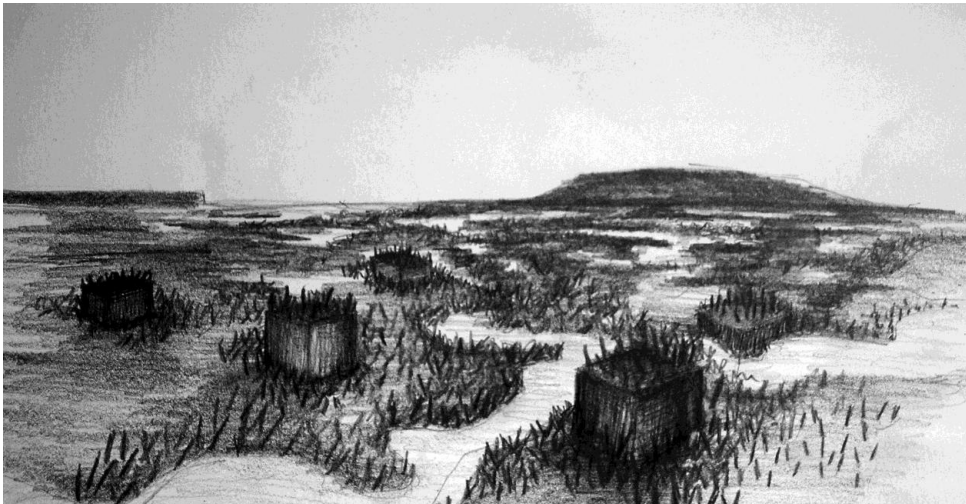


CHAPTER 4

The resistance of *Lanice conchilega* reefs to physical disturbance



Currently under review as:

Rabaut, M., Vincx, M., Hendrickx, F. and Degraer, S. subm.
The resistance of *Lanice conchilega* reefs to physical disturbance.
Submitted to ICES Journal of Marine Science

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Abstract

One way to generate detailed knowledge of the response to physical disturbance is quantifying the resistance of biogenically created emergent structures towards fisheries. The biogenic structures targeted in the present study are shaped by the ecosystem engineering polychaete *Lanice conchilega*. Direct mortality of *L. conchilega* as a consequence of sustained physical disturbance at varying frequencies has been tested to quantify the resilience of this particular reef system. Research is based on a laboratory experiment in which four different disturbance regimes were applied (disturbance every other 12, 24 and 48 h and no fishing disturbance as a control). Survival proportions were measured over time and tested with a generalized linear mixed model (GLMM). Survival dropped significantly after 10 and 18 days (with a disturbance frequency of every 12 and 24 h, respectively). The results indicate that *L. conchilega* is relatively resistant to physical disturbance but that reef systems can potentially collapse under continuous high frequency disturbance. The results of this experiment are discussed in the light of beam trawl fisheries, a common physical disturbance in areas where *L. conchilega* reefs occur. This experimental approach resulted in an indication of the physical disturbance level a system can handle and in this way, the quantification of this resistance contributes to the knowledge of the general resilience.

Key words

Physical disturbance, biogenic reef, *ex situ* experiment, fisheries, impact, *Lanice conchilega*, tube dwelling polychaete

Introduction

Biogenically structured habitats have the longest recovery trajectory in terms of recolonisation of the habitat by the associated fauna. Quantifying the resistance of biogenically created habitats towards physical disturbance in soft sediments can therefore be considered as a key factor in assessing fisheries impact in the soft sediment environment. Fishing with mobile gear disturbs the environment physically and is a major cause of habitat deterioration in soft-bottom ecosystems (Dayton *et al.*, 1995). Trawling alters, removes or destroys the complex, three-dimensional physical structure of benthic habitats by the direct removal of biological and topographic features (Turner *et al.*, 1999). Biogenic structures are vulnerable to fishing impacts (Bergman and van Santbrink, 2000, Kaiser *et al.*, 1999b) and chronic fishing disturbance severely reduces the complexity of such habitats by removing the fragile sessile fauna (Collie *et al.*, 1997, Thrush *et al.*, 1998). The total biomass of infauna and epifauna significantly decreases with trawling disturbance (Jennings *et al.*, 2001b) and trawl nets damage and kill invertebrates (Bergman and Hup, 1992, Brylinsky *et al.*, 1994, Kaiser and Spencer, 1996, Witbaard and Klein, 1994).

