

Experimental beam-trawling in *Lanice conchilega* reefs: Impact on the associated fauna

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Abstract

To study fisheries impact at the species level in temperate sandy bottom areas, a controlled field manipulation experiment was designed focusing on areas with high densities of the habitat-structuring, tube-dwelling polychaete *Lanice conchilega* (i.e. *L. conchilega* reefs). The hypothesis was that the impact on *L. conchilega* would be minimal, but that the fauna benefiting from the biogenically structured habitat would be impacted by beam-trawling. In this study, the impact of beam-trawl passage on intertidal *L. conchilega* reefs and its associated fauna was quantified. A treatment zone was exposed to a one-off experimental trawling. Subsequently, the impact on and recovery of the associated fauna was investigated for a period of 9 days post-impact. Community analysis showed a clear impact followed by a relatively quick recovery as apparent through MDS analysis (stress 0.06), a significant ($p < 0.001$) IMS of 0.61, through ANOSIM analysis: significant ($p = 0.001$) dissimilarities between treatment and control and through SIMPER analysis (decreasing dissimilarities over time). This impact and subsequent recovery was largely explained by two species: *Eumida sanguinea* and *Urothoe poseidonis*. Species analysis confirmed the beam-trawl passage significantly ($p = 0.001$) impacted *E. sanguinea* for the whole period of the experiment. The experiment confirmed that closely associated species of *L. conchilega* reefs are impacted by beam-trawl fisheries. This small-scale intertidal study provides some pointers which indicate that the tightly associated species will be impacted significantly when beam-trawling *L. conchilega* reefs in subtidal areas.

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1. Introduction

1.1. Fisheries impact on soft bottoms

Impact of fisheries on benthic ecosystems has been reported to vary substantially depending both on the type of gear used and on the nature of the impacted habitats (e.g. Brylinski et al., 1994; Kaiser et al., 2006). The impact of beam-trawling on soft-sediment systems has already triggered considerable attention (e.g. Bergman and Hup, 1992; Kaiser and Spencer, 1996; Sparks-McConkey and Watling, 2001). However, the former studies did not focus on specific habitats or niches within these soft-sediment systems. Kaiser et al. (2002) mention that biogenically structured habitats are more adversely affected by fishing

than unconsolidated sediment habitats. Moreover, biogenically structured habitats have the longest recovery trajectory in terms of recolonisation of the habitat by the associated fauna. Yet, soft-sediment organisms that create structures reaching only a few centimetres into the water column have been described as an important habitat supporting a diversity of taxa (cf. ecosystem engineers: Jones et al., 1997; Coleman and Williams, 2002), including post-settlement juveniles of commercially important fish (Watling and Norse, 1998). Quantifying the resilience of biogenically created habitats towards fisheries in soft sediments is therefore considered to be a key factor in assessing fisheries impact in the soft sediment environment.

1.2. *Lanice conchilega*

This study focuses on the habitat engineer (Rabaut et al., 2007) *Lanice conchilega* (Polychaeta). This tubeworm can be found in elevated patches of high densities (Ropert and Dauvin,

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2000), in which suspended material is trapped. The availability of habitat structures and their effect on the local hydrodynamic regime are important causal factors for polychaete larvae settling (Callaway, 2003). As such, patches of high abundances trap sediment and evolve towards biogenic emergent structures. They are referred to as “*L. conchilega* reefs” and create a heterogeneous habitat, which attracts species from the surrounding unconsolidated environment, thus enhancing biodiversity (Dittmann, 1999; Zühlke, 2001; Ager, 2002). The fauna associated with *L. conchilega* reefs depends to some extent on the nature of the habitat and the species community but *L. conchilega* always has an effect on the benthos (Zühlke et al., 1998; Dittmann, 1999; Rabaut et al., 2007). Some of these species live in commensal relationship with *L. conchilega*, such as *Eumida sanguinea* (Callaway, 2006), a predatory polychaete living between the fringes of the tubes. Besides the increased diversity, intertidal *L. conchilega* reefs harbour high benthic standing stocks and are considered to be highly productive (Zühlke et al., 1998; Zühlke, 2001; Callaway, 2006). Also in subtidal areas, *L. conchilega* acts as a bio-engineer (Rabaut et al., 2007). As enhanced standing stocks and productivity attract opportunistic demersal predators such as sole and plaice, the multitude of target species makes these reefs attractive for fisheries (Rijnsdorp et al., 2000).

1.3. Aims of the study

This experimental study was designed to quantify beam-trawl impact on the associated fauna community of *L. conchilega* reefs. Since *L. conchilega* has high chances to survive beam-trawling, avoiding damage by quickly retreating into its tube (Bergman and Hup, 1992), it was expected that experimental fishing would not harm *L. conchilega* individuals. The hypothesis was that species most associated with *L. conchilega* and occurring in high abundances would be mostly impacted by the disturbance. As these species shape the community structure in the reef systems, a community shift was expected after disturbance, followed by a rapid recovery. The final aim was to investigate the response mechanism to have some pointers of how similar *L. conchilega* reef systems in subtidal areas respond to beam-trawl fisheries.

