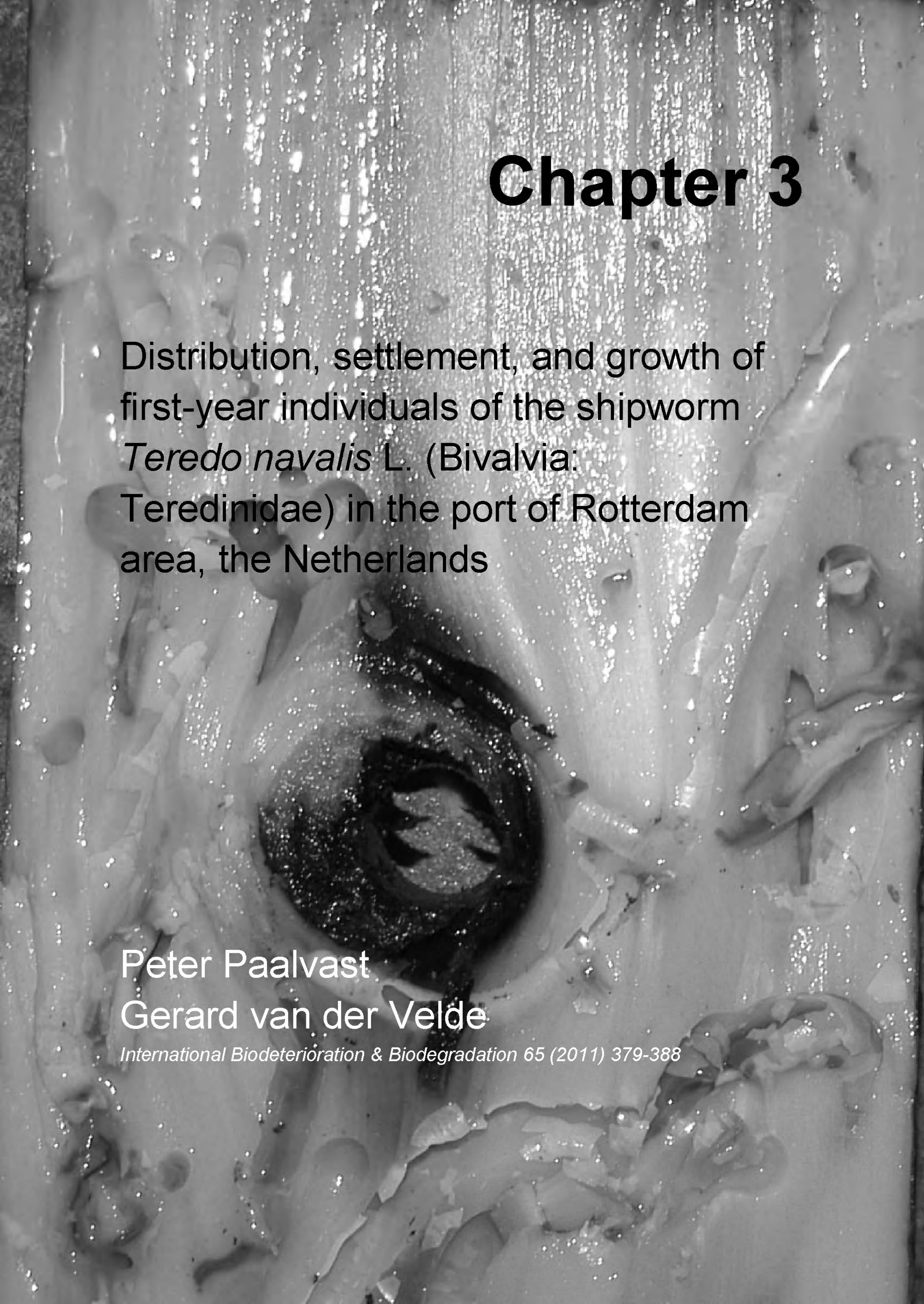

Chapter 3

Distribution, settlement, and growth of first-year individuals of the shipworm *Teredo navalis* L. (Bivalvia: Teredinidae) in the port of Rotterdam area, the Netherlands

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Abstract

During the period 2004 -2008 the distribution, settlement and growth of first year shipworms (*Teredo navalis* L., 1758.) was studied by exposing fir and oak panels in the port of Rotterdam area, which is situated in the Rhine-Meuse estuary in the Netherlands and covers the complete salinity gradient. Shipworms were found yearly in the western large polyhaline harbours. On only a few occasions they were found in harbours that showed large seasonal and daily fluctuations in salinity over the years. In 2006 the shipworm was found in fir panels 20 km upstream from the polyhaline harbours, demonstrating their ability to travel with the tidal currents over considerable distances and to settle once the abiotic conditions become favourable. Although the water temperatures allowed them to breed from April till November, infestations were not found before September and from the size of the animals in the panels it was concluded that in the port of Rotterdam area they spawned from August until the end of November.

The settlement height was negatively correlated with the distance of the panels to the sea floor. In the first season after settlement they showed a substantial growth rate of 0.18 cm day^{-1} in 2006. The longest shipworm found was in 2006 and measured 36.8 cm after 4 – 5 months of growth after settlement. Infestations and growth were lower in oak than in fir wood. In 2006 the maximum loss of wood caused by individuals settled in the same year in panels at the bottom accounted 12.4%. Shell size and body length of the animal after the first season of growth showed a significant positive logarithmic relation. In both 2006 and 2007 a similar relation between the average boring tube diameter and the length of the animals was found.

Lower river discharges leading to salinisation of the eastern part of the port of Rotterdam area create conditions favourable for the shipworm with serious consequences for the condition of the piles where the quays are built upon.

Introduction

Shipworms are 'xylophagous' marine bivalve molluscs belonging to the Teredinidae which are specialized to bore into wood. The first documented mass appearance of the shipworm (*Teredo navalis* L.) in the coastal waters of the Netherlands took place in 1730,1731, and 1732 and led to massive destruction of the wooden constructions that protected the dikes in Zealand and Westfrisland (Vrolik et al., 1860). Later outbreaks of the species occurred in 1770, 1827, 1858 and 1859. Also sluices and dolphins in harbours upstream the Rhine-Meuse estuary were found to be infected in 1826. The conclusion was drawn that several seasons of low river discharges resulting in increased salinity had created favourable conditions for the shipworm to settle and survive in the area. The shipworm commonly occurs in the Dutch coastal waters and the enclosed salt water bodies in the Dutch Delta Area (Van Benthem Jutting, 1943, De Bruyne, 1994).

The adult shipworm tolerates salinity conditions between 5 and 35 (Nair and Sarawathy, 1971) making the mouth of estuaries with daily changing salinities a hospitable habitat for this species. The animal thrives and reproduces at salinities of 10 and higher (Soldatova, 1961 in Tuente, 2002). Below a salinity of 9-10 boring activity stops (Blum, 1922). The pelagic larvae survive at salinities as low as 5 (Hoagland, 1986). The optimal water temperature for growth and reproduction lies between 15°C and 25°C. Spawning starts when the temperature rises above 11 to 12°C and the animals may breed from May until October (Grave, 1928). Temperatures up to 30°C are tolerated. Below 10°C the boring activity drops and it stops at 5°C. At temperatures around the freezing point they will hibernate until the water temperature becomes favourable again.