The biogenic structures found here are produced by the ecosystem engineer *Lanice conchilega* (Polychaeta, Terebellidae). This species is a well-known and widely distributed tube dwelling polychaete in soft bottom marine environments (Rabaut *et al.*, 2007). The physiology, the tube structure (Jones and Jago, 1993, Ziegelmeier, 1952), the hydrodynamic influence (Dittmann, 1999, Eckman, 1983, Heuers *et al.*, 1998), the ecosystem-engineering influence on faunal abundance, the species richness and the species composition (Callaway, 2006, Rabaut *et al.*, 2007, Van Hoey *et al.*, 2008) as well as the occurrence of *L. conchilega* aggregations (Carey, 1987, Hartmann-Schröder, 1996) have been documented. The aggregations produce clearly defined microhabitats which alternate with areas without *L. conchilega*, generating a surface structure of gentle mounds and shallow depressions. This ‘seascape’ can be visualized using side scan sonar imagery (Degraer *et al.*, 2008a). Experiments show that *L. conchilega* pumps oxygen into the bottom (Braeckman *et al.*, accepted, Forster and Graf, 1995) which is important for the composition of the benthic community and for the presence of specific benthic species (Steyaert *et al.*, 2005). Furthermore, this habitat seems to be of importance for higher trophic levels such as juvenile

flatfish (Van de Moortel, 2009, Vanaverbeke *et al.*, 2009a) and birds (Godet *et al.*, 2008). Rabaut *et al.* (2009b) demonstrated that the biogenic structures formed by dense aggregations of *L. conchilega* qualify as reefs. The good knowledge on this reef system show this species aggregations are particularly well suited as a proxy for measuring the impact of physical disturbance.

Therefore, this study hypothesizes that these biogenic structures are measurably affected by physical disturbance. Bergman and Hup (1992) found significant mortality after beam trawl disturbance for *L. conchilega*, especially for juveniles. Their study aimed at a general mapping of the fisheries impact on the benthos community of a soft bottom environment. However, no emergent *L. conchilega* reef structures (*sensu* Rabaut *et al.* 2009) occurred as there were no dense aggregations in their sampling area (355 individuals per m²). Studies on the reef system as such do exist as field studies with the aim to quantify the impact of one beam trawl passage on the associated *L. conchilega* reef fauna, without focusing on *L. conchilega* as such (Gamarra, 2008, Rabaut *et al.*, 2008). There is, however, no information available on the mortality of individual *L. conchilega* specimens within one reef. Fully controlled laboratory experiments are needed to measure the physical disturbance on the patchy reef habitat with known pressures on exact locations and time. The aim of this study is therefore to quantify direct mortality of *L. conchilega* as a consequence of sustained physical disturbances of dense aggregation reefs with varying frequency, using an experimental laboratory set up. This information may contribute to the knowledge on the resistance of this particular reef system. Recently, it has been argued that experiments can provide valuable insights in systems that underpin ecological resilience (Thrush *et al.*, 2009). Therefore the results on the resistance of *L. conchilega* reefs will be discussed in the light of the general resilience of this system.

Methods

In order to measure mortality within a *L. conchilega* reef as a consequence of repeated fisheries disturbance with known pressures, a fully controlled laboratory set up has been designed. Four undisturbed reef blocks were sampled in the intertidal zone of Boulogne-sur-Mer, France (50°44.10'N 1°35.25'E) on 14 June 2006. The reef blocks were sampled to a depth of 25 cm with rectangular frames of 0.12 m² (width: 0.30 m; length: 0.40 m) (i.e. a sample volume of 0.03 m³); sampling depth allowed to sample entire tubes. The bottom was sealed

with a removable bottom plate (Figure 1). The four reef blocks were stored at a constant temperature (17° C) and the frames were replaced by aquariums to allow for continuous water circulation (Figure 1). The sea water was enriched with algae (*Isochrysis galbana*) (renewal every other 48 h) using a concentration of 40×10^6 cells L⁻¹, i.e. 800 µg L⁻¹ organic weight (Helm *et al.*, 2004), to avoid food limitation (based on Denis *et al.* (2007)). Each reef block was divided into four sectors. Four disturbance regimes were randomly applied in each reef block: disturbance with a frequency of one disturbance every 12, 24 and 48 h (Tr1, Tr2 and Tr3) and no disturbance (C) (Figure 1). Pressure was applied to the treatments as a single passage of a metal plate (6 cm² in contact with bottom) loaded with weights (1.41 kg) on top that protrude above the water column during deployment. This allowed applying a pressure of 2.31 N.cm⁻², coinciding with that of a four meter beam trawl (based on Lindeboom and De Groot 1998, Chapter 3).

