ELSEVIER

In Collaboration with the Royal Netherlands Institute for Sea Research

Journal of Sea Research 55 (2006) 191–206

JOURNAL OF SEA RESEARCH

www.elsevier.com/locate/seares

Estimation of food limitation of bivalve larvae in coastal waters of north-western Europe

Oscar G. Bos [a,*], Iris E. Hendriks [b], Matthias Strasser [c], Per Dolmer [d], Pauline Kamermans [e]

[a] *Royal Netherlands Institute for Sea Research, P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands*
[b] *Instituto Mediterraneo de Estudios Avanzados, C/ Miquel Marques 21, 07190 Esporle, Islas Baleares, Spain*
[c] *Alfred-Wegener-Institut für Polar- und Meeresforschung, Wattenmeerstation Sylt, D-25992 List, Germany*
[d] *Danish Institute for Fisheries Research, Dept. of Marine Ecology and Aquaculture, Charlottenlund Castle, DK-2920 Charlottenlund, Denmark*
[e] *Netherlands Institute for Fisheries Research, Centre for Shellfish Research, P.O. Box 77, 4400 AB Yerseke, The Netherlands*

Received 5 May 2005; accepted 17 October 2005
Available online 27 December 2005

Abstract

Marine invertebrate recruitment may be affected by food limitation during the pelagic larval life stages. In the present study, field data on abundance of bivalve larvae along with their prey (small phytoplankton) were examined to see whether they were consistent with predictions made by an energetic model of larval requirements. Bivalve larvae were monitored during 2000 at ten different study sites in four different areas (Limfjorden, Sylt-Rømø bight, Western Wadden Sea and Delta area) along the coast of north-western Europe. Calculation of the energetic requirements of the larvae at 15 °C indicated maintenance costs of a 200-μm bivalve larva to be 1.9×10^{-5} J larva^{-1} d^{-1}, while the maximum assimilation rate, resulting in maximum growth, would amount to 6.2×10^{-3} J larva^{-1} d^{-1}. Calculation of potential assimilation rates of larvae in the field resulted in estimates between 10^{-5} and 10^{-3} J larva^{-1} d^{-1}. Maximum larval concentrations in the field occurred from May to September and ranged between 17 and 392 larvae dm^{-3}. Most larvae were able to cover their maintenance costs, but not to attain maximum growth rates. Between April and September, the potential assimilation rate averaged 7–26% of the maximum assimilation rate. Under the assumptions made for the present study, it is suggested that growth of larvae in north-west European waters is often food-limited.

Keywords: Monitoring; Bivalve larvae; Food availability; Phytoplankton; DEB-theory

1. Introduction

For most soft-bottom invertebrate species, it is not clear which larval processes are crucial for recruitment success (reviews in Rumrill, 1990; Ólafsson et al., 1994; Menge, 2000). Among the first to recognise that food limitation of larvae may affect marine invertebrate recruitment was Thorson (1950). In his view, larvae could die directly from starvation, or indirectly from predators due to a prolonged planktonic development time. Experimental evidence has demonstrated that food limitation of invertebrate larvae is more likely at higher trophic levels (crustaceans) than at lower trophic levels (molluscs, echinoids) (Hairston et al., 1960; review in Olson and Olson, 1989). Furthermore, food limitation is expected to be more important in

* Corresponding author.
E-mail address: bos@nioz.nl (O.G. Bos).

1385-1101/$ - see front matter © 2005 Elsevier B.V. All rights reserved.
doi:10.1016/j.seares.2005.10.006

oceanic waters than in coastal waters, due to the lower primary production (Huntley and Boyd, 1984) that would result in a lower *per capita* larval food intake rate (Holling, 1959). However, larval food limitation has also been reported in coastal waters (Fenaux et al., 1994; Hansen, 1999).

To assess whether food limitation is common to bivalve larvae, it is necessary to study both larval concentrations and concentrations of their prey, preferably in time and space (Olson and Olson, 1989). Time series of larval concentrations in north-western Europe have been provided by several authors (Pulfrich, 1997; Günther et al., 1998; De Vooys, 1999; Strasser and Günther, 2001). However, no extensive geographical comparison of larval concentrations has yet been made. Assuming that the areas may be regarded as closed systems and that the timing of spawning of several bivalve species in north-western Europe depends on species-specific threshold water temperatures (*Mytilus edulis*: Wilson and Seed, 1974; Podniesinki and McAlice, 1986; Thorarinsdóttir, 1986; *Crassostrea gigas*: Ruiz et al., 1992; *Macoma balthica*: Lammens, 1967; Drent and Luttikhuizen, ms. in prep.), it is expected that in a comparison, the differences in the height, duration and frequency of larval peaks (all bivalve species included), between areas primarily depend on (1) the spatial uniformity/irregularity of water temperature increase, (2) the number of species, (3) the adult stock size, and (4) total water volume.

Prey concentrations for bivalve larvae have not explicitly been determined, due to the limited information on natural diets of larvae (Baldwin and Newell, 1991, 1995). In general, the major food source for marine invertebrate larvae is considered to be phytoplankton (review in Strathmann, 1987), but other sources such as small heterotrophic flagellates, amino acids (Langdon, 1983; Manahan, 1983, 1989), bacteria (Baldwin and Newell, 1991) and dissolved organic matter (DOM), can also be ingested by larvae. Utilisation of DOM (osmotrophy), however, probably only supplements nutrients obtained by other feeding modes (Olson and Olson, 1989).

To relate food availability to growth of organisms, the Dynamic Energy Budget model (DEB-model; Kooijman, 2000) can be used. The DEB-model quantitatively describes energy flows through organisms and the changes in these flows in environments in which food concentrations and temperatures vary. In this model, all physiological and ecological processes are related in a systematic and coherent way. In short, organisms ingest energy, which is assimilated and directed towards growth and maintenance of structural cells, and towards the production of cells used for maturation/reproduction and their maintenance.

The aims of the present study were (1) to compare abundances of pelagic bivalve larvae along the coast of north-western Europe (Limfjorden, Sylt-Rømø bight, western Wadden Sea, Delta area) in one year (2000); (2) to estimate to which degree bivalve larvae were food-limited at these study sites.

2. Materials and methods

2.1. Study sites and sampling methodology

Bivalve larvae were sampled in 2000 in four areas along the coast of north-western Europe: (1) Limfjorden in the north of Denmark, (2) the Sylt-Rømø bight, (3) the western Wadden Sea and (4) the Delta area (Fig. 1). Samples were collected routinely from jetties or piers at high tide or close to high tide, and from boats at fixed times irrespective of the tide. Bivalve larvae sampling frequency was 20–252 y^{-1} (Table 1).

Larvae in different areas were sampled with comparable methods (Table 1). Generally, a sample of 10–100 dm^3 of surface seawater was taken with a bucket or pumped and filtered over a mesh size of 40–80 μm. Samples were preserved in formaldehyde or lugol and stored in the dark until further analysis. Only the total numbers of larvae were counted, irrespective of species composition, since microscopical discrimination between larval species is complicated (Loosanoff et al., 1966; Chanley and Andrews, 1971; Le Pennec, 1980; Pulfrich, 1997) and discrimination on the basis of DNA analysis in our study region is still under development (Van Bleijswijk, ms. in prep.). However, based on the stock biomass and on species determination of bivalve larvae in earlier years, the majority of the larvae probably consisted of *Mytilus edulis*, *Cerastoderma edule*, *Ensis americanus*, *Crassostrea gigas*, *Macoma balthica* and *Mya arenaria* (De Vooys, 1999; Strasser and Günther, 2001; Dolmer and Frandsen, 2002; Smaal et al., 2002; Ysebaert et al., 2003).

Phytoplankton data for the Limfjorden stations were collected simultaneously with the bivalve larvae. Phytoplankton data for the other stations were obtained from phytoplankton monitoring programmes by J. van Beusekom (AWI-Sylt), G.C. Cadée (Royal NIOZ), and the RIKZ (Middelburg, the Netherlands). Sampling in the Oosterschelde was at locations close to larval sampling locations (0–5 km). Phytoplankton data for stations OS-C and WS were not available. Therefore, only data on larval abundance are shown for these stations.

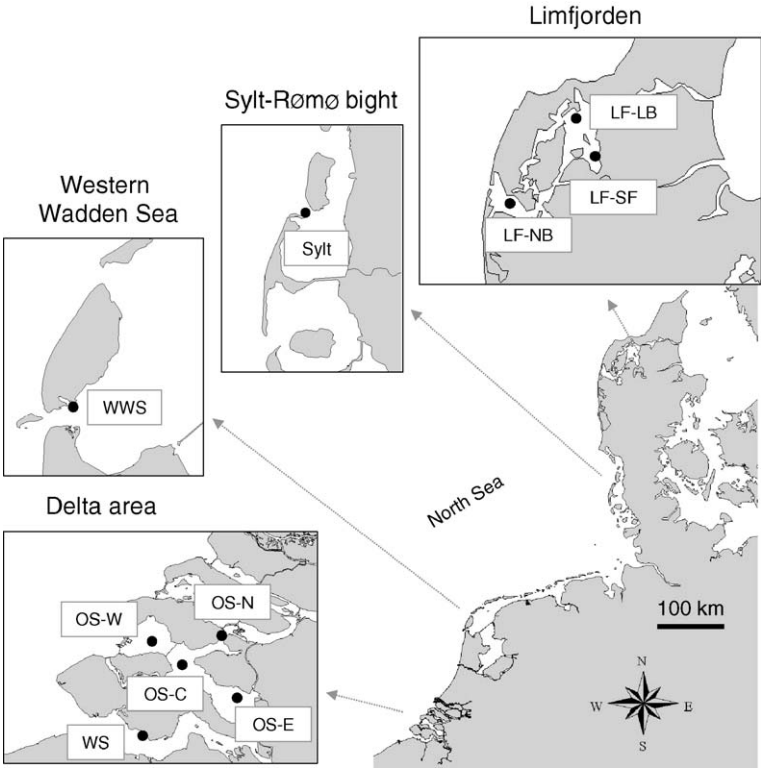

Fig. 1. Location and abbreviations of names of sampling stations (●) in four coastal waters of north-western Europe.

2.2. Larval food availability

Phytoplankton size estimations were based on Dodge (1982), Round et al. (1990), Tomas (1997), Kuylenstierna and Karlson (1998), Horner (2000), and Ichise et al. (2004). Only phytoplankton taxa <20 μm were included in further analyses, based on the assumptions (1) that larvae only ingest food particles up to the diameter of their mouth (20.5 ± 1.5 μm SD for *M. balthica* larvae of 184.9 ± 9.2 μm, n = 15; Van Iperen, pers. comm., 2003), which is confirmed by nutritional studies (Riisgård and Randløv, 1980; Hurley et al., 1997; Baldwin and Newell, 1991, 1995) and (2) that the average size of larvae in the field is ~200 μm (Pulfrich, 1997).

