

Short and mid-long term effects of cockle-dredging on non-target macrobenthic species: A Before-After-Control-Impact experiment on a tidal mudflat in the Oosterschelde (The Netherlands).

Sander Wijnhoven^{a*}, Vincent Escaravage^a, Peter M. J. Herman^b, Aad C. Smaal^c, Herman Hummel^a

^aMonitor Taskforce, Netherlands Institute of Ecology, Centre for Estuarine and Marine Ecology (NIOO-CEME), Korringaweg 7, P.O. Box 140, NL-4401 NT, Yerseke, The Netherlands

^bDepartment of Spatial Ecology, Netherlands Institute of Ecology, Centre for Estuarine and Marine Ecology (NIOO-CEME), Korringaweg 7, P.O. Box 140, NL-4401 NT, Yerseke, The Netherlands

^cAquaculture Department, Wageningen IMARES (Institute for Marine Resources & Ecosystem Studies) (WUR), Korringaweg 5, NL-4401 NT Yerseke, The Netherlands

*Corresponding author. Tel. : +31-113-577357; Fax: +31-113-573616. E-mail address: s.wijnhoven@nioo.knaw.nl

Publisher's version: <http://dx.doi.org/10.1111/j.1439-0485.2010.00423.x>

Abstract

To study the possible environmental impact of hydraulic cockle-dredging on macrobenthic communities and the environment, a fishing experiment was executed on a tidal mudflat in the Oosterschelde (SW Netherlands) according to a BACI- (Before-After-Control-Impact) design. Following the characterization of the initial situation, a part of the mudflat was commercially fished, after which dredged and undredged areas were compared on basis of macrofauna descriptors and sediment constitution approximately 2 months (short term) and one year (mid-long term) after fishing. Whereas a clear reduction of the larger *Cerastoderma edule* cockles (>23 mm) in the fished areas was found, no effect of dredging on total macrofauna densities and median grain size was observed. No negative effect of fishing on total macrofauna biomass was found; in contrast, an increase of the biomass of the non-target species almost compensated for the loss in weight due to the extraction of the larger cockles. No significant effect of dredging on species diversity, richness and evenness was found on the short and on the mid-long term, where these descriptors more tend to have been increased than decreased in the dredged plots after one year. The selective fishing for larger cockles reduced the average cockle size, but one year after fishing the initial average size was found again in the dredged area. Compared to the control area, the average size might however still be reduced as the size of the cockles in the control area did also increase during the year. Local environmental conditions, with its specific macrobenthic communities, seem to be crucial in the type of effects and the impact of dredging. It is therefore of eminent importance to follow a research design with pre-defined environmental conditions, rather than a comparison of different areas that were open and closed to fisheries. The present study based on a BACI approach indicates that mechanical cockle-fisheries had no overall negative impact in our study area.

Keywords: Cockle-fishery effects ; Benthic macrofauna ; *Cerastoderma edule* ; Species composition ; Short and mid-long term ; BACI-design

Introduction

Several studies have investigated the potential impact of dredging or sediment disturbing activities on macrobenthic communities and the non-target species in particular. Some of these show strong effects (*e.g.* Beukema 1995; Piersma *et al.* 2001; Leopold *et al.* 2004), other studies show minor or no effects at all (*e.g.* Craeymeersch & Hummel 2004; Ens *et al.* 2004; Beukema & Dekker 2005). These studies differ in the severity of the disturbances, especially the disturbance depth (Hall & Harding 1997; Kaiser *et al.* 2001), the season when the disturbance occurred (Hall & Harding 1997), the frequency of disturbance (*e.g.* Kaiser *et al.* 2001), the possible selectivity of the different fishing techniques used (Ferns *et al.* 2000) and the methodological approach of comparison of different areas that were fished or unfished for an extended period (Piersma *et al.* 2001) versus an experimental approach with exclusion of fishery in cockle beds (Craeymeersch & Hummel 2004).

The many studies on this topic differ also with respect to their research question. They ascertain negative effects of fishing disturbances on (i) the environment as a whole (*e.g.* Leopold *et al.* 2004; Zwarts 2004), (ii) the structure of communities (Leitão and Gaspar, 2007), (iii) the abundance of target species (Piersma *et al.* 2001), or (iv) processes as settlement, population dynamics and recolonisation of selected species (Cotter *et al.* 1997; Hiddink 2003; Beukema & Dekker 2005). Whereas these studies mostly consist of inventories after large impacts, the next step consists of their integration in policies aiming at a mitigation of the risk that takes into account the opportunities for sustainable fisheries (Beukema & Cadée 1999). Thereby an impact is expected on beforehand, where the study investigates the rehabilitation potential or duration of rehabilitation of the target or non-target populations or the environmental conditions (Hall & Harding 1997).

Given that different environments have their specific communities and species assemblages, various impacts of fisheries might be expected according to the substrate specifications (Ferns *et al.* 2000), tidal range and elevation or depth (Leitão & Gaspar 2007). Furthermore different effect evaluations can be expected according to the sampling design, ranging from *ad hoc* inventories in extensive areas that are either fished or protected over various spans of time (*e.g.* Piersma *et al.* 2001; Beukema & Dekker 2005) to *a priori* elaborated experimental designs on local sites with an exact knowledge about the fishing intensity and timing (Ferns *et al.* 2000).

In the first place, we are interested whether dredging has a destructive effect on non-target species, which might be damaged by being lifted up from the sediment or by processing through the fishing device. These effects might be visible on the short term through increased mortality resulting from injuries or from exacerbated predation by other macrobenthic species or by vertebrates (Ferns *et al.* 2000; Hiddink 2003). This implies that the predators of the highly dredging-impacted species might profit from this disturbance. Dredging can also induce shifts in the species composition as a result of the alteration of the environmental conditions such as the sediment composition on the short and especially the mid-long term (Hiddink 2003). Comparisons between observations at short and mid-long term indicate whether the effects on the species assemblages are transitory whereas mid-long term observations are required to detect effects on species recruitment and larval settlement (Piersma *et al.* 2001).

In this study we specifically investigate whether the sediment characteristics (grain size) and the macrobenthic communities (including non-target species) are negatively affected by hydraulic dredging for cockles on a soft-sediment tidal flat. In order to account for the various sources of variation beside the direct effect of dredging a BACI (Before-After-Control-Impact) design was used (Smith 2002). Whereas a substantial part of a mudflat was commercially fished, other parts were left undisturbed. In the dredged and undredged areas, 100 x 100 m plots were delimited and randomly sampled before and shortly (short term) and one year (mid-long term) after fishing.

This study is the first study investigating the impact of commercial cockle fisheries with suction dredgers on non-target benthic macrofauna species and communities according to a BACI approach in which also the sensitivity of the experimental design to detect quantitative changes is taken into account.

Materials and methods

Study area and experimental design

The experimental research on the effects of cockle dredging has been executed on the -Slikken van de Dortsman tidal flats in the Oosterschelde, a semi-open tidal bay in the south-west Netherlands (Fig. 1) with a salinity of above 30 ‰ (Coosen *et al.* 1994). Next to the blue mussel *Mytilus edulis*, the cockle *C. edule*, is the dominant suspension feeder in the Oosterschelde. However, nowadays, total cockle biomass is lower than it used to be during the eighties and before. Besides the intensive fishing on the cockle populations during several years, the construction of a storm surge barrier in the mouth of the Oosterschelde (from 1976 to 1986), had a great impact on suitability of the area for cockles. The construction of the storm surge barrier led to reduced current velocities by 30 to 70 %, and a reduction in the tidal range of 12 %, leading to clearer waters, crumbling away of the elevated areas, and sedimentation at the brims of the tidal flats (Geurts van Kessel *et al.* 2003). The tidal range in the research area varies between 1.7 and 3.8 meters.

Since the early 1990s, cockle-fishery in the Oosterschelde is submitted to authorization, which is only granted in years with abundant cockle biomass. No authorization was given since the year 2001 in our research area (Geurts van Kessel *et al.* 2003). As a consequence, the cockle banks in the present study were free of any dredging activity during a five years period before the t_0 sampling (September 2006). Nine plots of 100 x 100 meters were randomly selected within the research area. With respect to the expected spatial heterogeneity of habitat and living communities on the tidal flat, which is largely to a North-South gradient, it was decided to separate the 9 plots into 3 groups that were spatially clustered (North, middle and South part of the study area). Positioning and depth of the plots indicated in Fig. 1. Within each group two plots were to be dredged and the last one was used as an undredged/control reference. Within each of the 9 plots, 5 sample sites were randomly selected. On September the 6th 2006 (t_0), 45 macrofauna and sediment samples were taken, after which the whole area was dredged with the exception of the three control plots. The fishing operation was performed for commercial purposes by three cockle boats equipped with hydraulic dredges. The dredging activity of the ships was recorded with a satellite tracking system (STS) that revealed, after interpolation of the one minute interval signals, dredging tracks all over the experimental plots whereas this was not the case for the control plots (Fig. 1). After dredging the tracks in the field as clearly visible in the sediment were also checked, and were indeed found all over the dredged plots and not in the control plots. Fishing activity took place from September the 5th till November the 9th and were restricted to unsampled areas during the first day of fishing. On November the 9th 2006 (t_1), all sample sites were sampled for macrofauna and sediment to detect possible short term effects, and on 1 and 2 October 2007 (t_2), the sample sites were sampled again to detect possible mid-long term effects.