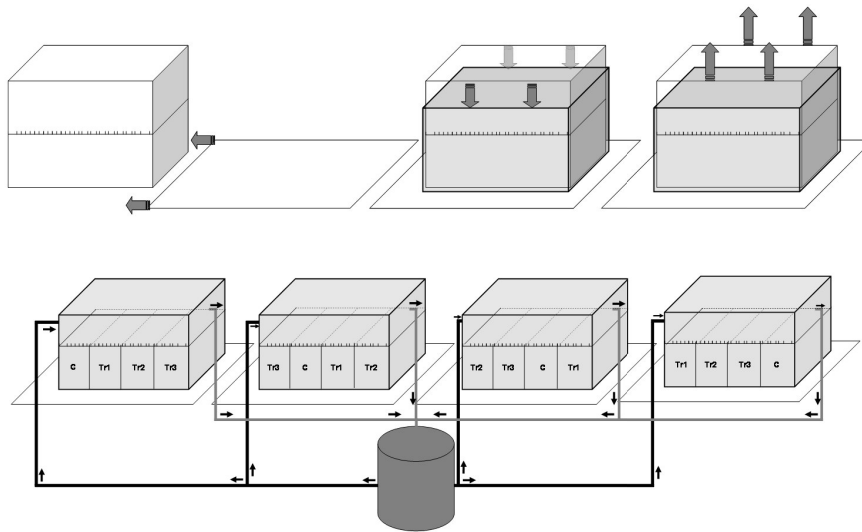


Figure 1. Experimental set up. Above: sampling of an undisturbed reef block; Below: experimental design: four undisturbed reef blocks, each with four treatment zones (C, Tr1, Tr2, Tr3); arrows indicate water circulation.

All environmental conditions were kept identical for all reef blocks. Survival of *L. conchilega* was the response variable measured to quantify the treatment effects. A *L. conchilega* specimen was considered to be alive when the tentacles protrude from the tube. To reduce counting errors, individuals were stained with neutral red.

Every 96 h, the number of living individuals was counted in each sector. As the response variable is the proportion number of surviving individuals compared to the number of individuals at the start of the experiment, the error distribution was assumed to be binomial. Hence, a generalized linear mixed model (GLMM) was used to evaluate the significance of the fixed effects treatment (i.e. C, Tr1, Tr2, Tr3), at each time (interval of 96 h; seven tests). To account for the statistical dependence of observations from the same reef block, this factor was included as a random effect (SAS software, Glimmix procedure). To have an idea of this reef block effect, block effects over time were tested for each treatment separately in a generalized linear model (GLM) (four tests) (SAS software, Genmod procedure). Furthermore, overdispersion was incorporated in the model as the fitted model turned out to be overdispersed.

Results

For the most intensive treatment (disturbance frequency of 12 h; Tr1), the proportion of survivors is significantly lower (GLMM Glimmix procedure; d.f. = 10; $p = 0.0102$; 36% survival relative to control) compared to the undisturbed sectors (C) after 240h, which is after 20 beam trawl passages in 10 days (Table 1). This difference remains for the whole experiment. For the intermediate disturbance frequency (24 h; Tr2), significant differences occur after 432 h (GLMM Glimmix procedure; d.f. = 11; $p = 0.0160$; 32% survival relative to control), which is after 18 beam trawl passages. Despite the consistently lower densities (Figure 2) and the clear drop in survival proportion (Figure 3), no significant (GLMM Glimmix procedure; d.f. = 11; $p = 0.0920$; 40% survival relative to control) differences were found for the least intensive disturbance regime (frequency of 48 h; Tr3).

Table 1. Significance levels for differences in survival proportions between three disturbance regimes (TR1, TR2, TR3) and control (C). Significant differences ($p < 0.05$) are highlighted.

