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Short communication

Effects of suction-dredging for cockles on non-target fauna in the Wadden Sea

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Abstract

Suction dredging for cockles removes large cockles from tidal flats and may also cause mortality of non-target fauna and make the habitat less suitable for some species. This study examines whether suction dredging for cockles on tidal flats of the Dutch Wadden Sea had affected densities of non-target fauna, directly after fishing and one year later. Densities of non-target fauna in two randomly chosen undredged locations were compared to densities at the surrounding heavily commercially dredged area. A significant negative effect of cockle dredging on densities of 0-group *Macoma balthica* was observed and this effect persisted one year after dredging. The dredged area appeared to be less suitable for settlement of mussels *Mytilus edulis*. No significant effects of dredging on the mudsnail *Hydrobia ulvae* and on 0 and 1-group *C. edule* were found. For the mobile young *Macoma balthica* it seems unlikely that the effect found after one year was still due to the mortality caused by dredging and this suggests that the habitat was less suitable as a consequence of dredging. Thus, even in the highly dynamic ecosystem of the Wadden Sea, effects of bottom disturbance by cockle dredging may persist after one year.

Keywords: Dredging; Fishing effects; *Cerastoderma edule*; *Macoma balthica*; Tidal flats; Wadden Sea; The Netherlands

1. Introduction

One of the biggest challenges in coastal-zone management is how to regulate the activities of all the different users of the coastal zone without affecting the functioning of marine ecosystems. Managers need to consider both political and environmental issues to prevent damage to marine habitats and conflicts between the different users. Fisheries managers have traditionally concentrated on stock management of the harvested species, but more recently concern about the secondary environmental effects of fishing on the non-target fauna and marine habitats has become increasingly prominent (Jennings and Kaiser, 1998).

Because most soft-sediment macrofauna lives buried in the sediment, harvesting of the target species requires physical disturbance of the substratum and hence disturbs the associated flora and fauna. As soft-sediment habitats tend to extend over large areas, they are suitable for extensive mechanical harvesting. Due to this large-scale sediment disturbance, harvesting may have an adverse effect on ecosystem functioning.

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The study of ecosystem effects in these habitats is of particular importance as intertidal areas provide important food sources for large numbers of migratory (and resident) bird and fish species (e.g. Zwarts et al., 1992).

In 2003 a policy decision about the future of the Dutch cockle dredging industry will be made (Ens et al., 2000). Presence or absence of effects of fishing on the functioning of the Wadden Sea ecosystem will be important for this decision. Therefore, this study reports on effects of cockle dredging on the benthic ecosystem of the Dutch Wadden Sea. Especially, effects of dredging on non-target organisms need to be considered carefully as the Dutch Wadden Sea is a protected nature conservation area.

As cockles are most abundant in the intertidal, most cockle dredging is carried out on tidal flats during periods when sufficient water covers the sand flats. Hydraulic suction dredges operate by fluidising the sand using water jets and then lifting the sediment and cockles. The dredge head (width 1 m) is lowered over the side of a vessel and towed alongside. The dredge has an adjustable cutting blade at the front of a grid (15 mm) and jets in front of the blade loosen the sediment. This sediment is then sieved through the grid and the cockles drawn up a suction pipe to the deck of the vessel. Small cockles (smaller than 23 mm length, length–width relation from Zwarts, 1991) and other debris fall through the screens (Hall and Harding, 1997).

There are some studies looking at effects of suction and tractor dredging and hand raking for cockles. Dredging has been reported to reduce the abundance of large cockles. In the short term, all studies found an increased mortality of non-target animals due to cockle harvesting (De Vlas, 1982; Cotter et al., 1997; Hall and Harding, 1997; Ferns et al., 2000; Kaiser et al., 2001). It has to be pointed out though that intertidal raking leaves the habitat in situ, whereas dredging physically removes the habitat, and that therefore the long-term effects of raking and dredging are probably different.

Ecologically, the long-term effects of dredging are much more important than the immediate (days to weeks) effects. Long-term changes in the abundance of species may affect the abundance of other species that prey on, compete with or are eaten by the dominant species. Experimental studies that examined the effect of cockle harvesting up to one year after fishing found that in some localities densities of 0-group *Cerastoderma edule*, 0-group *Macoma balthica*, 0-group *Mya arenaria*, *Nereis diversicolor* and *Heteromastus filiformis* were still significantly reduced one year after fishing (De Vlas, 1982). Ferns et al. (2000) showed that densities of some polychaetes and the mudsnail *Hydrobia ulvae* were still reduced 100 days after dredging in a tractor-dredged area. However, intensive hand raking for cockles is expected to have negative effects after 1 year on long-lived species only (Kaiser et al., 2001).

