



Towards a more complete understanding of the life cycle of brown shrimp (*Crangon crangon*): modelling passive larvae and juvenile transport in combination with physically forced vertical juvenile migration

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ABSTRACT

In this study we developed and utilized a complex model approach to investigate the impact of stage-specific transport processes on the development and spatial distribution of brown shrimp (*Crangon crangon*) post-larvae and juveniles in the German Bight. First, we focused on drift processes during the pelagic larval stage by coupling an individual-based model for egg and larval development ‘off-line’ to a 3D hydrodynamic model utilizing the Lagrangian method. Secondly, we investigated tidal-induced transport processes after juvenile settlement. To determine the tidal cycle, the model coupling was accomplished ‘on-line’ by resolving the individual-based model and hydrodynamic model with the same time step. The vertical migration of juveniles, a prerequisite for the selective tidal stream transport (STST), was modelled as a sub-grid scale physical process (balance of forces: gravitation, buoyancy, Stoke’s friction and dynamic uplift) and considered complex particle dynamics. We applied the model to test temperature and salinity cues as possible tidal indicators utilized by juvenile brown shrimp. Our results indicated that transport processes could significantly change the timing and spatial distribution of post-larval abundance. We also showed that the small-scale hydrodynamic forcing acting on the bodies of juvenile brown shrimps was sufficient to

account for the vertical migration required to use STST. For both investigated tidal cues STST performing juvenile brown shrimp were transported on-shore. A faster and more continuous STST was calculated for the salinity cue, resulting in larger abundances of brown shrimp in estuarine areas.

Key words: *Crangon crangon*, individual-based model, Lagrangian transport model, North Sea, selective tidal stream transport

INTRODUCTION

As it matures, brown shrimp (*Crangon crangon*) undergoes a number of different life stages which are characterized by differences not only in body structure but also in fundamental behavioural properties. Whereas eggs are carried by the females and hence can be considered benthic, larvae are released to a planktonic life form after hatching (Ehrenbaum, 1890; Kühl and Mann, 1964; Plett, 1965), and hence are exposed to passive transport processes. After completing five zoea stages (Ehrenbaum, 1890), brown shrimps metamorphose to the post-larval stage and settle at the bottom. The preferred habitats during the juvenile life stage are shallow tidal flats, which provide optimal nursery conditions with respect to temperature, predator avoidance and food availability (Janssen and Kuipers, 1981). A dominant signal of the seasonal population dynamics of brown shrimp in the southern North Sea is the massive immigration of 10–20-mm juveniles into their nursery grounds in late spring/early summer (May–June) (e.g. Beukema, 1992; Herrmann *et al.*, 1998; del Norte-Campos and Temming, 1998; Temming and Damm, 2002). These cohorts gradually leave the shallow nursery habitats and migrate to deeper, sublittoral areas, where they contribute to the exploitable stock and peak landings in autumn (Temming and Damm, 2002).

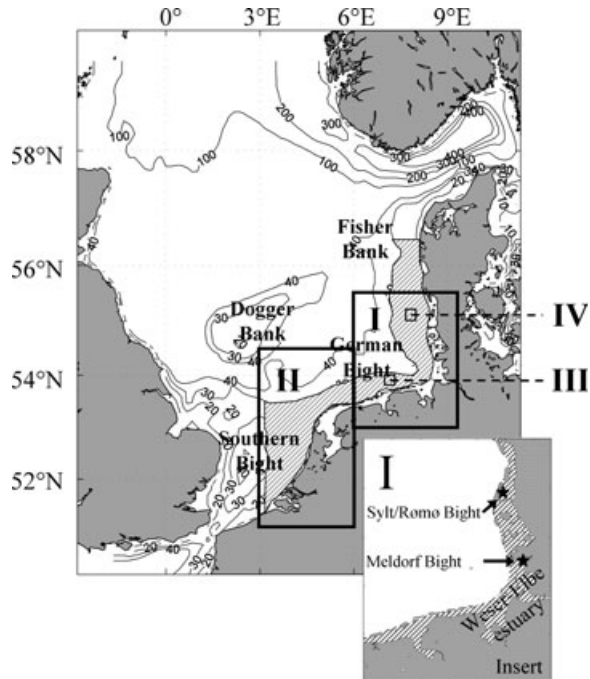
Brown shrimp constitutes a significant component of the coastal foodweb by transferring energy between the benthic and pelagic realms (Pihl and Rosenberg,

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Figure 1. North Sea topography including names of local topographic features. Striped area: considered spawning grounds of brown shrimp between 10 and 30 m depth line; Rectangles (I–IV): areas considered for analysis. Insert: amplification of area I. Stars: sampling locations for observed juvenile recruitment (Meldorf Bight: Nehrlich, 1987; del Norte-Campos, 1995; Sylt/Römö Bight: Herrmann *et al.*, 1998); Striped area: German Wadden Sea.



1982, 1984; Evans, 1983). Moreover, within the North Sea (see Fig. 1) ecosystem, brown shrimp forms an economically important species of increasing relevance. In 2006, historically high landings of over 37 000 tonnes were recorded (ICES, 2006). Despite its economic and ecological relevance, knowledge of brown shrimp life cycle and its linkage to biotic (e.g. prey and predator abundance) and abiotic (e.g. temperature, salinity, transport) factors still has important gaps. One major unresolved issue is the importance of transport processes during early life stages for spatial variability and timing of juvenile recruitment and, hence, commercial catches. Resolving this issue might also help to establish the importance of summer and winter egg production for population renewal, another open question in brown shrimp population dynamics.

Based on a study by Temming and Damm (2002), who developed and utilized an individual-based model (IBM) to investigate the relationship between the seasonal occurrence of juvenile immigration waves and the seasonal egg production, we developed the hypothesis that larval and juvenile transport processes

need to be considered when trying to understand the relevance of the egg production cycle for the spatial and temporal variability in brown shrimp juvenile recruitment.

Based on empirically derived relationships between developmental times of brown shrimp early life stages (egg, larvae, juveniles) and temperature, Temming and Damm (2002) simulated the population dynamic of juvenile brown shrimp at two distinct locations (Büsum harbour and Helgoland Roads) in the German Bight. Model runs were accomplished for 3 years that varied particularly with respect to winter water temperature [warm (1992), cold (1986), average (1993)] and the results were compared with observations from the German Wadden Sea [in 1986 (Nehrlich, 1987) and 1992 (del Norte-Campos, 1995) in the Meldorf Bight; and in 1993 (Herrmann *et al.*, 1998) in the Sylt/Römö Bight] (Fig. 1 insert).

The results indicated that the spring recruitment is related to winter egg production, with timing determined by winter water temperature. However, the model results deviated from observations and estimated delayed juvenile recruitment with a time lag of about 3–6 weeks. Temming and Damm (2002) speculated that the mismatch was caused by the fact that the observed juveniles originated from Dutch coastal waters and were transported into German waters by means of residual currents, a process that could potentially explain the deviation between observations and model results. To evaluate their hypothesis and quantify the implication of transport processes, we developed and utilized a spatially explicit IBM that accounts for stage-specific attributes.

The focus of our modelling study was both the pelagic larval and the benthic juvenile stages. Whereas brown shrimp larvae can be considered passive drifters, this is not a valid generalization for the larger juveniles, which have to be treated as active individuals. The observed juveniles in the tidal flats are usually at least 5 mm (Temming and Damm, 2002), indicating that post-larval settlement occurs in deeper, off-shore areas. Hence, juvenile brown shrimp need to cover distances of up to 60 km to reach their nursery grounds. It appears unlikely that brown shrimp accomplish this by active pleopod swimming, which would probably incur high metabolic costs (Morris *et al.*, 1985) and is in many cases two to three orders of magnitude slower than instantaneous current velocities in estuaries (Forward and Tankersley, 2001). It is more likely that juvenile brown shrimp are able to utilize the strong tidal currents of the North Sea for the required transport.

The hypothesis that juveniles use selective tidal stream transport (STST) to cover the required distance has been formulated previously by Cattrijse *et al.* (1997) based on observations from Boddeke (1976), who found a significant decrease in the pelagic abundance of young shrimp at the beginning of ebb tide. Likewise, Van der Baan (1975) observed a tide-related migration pattern for adult brown shrimps in the North Sea.

STST is defined as a horizontal transport that is accomplished by vertical migration into and out of the water column synchronously with changes in the direction of tidal currents (Forward and Tankersley, 2001). The juvenile brown shrimp migration into the tidal flats might be explained by active vertical swimming behaviour in combination with hydrodynamic drift. However, the juveniles are relatively large and it is unlikely that the pressure, frictional and gravitational forces acting on their rigid bodies can be neglected. These small-scale forces involve passive animal motions that deviate from the water transport patterns and would need to be resolved correctly before active individual migration behaviour is indicated. So far, the potential strength of this hydrodynamic forcing, the resulting vertical animal movements and their potential role in vertical migration behaviour has not been assessed and it is not clear whether it can contribute significantly to a saving of the metabolic costs of vertical upward swimming.

