsequently increased to a maximum of 6.5 10^6 m^3 in the 1980's (Duits-Nederlandse Eemscommissie 1990). At present, 2-4 10^6 m^3 (harbours) and 5-10 10^6 m^3 (channels) is dredged annually (Mulder 1998b). Disposal of the dredged material takes place partly on land (e.g. Rysumer Nacken), and partly in the estuary. The latter leads to increased suspended sediment concentrations, and hence turbidity (Essink 1993).

Industrial activities at Eemshaven, Delfzijl and Emden use estuarine water for cooling and processing and discharge, sometimes polluted, water in the estuary. A large electric power plant at the Eemshaven takes vast volumes of cooling water from the Ems estuary and discharges it after use at an 8 °C elevated temperature. The thermal pollution may cause problems to the ecosystem, especially during summer months at times when ambient water temperatures can approach 25 °C which is the tolerance limit for many fish species. Another negative side effect lies in the mortality caused to estuarine organisms that are impinged on the inlet grids or entrained with the cooling water (Jager 1992). Flounder larvae are most likely susceptible to both sources of mortality because of their small size.

Fishing activities are restricted to shrimp fishery and fishery with fixed nets. The by-catches contain juvenile flatfish, despite preventive measures (e.g. sieve-nets and flushing devices) that are applied, and may contribute to 0-group flatfish mortality (Berghahn and Purps 1998). The recreational function of the estuary has been of minor importance, but with growing demands of tourism this may change in the future.

Alteration of the habitat structure within a nursery can have serious effects on survival and recruitment (Gibson 1994). In case of the existing nursery area of the Wadden Sea, one should be aware that plans to construct new industrial areas (Maasvlakte II), living areas (Nieuw Holland) or airport (Schiphol II) in the Dutch North Sea coastal zone, may alter (residual) water circulation and larval advection and reduce supply to the nursery. Therefore, interventions even far outside an estuarine area may affect its nursery function if operating upon the processes underlying larval transport and larval supply.

Compensation

A recent trend in water management and nature conservation is the compensating principle. The underlying idea is to create new habitats in case the existing ones are sacrificed to man's demands, in an attempt to diminish ecological damage. The question of how new nursery habitats can be created was recently posed in the Western Scheldt where large-scale dredging activities are undertaken to improve the shipping route to the harbour of Antwerp.

Whereas much of the knowledge on nurseries was simply based on empirical observation of juvenile fish aggregations, the knowledge of the nursery function collected in the present investigation demonstrates that the incredible complexity of the processes involved does not provide a simple solution to such problems. Physical and biological factors are mutually correlated without evidence of causal relationships or complete understanding of the underlying mechanisms. Moreover, interacting processes and their intricacies confuse our insights. Many of these processes are not subject to human influence or control.

There are more gaps in knowledge and understanding. Within the Dutch Wadden Sea, investigations of the nursery function have focused on the Balgzand without knowing whether this area is representative for the entire Wadden Sea. A comparison between the Balgzand (western Wadden Sea) and the Dollard of abundance, growth and mortality of 0-group flatfish is possible and worthwhile. The sources of larval supply to the nursery are not exactly known (English Channel, German Bight, or both?). Moreover, data on (adult) population abundance and recruitment success are still lacking to assess the importance of the Ems-Dollard, for one, as a flounder nursery, compared to other areas. Monitoring of (juvenile and adult) flounder population abundance

would be required to assess the annual recruitment of this species and the relative importance of specific nursery areas along the European coast.

Recommendation

If a habitat should function as a nursery, the primary requirement would be to ensure that hydrographic conditions allow sufficient input of larvae to the area. Because of the long time-span during which spawning and nursery areas co-evolved, 'new' nurseries will be potentially successful only within the geographical range of the presently or historically known nursery areas.

How should an area be 'designed' to furnish a suitable nursery for one species or another? By trial and error may turn out to be the best available procedure. Of course, structuring a nursery can be achieved by guiding the tidal channels and influencing sediment composition and elevation of the tidal flats, i.e. moulding the morphology of the area. Salinity gradients and fluctuations can even be influenced by controlling the freshwater discharge to an area. Habitat requirements of temperature or food supply are nevertheless mainly out of human control.

Transplanting experiments with juveniles to unexploited areas, or stocking of existing nursery areas with (cultured) juveniles (*e.g.* Tominaga and Watanabe 1998) have proven ambiguous and the success will depend on a knowledge of the factors controlling movements of juveniles to join the adult stock (Gibson 1994) and subsequent successful reproduction.

Given the low population abundance of adult flounder, besides by fishing pressure probably restricted by the availability of juvenile habitat (Gibson 1994, Rogers *et al.* 1998), restoring the transitions between sea and fresh water might be a first step to increasing flounder populations. Because of the indications that flounder larvae make use of selective tidal stream transport (Chapters 4, 5), they may have problems in entering freshwater bodies in the absence of tidal currents. Migration to freshwater may be postponed to the juvenile stage when swimming capacities are sufficient - which is indicated by increased abundances of 0-group flounder in the IJsselmeer after modification of sluice management (Dekker 1994, Dekker *et al.* 1992).

Existing plans to restore a limited tidal regime in the Haringvliet (Rijkswater-staat 1998) may prove beneficial to flounder. The Haringvliet can provide an excellent case study to collect empirical knowledge about the utilisation as a nursery when new habitats become available once the connection with open sea and the tidal movement have been (partly) restored.

Positive experiences with the Haringvliet may eventually be applied to the large potential of formerly lost flounder nurseries in the Netherlands.

Transport and retention of flounder larvae (*Platichthys flesus* L.) in the Dollard nursery (Ems estuary)

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ABSTRACT

Variability in tidal transport of larval flounder (*Platichthys flesus* L.) in the Dollard was investigated to estimate the quantity of larvae that are annually retained in the nursery based on simultaneous measurements of water transport and larval concentrations. Sampling was done at a frequency of three times per hour in the main channel in the Dollard, during 35 tidal cycles divided over 1993, 1994 and 1995. In 1993, additional sampling was carried out simultaneously during 8 tidal cycles in a subsidiary channel. Larval concentrations showed marked tidal variations at all time scales and indicated a patchy spatial distribution. The estimated net tidal transport of larvae was not correlated to the net tidal transport of water. However, a higher net water transport coincided with higher retention, defined as the percentage of net larval transport divided by the flood larval transport. Also, relatively longer duration of the flood than the ebb period (tidal asymmetry) was positively correlated with both net tidal water transport and larval retention. The wind direction significantly affected the net water transport at the cross-section in the main channel, whereas wind speed was not significant. The flood transport, but not the ebb or net transport, was significantly higher at spring tide following full moon than at the other lunar phases.

The net tidal transport of larvae was much more variable in 1994 than in 1993 and 1995, resulting frequently in ebb surpluses in larval transport. Despite higher mean concentrations, the estimated net larval input was lower in 1994 than in 1993. This did not correspond with the observed abundance estimates of juvenile flounder in the Dollard in these two years, nor with the abundance index obtained from routine surveys. The total larval input better reflects the juvenile flounder abundance. Variability in water circulation, influenced by varying wind conditions, and its effect on larval transport and retention is an important source of variability in larval immigration in the nursery and is held responsible for a poor correlation between net larval input and juvenile abundance.

Keywords: *Platichthys flesus*, flounder, nursery, transport, retention.

INTRODUCTION

One factor that determines the importance of an area as a nursery is the input of fish larvae. The question arises whether a nursery is generally saturated with larvae or larval input determines variability in densities in the nursery areas (Baretta 1994). Before being able to answer that question, it is essential to obtain insight in the processes that determine the functioning of a nursery and to answer the question which are the key-factors.

For plaice (*Pleuronectes platessa* L.), intensive studies have demonstrated that year-class strength is correlated to larval input and that processes occurring in the nursery only result in fine-tuning of the numbers of recruits (Rauck and Zijlstra 1978, Van der Veer 1985, Zijlstra and Witte 1985). Van der Veer *et al.* (1991) draw a similar conclusion for flounder (*Platichthys flesus* L.) in the western Wadden Sea, but the year-to-year variability in the pelagic phase appeared to be much higher than in plaice. The depth distribution of flounder in the North Sea, which is closely associated with shallow water, and the relatively low adult abundance suggest that habitat availability for juvenile stages could be limiting population size (Gibson 1994, Rogers *et al.* 1998).

The transition of planktonic larvae to benthic juveniles in flatfish is a complex process associated with high mortalities. During the process of immigration and settlement, larvae may be distributed to less suitable habitats within the nursery and may fail to survive the prevailing abiotic conditions with respect to temperature, salinity, or UV-radiation (Berghahn *et al.* 1993). Predation by shrimp (Van der Veer and Bergman 1987) and gulls (Berghahn 1983) adds to the settlement mortality. However, mortality during settlement is difficult to measure directly and remains largely unknown.

The present study attempts to estimate the number of larval flounder that are transported into, and retained in the Dollard nursery, a shallow embayment in the inner part of the Ems estuary (**fig. a**a). To quantify larval input, reliable estimates are required of larval concentrations and of the water flow in the tidal channels that supply the area. Therefore, these parameters were measured simultaneously in a main channel in 1993, 1994 and 1995 during a total of 35 tidal cycles. Larval concentrations, transport and retention were calculated. Sources of variability in these processes are explored. The resulting number of larvae retained is compared with estimates of numbers of settled flounder in the Dollard during 1993 and 1994, to assess the order of magnitude of survival during settlement.

The tidal concentration variations are investigated to better understand the processes of transport and retention.
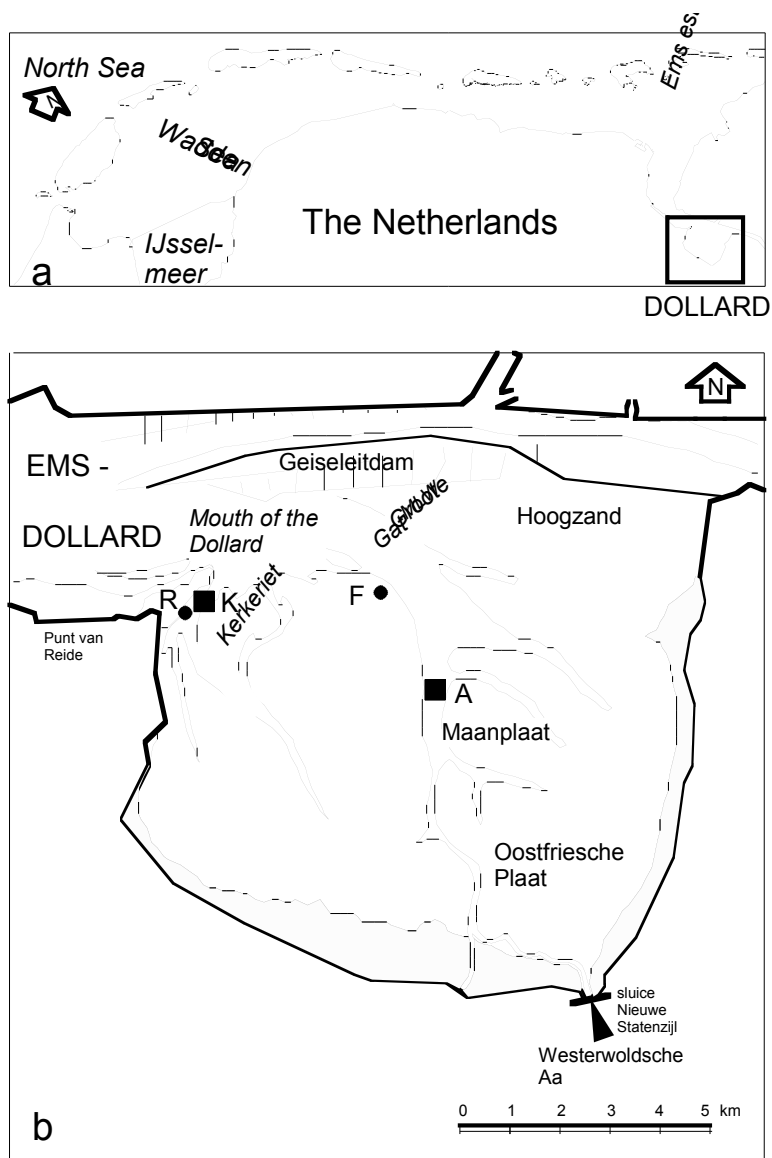
Fig. A. *Study area, with (a) position of the Ems-Dollard estuary in the Dutch Wadden Sea and (b) the Dollard with the sample locations (A, K), and the tidal gauges 'Dollard-Noord' (F) and 'Reide' (R).*

MATERIAL AND METHODS

Study area and sample locations

The history of the Dollard goes probably back to the year 1287, when a sequence of storm surges caused a large transgression of the sea through the natural levee of the River Ems (Stratingh and Venema 1855, Dollardzijlvest 1992). Because the hinterland consisted of low-lying peat-bog, the water could spread over a large area. The borders of the Dollard (**fig. b**) followed the line Termunten (1) - Noordbroek (2) - Scheemda (3) - Winschoten (4) - Bellingwolde (5) - Bunde (6) - Weenermoor (7) - Pogum (8) at the time of its maximum circumference in 1509. From that time onwards, successive land reclamations were undertaken by the population, until a final one in 1924 defined its present extent. The sluice at Nieuwe Statenzijl (9) was build in 1877 to regulate the discharges of the tributary river Westerwoldsche Aa, and was reconstructed in 1990.

At present, the Dollard is a brackish intertidal area of about 92 km^2, of which 85% emerges at low tide, in the Ems estuary (eastern Dutch Wadden Sea) that forms the transition between the river Ems and the North Sea (Fig.1a). Mean depth is 1.2 m, and the mean tidal volume about 120 10^6 m^3 (De Jonge 1988). The basin is bounded on the north by the Geiseleitdam (constructed 1875-1968), on the north-west by the Punt van Reide and on the other sides by dikes, fringed with 9 km^2 of marshes (Fig. 1b). Mean low water is 171 cm below mean sea level (msl), mean high water 128 cm above msl. Msl is 7 cm above Dutch Ordnance Level (D.O.L.). With a height of 1 m above msl, the Geiseleitdam forms a partial separation between Dollard and Ems that allows some water exchange between the two systems during high tides. The muddy flats are intersected with small gullies that drain water to the main channels during ebb. The tidal cycle has a period of 12h25′, a range of 3 to 3.5 m, and a mean excursion in the Dollard of 12 km (BOEDE 1983). During the second half of the ebb, freshwater from the river Westerwoldsche Aa is regularly discharged at Nieuwe Statenzijl. More details are given in Jager (1998).

Two channels, Groote Gat and Kerkeriet, guide the flood water into the Dollard. The large scale residual water circulation is characterised by two cells: Groote Gat normally shows a flood surplus, counteracted by the discharge of the river Westerwoldsche Aa, which is balanced by an ebb surplus in Kerkeriet (clockwise cell) and in the lower reach of the River Ems (anti-clockwise cell). Wind-driven water circulation may occasionally lead to a reversed direction of the residual water transport (De Jonge 1991).

Fig. B. *The Dollard at its maximum (shaded area) and present form (thick line) and the successive land reclamations (thin lines and year of formation). After Fig. 35, p. 130 in De Smet and Wiggers (1960).*

Because of the morphologically complex structure of the tidal channels, it was technically not possible to obtain representative estimates of the water flow entering and leaving the basin by measuring in the mouth of the Dollard with only one vessel available. Therefore, the measurements took place at a more inward position in the estuary. Originally (in 1993), one cross-section was selected in the main channel Groote Gat and one in the subsidiary channel Kerkeriet (**fig. a**b). The actual sample locations A and K represent the deepest points on the two cross-sections and had mean depths at HW of 6 m and 5 m, respectively (**fig. c**). The sample locations are indicated by capitals (A, K), whereas references to the entire cross-section will be indicated by apostrophes (A′, K′). The combination of these two was assumed to provide representative

measurements of the water transport. In 1994 and 1995, only location A was sampled, because the results obtained in 1993 indicated that the Groote Gat was the most important channel for larval transport.
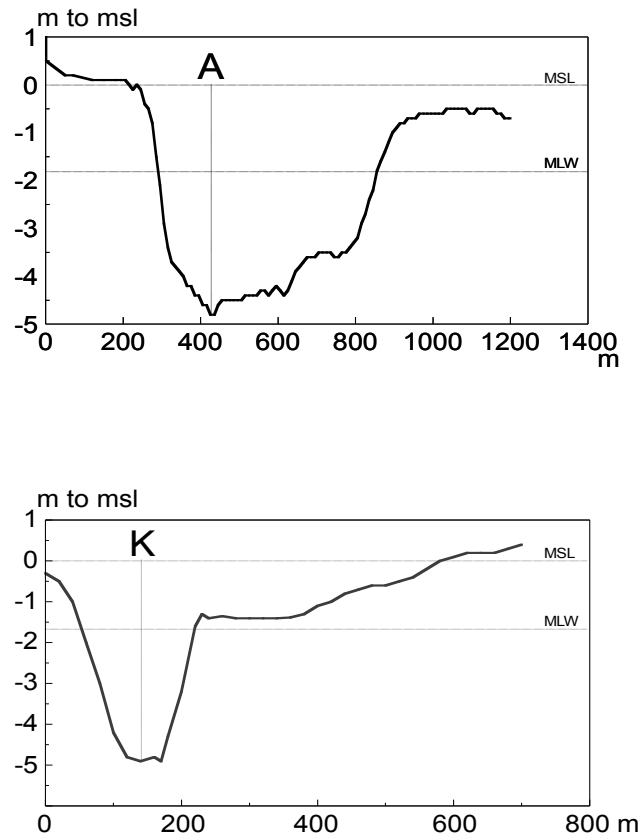
Fig. C. Cross-sections of the sample locations (A', K'), with mean low water (MLW) and mean sea level (MSL) indicated.

Plankton sampling

Probing during flood tide in the Groote Gat showed the first presence of flounder larvae in the Dollard on 13 April 1993, 29 March 1994 and 16 March 1995. These probes were followed by formal sampling programmes that continued until 18 May 1993, 25 May 1994 and 10 May 1995, respectively. The immigration of flounder larvae was followed with a sampling frequency of 1 to 2 tidal cycles per week. Over the three years, a total of 35 tidal cycles has been sampled at location A. At K, 8 tidal cycles were sampled simultaneously with Groote Gat in 1993.

Plankton samples were taken from an anchored ship every 20 minutes, simultaneous with measurements of current velocity and direction by means of calibrated Ott-meters, during a complete tidal cycle starting after LW slack. The 500 μm meshed standard (conical) plankton net (Sournia 1978) had a 0.5 m^2 opening and a length of 4.5 m. A 1 litre jar at the end could be removed to collect the filtrate. A calibrated flow-meter (General Oceanics 2030R) was placed in the net opening to measure the volume of filtered water. The net was attached by 3 bridles to a winch cable 0.9 m above a 100 kg-weight that kept the cable in a vertical position. The position of the weight prevented that the net would sample too close to the bottom and become clogged by sediment and organic debris. A line from the headrope to the bow of the ship secured the vertical position of the cable at high current velocities.

The net was lowered and lifted several times at a constant slow speed between surface and bottom during 1 to 3 minutes, depending on water depth and current velocities. This method ignores possible heterogeneous vertical larval distributions. Sample volumes ranged between 6 and 116 m^3 (mean 38 m^3, s.d. 14). When water turbidity was very high, the outside of the net was flushed when the net surfaced during the sampling procedure, to reduce clogging of the net. At depth-averaged current velocities below 30 cm s^{-1} fishing was impossible because the net dropped to a vertical position. Therefore no samples could be taken during 1 to 2 hr around slack waters. The samples were fixed in a 3.8% neutralised phosphate-buffered formaldehyde solution for subsequent laboratory analysis. The stage-frequency distribution was determined for a limited number of samples. The development stages that Ryland (1966) described for plaice were slightly adapted to fit flounder (Bies 1997, Jager and Kleef 1997). All larvae caught were in the process of metamorphosis, development stages IVb and IVb' (Ryland 1966) being the most abundant ones.

Water flow and water transport

Measurements of current velocity and direction started at the bottom, and were taken consecutively at a minimum of four depths: 0.2 and 0.7 m below the water surface (near-surface) and 0.3 and 0.8 m above the channel bed (near-bottom). With increasing water levels intermediate points were added to a maximum of 8 depths in the vertical. Each of these measurements lasted 30 s at high current velocities to a maximum of 60 s at low current velocities. For a more extensive description of the standard hydrographical methods used by Rijkswaterstaat see also De Jonge (1991) and Jager (1998).

The current velocity measurements were processed with the VIMET computer programme (Rijkswaterstaat 1980) to estimate the water flow. The measured vertical velocity profiles at the sample locations were orthogonized and

integrated over the depth range. Extrapolation from one measuring point to the entire cross-section of the channel was done by regression of current velocity at the sample location on current velocity in the cross-section for flood and ebb separately. The regression formulas were established in December 1992 by measuring water velocity through the cross-sections of the channels with 4 vessels simultaneously (**table a**). The depth-averaged velocity of the cross-section (m s^{-1}) was multiplied by the area of the wet profile (m^2) of the channel at each sampling time to obtain the instantaneous water flow (m^3 s^{-1}). Information on water level was obtained from two tidal gauges (Fig. 1b). The instantaneous water flow was integrated over time according to the trapezoidal rule to produce the water transport (m^3) per tidal phase (flood, ebb). These transports do not necessarily balance each other. Wind speed (m s^{-1}) and direction (0° = N) were measured on board every 30 min, using a Van Doorn anemometer and compass.

Table A. *Regression parameters to calculate the water flow during flood and ebb by sample location, based on extensive measurements in December 1992 (see text). Regression equation Y = a*X + b, where Y = depth-averaged current velocity (cm s^{-1}) of the cross-section; X = depth-averaged current velocity (cm s^{-1}) at the sampling position, a = slope, b = intercept, R^2 = correlation coefficient, n=18.*

| | **Flood** | | | **Ebb** | | |
Location	a	b	R^2	a	b	R^2
A	0.840	0.00526	0.973	0.741	0.00064	0.988
K	0.942	-0.09373	0.976	0.691	0.04686	0.973

Larval concentration, flux and transport

Flounder larvae were sorted from the samples and counted without subsampling. The larval concentration (n m^{-3}) in each sample was calculated by dividing the number of individuals by the sampled volume. The instantaneous larval flux (n s^{-1}) was calculated by multiplying the depth-averaged concentration by the instantaneous water flow through the cross-section, implicitly assuming a homogeneous distribution across the channel. Measurements, obtained at a depth-averaged current velocity of less than 30 cm s^{-1}, were excluded because the net dropped to a vertical position and sampling was inaccurate. Integration over time, without interpolation over slack tides, resulted in a landward (flood-) and seaward (ebb-) transport of flounder per tidal cycle. The flood and ebb transport were each separated in two parts, divided by the time that the water level reached D.O.L. Below D.O.L. the tidal flats are emerged and almost all water is transported through the channel, whereas above D.O.L. a considerable volume of water and thus larval transport may take place over the tidal flats. The (net) tidal transport was integrated over the tides that comprised the immigration period to assess the total (net) larval input in the nursery by year.

Data treatment and statistical analyses

The mean wind speed per sampling date was expressed on the scale of Beaufort for statistical purposes. The main wind direction was categorised in quadrants (N to W, W to S, S to E and E to N). The lunar phase (Dienst Getijdewateren 1993, Rijksinstituut voor Kust en Zee 1994) was divided in quarters (1=new moon, 2=first quarter, 3=full moon, 4=last quarter), with the dates of spring and neap tide as medians. Spring tides are about 2 d after full moon or new moon. Tidal asymmetry was defined as the difference in duration of the flood and ebb period (in minutes). Larval retention was expressed as (net larval transport/ flood transport)*100%. An ANOVA of water and larval transport by the factors wind speed, wind direction and lunar phase was done.

Post-larval density estimates

Settled juvenile flounder were sampled in 1993 and 1994 by means of a 2-m modified NIOZ beam trawl, mesh size 5 mm (Kuipers 1975, Kuipers *et al.* 1992, Jager and Kleef 1997). A stratified random sampling strategy was applied to allow reliable abundance estimates of juvenile flatfish in the Dollard. An index of abundance of juvenile flounder in the Ems estuary was obtained from RIVO-DLO data of the Demersal Young Fish Survey (DYFS; for survey methods see Boddeke *et al.* 1971).

Table B. *Flood, ebb and net (flood - ebb) water flow (10^6 m^3), flood, ebb and net larval transport (10^6), and larval retention (% of the flood transport) through A' (Groote Gat).*

Date	Flood Water flow	Ebb Water flow	Net Water flow	Flood Larval transport	Ebb Larval transport	Net Larval transport	% Larval retention
1993							
13/04	23.8	19.8	4.0	8.3	1.5	6.8	82.2
15/04	16.9	14.7	2.2	12.2	5.7	6.5	53.5
19/04	23.4	21.8	1.6	19.3	11.6	7.7	40.1
22/04	27.3	22.6	4.7	68.8	30.7	38.1	55.4
26/04	26.6	20.0	6.6	73.1	25.6	47.5	65.0
29/04	23.6	21.4	2.2	56.5	30.2	26.3	46.5
03/05	26.7	27.5	-0.8	44.8	14.6	30.2	67.4
06/05	26.0	22.4	3.6	53.4	12.9	40.5	75.7
11/05	27.0	21.5	5.5	30.3	18.6	11.7	38.5
13/05	26.7	28.8	-2.1	10.7	19.6	-8.9	-83.2
18/05	22.1	15.3	6.8	1.1	0.5	0.6	54.9

Table 2. (continued)

Date	Flood Water flow	Ebb Water flow	Net Water flow	Flood Larval transport	Ebb Larval transport	Net Larval transport	% Larval retention
1994							
31/03	38.2	21.7	16.5	3.8	0.5	3.3	87.3
05/04	27.1	22.7	4.4	9.7	1.4	8.3	85.9
07/04	21.9	18.0	3.9	11.7	4.9	6.8	57.8
11/04	21.4	24.8	-3.4	102.8	99.2	3.6	3.5
12/04	24.2	25.3	-1.1	113.4	75.7	37.7	33.2
14/04	30.3	30.5	-0.2	101.3	157.6	-56.4	-55.7
18/04	21.1	21.2	-0.1	154.8	106.5	48.3	31.2
19/04	20.1	15.5	4.6	108.4	138.4	-30.0	-27.7
21/04	20.1	16.4	3.7	67.8	121.4	-53.7	-79.2
28/04	28.9	25.0	3.9	39.8	84.0	-44.2	-111.0
03/05	21.1	14.0	7.1	229.8	90.6	139.2	60.6
10/05	25.9			56.1			
11/05	22.9	21.7	1.2	19.8	21.0	-1.2	-6.2
16/05	24.5	24.5	0.0	2.8	2.0	0.8	28.4
19/05	19.9	21.8	-1.9	2.9	1.0	1.9	64.8
25/05	28.3	25.2	3.1	0.3	0.4	-0.1	-29.8
1995							
30/03				1.1			
06/04	25.0	23.6	1.4	1.8	0.4	1.3	76.5
12/04	22.2	26.8	-4.6	4.7	16.4	-11.7	-250.0
18/04	26.4	28.7	-2.3	22.4	28.9	-6.5	-29.1
20/04	28.2	22.4	5.8	14.2	21.3	-7.2	-50.7
25/04	17.2	16.4	0.8	69.7	15.5	54.1	77.7
27/04	22.0	22.0	0.0	38.0	16.4	21.5	56.7
03/05	22.8	18.9	3.9	10.0	11.6	-1.6	-15.7
10/05	18.6	15.5	3.1	20.8	3.9	16.9	81.3

Table C. Flood, ebb and net (flood - ebb) water flow (10^6 m^3), flood, ebb and net larval transport (10^6), and larval retention (as % of the flood transport) through K′ (Kerkeriet).

Date	Flood Water flow	Ebb Water flow	Net Water flow	Flood Larval transport	Ebb Larval transport	Net Larval transport	% Larval retention
1993							
13/04							
15/04	5.0	6.7	-1.7	1.8	1.1	0.7	40.9
19/04	8.3	9.6	-1.3	3.4	1.4	2.0	58.6
22/04	8.9	11.7	-2.8	8.6	2.3	6.2	72.8
26/04	8.2	9.2	-1.0	3.9	3.4	0.4	10.7
29/04	6.6	10.0	-3.4	9.4	9.1	0.3	3.1
03/05							
06/05	7.4	9.7	-2.3	6.4	1.9	4.5	69.9
11/05	6.6	10.0	-3.4	2.6	6.2	-3.6	-137.3
13/05							
18/05	6.4	7.9	-1.5	0.3	0.04	0.2	85.9

RESULTS

Water flow

On average 24.2 10⁶ m³ (s.d. 4.1 10⁶, n=35) of water entered the Dollard during flood through A′ (**table b**), and 7.2 10⁶ m³ (s.d. 1.2 10⁶, n=8) through K′ (**table c**). On most sampling dates, more water entered during flood than left during ebb through the Groote Gat, resulting in a flood surplus; Kerkeriet showed an ebb surplus on all sampling dates. The net water flow of A′ is not entirely balanced by K′ (**fig. d**). Generally, most of the flood surplus of A′ returned by K′, indicating a clock-wise water circulation. On 26 April and 18 May, a relatively large part of the flood surplus of A′ returned by another route; this coincided with a south-easterly or south-westerly wind direction of moderate strength.
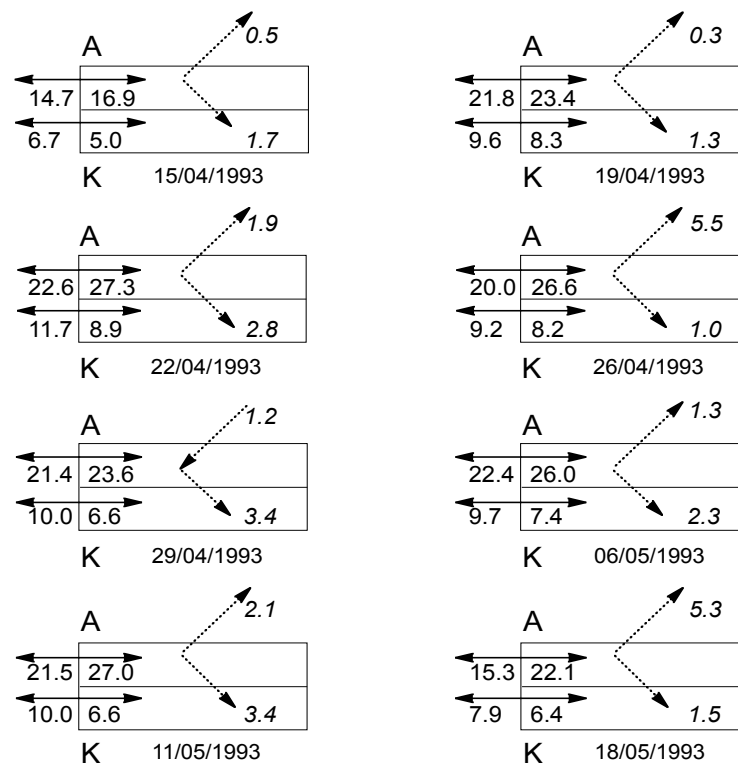
Fig. D. *Water balance of Groote Gat (A) and Kerkeriet (K) on the 8 sampling dates in 1993. The water volume (in 10⁶ m³) and direction (to the right = flood, to the left = ebb) are indicated by figures and arrows. Dotted arrows and italic figures indicate the estimated volumes to balance the Dollard water circulation. The freshwater discharge at Nieuwe Statenzijl was negligible (0.3 .10⁶ m³ on 15, 19 and 22 April and 0 on the other 5 sampling dates)*

As expected, the flood and ebb transport of water within a tidal cycle at A′ are closely related (**fig. e**). However, wind direction significantly influenced the intercept of the regression between flood and ebb transport (**table d**), and resulted in the following regression equation:

$$E = 9.1 + 0.6 * F + \alpha * wind,$$

(parallel slopes were forced; P<0.01, R-squared$_{adj.}$ = 0.553, n = 40) where E is the volume of ebb water (m^3), F the volume of flood water (m^3), α the intercept at different wind directions and *wind* (direction) is an indicator variable that takes the value 1 if true and 0 if false.

Table D. *Values of the regression parameter α at different wind directions.*

wind	α	wind	α	wind	α	wind	α
N to W	0	W to S	-3.5	S to E	-6.1	E to N	-2.1

ebb transport
(10^6 m^3)

flood transport (10^6 m^3)
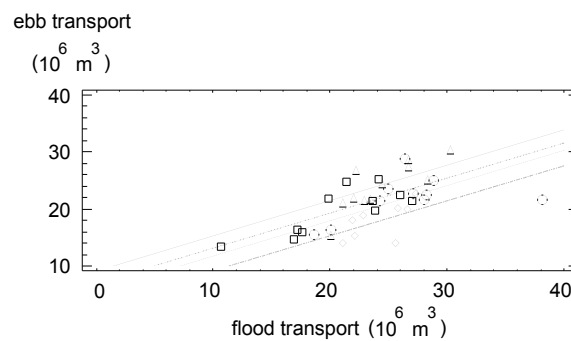
Fig. E. *Comparison of regression lines between flood and ebb water transport (10^6 m^3) at different wind directions (Δ drawn line = N to W, O striped line = W to S, ◊ dotted line = S to E, striped & dotted line = E to N).*

At northerly to westerly winds, the ebb transport is higher compared to the flood transport than at southerly to easterly winds. In 1993, the most frequently observed wind direction was northerly to easterly, whereas northerly to westerly winds prevailed in 1994, and westerly to southerly winds in 1995 (**table e**). Wind speed was not a significant factor within the observed range.

The net water flow at A′ was also affected by the wind direction (**table f**a). Southerly winds result in a relatively large net flood surplus, whereas northerly winds may lead to smaller and even negative values (**fig. f**a).

Tidal asymmetry is positively correlated with the net water flow (**table g**). Relatively longer flood than ebb duration occurred mainly at easterly to south-westerly wind directions (**table e**). Tidal asymmetry was significantly higher in 1993 than in 1994 (**table h**), indicating relatively longer flood periods in the first year.

Table E. Lunar phase, tidal asymmetry (flood - ebb duration in min), maximum and minimum water levels (in cm relative to Dutch Ordnance Level, which is 7 cm below m.s.l.), main wind direction ($\rightarrow$ means: turning to), wind speed (m s^{-1}), standard deviation (s.d.) and number of observations (n) at the sample location (A) in the Dollard.

Date	Lunar phase	Tidal asymm	Max. Water level	Min. Water level	Main Wind direction	Mean Wind speed	s.d.	n
1993								
13/04	4	80	122	-200	E	6.5	0.6	29
15/04	4	0	80	-180	NE	5.8	0.6	27
19/04	1	280	130	-180	NNW	5.9	0.8	27
22/04	1	180	150	-204	SE	3.4	2.2	29
26/04	1	180	135	-200	E→SW	4.5	1.8	28
29/04	2	220	130	-210	ENE	7.5	1.1	27
03/05	2	-40	150	-175	NNW	9.4	1.4	27
06/05	3	0	130	-240	NE	6.4	2.9	28
11/05	3	0	130	-230	NE	8.9	1.3	29
13/05	4	-60	155	-180	N	8.2	2.1	25
18/05	4	120	100	-230	SE	5.5	2.8	29
1994								
31/03	3	120	158	-240	SW	11.1	2.6	29
05/04	4	40	143	-171	SW	9.0	2.9	29
07/04	4	80	104	-205	S	2.5	0.9	28
11/04	1	-100	119	-245	NE	12.0	1.5	26
12/04	1	-60	136	-242	NE	10.5	1.8	27
14/04	1	-120	193	-160	NW	6.8	2.2	27
18/04	2	0	120	-213	NNW	4.6	1.4	26
19/04	2	60	97	-213	WNW	3.5	1.0	25
21/04	2	40	105	-202	SW	4.9	1.1	28
28/04	3	-40	157	-230	SW	5.9	1.8	27
03/05	4	80	93	-240	SE	12.1	3.4	28
10/05	1	0	136	-208	N	2.7	1.5	26
11/05	1	0	140	-216	N	5.7	0.7	27
16/05	2	0	158	-199	N	3.3	1.5	26
19/05	2	0	144	-186	NE	5.5	2.1	27
25/05	3	0	172	-202	N→W	4.7	1.3	27
1995								
30/03	1		123	-203	NW	3.2	1.0	13
06/04	2	-20	165	-183	W	5.4	1.5	28
12/04	2	20	152	-186	NW	7.9	2.9	28
18/04	3	20	198	-188	W	10.1	2.6	26
20/04	3	40	165	-223	SW	6.8	3.6	29
25/04	4	60	94	-205	E	9.5	0.8	28
27/04	4	20	144	-207	NW	7.5	1.1	29
03/05	1	20	137	-218	SE	2.2	1.1	27
10/05	2	100	108	-177	W	2.8	1.0	27

The lunar cycle affected the flood transport, but neither ebb nor net transport (**table i**). Flood transport was significantly higher at springtides following full moon (**fig. g**).

Table F. *Multifactor ANOVA of net water transport (a) and (b) net larval transport.*

(a)	SS	Df	F-ratio	P-value	Sign.
MAIN EFFECTS					
wind direction	151.73	3	4.87	0.007	**
wind speed (Bf)	76.86	5	1.48	0.225	n.s.
RESIDUAL	322.28	31			
TOTAL (corrected)	634.60	39			
(b)					
MAIN EFFECTS					
wind direction	9.97×10^{15}	3	3.67	0.025	*
wind speed (Bf)	6.22×10^{15}	4	1.72	0.176	n.s.
RESIDUAL	2.35×10^{16}	26			
TOTAL (corrected)	4.00×10^{16}	33			

The interaction of wind direction and wind speed is a linear combination of other factors, and is excluded.

Table G. *Spearman rank correlations between water transport, larval transport and retention, wind direction and tidal asymmetry.*

n=34	net water transport	net larval transport	larval retention
wind direction	n.s.	P=0.02, r=0.42	P=0.02, r=0.40
tidal asymmetry	P<0.001, r=0.61	n.s.	P=0.02, r=0.39
net water transport		n.s.	n.s.
net larval transport			P<0.001, r=0.69

Table H. *One-way ANOVA of tidal asymmetry (difference of flood and ebb duration) by year.*

	SS	Df	F-Ratio	P-value	Sign.
Between groups	43074	2	3.35	0.048	*
Within groups	205543	32			
TOTAL (corrected)	248617	34			

Table I. *ANOVA of (a) flood-, (b) ebb- and (c) net water transport by lunar phase.*

	Sum of Squares	Df	F-ratio	P-value	Sign. level
(a)					
Between groups	247.58	3	7.70	0.0006	***
Within groups	332.46	31			
TOTAL (corrected)	580.04	34			
(b)					
Between groups	112.80	3	2.28	0.100	n.s.
Within groups	494.47	30			
TOTAL (corrected)	607.27	33			
(c)					
Between groups	87.64	3	2.11	0.119	n.s.
Within groups	415.00	30			
TOTAL (corrected)	502.65	33			

net water transport

net larval transport
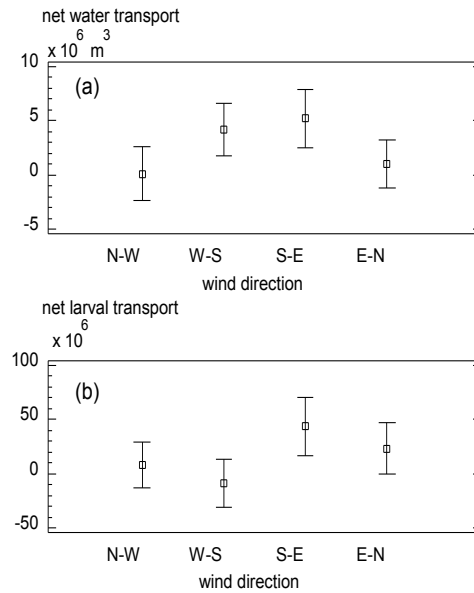
Fig. F. *Net water (a) and larval (b) transport by wind direction. Bars indicate 95% confidence intervals.*
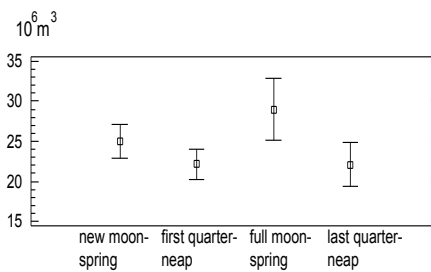
Fig. G. *Mean flood water transport (10^6 m^3) by lunar phase. Bars indicate 95% confidence intervals.*

Larval concentrations

The mean larval concentration per tidal cycle varied among sampling dates (**fig. h**). Mean concentrations increased to a maximum within 14 days after the first sampling date, except in 1995 when it took about 3 weeks, and then gradually decreased. The mean concentrations on 11 April and 3 May 1994 seem exceptionally high and do not fit in the described pattern.

Larval concentrations fluctuated widely from one sample to the next (20 min later) indicating a patchy distribution in the channel water (**fig. m** in Appendix). At location A, peak-concentrations were often observed at the beginning of the flood, during the first 1 to 2 h after LW slack when the tidal flats are not flooded

yet. When the flats became inundated (around D.O.L. -0.5 m at A', and D.O.L -1 m at K'), larval concentrations rapidly decreased. An increase in concentrations was observed during mid-flood, when current velocities are around their flood maximum. During ebb, a peak in larval concentrations sometimes coincided with the time of maximum velocity, e.g. on 19 April 1994, but otherwise concentrations were quite variable. At several dates a remarkable increase in larval concentrations was observed at the end of the ebb period.

