Helgol Mar Res (2008) 62:177–188
DOI 10.1007/s10152-008-0106-y

ORIGINAL ARTICLE

Documentation of sites of intertidal blue mussel (*Mytilus edulis* L.) beds of the Lower Saxonian Wadden Sea, southern North Sea (as of 2003) and the role of their structure for spatfall settlement

Marc Herlyn · Gerald Millat · Birgit Petersen

Received: 10 April 2007 / Revised: 17 December 2007 / Accepted: 8 January 2008 / Published online: 5 February 2008

Abstract Field surveys (dating back to 1950) and aerial photograph series (dating back to 1966) were evaluated to determine sites of intertidal blue mussel (*Mytilus edulis*) beds at the Wadden Sea coast of Lower Saxony. Maps were prepared indicating sites of blue mussel beds during the last decades. A table gives additional information on the presence (or absence) of blue mussel beds at each site at the time of large-scale surveys. Altogether 187 sites of *M. edulis* beds were recorded in the investigation area. In spring 1996, there were still only 19 sites where mussel beds still occurred, although at 51 sites residual mussel-bed structures were present, e.g. shell bases of former beds or protruding patches (which had been occupied by *M. edulis* before the beds vanished) and open spaces. At that time, the majority of the sites contained neither mussel beds nor mussel-bed structures. The analysis of recent data confirmed that mussel larvae have preferred to settle in sites of present mussel beds and sites with bases of former mussel beds. There was no preferential selection of one of these categories (settled beds vs. shell bases). On the other hand, the presence of mussel beds or mussel bed structures is not obligatory for settlement, because sites without those structures were also re-settled by the spatfall in 1996, even though on a smaller scale.

Communicated by H.-D. Franke.

M. Herlyn (✉) · B. Petersen
Niedersächsischer Landesbetrieb für Wasserwirtschaft,
Küsten- und Naturschutz, An der Mühle 5,
26548 Norderney, Germany
e-mail: marc.herlyn@nlwkn-ny.niedersachsen.de

G. Millat
Nationalparkverwaltung Niedersächsisches Wattenmeer,
Virchowstr. 1, 26382 Wilhelmshaven, Germany

Keywords *Mytilus edulis* · Blue mussel bed · Spatfall · Site documentation · Wadden Sea of Lower Saxony · Aerial photography · Field investigation

Introduction

The decline of the intertidal blue mussel (*Mytilus edulis*) beds at the coast of Lower Saxony from the mid-1980s (Obert and Michaelis 1991; Michaelis et al. 1995; Herlyn 1996, 1999; Herlyn and Michaelis 1996; Zens et al. 1997) to the mid-1990s (Herlyn and Millat 2000; De Vlas et al. 2005) was examined by extensive evaluation of the data sources on the intertidal mussel bed stocks in that region.

The spatial distribution of blue mussel beds in the Wadden Sea as a dynamic ecosystem (Reise 1985; Dittmann 1999) is remarkably constant because mussel beds often reestablish at the same locations (Dankers and Koelemaij 1989; Nehls and Thiel 1993; Nehls et al. 1997; Brinkman et al. 2002). Areas where blue mussel beds are present or occurred in the past are described as mussel bed sites. At suitable sites mussel beds can develop to the mature stage as an extraordinary biocoenosis showing high stability over decades (Linke 1939, 1954; Dankers and Koelemaij 1989; Obert and Michaelis 1991; Ruth 1994; Nehls et al. 1997). These locations "*where mature mussel beds (one or more) occur regularly over several years*" were defined as stable sites (CWSS 2002; De Vlas et al. 2005). Ruth (1994) infers that only drastic changes of abiotic conditions, e.g. caused by anthropogenic intervention, could destroy the suitability of sites for long-term development of mussel beds.

Blue mussel beds are characterised by their central role in terms of biodeposition, sediment stabilisation, filtration, consumption, secondary production, biomass, biodiversity

and as an important food resource for invertebrates, fish and birds (Gosling 1992; Nehls et al. 1997). Because of their characteristic features Dankers (1993) construes mature mussel beds as "superorganisms" with slow reproduction and low mortality.

Besides stable sites there are also sites settled by blue mussel beds with lower stability and lifespan (Ruth 1991; Nehls and Thiel 1993; Hilgerloh and Herlyn 1996; Hilgerloh et al. 1997; Nehls et al. 1997; Brinkman et al. 2002); these are described as unstable sites. Assessments about the suitability of locations for settlement of blue mussel larvae and development of mussel beds, based on the first documentation (Millat and Herlyn 1999; supplemented with surveys 1996 and 1997) as well as the more recent analysis (Herlyn and Millat 2004), were used for the preparation of management plans for blue mussel beds of Lower Saxony. The intention of the management plans is to protect sites of mature beds (indicated by high continuity) and hence the endangered biocoenoses, and to balance this with economic interests of the fishery.

One aim of this study was to update the first documentation of mussel bed sites (Millat and Herlyn 1999) with data from additional surveys which have meanwhile been regularly conducted.

Furthermore, taking as an example the extraordinary spatfall of *M. edulis* in summer 1996, an analysis of preferred mussel bed sites for larvae settlement was conducted: have structures been left at the mussel bed sites from which the mussel beds have disappeared? Are these structures obligatory for re-settlement of mussel bed sites?

Methods

The documentation of intertidal mussel bed sites was carried out for the Wadden Sea area of Lower Saxony, southern North Sea (Fig. 1a–d).

For determination of mussel bed sites aerial photograph series were analysed both in themselves and with additional ground truthing, and the results of pure field investigations were also consulted (Millat and Herlyn 1999).

Aerial photograph series from 1966, 1975 and 1980 (Table 1) were interpreted visually. For the areas of the Wanger and Wurster Watt in 1975 the habitat atlas of