The current experiment is a standard BACI (Before-After-Control-Impact) design (Smith 2002) which allows to compare the changes observed in experimental plots with those occurring in control plots, taking into account the autonomic developments during the study period.

Sampling and measurements

At each sample site, 5 macrofauna and 5 sediment samples were taken at each sample time. Macrofauna samples consisted of 3 cores ($3 \times 0.005 \text{ m}^2$) pushed 30 cm into the sediment within a 1 meter radius of the sample site, located with a GPS. The macrofauna samples are sieved over a 1 mm mesh, fixed with 4 % buffered formalin and stained with Rose Bengal, after which specimens are determined to the species level, with the exception of the Oligochaeta, Actinaria and Nemertea.

The numbers per species were counted and densities determined. To determine the density of species that are frequently fragmented such as polychaetes, the number of heads is counted. When only body parts are found and no head, the number of specimens is counted as one. Small or fragmented specimens for which determination can not be performed to the species level are classified at the genus level (*e.g. Cerastoderma sp, Spio sp and Arenicola sp*). The length of the cockles is also measured as the maximum measurable shell length to the nearest millimeter.

The total biomass (g ADW, ash-free dry-weight) of each species is determined either directly from the dried specimens (2 days at 80 °C) as the decrease in weight after two hours scorching at 560-580 °C or indirectly by length-weight regressions ($W=aL^b$ with W is weight in g ADW and L is length in mm). The length-weight regressions used here are based on (i) specimens scorched during this study, (ii) existing data in our BIS (Benthos Information System) database from the same area/season, and (iii) the fresh-weight of the specimens and taxon-specific conversion factors from other monitoring campaigns in BIS.

Sediment samples are taken with a 1 cm diameter tube pushed 3 cm into the sediment. The median grain size (μ m) of the samples was determined by laser-diffraction methodology using a Mastersizer 2000 of Malvern Instruments.

Descriptors

Plots, treatments and sample times were compared on total macrofauna and species densities and biomasses, species composition and frequencies and diversity. The length distribution of the cockles (*Cerastoderma sp* and *C. edule* combined) was also compared between the treatments. Diversity was measured as species diversity according to the Shannon index, species richness as the number of individual species and according to Margalef, and evenness according to Pielou, calculated with the software Primer 5.2.8 for Windows (Clarke & Warwick 2001). All total macrofauna and diversity indicators were calculated with and without taking *Cerastoderma sp* and *C. edule* into account, as it is expected that those are affected by dredging as the (larger) cockle is the target species. Further, top-10 lists of the most abundant individual species in chance of occurrence in samples, in densities and in biomasses were put together for each of the sample dates and treatments; eighteen lists in total. Species mentioned in at least one of the lists for one of the descriptors were selected to be related in a multivariate way to time and treatment.

Differences in the sediment grain size between the treatments were also analyzed.

With respect to the requirements of the parametric statistical testing regarding the normality in the distribution of the data, the density and biomass data were log-transformed before analyses. The diversity indicators (Shannon, Margalef and Pielou), the median grain size and cockle length data appeared to be normally distributed in all cases (Kolmogorov-Smirnov test at $p < 0.05$).

Data analysis

The comparisons between treatments were performed according to a standard BACI-ANOVA design where the effects of treatment, time and time \times treatment interaction are tested at $p < 0.05$. As a result of a rather strong plot effect, the individual samples can not be considered as taken randomly (without consideration of plot origin) within the treatments. Therefore a nested design according to: $\text{Change in Parameter} = \text{Parameter average} + \text{Treatment effect} + \text{Plot effect within each treatment} + \text{Unexplained variation}$ at which Unexplained variation which is the Error term, equals the variation among samples within plots (Sokal & Rohlf 1995). As a result of the decrease in the degree of freedom due to the nesting of plots within each treatment, the present ANOVA design is a relatively conservative test which might fail at detecting slight responses to the dredging. We are aware that data per treatment should not be gathered for testing, when differences between plots within treatments are present. However, we wanted to make sure that possible negative effects of cockle-dredging when present are at least not unnoticed. We therefore executed

the more sensitive (*i.e.* without distinction of plot origin) Student-t test ($p < 0.05$) for plain comparisons between the treatments or sampling times. Even the robustness of these more sensitive tests might be relatively low, due to the large variance among sample sites already at the start of the experiments (t_0), or due to the non-normal distributions. As we are especially interested in the developments over time for different treatments, independent of autonomous developments, we calculated the differences between t_1 and t_0 or t_2 and t_0 , and compared those per treatment using the Student-t test ($p < 0.05$).

Effects on individual species were investigated with Redundancy Analysis (RDA), which is a linear method of canonical ordination where combinations of the environmental variables are performed to build the ordination axes locating the samples within the multivariate space defined by the species data, either the log-transformed density, biomass or presence frequency data (Ter Braak & Milauer 1998). The analyses were restricted to the most abundant and dominant species determined as belonging to the top-10 species with respect to the descriptor to be analyzed (density, biomass or presence frequency) in at least one of the plots at one of the sample dates. The suitability of the linear response model was tested based on the value of the gradient length estimated with a Detrended Correspondence Analysis (DCA); for a gradient length between 1.5 and 3 SD both linear and unimodal models might be applied.

High species score (density, biomass or presence frequency) at a given location might be driven by out-of-scope factors coincidental with the treatment what could lead to misinterpretation based on the RDA plots. Therefore, the effect of the treatments on densities and biomasses of individual species were tested using Student-t-tests at $p < 0.1$. Again, this is a rather sensitive test in order to not leave possible negative impacts unnoticed. In order to cope with the bias introduced with the multiple t-testing, a Bonferroni correction according to $p \ddot{O} / n$ (Sokal & Rohlf 1995) was additionally also applied to identify the real significant effects on species. All statistics were executed in Systat for Windows 11.

Power analyses were performed in cases of absence of significant differences to determine the robustness of the tests. Herewith, the minimum difference that could possibly be detected with $p < 0.05$, was determined taking the variation between samples and the number of samples into account (Sokal & Rohlf 1995). The number of available observations and their standard deviation was tested at the level of 80 % probability assuming that the data are belonging to one normal distributed population of observations. As tested using Kolmogorov-Smirnov testing the distribution of the values for each of the parameter x treatment x time intervals can indeed be considered normally distributed, except for the difference in biomass between t_0 and t_2 at the dredged sites.

Results

Initial situation (t_0)

Data collected at the start of the experiments (t_0) show distribution patterns over the research area with a clear differentiation of the three northern plots when compared to the southern plots (Fig. 2). The three northern plots are characterized by smaller median grain sizes, lower total macrofauna densities and biomasses, and thereby higher Shannon, Margalef and Pielou diversity indices, than the southern plots (ANOVAs, $p < 0.05$). The intermediate plots showed intermediate values or resembled the southern or northern plots. Clearly, in all cases, as shown also in Fig. 2, the experimental plots resembled the reference plots (and thus showed the same geographic N-S gradient), and therefore at t_0 the averages of the reference plots for either median grain size (Fig. 3a), total density (Fig. 6a), total biomass (Fig. 6c), species diversity (Fig. 7e), species richness (Fig. 7a) and evenness (Fig. 7c) are the same as for the experimental plots. The initial large variance between plots is dealt with by nesting the variance within the treatments, which then serves as the error term for the treatment - time interaction to be tested.

The smallest detectable differences with the used design taking initial variability into account equals 1 % in median grain size, 10 % in evenness, 22 % in species richness, 24 % in species diversity, 48 % in total densities and 55 % in total biomass, with a probability of 80 % at $p < 0.05$, as calculated using Power Analyses.

Median grain size

It was expected that the median grain size might be directly influenced by dredging because of the sediment resuspension that occurs during the fishing activity. Yet, no difference in median grain size could be detected between the control and the dredged areas at any moment (t_0 , t_1 or t_2 ; t-test, $p < 0.05$) or between the sampling occasions (t_0-t_1 , t_0-t_2) (Fig. 3; Table 1). The average median grain size over all samples equals 175 μm , varying locally and independently of treatment or time between 150 and 190 μm .

Cockles

The present dataset allows estimating the impact of the fisheries on the cockle populations. Significantly lower cockle numbers were found in the dredged area compared to the control area at t_1 (t-test, $p < 0.05$) and lower cockle biomass in the dredged area than in the control area on both t_1 and t_2 ($p < 0.05$) (Fig. 5). The effect of fishing is more evident in the changes of the biomass since it were primarily the larger cockles that were fished (Fig. 4).

The size distribution of the cockles measured in this study can be used to estimate the size selectivity of the dredging with respect to the cockles. As indicated by the average cockle length and length distribution (Fig. 5a) clear shifts are found towards small sized individuals between t_0 and t_1 and back to the original size distribution at t_2 in the dredged areas. In the reference area, size distributions at t_0 and t_1 are quite similar whereas a slight increase in size distribution mode is detected between t_0 and t_2 (Fig. 4; Fig. 5). When different size classes (small (≤ 23 mm) and large (> 23 mm) cockles) are distinguished, data might inform over the differential effect of dredging as a function of the shell size. Indeed, a 23 mm shell length is approximately the size of separation of a 15 mm grid as used by the cockle ships (Hiddink 2003). However due to the low numbers of observations and their high variance, only differences of 82 (larger size classes) to 85 % (smaller size classes) can be detected (Power analysis; $P = 80\%$, $p < 0.05$). At t_1 on average 38.3 % of the cockles in the dredged area are large whereas in the control area, this is 72.2 % of the cockles (significant at $p < 0.1$). We find also a significant ($p < 0.1$) decrease in larger cockles between t_0 and t_1 in the dredged area compared to the control area.