Our aim here was to investigate both the impact of passive larval drift on brown shrimp post-larval recruitment variability and the role of STST for juvenile migration to the tidal flats. The latter emphasizes specifically the importance of small-scale physical forces for vertical migration and involves the question of whether the resulting vertical and horizontal transport pattern contributes or is even sufficient to explain the characteristics of STST, including the occurrence of juveniles in the water column during flood tide and the observed arrival times at the German coast.

METHODS

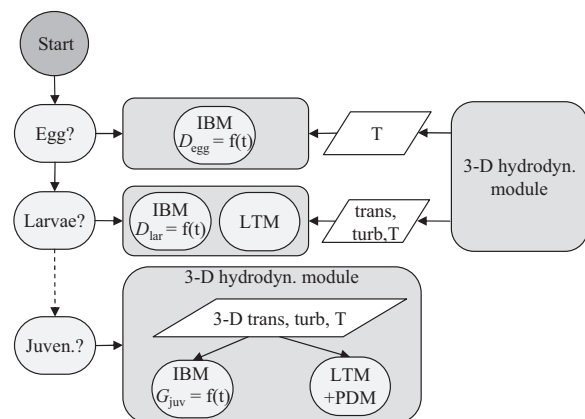
To address the issues of the impact of passive larval drift and of STST on recruitment timing of juvenile brown shrimp, we developed a coupled model system that includes an Eulerian 3D hydrodynamic module for the North Sea (ECOSMO; see Schrum *et al.*, 2006), a Lagrangian particle tracking module (LTM), a simple temperature-dependent IBM for brown shrimp eggs, larvae and juveniles and a particle-flow

field dynamics module (PDM). The latter resolves the hydrodynamics of small particles similar in shape to shrimp juveniles and is based on Newtonian first principles. In the following, we describe the different modes of coupling and provide detailed descriptions of the specific modules and the set-up of the numerical experiments that were conducted.

Model coupling

Coupling of biological and hydrodynamic modules can be performed either 'on-line' (modules were calculated simultaneously) or 'off-line' (modules were calculated independently). Both methods are distinguished by the possible temporal resolution of environmental characteristics. For the 'off-line' coupled model we used daily means of water transports and temperatures. In contrast, the 'on-line' coupling allows water drift to be resolved with a temporal resolution equal to that of the hydrodynamic model, in our case 20 min. Based on stage-specific requirements, we chose different methods for different brown shrimp life stages (Fig. 2). As brown shrimp is known to be an egg-carrying, benthic species, the embryonic phase was assumed to be demersal and stationary. For this first life stage the coupling of IBM and hydrodynamic modules was performed 'off-line' using previously model-derived time series of local (at the position of egg development) daily mean temperature. For the larval phase, an 'off-line' coupling was chosen which also allows for free larval drift, requiring additional information about current

Figure 2. Schematic diagram of the model structure including early life of brown shrimp from egg to juvenile stage. For each stage the coupled modules are listed. IBM, individual-based module; LTM, Lagrangian tracer module; PDM, particle-flow field dynamics module; $D_{\text{egg/lar}}$, egg/larval development; G_{juv} , juvenile growth; trans, transport; turb, turbulence; T, temperature.



velocities and turbulent dispersion. In addition to the IBM and the hydrodynamic module, an LTM was used to simulate larval transport.

During the juvenile phase the individuals can no longer be considered passive drifters. They are too large to neglect the pressure and frictional forces acting on their rigid body, leading to passive animal motion deviating from the water transports. To resolve these movements in a physically correct manner, we developed an equation of motion for shrimp particles based on Newtonian principles, which is used in a PDM. The latter was specifically developed for the purpose of modelling STST. The necessity of resolving the tidal cycle in the North Sea (mainly half-daily tides) makes the 'off-line' method unfeasible for our purpose. Therefore we chose the 'on-line' coupling to simulate water transport processes for juvenile brown shrimp.

Hydrodynamic module

The hydrodynamic core of the coupled model system was based on the HAMSOM/ECOSMO model applied to the North and Baltic Sea system. The model was described in detail by Schrum and Backhaus (1999) and further information on the set-up was given by Schrum *et al.* (2006). The model provided 3D daily mean Eulerian fields of environmental variables as input parameters for the IBM, LTM and PDM. This included advective current velocity, temperature and turbulent diffusion. The latter accounts for the unresolved sub-grid scale turbulence. The model equations were solved on a staggered Arakawa-C-grid (Arakawa and Lamb, 1977) using a spherical grid with resolution of 6' in latitude and 10' in longitude, which corresponds to an approximate 10-km horizontal resolution. To resolve stratification, a vertical resolution of 5 m for the upper 40 m has been chosen.

The surface boundary conditions were derived from NCEP/NCAR re-analysis data (Kalnay *et al.*, 1996). At the land/water interface, boundary conditions were taken from monthly mean freshwater runoff (North Sea: Damm, 1997; Baltic Sea: Bergström and Carlsson, 1994). Especially important for the simulation of STST is the consideration of partial tides in the model formulation. Tides were modelled as co-oscillating tides (prescribed tidal surface elevation at the open boundaries) and three dominant partial tides (M_2 , S_2 and O_1) were considered. Investigations concerning model validation were conducted by Janssen *et al.* (2001) and Janssen (2002), and indicated that the model gives a realistic estimation of the hydrodynamics and its variability for the North Sea and the Baltic Sea.

Individual-based model

The biological part of the model, i.e. development of brown shrimp individuals, was adopted from Temming and Damm (2002). It describes the development of brown shrimp from fertilization of eggs until the juveniles have grown to a predetermined length (15 mm). As the focus of this contribution was on the seasonal timing of juvenile recruitment and its regional structure rather than on its absolute magnitude, mortality was neglected. The development of brown shrimp eggs and larvae, and juvenile growth in the model were parameterized as a function of temperature and calculated with a daily time step.

In the first experiments, model particles symbolized cohorts of brown shrimp larvae between hatching and settlement at the end of larval stage, which coincides with a length of 4.6–4.7 mm (Tiews, 1970; Campos and van der Veer, 2008). For our modelling purposes, this value was rounded up to 5 mm. During the model performance, a developmental state was attributed to every model particle for each day (t). The fraction of the total stage duration (TD_t) was estimated based on the prevailing temperature (T_t):

$$TD_t = \sum_t \frac{1}{SD(T_t)} \quad (1)$$

The respective stage is completed if TD_t reaches 1.

The temperature-dependent stage duration SD_t (days) during the embryonic and larval phase was calculated as:

$$SD_t(T) = m \times T_t^b \quad (2)$$

Constants m and b for both developmental stages, egg and larvae, are given in Table 1. For the embryonic phase, the relationship was developed by Redant (1978) based on observations from Havinga (1930), Tiews (1954), Meixner (1969) and Wear (1974). The values for larval brown shrimp were based on measurements from Criales and Anger (1986), who created an equation for larval development depending on the number of moults and on temperature. They obtained the values for m and b by ascertaining that approximately five to six moults occurred during the larval stage. Both equations for the development time

Table 1. Parameters for the development of brown shrimp eggs and larvae (Eqn 2).

Stage	m	b	Reference
Egg	1031.34	-1.354	Redant (1978)
Larvae	914.78	-1.347	Criales and Anger (1986)

imply an acceleration of development with increasing water temperature.

In the second set of experiments, model particles symbolized cohorts of brown shrimp juveniles. The juvenile length-growth per day was parameterized as a function of temperature and the length of the individual (l) (Kuipers and Dapper, 1981):

$$\Delta l(T_t) = a + b \times T_t - c \times l \quad (3)$$

with the growth parameters $a = 0.25$, $b = 0.014$ and $c = 0.0042$ (Lüthke, 2003). Contrary to the original set of parameters from Kuipers and Dapper (1981), the parameters employed here were adjusted to allow for faster growth of juvenile brown shrimps and, hence, to fit the observed juvenile length between June and October in the German Bight (for details see Lüthke, 2003).