The port of Rotterdam covers the complete salinity gradient of the Rhine-Meuse estuary. The large harbours in the western part are always polyhaline and the shipworm could settle if wooden constructions to bore into are present. The bottom water of the harbours of the eastern part is fresh to oligohaline at average river discharge, but at discharges below 1000 $m^3 s^{-1}$ the area becomes α-mesohaline with salinities over 10. If the discharge of the river Rhine remains below 1000 $m^3 s^{-1}$ during the breeding season for a few weeks the conditions might become favourable for the shipworm. Larvae transported with the tidal currents to the eastern part of the port of Rotterdam area could perhaps settle and grow in the oak and pine on which several old quays are built upon. In the summer of 2003 the discharge of the river Rhine dropped to a level below 1000 $m^3 s^{-1}$ and the salinity in the eastern part of the port of Rotterdam area rose to levels above 10. In September 2003 the Port Authority decided to test the validity of the above hypotheses and sets of fir panels where placed at the bottom at various sites of the port of Rotterdam area yearly from 2004 till 2008 and were inspected for the presence of shipworms .

The following research questions were formulated:

1. What is the distribution of the shipworm related to salinity and what is the potential and actual breeding season and length of boring period of *T. navalis* in the port of Rotterdam area based on water temperature and settlement on fir panels, respectively?
2. Is it possible for the shipworm to settle in the eastern part of the port of Rotterdam area at low river discharges and is settlement equally distributed over the water column or is there a relation with water depth?
3. How fast does the shipworm grow in fir wood the first season after settlement, how much wood loss they cause in that period and is there a difference in settlement and growth of shipworms in fir and oak panels?
4. Can shell size be used to estimate the length of the shipworm and its cause of wood loss and is there a relation between the length of the shipworm and its average boring tube diameter?

Materials and methods

Study area

The port of Rotterdam is situated in the estuary of the rivers Rhine and Meuse (Fig. 1A). It stretches over a length of 40 km and covers 10,500 hectares of which 3440 hectares of the area is water of harbours and 1960 hectares rivers and canals. Under average conditions, at a river Rhine discharge (Qbr) of 2200 $m^3 s^{-1}$ at the Dutch-German border, the complete salinity gradient from fresh to seawater is found in this part of the estuary. This salinity gradient moves downstream at ebb tide and upstream at floodtide. The hydrology of the area is strongly controlled by means of the drainage regime of the Haringvliet sluices (Fig. 1A), based on the discharge of the Rhine at the Dutch-German border. The degree to which the sluice gates are opened at ebbtide increase with increasing discharge of fresh water. To avoid salinisation upstream of Rotterdam an amount of 1500 $m^3 s^{-1}$ of fresh water is directed to the port of Rotterdam area, i.e. the Nieuwe Waterweg (1300 $m^3 s^{-1}$) and the Hartelkanaal (200 $m^3 s^{-1}$). This flow of fresh water via the port of Rotterdam area can be maintained between a Qbr of 1700 $m^3 s^{-1}$ and 4500 $m^3 s^{-1}$. Below 1700 $m^3 s^{-1}$ the salinity gradient moves land inward, while above 4500 $m^3 s^{-1}$ it moves seaward. At a Qbr of approximately 1100 $m^3 s^{-1}$ the Haringvliet sluices are closed completely and both Meuse and Rhine water flows in the sea at Hoek van Holland. The isohalines of the bottom water in the area under average and low river discharge (1000 $m^3 s^{-1}$)

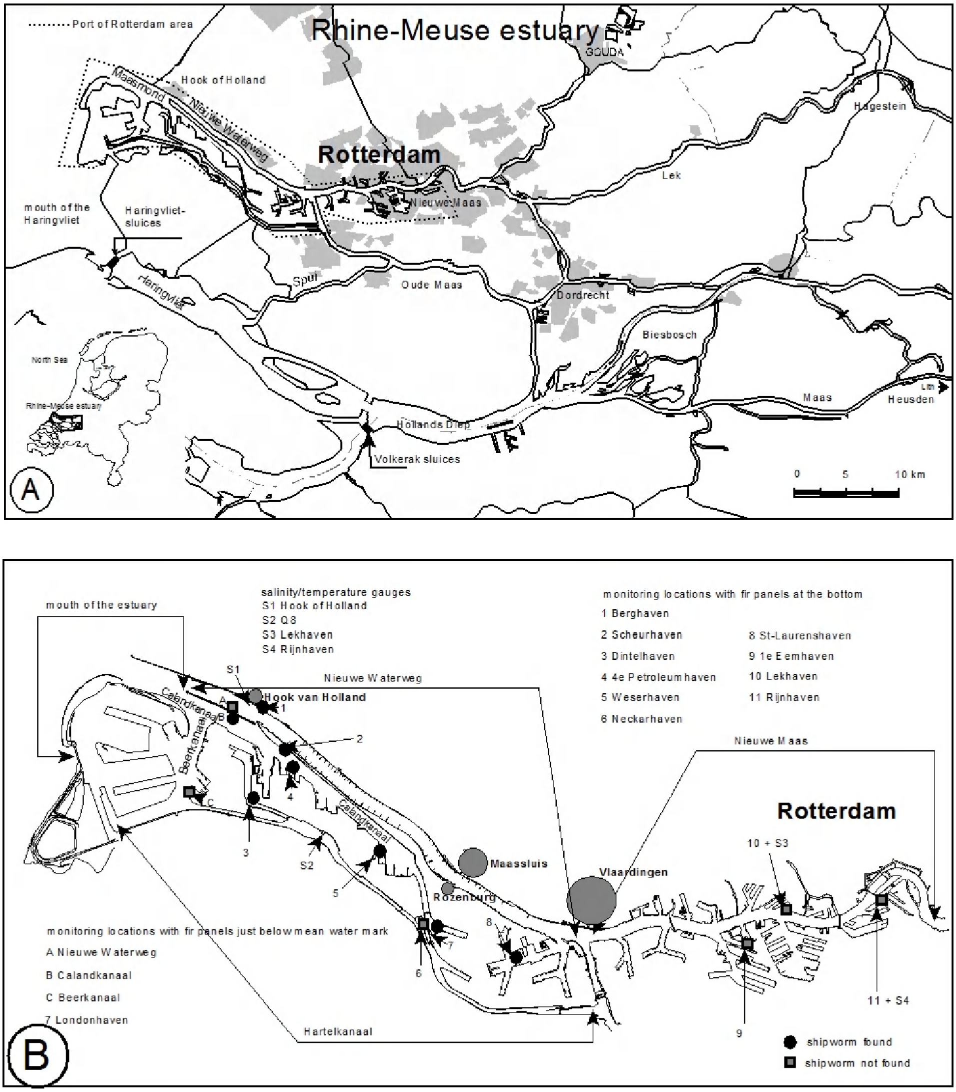

Figure 1 A. The port of Rotterdam in the Rhine-Meuse estuary. B. Monitoring locations and salinity/temperature gauges in the Port of Rotterdam area and the presence (black dots) and the absence (grey squares) of the shipworm in the monitoring panels during the period 2004 - 2008.

were calculated by the model RIJNAMO of Rijkswaterstaat (Bol and Kraak, 1998) (Fig. 2A, 2B).

The Rhine-Meuse estuary is microtidal with an average tidal range of 1.75 m at Hoek van Holland gradually decreases upstream till 1.10 m at Hagestein on the Lek and 0.25 m at Heusden on the Meuse. At springtide the tidal cycle at Hoek van Holland exhibits approximately a 4-h period of flood, a 4-h period of ebb and a 4.5-h low-water period.