Total macrofauna indicators

The total density of macrofauna excluding the cockles is found to be relatively stable through time and no significant differences are found between the dredged and control areas (Fig. 6a; Table 1). When differences in development of the densities might have been present between the two treatments, densities seem to not have been decreased over time in the dredged plots whereas the autonomous trend (visible in the control) shows a slight decrease (Fig. 6b). As no significant differences were observed, differences if present must have been smaller than 48 % at t_1 and 54 % at t_2 as calculated by a Power analysis.

In the total biomass, the autonomous effect of decrease over time seems to be even stronger than indicated by the numbers, and also here such a trend is absent in the dredged area (Fig. 6c,d). However, conducting a BACI-ANOVA, differences in trends do not appear to be significant ($p = 0.444$ from t_0 to t_1 and $p = 0.099$ from t_0 to t_2 ; Table 1).

When the total biomass is calculated including the cockles, the possible difference in trends is almost compensated by the cockle biomass. It is however clear that on both the short and the mid-

long term, with or without the cockles included, no decrease in densities or biomass is found as a result of dredging.

Species richness and species diversity show similar patterns when comparing the two treatments over time (Fig. 7a,e). Where initially the two treatments do not differ, this is still the case just after dredging, but one year after dredging the indicators tended to be increased for the dredged area whereas the control area remained unchanged. The observed trends can not be considered significantly different as shown by the BACI-ANOVA; $p=0.101$ for the trends in richness and $p=0.113$ for the trends in diversity between t_0 and t_2 (Table 1). However, definitely no negative effect of dredging on species richness and diversity is present. No effect is found on the evenness, or it must have been smaller than 10 % according to a Power analysis, but also then the impact of dredging seems to be positive instead of negative (Fig. 7c).

Effects on singular non-target species

Dredging might be species selective in its impact on the macrofauna through direct effects on recruitment and mortality rates or indirectly, through changes in habitat induced shifts in species composition. Figure 8 shows the results of RDAs based on densities (a) and biomass (b) for the most abundant species. Results of the presence frequency analyses are not shown, as they are rather similar to the density analyses. The graphs show the projection of the gradient axes of the species descriptor (from low to high values) together with that of the two environmental treatments (control and dredged) and sampling times (t_0 , t_1 and t_2). The closeness between both projections of species and factor gradients point to direct or indirect relations between the species descriptors and either the dredging and/or time (autonomous trend). Species like *C. edule*, *Tharyx marioni* and *Hydrobia ulvae* seem to be numerous at t_0 in particular, which points in the direction of an autonomous trend, although the first two are also related to the control, which points in the direction of a negative impact of dredging. Species found in higher numbers in the control plots at t_2 might also be impacted by dredging, like *Nephtys hombergii* and *Urothoe poseidonis*. At the other hand, many more species find the highest numbers in the dredged area at t_1 (*A. marina*, *Lanice conchilega*), and especially at t_2 . A similar trend can be found for the analyzed biomass data (fig. 8b), although other species appear in certain corners of the graph. It has to be noticed that coincidental appearance of larger numbers or larger specimens (higher biomass) in certain plots at certain dates, especially for low density species, can not be discriminated from real treatment effects in RDAs. Therefore, for further detailed statistical analyses per species t-testing would be needed.

The series of t-tests on individual species (Table 2) showed many species potentially affected by dredging, especially showing increases in densities or biomass. We have however to be aware that in multiple tests as performed with these t-tests a (conservative) Bonferroni correction should be performed, after which none of the observed differences are found to be really significant. Besides the negative effects on the cockle populations, as shown earlier (Fig. 4,5), the t-tests on individual species (Table 2) indicated possible negative impacts of dredging compared to the autonomous trend for three other taxonomic groups. These negative trends are only detected on the short term. Whereas an autonomous increasing trend in densities is observed six weeks after the onset of fishing for *H. ulvae* and the sub-class of the Oligochaeta, both have been decreased in the dredged area. *Arenicola sp.*, which is a special group as it very likely represents small individuals and body parts of *A. marina*, tended to increase less in the dredged area than in the control area ($p<0.1$). In contrast to the three groups that might be affected negatively by dredging on the short term, there are six species showing an increase after dredging on the short term. The biomasses of *A. marina*, *Capitella capitata*, *Pygospio elegans*, *Streblospio shrubsolii* and *Urothoe sp.* appear to increase during the first six weeks after the onset of dredging, whereas the opposite or at least no increase was found in the control area. For *Carcinus maenas*, the autonomous decreasing trend in density was not observed in the dredged area. The difference ($p<0.1$ in the t-test) between the treatments for *C. maenas*, was still observed after one year.

Many more species show an increase after dredging on the mid-long term. *Anaitides mucosa*, *Harmothoe lunulata* and *Spio sp* did not show a decreasing trend or such a strong decreasing trend in density in the dredged area as in the control area after a year. Further, there are 7 species that appear to show a stronger increase in biomass in the dredged area than in the control area on the mid-long term, and the decreasing trend in *Mya arenaria* biomass seems to be less strong in the dredged area compared to the control area. Whereas most species tending to increase after dredging belong to the polychaetes, there are also several malacostracans and *M. arenaria* which is a bivalve.

Discussion

Selective fisheries on large cockles

Our study demonstrates the efficiency of the fishing process with a clear reduction of the larger sized (>23 mm) cockles in the dredged areas. This observation confirms, apart from the visual observation of dredging tracks on the experimental areas, that fishing effectively took place on the dredged experimental plots. Partial recovery of the cockle population was observed after the fishing. Recruitment and growth of the cockles occurred in the dredged areas, but the average size of the cockles still lags after one year when compared to the control areas. No effect of dredging was detected on smaller sized cockles. The failure to detect any effect on the small sized cockles should be considered taking into account the low power of the test that is insensitive to differences lower than 85 %. A thorough analysis addressing the effects on smaller sized cockles would require larger sampling surfaces in order to reduce the variance in the data and therefore increase the discriminating power of the test.

Whether dredging influences cockle recruitment, as suggested by Piersma *et al.* (2001), could not be determined, as no large settlement occurred during the experiment. Beukema & Dekker (2005) suggest that negative effects of dredging on cockle recruitment mostly occur in sediments with very low mud content, where dredging might induce a further reduction of the fine material in the sediment below values required for the cockles. In the case of the present study area where sediment is rather muddy this effect is therefore not expected to be of great importance. The present study shows moreover no effect of dredging on median grain size, whereas the power to detect differences was large. Natural temporal variation in median grain size might be larger than the impact of dredging in the investigated area.

Effects on the environment

As indicated above, dredging might affect the composition of the environment and the top layer of the sediment in particular. On the other hand, sediment disturbance can also lead to an increased availability of nutrients in the top sediment layer or water layer (Kaiser *et al.* 2002; Warnken *et al.* 2003; Nayar *et al.* 2007) especially in areas with relatively low water turbulence and current velocities. Sediment disturbance can undo sediment compaction and increase sediment aeration or pore water renewal (Falcão *et al.* 2006). Increased nutrient availability can also lead to an oxygen decrease due to increased microbial activities (Riemann & Hoffmann 1991). The way and depth of disturbance and the type of environment are crucial in whether dredging will have a negative effect on certain macrobenthic species and whether also certain macrobenthic species might profit.

Irrespective all these potential impacts, our study failed to detect an effect of dredging on median grain size, although the power to detect differences was large. This is in contrast to findings in the Wadden Sea, where changes in median grain size and silt content were reported in areas that were fished for cockles, although the role of winter storms and the vicinity of mussel beds were also considered as relevant factors (Piersma *et al.* 2001).

Effects on communities and non-target species

In the present case, no severe environmental impact (on either density or biomass) of dredging was detected in the short term observations. Moreover, mid-long term sampling showed for both densities and biomass a slight increase in the dredged area leading to larger biomass compared to the control area after one year. This difference in biomass mostly resulted from a decrease in the control area (autonomous development) that seemingly was compensated by an increase in the dredged area. The higher biomass in the dredged areas does not result from a few dominant species that might benefit from the disturbed conditions but by many species as witnessed with the parallel increase in species richness and species diversity under steady levels of evenness.

Even in such a situation, at increasing biomass, species richness and species diversity, one can argue whether this is a positive or negative development, as certain species might be favored above others, and some species might be reduced. Therefore we focused also on impacts on the individual species. With respect to the individual species, only three species/groups show a reduction on the short term, *i.e.* with recovery within a year. One of the negatively impacted species is the gastropod *H. ulvae* as in accordance with Ferns *et al.* (2000) who showed a depletion of the *H. ulvae* populations under influence of mechanical cockle harvesting. *H. ulvae* is in the present study the most numerous species what might positively affect the diversity indices in the dredged areas. This species is also an important food source for several other species (Mendonça *et al.* 2007).

Previous studies have shown possible negative effects of dredging on smaller worms (Craeymeersch & Hummel, 2004; Ens *et al.* 2004) which is in concordance with the reduction of oligochaetes observed in the present study under the influence of dredging. Other studies suggested the opposite response, *i.e.* an increase of the dominance by worms as a result of sediment disturbances or increased nutrient availability in the environment (Reise 1982; Kaiser *et al.* 2002). The positive response of several worm species (*e.g.* *A. marina*, *C. capitata*, *P. elegans*, *S. shrubsolii*, *N. hombergii*, *P. dumerilii*, *P. ligni*, *S. armiger*) as observed in the present experiment might indeed point to a shift towards worm dominance in the disturbed conditions after the dredging. In this respect, it remains surprising that oligochaetes, which are known to first colonize and dominate in deteriorated conditions (Ysebaert *et al.* 2003), show decreased abundances in our study.