Lagrangian transport module

Passive phase. The ‘shrimp-particles’ were assumed to be passive drifters with neutral buoyancy during the larval phase. Consequently, their spatial displacement depends only on the transport and dispersion processes in the water column. By using daily mean transport estimates, tides were largely averaged out and only the residual currents, composed of wind-induced, baroclinic and tidal residual currents, were taken into account. Additionally, a diffusive velocity was considered to account for sub-grid scale turbulent processes. Thus, the particle velocity at a given time and location was defined as the sum of advective \vec{V}_a and diffusive \vec{V}_d velocities:

$$\frac{d\vec{X}(t)}{dt} = \vec{V}_a(t, \vec{X}) + \vec{V}_d(t, \vec{X}) \quad (4)$$

According to Maier-Reimer (1973) the local velocity components ($\vec{u}, \vec{v}, \vec{w}$) were calculated by linear interpolation between the velocity values at the grid-box boundaries. Diffusivity was assumed to be a random process and was therefore calculated using a Monte-Carlo method (Bork and Maier-Reimer, 1978). The required dispersion coefficient was derived from the hydrodynamic module. Although the applicability of this method has been controversially discussed by a number of authors for the case of pronounced vertical turbulence variations (e.g. Yamazaki and Kamykowski, 1994; Visser, 2009), the approach can be considered valid for the application presented here, as the near-shore areas of the southern North Sea do not exhibit a continuous, pronounced vertical turbulence profile or vertically stratified conditions. Hence, independent of the method used to simulate particle diffusion, we would

not expect turbulence-induced vertical accumulation of simulated ‘shrimp-particles’.

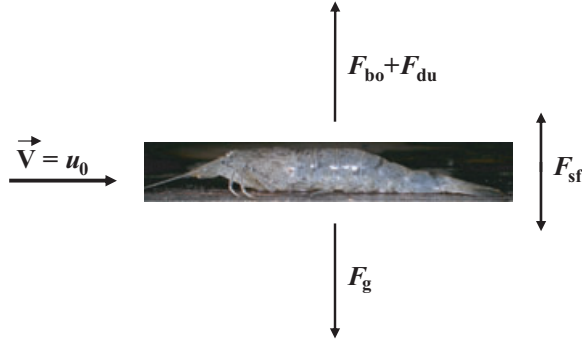
Active phase – STST. The vertical migration of juvenile brown shrimps into the water column after sensing the flood-tide current is a prerequisite for the utilization of STST. Within this study we aimed to resolve the contribution of the hydrodynamic forcing on the animal to its vertical migration while considering the specific body shape of juvenile brown shrimp. The physically induced vertical migration is determined by the balance of forces in a vertical direction according to Newton’s second law. Maxey and Riley (1983) have provided such an equation of motion for spherical particles of finite size and mass. The relative particle transport (relative to the fluid velocity) depends on the fluid velocity, buoyancy and friction (Stokes drag), while neglecting higher order force terms such as Basset-Boussinesq history forces and Faxen corrections. However, this is too simple an approach for marine crustaceans because their body is far from being spherical and hence body shape corrections for the friction term as well as pressure forces on the body have to be considered.

We formulated an equation of motion for the juveniles, which we solved numerically while making a justified assumption of the sub-grid scale velocity shear. To simplify the problem we concentrated on the vertical direction only and assumed that the horizontal ‘shrimp-particle’ relative motion could be neglected and horizontal shrimp transport occurs only through the fluid transport velocity. The forces acting on an individual comprise dynamic uplift, friction and gravitation. Each body within a fluid is affected by Archimedes’ principle as a result of density differences between the body and the fluid. If brown shrimps move with an angle of incidence (α) relative to the surrounding water, an additional force acts on its body, which could either be directed up or down depending on the angle. Here we postulate that the animals will always pose themselves against the flow with an optimal angle of incidence to achieve an uplift force. The hydrodynamic uplift force was described previously for the pelagic Antarctic krill (*Euphausia superba*) by Kils (1982). Due to physical similarities between the two species, we assumed that brown shrimps also experience an upward acceleration induced by this force.

The total force (F_{tot}) on the juvenile brown shrimp is then the sum of forces (Fig. 3):

$$F_{\text{tot}} = F_g + F_{\text{bo}} + F_{\text{sf}} + F_{\text{du}} \quad (5)$$

Figure 3. Lateral view of brown shrimp; the arrows indicate the set of forces (F_g : gravitation; F_{bo} : bouyancy; F_{sf} : Stokes friction; F_{du} : dynamic uplift) influencing vertical migration of brown shrimp individuals experiencing a relative horizontal current velocity \vec{V} . Photo: Marc Hufnagl, Univ. Hamburg.



where F_g = gravitation, F_{bo} = buoyancy; F_{sf} = Stokes friction and F_{du} = dynamic uplift.

In the following section we describe the single forces and formulate the equation for the vertical motion of an individual.

Gravitation (F_g) is proportional to the wet weight of brown shrimp (m_{cc}) and the gravitational constant (g):

$$F_g = m_{cc}g \quad (6)$$

Buoyancy (F_{bo}) is directed against gravity and acts on all bodies that are located in a fluid. It is inversely proportional to the mass of the displaced water-body (m_{H_2O}):

$$F_{bo} = -m_{H_2O}g \quad (7)$$

Stokes friction (F_{sf}) acts on all bodies that move relative to the fluid. At the body surface the velocity of flow equals zero. In a viscous fluid the body is decelerated, inducing a force that is directed against the direction of the movement. For a spherical body, the Stokes friction is defined as:

$$F_{sf} = -6\pi r\eta w \quad (8)$$

where r = radius, η = molecular viscosity coefficient and w = relative vertical velocity.

As brown shrimp are not spherical, we need a body shape constant (c) to replace the term $6\pi r$. Spaargaren (1979) empirically estimated the body shape constant for shrimp to be equal to $cm_{cc}^{\frac{2}{3}}$. The Stokes friction on the shrimp is therefore:

$$F_{sf} = -cm_{cc}^{\frac{2}{3}}\eta w \quad (9)$$

Dynamic uplift (F_{du}) is directed against the gravitation and is generated if the brown shrimp individual moves relative to the water with an angle of incidence. If the body shape of juvenile brown shrimp (Fig. 3) resembles in the broadest sense the shape of the wing of an airplane, we parameterized the dynamic uplift on brown shrimp according to the uplift of an airplane. The dynamic uplift is proportional to the base area ($S = Bl$, with prosoma width B and body length l = profile depth) and to the dynamic pressure q_0 and the lift coefficient (c_A) (Scharstein and Send, 2004):

$$F_{du} = -c_A q_0 S \quad (10)$$

The dynamic pressure is equivalent to the kinetic energy of a flow mass element (ΔM) related to the corresponding volume (ΔV) and can be calculated as:

$$q_0 = \frac{1}{2} \rho_{H_2O} u_0^2 \quad (11)$$

where ρ_{H_2O} = water density and u_0 = relative velocity.

Scharstein and Send (2004) provided a simplified solution for the lift coefficient as a function of the angle of incidence in a flow channel with height $H=2l$:

$$c_A = 2\pi \sin(\alpha) \quad (12)$$

Assuming that H is a characteristic length scale, we can utilize the model in the undisturbed water column.

By inserting Eqns 6, 7, 9 and 10 into the equation for the total force (Eqn 5) this can be rewritten as:

$$F_{tot} = m_{cc}g - m_{H_2O}g - cm_{cc}^{\frac{2}{3}}\eta w - c_A q_0 S = m_{cc} \frac{dw}{dt} \quad (13)$$

resulting in a vertical acceleration of the juvenile brown shrimp relative to the water mass:

$$\frac{dw}{dt} = g \left(1 - \frac{\rho_{H_2O}}{\rho_{cc}} \right) - cm_{cc}^{\frac{2}{3}}\eta w - \frac{c_A q_0 S}{m_{cc}} \quad (14)$$

This equation was now solved numerically to estimate the relative vertical shrimp movement. We approximated the derivative by a finite difference and obtained the vertical velocity of an individual (w_n) at time step n as a function of the velocity at the previous time step (w_{n-1}) and the time interval (Δt):

$$w_n = w_{lift} = \frac{w_{n-1} + \left(g \left(1 - \frac{\rho_{H_2O}}{\rho_{cc}} \right) \Delta t - \frac{c_A q_0 S}{m_{cc}} \Delta t \right)}{1 + cm_{cc}^{\frac{2}{3}}\eta \Delta t} \quad (15)$$

Most important for the uplift of the juveniles is the relative horizontal velocity (u_0) that the juveniles are exposed to. We obtained the relative horizontal velocity at time step n from the difference between the horizontal fluid velocities ($|\vec{V}_{\text{horiz}/n}|$) experienced by the individual at two subsequent time steps ($u_{0/n} = |\vec{V}_{\text{horiz}/n-1}| - |\vec{V}_{\text{horiz}/n}|$). Implicitly, this is using the assumption that a relative horizontal juvenile transport is quickly slowed down and not maintained longer than a time step and that the individual swimming velocity of the juveniles is negligible compared to the water transport. The relative horizontal velocity depends therefore solely on the vertical flow field profile, the juvenile orientation in the flow field and the juveniles' vertical ascent (or descent).