Given the large tidal fluctuations in concentrations, the arithmetic mean seems not very useful to compare dates or years. Nevertheless, mean concentrations indicated higher larval abundance in 1994 than in 1993 or 1995.
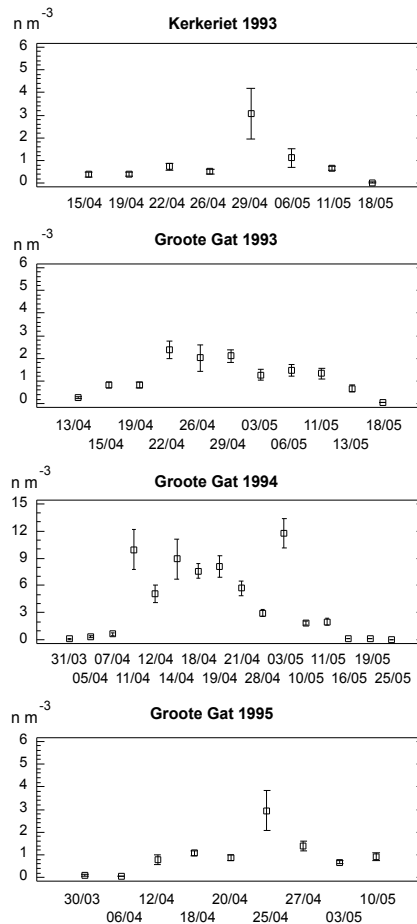
Fig. H. *Mean larval concentrations ($n\ m^{-3}$) by sampling date at Kerkeriet (1993) and Groote Gat (1993-1995). Bars indicate 95% standard errors.*
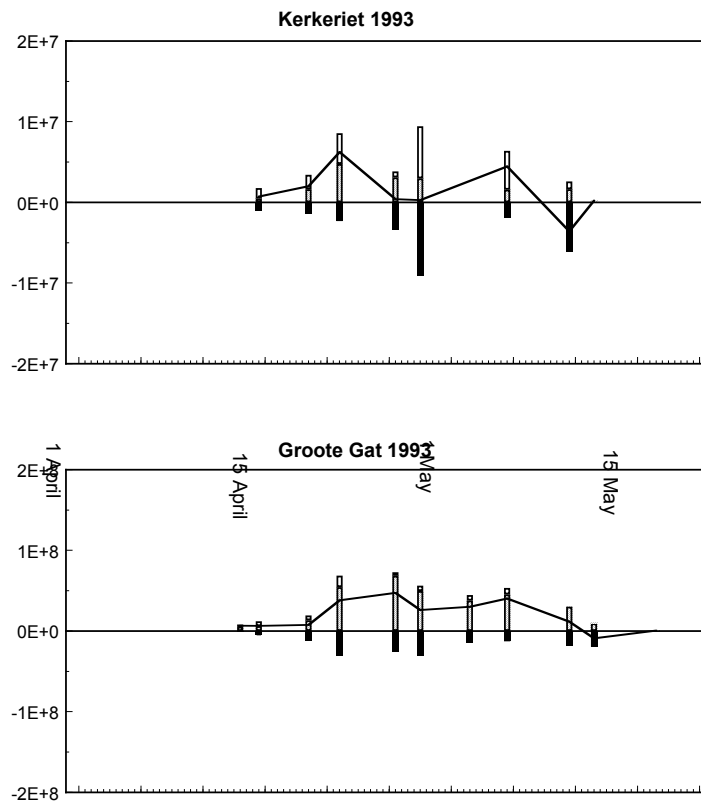
Fig. I. *Estimated flood transport (a = open bars, b = back-hatched bars) and ebb transport (c = grey bars, d = black bars) and net larval input (drawn line) per tidal cycle at A′ and K′ in 1993. The area under the drawn line represents the integrated net larval input during the entire immigration period.*

Larval transport and retention

Flood transports were generally higher than ebb transports at both A′ and K′, resulting in net landward larval transports in 1993. However, in 1994 and 1995 a larger ebb than flood transport was observed on 40 to 50% of the sampling occasions (**table b** and **table c**, **fig. i**).

The net tidal transport of flounder larvae at K′ varied from $4\ 10^6$ in seaward (negative) direction to $6\ 10^6$ in landward (positive) direction (**table c**). The net transport at A′ ranged from about $-10\ 10^6$ to $+50\ 10^6$ flounder larvae per tidal cycle in 1993 and 1995 (**table b**). In 1994, the largest net seaward transport ($56\ 10^6$) occurred on 14 April, whereas the largest net landward transport was realised on 3 May ($139\ 10^6$).
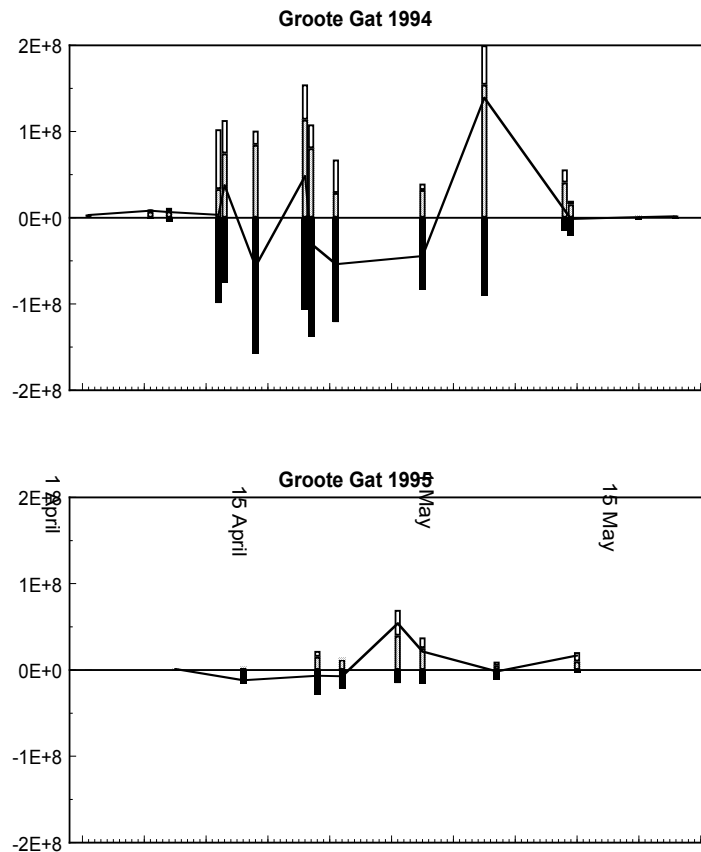
Fig. 9. (continued) *Estimated flood transport and net larval input per tidal cycle at A' in 1994 and 1995.*

The net larval transport at A′ was not correlated to the net water transport (**table g**). Part of the variability in the net tidal transport at A′ was accounted for by wind direction (**table f**b), with significantly higher but also more variable landward larval transport at southerly to easterly winds (**fig. f**b).

Lunar phase did not affect larval transport.

The mean larval retention at A′ was 45.1%, 9.5% and -6.7% in 1993, 1994 and 1995, respectively (**table b**), whereas it was 25.6% at K′ in 1993 (**table c**). The larval retention was correlated to the wind direction (**table g**): the lowest retention corresponded with northerly to westerly wind directions and the highest with easterly to northerly winds. Larval retention was not correlated to the net water transport. However, there was a positive correlation between larval retention and tidal asymmetry (**table g**).

Larval input and post-larval abundance estimates

The integrated flood transport ('total input') of larvae at A′ in 1994 was 5 times higher than in 1995 and 2.6 times higher than in 1993 (**table j**). The net larval input at A′, which is the difference of the flood and ebb transport integrated over the entire immigration period, ranged from nearly 400 10^6 (1995) to nearly 1400 10^6 (1993). The net larval input at K′ was about 5% of that at A′ in 1993 (**table j**). The overall retention (**table j**) was 25% at K′ and varied at A′ from 10% (1994) to 55% (1993).

The peak-numbers of settled flounder in the Dollard were estimated at 2.4 10^6 in 1993 and 3.1 10^6 in 1994 (**table j**). The abundance index of juvenile flounder from the DYFS indicated that 1994 was by far the strongest of the three years, whereas 1993 and 1995 were comparatively weak (**table j**).

The ratio of the peak abundance of settled flounder to the (net) larval input was 0.0009 (0.0017) in 1993 and 0.0005 (0.0046) in 1994. This roughly indicates the survival rate of the flounder larvae in the settlement process.

Table J. *Overall retention (net larval input/total larval input), integrated (net) larval input (10^6) excluding slack periods, peak abundance of settled flounder (10^6) in June in the Dollard, and abundance index of 0-group flounder in September/October in the Ems-Dollard from the Demersal Young Fish Survey (data RIVO-DLO). n.a.= no data available.*

Year	Location	Retention	Net larval input	Total larval input	Settled flounder	DYFS 0-group flounder
1993	K′	0.250	78	310		
1993	A′	0.547	1387	2534	2.4	1.25
1994	A′	0.100	677	6718	3.1	16.52
1995	A′	0.287	388	1352	n.a.	0.95

DISCUSSION

The timing of first arrival of the larvae in the Dollard nursery varied between the years investigated from mid-March to mid-April and, analogous to plaice, probably depends on the timing of adult spawning in the North Sea as well as on the speed of coastal transport of eggs and larvae (Hovenkamp 1991, Van der Veer *et al*. 1998). The immigration had more or less ended by the second half of May in 1993 and 1994. In 1995, the survey was stopped relatively early, when substantial larval concentrations were still present. The year 1995 was characterised by the earliest immigration and also the smallest numbers, whereas the year with the latest larval immigration (1993) was the one with the highest net larval input and overall retention.

The larval supply from the North Sea and its variation are unknown. The 1993-data give a hint of a secondary larval peak in the beginning of May which

coincided with a changed frequency-distribution of metamorphic stages (**fig. j**). It is possible that the larvae that arrive in the Dollard originate from different spawning grounds, e.g. the Southern Bight and the German Bight. At least for plaice (*Pleuronectes platessa* L.) a different spawning origin of juveniles in the Dollard has been suggested (Karakiri *et al.* 1991).
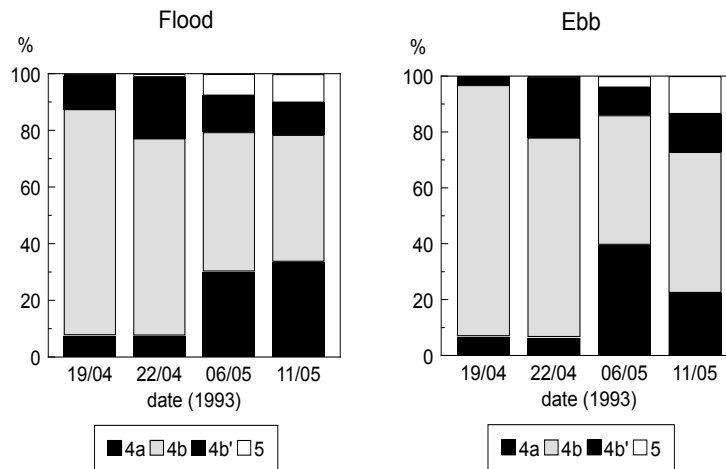
Fig. J. *Relative frequency distribution of flounder metamorphic stages during flood and ebb on four sampling dates in 1993 in the Groote Gat (Fernandez 1993).*

Because the net larval transport was only poorly correlated with the net water transport, other factors must determine the rate of retention. One of these is the timing of tidal variations in larval concentrations relative to the time of maximum water flow. **Fig. 11** was constructed to eliminate day-to-day variation. The initial peak after LW slack may be caused by larvae that start to move from the bottom as soon as the flood currents start running. Larval concentrations immediately decrease, which indicates the existence of a concentration gradient in the channel, with increasing concentrations from the mouth of the Dollard towards the sluice of Nieuwe Statenzijl. By sampling at one fixed position only, the passing water bodies may have different origins at different stages of the tide. This is a.o. reflected in the pattern of salinity during the tidal cycle (**fig. k**), which has its maximum around HW and is at a minimum around LW when discharged freshwater at Nieuwe Statenzijl reduces salinity. The spatial gradient in the channel may contribute to the observed irregular concentration patterns during the tidal cycle. Over several tides, the transport process leads to accumulation of larvae at the rims of the nursery, as was shown by Jager (1998).
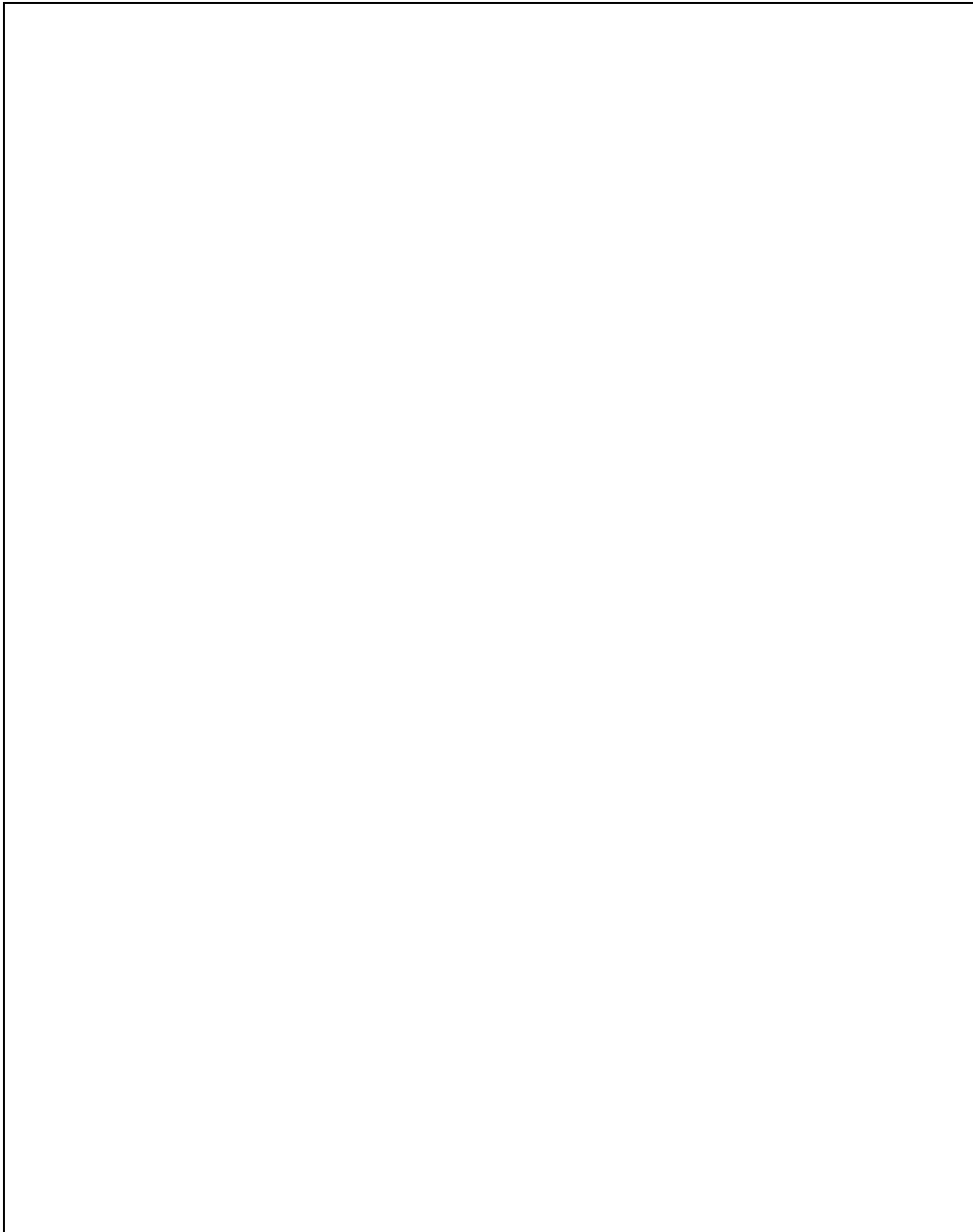
Fig. K. *Normal deviates Z (Zar 1984; Z=(x$_i$-μ)/σ) of (a) larval flounder concentrations, (b) salinity, (c) depth-averaged velocity, and (d) mean water level (m to D.O.L.) during the tidal cycle. * = Kerkeriet 1993, Groote Gat o = 1993, = 1994, Δ = 1995.*

When the tidal flats inundate, a further decrease in larval concentrations indicates that large numbers of larvae disappear from the channel. Subsequently, new larvae appear to be transported from the outer part of the estuary into the Dollard, resulting in a secondary peak. These concentrations are lower than the initial peak, suggesting that the incoming seawater contains relatively less larvae than had accumulated on the channel bottom. During ebb, part of these larvae return through the channel whereas part of them are retained on the flats in the nursery. Later during the ebb, when the tidal flats emerge, all larvae that did not settle flow back through the small gullies to finally collect in the main channel, where concentrations may form a late-ebb peak.

The tidal stage-composition of the sampled larvae confirms the picture described above (Jager *subm.*): during the beginning of the flood, 40% of the more developed metamorphic stages IVb' and V are present. This percentage gradually decreases toward HW, when stage V may even be completely absent. The early metamorphic stage IVa is most frequent around HW. During ebb, frequencies return to the initial LW-situation.

The vertical distribution of the larvae, although ignored in the present study, may enhance spreading over the flats if larvae are concentrated in the upper water layers (Jager and Mulder *subm.*). During flood, the centre of mass of larval distribution indeed lies in the upper half of the water column (Jager *subm.*). In 1995, the centre of mass dropped below 0.5 during ebb, but not in 1994, when high near-surface larval concentrations resulted in relatively high ebb transport.

Complex interactions of wind, spring-neap cycle, tide, water circulation and fresh water discharges most likely affect the process of larval transport. De Jonge (1991) indicates that the water circulation in the shallow Dollard is very sensitive to the wind direction. This is reflected in the water transport data obtained in the Groote Gat. Southerly to easterly, as well as westerly to southerly winds generally produced a larger flood surplus than the other wind directions. Under southerly to easterly wind conditions, a clockwise water circulation is enhanced: during the ebb probably more water is blown over the tidal flats and drained through the Kerkeriet channel, leading to flood surpluses in the Groote Gat. This wind direction coincided with relatively high, and more variable, landward net larval transport. On 26 April and 18 May 1993, the water circulation seemed reversed. A relatively large proportion of the Groote Gat flood water returned probably in north-easterly direction, and may have discharged over the Geiseleitdamm to the river Ems. During a north-westerly wind, flood water may indirectly enter the Dollard over the Geiseleitdamm from the river Ems and return through Groote Gat, which may lead to an ebb surplus in this channel (De Jonge 1991).

However, not all sampling dates with north-westerly winds showed an ebb surplus. Detailed information on (variability in) local water circulation is required to better understand the larval immigration and transport process. Favourable wind conditions during the immigration period may be critical for successful transport to and settlement of metamorphosing flounder larvae.

The present analysis was based on the assumption of homogeneous larval distribution across the channel. However, Rijnsdorp *et al.* (1985) found heterogeneous larval concentrations across the cross-section of a tidal channel in the south-west Netherlands. Also, Weinstein *et al.* (1980) found indications that larval concentrations were the highest in the flood branch of the channel during flood, and the highest in the ebb-branch during ebb. If so, this may lead to overestimation of the ebb transport and may explain some but not all of the negative larval transports observed, because the sample site in the Groote Gat is known to be in the ebb-dominated part of the channel. Moreover, the residual water circulation within a cross-section of a channel may vary at different wind conditions (De Jonge 1991), and so may the larval distribution across the Groote Gat. No data are available to further substantiate this possibility.

The integration of net larval transport over the immigration period will give unreliable results if the net transport per tidal cycle is very variable. In 1993 and 1995, the seasonal pattern was fairly smooth, whereas in 1994 there were some irregularities. Although mean larval concentrations were much higher in 1994 than in 1993, the difference in overall net larval input between these years is relatively small due to the frequent occasions of negative net tidal transport in 1994. One cause of the negative net larval transport is the timing of relatively high concentrations just at the maximum of ebb on most of these dates. Larval retention was positively correlated with tidal asymmetry, and so was the net water transport, but the causal relation between them is unknown. Because the tidal asymmetry was significantly higher in 1993 than in 1994, this factor may partly explain the higher larval retention in the former year.

The 1993-comparison showed that the overall net larval input via Kerkeriet was only 5% of that via Groote Gat and therefore is of minor importance. The estimates of larval input by measuring in the centre of the Dollard will underestimate the real input, because considerable numbers of larvae may have been transported to tidal flats north of the sampling location. The tidal volume measured at the sampled cross-section in the Groote Gat is (only) 20% of the water volume that is encountered in the mouth of the Dollard (De Jonge 1991).

The ratio of settled flounder to total larval input was lower in 1994 than 1993. According to the DYFS-abundance index in October, 1994 was a relatively strong year-class, which was (to a lesser extent) also indicated by the settled flounder data collected in the Dollard in June. Although the total larval input corroborates these observations, in contrast, the net larval input estimates

indicated 1993 and 1994 as equally strong years. Measuring the net larval input by the present method appears not to be a good predictor for year-class strength. The larval input (integrated flood transport) seems to correlate better with the DYFS-abundance index.

Saturation of the nursery may have occurred in the Dollard in 1994, when larval concentrations were high. Assuming that the range of distribution expands in years of high population abundance (MacCall 1990), part of the juvenile flounder in the Dollard may have overflown to the more seaward parts of the Ems estuary. This option is sustained by the relatively high flounder abundance index of 1994 in the DYFS, which monitors the middle part of the estuary. The high discharge of the rivers Ems and Westerwoldsche Aa in March and April 1994 (**fig. l**) created low-salinity conditions which may have been favourable for flounder.
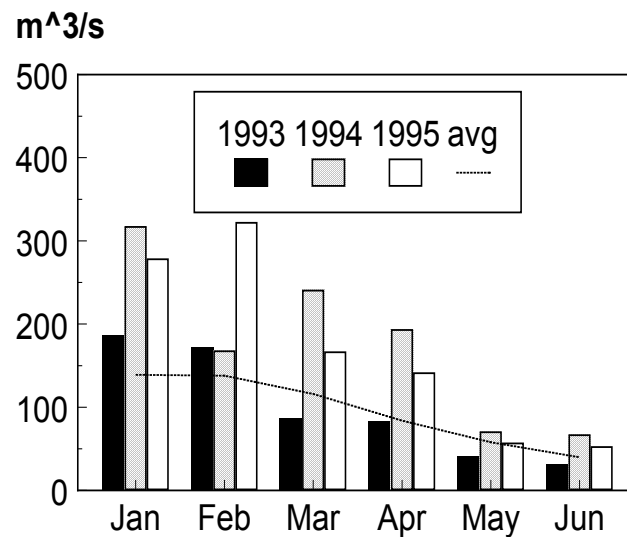
Fig. L. *Monthly averaged freshwater discharges of the river Ems (m³ s⁻¹) from January to June 1993 to 1995 (data obtained from Wasser- und Schiffahrtamt Emden), and 1941-1986 average (dotted line; after Steen et al. (1990) p. 27).*

The present study demonstrates the complexity of the described transport and retention processes. The resulting variability in larval concentrations hampers accurate assessment of larval input in the nursery. Nevertheless it shows that mean larval concentration and the total larval input are correlated to the abundance of post-settlement and juvenile flounder in the estuary and may be used to indicate the year-class strength at an early stage.

APPENDIX

Fig. M. *Measured larval concentrations (n m^{-3} , left axis; square markers) and water flow (m^3 s^{-1} , right axis; drawn lines) at the sample locations K (Kerkeriet) and A (Groote Gat) on the different sampling dates in 1993, 1994 and 1995. Dotted lines indicate interpolated values of larval concentrations. The arrows indicate the time at which the water level reached D.O.L.*

Fig. 13. (continued)

Fig. 13. (continued)

Fig. 13. (continued)

Fig. 13. (continued)

Accumulation of flounder larvae (*Platichthys flesus* L.) in the Dollard (Ems estuary, Wadden Sea)

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ABSTRACT

In the context of an investigation of the importance of the Dollard as a nursery for flounder (*Platichthys flesus* L.), the larval accumulation process was studied. The hypothesis was addressed that freshwater discharge is a steering factor in larval transport caused by a larval preference for low-salinity water. Flounder larvae were simultaneously sampled at three locations during five tidal cycles in combination with measurements of physical variables. One location was in the main channel, the other two were in more peripheral channels of the Dollard. One of those is directly connected to a sluice by which freshwater is discharged into the Dollard.

Concentrations of larvae varied during the tidal cycle at all locations; high initial values dropped after the middle of the flood to lower levels to increase again at the end of ebb. In the channel connected to the sluice, significantly lower salinities were observed around low water than at the other locations, which coincided with significantly higher larval concentrations at the beginning of flood. Water transport as well as larval transport at this location showed a flood surplus on all sampling dates. Also, relatively more larvae were transported than expected according to the water transport compared to the other stations. Moreover, there was an ebb surplus in larval transport during some sampling dates at the other locations.

The results indicated an accumulation of flounder larvae in the inner Dollard, and particularly in the area affected by the discharge of freshwater. Independent observations of settling flounder larvae in traps also indicated a concentration in the vicinity of the sluice. However, the sluice itself may form an effective barrier for flounder larvae that try to migrate to freshwater.

Keywords: *Platichthys flesus*, flounder, accumulation, transport, nursery, Dollard

INTRODUCTION

The flounder, *Platichthys flesus* L., is a euryhaline flatfish species (Pleuronecti-dae) with a coastal distribution in the northeastern Atlantic, ranging from the Mediterranean and Black Sea in the south to the Baltic and White Sea in the north. Its ability to live in low-salinity water and its alleged preference for such environments are interesting features that do not occur in other European flatfish species to the same degree.

In the North Sea, reproduction of flounder takes place in the marine environment (Redeke 1908, Ehrenbaum 1911, Rijnsdorp and Vethaak 1989). Highest concentrations of flounder eggs were observed in February west and northwest of the Dutch west coast, in the eastern English Channel and the area northwest of Helgoland (Van der Land 1991). The first bottom-living stages were caught by the end of April in brackish-water areas near river mouths. The juveniles either stay in the brackish environment or migrate further up the rivers (Redeke 1908). With growth, the juvenile flounders return to estuaries and gradually assume a more seaward distribution.

The preference of juvenile flounder for fresh water was mentioned by Redeke (1908), based on the observation that these stages were most abundant in those areas of the former Zuiderzee where salinity was lowest. Juvenile plaice (*Pleuronectes platessa* L.) were absent in these areas. The Zuiderzee estuary was dammed in 1932 and is now a freshwater lake (IJsselmeer). As a consequence, flounder can only enter the IJsselmeer through the sluices in the dam (Rijnsdorp and Vethaak 1989). Van der Veer *et al.* (1991) suggested that initial settling of flounder larvae in the western Wadden Sea probably takes place close to the sluices where freswater is discharged from the IJsselmeer. Following adaptations in the sluice management in 1991 aimed at improving the possibilities for fish migration, the abundance of juvenile flounder in the lake increased by an order of magnitude in 1991 and 1992 (Dekker *et al.* 1992). The flounder population in the IJsselmeer has remained high since then (Dekker 1994). These data indicate that the juveniles have a strong urge to migrate to fresh water.

Kerstan (1991) stressed the importance of rivers as nurseries, and concludes that freshwater habitats are preferred by 0-group flounder. However, it is less evident whether this preference already exists during the larval stage, at metamorphosis, or if it develops after settlement. A few observations suggest that larvae also prefer freshwater. Flounder as small as 10 mm were observed in May near the flat banks of the river Elbe, and free-swimming metamorphosing larvae were caught in the upper water layers of the estuary (Ehrenbaum 1911). Hutchinson and Hawkins (1993) observed metamorphosing larvae moving

upstream with the advancing tide in the River Itchen in water of very low salinity (<2 ppt), where the freshwater layer was in contact with the substrate.

During a pilot study (1992) within the framework of an investigation of the importance of the Ems-Dollard estuary as a nursery for flounder, large numbers of metamorphosing larvae were observed near the sluice of Nieuwe Statenzijl where freshwater from the river Westerwoldsche Aa is discharged into the Dollard (**fig. a**). Based on these observations the hypothesis was formulated that freshwater outflow is a steering factor in larval transport and retention, and that flounder larvae will accumulate in the part of the nursery area where salinity is lowest.

The present study tests this hypothesis using measurements of water flow and larval concentrations obtained during simultaneous sampling at three stations in the Dollard over five complete tidal cycles.
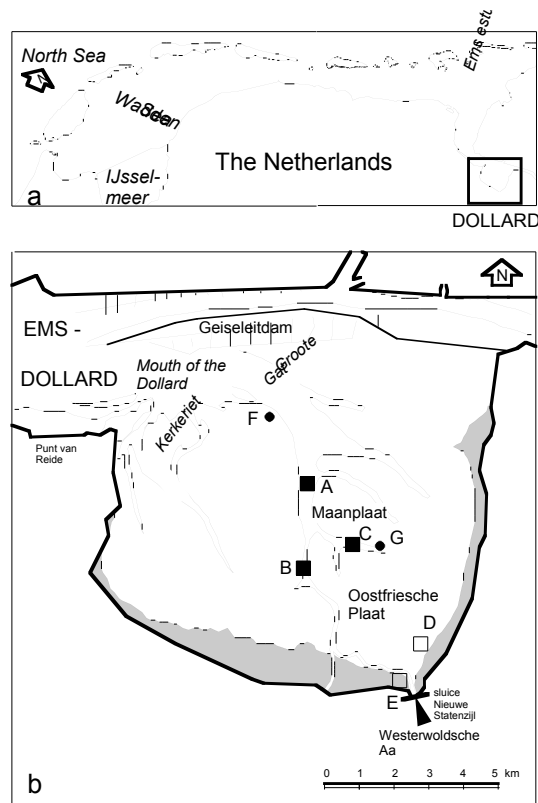
Fig. A. *Study area, with (a) position of the Ems-Dollard estuary in the Dutch Wadden Sea and (b) the Dollard with the sample locations (A, B, C), the locations of the buckets (D, E) and the tidal gauges 'Dollard-Noord' (F) and 'Maanplaat-Zuid'(G). Shaded area: salt marshes.*

MATERIAL AND METHODS

Study area

The Dollard is a brackish intertidal area in the Ems estuary (eastern Dutch Wadden Sea) that forms the transition between the river Ems and the North Sea (Fig. 1a). It has an area of about 92 km^2 of which 85% emerges at low tide. Mean depth is 1.2 m, and the mean tidal volume about 120 .10^6 m^3 (De Jonge 1988). This tidal basin is bounded on the north by the Geiseleitdam (constructed in 1961), on the north-west by the Punt van Reide and on the other sides by dikes, fringed with 9 km^2 of marshes (Fig. 1b). Mean low water is 171 cm below mean sea level (MSL), mean high water 128 cm above MSL. With a height of 1 m above MSL, the Geiseleitdam forms a partial separation between Dollard and Ems that allows some water exchange between the two systems, depending on the tide.

Freshwater input to the area originates from the river Ems (annual mean 100 m³ s^{-1}) and from the Westerwoldsche Aa (annual mean 12.5 m³ s^{-1}). The latter is discharged on ebbing tides through the sluice complex of Nieuwe Statenzijl. A decreasing NW-SE salinity gradient exists from the mouth of the Dollard to Nieuwe Statenzijl (De Jonge 1988). Mean salinity in the Dollard ranges from about S=6 in winter to S=25 in summer. Two main channels, Groote Gat and Kerkeriet, guide the flood water into the Dollard. The muddy tidal flats are intersected with small gullies that drain water to the main channels during ebb. The tidal cycle has a period of 12h25', a range of 3 - 3.5 m, and a mean excursion in the Dollard of 12 km (BOEDE 1983). There is a mean diel inequality in the tidal range of almost 0.3 m (0.2 m at HW and 0.08 m at LW; Dienst Getijdewateren 1993).

Sample locations

Based on extensive knowledge of the hydrology, morphology, and physical structure of the Dollard (Stratingh and Venema 1855, BOEDE 1983, Duits-Nederlandse Eemscommissie 1990, De Jonge 1988, 1991), three stations (A, B and C) were selected along the salinity gradient (Fig.1b, Fig. 2). Location A is situated 2500 - 2750 m more seaward than B and C, respectively. Sample location A (depth about 5 m below MSL) is the deepest point on a cross-section of the Groote Gat. The channel has a north-south orientation and a mean tidal volume of 28 .10^6 m^3, which is about 22% of the volume in the mouth of the Dollard (Duits-Nederlandse Eemscommissie 1990). Location B is situated in the channel Schanskerdiep, the extension of the main channel that ends at the sluice of Nieuwe Statenzijl. Location C was selected in a small channel, Oostfriesche Gat or Zurentjeriet (Stratingh and Venema 1855), that branches off

to the east between A and B and supplies the tidal flats Maanplaat and Oost-friesche Plaat with flood water.

Freshwater, discharged during the second part of the ebb at Nieuwe Statenzijl, flows seaward through the Schanskerdiep along locations B and A. Part of this ebb water is pushed back by the next flood into Oostfriesche Gat. Both B and C have depths of 3 m below MSL, but differ in the extent to which they are influenced by freshwater.

Accumulation is defined as an increase in numbers of larvae over a period of time, as the result of net landward transport. Comparison of the larval transport with water transport at location A with those at locations B and C, will demonstrate if the larval transport at one point is conservative with water transport or if there is preferential transport, or accumulation, of larvae in one of the locations. Comparison of larval transport to B and C is expected to yield information on the role of discharged freshwater in the process of larval accumulation in the Dollard.
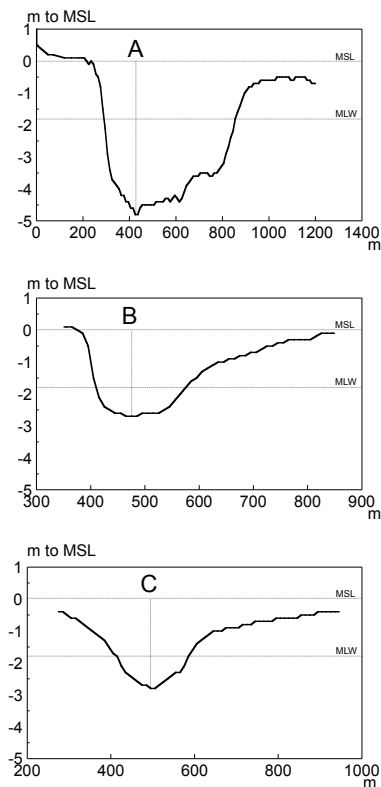
Fig. B. *Cross-sections of the sample locations (A', B', C'), with mean low water (MLW) and mean sea level (MSL) indicated.*

Physical variables

Five sampling dates were selected to cover the larval immigration period (April-May), and reflected a compromise between available ships and other investigations in the same period. Ships were moored at each of the cross-sections within 5 m of the actual sample locations (A, B, C) using a Hi-Fix positioning system (Decca, Racal, England).

At all stations, the following physical variables were measured every 20 min simultaneously with plankton sampling: current velocity and direction (calibrated Ott-meters), temperature and salinity (WTW-conductivity meter), turbidity (Partech instrument, calibrated at 2000 mg dm^{-3}). The profile measurements started at the bottom, and were taken consecutively at least at four depths: 0.2 and 0.7 m below the water surface (near-surface) and 0.3 and 0.8 m above the channel bed (near-bottom). With increasing water depths intermediate points were added, to a maximum of 8 sampling depths. Each measurement lasted 30 s at high current velocities to 60 s at low current velocities. See De Jonge (1991) for an extensive description of the standard hydrographical methods used by Rijkswaterstaat.

At location B, on 14 April no temperature and salinity measurements were taken due to failure of the WTW-meter. The beginning of the flood period was missed at station B on 3 May and at A on 19 May. To calibrate the Partech-readings, water samples were taken at regular intervals during the tidal cycle to determine the concentrations of suspended matter. Wind speed and direction were monitored on board the ship every 30 min by means of anemometer and compass, respectively. The times and volumes of freshwater discharge at Nieuwe Statenzijl were provided by the Water Board Dollardzijlvest.

Plankton sampling

Plankton samples were taken every 20 min from the anchored ships at the three locations simultaneously, during a complete tidal cycle starting after low water (LW) slack. The 500 μm mesh standard (conical) plankton net (Sournia 1978) had a 0.5-m^2 opening and a length of 4.5 m. A removable 1-dm^3 jar collected the filtrate. A flow-meter (General Oceanics 2030R) in the net opening measured the volume of filtered water. The net was attached by 3 bridles to a winch cable 0.9 m above a 100-kg weight that kept the cable in a vertical position even at high current velocities. The net was lowered and lifted several times at a constant slow speed between surface and bottom for 1 to 3 min, depending on water depth and current velocities. At mean profile current velocities below 30 cm s^{-1} fishing was impossible because the net dropped to a vertical position. Therefore, no samples could be taken for 1 to 2 h around slack waters. The samples were fixed in a 3.8% neutralised phosphate-buffered formaldehyde

solution for subsequent analysis in the laboratory.

All larvae caught, with total lengths of 8 to10 mm, were in the process of metamorphosis, and the development stages IVb and IVb' (Ryland 1966) were the most abundant ones in the plankton samples. In each sample, a larval concentration (n m^{-3}) was calculated by dividing the number of flounder by the filtered volume, assuming 100% net efficiency and no mesh selection. Sample volumes ranged between 6.8 and 116.0 m^3 (mean 35 m^3, standard deviation 13.6).

Trap sampling

In addition to planktonic samples, semi-quantitative data on settling flounder larvae were obtained at locations D and E (**fig. a**b) on the tidal flats by trap sampling on 14 and 21 April and 16 May. Given the general water circulation pattern (De Jonge 1991), location D is considered as hydrographically linked to, and indicative of the larval concentrations at location C, and location E as linked to location B. At each location ten traps, consisting of 5-dm^3 buckets (opening diameter 0.17 m), were dug in the sediment with the rims at the same level as the surface and filled with water to resist the upward pressure by the sediment. They were placed at mutual distances of around 0.5 m during LW and collected after one tidal cycle. The sieved contents of the buckets were fixed in a 3.8% formaldehyde solution, the number of flounder were counted in the laboratory, and the mean number per trap was calculated. Sampling failed at E on 14 April.

Data treatment

The sample locations are indicated by capitals (A, B, C), whereas references to the entire cross-section will be indicated by capitals with apostrophes (A', B', C'). Time is expressed as hours relative to the moment of high water (HW; turn of the tide) as measured at the locations during sampling. Within the tidal cycle, six 2-h periods were arbitrarily created and treated as different tidal phases, whereas 'tide' refers to flood/ebb.

Measurements of water velocity at the sample locations were orthogonised and integrated over depth by means of the VIMET computer programme (Rijkswaterstaat 1980). Extrapolation from the point measurements at the actual sampling station to the entire cross-section of the channel was based on previously established regression formulas for the three cross-sections by means of multiple ships for flood and ebb separately (**table a**). The depth-averaged velocity of the cross-section of the channel (m s^{-1}) was multiplied by the area of the wet profile (m^2) at each point in time to obtain the water flow (m^3 s^{-1}). Information on water level was obtained from the tidal gauges "Dollard-Noord" and "Maanplaat-Zuid" (Fig. 1b). The water flow estimates for every 20-min

period (m³ s^{-1}) were integrated over time to produce the water transport during flood and ebb (m^3). These values do not necessarily balance each other. There is usually a clockwise residual water circulation with flood surplus in the Groote Gat and ebb surplus in the Kerkeriet, but this circulation may be modified or even reversed by wind influence (De Jonge 1991).

A water budget was calculated for each sampling date. Part of the water transport at A' continues and will be encountered at B' and C'. The rest of the water fills the channel to the HW level, and at some point starts to spill over the tidal flats. The volume of water needed to fill the channel section between A' and B'/C' was estimated by the product of the tidal difference in the mean area of the wet profile of A' and B'+C', and the mean length of the section between A' and B'/C'. The lateral boundaries of the channel were set artificially by the computer programme.

Larval fluxes (n s^{-1}) were calculated by multiplying concentrations with the water flow during each 20 min period, implicitly assuming homogeneous distributions of larvae across the channel. Integration over time resulted in the landward (flood-) or seaward (ebb-) transport of flounder. The difference between flood- and ebb-transport provides the net transport (n) of larvae per tidal cycle. Transport during the hours of slack tide was assumed to be negligible and therefore data were not interpolated over these periods.

Table A. *Regression formulas used to calculate water flow during flood and ebb, by sample location. Y: depth-averaged velocity (cm s^{-1}) of the channel profile; X: depth-averaged velocity (cm s^{-1}) of the sampling point.*

Location	Tide	Regression formula	R^2	Date established
A	Flood	Y = 0.840*X + 0.00526	0.973	December 1992
	Ebb	Y = 0.741*X + 0.00064	0.988	December 1992
B	Flood	Y = 1.097*X + 2.411	0.981	September 1995
	Ebb	Y = 1.277*X - 5.641	0.968	September 1995
C	Flood	Y = 1.291*X - 0.816	0.979	September 1995
	Ebb	Y = 1.322*X - 2.535	0.947	September 1995

Statistical analyses

The missing salinity data of 14 April (location B) were interpolated by using a multiple regression derived from the salinity measurements on the other sampling dates at the three locations:

$$salinity_B = 0.132 + 0.733*salinity_C + 0.265*salinity_A + \varepsilon$$

$$(n=66, R^2_{Adj.} = 99.2\%).$$

Multifactor ANOVA was applied to salinity and ln-transformed suspended matter data and a multifactor ANCOVA to the ln-transformed (concentrations + 1) to

compare larval concentrations among locations during the tidal cycle. The latter was limited to the sampling on 14 and 21 April and 3 May; samples taken on 16 and 19 May were excluded from the ANCOVA because concentrations were too low.

RESULTS

Physical variables

Mean water temperatures increased from 6.9 °C to 14.6 °C over the sampling period (**table b**). The differences between locations were less than 0.8 °C. Variations within the tidal cycle and among locations were so small that the temperature is not expected to play a significant role in the accumulation process.

Mean salinity increased during the sampling period from S=5.7 to S=11.8. There were significant differences among sampling dates, locations and flood/ebb (**table c**). The interaction of location and tide was significant. Location A had significantly higher mean salinities than location B and C during flood and ebb on all sampling dates. A SNK-multiple range test indicated that mean salinities at B and C did not differ significantly during flood, but were significantly lower at B than at C during ebb.

Mean depth-averaged values of suspended matter varied from 200 to 800 mg dm^{-3} across the sampling dates, with maxima of up to 1500 mg dm^{-3} on 14 April (**table b**). There were significant differences in suspended matter concentrations among sampling dates and locations (**table c**). Suspended matter was higher on the last two sampling dates at location B than at A and C, which had similar concentration patterns. The interaction of location and tide indicated that suspended matter was significantly higher during flood than ebb at A and C, but the opposite at location B. Furthermore these tidal differences in suspended matter did not vary in entirely the same way at the three stations between the sampling dates.