In most published studies the differences in densities of animals between dredged and non-dredged areas alter due to the immigration of non-larval animals and settlement of larval recruits (De Vlas, 1982; Cotter et al., 1997; Hall and Harding, 1997; Ferns et al., 2000; Kaiser et al., 2001). If long-term effects nevertheless persist, this is possibly due to alterations of the habitat that make it less suitable for recolonisation by these organisms. Piersma et al. (2001) compared fished and unfished areas in the Wadden Sea and argue that recruitment of the bivalves *M. balthica* and *C. edule* decreased due to long-term changes of the intertidal ecosystem associated with shell fisheries.

The aim of the present study is ascertain whether suction dredging for cockles on tidal flats reduces the density of non-target fauna. What are the effects of dredging on densities directly after dredging and one year later? The difference between the present study and earlier studies is that this study examines effects of suction dredging with relatively small control plots in very large commercially (as opposed to experimentally) dredged areas.

2. Material and methods

2.1. General setup

This present study was not purposefully designed, but originated as an opportunity created by another experiment. Fishermen agreed not to dredge in locations where exclosure experiments were performed to estimate epibenthic predation pressure on *Macoma balthica* in 2000 (Hiddink et al., 2002a). These locations (n = 10) were chosen at random on the tidal flats of the Groninger Wad in the Dutch Wadden Sea. The studied area was last dredged for cockles one year earlier, in 1999. Around each of these 10 locations, an area of approximately 20 × 20 m was marked with stakes at the four corners and avoided by fishing vessels. The stakes were 3–4 m long so that they were still visible at high tide. The average tidal range in the area is 2.4 m. Two of these undredged squares were located within heavily dredged areas and therefore provided a good opportunity to examine the effect of cockle dredging on densities of non-target organisms (n = 2). Both plots were located around mid-tide level. The density of non-target fauna in these two undredged plots was compared with the surrounding dredged area before, directly after fishing, and one year later (Fig. 1).

The effects of dredging on the molluscs *Hydrobia ulvae*, *Macoma balthica*, *Mytilus edulis*, and non-target sizes of *Cerastoderma edule* (the 1999 and 2000 year class) were examined, because these species were common and could be sampled easily. *M. balthica* and *C. edule* were aged from the growth rings on their shells. The densities of *M. balthica* and *C. edule* (but not of *Hydrobia ulvae* and *M. edulis*) were estimated in July 2000 before fishing. The 1998 and 1999-yearclasses of *M. balthica* were analysed as one group. The 'exclosure' plots were marked in August 2000. Dredging started in early September and continued until early November. In late October 2000, densities of molluscs were sampled in fishing tracks and between tracks in the fished areas, and in the non-fished control areas. The actual borders of the non-fished area, based on the absence of visible fishing tracks, were marked with small sticks and recorded with a hand-held GPS in October 2000. One year later in October 2001, fishing tracks from 2000 could not be distinguished anymore (the tracks disappeared within months after fishing). Therefore, we took samples in the fished and non-fished area, without being able to distinguish between samples in tracks and between tracks in the fished area. On each occasion, 10 cores of 83 cm^2 were taken, pooled in the field and sieved over 1 mm. Samples were taken at random locations both in the unfished area and in a 20-m-wide fished band around it (to represent the fished area). There was little dredging in the area in 2001 before sampling in October 2001 (pers. obs.).