2. Methods

2.1. Intertidal study area

This impact study was carried out in the intertidal zone, which offered several advantages for a controlled field experiment. Firstly, there was no interference with commercial fisheries. This was related to the limited depth and the location in a protected zone where fishermen are not allowed. Secondly, the substantial tidal range made it possible to disturb the plots at high water spring tide (HWST) and to look for evidence of gear passage at low water spring tide (LWST). Thirdly, it was possible to sample manually and to visually follow up the recovery. The experimental area was situated in the intertidal zone of the seashore of Boulogne-sur-mer, France (50°44.10'N,

1°35.25'E; Fig. 1), a pocket-beach sheltered by two harbour walls. The largest zone covers an area of about 45,000 m² and is situated below the mean low waterline at spring tide. These lower reefs are only visible with extreme LWST conditions. The reef zones located higher on the beach were exposed at every low water: patches of the higher western zone occupied an area of about 4000 m², while the higher eastern zone has patches with a total area of 2500 m². The experiment was performed in the latter areas in which a treatment and control zone was delineated prior to disturbance (Fig. 1). *Lanice conchilega* patches in this study area reach on average densities of 3259 ± 269.1 individuals/m² (±SE) and the maximum density observed was 8262 individuals/m². These densities however, differed at a small scale (i.e. within the same reefs). This is an inherent characteristic of the investigated system as has been recorded by Carey (1987) and Heuers et al. (1998). Novel statistical modelling techniques allowed inclusion of the *L. conchilega* densities and modelling of the error structure as such (cf. *infra*).

2.2. Disturbance and sampling

On 13 February 2006, during HWST, a one-off disturbance event was simulated with the RV Sepia 2. A beam-trawl of 2.9 m width trawled the previously delineated treatment zone nine times. At the low tide (T0) following the experimental fishing, *L. conchilega* patches with evidence of beam-trawl passage were traced. Three treatment plots were defined (TR1–3) and four control sites (C1–4) were selected randomly and marked with star pickets to facilitate future tracing. Macrofauna samples were collected with an inox macrocorer of 15 cm diameter (i.e. 0.017 m²), sampling to a depth of 40 cm. Each set of replicate samples was accompanied by an additional sample collected for sediment (diameter 3.6 cm; penetration depth 5 cm).

To estimate the recovery of associated fauna, the site was subsequently sampled at every low tide during 3 days (T1–T4) (Table 1). At every sampling event, all treatment and control plots were sampled. Each sampling event took place around the moment of lowest water level to be able to reach the study area. The last sampling event (T5) was carried out 200 h after disturbance. Macrofauna was sieved alive on a 1 mm mesh size, fixed in 4% formalin–seawater solution and stained with Rose Bengal.

Table 1
Disturbance (D) and sampling times of the experiment

Sampling time	Hours after D
D	0
T0	6
T1	18
T2	30
T3	42
T4	54
T5	200

The hours are indicative and coincide in reality with the moment of lowest water level to be able to reach the study area.