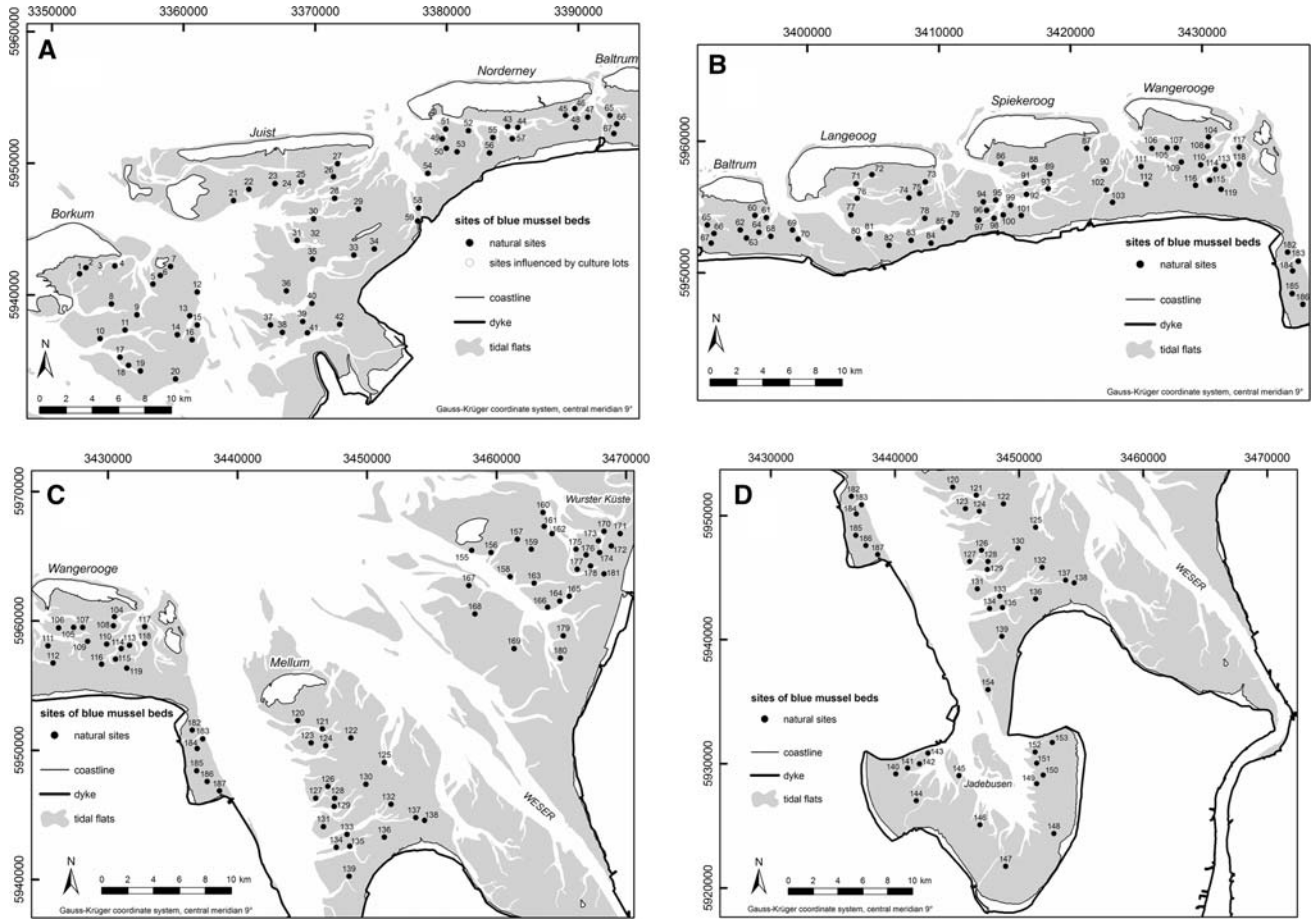

Fig. 1 Documentation of sites of intertidal blue mussel (*Mytilus edulis* L.) beds of the Lower Saxonian Wadden Sea (as of 2003); **a** Borkum—Baltrum, **b** Baltrum—Wangerooge, **c** Wangerooge—Wurster Küste, **d** Jadebusen

Table 1 Data sources for the documentation of sites of intertidal blue mussel (*Mytilus edulis*) beds at the coast of Lower Saxony, southern North Sea (state 2003)

Methods	Year of survey	Scale	References
Remote sensing	1966	1:50,000	archive of the NLÖ-FSK
	1975	1:52,000	archive of the NLÖ-FSK; Wurster and Wanger Watt: Dijkema et al. (1989)
	1980	1:50,000	archive of the NLÖ-FSK
Remote sensing and field investigations	1989/1991	1:28,000	Michaelis et al. (1995)
	1994	1:28,000 1:15,000	Zens et al. (1997)
	1996		Herlyn and Millat (2004)
	Spring	1:15,000	
	Autumn	1:15,000	
	1997	1:15,000	Herlyn and Millat (2004)
	1999	1:15,000	Herlyn and Millat (2004)
	2000	1:15,000	Herlyn and Millat (2004)
	2001	1:15,000	Herlyn and Millat (2004)
	2002	1:15,000	Herlyn and Millat (2004)
	2003	1:15,000	Herlyn and Millat (2004)
Field investigations	1950/1951	–	Krause (1951, 1952): Juist
	1952	–	Krause (1953): Baltrum
	1953	–	Krause (1954): Langeoog
	1958	–	Müller (1959): Bensersiel
	1960/1961	–	Müller (1964): Dornumersiel
	1964	–	Michaelis (1970): Minsener Oog
	1965	–	Michaelis (1968): NE Wurster Watt
	1967	–	Michaelis (1969): N Wurster Watt
	1969	–	Michaelis (1976): W Wurster Watt
	1972	–	Hauser and Michaelis (1975): Großer Knechtsand
	1973/1975	–	Meyer and Michaelis (1980): Hoher Weg
	1975/1977	–	Michaelis (1987): Jadebusen
	1981	–	Obert (1982): Borkum
	1986	–	Grotjahn (1990): Spiekeroog
	1987	–	Obert and Michaelis (1991): Norderney

Only in case of remote sensing

Dijkema et al. (1989) was consulted. Field investigations of different smaller areas from 1950 to 1987 and surveys of the whole intertidal mussel stock of the Wadden Sea area of Lower Saxony by aerial photography with ground truth investigations in 1989/91 and 1994 were additional data sources (Table 1). The data base of Millat and Herlyn (1999) was complemented by surveys of the whole intertidal mussel bed stock in 1996, 1997 and annually from 1999 to 2003 (Herlyn and Millat 2004). Exceptionally, in 1996 two surveys were carried out: the first in spring and the second in autumn, which was added in order to incorporate the extraordinary spatfall in summer 1996.

The data sources mentioned above (Table 1) were evaluated and sites of blue mussel beds were determined. Regarding the proofs of mussel beds we followed the definition of CWSS 2002 (cited in De Vlas et al. 2005; Herlyn 2005) "*A mussel bed is a benthic community structured by blue mussels. It may consist of a spatially well defined irregular collection of more or less protruding smaller beds, which may be called patches, separated by open spaces. This description entails also young beds with a high abundance of small mussels. The described structure may not be so distinct in young beds or just settled beds (spatfall).*" Within the patches there are also areas without mussels. Thus, the area covered by mussels generally occupies only a part of the whole mussel bed area (Maas Geesteranus 1942; Linke 1954; Michaelis et al. 1995). Mussel beds were considered to be absent if their typical structures (with patches settled by mussels and open spaces without settlement by mussels) were not existent or if the results of the accompanying ground truth investigations indicated that there were only isolated mussels or mussel clumps left on the site. Information which was assessed by field investigation was used as "ground truth" for verifying the interpretation of the aerial photographs. The prepared maps (Fig. 1a–d) show the sites of mussel beds and contain no additional

information such as extent, biomass and abundance. The symbols for the sites are located roughly in the center of the recorded mussel beds. As cleared with the corresponding Department of Fisheries (Staatliches Fischereiamt Bremerhaven) sites less than 200 m away from cultivated plots were assessed as influenced directly by man and were not recorded as natural sites (Table 2).

In spring 1996, the situation of the stock differed considerably from other years because the previous decline and effects of the ice winter 1995/1996 led to an extraordinary low mussel bed stock (Herlyn and Millat 2000; De Vlas et al. 2005). A large proportion of the mussel beds disappeared, but at the same time some of the affected sites still showed mussel bed structures with patches and open spaces. These unsettled patches were the bases of the vanished beds, consisting of the underlying, hardened part of the former settled patches, which was enriched with dead shell material. These structures were recognizable by remote sensing, like the structures of settled mussel beds. In such cases, the distinction between mussel-bed presence and absence was possible only by additional ground truth investigation. Because of that extraordinary situation, the results of the field investigations in spring 1996 are also represented within this study. The methods that were used in the field were developed for investigation of blue mussel beds and were described by Herlyn and Millat (2000).

