

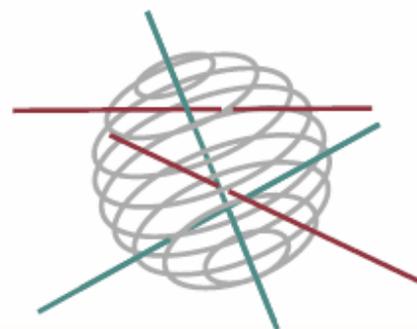
# SSD

SCIENCE FOR A SUSTAINABLE DEVELOPMENT

## UNDERSTANDING BENTHIC, PELAGIC AND AIRBORNE ECOSYSTEM INTERACTIONS IN SHALLOW COASTAL SEAS



J. VAN AVERBEKE, U. BRAECKMAN, E. CUVELIERS, W. COURTENS, T. HUYSE, G. LACROIX,  
M.H.D. LARMUSEAU, G. MAES, P. PROVOOST, M. RABAUT, T. REMERIE, M. SAVINA,  
K. SOETAERT, E.W.M. STIENEN, H. VERSTRAETE, F. VOLCKAERT, M. VINCX



ENERGY

TRANSPORT AND MOBILITY

AGRO-FOOD

HEALTH AND ENVIRONMENT

CLIMATE

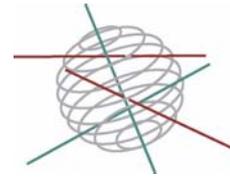
BIODIVERSITY

ATMOSPHERE AND TERRESTRIAL AND MARINE ECOSYSTEMS

TRANSVERSAL ACTIONS

SCIENCE FOR A SUSTAINABLE DEVELOPMENT

(SSD)



**Marine Ecosystems & Biodiversity**



FINAL REPORT PHASE 1

**UNDERSTANDING BENTHIC, PELAGIC AND AIRBORNE  
ECOSYSTEM INTERACTIONS IN SHALLOW COASTAL SEAS**



SD/BN/01A

**Promotors**

**J. Vanaverbeke & M. Vincx**

Ghent University (UGent)

Biology Department, Marine Biology Section

B-9000 Gent

**F. Volckaert**

Katholieke Universiteit Leuven (KULeuven)

Laboratory of Animal Diversity and Systematics

B-3000 Leuven

**EWM. Stienen**

Research Institute for Nature and Forest (INBO)

B-1070 Brussels

**K. Soetaert**

NIOO-CEME

NL 4400-AC Yerseke,

**J. Mees**

Vlaams Instituut voor de Zee (VLIZ)

B-8400 Oostende

**Authors**

Vanaverbeke J<sup>1</sup>, Braeckman U<sup>1</sup>, Cuveliers E<sup>2</sup>, Courtens W<sup>3</sup>, Huyse T<sup>2</sup>,  
Lacroix G<sup>4</sup>, Larmuseau MHD<sup>2</sup>, Maes G<sup>2</sup>, Provoost P, Rabaut M<sup>1</sup>, Remerie T<sup>1</sup>,  
Savina M<sup>4</sup>, Soetaert K, Stienen EWM<sup>3</sup>, Verstraete H<sup>3</sup>, Volckaert F<sup>2</sup>, Vincx M<sup>1</sup>.

\*

<sup>1</sup> UGent - <sup>2</sup> KULeuven - <sup>3</sup> INBO - <sup>4</sup> MUMM



KATHOLIEKE UNIVERSITEIT  
**LEUVEN**





Rue de la Science 8  
Wetenschapsstraat 8  
B-1000 Brussels  
Belgium  
Tel: + 32 (0)2 238 34 11 – Fax: + 32 (0)2 230 59 12  
<http://www.belspo.be>

Contact person: David Cox  
+ 32 (0)2 238 34 03

Neither the Belgian Science Policy nor any person acting on behalf of the Belgian Science Policy is responsible for the use which might be made of the following information. The authors are responsible for the content.

No part of this publication may be reproduced, stored in a retrieval system, or transmitted in any form or by any means, electronic, mechanical, photocopying, recording, or otherwise, without indicating the reference :

Vanaverbeke J, Braeckman U, Cuveliers E, Courtens W, Huyse T, Lacroix G, Larmuseau MHD, Maes G, Provoost P, Rabaut M, Remerie T, Savina M, Soetaert K, Stienen EWM, Verstraete H, Volckaert F, Vincx M. ***Understanding benthic, pelagic and airborne ecosystem interactions in shallow coastal seas “WESTBANKS”*** Brussels : Belgian Science Policy 2009 – 46 p. (Research Programme Science for a Sustainable Development : Final Report Phase 1)

## Table of content

<b>SUMMARY.....</b>	<b>4</b>
<b>INTRODUCTION.....</b>	<b>6</b>
<b>WP1: BENTHIC PELAGIC COUPLING.....</b>	<b>7</b>
Introduction .....	7
Material and Methods.....	7
Benthic diversity and ecosystem functioning.....	7
<i>Lanice conchilega</i> as ecosystem engineer.....	8
Results .....	8
<b>WP2: The role of dispersal for benthic organisms and demersal fish.....</b>	<b>17</b>
Introduction .....	17
Material and methods .....	17
Results .....	20
Dispersal dynamics: a field study.....	20
Discussion .....	24
<b>WP 3: Air-Sea biotic coupling.....</b>	<b>27</b>
Prey fish sampling.....	28
Foraging activities of terns.....	29
Diet composition of terns .....	30
Diet composition of auks.....	33
Benthivorous seabirds .....	34
<b>GENERAL CONCLUSIONS AND RECOMMENDATIONS .....</b>	<b>36</b>
<b>PERSPECTIVES for future WestBanks RESEARCH .....</b>	<b>39</b>
<b>ACKNOWLEDGEMENTS.....</b>	<b>41</b>
<b>LITERATURE .....</b>	<b>42</b>

## SUMMARY

Within the WestBanks project, we investigate interactions between sediment, water and air at the species and population level in the Western Coastal Banks area of the Belgian Part of the North Sea. This area was chosen because of its ecological importance for macrobenthos, fish and seabirds, which is reflected in its protection status by the Habitat and Bird Directive. We collect ecological data that should support a sound sustainable management of the area of the Western Coastal Banks.

Our results reflected the importance of functional identity and densities of macrobenthic organisms for ecosystem functioning. Three key species for the Western Coastal Banks area, belonging to three different functional groups (e.g. *Abra alba* – biodiffuser, *Lanice conchilega* – piston pumper and *Nephtys* sp. – gallery diffuser) were incubated at different density levels (natural, lower and very low) in lab experiments, where bioturbation and ecosystem processes were measured. Benthic respiration, a proxy for mineralisation and hence ecosystem functioning was related to temperature, food availability, species identity and densities. Hence, a decline in species densities due to human disturbance will most probably result in a lowered level of ecosystem functioning. Each species has a different impact on the ecosystem functioning and hence a decrease of one functional group will not be counteracted for by another functional group.

