Aquatic Invasions
Aquatic Invasions 2024 Volume 19, Issue 2: 169–190

Research Article

Matching field-based ranges in brackish water gradients with experimentally derived salinity tolerances of Conrad's false mussel (*Mytilopsis leucophaeata cochleata*) and zebra mussel (*Dreissena polymorpha*)

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Abstract

The invasive alien false mussels *Mytilopsis leucophaeata cochleata* and *Dreissena polymorpha* (Dreissenidae) have established populations in the North Sea canal in the Netherlands that connects the harbours of Amsterdam with the North Sea. The favourable and unfavourable salinity ranges of both species were earlier studied in long-term outdoor mesocosm experiments. Their occurrence in salinity gradients in estuaries or canals connecting seaways to freshwater harbours provides information on their salinity tolerance under field conditions. By the combination of laboratory experiments and field data using the same source population a high predictability can be expected for establishment of the gradients facilitated by constructions. The reliability of experimentally derived salinity-tolerance limits for both dreissenid species was tested using data on their distribution in a salinity gradient of the littoral zone along the North Sea canal. The mussels used for the survival experiments in mesocosms were also collected from this canal. Favourable salinity ranges for adult survival in the mesocosms were 0.2 – 17.5 for *M. leucophaeata cochleata* and 0.2 – 6.0 for *D. polymorpha*. Unfavourable salinities were outside these ranges and led to high and fast mortality of these species. *Mytilopsis leucophaeata cochleata* was present over nearly the whole length of the North Sea canal with the highest densities close to the sea sluices where also the highest salinities and water temperatures were measured. Their densities in the canal decreased gradually at larger distances from the sea. *Dreissena polymorpha* co-exists with *M. leucophaeata cochleata* at the east end of the canal with low salinity due to the influence of freshwater of the river Rhine. The occurrence of *D. polymorpha* was restricted to a salinity below 4 and *M. leucophaeata cochleata* only occurred at a salinity above 1.5 (maximum value measured in the canal 9.2). Shorter salinity gradients with lower salinity ranges provided additional information on the co-existence of both species. Co-existence was observed at a salinity range of 1.5–3.3 (own data), 1.0–3.5 (Van Couwelaar and Van Dijk 1989), both in the North Sea canal, and 0.2–2.8, in the

OPEN ACCESS

Academic editor: Demetrio Boltovskoy
Received: 30 October 2023
Accepted: 22 February 2024
Published: 13 May 2024

Citation: van der Gaag M, van der Velde G, Leuven RSEW (2024) Matching field-based ranges in brackish water gradients with experimentally derived salinity tolerances of Conrad's false mussel (*Mytilopsis leucophaeata cochleata*) and zebra mussel (*Dreissena polymorpha*). Aquatic Invasions 19(2): 169–190. https://doi.org/10.3391/ai.2024.19.2.124566

Canal through Voorne (Janssen and Janssen-Kruit 1967). These data correspond with studies of both species by Walton (1996) in the Hudson River (salinity range 0–3). Found salinity ranges in the North Sea canal for both species match with the tolerance results obtained by mesocosm experiments. A new invading dreissenid mussel *Dreissena rostriformis bugensis* and a mytilid *Ischadium recurvum* occur in the North Sea canal since 2006 and 2012, respectively. Competition between recent and earlier invaders is likely when salinity tolerances are similar. It has already been observed that *D. rostriformis bugensis* outcompetes *D. polymorpha* under freshwater conditions (Bij de Vaate et al. 2014; Matthews et al. 2014). *Ischadium recurvum* has the potential to colonize large parts of the canal and to be a strong competitor of *M. leucophaeata cochleata* (Goud et al. 2019). Since January 2022, the new 'Zeesluis IJmuiden' with the biggest locks in the world is in use, affecting the probability of population establishment of new introduced and invasive alien mussel species.

Key words: co-existence, dark false mussel, densities, distribution, Dreissenidae, North Sea canal, salinity, water temperature

Introduction

Bivalve species belonging to the Dreissenidae and Mytilidae are highly invasive and are famous as bioengineers. They colonize freshwater and brackish water bodies and coastal areas worldwide and transform ecosystems by their activities and high densities (Karatayev et al. 2002; Borthagaray and Carranza 2007; Sousa et al. 2009; Kelly et al. 2010; Van Leeuwen et al. 2010; Kennedy 2011) (Fig. 1). Although Mytilidae and Dreissenidae are not closely related with each other, they possess similar adaptations and life strategies due to evolutionary convergence. Their appearance shows at first glance a strong similarity, which is the reason that we call them all mussels. As they also occupy similar niches, e.g. by attachment with byssus threads to hard substrate, various species have the potential to outcompete each other or find a way of co-existence leading to sympatric populations. Differential tolerance to physicochemical conditions can prevent competition between various species leading to co-existence in sympatry.

The invasive freshwater zebra mussel *Dreissena polymorpha* (Pallas, 1771) originates from the Ponto-Caspian area. This species occurs nowadays widespread in Europe and North America (Van der Velde et al. 2010a, b; Matthews et al. 2014). Globally, *D. polymorpha* can potentially even spread further (Pollux et al. 2010). According to Van Benthem Jutting (1943) the oldest record in the Netherlands of *D. polymorpha*, under the name *Mytilus lineatus* Lamarck, was made by Waardenburg (1827) who found the species in fresh water on stones and shells in the Haarlemmermeer, in the rivers Rhine and Lee near Leiden. As the thesis of Waardenburg appeared in February 1827, *D. polymorpha* must have been already present there in 1826 or earlier. The species was probably introduced with the transport of timber from the Baltic area (Kerney and Morton 1970; Van der Velde et al. 2010a, b). *Dreissena polymorpha* is nowadays widespread in the Netherlands.

Mytilopsis leucophaeata (Conrad, 1831) is an invasive brackish water species originating from North America. The native distribution range of this species is the Atlantic coast of the United States of America and the Gulf of Mexico up to Brazil (Marelli and Gray 1983; Mackie and Claudi 2010; Kennedy 2011; Fernandes et al. 2018). Invasions of this species occurred in Europe, Asia Minor and South America (Souza et al. 2005; Fernandes et al. 2018; Lodeiros et al. 2019). In Europe its distribution is still expanding (Zhulidov et al. 2015) (Table 1).

