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ORIGINAL ARTICLE

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Introduced Pacific oysters (*Crassostrea gigas*) in the northern Wadden Sea: invasion accelerated by warm summers?

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Abstract Among the increasing number of species introduced to coastal regions by man, only a few are able to establish themselves and spread in their new environments. We will show that the Pacific oyster (*Crassostrea gigas*) took 17 years before a large population of several million oysters became established on natural mussel beds in the vicinity of an oyster farm near the island of Sylt (northern Wadden Sea, eastern North Sea). The first oyster, which had dispersed as a larva and settled on a mussel bed, was discovered 5 years after oyster farming had commenced. Data on abundance and size-frequency distribution of oysters on intertidal mussel beds around the island indicate that recruitment was patchy and occurred only in 6 out of 18 years. Significant proportions of these cohorts survived for at least 5 years. The population slowly expanded its range from intertidal to subtidal locations as well as from Sylt north- and southwards along the coastline. Abundances of more than 300 oysters m^{-2} on mussel beds were observed in 2003, only after two consecutive spatfalls in 2001 and 2002. Analyses of mean monthly water temperatures indicate that recruitment coincided with above-average temperatures in July and August when spawning and planktonic dispersal occurs. We conclude that the further invasion of *C. gigas* in the northern Wadden Sea will depend on high late-summer water temperatures.

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Introduction

Marine ecosystems have always been subject to changes in species composition and interactions, but natural migration of organisms due to climatic and geographic variations is becoming superimposed by anthropogenic vectors facilitating a much faster and wider distribution into new habitats. Important vectors are intercontinental shipping and the commercial transport of aquaculture products from one coast to another (Chew 1990; Carlton and Geller 1993; Carlton 1996; Reise et al. 1999; Gollasch et al. 2000; Ruiz et al. 2000; Naylor et al. 2001; Wolff and Reise 2002). However, only about 10% of these introduced species are expected to become established and to spread in their new environments, and only a small fraction may furthermore induce changes to the recipient ecosystem (Williamson and Fitter 1996).

In the North Sea, at least 80 non-indigenous species have established themselves in historical time and most of them inhabit the coastal and estuarine zones (Reise et al. 1999; Wolff 1999). Approximately 50% of these species were introduced through aquaculture, that is, either the imported target species was released into the wild or associated organisms were unintentionally co-introduced. Examples of species that were introduced with shellfish are the American slipper limpet *Crepidula fornicata* (Hagmeier 1941; Werner 1948; Thieltges et al. 2003) and various parasites such as the copepods *Mytilicola orientalis* and *M. ostreae* (Stock 1993).

The oyster fishery industry and accompanying shellfish imports have a long tradition in the North Sea. Until the end of the nineteenth century, the extensive subtidal beds of the European oyster *Ostrea edulis* supported a thriving fishing business. Overfishing, however, resulted in a dramatic decline in the native oyster population as the demand for fresh oysters grew (Hagmeier and Kändler 1927; Hagmeier 1941; Reise 1982, 1990). Fishermen thereupon started to import large numbers of seed oysters to restock the local oyster grounds but with no success (Möbius 1877; Hagmeier 1941; Korringa 1976; Utting and Spencer 1992). Only the cultivation of the Pacific oyster *Crassostrea gigas* turned out to be commercially successful. This oyster originates from Japan and has been distributed in oyster cultures all over the world since the early twentieth century (Andrews 1980; Quayle 1988; Arakawa 1990; Chew 1990). In most regions, the Pacific oysters did not remain restricted to their culture plots but reproduced and dispersed successfully in the new environments (e.g. British Columbia: Qualye 1988; Australia: Ayres 1991; and New Zealand: Dinamani 1991). In the North Sea imports of *C. gigas* started in 1964 in the Netherlands (Drinkwaard 1999), followed by transports to England (Walne and Helm 1979; Utting and Spencer 1992; Spencer et al. 1994), France (Maurin and LeDantec 1979; Grizel and Héral 1991), and Germany (Neudecker 1985). Whereas only sporadic natural spatfalls occurred in Great Britain (Spencer et al. 1994; Smith 1994; Eno et al. 1997), wild oyster populations are growing fast in France (Grizel and Héral 1991) as well as in the Netherlands (Drinkwaard 1999; Dankers et al. 2004). The success of natural recruitment and the rate of spread are different in these locations and seem to depend on abiotic factors such as water temperature and salinity (Quayle 1988; Ayres 1991; Spencer et al. 1994).

The spread of the Pacific oyster in the northern Wadden Sea began 5 years after the first German oyster farm had started its business off the island of Sylt in 1986 (Reise 1998). The first oyster that had dispersed as a larva was found on an intertidal mussel bed (*Mytilus edulis*) about 6.5 km north of the oyster farm. Oysters are found mainly as epibionts on natural mussel beds because they need hard substrates to settle on. Oyster larvae use the shells of living and dead mussels as attachment surface because mussel beds represent one of a limited number of secondary hard substrata available on the extensive mud and sand flats in the Wadden Sea. In this article, we describe the slow expansion of a wild *C. gigas* population since the first settlement of spat in 1990 and suggest that the increase in population size may be retarded by irregular recruitment, which we assume is limited by late-summer water temperatures.