As there are no studies available about the individual behaviour of juvenile brown shrimp in a specific flow field, we introduced a set of premises and assumptions to be able to estimate the relative horizontal velocity:

- 1 The current velocity in the bottom layer increases with distance from the bottom following a logarithmic profile and depends on the velocity value and the thickness of the respective grid cell. At the bottom, the current velocity equals zero.
- 2 The individuals are able to hold their orientation with respect to the current direction.
- 3 The individuals are able to change the angle of inclination and always chose an optimal angle of inclination.
- 4 The individuals respond to the tidal signal by ascending from the sediment to the water column (10 cm above the bottom).
- 5 Initially, for the first time step after ascending from the sediment, the individuals have no horizontal velocity and the relative velocity equals the advective current velocity $|\vec{V}_{\text{horiz}}|$.
- 6 The juvenile brown shrimp orients itself by the initial current directions and holds this orientation during the complete vertical migration cycle.
- 7 The impulse of the individual remains constant during a time step.

Due to a lack of observations, we decided to define the angle of inclination to optimize the vertical migration pattern. Therefore we specified a threshold for the relative velocity that determines the vertical acceleration of an individual. In cases with $u_0 > 0.01 \text{ m s}^{-1}$ the individual is accelerated upwards as long as the current velocity increases significantly with distance from the bottom. At $u_0 < 0.01 \text{ m s}^{-1}$, gravitation becomes the dominant force and the juvenile sinks downwards. At $u_0 = 0.01 \text{ m s}^{-1}$, the vertical acceleration of an individual equals 0.00 m s^{-2} . Following this, the optimal

angle was calculated as a function of body length (l) ($\alpha = 2.4414 + 0.4223 * l + 0.1883 * l^2$).

Besides the relative vertical particle velocity (w_{partrel}), which could be either positive or negative, the total vertical velocity of juvenile brown shrimp in the model (w) comprises the grid scale advective (w_{adv}) and the sub-grid scale diffusive (w_d) velocity:

$$w = w_{\text{adv}} + w_d + w_{\text{partrel}} \quad (16)$$

As the migration of brown shrimp depends on vertical differences in the horizontal flow, a time stepping that is able to resolve the vertical migration is essential. We therefore used a time resolution of 1 min to resolve the vertical particle dynamics and the resulting vertical migration of brown shrimps.

Model set-up

Passive phase (egg and larvae). Egg production was assumed to occur continuously throughout the year with an annual cycle characterized by maximum spawning activity in July and December. The relative spawning index ($I(t)$) per day (t) was developed by Temming and Damm (2002) considering the size distribution of the population, the size-specific percentages of egg-bearing females, the size- and temperature-specific moulting (i.e. spawning) rate and a rough estimate of monthly population size. Based on the spawning cycle, a number of cohorts $\{N(t) = 20I(t), t \in [1, 365]\}$ per water column started their egg phase at each day of the year within predefined spawning grounds. Note that the constant of proportionality (20) has no quantitative measure and the results are therefore solely interpretable in terms of relative intensity and temporal variability.

The start date of each simulation was set at 1st July of the previous year in order to account for winter spawning activity. Without knowledge of the exact spawning grounds in the North Sea, we assumed that brown shrimp spawns in the sub-tidal areas at water depths between 10 and 30 m (Fig. 1). This assumption was based on observations by Boddeke (1976), who found egg-bearing females mainly in deeper waters during winter. As the egg-carrying females are known to live at the sea bottom, the eggs were assumed to be benthic and stationary during the simulation. Thus the egg development was only determined by bottom water temperature at the specific spawning location. To quantify the impact of larval drift on juvenile recruitment for each year, two model runs were performed, one that considered the larvae as passive drifters (R1) and a reference run without larval drift (R2). In the reference run, the larvae remained at their initial spawning

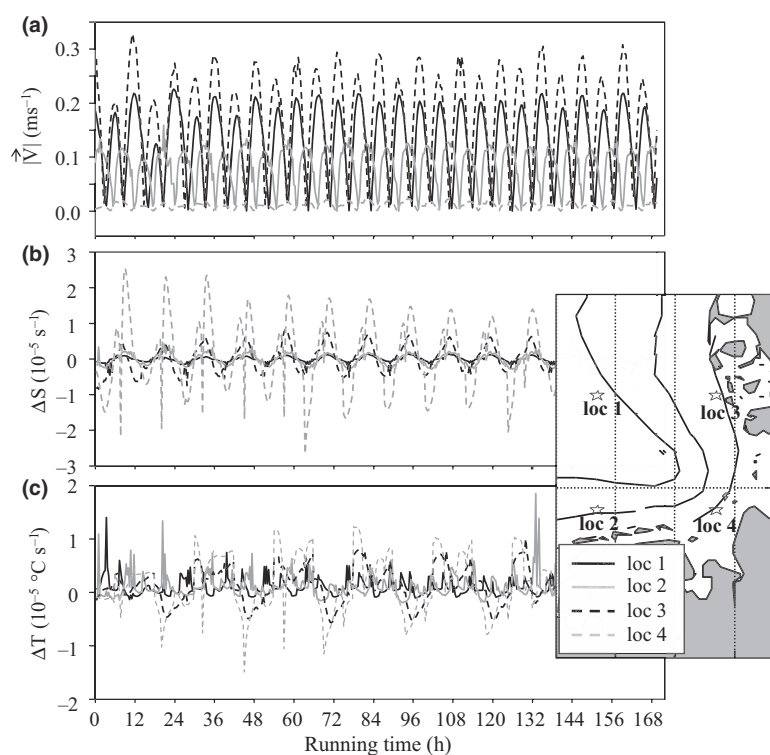


Figure 4. Simulated temporal variability of environmental factors at four distinct locations in the German Bight covering a simulation time period of about 167 h beginning on 1 of May. (a) Absolute value of current velocity ($|\vec{V}| = \sqrt{u^2 + v^2}$). (b) Local changes in salinity S . (c) Local changes in temperature T .

location but were, in contrast to the benthic eggs, distributed randomly in the water column.

Active phase – STST (juveniles). The simulation of the active transport of juvenile brown shrimp was conducted as a theoretical experiment. To test our hypothesis, simulations were performed for two contrasting years (1986 and 1992). In each simulation, particles (juveniles) were released on 1st May and the individuals were tracked over the year until they reached the coast. The particles were initially distributed homogeneously (10 per box) in a restricted area in the German Bight (53.03–55.53°N and 5.67–9.00°E) beyond the 10 m depth line.

The most important aspect for our numerical experiments is that the German Bight is characterized by strong tidal currents (Fig. 4a). Due to the variability of hydrographical conditions in the German Bight, these currents are associated with changes in temperature as well as salinity (Fig. 4b,c). These short-term changes in environmental conditions can be regarded as a mark in time that can indicate the onset of flood or ebb tide. The temperature distribution in the German Bight is characterized by a strong gradient perpendicular to the coast following the topographic gradients, with warmer waters in the shallow coastal areas in late spring and early summer. In late spring the coastal and off-shore waters in the German Bight

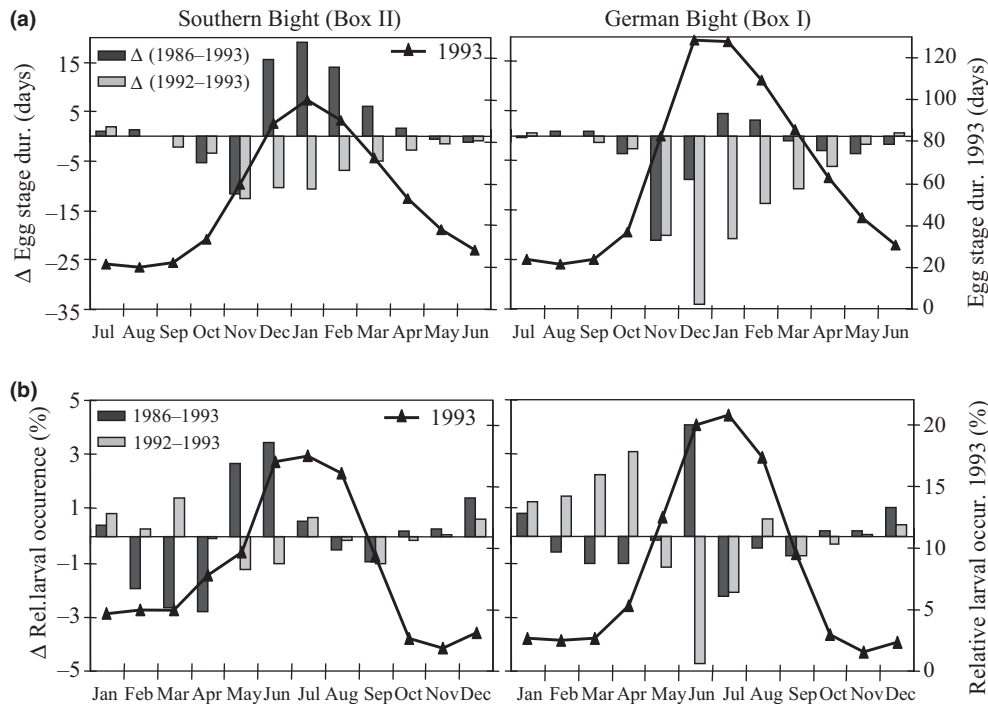
exhibit differential heating. Hence, the temperature in the shallow coastal regions increases more rapidly than the temperature in deeper stratified areas. Therefore the flood stream current is associated with a local decrease in temperature (Fig. 4c). The salinity distribution in the German Bight exhibits a very similar horizontal gradient when compared to temperature (Fig. 4b), but for a different reason. Freshwater runoff from the rivers, among others the Weser, Ems and Elbe, decreases salinities in the coastal areas and leads to a local increase in salinity in flood stream currents. To account for these two possible tidal signals, two kinds of model runs were performed using either temperature (ΔT) or salinity (ΔS) as tidal cue.

