

Colonization of an artificial hard substrate by *Mytilus edulis* in the German Bight

TANJA J. JOSCHKO¹, BELA H. BUCK^{1,2}, LARS GUTOW¹ & ALEXANDER SCHRÖDER¹

¹Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, Germany, and ²Institute for Marine Resources (IMARE), University of Applied Science, Bremerhaven, Germany

Abstract

The colonization of the underwater construction of an offshore research platform in the German Bight by *Mytilus edulis* was investigated. Mussel abundance, biomass and percentage coverage of the construction were determined from summer 2003 to summer 2005 from different water depths using digital underwater images and scrape samples of the hard substrate fauna. Growth was estimated from shell length distributions. In 2003 settlement of *M. edulis* was low at the platform mainly due to a temporal mismatch between platform construction and occurrence of competent larvae. In summer 2004 mussel abundance increased remarkably in the intertidal and upper subtidal. Abundance and biomass increased up to 30,000 individuals m^{-2} and approximately 40 kg m^{-2} in summer 2005. At the end of the investigation period, the upper part of the platform foundation was completely covered by *M. edulis*. Lower parts remained sparsely colonized. Mussel growth rates were high under offshore conditions because of favourable environmental conditions and reduced biological constraints. Cumulative effects from wind farm entities are estimated. Mussel accumulations will be an important component in the estimation of ecological implications of offshore wind farming at least at the local scale.

Key words: Artificial hard substrates, biomass, Mytilus edulis, North Sea, recruitment

Introduction

Marine anthropogenic hard substrates such as artificial reefs, oil and gas platforms, navigation marks, bridges and wrecks provide suitable habitats for hard bottom communities (e.g. Wolfson et al. 1979; Forteath et al. 1982; Stachowitsch et al. 2002). During succession, parts of marine hard substrates often become dominated by mussels (Reusch & Chapman 1997; Stachowitsch et al. 2002), which are strong competitors for space (e.g. Okamura 1986; Enderlein & Wahl 2004). In the North Sea the blue mussel Mytilus edulis Linnaeus, 1758 is one of the dominant species in the upper sections of hard substrates (Hardy 1981; Garcia 1991; Leewis et al. 1994) including offshore sites (Wolfson et al. 1979; Forteath et al. 1982; Page & Hubbard 1987; Whomersley & Picken 2003; Buck 2007).

In the southern North Sea populations of *M. edulis* exhibit a major spawning peak in spring (Pulfrich 1997). During their planktonic stage

mussel larvae can be distributed over large distances by currents (Pulfrich 1997; de Vooys 1999). In the absence of suitable substrates, pediveliger potentially delay metamorphosis for several weeks (up to 40 days at 10°C) (Bayne 1965, 1976) allowing for the colonization of distant substrates. During extended dispersal in the water column larvae are exposed to physical and biological stresses such as those resulting from water turbulences and unfavourable currents (Belgaro et al. 1995; Morgan 1995; Richards et al. 1995) and predation (Young & Chia 1987; Rumrill 1990). Larval mortality may exceed 99% (Thorson 1966; Mileikovsky 1971; Purchon 1977; Jørgensen 1981) due to starvation and predation by fish and invertebrates. Moreover, long drifts to offshore sites result in dilution of mussel larval densities in the water column (e.g. Young et al. 1998; Metaxas 2001; Walter et al. forthcoming).

While both the nearshore distribution of M. *edulis* and the larval occurrence in the water column is well studied in the North Sea (e.g. Walter & Liebezeit

Correspondence: T. J. Joschko, Alfred Wegener Institute for Polar and Marine Research, PO Box 120161, 27515 Bremerhaven, Germany. E-mail: Tanja.Joschko@awi.de

(Accepted 21 January 2008; Printed 17 October 2008)

ISSN 1745-1000 print/ISSN 1745-1019 online © 2008 Taylor & Francis DOI: 10.1080/17451000801947043

Published in collaboration with the University of Bergen and the Institute of Marine Research, Norway, and the Marine Biological Laboratory, University of Copenhagen, Denmark

2001; Walter 2004), only few and fragmentary data are as yet available from offshore areas (Buck 2007; Walter et al. forthcoming). However, if suitable substrates are available pediveligers settle and grow, while recruitment success and growth rates depend on environmental conditions and biological constraints such as predation.

Growth and production rates within a mussel population can be extremely high. Under favourable conditions mussels can grow 3.5–5 cm within 30–48 weeks (Orton 1914; Walter & Liebezeit 2001) and reach up to 6–8 cm in length within 1–2 years (Seed 1976; Page & Hubbard 1987). Such rapid growth seems to be characteristic for many blue mussel populations in estuarine and other enclosed areas. On tidal coasts, duration of air exposure of intertidal mussel beds is considered to be one of the most crucial factors controlling mussel growth (e.g. Baird & Drinnan 1957; Faldborg et al. 1994; McGrorty 1997) and may lead to considerable variations in size and shape between intertidal and subtidal *M. edulis* (Baird 1966; Seed 1968).