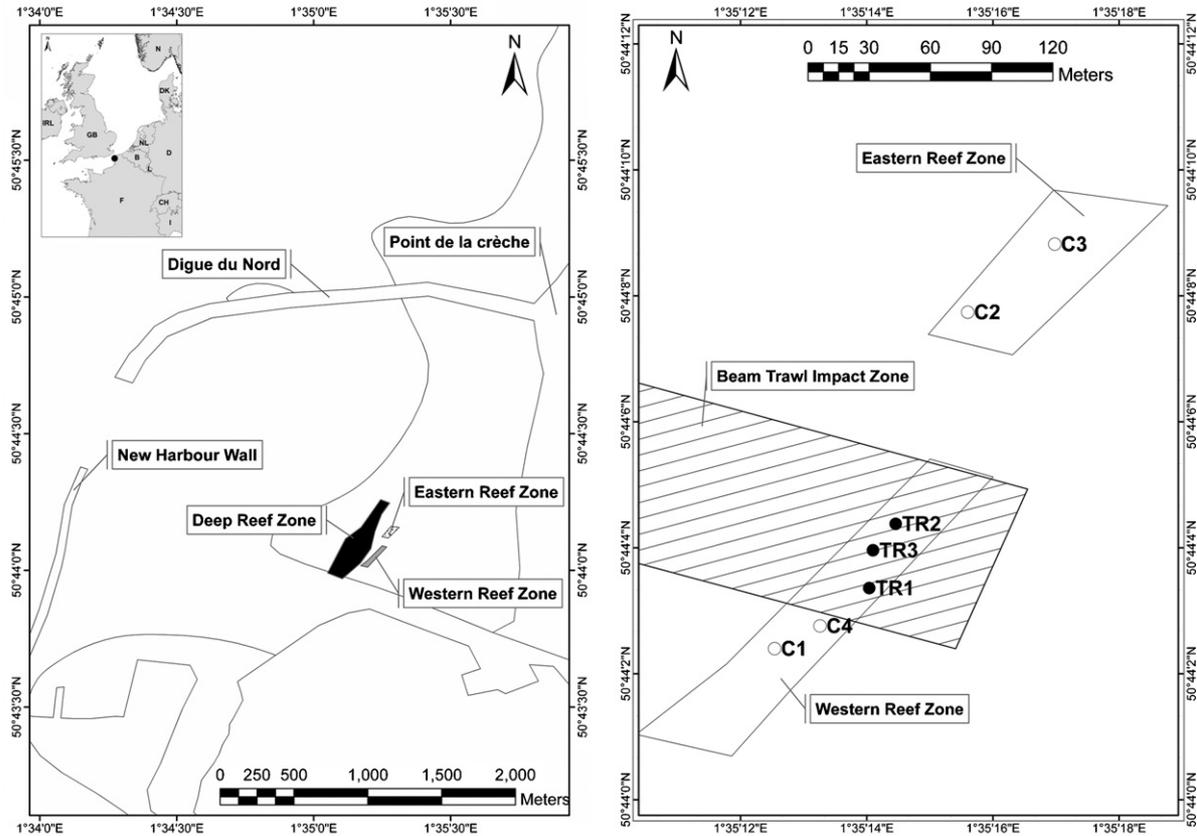


Fig. 1. Sampling location. Location of Boulogne-sur-mer in France (●), Europe (inset), Location of the *L. conchilega* reef zones at the 'pocket beach' (left) and sampling positions for treatment (●) and control (○) samples (right).

2.3. Sample processing

Sediment samples were dried at 60 °C and grain size analysis was carried out using a LS Coulter Counter. Sediment fractions were defined according to the Wentworth scale (Bunchanan, 1984). In the lab, sample contents were rinsed and all macrofauna was sorted out and identified at species level. The density of *L. conchilega* is generally based on tube counts, where only tubes with fringes are counted (as suggested by Van Hoey et al., 2006). Because the experimental fishing might have damaged the fringes of the tubes, individual counts have been used in this study to avoid an underestimation of *L. conchilega* densities.

2.4. Statistical analyses

The Primer v5 (Clarke and Warwick, 2001) statistical package was used for calculating diversity indices and carrying out SIMPER, ANOSIM and non-metric multidimensional scaling (MDS) analyses. Bray–Curtis dissimilarities were used to construct this MDS-diagram and averages of replicates were plotted. The recovery trajectory of treatment samples towards control samples was evaluated with a seriation test (calculating the index of multivariate seriation (IMS) with the RELATE routine of the Primer v5 software package). If the community changes exactly match the linear sequence then the IMS takes the value one. If, on the other hand, there is no discernable biotic pattern along the transect, then the IMS will be close to zero. These near-

zero values can be negative as well as positive but no particular significance is attached to this (Clarke and Warwick, 2001). To test for the effect of the treatment on densities of associated species, a generalized linear mixed model was used in which the fixed factors treatment, time, and their interaction effect, were related to the response variables of interest. The dependence of the response variables to the density of *L. conchilega* was incorporated by including it as a covariable in the statistical model. As the response variables are count data, the residual error structure was assumed to follow a Poisson distribution with the variance multiplied by an overdispersion parameter. Because the predictor and the mean response are not linearly related to each other, the relationship was specified by a log link function. The error structure of the model also incorporated dependency within replicates by including replicate setting as a random term. The fixed effects structure was reduced in a backward stepwise manner. The effect on associated species richness and on Pielou's evenness was analysed following a similar approach, but with the residual error structure assumed to follow a normal distribution.

3. Results

3.1. Sediment characteristics and species composition

The sediment of the Boulogne beach site is largely composed of fine sand (mean \pm SE: 62.14 \pm 3.00%) and medium

sand (mean \pm SE: $33.67 \pm 2.48\%$). Silt and clay content show values between 0 and 3.20% (mean \pm SE: $0.51 \pm 1.08\%$), which classifies this type of sediment as clean sand. No significant differences in sediment composition between sites, between sampling occasions, nor between treatments have been observed.

A total of 60 taxa was found during the sampling campaign following the experimental fishing, of which 28 were found only once. Polychaetes were most diverse (77% of all species), followed by amphipods (20%) and bivalves (1%). *Eumida sanguinea* was the most dominant polychaete (66%) and was very often found inside the tubes of *L. conchilega*; *Capitella capitata* made up 18% of the polychaete specimens. *Pygospio elegans*, *Pholoe minuta* and *Spio filicornis* offered low percentages (respectively 3%, 2% and 2% of the polychaete specimens), but were present in a large proportion of the samples (respectively, 40%, 36% and 51%). Amphipods were dominated by *Urothoe poseidonis* (91%).