Salinity, oxygen and temperature measurements

Salinity and temperature were recorded every 10 min at four stations (Fig. 1B). The water depth given is in metres related to NAP (Normaal Amsterdams Peil or Amsterdam Ordnance Datum). NAP is a vertical datum in use in a large part of Western Europe and is close to the mean sea level at the Dutch coast. In 2003 salinity depth files with 1-m intervals from surface to bottom (i.e., sea floor) were obtained with a WTW-conductivity meter (Cond 3301) with a TetraCon®325 conductivity and temperature sensor.

To determine if oxygen was a limiting factor for the shipworm from October 2004 till November 2005 monthly samples of the bottom water at eight locations were taken and the concentration was measured with a HQ20 Hach Portable LDOTM dissolved oxygen/pH meter.

Sampling

The distribution of the shipworm by its settlement was investigated by placing fir (monitoring) panels at the bottom or just below the mean water mark at different locations (Fig. 1B) along the salinity gradient. The vertical panels measured 10 x 20 x 2 cm. Five locations were in use from 2004 to 2008, seven from 2004 to 2007 and six from 2005 to 2008. In 2006 the number of locations was extended to 16, but at three locations the fir panels disappeared and were not used in the analysis, leading to 13 locations from which information about the shipworm could be obtained (Table 1).

The settlement season was studied by retrieving fir panels monthly in 2004 from August to December and in 2005 from July to December. A set of oak panels of 10 x 20 x 2 cm was placed next to the fir panels in 2006 in the Scheurhaven to compare settlement and growth in both types of wood (Table 1).

The settlement height in relation to the distance to the bottom (sea floor) was studied in 2006 by placing a construction (Fig. 3) with fir panels with a distance from the bottom of 0, 25, 50, 75 and 100 cm at the bottom of the Scheurhaven. Panels were retrieved in July, October and December 2006. In 2007 this was repeated at the same station but with four beams, with a length of 540 cm, a

Table 1 Monitoring locations in the period 2004 – 2008 with the dates of exposure (exp) and retrieval (retr) and the number of panels exposed and retrieved. 12* = oak panels, dis = disappeared.

monitoring year	2004						2005							2006				2007				2008	
location\dates	exp	retr	retr	retr	retr	retr	exp	retr	retr	retr	retr	retr	retr	exp	retr	retr	retr	exp	retr	retr	retr	exp	retr
01 Berghaven -5 m NAP	8-6	20-8	19-9	4-11	26-11	10-12	10-3	5-7	6-8	3-9	3-10	2-11	11-12	3-4	27-7	3-10	10-12	2-4	24-7	10-10	4-1-08	16-4	21-1-09
02 Scheurhaven -5 m NAP	8-6	20-8	19-9	4-11	26-11	10-12	9-3	8-7	9-8	5-9	5-10	3-11	16-12	4-4	27-7	3-10	10-12	2-4	24-7	10-10	4-1-08	16-4	21-1-09
03 Dintelhaven -4 m NAP							9-3	8-7	9-8	5-9	5-10	3-11	16-12	6-4	27-7	3-10	10-12	2-4	24-7	10-10	4-1-08	16-4	21-1-09
04 4e Petroleumhaven -3 m NAP														6-4			10-12						
05 Weserhaven -3 m NAP														4-4			10-12						
06 Neckarhaven -4 m NAP							9-3	8-7	9-8	5-9	5-10	3-11	16-12	5-4	27-7	3-10	10-12	2-4	24-7	10-10	4-1-08	16-4	21-1-09
07 Londonhaven -1.5 m NAP							9-3	8-7	9-8	5-9	5-10	3-11	16-12	5-4	27-7	3-10	10-12	2-4	24-7	10-10	4-1-08		
08 St-Laurenshaven -9 m NAP	8-6	20-8	19-9	4-11	26-11	10-12	9-3	8-7	9-8	5-9	5-10	3-11	16-12	4-4	27-7	3-10	10-12	2-4	24-7	10-10	4-1-08	16-4	21-1-09
09 1e Eemhaven -3 m NAP	8-6				26-11	10-12											10-12						
10 Lekhaven -9.5 m NAP	8-6	20-8	19-9	4-11	26-11	10-12	10-3	5-7	6-8	3-9	3-10	2-11	11-12	3-4			10-12	2-4	24-7	10-10	4-1-08	16-4	21-1-09
11 Rijnhaven -8.0 m NAP	8-6	20-8	19-9	4-11	26-11	10-12								3-4			10-12	2-4			dis		
A Nieuwe Waterweg mouth -0.8 m NAP														7-4			10-12						
B Calandkanaal mouth -0.8 m NAP														7-4			10-12						
C Beerkanaal -0.8 m NAP														6-4			10-12						
location\number of panels	exp	retr	retr	retr	retr	retr	exp	retr	retr	retr	retr	retr	retr	exp	retr	retr	retr	exp	retr	retr	retr	exp	retr
01 Berghaven -5 m NAP	6	1	1	1	1	1	16	2	2	2	2	2	2	18	6	6	6	12			12	12	12
02 Scheurhaven -5 m NAP	6	1	1	1	1	1	16	2	2	2	2	2	2	18	6	6	6	36+12*	12	12	12	12	12
04 Dintelhaven -4 m NAP							16	2	2	2	2	2	2	18	6	6	6	12			12	12	12
05 4e Petroleumhaven -3 m NAP														12			12						
06 Weserhaven -3 m NAP														12			12						
07 Neckarhaven -4 m NAP							16	2	2	2	2	2	2	18	6	6	6	36	12	12	12	12	12
08 Londonhaven -1.5 m NAP							16	2	2	2	2	2	2	18	6	6	6	12			12		
09 St-Laurenshaven -9 m NAP	6	1	1	1	1	1	16	2	2	2	2	2	2	18	6	6	6	36	12	12	12	12	12
10 1e Eemhaven -3 m NAP	6				1	1											4						
11 Lekhaven -9.5 m NAP	6	1	1	1	1	1	16	2	2	2	2	2	2	18	6	6	6	36	12	12	12	12	12
12 Rijnhaven -8.0 m NAP	6	1	1	1	1	1								18	6	6	6	12			dis		
A Nieuwe Waterweg mouth -0.8 m NAP														6			2						
B Calandkanaal mouth -0.8 m NAP														6			6						
C Beerkanaal -0.8 m NAP														12			12						