Table B. Mean depth-averaged water temperature (°C), salinity (ppt) and suspended matter (mg dm^{-3}) by sampling date (all stations combined).

Date 1994	Temp.	s.d.	n	Salinity	s.d.	n	Susp. matter	s.d.	n
14 April	6.9	0.4	77	6.0	0.8	99[*)	769	316	117
21 April	9.0	0.8	119	5.7	1.7	118	196	89	118
03 May	11.6	0.4	113	10.4	1.8	113	325	172	113
16 May	14.6	0.4	120	11.8	2.3	120	350	201	119
19 May	14.1	0.2	120	11.1	2.2	120	229	146	119

[*)]incl. 21 estimated values of salinity.

Table C. *Multifactor ANOVA of (a) salinity (including slack water periods and estimated values for 14 April 1994) and (b) ln (suspended matter). F-ratios are based on the residual mean square error.*

(a)	SS	Df	F-ratio	P-value	Sign.
MAIN EFFECTS					
date	3687	4	328	0.00	***
location	209	2	37	0.00	***
tide	73	1	26	0.00	***
INTERACTIONS					
date*location	41	8	1.8	0.07	n.s.
date*tide	12	4	1.0	0.39	n.s.
location*tide	46	2	8.2	0.00	***
date*tide*location	36	8	1.6	0.12	n.s.
RESIDUAL	1518	540			
TOTAL (corrected)	5866	569			
(b)					
MAIN EFFECTS					
date	134.3	4	119.0	0.00	***
location	3.6	2	6.3	0.002	**
tide	1.2	1	4.3	0.04	*
INTERACTIONS					
date*location	5.7	8	2.5	0.01	*
date*tide	0.4	4	0.4	0.84	n.s.
location*tide	7.8	2	13.8	0.00	***
date*tide*location	4.7	8	2.1	0.03	*
RESIDUAL	157	556			
TOTAL (corrected)	317	585			

Water flow

Water budgets for the five sampling dates are shown in **fig. c**. There was considerable variation in water transport among sampling dates, which is related to variations in tide and wind conditions (**table d**). The exceptionally low values of flood transport at B' on 3 May and at A' on 19 May are considered unreliable because part of the cycle was missed in the measurements.

Table D. *Tide, water levels (m to MSL) and wind direction and speed (m s^{-1}), as well as the standard deviation (s.d.) and number of observations (n), by sampling date.*

Date 1994	Tide	Water level max.	Water level min.	Mean wind direction	Mean wind speed	s.d.	n
14 April	spring	1.83	-1.67	NW	6.9	2.2	26
21 April	neap	0.98	-1.95	SW	5.0	1.0	30
03 May	neap	0.85	-2.44	SE	12.3	3.4	27
16 May	in-between	1.53	-2.07	N	3.3	1.5	26
19 May	neap	1.37	-1.97	NE	5.5	2.2	27
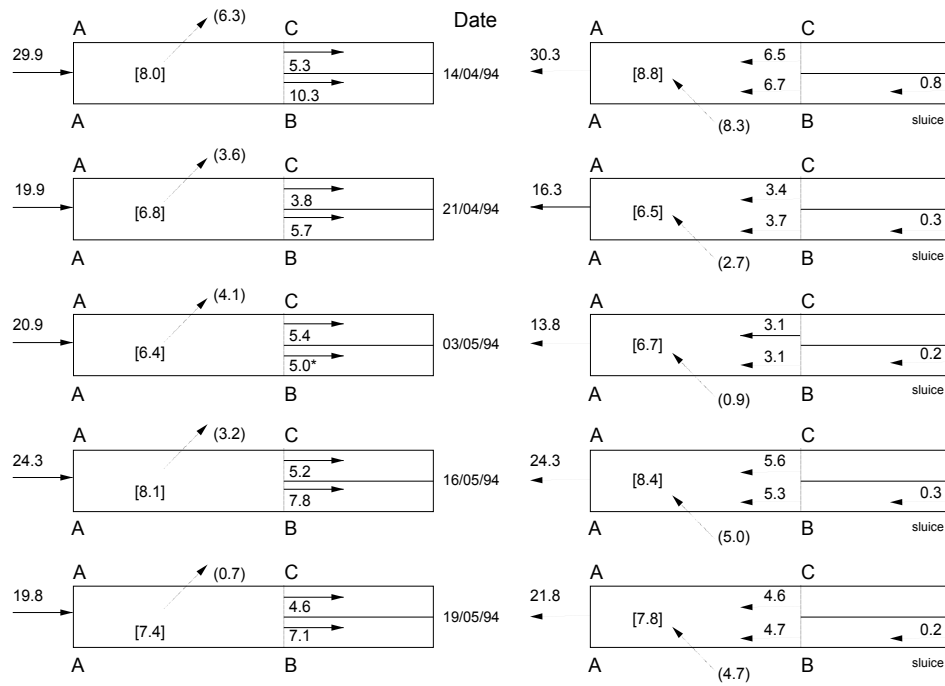
Fig. C. Water budget (in 10^6 m^3) of the cross-sections at locations A, B and C, during flood (left) and ebb (right). The channel sections are schematically represented by rectangles. The area outside of the rectangle represents the tidal flats. Continuous arrows and plain numbers indicate the measured water transport, dotted arrows are estimated values. Values between square brackets are calculated, whereas values between round brackets are estimated to balance the water budget. * Measurement slightly underestimated due to late start of the sampling.

The mean flood transports of cross-sections A', B' and C', excluding the estimates given above, were 24, 8, and 5 .10^6 m^3, respectively. The mean water flow of A' was slightly lower than the value of 28 .10^6 m^3 mentioned in the literature (Duits-Nederlandse Eemscommissie 1990). This is undoubtedly caused by the variability in water flow and the low number of tidal cycles measured.

The highest water level was recorded on 14 April during a spring tide in combination with a strong NW wind (**table d**) and corresponded with the date with the largest water flow. The lowest water level was observed on 3 May, caused by a combination of neap tide and a very strong southeasterly wind that blew water out of the area. These conditions resulted in a relatively large flood surplus of water at A' due to a below-average ebb transport.

Of the water transported through A' during flood, approximately half was used to fill the channel (30%) and to flood the flats (20%). The remaining 50%

continued through the channel and passed B' and C'. The flood water was divided over B' and C' approximately in proportion to the water storage capacity of both channels, on average 30% and 20%, respectively. The mean ebb transports at cross-sections A', B' and C' were 21, 5 and 5 .10^6 m^3, respectively. During ebb, part of the water flows seaward to the mouth of the Dollard over the tidal flats, and part of it is drained to the tidal channels. Of the water that was transported through A', on average 45% appears to have passed B' and C'. In contrast to the flood situation, B' and C' transported almost equal volumes of water during ebb. The volume of freshwater discharge amounted 4 to 12% of the water transport through B' during ebb.

The net water transport showed a substantial flood surplus at cross-section B' on all sampling dates. On most sampling dates, the net water transport of A' and C' showed a flood surplus of less than 10% of the estimated water transport. Because this is in the order of the assumed accuracy of the estimates, the difference is probably insignificant. Only the net water transport of 3 May showed a flood surplus on all three locations.

Table E. *Larval transport (10$^{6)}$ per tide (flood, ebb), and net transport (italic) by location.*

Location	Tide	14 April	21 April	03 May	16 May	19 May
A	Flood	117.0	67.8	239.7	2.9	2.9
	Ebb	172.5	121.4	92.4	2.1	1.1
	Net	*-55.5*	*-53.6*	*147.3*	*0.8*	*1.8*
B	Flood	68.7	55.2	100.2	3.6	2.3
	Ebb	40.8	13.7	31.6	1.3	0.4
	Net	*27.9*	*41.5*	*68.6*	*2.3*	*1.9*
C	Flood	34.8	13.5	55.0	1.2	0.4
	Ebb	83.2	17.9	11.5	0.5	0.9
	Net	*-48.4*	*-4.4*	*43.5*	*0.7*	*-0.5*

Larval transport

Larval transport varied considerably between sampling dates and locations (**table e**). B' was always characterised by a net flood transport of flounder larvae, in contrast with A' and C', where the net larval transport showed an ebb-surplus on 14 and 21 April (A', C') and 19 May (C'). The number of larvae transported to B' was 2 to 4 times higher than to C', whereas the water transport to B' was only 1.5 times higher than to C'.

If the water transport and larval transport at A' during flood or ebb are presented as 100%, the transports at B' and C' may be expressed relative to those at A' (**table f**). On 21 April and 19 May, almost all of the flood larval transport of A' was calculated to have passed B' and C' as well, and on 16 May the estimated larval transport of B' and C' combined was even higher than that of A'. This means that either the estimates are inaccurate, or that there is an

unknown source of larvae in the channel (e.g. larvae that were resting on the bottom), or that there is little, if any, loss of larvae to the tidal flats between locations A and B/C.

During ebb, generally less than 100% (except on 19 May) of the larval transport of A' had been measured at B'/C'. Part of the larvae at A' may therefore have returned from the tidal flats, or originated from the channel section between A' and B'/C'.

Table F. *Calculated water transport (W, %) and larval transport (L, %) at locations B and C and the rest (channel and tidal flats), relative to A (100%).*

Date	A	**Flood** B		C		rest		**Ebb** B		C		rest	
1994		W	L	W	L	W	L	W	L	W	L	W	L
14 April	100	34	59	18	30	48	11	22	23	22	48	57	28
21 April	100	29	80	19	20	53	0	23	11	21	15	56	74
03 May	100	*)24	*)42	26	23	50	35	23	34	23	12	54	54
16 May	100	32	124	21	41	13	-65	22	62	23	24	55	14
19 May	*)100	36	79	23	14	31	7	22	36	21	82	57	-4

*) value not reliable due to late start of the measurements

Larval fluxes and concentrations

Larval transport is the integration over time of larval fluxes, which are the product of water flow and larval concentrations at each sampling time (**fig. d**). The larval fluxes show a highly variable pattern during the tidal cycle, which is to a lesser extent caused by the variability in water flow than in larval concentrations. During a period of 1 to 2 hr around HW slack, no estimates of larval transport were available due to the limitations of sampling. The missed larval transport at the end of the flood comprises 15 to 20% of the total flood water transport, whereas the larval transport that was missed at the beginning of the ebb is 10 to 25% of the total ebb water transport. However, because the larval concentrations during these periods are unknown, the larval transport that is missed cannot reliably be estimated. Because the water transport varied relatively little across sampling dates, the larval concentrations will be considered in more detail.

fig. e compares the results of the simultaneous measurements of larval concentrations at the three locations and some physical variables on the first three sampling dates. One exceptionally high larval concentration of 920 m^{-3} was observed at location B on 21 April (1h40' M.E.T.) (**fig. e**). Mean current velocity was higher during ebb than during flood at all three locations.
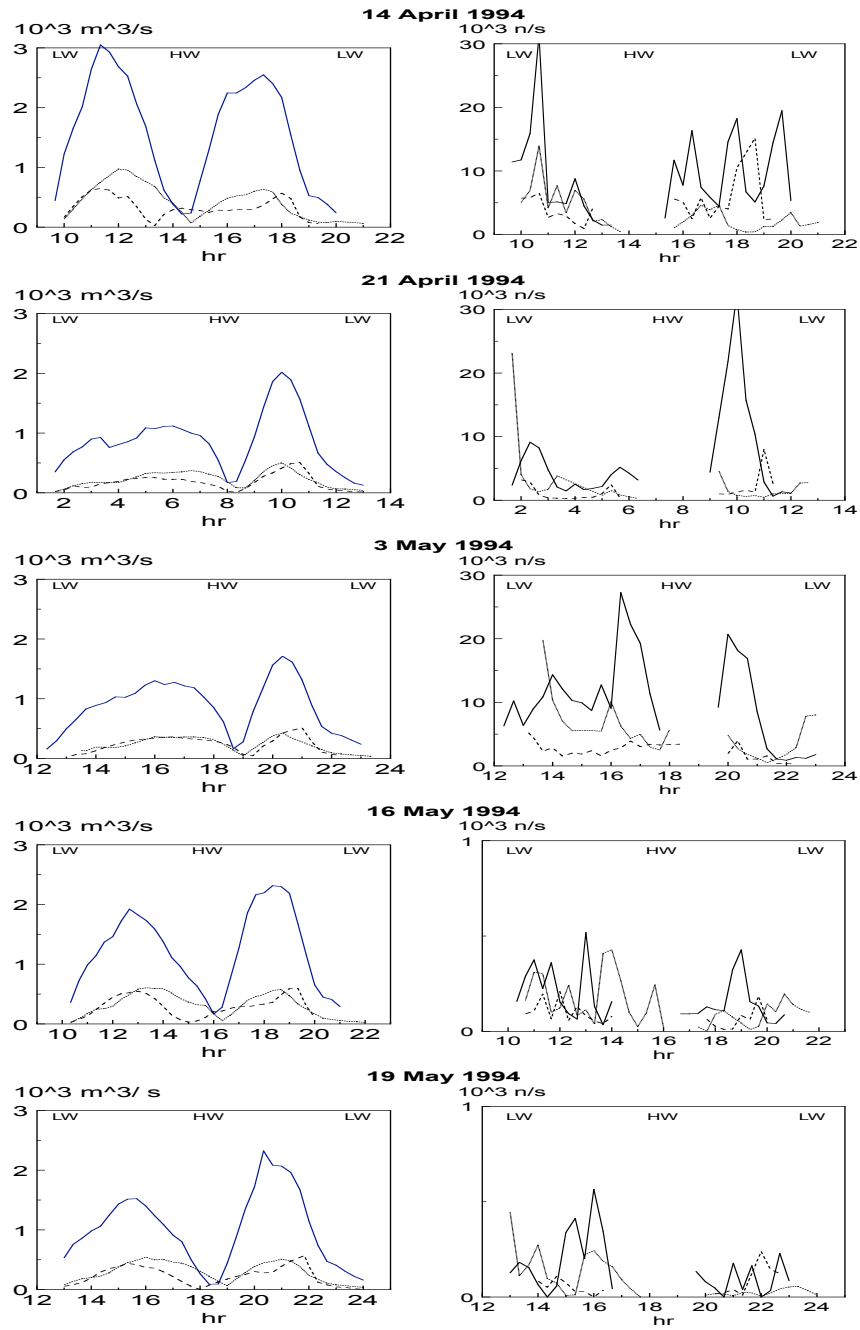
Fig. D. Water flow (left panes, in 10^3 m^3 s^{-1}) and larval flux (right panes, in 10^3 n s^{-1}) for the three locations (A —, B...., C---) by sampling date. The areas below the curves represent the time-integrated transports.

The turn of the tide at HW occurred 20 min later at B than A, whereas that moment varied at C relative to A. Timing of maximal current velocity varied during flood, whereas during ebb highest velocities were observed simultaneously at location A and B and with a time lag of 40 min at C. The peak in ebb current velocity at C coincided with a sharp increase in turbidity, as well as a peak in larval concentrations on the first two dates. These peaks at C were associated with the moment that the flats emerged and the last water was drained to the channel.

At the beginning of the flood, the initially high concentrations of larvae rapidly dropped to lower levels, first at location A and, with a time lag varying from 20 to 100 min, also at locations C and B. After the HW slack period, a brief increase in concentration levels was noted at all three locations, followed by a dip and a sudden and steep rise at the end of the ebb period. The time lag observed during flood was mirrored during ebb, especially on 3 May.

The passage of freshwater that was discharged at Nieuwe Statenzijl during ebb is clearly noticeable at location B by the sudden drop in salinity, and a steep increase in larval concentrations at the end of the ebb. At location A, the effect of the freshwater discharge could hardly be traced.

A Multifactor ANCOVA model of ln-transformed larval concentrations indicated that the factors sampling date, tidal phase and sampling location, as well as the first order interactions, contributed most to the variance (**table g**). Salinity was the most significant covariate in the model, although mean velocity and turbidity were also significant covariates. The model explained 73% of the variance in ln-transformed larval concentrations. However, the multicollinearity of 13% indicated significant linear correlations among the covariates. The tidal pattern in larval concentration differed among the three locations. The significance of the interaction between location and tidal phase was caused by the relatively high concentrations at A during the first phase of the ebb. Concentrations were significantly higher at A than at B and C, mainly around HW-slack. The concentrations of larvae were significantly higher at B than at C during the flood and the beginning of the ebb (**table h**).

Trap sampling

More flounder larvae were trapped at station E than D (**table i**). The highest numbers (7.5 and 80 per trap at D and E, respectively) were obtained on 21 April. Up to 200 larvae were caught in one 5-dm^3 bucket. The majority of the larvae were stage V (66%), at the end or completion of the metamorphosis.
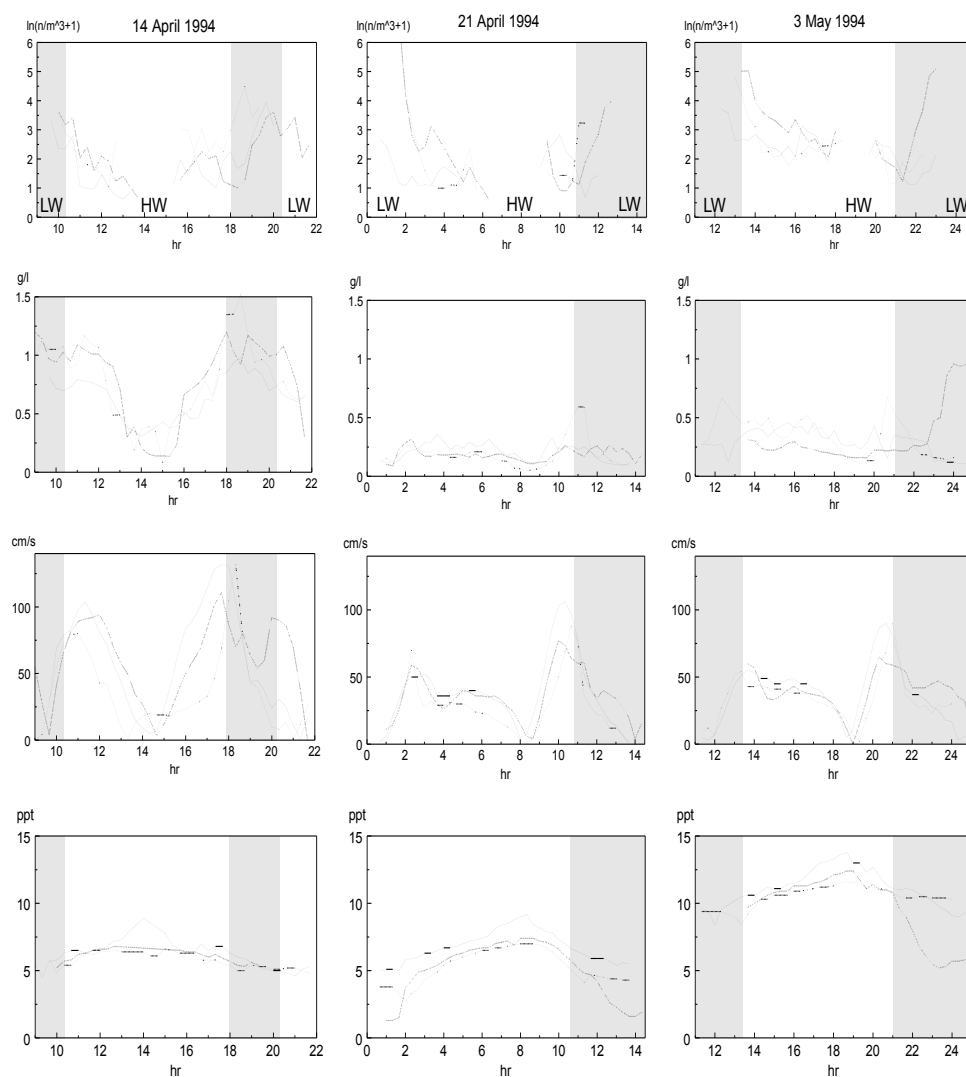
Fig. E. *Results of biological and physical data for the three locations (A — , B..., C---). From top to bottom: Ln(concentrations of flounder larvae+1) (n m^{-3}), dept-averaged concentration of suspended matter (g dm^{-3}), depth-averaged current velocity (cm s^{-1}), and depth-averaged salinity (ppt) during three sampling dates in 1994 (14 April, 21 April, 3 May). Shaded areas indicate periods of freshwater discharge at Nieuwe Statenzijl.*

Table G. ANCOVA of ln-transformed (larval concentrations + 1), using Type III - Sums of Squares. F-ratios are based on the residual mean square error. The interaction of sampling date*location and the 2nd order interaction had to be excluded. (Data for 16 and 19 May were excluded.)

	SS	Df	F-ratio	P-value	Sign
COVARIATES					
salinity	23.75	1	71.36	0.000	***
mean velocity	2.00	1	5.99	0.016	*
turbidity	1.29	1	3.88	0.051	~
area of cross-section	0.15	1	0.46	0.500	n.s.
MAIN EFFECTS					
date	33.15	2	49.82	0.000	***
tidal phase	3.70	5	2.22	0.055	~
location	2.50	2	3.75	0.026	*
INTERACTIONS					
date*tidal phase	23.27	10	6.99	0.000	***
tidal phase*location	22.15	10	6.66	0.000	***
Multicollinearity	24.87				
RESIDUAL	51.25	154			
TOTAL (corrected)	188.08	187			

Table H. ANCOVA of ln-transformed (larval concentrations + 1), using Type III - Sums of Squares. F-ratios are based on the residual mean square error. The interactions of sampling date*tidal phase, sample date*location and the 2nd order interaction had to be excluded. (Data for location A and 16 and 19 May were excluded.)

	SS	Df	F-ratio	P-value	Sign.
COVARIATES					
salinity	17.60	1	45.40	0.000	***
mean velocity	4.50	1	11.62	0.001	**
turbidity	2.05	1	5.28	0.024	*
area of cross-section	0.04	1	0.11	0.743	n.s.
MAIN EFFECTS					
date	23.91	2	30.83	0.000	***
tidal phase	6.30	5	3.25	0.010	**
location	2.30	1	5.92	0.017	*
INTERACTIONS					
tidal phase*location	9.89	5	5.10	0.000	***
Multicollinearity	29.29				
RESIDUAL	35.29	91			
TOTAL (corrected)	131.17	108			

Table I. Mean and standard deviation (s.d.) of the number of settling flounder per trap at locations D (Oostfriesche Plaat) and E (Nieuwe Statenzijl). n.a.= not available.

Date	Mean (D)	s.d.	Mean (E)	s.d.
14 April 1994	0.5	0.8	*n.a.*	*n.a.*
21 April 1994	7.5	5.0	80.0	66.7
16 May 1994	0	0	58.0	34.2

DISCUSSION

Temperature differences between locations and within the tidal cycle were so small that this factor is not expected to play a significant role in the accumulation process of flounder larvae. The sampling period covered the transition from high winter discharges of freshwater to a low summer regime, which was reflected in a rapid increase in salinity during the sampling period. Differences in mean salinity among locations were 0.6 to 1.8. These may seem small and insignificant but may be ecologically meaningful. Standard deviations in salinities were relatively large, especially in the Schanskerdiep, indicating a weak vertical stratification during some tidal phases of the ebb. By the end of the ebb, salinity was sometimes 4.5 lower at location B than at the other stations, which was undoubtedly related to the freshwater discharges at Nieuwe Statenzijl (4 to 12% of the ebb transport at B'). Because fish are more buoyant in high-salinity than in freshwater, fish near the bottom would tend to rise during flood and sink during ebb (Miller 1988). In the Dollard, salinity was lowest at the end of the ebb. Therefore, the concentrations in the channel would be expected to decrease during those periods. Instead, a steep rise in larval concentrations was observed, which was most pronounced in the Schanskerdiep. Although the Ems-Dollard is generally considered to be a well-mixed estuary (De Jonge 1988), it may locally and temporarily be only partially mixed. The rapid decrease in salinity at the end of ebb indicates the passage of a front. Such a front of freshwater, in particular in the small channel of the Schanskerdiep, may lead to upward advection of water at mid-depth (Bowden 1980). However, it is unknown if this advection would be strong enough to mix fish larvae.

The water storage area of the tidal flats supplied by A' was estimated at 3 km^2. The calculated mean flood transport through the Groote Gat would yield mean water depths of 1.2 m, which agrees with the mean water depth observed in the Dollard and indicates that the calculated water budget was not unrealistic. The calculated larval transports have an inherent inaccuracy due to the sometimes patchy distribution of the larvae. De Wolf (1989) indicates that patchiness may lead to an inaccuracy in estimates of mean concentrations of ±20%. Furthermore, larval concentrations across the cross-section of the channel may be heterogeneous (Rijnsdorp *et al.* 1985). Weinstein *et al.* (1980) found indications that larval catches were highest in the flood branch of the channel during flood, and highest in the ebb branch during ebb. Therefore, the larval concentrations at the sample location in the Groote Gat (in the ebb branch of the gully) may have been underestimated during flood and overestimated during ebb, which may account for part of the ebb surpluses in larval transport at some of the sampling dates and may also explain some of the gains in larval transport between Groote Gat and the two peripheral channels during flood.

Because of the smaller dimensions of the channels, sampling the deepest point of the Schanskerdiep and the Oostfriesche Gat is believed to be representative of the entire cross-section. The missing periods around slack waters make it difficult to compare water transport with larval transport. The current velocity generally dropped at an earlier stage of the tide in the Oostfriesche Gat than at the other locations, which complicated the comparison between them. Nevertheless, the data do indicate considerable differences between the estimated transports of water and larvae, and between the three channels. The differences in concentrations of flounder larvae between the stations B and C pointed to the highest accumulation in the channel that is directly connected to the sluice in Nieuwe Statenzijl. This study must be considered as a first attempt to make such a comparison of larval transport and water circulation in the Dollard.

Passive transport by physical processes in combination with tidal asymmetry may lead to accumulation of particles in an estuary (Postma 1961). However, the transport of flounder larvae in the nursery is not entirely passive. During flood the highest larval concentrations were found in the surface layer (Chapter 4, Bos *et al.* 1995), and this phenomenon could not be explained by physical processes only. During ebb, the vertical distribution of the larvae was more variable, suggesting a relatively stronger influence of physical forces (Chapters 4 and 5).

Generally, the highest concentrations were observed during the time around LW slack when the water has withdrawn from the tidal flats in the channels. This pattern was more pronounced in the peripheral channels compared to the main channel. This may be related to the larger proportion of channel water to water from the tidal flats in the latter (Jacobs 1968). Processes in the channels around low water slack seem to be crucial in the transport of flounder larvae. Unfortunately, the method of sampling used did not allow this phase to be studied in more detail.

The sharp drop in larval concentrations after the beginning of flood might be associated with the moment of inundation of the tidal flats. However, the actual timing of this event is difficult to define. During ebb the sharp peak in mean velocity, turbidity and larval concentrations in the Oostfriesche Gat coincided with the moment that the last water drained from the tidal flats into the tidal channel. Apparently this causes turbulent mixing in the channel, which leads to high concentrations of both suspended matter and floundering larvae.

Because the swimming capacity of flounder larvae is limited, the water circulation in the nursery will to a large extent determine the larval transport. There was an accumulation of flounder larvae towards the fringes of the Dollard compared to the main channel, which coincides with a decrease in mean salinity. The preferential larval transport to the Schanskerdiep was partly caused by the

water circulation which led to a flood surplus on all sampling dates. However, the water circulation could not entirely explain the stronger accumulation of larvae in this area. The most striking difference between the two peripheral channels was the sharp drop in salinities in the Schanskerdiep during ebb and the significantly higher larval concentrations at the beginning of flood, even when the outlier of 920 larvae m^{-3} was omitted. The negative correlation between salinity and larval concentrations was strong and consistent. However, both salinity and larval concentrations are related to the tidal cycle and the correlation is not necessarily a causal one.

Nevertheless, the data support the view that salinity in general and the discharge of freshwater in particular affect larval transport and may be held responsible for the relatively strong accumulation of flounder larvae in the channel Schanskerdiep. Independent observations of flounder larvae in traps also indicated higher numbers of larvae at the end of this channel near Nieuwe Statenzijl, and corroborated the observations that were made during the pilot study in 1992.

Another explanation for the accumulation in the vicinity of the sluice of Nieuwe Statenzijl might be that the sluice acts as a barrier that prevents the larvae from continuing their migration to fresh water. During the discharges of freshwater, currents are most likely to be too strong for the larvae. To pass the barrier their only option would be to let themselves lock through the sluice with ships that move to and from the Westerwoldsche Aa. However, there are usually few ship passages in April and May (**table j**), and the volume of water that is exchanged in this way is relatively small. Furthermore, fewer ships go to the river than to the Dollard. Therefore, the sluice of Nieuwe Statenzijl may form an effective barrier for flounder larvae.

Table J. *Number of in-going (to the river Westerwoldsche Aa) and out-going (to the Dollard) passages of ship through the lock of Nieuwe Statenzijl in April and May, 1992-1995.*

Year	Direction	1-15 April	16-30 April	1-15 May	16-31 May	Total
1992	in	3	0	8	4	15
	out	5	7	12	6	30
1993	in	3	2	5	10	20
	out	4	5	11	8	28
1994	in	6	15	23	19	63
	out	7	14	11	18	50
1995	in	3	4	2	2	11
	out	7	8	8	31	54

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Selective tidal stream transport of flounder larvae (*Platichthys flesus* L.) in the Dollard (Ems estuary)

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ABSTRACT

The vertical distribution of flounder larvae (*Platichthys flesus* L.) was investigated in the Dollard (Ems estuary, Wadden Sea) in relation to tidal phase and physical variables in order to address the question whether larval migration into the nursery is accomplished by passive transport, or is influenced by active (swimming) behaviour. Larval concentrations were measured twice per hour simultaneously at three water depths from low water (LW) slack to LW slack. Physical variables were measured at the same time.

Maximum concentrations of flounder larvae were 433 m^{-3} in 1994 and 40 m^{-3} in 1995. There were tidal variations in larval concentrations in all three water layers, and the vertical distribution varied as well. The highest larval concentrations were usually found near the surface during flood, and the lowest in the midwater layer during the ebb. In contrast to larval concentrations, turbidity was always highest near the bottom. The observation that larval vertical distributions deviate from those of suspended matter and vary in a different way led to the rejection of an entirely passive transport mechanism.

The vertical distribution of larvae during flood supported the selective tidal stream transport hypothesis, but the relatively high number of flounder larvae in the surface layer during ebb was in contradiction with it. The high surface concentrations during ebb may have been caused by different origins of the water layers, and thus larvae, or by an inability of the metamorphosing larvae to resist the strong ebb currents. The data suggest that the transport process inside the nursery may favour retention.

Keywords: flounder, *Platichthys flesus*, selective tidal stream transport, nursery, retention, Ems estuary

INTRODUCTION

A nursery may be described as a restricted area where juveniles of a (fish) species spend a limited period of their lifetime, during which they are spatially and temporally separated from older conspecifics (Bergman *et al.* 1988). Its function would be to provide conditions for growth and survival of the young individuals, which have been proven to be 'better' in an evolutionary sense than other areas. Coastal waters and estuaries act as nursery areas for several flatfish species (Zijlstra 1972, 1978). The spatial separation of adults and juveniles implies that larvae have to be transported from spawning areas to nursery grounds. This transport gradually evolves from a merely passive larval drift process in the open sea, through a process that may be more actively influenced by the larvae once they enter the estuarine areas, to the final process of settlement in the nursery area (Boehlert and Mundy 1988).

Mechanical transport, in combination with asymmetrical (flood dominated) tides, causes accumulation of suspended matter in estuaries (Postma 1961). The same processes might lead to estuarine larval retention without requiring active swimming (De Wolf 1973). Larvae are subject to advective tidal transport, they sink to the bottom in periods of low current velocity, and are redispersed in the water column by turbulent mixing when current velocities increase again. In a (partially) mixed estuary, the physical processes of longitudinal and lateral diffusion are relatively weak compared to longitudinal and lateral advection. Vertical diffusion, however, should not be neglected given the smaller scale of the vertical axis (Fortier and Leggett 1982).

In addition to the processes described above, larvae may actively influence their transport by swimming. A combination of passive transport mechanisms and active dispersal may be expected to result in more effective inshore transport of fish larvae into nursery areas (Norcross and Shaw 1984). One particular hypothesis formulated by Creutzberg (1961) relates to the selective tidal stream transport (STST). Larvae are supposed to ascend actively in the water column during flood and return to the bottom when the tide turns, thus preventing being flushed back during ebb. Swimming velocities of larvae, in the order of one to several cm s^{-1}, are small compared to current velocities often observed in estuaries. Because steep velocity gradients occur in the vertical plane, with virtually zero values near the bottom, the most effective migrations in terms of maximising distance displaced while minimising swimming energy will be those in the vertical direction (Miller 1988).

Estuarine transport will be most effective if the vertical movements are in phase with the tidal cycle, which requires cues for timing (Hill 1995). A combination of physical variables characterised by directional gradients, for example water temperature, salinity, turbidity and hydrostatic pressure, could

act as synchronising cues in inducing circatidal rhythms during these vertical migrations (Boehlert and Mundy 1988). For example, larval plaice (*Pleuronectes platessa* L.) has been shown to exhibit this type of transport (Creutzberg *et al.* 1978, Rijnsdorp *et al.* 1985).

Flounders (*Platichthys flesus* L.) spawn offshore in the southern North Sea. Highest concentrations of eggs have been observed in February west and northwest of the Dutch west coast, in the eastern English Channel and the area northwest of Helgoland (Van der Land 1991). The larvae drift to the coastal nurseries where they complete metamorphosis and settle in intertidal areas (Redeke 1908, Berghahn 1983, Van der Veer *et al.* 1991). The nursery areas of flounder extend from the brackish water regions of estuaries into freshwater habitats of rivers (Redeke 1908, Zijlstra 1978, Kerstan 1991). In the River Elbe, metamorphosing larvae have been found far upstream and also in tributary rivers in concentrations of 18 - 55 larvae per 100 m^3 (Möller and Dieckwisch 1991). How the upstream migration was accomplished by the larvae is not known (Campos *et al.* 1994). Because plaice and flounder are closely related, the transport mechanisms might be similar. However, flounder enter the nursery areas at a smaller size than plaice, and may therefore be less capable of manipulating their transport. Larval swimming speed (about 1 cm s^{-1}) is small compared to the tidal currents (1-2 m s^{-1}).

The present study addresses the transport mechanism of flounder larvae within the nursery prior to settlement, at the transition stage from a pelagic to a benthic lifestyle. The objective was to test two hypotheses about larval transport mechanisms by determining larval concentrations at three depths simultaneously during the tidal cycle. In the case of entirely passive transport, flounder vertical distributions would be expected to show similarities with suspended matter. Assuming negative buoyancy of the larvae, the vertical gradient in concentrations would be expected to be positive with increasing depth or at best be homogeneous under all conditions of turbulent vertical mixing. If the 'passive transport hypothesis' can be rejected, the 'STST hypothesis' that most larvae are expected in the water layers with highest current velocity during flood and in those with lowest current velocity during ebb is explored.

MATERIALS AND METHODS

Study area

The length of the Ems estuary from the inlet between the islands Rottumeroog and Borkum to the town of Emden is 50 km (**fig. a**a). The Dollard represents a rather isolated shallow tidal basin of the Ems estuary with a volume of about

120 10^6 m^3 and an area of about 92 km^2, of which 85% emerges at low tide (De Jonge 1988). It is bounded on the north by the Geiseleitdam, on the north-west by the Punt van Reide and on the other sides by dikes, fringed with 9 km^2 of marshes (**fig. a**b). Mean low water (LW) is 171 cm below mean sea level (MSL), and mean high water (HW) is 128 cm above MSL. With a height of 1 m above MSL, the Geiseleitdam forms a partial separation between Dollard and Ems that allows some water exchange between the two systems. The flooding water is guided into the Dollard by two main channels, Groote Gat and Kerkeriet. The muddy tidal flats are intersected with small gullies that drain water to the main channels during ebb. The tide has a period of 12h25', a tidal range of 3 - 3.5 m, and a mean tidal excursion in the Dollard of 12 km (De Jonge 1988). Location A (**fig. a**c), in the centre of the settlement area, and the deepest point (about 5 m below MSL) in the selected cross-section (53°17'N, 07°09'E) in the Groote Gat was selected for this study. The channel has a north-south orientation and a mean tidal volume of 28 10^6 m^3, which is about 22% of the volume in the mouth of the Dollard.

Data collection

Probing during flood tide in the Groote Gat showed the first presence of flounder larvae in the Dollard on 29 March in 1994 and 16 March in 1995, and these probes were followed by formal sampling programmes that continued until 25 May in 1994 and 10 May in 1995 (Table 1). Sampling from anchored ships typically continued during a full tidal cycle (13 hours) starting at LW slack. In 1994, two consecutive tidal cycles were sampled at three occasions. The plankton nets used (type Apstein, Hydro-Bios) had 500 μm mesh size, a diameter of 0.40 m, and a length of 1 m. The net was provided with a 0.2 m deep conus of synthetic material, with an opening diameter of 0.17 m. The sample was collected in a 1 litre removable jar attached to the end of the net. A flowmeter (General Oceanic R2030) mounted in the aperture enabled estimates of the volume of water filtered. This type of plankton net was chosen to allow sampling at different depths in shallow, turbid water during 20-30 minutes while maintaining high filtration efficiencies (Smith *et al.* 1968, Sournia 1978). Independent measurements of current velocities (see 'physical variables' section) allowed calculation of a filtration efficiency (F) for each sample (Smith *et al.* 1968): F = (volume of water filtered/volume of water encountered) *100 (**table a**). Mean F was 100% in 1994 and 88% in 1995. Taking the high efficiencies into account, as well as the high turbidities encountered in the Dollard and current velocities up to 1.6 m s^{-1}, active net avoidance by the larvae (8-10 mm total length) was assumed unlikely (Van der Veer 1985).
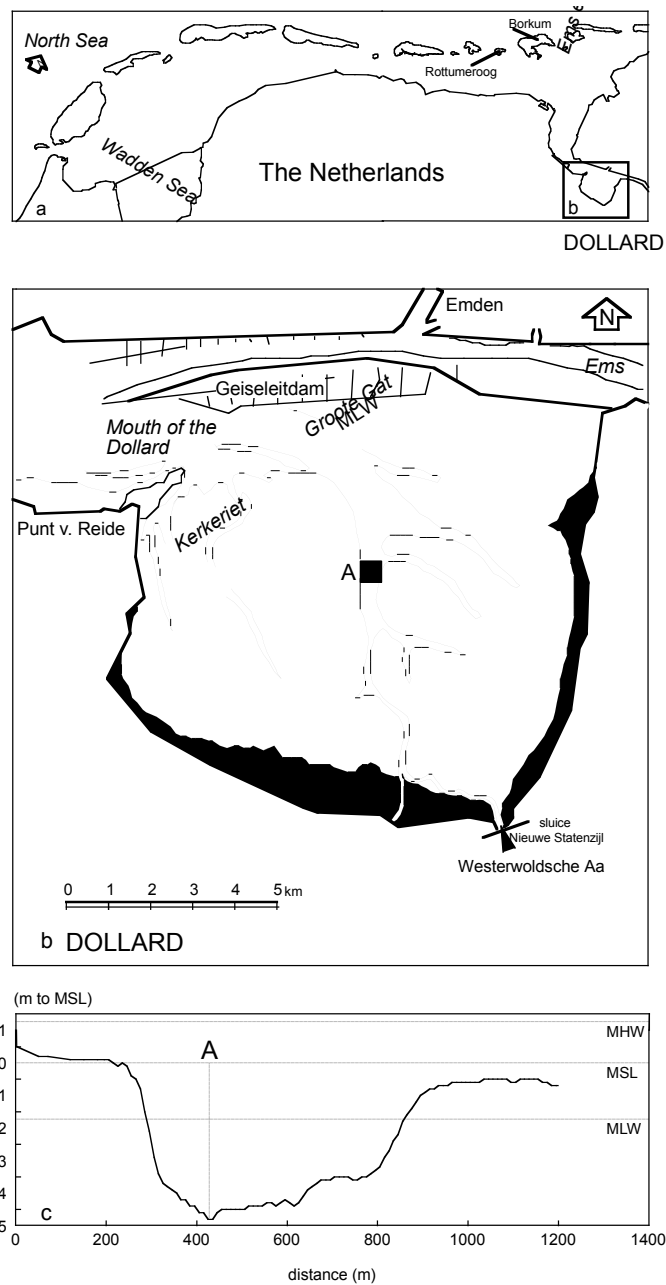
Fig. A. Study area, with (a) location of the Dollard in the Dutch Wadden Sea, (b) position of sample location A, (c) cross-section of the sample location, with mean sea level (MSL), mean high water (MHW) and mean low water (MLW) levels indicated. Salt marshes indicated by shaded areas.