Methods

Study site

The Wadden Sea is a large intertidal area in the southeast part of the North Sea, characterized by extensive mud and sand flats. First records of *Crassostrea gigas* on intertidal mussel beds, revetments, and harbour constructions are given for the northern Wadden Sea, which extends from Esbjerg (Denmark) in the north to the Elbe estuary (Germany) in the south (Fig. 1). The quantitative surveys of *C. gigas* abundances and size distributions were carried out on intertidal mussel beds close to the island of Sylt (North Frisian Wadden Sea, Germany; (Fig. 2). Sylt is adjacent to two tidal basins: the List basin in the northeast and the Hörnum basin in the southeast.

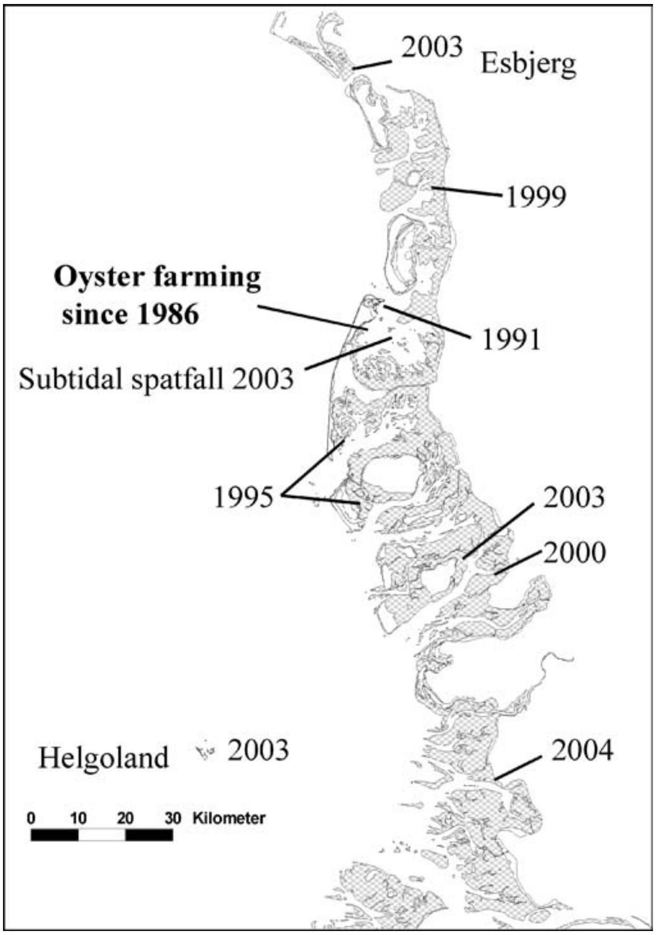


Fig. 1 Northern Wadden Sea from Esbjerg (Denmark) to Elbe estuary (Germany) with first records of *Crassostrea gigas*. *Grey areas* represent intertidal mud and sand flats

The List tidal basin (54°50′–55°10′N, 08°20′–08°40′E) is largely closed by dams to the north and south and covers an area of about 404 km^2. It is connected to the North Sea through a narrow tidal inlet of only 2.8 km in width (Reise and Riethmüller 1998). Tides are semidiurnal and the mean tidal range is 2 m; the average salinity is close to 30 psu. Long-term mean water temperatures (based on monthly mean temperatures) range from 18.2°C in August to 2.3°C in February. Intertidal flats, which are mostly sandy, make up 33% of the area (Reise and Lackschewitz 1998), and intertidal mussel beds cover 1.5 km^2 (Nehls 2003; Stoddard 2003).

The Hörnum tidal basin in the south of Sylt is widely open to the North Sea. It covers 290.2 km^2 (Spiegel 1997) and contains at present only five small mussel beds

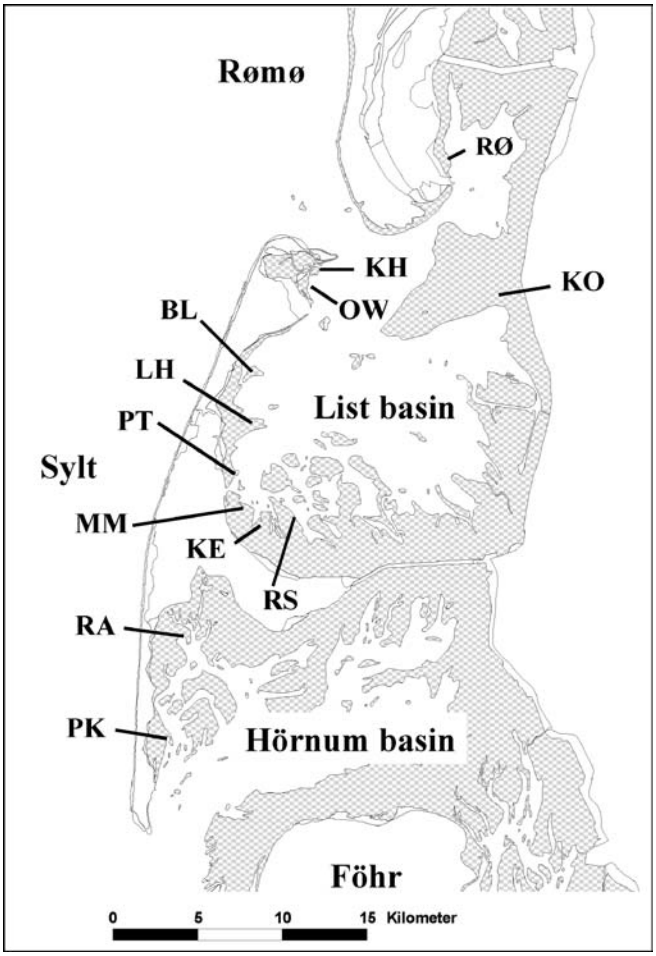


Fig. 2 Map of Wadden Sea near Sylt (List and Hörnum tidal basins) with labelled intertidal mussel beds (for abbreviations see Table 1)

that cover about 0.04 km^2 of the intertidal zone (Nehls 2003; Stoddard 2003).