The survey in spring 1996 was not conducted along the Wurster Küste (sites 154–181), because at that time it was impossible to distinguish reliably the shell bases of former mussel beds from the pure shell beds distributed there (Michaelis et al. 1995).

Results

For the presentation of the results the tidal flats of Lower Saxony were divided into four subregions: (1) from Borkum to Baltrum (Fig. 1a), (2) from Baltrum to Wangerooge (Fig. 1b), (3) from Wangerooge to the Wurster Küste (Fig. 1c), (4) Jadebusen (Fig. 1d). Table 1 contains the data base and Table 2 shows the occurrence or absence of mussel beds at each site at the time of the selected surveys.

After the severe winter 1995/1996, 34 sites were investigated in the field. Nine of them were settled by blue mussel beds according to the above definition, even though these beds were just colonized by mussels in low densities with biomass values (living mussels) between approx. 0.2 and 106 t (Table 3). The remaining 25 sites were not settled by *M. edulis* beds (apart from isolated specimens and/or conglomerates of just a few mussels, e.g. site 95 with fewer mussels on the bed than are needed to implement the sampling procedure). Twenty-four of these 25 sites still had mussel-bed structures such as bases of former beds shaped by shell material (as determined both by remote sensing and ground truth investigation).

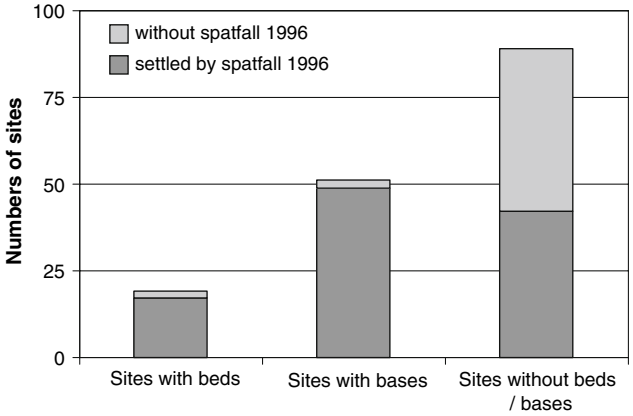

Fig. 2 Comparison of settlement by the *Mytilus edulis* spatfall from summer 1996 between (1) sites with mussel beds, (2) sites with shell bases of beds and (3) sites without mussel beds or shell bases of beds

By remote sensing, structures of mussel beds and shell bases of beds were recognizable on 70 out of 159 sites. From the above-mentioned ground truth information, we conclude that approximately 27% ($n = 19$ sites) of these 70 sites were settled by mussel beds. Consequently, the number of sites where mussel beds disappeared amounted to 140 out of 159 sites. Whereas a little more than a third of these 140 sites still had mussel bed structures ($n = 51$ sites), the major part ($n = 89$ sites) showed no recognizable evidence of former mussel beds.

The majority of the sites which were settled by the spatfall from summer 1996 showed mussel beds or shell bases of mussel beds, although the number of these sites was below the number of those without mussel bed structures (Fig. 2): Nearly 90% of the sites with beds and more than 95% of the sites with bases of beds were settled by the spatfall, whereas less than 50% of the sites without comparable structures were used for settlement.

Discussion

The documentation by Millat and Herlyn (1999) offered an overview of the distribution of blue mussel bed sites over a large-scale area of the Wadden Sea. These sites are locations where blue mussel beds existed in the past and in case of mature beds occurred over long periods. In the present study the documentation is continued with data sets obtained in large-scale surveys of the blue mussel stock of the Lower Saxonian intertidal in 1996, 1997 and annually from 1999 to 2003. The methodological approach of the first documentation was chosen again because prior to the survey of Michaelis et al. (1995), no area-wide data for

Table 2 Documentation of sites of intertidal blue mussel (*M. edulis*) beds at the coast of Lower Saxony, southern North Sea

Site (no.)	Aerial photography			Aerial photography and field investigation										Field investigation (number in brackets = year of survey)
	1966	1975	1980	1989/1991	1994sp	1996sp	1996au	1997sp	1999sp	2000sp	2001sp	2002sp	2003sp	
1	X	X	X	X	–	–	–	–	X	X	X	–	–	X (1981)
2	X	X	X	X	–	–	–	–	X	X	X	X	X	X (1981)
3*	X	X	X	X	X	S	X	X						X (1981)
4	X	X	X	X	–	–	X	X	–	–	X	X	X	X (1981)
5	X	X	X	–	–	–	–	–	–	X	X	X	X	X (1981)
6	X	X	X	–	–	–	–	–	–	–	–	–	–	X (1981)
7	X	X	X	–	–	–	–	–	–	–	–	–	X	X (1981)
8	X	X	X	X	–	–	X	X	X	X	X	X	X	X (1981)
9	–	X	X	–	–	–	–	–	–	–	–	–	–	X (1981)
10	X	X	X	–	–	–	–	–	X	–	–	–	–	X (1981)
11	X	X	X	–	–	–	–	X	X	–	–	–	–	X (1981)
12	X	X	X	X	X	XS	X	X	X	X	X	X	X	X (1981)
13	X	X	X	X	–	–	X	X	X	X	X	X	X	X (1981)
14	X	X	X	–	–	–	–	–	X	X	X	X	–	X (1981)
15	X	X	X	–	–	–	X	X	X	X	X	X	X	X (1981)
16	X	X	X	–	–	–	X	X	X	X	X	X	X	X (1981)
17	–	–	–	X	–	–	–	–	–	–	–	–	–	– (1981)
18	X	X	X	–	–	–	X	X	X	X	X	X	X	X (1981)
19	X	X	–	–	X	XS	X	X	X	X	X	X	X	X (1981)
20	X	X	X	X	X	X	X	X	X	X	X	X	X	X (1981)
21	X	X	X	X	X	X	X	X	X	X	X	X	X	X (1950/1951)
22	X	X	–	X	X	XS	X	X	X	X	X	X	X	X (1950/1951)
23	X	–	X	X	X	S	X	X	X	X	X	X	X	X (1950/1951)
24*	X	X	X	X	X	XS	X	X	X	X	X	X	X	X (1950/1951)
25	–	–	X	X	X	XS	X	X	X	X	X	–	–	X (1950/1951)
26	X	X	X	X	X	XS	X	–	X	X	X	X	X	– (1950/1951)
27	X	X	X	X	X	S	X	X	X	X	X	–	–	– (1950/1951)
28	–	–	–	–	–	–	–	–	–	–	–	–	–	X (1950/1951)
29	X	X	X	X	–	–	–	–	X	–	X	X	X	– (1950/1951)
30	X	X	X	–	–	–	X	X	X	X	X	–	–	X (1950/1951)
31	X	X	X	–	–	–	X	–	–	–	–	–	–	X (1950/1951)
32*	X	X	X	–	X	XS	X	X						X (1950/1951)
33	X	X	X	–	X	XS	X	X	X	X	X	X	X	– (1950/1951)
34	X	X	X	–	X	XS	–	–	–	–	X	X	X	– (1950/1951)
35	X	X	X	X	X	XS	X	X	X	X	X	X	X	X (1950/1951)
36	X	X	X	X	X	XS	X	X	X	X	X	X	–	X (1950/1951)
37	X	X	–	–	–	–	–	–	–	–	–	–	–	– (1950/1951)
38	X	X	X	–	–	–	X	X	X	X	X	X	–	– (1950/1951)
39	X	X	X	–	–	XS	X	X	X	X	X	X	–	– (1950/1951)
40	X	X	X	–	–	–	X	X	X	X	X	X	–	X (1950/1951)
41	–	–	–	–	–	–	X	X	X	–	–	–	–	X (1950/1951)
42	–	–	–	–	–	–	X	–	X	X	X	–	–	X (1950/1951)
58	X	X	–	–	–	–	X	X	X	X	X	X	X	X (1987)
59	–	X	–	–	–	–	X	X	X	X	X	X	X	X (1987)
43	–	–	–	–	–	–	X	X	X	X	X	X	X	X (1987)
44	–	–	–	–	–	–	–	–	–	–	–	–	–	X (1987)