Recruitment success and the development of M. edulis populations (including biomass production) have not yet been investigated in offshore waters with respect to time and water depth. The increased filtration of phytoplankton and the export of organic material via faeces and mussels falling off the structure, providing an additional food supply for predators and scavengers, may have implications for the local trophic functioning. These data sets also aid in estimating the potential of open ocean aquaculture in offshore areas in the German Bight (Whomersley & Picken 2003; Buck et al. 2004a). Moreover, from a technical point of view, fouling will have an impact on material weight and shape and can further result in large forces interfering with the grounding structure, thus, with the stability of offshore objects (Buck et al. 2006).

The aim of this study was to describe the colonization process of M. *edulis* on an offshore artificial hard substrate with respect to water depth, season and time since construction. Ecological implications of offshore wind farming in the North Sea will be estimated from the results.

Material and methods

Study area

The study was conducted at the research platform FINO 1 that was deployed for research on the feasibility and possible ecological implications of future offshore wind farming. The platform was installed in July 2003 in a soft bottom area $(54^{\circ}0.86'N, 06^{\circ}35.26'E)$ in the German Bight

(North Sea) about 45 km north of the island of Borkum (Figure 1a). It stands in a water depth of approximately 28 m on a steel structure (jacket design; Figure 1b) with four piles spreading from 7.5×7.5 m at the surface to 26×26 m at the seafloor.

During the investigation period from 2003 to 2005 salinity ranged from 32.9 to 34.7 psu and the surface water temperature varied from 3° C in spring to 19° C in summer. Oxygen saturation varied between 90 and 119% in 6 m depth. The principal tidal current direction was East-South-East and West-North-West. Daily maximum current velocities varied from 1 m s⁻¹ at the surface to 0.4 m s⁻¹ at 20 m depth. The average tidal range was 1.90 m with strong wind-driven fluctuations (unpublished data provided by the Federal Maritime and Hydrographic Agency BSH).

Sampling

Images

Recruitment and coverage of M. edulis on the underwater construction was documented using a remotely controlled underwater digital camera system (Kongsberg model OE 14-108 based on a Nikon Coolpix at 3.3 megapixel camera). The camera-system was fixed in a carriage passing along a vertical guiding track on the north pile of the platform (Figure 1c). The camera had a constant distance (20 cm) to the pile surface providing images of 0.04 m². Images were taken weekly from August 2003 to December 2004. As the emerging depth zonation pattern on the platform construction was not known prior to the colonization by marine organisms, images were taken at random depths from the water surface down to 28 m. Water depth of taken images was determined in relation to MLWS. On each sampling date, 30–55 images were taken. A total of 470 images were analysed for the development of the M. edulis population using Adobe Photoshop software version 7.0 (Adobe Systems Inc., San Jose, CA, USA). Percentage coverage of M. edulis was determined as the number of pixels occupied by M. edulis relative to the total number of pixels on each image. Shadowed areas on the images (maximum 6%) were excluded from the analysis. Individuals of *M. edulis* were counted and expressed as individuals per square metre (ind. m^{-2}).

Scrape samples

Since mussels usually form three-dimensional aggregates with individuals growing in different layers, abundances are inevitably underestimated if determined from two-dimensional images only. Therefore



Figure 1. Location and construction design of the offshore research platform FINO 1. (a) Map of the German Bight including the navigational coordinates of the research platform and engineering drawing (lateral view) of FINO 1; (b) bird's-eye view of the platform; (c) jacket construction of the platform foundation including the remotely controlled underwater camera and the vertical guiding track.

abundance (ind. m⁻²) and biomass (g m⁻², wet weight including shells) of *M. edulis* were determined from scrape samples from the surface of the platform foundation. For biomass calculation, mussels were opened and the water in the mantel cavity was removed before weighing. As *M. edulis* occurred on the underwater construction in substantial numbers only in the 1 m depth site (see Results) only scrape samples taken in this depth were considered. The 20×20 cm scrape samples (except for April 2004 with 10×10 cm) were taken by scuba divers in April (spring) and July (summer) 2004 and 2005. The samples were scraped into 500 µm mesh bags and stored in 4% borax-buffered formalin. In the labora-

tory all individuals of *M. edulis* were counted and weighed and total shell length of each individual was measured to the nearest 1 mm.

While in summer 2004 and summer 2005 four replicates were taken, only one sample could be taken due to bad weather conditions in spring 2004 and 2005.

Data processing

A three-dimensional sigmoid regression model was fitted to the 2004 data obtained from the image analysis, describing coverage (%) and abundance (ind. m^{-2}) of *M. edulis*, respectively, as a function of

water depth (m) and day of the year (JMP IN version 5.1, SAS Institute Inc., Cary, NC, USA). Maximum percentage cover was set at 100%. Due to heteroscedasticity (Bartlett's test) abundance and biomass of *M. edulis* in summer 2004 and 2005 determined from the scrape samples were compared by Mann–Whitney U-test. All results were accepted as statistically significant at alpha <0.05.

Results

Images: mussel abundance and percentage coverage

Substantial colonization of the underwater construction by *M. edulis* did not occur before spring 2004 and, therefore, the colonization analysis focuses on 2004 only. As shown exemplarily on images taken from the same spot in 1 m water depth (Figure 2a–e), juvenile mussels colonized the submerged parts of the platform in spring 2004. Thereafter, the density of *M. edulis* increased mainly in the upper area of the platform.