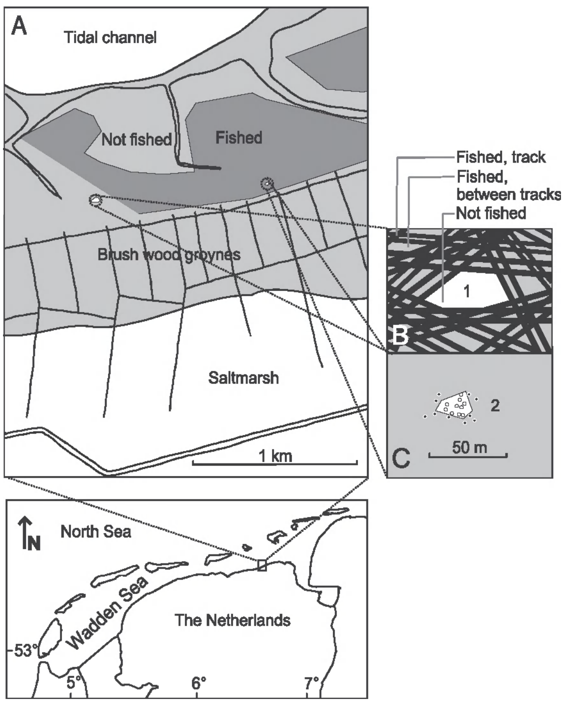


Fig. 1. Map of the study area at the Groninger Wad at its location in the eastern Dutch Wadden Sea. (A) Location of the unfished plots (white) in the fished area (dark grey) at the Groninger Wad (unfished area light grey). (B) Plot 1 with sampling areas in and between dredging tracks. (C) Plot 2 with an example of the distribution of the sampling stations in the fished and unfished area.

2.2. Fishing intensity

In October 2000 the fraction of the 'fished' area that was covered by dredging tracks was estimated visually in both locations. Boundaries of fished areas on a larger scale were recorded with a handheld GPS.

2.3. Statistical analysis

Densities of each species before fishing (July 2000) were compared with densities in the dredged and control area after fishing (October 2000) using t-tests. The effect of fishing on infaunal species densities was examined in a two-factor ANOVA, with Treatment (fished, not fished) and Year (2000, 2001) and the interaction between Year and Treatment as factors. If there is a significant effect of treatment and there exists no significant interaction between year

Table 1
ANOVA-tables. An * indicates a significant value

A) Density non-target *Cerastoderma edule* (1999 yearclass)

Source	Df	Mean square	F-ratio	P-value
Treatment	1	0.17701	9.56	0.036
Year	1	0.03781	2.04	0.226
Year × treatment	1	0.20161	10.89	0.030
Residual	4	0.01851		
Total (corrected)	7			

B) Density non-target *Cerastoderma edule* (2000 yearclass)

Source	Df	Mean square	F-ratio	P-value
Treatment	1	0.3669	0.54	0.504
Year	1	3.4140	5.00	0.089
Year × treatment	1	0.0301	0.04	0.844
Residual	4	0.6826		
Total (corrected)	7			

C) Density *Macoma balthica* (2000 yearclass)

Treatment	1	0.29645	18.92	0.012*
Year	1	0.08745	5.58	0.077
Treatment × Year	1	0.00510	0.33	0.599
Residual	4	0.01567		
Total (corrected)	7			

D) Density *Hydrobia ulvae*

Treatment	1	0.02205	0.80	0.421
Year	1	0.05445	1.98	0.232
Treatment × Year	1	0.00320	0.12	0.750
Residual	4	0.02753		
Total (corrected)	7			

Effect of fishing (treatment: fished (weighted average of in tracks and between tracks) or not fished), time after sampling (year: 2000 or 2001) and location (location 1 or 2) on densities of non-target *Cerastoderma edule*, *Macoma balthica* and *Hydrobia ulvae*.

and treatment, this suggests that the effect of fishing persists after 1 year. A non-significant interaction does not mean that there is significantly no interaction and therefore conclusions about the persistence of effects of dredging on densities after one year must be drawn with care. A significant year-effect indicates that densities differed between 2000 and 2001. In the two-factor ANOVA, the weighted average of density in and between tracks (weighted according the area covered with tracks in the fished area as visually estimated in the field) was used as the density in the fished area. Densities were (log + 0.1)-transformed to homogenise variances. Because there seemed to be a difference in densities between the two locations, the density data were normalised to the average of the observation per location to correct of this difference. The homogeneity of variances between treatments was tested with Levene's Test of Equality of Error Variances. Because there were only 2 replicates per treatment, normality of the data could not be examined within treatments. Therefore, the normality of the residuals was examined instead (Sokal and Rohlf, 1995) with the Kolmogorov-Smirnov Test. If the assumptions of the ANOVA were not met for a species or yearclass, no statistical test was performed on the data. The simultaneous testing of the effect of fishing on 4 species/year classes in one experiment results in an increased chance of a Type-I error. Therefore, the critical p-value was Bonferroni corrected by dividing the original critical p (0.05) by the number of tests done (4), giving a new critical p of 0.0125 (Sokal and Rohlf, 1995).