Table 2 continued

Site (no.)	Aerial photography			Aerial photography and field investigation										Field investigation (number in brackets = year of survey)
	1966	1975	1980	1989/1991	1994sp	1996sp	1996au	1997sp	1999sp	2000sp	2001sp	2002sp	2003sp	
45	X	X	X	X	X	XS	X	X	X	X	X	X	X	X (1987)
46	X	X	X	X	X	S	X	X	X	X	X	X	X	X (1987)
47	X	X	X	X	X	S	X	X	X	X	X	X	X	X (1987)
48	–	–	X	X	X	S	X	X	X	X	X	X	X	– (1987)
49	X	–	X	–	–	–	X	X	X	–	–	–	–	– (1987)
50	X	–	X	–	–	–	X	X	–	–	X	X	X	– (1987)
51	X	X	X	X	X	XS	X	X	X	X	X	X	X	– (1987)
52	X	X	X	–	–	–	X	X	X	–	X	X	–	– (1987)
53	–	–	–	–	–	–	–	–	–	–	–	–	–	X (1987)
54	–	–	X	–	–	–	X	X	X	X	X	X	X	– (1987)
55	X	X	X	X	X	X	X	X	X	X	X	X	X	– (1987)
56	X	X	X	X	X	S	X	X	X	X	X	X	X	– (1987)
57	–	–	–	–	–	XS	–	X	X	X	X	X	X	X (1987)
60	X	X	X	X	X	XS	X	X	X	X	X	X	X	X (1952)
61	–	X	X	X	X	S	X	X	X	X	X	X	X	X (1952)
62	X	X	–	X	X	XS	X	X	X	X	X	X	–	X (1960/1961)
63	X	X	X	–	X	S	–	–	–	–	–	–	–	– (1960/1961)
64	X	X	X	–	–	–	–	–	X	X	X	X	X	– (1960/1961)
65	X	X	X	–	–	XS	–	–	–	–	–	–	–	X (1960/1961)
66	X	X	X	X	X	–	–	–	X	X	X	X	X	X (1960/1961)
67	X	X	–	–	–	–	–	–	X	X	X	X	–	– (1960/1961)
68	X	X	X	X	X	S	X	X	X	X	X	X	X	X (1960/1961)
69	X	X	X	X	X	S	X	X	X	X	X	X	X	X (1960/1961)
70	X	X	X	–	–	–	X	X	X	X	X	X	X	X (1960/1961)
71	–	X	ND	X	X	XS	–	X	X	X	X	X	X	X (1953)
72	–	X	ND	–	X	–	–	X	–	–	–	–	–	– (1953)
73	X	X	X	–	X	S	X	X	X	X	X	X	X	X (1953)
74	X	X	X	X	X	–	–	X	X	X	X	X	X	– (1953)
75	X	X	X	X	X	XS	X	X	X	X	X	X	X	X (1953)
76	X	X	ND	–	–	–	X	X	X	X	X	X	X	X (1953)
77	X	X	ND	–	–	–	–	–	–	–	–	–	–	X (1953)
78	X	X	X	X	X	S	X	X	X	X	X	X	X	X (1953)
79	X	X	X	X	X	XS	X	X	X	X	X	X	X	– (1953)
80	–	–	ND	–	–	–	–	–	X	–	–	–	–	X (1958)
81	X	X	ND	–	–	–	X	X	X	X	X	X	X	X (1958)
82	–	–	ND	–	–	–	–	–	–	–	–	–	–	X (1958)
83	X	X	X	X	–	–	–	–	–	–	–	–	–	– (1958)
84	–	–	–	–	–	–	–	X	X	X	X	X	X	– (1958)
85	X	X	X	X	X	–	X	X	X	X	X	X	X	– (1958)
94	X	X	X	X	–	–	X	X	X	X	X	X	X	– (1986)
95	X	X	X	X	X	S	X	X	X	X	X	X	X	X (1986)
96	X	X	X	X	X	S	X	X	X	X	X	X	X	X (1986)
97	X	X	X	X	X	–	X	X	X	X	X	X	X	– (1986)
98	X	X	X	X	–	–	X	–	X	X	X	X	X	X (1986)
86	X	X	X	X	X	XS	X	X	X	X	X	X	X	X (1986)
87	X	X	X	X	X	X	–	X	X	X	X	X	X	– (1986)