Several Malacostraca species (*i.e.* *C. maenas*, *Urothoe sp.*, *C. crangon*, *Gammarus sp.*, *G. locusta*), also seem to profit in numbers or biomass from the new conditions in the dredged area. These are mobile species and therefore fast colonizers upon disturbed areas. Their increase might result from the next two non-exclusive processes. On the one hand, they might profit from an increased food availability; *i.e.* the presence of damaged and dead organisms (large macrofauna) in the dredged environment on which they can scavenge. On the other hand, the increase in space availability due to the dredging (cockles are removed) might sustain the observed increase of the malacostracans. The hypothesis of increased space availability as a result of the dredging might also explain the attenuation in the decrease (autonomous trend) of the bivalve *M. arenaria* that is observed in the dredged area when compared with the control area. In addition, our hypothesis of decreased competition and/or increased space availability for non-target species seems to be supported by the partial compensation of the fished-away cockle biomass by biomass of non-target species and the apparent slight growth acceleration by the cockles left over in the dredged area.

The present study did not detect any negative effect on bivalve species other than cockles, which are however potentially influenced by dredging as shown by other studies. This result indicates that those bivalves are either not impacted, as they mainly inhabit deeper parts of the sediment (*e.g.* *M. arenaria*), or that they are not significantly damaged after the processing through the dredge when they are returned to the sediment (*e.g.* *Macoma balthica*). The equivocal effects of the dredging on *Arenicola sp.* and *A. marina* should be interpreted as a methodological artifact since *Arenicola sp.*

mostly consists of juveniles and incomplete parts of *A. marina* as no other *Arenicola* species than *A. marina* are observed in the research area.

The use of the t-test where the sensitivity is improved (compared with the nested ANOVA) by an increase of the degree of freedom (no distinction between the plots) did allow to reject the hypothesis that large scale negative effects on macrofauna density, biomass and diversity would result from the dredging in the investigated area. Actually, only two groups (*H. ulvae* and the oligochaetes) showed a negative effect of dredging on the short term in this experiment, although differences were not significant (ANOVA, $p > 0.05$). This also accounts for the range of species that showed positive effects of dredging on the short and mid-long term. From this, it can be concluded that the whole range of species, with the exception of the two groups just mentioned, were not negatively impacted. Whether some species might have benefitted from the dredging remains unsubstantiated.

Consequences of the current design

Although the current study did show significant differences or could rule out significant differences in the development of certain parameters with a reasonable statistical power, the unbalanced design is not ideal. A pairwise experimental design with as much undredged as dredged plots would increase the power of the tests and would make detection of smaller differences in development between the treatments possible without increasing the total number of plots/samples. As there is a large variation between plots and less variation within plots, the power can be increased the most by increasing the number of plots instead of increasing the number of samples within plots.

Cockle fisheries in a broader context

Within the conditions in the present experiment, it may be concluded that the impact of dredging on non-target species and the sediment does not appear to be overly-destructive on the mid-long term and therefore likely also not on the longer term. The negative effects observed for a few species on the short term were not detected on the mid-long term, and also not with the most sensitive tests. The results thus indicate that on the longer term effects on non-target species of cockle fisheries as carried out in this study are not to be expected. On the other hand, a longer term effect on the cockle populations can not be excluded. Although the cockle stock itself recovered after the dredging and individual growth was observed, a lag in the average size was still detected after one year in the dredged area when compared with the control area. Below we will present an overview of some relevant elements that can be of influence for the positioning of the present observations in a larger context.

The distance between dredged sample sites and undredged areas varied in this study between 10 and 300 meters. In previous studies, showing negative effects of cockle-dredging on non-target species, this distance was larger (Hiddink 2003), and thus it might be argued that recolonisation from neighbouring areas in our study was easier to occur. The extent of recolonisation from undredged neighbouring areas for both the recovery of the cockles and for the increase in non-target species was not addressed directly in this study, because the undredged experimental areas were very small compared to the total area dredged. We believe therefore that the undredged areas therefore can only have contributed in a minor way to the recolonisation in the much larger dredged area. Recolonisation from within the dredged area might also have been possible, as the dredging intensity was not uniformly distributed over the dredged area. However, satellite tracking system registrations did indicate that undisturbed parts were scarce. Therefore, we conclude that recolonisation has only contributed in a minor way to the absence of significant results of cockle fisheries on the zoomacro-benthic community.

The present study deals with the impact of a single dredging event whereas more disruptive effects on communities can be reasonably postulated by recurrent (yearly or even more frequent) dredging

activities. At the more disruptive intensity level, dredging activities reasonably may expect to prevent the establishment of long living ecostructures such as mussel/oyster banks and seagrass-fields together with their associated flora and fauna (Dittmann 1990; Boström & Bonsdorff 2000; Jaramillo *et al.* 2007). The negative impact shown by many other studies on a range of non-target species might be the result of other more destructive (*e.g.* deeper) dredging techniques (Hall & Harding 1997; Ferns *et al.* 2000) than the hydraulic dredging in use in the present case.

Local conditions of the fishing area should also be taken into account when considering the effects of fisheries on benthos. Queirós *et al.* (2006) and Hiddink *et al.* (2007) clearly point at the strong effect of habitat characteristics such as sediment and productivity in relation with the sensitivity to dredging disturbances. A common conclusion by both papers was that the degree of natural disturbance determines the degree of sensitivity to fishing activities. It is thus possible that communities of sandy substrates as in the Wadden Sea are differentially sensitive to disturbances than communities found on muddy sediments as in our study. This could then explain differences between the negative impacts of cockle fisheries as found in the Wadden Sea (Piersma *et al.* 2001) and the absence of significant results in our area. However, the relation with the mud content is not consistent, as effects of fisheries, as indicated by Queirós *et al.* (2006), were more negative on the more muddy areas, whereas in our muddy area no significant effects could be found. Further studies should have to focus more on those aspects. Several studies also show negative effects of dredging on the bivalve recruitment (Piersma *et al.* 2001; Hiddink 2003). In absence of massive bivalve recruitment in the area during the research period, no conclusion can be drawn relative to the effect of dredging on the recruitment from the present study.

From the results of our study we can conclude that sustainable cockle fisheries might be possible taking into consideration the above mentioned aspects. The sensitivity and the recovery potential of a dredged area, being amongst others related to the type of habitat and probably also to the period of non-disturbance, should be specified on basis of adequate field-experiments preferably using a BACI approach.

Acknowledgements

We would like to thank the research assistants of the Monitor Taskforce (NIOO-CEME) for sampling and macrofauna determination. Thanks to the crew of the ships YE172, YE98 and YE42, and to Joke Kesteloo-Hendrikse and Douwe van de Ende (IMARES) for their assistance during the fieldwork. The research has been executed in the frame of the -Project Research Sustainable Shellfish Fisheriesø(PRODUS), and we would like to thank the -Cooperative Producers Organization of the Dutch Cockle Fisheriesøand Jaap Holstein in particular for their cooperation. Thanks to the organizing committee of the 44th EMBS 2009, who gave us the opportunity to present and discuss this study. This is publication 4892 of the Netherlands Institute of Ecology (NIOO-KNAW), and Monitor Taskforce Publication Series 2010-10.

References

- Beukema J.J. (1995) Long-term effects of mechanical harvesting of lugworms *Arenicola marina* on the zoobenthic community of a tidal flat in the Wadden Sea. *Netherlands Journal of Sea Research*, **33**, 219-227.
- Beukema J.J., Cadée G.C. (1999) An estimate of the sustainable rate of shell extraction from the Dutch Wadden Sea. *Journal of Applied Ecology*, **36**, 49-58.
- Beukema J.J., Dekker, R. (2005) Decline of recruitment success in cockles and other bivalves in the wadden Sea: possible role of climate change, predation on postlarvae and fisheries. *Marine Ecology Progress Series*, **287**, 149-167.
- Boström C., Bonsdorff E. (2000) Zoobenthic community establishment and habitat complexity ó the importance of seagrass shoot-density, morphology and physical disturbance for faunal recruitment. *Marine Ecology Progress Series*, **205**, 123-138.