*Lanice conchilega* is shown to be a very important benthic organism in the area of the Western Coastal Banks since its presence in ambient densities doubled the nitrogen mineralisation rates compared to situations where it is absent. Moreover, our results showed that *L. conchilega*-patches classify as biogenic reefs in the framework of the Habitat Directive. The presence of *L. conchilega* in increased densities is linked with an increased diversity and densities of other macrobenthic organisms. We further showed that *L. conchilega* and its associated fauna are vulnerable to beam trawling activities.

The molecular analyses of dispersal dynamics revealed that the distribution of *L. conchilega* results from large-scale dispersal events in the North Sea and local dispersal off Brittany. Similar research on sole (*Solea solea*) resulted in the development of markers discriminating between the temporal and the spatial scale. This made it possible to detect an exchange of populations throughout the year on the BPNS. This observation is new, and more samples will be processed in the second phase of WestBanks to validate this result.

The modeling of the larval transport revealed that passive transport of larvae is influenced by local circumstances (e.g. passive transport is not the same at different places on the BPNS). Active vertical movements of larvae in the water column decrease the transport and horizontal dispersion of larvae as well, but again the effect of the active movements on the dispersion is site specific. This result in a low

connectivity between the areas considered which might be the explanation for the presence of subpopulations of sole in the Eastern Channel and the southern North Sea.

In order to assess the health of the pelagic ecosystem, we investigate whether marine top-predators (seabirds) can be used as indicators. In order to do so, there is a need to increase the knowledge of the links between these seabirds and their prey: pelagic fish. Therefore, pelagic fish was sampled in the Westdiep and the Wenduinebank, which are two key locations for seabirds. Both locations harboured different pelagic fish communities and energetically more favourable fish were encountered in the Westdiep. However, during the breeding season there was a higher availability of potential prey near the Wenduinebank. Research on foraging activities of terns revealed that the Wenduinebank is indeed a very important feeding ground for breeding terns. Both adult Common Terns and chicks feed on clupeid fish while adults also feed on polychaete worms (Nereidae). These nereids were also encountered in the faeces of Sandwich Tern suggesting the presence of this worm in the pelagic realm during restricted periods of the year. Adult Sandwich Terns feed on Ammodytidae, while Sandwich Tern chicks depend on the presence of suitable Clupeidae. Hence, changes in availability of clupeid fish of suitable size leads to a decrease in chick survival of both tern species. Prey length distribution may thus be a good candidate to serve as indicator for the health of the pelagic ecosystem.

## INTRODUCTION

In this report, we give an overview of the scientific progress made during the first phase of the WestBanks project. WestBanks builds further on the expertise and knowledge gathered in previous Belspo-funded projects in the SPSD I and SPSD II framework (Vincx et al. 2002, Vanaverbeke et al. 2007). These projects focused on benthos, genetic diversity of selected taxa and seabirds. Whereas the initial focus was on the description of spatial and temporal biological patterns on the Belgian Part of the North Sea (BPNS), a gradual progress is visible into research focused on comparing and understanding processes at the sediment-water interface, linking genetic diversity with dispersal capacity of organisms and the use of the breeding success of terns as an indicator of the health of the pelagic realm of the BPNS.

WestBanks continues along these lines, but focuses on the interactions between sediment, water and air at the ecosystem, species and population level. In order to maximise the integration of the results, we target on a single area of the BPNS, the Western Coastal Banks area. This area is very important from a biological point of view since (1) it harbours a very rich macrobenthic community (Van Hoey et al. 2004) in a shallow sand banks system. Therefore this area has been designated as Special Area of Conservation (SAC) under Habitats Directive of NATURA2000 (Rabaut et al. in press a); (2) its hydrodynamics and high primary productivity create an area with high densities of juvenile fishes (Beyst et al. 2002, Dewicke et al. 2003) and (3) acts as a foraging area for internationally important numbers of seabirds. Therefore the area is designated as a Special Protection Area for the conservation of birds under the Birds Directive of NATURA2000 (Haelters et al. 2004).

Based on the published knowledge on the biological communities (Degraer et al. 1999, Steyaert et al. 1999, Van Hoey et al. 2004, Vanaverbeke et al. 2007), ecosystem processes (Franco et al. 2007, Franco et al. 2008 a,b, Van Oevelen et al. subm.) and genetic structure (Gysels et al. 2004a, b, c, Huyse and Volckaert, 2005) and in combination with the newly initiated research within WestBanks, we aim at improving the sustainable management of the BPNS by providing sound scientific knowledge on the relationship between diversity-ecosystem functioning, connectivity between populations and the link between marine top predators and lower levels of the marine ecosystem. Here we report on our scientific progress and we formulate general conclusions and recommendations following on these results.

## WP1: BENTHIC PELAGIC COUPLING

### Introduction

The macrobenthic fauna is known to be important in processes occurring near the sediment water interface since this size group (1) influences processes related to mineralisation of pelagically produced organic carbon, (2) can increase habitat heterogeneity and (3) acts as a food source for demersal fish (Cabral 2000, Molinero & Flos 1992, Rijnsdorp & Vingerhoed 2001). We investigated the role of selected macrobenthic taxa on all of these aspects in order to quantify their relative importance for the functioning of the ecosystem of the Western Coastal Banks and to assess the consequences of anthropogenic disturbances leading to a change in densities and/or diversity of the macrobenthos of the Western Coastal Banks area.

### Material and Methods.

#### Benthic diversity and ecosystem functioning

Two experiments were planned to link species diversity/density with ecosystem functioning: one before sedimentation of the phytoplankton bloom (winter - March: low food availability and temperature) and one when organic matter had been settled on the sea bottom (summer - September: high food availability and higher temperatures). These lab experiments were carried out in the mesocosm facilities at the NIOO, Yerseke (NL). Chlorophyll *a* concentrations in water and sediment were sampled in February and September and analysed as described in Franco et al. (2007). Microcosms containing sediment without macrofauna and seawater from the Oosterschelde were incubated in controlled conditions (constant temperature of resp. 10 and 18°C and salinity of 32 psu). Single-species treatments of key-species belonging to 3 different functional groups (Forster & Graf 1995, Gérino et al. 2003) were added to these microcosms at three density levels (average natural, lower and very low) to account for possible density declines. These species are *Abra alba* (FG: biodiffuser), *Lanice conchilega* (FG: piston-pumper) and *Nephtys* sp. (FG: gallery-diffuser). Ecosystem functions measured during a 36h (winter) and 8h (summer) incubation included SCOC and nutrient fluxes in and out the sediment and denitrification. The effect of bioturbation on these biogeochemical processes was assessed by adding a layer of luminophores to the sediment surface and at 3.5 cm depth (Caradec et al. 2004, Gilbert et al. 2007). SCOC was monitored by Winkler analysis (winter) and Membrane Inlet Mass Spectrometer (MIMS) (summer); nutrients were analyzed with a Segmented Flow Analyser SANPLUS SKALAR and N<sub>2</sub> – gas was measured with MIMS. Bioturbation by *Abra alba* and *Nephtys* sp. was quantified by image analysis of UV-illuminated pictures of sliced sediment containing luminophores. Macrofaunal respiration estimates of *Abra alba*, *Lanice conchilega* and *Nephtys* sp. were derived from biomass measurements following Sijm et al. (2004), Van Hoey et al. (2006) and Mahaut et al. (1995). Vertical oxygen profiles were measured in

September using Unisense micro-electrodes. A mass budget was calculated from SCOC and nutrient fluxes as described in Vanaverbeke et al. 2007.