3. Results

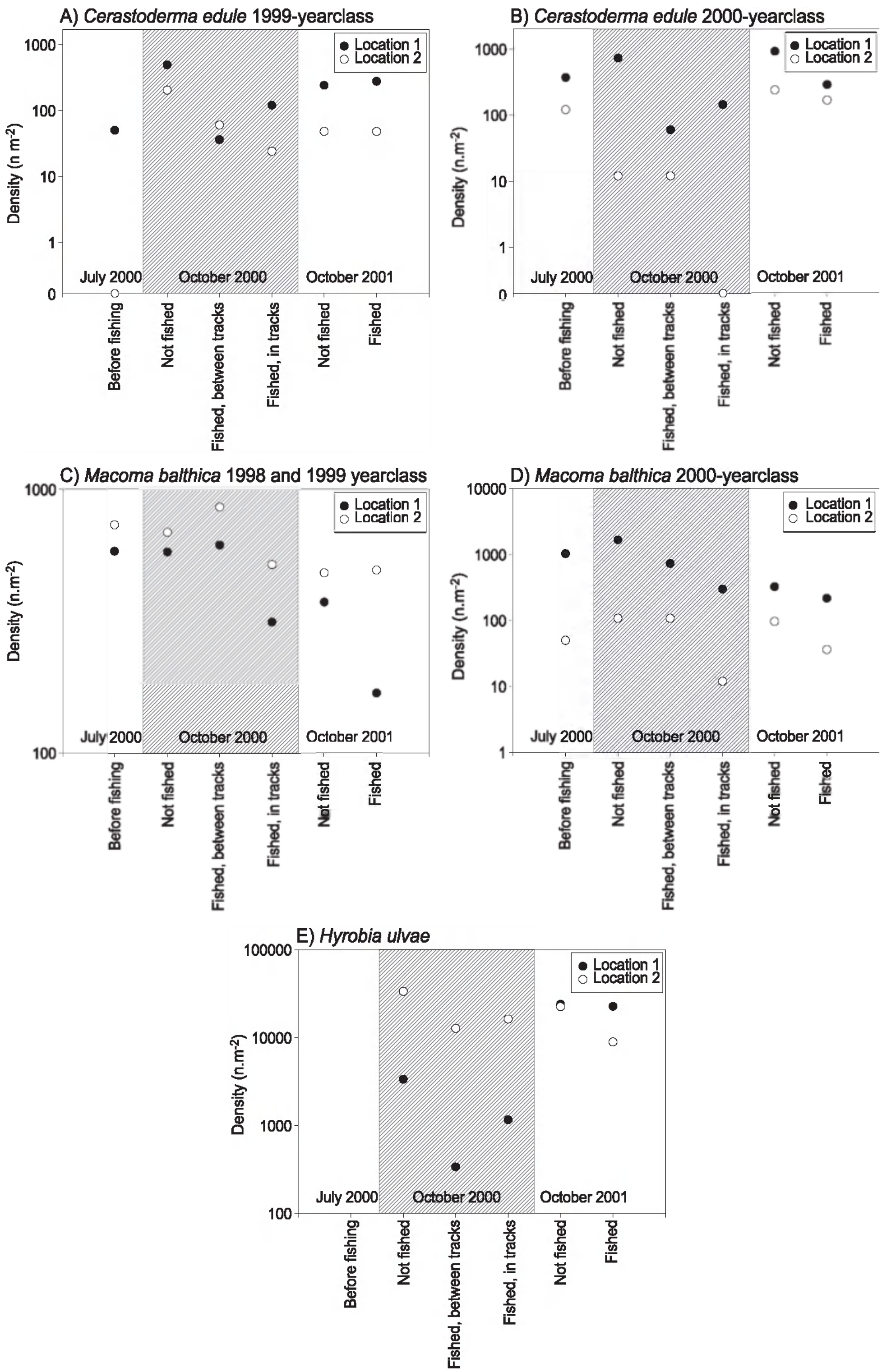
3.1. Fishing intensity

The whole area around the control plots was heavily dredged in September and October 2000. The undredged plot in location 1 measured approximately 55 × 29 m. Approximately 90% of the fished area in this location appeared to be covered by dredging tracks in late October. The undredged plot in location 2 measured 27 × 15 m. Approximately 60% of the fished area in this location appeared to be covered by dredging tracks in late October.

3.2. Effects on non-target species

None of the examined species and year classes showed a statistically significant increase or decrease in density between July 2000 (before fishing) and October 2000, for both the fished and the control plots.

Fig. 2. Densities of (A) 1999-yearclass *Cerastoderma edule*, (B) 2000-yearclass *Cerastoderma edule*, (C) 1998 and 1999-yearclass *Macoma balthica*, (D) 2000-yearclass *Macoma balthica*, and (E) *Hydrobia ulvae*, before fishing (July 2000), directly after fishing (October 2000) and one year after fishing (October 2001).