Abundance and size of *C. gigas* on intertidal mussel beds

Comprehensive field surveys on the abundance of *C. gigas* were carried out twice near the island of Sylt. The first survey took place from March to May and from September to October 1999 on 12 intertidal mussel beds: 11 in the List tidal basin and 1 in the Hörnum tidal basin (Fig. 2). The second survey was conducted in July and August 2003 on 10 intertidal mussel beds: 8 in the List basin and 2 in the Hörnum basin. Two mussel beds were also visited in spring and autumn 2001 and 2002 to detect changes in abundance on a smaller time scale. The data are compared with those from a survey that was done in the same area and in the same way in 1995 by Reise (1998).

The abundance of *C. gigas* on intertidal mussel beds was determined by randomly placing a frame of 50×50 cm (0.25 m^2) within the area covered by mussels. During the 2003 survey we used a smaller frame (25×25 cm) on the mussel beds at Munkmarsch and Königshafen because of the very high oyster abundances. The oysters inside the frame were counted. If the mussel bed patch was covered with fucoid algae, these were lifted and the oysters beneath the algal canopy were counted. The number of replicates varied with the amount of time available due to the turning tide and the size of the mussel bed (11–238 per site). Field surveys were carried out before the recruitment of the same year took place or before the recruits were large enough to be counted. The recorded abundances, therefore, did not include the 0-group of the respective year and the spring and fall data from 1999 can be compared with those of July and August in 1995 and 2003. The total amount of *C. gigas* in the List basin in 2003 was calculated by multiplying the overall mean abundance of *C. gigas* by the total area within the basin that was covered with mussel beds in 2003:1.54 km^2 mussel bed area, mussel coverage 31%, that is, 0.48 km^2 mussel ground. These data are derived from a regular monitoring program that surveys the size of mussel beds with aerial views and ground inspection with a global positioning system (GPS). Mussel coverage is determined by walking in linear transects across the mussel beds and counting the number of steps that hit areas covered with mussels and steps that hit areas with no living mussels (Nehls 2003 and more recent data).

The length-frequency distribution of *C. gigas* was investigated by measuring the shell length (longest diameter of the shell) of oysters that were randomly encountered on the mussel bed. Shell length was measured with vernier callipers to the nearest millimetre.

Results are given as arithmetic means with standard deviations (SDs). Data of abundance were analysed with non-parametric tests because of the heterogeneity of variances despite transformation. We used Kruskal–Wallis analysis of variance (ANOVA) followed by Mann–Whitney *U*-tests (software STATISTICA 1999 by StatSoft). Differences were considered significant at $P < 0.05$.

Biomass

Biomass of *C. gigas* on different mussel beds in 2003 was estimated by using an exponential relation between dry weight (meat and shells) and length of 83 oysters collected on two mussel beds ($y = 0.0002x^{2.8072}$, $R^2 = 0.9122$). With this equation we determined the biomass of *C. gigas* on each mussel bed by converting the length of the oysters into dry weight data.

Abundance and size of *C. gigas* on subtidal habitats

Abundance of *C. gigas* on subtidal mussel beds in tidal channels around Sylt was estimated by taking hauls with a traditional oyster dredge (see Reise et al. 1989). These dredge hauls were carried out in 1999 (20 hauls at two locations), 2001 (22 hauls at two locations), 2002 (10 hauls at one location), and 2004 (30 hauls at three locations). The distance dredged and the geographic position was noted for each haul. Furthermore, we counted the number of *C. gigas* in each haul and measured the shell length as longest diameter of the oyster shell.

Water temperature

Since 1984, surface water temperatures have been regularly measured (about twice weekly) in the main tidal channel near List and at the entrance of Königshafen Bay. Temperature data presented in this article are based on mean monthly values from 1987 to 2003. Results are given as arithmetic means with standard deviations and analysed with *t*-tests for independent variables. All data were tested for homogeneity of variances using the Levene test. Deviations from the monthly mean water temperatures for the months July and August were calculated by subtracting the mean water temperature in each year from the long-term average (1987–2003).

Results

Distribution of *C. gigas* in the North Frisian Wadden Sea

Since 1986, the oyster farm located on the tidal flats east of the island of Sylt (List tidal basin) has produced about 2 million oysters per annum (Fig. 1). A wild oyster population developed in the area due to larval dispersal and the first wild oysters were found in Königshafen Bay in 1991. A quantitative survey in 1995 revealed that 14 out of 17 mussel beds in the List tidal basin were colonized with *C. gigas*. In the Danish Wadden Sea north of the List basin, adult *C. gigas* were found in the Juvre tidal basin near the island Mandø (1999) and at the northern end of the Wadden Sea near Esbjerg (2003:6.8 individuals m^{-2}). South of Sylt, Pacific oysters were found in Hörnum tidal basin (first record in 1995), east of the island of Amrum (1995), at Nordstrand (2000), near the island of Pellworm (2003), and near Büsum (2004). On the offshore island of Helgoland, wild *C. gigas* were found from 2003 onwards. Oyster densities in the northern Wadden Sea outside the List basin are, however, still much lower than inside. Abundances stayed below 1 individual m^{-2} in 2003 on all mussel beds in the North Frisian Wadden Sea south of the List basin (except one mussel bed in Hörnum basin which contained 1.8 individuals m^{-2}).