### ***Lanice conchilega* as ecosystem engineer**

The role of *Lanice conchilega* as ecosystem engineer was investigated by means of analyses of historical data and collection of field data. Experimental work was performed to assess the vulnerability of *L. conchilega* aggregations to beam trawling.

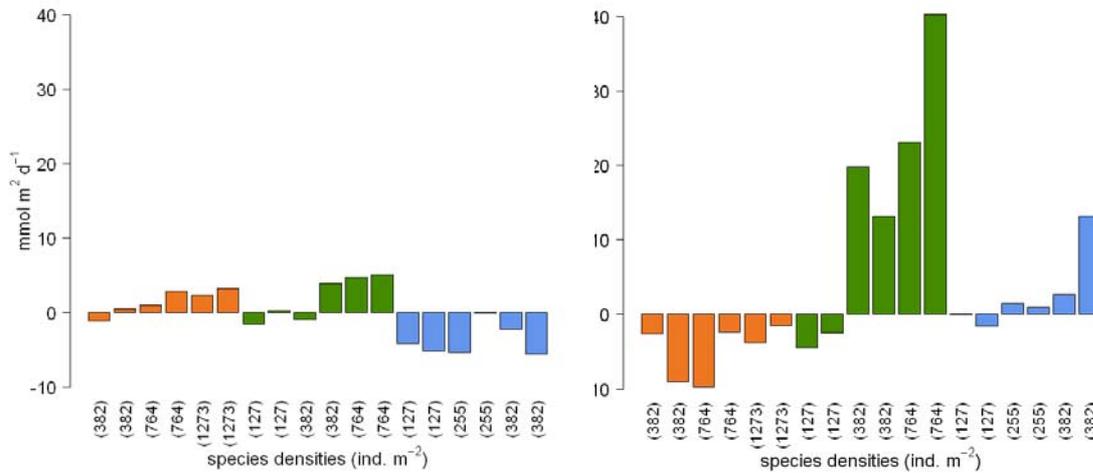
Long term data collected on the BPNS (1994-2005) were filtered on the basis of habitat classification taking into account sedimentological characteristics and bathymetry (Rabaut et al. 2007). A dataset of 657 samples was analysed by means of non-metric Multidimensional Scaling (MDS) and Analysis of Similarity (ANOSIM) (Clarke & Gorley 2001). The effect of *L. conchilega* aggregations on the physical environment (elevation, sediment consolidation, spatial extent and patchiness) were measured in the intertidal zone of the “Baai van Heist” and the adjacent Belgian integral marine reserve (see Rabaut et al. 2008 for details).

The effect of beam trawling on the survival of *L. conchilega* was investigated by means of lab experiment. Undisturbed *L. conchilega* patches were transported to the lab and different intensities of beam trawling were mimicked using a specially designed tool (Rabaut et al. in prep.). The effects of beam trawling on fauna associated with *L. conchilega* were assessed through field experiments in the intertidal and subtidal zones. Here, beam-trawled *Lanice* patches were compared with non-trawled patches at different time intervals allowing for evaluating the resilience of the associated fauna (Rabaut et al. 2008).

## **Results**

Our results clearly show the importance of macrobenthic organisms for the ecosystem functioning on the one hand and the vulnerability of these organisms for anthropogenic disturbance on the other hand. In addition, it was very obvious that not only densities but also functional identity is an important factor in maintaining the functioning of the seabed. Benthic respiration (a proxy for mineralization (Banta et al. 1995) and hence ecosystem functioning) was related to temperature and food availability, species identity (reflecting functional diversity) and densities. A SCOC predictive value was calculated as the sum of background (averaged control) SCOC measurements and the estimated macrofaunal respiration derived from biomass data. For the lowest *A. alba* and *L. conchilega* densities in winter (low food situation), the measured SCOC is not higher than the predicted value (Fig. 1). However, in the “low” and “natural” densities, clearly more O<sub>2</sub> was respired than was predicted (*A. alba* winter effect on SCOC: R<sup>2</sup> = 0.6; p = 0.04, up to 18 % enhancement over control; *L. conchilega*

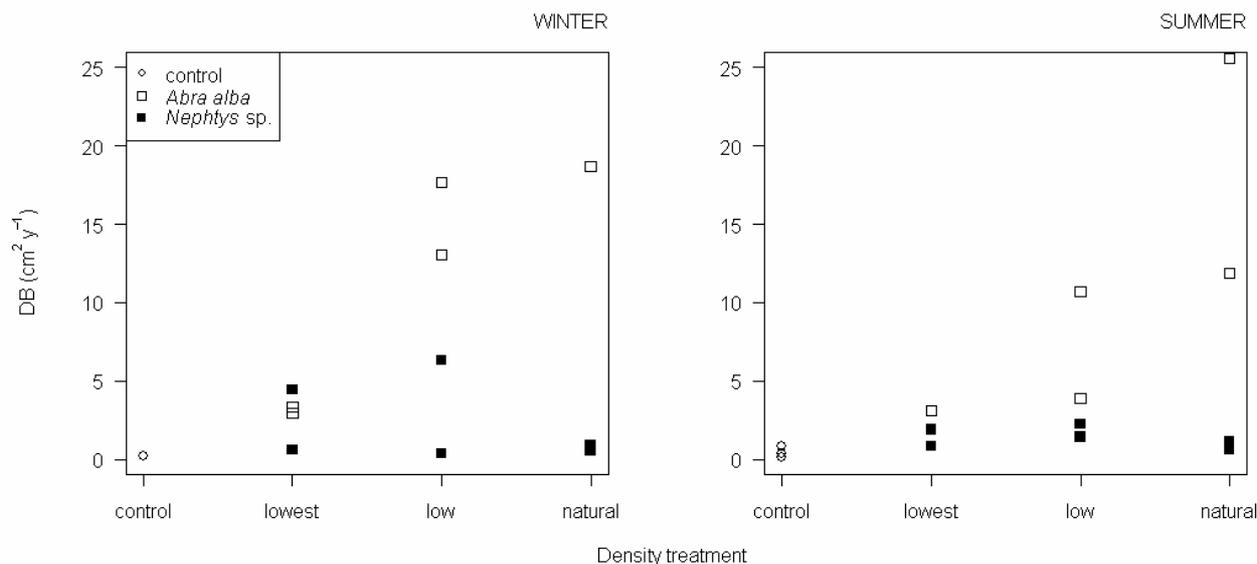
winter effect on SCOC:  $R^2 = 0.6$ ;  $p = 0.04$ , up to 25 % of enhancement over control). On the contrary, *Nephtys* sp. treatments respired less than predicted.