A) Cerastoderma edule 1999-yearclass
B) Cerastoderma edule 2000-yearclass
C) Macoma balthica 1998 and 1999 yearclass
D) Macoma balthica 2000-yearclass
E) Hyrobia ulvae
Location 1
Location 2
Density (n m-2)
Density (n.m-2)
July 2000
October 2000
October 2001
Before fishing
Not fished
Fished, between tracks
Fished, in tracks
Not fished
Fished
0
1
10
100
1000
10000
100000

3.2.1. *Cerastoderma edule*

The yearclasses of *Cerastoderma edule* born in 2000 and 1999 measured 5.0 ± 3.2 mm (mean ± SD) and 16.7 ± 2.7 mm in October 2000, respectively. The largest 1999-cockle measured 22 mm. Therefore, these cockles were too small to be of interest to commercial fishermen in 2000. There was no significant effect of fishing on the densities of the 1999 and 2000-yearclasses of *C. edule* (Table 1A and B, Fig. 2A and B). The density of 2001-yearclass *C. edule* was not significantly different between fished (175 ± 93 m^{-2}) and non-fished (78 ± 25 m^{-2}) locations in October 2001 ($F_{1,2}$ = 11.34, P = 0.078).

3.2.2. *Macoma balthica*

The effect of fishing on the densities of older *Macoma balthica* could not be tested because variances were not homogeneous between treatments. The

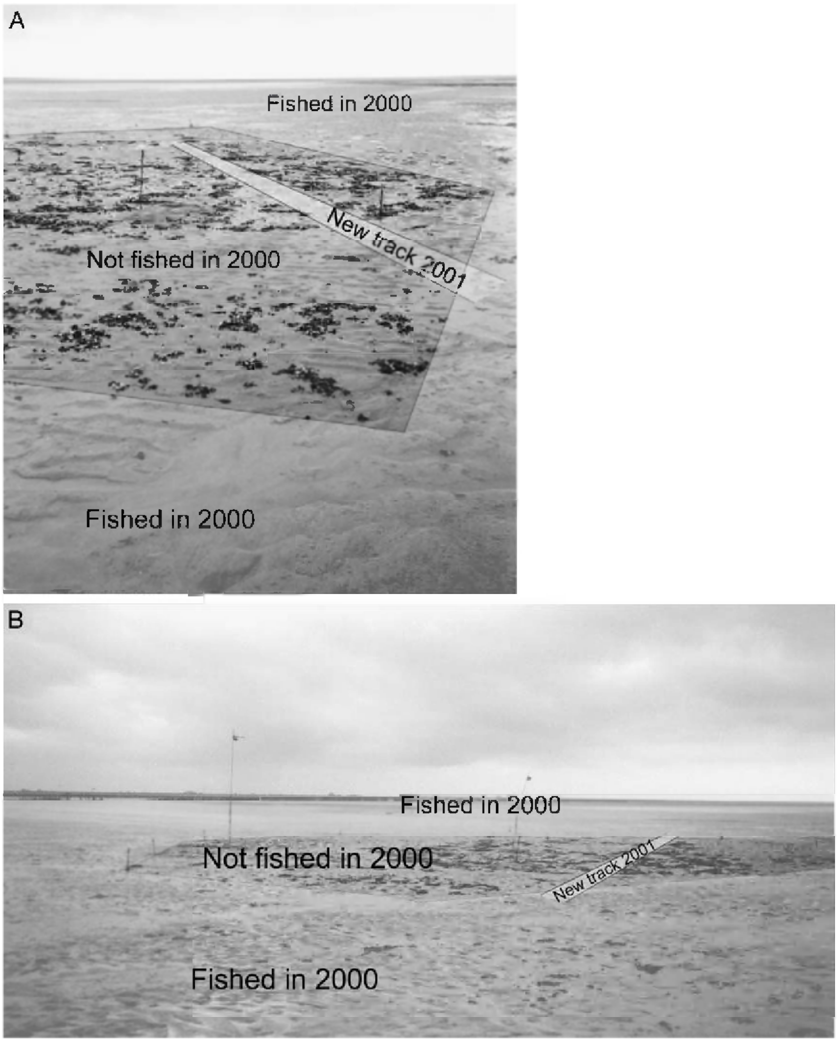


Fig. 3. Two photographs of location 2 at the Groninger Wad one year after fishing at 9 October 2001. (A) Viewing in westerly direction. (B) Viewing in southerly direction from a longer distance. Black patches are clumps of mussels (*Mytilus edulis*), cockles (*Cerastoderma edule*) and green seaweeds (*Ulva* and *Enteromorpha*). Boundaries of the areas are drawn based on sticks marking the boundaries of the non-fished plot and recorded GPS locations. To make the observed patterns clearer, lines were drawn around the non-fished area and the colour of the surrounding fished area was made slightly whitish.