	48h	144h	240h	336h	432h	528h	624h
C - TR1	0.5499	0.7875	0.0102	0.044	0.0011	0.0261	0.0309
C - TR2	0.8113	0.9631	0.2372	0.8227	0.016	0.023	0.0036
C - TR3	0.9132	0.9715	0.9999	0.7198	0.1264	0.2992	0.092

Densities of *L. conchilega* dropped with time in all treatments (Figure 2), including the non-disturbed control sectors. Survival in the control sectors drops from 88.3% \pm 4.1% SE at 48 h

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to 5.6% \pm 2.0% SE at hour 624. The block effect is significant for all treatments (except for Tr1) (Table 2) and Tr2 and Tr3 show an interaction effect with time. This implies that there is an experimental 'cage effect'. Therefore, this reef block effect was incorporated as a random factor in the model that tests for the treatment effect.

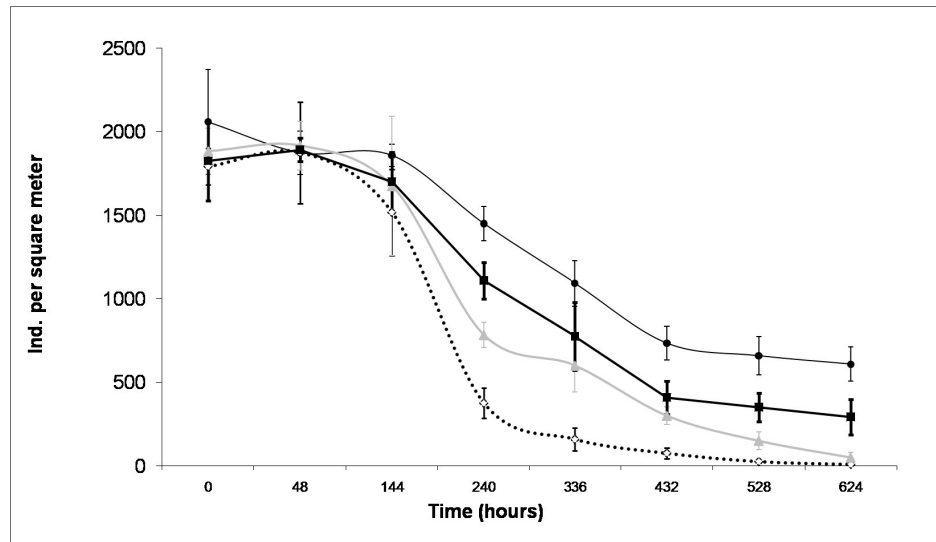


Figure 2. Density evolution of *Lanice conchilega* for three treatments (dashed line: Tr1; grey line: Tr2; black square: Tr3; black bullet: control).

Table 2. Significance levels for overall block and time effect per treatment. The block effect is significant for all treatments (except for Tr1) and therefore, results on treatment effects are based on a mixed model, taking the block effect into account.

Significant differences ($p < 0.05$) are highlighted.

	Block effect	Time	Block x Time Interaction effect
C	< 0.0001	< 0.0001	0.0673
Tr1	0.0575	< 0.0001	0.506
Tr2	0.0002	< 0.0001	< 0.0001
Tr3	< 0.0001	< 0.0001	0.0185

Differences in survival proportions between treatments are visualized in Figure 3. The survival proportion in Tr1, Tr2 and Tr3 presented relative to C (recalculation with a survival rate of 100% for C).