- Clarke K.R., Warwick R.M. (2001) Change in marine communities: an approach to statistical analysis and interpretation, 2nd edition. PRIMER-E, Plymouth, UK: 178 pp.
- Coosen J., Twisk F., Van der Tol M.W.M., Lambeck R.H.D., Van Stralen M.R., Meire P.M. (1994) Variability in stock assessment of cockles (*Cerastoderma edule* L.) in the Oosterschelde (in 1980-1990), in relation to environmental factors. *Hydrobiologia*, **282/283**, 381-395.
- 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 Journal of Marine Science*, **54**, 72-83.
- Craeymeersch J.A., Hummel H. (2004) Effectonderzoek kokkelvisserij Voordelta. RIVO-rapport C012/04, Yerseke, The Netherlands: 41 pp (in Dutch).
- Dankers N., Zuidema D.R. (1995) The role of the mussel (*Mytilus edulis* L.) and mussel culture in the Dutch Wadden Sea. *Estuaries*, **18**, 71-80.
- Dittmann, S. (1990) Mussel beds ó amensalism or amelioration for intertidal fauna? *Helgoländer Meeresunters*, **44**, 335-352.
- Ens B.J., De Jong M.L., Ter Braak C.J.F. (2003) EVA II deelproject C4: Resultaten kokkelvisserijexperiment Ameland. Alterra-rapport 945, Wageningen, The Netherlands: 144 pp (in Dutch).
- Ens B.J., Smaal A.C., De Vlas J. (2004) The effects of shellfish fishery on the ecosystems of the Dutch Wadden Sea and Oosterschelde; Final report on the second phase of the scientific evaluation of the Dutch shellfish fishery policy (EVA II). Alterra-rapport 1011, RIVO-rapport C056/04, RIKZ-rapport RKZ/2004.031, Wageningen, The Netherlands: 212 pp.
- Falcão M., Caetano M., Serpa D., Gaspar M., Vale C. (2006) Effects of infauna harvesting on tidal flats of a coastal lagoon (Ria Formosa, Portugal): Implications on phosphorus dynamics. *Marine Environmental Research*, **61**, 136-148.
- Ferns P.N., Rostron D.M., Siman H.Y. (2000) Effects of mechanical cockle harvesting on intertidal communities. *Journal of Applied Ecology*, **37**, 464-474.
- Geurts van Kessel A.J.M., Kater B.J., Prins T.C. (2003) Veranderende draagkracht van de Oosterschelde voor kokkels. Rapportage van Themaø 2 en 3 uit het -Lange Termijn Onderzoeksprogramma Voedselreservering Oosterscheldeø in het kader van de Tweede Evaluatie van het Nederlands Schelpdiervisserijbeleid, EVA II. Rapport RIKZ/2003.043, RIVO rapport C062/03, Middelburg, The Netherlands: 128 pp (in Dutch).
- Hall S.J., Harding M.J.C. (1997) Physical disturbance and marine benthic communities: the effects of mechanical harvesting of cockles on non-target benthic infauna. *Journal of Applied Ecology*, **34**, 497-517.
- Hiddink J.G. (2003) Effects of suction-dredging for cockles on non-target fauna in the Wadden Sea. *Journal of Sea Research*, **50**, 315-323.
- Hiddink J.G., Jennings S., Kaiser M.J. (2007). Assessing and predicting the relative ecological impacts of disturbance on habitats with different sensitivities. *Journal of Applied Ecology*, **44**, 405-413.
- Jaramillo E., Contreras H., Duarte C. (2007) Community structure of the macroinfauna inhabiting tidal flats characterized by the presence of different species of burrowing bivalves in Southern Chile. *Hydrobiologia*, **580**, 85-96.
- Kaiser M.J., Broad G., Hall S.J. (2001) Disturbance of intertidal soft-sediment benthic communities by cockle hand raking. *Journal of Sea Research*, **45**, 119-130.
- Kaiser M.J., Collie J.S., Hall S.J., Jennings S., Poiner I.R. (2002) Modification of marine habitats by trawling activities: prognosis and solutions. *Fish and Fisheries*, **3**, 114-136.
- Leitão F.M.S., Gaspar M.B. (2007) Immediate effect of intertidal non-mechanised cockle harvesting on macrobenthic communities: a comparative study. *Scientia Marina*, **71**, 723-733.
- Leopold M.F., Dijkman E.M., Cremer J.S.M., Meijboom A., Goedhart P.W. (2004) De effecten van mechanische kokkelvisserij op de benthische macrofauna en hun habitat. Eindverslag EVA II (Evaluatie Schelpdiervisserij tweede fase), Deelproject C1/3. Alterra-rapport 955, Wageningen, The Netherlands: 146 pp (in Dutch).

- Mendonça V.M., Raffaelli D.G., Boyle P.R. (2007) Interactions between shorebirds and benthic invertebrates at Culbin Sands lagoon, NE Scotland: Effects of avian predation on their prey community density and structure. *Scientia Marina*, **71**, 579-591.
- Nayar S., Miller D.J., Hunt A., Goh B.P.L., Chou L.M. (2007) Environmental effects of dredging on sediment nutrients, carbon and granulometry in a tropical estuary. *Environmental Monitoring and Assessment*, **127**, 1-13.
- 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. *Journal of Applied Ecology*, **38**, 976-990.
- Queirós A.M., Hiddink J.G., Kaiser M.J., Hinz H. (2006) Effects of chronic bottom trawling disturbance on benthic biomass, production and size spectra in different habitats. *Journal of Experimental Marine Biology and Ecology*, **335**, 91-103.
- Riemann B., Hoffmann E. (1991) Ecological consequences of dredging and bottom trawling in the Limfjord, Denmark. *Marine Ecology Progress Series*, **69**, 171-178.
- Smith, E.P. (2002) BACI design. In: El-Shaarawi A.H., Piegorsch W.W. (eds.) Encyclopedia of environmetrics, volume 1. John Wiley & Sons, Ltd, Chichester, UK: pp. 141-148.
- Sokal R.S., Rohlf F.J. (1995) Biometry: the principles and practice of statistics in biological research. 3rd ed., W.H. Freeman and Company, New York, US: 887 pp.
- Ter Braak C.J.F., Milauer P. (1998) CANOCO reference manual and user's guide to Canoco for Windows. Software for canonical community ordination (version 4). Centre for Biometry Wageningen, the Netherlands: 351 pp.
- Warnken K.W., Gill G.A., Dellapenna T.M., Lehman R.D., Harper D.E., Allison M.A. (2003) The effect of shrimp trawling on sediment oxygen consumption and the fluxes of trace metals and nutrients from estuarine sediments. *Estuarine, Coastal and Shelf Science*, **57**, 25-42.
- Wijnhoven S., Sijm W., Hummel H. (2008) Historic developments in macrozoobenthos of the Rhine ó Meuse estuary: From a tidal inlet to a freshwater lake. *Estuarine, Coastal and Shelf Science*, **76**, 95-110.
- Ysebaert T., Herman P.M.J., Meire P., Craeymeersch J., Verbeek H., Heip C.H.R. (2003) Large-scale spatial patterns in estuaries: estuarine macrobenthic communities in the Schelde estuary, NW Europe. *Estuarine, Coastal and Shelf Science*, **57**, 335-355.
- Zwarts L. (2004) Bodemgesteldheid en mechanische kokkelvisserij in de Waddenzee. Rapport RIZA/2004.028, Lelystad, The Netherlands: 129 pp (in Dutch).

Figure captions

Figure 1. Positioning of the experimental plots (plot numbers indicated) on the -Slikken van de Dortsmanøtidal flats in the Oosterschelde area (SW Netherlands).

Figure 2. Between plots variation before fishing (t_0). Variation in (a) median grain size (μm), (b) total density (n/m^2), (c) total biomass ($\text{g ADW}/\text{m}^2$), and (d) species diversity according to Shannon. Significant differences ($p < 0.05$) are indicated with different letters, whereas a letter in common means no significant differences.

Figure 3. Median grain size of the toplayer of the experimental plots. (a) Median grain size (μm) in control and dredged plots before (t_0), and shortly (t_1) and 1 year (t_2) after fishing; (b) increase or decrease of median grain size between t_0 and t_1 and between t_0 and t_2 .

Figure 4. Numbers of cockles distributed over size classes within the control and dredged plots (rows) before (t_0), and shortly (t_1) and 1 year (t_2) after fishing (columns).

Figure 5. Cockle length in mm (a) and biomass in $\text{g ADW}/\text{m}^2$ (b) in control and dredged plots before (t_0), and shortly (t_1) and 1 year (t_2) after fishing. Significant differences in lengths between treatments are indicated with * ($p < 0.05$).

Figure 6. Total macrobenthic density and biomass of the experimental plots. (a) Total density (n/m^2) in control and dredged plots before (t_0), and shortly (t_1) and 1 year (t_2) after fishing, (b) Relative increase or decrease of total density between t_0 and t_1 and between t_0 and t_2 calculated as the difference between the natural logarithms, (c) Total biomass ($\text{g ADW}/\text{m}^2$) in control and dredged plots before (t_0), and shortly (t_1) and 1 year (t_2) after fishing, and (d) Relative increase or decrease of total biomass between t_0 and t_1 and between t_0 and t_2 calculated as the difference between the natural logarithms.

Figure 7. Macrobenthic assemblage biodiversity descriptors. (a) Species richness according to Margalef in control and dredged plots before (t_0), and shortly (t_1) and 1 year (t_2) after fishing. (b) Increase or decrease of species richness between t_0 and t_1 and between t_0 and t_2 . (c) Pielouø Evenness in control and dredged plots before (t_0), and shortly (t_1) and 1 year (t_2) after fishing. (d) Increase or decrease of evenness between t_0 and t_1 and between t_0 and t_2 . (e) Shannonø species diversity in control and dredged plots before (t_0), and shortly (t_1) and 1 year (t_2) after fishing. (f) Increase or decrease of species diversity between t_0 and t_1 and between t_0 and t_2 .

Figure 8. Results of Redundancy Analyses (RDA) showing relations between species, treatments and sample dates. (a) RDA plot based on log-transformed species densities. (b) RDA plot based on log-transformed species biomass.

Figures

Fig. 1.