Abundance of *C. gigas* on intertidal mussel beds near Sylt

In 1995, some mussel beds on the tidal flats near Sylt and Rømø were still without oysters, but by 1999 living *C. gigas* were found on all investigated intertidal mussel beds (Fig. 2, Table 1). The mean abundance of oysters in the List tidal basin, however, did not increase. In 1995, Reise (1998) counted 3.6 individuals m^{-2}, and in 1999, we found 3.7 oysters m^{-2}. This changed pro-

Table 1 Abundance (individuals/0.25 m^2 ± SD), number of samples, and biomass (grams dry weight per square metre) of *Crassostrea gigas* on 15 intertidal mussel beds in the Sylt area: 13 in the List tidal basin and 2 in Hörnum tidal basin.*Blank cells*: no data available. *Asterisks* indicate that mussel beds no longer exist. For location of sites see Fig. 2. Data for 1995 from Reise (1998)

Code	Site	Abundance						Number of samples			Individuals/m^2			Grams/m^2
		Individuals/0.25 m^2			SD									
		1995	1999	2003	1995	1999	2003	1995	1999	2003	1995	1999	2003	2003
List basin														
RØ	Rømø	0	0.2	1.6		0.4	1.1	40	29	25	0	0.9	6.4	30.2
KO	Koldby	0		0.4			0.7	32		21	0		1.6	31.7
KH	Königshafen	2.1	1.9	77.2	2.0	2.3	48.4	48	238	23	8.2	7.8	308.9	1967.1
KH1	Mövenbergwatt	0.9	0.4	*	1.1		*	32	65	*	3.6	1.5	*	*
KH2	Ostfeuerwatt		0.8	*			*		89	*		3.4	*	*
KH3	Uth. Außenwatt		1.0	61.3		1.5	33.3		54	15		3.9	245.3	1232.0
OW	Oddewatt	0.6	0.1	*	0.8		*	70	80	*	2.4	0.5	*	*
BL	Blidsel	1.6	0.8	32.8	1.8	1.4	16.9	80	165	14	6.2	3.1	131.1	1381.7
LH	Leghörn	0.6	0.8	23.2	0.9	1.3	15.2	48	236	18	2.2	3.3	92.9	793.9
PT	Pander Tief	2.1		69.3	2.0		57.6	40		75	8.2		277.0	11386.1
MM	Munkmarsch	1.2	3.3	41.7	1.1	4.4	26.4	44	126	29	4.6	13.2	166.6	4168.5
KE	Keitum	0	0.8	7.0		1.5	6.6	36	82	24	0	3.0	27.8	469.2
RS	Rauling-Sand		0.1	0.1					58	11		0.3	0.4	0
Mean											3.6	3.7	125.8	2146.0
Hörnum basin														
RA	Rantum	0.1		0.1				32		38	0.5		0.2	27.8
PK	Puan Klent	0.4	0.1	0.5	0.7	0.3	0.8	48	20	22	1.7	0.3	1.8	148.0
Mean											1.1	0.3	1.0	87.9

foundly by 2003, when the mean abundance of *C. gigas* reached 125.8 oysters m^{-2} on intertidal mussel beds. This is equivalent to about 2,100 g dry weight (including shell and meat) per square metre. Using the data of mean abundance (125.8 oysters m^{-2}) and the total area of intertidal mussel beds (0.48 km^2), we estimate for the List tidal basin a number of 60.4 million oysters in 2003 (i.e. approximately 1,000 t dry weight). The population development of *C. gigas* stagnated in the tidal basin in the south of Sylt (Hörnum basin). Abundances stayed on a low level throughout the entire period from 1995 to 2003.

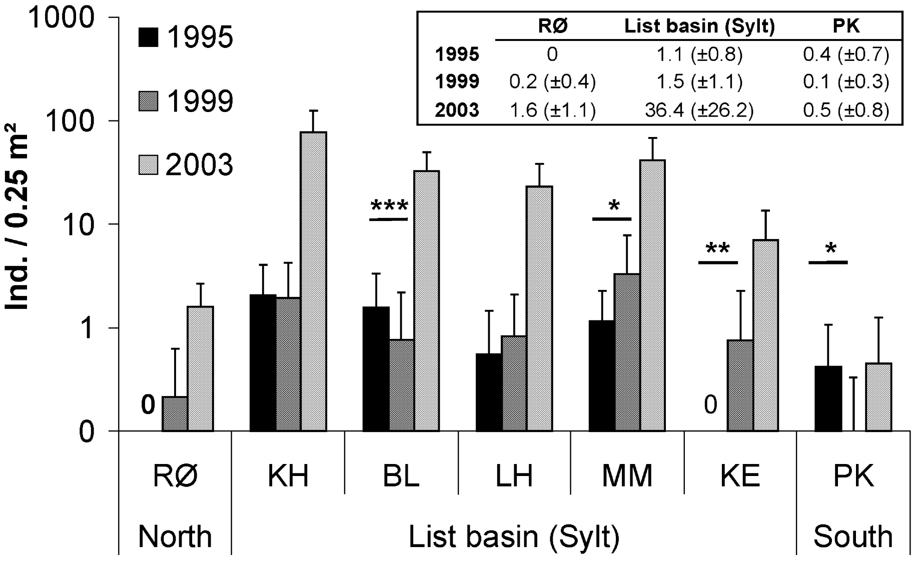
We focus on seven mussel beds, one at the northern end of the List basin (RØ), five adjacent to the island of Sylt in the List basin (KH, BL, LH, MM, KE), and one in the southern basin (PK) in order to describe the population development of *C. gigas* in more detail (Fig. 3). By comparing the oyster densities in 1995 and 1999, it turns out that a significant increase in abundance only occurred on two mussel beds in the List basin, MM (Kruskal–Wallis ANOVA, $P<0.0001$; Mann–Whitney *U*-test, $P=0.011$) and KE (Kruskal–Wallis ANOVA, $P<0.0001$; Mann–Whitney *U*-test, $P=0.009$), whereas on two other mussel beds, BL (Kruskal–Wallis ANOVA, $P<0.0001$; Mann–Whitney *U*-test, $P<0.001$) and PK (Kruskal–Wallis ANOVA, $P=0.001$; Mann–Whitney *U*-test, $P=0.014$), a significant decrease in numbers occurred. Four years later, in 2003, abundances of *C. gigas* were significantly higher on all mussel beds in the List basin, with Königshafen containing over 300 oysters m^{-2}. It is remarkable that the mussel bed in the north of the List basin (RØ) and the one in the southern basin (PK) still showed comparatively low oyster densities (6.4 oysters m^{-2} for Rømø, and 1.8 oysters m^{-2} for Puan Klent). The mean values of oyster abundance on the five mussel beds adjacent to Sylt in the List basin increased from 4.3 oysters m^{-2} in 1995 and 6.1 oysters m^{-2} in 1999 to 145.5 oysters m^{-2} in 2003.