Table 1
Overview of methods used to sample bivalve larvae at sampling stations along the coast of NW Europe in 2000

Area	Station code	Sampling Period	Sampling Interval	Station	Moment of sampling	Sampling method	Mesh size (μm)	Sample Volume (l)	Fixation Method	Analysed Volume (% of total)
Limfjorden	LF-LB	Jan-Dec	1–4 mo^{-1}	Boat	–	PP	60	450–1500	L	0.2–100
	LF-SF	Jan-Dec	1–4 mo^{-1}	Boat	–	PP	60	450–1500	L	0.2–100
	LF-NB	Jan-Dec	1–4 mo^{-1}	Boat	–	PP	60	450–1500	L	0.2–100
Sylt-Rømø bight	Sylt	Jan-Dec	1–7 w^{-1}	Ferry pier	HT-1 h	Bu	80	10	F, H	100
Western Wadden Sea	WWS	Jan-Dec	1–3 w^{-1}	Jetty	HT	Bu	40	10	F, B, R	5
Delta area	OS-N	Apr-Oct	1 w^{-1}	Boat	–	Bu	55	100	F, B	13
	OS-E	Apr-Oct	1 w^{-1}	Boat	–	Bu	55	100	F, B	13
	OS-C	Apr-Oct	1 w^{-1}	Boat	–	Bu	55	100	F, B	13
	OS-W	Apr-Oct	1 w^{-1}	Boat	–	Bu	55	100	F, B	13
	WS	Apr-Oct	Weekly (moon)	Jetty	HT-1/2 h	Bu	55	100	F, H	10

HT = high tide, LT = low tide, Bu = sampling with 10-litre bucket at surface, PP = sampling with plankton pump (150 l min^{-1}) at 1 m depth, F = preserved with 4–10% formaline, H = sample buffered with hexamethylenetetramin, B = buffered with borax, R = coloured with Bengal Red, L = preserved with Lugol.

Phytoplankton taxa forming chains, colonies or possessing large spines were also excluded from the analysis.

Biovolumes of the selected phytoplankton species were obtained from the literature or estimated using a standardised set of equations for biovolume calculations (Hillebrand et al., 1999). Biovolumes were converted to carbon content (C; pgC μm^{-3}), using the conversion $\log_{10}C = -0.422 + 0.758 \log_{10} V$ for diatoms (Strathmann, 1967), $\log_{10}C = -0.363 + 0.863 \log_{10} V$ for other nanoplankton, including dinoflagellates (2–20 μm; Verity et al., 1992) and $C = 0.165 V$ for ciliates (Putt and Stoecker, 1989), where V (μm^3) is the volume of the cell. Subsequently, carbon content was converted into energy content (E; J cm^{-3}) using the conversion 1 g $C = 46 \times 10^3$ J (Salonen et al., 1976). Next, cell carbon content was multiplied by cell concentration and summed for all species per sampling date.

2.3. Dynamic Energy Budget model

Calculations of maximum assimilation rate (J $larva^{-1}$ d^{-1}), assimilation rates as a function of food concentration (J $larva^{-1}$ d^{-1}) and maintenance costs (J $larva^{-1}$ d^{-1}) were based on predictions of the Dynamic Energy Budget (DEB) model developed by Kooijman (2000) and adapted for *M. balthica* larvae by Philippart et al. (ms. in prep.) (Table 2). The DEB-model describes the energy flows through an organism (Fig. 2) and the changes in these flows in environments in which food concentrations and temperatures vary.

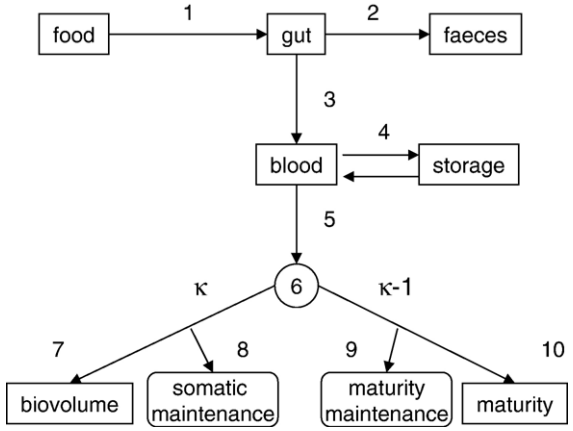

Fig. 2. Energy flow through an organism in the DEB-model, after Van Haren and Kooijman (1993). Rates: 1 ingestion, 2 defecation, 3 assimilation, 4 mobilisation of energy into reserves, 5 demobilisation of energy from reserves, 6 utilisation, 7 growth, 8 maintenance, 9 maturation maintenance, 10 maturation. The rounded boxes indicate sources or sinks, the squares indicate state variables.

In the model, energy intake J_X is described by a type-II functional response (Holling, 1959) (Fig. 3), in which the ingestion rate depends hyperbolically on the available food concentration:

$$J_X = \{J_{Xm}\} \cdot \frac{X}{X_K + X} \cdot V^{2/3},$$

where J_X is the ingestion rate (cells $larva^{-1}$ d^{-1}; for other symbols see Table 2). The ingested food is converted into energy reserves with constant assimilation

Table 2
Description of symbols in Dynamic Energy Budget (DEB) model and parameter estimates and conversion factors for the DEB model of a *Macoma balthica* larva at 15°C (after Philippart et al., ms. in prep.)

Factor	Description	Value	Ref.	Units
X	Food density	–		cells cm^{-3}or J cm^{-3}
X_K	Half-saturation constant for feeding	10,000	1	cells *Isochrysis* cm^{-3}
$\{J_{Xm}\}$	Surface-specific maximum ingestion rate	3.06		cells *Isochrysis* μm^{-2} d^{-1}
$\{p_{am}\}$	Surface-specific maximum assimilation rate	1.04		J μm^{-2} d^{-1}
δ_m	Shape coefficient	0.386		–
κ	Energy allocation coefficient	0.76		–
$[E_G]$	Volume-specific costs of growth	5.67×10^{-8}		J μm^{-3}
$[p_M]$	Volume-specific costs of somatic maintenance	3.30×10^{-11}	2	J μm^{-3}
$[p_j]$	Volume-specific costs of maturity maintenance	3.30×10^{-11}		J μm^{-3}
V	Volume at 200 μm shell length	$(0.386 \times 200)^3$		μm^3
T_A	Arrhenius temperature	7596	3	K
$k(T_1)$	Physiological rate at reference temperature T_1	–		–
T_1	Reference temperature	288 (15)		K (°C)
k(T)	Physiological rate at temperature T	–		–
T	Seawater temperature	–		K
Conversions				
	Energy content of *Isochrysis* cells	6.07×10^{-7}	4	J $cell^{-1}$
	Assimilation efficiency coefficient	0.56	3	–

(1) Jespersen and Olsen, 1982; (2) Beukema and De Bruin, 1979; (3) Van Haren and Kooijman, 1993; (4) Sprung, 1983.

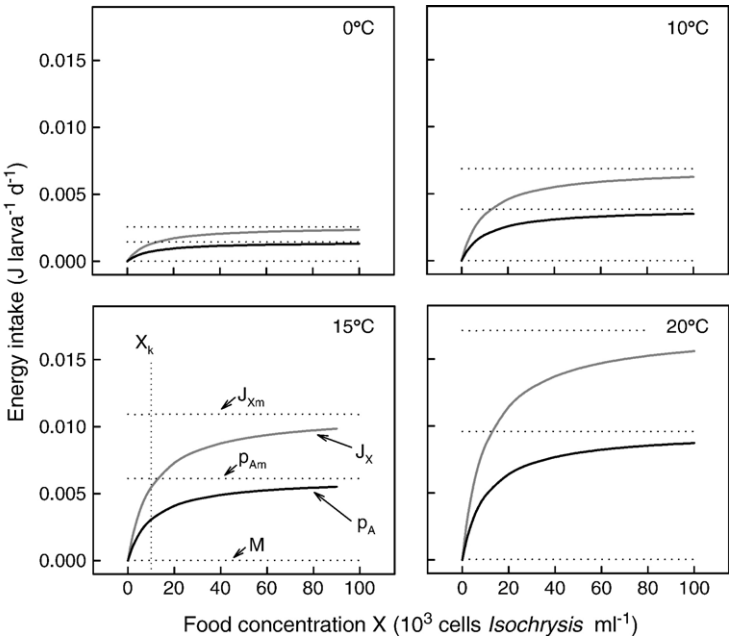

Fig. 3. DEB-model predictions of energy intake (J larva^{-1} d^{-1}) as a function of food concentration (functional response; cells *Isochrysis galbana* cm^{-3}) of a 200 μm *Macoma balthica* larva at 4 different temperatures (0, 10, 15 and 20°C; Philippart et al., ms. in prep). From top to bottom, lines indicate maximum ingestion rate (J_{Xm}), ingestion rate (J_X), maximum assimilation rate (p_{Am}), assimilation rate (p_A), and maintenance costs (M). The vertical line indicates the half-saturation constant X_k.

efficiency. The assimilation rate can therefore be described by:

$$p_A = \{p_{Am}\} \cdot \frac{X}{X_K + X} \cdot V^{2/3},$$

where p_A=assimilation rate (J larva^{-1} d^{-1}; for other symbols see Table 2).

The assimilated energy flows into a storage compartment (Fig. 2) and no maintenance costs are paid over storage of energy. From this compartment, the fraction κ of the mobilised reserve is mobilised into somatic growth and maintenance of somatic tissue, while the remainder (1-κ) is converted into growth of maturation tissue and maintenance of this tissue.

Maintenance costs of both somatic and maturation tissue are proportional to volume, since each cell uses a fixed amount of energy per unit of time. Somatic maintenance has priority over growth, hence an organism stops growing as soon as the fraction κ of the mobilised reserve is equal to, or lower than, somatic maintenance. In this model, somatic maintenance (Fig. 2) is expressed as:

$$p_M = [p_M] \cdot V,$$

where p_M=somatic maintenance costs (J larva^{-1} d^{-1}; for other symbols see Table 2).

Maturation maintenance (Fig. 2) is expressed as:

$$p_j = \left(\frac{1-\kappa}{\kappa}\right) \cdot [p_j] \cdot V,$$

where p_j=maturity maintenance costs (J larva^{-1} d^{-1}; for other symbols see Table 2). Together, maturity maintenance costs p_j and somatic maintenance costs p_M are referred to as maintenance costs M (J larva^{-1} d^{-1}) in the present study.