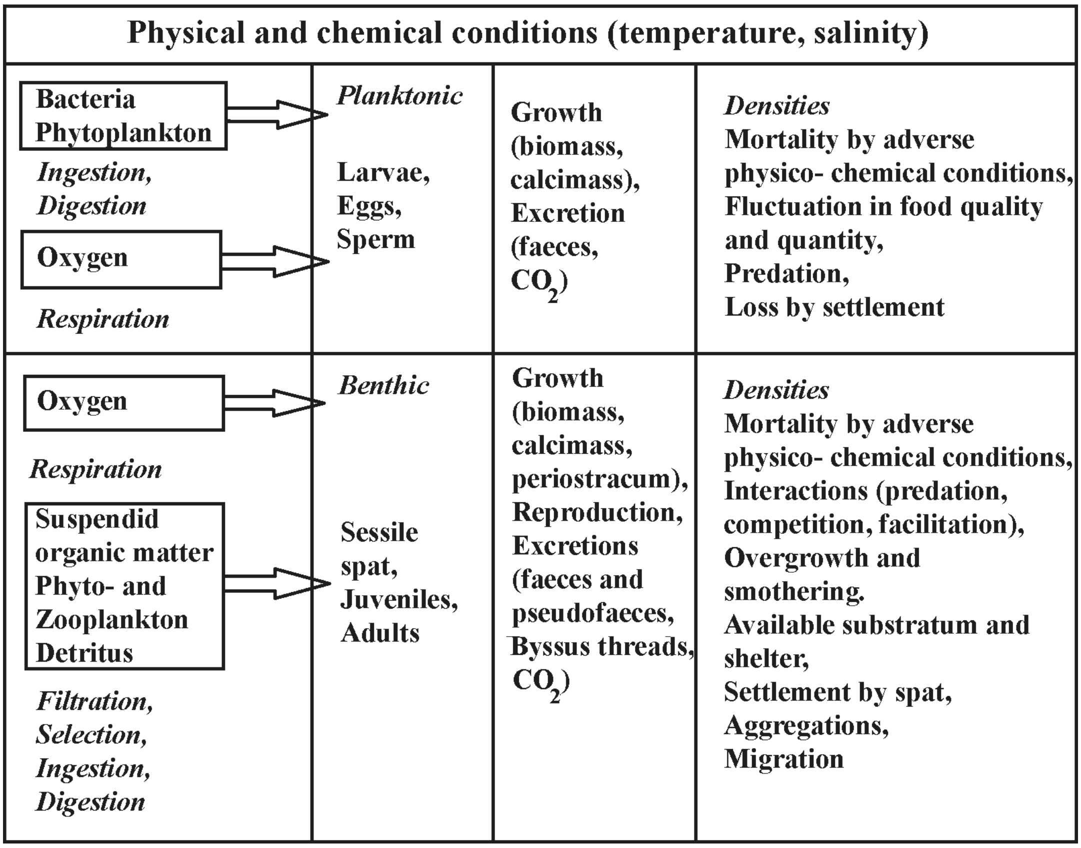

Figure 1. Scheme of environmental needs (rectangles) and activities (in italics) of mussels for the metabolism and growth (left column) during their life cycle (central columns), and factors influencing their densities (right column). (Adapted from Van der Gaag 2021).

Table 1. First records of *Mytilopsis leucophaeata cochleata* in countries of Europe and Asia Minor.

No.	Country	Water system/site	Year	Reference
1	Great Britain*	Wales, Tenby	1800?	Oliver (2015)
2	Belgium	Harbour of Antwerp	1835	Kickx in Nyst (1835)
3	France	Canal of Bergues	1872	De Guerne (1873)
4	The Netherlands	River Amstel, Amsterdam	1895	Maitland (1897)
5	Germany	Kiel Canal	1928	Boettger (1932)
6	Kaliningrad (Russia)	Baltiejsk (Pillau)	<1939	Steussloff (1939)
7	Lithuania	Klaipeda (Memel)	<1939	Jaeckel (1962)
8	Spain	Guadalquivir	1993	Escot et al. (2003)
9	Great Britain	Wales, Cardiff	1996	Oliver et al. (1998)
10	Finland	Loviisa archipelago	2003	Laine et al. (2006)
11	Ukraine	Dniester, liman	2004	Therriault et al. (2004)
12	Iran	Caspian Sea	2009	Heiler et al. (2010)
13	Poland	Gulf of Gdansk	2010	Dziubińska (2011)
14	Georgia	Black Sea	2010	Mumladze et al. (2019)
15	Sweden	Bay of Asphällafjärden	2011	Florin et al. (2013)
16	Russia	Caspian Sea	2014	Zhulidov et al. (2018)
17	Italy	Lagune of Venice**	2018	Zulian and Quaggiotto (2020)

*Museum collection;
** Earlier recorded in Italy at the beach of Cervia (Ravenna) as *Mytilopsis* spec. (Camerani 2009).

The first record of Conrad's false mussel *Mytilopsis leucophaeata cochleata* (Kickx in Nyst, 1835) (Dreissenidae) in the Netherlands was in the River Amstel in Amsterdam by R.T. Maitland in 1895 (Table 1). Maitland found this false mussel species on floating wooden piles (Secretaris Nederlandsche Dierkundige Vereeniging 1897). The species was identified as *Dreissena cochleata*.

The massive occurrence of dreissenid mussels in the Netherlands, a sedimentary area with soft substrate, is highly facilitated by the use of imported stones instead of wood as protection against bank erosion of the large water bodies such as rivers and canals since the arrival of the shipworm centuries ago (Paalvast and Van der Velde 2014). Differential tolerance to physico-chemical conditions can prevent competition between various species leading to co-existence in sympatry.

Salinity tolerance

The benthic mussel stages can be dispersed over long distances, while attached to ship hulls or floating substrata. Alternatively, larvae can be transported by water currents and in the ballast and bilge water of ships and vessels. To gain insight into dispersal potential and habitat suitability, survival of the benthic stages of two invasive dreissenid species (chosen based on their occurrence in salinity gradients) were tested for their tolerance to salinity. They were exposed to various salinities in outdoor mesocosms during three long-term experiments (Van der Gaag et al. 2016, 2017, 2018). Mussel survival was studied without prior acclimation, reflecting conditions they experienced when they are attached to ship hulls while travelling along a salinity gradient from fresh or brackish water to seawater, or vice versa. Initially, mussels react to salinity shock by temporarily closing their valves, suspending ventilation and feeding. This cannot be maintained for long periods and adaptation to higher salinity must eventually occur. In our tests, bivalve survival was monitored till the last specimen of a test cohort died. The survival periods were compared with the duration of actual ship voyages to estimate the real-world survival potentials of species dependent of salinity changes, travel distances and durations. Salinity shocks during the trip will be survived within the favourable salinity range but these species tolerate only for a few weeks the unfavourable salinity range. Variability in salinity of dispersal corridors may function as a barrier for the spread of species. At faster and more frequent shipping in the future, salinity can become less important as a dispersal barrier (Van der Gaag et al. 2016).

Genetics

Genetic information should be considered with respect to environmental tolerances such as salinity. Recently, it became clear that with respect to the COI gene of the invasive populations of *M. leucophaeata* in Europe, only one haplotype was involved. This haplotype is the same for the populations along the temperate east Atlantic coast of North America (Heiler et al. 2010; Fernandes et al. 2018, 2022). This relatively cold-tolerant lineage may be presenting a distinct species that originated in the mid-eastern or north-eastern USA and deviating because of past glaciations or the formation of the Labrador Current. This haplotype has colonised Eurasia via harbours by the shipping trade, which function as the hubs for further dispersal (Fernandes et al. 2018). The haplotype can be considered a subspecies or a species separate from *M. leucophaeata* for which in both cases the name *cochleata* is available as described by Kickx in Nyst (1835). So, we established the salinity-temperature tolerance of this (sub) species.

Populations of *D. polymorpha* in the Netherlands resembled genetically most those of invasive populations in other Eurasian countries such as Poland, Spain, and Russia (Volga River). Its sister group consists of populations from the Danube River, Hudson River, and the Erie Canal (Stepien et al. 2014).

Salinity limits and gradients

Mytilopsis leucophaeata cochleata and *D. polymorpha* show a different occurrence with respect to salinity. To understand and predict their colonization, dispersal, population development and survival, it is important to know their salinity tolerances. To get information about their salinity limits in the field in relation to other environmental factors several approaches can be used varying from short to long-term observations and measurements in the field, transplants in cages and settlement plates at various locations. To get a better understanding controlled outdoor and indoor mesocosms and aquarium experiments were carried out at varying combinations of conditions (Van der Gaag et al. 2016 and literature therein).

Data on species occurrence in salinity gradients in estuaries or canals connecting seaways to freshwater harbours can also provide valuable information on their salinity tolerance (Wolff 1969; Strayer and Smith 1993). Therefore, the distribution of two invasive dreissenids (*M. leucophaeata cochleata* and *D. polymorpha*) has been studied in a salinity gradient within the North Sea canal (Noordzeekanaal, the Netherlands).