Recruitment of *M. edulis* was most successful at 0-2 m depth (Figure 3a). At this depth, the number of individuals increased in June 2004 (approximately day 150). Maximum abundance of *M. edulis* was reached in autumn 2004 (between day 250 and day 300, i.e. from early September to the end of October) and decreased thereafter until December. Only a few individuals settled below 3 m depth where densities of *M. edulis* remained low throughout the entire investigation period.

Mytilus edulis started to cover the underwater construction substantially in the upper parts in July 2004 (approximately day 200) (Figure 3b). Thereafter, *M. edulis* covered the structure in this depth until the end of the investigation period at nearly 100% coverage. Below 3 m depth, the underwater construction remained sparsely covered by *M. edulis*.

The early temporal and spatial colonization of the underwater construction by *M. edulis* in 2004 is best described in terms of abundance and percentage coverage by a three-dimensional sigmoid regression model (Table I; Figure 3). For the abundance data the model simplifies the colonization process as the regression plane steadily approaches the maximum abundance. The calculated maximum abundance is thus a compromise between the initial maximum abundance peak in autumn 2004 and the subsequent lower abundances.

Scrape samples: mussel abundances and biomass

The number of individuals of *M. edulis* increased from April 2004 (2000 ind. m^{-2}) to July 2004 (6581±1625 ind. m^{-2}) (mean±SE; n=4) and remained fairly constant until spring 2005 (9075 ind. m^{-2}) (Figure 4). Subsequent recruitment resulted in densities of $31,507\pm6405$ ind. m^{-2} (mean \pm SE; n=4) in summer 2005. In summer 2005 densities were significantly higher than in summer 2004 (P < 0.05).

The biomass of *M. edulis* changed only little from spring to summer 2004 (Figure 4). Biomass increased significantly from 935 ± 301 g m⁻² (mean \pm SE; n =4) in summer 2004 to $39,833 \pm 7440$ g m⁻² (mean \pm SE; n =4) in summer 2005 (P <0.05).

In summer 2004, maximum shell length of the mussels was 27 mm (Figure 5). While earliest recruits were still missing in April 2005 the shell length ranged from 5 to 59 mm with 45% of the individuals being in the 10–20 mm range. In July 2005, individuals of all sizes up to 64 mm shell length occurred in considerable numbers with a distinct peak at small sizes up to 3 mm.

Discussion

Recruitment success

Generally, mussel settlement on natural and artificial substrates is highly variable in time and space (e.g. McGrath et al. 1988; Hunt & Scheibling 1997; Ramirez & Caceres-Martinez 1999). Settlement and recruitment success of *M. edulis* depends on abiotic factors such as the availability of a suitable substrate in an appropriate water depth, favourable environmental conditions (Seed & Suchanek 1992) and on biological factors including larval supply, the timing of spawning, predation, and the quality and quantity of food (Bayne 1965, 1976).

Development of M. edulis larvae takes approximately 4-6 weeks allowing the larvae to spread over wide geographical regions (Seed 1976; Lane et al. 1985; Widdows 1991; Seed & Suchanek 1992). A comparison of larval densities measured at different inshore and offshore locations in the German Bight indicate that numbers of larvae decrease by some orders of magnitude towards offshore regions (Table II) (e.g. Walter et al. forthcoming). Low offshore concentrations of mussel larvae are due to dilution during offshore dispersal from their source region (e.g. Young et al. 1998; Metaxas 2001) and intensive predation on the larvae. Despite comparatively low larval abundances M. edulis densely settled in 2003 on offshore mussel collectors installed near the research platform FINO 1 and at 16 other offshore sites in the German Bight (Walter et al. forthcoming). Similarly, in 2003, food quality (expressed as C:N ratio) and quantity (expressed as chlorophyll a content) were sufficient in the platform area to sustain mussel growth (Walter et al. forthcoming). Therefore, the absence of M. edulis on the research



Figure 2. Underwater images documenting the colonization of the offshore research platform FINO 1 by *Mytilus edulis*. (a–e) Images taken from the same position in 1 m water depth in May, June, August, September and December 2004, respectively; (f) presence of the predatory starfish *Asterias rubens* within the *M. edulis* population at a depth of 2.5 m in November 2004. Scale bars: 7 cm.

platform in 2003 seems not to be an effect of low larval abundances and insufficient food supply at this offshore site. This assumption was supported by the intensive colonization of the platform foundation by *M. edulis* in the following year. The almost complete absence of blue mussels from the platform foundation in 2003 was probably due to a temporal mismatch between the construction of the platform in summer and the main *Mytilus*-larval peak being in spring (Pulfrich 1996). Similarly, mussel larvae occurring in smaller numbers throughout the summer months or even later (de Vooys 1999; Walter &



Figure 3. (a) Abundance and (b) percentage coverage of *Mytilus* edulis on the offshore research platform FINO 1 in different water depths in 2004 determined from digital underwater images. The surface plot displays the three-dimensional sigmoid regression model of Table I.

Table I. Specific equations and correlation coefficients (\mathbb{R}^2) of the three-dimensional sigmoid regression model describing abundance and percentage cover of *Mytilus edulis* on the underwater construction of the offshore research platform FINO 1 in 2004 as a function of x = day of the year and y = water depth (m).