Temperature affects all physiological rates (Kooijman, 2000; Fig. 3). In DEB, the Arrhenius description has been selected to describe the temperature correction for a physiological rate k(T) at a particular temperature T according to:

$$k(T) = kT_1 \cdot e^{\left(\frac{T_A}{T_1} - \frac{T_A}{T}\right)},$$

where k(T) is the physiological rate at temperature T(K; for other symbols see Table 2).

In the present, study the length of the *M. balthica* larva in the DEB-model (Philippart et al., ms. in prep.) was set at 200 μm, as an approximate average length of larvae found in the water column (Pulfrich, 1997). It is assumed that the energy budget of other bivalve larvae of the same length is in the same order of magnitude.

In the DEB-model for *M. balthica* larvae (Philippart et al., ms. in prep.), the half-saturation constant X_K was based on the ingestion rates of mussel larva at 15 °C (*Mytilus edulis*; Jespersen and Olsen, 1982) and set at 10 000 *Isochrysis galbana* cells cm^{-3} (Table 2). Assuming an energy content of *I. galbana* of 6.07×10^{-7} J $cell^{-1}$ (Sprung, 1983), and an area-specific maximum ingestion rate $\{J_{Xm}\}$ of 3.06 *I. galbana* cells μm^{-2} d^{-1} (Jespersen and Olsen, 1982), the area-specific maximum ingestion rate $\{J_{Xm}\}$ could be expressed as $3.06 \times 6.07 \times 10^{-7} = 2.5 \times 10^{-6}$ J μm^{-2} d^{-1}. The assimilation efficiency was assumed to be 0.56 (Van Haren and Kooijman, 1993), yielding an area-specific maximum assimilation rate $\{p_{Am}\}$ of $2.5 \times 10^{-6} \times 0.56 = 1.4 \times 10^{-6}$ J μm^{-2} d^{-1}. Somatic maintenance costs $[p_m]$ were calculated from the decrease of somatic mass during the non-feeding period of adult *M. balthica* (Beukema and De Bruin, 1979), and were 3.30×10^{-11} J μm^{-3}. The maturity maintenance costs $[p_j]$ were assumed to be equal to $[p_m]$. The volume of an adult *M. balthica* was estimated from the wet weight, assuming that 1 g wet weight corresponds to 1 cm^3. The shape coefficient δ_m, used to relate volumetric shell length (SL; μm^3) to volume (V; μm^3) was $(SL \times \delta_m)^3 / V = 0.386$. Finally, physiological rates were corrected for temperature, using an Arrhenius temperature of 7596 K (*M. edulis*; Van Haren and Kooijman, 1993).

3. Results

3.1. Concentrations of bivalve larvae

Larval concentrations in Limfjorden generally reached peak values in May with 117–241 larvae dm^{-3}. At stations LF-LB and LF-SF, only single peaks were observed, while at station LF-NB, three

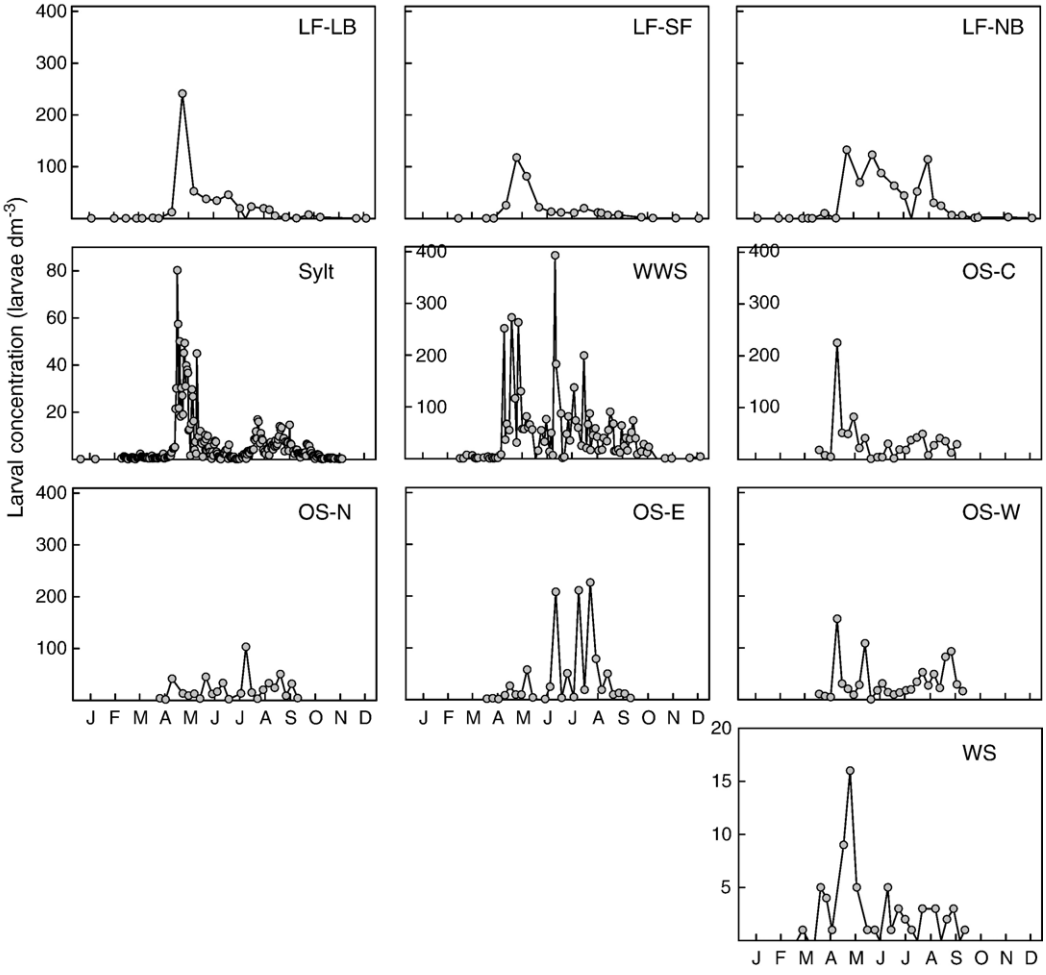

Fig. 4. Larval concentration (larvae dm^{-3}) at sampling stations in Limfjorden (LF), the Sylt-Rømø bight (Sylt), western Wadden Sea (WWS) and Delta area (OS and WS) throughout 2000. Note that scales of Sylt and WS differ from the other stations.

peaks were observed in May, June and August (Fig. 4). In the Sylt-Rømø bight larval concentrations were slightly lower than in Limfjorden and the Delta area and consistently lower than in the western Wadden Sea. Due to the high sampling frequency, several smaller peaks were observed in the Sylt-Rømø bight. However, a first large larval peak (80 larvae dm^{-3}) was observed at the beginning of May. A second peak (16 larvae dm^{-3}) was observed in the first week of August and a third peak (13 larvae dm^{-3}) at the beginning of September (Fig. 4). In the western Wadden Sea (WWS) the first clear peak (272 larvae dm^{-3}) was noticed at the beginning of May, and the second peak at the end of June (392 larvae dm^{-3}), the highest of all stations. Larvae were only occasionally found in winter and early spring samples. From the end of April to the end of October larval concentrations varied between 10 and 100 larvae dm^{-3} (Fig. 4). In the Oosterschelde, peak values in the central (OS-C; 156 larvae dm^{-3}) and western part (OS-W; 224 dm^{-3}) were found in the third week of April, while peak values in the north (OS-N; 103 dm^{-3}) and eastern part (OS-E; 224 dm^{-3}) were found in the third week of July. Concentrations of bivalve larvae in the Westerschelde (WS) were consistently lower than concentrations in the Oosterschelde. The maximum value was 16 larvae dm^{-3} (Fig. 4).

To see whether larval concentrations depend on the water volume of the sampling areas, the total reproductive output per basin was estimated from literature data on stock size, individual egg production and area surface (Tables 3, 4) and divided by the total water volume of each basin to obtain an egg concentration index (eggs dm^{-3}). Next, the egg concentration index (eggs dm^{-3}) was compared to the average larval concentration (larvae dm^{-3}) (Fig. 5). The measured larval concentrations show a positive relation with the egg production index of the bivalve stock in each area (Tables 3, 4; Fig. 5).

3.2. Food availability for bivalve larvae

Among the 311 sampled phytoplankton taxa, 52 taxa were selected as suitable for larval ingestion (Table 5). The carbon content of this phytoplankton fraction varied from 2.0×10^{-7} to 2.1×10^{-1} μg C cm^{-3} corresponding to an energy content of 9.4×10^{-9} to 9.5×10^{-3} J cm^{-3}. In general, possibilities for growth were maximal between May and September. At most stations, the energy concentration of the phytoplankton was sufficient to meet maintenance costs (M; J $larva^{-1}$ d^{-1}; Fig. 6). However, in the Sylt-Rømø bight, larval maintenance costs were not reached for at least half of the year. Furthermore, the period in which a larva could grow was relatively short compared to other stations. At all stations, the most important contributor to total energy content of the phytoplankton was the category 'other nanoplankton' including dinoflagellates (Table 5) (94.4–99.5%) followed by diatoms (4.0–0.4%) and ciliates (0.0–1.5%). The average biovolume of the selected phytoplankton was 28 ± 20 μm^3 (mean ± SE), ranging between 6.2 μm^3 (station LF-LB) and 92.7 μm^3 (station WWS). In general, the potential assimilation rates (p_A) ranged between >1% and 60% of the maximum assimilation rates (p_{Am}) in the period between the beginning of April and the end of September. Average values for this period were 18 ± 3 (mean ± SE) to 26 ± 5% for the Limfjorden stations, 7 ± 2% for the Sylt-Rømø bight, 19 ± 2% for the western Wadden Sea and 15 ± 3 to 25 ± 4% for the Oosterschelde stations.

In Limfjorden, peak values of the phytoplankton energy concentration occurred at the end of June and the beginning of July, varying between 7.0×10^{-3} J cm^{-3} (station LF-LB) and 9.5×10^{-3} J cm^{-3} (station LF-SF). According to the DEB-model, the larvae assimilated the energy content of the phytoplankton during these peaks at rates (p_A) of 1.57×10^{-3} and 1.64×10^{-3} J $larva^{-1}$ d^{-1}, respectively (Fig. 7). In the Sylt-Rømø bight, phytoplankton energy concentration showed very distinct peak values at the beginning of May (8.4×10^{-3} J cm^{-3}) and in June (6.4×10^{-3} J cm^{-3}), while the energy concentration was close to zero during the rest of the year.