The present study aims to test the reliability of the experimentally derived salinity-tolerance limits for these species (Van der Gaag et al. 2016), using available data on their distribution in the salinity gradients of the North Sea canal and elsewhere in the Netherlands to get insight in the environmental conditions for co-existence and sympatry, niche segregation and invasiveness of these mussels and to predict their occurrence (Van der Velde et al. 1998).

Materials and methods

Study area

The distribution related to salinity of *M. leucophaeata cochleata* and *D. polymorpha* was studied in the North Sea canal (Province of North-Holland) in the Netherlands. This canal connects the Amsterdam harbours with the North Sea (Figs 2, 3).

The North Sea canal opened in 1876 for shipping after 11 years of implementation. The construction of this waterway started with 7 km digging through the coastal dunes near Velsen. At the east end the Oranjesluizen (Oranje sluices) were built in 1872 and 17 km of dykes constructed in the lakes 'Wyker meer' and 'IJ meer'. This resulted in several land reclaims and a canal with a depth of 7.5 m and a bottom width of 27 m (Van Haaren and Tempelman 2006). After several enlarging and deepening works, the North Sea canal is today 15–18 m deep and 170 m wide (Zindler et al. 2004). The distance along the canal from the sluices at IJmuiden to the city of Amsterdam is indicated as kilometres (km). The 21 km western part of the canal (km 0–21) is called the North Sea canal and the 7 km eastern part (km 21–28) is the river IJ. The IJ in Amsterdam is 10–12 m deep and about 100 m wide (Van Haaren and Tempelman 2006). The banks along the canal mainly consist of Belgian and German rock armour, sheet piles (harbours) and reed beds (some side canals).

Figure 2. Map of the Netherlands showing areas and locations (sea areas, main lakes, rivers (R.), canals and harbours) mentioned in the text.

The main function of the canal is transport by shipping from the harbours of Amsterdam to the North Sea and vice versa. Large seagoing ships can use all harbours along the canal up to the Mercurius harbour that is located at 21.5 km from the sea and 3 km from the city centre of Amsterdam. In the canal yearly 45,000 ship movements were recorded (Rijkswaterstaat 2023 https://www.rijkswaterstaat.nl/water/waterbeheer/bescherming-tegen-het-water/waterkeringen/dammen-sluizen-en-stuwen/sluizencomplex-ijmuiden#feiten-en-cijfers). Other functions of the canal are the discharge of water and sediment and use of cooling water by power stations and industries. The yearly water discharge through the sluices is 4.6 billion m^3 (Rijkswaterstaat 2023 https://www.rijkswaterstaat.nl/water/waterbeheer/bescherming-tegen-het-water/waterkeringen/dammen-sluizen-en-stuwen/sluizencomplex-ijmuiden#feiten-en-cijfers).

The sampling sites of *M. leucophaeata cochleata* and *D. polymorpha* in the North Sea canal, the river IJ and the harbour of IJmuiden are situated in the littoral zones along the main channel of the canal (Fig. 3, Table 2). Sampling sites 1 and 2 are situated

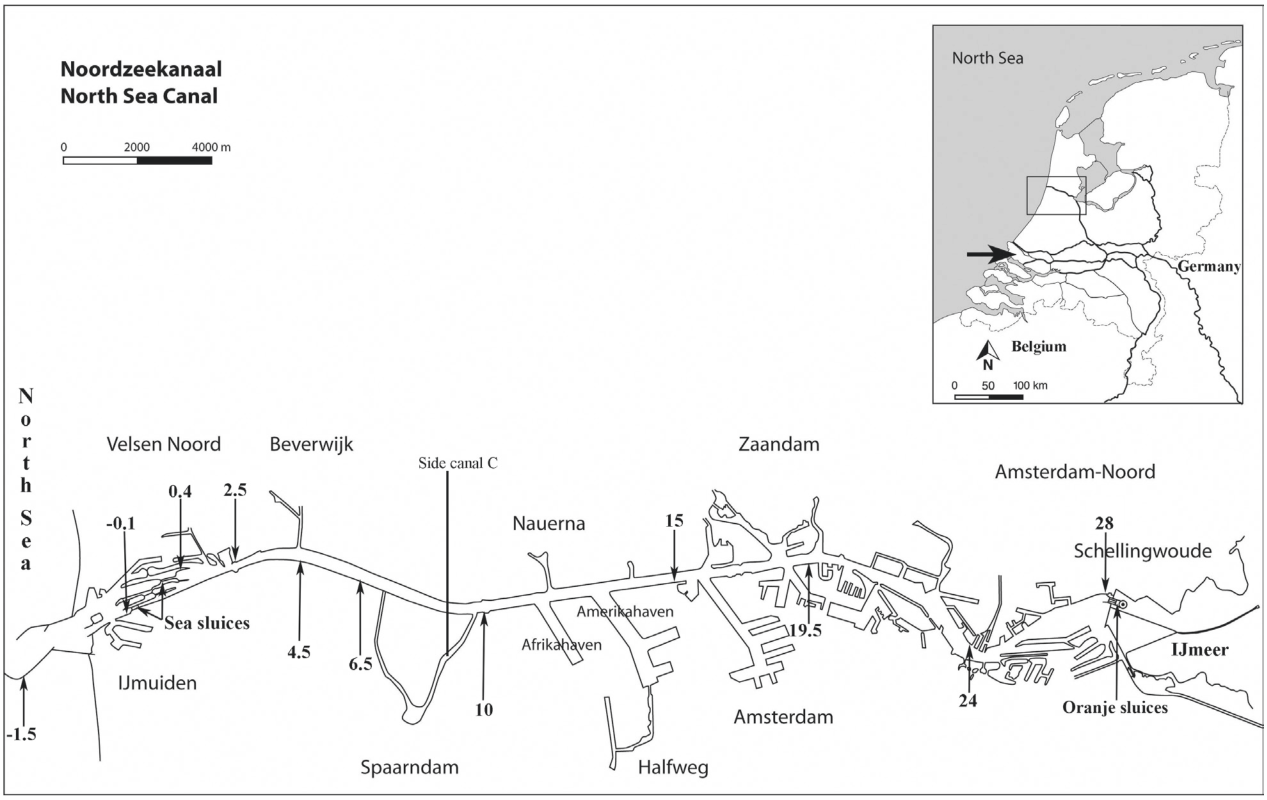

Figure 3. Sampling sites in the North Sea canal between the sea sluices in IJmuiden and the IJmeer, indicated by arrows with km. The square in the inserted figure indicates the geographical location of the North Sea canal area and the black arrow points the location of the canal through Voorne in the Netherlands.

outside the sluices (seawater) and, sampling sites 10 and 11 are in the IJ (Amsterdam). All the other sampling sites are situated along the borders of the North Sea canal.

Hydrology and salinity

The harbour of IJmuiden is located West of the sea sluices, where seawater (normally with a salinity of 30–35) is mixed with brackish water from the canal resulting in a salinity of 17 measured at low tide. The freshwater lake IJmeer is situated east of the Oranje sluices (Fig. 3). The North Sea canal receives freshwater from the River Rhine through the Amsterdam-Rhine canal. The surface water of the North Sea canal is clearly a mixture of seawater from the North Sea and discharged freshwater originating from the River Rhine and surrounding polder areas.

The North Sea canal is a water system with salt stratification. When ships pass the sluices, seawater penetrates the canal. This results in a salt wedge, which moves over the bottom in an eastern direction. The water with a lower salinity (brackish water) and lower density flows over the salt wedge in the direction of the sea. The salt wedge reaches until the threshold of the emergency barrier separating the Amsterdam-Rijnkanaal from Het IJ/North Sea canal. Both water layers poorly mix so that a salt jump develops at a certain depth.