2000-yearclass of *M. balthica* measured 4.9 ± 1.2 mm in October 2000. There was a significant effect of fishing on the densities of the 2000-yearclass *M. balthica* (Table 1C). The lower densities in the fished compared to the non-fished area in 2001 (Fig. 2D) show that this effect persisted in October 2001. The non-significant treatment x year effect ($p = 0.599$, Table 1C) suggests the same. The density of 2001-yearclass *M. balthica* was not significantly different between fished (169 ± 34 m^{-2}) and non-fished (72 ± 68 m^{-2}) locations in October 2001 ($F_{1,2}$=2.58, $P = 0.250$).

3.2.3. *Hydrobia ulvae*

There was no significant effect of fishing on the density of *Hydrobia ulvae* (Table 1D, Fig. 2E). In 4 out of the 5 groups examined above, the density directly after fishing was lower between the tracks in the fished area (which seemed not to be fished) than in the unfished area.

3.2.4. *Mytilus edulis*

Mytilus edulis was not found in the samples in 2000. In 2001, a density of 12 m^{-2} of small mussels (2001-yearclass) was found in the unfished area of location 1 and a density of 1458 m^{-2} was found in the unfished area of location 2, while in the two surrounding fished areas no *M. edulis* was found in the samples. The significance of this difference could not be tested because variances were not homogeneous.

Fig. 3 shows that in 2001, one year after fishing, the density of mussels and attached seaweed (mainly *Ulva* and *Enteromorpha*) in location 2 was much higher in the unfished area. The border of the high density area approximately coincided with the border of the unfished area.

4. Discussion

After intertidal cockle-dredging in the late summer of 2000, densities of 2000-yearclass *Macoma balthica* were lower in dredged than in undredged locations. Fig. 2D shows that the densities of 2000-yearclass *M. balthica* were still lower in the fished than in the unfished areas one year after fishing. The non-significant interaction between treatment and year (Table 1D) also suggests that the effect of fishing persisted one year later.

Although the effect of dredging on *Mytilus edulis* could not be tested statistically, the observed densities in October 2001 and the patterns shown in Fig. 3 suggest that dredging alters the sediments of the tidal flats such that they become unsuitable for settlement of *M. edulis*. This is probably due to a reduced availability of substrate that is suitable for settlement (e.g. shells of living and dead cockles or *Lanice*-tubes, Callaway, 2003). Cockle dredging removes sediment and may further degrade the shells of dead bivalves such that they are no longer suitable for settlement.

The studied area was heavily dredged in 1999 and earlier years (pers. obs.). Therefore, the species (and age groups?) that seem to be most vulnerable to dredging, such as *M. edulis*, *Zostera marina* and *Z. noltii*, could already have been removed in earlier years. Hence, it is likely that the effect of dredging is underestimated in this study. This is illustrated in Fig. 3, in which the fishing track made in 2001 was only visible (due to removal of mussels) in the previously undredged plot, and it was not visible in the area that was dredged in 2000. Because the present study had only 2 replicates while the within-treatment variance was high, the power to detect differences between treatments was probably low anyway.

The reduction in the density of non-target fauna in dredged areas may be explained by mortality caused by dredging, a redistribution from the dredged to the undredged location or both. At some time between July and October 2000, the density of 2000-yearclass *M. balthica* increased in the undredged control area, while density decreased in the dredged area, but these temporal changes in each treatment were non-significant. Therefore, it is not possible to determine whether the difference between the control and treatment area was caused by a decreasing density in the dredged area or by an increasing density in the undredged area and, consequently, it is not clear whether the observed difference was due to mortality or redistribution or both. In other words, it is possible to detect a divergence between treatments, but it is not possible to determine the reason of divergence from the present study.