**Figure 1: Stimulation of benthic respiration (left: spring; right: late summer) by different densities of *Abra alba* (orange), *Lanice conchilega* (green) and *Nephtys* sp. (blue) in mmol O<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup>. Values are calculated as measured SCOC – predicted SCOC.**

In summer, we observed much more stimulation by *L. conchilega* than in winter (*L. conchilega* summer effect on SCOC:  $R^2 = 0.85$ ;  $p = 0.006$ , up to 68 % of enhancement over control). The fauna effect of *L. conchilega* on SCOC vs. density relation is stronger in summer (ANCOVA  $p < 0.0005$ ) compared to winter. We suggest the enhanced introduction of oxygen into the sediment explains this stimulation of SCOC. The *A. alba* treatments respired less than predicted in summer. The “negative stimulation” by *Nephtys* sp. in winter and *A. alba* in summer might be explained by an overestimation of faunal respiration. This implies that the animals decreased or even resumed their metabolic activity. Consequently, high background respiration of the bacterial community may mask the low oxygen consumption by the added fauna. Since *L. conchilega* individuals do not exhibit bioturbation activities, bioturbation activities were only investigated for *A. alba* and *Nephtys* sp.. A biodiffusion constant  $D_B$  was obtained by fitting modeled profiles to observed luminophore profiles in all treatments (Fig. 2).

Presence of fauna increased bioturbation in the experiments and this increase was density-dependent for *A. alba* (winter:  $R^2 = 0.81$ ,  $p = 0.009$ ; summer:  $R^2 = 0.69$ ,  $p = 0.007$ ), while this was not the case for *Nephtys* sp.. There was no sign of bioturbation of deep sediment layers in all experimental treatments.



**Figure 2: Biodiffusion coefficients ( $D_b$ ) derived from surface layer luminophore profiles of control (white dots), *Abra alba* (white squares) and *Nephtys* sp. (black squares) in winter (left) and summer (right) experiments.**

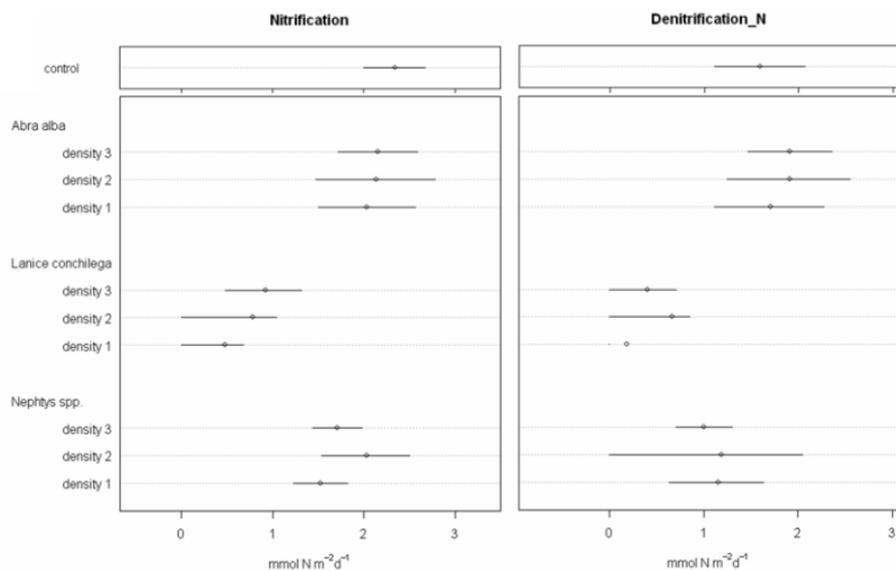
In an ecological perspective, natural density of *A. alba* contributes more to sediment reworking than the natural *Nephtys* sp. density, irrespective of season.

Oxygen penetrated (not depicted) generally 3 mm in the sediment. Only in the presence of *L. conchilega* in natural densities, an oxygen penetration of 6 mm was observed. Although not significant, oxygen penetration tended to increase with *L. conchilega* densities. This implies that even small reefs of *L. conchilega* can enhance oxygen penetration on a large scale.

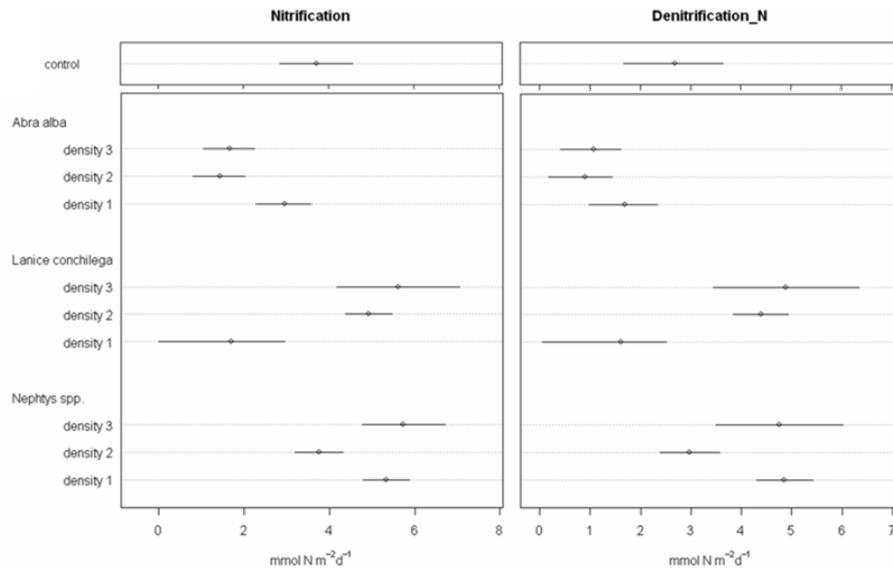
Measurements of nutrient fluxes revealed only net effluxes from the sediment to the water column in winter and summer. Ammonium effluxes increased with higher *A. alba* densities, which is in accordance with the hypothesis of Thrush et al. (2006): while subducting organic matter, this suspension – deposit feeder fuels microbial decomposition and mineralization processes that consume oxygen and release  $\text{NH}_x$ . Nevertheless, highest ammonium net effluxes were observed in the treatments of *L. conchilega*. This can be related to its pumping behavior, removing inhibitory metabolites.

Denitrification is considered to be a very important ecosystem process since it removes nitrogen from eutrophicated ecosystems (Seitzinger 1988). Therefore we calculated a mass budget to estimate the nitrification and denitrification contribution to the total mineralisation (represented by SCOC). The mass budget outcome of denitrification predicts the measured rates quite good. In winter (Fig. 3), nitrification and denitrification rates in animal treatments are not higher than background (defaunated controls). *Lanice conchilega* treatments even result in lower values, due to a relatively high ammonium efflux to the water

column compared to the actual oxygen influx. While flushing its tube with oxygen rich water, this polychaete washes away high ammonium concentrations that were otherwise available for nitrification and denitrification. Another pattern is observed in summer (Fig.4): background denitrification and nitrification rates are higher than in winter. During late summer, these ‘ecosystem cleaning processes’ are stronger in natural densities of *L. conchilega* and *Nephtys* sp. treatments than in control and *A. alba* treatments. For both *L. conchilega* and *Nephtys* sp. treatments, this can be related to a stronger oxygen influx compared to the actual ammonium efflux. More oxygen is available for nitrification and the resulting nitrate can be used for denitrification. The density dependence of denitrification in *L. conchilega* treatments was best described by a quadratic function ( $R^2 = 0.81$ ,  $p = 0.003$ ). Aller (1988) showed that denitrification potential drops at a certain tube density. This is explained by an over-oxygenation and large removal of substrate for coupled nitrification/denitrification (resp. ammonium and nitrate).