Table 3
Main characteristics of study areas

Area	Area (km^2)	Mean depth (m)	Volume (10^{12} l)	Residence time (d)
Limfjorden	1575(1)	4.9(1)	7.72	
Løgstør Bredning (LF-LB)				35(2)
Skive Fjord (LF-SF)				70(2)
Nissum Bredning (LF-NB)				15(2)
Sylt-Rømø bight (Sylt)	400(3)	4.2	1.69(4)	19–29(5)
Western Wadden Sea (WWS)	1390(6)	3.3(7)	4.59	5–15(6)
Delta area				
Oosterschelde	350(8)	7.7	2.70(7)	
Western region (OS-W, OS-N)				20(9)
Central region (OS-C)				140(9)
Westerschelde (WS)	300(10)	8	2.40	

References are indicated with numbers in brackets.
References: (1) Dolmer and Frandsen, 2002; (2) Dolmer, 2002; (3) Strasser and Günther, 2001; (4) Strasser, 2000; (5) Sprung et al., 2001; (6) Dame and Prins, 1998; (7) Ridderinkhof et al., 1990; (8) Bakker, 1994; (9) Smaal et al., 2001; (10) Bouma et al., 2001.

Table 4
Estimation of total potential bivalve reproductive output (eggs dm^{-3}) per study area in 2000

Area	Species	FW (10^6 kg)	SL (mm)	Ind. FW (g)	Stock size (10^9 ind.)	Repr. output (10^5 eggs $female^{-1}$)	Total repr. output (10^{14} eggs)	Total egg density (eggs dm^{-3})	Mean egg density* (eggs dm^{-3})	Mean egg density* (eggs dm^{-2})
Limfjorden	*Mytilus edulis*	400(1)	50(1)	10.8(2)	37.02	15.0(3)	278	3598	23.7	176305
Sylt-Rømø	*Cerastoderma edule*	7.80(4)	28	7.0(5)	1.12	4.50(3)	2.52	149	0.9	6300
Bight	*Crassostrea gigas*[a]				0.001(6)	100(6)	0.05	3	0.02	125
	Macoma balthica	3.64(4)	16	0.8(5)	4.61	0.45(3)	1.04	61	0.4	2592
	Mytilus edulis	1.48(4)	50	10.8(2)	0.14	15.0(3)	1.03	61	0.4	2569
Western	*Cerastoderma edule*[b]				21.3(7)	4.50(3)	48.0	1047	6.9	34558
Wadden	*Macoma balthica*[b]				43.5(7)	0.45(3)	9.78	213	1.4	7034
Sea	*Mytilus edulis* cult.	39.0(8)	50	10.8	3.61	15.0(3)	27.1	590	3.9	19478
	Mytilus edulis subtid.	33.7(9)	50	10.8	3.12	15.0(3)	23.4	510	3.4	16831
	Mytilus edulis intert.	2.15(10)	50	15.1	0.15	15.0(3)	1.16	25	0.2	832
Delta area										
Oosterschelde	*Cerastoderma edule*		28(11)	7.0(5)	7.61(7)	4.50(3)	17.1	634	4.2	48921
	Crassostrea gigas[a]	150(12)		150	1.00	100(6)	50.0	1852	12.2	142857
	Crassostrea gigas	6.50(12)		150	0.043	100(6)	2.17	80	0.5	6190
	Macoma balthica				2.04(7)	0.45(3)	0.46	17	0.1	1312
	Mytilus edulis[b]				3.74(9)	15.0(3)	28.1	1039	6.8	80143
Westerschelde	*Cerastoderma edule*				1.02(7)	4.50(3)	2.29	109	0.6	7643
	Macoma balthica				4.42(7)	0.450(3)	0.995	47	0.3	3318

Only the most important bivalve species are included. Estimates of the reproductive output are based on stock estimates for 2000, except for the Sylt-Rømø bight where estimates were based on surveys in the mid-1990s. When direct stock size estimates were not available, stock size was estimated assuming a species-specific standard shell length. It is assumed that 50% of the bivalve stock consists of females. FW=fresh weight, SL=shell length, ind.=individual, repr.=reproductive, cult.=subtidal culture plots, subt.=subtidal, intertid.=intertidal. References are indicated with numbers in brackets.

References: (1) Kristensen and Hoffmann, 2004; (2) Williams and Ens, unpubl. results; (3) Honkoop et al., 1999; (4) Gätje and Reise, 1998; (5) Zwarts and Blomert, 1992; (6) Reise, 1998; (7) Kamermans et al., 2004; (8) Smaal et al., 2001; (9) Kater and Kesteloo, 2003; (10) Kater and Den Os, 2001; (11) Dekker and De Bruin, 2001; (12) Perdon and Smaal, 2000.

[a] Excluding hard substrates.

[b] Assuming that the stock in western Wadden Sea is 50% of the stock in the Dutch Wadden Sea (Brinkman, pers. comm.).

* Averaged over the length of the spawning season (1 April–30 Sept, 152 days) for comparison with larval densities.

Assimilation rates (p_A) for these peak values were 1.7×10^{-3} and 2.7×10^{-3} J $larva^{-1}$ d^{-1}, respectively (Fig. 7). In the western Wadden Sea, the energy concentration fluctuated over the year, with peak values in February (7.8×10^{-3} J cm^{-3}), April (6.1×10^{-3} J cm^{-3}) and June/July (4.9×10^{-3} J cm^{-3}), yielding assimilation rates p_A of 1.55×10^{-3}, 1.46×10^{-3} and 2.5×10^{-3} J $larva^{-1}$ d^{-1}, respectively (Fig. 6).

In the Delta area, peak values were mainly found in May at stations OS-N and OS-E (~2.8×10^{-3} J cm^{-3}), at end of June at all three stations (4.0–4.6×10^{-3} J cm^{-3}) and in August at stations OS-W and OS-N (2.1–4.2×10^{-3} J cm^{-3}). Assimilation rates of larvae were 1.33–1.34×10^{-3} J $larva^{-1}$ d^{-1} (May, OS-N and OS-E), 3.01–3.97 J $larva^{-1}$ d^{-1} (June, all three stations), and 3.90–2.87×10^{-3} J $larva^{-1}$ d^{-1} (August, OS-W and OS-N). Due to the absence of phytoplankton data for stations OS-C and WWS, no assimilation rates could be estimated.

4. Discussion

4.1. Assumptions and model limitations

The results of the present study suggest that larvae in north-west European waters are food limited throughout the year. It has to be stressed, however, that all estimates are based on assumptions. Estimates of larval abundance were made under the assumption that larvae are distributed uniformly over the water column, so any vertical movements of the larvae (Verwey, 1966) were ignored. Average larval concentrations in the water column may, hence, have differed from those at the surface, where the sampling took place. In addition, it was assumed that larvae would not be size-selective and would ingest all phytoplankton and heterotrophic ciliates <20 μm, except for species possessing spines or forming chains. However, some species of larvae are known to feed selectively. For example, larvae of the

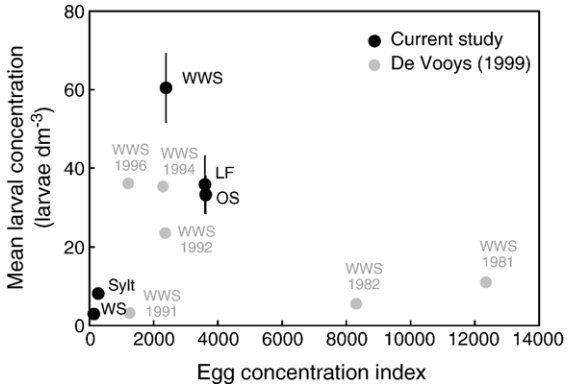

Fig. 5. An estimated index of average bivalve egg concentrations (eggs dm^{-3}) plotted against the average number of larvae measured in each area (larvae dm^{-3}; mean ± SE). Egg concentrations are based on total yearly egg production (Table 4) and the water volume of the sampled areas (Table 3). Results of De Vooys (1999) (station WWS in earlier years) have been included for comparison (De Vooys' data on *Mytilus edulis* and *Cerastoderma edule* biomass were converted to egg numbers according to Table 4).

oyster *Crassostrea virginica* strongly select for 2–4 μm food particles in food suspensions, and for much larger (22–30 μm) food material in the presence of a large (>10 μm)-cell dinoflagellate bloom (Baldwin, 1995), while *Mytilus edulis* veligers had the highest clearance rates at particle sizes of 2.5 to 3.5 μm and did not ingest particles <1 and >8–9 μm (Riisgård and Randløv, 1980). The volumes of the prey cells were estimated from the literature, and their specific size was assumed to be constant. The nutritional value (J μm^{-3}) of phytoplankton was also assumed to be constant, although this can differ between and within species (Walne, 1963; Baldwin and Newell, 1995).

It was assumed that the Dynamic Energy Budget (DEB) model for *Macoma balthica* larvae (Philippart et al., ms. in prep.) would provide good estimates of the energetic requirements. This probably holds for maintenance costs (M) (Kooijman, 2000; Van der Veer et al., 2001), but not for ingestion rates. Van der Veer et al. (2001) showed that various flatfish species differ especially with respect to their surface area-specific maximum ingestion rates $\{J_{Xm}\}$. For larvae of various bivalve species this may mean that ingestion rates differ and, hence, that the degree of food limitation for other species than *M. balthica* may have been under- or overestimated. In addition, the energy budget calculations were made for a 200-μm larva, although in the field larvae may range from 50 to 400 μm (Pulfrich, 1997; pers. obs.). According to the DEB-model, a smaller larva (e.g., 150 μm) and a larger one (e.g., 250 μm) require 56% and 156%, respectively, of the energy required by a 200-μm larva (Fig. 7), which corresponds to the observation that smaller organisms generally have a higher demand per unit of body mass (e.g. Banse and Mosher, 1980; Banse, 1982). Finally, in the DEB-model itself, many assumptions have been made that are discussed in detail by Philippart et al. (ms. in prep.). For example, the assimilation efficiency in de DEB-model is constant (0.56%; Van Haren and Kooijman, 1993), but may in reality show great variation (33 to 92% in mixed zooplankton; Conover, 1966). Altogether, numerous uncertainties exist in the estimates of the parameters. Confidence intervals could be provided for the results, based on the uncertainties of the parameters, but that would only suggest a certainty of the data that is not realistic.