Table A. *Summary of sampling statistics per tidal cycle: total number of flounder larvae caught, number of samples (n), mean sampled volume (V, m³), mean filtration efficiency (F, %), mean temperature (T, □C), mean salinity (S) and their according standard deviations (s.d.).*

Date	Larvae	n	V	s.d. V	F	s.d. F	T	s.d. T	S	s.d. S
1994										
11/04	5984	41	23.0	9.3	104.2	25.4	8.4	1.3	4.7	1.0
12/04	5439	51	22.5	10.5	103.6	25.1	8.4	0.8	4.9	0.9
18/04	3726	39	22.1	8.3	103.6	19.7	7.7	0.6	5.7	0.8
19/04	5059	48	16.6	7.2	95.3	24.7	7.8	0.3	6.0	0.7
03/05	5424	48	17.8	7.1	109.4	20.3	11.5	0.4	11.4	0.8
10/05	1148	34	19.1	7.0	94.8	19.6	12.0	0.3	12.2	0.8
11/05	1244	54	20.3	9.0	99.8	20.7	12.4	0.5	12.0	0.9
16/05	121	52	20.5	9.8	97.4	19.5	14.9	0.3	13.1	1.1
1995										
30/03	30	25	15.2	7.0	88.8	29.5	4.0	0.3	8.4	0.6
06/04	25	48	19.8	9.4	92.4	31.8	8.7	0.7	7.0	0.9
12/04	473	50	18.6	9.4	89.0	23.6	8.8	1.0	7.8	1.0
18/04	888	42	20.9	9.1	95.0	29.8	8.6	0.2	10.5	1.2
20/04	1414	50	18.1	8.6	84.5	27.5	8.1	0.4	10.0	1.0
25/04	1876	50	14.4	7.0	86.3	29.2	12.5	1.1	8.5	0.5
27/04	985	50	17.6	8.0	86.1	21.7	12.0	0.3	9.4	0.9
03/05	392	48	17.2	7.6	83.7	23.4	14.3	1.4	11.4	0.9
10/05	503	48	14.4	6.1	90.3	23.1	11.9	0.5	12.8	0.5

Three of these nets were attached to a line that had a 50 kg (1994) or 100 kg (1995) weight at the bottom end to prevent the nets from drifting with the strong tidal currents. The nets were lowered as quickly as possible until the weight rested on the sea floor and the line was tight. Sample duration was 20-30 minutes. Each sample set ideally consisted of three samples: surface, midwater and near-bottom. The distances between the nets and the bottom were adjusted to the varying water depths (**fig. b**f) by changing the attachment of the nets to the line accordingly. In 1994, the bottom net was kept 0.5 to 1.5 m from the bottom and the surface net between 0.5 and 1 m below the sea surface whereas the midwater net kept an equidistance between surface and bottom nets. The scheme was slightly adapted in 1995 by keeping the bottom net at a constant distance from the sea floor. The distance of 0.75 m initially chosen was increased to 1.00 m during the ebb of 20 April 1995 and on subsequent sampling dates because high near-bottom turbidities caused clogging of the net. On 3 May 1994, the surface net had actually fished in the midwater layer due to a malfunctioning crane. To correct for deficiencies in sampling procedures, the positions of the nets were arbitrarily categorised according to their absolute fishing positions relative to surface and bottom: 'surface': <1.5 m below the surface; 'near-bottom': ≤1.5 m above the bottom; 'midwater': all other sampling positions. On 10 May 1994, most of the ebb period was not sampled due to anchoring problems of the boat.

11/12 April 1994

18/19 April 1994
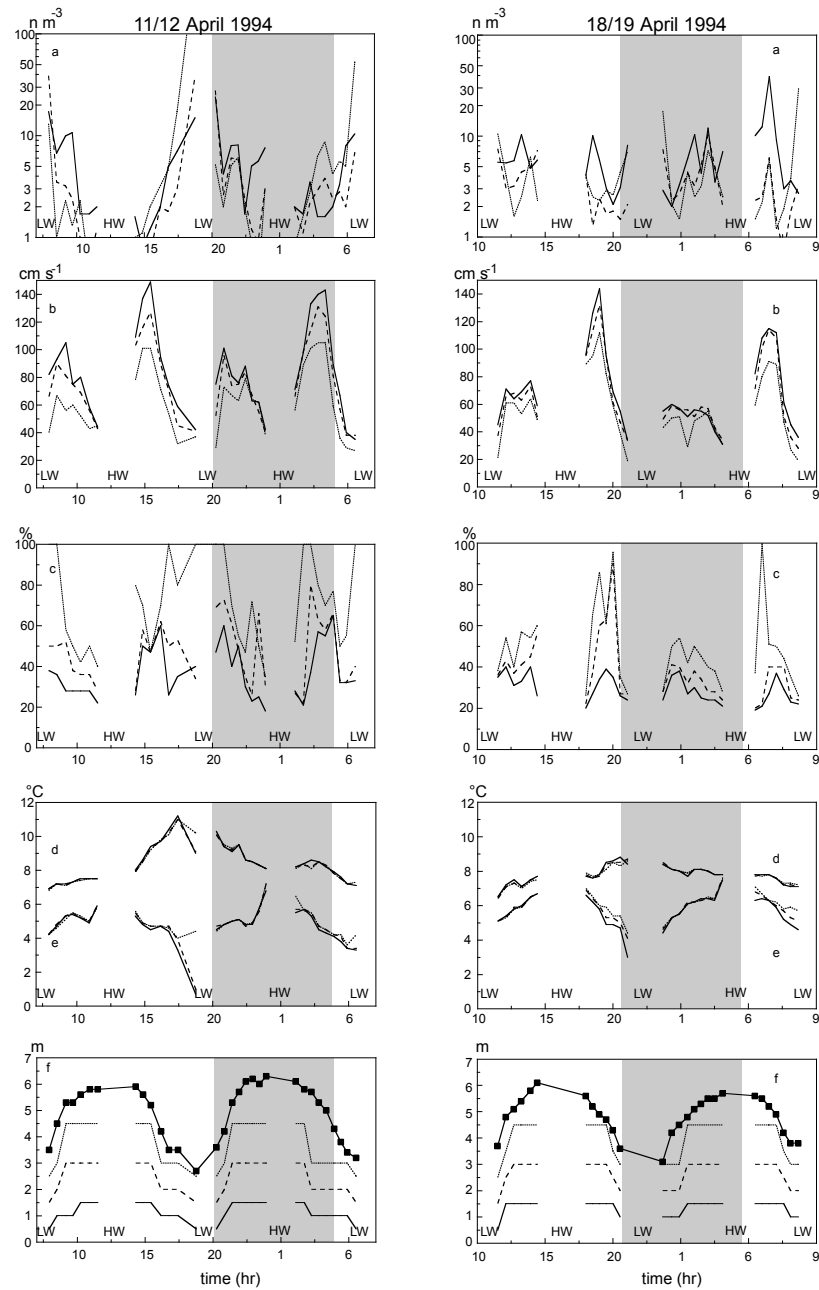
Fig. B. *Concentrations (n m⁻³) of flounder larvae (a), (b) velocity (cm s⁻¹), (c) turbidity (%), (d) temperature (°C), (e) salinity (ppt), (f) water depth (m) and positions of the nets in the surface (—), midwater (----) and near-bottom layer (......) during two 26-h sampling occasions (11/12 April and 18/19 April 1994). Actual samples indicated by solid squares in Fig. 2(f). Slack water indicated by LW or HW. Periods of darkness ('night') indicated by shaded areas.*

Samples were taken twice per hour as soon as current velocities allowed sampling after LW slack. During a period of 1 - 2 h around slack waters, when current velocities dropped to virtually zero, fishing was not possible. Water volumes up to 50 m^3 were filtered per sample (Table 1). Sampled volumes of less than 5 m^3 were rejected (36 out of 778 samples) because sampling was considered to have been unsatisfactory due to low current velocities or clogging of the net. After flushing of the nets, the samples were collected and fixed in a 3.8% neutralised phosphate-buffered formaldehyde solution for subsequent laboratory analysis. Larval concentrations were calculated by dividing the number of flounder by the filtered volume of water per sample, and were standardised to 10 m^3. The stage-frequency distribution was determined for a limited number of samples. The development stages that Ryland (1966) described for plaice were slightly adapted to fit flounder (Bies 1997, Jager and Kleef 1997). All larvae were in the process of metamorphosis.

Physical variables

The following physical variables were measured every 20 minutes during plankton sampling: temperature and conductivity (WTW-conductivity meter), turbidity (Partech instrument calibrated at 2000 mg dm^{-3}), current velocity and direction (calibrated Ott-meters). These measurements started at the bottom, and were taken consecutively at four to eight points in the vertical, depending on water depth. See De Jonge (1991) or Jager (1998) for an extensive description of the hydrographical methods used by Rijkswaterstaat. Wind speed and wind direction were monitored on board the ship every 30 minutes (Van Doorn anemometer and compass). Conductivity was transformed (applying temperature correction) to salinity, and expressed in the (dimensionless) Practical Salinity Scale.

Data analyses

Lowering of the nets usually took a couple of minutes to avoid entanglement but no precise recordings were made. Lifting the nets took less time than lowering, and variation was negligible. Larval concentrations in midwater and bottom layer were therefore corrected for the time that was needed to lower the nets into position. The average error was estimated at 2.5% (midwater) and 5% (bottom) of sample duration, and the corrected concentrations were calculated as follows:

$CC_m = (n_m - 0.025*n_s)/(V_m - 0.025*V_s)$

$CC_b = (n_b - 0.025*n_m - 0.025(1-0.025)*n_s) / (V_b - 0.025*V_m - 0.025(1-0.025)*V_s)$

where CC_m and CC_b = corrected midwater, respectively bottom concentrations; n_s, n_m, n_b = number of flounder larvae in the surface, midwater and bottom samples, respectively; V_s, V_m, V_b = sampled water volumes in the three strata.

Negative concentrations after correction were set at zero.

The centre of mass of the larval distribution (z_{cm}) relative to depth (indicated by *; dimensionless) was calculated according to equation 1:

$$z^*_{cm}(t) = \frac{z_{cm}(t)}{h(t)} = \frac{\int_0^h zc(z,t)dz}{h(t)\int_0^h c(z,t)dz} \qquad \textbf{A}$$

where c is concentration, z is height above the bottom, t is time and h is water depth (Jager and Mulder *subm.*).

Time was standardised to HW-slack as measured at the sampling location. Within the tidal cycle, six two-hour periods were arbitrarily distinguished and treated as different tidal phases (e.g. tidal phase -5 is 6-4 h before HW; flood: -5, -3, -1; ebb: 1, 3, 5). Samples that were taken between half an hour after sunset and half an hour before sunrise got the assignment 'night', the other samples 'day'. Multifactor ANOVA was applied to ln-transformed (larval concentrations + 1) and physical data. Transformation was necessary to normalise the residuals. The residuals from the multifactor ANOVA models for the different variables were correlated with each other (Spearman Rank Correlation) to detect possible relationships between larval concentrations and physical variables. On 16 May 1994, 30 March 1995 and 6 April 1995, larval concentrations were too low for statistical treatment (Table 1), and these data were excluded from the analyses.

RESULTS

Mean concentrations of flounder larvae were significantly higher in 1994 (3.75 m^{-3}, s.d. 5.7) than in 1995 (0.96 m^{-3}, s.d. 2.1) (Kruskal-Wallis test statistic 147.4; p=0). Maximum concentrations per sample were 433 m^{-3} in 1994 and 40 m^{-3} in 1995. Patterns of larval concentrations during the tidal cycle were not significantly different between years, whereas the difference in vertical distribution was marginally significant across years (**table b**, interaction of year and tidal phase not significant; interaction of year and water layer P~0.05). In both years there were significant differences in mean larval concentrations among sampling dates (**fig. c**). The second order interaction was not significant, implying that the vertical distribution of larvae throughout the tidal cycle is similar across years. The ANOVA for corrected concentrations gave essentially similar results as for uncorrected concentrations (**table b**).

Table B. *Analysis of variance of ln-transformed larval concentrations (1994 and 1995), and comparison of corrected and uncorrected values. The model* ln (cb*10+1)$_{corrected}$= μ + *year+water layer+tidal phase+tidal phase*water layer+*ε *explained 44% of the variance. Indications of significance levels (sign.):* *** P<0.001, ** P<0.01, * P<0.05, ~ P=0.05.*

		Corrected		Uncorrected	
	Df	F-ratio	sign.	F-ratio	sign.
MAIN EFFECTS					
year (yr)	1	171.90	***	180.34	***
water layer	2	12.90	***	11.61	***
tidal phase	5	11.80	***	12.24	***
INTERACTIONS					
yr*water layer	2	3.29	*	3.05	~
yr*tidal phase	5	1.54	n.s.	1.57	n.s.
water layer*tidal phase	10	3.41	***	2.96	**
yr*water layer*tidal phase	10	1.46	n.s.	1.49	n.s.
	Df		SS		SS
RESIDUAL	586		581.59		555.18
TOTAL	621		1045.33		1001.83
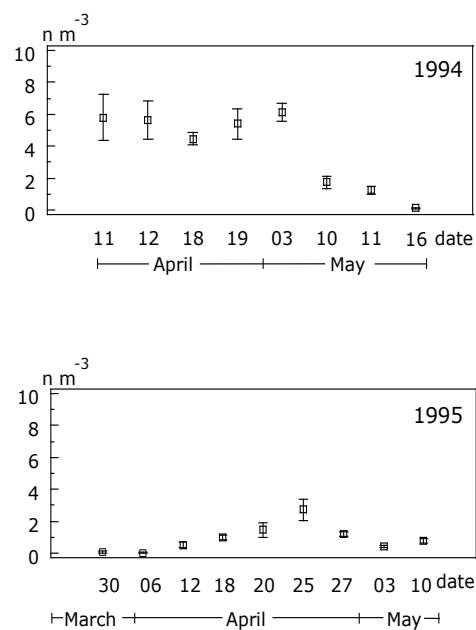
Fig. C. *Temporal pattern of mean larval concentrations (n m^{-3}) in 1994 and 1995; 95% Confidence Intervals indicated by bars. The mean was calculated as the arithmetic mean of concentrations in all samples and water layers per tidal cycle (flood and ebb).*

The height of the centre of mass of the larvae, reflecting the vertical concentration distribtution, was higher during flood than during ebb (**fig. d**).

Fig. D. Relative depth of the centre of mass of flounder larval distribution in the water column during the tidal cycle in 1994 ( ) and 1995 (Δ). After Jager & Mulder (subm.).

The centre of mass was even higher than 0.5 during flood, but also during part of the ebb in 1994. The change in vertical distribution of the larvae with tidal phase was also expressed in a significant contribution to the variance by the interaction of tidal phase and water layer (**table c**).

Table C. Analysis of variance of ln-transformed corrected larval concentrations, and comparison of the years 1994 and 1995. Significance levels as Table 1.

		1994		**1995**	
	Df	F-ratio	sign.	F-ratio	sign.
MAIN EFFECTS					
date	6	30.40	***	18.20	***
water layer	2	7.59	***	22.23	***
tidal phase	5	14.28	***	7.71	***
INTERACTIONS					
date*water layer	12	0.94	n.s.	3.35	***
water layer*tidal phase	10	2.91	**	5.35	***
	Df		SS	Df	SS
RESIDUAL	270		166.33	280	174.21
TOTAL	305		385.53	315	378.03

At closer inspection, the near-bottom pattern in larval abundance during the tidal cycle deviated from the other two strata: both surface and midwater concentrations decreased after the beginning of flood and increased again after the middle of ebb (interaction of tidal phase and water layer not significant, **table d**a), whereas near-bottom concentrations increased rather suddenly after

HW slack to stay at a higher level during ebb (**fig. e**). Larval concentrations were significantly higher in the surface layer than in midwater (**table e**).

Table D. Analysis of variance of ln-transformed corrected larval concentrations (1994), and comparison of different water layers; (a) bottom layer excluded; (b) flood, midwater layer excluded; (c) ebb, midwater layer excluded. Data for 16 May excluded. Significance

(a)

	Df	F-ratio	sign.
MAIN EFFECTS			
date	6	18.34	***
water layer	1	13.36	***
tidal phase	5	8.98	***
INTERACTIONS			
date*water layer	6	1.32	n.s.
water layer*tidal phase	5	0.63	n.s.
		SS	
RESIDUAL	179	100.77	
TOTAL	202	223.66	

(b)

	Df	F-ratio	sign.
MAIN EFFECTS			
date	6	13.31	***
water layer	1	18.99	***
tidal phase	2	11.73	***
INTERACTIONS			
date*water layer	6	1.43	n.s.
water layer*tidal phase	2	5.44	**
		SS	
RESIDUAL	77	46.45	
TOTAL	94	147.86	

(c)

	Df	F-ratio	sign.
MAIN EFFECTS			
date	6	5.75	***
water layer	1	0.32	n.s.
tidal phase	2	13.06	***
INTERACTIONS			
date*water layer	6	1.78	n.s.
water layer*tidal phase	2	1.53	n.s.
		SS	
RESIDUAL	69	45.53	
TOTAL	86	103.75	

levels as in Table 1.

Table E. Multiple range test (95% LSD) of ln-transformed corrected larval concentrations (1994) by water layer, excluding the bottom layer.

	Count	LS Mean	Homogeneous groups
WATER LAYER			
midwater	124	3.03	X
surface	79	3.50	X
CONTRAST	Diff.	+/- Limits	

$\ln(10n+1)\ 10m^{-3}$

$\ln(10n+1)\ 10m^{-3}$
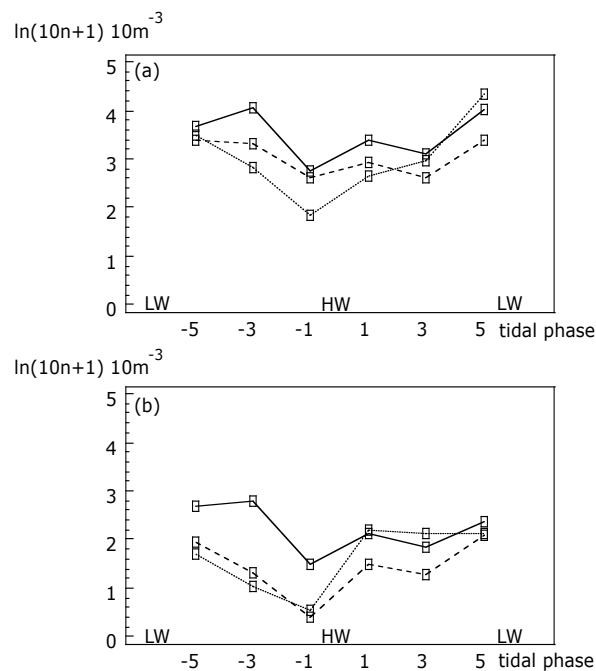
Fig. E. *Interaction plot of ln-transformed larval concentrations by tidal phase and water layer in 1994 (a) and 1995 (b); surface (—), midwater (- - -) and near-bottom (......). Slack water indicated by LW or HW.*

The concentration pattern of the surface and near-bottom layer were examined for flood and ebb separately (**table d**b, c). Concentrations at the surface increased during the middle of flood whereas near-bottom concentrations steadily decreased (significant interaction of tidal phase and water layer). During the middle of the flood period, larval concentrations were significantly higher in the surface layer than near-bottom (Kruskal-Wallis test statistic 13.93, $p < 0.001$). During ebb, the surface and near-bottom concentrations followed the same pattern, increasing to the end of ebb (**table d**c, interaction of water layer and tidal phase not significant).

There were no significant day-night effects in larval concentration, nor was the day-night effect significantly different for the three water layers (**table f**). However, the interaction of day-night and tidal phase was significant. This suggests that, irrespective of the water layer, during day time larvae were less abundant at the end of the flood, and more abundant at the beginning of the ebb and around LW slack, than during the night (**fig. f**).

Table F. *Analysis of variance of day-night variations in ln-transformed larval concentrations (corrected), based on the 26-h sampling occasions of 11/12 April and 18/19 April 1994. The second-order interaction was excluded. Significance levels as in Table 1.*

	Df	F-ratio	Sign.
MAIN EFFECTS			
tidal phase	5	7.59	***
water layer	2	5.42	**
day-night	1	0.04	n.s.
INTERACTIONS			
tidal phase*water layer	10	3.15	**
tidal phase*day-night	5	3.07	*
water layer*day-night	2	0.38	n.s.
		SS	
RESIDUAL	146	82.62	
TOTAL	171	152.52	
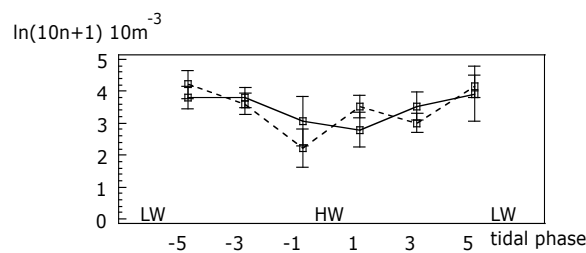
Fig. F. *Interaction plot of ln-transformed larval concentrations by tidal phase and day (---) or night (—) in 1994. Slack water indicated by LW or HW.*

The metamorphic stages 4b and 4b' were the most abundant. The stage-frequency distribution varied during the tidal cycle (**fig. g**): the most developed stages (4b', 5) were more abundant around LW in all three water layers. There was a gradual shift in stage distribution from the surface to the near-bottom layer, the more developed stages being relatively more abundant in the latter.

Turbidity showed a semi-tidal periodicity (**fig. b**c), always being highest near-bottom and lowest near the surface. The pattern during the tidal cycle was similar in all water layers in 1994 (**table g**, interaction of tidal phase and water layer not significant), but not in 1995 ($p=0.02$). There were significant differences in turbidity among sampling dates, and a significant interaction of sampling date and water layer.

Generally, mean current velocities were higher during ebb than flood tides (**fig. h**). They varied among sampling dates (**table g**), but no significant differences were observed between 1994 and 1995. Current velocities were generally highest near the surface and lowest near the bottom. Only during short intervals at the end of the flood period highest velocities were sometimes observed in midwater (**fig. b**b).

Surface

Midwater
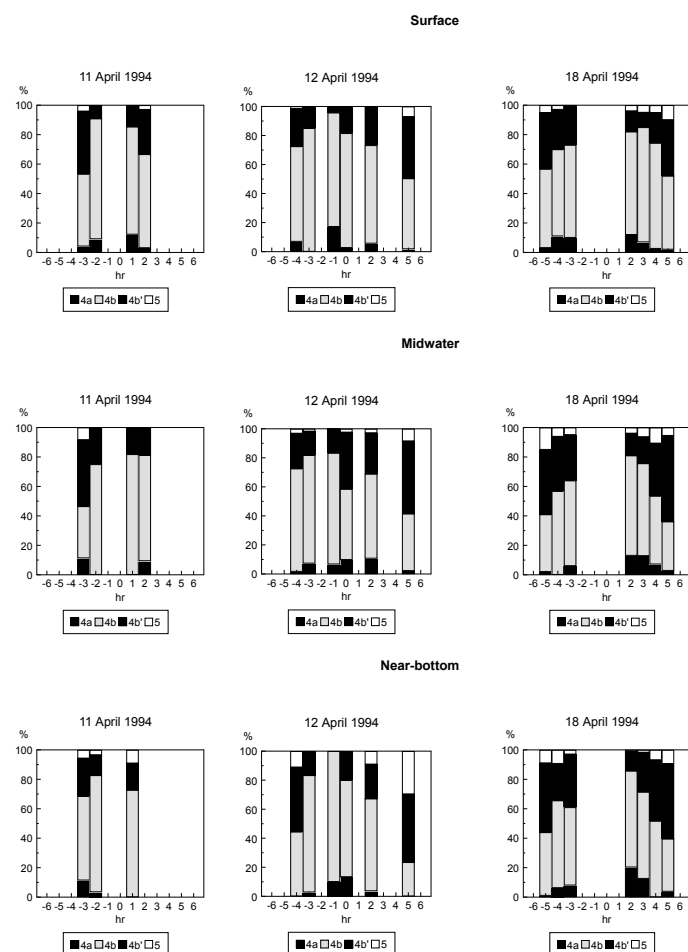
Near-bottom

Fig. G. *Tidal stage composition of flounder larvae in the surface, midwater and near-bottom water layers on 11&12 April (left) and 18 April 1994 (right; Bies 1997).*

Mean water temperatures ranged from 7.7 to 14.9 °C in 1994 and from 4.0 - 14.3 °C in 1995 (**table a**). Temperature showed diel fluctuations in all three water layers (**fig. b**d), and did not differ between water layers (**table h**). During the sampling period salinity increased from 4.7 to 13.1 in 1994 and from 7.0 to 12.8 in 1995 (**table a**). Maxima occurred around HW, and the lowest values were observed at the end of the ebb-period (**fig. b**e). Salinity differences between water layers were significant and there was also a significant interaction of water layer and tidal phase in both years (**table h**), indicating some degree of stratification.
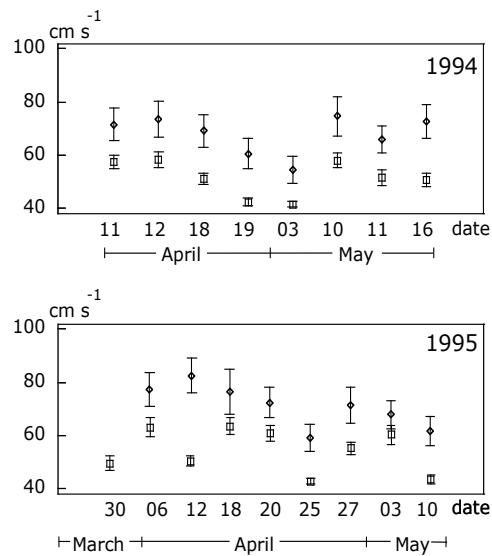
Fig. H. Mean velocity (cm s^{-1}) in the water column during flood ( ) and ebb (◊) in 1994 and 1995; Standard Errors indicated by bars.

Table G. Analysis of variance in turbidity and depth-averaged current velocity by year. Significance levels as in Table 1.

		Turbidity		Velocity	
1994	Df	F-ratio	sign.	F-ratio	sign.
MAIN EFFECTS					
date	7	42.19	***	11.98	***
water layer	2	58.42	***	15.44	***
tidal phase	5	18.38	***	79.02	***
INTERACTIONS					
date*water layer	14	2.27	**	0.77	n.s.
water layer*tidal phase	10	0.62	n.s.	1.45	n.s.
		SS		SS	
RESIDUAL	334	57918		111803	
TOTAL	372	169790		287793	
1995	Df	F-ratio	sign.	F-ratio	sign.
MAIN EFFECTS					
date	8	47.49	***	9.23	***
water layer	2	113.07	***	26.02	***
tidal phase	5	12.05	***	63.84	***
INTERACTIONS					
date*water layer	16	5.15	***	0.19	n.s.
water layer*tidal phase	10	2.14	*	1.44	n.s.
		SS		SS	
RESIDUAL	379	91647		161216	

TOTAL	420	295495		370350	

Table H. *Analysis of variance of salinity and temperature by year. Significance levels as in Table 1.*

		Salinity		**Temperature**	
1994	Df	F-ratio	sign.	F-ratio	sign.
MAIN EFFECTS					
date	7	2354.3	***	769.32	***
water layer	2	12.92	***	0.02	n.s.
tidal phase	5	153.68	***	1.97	n.s.
INTERACTIONS					
date*water layer	14	0.65	n.s.	0.26	n.s.
water layer*tidal phase	10	2.58	**	0.06	n.s.
		SS		SS	
RESIDUAL	334	82.0		145.2	
TOTAL	372	4819.5		2575.4	
1995	Df	F-ratio	sign.	F-ratio	sign.
MAIN EFFECTS					
date	8	508.40	***	738.81	***
water layer	2	16.35	***	2.14	n.s.
tidal phase	5	103.44	***	33.32	***
INTERACTIONS					
date*water layer	16	0.48	n.s.	0.24	n.s.
water layer*tidal phase	10	2.85	**	0.25	n.s.
		SS		SS	
RESIDUAL	379	122.1		173.5	
TOTAL	420	1586.1		3105.1	

Because larval concentration, salinity, turbidity and velocity are all correlated to the tidal cycle and also vary with water layer and sampling date, the residuals that remain after removal of the variance by these factors (**table c** and **table g**) were tested to investigate correlations among them (**table i**). There was no correlation between residuals of larval concentrations and those of current velocity or turbidity, whereas residuals of velocity and turbidity were positively correlated.

Table I. *Spearman Rank Correlations between the residuals of the ANOVA models for Platichthys flesus (Table 2), and turbidity and velocity (Table 6), for 1994 (n=306) and 1995 (n=316).*

RESIDUALS	ln(flounder)	velocity	turbidity
ln(flounder)		P=0.8 n.s. 1994	P=1.0 n.s. 1994
velocity	P=1.0 n.s. 1995		P=0 r=0.25 1994
turbidity	P=0.9 n.s. 1995	P=0 r=0.37 1995	

DISCUSSION

The larval concentrations observed in the present study (3 m^{-3} overall average of 1994 and 1995) were considerably higher than those published for flounder in the western Wadden Sea (mean flood abundance maximum of 0.037 m^{-3} in 1985, Van der Veer *et al.* 1991) or in the tributary rivers of the Elbe (0.55 m^{-3}, Möller and Dieckwisch 1991; maximum 1.8 m^{-3}, Bos *et al.* 1995), which may be taken as an indication of accumulation of flounder larvae in the study area (Jager 1998). The assumptions made to correct the larval concentrations for lowering time of the net could not be verified, but did seldom lead to negative concentrations. The correction term contributed to the significance of differences in concentrations between water layers. At sample volumes >5 m^3, there was no correlation between sample volume and larval concentration. Although the bottom net systematically fished smaller volumes than the other nets, as a result of the lower current velocities, there is no evidence that the volume sampled has affected the calculated larval concentrations.

Differences in mean current velocities among sampling dates corresponded with the spring-neap cycle in tidal differences. The higher velocities during ebb than during flood indicate that currents at the sample location (on the west side of the channel) were ebb-dominated. This result is in agreement with observations of the Duits-Nederlandse Eemscommissie (1990) that flood currents are strongest at the east side of the channel while during ebb highest velocities are manifest at the west bank.

Highest turbidities were always found near the bottom, caused by resuspension of sediments by bottom shear. Higher current velocities give rise to higher turbidity, which is also shown by the positive correlation of both variables after removal of the variation caused by tide, water layer and sampling date. Small differences in the net positions between 1994 and 1995 may have been responsible for relatively higher turbidity in the bottom layer in 1995 because the bottom net was on average kept closer to the bottom in that year.

The vertical distribution of larvae was not homogeneous, but generally showed the highest concentrations near the sea surface. This pattern was the inverse of that in turbidity. Flounder larvae are negatively buoyant in both fresh and salt water (Jager and Mulder *subm.*), and without swimming the highest concentrations would be expected near the bottom in an equilibrium flow situation. Even under turbulent mixing conditions, one might at best expect a homogeneous vertical distribution of larvae. In addition, the vertical distribution of larvae changed in a different way in the three strata during the tidal cycle, whereas the vertical profile in turbidity (representative of passive particles) remained constant. Furthermore, the residuals of larval concentrations were correlated with neither those of turbidity nor velocity. These results imply that

the transport process is not entirely passive, and thus leads to rejection of the 'passive transport' hypothesis.

During flood, the vertical distribution of the larvae (as reflected in a centre of mass which was well above 0.5) supported selective use of the tidal currents, since the highest concentrations were found in the fast moving surface layer. During ebb, concentrations in the bottom layer increased as expected, but on some dates there were still high concentrations of larvae present in the surface layer as well. Note therefore that the depth of the centre of larval distribution of about 0.5 does not mean that the larvae are homogeneously distributed in the vertical plane. The larvae in the surface layer during ebb may have a different origin than the near-bottom ones. A preliminary analysis of larval characteristics indicated that their morphometrics are variable during the tidal cycle and between water layers, and indicate that larvae in the surface layer during ebb on 18 April 1994 consisted of relatively early metamorphic stages (Bies 1997).

The observed tidal variation in concentrations may have been caused by lateral transport of the larvae during high tide out of the channel, with the water that spreads to cover the tidal flats. Larvae that fail to settle during one flood tide will be drained with the ebbing tidal flat water, which is characterised by a somewhat lower salinity, therefore has a lower density, and tends to spread over the channel water (Postma 1982). Thus, a surface layer may form during ebb with dense larval concentrations returning from the tidal flats, whereas the larvae at the bottom may have stayed behind in the channel. This explanation is supported by the observed salinity differences in the vertical profiles, especially around HW, during ebb and before LW slack. As soon as the flood water comes in, salinity stratification disappears. Under quiet wind conditions, there might be less mixing of the water from the flats with the channel water and the stratification may be stronger. This may explain the fluctuating patterns in larval concentrations during 18/19 April 1994 when, due to low mean wind speed and relatively low current velocities, there was probably less turbulent mixing.

The high larval concentrations in the surface layer during ebb contradict the STST hypothesis, and would result in net seaward transport of the larvae. On the other hand, the observed vertical distribution may favour retention. The mean tidal excursion in the Dollard is over a distance of circa 12 km, and would carry the larvae back to the middle part of the Ems estuary. However, this is not necessarily the distance the larvae are transported because the conditions change continuously. Nevertheless, the larvae do not leave the nursery area and during the next flood tide they may be redistributed over the tidal flats for repeated settlement attempts, until finally they succeed, or perish.

The proportion of unexplained variance in larval concentration was about 50%, indicating that there are other factors contributing to the observed fluctuations. One of these may be wind (Rijnsdorp *et al.* 1985), which can cause

considerable shear in shallow water on the tidal flats. Much longer time series analyses would be needed to demonstrate relations between wind and larval concentrations. Part of the variance may also have been caused by imperfections in the sampling method.

Contrary to plaice (Rijnsdorp *et al.* 1985) or flounder larvae in coastal waters (Campos 1996) no day-night differences were found in mean larval flounder concentrations or in their vertical distribution. Because the water in the Dollard is very turbid, even during daytime light does not penetrate far into the water column, and therefore this factor is not likely to influence the vertical distribution of the larvae in this area to a large extent. The interaction of day-night and tidal phase had low significance and is not very meaningful, considering the low number of observations.

Larval concentrations in the surface layer increased during the last two hours of the ebb, suggesting that the larvae are optimally positioned to achieve maximal transport to the tidal flats during the following flood period. The present data do not allow cross-correlations of concentrations with physical variables to reveal the cues that induce larvae to make their vertical migrations.

It would be worthwhile to obtain detailed information on the (LW) slack periods, when changes in larval concentrations and salinity are most rapid. Although the slack water periods may not seem very important in terms of realised transport, these may represent the time, because current velocities are low, when active swimming in the vertical plane (downward during HW slack, upward during LW slack) can have a relatively large impact on net transport. In addition, internal physical mixing of different water layers may be relatively important during these periods as well, compared to external mixing by longitudinal advection (Abraham 1988). The generated advection will be directed downward during HW slack and upward during LW slack (*pers. comm.* K. Robaczewska), and may create a synergy with larval swimming. Other factors that affect buoyancy, like salinity (Burke *et al.* 1995) or feeding condition (Sclafani *et al.* 1993) may also influence the transport process.

Although larval transport in the nursery area appears to be largely determined by water circulation and the discharge of freshwater (Jager 1998), the results presented clearly demonstrate that flounder larvae are able to influence their transport by adjusting their vertical distribution in the water column. Active transport was also suspected (Grioche *et al.* 1997) or demonstrated (Bos *et al.* 1995, Campos 1996) with flounder larvae in other areas, and may be generally used by at least the more advanced metamorphic larval stages of this species to accomplish inshore migration. Quantifying the contribution of nonhomogeneous vertical distributions to the transport velocity (Jager and Mulder *subm*.) may allow to assess the effectiveness of larval transport of flounder in the Dollard.

ACKNOWLEDGEMENTS

Transport velocity of flounder larvae (*Platichthys flesus* L.) in the Dollard (Ems estuary)

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ABSTRACT

Larval concentrations of flounder (*Platichthys flesus* L.), longitudinal current velocity, and physical variables were measured simultaneously in the Dollard to calculate the mass transport of the larvae, salinity and suspended matter. Transport velocities of the three substances (salinity, suspended matter and larvae) and of water were calculated and compared. The concept of larval velocity was extended to incorporate the effect of varying vertical larval distribution. The contributions of variations in vertical and temporal concentration to the transport velocity were calculated separately. The differences in velocity between the substances in relation to the vertical and temporal variation provide more insight in estuarine transport processes in the nursery.

Temporal salinity variation dominated over vertical variation during flood, and indicated that longitudinal advection was important. Overall, during flood the transport velocity of salinity was 3% lower than that of water. During ebb, there was hardly any difference between the transport velocity of salinity and water. The contributions of temporal and vertical variation in suspended matter were each in the order of 10%, but of opposite signs. The net result is a transport velocity of suspended matter which is 3% (flood) or 4% (ebb) higher than that of water. Erosion-deposition seemed the dominant process. During flood, transport velocity of larvae is 9% higher than that of water, which is mainly caused by vertical concentration variation (6%), while during ebb, larval transport velocity is 9% lower, which is almost exclusively due to the temporal concentration variation (8%). Swimming influences transport during flood, while during ebb it is not clear which process dominates. The results indicate that flounder larvae make use of selective tidal stream transport inside the nursery.

Keywords: *Platichthys flesus*, flounder, transport velocity, nursery, retention

INTRODUCTION

In a study of flounder (*Platichthys flesus* L.) in the Dollard, the hypothesis that larval transport in the nursery is entirely passive was rejected, because larvae were found to adjust their vertical distribution in the water column during the tidal cycle (Jager *subm.*). Tidal phases and the vertical distribution contributed most to the variance of larval concentrations on a single location inside a nursery area during the larval immigration period. However, larval transport appears also to be at least partly determined by the water circulation and affected by the discharge of freshwater (Jager 1998). This raises the question to what extent larvae are capable of influencing their transport in the nursery.

While Jager (*subm.*) qualitatively analysed the factors that contributed to the variance in larval concentrations, the present paper attempts to make a quantitative analysis based on the same data set. The concept of 'larval velocity' (Rowe and Epifanio 1994), which quantifies the mean tidal transport velocity of fish larvae, was applied to the available data set and developed further. We use 'transport velocity' instead of 'larval velocity', and define it as the ratio of the time- and/or depth-averaged mass transport and concentration. The transport velocity of the substance is compared with that of water. The difference between the two is called the relative transport velocity.

The mass balance of dissolved or suspended material can be described by the three-dimensional advection-diffusion equation. An advection-diffusion approach is commonly used in the description of physical transport processes. Fortier and Leggett (1982) applied the same approach to the transport of fish larvae. This allows a comparison between the relative transport velocity of larvae and the relative transport velocity of salinity (as a 'tracer' of different water masses) and of suspended matter (as 'passive particles') to investigate whether there is an active component involved in larval transport. Such an active component in larval transport would, according to the selective tidal stream transport (STST) hypothesis (Creutzberg 1961, Creutzberg *et al.* 1978, Hill 1995), be mainly expressed in the vertical concentration variation.

The acting physical (advection, turbulent diffusion, erosion-sedimentation) or biological (swimming) processes are expressed in temporal and vertical concentration variations, which determine the relative transport velocity of a substance. The objective of the present paper is to separate the contributions of inhomogeneous vertical distribution and of varying concentrations during the tidal cycle to the (larval) transport by calculating and analysing the (relative) transport velocity. Knowledge of the separate contributions of temporal and vertical concentration variations, on the basis of extensive data collected at one location in the Dollard nursery, will therefore give insight in the transport mechanism and the relative importance of larval activity during the immigration.

MATERIALS AND METHODS

Study area

The Dollard is a shallow tidal basin of about 100 km^2 inside the Ems estuary. The sampling location is situated in the ebb-branch of the main channel, with a depth of 5 m below MSL. The tidal range is 3 to 3.5 m, and the mean tidal excursion is 12 km. For a detailed description of the study area and sample location (A) is referred to Jager (1998).

Data collection

The methods are extensively described in Jager (*subm.*). Larval concentrations were determined twice per hour by fishing with 500 µm meshed plankton nets (type Apstein, Hydro-Bios) at three depths (surface, midwater and near-bottom) simultaneously during 20-30 minutes. Sampling from anchored ships typically continued during a full tidal cycle (13 hours) starting at low water (LW) slack. During a period of 1 to 2 hours around slack waters, when current velocities dropped to virtually zero, fishing was not possible. In addition, physical parameters were measured three times per hour at 8 depths consecutively. Measuring one vertical profile took up to 15 minutes. A total of 17 tidal cycles has been sampled between early April and the end of May, of which 8 in 1994 and 9 in 1995 (see **table a**). On one occasion the ebb was missed (10 May 1994).

Table A. *Parameters for the regression of suspended matter (mg dm^{-3}) on turbidity (%).*

Date	Slope	Intercept	P	R^2	n
11/04/1994	11.57	-152.5	0.0015	0.694	11
12/04/1994	11.57	-152.5	0.0015	0.694	11
18/04/1994	8.78	-79.9	0.0002	0.776	12
19/04/1994	8.78	-79.9	0.0002	0.776	12
03/05/1994	15.03	15.9	0.0032	0.909	6
10/05/1994	11.86	-60.6	0.0001	0.848	11
11/05/1994	11.86	-60.6	0.0001	0.848	11
16/05/1994	10.27	-20.5	0.0007	0.957	6
12/04/1995	17.16	-117.1	0.0000	0.990	6
18/04/1995	17.51	-229.4	0.0004	0.969	6
20/04/1995	15.41	-105.1	0.0014	0.939	6
25/04/1995	24.14	-184.1	0.0000	0.989	6
27/04/1995	23.32	-171.4	0.0003	0.973	6
03/05/1995	16.03	-41.2	0.0005	0.965	6
10/05/1995	17.67	-81.9	0.0155	0.804	6

Data treatment

Larval concentrations were corrected for the time needed to lower the plankton nets into position (Jager *subm.*). To calibrate the Partech turbidity meter, 6

water samples of 1 dm³ were taken at mid-depth during each tidal cycle. The fractions <53 μm and >53 μm were determined. A linear regression for total suspended matter concentration and turbidity was fitted for each sampling date (**table a**).

The measured vertical profiles of larval concentration and physical variables were utilised to calculate the required transport quantities by means of the VIVECS program (Mulder 1998a) using the equations described in the section 'parameter calculation'. To allow for integration over the entire water column, the measured vertical profiles of (corrected) larval concentrations and physical variables were extrapolated to the bottom and the surface. Larval concentrations at the bottom and the surface were set equal to the nearest measured value. Velocity at the surface was also set equal to the nearest measured value, while velocity at the bottom was set to zero. Values for suspended matter were extrapolated from an exponential function through the two nearest measured values because the vertical concentration distribution of passive substances characterised by a particular fall velocity is better approached by an exponential rather than by a linear function (e.g. Van Rijn 1985). Salinity was linearly extrapolated. Occasionally, a bottom layer of fluid mud producing turbidity values >100% disturbed the conductivity measurements. In such cases, a correction was applied by taking the nearest reliable salinity value within the profile.

To enable integration over time, the mid-point of the time interval required for measuring an entire profile was used. Integration was done for flood and ebb separately, because based on the STST hypothesis different processes were expected to be important during the different tidal phases. Discrimination between the tidal phases was based on histograms of all measured current directions during one cycle. Opposite signs were given to the current velocity during flood and ebb. The time of slack water was linearly interpolated between the times when the sign of the depth-averaged current velocity changed.

Transport calculations require synchronous concentration and velocity data at the same depths. To synchronise the two, a velocity profile was constructed for the time of a larval concentration profile by interpolation of the nearest measured velocity profiles. These profiles were subsequently divided into a number of layers, and a value at the boundary of each layer was calculated from linear interpolation. The instantaneous local transport was then obtained by multiplying the velocity and concentration at each layer boundary. Subdivision of the water column in 20 layers proved to be sufficiently large to reach convergence of the estimates and therefore this number was applied throughout.