By maintaining a minimal flow rate of 10 $m^3.s^{-1}$ in the Amsterdam-Rijnkanaal the salt wedge of the Amsterdam-Rijnkanaal is banned. The result of the combination of a salt wedge flowing to the east and the brackish upper layer flowing to the west is a salt gradient in horizontal as well as vertical direction. The mean residence time of the salt wedge is 40 days and for the freshwater layer 20 days. The flow rate is < 0.2 $m.s^{-1}$

Table 2. Overview of data for the North Sea canal (own data, data Van Couwelaar and Van Dijk 1989) and data canal through Voorne (Janssen and Janssen-Kruit 1967. All data : x = present, xx = numerous, *M.l.* = *Mytilopsis leucophaeata cochleata*, *D.p.* = *Dreissena polymorpha*, *M.e.* = *Mytilus edulis*, Temp. = water temperature. Own data and data Couwelaar and Van Dijk : number per square metre.

North Sea canal							
Own data (collected October 1989)							
Distance from sea	*M.l.*	*D.p.*	*M.e.*	*M.l./D.p.*	Temp.°C	Salinity	
Km -1.5	0	0	xx		16.0	16.2	
Km -0.1	0	0	xx		17.4	13.0	
Km 0.4	16800	0	0		18.9	8.0	
Km 2.5	14600	0	0		18.8	7.9	
Km 4.5	2800	0	0		15.5	7.5	
Km 6.5	8700	0	0		17.0	6.5	
Km 10	11000	0	0		15.2	5.1	
Km 15	8600	0	0		17.2	4.3	
Km19.5	5700	50	0	114	15.6	3.3	
Km 24	9200	2800	0	3.29	15.6	3.0	
Km 28	0	xx	0		15.1	1.7	
Data Van Couwelaar & Van Dijk (collected September 1988)							
Km 5	1462	0			17	4.0	
Km 7.5	1406	20		70.3	16	3.5	
Km 13	811	23		35.5	17	3.0	
Km 18.5	1740	1480		1.2	19	2.7	
Km 22	283	998		0.28	16	1.8	
Km 25	578	1277		0.45	17	1.0	
Km 28	11	945		0.01	17	2.5	
Canal through Voorne							
Data Janssen & Janssen-Kruit (collected September 1965)							
Distance from Brielse Maas	*M.l.*	*D.p.*	*M.e.*	*M.l./D.p.*	Salinity high	Salinity Low	Salinity Mean
Km -0	0	xx			0.5	0.2	0.4
Km 0	2	x			0.9	0.2	0.4
Km 1	4	x			1.1	0.2	0.5
Km 3	60	90		0.67	1.6	0.3	0.6
Km 6	70	20		3.5	2.1	0.4	0.9
Km 7.5	xx	14			2.5	0.5	1.1
Km 9	xx	1			2.8	0.6	1.3

and the mean water drainage 85 $m^3.s^{-1}$ (Van Beersum et al. 1993). Water from the Amsterdam-Rijnkanaal, lake IJmeer and the polder waters are directed towards the North Sea. By these flow rates a relatively brackish, well mixed upper layer (epilimnion) develops with a thickness of 5–6 m with a decreasing thickness from west to east. An intermediary layer with a thickness of 8 m develops, with a linearly increasing salinity (metalimnion) and a basic layer of 1–2 m with a constant salinity, of which the thickness increases and the salinity decreases from west to east (hypolimnion) (Karelse and Van Gils 1991). At each lock sea water enters the canal reinforcing the salt wedge (ten times per day for the Noordersluis). Now and then the salt wedge enters the Amsterdam-Rijnkanaal under the influence of water flow and wind.

Collection and measurements of mussels

In October 1989, we collected one to three basalt stones in the littoral zones of the North Sea canal at seven sampling sites (km 0.4, 2.5, 6.5, 10, 15, 19.5, 24) alongside the canal for the sampling of *M. leucophaeata cochleata* and *D. polymorpha* (Fig. 3). *Mytilus edulis* could be collected only from the basalt stones at the seaside of the sluices in IJmuiden at low tide (Van der Velde et al. 1998). In April, June and September 1990, four to five sampling sites alongside the canal have been sampled and in June 1991 only km 24. All sampled stones were transported to the laboratory in plastic bags, provided with the number of the sampling location and were stored at 4 ^{0}C until analyses. Subsequently, all mussels present on the stones were removed and counted. The sampling area was measured in cm^2. The shell length and height of each individual of *M. leucophaeata cochleata* and *D. polymorpha* were measured with an accuracy of 0.05 mm. For practical reasons the minimum length of the specimens used for size measurements was 1 mm. The density of each species and the ratio between the numbers of individuals of both species were calculated.

Collection of physico-chemical data

Salinity of the upper water layer was measured with an YSI salinity meter in the North Sea canal and water temperature was measured with a mercury thermometer at each sampling date and site. To study the seasonal variability of salinity and water temperature of the North Sea canal, monthly measurements were carried out near the Municipality of Velsen (km 2.5) for four years. All other salinity values of the North Sea canal used were derived from chloride data of Van Couwelaar and Van Dijk (1989). Salinity data of the canal through Voorne data were derived from chloride values mentioned in Janssen and Janssen-Kruit (1967). Salinity was calculated by multiplication of chloride content values ($g.l^{-1}$) with 1.80655 (Salinity = 1.80655 * Cl) (Wooster et al. 1969).

Statistics and graphs

SigmaPlot for Windows (Version 11.0 (Build 11.0.0.77) Copyright © 2008. Systat Software Inc., 1735 Technology Drive Suite 430 San José, CA95110, U.S.A.) was used for statistical analyses and graphical representation of data.

Results

Current species occurrence

A large population of *M. leucophaeata cochleata* is still present in the North Sea canal and the connected river IJ (Figs 3, 4). The ships in the canal produce waves and currents resulting in a supply of suspended organic matter to mussels in the littoral zone. Power plants and other industries use water of the canal for cooling purposes and discharge cooling water with temperatures above ambient conditions. The higher water temperatures in mixing zones of these thermal discharges are beneficial for the reproduction and growth of mussels. In cooling water systems with water intake from the canal, the higher temperature and the continuous flow of food stimulate the growth of the mussels that settled in the condenser tubes causing blockage of the water flow (Jenner et al. 1998).