RESULTS

Passive phase

To simplify the interpretation of model results, the investigation area was subdivided into the German Bight (Box I see Fig. 1) and the Southern Bight (Box II). To investigate the impact of spatial variability in water temperature on egg developmental rates, stage duration (days) for eggs in both areas was calculated for three different years (1986, 1992, 1993) and compared to each other (Fig. 5a). Monthly means for the year 1993 (year with average temperatures) were plotted against time to illustrate the seasonal cycle and indicated a clear

Figure 5. Simulated average egg stage duration (a) and relative occurrence of post-hatched larvae (b) in the Southern and German Bight (compare Fig. 1). (a) Solid line: monthly averaged duration of egg development (days) for 1993 (right axis). Bars: difference between monthly mean egg stage duration in 1986 and 1992, and the reference year 1993 (left axis). (Values were averaged for all simulated individuals spawned in Box I and Box II respectively). (b) Solid line: relative occurrence of post-hatched larvae in year 1993 (right axis). Bars: difference of relative monthly occurrences of post-hatched larvae in year 1986 and 1992, and the reference year 1993 (left axis).



seasonal signal, with up to sixfold differences between eggs spawned in the summer (approximately 20 days in August) and in the winter (>100 days in December/January). The estimates for 1993 served as a reference to investigate inter-annual differences among the years. A prolonged egg phase for eggs spawned in winter (December–March) was found in the colder year 1986 compared to 1993. This was most clearly found in the Southern Bight area (Box II) but was also seen in the entire German Bight in January and February. In contrast, the egg phase in winter 1992 was between 10 (Box II) and 30 days (Box I) shorter than in 1993. Egg development rates showed marked differences between Box I and Box II in both intra- and inter-annual patterns. In general, the calculated egg stage durations were longer in Box I than in Box II, with a maximum difference of 39 days between the boxes in December 1993. As a consequence of the temperature-dependent, slower egg development during winter, the concentrations of newly hatched larvae increased rapidly in spring (Fig. 5b). The seasonal cycle of newly hatched larval appearance in Box I and Box II was shown for 1993,

indicating low concentrations in winter and maximum concentrations in summer (June/July). As a consequence of the differences in egg development rates, pronounced differences between the calculated seasonal patterns were found for the different areas and years. Due to longer egg phases in winter, the relative winter concentrations of newly hatched larvae in Box I were lower than in Box II, followed by a steeper increase in May and a more pronounced maximum in June 1993. The same mechanism is responsible for the simulated inter-annual differences, with longer egg stage durations in winter 1986 resulting in a more pronounced maximum in June 1986 than in the average year 1993.

After hatching, brown shrimp larvae were considered passive drifters following the prevailing circulation pattern (Fig. 6a). The results of the drift experiments (R1) indicated that the larvae potentially hatched in January were exposed to strong currents that were mainly forced by southwesterly winds during this part of the year (Siegismund and Schrum, 2001) and thus exhibited a cyclonic circulation pattern along the southern and Danish coasts.

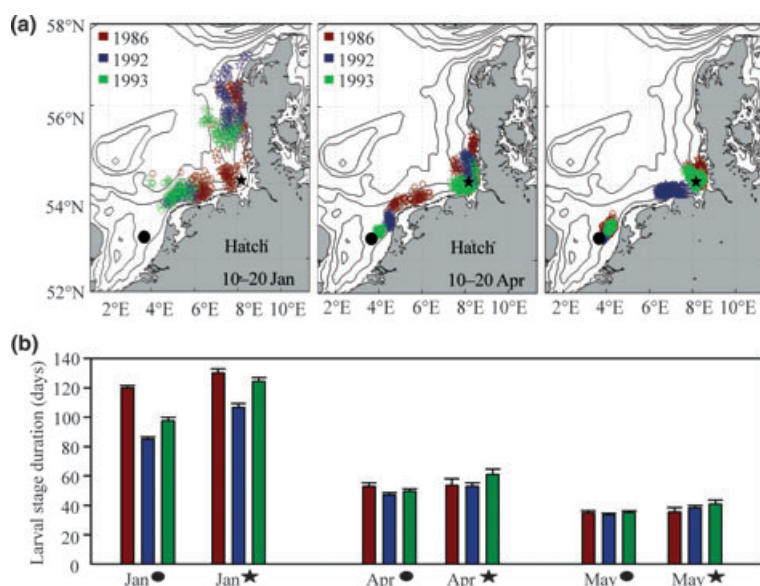


Figure 6. (a) Simulated location of larval hatch and post-larval settlement for the 3 years. Displayed are larvae hatched at one specific location in the Southern Bight (black circle) and in the German Bight (black star) in January, April and May. (b) Simulated average larval stage duration with respect to hatching time (month) and location.

Additionally, these individuals experienced long larval stage duration due to low winter water temperatures (Fig. 6b). Simulated drift pattern for larvae hatched in April and May (Fig. 6a) showed a decrease in both larval stage duration and length of the drift pathways as the year progressed. In 1986 in particular, the dislocation of larvae hatched in the Southern Bight in April was modelled to be substantially larger than that of larvae hatched in May. May-hatched larvae were generally exposed to relatively high temperatures and weak residual currents, resulting in a rather limited displacement of these larvae (Fig. 6b). In addition, we detected spatial differences for larval stage duration, with longer durations for larvae originating from the German Bight than the Southern Bight.

The above-mentioned differences in developmental rates and in larval displacement resulted in dissimilarities in juvenile appearance among years and among regions. To assess the spatial variability in the timing of juvenile recruitment, the occurrence of 5-mm juvenile brown shrimp was calculated for Box I and Box II separately. In both areas we found a clear seasonal cycle for the estimated recruitment (Fig. 7a) in which the number of newly metamorphosed juveniles started to increase in April and reached a maximum in July. In Box I, the number of 5-mm juveniles in May 1986 and 1992 was higher than in 1993. In contrast, the maximum values in July 1993 exceeded those in the other years. The opposite trend was seen in Box II, where the abundances of post larval brown shrimp in spring were lower in 1986 and 1992 than in 1993, but higher in summer.

The difference in simulated numbers of juvenile individuals between the two runs, the run with drift (R1) and without drift (R2), allowed an assessment of the impact of larval drift on juvenile recruitment (Fig. 7b). Due to the cyclonic circulation and the fact that spawning grounds further west and along the English channel were not considered in the simulations, a negative balance of juvenile abundances was calculated for the westernmost Box II throughout the year, with the largest deficit in May. Consequently, we could detect an increased number of recruits in the German Bight (Box I) as a result of larval drift in spring and summer. On the other hand, a negative balance was calculated for this area in autumn. The most conspicuous signal was the increased number of juveniles in May 1986.