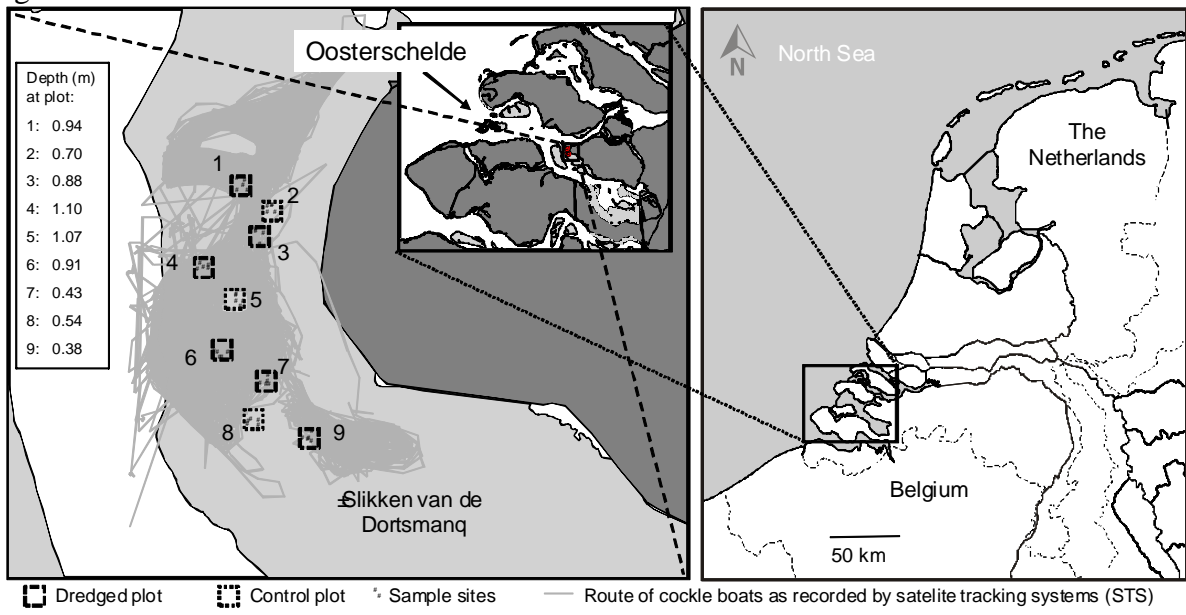


Fig. 2.

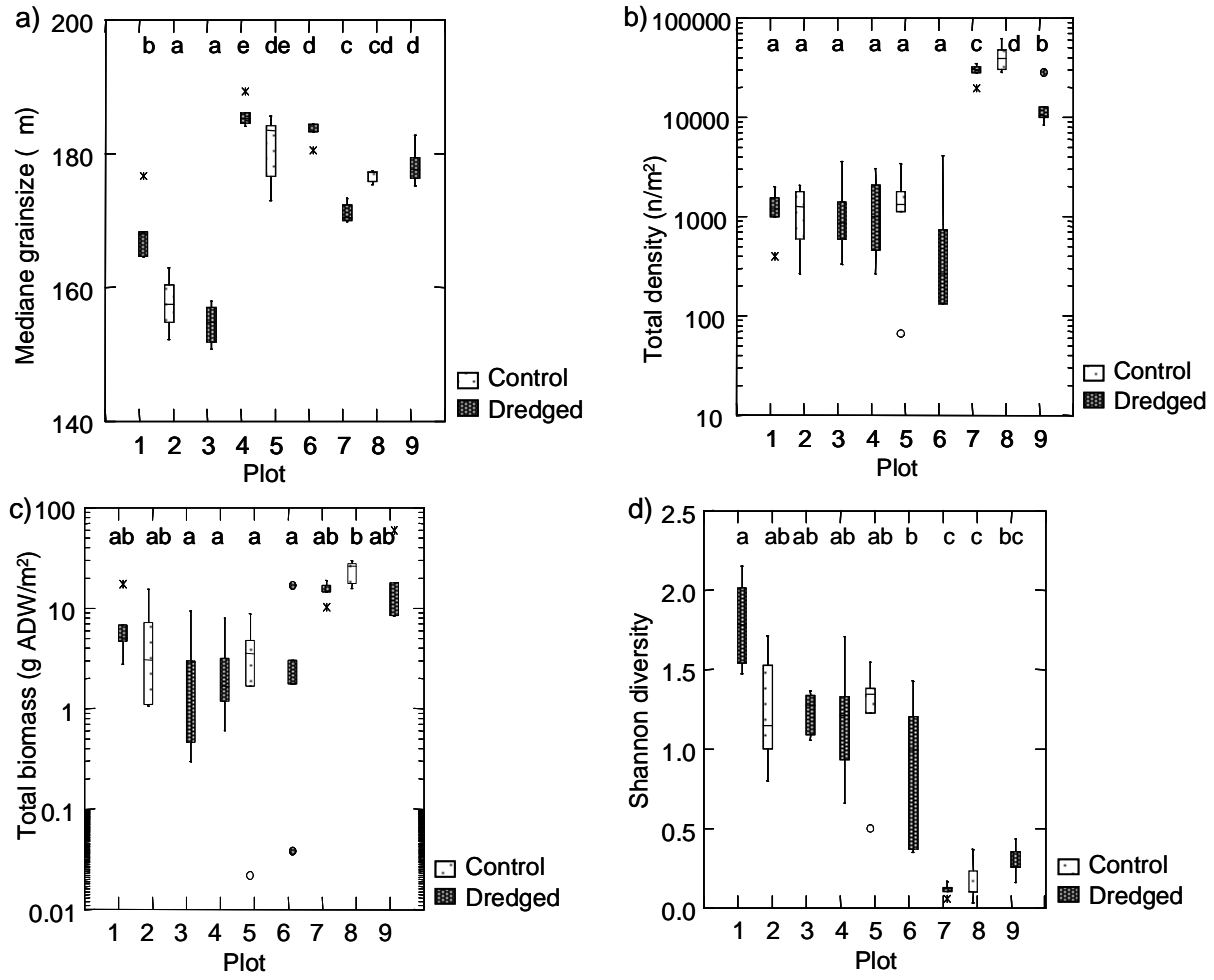


Fig. 3.

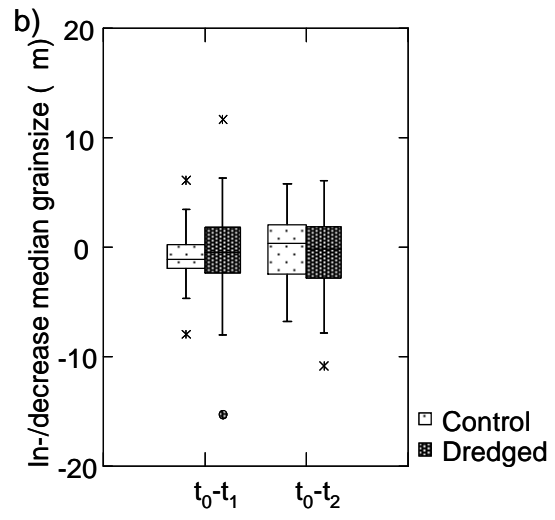
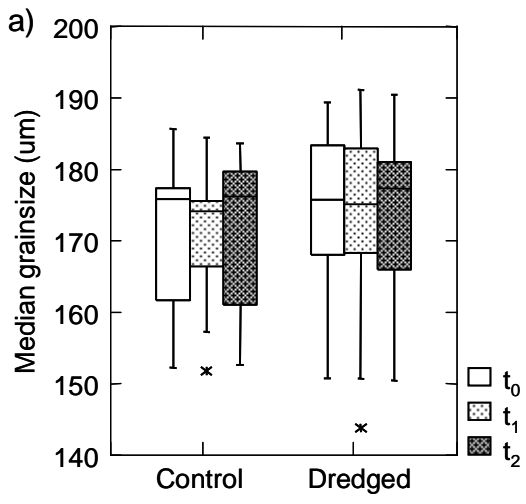


Fig. 4.

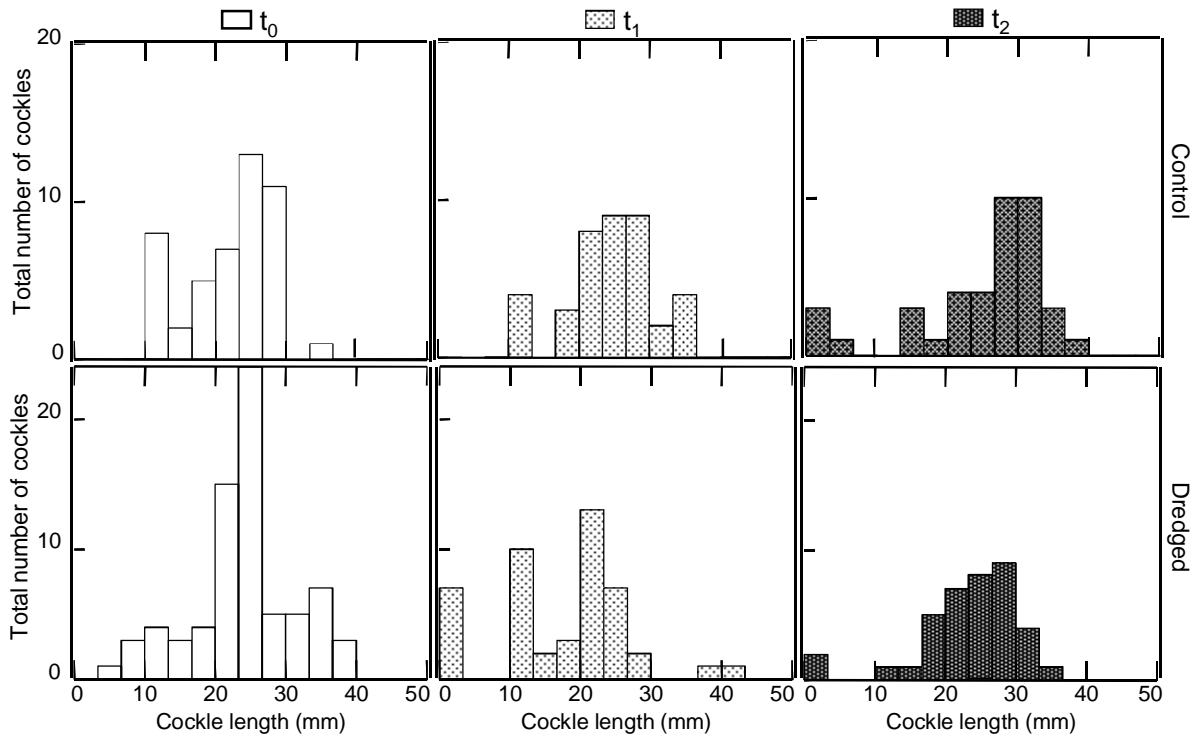


Fig. 5.