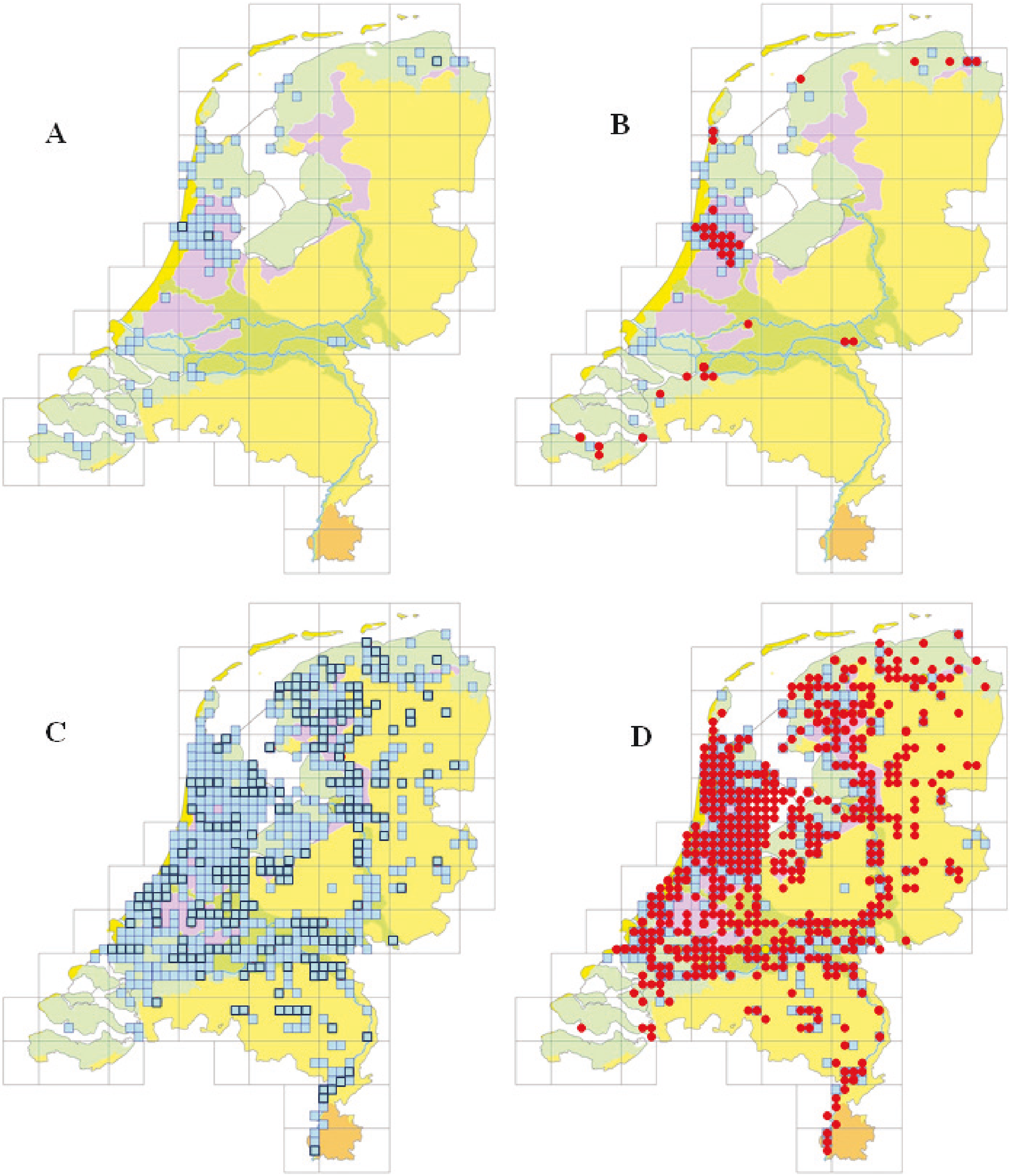

Figure 4. Distribution of *Mytilopsis leucophaeata cochleata* (**A, B**), *Dreissena polymorpha* (**C, D**) in the Netherlands (Source NDFF service team, Nijmegen). **A, C.** All records in the period 1800–2024 are indicated with blue squares. **B, D.** All records in the period 1990–2024 are indicated with red dots; atlas blocks without records in this period but with records before 1990 are indicated with blue squares. A small atlas block measures 5 × 5 km, a large atlas block 10 × 5 km covering two topographical map sheets (east and west). Soil type is indicated by different colours: orange: loess, yellow: sand, purple: peat, green: clay (Vogelbescherming Nederland 2007).

At km 0.4, 2.5, 4.5, 6.5, 10, 15, 19.5, and 24 *M. leucophaeata cochleata* was found and, at km 19.5 and km 24 this species was found to co-exist with *D polymorpha* (Tables 2, 3). At km 19.5 one specimen of *D. polymorpha* was found in October 1989 but none in 1990. At km 28 only *D. polymorpha* was found.

Table 3. Overview of data for the North Sea canal . Own data and data Van Couwelaar en Van Dijk: number per square metre; *M.l.* = *Mytilopsis leucophaeata cochleata*, *D.p.* = *Dreissena polymorpha*, Temp. = Water temperature ⁰C, n.d. = not measured.

North Sea canal. Own data 1989/1990								
Distance	*M.l.*	*M.l.*	*M.l.*	*M.l.*	Salinity	Salinity	Salinity	Temp
from sea	Oct.89	Apr.90	Jun.90	Sep.90	Apr.90	Jun.90	Sep.90	Oct. 89
Km -0.1	0							17.4
Km 0.4	16800	10800	22500	11800	7.4	n.d.	9.2	18.9
Km 2.5	14600	5600	8000	12000	5.9	n.d.	8.5	18.8
Km 4.5	2800							15.5
Km 6.5	8700	8000	6600	1600	4.3	n.d.	6.1	17.0
Km 10	11000							15.2
Km 15	8600	1600		3800	3.1		4	17.2
Km19.5	5700							15.6
Km 24	9200	3900	4500	3800	1.5	n.d.	2.2	15.6
Km 28	0							15.1
North Sea canal. Data Van Couwelaar & Van Dijk, 1989								
Distance	*M.l.*	*D.p.*	*M.l.*	*D.p.*	*M.l./ D.p.*	*M.l./ D.p.*	Temp	Salinity
from sea	May.88	May.88	Sep.88	Sep.88	May.88	Sep.88	Sep.88	Sep.88
Km 5	906	0	1462	0			17	4.0
Km 7.5			1406	20		70.3	16	3.5
Km 13	977	9	811	23	108.6	35.5	17	3.0
Km 18.5	387	30	1740	1480	12.9	1.2	19	2.7
Km 22	0	273	283	998		0.28	16	1.8
Km 25			578	1277		0.45	17	1.0
Km 28			11	945		0.01	17	2.5

Dreissena polymorpha co-existed with *M. leucophaeata cochleata* at the farthest end of the canal with most Rhine water influence (Fig. 5). The occurrence of *D. polymorpha* was restricted to a salinity below 4 (Fig. 6). At km -1.5 and km -0.1, outside of the sea sluices, no dreissenid mussels were observed (see below Discussion Salinity tolerance).

Physico-chemical data

The salinity measurements in the North Sea canal showed a gradual decrease from km 0–km 25 (Fig. 5). Table 4 summarizes the yearly mean, maximum, minimum and median water temperature of sampling site km 2.5 (municipality of Velsen).

Monthly, salinity and water temperature in the period 1989–1992 were measured in the North Sea canal at km 2.5 (Velsen). Salinity fluctuated between 3.0 and 9.5 (Fig. 7), while the temperature course is predictable with a maximum in June–October (20–24 ⁰C) and a minimum in December–February (4–8 ⁰C).

Densities and co-existence

Mytilopsis leucophaeata cochleata was present over nearly the whole length of the North Sea canal with the highest densities close to the sea sluices where also the highest salinities and water temperatures were measured. The densities in the canal decreased gradually at larger distances from the sea (Fig. 5) where salinity was lower (Fig. 6).