Besides the impact on average recruitment in the two areas, the larval drift resulted in a pronounced spatial variability. In Fig. 8, the monthly mean number of recruits in the investigation area is depicted for May in the 3 years. A conspicuous concentration of recruits was found along the coastline in the southern part of the German Bight in all 3 years. In contrast, recruits off the Danish coast were significantly more dispersed. Additionally, the model estimated a strong spatial variability in the timing of maximum recruitment. To highlight these spatial differences, we calculated monthly means of the average numbers of 5-mm juveniles per day in two small sub-areas (Box III and IV in Fig. 1) (Fig. 9). Although Boxes III and IV were both located in the German Bight area, the seasonal cycles were markedly different. A maximum of early juveniles in Box III was simulated for June in

Figure 7. (a) Simulated average relative (relative to the total number of cohorts) occurrence of 5-mm juvenile brown shrimp in Box I and Box II. Solid line: monthly average for 1993 (right axis). Bars: difference between monthly means in 1986 and 1992, and the reference year 1993 (left axis). (b) Differences in the monthly mean number of 5-mm juveniles between experiment R1 (with larval drift) and the reference experiment R2 (without larval drift).

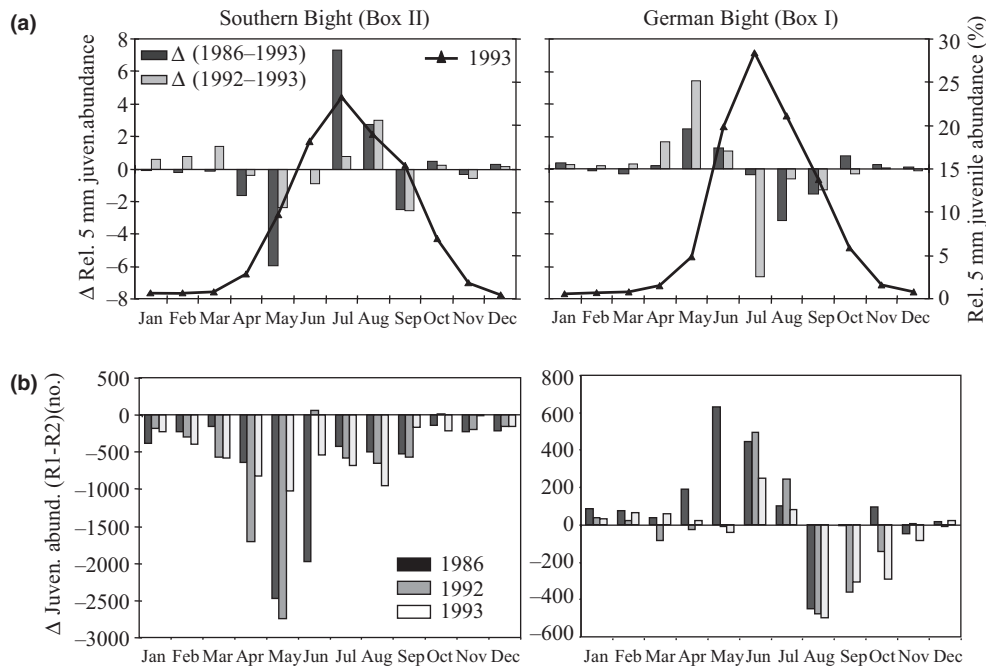
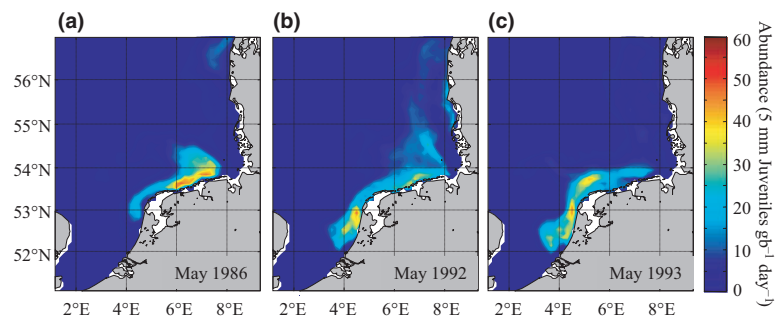


Figure 8. Simulated spatial distribution of 5-mm juveniles in the German Bight. Displayed are monthly mean values for May in (a) 1986, (b) 1992 and (c) 1993. Colours represent the average daily abundance of juveniles per area. gb, horizontal gridbox.



1992 and 1993, whereas 1986 exhibited a different pattern, with an early peak in May and a second peak in July. In contrast, the maxima in Box IV generally occurred later in the year, with a delay of 1 month in 1992 and of 2 months in 1986, indicating more pronounced spatial differences for the exceptionally cold year 1986.

Active-phase STST

The results of the larval drift simulation revealed a strong spatial variability in the distribution of 5-mm juveniles off the German Coast, suggesting a similar spatial variability in the immigration pattern of juvenile recruits to the tidal flats of the Wadden Sea. In

both experiments (ΔT , temperature differences and ΔS , salinity differences as cues) most juveniles reached the coast after the migratory period independent of their initial position. This indicates that active swimming is not required but that the physical forcing alone is sufficient to explain the observed migration pattern, assuming that the juveniles follow a few behavioural rules: (i) to react to a tidal signal (either temperature or salinity change), (ii) to keep their orientation in the tidal current, and (iii) to maintain an optimal angle to the current. Based on our calculations here, we conclude that energy-requiring vertical or horizontal swimming behaviour is completely unnecessary for the juveniles to reach their habitats on

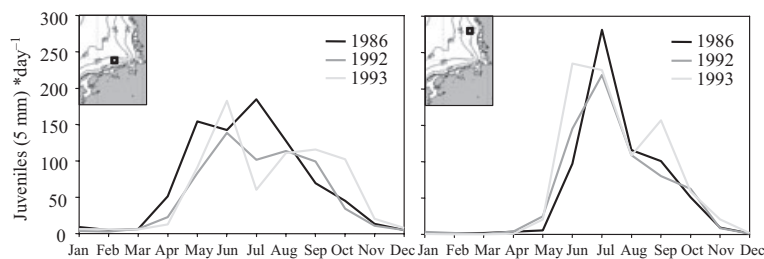


Figure 9. Simulated temporal variability of 5-mm juvenile abundance at two restricted locations in the German Bight (Boxes III and IV in Fig. 1). Values represent monthly averages of daily abundance.

the tidal flats. Both ΔT and ΔS appeared to be possible cues, but timing and location of immigration were strongly determined by the initial position in combination with the environmental cue chosen. A visualization of vertical particle displacement for two 'juveniles' initialized at different locations in the German Bight (Fig. 10) indicated a generally strong tidal effect on vertical migration. In all four visualized cases, the individuals hardly reached the surface layer during a vertical migration cycle. By calculating the relative maximum distance from the bottom which 'juveniles' are able to reach within one vertical migration cycle for a representative number of particles, we found that individuals are able vertically to migrate distances between 0.1 and 0.8 times the total bottom depth. On average (for all experiments), the maximum distance from the bottom was 0.46 times the total bottom depth, indicating that only in shallow areas did the simulated 'juveniles' come close to the surface. This can be explained simply by the fact that tidal current shear decreases with distance from the bottom and hence the uplift force decreases significantly with increasing height in the water column. Simultaneously, gravitation slows down the upward movement and finally, lets the juveniles sink again.

Both tidal cues seemed to function similarly well in the southern German Bight off the West and East Frisian coasts. However, in the northern German Bight the salinity-based cue seemed more efficient in triggering the vertical ascent in each tidal cycle. In the

experiments presented here, this resulted in a more direct horizontal on-shore transport of juveniles compared to the transport pattern estimated using the temperature signal (Fig. 11). The results further indicated that the ΔS cue supported STST of juvenile brown shrimp in the entire German Bight area due to its continuity in time and space, although the signal varied spatially in strength. In general, ΔS as tidal signal was a more constant and, in spring, also a more pronounced signal, leading to a faster on-shore transportation of juveniles almost everywhere. In contrast, the ΔT cue might result in delayed juvenile arrival and more variability in migration periods (spatially and inter-annually). In particular, juveniles that start migration further off-shore are likely to need a longer migratory period to reach their nursery grounds.

A comparison of all four experiments (exp. I: ΔS 1986; exp. II: ΔT 1986; exp. III: ΔS 1992; exp. IV: ΔT 1992) provided information about the effectiveness of the incorporated tidal cue for vertical migration and about the importance of inter-annual differences (Fig. 12). Where the individuals utilized the temperature signal for vertical migration, the time to reach the coast did not solely depend on the distance to the coast. A narrow area in the post-glacial valley of the River Elbe, for example, could be detected as an area that leads to a faster horizontal on-shore transport compared with other areas with equal distances to the coast. Furthermore, it appeared apparent that temperature conditions in 1992 were more favourable for a

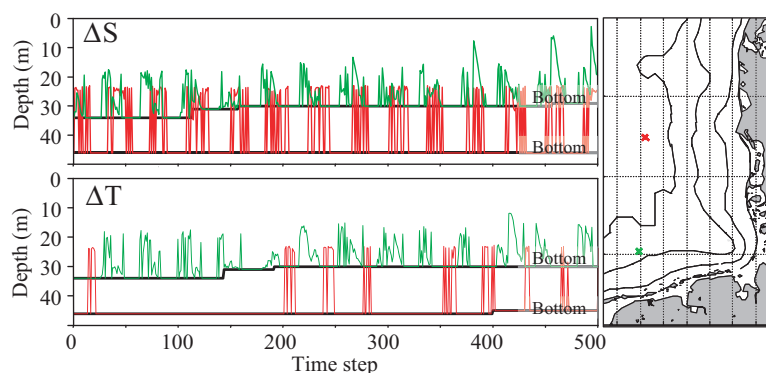


Figure 10. Simulated vertical displacement in the water column for two selected individuals within a time period of 500 time steps ≈ 167 h (1 time step $\equiv 20$ min) starting on 1 May. The start points are indicated in the map by crosses in the respective colour. The corresponding horizontal displacement is indicated in Fig. 11.