Larval concentrations could not be measured during a period of 1 to 2 hr around slack tides, whereas for the physical variables information was on

average missing during 25 minutes only. Two alternative approaches were followed: one without integration over the slack time interval and one including the slack period. In the latter case, the data around the missing interval were linearly interpolated to the time of slack water when current velocity and transport were assumed to be zero. Only a selection of the results including slack periods will be presented for comparative purposes.

Parameter calculation

A summary of the used parameters and their dimensions is given in the Appendix. The vertical concentration distribution is reflected in the centre of mass (z_{cm}) relative to depth (indicated by *; dimensionless), which is defined as

$$z^*_{cm}(t) = \frac{z_{cm}(t)}{h(t)} = \frac{\int_0^h zc(z,t)dz}{h(t)\int_0^h c(z,t)dz} \qquad \textbf{A}$$

where c is concentration, z is height above the bottom, t is time and h is water depth. The integral was solved by applying the trapezoidal rule to the values at the layer boundaries.

The depth-averaged ($^-$) instantaneous concentration is given by

$$\bar{c}(t) = \frac{1}{h(t)}\int_0^h c(z,t)dz \qquad \textbf{B}$$

The time-averaged ($< >$) local concentration is given by

$$<c(z^*)> = \frac{\int_0^T c(z^*,t)h(t)dt}{\int_0^T h(t)dt} \qquad \textbf{C}$$

where T is the integration period (flood or ebb). The mass-preserving method is applied here because water depth varies with time. Theoretically, at each level an infinitely small layer thickness (Δ) should be considered to enable mass-calculations. With a constant number of water layers Δ is proportional to h, and therefore h is used in equation **3**. The integral was solved by applying the trapezoidal rule to the values at the mean profile times.

In equations **2** and **3,** c can be substituted by current velocity (v) or transport ($s = v \times c$), taking into account the two horizontal components of these vector quantities. In this way $\bar{v}(t)$, $\bar{s}(t)$ and $<s(z^*)>$ are obtained.

The instantaneous depth-averaged transport velocity is defined as

$$\bar{v}_s(t) \;=\; \frac{\bar{s}(t)}{\bar{c}(t)}$$

D

Note that $\bar{s} \neq \bar{v} \times \bar{c}$ and $\bar{v}_s \neq \bar{v}$ in case of a non-homogeneous vertical distribution of concentrations.

The time-averaged transport velocity at a relative depth is defined as

$$<v_s(z^*)> \;=\; \frac{<s(z^*)>}{<c(z^*)>}$$

E

This is the so-called 'larval velocity' (*sensu* Rowe and Epifanio 1994) if *c* represents the larval concentration, but we use the equation more generally here for concentrations of larvae, suspended matter and salinity. Note that $<s> \neq <v> \times <c>$ and $<v_s> \neq <v>$ if *c* is inhomogeneously distributed over time.

The time- and depth-averaged transport velocity is

$$<\bar{v}_s> \;=\; \frac{\displaystyle\int_0^T \bar{s}(t)\,h(t)\,dt}{\displaystyle\int_0^T \bar{c}(t)\,h(t)\,dt}$$

F

If the concentration is constant over time and depth, the total transport velocity of a substance is equal to the time- and depth-averaged current velocity ($<\bar{v}_s>$ = $<\bar{v}>$). However, temporal ($\Delta V_{s,t}$) and vertical ($\Delta V_{s,z}$) concentration variations contribute to the total transport velocity, according to

$$<\bar{v}_s> \;=\; <\bar{v}> \;+\; \Delta V_{s,t} \;+\; \Delta V_{s,z}$$

G

To determine the contribution of time-variation in concentration, we define a transport velocity without the contribution of inhomogeneous vertical distribution as

$$<\bar{v}_s>' \;=\; <\bar{v}> \;+\; \Delta V_{s,t}$$

H

where $<\bar{v}_s>'$ can be calculated from

$$<\bar{v}_s>' \;=\; \frac{\displaystyle\int_0^T \bar{v}(t)\,\bar{c}(t)\,h(t)\,dt}{\displaystyle\int_0^T \bar{c}(t)\,h(t)\,dt}$$

I

Note that the transport in Eq. **9** is based on the depth-averaged velocity and concentration, which is not equal to the transport ($\bar{s}$) used in Eq. **6**.

Once $<\bar{v}_s>$, $<\bar{v}>$ and $<\bar{v}_s>'$ are known, $\Delta V_{s,t}$ and $\Delta V_{s,z}$ can be derived from Eq. **8** and **7**.

The difference between transport velocity and tidal current velocity is called the 'relative transport velocity', which is positive if a substance is transported faster than water.

The tidal displacement (L_s) of a substance is calculated by multiplying the transport velocity with the tidal period T (flood or ebb). The relative tidal displacement is the difference between displacement of a substance and of water caused by the temporal and vertical concentration variation during the tidal cycle. Calculations were performed for flood and ebb separately.

Specific gravity

A simple experiment was conducted with two metamorphosing flounder larvae, to determine whether their specific gravity was larger than or equal to water. The larvae were anaesthetised in MS222, and were then carefully released at the surface of an aquarium (50x40x40 cm) that was filled with water of 14 °C, and salinity 0.2 or 30. Each larva was repeatedly dropped in water of both salinities alternately, and was observed whether to float or sink.

RESULTS

Salinity

The centre of mass of salinity is on average slightly lower than 0.5 during both flood and ebb and it was significantly lower during ebb than during flood, although the difference is very small (**table b**).

Table B. *Mean centre of mass per tidal phase of salinity, suspended matter and flounder larvae, and corresponding standard errors (s.e.) and number of observations (n).*
(* = significantly different from 0.5 at p=0.05).

SUBSTANCE	year	flood	ebb	s.e.$_{flood}$	s.e.$_{ebb}$	n$_{flood}$	n$_{ebb}$
Salinity	1994	* 0.494	* 0.487	0.001	0.018	139	118
	1995	* 0.498	* 0.493	0.0003	0.0007	122	125
Suspended matter	1994	* 0.375	* 0.402	0.007	0.007	139	118
	1995	* 0.358	* 0.382	0.007	0.009	122	125
Larvae	1994	* 0.600	0.532	0.015	0.017	66	54
	1995	* 0.659	0.482	0.015	0.020	58	56

Relatively low values were observed during the ebb in 1994 which may indicate a salinity stratification. The time-averaged salinity profiles demonstrate slightly lower values at the surface and a tendency to increase with depth during both flood and ebb (**fig. a**).
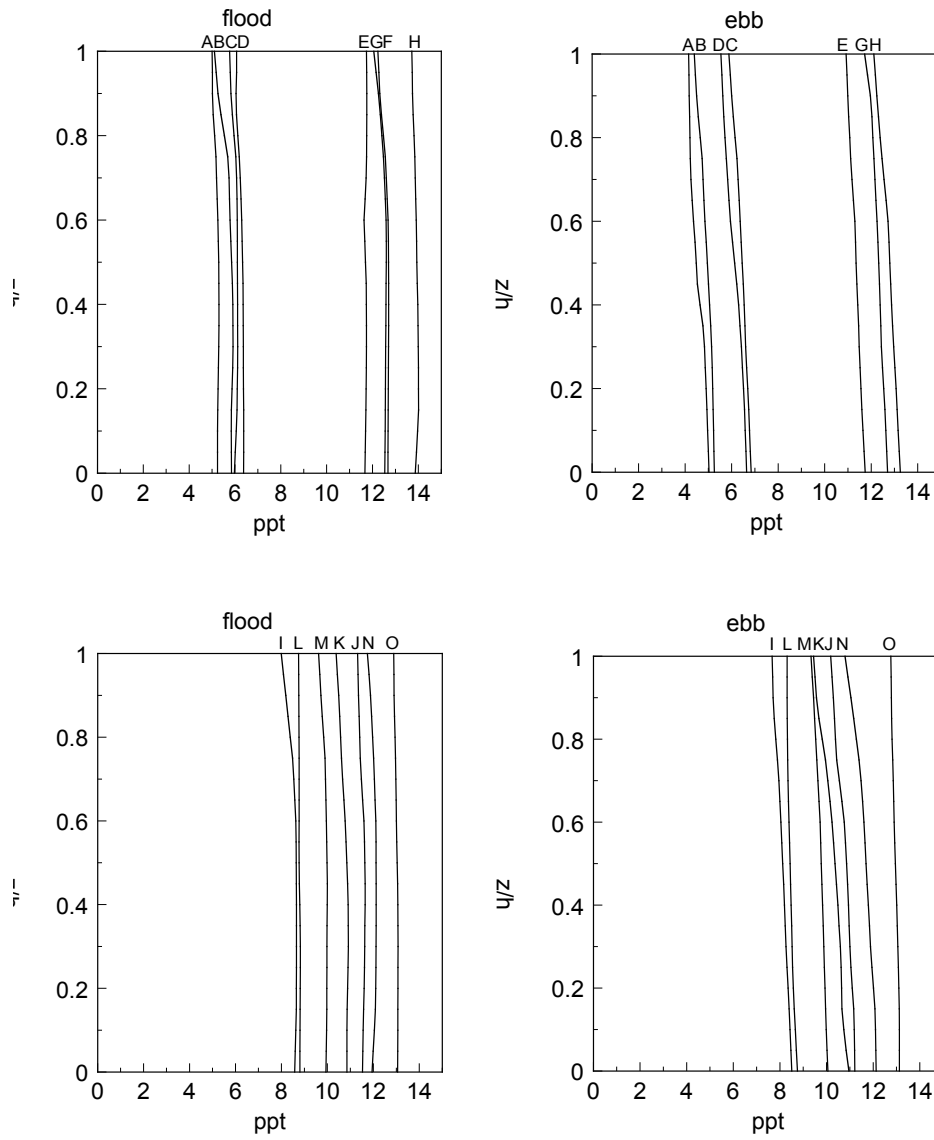
Fig. A. *Time-averaged salinity profiles by sampling date in 1994 (top, A to H) and 1995 (bottom, I to O). A=11/04, B=12/04, C=18/04, D=19/04, E=03/05, F=10/05, G=11/05, H=16/05, I=12/04, J=18/04, K=20/04, L=25/04, M=27/04, N=03/05, O=10/05.*

Fig. B. Relative depth-averaged transport velocity (m s^{-1}) profiles of salinity by sampling date. Legend to the dates as in Fig. 1.
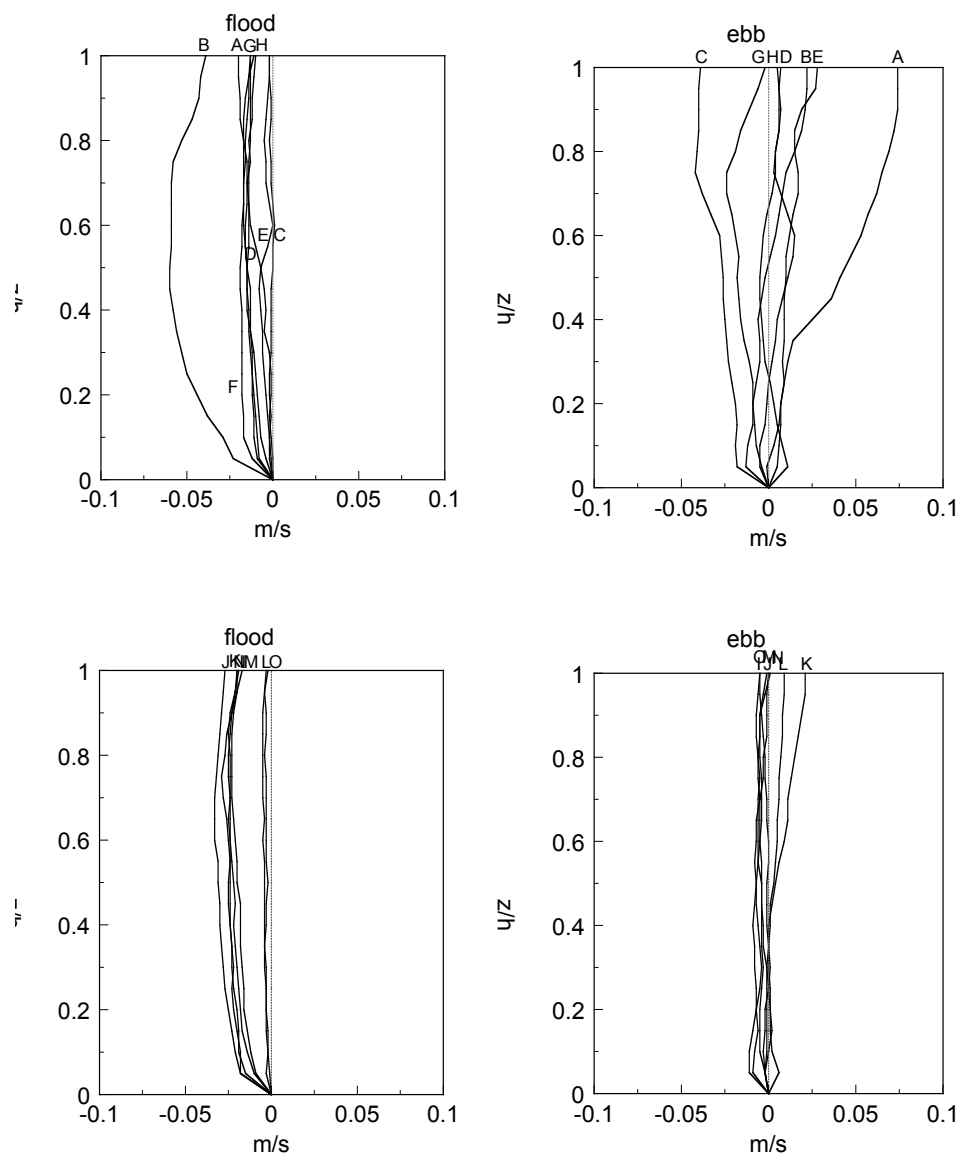
Fig. C. *Relative time-averaged transport velocity profiles of salinity by sampling date Legend to the dates as in Fig. 1.*

Table C. *Absolute time- and depth-averaged transport velocities ($<\bar{v}_s>$, m s^{-1}) for salinity per tidal phase and sampling date, and contributions of current velocity ($<\bar{v}>$), temporal ($\Delta V_{s,t}$) and vertical ($\Delta V_{s,z}$) concentration variation. Negative contributions of temporal and vertical variations in concentration indicate seaward landward directions during flood and ebb, respectively. The data have also been averaged over all sampling dates (mean) and expressed as percentages (%).*
(a) results excluding the slack period, (b) summary of data including the slack period.

| (a)	Flood				Ebb			
Date	$<\bar{v}_s>$	$<\bar{v}>$	$\Delta V_{s,t}$	$\Delta V_{s,z}$	$<\bar{v}_s>$	$<\bar{v}>$	$\Delta V_{s,t}$	$\Delta V_{s,z}$
11/04/1994	0.519	0.532	-0.013	0.000	0.799	0.773	0.033	-0.007
12/04/1994	0.443	0.488	-0.044	-0.001	0.737	0.743	0.001	-0.007
18/04/1994	0.472	0.471	0.001	0.000	0.561	0.586	-0.020	-0.005
19/04/1994	0.385	0.398	-0.013	0.000	0.523	0.518	0.011	-0.006
03/05/1994	0.394	0.400	-0.006	0.000	0.506	0.497	0.012	-0.003
10/05/1994	0.478	0.495	-0.017	0.000				
11/05/1994	0.452	0.466	-0.014	0.000	0.589	0.599	-0.007	-0.003
16/05/1994	0.410	0.423	-0.013	0.000	0.769	0.748	0.024	-0.003
12/04/1995	0.417	0.440	-0.023	0.000	0.731	0.737	-0.002	-0.004
18/04/1995	0.485	0.512	-0.027	0.000	0.785	0.794	-0.006	-0.003
20/04/1995	0.527	0.550	-0.024	0.001	0.684	0.684	0.007	-0.007
25/04/1995	0.378	0.381	-0.003	0.000	0.536	0.534	0.003	-0.001
27/04/1995	0.455	0.473	-0.018	0.000	0.621	0.628	-0.005	-0.002
03/05/1995	0.486	0.506	-0.021	0.001	0.555	0.560	0.000	-0.005
10/05/1995	0.382	0.386	-0.004	0.000	0.511	0.510	0.002	-0.001
mean	0.446	0.461	-0.016	0.000	0.636	0.637	0.004	-0.004
%	100	103.6	-3.6	0.1	100	100.0	0.6	-0.6
(b)								
mean	0.424	0.441	-0.017	0.000	0.583	0.591	-0.004	-0.004
%	100	103.9	-4.0	0.1	100	101.4	-0.7	-0.7
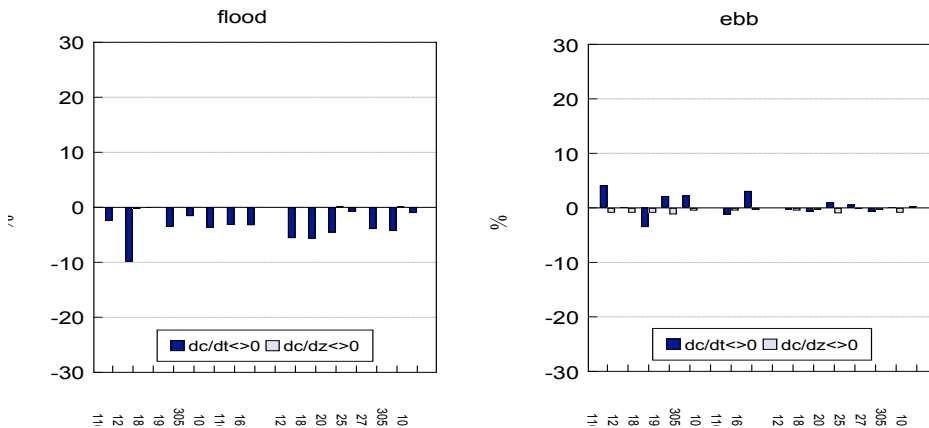
Fig. D. *Relative contribution (%) to the transport velocity of temporal (dc/dt<>0 = $\Delta V_{s,t}$) and vertical (dc/dz<>0 = $\Delta V_{s,z}$) salinity variations, for flood and ebb separately for all sampling dates.*

The relative depth-averaged transport velocity, reflecting the contribution of inhomogeneous vertical salinity distribution to the transport velocity, indicates that the largest stratification effects occurred around LW slack (transport velocity up to 0.06 m s^{-1} lower than the water velocity; **fig. b**). This effect was more pronounced in 1994 than in 1995. The transport velocity was also lower than water velocity (up to 0.025 m s^{-1}) shortly after HW slack in both years.

The relative time-averaged transport velocity profiles of salinity, reflecting temporal concentration variations, were negative during flood at all depths with absolute values up to 0.06 m s^{-1} (**fig. c**). During ebb, however, both negative and positive relative transport velocities were observed. Deviations from a straight vertical line indicate that the temporal changes follow different patterns at different depths.

The contributions of temporal and vertical variation to the transport velocity (**table c**) are shown for each sampling date in **fig. d**. As might be expected for a dissolved substance, the time- and depth-averaged transport velocities of salinity were almost equal to those of water. Temporal variation has a larger effect than vertical variation. During flood, the contribution of temporal variation was consistently negative, and the contribution of vertical variation was only minor. During ebb, temporal variation resulted in positive effects, whereas vertical variation had a negative effect. Overall, the temporal salinity variation has a negative contribution of 3.6% to the transport velocity during flood, whereas the vertical variation contributes only 0.1% (**table c**). During ebb, the net effect is considerably smaller than during flood: the temporal variation adds 0.6% and the vertical variation subtracts 0.6%. Including slack periods in the time-integration leads to a small reduction of the transport velocity of water and salinity (**table c**b), but hardly affects the calculated contributions of temporal and vertical concentration variation to the transport velocity of salinity. Tidal displacements of salinity and water were almost equal, which is on average 12 km (**table f**).

Suspended matter

The centre of mass of suspended matter was significantly lower than 0.5 during flood and ebb in both years, indicating that particles are concentrated in the lower part of the water column. This effect is more pronounced during flood than during ebb (**table b**). The time-averaged concentration profiles confirm these results: the highest concentrations occur near the bottom, and the vertical variations are larger during flood than during ebb (**fig. e**).

The relative depth-averaged transport velocity was always negative with minimum values after HW slack (**fig. f**). This coincides with strongly increasing tidal current velocities (see Jager *subm.*), which lead to resuspension of suspended matter near the channel bed.

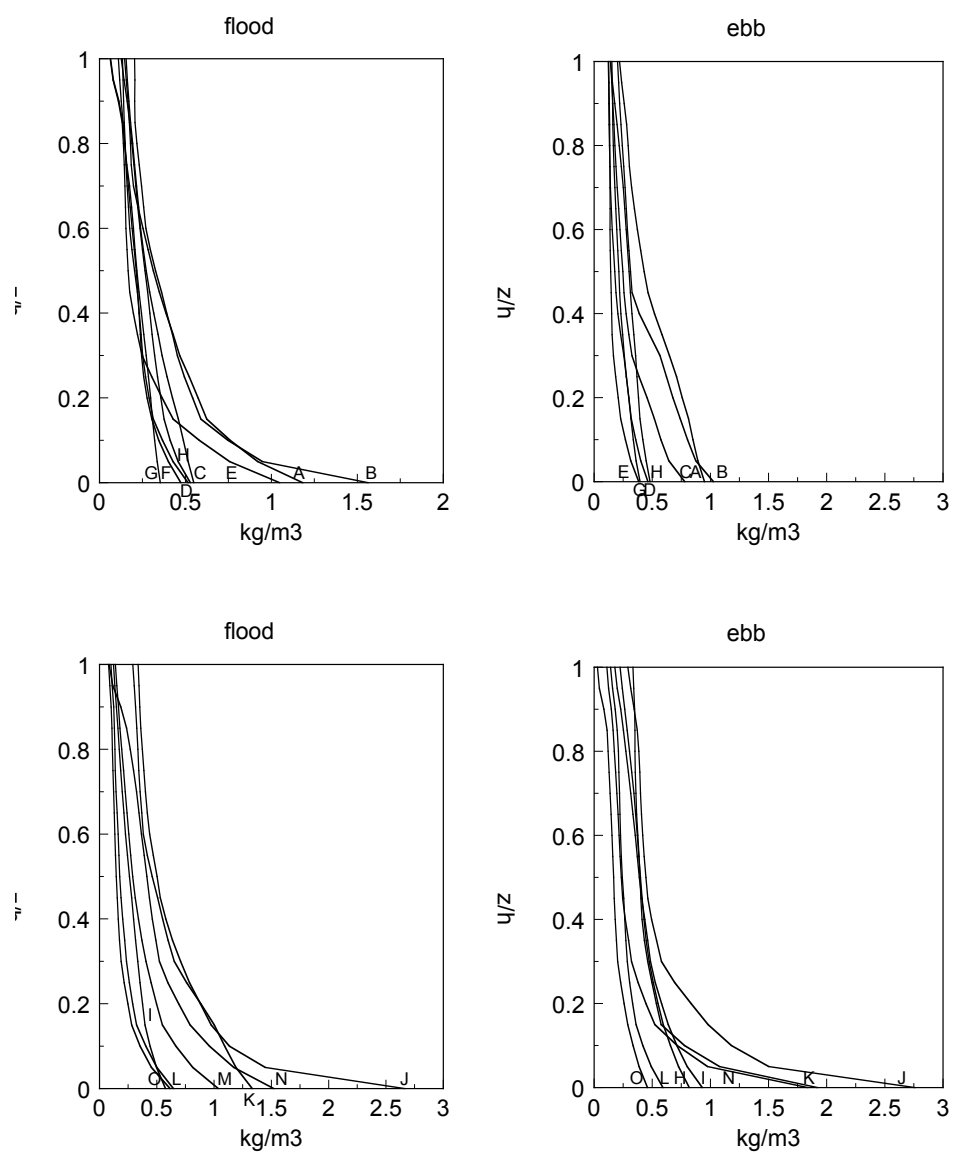**Fig. E.** *Time-averaged suspended matter concentration profiles by sampling date. Legend to the dates as in Fig. 1.*

Fig. F. *Relative depth-averaged transport velocity (m s^{-1}) profiles of suspended matter by sampling date. Legend to the dates as in Fig. 1.*
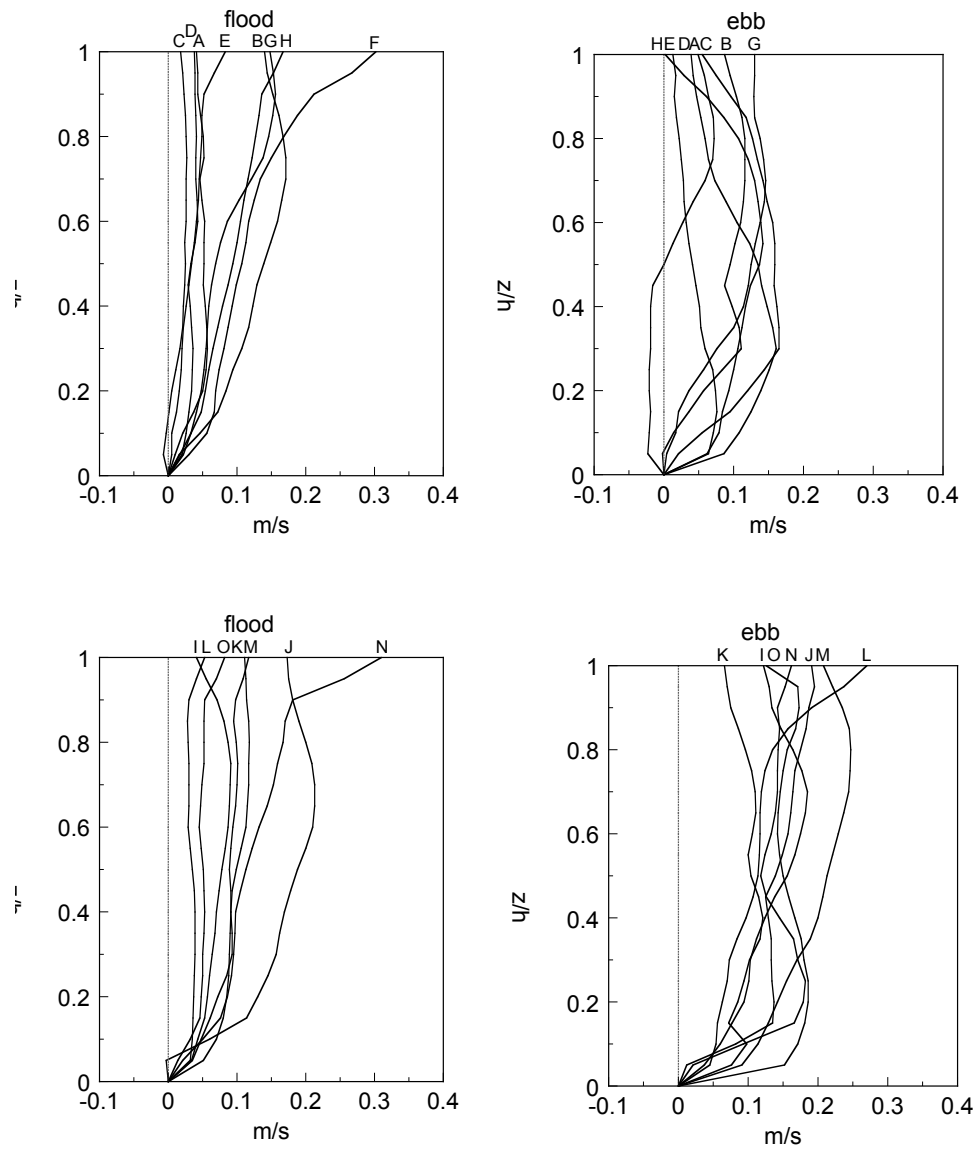
Fig. G. Relative time-averaged transport velocity profiles of suspended matter by sampling date. Legend to the dates as in Fig. 1.

Table D. *Absolute time- and depth-averaged transport velocities ($<\bar{v}_s>$, m s^{-1}) for suspended matter per tidal phase and sampling date, and contributions of current velocity ($<\bar{v}>$), temporal ($\Delta V_{s,t}$) and vertical ($\Delta V_{s,z}$) concentration variation. For legends see also* **table c**.

(a) results excluding the slack period, (b) summary of data including the slack period.

| (a) Date	Flood $<\bar{v}_s>$	$<\bar{v}>$	$\Delta V_{s,t}$	$\Delta V_{s,z}$	Ebb $<\bar{v}_s>$	$<\bar{v}>$	$\Delta V_{s,t}$	$\Delta V_{s,z}$
11/04/1994	0.482	0.532	0.047	-0.097	0.686	0.773	-0.005	-0.082
12/04/1994	0.518	0.488	0.099	-0.069	0.716	0.743	0.067	-0.094
18/04/1994	0.448	0.471	0.011	-0.034	0.619	0.586	0.115	-0.082
19/04/1994	0.404	0.398	0.037	-0.031	0.564	0.518	0.127	-0.081
03/05/1994	0.355	0.400	0.025	-0.070	0.500	0.497	0.059	-0.056
10/05/1994	0.560	0.495	0.101	-0.036				
11/05/1994	0.507	0.466	0.073	-0.032	0.635	0.599	0.082	-0.046
16/05/1994	0.470	0.423	0.079	-0.032	0.807	0.748	0.106	-0.047
12/04/1995	0.476	0.440	0.062	-0.026	0.787	0.737	0.126	-0.076
18/04/1995	0.567	0.512	0.107	-0.052	0.773	0.794	0.090	-0.111
20/04/1995	0.580	0.550	0.086	-0.056	0.668	0.684	0.120	-0.136
25/04/1995	0.373	0.381	0.039	-0.047	0.589	0.534	0.095	-0.040
27/04/1995	0.499	0.473	0.097	-0.071	0.758	0.628	0.183	-0.053
03/05/1995	0.530	0.506	0.106	-0.082	0.535	0.560	0.137	-0.162
10/05/1995	0.380	0.386	0.049	-0.055	0.611	0.510	0.179	-0.078
mean	0.477	0.461	0.068	-0.053	0.661	0.637	0.106	-0.082
%	100	96.8	14.2	-11.0	100	96.4	16.0	-12.4
(b)								
mean	0.466	0.441	0.077	-0.052	0.640	0.591	0.129	-0.080
%	100	94.6	16.4	-11.1	100	92.3	20.2	-12.5
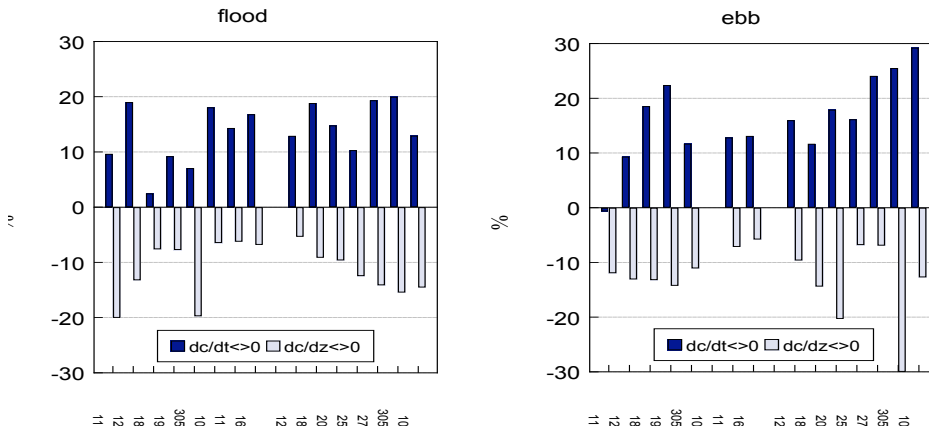
Fig. H. *Relative contribution (%) to the transport velocity of temporal (dc/dt<>0 = $\Delta V_{s,t}$) and vertical (dc/dz<>0 = $\Delta V_{s,z}$) suspended matter concentration variations, for flood and ebb separately for all sampling dates.*

The relative time-averaged transport velocity was almost always positive, indicating that suspended matter is transported faster than water during both flood and ebb (**fig. g**) with values up to 0.3 m s^{-1}. The profiles show highest values at the surface during flood and in midwater during ebb. However, the patterns were quite variable in both tidal phases and both years.

The contribution of the temporal variation to the transport velocity of suspended matter (**table d**) was consistently opposite to that of the vertical variation and were in the same order of magnitude (**fig. h**). Overall, the temporal variation had a positive contribution of about 15% to the transport velocity, whereas the vertical variation subtracted 12% during both flood and ebb (**table d**). Including slack periods merely increases the contribution of the temporal concentration variation by a few percent (**table d**b). The net effect of both variations on the tidal displacement is landward during flood and seaward during ebb (**table f**).

Larvae

In water of 30 as well as 0.2 salinity, the two larvae sank fairly quickly to the bottom after release. The specific gravity of flounder larvae is thus larger than water in both saline and fresh water. The mean centre of mass of the larval distribution was higher than 0.5 during flood, and not significantly different from the midpoint during ebb (**table b**). The time-averaged larval concentration profiles (**fig. i**) indicate that relatively high concentrations were indeed consistently observed in the upper part of the water column during flood. During ebb, however, relatively high concentrations may occur in the surface or the near-bottom layer or even in both layers with relatively low concentrations in between (see also Jager *subm*.). Therefore, a value of 0.5 may not be interpreted as indicating a homogeneous distribution over the water column. These patterns were observed in both years, although the concentrations were generally higher in 1994.

The vertical distribution of the larvae caused relative depth-averaged transport velocities that were positive during flood in both years, and highly variable during ebb, positive or negative, depending on date and time within a tidal cycle (**fig. j**). The difference between larval velocity and current velocity ranges from -0.2 to +0.2 m s^{-1}.

Larval time-averaged transport velocity (**fig. k**) during flood was on most dates higher than of water (up to 0.1 m s^{-1}), with a few exceptions. The irregular vertical profiles again indicate different tidal variations at different relative depths in the water column. During ebb, patterns were much more variable. Particularly in the upper water layer, larvae travelled sometimes 0.2 m s^{-1} faster than water or 0.4 m s^{-1} slower. In the near-bottom layer, relative velocities were smaller and more frequently negative, especially in 1994.
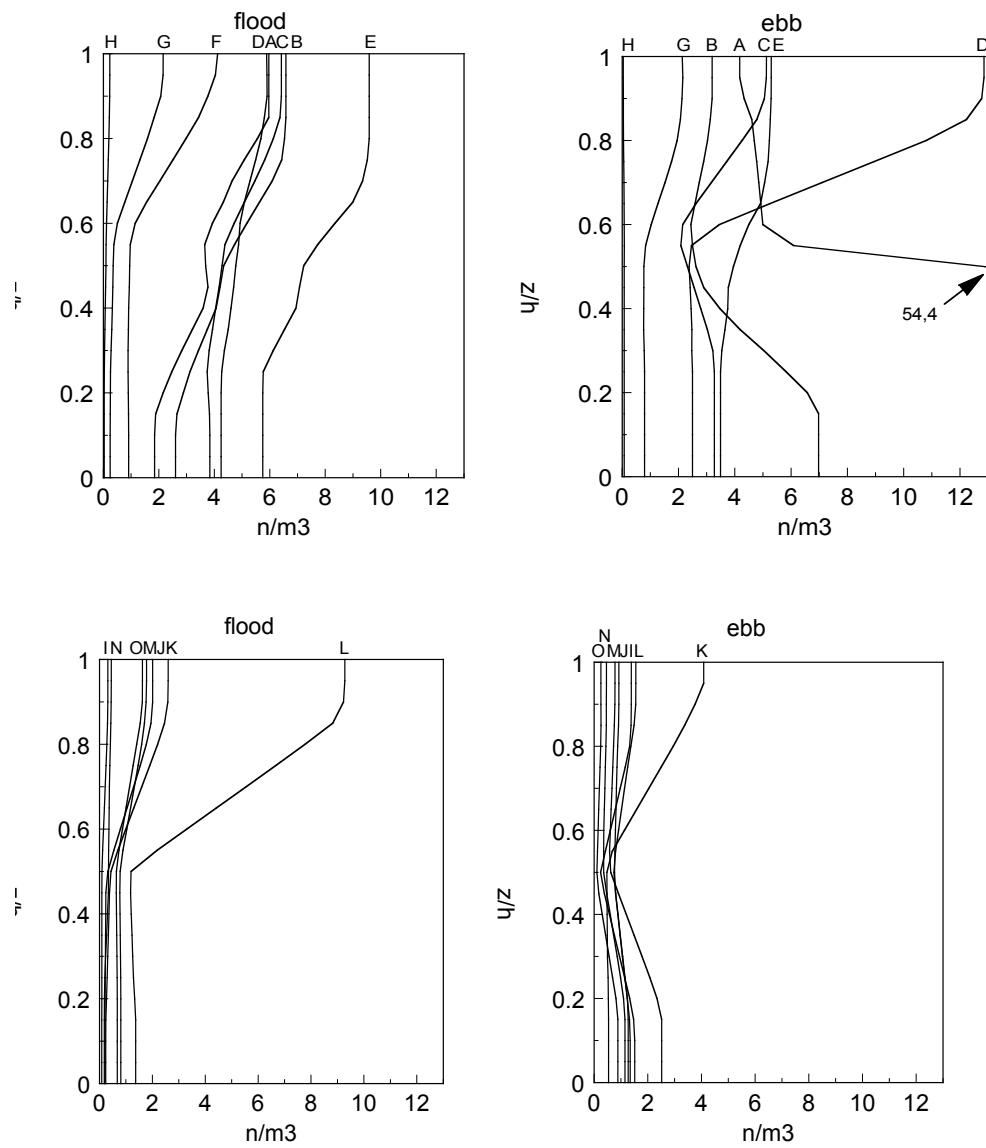
Fig. I. *Time-averaged larval concentration profiles by sampling date. Legend to the dates as in Fig. 1.*

Fig. J. Relative depth-averaged transport velocity (m s^{-1}) profiles of flounder larvae by sampling date. Legend to the dates as in Fig. 1.
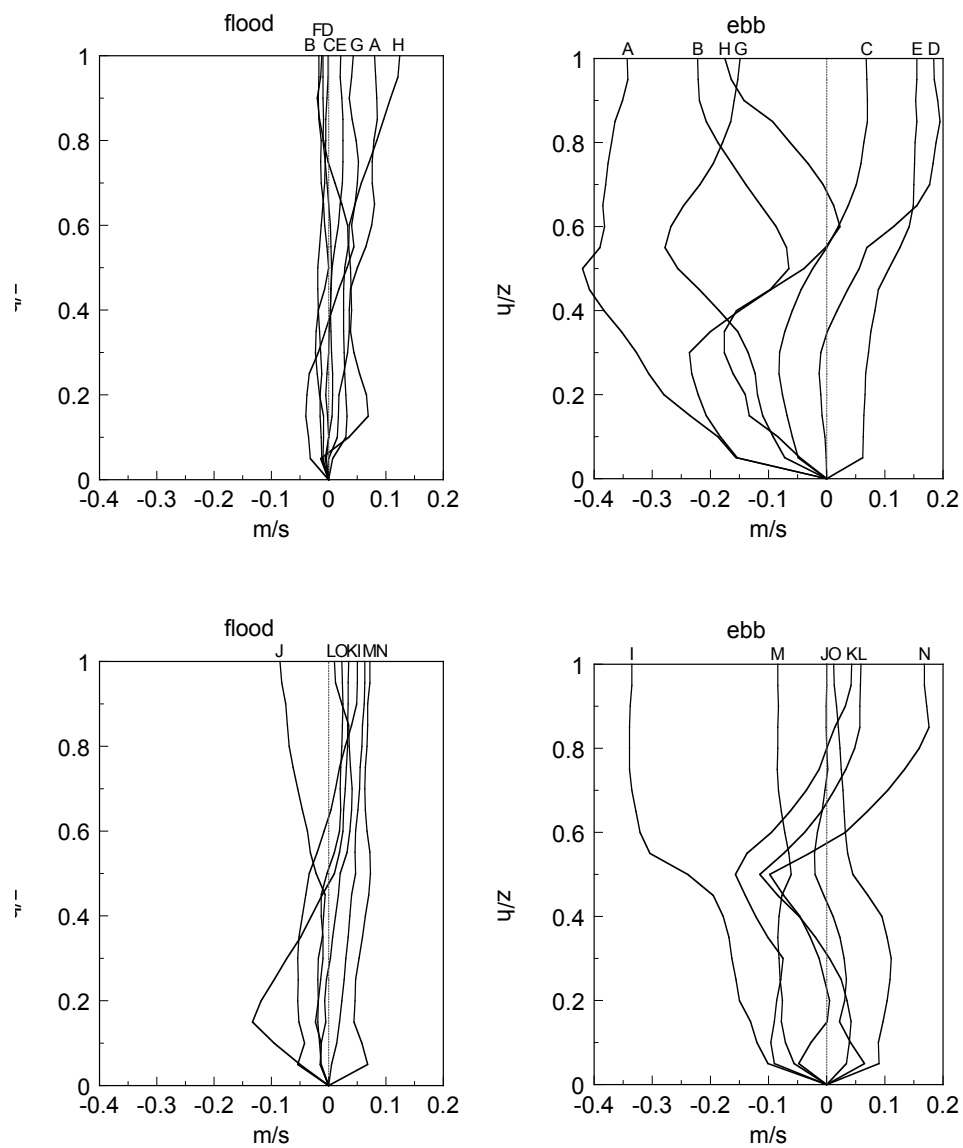
Fig. K. *Relative time-averaged transport velocity profiles of flounder larvae by sampling date. Legend to the dates as in Fig. 1.*