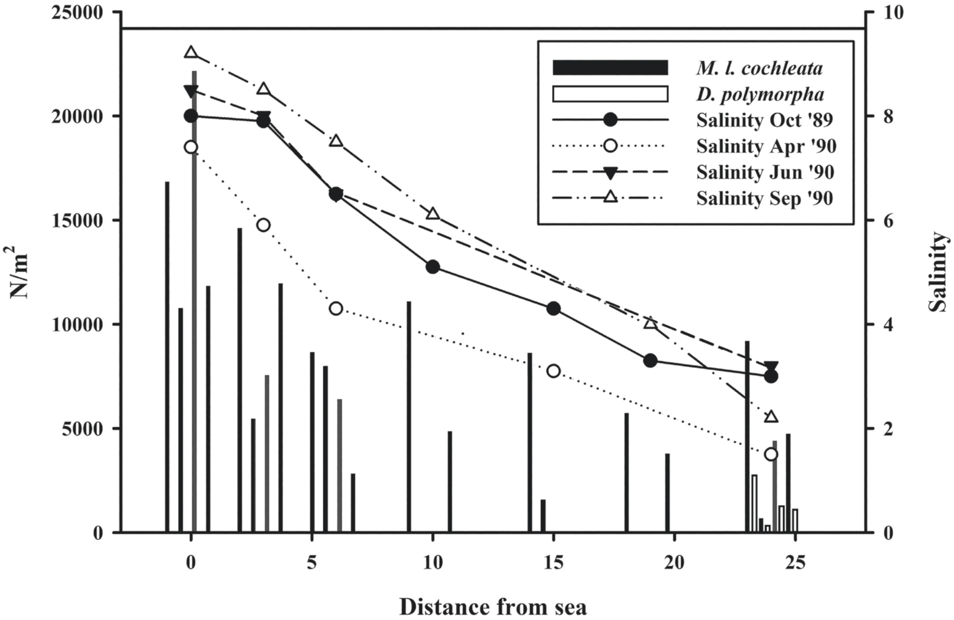

Figure 5. Densities of *Mytilopsis leucophaeata cochleata* and *Dreissena polymorpha* in relation to the salinity gradient in the North Sea canal (Fig. 2, Table 3). At every distance from sea, the order is October 1989, April 1990, June 1990 and September 1990.

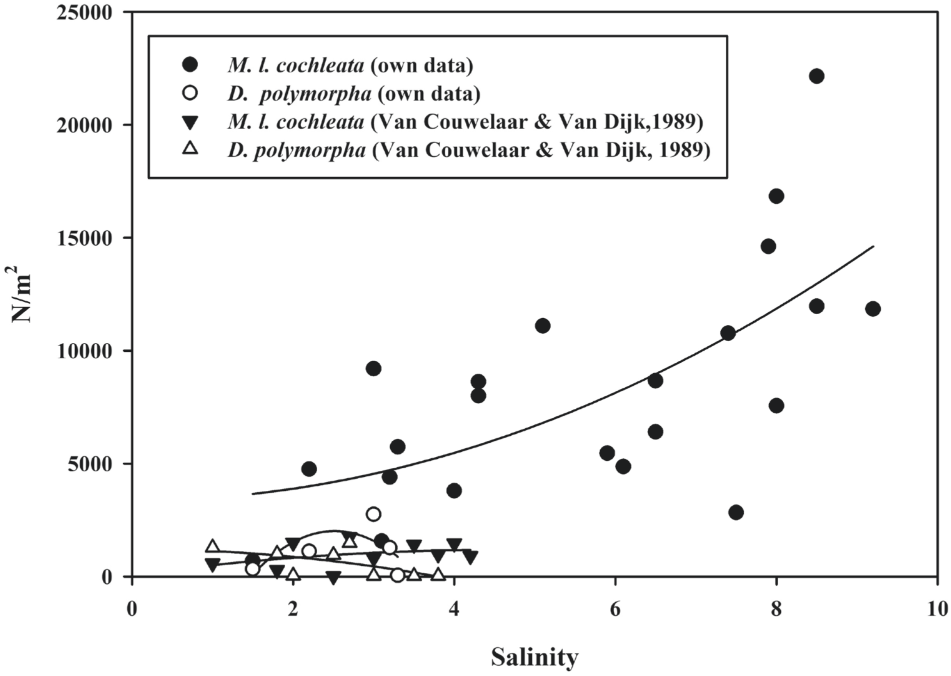

Figure 6. Population density in relation to salinity for *Mytilopsis leucophaeata cochleata* (regression line: $Y = 3373.3 + 12.5X + 134.2X^2$; p=0.012) and *Dreissena polymorpha* (regression line $Y = -9729.7 + 9330.4X – 1854.1X^2$; p=0.494) in the North Sea canal, together with the observations of Van Couwelaar and Van Dijk (1989), *M. l. cochleata* (regression line: $Y = 69.8 + 483.3X + 52.8X^2$; p=0.467) and *D. polymorpha* (regression line: $Y = 1221.3 – 15.2X – 81.1X^2$; p=0.283).

The occurrence of co-existing *D. polymorpha* and *M. leucophaeata cochleata* was studied at km 24 in the period October 1989–June 1991. The density of *M. leucophaeata cochleata* was on average 2.4 times higher than that of *D. polymorpha* (Table 5). Further eastward at 'freshwater' sites only *D. polymorpha* was found.

Table 4. Water temperature (°C) and salinity with mean value, date of maximum, date of minimum and median value in the years 1989–1992 in the North Sea canal at km 2.5 (near the municipality of Velsen).

	Year(s)	Mean	Maximum (date)	Minimum (date)	Median
Water temperature °C	1989–1992	13.5	23.9 (24/08/1989)	4.5 (16/01/1991)	13.6
	1989	14.2	23.9 (24/08/1989)	6.5 (26/01/1989)	10.6
	1990	13.5	19.4 (21/06/1990)	4.7 (19/12/1990)	12.8
	1991	12.1	20.4 (28/08/1991)	4.5 (16/01/1991)	11.0
	1992	14.3	23.2 (30/06/1992)	5.0 (22/01/1992)	14.2
Salinity	1989–1992	5.5	9.2 (18/01/1990)	3.2 (16/12/1992)	5.2
	1989	6.2	7.9 (23/11/1989)	4.3 (18/05/1989)	5.5
	1990	6.2	9.2 (18/01/1990)	3.5 (22/11/1990)	5.8
	1991	5.0	7.2 (30/09/1991)	3.2 (16/01/1991)	4.5
	1992	4.6	5.5 (30/06/1992)	3.2 (16/12/1992)	5.0

Table 5. Number of individuals and ratio of *Dreissena polymorpha* (Dp) and *Mytilopsis leucophaeata cochleata* (Mlc) collected from stones in the North Sea canal in the IJ opposite of the central railway station of Amsterdam (km 24).

Date	Salinity	*Dreissena polymorpha*	*Mytilopsis leucophaeata cochleata*	*Mlc./Dp*
October 1989	3.0	55	184	3.3
April 1990	1.5	87	168	1.9
June 1990	n.d.	98	227	2.3
September 1990	2.2	65	209	3.2
June 1991	n.d.	84	161	1.9
Average number and ratio with standard deviation		77 (±17)	190 (±28)	2.4 (±0.7)

Discussion

Population establishment and decline in the Netherlands

From 1895 until 1932, *M. leucophaeata cochleata* expanded its range in the Netherlands through the brackish water systems in the province of North-Holland and from the coastal areas near Hellevoetsluis to Groningen (Van der Gaag 2021). Most of the populations in the province of North-Holland disappeared due to a decline in water salinity after the closure of the Zuiderzee, leading to the development of the freshwater lake IJsselmeer in 1932. In 1932, in the Oosterdock (part of the harbour of Amsterdam) Vorstman performed a study with slide glasses, to get insight in the life cycle of *M. leucophaeata cochleata* (Vorstman 1933a, b, 1934) demonstrating that this area was still a brackish water system.