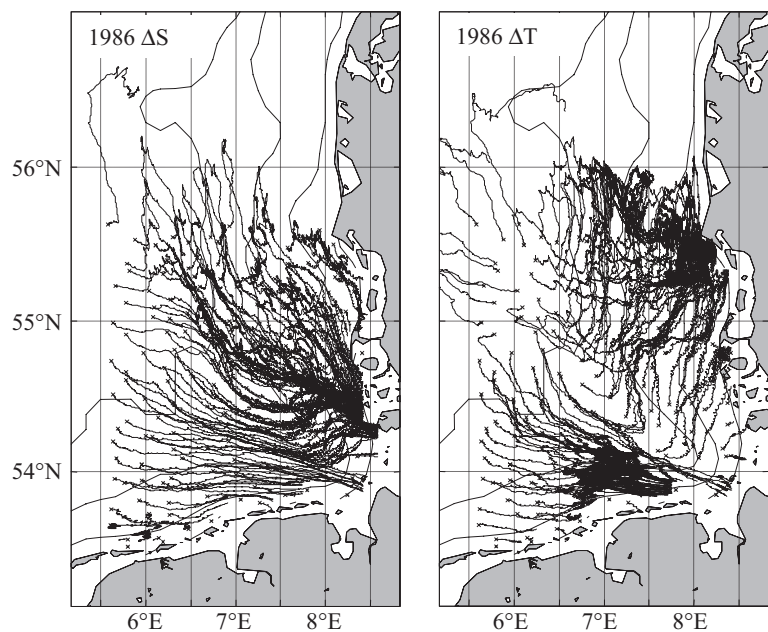


Figure 11. Estimated horizontal trajectories for a selected number of simulated juveniles using STST in the German Bight in 1986 (start locations indicated by x). ΔS , model experiment with salinity changes as tidal cue; ΔT , model experiment with temperature changes as tidal cue.

fast on-shore transport than temperatures in the colder year, which was probably caused by an earlier onset of differential heating in spring.

DISCUSSION AND CONCLUSIONS

Passive phase

To test the hypothesis that larvae are strongly affected by passive transport processes prior to metamorphosis, as proposed initially by Temming and Damm (2002) to explain differences in observed [Meldorf Bight in 1986 (Nehrlich, 1987) and 1992 (del Norte-Campos, 1995) and Sylt/Römö Bight in 1993 (Herrmann *et al.*, 1998)] and simulated juvenile recruitment, we conducted model experiments where brown shrimp larvae were treated as passive drifters.

The maximum abundance of 5-mm brown shrimp juveniles was estimated in June/July for the eastern German Bight but a strong increase in densities was simulated as early as May. The pattern is regionally different even within the German Bight (Fig. 9) where the eastern region exhibits an even earlier increase in densities. This initial increase matches the ascending limb of the peak in the field data of early juveniles presented by Temming and Damm (2002). However, the peaks in the field data, especially in 1986, are narrower and tend to decline from June/July onwards.

One possible reason for this mismatch with observations is the neglect of mortality for brown shrimp early life stages in the model. As predation probably constitutes the major cause of mortality (e.g. Hen-

derson *et al.*, 2006; Campos *et al.*, 2010), the seasonal dynamics of predator populations need to be considered. A number of different fish species, e.g. armed bullhead (*Agonus cataphractus*), whiting (*Merlangius merlangus*) and cod (*Gadus morhua*) (Tiews, 1978), are reported to feed on brown shrimp. Seasonal variations in predator population dynamics, and hence in predation pressure, may influence the seasonal dynamics of observed juvenile brown shrimp recruitment. Observations have shown that the densities of potential predators increase from spring to late summer (Jansen, 2002), which could explain the partial mismatch between observations and model results in summer.

We can also deduce alternative explanations for mismatch between model results and observations. Most apparent is the pronounced spatial variability estimated for 5-mm juvenile abundance. The temporal signal in a small sub-area (Box III, cf. Fig. 9) of the German Bight corresponded much better to the observations and could explain the earlier recruitment observed in the cold year 1986 in Meldorf Bight. The observations utilized for the comparison were collected at restricted locations and therefore do not represent the average situation in the German Bight. It appears possible that the small-scale spatial variability in the timing of metamorphosing juveniles plays an important role in the timing and location of juvenile recruitment in the Wadden Sea.

The correlation between settlement and environmental transport processes such as the prevailing cir-

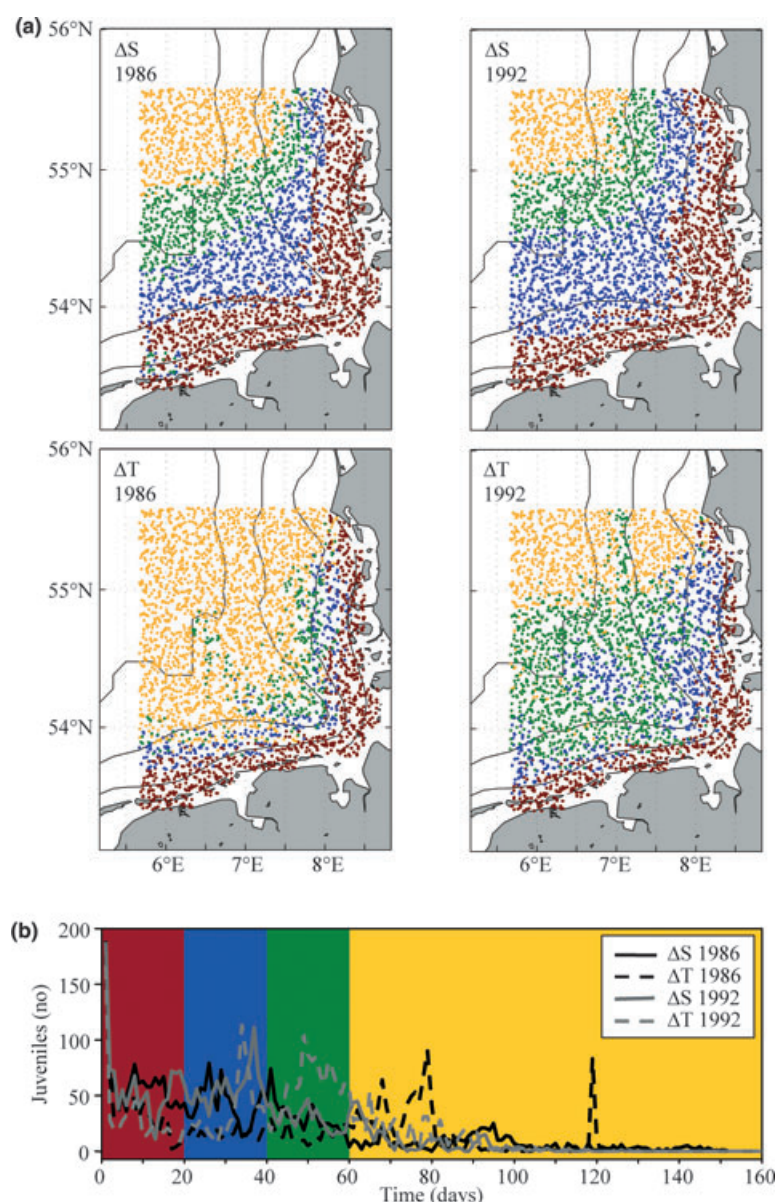


Figure 12. (a) Simulated spatial distribution of juveniles reaching the coast within a predefined time window. The colours indicate the corresponding time period: red, 0–20 days; blue, 20–40 days; green, 40–60 days; yellow, >60 days (including individuals that do not reach the coast). (b) Simulated number of individuals reaching the coast versus time in days (underlying colours correspond to the colour code in panel (a)).

culcation pattern and the spring/neap-tidal cycle were previously reported for another benthic species (shore crab *Carcinus maenas*), which is characterized by a comparable life cycle in the German Bight (Giménez and Dick, 2007). Specific environmental conditions were found to determine a local maxima or minima in settlement around Helgoland with strong inter-annual differences. These results confirm our findings about the importance of environmental factors for the location and timing of brown shrimp settlement and provide a further indication that the distribution of newly settled individuals might show a strong spatial variability.