Earlier studies have shown that cockle harvesting has direct negative effects on the density of non-target fauna (De Vlas, 1982; Hall and Harding, 1997;

Ferns et al., 2000; Kaiser et al., 2001), and it seems therefore likely that mortality may at least partly explain the differences in densities between control and treatment areas. As densities in control areas after fishing seem to be higher than before fishing, a redistribution from the dredged to the control area may explain in part the observed difference between control and treatment as observed in October 2000. De Vlas (1982) suggested that a redistribution of 0-group *M. balthica* may occur when bivalves are suspended by the dredge, and subsequently transported by currents. Coffen-Smout and Rees (1999) showed an active movement of cockles away from disturbed areas. Both 0-group *M. balthica* and 0-group *Cerastoderma edule* are very mobile and 0-group *M. balthica* undertake long-distance migrations (km's) during their first winter (Armonies, 1992; Beukema and De Vlas, 1989; De Montaudouin, 1997; Hiddink and Wolff, 2002). After the winter migration, juvenile *M. balthica* is distributed rather homogeneously over the tidal flats (Hiddink et al., 2002b). Therefore, it seems unlikely that the effect of cockle dredging on 2000-yearclass *M. balthica* that persisted on the small scale of the experimental plots one year after dredging was a direct result of mortality or an immediate redistribution caused by dredging in 2000 (unless only a small and fixed fraction of the population migrates). The observations suggest that the effect of cockle dredging goes beyond the mortality of non-target fauna during dredging. It is possible that *M. balthica* prefers undredged over dredged tidal flats in the long term. Piersma et al. (2001) suggested that cockle dredging causes a decrease in the silt content of the sediment that makes the sediment unattractive for settlement of small bivalves. Possibly, the productivity of the system is reduced because the macro algae, decomposing organic material and fine sediment are resuspended in the water column during dredging and transported away by the tide, possibly making the area less suitable for bivalves. Therefore, future studies should monitor the impact of dredging on these factors.

The densities in tracks and between tracks directly after fishing were approximately equal for *C. edule* and *H. ulvae*. Cockles and other fauna passing through the 15-mm grid of the dredge are likely to land in the path of the dredge because this is the area over which the grid passes. Further, after intensive fishing, earlier tracks may be erased by newer tracks, making it difficult to discern between areas in and between tracks. Additionally, there may be an active or passive relocation from unfished areas between tracks to areas in tracks after fishing, which is helped by the fact that the dredge makes a furrow. Together, these three processes may explain why there were no significant differences in the densities in and between tracks after fishing.

Densities of 1999 and 2000-yearclass cockles seemed not to have decreased from October 2000 to October 2001, while a natural mortality of 20–90% would have been expected over this period (Beukema, 1993). For the 2000-yearclass this pattern may be explained: a fraction of the 2000-yearclass may have been too small to be retained on the 1-mm sieve in October 2000 and therefore not sampled quantitatively, while after growing for a year, they were sampled quantitatively in 2001. This may also mean that the effect of dredging as measured in October 2000 only examined the effect on the larger animals, while in October 2001 the effect on all animals was examined. For the 1999-yearclass the increase is difficult to explain, but suggests that there has been a relocation of animals. The large increase in densities of the 1999-yearclass of cockles found between July and October 2000 is unexpected and difficult to explain. The decrease in 2000-yearclass *M. balthica* density from October 2000 to 2001 may, at least party, be explained by the emigration of these *M. balthica* out of this high intertidal nursery area in winter. Nevertheless, these observations do not seem to affect the validity of the conclusions.

There is an important scale issue here in that effectively the control areas acted as islands in large disturbed areas. This means that, in contrast to many other studies that examine fishing effects by experimentally fishing small areas in large untouched areas, a fast recolonisation of the fished area from the non-fished plots was not possible in the present study. In contrast, for 2000-yearclass *M. balthica* the density increase in the control locations suggests a relocation of animals from the disturbed to the control locations, an effect that probably would not have been noted in a larger control area. This shows that the spatial scale and layout of experiments may be very important for the outcomes of experiments with animals that are not strictly sessile, because the relative sizes of the treatments may have an effect on the densities in the fished and control plots.

In conclusion, this study demonstrates, as in previous studies, that cockle dredging causes declines of non-target fauna during dredging and that effects of dredging persist one year after dredging. However, unlike previous studies, the results herein provide one of the first insights into recolonisation rates of large-scale disturbed area relating to small undisturbed areas. This study suggests that the habitat became less suitable for 1-group *M. balthica* and 0-group *M. edulis* after dredging, but that the suitability for 0-group *M. balthica* and *C. edule* was not affected. Thus, even in the highly dynamic ecosystem of the Wadden Sea, the effects of cockle dredging on benthic fauna may persist for at least one year and this within a previously disturbed habitat, in which one would expect effects to be less pronounced.