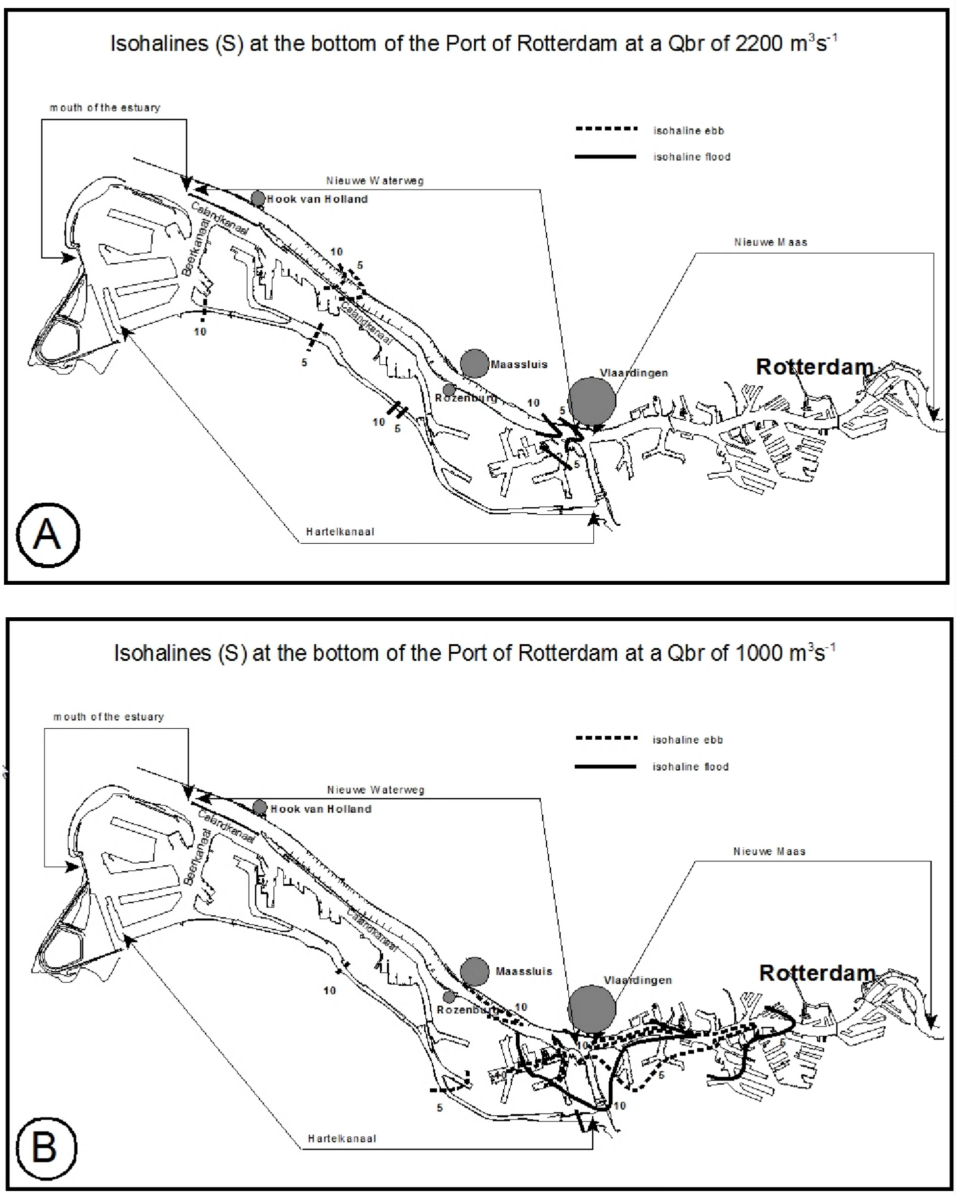

Figure 2 A. The isohalines 5 and 10 at ebb and flood in the port of Rotterdam area at an average discharge of the Rhine at the Dutch-German border (Qbr) of 2200 $m^3 s^{-1}$. B. The isohalines 5 and 10 at ebb and flood in the Port of Rotterdam area at a discharge of the Rhine at the Dutch-German border (Qbr) of 1000 $m^3 s^{-1}$.

width of 10 cm and a thickness of 5 cm, covering the water column and intertidal zone. The beams were retrieved in January 2008 and sawed into pieces 20 cm long.

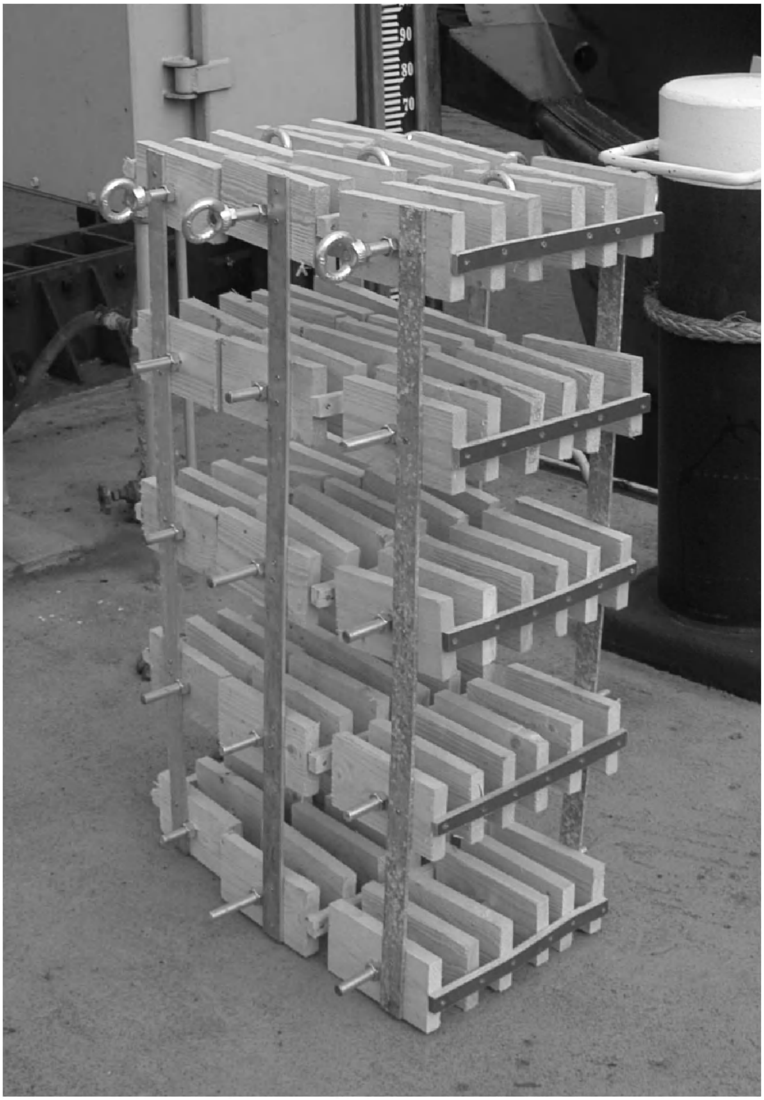

Figure 3 The construction with the fir panels to study the settlement height (0, 25, 50, 75 and 100 cm) in relation to the distance to the bottom placed in the Scheurhaven in 2006.

Analysis

From the data of the measuring stations the daily minimum and maximum salinity was taken for a yearly overview of the salinity fluctuations in relation to the discharge of the river Rhine at the Dutch German border (Lobith; Bimmen). The mean daily water temperature was calculated.

Shipworm individuals were identified to the species level using the key in Hayward and Ryland (1995).

All panels and beam pieces were freed of fouling, placed in plastic bags, deep frozen if necessary and digitally radio graphed by Applus RTD Benelux. On screen the body length (length of the boreholes) and shell size was measured for each individual shipworm. Also, for the years 2006, 2007 and 2008 the average diameter of the boreholes was estimated, based on measurements of the diameter at 0.25, 0.50 and 0.75 of the length in order to calculate the loss of wood. Growth was calculated by comparing the average length of the shipworms in October with those in December in 2006 and 2007.