Table 2 continued

Site (no.)	Aerial photography			Aerial photography and field investigation										Field investigation (number in brackets = year of survey)
	1966	1975	1980	1989/1991	1994sp	1996sp	1996au	1997sp	1999sp	2000sp	2001sp	2002sp	2003sp	
88	X	X	X	X	X	S	X	X	X	X	X	X	X	– (1986)
89	X	X	X	X	X	XS	X	X	X	X	X	X	X	X (1986)
90	X	X	X	X	X	X	X	X	X	X	X	X	X	X (1986)
91	X	X	X	X	–	–	X	X	X	–	–	–	–	X (1986)
92	X	X	X	X	–	–	X	X	X	X	X	X	X	– (1986)
93	X	X	X	X	–	–	X	X	X	X	X	X	X	– (1986)
99	X	X	X	–	–	S	X	X	X	X	X	X	–	– (1986)
100	–	–	–	–	X	–	–	–	–	–	–	–	–	– (1986)
101	–	X	X	X	–	–	–	–	–	–	X	–	–	X (1986)
102	X	X	X	X	–	–	–	–	–	–	–	–	–	– (1986)
104	ND	X	ND	X	–	–	–	X	X	X	X	X	X	ND
105	–	X	X	X	–	–	X	X	X	X	X	–	–	ND
106	X	X	ND	X	–	–	–	–	X	X	X	X	X	ND
107	X	X	ND	X	–	–	X	X	X	X	X	X	X	ND
108	ND	X	ND	X	X	X	X	X	X	X	X	X	X	ND
109	ND	X	ND	X	X	XS	X	–	X	–	–	–	–	ND
110	ND	X	ND	X	X	XS	X	X	X	X	X	X	X	ND
111	X	X	–	–	–	–	–	–	–	–	–	–	–	ND
112	–	X	X	–	–	–	X	X	X	X	X	X	X	ND
113	ND	X	ND	–	–	–	X	X	X	X	X	X	X	– (1964)
114	ND	X	ND	–	X	S	X	X	X	X	X	X	X	– (1964)
115	ND	X	ND	–	X	–	X	X	X	X	X	X	X	X (1964)
116	ND	X	ND	–	–	–	–	X	X	X	X	X	–	X (1964)
117	ND	ND	ND	–	–	–	–	–	–	–	–	–	–	X (1964)
118	ND	ND	ND	X	X	S	X	X	X	X	X	X	X	X (1964)
119	ND	ND	ND	–	–	–	–	–	–	–	–	–	–	X (1964)
103	–	X	–	X	X	XS	X	X	X	X	X	X	X	– (1986)
120	X	X	ND	X	X	S	X	X	X	X	X	X	X	X (1973/1975)
121	X	X	ND	X	X	S	X	X	X	X	X	X	X	X (1973/1975)
122	X	X	ND	X	X	XS	X	X	X	X	X	X	X	X (1973/1975)
123	X	X	ND	–	–	–	–	–	X	–	–	–	–	– (1973/1975)
124	–	X	ND	–	–	–	X	X	X	–	–	–	–	X (1973/1975)
125	–	X	ND	–	–	–	–	–	–	–	–	–	–	– (1973/1975)
126	–	X	ND	–	–	–	–	–	X	–	X	–	–	X (1973/1975)
127	–	X	ND	–	–	–	–	–	X	–	–	–	–	X (1973/1975)
128	X	X	ND	X	–	XS	X	X	X	X	X	X	X	– (1973/1975)
129	–	–	ND	–	–	–	–	–	X	–	–	–	–	X (1973/1975)
130	X	X	ND	–	X	XS	X	X	X	X	X	X	X	– (1973/1975)
131	–	–	ND	–	–	–	–	–	–	–	–	–	–	X (1973/1975)
132	X	X	ND	X	X	XS	X	X	X	X	X	X	X	X (1973/1975)
133	–	–	ND	X	–	–	–	–	–	–	–	–	–	– (1973/1975)
134	–	–	ND	–	–	–	–	–	–	–	–	–	–	X (1973/1975)
135	–	–	ND	–	–	–	–	–	–	–	–	–	–	X (1973/1975)
136	–	–	ND	–	X	–	X	X	X	–	–	–	–	X (1973/1975)
137	–	X	ND	–	–	–	X	–	–	–	–	–	–	X (1973/1975)
138	X	–	ND	–	–	–	–	–	–	–	–	–	–	X (1973/1975)

Table 2 continued

Site (no.)	Aerial photography			Aerial photography and field investigation										Field investigation (number in brackets = year of survey)
	1966	1975	1980	1989/1991	1994sp	1996sp	1996au	1997sp	1999sp	2000sp	2001sp	2002sp	2003sp	
139	–	X	ND	–	–	–	X	X	X	X	X	X	X	X (1973/1975)
140	ND	ND	ND	X	X	X	X	X	X	X	X	X	X	– (1975/1977)
141	ND	ND	ND	X	X	X	X	X	X	X	X	X	X	X (1975/1977)
142	ND	ND	ND	–	X	X	X	–	X	X	X	X	X	X (1975/1977)
143	ND	ND	ND	X	X	XS	X	X	X	X	X	X	X	– (1975/1977)
144	ND	ND	ND	X	X	S	X	X	X	X	X	X	X	– (1975/1977)
145	ND	ND	ND	X	–	–	X	X	X	X	X	X	X	X (1975/1977)
146	ND	ND	ND	X	X	XS	X	X	X	X	X	X	X	X (1975/1977)
147	ND	ND	ND	–	–	–	–	–	–	–	X	X	X	X (1975/1977)
148	ND	ND	ND	–	–	–	–	–	–	–	–	–	–	X (1975/1977)
149	ND	ND	ND	–	X	S	X	X	X	X	X	X	X	X (1975/1977)
150	ND	ND	ND	X	X	XS	–	–	X	X	X	X	X	– (1975/1977)
151	ND	ND	ND	–	X	S	X	X	X	X	X	X	X	X (1975/1977)
152	ND	ND	ND	X	X	XS	–	X	X	X	X	X	X	X (1975/1977)
153	ND	ND	ND	X	X	–	X	–	–	–	–	–	–	X (1975/1977)
154	ND	ND	ND	–	–	ND	–	–	–	–	–	–	–	X (1975/1977)
155	ND	–	ND	–	–	ND	–	–	–	–	–	–	–	X (1972)
156	ND	X	ND	–	–	ND	X	–	X	–	–	–	–	X (1972)
157	ND	–	ND	X	–	ND	X	X	X	X	X	X	X	X (1972)
158	ND	X	ND	–	–	ND	–	–	X	X	X	–	–	X (1972)
159	ND	–	ND	–	–	ND	–	–	–	–	–	–	–	X (1972)
160	ND	–	ND	–	–	ND	–	–	–	–	–	–	–	X (1967)
161	ND	X	ND	–	–	ND	–	–	X	X	X	X	–	X (1967)
162	ND	X	ND	–	–	ND	–	–	–	–	–	–	–	X (1967)
163	ND	–	ND	–	–	ND	–	–	–	–	–	–	–	X (1967)
164	ND	X	ND	–	–	ND	–	–	–	–	–	–	–	X (1967)
165	ND	X	ND	–	–	ND	X	–	X	X	X	X	X	X (1967)
166	ND	X	ND	–	–	ND	X	X	X	X	X	–	–	X (1967)
167	ND	–	ND	–	–	ND	–	–	–	–	–	–	–	X (1969)
168	ND	–	ND	–	–	ND	–	–	–	–	–	–	–	X (1969)
169	ND	X	ND	–	–	ND	–	–	–	–	X	–	–	X (1969)
170	ND	X	ND	X	–	ND	X	X	X	X	X	X	X	X (1965)
171	ND	–	ND	–	–	ND	–	–	–	X	X	–	–	X (1965)
172	ND	–	ND	–	–	ND	X	–	X	X	X	X	X	X (1965)
173	ND	–	ND	–	–	ND	–	–	X	X	–	–	–	X (1965)
174	ND	–	ND	–	–	ND	X	X	X	X	X	X	X	X (1965)
175	ND	–	ND	–	–	ND	–	–	–	–	–	–	–	X (1965)
176	ND	–	ND	–	–	ND	–	–	X	X	X	X	X	X (1965)
177	ND	–	ND	–	–	ND	–	–	–	–	–	–	–	X (1965)
178	ND	–	ND	–	–	ND	–	–	–	–	–	–	–	X (1965)
179	ND	–	ND	–	–	ND	–	–	–	–	–	–	–	X (1965)
180	ND	X	ND	–	–	ND	–	–	–	–	–	–	–	X (1965)
181	ND	X	ND	–	–	ND	–	–	X	X	X	X	X	– (1965)
182	ND	–	ND	X	X	X	X	X	X	X	X	X	X	ND
183	ND	–	ND	X	–	–	–	–	–	–	–	–	–	ND
184	ND	–	ND	X	–	–	X	X	X	X	X	X	X	ND