3.2. Beam-trawl impact on community composition

Three clusters of samples were distinguished. The first group consisted of only one element: the average of treatment replicates at T0 sampling. The second group comprised the averages of the treatment replicates of sampling times T1, T2 and T3. The third group was made up by all averages of control replicates and the average of treatment replicates of T5, the sampling time by which full recovery was observed. The second group is situated between the first group (impacted) and the third group (recovered and control). There is a shift of treatment samples towards control samples, which indicates the direction of recovery towards these control samples over time. This recovery trajectory has a significant IMS value of 0.61 ($p = 0.0003$). For this IMS values all control samples were averaged, as there was no recovery trajectory within the C samples (IMS = -0.36 ; $p = 0.85$). The MDS-plot clearly demonstrates an impact at the community level, which is, however, not a long-lasting one. As indicated in Table 2, SIMPER analysis revealed diminishing dissimilarity

Table 2
SIMPER results showing differences between treatment samples (over time) and control samples (as one group)

Group 1	Group 2	Dissimilarity
T0TR	C	56.9
T1TR	C	48.7
T2TR	C	48.04
T3TR	C	45.67
T4TR	C	50.76
T5TR	C	38.78
T5TR	TR-T5TR	43.48
TR	C	48.14
TR-T5TR	C+T5TR	49.26

Dissimilarity is most pronounced between the treatment samples at T0 and the control samples; dissimilarities are decreasing over time (except for T4, storm effect). Samples of T5TR are more similar to the control samples than to the other treatment samples (TR-T5TR) and dissimilarity between control and treatment samples increases when T5TR is considered to the control samples.

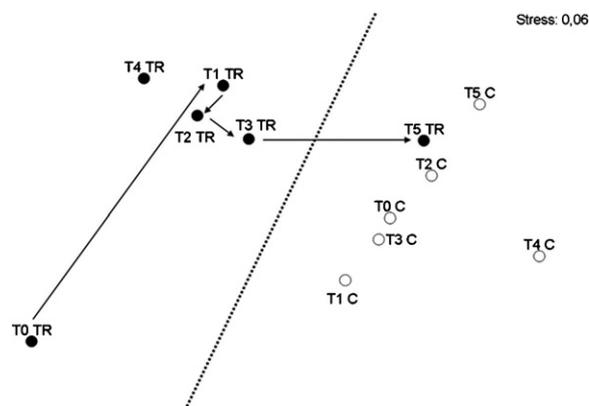


Fig. 2. Two-dimensional MDS ordination (stress = 0.06) of community data for each treatment and sampling occasion (means of replicates). Treatment (●) community composition evolves over time to the community composition of the control (○) samples (with the exception of T4: stormy weather). The recovery trajectory plotted here has an IMS value of 0.61 ($p < 0.01$).

between TR and C communities over time, with the exception of T4 (due to stormy weather). Samples of T5TR are more similar to the control samples than to the other treatment samples (TR excluding T5TR) and dissimilarity between control and treatment samples increases when T5TR is considered as belonging to the control samples (Table 2; Fig. 2).

SIMPER-analyses also revealed that 90% of the communities in both C and TR plots were characterized by a small number of species (*E. sanguinea*, *Capitella capitata*, *U. poseidonis*, *Nephtys cirrosa* and *S. filicornis*). The analysis of similarities (ANOSIM) confirms there is a significant dissimilarity between TR and C samples ($p = 0.001$).

3.3. Beam-trawl impact on total macrofauna density

Macrofauna densities were significantly affected by the treatment ($p = 0.01$) and the densities of *L. conchilega* ($p < 0.0001$), irrespective of recovery time (time effect: $p = 0.20$; time \times treatment effect: $p = 0.42$). The mean macrofauna densities (individuals/m²) for control and treatment were 3277 (± 220 SE) and 2487 (± 186 SE) respectively. The final model considered all samples to be independent among sample locations ($s^2 = 0.032 \pm 0.033$ SE).

Tables 3 and 4.

Table 3
GLMM results for total number of individuals (i.e. summing up all macrofauna per sample)

Effect	F	DF	p
nlan	45.69	1	<0.0001
tr	7.34	1	0.0096
time	–	–	NS
nlan \times tr	–	–	NS
time \times tr	–	–	NS

Treatment (tr) and *L. conchilega* (nlan) densities describe the total number of individuals significantly. Neither time nor interaction effects (nlan \times tr and time \times tr) were significant and were left out of the final GLMM.

Table 4

GLMM results *E. sanguinea*. Treatment (tr) and *L. conchilega* (nlan) densities describe distribution of *E. sanguinea* significantly

Effect	F	DF	p
nlan	30.49	1	<0.001
tr	11.92	1	0.0012
time	–	–	NS
nlan × tr	–	–	NS
time × tr	–	–	NS

Neither time nor interaction effects (nlan × tr and time × tr) were significant and were left out of the final GLMM.