Length-frequency distribution of *C. gigas*

In Fig. 4, we present length-frequency distributions of *C. gigas* on two mussel beds (KH and MM) from 1999 to 2004. Based on these frequency distributions the age structure of the population is described by distinguishing different year classes and calculating their length increments. By growth experiments we verified that peaks in these graphs indicated year classes: juvenile oysters reach 20–33 mm shell length in the first spring after settlement in the previous summer. They will continue to grow to 40–60 mm by the end of the growing season in November and will remain this size until the next growing period starts in April (own unpublished data).

In spring 1999, oysters at the Königshafen site were represented by a distinct year class between 25 and 65 mm shell length (cohort of 1997) and some older individuals. The cohort of 1997 represented 53% of all oysters in this area. The distribution looked similar at Munkmarsch, but with a higher proportion of oysters of the year class 1997 (86%). Until fall 1999, the 1997 year class grew by 20–30 mm in shell length to approximately 50–100 mm. It is important to note that we did not consider oyster spat in the fall monitoring because these oysters were still too small to be counted. The offspring of the summer of a certain year is, therefore, first represented in the spring graphs of the following year. The spring graphs, however, still show a lower abundance of juvenile oysters than the subsequent autumn graphs, because the recruits of the previous summer were still too small to be included adequately in the spring monitoring. By autumn, however, the oysters had grown to a larger size and were more adequately represented. This is especially the case in the Königshafen 1999 and in the Königshafen and Munkmarsch 2003 graphs.

The data set from April 2001 shows a much older population than in April 1999 for both Königshafen and



	RØ	List basin (Sylt)	PK
1995	0	1.1 (±0.8)	0.4 (±0.7)
1999	0.2 (±0.4)	1.5 (±1.1)	0.1 (±0.3)
2003	1.6 (±1.1)	36.4 (±26.2)	0.5 (±0.8)

Fig. 3 Mean abundance (individuals per 0.25 $m^2 \pm$ SD; logarithmic scale) of *C. gigas* on seven intertidal mussel beds (RØ, KH, BL, LH, MM, KE, PK) near Sylt surveyed in 1995, 1999, and 2003. Sample size varied between $n=14$ and $n=238$. *Asterisks* mark significant differences between 1995 and 1999 data sets (Mann–Whitney *U*-test): $*0.05>P\geq0.01$, $**0.01>P\geq0.001$, $***P<0.001$. *Inset* Mean abundance of *C. gigas* (individuals per 0.25 $m^2 \pm$ SD) on mussel bed RØ, over all five mussel beds in List basin (Sylt), and on mussel bed PK