Variable	Equation		
Abundance	$f(\mathbf{x}, \mathbf{y}) = \frac{12338.26}{(1 + e^{-2.67 + 1.10x})(1 + e^{12.46 - 0.06y})}$	0.75	
Cover	$f(\mathbf{x}; \mathbf{y}) = \frac{100.00}{(1 + e^{-20.72 + 9.52\mathbf{x}})(1 + e^{84.17 - 0.33\mathbf{y}})}$	0.96	

The maximum percentage cover was set at 100%. Data derived from underwater digital images.



Figure 4. Temporal development of abundance (mean \pm SE, n = 4) and biomass of *Mytilus edulis* on the offshore research platform FINO 1 in 1 m depth in April (A) and July (J) 2004 and 2005.

Liebezeit 2001) refused to settle on the yet unattractive, recently introduced platform construction. Settlement and metamorphosis of M. edulis is induced by habitat-specific chemical cues released by a particular biofilm (Dobretsov & Railkin 1996; Dobretsov & Wahl 2001). Macromolecular biofilms colonized by diatoms and protozoa typically develop on the surfaces of substrates within one week of submersion in seawater (reviewed by Wahl 1989). It is, however, not known whether the biofilm developed on the platform construction in 2003 emitted the relevant cues that induce settlement and metamorphosis of Mytilus-larvae (e.g. Bao et al. 2007). For example, the induction of mussel settlement requires further metabolites released by macroorganisms such as filamentous algae (Dobretsov & Wahl 2001). Filamentous algae, however, did not occur on the platform foundation before October 2003 (T. J. Joschko, personal observation).

Mussel recruitment success was negligible below approximately 3 m depth. Only the upper areas (down to 3 m) of the submerged parts were fully covered by M. edulis while in deeper parts of the platform only single individuals and rare aggregates were observed. In the White Sea, Dobretsov & Miron (2001) also found highest settlement in about 1.5 m depth with densities of settled post-larvae decreasing below 3 m depth. This distributional pattern was, however, due to a strong thermocline/halocline retaining the larvae in upper water layers. Due to tidal currents the water column at FINO 1 is well mixed throughout the year without a stable thermocline. In non-stratified waters no clear preference for the upper zone is apparent in the settlement pattern of M. edulis (Freeman et al. 2002) and the distribution of settlers reflects their photo- and geotactic behaviour (Bayne 1964, 1976). U. Walter and B. H. Buck (unpublished data) recorded a declining chlorophyll concentration in the German Bight with increasing depth. Hence, higher food concentrations



Figure 5. Temporal development of shell length (mm) frequency distribution of *Mytilus edulis* in April and July 2004 and 2005 on the offshore research platform FINO 1 in 1 m depth. [n, total number of individuals per sampling date (i.e. all replicate samples pooled) used for shell length determination; numbers of individuals per length class were standardized to 1 m^2 .]

in surface waters probably favoured survival and growth of *M. edulis* in the upper part of the platform construction. Furthermore, survival of *M. edulis* in the intertidal zone of the platform might have been favoured by limited predation. Predation by the starfish *Asterias rubens* often controls the vertical distribution and abundance of litoral and sublitoral mussel assemblages (Saier 2001). At the platform, *A. rubens* mainly occurred below the exposed intertidal zone. Heavy wave action probably withholds *A. rubens* from parts of the mussel population. Hence, we suggest that the vertical distribution of *M. edulis* on the platform was shaped by more favourable food supply and reduced competition and predation by species less tolerant to wave exposure in upper water layers.

Substrate coverage, biomass and predation

In the upper part of the platform foundation the number of juvenile M. edulis increased progressively after settlement in spring 2004 with, however, only low biomass and percentage coverage directly after settlement. Mussel abundances determined from underwater images were about three times lower than densities determined from scrape samples from the same time period (June to August 2004). This difference illustrates the inadequacy of the former method for estimating the total abundances of small mussels growing in a fouling assemblage or in dense mussel aggregates. Nevertheless, underwater images provide a useful method for describing trends in the development of abundances and coverage. The high temporal resolution of the photo sampling allowed for the observation of rapid processes within the mussel assemblage such as the massive increase in surface coverage by M. edulis in 1 m depth from June to August 2004 (Figure 2b, c). The bare surface area was rapidly covered in these months probably due to settlement of new recruits and density-induced active or passive movements of individuals as an effect of mussel growth (Littorin & Gilek 1999).

Despite predation, the biomass of M. edulis increased substantially from summer 2004 to spring 2005 from ca. 1 to 25 kg m⁻². During the main growth season from May to September and the season of apparently reduced growth from December to February (Dare 1976) mussel abundance remained fairly constant, indicating that the increase in biomass was exclusively due to individual growth instead of new recruitment. The lack of any small mussels in April 2005 indicates that the sampling preceded the major annual mussel recruitment in May/June. In July 2005, all size classes occurred, the highest proportions being due to small individuals. Maximum abundance and biomass in summer 2005 (i.e. 2 years after platform installation) were, thus, due to a combination of growth and successful recruitment in spring 2005.