Statistical analysis was carried out with the aid of the computer program SPSS for Windows Release 11.0.0. The Levene's test for equality of variance and the independent t-test were applied for comparing the average length of the shipworms in 2006 and 2007. To compare the average length of the shipworms at the different monitoring locations and at different distances from the bottom the Levene's test for equality of variance and analysis of variance (One way Anova) were conducted. For testing the relation of settlement of shipworms and the distance to the bottom, the relation of body length and shell size, and the relation of body length and average boring tube diameter the curve fit and correlation coefficient were calculated and analysis of variance applied.

Results

Hydrography

The water temperature fluctuated between 3°C in winter and 25°C in summer in the Lekhaven and between 4 and 22°C at Hoek van Holland during 2004-2008. From April to November the water temperature was above 10°C, and it was above 15°C from June until mid-October. In spring and summer the river water temperature was higher than that of seawater, in autumn they were about the same, while in winter seawater temperature was higher. Over the period 2004-2008, out of 1814 days, for 1697 days the water temperature was high enough for the shipworm to exhibit boring activity. Spawning could have taken place in the period mid-April until mid-November.

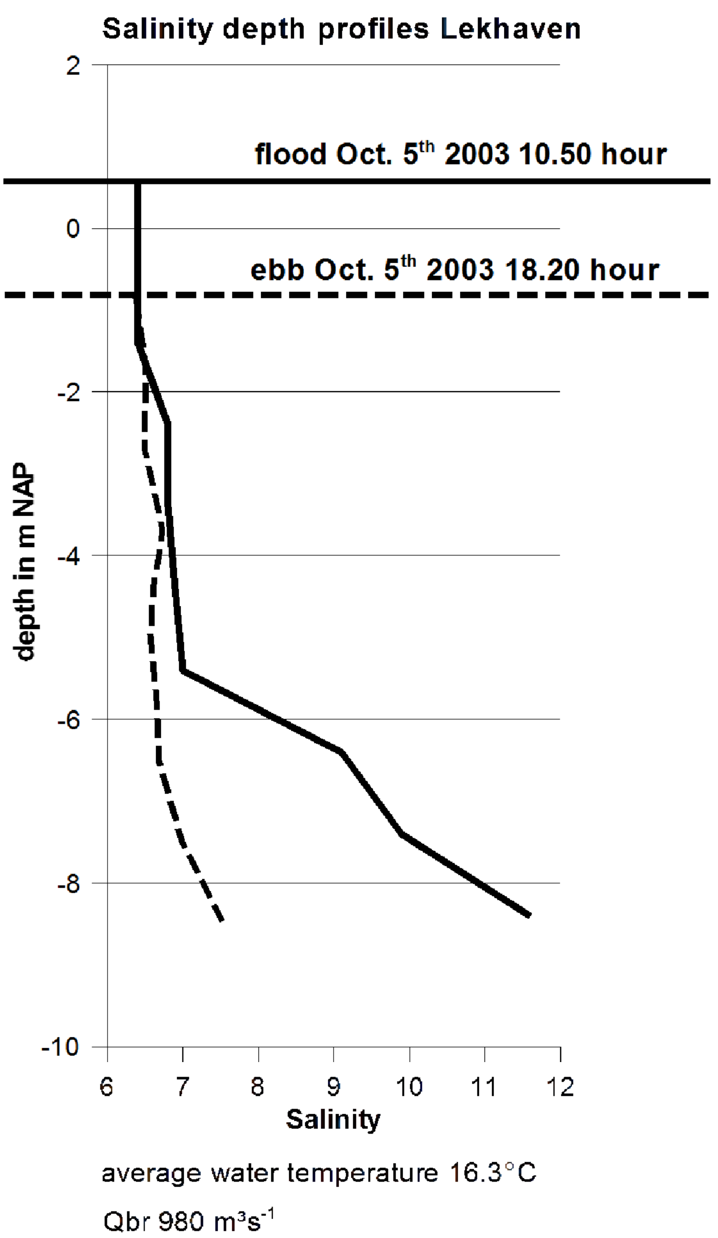

Figure 4 Salinity depth profiles of the Lekhaven in the eastern part of the port of Rotterdam area on Oct. 5, 2003.

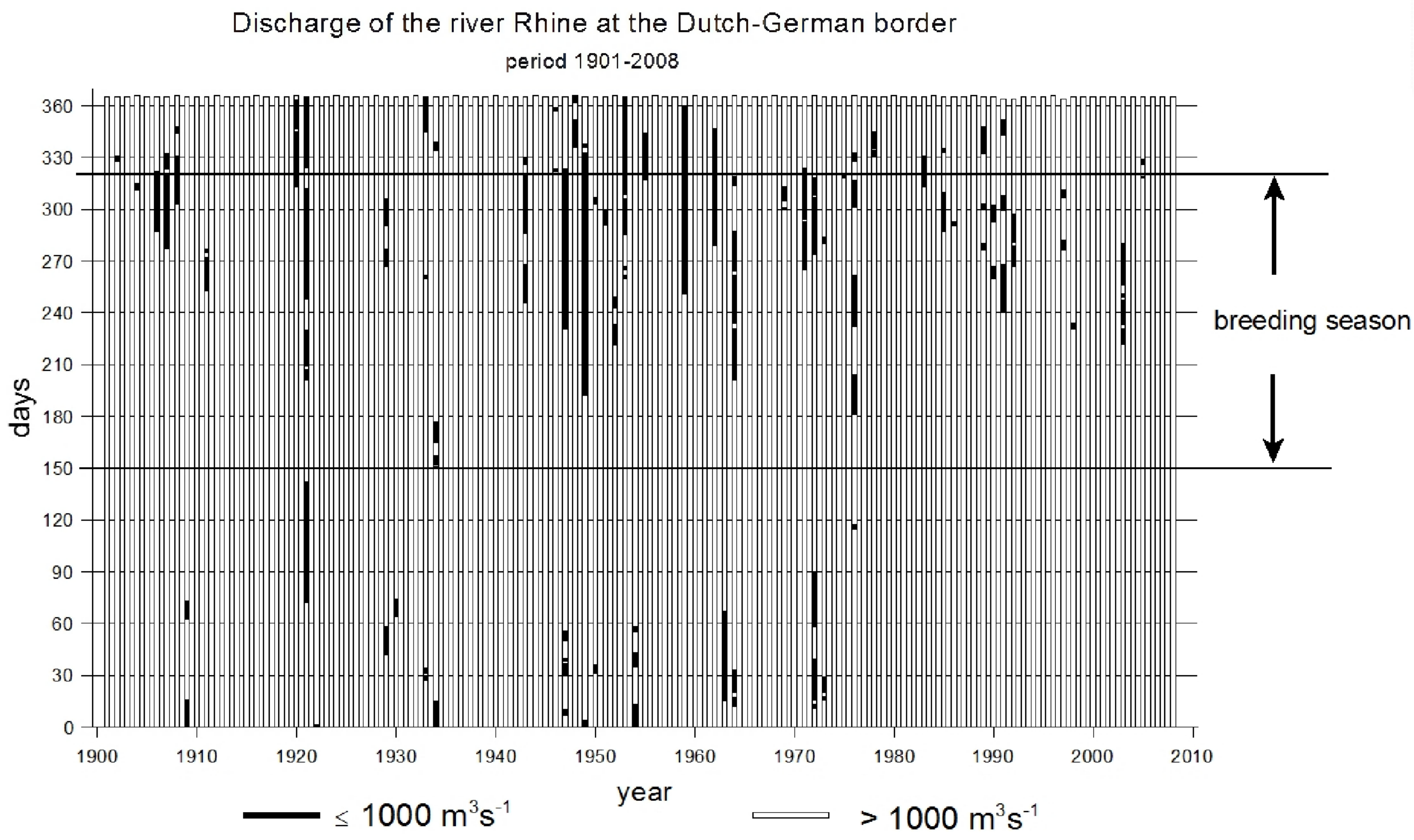

Figure 5 Discharges of the river Rhine at the Dutch-German border below and above 1000 $m^3 s^{-1}$ during the period 1901 and 2008 and their occurrence in the breeding season of the shipworm.