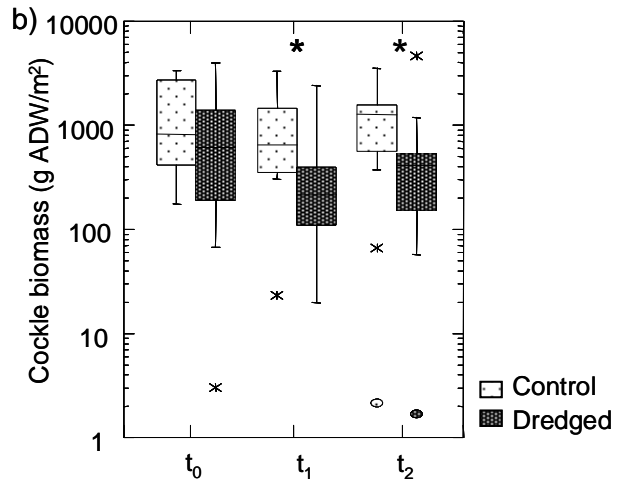
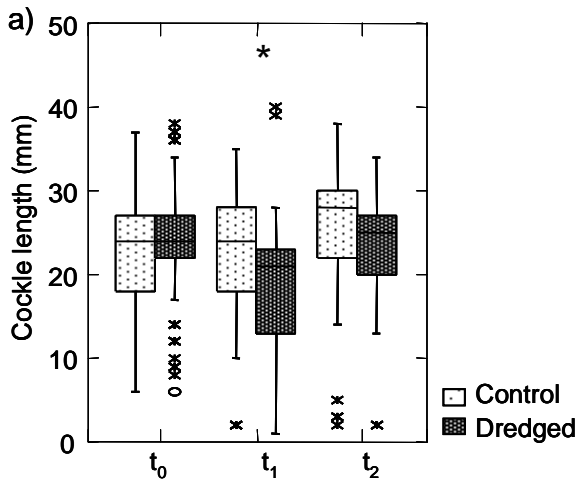


Fig. 6.

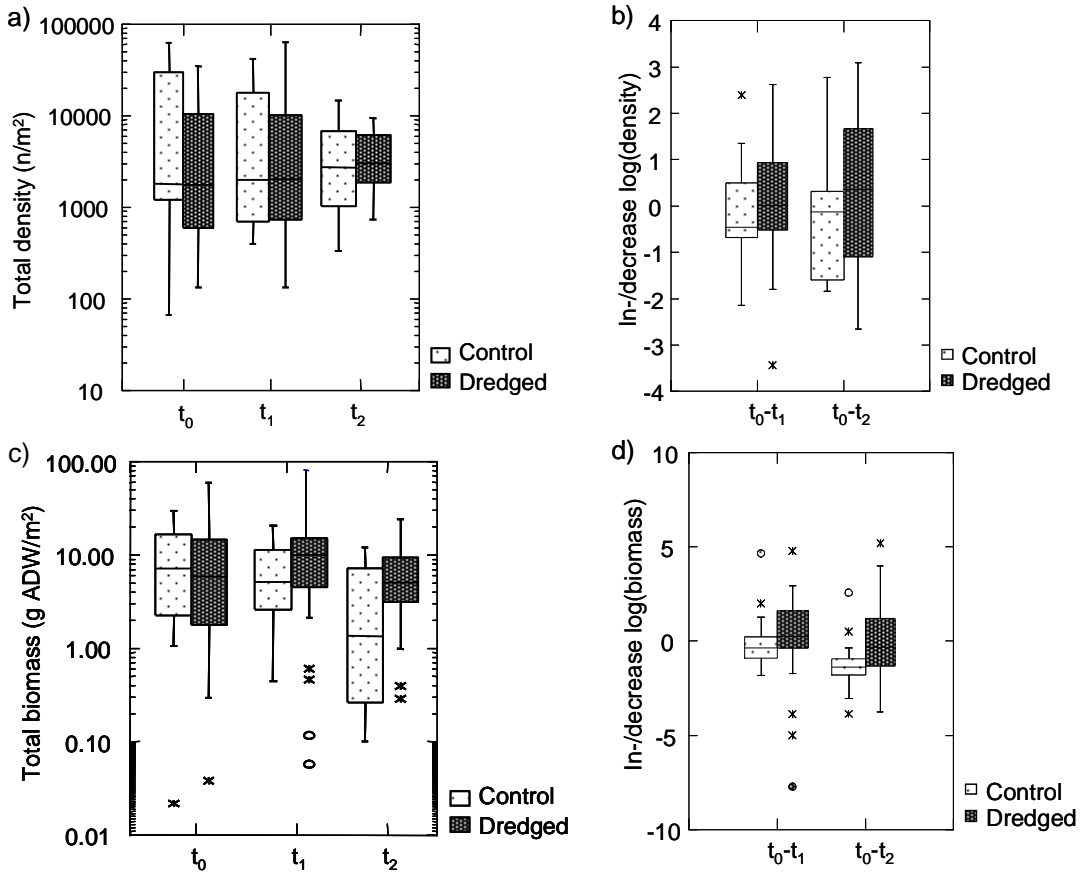


Fig. 7.