Multiple factors such as reduced competition for space and food during initial colonization of the platform as well as low sedimentation of suspended particles on the vertical surface and especially at an offshore construction (Cheung & Shin 2005; Westerbom & Jattu 2006) might account for the success of the first recruits under offshore conditions. A shell length of 26 mm was reached within 2–3 months after settlement. The growth of some individuals to a shell length of 55–64 mm within 12 months is

Table II. Yearly maximum abundances of *Mytilus edulis* larvae measured at different inshore and offshore sites of the German Bight (North Sea).

Region	Distance from shore (km)	Maximum larval abundance (ind. m^{-3})	Reference	Remarks
Inshore				
Lower Saxony Wadden Sea	<1	9000	Heiber (1988)	
Schleswig-Holstein Wadden Sea	<1	$\sim 800 - 4000$	Pulfrich (1997)	Data from 3 years
Dutch Wadden Sea	<1	30,000–190,000	de Vooys (1999)	Data from 7 years
Dutch Wadden Sea	<1	272,000	Bos et al. (2006)	
Sylt-Rømø Bight	<1	80,000	Bos et al. (2006)	
Yade estuary	<1	~9000	Walter & Liebezeit (2001)	
German Bight	2–3	24,920	Walter et al. (forthcoming)	
German Bight	7	1467 ± 455	Walter et al. (forthcoming)	
Offshore				
German Bight	22	637 ± 50	Walter et al. (forthcoming)	
German Bight (FINO 1 region)	45	708	T. J. Joschko (unpublished)	
German Bight (FINO 1 region)	45	147 ± 58	Walter et al. (forthcoming)	
German Bight	75	253 ± 127	Walter et al. (forthcoming)	

consistent with the commonly high growth rates of M. edulis in offshore waters (Buck et al. 2004a; Buck 2007). Growth rates of mussels originating from inshore areas within the German Bight range from 20 to 30 mm (Walter 2004) and from intertidal mussel beds from 10 to 30 mm within the first year (Buschbaum & Saier 2001). Growth rates of M. edulis at offshore sites are, thus, twice as high as in inshore waters. One reason for higher mussel growth rates in offshore waters is a lower rate of infestation by micro- and macro-parasites due to dilution of parasite densities during offshore transport and missing intermediate hosts such as periwinkles that are common in coastal waters but absent at offshore sites (Buck et al. 2005).

Ecological implication

The almost complete coverage of the upper part of the research platform by blue mussels proved the general ability of M. *edulis* to densely colonize offshore habitats several tens of kilometres away from coastal source areas despite the dilution of larval densities during planktonic offshore transport. Within the German Bight offshore recruitment of M. *edulis* is, therefore, limited by the availability of suitable hard substrates rather than by larval dispersal capacities. Planned wind farms with up to several hundred turbines will, thus, provide offshore sites for substantial mussel recruitment.

Our study demonstrates the rapid growth of blue mussels under favourable offshore conditions of low environmental stress, unlimited oxygen supply, and reduced impairment by predation and parasite infection (Buck et al. 2005). Recruitment success and rapid growth of the mussels result in the accumulation of an enormous biomass on the underwater construction. The upper part of the jacket structure supported a total of approximately 6 tons of *M. edulis* in summer 2005, approximately equivalent to the total soft bottom macrofaunal biomass in an area of 155 m radius (i.e. ~ 0.1 km²) (assuming 7 g Ash-free Dry Mass (AFDM) m⁻², after Heip & Craeymeersch 1995).

Considerable effects might arise from the aggregation of the suspension-feeder M. edulis on hundreds of neighboured wind turbines in extensive wind farms. According to the German Federal Maritime and Hydrographic Agency (see www.bsh.de) almost 3000 wind turbines are already planned for the German Exclusive Economic Zone (EEZ) encompassing an area of 28,600 km². The ecological significance of the cumulative effects caused by the aggregation of M. edulis on hundreds of neighboured wind turbines can be illustrated by calculating their respective shares of the total benthic biomass and the consumption of the primary production. The average macrofaunal biomass in the North Sea amounts to 7 g AFDM m^{-2} (Heip & Craeymeersch 1995). The annual phytoplankton primary production in the German Bight amounts to 332 g C m⁻² (Rick et al. 2006). To fulfil their energy demands M. edulis assimilate approximately seven times their own biomass per year with an assimilation efficiency of 70% (Kautsky 1995, cited in Björk et al. 2000). The results of this study predict a biomass load of M. edulis of 39 kg m⁻² on the upper parts of the underwater structure of the wind turbines which is equivalent to 1.8 kg AFDM m^{-2} and 1.2 kg C m^{-2} (conversion factor from Ricciardi & Bourget 1998). For the total surface area of the platform available in the upper 5 m, this amounts to 265 kg AFDM or 173 kg C per single structure. Based on these data, the calculation for the entire area of the German EEZ indicates that the *M. edulis* accumulated on 3000 wind turbines would result in an increase of the total macrofaunal biomass of the area by 0.4% which would consume 0.06% of the annual primary production. This is negligible compared to the 30% of the primary production generally processed in the benthic food web (Steele 1974). Calculated on a more local scale of a single wind farm area consisting of 80 turbines in an area of 30 km² (according to the planned wind farm 'Borkum Riffgrund West' in the German Bight, see www.bsh.de), the accumulated mussels would add 10% to the local macrofaunal biomass and consume 1.4% of the annual primary production.