3.4. Beam-trawl impact on community diversity

The beam-trawl did not impact the species richness in a significant way ($p=0.070$). The factor time and the interaction effects (Nlan × tr and tr × time) did not explain the variation in species richness significantly ($p>0.107$). The *L. conchilega* densities did explain the variation in species richness in a significant way ($p=0.015$). Similar results were obtained for Pielou’s evenness. The treatment effect could not explain Pielou’s evenness significantly ($p=0.068$). The factor time and the interaction effects (Nlan × tr and tr × time) did not explain the variation in Pielou’s evenness ($p>0.16$). Mean evenness indices for C and TR are $0.61 (\pm 0.02 \text{ SE})$ and $0.67 (\pm 0.02 \text{ SE})$ respectively. Moreover, Pielou’s evenness was not significantly explained by the *L. conchilega* density ($p=0.088$).

3.5. Beam-trawl impact on species level

Species were tested for each explanatory factor or interaction effect. *Eumida sanguinea* was significantly affected by the beam-trawl disturbance ($p=0.0012$) and the densities of *L. conchilega* ($p<0.0001$), irrespective of recovery time (time effect: $p=0.511$; time × treatment effect: $p=0.277$), indicating that there was no real recovery of this species during the sampling period. There was no effect of sampling location over time ($s^2=0.037 \pm 0.033 \text{ SE}$), implying that all samples can be considered as independent. The mean abundances (individuals/m²) of *E. sanguinea* for control versus treatment are $1758 (\pm 133 \text{ SE})$ versus $1168 (\pm 105 \text{ SE})$. Fig. 3 clearly shows the persistent impact on *E. sanguinea*. The regression lines have the same slope (i.e. the same relation with *L. conchilega* densities), but a

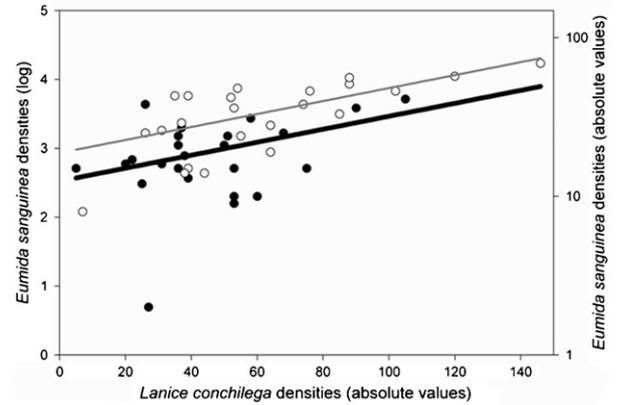


Fig. 3. Impact on *Eumida sanguinea*. Treatment values (●) and control values (○) are set out as a function of *L. conchilega* densities. *E. sanguinea* is always related with *L. conchilega* densities (same slope), but densities of *E. sanguinea* are significantly lower in treatment samples (lower intercept).

different intercept (i.e. lower abundances in treatment samples as a consequence of disturbance).

The same model was used for *Urothoe poseidonis* densities. None of the explanatory factors explained the *U. poseidonis* densities in a significant way ($p>0.0544$). Nevertheless, the study of multivariate results of community composition over time indicates an impact on *U. poseidonis*. At T0, SIMPER analysis showed that *U. poseidonis* was not present in the characteristic community of TR (not included in 95% of the community), whereas this species appeared in all other samples (TRs from T1 onwards and all Cs). SIMPER analysis indicated that two other species were important in community structure (*C. capitata* and *N. cirrosa*). The same generalized linear mixed model was used to test the explanatory factors for these two species. *C. capitata* densities could be described only through the densities of *L. conchilega*. No effect of treatment, time or interaction effects were observed for the two species. *L. conchilega* densities could not explain the densities of *N. cirrosa*.

As *E. sanguinea* and *U. poseidonis* showed a treatment effect, the community response on the treatment was tested without these species. The general recovery pattern as described for the whole community was largely maintained for the analyses where one of these species was excluded. Still, if a community with both species excluded is analyzed, the pattern largely disappears (Fig. 4). This proves that the community response