Table 2 continued

Site (no.)	Aerial photography			Aerial photography and field investigation										Field investigation (number in brackets = year of survey)
	1966	1975	1980	1989/1991	1994sp	1996sp	1996au	1997sp	1999sp	2000sp	2001sp	2002sp	2003sp	
185	ND	–	ND	X	X	XS	–	–	X	–	–	–	–	ND
186	ND	–	ND	X	–	–	X	X	X	X	–	–	–	ND
187	ND	–	ND	X	X	X	X	X	X	X	X	X	X	ND

Data base see Table 1; altered according to Herlyn and Millat 2004) (sp = spring; au = autumn; X = occurrence of mussel bed; – = absence of mussel bed; ND = no data base available; only spring 1996: S = structure of former mussel bed; XS = no distinction possible between (settled) mussel bed and site with structures of former bed (without settlement by *M. edulis* bed); * = former natural site, but culture lot since 1998 (No. 3), less than 200 m away from culture lot since 2000 (No. 24), partly overlapping with neighbouring culture lot since 1999 (No. 32)

Table 3 Area, cover, proportion and biomass (weight of living mussels) of intertidal blue mussel beds at the coast of Lower Saxony in spring 1996

Site	Area (m^2)	Cover (%)	Proportion (%)	Biomass (kg m^{-2})	Total biomass (*t*)
20	72,582	14	63	5.25	34
21	169,290	20	18	5.94	36
55	240,645	20	46	4.78	106
87	38,427	26	21	5.07	11
90	510,131	100	1	2.26	12
108	12,574	23	36	9.66	10
140	210,033	5	98	7.86	81
182	78,083	17	65	4.39	38
187	9,442	40	3	1.79	0.2

parameters other than presence/absence of mussel beds are available for the area of the Lower Saxonian Wadden Sea. Thus, only this approach enables consideration of the data base from the decades before 1989/1991, so that a longer period (dating back to the 1950s) can be included in this study. Due to natural changes of the Wadden Sea (e.g. shifting of gullies) it may be necessary to revise the present documentation of mussel bed sites periodically by means of ongoing surveys.

This documentation makes it possible to present the history of blue mussel bed occurrences at the determined sites since the beginning of the 1950s. Locations where mature mussel beds occur regularly over several years were defined as stable sites (De Vlas et al. 2005), with extraordinary importance for the whole population. Within this study, repeated records of mussel beds at the same sites are interpreted as evidence for sites of mature beds. But on the basis of the available data, the distinction between stable and unstable sites as a natural bifurcation is not possible for the stock as a whole. Only for those sites with high continuity on the one hand (e.g. sites 20, 55, 120) and those with low continuity on the other hand (e.g. sites 9, 49, 72) can this assessment be achieved. In the field, the relief of the beds provides additional information about the stability of sites: According to Herlyn and Millat (2004) relief (maximal height differences between open spaces and protruding patches) and stability of mussel beds are significantly correlated. The higher the mussel patches were, the more stable were the investigated mussel beds. Presumably, this connection is a question of mutual influence between relief and stability. The relation between relief and age of mussel beds was already recognized by Linke (1954), who described height differences of up to 1.80 m for old mussel beds.

Against the background of declines of blue mussel stocks in large areas of the Wadden Sea (Smit et al. 1998; Obert and Michaelis 1991; Michaelis et al. 1995; Zens et al. 1997; Herlyn and Millat 2000; de Vlas et al. 2005) and partially controversial discussions about the causes, it is necessary to acquire more information about blue mussel stock development and the importance of sites of mussel beds, among other things in terms of ensuring the undisturbed bed development especially at sites of mature beds. The evaluation of widespread data sources presented here shows one way to reach this goal despite the scanty data base provided by large-scale surveys of mussel beds in the past: In Lower Saxony, for example, the first synchronous survey of the complete stock of intertidal blue mussel beds was not carried out until 1994 (Zens et al. 1997).

For the Dutch part of the Wadden Sea a habitat model for littoral mussel beds was developed which is likewise based on earlier surveys (in the years 1960–1970) of mussel beds, as well as on environmental characteristics: wave action, flow velocity, median grain size, emersion time and

distance to a gully border (Brinkman et al. 2002). The main aim of the Dutch documentation was the recognition of sites of former mussel beds in the face of extinction of the intertidal mussel bed stock at the end of the 1980s (Brinkman et al. 2002) as a basis for protection. Because local abiotic data were the basis of the Dutch model, it cannot be transferred to other areas without additional investigations (Brinkman et al. 2002). Also, for the Wadden Sea region of Schleswig-Holstein a determination of sites exists. It confirms the approach of this study because it follows comparable methods, based on the analysis of aerial photograph series with additional ground truthing and contact flights (Nehls 1999). As recommended in the Trilateral Monitoring and Assessment Program—Quality Status Report 2004 (Essink et al. 2005), the Dutch model should be extended to the German Wadden Sea, for a comparison of the results of the habitat suitability analysis (Brinkman et al. 2002) with the results of this approach. The combination of the Dutch and the German approaches may inform us better about the stability characteristics of mussel beds and the specific features of stable and unstable sites.

The special situation in 1996 (characterized by a strong decline of intertidal mussel beds until an extraordinary spatfall) enables a large area to be analysed if mussel bed structures were left following the disappearance of blue mussel beds and if these structures were obligatory for recolonization of mussel-bed sites. An investigation of the connection between spatfall settlement outside of mussel-bed sites and substrata was not conducted within this study because of methodological problems with the demarcation of the additional spatfall locations and restricted knowledge about the substrata of these areas. Furthermore, these areas are of lesser importance for long-term colonization—precisely because they are outside of the sites. Similarly, Lutz and Kennish (1992) describe permanent attachment of larvae in adult beds only.

Settlement was defined as "...the descent of larvae from the plankton to the bottom substrate..." (Bayne 1965). Descending *Mytilus* larvae attach preferentially to filamentous substrates like thecate hydroids and filamentous algae (Bayne 1964; Lutz and Kennish 1992). After this primary settlement plantigrades may pass through a secondary drifting phase for selecting sites of permanent attachment. In the literature direct settlement of *M. edulis* larvae on hard substrata without a secondary pelagic phase is also described (Lutz and Kennish 1992). Within the present study the distinction between primary and secondary settlement was not possible because spatfall areas can be surveyed by remote sensing only some months after settlement.

At the end of the decline, only approx. a third of the sites where mussel beds disappeared still had bases of former beds structured by shell material. The situation after the following spatfall 1996 indicates that *M. edulis* larvae prefer such sites and those with actual mussel beds, in each case to the same extent, because there they find suitable substrata for settlement. Linke (1954) emphasizes the importance of dead shell material as a secondary hard substratum for blue mussel recruitment in the Wadden Sea, which is dominated by fine-grained sediments, and already mentions in this context the importance of dead shell material on the sites of former beds. On the other hand, the investigation of the spatfall shows that these structures were not obligatory for re-settlement of sites because sites without mussel-bed structures were also selected, although less extensively. Hard substrata like shells of living mussels, their byssus threads, barnacles and shell material are not obligatory preconditions for settlement; other suitable substrata for settlement are, e.g. protruding feeding tubes of *Lanice conchilega*, macroalgae and eelgrass (Verwey 1952; Linke 1954; Blok de and Geelen 1958; Hertweck 1993, 1995; Flemming and Delafontaine 1994; Meixner 1995; Pulfrich 1995). Presumably, the sites were selected for settlement because of suitable abiotic conditions for mussel beds such as wave action, flow velocity and emersion time (Brinkman et al. 2002). These conditions should prevail at sites which had been colonized successfully in the recent past by mussel beds, given that no drastic changes have since occurred.