Current offshore research considers the multifunctional use of offshore wind farm areas by including mariculture enterprises such as seaweed and mussel farming (Buck et al. 2004b). Our results show the potential of spat settlement and mussel biomass yield. For commercial operation of offshore mussel cultures, however, further biological data are required such as offshore larval densities, growth rates, losses driven by mortality and predation, and the reliability of successful recruitment.

The cumulative effects on the environment – both in space through large numbers of turbines and including various indirect ecosystem effects – are at present difficult to estimate. There also remain the as yet unanswered question as to whether and what kind of fisheries may be conducted in offshore wind farms and possible secondary uses. Therefore, further investigations are required before conclusive predictions of expected environmental effects from the intensive development of offshore wind energy can be made. The expected mussel accumulations remain an important component in the estimation of ecological implications at least on a local scale.

Acknowledgements

The study was carried out within the projects BeoFINO and BeoFINO II which were funded by the German Federal Ministry for the Environment, Nature Conservation and Nuclear Safety (BMU) (grant numbers 0327526 and 0329974A). The conclusions of this paper are those of the authors and do not necessarily represent the views of the BMU. We would like to thank C. Orejas for project management and for contributing data and numerous divers and laboratory assistants for sampling and sample processing. Thanks are due to M. Potthoff for calculation assistance. We are grateful to the crew of the RV Heincke, and to D. Kindler and A. Trautsch (Wind Test) for co-operation during sampling and to K. Herklotz from the Federal Maritime and Hydrographic Agency for providing hydrographical data. We thank R. Alheit for improving the English of this manuscript. We would also like to thank three anonymous reviewers for their helpful comments.

References

- Baird RH. 1966. Factors affecting growth and condition of mussels (*Mytilus edulis*). Fishery Investigations, Series II 25:1– 33.
- Baird RH, Drinnan RE. 1957. The ratio of shell to meat in *Mytilus* as a function of tidal exposure to air. Journal du Conseil Permanent International de l'Exploration de la Mer 22:329–36.
- Bao WY, Satuito CG, Yang JL, Kitamura H. 2007. Larval settlement and metamorphosis of the blue mussel *Mytilus* galloprovincialis in response to biofilms. Marine Biology 150:565–74.
- Bayne BL. 1964. The responses of the larvae of *Mytilus edulis* L. to light and to gravity. Oikos 15:162–74.
- Bayne BL. 1965. Growth and delay of metamorphosis of the larvae of *Mytilus edulis* L. Ophelia 2:1–47.
- Bayne BL. 1976. Marine Mussels: Their Ecology and Physiology. Cambridge (UK): Cambridge University Press. p 506.
- Belgaro A, Legendre P, Dewarumez JM, Frontier S. 1995. Spatial structure and ecological variation of meroplankton on the Belgian–Dutch coast of the North Sea. Marine Ecology Progress Series 128:51–9.
- Björk M, Gilek M, Kautsky N, Näf C. 2000. In situ determination of PCB biodeposition by Mytilus edulis in a Baltic coastal ecosystem. Marine Ecology Progress Series 194:193–201.
- Bos OG, Hendriks IE, Strasser M, Dolmer P, Kamermans P. 2006. Estimation of food limitation of bivalve larvae in coastal waters of north-western Europe. Journal of Sea Research 55:191–206.
- Buck BH. 2007. Experimental trials on the feasibility of offshore seed production of the mussel *Mytilus edulis* in the German Bight: installation, technical requirements and environmental conditions. Helgoland Marine Research 61:87–101.
- Buck BH, Berg-Pollack A, Assheuer J, Zielinski O, Kassen D. 2006. Technical realization of extensive aquaculture constructions in offshore wind farms: consideration of the mechanical loads. In: Proceedings of the 25th International Conference on Offshore Mechanics and Arctic Engineering (OMAE 2006), Offshore Wind Energy Symposium. New York: American Society of Mechanical Engineers. p 1–7.
- Buck BH, Krause G, Rosenthal H. 2004a. Extensive open ocean aquaculture development within wind farms in Germany: the prospect of offshore co-management and legal constraints. Ocean and Coastal Management 47:95–122.
- Buck BH, Thieltges DW, Walter U, Nehls G, Rosentahl H. 2005. Inshore–offshore comparison of parasite infestation in *Mytilus edulis*: implications for open ocean aquaculture. Journal of Applied Ichthyology 21:107–13.
- Buck BH, Walter U, Rosenthal H. 2004b. Experimental trials on the feasibility of offshore seed production of blue mussels (*Mytilus edulis*) in the German Bight. In: Shumway SE, editor. Aquaculture – An Ecologically Sustainable and Profitable Venture, Offshore Aquaculture. Baton Rouge (FL): World Aquaculture Society. p 76.
- Buschbaum C, Saier B. 2001. Growth of the mussel *Mytilus edulis* L. in the Wadden Sea affected by tidal emergence and barnacle epibionts. Journal of Sea Research 45:27–36.
- Cheung SG, Shin PKS. 2005. Size effects of suspended particles on gill damage in green-lipped mussel *Perna viridis*. Marine Pollution Bulletin 51:801–10.