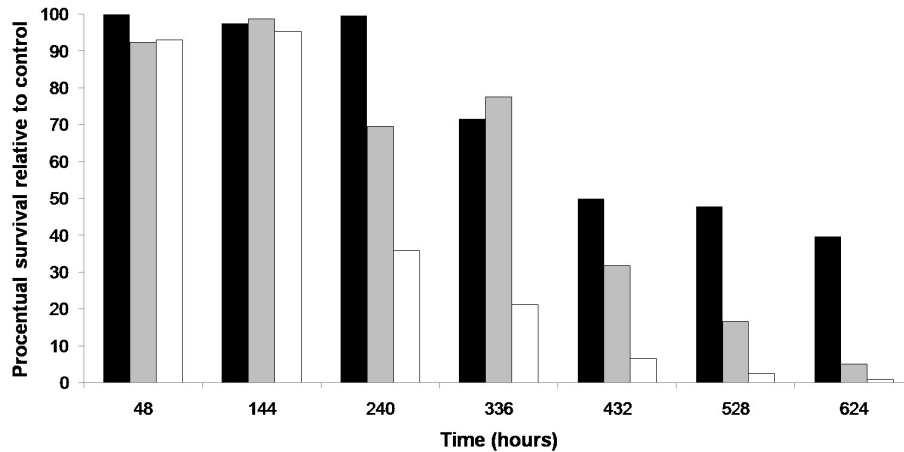


Figure 3. Survival proportions over time for the disturbed sectors (white: Tr1; grey: Tr2; black: Tr3). Proportions are visualized as a percentage of the control proportions for each time (i.e. survival proportions in control are set to 100%).

Discussion

Effects of the survival of *L. conchilega* emerged as a significant factor after 18 disturbances (in 18 days) and after 20 disturbances (in 10 days). These results indicate that the direct impact (i.e. mortality) of this ecosystem engineer occurs after several subsequent disturbances. The current experimental design allowed incorporating the block effect in the analyses while the level of replication allowed for detection of significant differences. The low survival levels in the control areas potentially lead to an underestimation of the physical disturbance applied, as the specimens may have been less resistant under the laboratory conditions. Nevertheless, the statistical analysis of proportions rather than absolute survival leads to correct estimation of the response. Survival under disturbance is relatively high when analyzed relative to the survival in controls. This relatively high survival proportions of *L. conchilega* after physical disturbance is attributed to the fact that the species builds tubes of about 20 cm length in which they can retreat very fast. Therefore, they are assumed to be able to escape from beam trawl disturbance (Bergman and Hup, 1992), although there is no information available on exact reaction times. This escape behavior is confirmed in our study. After the upper part of the tube has been destroyed, *L. conchilega* can rebuild the protruding part of the tube quickly, as was visible in our experiment, and can even re-establish its tube when washed out from the sediments within 24 h (Nicolaidou, 2003). The density evolution of *L. conchilega* (Figure 2)

does show a drop in disturbed areas after six days, a trend that turned out not to be significant. This can be attributed to the high fluctuation and variation in the data during the first days which might be related to the use of only four replicates per treatment.

The design of the fully controlled experimental approach allowed quantifying the impact of physical disturbance for *L. conchilega*. The results provide insight in the resistance of the reefs towards physical disturbance though translation to real physical disturbance such as beam trawl passage remains difficult. The velocity at which disturbance was performed was not included as a factor. The pressure at which the treatment was applied (2.31 N.cm^{-2}) was held constant while the velocity of disturbance was likely to be lower than an operating beam trawl vessel (which proceeds at about 7.5 km.h^{-1}). If the velocity of disturbance would be critical for the reaction time of *L. conchilega*, our response to beam trawl impact would be a minimal value. Furthermore, as far as the applied pressure is concerned, only the equivalence of an intermediate fishing pressure in a small coastal zone trawler was applied and the impact of tickler chains could not be mimicked in this laboratory set up. If larger trawlers are to be tested, a heavier impact is estimated. Moreover, in reality, different pressures exist with the same gear, depending on current directions and speed (Lindeboom and De Groot, 1998: Chapter 3) and different beam trawl types are being used. The impact of the net itself was not investigated here but *L. conchilega* reefs are relatively undisturbed by nets (Rumohr *et al.*, 1994), though the same authors report that the meshes can be festooned with *L. conchilega*. The experimental set up resulted in the quantification of survival of *L. conchilega* under a physical disturbance. Direct translation to real-world scenarios, however, remains difficult though the results provide insights in the resistance *L. conchilega* has towards physical disturbance such as applied by mobile fishing gear. The experimentally measured impact is therefore valuable though relative and context-dependent.