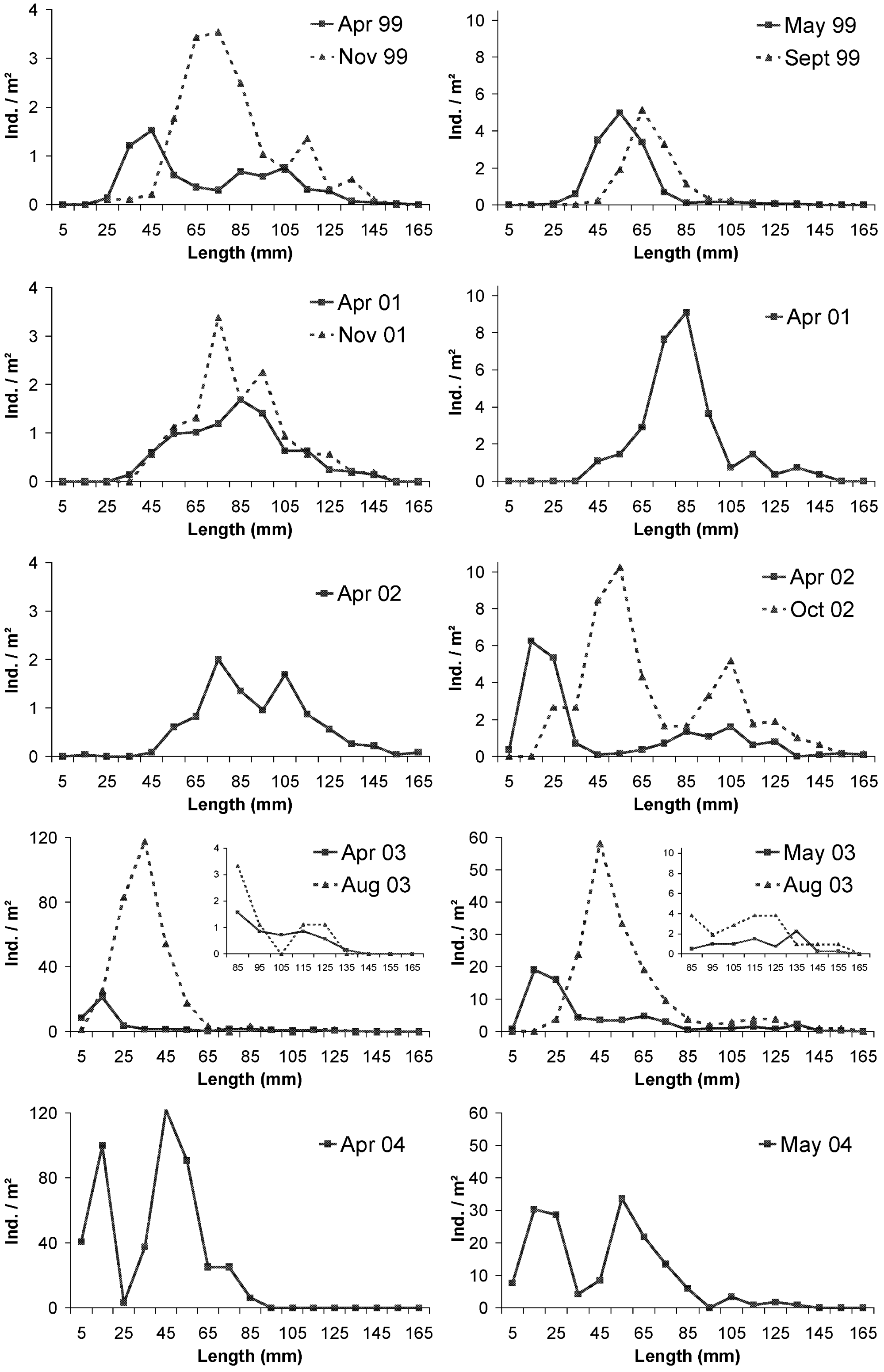


Fig. 4 Length-frequency distribution of *C. gigas* on two intertidal mussel beds near Sylt (*left* Königshafen; *right* Munkmarsch) from 1999 to 2004. Number of individuals measured varied between $n=68$ and $n=307$. *Insets* in 2003 graphs depict large size classes on a lower scale to show survival of adults

Munkmarsch. There were no signs of any significant recruitment or mortality in 1999 and 2000. The size distribution of *C. gigas* in Königshafen for April 2002 was similar to that for 2001, but a strong recruitment was apparent at Munkmarsch with 60% of the oysters measuring under 30 mm. This 2001 cohort grew approximately 30 mm by October 2002. In spring 2003, recruitment on both mussel beds was evident: the majority of oysters belonged to the year class of 2002. This cohort grew by about 20 mm until August 2003 and represented 97% of the Königshafen population and 76% of the Munkmarsch population. In April/May

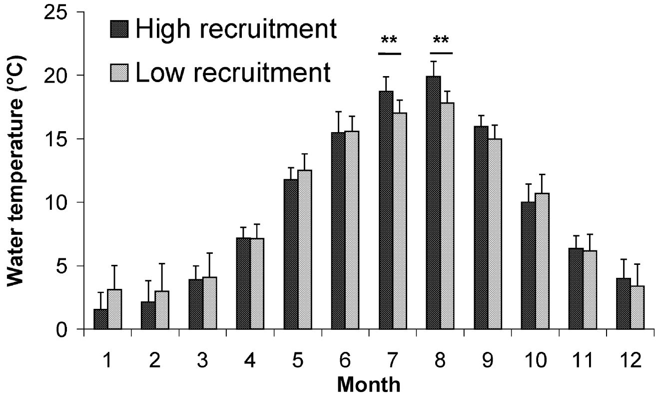


Fig. 5 Monthly means of water temperature (°C) during years with notable or high *C. gigas* recruitment (1991, 1994, 1997, 2001, 2002, 2003) and years with no or very low recruitment (1987–1990, 1992, 1993, 1995, 1996, 1998–2000). Significant differences in water temperature occurred in July (*7*) and August (*8*; $^{**}P=0.008$ and $P=0.001$, respectively; *t*-test for independent variables)

2004, oyster recruitment from the previous summer was evident on both mussel beds.

It is important to note that the 1997 cohort was still present in 2002 in almost the same numbers as in the years before, that is, no detectable mortality occurred from 1999 to 2002, suggesting a high survival rate of 2- to 5-year-old oysters. Even in 2003, the 1997 cohort was still present (see insets in Fig. 4).

Mean water temperatures and *C. gigas* recruitment

The comparison of monthly mean water temperatures during years with notable *C. gigas* recruitment (1991, 1994, 1997, 2001, 2002, 2003) and years with no measurable recruitment (1987–1990, 1992, 1993, 1995, 1996, 1998–2000) revealed significantly higher water temperatures in July and August in recruitment years (Fig. 5). No significant differences in water temperatures occurred for all other months. Deviations of water temperatures from the long-term mean (1987–2003) in July and August show that successful recruitment only occurred in relatively warm summers (Fig. 6).