4.2. Larval concentrations

In the current study, the observed average larval concentrations (larvae dm^{-3}) were positively related to the egg concentration index (eggs dm^{-3}) (Fig. 5), i.e. larval concentrations appeared to depend on the size of the adult stocks and the water volume of the estuary. To keep it simple, this analysis did not include the water exchange of the basins with the open sea, resulting in offshore transport of larvae (Roegner, 2000). The egg concentration index can probably be improved if more information on the various stock sizes was available. In the western Wadden Sea, for example, the deeply buried *Mya arenaria* was not taken into account because only limited information exists on its distribution, although in parts of the western Wadden Sea it may constitute 7–70% of the total bivalve biomass (Dekker and De Bruin, 2001). Similarly, *Ensis americanus* in the Sylt-Rømø bight was not taken into account because only limited information was available on its abundance and distribution (Armonies and Reise, 1999). In addition, the population size of *Crassostrea gigas* in the Sylt-Rømø bight may have been underestimated, since it increased from 1 million individuals in 1995 (Reise, 1998) to 60 million individuals in 2003 (Diederich et al., 2005).

The data of De Vooys (1999), who measured larval concentrations at station WWS in earlier years, confirm the positive relation between the egg production index and the measured larval abundance at low egg concentrations, i.e. at small adult stock (Fig. 5). The egg production index was estimated by converting estimates on the fresh weight of the mussel and cockle stocks (De Vooys, 1999) into egg numbers according to Table 4. At extremely high bivalve stocks (as occurred around 1981 due to simultaneous successful recruitment in all im-

Table 5
Individual cell volumes (μm^3) of phytoplankton taxa that can theoretically be ingested by bivalve larvae on basis of their size and morphology (see methods section), sampled in Limfjorden, Sylt-Rømø bight, western Wadden Sea and Delta area in 2000

Location	Group	Species	Shape*	Calculation of biovolume	V(μm^3)	pgC $cell^{-1}$	Reference
Limfjorden	O	Autotrophic picoplankton indet.	6	$\pi/6 \times (1)^3$	0.52	0.25	a
Limfjorden	D	Centric diatom <10 μm	1	$\pi/4 \times (5)^2 \times 2.5$	49.09	7.24	b
Sylt-Rømø bight	D	Centric diatom 0–2	1	$\pi/4 \times (1)^2 \times 0.5$	0.39	0.19	b
Sylt-Rømø bight	D	Centric diatom 0–3	1	$\pi/4 \times (1.5)^2 \times 0.75$	1.33	0.47	b
Sylt-Rømø bight	D	Centric diatom 0–5	1	$\pi/4 \times (2.5)^2 \times 1.25$	6.14	1.50	b
Limfjorden	D	Centric diatom 10–20 μm	1	$\pi/4 \times (15)^2 \times 7.5$	1325.36	88.05	b
Sylt-Rømø bight	D	Centric diatom 1–3	1	$\pi/4 \times (2)^2 \times 1$	3.14	0.90	b
Sylt-Rømø bight	D	Centric diatom 2	1	$\pi/4 \times (2)^2 \times 1$	3.14	0.90	b
Sylt-Rømø bight	D	Centric diatom 2 × 4	1	$\pi/4 \times (2)^2 \times 1$	3.14	0.90	b
Sylt-Rømø bight	D	Centric diatom 5	1	$\pi/4 \times (5)^2 \times 2.5$	49.09	7.24	b
Sylt-Rømø bight	D	Centric diatom 5–10	1	$\pi/4 \times (7.5)^2 \times 3.75$	165.67	18.20	b
Limfjorden	O	Choanoflagellates <5 μm	5	$\pi/6 \times (1.25)^2 \times 2.5$	2.05	0.81	b
Limfjorden	O	Choanoflagellates 5–10 μm	5	$\pi/6 \times (3.75)^2 \times 7.5$	55.22	13.82	b
Limfjorden	O	*Chrysochromulina* spp. <5 μm	6	$\pi/6 \times (2.5)^3$	8.18	2.66	b
Limfjorden	O	*Chrysochromulina* spp. 5–10 μm	6	$\pi/6 \times (7.5)^3$	220.89	45.71	b
Limfjorden	C	Ciliates spp. 0–10 μm	5	$\pi/6 \times (2.5)^2 \times 5$	16.36	2.70	a
Limfjorden	C	Ciliates spp. 11–20 μm	5	$\pi/6 \times (7.5)^2 \times 15$	441.79	72.90	a
Limfjorden	O	Coccoid cyanobacteria spp.	5	$\pi/6 \times (1)^2 \times 2$	1.05	0.45	a
Delta area	O	Cryptomonadales	6	$\pi/6 \times (4)^3$	33.51	8.98	b
Delta area	O	Cryptophyceae sp.	5	$\pi/6 \times (1.25)^2 \times 2.5$	2.05	0.81	b
Limfjorden	O	Cryptophyceae spp. <5 μm	5	$\pi/6 \times (1.25)^2 \times 2.5$	2.05	0.81	b
Limfjorden	O	Cryptophyceae spp. 10–15 μm	5	$\pi/6 \times (6.25)^2 \times 12.5$	255.66	51.86	b
Limfjorden	O	Cryptophyceae spp. 15–20 μm	5	$\pi/6 \times (8.75)^2 \times 17.5$	701.54	123.92	b
Limfjorden	O	Cryptophyceae spp. 5–10 μm	5	$\pi/6 \times (3.75)^2 \times 7.5$	55.22	13.82	b
Western Wadden Sea	D	*Cymatosira belgica*	–	–	300	59.53	c
Delta area	D	*Delphineis minutissima*	–	–	27	7.45	d
Western Wadden Sea	O	Dinoflagellate	5	$\pi/6 \times (7)^2 \times 10$	256.56	52.02	e
Sylt-Rømø bight	O	Dinoflagellate sp.	6	$\pi/6 \times (7)^2 \times 10$	256.56	52.02	e
Sylt-Rømø bight	O	Dinoflagellate sp. >3 μm	5	$\pi/6 \times (1.5)^2 \times 3$	3.53	1.29	b
Sylt-Rømø bight	O	Dinoflagellate sp. >4 μm	5	$\pi/6 \times (2)^2 \times 4$	8.38	2.71	b
Sylt-Rømø bight	O	Dinoflagellate sp. 0–3 μm	5	$\pi/6 \times (0.75)^2 \times 1.5$	0.44	0.21	b
Limfjorden	O	Dinoflagellate sp. 10–20 μm	5	$\pi/6 \times (7.5)^2 \times 15$	441.79	72.90	b
Sylt-Rømø bight	O	Dinoflagellate sp. 5 μm	5	$\pi/6 \times (2.5)^2 \times 5$	16.36	4.84	b
Sylt-Rømø bight	O	Dinoflagellate sp. 7 μm	5	$\pi/6 \times (3.5)^2 \times 7$	44.90	11.56	b
Limfjorden	O	*Ebria* sp. (10–20 μm)	3	$\pi/12 \times (8)^2 \times (4+7)$	181.34	38.55	b
Western Wadden Sea	D	*Eunotogramma dubium*	–	–	539	44.52	f
Sylt-Rømø bight	D	*Eunotogramma dubium*	–	–	539	44.52	f
Western Wadden Sea	O	Flagellates <10 μm	–	–	60	14.84	c
Limfjorden	O	Flagellates <5 μm	5	$\pi/6 \times (1.25)^2 \times 2.5$	2.05	0.81	b
Limfjorden	O	Dinoflagellate sp. <10 μm	5	$\pi/6 \times (2.5)^2 \times 5$	16.36	4.84	b
Western Wadden Sea	O	Flagellates >10 μm	–	–	612	110.15	c
Limfjorden	O	Flagellates 5–10 μm	5	$\pi/6 \times (3.75)^2 \times 7.5$	55.22	13.82	b
Delta area	O	*Heterocapsa minima*	–	–	125	27.97	d
Western Wadden Sea	O	*Heterocapsa rotundata* (syn. *Katodinium rotundatum)*	3	$\pi/12 \times (6)^2 \times (6.5+6)$	117.81	26.57	a
Sylt-Rømø bight	O	*Heterocapsa* sp.	5	$\pi/6 \times (5.25)^2 \times 10.5$	151.53	33.02	b
Delta area	O	*Heterocapsa triquetra*	–	–	1953	299.83	d
Limfjorden	O	Heterotrophic flagellates	–	–	60	14.84	c
Sylt-Rømø bight	D	*Katodinium* sp.	–	–	151.53	33.02	b
Delta area	O	*Leucocryptos marina*	3	$\pi/12 \times (7.5)^2 \times (14+7.5)$	316.61	62.37	a
Limfjorden	O	*Leucocryptos* sp. (10–15 μm)	3	$\pi/12 \times (6)^2 \times (10+6)$	150.80	32.88	b
Limfjorden	O	*Leucocryptos* sp. (5–10 μm)	3	$\pi/12 \times (3)^2 \times (5+3)$	75.40	18.08	b
Limfjorden	C	*Lohmaniella oviformis*	5	$\pi/6 \times (15.5)^2 \times 16.5$	2075.61	342.48	a
Limfjorden	O	*Micromonas pusilla*	5	$\pi/6 \times (1)^2 \times 2$	1.05	0.45	b
Delta area	O	*Nephroselmis* sp.	4	$\pi/4 \times 6.5 \times 4 \times 2$	40.84	10.65	a
Western Wadden Sea	D	Pennate diatoms indet.	–	–	895	65.39	c

Table 5 (*continued*)

Location	Group	Species	Shape*	Calculation of biovolume	V(μm^3)	pgC $cell^{-1}$	Reference
Limfjorden	D	Pennate diatoms indet.	–	–	895	65.39	c
Delta area	O	Peridiniaceae	–	–	4096	568.15	d
Western Wadden Sea	O	*Phaeocystis* flagellate	–	–	65	15.91	c
Sylt-Rømø bight	O	*Phaeocystis globosa*	–	–	65	15.91	c
Delta area	O	*Phaeocystis* sp.	–	–	65	15.91	c
Delta area	O	*Prasinocladus marinus*	5	$\pi/6 \times (6)^2 \times 10$	188.50	39.87	b
Limfjorden	O	Prasinophyceae spp.	5	$\pi/6 \times (6)^2 \times 10$	188.50	39.87	b
Sylt-Rømø bight	O	Prasinophyceae spp.	5	$\pi/6 \times (6)^2 \times 10$	188.50	39.87	b
Limfjorden	O	*Prorocentrum balticum*	–	–	375	72.18	g
Limfjorden	O	*Prorocentrum minimum*	5	$\pi/6 \times (12.5)^2 \times 18$	1472.62	235.00	a
Limfjorden	O	*Prorocentrum triestinum*	5	$\pi/6 \times (8)^2 \times 10$	335.10	65.50	a
Delta area	O	*Pyramimonas* sp.	2	$\pi/12 \times (10)^2 \times 15$	392.70	75.11	b
Western Wadden Sea	O	*Rhodomonas* spp.	–	–	221	45.73	c
Delta area	O	Small algae indet.	6	$\pi/6 \times (2.1)^3$	4.85	1.69	d
Limfjorden	C	*Strombidium* sp. (<10 μm)	2	$\pi/12 \times (3)^2 \times 5$	11.78	1.94	h
Limfjorden	C	*Strombidium* sp. (10–20 μm)	2	$\pi/12 \times (9)^2 \times 15$	318.09	52.48	h

D=diatoms, C=ciliates, O=other nanoplankton (including dinoflagellates). Carbon content of diatoms is calculated according to Strathmann (1967), of 'other nanoplankton', according to Verity (1992) and of ciliates according to Putt and Stoecker (1989) (see 'Materials and methods'). References: (a) Kuylenstierna and Karlson, 1998; (b) Tomas, 1997; (c) Philippart et al., 2000; (d) Koeman, pers. comm., 2003; (e) Van Iperen, pers.comm., 2003; (f) Philippart pers. comm., 2003; (g) Plymouth Mar. Lab.; (h) Ichise et al., 2004.