**Figure 3: Nitrification and denitrification in winter (in mmol N m<sup>-2</sup> d<sup>-1</sup>). Points represent mean modelled values, segments indicate the range between 1st and 3rd quantiles.**



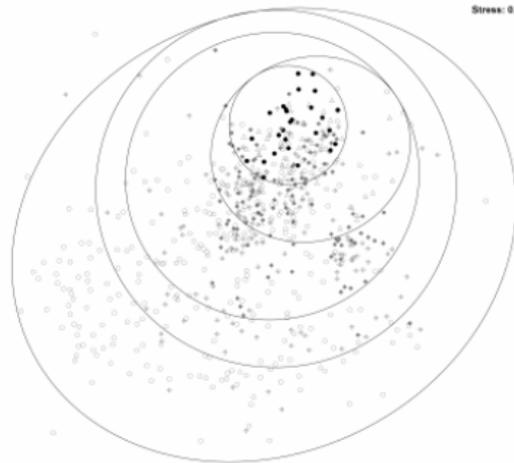
**Figure 4: Nitrification and denitrification in summer (in  $\text{mmol N m}^{-2} \text{d}^{-1}$ ). Points represent mean modelled values, segments indicate the range between 1<sup>st</sup> and 3<sup>rd</sup> quantiles**

Several authors argue that *A. alba* and *Nephtys* sp. introduce oxygen into the sediment (Davis & Miller 1979, Wikander 1980). Indeed, we also observed an enhanced thickness of the grayish sediment layer and particularly in the vicinity of these *A. alba* channels and *Nephtys* sp. burrows. However, oxygen penetration depth in *A. alba* cores did not differ from control depth, neither did the *Nephtys* sp. treatments. The sediment had been reworked, and reduced metabolites from the deeper strata were reoxidized, hence the gray color, but oxygen became quickly depleted. This may be explained by the fact that these species do not actively irrigate their burrows/feeding pits, hence the also rather limited influence on other chemical conditions in the sediment (Mermillod–Blondin et al. 2004, Michaud et al. 2005, 2006).

The importance of benthic mineralization is that it makes nitrogen, often considered to be a limiting nutrient, available to the pelagic algae in the water overlying the sediments (Blackburn 1988). The total nitrogen mineralization as calculated from the mass budget was on an average  $2.52 \pm 0.19$  (se) times higher in summer compared to winter. Bio-irrigation and bioturbation influence this process, which is confirmed by our results. Fauna treatments enhanced N mineralization on an average by a factor 1.20 in both seasons. However, the stimulation of the three species was different, which can be explained by their behavior. The natural density of *L. conchilega* increased the total N mineralization in summer two times compared to control. This is of the same order or even more than what has been found by Kristensen (1988) and confirms the theory that bioirrigation influences N mineralization more drastically than bioturbation (Mermillod-Blondin et al. 2004).

The importance of *L. conchilega* for the coastal ecosystem of the BPNS was confirmed by the analysis of historical data and a field study investigating the reefiness of dense *L. conchilega*

aggregates. The presence and abundance of *L. conchilega* on the BPNS can be linked with the diversity and community composition of the entire macrobenthic community (Fig. 5) as shown by MDS and 1-way ANOSIM (see Rabaut et al. 2007 for detailed results).



**Figure 5. Two-dimensional MDS ordination plot of similarities between species assemblages of different density classes of *L. conchilega* aggregations (classes 1–4, respectively, crossed squares, filled grey squares, open triangles and black filled dots) and *L. conchilega*-free samples (open dots) (using Bray Curtis similarity measure of square root transformed data).**

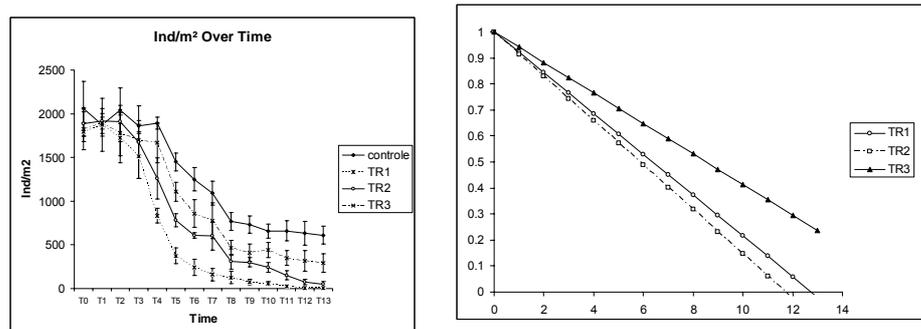
Field measurements in dense *L. conchilega* aggregations were performed and combined with existing knowledge on the biological characteristics to assess the ‘reefiness’ of these aggregations (following Hendrick & Foster-Smith 2006). Significantly higher elevation ( $p < 0.001$ ) and shear strength ( $p < 0.001$ ) inside *L. conchilega* patches, a positive correlation between *L. conchilega* densities and shear stress and the observation that juvenile *Lanice* settlement is enhanced in the presence of adult *L. conchilega* tubes emphasises the habitat structuring capacity of this polychaete.

Based on these measurements and experiments, and in combination with current biological knowledge (Zühlke 2001, Van Hoey (2006), Rabaut et al. (2007), a “reefiness scoring table” (Table 1) was proposed that can be used to evaluate the status of *L. conchilega* patches as being biogenic reefs in the framework of the Habitat Directive (Rabaut et al. in press b). It should be mentioned that it remains difficult to estimate the spatial extent and patchiness of these systems in subtidal areas. This is an important knowledge gap that should receive attention in the future. Long-term monitoring with advanced remote sensing techniques offer a valuable method to map not only the spatial but also the temporal distribution of *L. conchilega* aggregations/reefs in subtidal areas.

	Characteristic Score		
	Low 0	Medium 50	High 100
A. <i>Elevation Score</i> . Relative height of the patch	~ 5 cm	5 - 9 cm	> 9 cm
B. <i>Sediment Consolidation Score</i> . Shear vane stress	~ 1 kg/cm <sup>2</sup>	~ 1.5 kg/cm <sup>2</sup>	~ 2 kg/cm <sup>2</sup>
C. <i>Area Score</i> . Extent of total area Average area of individual reefs	1000 m <sup>2</sup> ~ 1 m <sup>2</sup>	50000 m <sup>2</sup> ~ 2 m <sup>2</sup>	> 100000 m <sup>2</sup> 2 - 10 m <sup>2</sup>
D. <i>Patchiness Score</i> . Percentage cover of patches within the total area	~ 5 %	5 - 10 %	> 10 %
E. <i>Lanice conchilega Density Score</i> . Average density of <i>L. conchilega</i> (/m <sup>2</sup> )	~ 500 individuals	500 - 1500 individuals	> 1500 individuals
F. <i>Biodiversity Score</i> . Species richness (S) Margalef's index (d)	~ 18 ~2	~ 25 ~ 2.5	> 30 > 3
G. <i>Longevity Score</i> .	1 year	2 years	> 2 years