Table E. *Absolute time- and depth-averaged transport velocities ($<\bar{v}_s>$, m s^{-1}) for larvae per tidal phase and sampling date, and contributions of current velocity ($<\bar{v}>$), temporal ($\Delta V_{s,t}$) and vertical ($\Delta V_{s,z}$) concentration variation. For legends see **table c**. (a) results excluding the slack period, (b) summary of data including the slack period.*

| (a) | Flood | | | | Ebb | | | |
Date	$<\bar{v}_s>$	$<\bar{v}>$	$\Delta V_{s,t}$	$\Delta V_{s,z}$	$<\bar{v}_s>$	$<\bar{v}>$	$\Delta V_{s,t}$	$\Delta V_{s,z}$
11/04/1994	0.728	0.606	0.053	0.069	0.352	0.792	-0.390	-0.050
12/04/1994	0.662	0.635	-0.009	0.036	0.660	0.868	-0.156	-0.052
18/04/1994	0.600	0.587	-0.005	0.018	0.808	0.793	-0.002	0.017
19/04/1994	0.472	0.469	-0.003	0.006	0.905	0.678	0.123	0.104
03/05/1994	0.484	0.456	0.010	0.018	0.751	0.617	0.108	0.026
10/05/1994	0.644	0.606	0.019	0.019				
11/05/1994	0.630	0.532	0.033	0.065	0.648	0.758	-0.157	0.047
16/05/1994	0.674	0.541	0.049	0.084	0.729	0.846	-0.122	0.005
12/04/1995	0.607	0.574	0.001	0.032	0.698	0.959	-0.232	-0.029
18/04/1995	0.686	0.694	-0.037	0.029	0.944	0.969	0.022	-0.047
20/04/1995	0.760	0.692	0.010	0.058	0.928	0.858	-0.059	0.129
25/04/1995	0.540	0.475	0.026	0.039	0.694	0.678	0.015	0.001
27/04/1995	0.674	0.607	0.042	0.025	0.681	0.837	-0.087	-0.069
03/05/1995	0.744	0.643	0.058	0.043	0.712	0.775	0.028	-0.091
10/05/1995	0.522	0.489	0.016	0.017	0.713	0.721	0.091	-0.099
mean	0.628	0.574	0.018	0.037	0.730	0.796	-0.059	-0.008
%	100	91.3	2.8	5.9	100	109.1	-8.0	-1.0
(b)								
mean	0.549	0.484	0.033	0.033	0.606	0.624	-0.012	-0.007
%	100	88.1	6.0	5.9	100	103.1	-2.0	-1.1
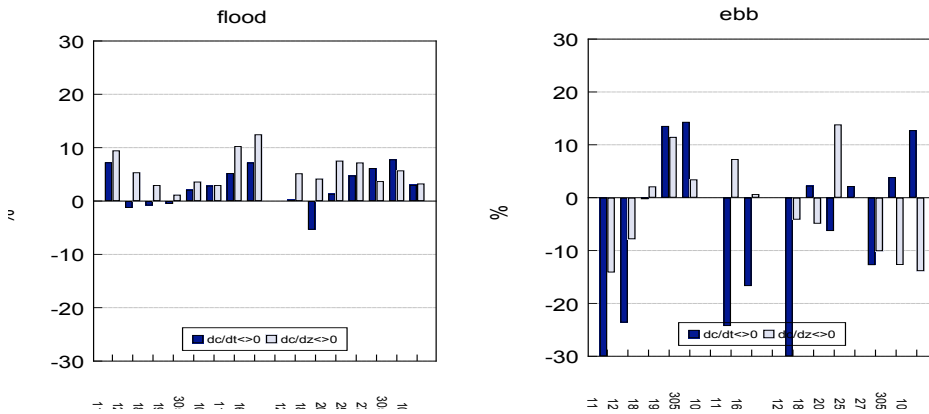
Fig. L. *Relative contribution (%) to the transport velocity of temporal (dc/dt<>0 = $\Delta V_{s,t}$) and vertical (dc/dz<>0 = $\Delta V_{s,z}$) larval concentration variations, for flood and ebb separately for all sampling dates.*

Table F. *Duration of the flood and ebb period (T, min), relative time- and depth-averaged transport velocity ($<\bar{v}_r> = |<\bar{v}_s>| - |<\bar{v}>|$, m s^{-1}), and displacement relative to water (L$_s$ - L, km) of salinity, suspended matter and larvae, assuming that estimated transport velocities are valid also during the slack periods. Relative displacement in landward direction is positive during flood and negative during ebb.*

Date	T	Salinity $<\bar{v}_r>$	L$_s$ - L	Susp. $<\bar{v}_r>$	L$_s$ - L	Larvae $<\bar{v}_r>$	L$_s$ - L
Flood							
11/04/1994	325	-0.013	-0.25	-0.050	-0.98	0.122	2.38
12/04/1994	350	-0.045	-0.94	0.030	0.63	0.027	0.57
18/04/1994	364	0.001	0.02	-0.023	-0.50	0.013	0.28
19/04/1994	396	-0.013	-0.31	0.006	0.14	0.003	0.07
03/05/1994	421	-0.006	-0.15	-0.045	-1.14	0.028	0.71
10/05/1994	361	-0.017	-0.37	0.065	1.41	0.038	0.82
11/05/1994	365	-0.014	-0.31	0.041	0.90	0.098	2.14
16/05/1994	382	-0.013	-0.30	0.047	1.08	0.133	3.05
12/04/1995	400	-0.023	-0.55	0.036	0.86	0.033	0.79
18/04/1995	366	-0.027	-0.59	0.055	1.21	-0.008	-0.18
20/04/1995	389	-0.023	-0.54	0.030	0.70	0.068	1.59
25/04/1995	393	-0.003	-0.07	-0.008	-0.19	0.065	1.53
27/04/1995	375	-0.018	-0.40	0.026	0.59	0.067	1.51
03/05/1995	369	-0.020	-0.44	0.024	0.53	0.101	2.23
10/05/1995	406	-0.004	-0.10	-0.006	-0.15	0.033	0.80
mean	*377*	*-0.016*	*-0.35*	*0.015*	*0.34*	*0.055*	*1.22*
s.d.	*24*	*0.011*	*0.24*	*0.035*	*0.78*	*0.043*	*0.94*
Ebb							
11/04/1994	423	0.026	0.66	-0.087	-2.21	-0.440	-11.17
12/04/1994	391	-0.006	-0.14	-0.027	-0.63	-0.208	-4.88
18/04/1994	378	-0.025	-0.57	0.033	0.75	0.015	0.34
19/04/1994	339	0.005	0.10	0.046	0.94	0.227	4.62
03/05/1994	342	0.009	0.18	0.003	0.06	0.134	2.75
10/05/1994	362						
11/05/1994	384	-0.010	-0.23	0.036	0.83	-0.110	-2.54
16/05/1994	364	0.021	0.46	0.059	1.29	-0.117	-2.55
12/04/1995	382	-0.006	-0.14	0.050	1.14	-0.261	-5.97
18/04/1995	366	-0.009	-0.20	-0.021	-0.46	-0.025	-0.55
20/04/1995	370	0.000	0.00	-0.016	-0.36	0.070	1.55
25/04/1995	357	0.002	0.04	0.055	1.18	0.016	0.34
27/04/1995	376	-0.007	-0.16	0.130	2.93	-0.156	-3.52
03/05/1995	370	-0.005	-0.11	-0.025	-0.56	-0.063	-1.40
10/05/1995	334	0.001	0.02	0.101	2.02	-0.008	-0.16
mean	*369*	*0.000*	*-0.01*	*0.024*	*0.49*	*-0.066*	*-1.65*
s.d.	*22*	*0.013*	*0.30*	*0.057*	*1.29*	*0.169*	*3.97*

The contribution of the vertical variation was higher than of the temporal variation during flood and always positive (**fig. l**). In contrast, the temporal variation appears to dominate during ebb and, although highly variable, the contributions were generally negative. The contribution of the temporal variation ranges between -0.04 and 0.06 m s^{-1} during flood and between -0.39 and 0.12

m s^{-1} during ebb, whereas the contribution of the vertical variation varies between 0.01 and 0.08 m s^{-1} during flood and between -0.10 and 0.13 m s^{-1} during ebb (**table e**). Overall (**table e**), transport velocity of larvae was 9% higher than of water during flood, mainly due to the vertical concentration variation (6%). During ebb, larval transport velocity was 9% lower than of water, but in this case almost exclusively due to the temporal concentration variation (8%). Including slack periods gives a substantial reduction of the transport velocities of water and larvae (**table e**b), an increase (flood) or decrease (ebb) of the contribution of the temporal concentration variation to the larval transport velocity, whereas the contribution of the vertical variation does not change.

Taking the duration of the flood and ebb periods into account, the differences in transport velocity result in differential larval displacement compared to the tidal excursion of water. The relative displacement of larvae during flood was landward on most sampling dates (on average 1.2 km). During ebb, larval displacement remained on average 1.7 km behind, but a relative displacement seaward was observed on 5 out of 14 sampling dates (**table f**).

DISCUSSION

The centre of mass of a dissolved substance in a well-mixed water column lies theoretically halfway. Although the absolute differences observed were small, the centre of mass of salinity was significantly lower than 0.5, which may be taken as an indication of stratification. This was more so in 1994 than in 1995. Vertical variation was particularly pronounced around HW when relatively fresh water starts returning from the flats and intrudes at the surface (Postma 1982). Furthermore, a front of fresh water, discharged into the Dollard at Nieuwe Statenzijl (Dorrestein 1960, De Jonge 1988, Jager 1998), passes the sample location at the end of the ebb and causes temporary stratification with low surface salinity values followed by reduced salinities in the entire water column. Incomplete mixing does indeed occur in the vicinity of the sample location (Dorrestein 1960). However, the temporal variation due to the longitudinal salinity gradient in the channel, which is caused by the freshwater discharges, is far more important for the transport velocity than the short term vertical variations. The volume of the discharge is highly variable and depends largely on precipitation. The high transport velocity measured during ebb on April 11th and the low value during flood on April 12th 1994 (curves A and B in **fig. c**) are probably related to a relatively high discharge at Nieuwe Statenzijl.

Both the temporal and vertical variations in suspended matter concentrations are influenced by the processes of advection, diffusion, erosion and deposition, although in different ways.

The temporal concentration variations will reflect the effects of lateral and longitudinal advection, but processes of erosion and deposition, which are current-related, dominate the temporal variation (Van Leussen 1991) and thus its contribution to the transport velocity. The erosion-deposition cycle results in temporal concentration variations which are more or less synchronous with the current velocity, leading to a positive contribution to the (time-averaged) transport velocity.

The vertical concentration profile will exhibit increasing values towards the bottom as a result of erosion and deposition. Because the vertical current profile shows an opposite trend, the contribution of these profiles to the transport velocity will be negative. Turbulent diffusion is current-dependent, and results in a more homogeneous vertical distribution at higher velocities. However, the vertical redistribution, merely due to turbulent diffusion, also affects the temporal concentration variation at each depth. In the upper layer the temporal variation will be synchronous with the current speed, yielding a positive contribution to the time-averaged transport velocity, while near-bottom the opposite occurs. In theory, this would result in an S-shaped vertical profile of the time-averaged transport velocity.

Under steady and uniform conditions a passive substance with a specific gravity larger than water may be expected to have its centre of mass in the lower half of the water column. Although these conditions are not met in the Dollard, the centre of mass of suspended matter was always significantly lower than 0.5. Higher current velocities, and consequently higher turbulent mixing, may explain the somewhat higher value during ebb than during flood.

For suspended matter, temporal and vertical variation are both important and moreover they counteract. The high concentrations in the lower part of the water column, where current velocity is relatively low, cause a negative relative (time and) depth-averaged transport velocity. In contrast, the positive correlation between temporal variations in suspended matter and current velocities causes a positive relative transport velocity. The time-averaged transport velocity profiles do not show the theoretical S-shape (with positive values in the upper, and negative values in the lower water layers) that would be expected if merely turbulent diffusion was acting. Therefore, we deduce that the effects of turbulent diffusion are subordinate to those of current-dependent erosion-deposition.

In addition, (stormy) wind conditions strongly influence the exchange of sediment between the flats and the channels (De Haas and Eisma 1993) and therefore may also affect temporal variation in suspended matter. The highest wind velocity observed during sampling was 12 m s^{-1} (Jager 1998), which is 6 on the scale of Beaufort, but on most sampling dates wind velocity was much less.

Different water masses can be expected to have different loads of suspended matter and therefore front conditions such as between fresh and estuarine water may also affect temporal variation. For example, the negative relative transport velocity of suspended matter in the lower half of the water column during the ebb of 11 April 1994 (curve A in **fig. g**) may express this phenomenon. Effects of both wind and front conditions are expected to be more important during the ebb, and would result in increased concentrations by advection rather than by local redistribution of sediment by erosion-deposition. However, the observed small differences between flood and ebb in the concentration profiles and in the relative contribution of the temporal variation do not indicate that either of the two processes has been very influential. The overall transport velocity of suspended matter is only slightly higher (on average 2.5 to 5%) than of water.

The most important processes that determine the larval transport are the horizontal (longitudinal and lateral) advection by tidal currents, the vertical advection (expressing the effects of both gravity and swimming) and the vertical diffusion by turbulence. Theoretically, upward larval migration will have a similar effect as turbulent diffusion during increasing, and opposite effects during decreasing current velocities. The selective tidal stream transport hypothesis predicts a positive relative time-averaged transport velocity in the upper layers and negative values in the lower layers during flood, and vice versa during ebb, caused by vertical migration.

The mean centre of mass of larvae differs significantly from those of salinity and suspended matter and can be much higher than 0.5. The centre of mass of the larval distribution was usually higher than of suspended matter, particularly during flood. In contrast, however, the larval centre of mass is lower during ebb than during flood. This indicates that the larvae are not only subject to physical forces but that an active component in the vertical direction is involved.

For larvae, the vertical concentration variation has a large and positive effect on the transport velocity during flood. This is in contrast with suspended matter where the vertical variation has a large but negative effect. Because the flounder larvae have a positive fall velocity in both saline and fresh water their specific gravity would lead to a negative contribution to the transport velocity. The estimated positive contribution of vertical variation during flood (5.9%) can only be explained by upward swimming. Because the physical forces acting on the larvae have to be counteracted and overcome, upward swimming may in reality contribute even more than the estimated value.

During ebb, the vertical concentration variations contribute on average negatively to the larval velocity, suggesting that larval swimming may be less important. The negative effects of temporal variations on the transport velocity are more pronounced during this phase. Although the larvae originate from the open sea, within the estuary a landward concentration gradient has been

observed (Jager 1998) causing decreasing larval concentrations during flood and increasing concentrations during ebb. In combination with the relatively high current velocities during the first half of the flood and ebb, this will lead to positive values of the relative time-averaged transport velocity during flood and negative values during ebb. This deviation from a (symmetrical) sinusoidal velocity curve is more pronounced during ebb than during flood and explains the higher contribution of temporal variation during the former tidal phase.

The result of temporal variation in turbulent diffusion would be an S-shaped transport velocity profile with positive values in the upper half of the water column and negative values in the lower half, as observed on 18 April 1994 (curve C in Fig. 11). Such a profile seems to be the exception rather than the rule and turbulent diffusion is therefore not believed to be of much influence on the larval transport velocity. Effects of vertical migration and longitudinal variation appear to be much more important.

The number of larval concentration measurements in the vertical profile was in practice limited to 3 (a.o. by the small depth of the sample location at LW). Given the irregular distribution of flounder larvae, this should be considered as the minimum to apply the presented method. Increasing the number of concentration measurements in the vertical profile will increase the accuracy.

In contrast to Rowe and Epifanio (1994), our approach explicitly adresses the influence of the vertical distribution of concentration and current speed on transport velocities. Assuming a homogeneous vertical distribution would have led to a 68% bias in the estimated relative transport velocity, or a 6% bias in the estimated transport velocity during flood. Another difference with Rowe and Epifanio (1994) is the use of relative depth in our calculations, which is necessary because in the Dollard the tidal difference (3 to 3.5 m) is large compared to the depth of the sample location (5 m below MSL). Applying the concept of transport velocity to suspended matter and salinity, beside larvae, is an interesting extension of our approach which allows a more detailed analysis of the processes underlying the estuarine transport.

We made no attempt to calculate a tidally averaged residual transport velocity, because the applied Eulerian approach does not justify such estimates. Ridderinkhof and Zimmerman (1990) showed that the Lagrangian residual transport velocity of water differs appreciably from the Eulerian one in a non-uniform velocity field as typically present in the Dollard. A similar reasoning applies to estimates of displacement. The given estimates of the latter should therefore not be taken too literally, because they are based on extrapolations of current velocities measured at one particular location.

Nevertheless, assuming a uniform velocity field in the entire estuary, it is tempting to make a rough calculation of the time required for flounder larvae to reach the Dollard after entering the estuary through the tidal inlet at Borkum.

The larvae appear to succeed in covering 1.2 km more than the average tidal excursion during flood. During ebb, their displacement is 1.7 km less seaward than that of water (**table f**). This would mean a net landward displacement per tidal cycle of about 3 km. To cover the distance between the tidal inlet at Borkum and the Dollard nursery (50 km), the larvae would require about 9 days. This time agrees with findings in the Elbe estuary, where flounder larvae were estimated to need two weeks to cover a distance of 79 km (Bos *et al.* 1995).

The results support the conclusion that the vertical distribution has a dominant effect on the larval velocity of flounder. The absolute contribution of at least 6% of active swimming to larval transport velocity may seem insignificant. Apparently, flounder larvae can only enhance or inhibit their transport to a limited extent, and their distribution inside the nursery area is largely determined by the water circulation. However, even with small differences in transport velocities between larvae and water, the cumulative effect of a 6% contribution during each subsequent tidal cycle will eventually lead to considerable differences in the residual displacement of flounder larvae in the Dollard.

APPENDIX

Symbol	Description	Dimension
$z_{cm}^{*}(t)$	centre of mass relative to depth	
$\bar{c}(t)$	depth-averaged instantaneous concentration	g kg^{-1}, kg m^{-3}, n m^{-3}
$<c(z^{*})>$	time-averaged local concentration (mass preserving)	idem
$\bar{v}_{s}(t)$	instantaneous depth-averaged transport velocity	m s^{-1}
$<v_{s}(z^{*})>$	time-averaged transport velocity at relative depth ('larval velocity')	m s^{-1}
$<\bar{v}_{s}>$	time- and depth-averaged transport velocity	m s^{-1}
$\Delta V_{s,t}$	contribution of temporal concentration variation to transport velocity	m s^{-1}
$\Delta V_{s,z}$	contribution of vertical concentration variation to transport velocity	m s^{-1}
$<\bar{v}_{s}>'$	transport velocity without the contribution of vertical concentration variation	m s^{-1}
L_s	tidal displacement of a substance	km

ACKNOWLEDGEMENTS

Across-channel distribution of flounder larvae (*Platichthys flesus* L.) in the Ems-Dollard estuary and its effects on larval transport estimates

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ABSTRACT

Estimates of larval transport of the flounder (*Platichthys flesus* L.) in the Ems-Dollard were based on the assumption of homogeneous concentrations across the width of the tidal channel. This needed further investigation, because there were indications from other studies that flatfish larvae are heterogeneously distributed across a tidal channel. The opportunity of a large-scale water flow measurement in the middle part of the Ems-Dollard, involving many ships, was seized to study the larval distribution of flounder across the tidal channel and to test the assumption of homogeneous concentrations. In addition, larval concentrations were measured on two positions on another cross-section which was situated deeper into the Dollard, and which was the sampling location of extensive studies of larval flounder by Jager (Chapter 2*, 1998, subm.*). The effects of a heterogeneous distribution on larval transport estimates are evaluated.

The hypothesis that larval concentrations are homogeneous across the width of the channel was rejected by the present study. Larval concentrations showed heterogeneous tidal variations at the different positions on the cross-sections in the middle part of the estuary, and moreover, mean concentrations differed. Larvae tend to concentrate in the main stream. Given the large variability in larval concentrations, data were not sufficient to determine tidal patterns in the across-channel distribution.

The accuracy of the estimates of overall transport through the channel section improved by increasing the number of sampling positions per cross-section. However, some of the individual sampling positions can provide transport estimates that approach the overall transport based on all four sampling positions. These are generally the positions in the centre of the channel with the largest water transport.

In the cross-section deeper in the Dollard, tidal variations in larval concentrations were similar, and mean concentrations differed between the positions only during part of the tidal cycle. Concentrations tended to be higher in the flood-branch of the channel. The estimates of the net transport were affected in an unpredictable way, although measurements at the ebb-dominated position on the channel cross-section underestimated both the flood and ebb transport of flounder larvae. The data do not allow a well-founded correction of larval transport estimates that are based on only one position per cross-section.

INTRODUCTION

Estimates of larval transport of flounder (*Platichthys flesus* L.) in the Dollard were based on larval concentration measurements in the deepest part of a cross-section of the main tidal channel in the centre of this nursery area (Chapter 2, Jager 1998). The approach followed was based on the assumption that larval transport can be representatively estimated by measuring depth-averaged larval concentrations and current velocity at one point on a cross-section in the tidal channel. Larval transport estimates were obtained by multiplying the depth-averaged larval concentration at one point by the water flow through the cross-section. The water flow is derived by multiplying the wet area of the channel profile by the cross-sectional current velocity which in turn is derived from the current velocity at the sampling location by means of previously established linear regression equations (see Chapter 2). An underlying assumption of using this method is, that larval concentrations are homogeneous in the cross-section.

However, the water flow through the cross-section of a tidal channel is by no means homogeneous. Due to the particular geophysical location and structure, relatively more water may be transported through one side of the cross-section during flood, whereas the other side may show an ebb-surplus (De Jonge 1991). Heterogeneous larval concentrations of plaice (*Pleuronectes platessa* L.) across the cross-section of a tidal channel in the south-west Netherlands were observed by Rijnsdorp *et al.* (1985). Weinstein *et al.* (1980) found indications that larval concentrations of *Paralichthys spp.* were the highest in the flood branch of the channel during flood, and the highest in the ebb-branch during ebb. These studies indicate that the assumption of homogeneous distribution of larvae across the channel may not be justified, and needs further foundation.

The opportunity of an international STROEDE survey (Dutch acronym of '**STRO**ommeting **E**ems-**D**ollard **E**stuarium'), involving a fleet of 10 ships per cross-section, was seized to measure larval concentrations across the main channel in the middle part of the Ems-Dollard estuary. This campaign, which took place in the middle of the larval immigration period of flounder (*Platichthys flesus* L.), offered an unique opportunity to test the hypothesis that larval concentrations are homogeneously distributed over the width of a channel in the Ems-Dollard estuary. The present study also investigates whether a single station may provide an unbiased and reliable estimate of transported water and larvae. Implications for the method applied in Chapter 2 and 3 to estimate larval transport are evaluated and discussed.
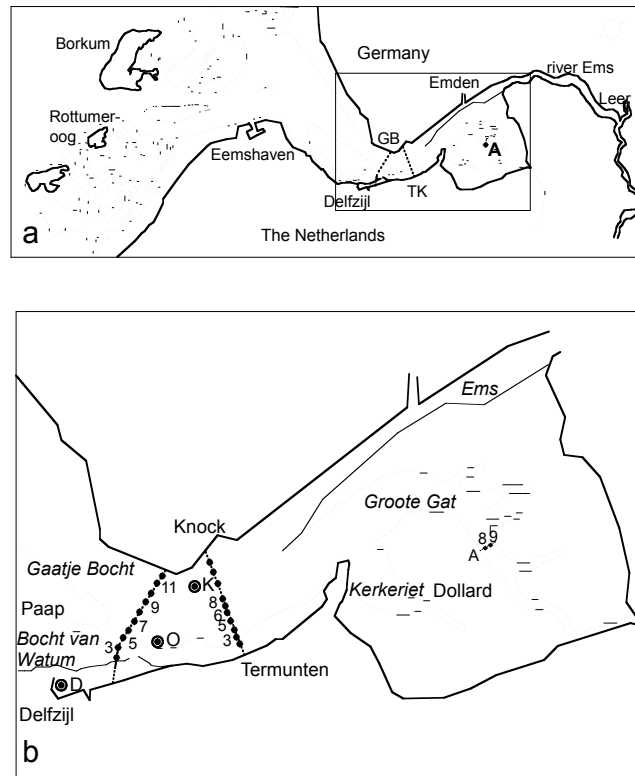
Fig. A *Study area, with (a) the Ems-Dollard estuary and (b) the sampled cross-sections Bocht van Watum/Gaatje Bocht, Termunten-Knock and Groote Gat (A), and the tidal gauges Paap, Delfzijl (D), Oterdum (O) and Knock (K). Dots represent the ship positions on the cross-sections.*

MATERIALS AND METHODS

Large-scale water flow measurements have been made in the Ems estuary in 1994 as part of an international STROEDE co-operation between 'Rijkswaterstaat (Directie Noord Nederland)' and the 'Wasser- und Schiffahrtamt Emden'. To accurately estimate the water transport in the middle part of the estuary, the water flow through two cross-sections, Bocht van Watum/Gaatje Bocht (GB) and Termunten-Knock (TK; *fig. a*), was measured on 26 and 28 April 1994, respectively. Measurements took place during a complete tidal cycle from one Low Water (LW) to the next simultaneously from 10 anchored ships per cross-section, following standard procedures (Duits-Nederlandse Eemscommissie 1996). The positions of the vessels on the cross-sections were carefully selected to representatively cover the width of the channel.

Fig. B. *Profiles of the sampled cross-sections, with mean low water (MLW) and mean sea level (MSL) indicated. (a) GB, (b) TK. The numbers indicate the selected positions at which larval concentrations were measured. Physical variables were measured at positions indicated by ***

In addition to the water flow measurements, plankton samples were taken simultaneously on 5 (26 April) or 4 (28 April) of the 10 positions in each cross-section (**fig. b**) by the National Institute for Coastal and Marine Management / *RIKZ*. Larval sampling was accompanied by measurements of water temperature, salinity (WTW-conductivity meter) and turbidity (Partech meter) on 2 positions per cross-section only.

During an additional survey in 1995, two positions in the cross-section A (8 and 9; **fig. a**) were sampled simultaneously on 20 and 27 April following the same sampling procedures as described by Jager (1998). Plankton sampling in GB and TK differed slightly because the net was lowered and lifted only 1 to 2 times for each sample. This adaptation was necessary to standardise sampling at the different positions within the cross-sections and because of the larger depth of the channels in the middle part of the estuary (about 15 m instead of only 5 m in the Dollard).

The sampling positions will be referred to by the abbreviation of the cross-section followed by the respective numbers as indicated in Figs. 1 and 2.
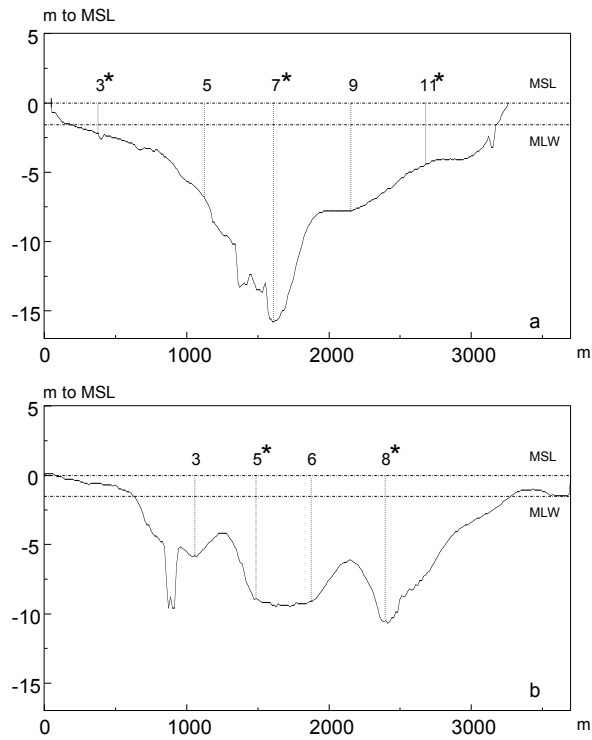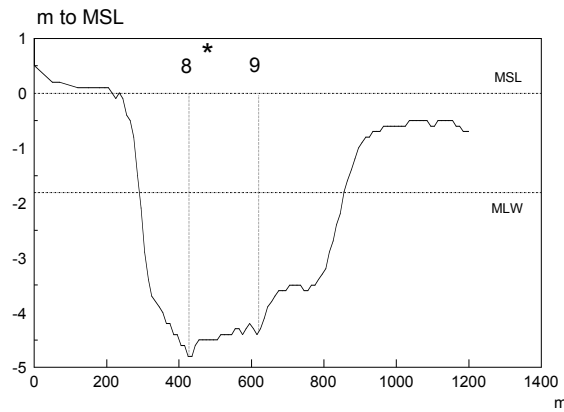
Fig. C. *Profile of the sampled cross-section A with mean low water (MLW) and mean sea level (MSL) indicated. The numbers indicate the positions at which larval concentrations were measured. Additional physical variables were measured at the position indicated by *.*

Gaatje Bocht

Cross-section GB has a width of 3000 m, and a maximum depth of 16 m below mean sea level (MSL) at position GB_7.(**fig. b**a). The outflow of the Dollard via Kerkeriet and Groote Gat may be largely expected at GB_7 and GB_9, whereas GB_{11} will largely reflect the outflow of the river Ems. Current velocities at GB_3 were very low, resulting in very incomplete plankton sampling. Therefore, GB_3 was excluded from the analyses.

Termunten-Knock

In the cross-section TK, width 3000 m, the outflow channels of the Kerkeriet (TK_3), the Groote Gat (TK_5, TK_6) and the river Ems (TK_8) can clearly be discerned (**fig. b**b). Maximum depth is 10 m below MSL at position TK_8.

Groote Gat

During the additional survey on 20 and 27 April 1995, two positions (8 and 9) at a mutual distance of 200 m were sampled simultaneously in the channel Groote Gat (cross-section A, **fig. c**), which is located deeper into the estuary. In this cross-section extensive studies of larval flounder have been performed at position 8 during surveys in 1993, 1994 and 1995 (Chapter 2, Jager 1998, Jager *subm.*). A_8 is the deepest point on the 1000 m wide cross-section and situated in the ebb-dominated part of the channel.

Data treatment

The current velocity measurements were processed with the VIMET (Rijkswaterstaat 1980) computer programme to estimate the water flow. The programme VIVIAN (Ariaans and Boorsma 1993) was applied to process, interprete and present the results of the VIMET analyses. Multiplying the local (i.e. at the sampling position) instantaneous (i.e. at each sampling time) depth-averaged current velocity by the instantaneous depth of the water column gives the local instantaneous water flow per unit width (m^3 s^{-1} m^{-1}). The water level was continuously registrated by the tidal gauges of Delfzijl, Paap, Oterdum and Knock (*fig. a*). Integration of the local instantaneous water flow over the tidal period gives the local water transport (m^2 per tide). The overall tidal water transport through the STROEDE cross-sections (m^3) is obtained by linear interpolation of the local water transports over the width of the channel. See Duits-Nederlandse Eemscommissie (1996) or Kiezebrink (1996) for a more extensive description of the hydrographical methods used.

The local instantaneous larval flux (n s^{-1} m^{-1}) was calculated by multiplying the local depth-averaged larval concentration (n m^{-3}) by the local instantaneous water flow (m^2 s^{-1}). Integration over the tidal period, excluding slack-periods, resulted in a flood and ebb larval transport for each sampled location on the cross-section (n m^{-1} per tide). Estimates of the larval tidal transport through the entire cross-section (n) were derived in two ways:

1. by linear interpolation of the local larval transports and extrapolation to a zero-transport at the channel borders, which are arbitrarily set (about msl) at 0-3000 m (GB), 500-3500 m (TK) and 250-1000 m (A).
2. by multiplying the local instantaneous larval concentration by the cross-sectional water flow (m^3 s^{-1}), followed by integration over the tidal period. The cross-sectional flow can be obtained from the local water flow
   a) either by means of the regression equations in **table a** and 2, or
   b) by linear interpolation over the width of the channel.

To evaluate method 2a, generally applied by Jager (1998, Chapter 2), the transport estimates obtained by the different methods are compared with method 1, which is considered the best available estimate.

Statistical analyses

Multifactor ANOVA was applied to ln-transformed depth-averaged larval (concentrations + 1) and depth-averaged current velocity, to investigate temporal and local patterns in those variables. A sensitivity analysis of the overall larval transport estimates obtained by method 1, based on N (varying from 1 to 4) sampling positions, was done for GB and TK to assess the effect of the number of sampling locations on the overall transport estimate.

Table A. *Regression parameters used to calculate the water flow during flood and ebb by sample location on the cross-sections GB and TK, based on extensive measurements on 26 and 28 April 1994. Regression equation $Y = a*X$, where Y = water flow (m^3 s^{-1}) through the cross-section, X = absolute value of the water flow (m^2 s^{-1}) at the sampling point, a = slope, regression forced through the origin, R^2 = correlation coefficient; $P<0.001$ for all locations.*

| | **Flood** | | | **Ebb** | | |
Location	a	R^2	n	a	R^2	n
GB_3	311	0.98	24	341	0.99	17
GB_5	3622	0.98	20	3487	0.98	22
GB_7	975	0.99	20	1200	0.99	22
GB_9	2382	0.99	20	1879	0.99	22
GB_{11}	3305	0.98	20	3478	0.96	22
TK_3	3882	0.98	20	3751	0.99	22
TK_5	1730	0.99	20	2275	0.99	22
TK_6	1481	0.99	20	1804	0.99	22
TK_8	1512	0.99	20	1329	0.92	22

Table B. *Regression parameters used to calculate water flow during flood and ebb of two sampling positions on cross-section A, based on extensive measurements in December 1992. Regression equation $Y = a*X + b$, where Y = depth-averaged current velocity (cm s^{-1}) of the cross-section; X = depth-averaged current velocity (cm s^{-1}) of the sampling position, a = slope, b = intercept; R^2 = correlation coefficient.*

| | **Flood** | (n=19) | | **Ebb** | (n=18) | |
Location	a	b	R^2	a	b	R^2
A_8	0.840	0.0053	0.97	0.741	0.0006	0.99
A_9	0.845	0.0089	0.98	0.787	0.0375	0.99

RESULTS

Gaatje Bocht and Termunten-Knock

Depth-averaged current velocity showed parallel tidal variations at the sampling locations in both cross-sections (**table c**), the interaction of tidal phase by position not being significant. Mean velocity was significantly lower at GB_5 than at the other positions in this cross-section, and was significantly higher at GB_{11} than at GB_7. In cross-section TK, the mean depth-averaged velocity was significantly lower at TK_3 than at all other sampling positions.

Table C. *Multifactor ANOVA of depth-averaged current velocity for (a) GB and (b) TK.*

(a)	SS	Df	F-ratio	P-value	Sign.
MAIN EFFECTS					
tidal phase	79836	5	13.68	0.000	***
position	22548	3	29.06	0.000	***
INTERACTIONS					
tidal phase*position	12240	15	1.49	0.12	n.s.
RESIDUAL	63734	116			
TOTAL (corrected)	179198	139			

(b)	SS	Df	F-ratio	P-value	Sign.
MAIN EFFECTS					
tidal phase	57114	5	23.30	0.000	***
position	12373	3	8.41	0.000	***
INTERACTIONS					
tidal phase*position	7556	15	1.03	0.43	n.s.
RESIDUAL	54912	112			
TOTAL (corrected)	131825	135			

During flood, the largest water transport took place through the deepest point of the westerly cross-section (GB_7), and more or less proportional to the topography of the channel bed through the cross-section TK (**table d**, **fig. d**). During ebb, relatively more water was transported through the northern part of both cross-sections. Both GB and TK were estimated to have an overall flood surplus in water transport, of 3-4%, respectively. Nevertheless, some points on the cross-section were characterised by an ebb surplus (GB_6, GB_9, TK_2 and TK_8; **table d**, **fig. d**). GB_7, TK_5 and TK_6 had a flood surplus.

Table D. *Local (n m^{-1}) and overall (n) transport per tide, of water (10^3 m^3) and larvae (10^3), through the cross-sections GB and TK. Overall transport according to method 1.*

	Flood		**Ebb**	
Location	Water	Larvae	Water	Larvae
GB_3	1.2	(18.6)	25.0	(11.9)
GB_5	76.8	132.1	70.3	50.3
GB_7	277.4	1027.9	207.9	375.3
GB_9	111.6	350.6	133.5	115.9
GB_{11}	80.6	86.2	73.3	68.4
Overall GB	275342	839666	266583	318951
TK_3	70.4	363.8	67.3	131.0
TK_5	158.2	653.8	112.4	234.2
TK_6	184.2	1113.6	140.4	373.6
TK_8	176.5	618.5	198.9	265.0
Overall TK	287463	1459115	275619	546903

Larval transport at GB_3 (in parentheses) is not reliable.

The largest larval transport occurred at the deepest point on cross-section GB (**table d**). On the other cross-section, the highest larval transport was measured at TK_6. All sample locations on both cross-sections showed a flood surplus in larval transport (**fig. d**), which reached a maximum at GB_7 on the westerly and at TK_6 on the easterly cross-section.

On both cross-sections, larval concentrations showed different variations during the tidal cycle at the different sampling positions, indicated by a significant interaction of position on the cross-section by tidal phase (**table e**). However, the common pattern consisted of high concentrations at the beginning of the flood, followed by a decrease toward HW slack and an increase towards the end of the ebb (**fig. e**).
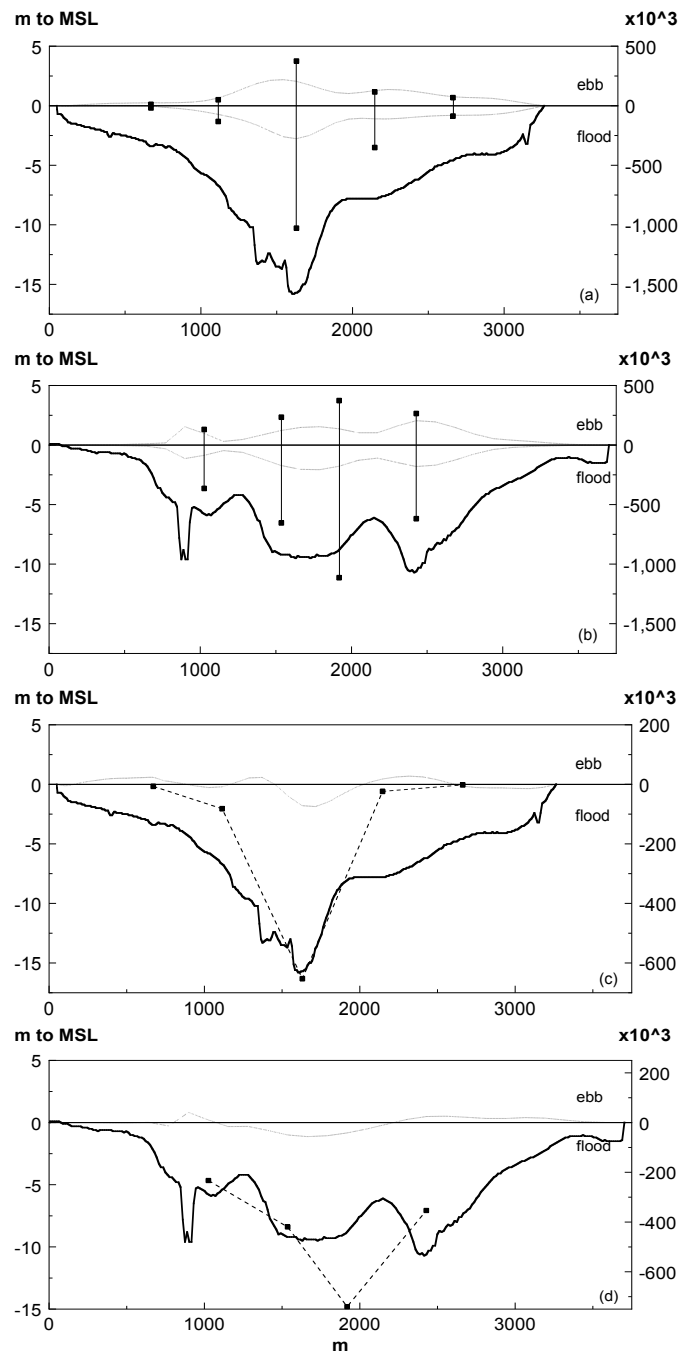
Fig. D. *Tidal (flood, ebb) water transport (m³, dotted line) and local larval transport (n, square markers) through the cross-sections (a) GB and (b) TK, and residual (i.e. net) transport of water and larvae through the cross-sections (c) GB and (d) TK. Left axis: depth of the channel profile; right axis: transport.*

Table E. Multifactor ANOVA of ln-transformed (larval concentrations+1) for the cross-sections (a) GB and (b) TK.

(a)	SS	Df	F-ratio	P-value	Sign.
MAIN EFFECTS					
tidal phase	14.60	5	21.50	0.000	***
position	3.79	3	9.30	0.000	***
INTERACTIONS					
tidal phase*position	5.34	15	2.62	0.002	**
RESIDUAL	13.59	100			
TOTAL (corrected)	39.22	123			
(b)	SS	Df	F-ratio	P-value	Sign.
MAIN EFFECTS					
tidal phase	22.61	5	16.10	0.000	***
position	7.15	3	8.49	0.000	***
INTERACTIONS					
tidal phase*position	13.00	15	3.09	0.000	***
RESIDUAL	27.25	97			
TOTAL (corrected)	72.78	120			

During flood (**table f**), the temporal concentration pattern of GB differed among positions, and thus allowed no conclusion about differences in mean concentrations. During ebb, concentrations across GB varied in a similar way (interaction of tidal phase by position not significant). The differences between positions were not significant (p=0.07), though mean concentration at GB_7 appeared to be higher than at GB_5 with intermediate values at GB_9 and GB_{11}.