- Dare PJ. 1976. Settlement, growth and production of the mussel, *Mytilus edulis* L., in Morecambe Bay, England. Fishery Investigations, Series II 28:1–24.
- de Vooys CGN. 1999. Numbers of larvae and primary plantigrades of the mussel *Mytilus edulis* in the western Dutch Wadden Sea. Journal of Sea Research 41:189–201.
- Dobretsov SV, Miron G. 2001. Larval and post-larval vertical distribution of the mussel *Mytilus edulis* in the White Sea. Marine Ecology Progress Series 218:179–87.
- Dobretsov SV, Railkin A. 1996. Effect of surface characteristics on the settlement and attachment of larval mussel *Mytilus edulis* (Mollusca, Filibranchia). Zoologicheskij Zhurnal 75:499–506.
- Dobretsov SV, Wahl M. 2001. Recruitment preferences of blue mussel spat (*Mytilus edulis*) for different substrata and microhabitats in the White Sea (Russia). Hydrobiologia 445:27–35.
- Enderlein P, Wahl M. 2004. Dominance of blue mussels versus consumer-mediated enhancement of benthic diversity. Journal of Sea Research 51:145–55.
- Faldborg K, Jensen KT, Maagaard L. 1994. Dynamics, growth, secondary production and elimination by waterfowl of an intertidal population of *Mytilus edulis* L. Ophelia Supplement 6:187–200.
- Forteath GNR, Picken GB, Ralph R, Williams J. 1982. Marine growth studies on the North Sea oil platform Montrose Alpha. Marine Ecology Progress Series 8:61–8.
- Freeman KR, Kenchington E, MacQuarrie SP. 2002. Comparative settlement depths of *Mytilus edulis* C. Linnaeus, 1758 and *M. trossulus* Gould, 1850: I. A mesocosm study. Journal of Shellfish Research 21:59–65.
- Garcia CB. 1991. Comparison of successional patterns on hard substrata: the Caribbean Sea and the North Sea [PhD thesis]. Bremen (Germany): University of Bremen. 148 p.
- Hardy FG. 1981. Fouling on North Sea platforms. Botanica Marina 24:173–6.
- Heiber W. 1988. Die Faunengemeinschaft einer großen Stromrinne des Wurster Wattengebietes (Deutsche Bucht) [PhD thesis]. Bonn (Germany): University of Bonn.
- Heip C, Craeymeersch JA. 1995. Benthic community structures in the North Sea. Helgoländer Meeresuntersuchungen 49:313– 28.
- Hunt HL, Scheibling RE. 1997. Role of early post-settlement mortality in recruitment of benthic marine invertebrates. Marine Ecology Progress Series 155:269–301.
- Jørgensen CBA. 1981. A hydromechanical principle for particle retention in *Mytilus edulis* and other ciliary suspension feeders. Marine Biology 61:277–82.
- Kautsky U. 1995. Ecosystem processes in coastal areas of the Baltic Sea [PhD thesis]. Stockholm: University of Stockholm.
- Lane DJW, Beaumont AR, Hunter JR. 1985. Byssus drifting and the drifting threads of the young post-larval mussel *Mytilus edulis*. Marine Biology 84:301–8.
- Leewis RJ, Waardenburg HW, van der Tol MWM. 1994. Biomass and standing stock on sublittoral hard substrates in the Oosterschelde Estuary (SW Netherlands). Hydrobiologia 282/ 283:397–412.
- Littorin B, Gilek M. 1999. A photographic study of the recolonisation of cleared patches in a dense population of *Mytilus edulis* in the northern Baltic proper. Hydrobiologia 393:211–9.
- McGrath D, King PA, Gosling EM. 1988. Evidence for the direct settlement of *Mytilus edulis* larvae on adult mussel beds. Marine Ecology Progress Series 47:103–6.
- McGrorty S. 1997. Winter growth of mussels *Mytilus edulis* as a possible counter to food depletion by oystercatchers *Haematopus ostralegus*. Marine Ecology Progress Series 73:153–63.