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References

Armonies, W., 1992. Migratory rhythms of drifting juvenile molluscs in tidal waters of the Wadden Sea. Mar. Ecol. Prog. Ser. 83, 197–206.

Beukema, J.J., 1993. Increased mortality in alternative bivalve prey during a period when the tidal flats of the Dutch Wadden Sea were devoid of mussels. Neth. J. Sea. Res. 31, 395–406.

Beukema, J.J., De Vlas, J., 1989. Tidal-current transport of thread-drifting postlarval juveniles of the bivalve *Macoma balthica* from the Wadden Sea (Netherlands) to the North Sea. Mar. Ecol. Prog. Ser. 5, 193–200.

Callaway, R., 2003. Long-term effect of imitation polychaete tubes on benthic fauna: they anchor *Mytilus edulis* (L.) banks. J. Exp. Mar. Biol. Ecol. 283, 115–132.

Coffen-Smout, S.S., Rees, E.I.S., 1999. Burrowing behaviour and dispersion of cockles *Cerastoderma edule* L. following simulated fishing disturbance. Fish. Res. 40, 65–72.

Cotter, A.J.R., Walker, P., Coates, P., Cook, W., Dare, P.J., 1997. Trial of a tractor dredger for cockles in Burry Inlet, South Wales. ICES J. Mar. Sci. 54, 72–83.

De Montaudouin, X., 1997. Potential of bivalves' secondary settlement differs with species: A comparison between cockle (*Cerastoderma edule*) and clam (*Ruditapes philippinarum*) juvenile resuspension. Mar. Biol. 128, 639–648.

De Vlas, J., 1982. De effecten van kokkelvisserij op de bodemfauna van Waddenzee en Oosterschelde. Report 82/19. Rijksinstituut voor Natuurbeheer, Texel, pp. 1–99.

Ens, B.J., Lanters, R., Smaal, A., 2000. EVA II: Evaluating the Dutch Policy of Shellfish Fishing in 2003. Wadden Sea Newsletter 2002-2, 22–24.

Ferns, P.N., Rostron, D.M., Siman, H.Y., 2000. Effects of mechanical cockle harvesting on intertidal communities. J. Appl. Ecol. 37, 464–474.

Hall, S.J., Harding, M.J., 1997. Physical disturbance and marine benthic communities: The effects of mechanical harvesting of cockles on non-target benthic infauna. J. Appl. Ecol. 34, 497–517.

Hiddink, J.G., Wolff, W.J., 2002. Changes in distribution and decrease in numbers during migration of the bivalve *Macoma balthica*. Mar. Ecol. Prog. Ser. 233, 117–130.

Hiddink, J.G., Marijnissen, S.A.E., Troost, K., Wolff, W.J., 2002a. Predation on the 0-group and older year classes of the bivalve *Macoma balthica*: interaction of size selection and intertidal distribution of epibenthic predators. J. Exp. Mar. Biol. Ecol. 269, 223–248.

Hiddink, J.G., Ter Hofstede, R., Wolff, W.J., 2002b. Predation of intertidal infauna on juveniles of the bivalve *Macoma balthica*. J. Sea Res. 47, 139–157.

Jennings, S., Kaiser, M.J., 1998. The effects of fishing on marine ecosystems. Adv. Mar. Biol. 34, 201–352.

Kaiser, M.J., Broad, G., Hall, S.J., 2001. Disturbance of intertidal soft-sediment benthic communities by cockle hand raking. J. Sea Res. 45, 119–130.

Piersma, T., Koolhaas, A., Dekinga, A., Beukema, J.J., Dekker, R., Essink, K., 2001. Long-term indirect effects of mechanical cockle dredging on intertidal bivalve stocks in the Wadden Sea. J. Appl. Ecol. 38, 976–990.

Sokal, R.R., Rohlf, R.J., 1995. Biometry. Freeman, New York. 887 pp.

Zwarts, L., 1991. Seasonal variation in body weigth of the bivalves *Macoma balthica*, *Scrobicularia plana*, *Mya arenaria* and *Cerastoderma* edule in the Dutch Wadden Sea. Neth. J. Sea Res. 28, 231–245.

Zwarts, L., Blomert, A.M., Wanink, J.H., 1992. Annual and seasonal variation in the food supply harvestable by knot *Calidris canutus* staging in the Wadden Sea in late summer. Mar. Ecol. Prog. Ser. 83, 129–139.