On Aug. 10, 2003 the Qbr (discharge of the river Rhine at the Dutch-German border) reached, approximately, the critical value of 1000 m^3 s^{-1}, with the consequence that in some eastern parts of the port of Rotterdam area the salinity reached values of over 10 and this situation lasted until Oct. 7, a period of almost two months.
Two salinity depth profiles were measured at flood and ebb on October 5, 2003 at a Qbr of 980 m^3 s^{-1} in the Lekhaven. The profile taken at flood demonstrates the stratification under conditions of high salt intrusion in this part of the port of Rotterdam area (Fig. 4). At these low discharges the conditions become favourable for the shipworm to settle.
In the period 2003-2008 in the eastern part of the port of Rotterdam area, salinity changed at the bottom several times from fresh-oligohaline to meso-haline conditions, but as the river discharge after 2003 until 2008 reached values below 1000 m^3 s^{-1} only for a few days, no suitable conditions for the shipworm occurred for settlement and growth. Long periods of discharges below 1000 m^3 s^{-1} occur (Fig. 5). In the last decade, in 15 separate years, there were periods of 30 days or longer then discharges below 1000 m^3 s^{-1} were recorded during the breeding season of the shipworm. The longest uninterrupted period with this critical discharge was in 1949, which had a duration of 141 days, but before 1970 the hydrology of the port of Rotterdam area differed greatly from the present situation because of the absence of the Haringvliet sluices and weirs in the Lek and Nederrijn.
In the western part of the port of Rotterdam area the waterways Hartelkanaal and Nieuwe Waterweg and adjacent harbours exhibited strong daily changes in salinity due to the tide and the river discharges. The large harbours Beer- en Calandkanaal where polyhaline throughout 2003-2008.
Oxygen levels measured between October 2004 and October 2005 at the monitoring locations were high and fluctuated between 80 and 120% saturation, with a median value of 98%. On only one occasion was an oxygen saturation level as low as 69% measured.

Distribution

The settlement of larvae as an indication of the distribution of the shipworm on the monitoring panels varied from year to year (Table 2).
The shipworm settled in the fir panels in the Scheurhaven throughout the monitoring period and in three individual years in those in the Berghaven. Only in 2006 were shipworms found in panels at other locations that were monitored from 2004 or 2005 until 2008, none of them, however, were in the eastern part of the port of Rotterdam area. In 2006 shipworms were also encountered in the

panels of the extra locations in the Calandkanaal, but not in those of the Beerkanaal (Fig. 1B).

Wooden piles made of Basralokus (*Dicorynia paraensis* Bentham) pulled out the polyhaline Calandkanaal contained many boreholes in the outer 5 cm. Inspection of fir piles from the harbours of Maassluis, Vlaardingen and the centre of Rotterdam did not show any damage caused by shipworms.

Examination of the shells of live animals in panels and beams and in empty burrows of the piles and driftwood from the Calandkanaal, showed that only one species, *T. navalis*, was involved.

Table 2 Number of shipworms that settled on 6 fir panels at the different monitoring locations in the Port of Rotterdam area during the period 2004 – 2008.
- = no shipworms found, blank = no panels at monitoring location.

Location\year	number of individuals per 6 fir panels				
	2004	2005	2006	2007	2008
01 Berghaven -5 m NAP	3.0	-	2.0	-	2.0
02 Scheurhaven -5 m NAP	24.0	9.0	74.0	40.0	3.0
03 Dintelhaven -4 m NAP		-	1.0	-	-
04 4e Petroleumhaven -3 m NAP			13.5		
05 Weserhaven -3 m NAP			23.5		
06 Neckarhaven -4 m NAP		-	-	-	-
07 Londonhaven -1.0 m NAP		-	8.0		
08 St-Laurenshaven -9 m NAP	-	-	14.0	-	-
09 1e Eemhaven -3 m NAP	-		-		
10 Lekhaven -9.5 m NAP	-	-	-	-	-
11 Rijnhaven -8.0 m NAP	-	-	-		
A Nieuwe Waterweg mouth -0.8 m NAP			-		
B Calandkanaal mouth -0.8 m NAP			19.0		
C Beerkanaal -0.8 m NAP			-		

Breeding season

Shipworms were never found in the panels before September. Small individuals with a body length of less than 50 mm were encountered in the panels from September to December, indicating a breeding season from August until the end of November.

Settlement in relation to the distance to the bottom

In both 2006 and 2007 the settlement of the shipworm was significant negatively correlated with the distance to the bottom (Fig. 6). Almost 75% of the shipworms were found in the first 60-cm and 80-cm water layer above the bottom in 2006 and 2007, respectively. In 2007, above 120 cm from the bottom shipworms were found only sporadically.

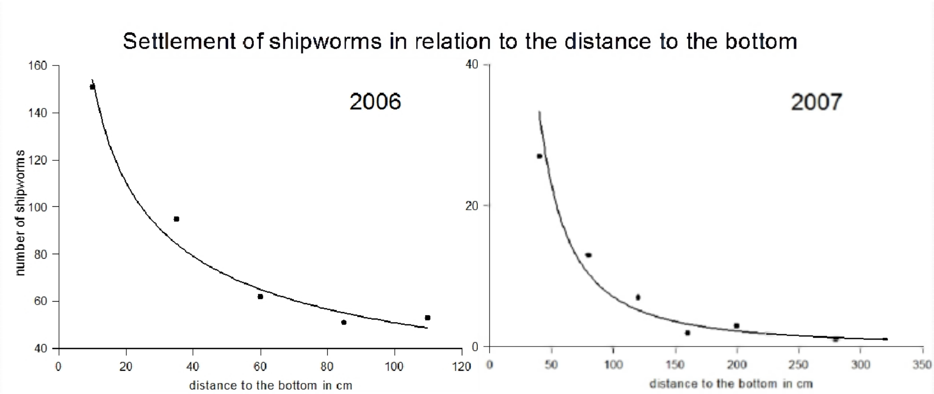

Figure 6 Settlement of shipworms in 2006 (left)($Y = 465X^{-0.48}$, $R^2 = 0.96$, $p < 0.003$) and 2007 (right) ($Y = 17028X^{-1.69}$, $R^2 = 0.94$, $p < 0.001$) in the Scheurhaven in relation to the distance to the bottom (sea floor).

Growth and wood loss

The number of shipworms found in the panels during 2006 and 2007 allowed calculation of body length frequency distribution, growth and caused wood loss. The body length frequency (Fig. 7) as a percentage of the total number of individuals in fir panels from the locations 2, 5, 7, 8 and B in the Calandkanaal (Fig. 1B), the polyhaline region of the port of Rotterdam area, shows that the majority of the individuals in 2006 belonged to higher body-length classes than in 2007. The average body length of the shipworms at the end of the growing season in 2006 (n=334, M=15.5 cm, SD=5.5 cm) was significantly greater ($t(427)=4.1$, $p<0.001$) than the average body length of the shipworms at the end of the growing season in 2007 (n=95, M=12.8 cm, SD=6.3 cm). The longest individuals in 2006 and 2007 measured 36.9 cm and 28.8 cm, respectively (Table 3).