* Geometric shapes and biovolume calculations as described in Hillebrand et al., 1999: (1) cylinder; (2) cone; (3) cone + half sphere; (4) elliptic prism; (5) prolete spheroid; (6) sphere.

portant bivalve species in 1979; compare Beukema et al., 2001) however, De Vooys (1999) measured low larval concentrations, probably due to the important filtration activity of the adults. Furthermore, De Vooys (1999) showed a clear year-to-year variation in larval concentrations in a single area (western Wadden Sea), which demonstrates that geographical comparisons of larval concentrations based on different studies from different years must be treated with great caution.

Maximum larval concentrations in the current study varied from 17 (station WS) to 392 larvae dm^{-3} (station WWS), with intermediate maximum values of 100–220 larvae dm^{-3} at the other stations. The low larval concentrations in the Westerschelde may be attributed to a combination of relatively low bivalve stocks and a relatively large water volume (Fig. 5). In the Sylt-Rømø bight, at similarly low bivalve stocks (Table 4), larval concentrations were higher, because the eggs were probably less diluted (Fig. 5). Larval numbers were probably underestimated in the Sylt-Rømø bight because the mesh size of the sieve was larger than in the other study areas (Table 1). In addition, the adult stock may have been underestimated. In the western Wadden Sea, the highest larval concentrations were observed, which was attributed to a relatively low water volume and high bivalve stocks (Fig. 5). In the Oosterschelde and Limfjorden, larval concentrations were of the same magnitude. In the Oosterschelde, bivalve stocks were larger, but the dilution of eggs was also greater. Since, in general, the average benthic biomass is limited by the primary productivity of the system (Herman et al., 1999), it may be that larval concentrations are indirectly determined by the primary production, via adult biomass and adult reproductive output.

The study areas differed not only in the intensity of the larval peaks, but also in their number. The successive larval peaks may have been the result of the different timing of spawning of bivalve species. Single larval peaks were observed in Limfjorden, while in the other areas multiple larval peaks were observed. This may be an effect of the sampling frequency (Table 1), but also of differences in physical and hydrodynamic characteristics of the areas (Table 3). Limfjorden is a subtidal area, whereas tidal flats dominate the other areas. In general, the water temperature increase in subtidal areas is spatially more uniform than in intertidal areas (Raffaelli and Hawkins, 1996), leading to a more synchronised spawning in subtidal areas. Furthermore, Limfjorden is dominated by a single bivalve species, *M. edulis* (Dolmer et al., 1999), while in the other areas 3–5 bivalve species are abundant (Table 4). Therefore the single larval peaks observed at stations LF-LB and LF-SF may have resulted from a synchronised spawning event of *M. edulis*, while the multiple peaks measured in the other areas (Fig. 4) may have resulted from multiple spawning by multiple species. Finally, the duration of peaks may vary between areas due to effects of water temperature (Drent, 2002) and

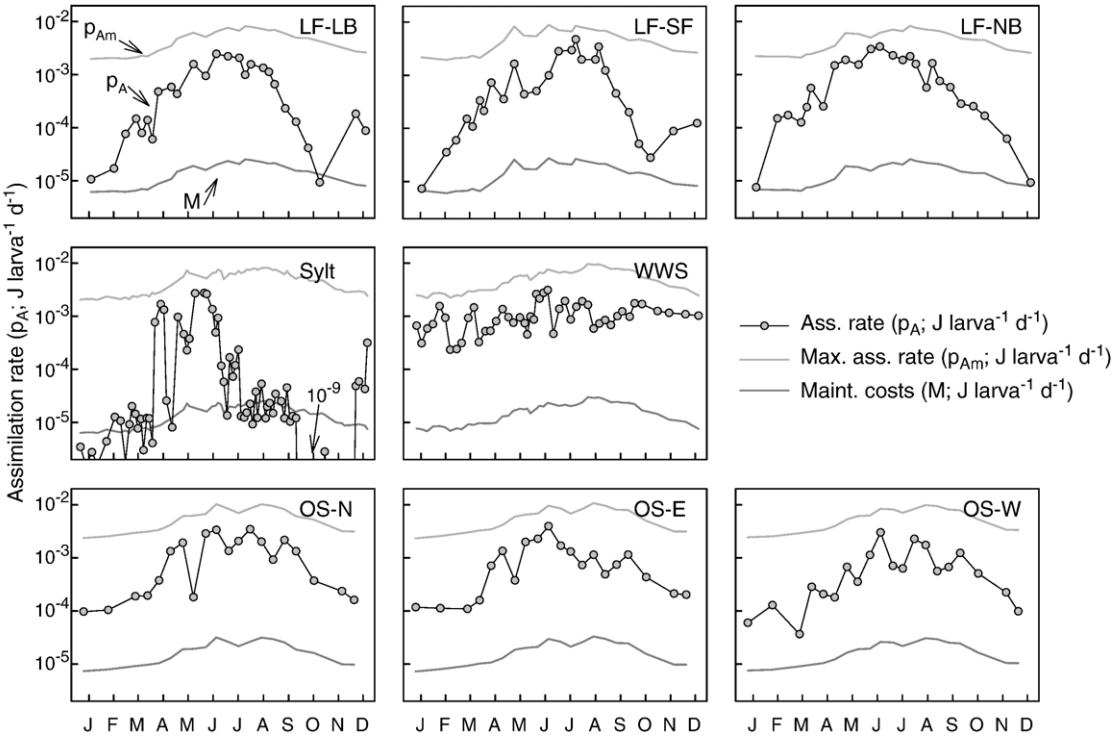

Fig. 6. Assimilation rate of a bivalve larva (p_A; J larva^{-1} d^{-1}; middle line) based on phytoplankton energy content and larval energy needs. The upper line shows maximum assimilation rate (p_{Am}; J larva^{-1} d^{-1}) leading to maximum larval growth, and lower line shows maintenance costs (M; J larva^{-1} d^{-1}), at which growth is not possible. Rates are calculated with a DEB-model for a 200 μm *Macoma balthica* larva and are corrected for temperature.

nutrition (Pechenik et al., 2002) on larval development rate.

4.3. Food limitation

The above results show that in the period between April and September 2000, larvae were able to achieve an average assimilation rate p_A between 7% and 25% of the maximum assimilation rate p_{Am}, with a maximum of 60%. This suggests that a representative larva, with a length of 200 μm, is food-limited for most of its life, irrespective of the study site. Such low assimilation rates may greatly increase the time a larva needs to complete development into a competent larva, with the

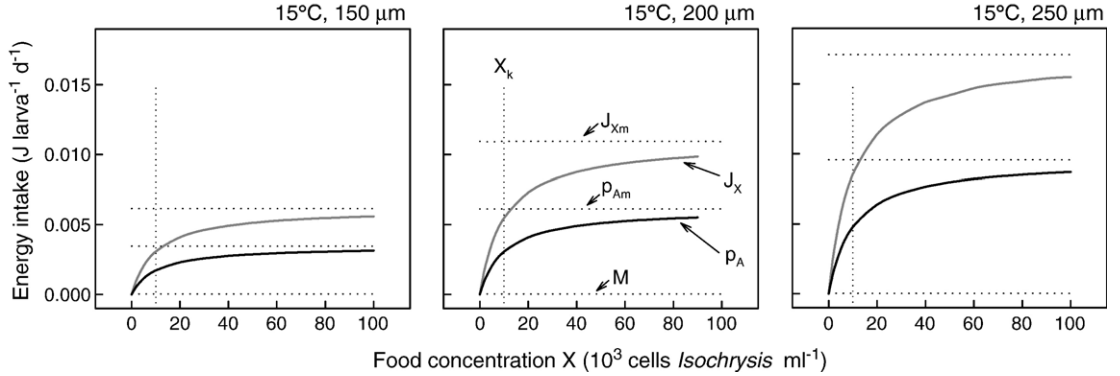

Fig. 7. DEB-model predictions of energy intake (J larva^{-1} d^{-1}) as a function of food concentration (functional response; cells *Isochrysis galbana* cm^{-3}) for different larval sizes (150, 200 and 250 μm). From top to bottom, lines indicate maximum ingestion rate (J_{Xm}), ingestion rate (J_X), maximum assimilation rate (p_{Am}), assimilation rate (p_A), and maintenance costs (M). The vertical line indicates the half-saturation constant X_k.

risk of being transported offshore (Young et al., 1998; Roegner, 2000) or of predation by e.g. benthic filter feeders (Cowden et al., 1984; André and Rosenberg, 1991). However, by definition, larvae will never attain maximum growth rates and will therefore always be food-limited to a certain extent, since the p_{Am} is the upper limit of an asymptotic function (Fig. 3). A relevant question is therefore at what food levels a larva is still able to grow and develop successfully. In a laboratory experiment, at 15 °C, *M. balthica* larvae were able to develop successfully to metamorphosis at food concentrations of 4.0×10^3 cells *Isochrysis galbana* cm^{-3} (Bos et al., subm. ms.). For a 200-µm larva, this would correspond to a p_A of 29% of the p_{Am}. Furthermore, growth rates were high and development was fast at food concentrations of 80×10^3 cells cm^{-3} (Bos et al., subm. ms), corresponding to a p_A of 89% of p_{Am} for a 200-µm larva at 15 °C. In another experiment, *M. balthica* larvae reared in natural seawater were mostly not able to complete metamorphosis, while control larvae fed with 50×10^3 *I. galbana* cells cm^{-3} always successfully completed metamorphosis (Bos et al., subm. ms). Together, these experiments suggest that the observed food levels in the field were frequently too low for bivalve larvae to complete metamorphosis.