**Table 1 Reefiness scoring table (modified from Hendrick & Foster-Smith 2006)**

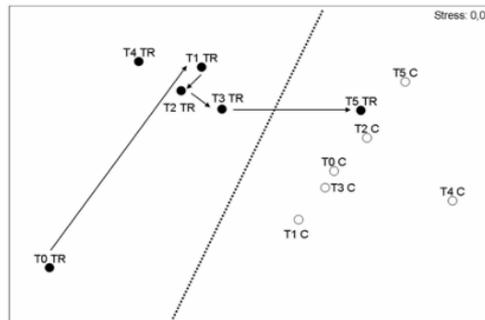
As our research indicated the importance of *L. conchilega* for the structuring and functioning of the benthic ecosystem at the Western Coastal Banks, and since this structuring influence is positively related to *L. conchilega* densities, it is important to assess the vulnerability and resilience to human disturbances. As beam trawling is a frequent activity in our study area, we investigated whether beam trawling has a significant impact on both the *L. conchilega* individuals and the fauna associated with *L. conchilega* patches. Lab experiments were conducted in which undisturbed *L. conchilega* aggregations were subjected to a physical disturbance mimicking beam trawling at different intensities. Mortality of *L. conchilega* individuals clearly increased when beam trawling intensity increased (Fig. 6).



**Figure 6. Survival (left) and relative mortality (right) of *Lanice conchilega* C: control, T1 to T3 indicate increasing disturbance regimes. Time steps coincide with 48 hours.**

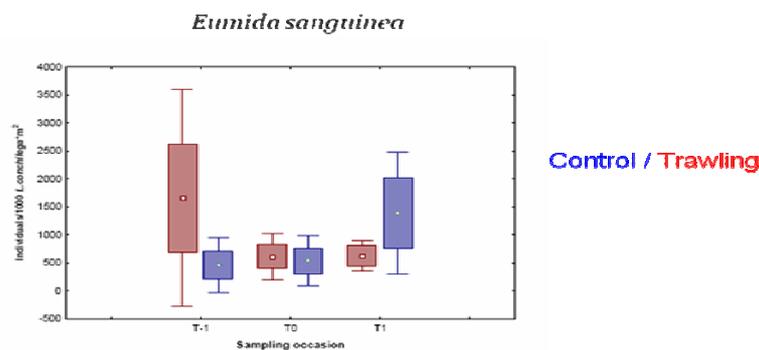
As beam trawling induces mortality of *L. conchilega* individuals within aggregations, there is a chance that the fauna associated with these patches is affected as well. Therefore a one-off beam trawling experiment was performed both in intertidal and subtidal areas to evaluate the effects of such disturbance on the associated fauna. Multivariate analyses (Fig. 7) and SIMPER revealed an impact on the community level and a quick recovery to the original situation. Impacts by beam trawling on the associated fauna of *L. conchilega* are not only related to the impact *s.s.*, but also to the densities of *L.*

*conchilega*. Therefore, *L. conchilega* densities were incorporated as a co-factor in further tests for differences in community composition as a consequence of beam trawling. This did not reveal any significant differences in community composition. However, applying a Generalised Linear Model,



**Figure 7. 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 ( $p < 0.01$ ).**

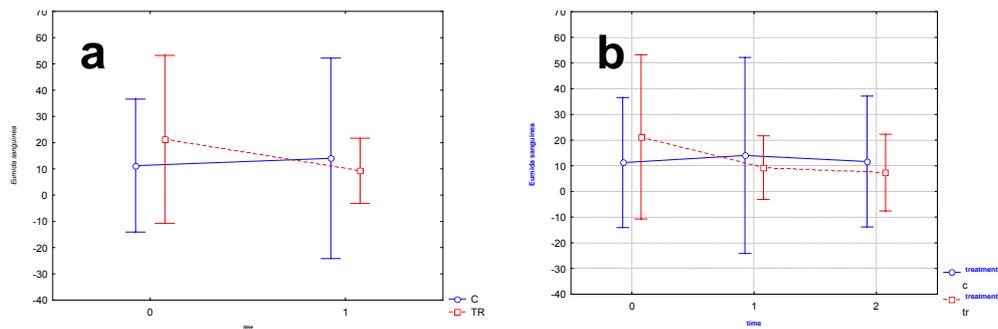
integrating *L. conchilega* densities as covariable, significant treatment by time effects were detected of the well-known associate of *L. conchilega*: *Eumida sanguinea* (Fig. 8).



**Fig. 8 Effect of beam trawling on densities of *Eumida sanguinea* in *Lanice conchilega* patches.**

Integrating these short term results with samples taken five days after disturbance, significant differences are still present and a leveling off becomes visible in the absence of repeated disturbance (Fig. 9).

Other species not particularly associated with *L. conchilega* (e.g. *Phyllodoce lineata*, *Abra alba* and *Mysella bidentata*) are significantly impacted by the trawling disturbance. Species that have been describes as “negative associates” (Rabaut et al. 2007) show a positive respons to beam trawl impact. Those species are *Capitella* sp., *Heteromastus filiformis* and *Notomastus filiformis*.



**Figure. 9: Significant impact ( $p < 0.01$ ) on *E. sanguinea* immediately after disturbance (a) and leveling of thereafter (b)**

Generalising, the effect of beam trawling on the associated fauna follows to main lines: vulnerable species are negatively affected and recovery can either be fast or slow. Opportunistic species on the other hand increase their densities after a beam trawl disturbance.

In summary, we showed that macrobenthic diversity and density is important in mediating the biogeochemical processes needed for the mineralisation of the organic matter produced in the water column. This is very important, since these processes remove nitrogen from eutrophicated systems and partly provide the water column with the nutrients necessary for primary production. Most ecosystem process proxied measured decrease when densities of the organisms decrease. Hence, human activities causing a decrease in abundances directly influence the efficiency of the benthic ecosystem functioning, and as a consequence of this, the provision of nutrients to the water column. In addition, beam trawling causes increased mortality of *L. conchilega* individuals and affects the fauna associated with *L. conchilega* aggregations. Our results stress the importance of *L. conchilega* for the benthic ecosystem functioning since it is not only increasing ecosystem efficiency but also supports a high benthic biodiversity through its ecosystem engineering characteristics.

## WP2: The role of dispersal for benthic organisms and demersal fish

### Introduction

The focus here is on two main questions: (i) Which processes do explain regional and local population structure in the North Sea and Eastern Channel? Although many organisms have a homing behaviour and are thought to live in metapopulations, the structure and dynamics of the genetic landscape remains poorly documented. Apart from contemporary processes, the current genetic structure of marine species is also affected by historical gene flow patterns. (ii) Which physical and biological processes affect the inter- and intra-annual variation in recruitment success? Recruits determine cohort strength and effective population size, hence the population dynamics and ecosystem functioning. We make use of a modeling approach to test various larval behaviours of sole and other organisms from the bibliography in the North Sea. The 3D hydrodynamic model COHERENS and its particle-tracking transport unit SEDLAG are implemented in the southern North Sea, and are used to estimate the influence of hydrodynamic processes and larval behaviour on the transport of sole larvae from real spawning grounds.