Between Oct. 3 and Dec. 10, 2006, the average body length of the individuals from the Calandkanaal increased by 10.5 cm, from 5 cm to 15.5 cm, a growth of 0.15 cm day^{-1}. If the individuals in the body-length classes 0–5 cm and 5–10 cm are considered to have settled after Oct. 3, 2006, then the growth would have been 0.18 cm day^{-1}.

Individuals found in the St-Laurenshaven, a harbour with strong fluctuations in salinity, all belonged to the 0–5 cm body-length class on Oct. 3 and Dec. 10, 2006. Growth of these individuals between these two dates amounted to only 0.02 cm day^{-1}. Body lengths of the individuals on Dec. 10, 2006 at the bottom on the locations 2, 4, 5, 7 en B in the Calandkanaal differed significantly (one-way ANOVA, $F(4,170)=5.3$, $p<0.001$). Those of location 5 (Weserhaven) were

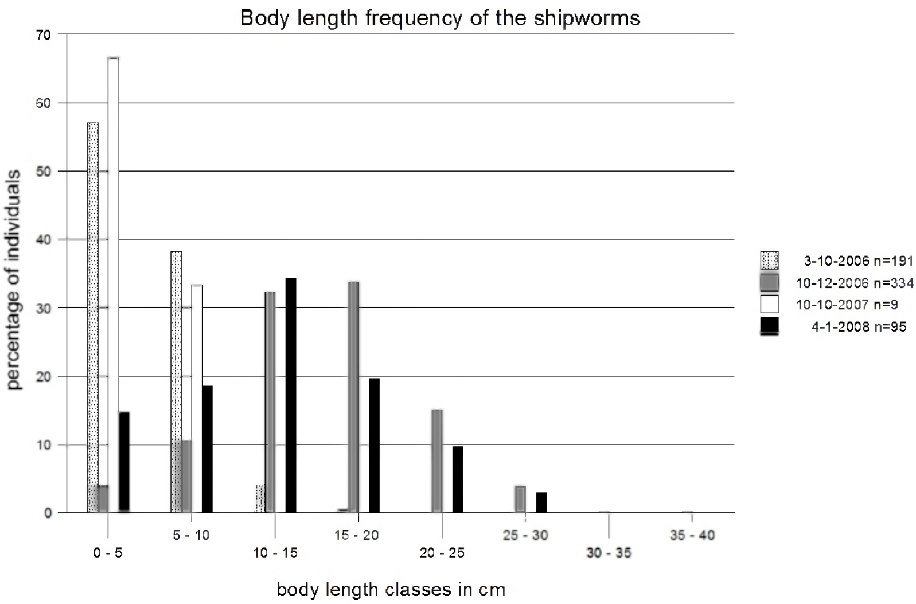

Figure 7 Body length frequency of the shipworms found in 2006 and 2007 in the fir panels as a percentage of the number of individuals. Data from all monitoring locations.

significantly longer than those of the locations 7 (Londonhaven) and B (Calandkanaal mouth). On the latter locations the panels felt dry during spring tide. Significant differences in body length in shipworms between the locations 2 (Scheurhaven), 4 (fourth Petroleumhaven) and the locations 7 (Londonhaven) and B (Calandkanaal mouth) were not seen.
In both 2006 and 2007 the body lengths of the individuals at the end of the growing season at different distance from the bottom over approximately the first metre differed significantly from one another (one-way ANOVA, $F(4, 232)=3.5$, $p<0.01$ and $F(4, 44)=2.8$, $p<0.05$) (Table 3). The largest shipworms were found closest to the bottom and around 1 m above the bottom. In both years a quadratic trend could be demonstrated between the distance from the bottom and the body lengths of the shipworms (one-way independent ANOVA, $F(1, 232)=8.3$, $p<0.01$ and $F(1, 44)=5.3$, $p<0.05$ for the years 2006 and 2007, respectively).
The individuals found in the oak wood panels at the bottom of the Scheurhaven ($n=7$, $M=7.0$ cm, $SD=2.9$ cm) on Dec. 10, 2006, were significantly shorter in body length ($t(43)=2.5$, $p<0.02$), than those found in the fir panels at the bottom of the Scheurhaven ($n=40$, $M=11.6$ cm, $SD=4.8$ cm) on the same date.

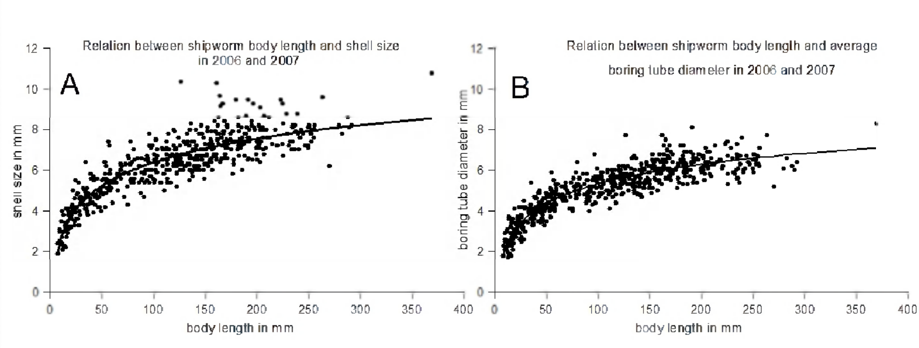

Figure 8 A. Relation between the shipworm body length and its shell size (Y = 1.69lnX – 1.38, R^2 = 0.78, p < 0.0001, N = 531), B. Relation between the shipworm body length and the average boring tube diameter in 2006 and 2007 (Y = 1.38lnX - 1.02, R^2 = 0.83, p < 0.001, N = 592). Data from all monitoring locations.

Shell length and body length of 531 individuals were measured in 2006 and 2007. A clear positive logarithmic correlation (R^2=0.78, p<0.0001) was found between the body length and size of the shell (Fig. 8A). The largest shell measured 10.8 mm. The boring tube changes from conical to cylindrical at a body length between 50 and 100 mm.

In 2006 and 2007 almost the same logarithmic relationship between the body length of the shipworms and the average tube diameter was found (Fig. 8B). In both cases there was a significant positive correlation (R^2=0.84, p<0.001 and R^2=0.76, p<0.001, respectively).

The wood loss by shipworms could be calculated by means of the average diameter of the boring tubes (Table 3). In 2006 most of the wood was lost within the panels on the bottom due to the higher shipworm infestation there than in the other panels. Within a period of 3 to 4 months 12.4 % of the fir wood was lost due to shipworm boring activity.

In 2007 the percentage wood loss was much lower, not only as a result of fewer shipworms within the panels but also because the individuals were smaller than in 2006 (Table 3). The amount of wood loss per individual shipworm in oak wood was less than half of that in fir (Table 3).