The delta works in the south-western part of the Netherlands resulted in the closure of estuaries by dams and other storm surge barriers. These flood defence structures changed brackish estuaries into freshwater lakes causing the local extinction of several populations of *M. leucophaeata cochleata* in the province of Zuid-Holland (e.g., the population in the canal through Voorne by the closure of the Haringvliet

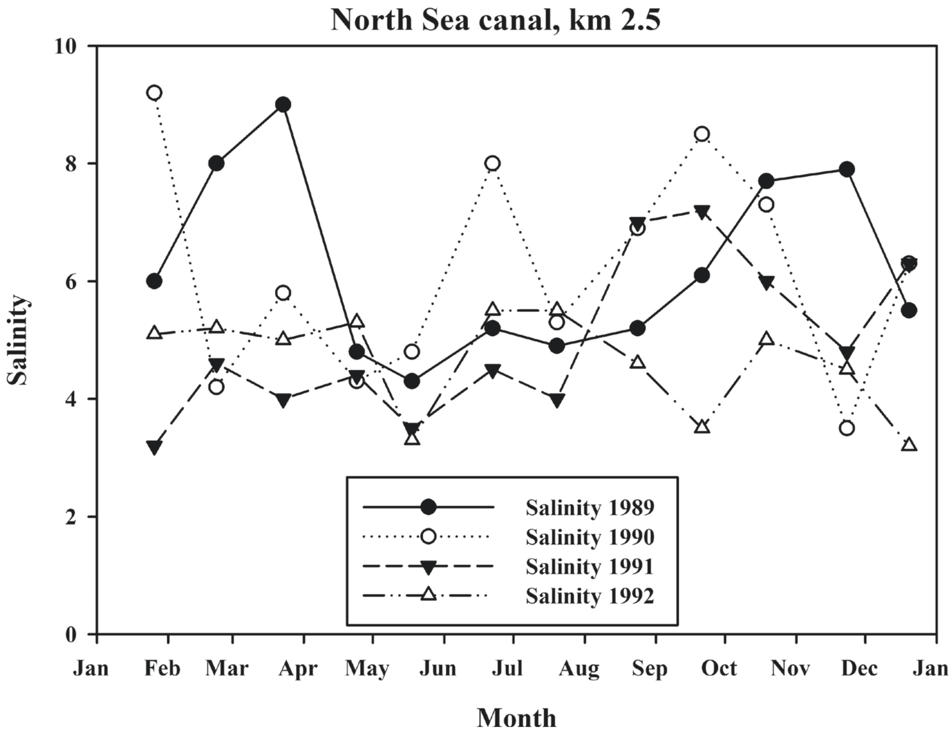

Figure 7. Monthly salinity in the period 1989–1992 in the North Sea canal at km 2.5 (municipality of Velsen). At this locality only *Mytilopsis leucophaeata cochleata* was found.

estuary in 1971) (Fig. 4). Most of the populations in the provinces of Friesland and Groningen also disappeared before the 21[th] century due to a strong decline of the brackish water systems by increased inlet of fresh water for agricultural purposes. Although considered an alien species the high local extinction rate led to putting *M. leucophaeata cochleata* on the red list of vulnerable species (Gmelig Meyling and De Bruyne 2022).

An established population of *M. leucophaeata cochleata* is still present in the canal from Ghent to Terneuzen in the south of the Netherlands (Kuijper 2000). A small population occurs in the Eems canal and the Oosterhornhaven in Weiwerd near Delfzijl (Kuijper 2002) in Groningen. The species also occurs in the Van Harinxma canal at Harlingen in the north, in the eastern part of the Western Scheldt near Rilland in the south and in a water body near Den Helder in North-Holland (De Bruyne et al. 2013) (Figs 2–4).

Gradient study in the canal through Voorne

Janssen and Janssen-Kruit (1967) qualitatively collected dreissenid mussels at seven locations with different salinities in the littoral zone of the canal through Voorne.

The canal through Voorne between the river Brielse Maas and Haringvliet estuary was digged out by hand and finished in 1829 (Figs 2, 3). The Haringvliet was at that time in open connection with the North Sea. The canal has a width of 30 m, a sluice width of 10 m and a depth of 5.3–5.6 m, which was large enough for most ships at that time (Benschop 2023). The canal through Voorne had connections by the sluice with the Brielse Maas and with the Haringvliet via a sluice at Hellevoetsluis. By the construction of this canal the sailing time for ships from the North Sea to the Rotterdam harbour was since 1829 shortened half a day. The canal lost its function after the construction of the Nieuwe Waterweg between the North Sea and the Port of Rotterdam in 1872. The Haringvliet was at that time in open connection with the North Sea. In 1960 the canal through Voorne was dammed of in the north (Wikipedia 2022). The Haringvlietdam was finished in 1971 changing the Haringvliet into a freshwater body. The desalination of the canal through Voorne resulted in the disappearance of *M. leucophaeata cochleata* after 1971 (Fig. 4). A salinity gradient was present from the northern sluice (km 0), which connected the canal to the freshwater of the Brielse Maas, and the southern sluice (km 9), which connected the canal to the seawater of the Haringvliet. Salinity data of the first nine months of 1965 were delivered as chloride content by Rijkswaterstaat. Their qualitative sampling approach allowed to calculate the ratio between the number of individuals of both species. In the low salinity part of the canal, a few *M. leucophaeata cochleata* were found and many *D. polymorpha.* In the high salinity part of the canal the opposite was found. In the middle of the canal both species were present in equal amounts as salinity values of the canal through Voorne were low (Table 2).

Gradient studies in North Sea canal

In 1988, Stichting Ecotest commissioned by the department Water Management of Rijkswaterstaat Directorate Noord-Holland investigated the littoral fauna of the North Sea canal, side channels and harbours (Van Couwelaar and Van Dijk 1989). They found populations with a density higher than 200 mussels.m^{-2} for *M. leucophaeata cochleata* between km 5–km 25. For *D. polymorpha* they found a density of more than 200 mussels.m^{-2} at km 25–km 28, low numbers at km 22 and very low numbers from km 7.5–km 13.5 (Tables 2, 3). In the side channel C, near the municipality of Spaarndam (Fig. 3), *D. polymorpha* had high numbers too, because of fresh water discharged by the sluice of the Spaarne (Tables 2, 3). In the period 1989–1990, we found high numbers for *M. leucophaeata cochleata* from km 0–km 25, high numbers for *D. polymorpha* at km 25 – km 28 and low numbers at km 19.5 (Table 3). In the western part of the North Sea canal (the deep part with the big harbours) the salinity (3–8) is too high for the settlement of a permanent *D. polymorpha* population with high density. *Mytilopsis leucophaeata cochleata* is more tolerant to salinity (2–8) and showed high densities from km 0–km 25. In the most eastern part of the canal, near the Oranje sluices, the salinity (1–2) is too low for a viable population of *M. leucophaeata cochleata*. In 1989 and in 1990, both species had well established populations. They co-existed at km 25 at the north side of the canal just opposite of the central station of Amsterdam as also found by Van Couwelaar and Van Dijk (1989). De Bruyne and Neckheim (2001) mentioned a record of co-existence of both species near the quay De Ruyterkade in Amsterdam in 1951 at a salinity of 2.4. Walton (1996) mentioned coexistence of both species in the Hudson River, New York where *D. polymorpha* occurs at salinities of 0–3 (none found at salinities of 5–9). All these data are in agreement with each other and fall within the favourable ranges found by our mesocosms study (look under the heading Salinity tolerance below).

Mytilopsis leucophaeata cochleata was also found in fresh water outside the brackish water areas in the large rivers Rhine, Meuse and Scheldt (Fig. 4). Jaeckel (1962) mentioned it even stream upwards, from the inner Rhine-Ruhr harbour of Duisburg (Germany). Because their shells often carry growth of brackish water species such as bryozoans and tube worms which live in the North Sea canal area but lack in fresh water, they must have been transported by ships most likely through the Amsterdam-Rhine canal to the Rhine and there became detached from the ship hulls. Adult *M. leucophaeata cochleata* can survive in fresh water for a long time (120–150 days in mesocosm and transplantation experiments), but reproduction was not observed under such conditions (Verhofstad et al. 2013; Van der Gaag et al. 2016).