The aim of this experiment is to contribute to the knowledge on the resistance of *L. conchilega* reefs. The quantification of the resistance to physical disturbance relates to the capacity to sustain under certain exogenous disturbances. Therefore, this study contributes also to the knowledge of the resilience of this reef system as resilience is defined as the capacity of a system to renew and sustain specific conditions or processes in spite of exogenous disturbances or changes in driving forces (Carpenter and Folke, 2006). Ecological resilience

assumes that an ecosystem can exist in alternative self-organized or “stable” states (Peterson *et al.*, 1998). The stability of an ecosystem’s ecological functions is determined by the presence or absence of so-called driver species (Walker, 1995), which can take many forms such as ecosystem engineers (Peterson *et al.*, 1998). The present study quantifies the survival of the ecosystem engineer *L. conchilega* (i.e. a driver species of the *L. conchilega* reef habitat) under different physical disturbance regimes. Moreover, the *L. conchilega* reef ecosystem consists of several important (associated) species (Rabaut *et al.*, 2007), which are also vulnerable to physical disturbance, as demonstrated for beam trawl passage (Rabaut *et al.*, 2008). Thus, the resilience of the reef system is defined by several drivers (i.e. the tube builder and the closely associated species). This quantification is important for continental shelf areas such as the North Sea (Rabaut *et al.*, 2007, Van Hoey *et al.*, 2008), where *L. conchilega* reefs occupy areas with strong hydrodynamics (Lanckneus *et al.*, 2001) and intense trawling (Gislason, 1994, Jennings *et al.*, 1999, Rabaut *et al.*, 2009a). The high species richness and increased abundance in *L. conchilega* reefs (Rabaut *et al.*, 2007, Rabaut *et al.*, 2009b), together with the attraction of juvenile flatfish (Rabaut *et al.*, accepted, Van de Moortel, 2009), make the areas with *L. conchilega* reefs attractive for fisheries. Therefore, a high frequency of disturbance is expected, though exact figures are not yet available. This indicates that current physical disturbance does not have a great negative impact on the tube builder itself. In the longer run, the reefs are dependent on successful recruitment (Rabaut *et al.*, 2009b), a mechanism that was not taken into account in this study on short term impacts. However, results may also imply that some reefs are possibly disturbed at frequencies that are comparable to the the current study leading to local destruction of the reefs.

Conclusion

Lanice conchilega reefs consist of dense aggregations of the tube worm as well as of the associated fauna. The resilience of the reefs relates to the vulnerability of those two components. The impact on the associated fauna has been described before. The present study quantifies the survival of *L. conchilega*, a driver species of the reef habitat, under different physical disturbance regimes. The experimental approach allowed the disturbing specific reefs that naturally occur in a patchy habitat with known pressures on exact locations and times. Significant impacts on the survival of *L. conchilega* emerged in this study

after several subsequent disturbances. This indicates that *L. conchilega* is relatively resistant to physical disturbance but that the reefs can collapse under continued high frequency fishing pressure. The relatively high survival proportions of *L. conchilega* after physical disturbance can be attributed to the escape behavior and the high capacity for tube regeneration.

Acknowledgement

The authors thank for the assistance with the experimental work by C. Sohier and L. Hiele. We are grateful for help during the design of the sampling and aquarium equipment of D. Van Gansbeke and S. Vanhamme. Technical support was further provided by Jürgen Verstraeten. We thank L. Hiele for her invaluable linguistic comments. We are grateful for the proof reading efforts of J. Craeymeersch, L. Godet, J. Seys, G. Van Hoey, J. Vanaverbeke, A. Vanreusel and F. Volckaert.. We are very grateful for the comments provided by two anonymous peer reviewers together with the suggestions of Dr. Bill Turrell that improved the manuscript considerably. This research was carried out within the Ghent University *BBS_{ea}* project (contract no. GOA 01G00705; <http://biology.ugent.be/bbsea>) and within the WESTBANKS project (understanding benthic, pelagic and air-borne ecosystem interactions in shallow coastal seas; <http://www.vliz.be/projects/westbanks>) which is supported by the Belgian Science Policy (BELSPO; contract no. SD/BN/01). The authors acknowledge the support by the MarBEF Network of Excellence 'Marine Biodiversity and Ecosystem Functioning' (<http://www.marbef.org>) which is funded by the Sustainable Development, Global Change and Ecosystems Programme of the European Community's Sixth Framework Programme (contract no. GOCE-CT-2003-505446). The first author acknowledges a fellowship from the Research Foundation – Flanders (*FWO-Vlaanderen*), Belgium.