Discussion

The water temperatures measured at the mouth of the estuary indicate that during the monitoring period *T. navalis* could perform its boring activity almost year round, although it was reduced during winter. Taking 12°C as the lower limit

Table 3 Wood loss due to the shipworm activity in 2006 and 2007 and their length in fir and oak panels and in fir beams (*) in the Scheurhaven. std = standard deviation, med = median, min = minimum, max = maximum.

date	distance in cm to bottom	type of wood	volume of wood in cm^3	number of shipworms	length of shipworms in cm					volume of wood loss in cm^3	% wood loss	volume of wood disappeared in cm^3 per shipworm
					mean	std	med	min	max			
3-10-2006	0 - 10	fir	2400	77	5.0	2.5	4.6	1.0	10.4	65.4	2.7	0.85
3-10-2006	25 - 35	fir	2400	46	4.7	3.0	4.1	0.8	14.6	37.0	1.5	0.81
3-10-2006	50 - 60	fir	2400	21	4.2	1.6	3.8	1.7	8.0	14.2	0.6	0.67
3-10-2006	75 - 85	fir	2400	14	4.5	2.3	4.1	1.1	9.8	10.8	0.5	0.77
3-10-2006	100 - 110	fir	2400	21	5.9	3.8	5.4	1.0	17.2	22.3	0.9	1.06
10-12-2006	0 - 10	fir	2400	74	15.8	4.4	15.9	4.3	27.9	297.6	12.4	4.02
10-12-2006	25 - 35	fir	2400	49	16.0	6.5	15.3	2.0	36.9	236.5	9.9	4.83
10-12-2006	50 - 60	fir	2400	41	13.3	5.1	13.2	1.8	25.0	146.0	6.1	3.56
10-12-2006	75 - 85	fir	2400	37	13.4	4.8	13.8	2.4	23.5	143.0	6.0	3.87
10-12-2006	100 - 110	fir	2400	32	16.5	5.2	17.1	3.5	24.7	145.9	6.1	4.56
10-10-2007	0 - 10	fir	4800	9	4.0	2.1	3.4	1.3	7.6	5.1	0.1	0.57
4-1-2008	0 - 10	fir	4800	40	11.6	4.8	11.8	1.8	21.3	123.1	2.6	3.08
4-1-2008	0 - 10	oak	4800	7	7.0	2.9	5.6	4.7	12.6	9.9	0.2	1.42
4-1-2008	0 - 20	fir*	4000	8	18.9	6.7	19	10.3	28.8	42.7	1.1	5.34
4-1-2008	20 - 40	fir*	4000	19	10.6	5.9	9.8	2.2	22.6	53.9	1.3	2.84
4-1-2008	40 - 60	fir*	4000	5	12.0	6.3	12.3	2.1	18.2	19.8	0.5	3.96
4-1-2008	60 - 80	fir*	4000	8	11.6	6.9	12.0	2.5	23.5	25.8	0.6	3.22
4-1-2008	80 - 100	fir*	4000	5	15.0	6.2	15.3	9.1	22.5	21.8	0.5	4.36

for reproduction, the spawning season could start in April/May and end at the beginning of November, but as no individuals were found before September, it is more likely that reproduction started in July/August based on settlement time.
The settlement of *T. navalis* in the port of Rotterdam area decreased with increasing distance from the bottom (sea floor) in both test panels and test beams; this was found also by Scheltema and Truitt (1956) in test panels in Maryland coastal waters, U.S.A., and by Tuente et al. (2002), who counted bore holes in oak piles and fir pier posts in the harbours of Bremerhaven in Germany. This pattern of settling could be an advantage in estuaries where salinities are usually higher and more stable near the bottom.
The shipworms in the port of Rotterdam grew rapidly in 2006 and 2007 and achieved maximum body lengths of 38.9 cm and 29.0 cm, respectively. The higher average body length in 2006 related to more wood lost is very likely the result of the higher water temperatures in that year compared to 2007. Kristensen (1979) observed a maximum body length growth of 0.7 mm day^{-1} of

first-year animals in Denmark. In the present study the average body length growth in 2006 of 1.5 mm day^{-1} exceeded this more than twofold, and considering a growth period of 130 days, the longest animal found should be the result of an average body length growth rate of 3 mm day^{-1}.
A significant relationship between the shell size and body length of the shipworm was found. The curve of the logarithmic formula supports the findings of Mann and Gallagar (1985) that the shape of the boring tube is a truncated cone progressing to a cylinder. The formula can be used to estimate the body length of the animals and thus the wood consumption by measuring the shell size, but it should only be used when densities are too high to measure individual tube lengths.
Significantly less shipworm larvae settled on the oak panels and showed less growth after metamorphoses than those that had settled on fir panels. This may be related to the greater hardness of oak wood, which means that the animals need to spent more energy boring into oak than into fir. Within specialized epithelial cells of several members of the Teredinidae, associations of symbiotic cellulolytic nitrogen-fixing bacteria were found within the gills (Distel et al., 1991, 2002*,* Sipe et al., 2000). Popham and Dickson (1973) demonstrated bacterial associations in the gills of the shipworm *T. navalis,* indicating that this species may be able to feed solely on wood. Mann and Gallager (1985) found no significant growth enhancement in the presence of a phytoplankton supplement (in addition to wood). However it is not unlikely that individuals that bore into hardwood need to acquire extra nourishment by filtration for at least their basal metabolism. This is also the case in highly infested wood when there is no more space to bore into left.
In the port of Rotterdam *T. navalis* seems to have a vital population in the Caland- and Beerkanaal from which larvae are transported by the tidal currents via the Hartelkanaal and Nieuwe Waterweg where, as demonstrated for a few locations, they can settle and survive for a short period of time. Taking into account the high river discharges that occur with the low salinities they bring about, it is not possible that a viable *T. navalis* population could be built up other than in the polyhaline environment of the Caland- and Beerkanaal. The presence of *T. navalis* in panels in the St-Laurenshaven showed the ability of the larvae to travel upstream of at least 20 km.

Conclusions

The area of distribution in the port of Rotterdam of the shipworm *T. navalis* encompasses the polyhaline harbours Beer- and Calandkanaal. Under conditions of low river discharge the area of distribution can temporarily be

extended to some 20 km upstream via the Nieuwe Waterweg. Based on the water temperature in the period 2004-2008, the potential breeding season lies between April and November. Based on the settlement on fir panels, a breeding season between July and November is more likely for the port of Rotterdam area.
Considering the water temperature in the period 2004-2008 the shipworm could have performed its boring activity 94% of the time. This is almost year round. The historical river discharge changes make it plausible that the shipworm could settle for a short period of time in the eastern part of the port of Rotterdam area. The settlement of the shipworm in the port of Rotterdam area showed a clear negative correlation to its distance to the bottom.
Shipworms in the port of Rotterdam area grew with an average body-length growth rate of 1.5 mm day^{-1} in 2006 and caused a loss of 12.4% of the fir wood of panels at the bottom of the Scheurhaven in a period of approximately 4 months. Significantly less shipworm larvae managed to settle in oak wood than in fir wood. The growth of shipworm individuals in oak wood was significantly lower than in fir wood.
Although there is a strong statistical relation between the shell size and the body length of the shipworm, the shell size should only be used to calculate the length of an individual if not exceeding 5 to 6 mm. At high densities measurement of the shell sizes could be appropriate to calculate wood consumption in the first season after settlement. There is a significant relation between the length of the shipworm and its average boring tube diameter, but as the individuals grow longer this relation becomes weaker.
Lower river discharges leading to salinisation of the eastern part of the port of Rotterdam area create conditions favourable for the shipworm to settle and grow, with consequences for the condition of the piles upon which the quays are built.

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