### Material and methods

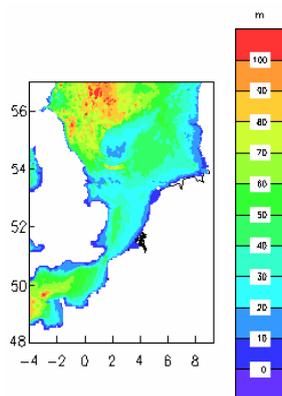
**Genetic structure of *Lanice*:** Specimens of *Lanice conchilega* were collected from 13 Northeastern Atlantic populations (ranging from Sylt to Roscoff). Samples from each location were collected with a hand corer (intertidal) or Van Veen grab (subtidal). After collection, the samples were stored in ethanol (70 – 95%) at 4°C. On average, 30 specimens were analysed from each location. DNA was extracted using a modified CTAB protocol (Jolly et al. 2005). A 650 bp fragment of the mitochondrial COI gene was amplified by PCR with the universal primers HCO1490 and LCO2498. Species-specific internal primers were designed to amplify difficult templates. Additional mitochondrial (16S) and nuclear (ITS & 28S) fragments were amplified using the primers described in Palumbi and Metz (1991) and Jollivet (1998). PCR products were sequenced bi-directionally. Phylogenetic relationships were investigated using traditional (NJ, MP & ML) and haplotype network methods (Parsimony Network). Standard genetic diversity indices and population genetic statistics were calculated in ARLEQUIN v. 3.11.

**Genetic structure of sole:** Adult sole (n = 348) were collected along the Belgian coast with a beam trawl in May/June 2007 (code BELA07) and at the end of August 2007 (code BELB07). Of these fish, total length was measured, a fin tissue was taken and otoliths were collected. Sampling along the Belgian coast was repeated in spring 2008 to test for temporal genetic stability. In the laboratory, DNA was purified with a commercial kit (Nucleospin). From the 25 microsatellite markers available for *Solea* sp., 4 multiplex PCR reactions were optimized, resulting in 18 microsatellite markers. 96 individuals of

population ‘BELA07’ and 48 individuals of ‘BELB07’ were already genotyped at 15 loci. After performing quality tests, 12 microsatellite loci were retained for a preliminary data analysis. In addition to the nuclear markers, we also optimized a mitochondrial marker (Cyt *b*), to check for genetic differentiation between populations and to investigate sex-biased dispersal. We have optimized a sequencing reaction for the amplification of a 700 bp fragment, which appears to have enough variation to detect population structure

**Genetic structure of gobies:** For the study on the sand goby *Pomatoschistus minutus*, we first developed a PCR-RFLP protocol for the genetic identification of (postlarval) *Pomatoschistus* species in the North Sea. The diagnostic tool is based on restriction enzyme digestion of the control region of the mitochondrial genome. Our tests allow for unambiguous species identification and warrant new opportunities in the current research of *Pomatoschistus* species (Larmuseau et al. 2008). Next, an up-to-date phylogeographic analysis was realized by sequencing the mtDNA cytochrome *b* (Cyt *b*) gene of sand gobies from 12 localities throughout the species range, combined with published data of allozyme markers and mtDNA control region sequences. Several phylogenetic methods and a network analysis were used to explore the phylogeographic pattern; the historical demography of *P. minutus* was studied through a mismatch analysis and a Bayesian Skyline Plot.

**Modelling tools:** The NOS model is a 3D hydrodynamical model of the southern North Sea, based on the COHERENS code (Luyten 1999). It covers the region between 4°W and 9°E, and between 48.5°N and 57°N (Fig. 10), using a 157 by 205 horizontal grid with a resolution of 5’ in longitude and 2.5 in latitude, and 20 sigma coordinate vertical layers. Currents and sea surface elevation as well as temperature and salinity are simulated. Open boundaries of the model area are the western and northern boundaries at 4°W and 57°N and 14 rivers are considered. The model simulation runs for two years (1993 and 1994) to allow a realistic initialisation of water masses, and is then run for the analysis of the years 1995 and 1996. The Lagrangian particle-tracking technique is well suited to study the transport of fish larvae because it allows the trajectory of each particle to be followed individually and allow easy integration of biological properties dependant on the larval history. For this application, the COHERENS particle-tracking module SEDLAG (Luyten 1999) has been updated with the latest knowledge. Details on the implementation are given in Savina et al. (subm.).



**Figure 10. The NOS model implementation with rivers considered. Bathymetry is presented in meters.**

**Scenarios:** In a first approach, only the transport of larvae is considered. The model contains no biological features (i.e.: mortality, growth, influence of temperature ...). Six spawning areas have been identified: the inner German Bight, close to the Belgian coast, in the Eastern Channel, in the Thames estuary, on the Norfolk banks, and close to Texel (ref. in Rijnsdorp et al. 1992), Bolle et al. pers. comm.). A total of 368,000 eggs are released, corresponding to 1000 eggs per grid cell identified as a spawning area. The timing of the spawning is very much related to the water temperature (Wegner 2003). The spawning period can thus vary from one year to another, and the spawning activity is thought to progressively spread from south to north of the region (Russell 1976). Globally however, sole spawn from early April to August, with a spawning peak occurring in late April – early May (Borremans 1987). Here, in addition to a standard spawning event on the 01/05/95, we test both an early (15/04/95) and a late (15/05/95) spawning event. Again, the duration of the pelagic stage depends on temperature (Fonds 1979). Based on the literature, the standard larval duration chosen, 10 days of egg development and 30 days of larvae development., corresponds with the low temperature situation.

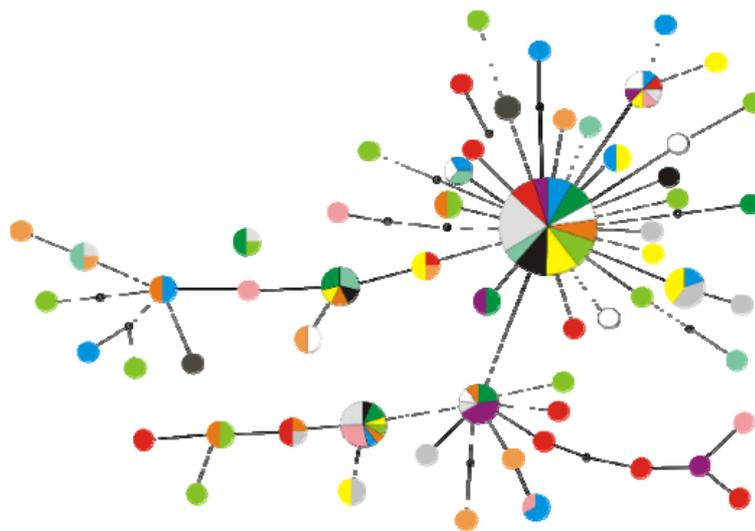
It has been observed experimentally that the early sole larvae from the Bay of Biscay develop diel vertical migrations, whose range increases up to early metamorphosis (Koutsikopoulos et al 1991, Champalbert et al 1992 in Amara et al. (1998)). During metamorphosis, larvae reduce the amplitude of their vertical ascents, and stay closer to the bottom, although they still perform diel movements (Lagardère 1999).