Other studies in coastal waters that aimed at detecting food limitation of larvae have yielded contrasting results. In a Danish embayment, mussel *M. edulis* larvae reared in natural seawater were generally food-limited, compared to those reared in enriched natural seawater (Fotel et al., 1999). Jørgensen (1981), however, reported growth rates of *M. edulis* veligers estimated from field samples similar to growth rates under optimal conditions in the laboratory. Thus the literature suggests food limitation in at least some coastal areas. Limited food availability in our study areas is probably not caused by competition between larvae (Strathmann, 1996; Bos et al., ms. in prep.), but by competition of larvae and the benthic bivalve stock (Cowden et al., 1984; André and Rosenberg, 1991), a match/mismatch situation of larvae and their food source (Philippart et al., 2003; Bos et al., subm. ms.) as has been reported for fish larvae (Cushing, 1990), or by competition with other planktonic species (Hansen et al., 1994).

In conclusion, the results suggest that larvae in north-western European waters are food limited throughout the year under the assumptions made in the present study. Although the assimilation rates at most study sites appear to be high enough to cover the maintenance costs of the larvae, it is not clear whether they can support the metamorphosis of veliger larvae into settlers. As a consequence, the link between the degree of larval food limitation and bivalve recruitment remains to be elucidated (Olson and Olson, 1989). Further research should focus on the determination of natural larval food sources, their nutritional value, and their effect on larval growth, development and survival rates. Also factors that influence larval food availability, such as competition for food with other planktonic species or with the adult stock, and the behaviour of larvae in response to patches of food (Metaxas and Young, 1998) should be clarified.

Acknowledgements

The Netherlands Organisation for Scientific Research (Priority Program on Sustainable Use and Conservation of Marine Living Resources) provided funding for the present study. We are grateful to Miriam Collombon and the staff at the County of Ringkjøbing for collecting and identifying plankton samples. We thank Justus van Beusekom, Hanne Halliger, Gerhard Cadée, Reinoud Koeman, Bert Wetsteijn, Jolanda van Iperen and Rijkswaterstaat for data on phytoplankton. We also thank 'Deutscher Wetterdienst, Wetterstation List', Hendrik van Aken and Rijkswaterstaat for data on water temperature. Katja Philippart, Jaap van der Meer, Sebastian Holmes, Jan Beukema and four anonymous reviewers contributed to discussions and improvements of earlier versions. Sophie Brasseur provided the maps of the study areas.

References

André, C., Rosenberg, R., 1991. Adult-larval interactions in the suspension-feeding bivalves *Cerastoderma edule* and *Mya arenaria*. Mar. Ecol. Prog. Ser. 71, 227–234.

Armonies, W., Reise, K., 1999. On the population development of the introduced razor clam *Ensis americanus* near the island of Sylt (North Sea). Helgol. Meeresunters. 52, 291–300.

Bakker, C., 1994. Zooplankton species composition in the Oosterschelde (SW Netherlands) before, during and after the construction of a storm-surge barrier. Hydrobiol. 282/283, 117–126.

Baldwin, B.S., 1995. Selective particle ingestion by oyster larvae (*Crassostrea virginica*) feeding on natural seston and cultured algae. Mar. Biol. 123, 95–107.

Baldwin, B.S., Newell, R.I.E., 1991. Omnivorous feeding by planktotrophic larvae of the eastern oyster *Crassostrea virginica*. Mar. Ecol. Prog. Ser. 78, 285–301.

Baldwin, B.S., Newell, R.I.E., 1995. Relative importance of different size food particles in the natural diet of oyster larvae (*Crassostrea virginica*). Mar. Ecol. Prog. Ser. 120, 135–145.

Banse, K., 1982. Mass-scaled rates of respiration and intrinsic growth in very small invertebrates. Mar. Ecol. Prog. Ser. 9, 281–297.

Banse, K., Mosher, S., 1980. Adult body-mass and annual production-biomass relationships of field populations. Ecol. Monogr. 50, 355–379.

Beukema, J.J., De Bruin, W.D., 1979. Calorific values of the soft parts of the tellinid bivalve *Macoma balthica* (L) as determined by 2 methods. J. Exp. Mar. Biol. Ecol. 37, 19–30.

Beukema, J.J., Dekker, R., Essink, K., Michaelis, H., 2001. Synchronized reproductive success of the main bivalve species in the Wadden Sea: causes and consequences. Mar. Ecol. Prog. Ser. 211, 143–155.

Bouma, H., De Vries, P.P., Duiker, J.M.C., Herman, P.M.J., Wolff, W.J., 2001. Migration of the bivalve *Macoma balthica* on a highly dynamic tidal flat in the Westerschelde estuary. The Netherlands. Mar. Ecol. Prog. Ser. 224, 157–170.

Chanley, P.E., Andrews, J.D., 1971. Aids for identification of bivalve larvae of Virginia. Malacologia 11, 45–119.

Conover, R.J., 1966. Assimilation of organic matter by zooplankton. Limnol. Oceanogr. 11, 338–345.

Cowden, C., Young, C.M., Chia, F.S., 1984. Differential predation on marine invertebrate larvae by two benthic predators. Mar. Ecol. Prog. Ser. 14, 145–149.

Cushing, D., 1990. Plankton production and year-class strength in fish populations: An update of the match/mismatch hypothesis. Adv. Mar. Biol. 26, 249–294.

Dame, R.F., Prins, T.C., 1998. Bivalve carrying capacity in coastal ecosystems. Aquat. Ecol. 31, 409–421.

Dekker, R., De Bruin, W., 2001. Het macrozoobenthos op twaalf raaien in de Waddenzee en de Eems-Dollard in 2000. NIOZ Report 2001-1.

De Vooys, C.G.N., 1999. Numbers of larvae and primary plantigrades of the mussel *Mytilus edulis* in the western Dutch Wadden Sea. J. Sea Res. 41, 189–201.

Diederich, S., Nehls, G., Van Beusekom, J.E.E., Reise, K., 2005. Introduced Pacific oysters (*Crassostrea gigas*) in the northern Wadden Sea: invasion accelerated by warm summers? Helgol. Mar. Res. 59, 97–106.

Dodge, J.D., 1982. Marine Dinoflagellates of the British Isles. Her Majesty's Stationary Office, London.

Dolmer, P., 2002. Mussel dredging: Impact on epifauna in Limfjorden, Denmark. J. Shellfish Res. 21, 529–537.

Dolmer, P., Frandsen, R.P., 2002. Evaluation of the Danish mussel fishery: suggestions for an ecosystem management approach. Helgol. Mar. Res. 56, 13–20.

Dolmer, P., Kristensen, P.S., Hoffmann, E., 1999. Dredging of blue mussels (*Mytilus edulis* L.) in a Danish sound: stock sizes and fishery-effects on mussel population dynamics. Fish. Res. 40, 73–80.

Drent, J., 2002. Temperature responses in larvae of *Macoma balthica* from a northerly and southerly population of the European distribution range. J. Exp. Mar. Biol. Ecol. 275, 117–129.

Fenaux, L., Strathmann, M.F., Strathmann, R.R., 1994. Five tests of food-limited growth of larvae in coastal waters by comparisons of rates of development and form of echinoplutei. Limnol. Oceanogr. 39, 84–98.

Fotel, F.L., Jensen, N.J., Wittrup, L., Hansen, B.W., 1999. In situ and laboratory growth by a population of blue mussel larvae (*Mytilus edulis* L.) from a Danish embayment. Knebel Vig. J. Exp. Mar. Biol. Ecol. 233, 213–230.

Gätje, C., Reise, K., 1998. Ökosystem Wattenmeer. Springer-Verlag, Berlin.

Günther, C.-P., Boysen-Ennen, E., Niesel, V., Hasemann, C., Heuers, J., Bittkau, A., Fetzer, I., Nacken, M., Schlüter, M., Jacklin, S., 1998. Observations of a mass occurence of *Macoma balthica* larvae in midsummer. J. Sea Res. 40, 347–351.

Hairston, N.G., Smith, F.E., Slobodkin, L.B., 1960. Community structure, population control, and competition. Am. Nat. 94, 421–425.

Hansen, B.W., 1999. Cohort growth of planktotrophic polychaete larvae — are they food limited? Mar. Ecol. Prog. Ser. 178, 109–119.

Hansen, B., Bjørnsen, P.K., Hansen, P.J., 1994. The size ratio between planktonic predators and their prey. Limnol. Oceanogr. 39, 395–403.

Herman, P.M.J., Middelburg, J.J., Van de Koppel, J., Heip, C.H.R., 1999. Ecology of estuarine macrobenthos. Adv. Ecol. Res. 29, 195–240.

Hillebrand, H., Dürselen, C.-D., Kirschtel, D., Pollinger, U., Zohary, T., 1999. Biovolume calculation for pelagic and benthic microalgae. J. Phycol. 35, 403–424.

Holling, C.S., 1959. Some characteristics of simple types of predation and parasitism. Can. Entomol. 91, 385–398.

Honkoop, P.J.C., Van der Meer, J., Beukema, J.J., Kwast, D., 1999. Reproductive investment in the intertidal bivalve *Macoma balthica*. J. Sea Res. 41, 203–212.

Horner, R.A., 2000. A Taxonomic Guide to Some Common Marine Phytoplankton. Biopress Ltd., Bristol.

Huntley, M., Boyd, C., 1984. Food-limited growth of marine zooplankton. Am. Nat. 124, 455–478.

Hurley, D.H., Walker, R.L., O'Beirn, F.X., 1997. Growth and survival of *Spisula solidissima* similis larvae fed different rations of Tahitian strain *Isochrysis species*. J. Shellfish Res. 16, 151–155.

Ichise, S., Horikami, H., Katoh, K., Kihara, A., Mikami, K., Nakamachi, M., Skaloud, P., Sugiyama, N., Takahashi, M., Tsukii, Y., Tsuruhara, T., Ugawa, Y., Wang, C.L., Yanagi, A., Yazaki, K., Yoshino, H., 2004. Protist Information Server. Online, dataset, http://protist.i.hosei.ac.jp.

Jespersen, H., Olsen, K., 1982. Bioenergetics in veliger larvae of *Mytilus edulis* L. Ophelia 21, 101–113.

Jørgensen, C.B., 1981. Mortality, growth, and grazing impact of a cohort of bivalve larvae, *Mytilus edulis* L. Ophelia 20, 185–192.