Table F. Multifactor ANOVA of ln-transformed (larval concentrations+1), flood and ebb separately, for the cross-sections (a) GB and (b) TK.

|	Flood				Ebb			
(a)	Df	F-ratio	P-value	Sign.	Df	F-ratio	P-value	Sign.
MAIN EFFECTS								
tidal phase	2	22.54	0.000	***	2	20.80	0.000	***
position	3	11.14	0.000	***	3	2.49	0.070	n.s.
INTERACTIONS								
tidal phase*position	6	3.52	0.006	**	6	1.20	0.320	n.s.
		SS				SS		
RESIDUAL	50	6.69			50	6.89		
TOTAL (corrected)	61	20.94			61	15.31		
(b)	Df	F-ratio	P-value		Df	F-ratio	P-value	
MAIN EFFECTS								
tidal phase	2	10.93	<0.001	***	2	22.27	0.000	***
position	3	5.25	0.003	**	3	3.60	0.020	*
INTERACTIONS								
tidal phase*position	6	3.29	0.008	**	6	4.40	0.001	**
		SS				SS		
RESIDUAL	50	16.59			47	10.65		
TOTAL (corrected)	61	37.62			58	30.04		
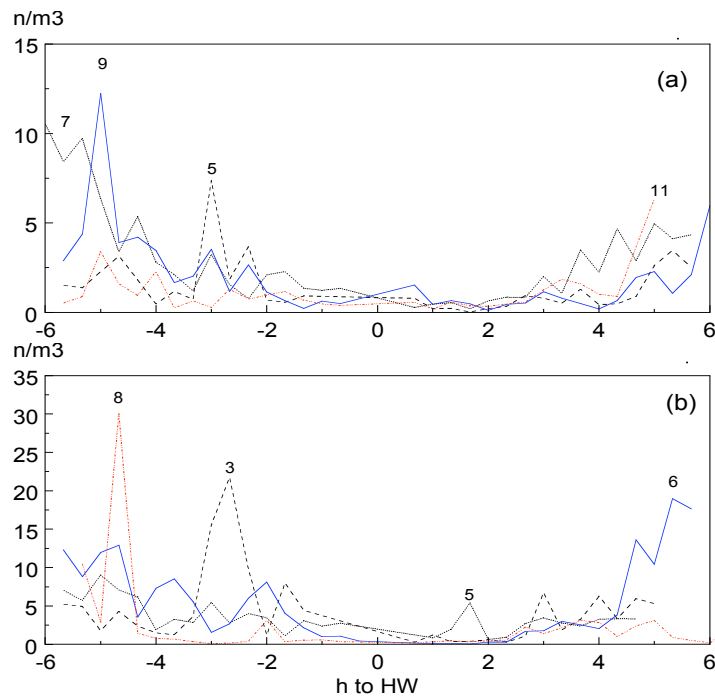
Fig. E. *Concentrations (n m^-3) of flounder larvae at the different positions (numbers are indicated in the Fig.) on the cross-section of (a) GB and (b)TK.*

Across TK, concentration patterns differed among positions during both tidal phases, which complicates discrimination between positions of differences in mean concentrations. TK_8 tended to have lower mean concentrations than all other positions.

An analysis of the effect of the number of positions on the overall transport estimate (**table g**) indicated that the mean generally increased with increasing number of positions and that the standard deviations converged.

Table G. *Average overall larval transport (10^6; avg.) and standard deviation (10^6; s.d.), calculated by method 1 from a variable number of sampling positions (N) on the cross-sections (a) GB and (b) TK. n is the number of observations, whereas min. and max. are the limits of the standard-error (s.e.) interval around the mean.*

(a)		**Flood**				**Ebb**			
N	n	avg.	s.d.	min.	max.	avg.	s.d.	min.	max.
1	4	599	652	273	925	229	227	115	342
2	6	851	505	645	1057	318	182	244	393
3	4	914	367	730	1097	343	136	275	411
4	1	840				319			
(b)									
1	4	1031	468	797	1265	376	150	302	451
2	6	1345	272	1235	1456	491	81	458	524
3	4	1444	141	1374	1514	533	30	518	548
4	1	1459				547			

Referring to the investigations of Jager (*in prep.*, 1998) in the Groote Gat, it is important to know whether one sampling position may produce reliable estimates of larval transport through the cross-section. For GB and TK, the cross-sectional transport was calculated, based on each of the four sampled positions following methods 2a and 2b. The obtained larval transport estimate was compared with the overall larval transport (GB, TK), based on all sampling positions per cross-section according to method 1 (**table h**). The estimates ranged from 15% of the overall net (landward) transport, but in seaward (negative) direction, to 141% of the overall (ebb) transport. Using either method of calculation (**table h**, a or b), the flood transport was most accurately estimated by position GB_9, the ebb transport by GB_{11} and the net larval transport by GB_7. The flood and net transport of TK were best approached by TK_3, the ebb transport by TK_5. GB_5, GB_{11} (flood, net) and TK_8 generally gave poor estimates of larval transport through the cross-section.

Table H. *Estimated larval transport (10^6) through the cross-sections (GB_i, TK_i), based on larval concentration measurements on the different sample locations (i), (a) obtained by method 2a, (b) obtained by method 2b. Overall larval transport (10^6) as in **table d** (method 1).*

(a)	Flood	%	Ebb	%	Net	%
GB_5	478	57.0	175	55.0	303	58.2
GB_7	1002	119.3	450	141.2	552	106.0
GB_9	835	99.4	218	68.3	617	118.5
GB_{11}	285	33.9	238	74.6	47	9.0
TK_3	1412	96.8	491	89.8	921	101.0
TK_5	1131	77.5	533	97.4	599	65.6
TK_6	1649	113.0	674	123.2	975	106.9
TK_8	935	64.1	352	64.4	583	63.9
(b)	Flood	%	Ebb	%	Net	%
GB_5	106	12.7	182	56.9	-75	-14.5
GB_7	979	116.6	432	135.3	547	105.1
GB_9	858	102.2	203	63.5	655	125.8
GB_{11}	295	35.1	275	86.4	19	3.7
TK_3	1437	98.5	507	92.7	930	102.0
TK_5	1114	76.3	527	96.3	587	64.4
TK_6	1642	112.5	626	114.4	1016	111.4
TK_8	952	65.3	319	58.4	633	69.4
Overall GB	840	100.0	319	100.0	521	100.0
Overall TK	1459	100.0	547	100.0	912	100.0

Groote Gat

Larval concentrations varied in a similar way at A_8 and A_9 during the tidal cycle, the interaction of position by tidal phase not being significant (**table i**). Mean concentrations were significantly higher at A_9 than A_8 during the beginning of the flood and the middle of the ebb period (**fig. f**).

Depth-averaged velocity did not differ between A_8 and A_9 (**table i**), and had a similar tidal pattern (interaction of position by tidal phase not significant): the highest values occurred during the middle of ebb, the lowest values around slack waters (**fig. g**). Larval transport calculations indicated more negative values of the net transport at A_9 than A_8, although both the flood and ebb transport were higher at A_9 than A_8 (**table j**). On 20 April, larval flood and ebb transport were seriously underestimated by using measurements on A_8, and overestimated using A_9 as a basis (**table k**). The net transport was best estimated at A_9. In contrast to the first date, on 27 April larval flood and ebb transport were approached quite well by calculations founded on A_9. The net transport was underestimated by A_9, but contrary to 20 April overestimated by A_8. The variation between the dates is large. Nevertheless, it appears that the larval concentration measurements on A_8 produce transport estimates that are too low.

Table I. *Multifactor ANOVA of (a) ln-transformed (larval concentrations + 1) and (b) depth-averaged velocity on cross-section A, sampled on 20 and 27 April 1995.*

(a) larvae	SS	Df	F-ratio	P-value	Sign.
MAIN EFFECTS					
tidal phase	2.18	5	2.61	0.030	*
position	1.37	1	8.21	0.005	**
INTERACTIONS					
tidal phase*position	0.80	5	0.96	0.450	n.s.
RESIDUAL	15.04	90			
TOTAL (corrected)	21.09	101			
(b) velocity					
MAIN EFFECTS					
tidal phase	56629	5	25.65	0.000	***
position	36	1	0.08	0.780	n.s.
INTERACTIONS					
tidal phase*position	460	5	0.21	0.960	n.s.
RESIDUAL	50346	114			
TOTAL (corrected)	107918	125			

Table J. *Local (n m^{-1}) and overall (n; method 1) transport per tide through cross-section A of water (10^3 m^3) and larvae (10^3), on (a) 20 April, (b) 27 April 1995.*

Location	Flood		Ebb	
(a)	Water	Larvae	Water	Larvae
A_8	64692	32419	61500	56752
A_9	60996	99378	49608	144859
Overall A	29199	34072	25392	51422
(b)				
A_8	54312	95422	63972	47789
A_9	50724	95910	54408	70349
Overall A	24377	44748	27205	28715

Table K. *Estimated larval transport (10^3) through cross-section A, based on larval concentration measurements on sample position A_8 or A_9 multiplied by the cross-sectional water flow (method 2a). Overall transport (method 1) as in Table 10.*
(a) 20 April, (b) 27 April 1995.

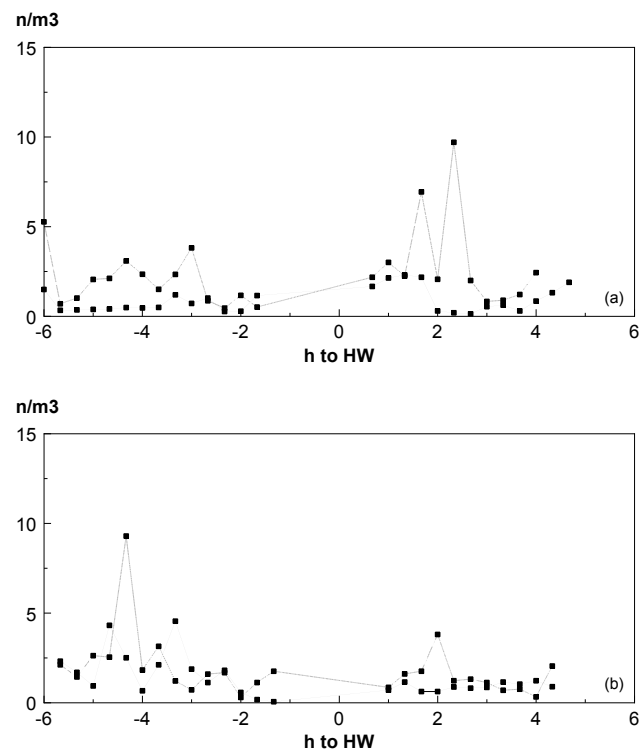| (a)	Flood	%	Ebb	%	Net	%
A_8	14153	41.5	21325	41.5	-7172	41.3
A_9	45068	132.3	62561	121.7	-17493	100.8
Overall A	34072	100.0	51422	100.0	-17350	100.0
(b)						
A_8	38108	85.2	16445	57.3	21663	135.1
A_9	42312	94.6	30384	105.8	11928	74.4
Overall A	44748	100.0	28715	100.0	16033	100.0

Fig. F. *Concentrations (n m^{-3}) of flounder larvae at the two positions on cross-section A (— A_8, ... A_9) on (a) 20 April and (b) 27 April 1995.*
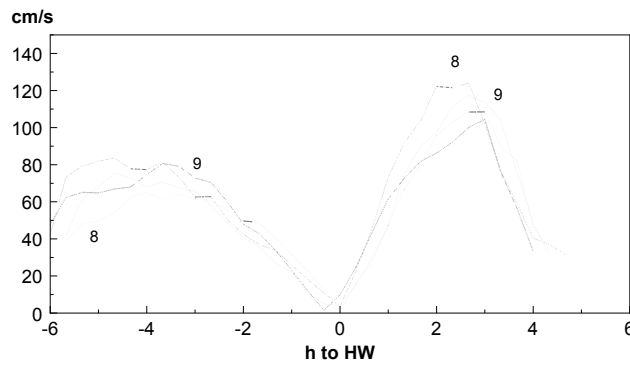
Fig. G. *Depth-averaged velocity (cm s⁻¹) at the two positions (numbers indicated in the Fig.) on cross-section A on 20 April (-.- and ...) and 27 April (— and ---) 1995.*

DISCUSSION

The estuary makes a sharp bend between the cross-sections GB and TK. The current profile over the cross-sections GB and TK indicates that the flood current tends to follow the most direct way. During ebb, the lateral current velocity profile is dictated by the topography of the channel bed, with the highest current velocity at the deepest locations (Duits-Nederlandse Eemscommissie 1996).

Within cross-section GB, the largest volume was transported through the deepest point, whereas relatively much water was transported through the middle part of the cross-section TK probably due to the bend in the estuary. Cross-section GB showed 3 and TK 2 distinct cells of water circulation. The northern part of cross-section TK was characterised by a net ebb surplus, probably caused by the outflow of the river Ems. The middle channel, longitudinally connected with the Groote Gat (Dollard), showed a flood surplus that was partly balanced by the ebb surplus in a small but deep channel at the south of the cross-section.

The overall water transport through the two cross-sections showed a flood surplus of 3 - 4%. This is contrary to the expectation that estuaries generally have a net seaward discharge. Diel inequality of the tide or certain wind conditions can cause temporary raising of the water level and may in this way account for a flood surplus on some occasions. However, the observed surplus could not be explained by tidal or meteorological conditions (Duits-Nederlandse Eemscommissie 1996). The water may have been stored in the Dollard or Ems, but more likely is that the apparent flood surplus has been caused by measurement errors which are about 10% (Kiezebrink 1996).

The hypothesis that larval concentrations are homogeneous across the width of the channel has to be rejected on the basis of the results obtained. Larval concentrations showed heterogeneous tidal variations across the wide channels in the middle part of the Ems estuary and mean concentrations differed among the positions on a cross-section. The complex morphology of the channel bed, with large depth-variations over short distances, may lead to turbulent flow conditions and circulation patterns, which cause variability in larval concentrations.

The largest larval flood surplus was found at the deepest point on cross-section GB, but at the north-side of the middle channel of cross-section TK, which is not the deepest point but had the highest mean current velocity. Apparently, the larvae concentrate in the main stream. These results are in agreement with the suggestion by Weinstein *et al.* (1980), that larvae tend to concentrate in the flood branch during flood and in the ebb branch during ebb. However, conclusive evidence cannot be given due to the high variability in larval concentrations.

Increasing the number of sampling positions on which the overall larval transport calculations are based increases the accuracy of the estimates. The standard error of the overall transport estimate (N=4) ranged between 3-5% (TK) and 21-22% (GB). However, the estimate by method 1 also depends on the width of the channel, which is not clearly defined. Therefore, the overall transport as estimated by interpolation of local transport over the width of the channel has shortcomings irrespective of the number of sampling positions. If only one position can be sampled, the best option seems to choose the one with the largest water transport, in the centre of the channel. The positions near the borders of the gully generally are less suitable.

In the Groote Gat, where the channel is smaller and has a less complex morphology, tidal variations in larval concentrations were similar in the flood- and ebb-dominated parts of the cross-section. Only at the beginning of the flood and the middle of the ebb were mean concentrations significantly higher in the flood-branch of the Groote Gat. Therefore, calculations based on samples taken in the ebb-dominated part of this channel underestimate larval transport by assuming homogeneous larval concentrations over the width of the channel. The estimate based on A_8 may underestimate the overall flood transport by 15 to 60%, the overall ebb transport by 40 to 60%, whereas the overall net transport may be underestimated by 60% or overestimated by 35%. Because concentrations at A_8 are lower during both flood and ebb, the estimates of the net larval transport are apparently affected in an unpredictable way. The data do not allow a well-founded correction of larval transport estimates in the channel Groote Gat in the Dollard.

ACKNOWLEDGEMENTS

Comparison of sampling methods

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INTRODUCTION

Two different net types and corresponding methods of operation were applied in the investigations. Both have their advantages and disadvantages. The larval concentrations and transport estimates, obtained by both net types and methods, are compared in this Chapter.

MATERIALS AND METHODS

The net (A) used to measure larval concentrations for larval transport estimates (Chapters 2, 3, 6) consisted of a 500 μm meshed standard (conical) plankton net (Sournia 1978) with a 0.5 m^2 opening and a length of 4.5 m. The net (B; type Apstein, Hydrobios) used to measure the vertical distribution of larval concentrations (Chapters 4, 5) was also 500 μm meshed, but had a diameter of 0.4 m, a length of 1 m, and was provided with a 0.2 m deep conus of synthetical material with an opening diameter of 0.17 m.

The methods of operation of the nets differed. Sampling with net A consisted of repeated double oblique hauls during a minimum of 1 minutes and a maximum of 3 minutes. (Chapter 2, Jager 1998). In this way, one depth-averaged concentration is obtained. Sampling frequency was 3 times per hour. Net B was applied in stratified sampling at 3 depths simultaneously, during 20-30 minutes per sample (Chapters 4 and 5). For each sampling time, three concentrations were obtained. Sampling frequency was 2 times per hour.

To compare depth-averaged concentrations between the two net types, the stratified concentrations at 3 depths were averaged by means of the VIVECS programme (Mulder 1998, see also Chapter 5) after linear inter- and extrapolation over depth, using the equation

$$\overline{c}(t) = \frac{1}{h}\int_0^h c(z,t)dz \quad,$$

where $\overline{c}(t)$ is depth-averaged concentration at time t, h is water depth (m) and z is sampling depth (m). The tidal transport was calculated by VIVECS.

A multifactor ANOVA was applied to the ln-transformed depth averaged (concentrations+1), and included tidal phase, type of net/method, and the interaction of both as sources of variance. Linear regression of transport estimates calculated from depth-averaged concentrations ($\overline{c}(t)$), obtained by net A or by net B, was done. Linear regression of transport estimates based on stratified concentrations (B) on those, based on $\overline{c}(t)$ was done to correct for the effect of vertical stratification in concentrations.
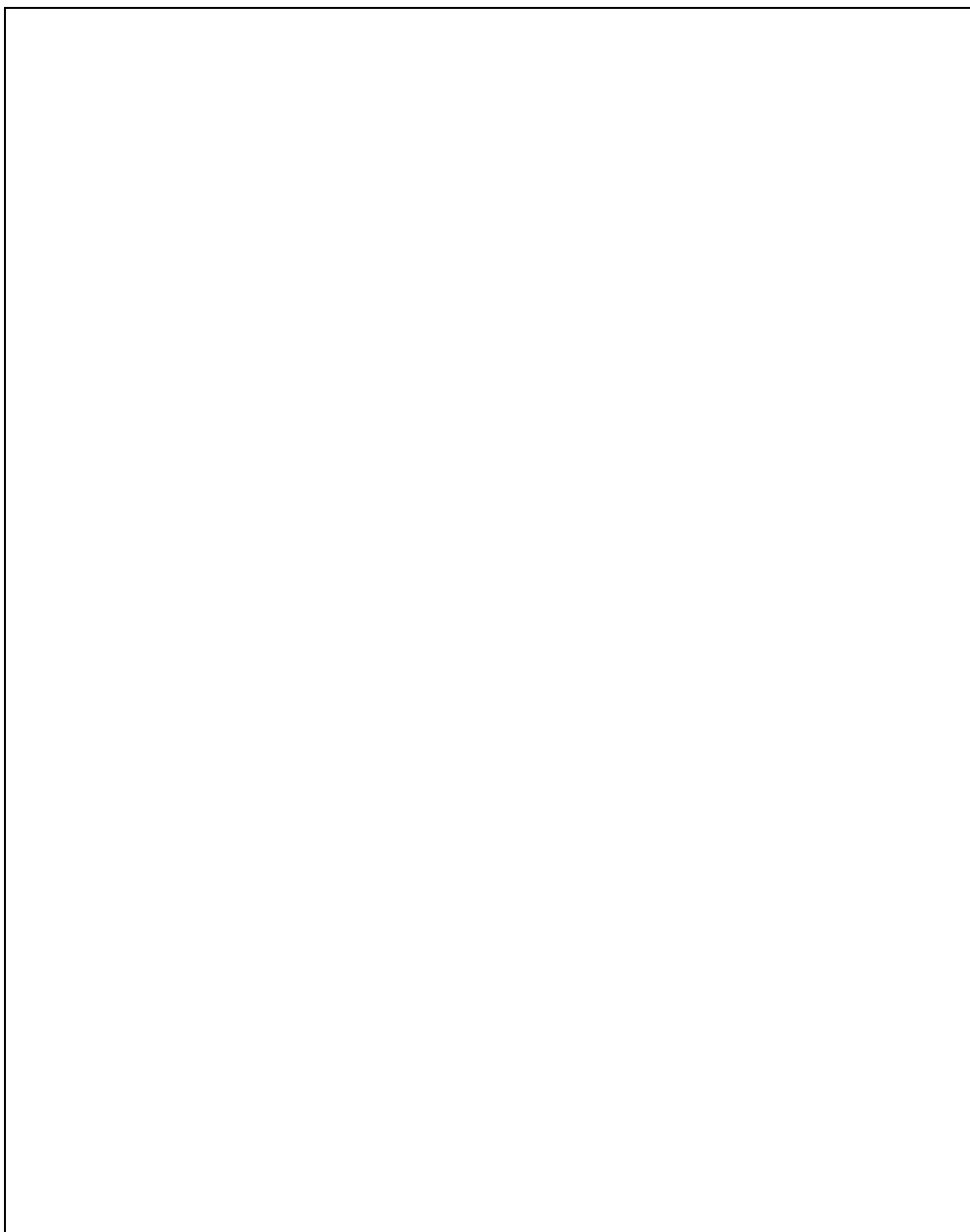
Fig. 1. Larval concentrations (n m^{-3}) obtained by A (dotted line, square markers) and B (drawn line, open circles) on the different sampling dates in 1994.

Fig. 2. Larval concentrations (n m^{-3}) obtained by A (dotted line, square markers) and B (drawn line, open circles) on the different sampling dates in 1995.

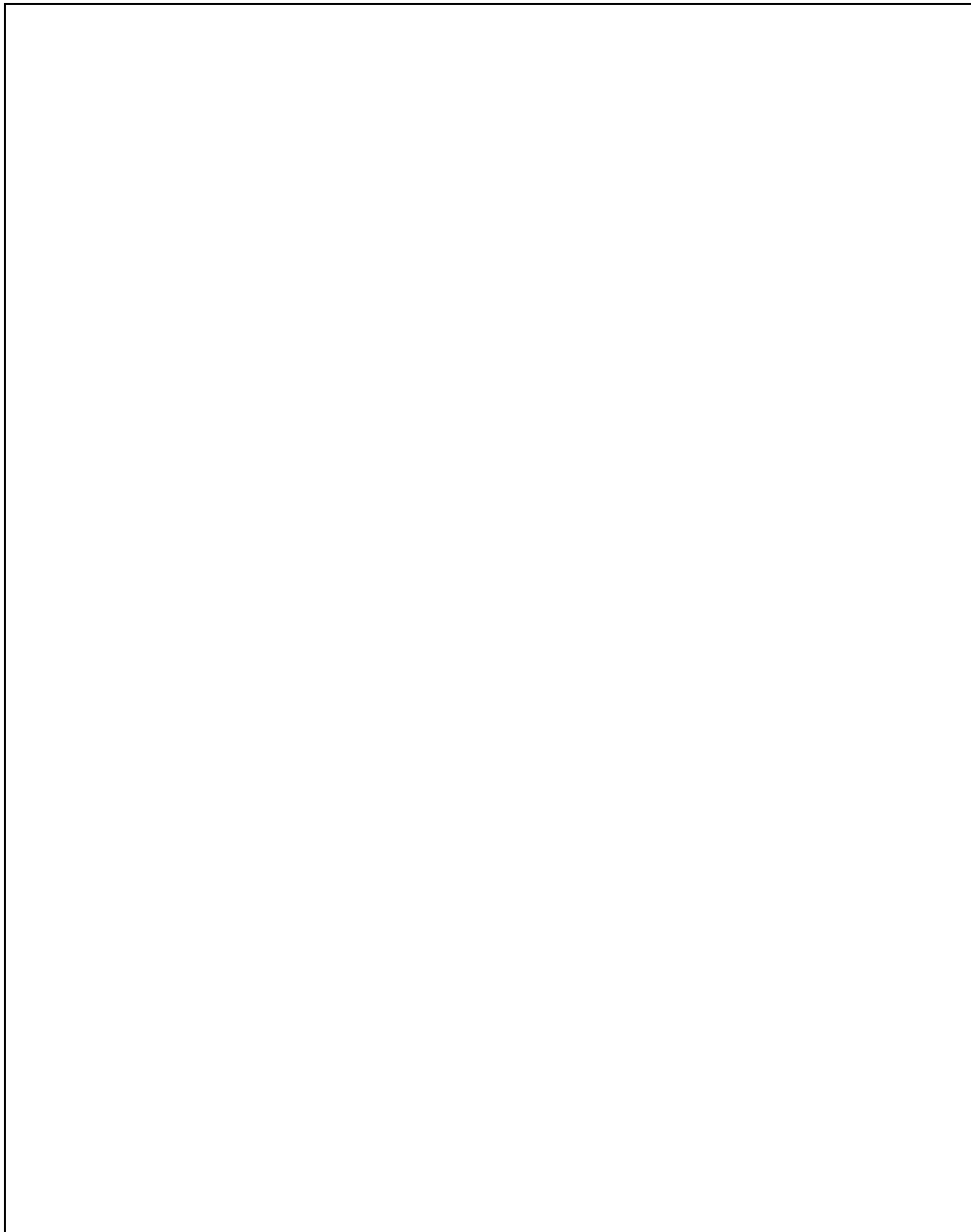# RESULTS

The larval concentrations obtained by both A and B for the different sampling dates in 1994 and 1995 are shown in Fig. 1 and Fig. 2. There is a striking similarity between the two types on some dates (e.g. 11 and 12 April 1994), but a striking dissimilarity on others (e.g. 10 May 1994).

The ANOVA indicated that mean concentrations did not differ between the net types (Table 1). Both net types showed the same tidal pattern in larval concentrations (interaction of net type and tidal phase not significant). The model explained only a very small proportion of the total variance in larval concentrations.

Table A. *Multifactor ANOVA of ln-transformed (larval concentrations+1) for 1994 and 1995.*

1994	SS	Df	F-ratio	P-value
MAIN EFFECTS				
tidal phase	14.50	5	3.09	0.01
net type	0.01	1	0.01	0.91
INTERACTION				
tidal phase*net type	0.37	5	0.08	0.99
RESIDUAL	316.77	337		
TOTAL (corrected)	333.34	348		
1995	SS	Df	F-ratio	P-value
MAIN EFFECTS				
tidal phase	7.28	5	7.54	0.00
net type	0.13	1	0.68	0.41
INTERACTION				
tidal phase*net type	0.38	5	0.40	0.85
RESIDUAL	62.35	323		
TOTAL (corrected)	70.89	334		

Although the mean concentrations did not differ, the influence of net type on the larval transport estimates is substantial (**table b**). For both the flood and net transport, the estimates obtained by both nets differed significantly, and were 55% higher (flood) or 33% lower (net) in the case of net A. The ebb transport was estimated equally well by both types of net (slope not significantly different from 1).

Table B. *Linear regression of the form y = ax, where y are transport estimates obtained by A and x those obtained by B. Regression was forced through the origin.*

	n	slope	R^2	P-value	s.e. estimate	test slope=1
Flood	15	1.55	0.96	0.00	45.4	0.00
Ebb	14	0.96	0.86	0.00	76.6	0.74
Net	14	0.67	0.51	0.00	78.8	0.09

Vertical stratification had a statistically significant but very small effect on the larval transport estimates (**table c**). The vertical stratification of larval concentrations contributed only 5-7% (flood, ebb) or 16% (net) to the difference in transport estimates.

Table C. Linear regression of the form y = ax, where y are transport estimates based on depth averaged concentrations $\overline{c}(t)$ derived from net B, and x are transport estimates based on stratified concentrations (B). Regression forced through the origin.

	n	slope	R^2	P-value	s.e. estimate	test slope=1
Flood	15	0.95	0.99	0.00	3.6	0.00
Ebb	14	1.07	0.99	0.00	19.9	0.02
Net	14	1.16	0.99	0.00	23.0	0.01

DISCUSSION

A confounding effect is caused by the fact that fishing with the large plankton net (A) lasted max. 3 min per sample, whereas each sample with the small net (B) lasted 20-30 min. If larval distribution is very patchy this may cause a difference in concentrations obtained between the two methods.The small net levels down the peak abundances of larvae, and results in slightly lower concentrations although not statistically significant. The risk of net avoidance may have been larger in the small nets than in the large net, but this effect was probably counteracted by the larger risk of clogging of the latter. The risk of clogging was higher during ebb than during flood, due to higher current velocities.

The large differences in transport estimates that were nevertheless obtained by A or B may be explained by the differences of the tidal period over which the integration took place. Although sampling duration over a tidal cycle was sometimes only 20 min longer for net A, this part might result in a difference of just one or two samples at the beginning of the flood (around LW slack) when concentrations were extremely high.

The method applied in Chapter 2 appears very sensitive to sampling around LW slack. The effect of ignoring the heterogeneous vertical larval distribution is in the order of 5%, which leaves a difference of up to 50% in transport estimates between A and B. Stratified sampling results in serious under-estimation of the larval transport, and therefore method A seems more appropriate for estimating the tidal transport of flounder larvae.

Processen van getijdentransport en accumulatie van larvale bot (*Platichthys flesus* L.) in de Eems-Dollard kinderkamer

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Fig. A. Metamorfose-stadia van larvale bot (Platichthys flesus). Van boven naar beneden: stadium 4a, stadium 4b (3x), stadium 4b' en stadium 5. Totale lengte 8 tot 10 mm.

INLEIDING

Kustwateren en estuaria vervullen een aantal functies voor de visfauna. Ze fungeren als leefgebied voor volwassen individuen van sommige soorten (migratie, voortplanting) en als kinderkamer voor jonge exemplaren van andere soorten (voedselvoorziening, groei en overleving). Tegelijkertijd doet de mens een beroep op deze watersystemen voor talloze activiteiten, die in conflict kunnen komen met de natuurlijke functies die het watersysteem vervult. Gedetailleerde en kwantitatieve informatie is nodig om de processen en factoren te analyseren die het functioneren van een gebied als kinderkamer bepalen. Omdat dit soort informatie niet eenvoudig kan worden verkregen voor uitgestrekte gebieden en veel soorten tegelijkertijd, is de keuze gemaakt om het functioneren van een tamelijk geïsoleerd gebied in de Waddenzee (de Eems-Dollard) als kinderkamer voor een enkele platvissoort (de bot, *Platichthys flesus* (Linnaeus 1758), **fig. a**) te bestuderen.

Kinderkamer

Een kinderkamer kan worden gedefinieerd als een beperkt gebied waar jonge (juveniele) individuen van een (vis)soort een bepaalde periode van hun leven doorbrengen, gescheiden van oudere (adulte) soortgenoten. Deze scheiding kan zowel in tijd (juvenielen en adulten bevolken het gebied bijvoorbeeld in verschillende seizoenen) als in ruimte (door het benutten van verschillende habitats) worden gerealiseerd, maar kan bij sommige soorten onvolledig zijn. Een enkel levensstadium is dus een tijdlang geconcentreerd in een relatief beperkt gebied dat aan bepaalde fysisch-morfologische criteria voldoet. Veel platvissoorten maken gebruik van kinderkamergebieden.

De kinderkamer voorziet in voedsel en geschikte abiotische omstandigheden, en huisvest relatief weinig predatoren of biedt mogelijkheden om die te ontkomen. Estuariene omstandigheden kunnen gunstig zijn voor jonge vissen: de hoge troebelheid maakt ze moeilijk zichtbaar voor visuele predators, de complexe structuur van het gebied vermindert de efficiëntie van de predators, terwijl grote predators meestal minder talrijk zijn in ondiep water. Kinderkamers verzekeren het voortbestaan van vispopulaties maar vormen door hun begrensde oppervlakte en mogelijke competitie tussen soorten evenzeer een beperking en een mogelijk regulerend mechanisme voor visbestanden.

De geografische scheiding tussen paaigebieden en kinderkamergebieden vereist een of ander transportmechanisme om de eieren en larven van open zee naar de kustwateren te vervoeren. De toevoer van larven in een kinderkamer wordt gedeeltelijk bepaald door factoren die werkzaam zijn buiten de kinderkamergebieden, zoals de omvang van de paaipopulatie en de vruchtbaar-

heid (fecunditeit) van de vrouwelijke dieren, de ligging van de paaigronden en daarmee samenhangende stromingspatronen, meteorologische condities ten tijde van de verspreiding, en sterfte van eieren en larven.

De traditionele benadering van het fenomeen kinderkamer was vanuit het oogpunt van populatie-aanwas ('recruitment') en werd ingegeven door het commerciële belang in de Noordzee-visbestanden. Het toetreden van jonge vis tot het bevisbare deel van de populatie vormt een sleutelbegrip, en veel van de klassieke populatie dynamische modellen trachtten deze 'stock-recruitment' relatie te beschrijven. De nadruk lag op de overleving van de larvale stadia, gerelateerd aan sterfte door verhongering en predatie. Maar het succesvolle transport van een cohort van de paaigronden naar de kinderkamer wordt behalve door biotische ook door abiotische (fysische) processen gedurende deze periode bepaald. Recent zijn omgevingsvariabelen in 'stock-recruitment' modellen opgenomen, teneinde een deel van de variabiliteit in de 'stock-recruitment' relaties te verklaren. Toch blijft dit een 'black-box' benadering en worden de onderliggende processen en werkzame mechanismen hiermee niet verklaard.

Kinderkamer-parameters

Wanneer de soort-specifieke voorkeuren vastgesteld zijn, kan het oppervlak aan geschikt habitat in een estuarium worden gekwantificeerd. Naast de hoeveelheid habitat is echter ook de habitat-kwaliteit van belang. Habitat-kwaliteitsindices kunnen worden afgeleid uit de groei- en sterftesnelheden van de juveniele populatie alsmede uit de conditie-index. Deze parameters zijn echter zeer moeilijk nauwkeurig te schatten of via een directe methode te meten. Bovendien zullen de kwaliteit en draagkracht ('carrying capacity': populatie-omvang waarbij de groeisnelheid (K) is afgenomen tot 0; MacCall 1990) van de kinderkamer jaarlijks variëren.

De betekenis van een kinderkamer wordt pas duidelijk door het definitieve aandeel van geleverde recruten aan de volwassen populatie uit een gebied af te zetten tegen dat uit andere gebieden. Dit veronderstelt impliciet een goede kennis van de populaties. Omdat van niet-commerciële soorten dit soort gegevens vaak ontbreken, kan deze vergelijking in die gevallen niet goed gemaakt worden.

Het aantal soorten dat een estuarium benut als kinderkamer kan een bruikbare parameter zijn met betrekking tot de bescherming van bepaalde habitats, maar is minder relevant vanuit de soortsbenadering.

Bot

De bot is een euryhaliene (zout-tolerante) platvissoort die behoort tot de familie der Pleuronectidae. De soort heeft een kustgebonden verspreiding in de noord-

oostelijke Atlantische Oceaan, die zich uitstrekt van de Middellandse en Zwarte Zee in het zuiden tot aan de Baltische en Witte Zee in het noorden. Het vermogen - en zelfs de voorkeur - van bot om in brak tot zoet water te leven, is een karakteristiek die in geen van de andere Europese platvissoorten in die mate optreedt.

De voortplanting vindt plaats in de Noordzee, waar de doorzichtige eieren (diameter 1 mm) zich in het pelagiaal ontwikkelen. De hoogste concentraties eieren werden waargenomen in februari ten westen en noord-westen van de Nederlandse westkust, in het oostelijke deel van het Kanaal en het gebied ten noord-westen van Helgoland. De larven komen na 5 tot 7 dagen uit het ei, afhankelijk van de watertemperatuur. Het centrum van de verspreiding van botlarven beweegt zich eind maart en in april in oostwaartse richting langs de Friese kust, terwijl de larven egaal verspreid voorkomen in de Duitse Bocht. In tegenstelling tot de verspreiding van de vroege larvale stadia, die voornamelijk bepaald lijkt te worden door processen van advectie en diffusie, worden oudere larven vooral aangetroffen langs de kust in de nabijheid van estuaria. Vrij zwemmende metamorfoserende larven werden in mei in de bovenste waterlagen aangetroffen in het Elbe-estuarium. Hutchinson & Hawkins (1993) namen waar dat metamorfoserende larven in de rivier de Itchen met het opkomend tij meezwommen in de zoete waterlaag waar die in contact stond met de bodem. Botlarven vestigen zich bij een relatief geringe lengte van 8-10 mm op de bodem. De juvenielen blijven ofwel in brakwater of migreren verder stroom-opwaarts. Kerstan (1991) bracht de grote betekenis van de rivieren als kinderkamer voor bot onder de aandacht en concludeert dat zoetwater-habitats de voorkeur genieten van de 0-groep. De verspreiding van jonge bot is duidelijk verschillend van jonge schol. Redeke (1908) stelde reeds de vraag hoe de jonge botjes erin slagen hun weg te vinden van de Noordzee naar het brakke water.

ONDERZOEKSOPZET

Er is toenemende aandacht voor een benadering die de basale processen en mechanismen van de kinderkamerfunctie onderzoekt, rekening houdend met fysische en ruimtelijke processen, zoals de hydrodynamische variabiliteit, morfo-dynamiek en habitatstructuur. De huidige studie gaat uit van deze laatste benadering, en tracht de processen te identificeren en doorslaggevende mechanismen te doorgronden die het functioneren van een kinderkamer voor platvis bepalen. Processen die binnen een kinderkamer werken en het functioneren bepalen zijn:

1. Toevoer van larven en retentie in het kinderkamergebied

De kinderkamer ontvangt een toevoer van larven, waarvan de omvang reeds grofweg wordt bepaald door de eerder genoemde factoren op open zee alsmede het getijdenvolume in het zeegat en de mate van uitwisseling tussen zee- en kustwater. Eenmaal gearriveerd in de kinderkamer worden de efficiëntie van het transport en de synchronisatie van migraties met de getijdencyclus bepalende randvoorwaarden voor retentie en succesvolle vestiging.

2. Vestiging van platvislarven op de getijdenplaten

Gedurende de voltooiing van de metamorfose, die wordt gekenmerkt door een verschuiving van de ogen naar een zijde van de vis, gaan de platvislarven over tot een bodemgebonden leefwijze die karakteristiek is gedurende hun verdere leven. Dit proces, dat de ruimtelijke verspreiding van platvislarven op de getijdenplaten bepaalt, wordt vestiging ('settlement') genoemd. Tijdens de vestiging op de platen komt een nieuw potentieel beschikbaar om voedsel te verwerven en predatoren te ontwijken en kan de groei sprongsgewijs toenemen. De drastische morfologische en ethologische veranderingen die gekoppeld zijn aan de transformatie van een pelagische naar een benthische leefwijze vereisen tal van aanpassingen van het organisme en maken de vestigingsfase tot een kritieke periode tijdens de platvisontwikkeling: vitale processen die de omvang van het recruitment bepalen vinden plaats in de korte tijdspanne rondom de metamorfose. Sterfte die optreedt tijdens de vestiging kan de variabiliteit in populatieomvang reduceren indien dichtheids-afhankelijke processen werkzaam zijn.

3. Ruimtelijke verspreiding, groei en sterfte

Schol en bot vestigen zich in het (inter)getijdengebied, waar ze aanvankelijk in getijdenpoeltjes verblijven gedurende laagwater. Enige tijd na de vestiging ontruimen de juvenielen de intergetijdenzone tijdens eb en beginnen getijden-migraties te ondernemen, zodat ze de platen alleen nog tijdens vloed bevolken. De ruimtelijke verspreiding van de 0-groep platvis is gecorreleerd met het sedimentgehalte van het substraat. Voedselbeschikbaarheid en water-temperatuur bepalen grotendeels de groei, en de sterfte stabiliseert zich op een lager niveau. Na een paar maanden, wanneer de temperatuur daalt in de herfst, verlaat de juveniele platvis het gebied om zich in de wintermaanden in dieper water op te houden (zie Gibson 1997 voor een overzicht). Gedurende hun tweede levensjaar bevinden de jonge platvisjes zich nog steeds in de kustzone, maar ze nemen nu andere habitats in dan de 0-groep. De verspreiding van bot verschuift mettertijd van brak naar zout water.
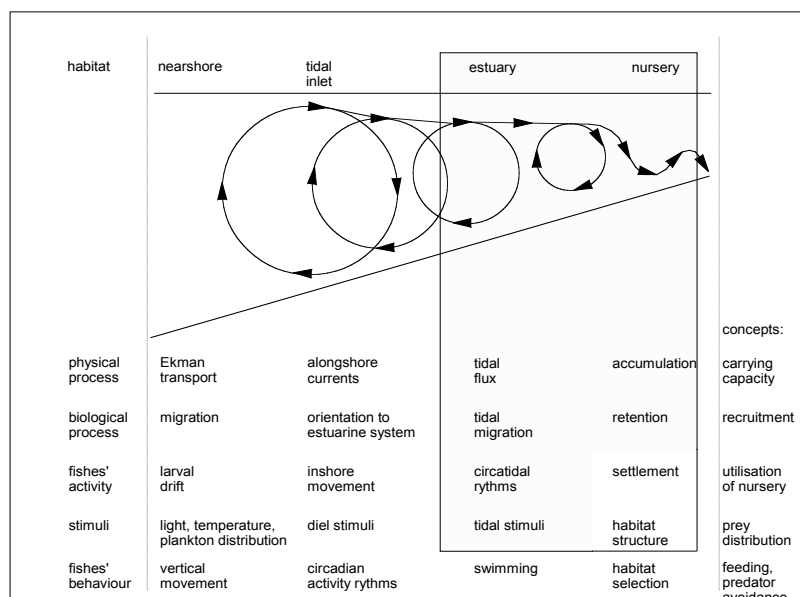
Fig. B. *Conceptueel model van het gradueel veranderende larventransport van open zee naar de kust-gebonden kinderkamergebieden (aangepast naar Boehlert & Mundy 1988). Cirkels met pijlen verwijzen naar de verticale bewegingen van de larven in de waterkolom. Het onderzoek heeft zich geconcentreerd op de onderwerpen binnen het grijze vlak.*
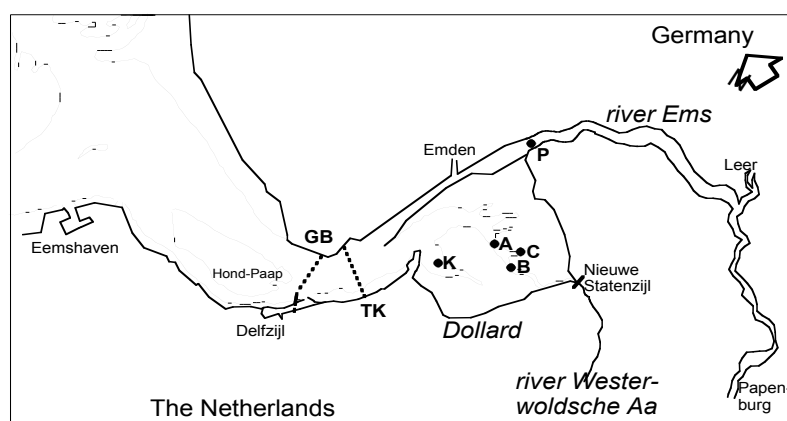

Fig. C. *Gedetailleerd kaartje van het Eems-Dollard estuarium inclusief de bemonsteringslocaties (GB, TK, A, B, C, K, P; zie Tabel 1).*

Aanvankelijk behelsde het onderzoeksplan alledrie genoemde aspecten van de kinderkamerfunctie, maar in de loop van het onderzoek bleek een beperking noodzakelijk, waarbij de studie werd toegespitst op het eerste onderdeel, de **toevoer van larven in de kinderkamer**. Dit omvat tevens de transport-mechanismen en accumulatieprocessen in de kinderkamer (**fig. b**). De reeds aanwezige uitgebreide en gedetailleerde kennis over het Eems-Dollard estuarium bood een goed uitgangspunt voor het huidige onderzoek.