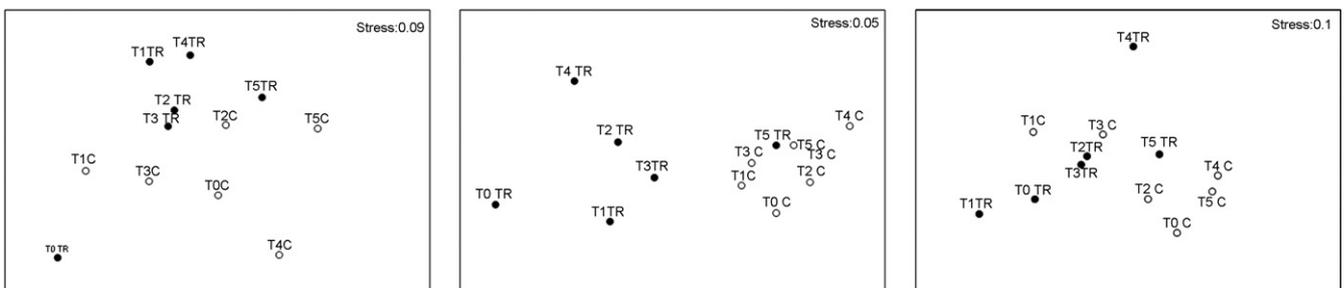


Fig. 4. Two-dimensional MDS ordinations with exclusion of *E. sanguinea* (left), *U. poseidonis* (middle) and both species (right). Only when both species are excluded from the dataset, the distinction between treatment (●) community and control (○) community is not visible anymore.

was dictated by only two associated species. As *E. sanguinea* was the only species showing a significant treatment effect, it was verified whether the impact on total number of individuals was determined by this species or not. The tests performed for total number of individuals were repeated with *E. sanguinea* excluded from the dataset. The results of the model runs show that the significant treatment effect disappears ($p = 0.46$). This species group was however still significantly described by *L. conchilega* densities ($p < 0.0001$).

4. Discussion

Before discussing the results in-depth, we admit that using a BACI design would have provided unequivocal evidence of the impact observed in our study. The so-called T-1 situation was planned, but we would like to articulate the considerable logistic problems we met at the time of the experiment. Upcoming stormy weather forced us to start the field experiment earlier than planned; at the same time, limited availability of the research vessel, combined with an unfavorable tidal regime did not allow postponement of the experiment. The C and TR plots delineated for this small-scale experiment, were situated at the same height in the intertidal zone and even though a T-1 would have provided evidence of the control and treatment reefs being similar, it is very unlikely that the results presented here are the consequence of bias. The *L. conchilega* densities are very similar in TR and C plots and remain stable over time, indicating there was no beam-trawl impact on this species.

4.1. *Eumida sanguinea*

The results showed clearly that the most pronounced impact was on *E. sanguinea*, a species that was significantly impacted by the beam-trawl disturbance during the entire period of the experiment. The same result appeared for total macrofauna density. The community analyses however, suggested an overall quick recovery from disturbance. Species richness was only described by densities of *L. conchilega*, indicating that only few species were impacted. Results on Pielou's evenness showed that the beam-trawl passage did not impact the evenness of the associated species community. However, the relatively low p-level (0.068) suggests that we might have a Type II error in this case. As increasing the value of α reduces the risk of a Type II error (Wiens and Parker, 1995), a p-level under 0.1 could be considered as valuable because we deal with an impact study in a dynamic area. The indication of Pielou's evenness being impacted by the disturbance was confirmed by the observed impact on the most abundant associated species, *E. sanguinea*.

The high impact on this species can be explained by its high abundance and by its ecology. *Eumida sanguinea* lives in between the fringes of the *L. conchilega* tubes, which may serve as miniature hatcheries for *E. sanguinea*, providing food and possibly some shelter (Callaway, 2006). Moreover, during the sample treatment most *E. sanguinea* individuals were found inside the *L. conchilega* tubes and between the fringes. Hence, *E. sanguinea* is susceptible to being removed mechanically by the beam-trawl. Olivier and Retière (1998) showed that

E. sanguinea does not drift away during high tide, but stays at the sea bottom. This indicates that the low abundances are not merely due to differential removal during spring tide. The importance of *E. sanguinea* was confirmed by the disappearing treatment effect on the total number of individuals when this species was excluded from the dataset. However, analysing the recovery on community level as shown in the MDS plot could not be attributed to this most abundant species alone; Fig. 4 shows clearly that the recovery trajectory is defined through the impact on *E. sanguinea* together with *U. poseidonis*.

4.2. *Urothoe poseidonis*

Variation in densities of *Urothoe poseidonis* was not explained by treatment effect, time nor interaction effects. Multivariate results however, indicate that there was a disturbance impact and a quick recovery. Besides, the community analyses showed that *U. poseidonis* had to be excluded from the community together with *E. sanguinea* before the treatment response disappeared (Fig. 4). The absence of *U. poseidonis* at T0 is an indication for an impact, but does not provide a proof. The lack of a significant disturbance effect can be attributed to (1) the quick recovery, (2) the fact that this species only accounted for a small part of the community, and (3) a low impact due to its burrowing behaviour: *U. poseidonis* lives at 4–15 cm depth (Callaway, 2006). We did not find impacts on any other species present in the community.

4.3. Recovery mechanism

The observed impact in our study directly focused on the biological system and not on alteration of the physical habitat as the results indicated that the beam-trawl passage did not have a dramatic impact on sediment composition. Other authors also did not detect significant changes in sediment grain size (e.g. Schwinghamer et al., 1998). The quick overall recovery from disturbance is possibly related to the dynamic intertidal environment, where communities are known to recover very quickly from disturbances (Kaiser and Spencer, 1996). In Brylinski et al. (1994), impacts of otter trawling in these high-energy environments also appeared to be minor.