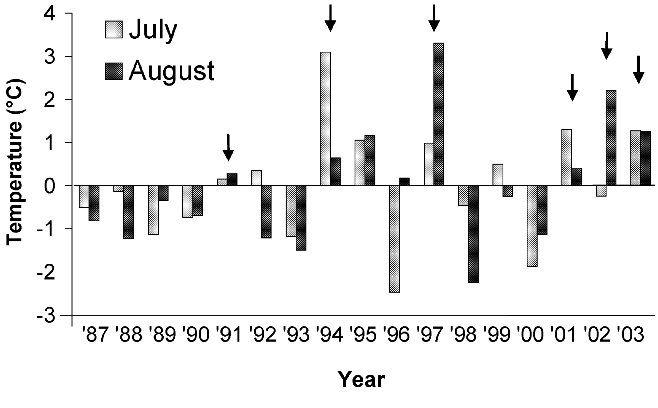


Fig. 6 Deviations of mean monthly water temperatures in July and August from the long-term mean (1987–2003). *Arrows* mark years with high *C. gigas* recruitment (1991, 1994, 1997, 2001, 2002, 2003)

Abundance and size of *C. gigas* in the subtidal zone near Sylt

Dredge hauls in subtidal channels around the island of Sylt in the time period from 1992 to 1996 did not yield any living *C. gigas* (Reise 1998). In 1999, we fished at two locations (Munkmarsch and Königshafen) of subtidal mussel stocks and found only one and three adult oysters, respectively (Table 2). The Munkmarsch site was again investigated in 2001 and 2002 and we still only caught four and two oysters, respectively. In 2004, however, we found 95 oysters at Munkmarsch and 25 at Königshafen. There was a noticeably high proportion of juvenile oysters present. Another ten dredge hauls in the middle of the tidal basin yielded 428 living oysters of which 33% belonged to the 2003 year class.

Discussion

Since 1986, a potential spawning population of *Crassostrea gigas* has been cultured for commercial purposes at Sylt. Significant recruitment in the area only took place in 1991, 1994, 1997, 2001, 2002, and 2003 (i.e. in 6 out of 18 years). This indicates that the reproductive success of *C. gigas* in the northern Wadden Sea is not a regular phenomenon but occurred only in about one-third of the years since the local introduction of the species.

The expansion of Pacific oysters in the Wadden Sea near Sylt started off slowly with the colonization of certain intertidal mussel beds near the oyster farm. Successful recruitment did not occur in all suitable habitats, and it was not until 1999 that all mussel beds in the List tidal basin contained wild *C. gigas*. Nevertheless, strong recruitment was still confined to certain locations within the basin. By 2003, some mussel beds in the area still had very low oyster densities, whereas a massive population increase took place in other areas. In 2001, for example, recruitment occurred on mussel beds in the southern part of the List basin but not in the northern part (approximately 15 km apart).

The spread towards areas outside the List tidal basin also occurred slowly. Abundances of *C. gigas* on mussel beds in the Hörnum basin in the south of Sylt remained at a low level until 2003, although living *C. gigas* had been found from 1995 onwards. Also near the islands further south (Föhr, Amrum, Pellworm) abundances are still low in comparison to northern Sylt. The same is true for the Danish Wadden Sea, where *C. gigas* is now present although still in low numbers.

The origin of the oysters south of the island of Sylt is not clear, as natural transport against the south-north

Table 2 Dredge hauls in subtidal channels in the List tidal basin. Given are locations, number of hauls, and area fished. The distance dredged varied between 150 and 470 m. Also total number and length of *C. gigas* for each location are shown. Data for 1992–1996 from Reise (1998)

	1992–1996	1999		2001		2002	2004		
Location	Sylt area	MM	KH	MM	KO	MM	MM	KH	Bay
No. of hauls	216	10	10	10	12	10	10	10	10
Area (m^2)	108,000	4,000	2,000	4,000	3,000	3,000	3,700	2,100	3,000
No. of *C. gigas*	0	1	3	4	12	2	95	25	428
Length (mm)									
Min–max	–	108	70–109	75–137	28–144	5; 120	5–134	8–146	2–97
Mean (±SD)				99.8 (±26.5)	94.5 (±31.9)		56.7 (±28.7)	59.6 (±29.5)	38.5 (±23.4)

current is unlikely and may only occur on rare occasions. Transport from the List basin due to mussel farming activities is possible, as well as further introductions from several experimental cultures in the North Frisian Wadden Sea. Larval drift from the Oosterschelde or the Dutch Wadden Sea, however, seems to be rather unlikely. Transport times between Texel and the North Frisian Wadden Sea amount to about 150 days (de Ruijter et al. 1988) and are, therefore, longer than the mean lifetime (3–4 weeks) of pelagic larvae (Neudecker 1985; Quayle 1988). The extended planktonic larval period nevertheless allows a high dispersal by currents, as has been described for *C. gigas* in British Columbia, where settlement of wild oysters occurred 60 km away from the next oyster farm (Elsey and Qualye 1939).

Larval retention in the List tidal basin, however, should be high as it is practically enclosed and is only connected to the North Sea by a 2.8-km-wide channel. This is very favourable to the oyster larvae because they remain on suitable sites close to their origin, and this certainly facilitates population growth when adult stocks are still low. Larvae in more open areas may be widely distributed and are, therefore, less likely to find suitable settling substrates and subsequently perish. The List tidal basin thus offers ideal conditions for the spread of species with planktonic larvae due to the continuous input of larvae from the local oyster farm and the closed bay environment.