Active phase – STST

It appeared to be essential to include the post-larval migration period into the explanation of juvenile recruitment processes, as our results showed clearly that the initial location where juveniles settle to the bottom can strongly determine when and where juveniles reach their nursery grounds. In contrast to other numerical experiments conducted to investigate impacts of STST (e.g. Arnold and Cook, 1984; Luetich *et al.*, 1999), we resolved the physical forcing on the streamlined brown shrimp body, which allowed us to base the vertical migration behaviour of the brown

shrimps almost solely on first principles rather than on vague assumptions on vertical swimming behaviour. Brown shrimp juveniles and adults are influenced by pressure force differences on their bodies, resulting in a hydrodynamic uplift under increasing current velocities (comparable to a forcing on an airplane). This forcing, in combination with friction and buoyancy forcing, also allows animals to descend under decreasing tidal current velocities without the necessity of another environmental cue. In the case of low relative current velocities, the gravitational force dominates the dynamic uplift and the individuals sink to the bottom. This aspect is quite important, as individuals are horizontally drifting mostly passively with the water mass and are therefore not exposed to changing environmental conditions that could indicate the ebb phase and give a signal for descent. Overall, our results showed that, due to the combined effects of uplift, friction and buoyancy forces, the small-scale physical forcing on the juvenile body already results in a sufficiently large vertical transport to allow for effective utilization of selective tidal stream transport. We found that the simulated 'juveniles' traversed on average half of the water column during one vertical migration cycle. As the gradient in horizontal current velocities decreases with distance from the bottom, our approach did allow for a migration of juveniles into the surface layers. However, tidal currents are sufficiently strong in the whole water column except in the bottom boundary layer due to friction. Hence, there is no need for the juveniles to migrate all the way up to the surface.

Two potential tidal cues (temperature and salinity) were numerically tested. In both cases the individuals performed the required vertical migration and were transported on-shore with the flood stream. It is rather difficult from model results alone to rank the relevance of the two investigated tidal cues and arguments can be found for both cues from our results as well as from the literature. The salinity change acts as a clearer signal indicating the arrival of the flood stream current and it appears to be more continuous in time and space, which leads to a faster transport of juveniles to the nursery grounds when compared to the temperature cue. On the other hand, STST initiated by a salinity signal results in a very differential pattern of juvenile recruitment, with juveniles accumulating in the estuaries of the rivers Elbe, Jade and Weser, a fact that can not be unrestrictedly confirmed by observations due to a lack of relevant field studies. Although higher concentrations of brown shrimp were recently observed to be associated with salinity minima in the estuarine areas within the DYFS (demersal young fish survey)

program in 2005 (ICES, 2006), results from the DYFS accomplished in 2006 (ICES, 2007) show a slightly different pattern, with less correlation to the prevailing salinity gradient. An argument that could support salinity as the relevant tidal cue is that it has been observed previously to be the tidal cue for another marine species in the same area. Flounder (*Platichthys flesus*) larvae are known to use STST to reach the same nursery grounds (Jager, 1998, 1999) as brown shrimp in the German Bight using salinity cues for this purpose, which could be a hint as to the relevance of salinity in this marine area. In contrast, the temperature signal in the German Bight is superimposed by a general, differential heating in spring and spatial differences due, for example, to stratification, and hence lead to a broader distribution of immigrating juveniles in the tidal flats in combination with longer migration periods. The main argument for temperature as the more relevant signal is the temperature dependence of the seasonal migration of adult brown shrimp observed by Boddeke (1976) and Van der Baan (1975), which support the assumption that juvenile brown shrimp are likewise sensitive to temperature changes.

STST has been reported for a variety of species including a number of invertebrates, e.g. crab *Carcinus maenas*, as well as fish species in the North Sea (for a review see Forward and Tankersley, 2001). Although temperature and salinity appear to be the most obvious tidal cues in the German Bight, a number of other environmental factors (e.g. hydrostatic pressure, turbulence, olfactory cues, nutrient concentrations) vary temporally with tidal currents and have previously been reported to impact transport processes of marine species (Forward and Tankersley, 2001). To be a relevant indicator of vertical migration of marine species, the environmental change during a tidal cycle must fulfil two criteria: the factor must change in a detectable relative rate and by a detectable amount. Laboratory studies on the response of blue crab (*Callinectes sapidus*) and fiddler crab (*Uca* spp.) post-larvae to salinity changes were conducted by Tankersley *et al.* (1995). The minimum relative rate that evokes the ascent response was $5.53 \times 10^{-4} \text{ s}^{-1}$ for blue crab and $1.33 \times 10^{-3} \text{ s}^{-1}$ for fiddler crab. The minimum absolute amount of change in salinity necessary for a responsive behaviour was 0.3 for both species. However, it is likely that the sensitivity of individuals to environmental cues depends on both the species and the habitat the individuals are adapted to. Tide-dependent salinity changes (at the bottom) calculated for May in the German Bight are in general relatively small (in the range of 10^{-5} s^{-1} ; see Fig. 4) and, especially in offshore areas, are most likely too small to be detected by

brown shrimp post-larvae. Similarly, off-shore changes in temperature during a tidal cycle were calculated to be comparably small in May (in the range of $10^{-5} \text{ }^{\circ}\text{C s}^{-1}$). Due to ongoing differential heating, tidal-related temperature variations in the German Bight become more pronounced in late spring and summer. The relatively small tidal signal for temperature and salinity in May either indicates a strong sensitivity of brown shrimp post-larvae to one of these cues or suggests the presence of another environmental cue, which may also vary with the tidal currents and may play a more dominant or auxiliary role. Additional model experiments could be carried out to identify the possibility of other environmental factors being valuable as tidal cues. This could include scenario tests with respect to turbulence, hydrostatic pressure or the impacts of endogenous rhythms. Complementarily, the sensitivity of brown shrimp post-larvae to environmental cues should be deduced from laboratory studies applying protocols used by Tankersley *et al.* (1995) for blue crab. Additionally, assumptions made about shrimp behaviour (e.g. orientation of juveniles in the flow, reaction on environmental cues) need to be investigated with further process-oriented laboratory as well as numerical studies to understand sub-grid scale physical processes and measure the actual inclination angles to the flow.

In conclusion, the hypothesis proposed by Temming and Damm (2002) was confirmed by the model results. We obtained valuable information from the model experiments. First, the accelerated egg and larval development in the Southern Bight is important for the occurrence of early juvenile brown shrimp in the German Bight, as these larvae are strongly affected by the cyclonic residual currents in the southern North Sea. Secondly, the impacts of passive transport processes on juvenile recruitment vary seasonally, with stronger effects on larvae hatched in winter and early spring ascribable to both stronger residual currents and a longer duration of the larval stage. But as larval survival is also associated with water temperature (Criales and Anger, 1986), these larvae have in reality a low probability of surviving. The earliest hatching date that potentially supports larval survival with respect to temperature appears in April, with better (warmer) conditions occurring in the westernmost area near the English Channel. Thirdly, as hypothesized, the inter-annual differences in juvenile recruitment can, at least partly, be ascribed to larval drift and temperature differences. A stronger impact can be presumed in years with low water temperatures, such as 1986. We were able to show that juveniles observed in the German Wadden Sea in May 1986 (Temming

and Damm, 2002) were likely to have been hatched in the Southern Bight initially and drifted towards the German Bight during their larval phase. The higher water temperatures near the English Channel lead to an acceleration of larval development and thus to an earlier juvenile recruitment maximum in the German Bight. In contrast, in 1993 larval transport had a comparatively low impact on the temporal dynamics of 5-mm juvenile abundance in the same area.

The use of a coupled model system to investigate the life cycle of brown shrimp in the southern North Sea provided insights into the interrelations of brown shrimp early life stages and environmental factors. Our results indicated that stage-specific approaches for the egg, larval and juvenile phases must be considered when resolving the life cycle. This also highlights the dominant impact that small-scale hydrodynamic forcing may have on marine organisms, particularly on the vertical movements of organisms relative to the water column. In addition, suspended particle dynamic approaches are an essential requirement for realistic modelling of larger marine species. Our numerical approach gives a clear picture of the role of transport processes during brown shrimp early life stage. However, as it is in some respects a very theoretical approach, it is necessary to test our assumptions and findings with process-oriented laboratory studies as well as field observations with a special emphasis on STST.

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