During recent years the situation of the *M. edulis* stock has changed drastically, due to the invasion of the Pacific oyster (*Crassostrea gigas*, Thunberg 1793) in the Lower Saxonian Wadden Sea since 1998 (Wehrmann et al. 2000). Within a few years, *C. gigas* has spread in the investigation area of the present study, with intertidal blue mussel beds as one of the preferred substrata for colonization, as in other parts of the Wadden Sea from the Netherlands to Denmark where this species is to be found (De Vlas et al. 2005; Reise et al. 2005; Nehls et al. 2006). Against this background, investigations of the biocoenosis "blue mussel bed" as a continuum are no longer possible in the same configuration as before, with regard to its structure and species composition. Because of the changed configuration of the biocoenosis at sites of previously unaltered mussel beds, a new period of observation should be initiated.

Acknowledgments The authors acknowledge the helpful contributions of two anonymous referees. We are indepted to Dr. H. Marencic (CWSS, Wilhelmshaven) and Dr. G. Hertweck (Senckenberg am Meer, Wilhelmshaven) who gave very valuable comments on the manuscript. We wish to thank K. Kolbe (bio-büro, Norden) who improved and prepared the GIS maps. This study was supported by the Niedersächsische Wattenmeer-Stiftung.

References

Bayne BL (1964) Primary and secondary settlement in *Mytilus edulis* L. (Mollusca). J Anim Ecol 33:513–523

Bayne BL (1965) Growth and delay of metamorphosis of the larvae of *Mytilus edulis* (L.). Ophelia 2:1–47

Blok de JW, Geelen HJFM (1958) The substrastum required for the settling of mussels (*Mytilus edulis* L). Arch Neerl Zool 8(suppl):446–460

Brinkman AG, Dankers N, Van Stralen M (2002) An analysis of mussel bed habitats in the Dutch Wadden Sea. Helgol Mar Res 56:59–75

CWSS (2002) Common wadden sea secretariat, blue mussel monitoring, report of the second TMAP blue mussel workshop on Ameland April 8–10, 2002, Wilhelmshaven, Germany

Dankers N (1993) Integrated estuarine management—Obtaining as a sustainable yield of bivalve resources while maintaining environmental quality. In: Dame RF (ed) Bivalve filter feeders in estuarine and coastal ecosystem processes. NATO ASI series, Springer, Heidelberg, G 33:479–511

Dankers N, Koelemaij K (1989) Variations in the mussel population of the Dutch Wadden Sea in relation to monitoring of other ecological parameters. Helgoländer Meeresunters 43:529–535

De Vlas J, Brinkman B, Buschbaum Chr, Dankers N, Herlyn M, Kristensen PS, Millat G, Nehls G, Ruth M, Steenbergen M, Wehrmann A (2005) Intertidal blue mussel beds. In: Essink K, Dettmann C, Farke H, Laursen K, Lüerßen G, Marencic H, Wiersinga W (eds) Wadden Sea quality status report 2004. Wadden Sea ecosystem No. 19. Trilateral Monitoring and Assessment Group, Common Wadden Sea Secretariat, Wilhelmshaven, pp 190–200

Dijkema KS, Van Thienen G, Van Beek JG (1989) Habitats of the Netherlands, German and Danish Wadden Sea. Research Institute for Nature Management, Texel. Veth Foundation, Leiden

Dittmann S (1999) The Wadden Sea ecosystem—stability properties and mechanisms. Springer-Verlag, Berlin

Essink K, Dettmann C, Farke H, Laursen K, Lüerßen G, Marencic H, Wiersinga W (eds) (2005) Wadden Sea Quality Status Report 2004. Wadden Sea Ecosystem No. 19. Trilateral Monitoring and Asessment Group, Common Wadden Sea Secretariat, Wilhelmshaven

Flemming BW, Delafontaine MT (1994) Biodeposition in a juvenile mussel bed of the East Frisian Wadden Sea (southern North Sea). Neth J Aquat Ecol 28:289–297

Gosling E (1992) The mussel *Mytilus*: ecology, physiology, genetics and culture. Developments in aquaculture and fisheries science, vol. 25. Elsevier Science Publishers, Amsterdam

Grotjahn M (1990) Sedimente und Makrofauna der Watten bei der Insel Spiekeroog. Untersuchungen im Rahmen des "Sensitivitätsrasters Deutsche Nordseeküste". Jber 1987, Forschungsstelle Küste 39:97–119

Hauser B, Michaelis H (1975) Die Makrofauna der Watten, Strände, Riffe und Wracks um den hohen Knechtsand in der Wesermündung. Jber 1974, Forschungsstelle Norderney 26:85–119

Herlyn M (1996) Zur Bestandssituation der Miesmuschelbänke des niedersächsischen Wattenmeeres. Mitteilungen aus der Norddeutschen Naturschutz Akademie 1/1996. Schneverdingen, Germany

Herlyn M (1999) Zur Entwicklung des Miesmuschelbestandes der niedersächsischen Watten. Umweltatlas Wattenmeer Bd. 2 – Wattenmeer zwischen Elb- und Emsmündung. Verlag Eugen Ulmer, Stuttgart, pp 70–71

Herlyn M (2005) Quantitative assessment of intertidal blue mussel (*Mytilus edulis* L.) stocks. Combined methods of remote sensing, field investigation and sampling. J Sea Res 53:243–253

Herlyn M, Michaelis H (1996) Untersuchungen zur Entwicklung von Miesmuschelbänken der niedersächsischen Watten—Unter Berücksichtigung der Miesmuschelfischerei. Umweltforschungsplan des Bundesministers für Umwelt, Naturschutz und Reaktorsicherheit, Forschungsbericht 108 02 085/21

Herlyn M, Millat G (2000) Decline of the intertidal blue mussel (*Mytilus edulis*) stock at the coast of Lower Saxony (Wadden Sea) and influence of mussel fishery on the development of young mussel beds. Hydrobiologia 426:203–210

Herlyn M, Millat G (2004) Wissenschaftliche Begleituntersuchungen zur Aufbauphase des Miesmuschelmanagements im Nationalpark "Niedersächsisches Wattenmeer". Abschlußbericht der Niedersächsischen Wattenmeerstiftung, Wilhelmshaven, Germany, unpublished

Hertweck G (1993) Zeitliche Variabilität und räumliche Inhomogenität in den Substrateigenschaften und der Zoobenthosbesiedlung im Umfeld von Miesmuschelbänken. A: Biofazies und Aktuopaläontologie. Senckenberg am Meer, Bericht 93/1:49–63

Hertweck G (1995) Verteilung charakteristischer Sedimentkörper und Benthossiedlungen im Rückseitenwatt der Insel Spiekeroog, südliche Nordsee. I Ergebnisse der Wattkartierung 1988–1992. Senckenbergiana marit 26:81–94

Hilgerloh G, Herlyn M (1996) Auswirkungen der Prädation auf eine junge Miesmuschelbank. Verh Dtsch Zool Ges 89:306

Hilgerloh G, Herlyn M, Michaelis H (1997) The influence of predation by herring gulls *Larus argentatus* and oystercatchers *Haematopus ostralegus* on a newly established mussel *Mytilus edulis* bed in autumn and winter. Helgoländer Meeresunters 51:173–189