The recovery pattern drawn in the MDS plot (Fig. 2) was confirmed through the seriation test (RELATE analysis) and the SIMPER results (Table 2). This fast recovery is possibly related to the renewal of the population of *E. sanguinea* (with *L. conchilega* reefs close by, serving as a source). Negrello et al. (2006) emphasized the importance of this small-scale dispersal for infaunal recolonization on a tidal flat and noticed that recolonization can also occur through migration across the water column. This migration is suggested to be passive rather than active (Savidge and Taghon, 1988). We suggest that recovery from disturbance occurs gradually through adult migration from sediments surrounding the plots rather than by recruitment of juveniles as the timing and duration of the experiment excluded recruitment as a recovery mechanism. This dispersal may depend on sediment bed-load transport of large amounts of sediment and adult fauna into areas that have been trawled or

because of exposure to wave action and currents, as suggested in Hall and Harding (1997) (mechanical harvesting of cockles) (as cited in Kaiser et al., 2001). Intertidal *L. conchilega* reefs are probably more resilient to trawling because of (1) their adaptation to continuous natural disturbances (wave action and wind stress) and (2) the smaller number of associated species. Therefore, the recovery following a trawling disturbance is expected to happen faster in the intertidal, but with the same impact-recovery responses and mechanisms as in subtidal areas.

Moreover, Kaiser et al. (2001) suggested, based on a meta-analysis of Collie et al. (2000), that intertidal soft-sediment environment communities, composed of small-bodied, motile and opportunistic fauna seemed to be relatively tolerant to physical disturbance and were able to recolonize the habitat within six months. In contrast, far less tolerance is observed in communities that contain relatively sessile organisms with infrequent recruitment and those containing biota that influence the stability of the sedimentary environment and represent biogenic habitats.

We assumed that the impact mechanism in the intertidal would be similar to the one in subtidal environments, namely that closely associated fauna would be affected. Diversity in intertidal *L. conchilega* reefs is expected to be lower than in the subtidal. Therefore, we surmised that not only the *E. sanguinea* population would be impacted, but also some other dominant associated species that have been defined as associated species in subtidal areas (Rabaut et al., 2007), such as *Spiophanes bombyx*, *Phyllodoce maculata - mucosa* and *Pariambus typicus*. Another factor is experimental fishing in the intertidal zone, which implies the use of a beam-trawl of smaller dimension than the commercial counterpart. It is therefore possible that the severity and duration of the impact observed here is an underestimation. Although we recognize that scaling-up a small-scale experiment to large, intensely fished subtidal areas is not straightforward (Thrush and Whitlatch, 2001), our results provide some pointers of how the recovery mechanism of a *L. conchilega* reef in general takes effect.