In de opzet van het bemonsteringsprogramma werd rekening gehouden met aanbevelingen van Weinstein (1988). Die schetste een benadering waarbij eerst een model wordt ontwikkeld dat de fysische processen beschrijft, aannemend dat het transport van de 'passieve' organismen volledig wordt gestuurd door de hydrodynamica. De tweede stap zou zijn om op een beperkt aantal stations zeer intensief larven te bemonsteren, met een groot aantal herhalingen om de achtergrond-variabiliteit te leren kennen. De verzamelde data zouden een eerste aanzet kunnen zijn om larventransport in het estuarium te modelleren. Het hydrodynamisch estuariummodel wordt vervolgens aangepast door het gedrag van larven te verdisconteren, en met dit aangepaste model kunnen verschillende scenario's worden doorgerekend om de invloed van bepaalde ingrepen in het estuarium op het recruitment te schatten.

Tabel A. *Opzet van de onderzoekingen aan botlarven in de Eems-Dollard in 1993-1995 op de bemonsteringslocaties A (Groote Gat), B (Schanskerdiep), C (Oostfriesche Gat), K (Kerkeriet) en P (Pogum). Bemonsteringsmethoden door middel van 'double oblique' (⊗) of gestratificeerde verticale bemonstering (≡).*

Datum	Locatie			Datum	Locatie			Datum	Locatie	
1993	A	K	P	**1994**	A	B	C	**1995**	A	A9
13/04	⊗		⊗	31/03	⊗			30/03	⊗	
15/04	⊗	⊗	⊗	05/04	⊗			06/04	≡⊗	
19/04	⊗	⊗	⊗	07/04	⊗			12/04	≡⊗	
22/04	⊗	⊗	⊗	11/04	≡⊗			18/04	≡⊗	
26/04	⊗	⊗	⊗	12/04	≡⊗			20/04	≡⊗	⊗
29/04	⊗	⊗	⊗	14/04	⊗	⊗	⊗	25/04	≡⊗	
03/05	⊗		⊗	18/04	≡⊗			27/04	≡⊗	⊗
06/05	⊗	⊗		19/04	≡⊗			03/05	≡⊗	
11/05	⊗	⊗	⊗	21/04	⊗	⊗	⊗	10/05		
13/05	⊗		⊗	26/04	⊗					
18/05	⊗	⊗		28/04	≡⊗					
				03/05	≡⊗	⊗	⊗			
				10/05	≡⊗					
				11/05	≡⊗					
				16/05	⊗	⊗	⊗			
				19/05	⊗	⊗	⊗			
				25/05						
TOTAAL	11	8	9		24	5	5		18	2

Larvenconcentraties werden gemeten gelijktijdig met fysische variabelen in het centrum van de hoofdgeul in de Dollard (A) gedurende 35 getijdencycli in 1993, 1994 en 1995 (**fig. c**, Tabel 1). Soms werd gemeten in de rivier de Eems nabij Pogum (P), in een belangrijke nevengeul in de Dollard (K), in twee locaties nabij de randen van de Dollard (B, C), en meer zeewaarts in het estuarium (GB en TK op 26 en 28 april 1994; niet vermeld in Tabel 1).

De belangrijkste doelstelling tijdens het eerste jaar (1993) was, om gedetailleerde beschrijvende kennis te verkrijgen over de larvale intrek: wanneer vindt die plaats, in welke hoeveelheden arriveren de larven in de kinderkamer, en worden Dollard en Eems (die beide samenkomen in het Eems estuarium) in gelijke mate van larven voorzien?

Het werd spoedig duidelijk dat de omstandigheden in de rivier Eems ongunstig waren voor de toegepaste bemonsteringsmethode: door de hoge stroomsnelheden in combinatie met de extreem hoge troebelheid sloegen de fijne mazen van het net dicht waardoor geen representatieve bemonstering kon plaatsvinden en de data onbetrouwbaar werden. Daarom is locatie P in de volgende jaren vervallen en zijn de Eemsgegevens buiten beschouwing gelaten. De twee belangrijke geulen in de Dollard (A, K) werden aanvankelijk beide bemonsterd teneinde hun relatieve belang vast te stellen. Toen in 1993 bleek dat het Kerkeriet (K) slechts een kleine bijdrage aan het totale larventransport leverde, is de aandacht in de latere jaren toegespitst op het Groote Gat. De kwantitatieve larventoevoer werd daar in 1994 verder onderzocht. Bovendien werd het transportmechanisme bestudeerd, waarbij de vooronderstelling van passieve larven werd getoetst. Het proces van ophoping in de kinderkamer (accumulatie) werd benaderd door over een longitudinale gradiënt in de Dollard (locaties A, B, C) te bemonsteren. Het laatste jaar (1995) werd benut om aanvullende gegevens over het transportproces te verkrijgen.

De datasets die ten grondslag liggen aan de verschillende Hoofdstukken worden samengevat in Tabel 2.

Tabel B. *Overzicht van databestanden die ten grondslag liggen aan de verschillende hoofdstukken. Symbolen als in Tabel 1.*

Hoofdstuk	Locatie	Bemonsterings Methode	Aantal Getijdencycli	Jaar
2	A	⊗	35	1993, 1994, 1995
3	A, B, C	⊗	15 (=3*5)	1994
4	A	=	17 (=8+9)	1994, 1995
5	A	=	17 (=8+9)	1994, 1995
6	TK, GB, A, A9	⊗	14 (=2*5+2*2)	1994, 1995
7	A	⊗ =	17	1994, 1995

UITKOMSTEN VAN HET ONDERZOEK

Transport en retentie

In **Hoofdstuk 2** wordt de jaarlijkse toevoer van larven geschat, alsmede het percentage dat achterblijft in de kinderkamer, door het getijdentransport te kwantificeren. De immigratie van metamorfoserende larven besloeg een periode van ca 6 weken, en begon tussen eind maart en begin april terwijl de maximale intensiteit 2 tot 3 weken na de eerste observatie van larven werd bereikt. Vanuit het gegeven dat pelagische botlarven zich op de getijdenplaten vestigen werd een netto landwaarts larventransport verwacht. In 1993 werd deze verwachting bevestigd, maar het hoge aantal getijdencycli in 1994 en 1995 met een netto zeewaarts larventransport was een onverwacht resultaat.

Het algemene patroon in het getijdenverloop van larvenconcentraties werd gekenmerkt door maxima gedurende de eerste paar uren van de vloed, gevolgd door een snelle afname. Een secundaire piek in concentraties volgde halverwege de vloedperiode. Tijdens eb varieerden de concentraties enorm, maar een opmerkelijke toename aan het eind van de eb werd herhaaldelijk waargenomen. De getijdenvariaties in larvenconcentraties resulteren in een zeer variabel transport en retentie.

De verschillen tussen de jaren kunnen niet worden verklaard uit veranderingen in de morfologie van de Dollard, aangezien deze in de onderzoeksperiode niet erg veranderd is. Andere factoren, zoals de waterbeweging en asymmetrie van het getijde, zijn mogelijk verantwoordelijk voor de waargenomen variabiliteit in het larventransport en deze zijn geanalyseerd. Het netto watertransport was positief gecorreleerd met de retentie van larven, maar niet met het netto larventransport. Een relatief langere vloed- dan ebperiode was positief gecorreleerd met zowel het netto watertransport als de larvale retentie gedurende een getijdencyclus. De windrichting beïnvloedde het netto watertransport ter plaatse van de bemonsterde locatie, evenals het netto larventransport en de retentie. De overheersende windrichting tijdens de periode van larvenintrek is mogelijk van invloed op het transport en de vestiging van metamorfoserende botlarven in de kinderkamer.

Omdat het netto larventransport zo variabel was van dag tot dag, bleek het onmogelijk de netto larventoevoer in de kinderkamer nauwkeurig te bepalen. Het vloedtransport bleek een betrouwbaarder maat, en de schatting van de totale larventoevoer (het vloedtransport, geïntegreerd over de totale im-migratieperiode) in het centrum van de Dollard bedraagt tussen de 1 en 7 10^9 larven tijdens de onderzochte jaren. De gemiddelde larvenconcentratie en geschatte totale larventoevoer komen in beperkte mate overeen met aantalsschattingen van net gevestigde botjes in de Eems-Dollard.

Accumulatie

Het waargenomen getijdenpatroon in larvenconcentraties, zoals in het vorige hoofdstuk werd vastgesteld, duidt op een oplopende concentratiegradiënt in de hoofdgeul van de Dollard richting de sluis bij Nieuwe Statenzijl.

De ophoping van larven naar de randen van de kinderkamer, en de invloed van zoetwaterlozingen op dit proces, zijn onderzocht in **Hoofdstuk 3**. De hypothese is getoetst dat botlarven zich ophopen in het deel van de kinderkamer waar de zoutgehalten het laagst zijn. De resultaten toonden aan dat de larvenconcentraties in de richting van de randen van de Dollard toenamen ten opzichte van het centrale punt in de hoofdgeul, hetgeen samenviel met een afname in het gemiddeld zoutgehalte. De hoogste concentraties werden gemeten rond LW in de geul Schanskerdiep, die in directe verbinding staat met de sluis in Nieuwe Statenzijl. De periode rond LW lijkt van groot belang, gezien de hoge concentraties en de snelle veranderingen die daarin optreden.

Het voorkeurstransport van larven naar het Schanskerdiep kon niet volledig worden verklaard uit de watercirculatie. Dit resultaat ondersteunt de opvatting dat de lozing van zoetwater het larventransport van bot beïnvloedt en verantwoordelijk is voor de relatief sterke ophoping in het brakke gebied in de nabijheid van Nieuwe Statenzijl. Het onderliggend mechanisme blijft onbekend. De doorgang naar het zoete water is echter geblokkeerd door de sluis, die een mogelijke barrière vormt gezien de beperkte zwemvermogens van de botlarven. De oorzaak van de ophoping kan dus ook een fysieke zijn.

Selectief getijdentransport

De ruimtelijke scheiding van volwassen individuen tijdens de paaitijd en juveniele individuen tijdens de vestiging impliceert dat de larven op een of andere manier van de paaigronden naar de kinderkamers moeten worden getransporteerd. De migratie van platvislarven van open zee naar de kinderkamers wordt algemeen gezien als een geleidelijk veranderend proces (**fig. b**): van een volledig passief transport dat uitsluitend door fysische factoren wordt bepaald, tot een aktieve bijdrage van de larven in de vorm van selectief getijdentransport (STST; Boehlert & Mundy 1988). Voorwaarde voor STST is het gericht zwemmen in verticale richting, synchroon met de getijdencyclus (Hill 1991). Hoewel in schol aanwijzingen voor STST zijn gevonden (Creutzberg e.a. 1978, Rijnsdorp e.a. 1985) was er geen informatie over bot die kon ophelderen of platvislarven in het algemeen van dit mechanisme gebruik maken. Daarom is het transportmechanisme van botlarven in 1994 en 1995 onderzocht door de verticale verdeling van larven in de waterkolom gedurende het getijdenverloop frequent te meten. In **Hoofdstuk 4** is van ANOVA-technieken gebruik gemaakt

om de belangrijkste factoren op te sporen die verantwoordelijk zijn voor de variaties in larvenconcentraties.

De larvenconcentraties namen af na LW en stegen aan het eind van de eb in zowel de bovenste als middelste waterlaag, maar de concentraties waren duidelijk hoger in de bovenste waterlaag. De concentraties bij de bodem namen relatief sterk toe tijdens eb. Er konden geen dag-nacht verschillen worden ontdekt. Vanwege de hoge concentraties bovenin de waterkolom en de variabele verticale verdeling van botlarven gedurende de getijdencyclus, moest de hypothese van een volledig passief transport worden verworpen. In ieder geval lijken er tijdens vloed duidelijke aanwijzingen te zijn voor STST. Tijdens eb concentreerden larven zich niet alleen bij de bodem, maar ook nog steeds bovenin de waterkolom, hetgeen in tegenspraak is met de verwachtingen volgens de STST-hypothese. De larven die tijdens eb bovenin het water worden aangetroffen zijn mogelijk met het terugstromende water van de platen afgespoeld na een mislukte vestigingspoging. Tijdens de volgende vloedperiode krijgen ze opnieuw gelegenheid om de getijdenplaten te koloniseren. Het aandeel van de verschillende metamorfose-stadia varieerde zowel binnen het getijde als tussen waterlagen. De veranderingen zijn gradueel. De verder ontwikkelde stadia komen relatief meer voor nabij de bodem dan aan de oppervlakte. Rond HW zijn deze uit de geul verdwenen.

Transportsnelheid

Hoewel het vorige hoofdstuk aannemelijk maakt dat botlarven gebruik maken van STST als transportmechanisme, was een onopgeloste vraag in welke mate de larven in staat zijn hun transport te beïnvloeden wanneer zij worden blootgesteld aan de sterke getijdenstromingen en turbulentie die in de geulen optreedt. Deze vraag is aan de orde gesteld in **Hoofdstuk 5**, waarbij het concept van 'larval velocity' (Rowe & Epifanio 1994) is toegepast. Dit concept is bovendien uitgebreid naar een meer algemeen toepasbare transportsnelheid ('transport velocity') om vergelijkingen met de verplaatsing van zwevende stof (als voorbeeld van passieve deeltjes) en zout (als voorbeeld van een opgeloste stof) mogelijk te maken. De transportsnelheid kan gerelateerd worden aan de getijdengemiddelde stroomsnelheid. Verschillen tussen beide worden veroorzaakt door variaties in de temporele of verticale verdeling van de stoffen, of een combinatie van die twee. De bijdragen van de verticale en temporele concentratie-variaties aan de transportsnelheid zijn afzonderlijk berekend.

Theoretische kennis van de onderliggende fysische processen op de concentratieverdeling, en dus de transportsnelheid, is toegepast om meer inzicht te krijgen in de estuariene transportprocessen. De relatieve transportsnelheden van botlarven, zwevende stof en zout vertoonden duidelijk verschillende patronen.

In het geval van zout was de temporele variatie belangrijker dan de verticale variatie, hetgeen erop wijst dat longitudinale advectie een belangrijk proces is. In het geval van zwevende stof waren de bijdragen van temporele en verticale variaties aan de transportsnelheid even groot, maar van tegengesteld teken. Erosie-depositie lijkt het bepalende proces te zijn. Bij botlarven was de verticale variatie in concentraties het belangrijkst tijdens vloed, terwijl de bijdrage van de temporele variatie overheerste tijdens eb. Dit is een sterke aanwijzing dat het transportproces met name tijdens vloed wordt beïnvloed door activiteit van de larven (d.w.z. zwemgedrag), maar tijdens eb in mindere mate. Door te zwemmen wordt de larvale transportsnelheid met 6% verhoogd. Hoewel dit in absolute zin een laag percentage mag lijken, moet niet worden vergeten dat deze eigen bijdrage tijdens iedere getijdencyclus herhaald optreedt en uiteindelijk leidt tot een cumulatief effect op de residuele verplaatsing van larven in de Dollard. Daar komt bij, dat de (positieve) bijdrage van de verticale variatie aan de transportsnelheid van larven opmerkelijk verschilt van zwevende stof, waar die bijdrage sterk negatief is. De 6% bijdrage van larven aan hun transportsnelheid moet dus worden gezien als een minimum bijdrage aan een resultante, waarin het overwinnen van fysische processen (die de transport-snelheid remmen) verrekend is. De temporele variatie tijdens eb is mogelijk gerelateerd aan het accumulatieproces, maar de data staan geen duidelijke conclusies toe over de processen die domineren.

Verspreiding over de breedte van de geul

De onderzoeken, die in de voorgaande hoofdstukken zijn beschreven, waren alle gebaseerd op metingen in het diepste punt van een dwarsdoorsnede van de hoofdgeul in het centrum van de Dollard, onder de aanname (ten aanzien van de transportberekeningen) dat de larven homogeen over de (breedte en diepte van de) geul verdeeld zijn. Deze aanname is van grote invloed op de resultaten en behoefde daarom een onderbouwing door middel van het bestuderen van de larvenverdeling over de breedte van de geul (**Hoofdstuk 6**). Idealiter zou de studie kunnen resulteren in correctiefactoren die kunnen worden toegepast voor het meetpunt dat als representatief wordt beschouwd voor de gehele dwars-doorsnede van de geul. Dit type onderzoekingen is zeer kostbaar vanwege de simultane metingen met meerdere schepen die hiervoor vereist zijn. Dit is de reden dat het onderwerp slechts beperkt kon worden verkend door aan te sluiten bij een debietmeting met een groot aantal schepen die toevallig plaatsvond tijdens de periode van larvale migratie. Deze meetcampagne werd uitgevoerd in het middengedeelte van het Eems-estuarium, waar de geul veel breder is dan in de centrale Dollard.

De resultaten tonen overtuigend aan dat er geen sprake is van homogene larvenconcentraties, en dat derhalve de aanname die aan de kwantitatieve

transportschattingen ten grondslag ligt niet juist is. Bovendien varieerden de larvenconcentraties tijdens eb en vloed op verschillende wijze, afhankelijk van de meetpositie in het dwarsprofiel. Het grootste larventransport werd gerealiseerd in het diepste gedeelte in het midden van de geuldoorsnede. Vanwege de hoge variabiliteit die optrad in de larvenconcentraties en het beperkte aantal metingen kon geen correctiefactor worden vastgesteld.

Het larventransport op 28 april 1994 was aanzienlijk hoger in het midden van het estuarium (1459 10^6, vloed; 547 10^6, eb) dan op diezelfde dag in de Dollard (39 10^6, vloed; 84 10^6, eb), hetgeen voornamelijk wordt verklaard uit het veel grotere watertransport door de geuldoorsnede in het middengebied.

Evaluatie

De schattingen van het larventransport, zoals gepresenteerd in H.2 en H.3, worden beïnvloed door verschillende foutenbronnen. Om de berekende omvang van het larventransport op waarde te kunnen schatten wordt een korte beschouwing gegeven van de mogelijke foutenbronnen die reeds in de verschillende hoofdstukken aan de orde zijn gekomen:

1. de larvale flux (transport per tijdseenheid) door de dwarsdoorsnede van de geul werd verkregen door vermenigvuldiging van de dieptegemiddelde larvenconcentratie op 1 punt met het waterdebiet door de geuldoorsnede. Deze laatste werd op zijn beurt berekend door extrapolatie van de stroomsnelheid op de meetlocatie naar die van de geuldoorsnede via een regressievergelijking die eerder met behulp van meerdere schepen bepaald was. Hoewel de correlatie-coëfficiënten van de regressie gemiddeld hoog zijn (0.98), kan er een onbekende variatie optreden als gevolg van de springtij/-doodtij cyclus en wind-omstandigheden.

   Andere belangrijke aannamen spelen een rol bij de toegepaste methode:

   • *de verticale verdeling van larven in de waterkolom is homogeen.* In H.4 en H.5 is aangetoond dat dit niet het geval is. Het negeren van de verticale stratificatie leidt tot een afwijking van ca 5% in de schattingen van het larventransport.

   • *de larven zijn homogeen verdeeld over de breedte van de geuldoorsnede.* Deze aanname houdt evenmin stand (H.6) en kan serieuze (tot 50%) onder- of overschatting van het larventransport veroorzaken, afhankelijk van de positie van de meetlocatie binnen de dwarsdoorsnede van de geul.

2. Er werd in de onderzoeken uitgegaan van de Euleriaanse benadering. Die houdt in dat de metingen op een vaste positie worden uitgevoerd en dat gedurende de getijdencyclus in feite verschillende waterpakketten worden bemonsterd. Door op een positie in een dwarsprofiel te bemonsteren wordt bovendien een gedeelte van het watertransport gemist waardoor de berekende netto (residuele) transporten onbetrouwbaar worden (H.5).

3. Type net. Het fijnmazige planktonnet met een grote opening is gevoelig voor dichtslibben waardoor de visefficiëntie nadelig beïnvloed kan zijn. Het type dat is voorzien van een conus met een kleine openingsdiameter is minder gevoelig voor dichtslibben maar heeft mogelijk te kampen met ontwijkingsgedrag door de larven, hoewel zulke effecten niet aangetoond konden worden. De gemiddelde concentraties die met behulp van de verschillende nettypen werden gemeten zijn statistisch niet verschillend. Bij beschouwing van de ruwe gegevens valt echter op dat met het net met de grote openingsdiameter enigszins hogere concentraties worden gemeten dan met het net met de kleine openingsdiameter (zie H.7). Het geclusterd voorkomen van larven zal in bemonsteringen met het grote net (bevissing gedurende 1-3 min) een groter effect teweegbrengen dan in die met het kleine net, waar de langere bemonsteringsduur (20-30 min) zorgt voor een nivellering van piekconcentraties. De transportschattingen met beide meetmethoden lopen 50% uiteen en waren het hoogste voor het grote net. De zeer hoge larvenconcentraties die optreden rond LW, en die afhankelijk van de bevissing met het ene of andere type net al dan niet inbegrepen worden in de transportschatting, zijn verantwoordelijk voor dit verschil.

4. De berekeningen in H.2 en H.3 verwaarloosden de kenteringsperioden, aangezien in dat tijdsinterval vanwege geringe stroomsnelheden geen bemonstering mogelijk is. Een andere optie was om de larven-fluxen over de kenteringsintervallen te interpoleren. Dit zou hebben geleid tot 5% (vloed) of 10% (eb) hogere transportschattingen, maar het netto transport wordt niet waarneembaar beïnvloed door het incorporeren van de kentering.

5. Dag-tot-dag variatie. Vooral in 1994 was er een aanzienlijke variatie in concentratieniveaus tussen de bemonsteringsdagen, waardoor de transport-schattingen erg uiteenliepen. Het bemoeilijkt een betrouwbare interpolatie van de transporten per getijde over de hele immigratieperiode. De omvang van deze afwijking kan niet worden geschat.

De bovenstaande opsomming van foutenbronnen pretendeert niet volledig te zijn, maar leidt desalniettemin tot de conclusie dat de kwantitatieve schattingen van het larventransport een grote intrinsieke onnauwkeurigheid bevatten. De fout die wordt geïntroduceerd door een homogene verticale verdeling van larven aan te nemen (door middel van diepte-gemiddelde bemonstering), terwijl dat niet het geval is, is relatief klein ten opzichte van de overige en mag verwaarloosd worden. De bemonsteringsmethode waarbij gebruik wordt gemaakt van het type net met een grote opening lijkt geëigend voor het doel van transport-schattingen. De grootste fout wordt waarschijnlijk geïntroduceerd door slechts op één meetlocatie in een dwarsprofiel te meten. Een groot aantal herhalingen op dezelfde locatie zal de fout uitmiddelen en verkleinen, en resulteert in een

schatting die tenminste de juiste orde van grootte en richting (landwaarts of zeewaarts) van het residuele transport van botlarven vaststelt.

SYNTHESE

Uit de uitkomsten van de verschillende onderdelen van het onderzoek kan een algemeen beeld geschetst worden van de processen van transport en accumulatie bij botlarven in de Dollard-kinderkamer.

Het larventransport tijdens vloed wordt bevorderd door selectief gebruik te maken van het getijde, een proces dat goed getypeerd wordt door de term 'floundering': ongecontroleerd bewegen in een poging om niet te zinken. Tijdens eb krijgen fysische processen de overhand. Alle metamorfose-stadia zijn in de geul aanwezig, maar in onderling wisselende verhoudingen gedurende de verschillende fasen van het getijde en in verschillende waterlagen (**fig. d**).

Tijdens de LW-kentering rusten de larven op de bodem van de geul. Zodra de vloedstroom begint te lopen, hetgeen op een of andere manier door de larven kan worden waargenomen, maken zij zich los en zwemmen massaal omhoog in de waterkolom (-6). De vloed zet door, en voert 'verse' larven mee uit het meer naar buiten gelegen gedeelte van het estuarium. Deze bevinden zich over het algemeen in een minder ver ontwikkeld stadium van de metamorfose, en komen voor in lagere concentraties dan de larven die zich gedurende de voorafgaande getijden op de bodem hadden opgehoopt. Hierdoor ontstaat een schijnbare verdunning van larvenconcentraties in de eerste uren van de vloed (-5). Het waterniveau stijgt gedurig en begint de platen te overspoelen (-4). De larven die zich in de bovenste waterlagen ophouden worden meegevoerd met het water dat over de platen begint te kruipen. De oudere stadia (4b' en 5) verdwijnen geleidelijk uit de geul, en nu nemen ook de concentraties in de bovenste waterlaag af (-3). De vloed houdt aan, en voert nog larven met zich mee (-2), maar er bevindt zich nu meer water boven de platen dan in de geul. De HW stroomkentering wordt voorafgegaan door het afnemen van de waterhoogte (-1, 1). De stroomsnelheid daalt tot nul en de larven zakken uit naar de bodem van hetzij de platen, waar zij zullen overtijen, of de geul, waar zij met de krachtige ebstroom geconfronteerd zullen worden. De larven, die er niet in slagen om zich op de platen te handhaven, worden met het afstromend water teruggevoerd naar de geul waardoor de larvenconcentraties daar gedurende eb toenemen.

Ten tijde van de maximale stroomsnelheden (2) kan een deel van de larven de daardoor opgewekte turbulentie niet weerstaan, en wordt opgewerveld in de waterkolom. Nadat de platen droogvallen (3) neemt de stroomsnelheid af en zinken de larven wederom naar de bodem (4). De laatste larven spoelen terug van de platen in de oppervlakkige waterlaag (5), terwijl zich bij de bodem larven ophopen die via de geul terugkeren uit de randgebieden van de Dollard.
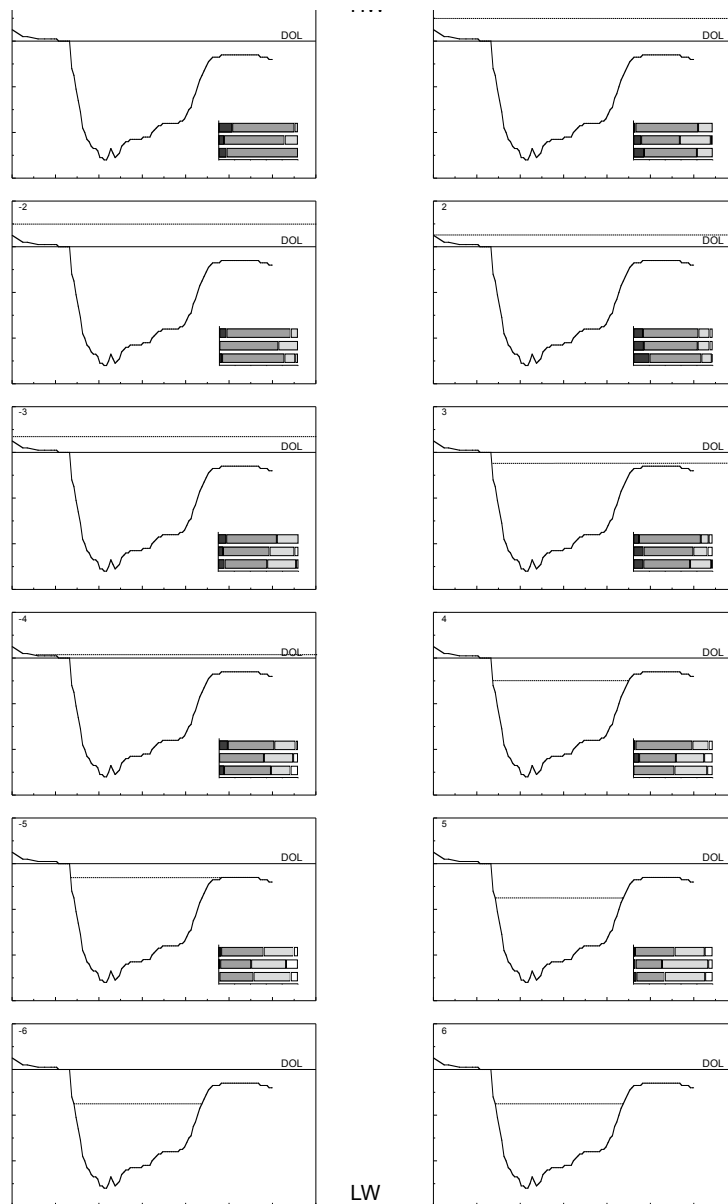
Fig. D. Conceptueel model van het larventransportproces binnen de kinderkamer. Van linksonder naar rechtsonder en met de klok mee, worden de verschillende stadia van de getijdencyclus aangegeven met cijfers die het aantal uren t.o.v. HW representeren. De dwarsdoorsnede van locatie A is als voorbeeld gebruikt. Het waterniveau (...) en N.A.P. (—) zijn aangegeven. De larvenconcentraties worden voorgesteld door stipjes. De relatieve samenstelling van metamorfose-stadia van de bemonsterde botlarven is in de histogrammen rechtsonder in iedere figuur aangegeven. Op de verticale schaal staan 3 waterlagen (van boven naar onder) aangeduid, en de horizontale schaal loopt van 0-100%. De metamorfose stadia worden met verschillende grijstinten weergegeven (4a=donkerst grijs, 4b= middelgrijs, 4b'=lichtgrijs, 5=wit). Stadium 5 is het eindstadium van het metamorfose-proces.

De concentraties in het midden van de waterkolom zijn relatief laag. Tenslotte daalt de stroomsnelheid tot nul en vestigen alle larven zich op de bodem (6) voor een kort moment tijdens de LW-kentering, in afwachting van een nieuwe sprong voorwaarts met de komende vloedstroom.

Door de combinatie van tij-gerelateerde processen en larvengedrag worden de botlarven tijdens eb over een minder grote afstand teruggevoerd, dan was gewonnen tijdens vloed. Dit proces wordt elk getijde herhaald en leidt op den duur tot accumulatie van larven langs de randen van de kinderkamer, totdat de toevoer van larven geleidelijk aan afneemt (tegen eind mei) en de vestiging is voltooid. De zoetwaterlozingen in het gebied zijn gecorreleerd met de larvenophoping, maar een oorzakelijk verband is niet aangetoond.
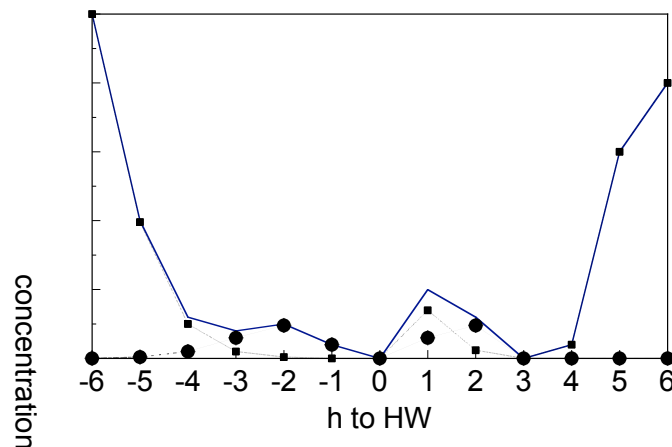

Fig. E. *Samengestelde curve (dikke getrokken lijn) van het getijdenverloop in larvenconcentraties, bestaande uit de curve die transport weergeeft (gestreepte lijn met blokjes) en de curve die accumulatie voorstelt (stippellijn met blokjes).*

De schatting van larventransporten wordt bemoeilijkt doordat processen van transport en ophoping elkaar in feite doorkruisen (**fig. e**). De Haas & Eisma (1993) constateerden in het getijdenverloop van zwevende stof in de Dollard twee maxima in concentraties. De eerste piek wordt verklaard door resuspensie middels turbulentie van vers afgezet sediment. De tweede piek wordt veroorzaakt door erosie van geconsolideerd bodemsediment door de toegenomen stroomsnelheid. De Haas & Eisma stellen het waargenomen concentratieverloop voor als een samengestelde curve. Dit idee kan analoog worden toegepast op botlarven. In tegenstelling tot zwevende stof zijn de processen van accumulatie en getijde-advectie de belangrijkste factoren die de samengestelde curve van het concentratieverloop bepalen.

De meeste zijgeulen in de Dollard takken in oostelijke richting af van het Groote Gat (**fig. c**). Ook ligt de oostelijke geulrand op een lager niveau dan de westelijke, waardoor de oostoever tijdens opkomend water op een vroeger

tijdstip zal overlopen dan de westoever. Dit heeft als consequentie dat de meegevoerde larven in eerste instantie de platen oostelijk van het Groote Gat zullen bevolken en pas in een later stadium tijdens de vloed ook westwaarts migreren. Zodoende is de veronderstelling dat de platen Hoogzand, Maanplaat en Oostfriesche Plaat (zie Fig. 1 in H.2) vanuit het Groote Gat met larven gevoed worden, terwijl de Heringsplaat aanvankelijk vanuit het Kerkeriet en pas later vanuit het Groote Gat van larven zal worden voorzien. Vanwege het relatief geringe larventransport via het Kerkeriet zou dit kunnen betekenen dat de dichtheden van zich vestigende botlarven hoger zijn ten oosten dan ten westen van het Groote Gat, waarbij deze geul een metaforische waterscheiding vormt.

De extreem hoge larvenconcentraties (tot 1000 m^{-3}) die in de huidige studie zijn aangetroffen, evenals de schattingen van de totale larventoevoer (in de orde van 10^9), duiden erop dat de Dollard een belangrijke kinderkamer is voor de bot. Behalve de Dollard ontvangt de aangrenzende Eems een substantiële invoer van larven, die naar verwachting van dezelfde grootte-orde is. Het relatieve belang van Dollard en Eems, waarbij rekening wordt gehouden met de kwantiteit en kwaliteit van de kinderkamers alsmede de onderlinge samenhang van beide ecosystemen, blijven het onderwerp van verder onderzoek.

IMPLICATIES VOOR HET BEHEER

Bedreigingen

Omdat estuaria het scheidingsvlak tussen zoetwater en het mariene ecosysteem vormen, zijn zij het toneel van een breed scala aan menselijke activiteiten die kunnen conflicteren met de natuurlijke functies, waaronder de kinderkamer-functie (zie *fig. f*).

In het verleden zijn aanzienlijke oppervlakten aan kinderkamergebied voor bot verloren gegaan door het afsluiten van de Rijndelta (Haringvliet), de Zuiderzee (3200 km^2) en Lauwerszee (94 km^2). De Dollard is successievelijk herwonnen op de zee, na het ontstaan in de Middeleeuwen door een reeks van transgressies (zie Fig. 2 in H.2).

Alle historische overgangen van zout naar zoet water in de Nederlandse Waddenzee zijn geblokkeerd door sluizen, dammen of dijken. De sluis bij Nieuwe Statenzijl is slechts een voorbeeld van een fysieke barrière voor vismigratie naar zoetwater.

De rivier de Eems, hoewel al niet meer in maagdelijke toestand vanwege vroegere kanalisaties, heeft nog steeds een relatief ongestoorde estuariene overgang tot aan Herbrum. Maar deze situatie wordt momenteel bedreigd door concrete plannen om een stormvloedkering ('Sperrwerk') in de Eems te bouwen

Fig. F. *Menselijke activiteiten in het Eems-Dollard estuarium die kunnen interfereren met de kinderkamerfunctie voor bot.*

in het belang van de kustverdediging alsmede dat van een scheepswerf in Papenburg die afhankelijk is van, en wordt beperkt door, dit ondiepe vaarwater voor het transport van (gigantische) cruiseschepen naar zee. Zelfs een kort-durende sluiting van het 'Sperrwerk' in de periode van larvale intrek kan het getijdentransport van botlarven verstoren met onvoorspelbare gevolgen voor de kinderkamerfunctie van de Eems.

De Eems is een belangrijke scheepvaartweg van de Noordzee naar de Eemshaven en de havens van Delfzijl en Emden. Om deze functie te handhaven moet intensief gebaggerd worden. De omvang van de baggerwerkzaamheden bedroeg van 1950-1965 gemiddeld 1.6 10^6 m^3 per jaar, en nam toe tot 6.5 10^6 m^3 in de jaren '80. In de huidige situatie wordt 2-4 10^6 m^3 (havens) plus 5-10 10^6 m^3 (geulen) per jaar gebaggerd (Mulder 1998b). Het uitgebaggerde slib wordt deels op het land gestort (Rysumer Nacken) en deels teruggestort in het estuarium, hetgeen verhoogde gehalten van zwevende stof en troebelheid teweegbrengt.

Industriële activiteiten in de Eemshaven, Delfzijl en Emden onttrekken proces- en koelwater aan het estuarium, en lozen het (soms vervuilde, of opgewarmde) water na gebruik. Met het water worden organismen ingezogen, hetgeen in het algemeen tot sterfte zal leiden. Botlarven zijn vanwege hun geringe lengte waarschijnlijk kwetsbaar voor deze sterfte-oorzaak.

Visserij-activiteiten zijn beperkt tot garnalenvisserij en visserij met vaste vistuigen. De bijvangsten bevatten jonge platvis, ondanks maatregelen ter preventie, en kunnen bijdragen aan de sterfte van de 0-groep.

Het veranderen van de habitat-structuur in een kinderkamergebied kan grote gevolgen hebben voor de overleving en de populatie-aanwas. In het geval van de Waddenzee moet men erop bedacht zijn dat de uitvoering van plannen om

nieuwe industriegebieden (Maasvlakte II), leefgebieden (Nieuw Holland) of vliegvelden (Schiphol II) aan te leggen in de Nederlandse kustzone gevolgen kan hebben voor de (residuele) waterbeweging en het larventransport. Dus ook ingrepen buiten een gebied kunnen de kinderkamerfunctie ervan beïnvloeden wanneer er interactie optreedt met de processen die de larventoevoer bepalen.

Compensatie

Een recente ontwikkeling in het waterbeheer en bij natuurbescherming is het compensatiebeginsel, dat tracht de ecologische schade van een menselijke ingreep te beperken door elders nieuwe habitats te creëren. Onlangs is de vraag gesteld met betrekking tot de Westerschelde hoe nieuwe kinderkamer-habitats kunnen worden aangelegd, wanneer de bestaande worden aangetast door de ingrijpende baggeractiviteiten die worden uitgevoerd om de scheepvaartweg naar Antwerpen te verbeteren.

Terwijl de kennis van kinderkamers in veel gevallen voornamelijk berust op het empirisch vaststellen van concentraties jonge vis, toont de kennis die in dit onderzoek is verzameld aan dat, als gevolg van de ongelooflijke complexiteit van de betrokken processen, geen simpele oplossing voor een dergelijke vraag gegeven kan worden. Fysische en biologische factoren hangen onderling samen maar een volledig begrip van de fundamentele processen ontbreekt. Bovendien wordt het inzicht vertroebeld doordat er interactie tussen processen plaatsvindt. Veel van deze processen vallen buiten de invloed of controle van de mens. Er zijn meer lacunes in kennis. Veel kinderkamer-onderzoek in de Waddenzee is uitgevoerd op het Balgzand (westelijke Waddenzee), maar onbekend is in hoeverre dit gebied representatief is voor de hele Waddenzee. Een vergelijking tussen Balgzand en Dollard wat betreft dichtheden, groei en sterfte van 0-groep platvis is mogelijk en zinvol. De herkomst van de larven is niet precies bekend (Engels Kanaal, Duitse Bocht, of beide?). Door het ontbreken van getallen voor de populatieomvang en van het recruitmentsucces is het onmogelijk om de betekenis van de Eems-Dollard als kinderkamer voor bot te relateren aan andere gebieden langs de Europese kust.

Aanbevelingen

Als een habitat moet fungeren als kinderkamer is het allereerst zaak dat de hydrografische omstandigheden zodanig zijn dat er voldoende larven in het gebied terechtkomen. Vanwege de lange tijd waarin paai- en kinderkamer-gebieden gezamenlijk zijn geëvolueerd, zullen 'nieuwe' kinderkamers slechts kans van slagen hebben binnen het geografische areaal van de huidige of historisch bekende kinderkamergebieden. Het is niet goed mogelijk om aan te geven hoe een gebied ingericht zou moeten worden om geschikt te zijn als

kinderkamer voor de ene of andere soort. Een gebied kan gestructureerd worden door geulen te verleggen, en de sedimentsamenstelling en hoogteligging van de platen te beïnvloeden. Zelfs zoutgradiënt en -fluctuaties kunnen door de mens gestuurd worden. Maar factoren als temperatuur of voedselaanbod onttrekken zich aan onze invloed. Transplantatie-experimenten, waarbij juveniele vis werd overgebracht naar onbenutte gebieden, of het uitzetten van juveniele (gekweekte) vis in bestaande kinderkamers, zijn twijfelachtig gebleken en het succes zal vooral afhangen van de kennis van factoren die uiteindelijk het voortplantingssucces bepalen. Bestaande plannen om een beperkt getijde in het Haringvliet te herstellen zijn naar verwachting gunstig voor bot. De geringe bestandsomvang van de botpopulatie in de Noordzee-kustzone wordt, naast de effecten van visserijdruk (bijvangst), mogelijk bepaald door de beperkte hoeveelheid kinderkamergebied. Door overgangen tussen zee en zoetwater te herstellen wordt een eerste stap gezet naar het stimuleren van botpopulaties. Wanneer getijdenstromen ontbreken kan het voor larven moeilijk zijn om van zout naar zoet te migreren, vanwege de gevonden aanwijzingen dat zij voor hun transport daarvan afhankelijk zijn. In dat geval wordt de migratie vermoedelijk in een later stadium ondernomen, wanneer de zwemvermogens voldoende ontwikkeld zijn. Dit wordt ondersteund door de toegenomen dichtheden van 0-groep bot in het IJsselmeer nadat het sluisbeheer is aangepast. Er is in Nederland nog een groot potentieel aan historische kinderkamergebieden van bot, die in het verleden verloren zijn gegaan.

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