- Metaxas A. 2001. Behaviour in flow: perspectives on the distribution and dispersion of meroplanktonic larvae in the water column. Canadian Journal of Fisheries and Aquatic Science 58:86–98.
- Mileikovsky SA. 1971. Types of larval development in marine bottom invertebrates, their distribution and ecological significance: a re-evaluation. Marine Biology 10:193–213.
- Morgan SG. 1995. Life and death in the plankton: larval mortality and adaptation. In: McEdwards L, editor. Larval Ecology of Marine Invertebrates. Boca Raton (FL): CRC Press. p 279– 321.
- Okamura B. 1986. Formation and disruption of aggregations of *Mytilus edulis* in the fouling community of San Francisco Bay, California. Marine Ecology Progress Series 30:275–82.
- Orton JH. 1914. Preliminary account of a contribution to an evaluation of the Sea. Journal of the Marine Biological Association of the United Kingdom 10:312–20.
- Page HM, Hubbard DM. 1987. Temporal and spatial patterns of growth in mussels *Mytilus edulis* on an offshore platform: relationships to water temperature and food availability. Journal of Experimental Marine Biology and Ecology 111:159–79.
- Pulfrich A. 1996. Attachment and settlement of post-larval mussels (*Mytilus edulis* L.) in the Schleswig-Holstein Wadden Sea. Journal of Sea Research 36:239–50.
- Pulfrich A. 1997. Seasonal variation in the occurrence of planktic bivalve larvae in the Schleswig-Holstein Wadden Sea. Helgoländer Wissenschaftliche Meeresuntersuchungen 51:23–39.
- Purchon RD. 1977. The Biology of the Mollusca. London: Pergamon Press. p 576.
- Ramirez SC, Caceres-Martinez J. 1999. Settlement of the blue mussel *Mytilus galloprovincialis* Lamarck on artificial substrates in Bahia de Todos Santos B.C., Mexico. Journal of Shellfish Research 18:33–9.
- Reusch TBH, Chapman ARO. 1997. Persistence and space occupancy by subtidal blue mussel patches. Ecological Monographs 67:65–87.
- Ricciardi A, Bourget E. 1998. Weight-to-weight conversion factors for marine benthic macroinvertebrates. Marine Ecology Progress Series 163:245–51.
- Richards S, Possingham H, Noye B. 1995. Larval dispersion along a straight coast with tidal currents: complex distribution patterns from a simple model. Marine Ecology Progress Series 122:59–71.
- Rick HJ, Rick S, Tillmann U, Brockmann U, Gärtner U, Dürselen C, Sündermann J. 2006. Primary productivity in the German Bight (1994–1996). Estuaries and Coasts 29:4–23.
- Rumrill S. 1990. Natural mortality of marine larvae. Ophelia 32:163–98.
- Saier B. 2001. Direct and indirect effects of seastars Asterias rubens on mussel beds (*Mytilus edulis*) in the Wadden Sea. Journal of Sea Research 46:29–42.
- Seed R. 1968. Factors influencing shell shape in the mussel Mytilus edulis. Journal of the Marine Biological Association of the United Kingdom 48:561–84.
- Seed R. 1976. Ecology. In: Bayne BL, editor. Marine Mussels: Their Ecology and Physiology. Cambridge (UK): Cambridge University Press. p 13–65.
- Seed R, Suchanek TH. 1992. Population and community ecology of *Mytilus*. In: Gosling E, editor. The Mussel *Mytilus*: Ecology, Physiology, Genetics and Culture. Amsterdam: Elsevier. p 87– 169. (Developments in Aquaculture and Fisheries Science; 25).
- Stachowitsch M, Kikinger R, Herler J, Zolda P, Geutebrueck E. 2002. Offshore oil platforms and fouling communities in the southern Arabian Gulf (Abu Dhabi). Marine Pollution Bulletin 44:853–60.

- Steele JH. 1974. The Structure of Marine Ecosystems. Oxford: Blackwell. p 128.
- Thorson G. 1966. Some factors influencing the recruitment and establishment of marine benthic communities. Netherlands Journal of Sea Research 3:267–93.
- Wahl M. 1989. Marine epibiosis. I. Fouling and antifouling: some basic aspects. Marine Ecology Progress Series 58:175–189.
- Walter U. 2004. Erprobung einer Langleinen-Pilotanlage zur Gewinnung von Saatmuscheln für die Miesmuschelaquakultur. Zwischenbericht über die wissenschaftlichen Begleituntersuchungen des Projektes. Wilhelmshaven (Germany): Mytilamar. p 35.
- Walter U, Buck BH, Liebezeit G. Forthcoming. Larval occurrence and settlement success in the German Bight: a trial to estimate potentials for *Mytilus edulis* culture in offshore areas. Aquaculture International.
- Walter U, Liebezeit G. 2001. Abschlußbericht des Projektes: Nachhaltige Miesmuschel-Anzucht im niedersächsischen Wattenmeer durch die Besiedlung natürlicher und künstlicher Substrate. Wilhelmshaven (Germany): Forschungszentrum Terramare. p 99.
- Westerbom M, Jattu S. 2006. Effects of wave exposure on the sublittoral distribution of blue mussels *Mytilus edulis* in a

heterogeneous archipelago. Marine Ecology Progress Series 306:191-200.

- Whomersley P, Picken GB. 2003. Long term dynamics of fouling communities found on offshore installations in the North Sea. Journal of the Marine Biological Association of the United Kingdom 83:897–901.
- Widdows J. 1991. Physiological ecology of mussel larvae. Aquaculture 94:147–63.
- Wolfson C, Van Blaricom N, Davis N, Lewbel GS. 1979. The marine life of an offshore oil platform. Marine Ecology Progress Series 1:81–9.
- Young CM, Chia ES. 1987. Abundance and distribution of pelagic larvae as influenced by predation, behavior, and hydrographic factors. In: Giese AC Pearse JS Pearse VB, editors. Reproduction of Marine Invertebrates. Vol. 9, General Aspects: Seeking Unity in Diversity. Palo Alto/Pacific Grove (CA): Blackwell/Boxwood. p 385–463.
- Young EF, Bigg GR, Grant A, Walker P, Brown J. 1998. A modelling study of environmental influences on bivalve settlement in the Wash, England. Marine Ecology Progress Series 172:197–214.

Editorial responsibility: Martin Solan