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References

- Ager, O., 2002. *Lanice conchilega*. sand mason. marine life information network: biology and sensitivity key information sub-programme [on-line], Plymouth. Available from: <http://www.marlin.ac.uk/species/Laniceconchilega.htm>.
- Bergman, M., Hup, M., 1992. Direct effects of beam trawling on macrofauna in a sandy sediment in the Southern North Sea. ICES J. Mar. Sci. 49, 5–11.
- Brylinski, M., Gibson, J., Gordon, D., 1994. Impact of flounder trawls on the intertidal habitat and community of the Minas Basin, Bay of Fundy. Can. J. Fish. Aquat. Sci. 51, 650–661.
- Bunchanan, J., 1984. Sediment analysis. In: Hadine & McIntyre, Methods for the Study of Marine Benthos. Blackwell Scientific Publications, pp. 41–65.
- Callaway, R., 2003. Juveniles stick to adults: recruitment of the tube-dwelling polychaete *Lanice conchilega* (Pallas, 1766). Hydrobiologia 503, 121–130.
- Callaway, R., 2006. Tube worms promote community change. Mar. Ecol. Prog. Ser. 308, 49–60.
- Carey, D., 1987. Sedimentological effects and palaeoecological implications of the tube-building polychaete *Lanice conchilega* Pallas. Sedimentology 34, 49–66.
- Clarke, K., Warwick, R., 2001. Change in marine communities: an approach to statistical analysis and interpretation, 2nd ed. Natural Environmental Research Council, Swindon, p. 175.
- Coleman, F., Williams, S., 2002. Overexploiting marine ecosystem engineers: potential consequences for biodiversity. Trends Ecol. Evol. 17, 40–44.
- Collie, J., Hall, S., Kaiser, M., Poiner, I., 2000. A quantitative analysis of fishing impacts on shelf-sea benthos. J. Anim. Ecol. 69, 785–799.
- Dittmann, S., 1999. Biotic interactions in a *Lanice conchilega*-Dominated Tidal Flat. In: The Wadden Sea Ecosystem. Stability Properties and Mechanisms. Springer-Verlag, Berlin, Heidelberg, New York, p. 43–49.
- 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 in fauna. J. Appl. Ecol. 34, 497–517, as cited in Kaiser et al., 2001.
- Heuers, J., Jaklin, S., Zühlke, R., Dittmann, S., Günther, C., Hildenbrandt, H., Grimm, V., 1998. A model on the distribution and abundance of the tube-building polychaete *Lanice conchilega* (Pallas, 1766) in the intertidal of the Wadden Sea. Verh. Ges. Okol. 28, 207–215.
- Jones, C., Lawton, J., Shachak, M., 1997. Positive and negative effects of organisms as physical ecosystem engineers. Ecology 78, 1946–1957.
- Kaiser, M., Spencer, B., 1996. The effects of beam-trawl disturbance on infaunal communities in different habitats. J. Anim. Ecol. 65, 348–358.
- Kaiser, M., Broad, G., Hall, S., 2001. Disturbance of intertidal soft-sediment benthic communities by cockle hand raking. J. Sea Res. 45, 119–130.
- Kaiser, M., Collie, J., Hall, S., Jennings, S., Poinerand, I., 2002. Modification of marine habitats by trawling activities: prognosis and solutions. Fish Fish. 3, 114–136.
- Kaiser, M., Clarke, K., Hinz, H., Austen, M., Somerfield, P., Karakassis, I., 2006. Global analysis of response and recovery of benthic biota to fishing. Mar. Ecol. Prog. Ser. 311, 1–14.
- Negrello, F.O.A., Underwood, A., Chapman, M., 2006. Recolonization of infauna on a tidal flat: An experimental analysis of modes of dispersal. J. Exp. Mar. Biol. Ecol. 328, 240–250.
- Olivier, F., Retière, C., 1998. The role of physical–biological coupling in the benthic boundary layer under megatidal conditions: The case of the dominant species of the *Abra alba* community in the Eastern Baie de Seine (English Channel). Estuaries 21, 571–584.
- Rabaut, M., Guilini, K., Van Hoey, G., Vincx, M., Degraer, S., 2007. A bio-engineered soft-bottom environment: the impact of *Lanice conchilega* on the

- benthic species-specific densities and community structure. *Estuar. Coast. Shelf S.* 75, 525–536, doi:10.1016/j.ecss.2007.05.041.
- Rijnsdorp, A., van Mourik Broekman, P.L., Visser, E., 2000. Competitive interactions among beam trawlers exploiting local patches of flatfish in the North Sea. *ICES J. Mar. Sci.* 57, 894–902.
- Ropert, M., Dauvin, J., 2000. Renewal and accumulation of a *Lanice conchilega* (Pallas) population in the Baie des Veys, Western Bay of Seine. *Oceanol. Act.* 23, 529–546.
- Savidge, W., Taghon, G., 1988. Passive and active components of colonization following two types of disturbance on intertidal sandflat. *J. Exp. Mar. Biol. Ecol.* 115, 137–155.
- Schwinghamer, P., Gordon, D., Rowell, T., Prena, J., McKeown, D., Sonnichsen, G., Guigné, J., 1998. Effects of experimental otter trawling on surficial sediment properties of a sandy bottom ecosystem on the Grand Banks of Newfoundland. *Conser. Biol.* 12, 1215–1222.
- Sparks-McConkey, P., Watling, L., 2001. Effects on the ecological integrity of a soft-bottom habitat from a trawling disturbance. *Hydrobiology* 456, 73–85.
- Thrush, S.F., Whitlatch, R.B., 2001. Recovery dynamics in benthic communities: balancing detail with simplification. In: Reise, K. (Ed.), *Ecological Studies – Ecological Comparisons of Sedimentary Shores, Analysis and Synthesis*, 151. Springer-Verlag, Berlin, Germany, pp. 297–316.
- Van Hoey, G., Vincx, M., Degraer, S., 2006. Some recommendations for an accurate estimation of *Lanice conchilega* density based on tube counts. *Helgoland Mar. Res.* 60, 317–321.
- Watling, L., Norse, E., 1998. Disturbance of the seabed by mobile fishing gear: a comparison with forest clear-cutting. *Conser. Biol.* 12, 1180–1197.
- Wiens, J.A., Parker, K.R., 1995. Analyzing the effects of accidental environmental impacts: approaches and assumptions. *Ecol. Appl.* 5, 1069–1083.
- Zühlke, R., 2001. Polychaete tubes create ephemeral community patterns: *Lanice conchilega* (Pallas, 1766) associations studied over six years. *J. Sea Res.* 46, 261–272.
- Zühlke, R., Blome, D., Heinz, K., Dittmann, S., 1998. Effects of the tube-building polychaete *Lanice conchilega* (Pallas) on benthic macrofauna and nematodes in an intertidal sandflat. *Senckenb. Marit.* 29, 131–138.