Krause HR (1951) Die biologische Kartierung des westlichen Juister Wattes im Sommer 1950. Jber 1950, Forschungsstelle Norderney 2:1–28

Krause HR (1952) Die Kartierung der Lebensgemeinschaften des östlichen Juister Watts im Jahre 1951. Jber 1951, Forschungsstelle Norderney 3:49–72

Krause HR (1953) Bericht über die Kartierung der Lebensgemeinschaften des Baltrumer Watts im Jahre 1952. Jber 1952, Forschungsstelle Norderney 4:116–129

Krause HR (1954) Die Kartierung der bodenbewohnenden Lebensgemeinschaften im Langeooger Watt. Jber 1953, Forschungsstelle Norderney 5:81–93

Linke O (1939) Die Biota des Jadebusenwattes. Helgoländer Wiss Meeresunters 1:201–348

Linke O (1954) Die Bedeutung der Miesmuscheln für die Landgewinnung im Wattenmeer. Natur und Volk 84:253–261

Lutz RA, Kennish MJ (1992) Ecology and morphology of larval and early postlarval mussels. In: Gosling E (eds) The mussel *Mytilus*: ecology, physiology, genetics and culture. Developments in Aquaculture and Fisheries Science, vol. 25. Elsevier Science Publishers, Amsterdam, pp 53–85

Maas Geesteranus RA (1942) On the formation of banks by *Mytilus edulis* L. L Arch Neerl Zool 6:283–326

Meixner R (1995) Zeitweilige Schillzunahme als Voraussetzung starker Miesmuscheljahrgänge. Inf Fischwirtsch 42:62–65

Meyer M, Michaelis H (1980) Das Makrobenthos des westlichen Hohen Weges. Jber 1979, Forschungsstelle Norderney 31:91–155

Michaelis H (1968) Biologisch-sedimentologische Untersuchung des Wurster Wattes von Spieka bis Arensch. Jber 1966, Forschungsstelle Norderney 18:71–82

Michaelis H (1969) Makrofauna und Vegetation der Knechtsandwatten. Jber 1967, Forschungsstelle Norderney 19:147–173

Michaelis H (1970) Biologische Untersuchung der Watten und Landgewinnungsfelder bei Schillighörn. Jber 1968, Forschungsstelle Norderney 20:61–76

Michaelis H (1976) Die Makrofauna des nördlichen Eversandes (Wesermündung). Jber 1975, Forschungsstelle Norderney 27:167–179

Michaelis (1987) Bestandsaufnahme des eulitoralen Makrobenthos im Jadebusen in Verbindung mit einer Luftbildanalyse. Jber 1986, Forschungsstelle Küste, Norderney 38:13–97

Michaelis H, Obert B, Schultenkötter I, Böcker L (1995) Die Miesmuschelbestände der niedersächsischen Watten, 1989–1991. Ber Forschungsstelle Küste Norderney 40:55–70

Millat G, Herlyn M (1999) Documentation of Intertidal Mussel Bed (*Mytilus edulis*) Sites at the coast of Lower Saxony. Senckenbergiana marit 29(suppl):83–93

Müller CD (1959) Biologische und sedimentologische Wattuntersuchung zwischen Westeraccumersiel und Neuharlingersiel an der ostfriesischen Küste. Jber 1958, Forschungsstelle Norderney 10:61–86

Müller CD (1964) Das ostfriesische Watt von Dornumersiel bis Norddeich. Eine biologisch-sedimentologische Untersuchung mit Folgerungen für den Küstenschutz. Jber 1963, Forschungsstelle Norderney 15:81–125

Nehls G (1999) Miesmuschelmonitoring im Nationalpark Schleswig-Holsteinisches Wattenmeer 1998. Ein Projekt im Rahmen des Trilateral Monitoring and Assessment Program. Tönning, Germany, unpublished

Nehls G, Thiel M (1993) Large-scale distribution patterns of the mussel *Mytilus edulis* in the Wadden Sea of Schleswig-Holstein: do storms structure the ecosystem? Neth J Sea Res 31:181–187

Nehls G, Hertzler I, Scheiffarth G (1997) Stable mussel *Mytilus edulis* beds in the Wadden Sea—they're just for the birds. Helgoländer Meeresunters 51:361–372

Nehls G, Diederich S, Thieltges DW, Strasser M (2006) Wadden Sea mussel beds invaded by oysters and slipper limpets: competition or climate control? Helgol Mar Res 60:135–143

Obert B (1982) Bodenfauna der Watten und Strände um Borkum—Emsmündung. Jber 1981, Forschungsstelle Norderney 33:139–162

Obert B, Michaelis H (1991) History and ecology of the mussel beds (*Mytilus edulis* L.) in the catchment area of a Wadden Sea tidal inlet. In: Elliot M, Ducrotoy J-P (1991) Estuaries and Coasts: spatial and temporal intercomparisons. Olsen and Olsen, Viborg, pp 185–194

Pulfrich A (1995) Reproduction and recruitment in Schleswig Holstein Wadden Sea edible mussel (*Mytilus edulis* L.) populations. Thesis, Inst. f. Meereskunde, Christian-Albrechts-Universität Kiel, Germany

Reise K (1985) Tidal flat ecology—an experimental approach to species interactions. Springer-Verlag, Berlin

Reise K, Dankers N, Essink K (2005) Introduced species. In: Essink K, Dettmann C, Farke H, Laursen K, Lüerßen G, Marencic H, Wiersinga W (eds) Wadden Sea quality status report 2004. Wadden Sea ecosystem No. 19. Trilateral Monitoring and Assessment Group, Common Wadden Sea Secretariat, Wilhelmshaven, pp 155–161

Ruth M (1991) Miesmuschelfischerei im schleswig-holsteinischen Wattenmeer. Ein Beispiel für die Problematik einer Fischerei im Nationalpark Wattenmeer. Schriftenreihe der Schutzgemeinschaft Deutsche Nordseeküste e.V.: Probleme der Muschelfischerei im Wattenmeer, pp 26–46

Ruth M (1994) Untersuchung zur Biologie und Fischerei von Miesmuscheln im Nationalpark Schleswig-Holsteinisches Wattenmeer. Texte 73/97 des Umweltbundesamtes, Berlin

Smit CJ, Dankers N, Ens BJ, Meijboom A (1998) Birds, mussels, cockles and shellfish fishery in the Dutch Wadden Sea: how to deal with low food stocks for eiders and oystercatchers? Senckenbergiana marit 29:141–153

Verwey J (1952) On the ecology and distribution of cockle and mussel in the Dutch Wadden Sea: their role in sedimentation and the source of their food supply, with a short review of the feeding behaviour of bivalve molluscs. Arch Neerl Zool 10:171–239

Wehrmann A, Herlyn M, Bungenstock F, Hertweck G, Millat G (2000) The distribution gap is closed—first record of naturally settled Pacific oysters (*Crassostrea gigas*) in the East Frisian Wadden Sea, North Sea. Senckenbergiana marit 30:153–160

Zens M, Michaelis H, Herlyn M, Reetz M (1997) Die Miesmuschelbestände der niedersächsischen Watten im Frühjahr 1994. Ber Forschungsstelle Küste Norderney 41:141–155