Salinity and hydrology

In the past, *M. leucophaeata cochleata* occurred on piles and wooden and stony bank protection in the docks of Amsterdam, as these harbour areas were still connected with the Zuyder Sea (Zuiderzee) and sea water penetrated into the canals of Amsterdam and other waters around Amsterdam. In 1932 the Zuiderzee was closed by a dam, and changed very soon in a freshwater lake, called lake IJsselmeer. This led to the disappearance of *M. leucophaeata cochleata* in the period 1935–1940 by freshening of the water in the canals of Amsterdam, except the IJ. In the Zuiderzee, *M. leucophaeata cochleata* was lacking and this species did not invade the newly created lake IJsselmeer in spite of a short brackish phase after the closing. *Dreissena polymorpha* invaded the whole lake (Van Benthem Jutting 1943) profiting from freshening of the IJsselmeer and availability of shells as a substrate due to mass mortality of marine bivalves such as *Mya arenaria* L., 1758 (Smit et al. 1993) (Figs 2, 4). Elsewhere, freshening of the water caused by dams in river estuaries by the Delta works and the influence of the enclosed freshwater IJsselmeer on salinity of surrounding water bodies led to the disappearance of *M. leucophaeata cochleata* at many localities where it was recorded before (Fig. 4, blue squares) in contrast to *D. polymorpha*. *Mytilopsis leucophaeata cochleata* was found in the Netherlands in brackish water but not in the so-called shock habitats where the salinity changes from sea to fresh water and daily fluctuates with the tidal regime (Wolff 1969). This species occurs where seasonal fluctuation of salinity is predictable allowing to fulfil its life cycle. Therefore, it favours brackish canals and harbours.

Salinity tolerance of *Mytilopsis leucophaeata cochleata* and *D. polymorpha* was studied in long-term studies in outdoor mesocosms during 1992 – 1995 by which favourable and unfavourable salinity ranges for the survival of full-grown mussels could be distinguished for the mussel species occurring in the North Sea canal (Van der Gaag et al. 2016). The results of the outdoor salinity tolerance experiments allowed us to distinguish favourable (f.: high tolerance) and unfavourable (u.: no or low tolerance) salinity ranges for each species, viz. for *D. polymorpha* 0.2–6.0 (f.), 7.0–30.0 (u.), for *M. leucophaeata cochleata* 0.2–17.5 (f.), 20.0–30.0 (u.). At the unfavourable salinities, those mussels died within 14 days of initial exposure. The maximum duration of survival of single specimens of *D. polymorpha* was 318 days at a salinity of 3.2, and 781 days for *M. leucophaeata cochleata* at a salinity of 15.0 (Van der Gaag et al. 2016).

Favourable salinity ranges measured by adult survival time in the mesocosms, appeared to be 0.2–17.5 for *M. leucophaeata cochleata*, and 0.2–6.0 for *D. polymorpha* (Van der Gaag et al. 2016). The salinity range based on the distribution of *M. leucophaeata cochleata* in the North Sea canal was 1.5–9.2, 1.5–3.3 for *D. polymorpha*, and 13.0–16.2 for *Mytilus edulis*. Van Couwelaar and Van Dijk (1989) found in the North Sea canal for *M. leucophaeata cochleata* 1.0–4.2 and *D. polymorpha* 1.0–3.5. Janssen and Janssen-Kruit (1967) found for *M. leucophaeata cochleata* in Canal through Voorne 0.2–2.8, and for *D. polymorpha* 0.2–2.8. Van Couwelaar and Van Dijk (1989) found this sympatric occurrence in the North Sea canal at a salinity of 1.0–3.5. In our study this was recorded for a salinity range of 1.5–3.3 (Tables 2, 3). All these salinity values are within the favourable ranges of both species, such as determined in the long-term survival experiments in the mesocosms.

Recent developments and new invaders

New invading mussels in the North Sea canal and the Netherlands are the brackish water Hooked mussel or Bent mussel *Ischadium recurvum* (Rafinesque, 1820)

(Mytilidae) since 2012 (first record in Europe), originating from the Gulf of Mexico (Goud et al. 2019) and the freshwater Quagga mussel (*Dreissena rostriformis bugensis* (Andrusov, 1897) (Dreissenidae) since 2006, originating from the Ponto-Caspian area (Bij de Vaate 2006).

Ischadium recurvum shows increased mortality below a salinity of 6 and needs a minimum salinity of 4.5 (Allen 1960). The species tolerates a maximum salinity of 36 (Gulf of Mexico salinity) (Goud et al. 2019). Maximum salinity for occurrence of *Dreissena rostriformis bugensis* is 4 (Mills et al. 1996). Maximum salinity for reproduction is 2 (Wright et al. 1996).

The occurrence of these newcomers means that competition between four mussel species is likely when salinity tolerances are similar but excluded when salinity tolerances are different. It is already observed that *D. rostriformis bugensis* outcompetes *D. polymorpha* under freshwater conditions (Bij de Vaate et al. 2014; Matthews et al. 2014; D'Hont et al. 2018). Besides new species in the North Sea canal also new constructions were made leading to opportunities for alien and native species. In 1993–1994 the Seaport Marina of IJmuiden was constructed and is with the harbour of Scheveningen nowadays one of the few seawater harbours along the Dutch coast. The Seaport Marina is constructed at the southern part of the old inner pier of IJmuiden outside the sluices. Other opportunities for marine species are provided by the harbour near the steel fabric Tata Steel at the northern side of the canal. Both can act as a hub for the dispersal of newly introduced species. Since January 2022, at opening of the new lock (Zeesluis IJmuiden), the biggest lock in the world, each time 10,000 ton sea water is entering the North Sea canal unlike the old lock (Noordersluis) with 6,000 ton sea water. Construction of a dam (2022–2024) with at the bottom a gate in the inner blow down channel (Binnenspuikanaal) will made it possible to drain the salt sea water to the North Sea. In the case that the salinity is rising too high when the salt wedge is moving too far inland, and salt water is entering the Amsterdam-Rhine canal the old lock will be used (Rijkswaterstaat 2023). The biological consequences of these hydrological changes have to be studied as this situation creates opportunities for establishment of new alien mussel species and other biofouling species. Studies on the interactions between these new invaders and existing populations in the North Sea canal are urgent.

Conclusions

Besides the recent introductions of new alien species in the North Sea canal also new constructions were made leading to new opportunities for new and earlier invaders and native species. Hydraulic engineering works such as sluices control the salinity of the canal and provide a stable environment for these species. In the Netherlands, these habitats were created by digging canals, construction of harbours and sluices so that sudden salinity changes remained small. The North Sea canal harbours the largest population of *M. leucophaeata cochleata* in the Netherlands and is in this way a source for further dispersal by shipping. The highest densities occur in the western part of the canal with relatively high salinity. The species coexists with *D. polymorpha* at salinities below 4. Outdoor mesocosm experiments provided useful information about the limits of salinity tolerance of species but their limits found in gradients in the field can be restricted by other factors resulting in a smaller tolerance range than found by experiments.

Data sharing

The data are included in the manuscript.

Author's contributions

MvdG, GvdV and RSEWL conceived the study and carried out the field work. All authors contributed to the analysis of the data and were involved in the writing of the paper. All authors have given approval for publication.

Acknowledgements

We thank Martin G. Versteeg for assistance during the field work and transport and three anonymous reviewers for constructive remarks.

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