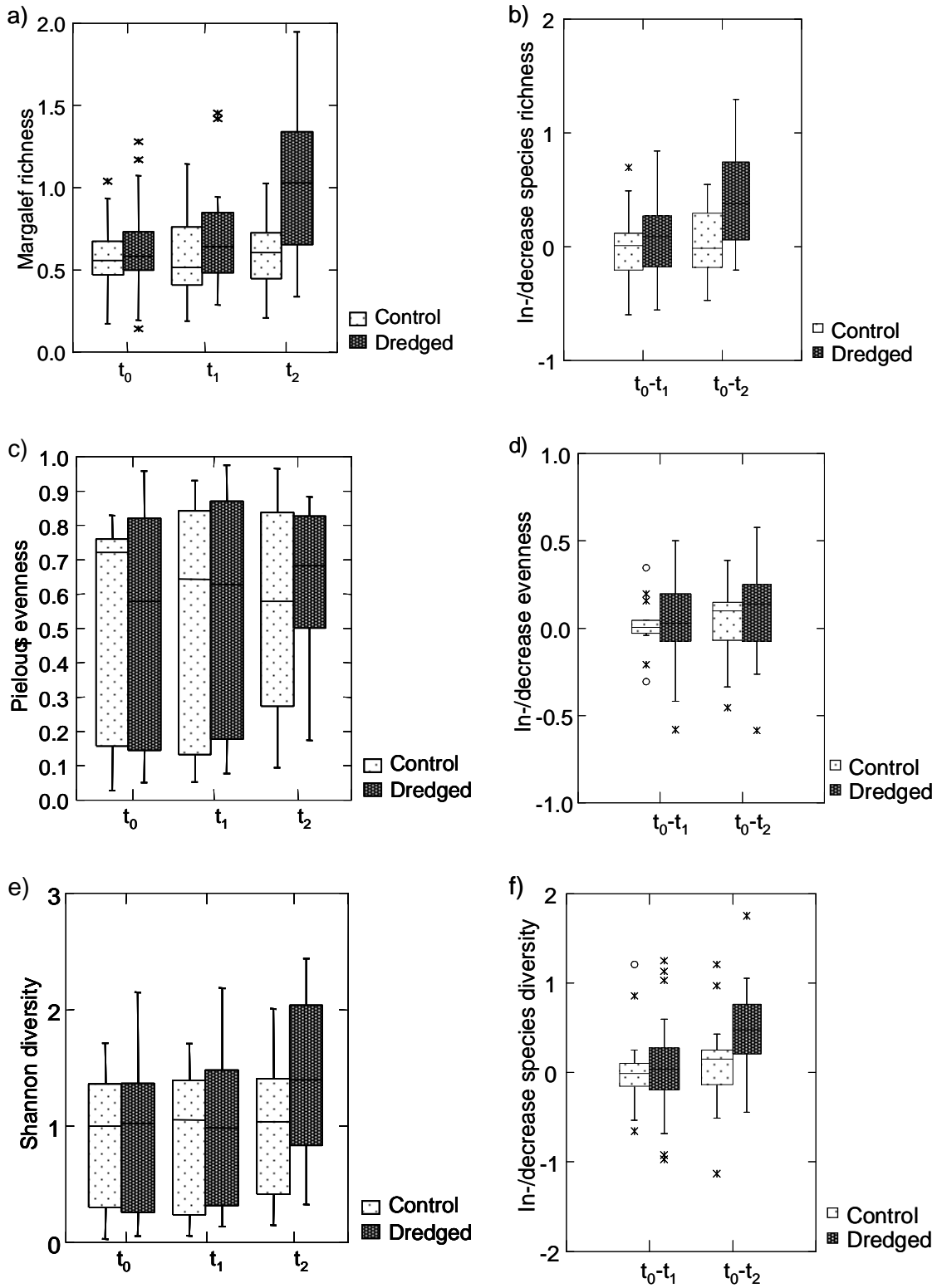
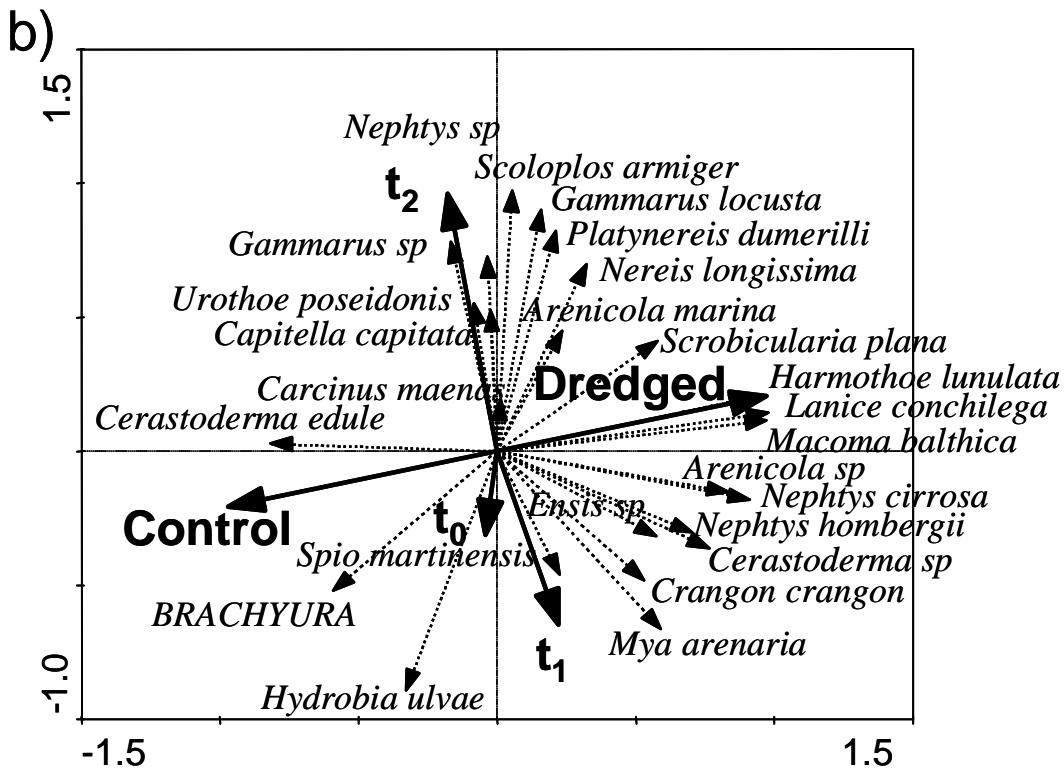
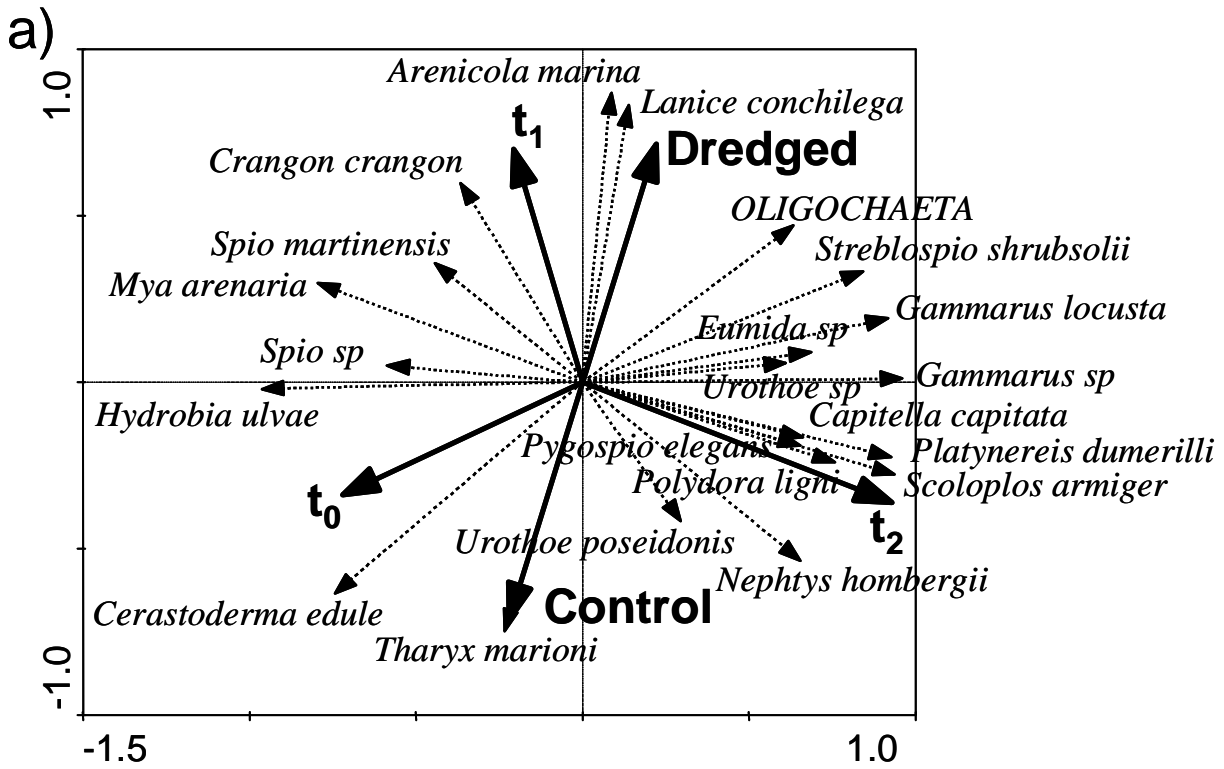


Fig. 8.



Tables

Table 1. Test results of BACI-ANOVA for time δ treatment interactions taking δ plot nested within treatment x time δ (time*plot(treatment)) as error; $df_{(time*treatment)}=1$; $df_{error}=7$; cockle data excluded.

	Short term effects (t ₀ -t ₁)		Mid-long term effects (t ₀ -t ₂)	
	F-ratio	p	F-ratio	p
Median grainsize	1.007	0.444	0.000	1.000
Log(density)	1.285	0.352	0.157	0.922
Log(biomass)	0.061	0.979	3.627	0.099
Margalef richness	0.642	0.612	3.560	0.101
Pielou's evenness	0.251	0.858	0.866	0.502
Shannon diversity	0.494	0.698	3.271	0.113

Table 2. Possible differences in density and/or biomass developments between control (C) and dredged (D) plots for the non-target macrobenthic species, from t_0 to t_1 and from t_0 to t_2 , as indicated from paired t-tests without Bonferroni correction.

Negative effects of dredging				Positive effects of dredging			
Species	Class	Development	p-level	Species	Class	Development	p-level
Density t_0-t_1 :							
<i>Hydrobia ulvae</i>	Gastropoda	D, C	0.042	<i>Carcinus maenas</i> ¹	Malacostraca	=D, C	0.054
Oligochaeta	Clitellata	D, C	0.006				
Biomass t_0-t_1 :							
<i>Arenicola sp</i>	Polychaeta	D, C	0.069	<i>Arenicola marina</i>	Polychaeta	D, C	0.059
				<i>Capitella capitata</i>	Polychaeta	D, C	0.016
				<i>Pygospio elegans</i> ¹	Polychaeta	D, C	0.016
				<i>Streblospio shrubsolii</i> ¹	Polychaeta	D, =C	0.030
				<i>Urothoe sp</i> ¹	Malacostraca	D, C	0.098
Density t_0-t_2 :							
				<i>Anaitides mucosa</i> ¹	Polychaeta	D, C	0.064
				<i>Carcinus maenas</i> ¹	Malacostraca	=D, C	0.054
				<i>Harmothoe lunulata</i> ¹	Polychaeta	D, C	0.066
				<i>Spio sp</i>	Polychaeta	D, C	0.036
Biomass t_0-t_2 :							
				<i>Crangon crangon</i>	Malacostraca	D, C	0.014
				<i>Gammarus sp</i>	Malacostraca	D, C	0.054
				<i>Gammarus locusta</i>	Malacostraca	D, C	0.009
				<i>Mya arenaria</i>	Bivalvia	D, C	0.086
				<i>Nephtys hombergii</i>	Polychaeta	D, C	0.097
				<i>Platynereis dumerilii</i> ¹	Polychaeta	D, C	0.049
				<i>Polydora ligni</i> ¹	Polychaeta	D, C	0.027
				<i>Scoloplos armiger</i>	Polychaeta	D, C	0.051

decrease; stronger decrease than for the other treatment of the same species; increase; stronger increase than for the other treatment of the same species; = unchanged; p-levels for significant differences after Bonferroni correction are $p < 0.0001$ for the dominant species only and $p < 0.00002$ for all observed species, which are achieved by none of the species; ¹ Species not belonging to the 10 most dominant species in densities or biomass in one of the treatment x time combinations