Kamermans, P., Bult, T., Kater, B.J., Baars, J., Kesteloo-Hendrikse, J.J., Perdon, J., Schuiling, E., 2004. EVA II (H4): Invloed van natuurlijke factoren en kokkelvisserij op de dynamiek van bestanden aan kokkels (*Cerastoderma edule*) en nonnen (*Macoma balthica*) in de Waddenzee, Oosterschelde en Westerschelde. RIVO Report C058/03.

Kater, B.J., Den Os, D., 2001. Het mosselbestand op de droogvallende platen in de Waddenzee in het voorjaar van 2000. RIVO Report C069/01.

Kater, B., Kesteloo, J., 2003. Mosselbestanden in de Oosterschelde 1992–2002. RIVO Report C002/03.

Kooijman, S.A.L.M., 2000. Dynamic Energy and Mass Budgets in Biological Systems. Cambridge University Press, Cambridge.

Kristensen, P.S., Hoffmann, E., 2004. Bestanden af blåmuslinger i Limfjorden 1993 til 2003. Danmarks Fiskeriunders., Charlottenlund, DFU-Rapport 130–04.

Kuylenstierna, M., Karlson, B., 1998. Checklist of phytoplankton in the Skagerrak-Kattegat (Göteborg University, Sweden), online, dataset, http://www.marbot.gu.se.

Lammens, J.J., 1967. Growth and reproduction of a tidal flat population of *Macoma balthica* (L.). Neth. J. Sea Res. 3, 315–382.

Langdon, C.J., 1983. Growth studies with bacteria-free oyster (*Crassostrea gigas*) larvae fed on semi-defined artificial diets. Biol. Bull. 164, 227–235.

Le Pennec, M., 1980. Premières observations sur la morphogenèse de la coquille larvaire de *Spisula subtruncata* (Da Costa) en élevage experimental. Cah. Biol. Mar. 21, 403–408.

Loosanoff, V.L., Davis, H.C., Chanley, P.E., 1966. Dimensions and shapes of larvae of some marine bivalve mollusks. Malacologia 4, 351–435.

Manahan, D.T., 1983. The uptake and metabolism of dissolved amino acids by bivalve larvae. Biol. Bull. 164, 236–250.

Manahan, D.T., 1989. Amino-acid fluxes to and from seawater in axenic veliger larvae of a bivalve (*Crassostrea gigas*). Mar. Ecol. Prog. Ser. 53, 247–255.

Menge, B.A., 2000. Recruitment vs. postrecruitment processes as derminants of barnacle population abundance. Ecol. Monogr. 70, 265–288.

Metaxas, A., Young, C.M., 1998. Responses of echonoid larvae to food patches of different algal densities. Mar. Biol. 130, 433–445.

Ólafsson, E.B., Peterson, C.H., Ambrose Jr., W.G., 1994. Does recruitment limitation structure populations and communities of macro-invertebrates in marine soft sediments: the relative significance of pre- and post-settlement processes. Oceanogr. Mar. Biol. Ann. Rev. 32, 65–109.

Olson, R.R., Olson, M.H., 1989. Food limitation of planktotrophic marine invertebrate larvae: does it control recruitment success? Ann. Rev. Ecol. Syst. 20, 225–247.

Pechenik, J.A., Jarrett, J.N., Rooney, J., 2002. Relationships between larval nutrition experience, larval growth rates, juvenile growth rates, and juvenile feeding rates in the prosobranch gastropod *Crepidula fornicata*. J. Exp. Mar. Biol. Ecol. 280, 63–78.

Perdon, K.J., Smaal, A.C., 2000. Het bestand aan Japanse oesters op de platen van de Oosterschelde. RIVO report C030/00.

Philippart, C.J.M., Cadée, G.C., Van Raaphorst, W., Riegman, R., 2000. Long-term phytoplankton-nutrient interactions in a shallow coastal sea: algal community structure, nutrient budgets, and denitrification potential. Limnol. Oceanogr. 45, 131–144.

Philippart, C.J.M., Van Aken, H.M., Beukema, J.J., Bos, O.G., Cadée, G.C., Dekker, R., 2003. Climate-related changes in recruitment of the bivalve *Macoma balthica*. Limnol. Oceanogr. 48, 2171–2185.

Podniesinki, G.S., McAlice, B.J., 1986. Seasonality of blue mussel, *Mytilus edulis* L., larvae in the Damariscotta River estuary, Maine, 1969–77. Fish. Bull. 84, 995–1001.

Pulfrich, A., 1997. Seasonal variation in the occurrence of planktic bivalve larvae in the Schleswig-Holstein Wadden Sea. Helgol. Meeresunters. 51, 23–39.

Putt, M., Stoecker, D.K., 1989. An experimentally determined carbon-volume ratio for marine oligotrichous ciliates from estuarine and coastal waters. Limnol. Oceanogr. 34, 1097–1103.

Raffaelli, D., Hawkins, S., 1996. Intertidal Ecology. Chapman and Hall, London.

Reise, K., 1998. Pacific oysters invade mussel beds in the European Wadden Sea. Senckenber. Marit. 28, 167–175.

Ridderinkhof, H., Zimmerman, J.F.T., Philippart, M.E., 1990. Tidal exchange between the North Sea and Dutch Wadden Sea and mixing time scales of the tidal basins. Neth. J. Sea Res. 25, 331–350.

Riisgård, H.U., Randløv, A., 1980. Rates of water processing, oxygen consumption, and efficiency of particle retention in veligers and young postmetamorphic *Mytilus edulis*. Ophelia 19, 37–47.

Roegner, G.C., 2000. Transport of molluscan larvae through a shallow estuary. J. Plankt. Res. 22, 1779–1800.

Round, F.E., Crawford, R.M., Mann, D.G., 1990. The Diatoms. Cambridge University Press, Cambridge.

Ruiz, C., Abad, M., Sedano, F., Garciamartin, L.O., Lopez, J.L.S., 1992. Influence of seasonal environmental-changes on the gamete production and biochemical-composition of *Crassostrea gigas* (Thunberg) in suspended culture in El Grove, Galicia, Spain. J. Exp. Mar. Biol. Ecol. 155, 249–262.

Rumrill, S.S., 1990. Natural mortality of marine invertebrate larvae. Ophelia 32, 163–198.

Salonen, K., Sarvala, J., Hakala, I., Viljanen, M.L., 1976. Relation of energy and organic-carbon in aquatic invertebrates. Limnol. Oceanogr. 21, 724–730.

Smaal, A.C., Van Stralen, M., Schuiling, E., 2001. The interaction between shellfish culture and ecosystem processes. Can. J. Fish. Aquat. Sci. 58, 991–1002.

Smaal, A.C., Brummelhuis, E., Collombon, M., Poelman, J., Kamermans, P., 2002. Larval abundance and spatfall of mussels *Mytilus edulis* in the Dutch Wadden Sea and Oosterschelde estuary. ESSENSE Final Report (FAIR CT98-4201).

Sprung, M., 1983. Untersuchungen zum Energiebudget der larven der Miesmuschel (*Mytilus edulis* L.). Ph.D. Thesis, Cristian-Albrechts-Universität, Kiel.

Sprung, M., Asmus, H., Asmus, R., 2001. Energy flow in benthic assemblages of tidal basins: Ria Formosa (Portugal) and Sylt-Rømø bay (North Sea) compared. In: Reise, K. (Ed.), Ecological Comparisons of Sedimentary Shores. Springer, Berlin, pp. 237–254.

Strasser, M., 2000. Rekrutierungsmuster ausgewählter Wattfauna nach unterschiedlich strengen Wintern. Ph.D. Thesis, University Hamburg, Hamburg.

Strasser, M., Günther, C.-P., 2001. Larval supply of predator and prey: temporal mismatch between crabs and bivalves after a severe winter in the Wadden Sea. J. Sea Res. 46, 57–67.

Strathmann, R.R., 1967. Estimating the organic carbon content of phytoplankton from cell volume or plasma volume. Limnol. Oceanogr. 12, 411–418.

Strathmann, R.R., 1987. Larval feeding. In: Giese, A.C., Pearse, J.S., Pearse, V.B. (Eds.), Reproduction of Marine invertebrates. Blackwell Sci., Palo Alto, California.

Strathmann, R.R., 1996. Are planktonic larvae of marine invertebrates too scarce to compete within species? Oceanol. Acta 19, 399–407.

Thorarinsdóttir, G.G., 1986. Gonad development, larval settlement and growth of *Mytilus edulis* L. in a suspended population in Hvalfjordur, south-west Iceland. Aquacult. Res. 27, 57–65.

Thorson, G., 1950. Reproductive and larval ecology of marine bottom invertebrates. Biol. Rev. 25, 1–45.

Tomas, C.R., 1997. Identifying Marine Phytoplankton. Academic Press, San Diego.

Van der Veer, H.W., Kooijman, S.A.L.M., Van der Meer, J., 2001. Intra- and interspecies comparison of energy flows in North Atlantic flatfish species by means of dynamic energy budgets. J. Sea Res. 45, 303–320.

Van Haren, R.J.F., Kooijman, S.A.L.M., 1993. Application of a dynamic energy budget model to *Mytilus edulis* (L.). Neth. J. Sea Res. 31, 119–133.

Verity, P.G., Robertson, C.Y., Tronzo, C.R., Andrews, M.G., Nelson, J.R., Sieracki, M.E., 1992. Relationships between cell-volume and the carbon and nitrogen-content of marine photosynthetic nanoplankton. Limnol. Oceanogr. 37, 1434–1446.

Verwey, J., 1966. The role of some external factors in the vertical migration of marine animals. Neth. J. Sea Res. 3, 245–266.

Walne, P.R., 1963. Observations on food value of 7 species of algae to larvae of *Ostrea edulis*. 1. Feeding experiments. J. Mar. Biol. Ass. UK 43, 767–784.

Wilson, J.H., Seed, R., 1974. Reproduction in *Mytilus edulis* L. (Mollusca: Bivalvia) in Carlingford Lough, Northern Ireland. Ir. Fish. Invest. Ser. B. (Mar.) 15, 1–30.

Ysebaert, T., Herman, P.M.J., Meire, P., Craeymeersch, J., Verbeek, H., Heip, C.H.R., 2003. Large-scale spatial patterns in estuaries: estuarine macrobenthic communities in the Schelde estuary, NW Europe. Estuar. Coast. Shelf Sci. 57, 335–355.

Young, E.F., Bigg, G.R., Grant, A., Walker, P., Brown, J., 1998. A modelling study of environmental influences on bivalve settlement in The Wash, England. Mar. Ecol. Prog. Ser. 172, 197–214.

Zwarts, L., Blomert, A.-M., 1992. Why knot *Calidris canutus* take medium-sized *Macoma balthica* when six prey species are available. Mar. Ecol. Prog. Ser. 83, 113–128.