The fast development of oysters in the closed Oosterschelde and the much later spread into the Dutch and western German Wadden Sea followed the same pattern (Wehrmann et al. 2000; Dankers et al. 2004). Within the bay, the slow and patchy expansion presumably does not result from a lack of dispersal but from limited larval supply or poor initial survival after settlement. This might also explain the slow colonization of subtidal habitats. It is important to note that the site where we found juvenile *C. gigas* used to be an important subtidal spatfall area of blue mussels (Ruth 1994) and is located about 7 km from the nearest intertidal mussel bed. These findings are thus the first clear indications of subtidal spatfall in Pacific oysters in the Northern Wadden Sea. Even though *C. gigas* is considered to be more an intertidal species, it has the capability to colonize subtidal habitats (Buroker 1985). In the Oosterschelde (The Netherlands), where Pacific oysters were introduced in the 1960s, *C. gigas* is now a dominant species in intertidal and subtidal benthic communities (de Kluijver and Leewis 1994; Leewis et al. 1994; Meijer and Waardenburg 1994; Drinkwaard 1999). In British Columbia, *C. gigas* is found only in intertidal habitats, presumably because low temperatures in deeper waters limit the survival of larvae and juveniles (Quayle 1988).

The irregular recruitment of *C. gigas* in the northern Wadden Sea is apparently no threat to the population because of the high survival rate after 1-year-old cohorts have become established. As the cohort of 1997 showed high persistence during the subsequent 5 years, a failure in reproductive success during 4 consecutive years is not expected to threaten population maintenance. The long persistence of *C. gigas* populations has also been reported from Great Britain, where adult oysters were still present 9 years after the closure of an oyster farm (Smith 1994).

What could be the reason for this irregular recruitment success? We compared water temperature regimes in years with notable or high oyster recruitment and those with no or low reproductive success and found that high recruitment corresponded with higher than average water temperatures in late summer. This is an important time period in the oyster life cycle; spawning occurs, larvae are dispersed, and juveniles settle on hard substrates. In the Wadden Sea, *C. gigas* spawns in late July and August. After fertilization, pelagic larvae develop and will stay in the water column for 21–30 days before settlement occurs (Neudecker 1985; Quayle 1988).

The importance of temperature for oyster spawning and recruitment has been described by various authors. In Japan, 23–25°C is considered as the optimum water temperature for successful recruitment (Korringa 1976; Kobayashi et al. 1997), and even though spawning has been observed in British Columbia (Canada) at 15°C, the optimal temperature for larval development is considered to be 23°C (Quayle 1988). In Great Britain, *C. gigas* has been observed to spawn from 18°C onwards but natural recruitment is sporadic and occurred only in exceptionally warm summers (Mann 1979; Spencer et al. 1994).

In the Oosterschelde (The Netherlands), *C. gigas* was introduced in 1964 and the first natural recruitment was observed in 1975 and 1976 during exceptionally warm summers with water temperatures above 20°C in July and August of 1976 (Drinkwaard 1999). The next major larval outbursts occurred in 1982, 1986, and 1989 (Drinkwaard 1999). The oyster population increased dramatically from then onwards. Monitoring of the area expansion of oyster reefs in the Oosterschelde revealed an increase from 0 ha in 1976 to 15–35 ha in 1980, 210–370 ha in 1990, and 640 ha in 2002 (Kater and Baars 2003).

In France, *C. gigas* expanded much faster. Since the introduction of broodstock from British Columbia and Japan in 1971, spat recruitment has been successful with the exception of three specific years (1972, 1981, and 1986) when abnormally low temperatures were held responsible for low spatfalls (Grizel and Héral 1991). A similar rapid rise in oyster densities occurred in New Zealand, where the first naturally dispersed oysters were found in 1971 and a strong increase in spat abundance has been observed ever since. A marked rise in temperature during the main spatting period was held responsible for the dramatic increase of *C. gigas* spatfalls, which superseded those of the native rock oyster *Saccostrea glomerata* in 1978 (Dinamani 1978, 1991). In Tasmania and New South Wales (Australia), however, only erratic spatfalls occurred after the introduction of *C. gigas* and low water temperature and high salinity were considered to be major limiting factors (Ayres 1991). Nevertheless, large oyster reefs were formed about 9 years after the first oyster spat was observed in Tasmania and a rapid spread was documented in some estuaries in New South Wales. Comparing the spread and recruitment success of *C. gigas* in the Wadden Sea with that in other areas, it can be assumed that Pacific oysters here are at the edge of their physiological range and are expected to rely on high late-summer water temperatures occurring at least once every 5 years.

It is well known that the spread of exotic species may depend on temperature regimes and may profit from climate change (Lodge 1993; Nehring 1998; Franke et al. 1999; Stachowicz et al. 2002; Walther et al. 2002). In the Wadden Sea, the American slipper limpet (*Crepidula fornicata*) is limited by cold winter temperatures and is expected to increase in abundance if climate change should lead to milder winters (Thieltges et al. 2004). Another example is the introduced cord-grass, *Spartina anglica*, which is increasing in the northern Wadden Sea presumably as a result of warmer spring seasons (M. Loebl, J.E.E. van Beusekom, and K. Reise, submitted). Regarding the Pacific oyster, a possible climate change involving warmer late-summer water temperatures or a higher frequency of hot summers could have a profound impact on its abundance in the northern Wadden Sea.

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