Here three scenarios have been tested: a passive scenario (larvae modelled as “dissolved components”), a first active scenario (ascending eggs, early larvae in surface waters, late larvae in bottom waters) and a second active scenario (ascending eggs, early larvae performing diel vertical migrations in the surface waters, late larvae performing diel vertical migrations in the bottom waters). Since the meteorological variability is expected to have strong influence on larvae dispersion, simulations (all scenarios) have been performed for two contrasted years in term of meteorological conditions, 1995 and 1996. Details on the scenarios are given in Savina et al. (subm.).

## Results

### Dispersal dynamics: a field study

The phylogenies of the mitochondrial (COI & 16S) and nuclear (ITS & 28S) markers converged but pointed to the presence of one divergent sequence from a *L. conchilega* specimen in the Roscoff population. The degree of uncorrected nucleotide divergence (>22%) clearly exceeds the divergence observed between the other *Lanice* sequences (<3%) and suggests the presence of inter-specific genetic variation (i.e., cryptic species). This pattern of cryptic speciation is not uncommon in marine invertebrates (see Knowlton 1993), and was recently observed in related tube building polychaetes (Jolly et al. 2005). A strong vicariant effect caused by lowered sea level during the Pleistocene glaciations may be responsible for the large divergence, because of physical restriction of larval dispersal between the isolated populations. In addition, the coasts of Brittany and the British Isles may have served as secondary contact zones between the diverged clades, as observed in many other benthic species (Jolly et al. 2005, Muths et al. 2006).



**Figure 11. Statistical Parsimony network among COI haplotypes of *Lanice conchilega*, circles represent haplotypes (surface relative to haplotype frequency), lines represent single mutations, small empty circles represent missing haplotypes, circles are coloured according to their geographic distribution: blue: Sylt; Green: Ameland; Purple: Oosterschelde; Orange: Heist; Yellow: Balandbank; Black: Westdiep; Light Green: Zeebrugge; Grey: Boulogne; Red: Torquay; White: Swansea; Pink: Roscoff.**

The phylogeographic analysis of the mitochondrial COI gene from a total of 211 individuals revealed 61 different haplotypes, 19 of which were shared between different populations (Table 2). The haplotype network has a star-like shape, with many mutations occurring around the most common (ancestral) haplotype H1 (Fig. 11). Such a pattern is typically observed in a species that has recently experienced a demographic expansion. The haplotype network did not reveal any regional clustering of specific

haplotypes, the population specific haplotypes are scattered throughout the network and the high-frequency haplotypes have a broad distribution. Remarkably, the most common (central) haplotype (H1) was not observed in the Roscoff population.

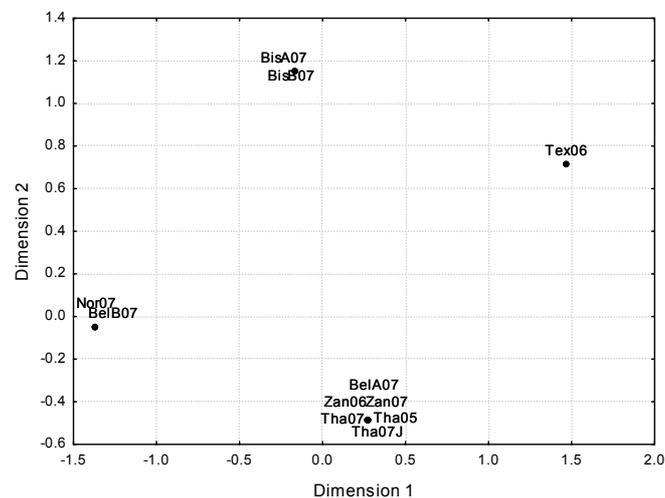
Location	Date	N	Nh	Nh unique	h	$\pi$
Sylt	10/07/2007	18	11	3	0.8562	0.011880
Ameland	21/06/2007	17	7	2	0.8162	0.008637
Oosterschelde	14/11/2007	12	5	1	0.7576	0.006279
Heist	11/08/2006	22	15	4	0.9264	0.012835
Balandbank	16/10/2006	20	10	2	0.8000	0.007874
Wenduinebank	18/10/2007	10	6	2	0.8444	0.009722
Westdiep	16/10/2007	5	1	0	0.0000	0.0000
BCP701	18/10/2007	21	14	9	0.8667	0.012500
De Panne	10/10/2007	11	6	2	0.8546	0.012427
Boulogne	1/02/2006	34	13	3	0.7433	0.008533
Torquay	1/08/2006	19	12	8	0.8713	0.011990
Swansea	13/09/2000	10	7	1	0.8788	0.008343
Roscoff	3/04/2007	12	6	2	0.8444	0.014486

**Table 2. Genetic diversity indices for the 13 *Lanice conchilega* populations. h: haplotype diversity,  $\pi$ : nucleotide diversity.**

The levels inter-population haplotype diversity were high ( $h = 0.74 - 0.93$ ), except for the uniformity observed in the Westdiep population (however,  $N=5$ ). No latitudinal trends were observed in haplotype and nucleotide diversity, the values did not significantly differ among the 13 populations. An overall AMOVA analysis indicated a low, but significant genetic structuring among *L. conchilega* populations ( $\Phi_{ST}$ : 0.037  $P<0.001$ ). This genetic structuring is mainly caused by the moderate isolation of the Roscoff population. The pairwise genetic ( $\Phi_{ST}$ ) distances between Roscoff and all the other sites ranged from 0.09 – 0.25. In addition, three pairwise distances involving the intertidal Heist population revealed a low, but significant value ( $\Phi_{ST}$ : 0.06 – 0.09). The genetic homogeneity, even at larger geographical scales, between *L. conchilega* populations might fit with the hypothesis of high dispersal among populations, linked to the prolonged larval stage of *L. conchilega* (up to 60 days). However, the moderate divergence of the Roscoff population probably also indicates that regional hydrodynamics, such as the presence of a seasonal frontal system at the northern tip of Brittany (Ushant front, Pingree et al. 1975) or the existence of circular currents along the coasts of the English Channel (Salomon and Breton 1993) may promote the isolation of *L. conchilega* populations. It remains difficult to separate the historical (e.g. postglacial colonization from

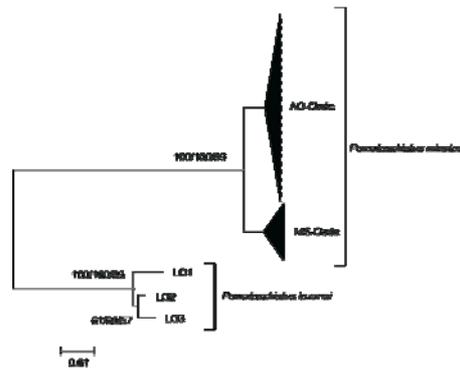
a single refugium) from the recurrent (e.g. high dispersal) imprints in the genetic structure of *L. conchilega*.

Genetic differentiation between the Belgian samples of sole taken in spring 2007 and in late summer 2007 is low but significant ( $F_{st}=0.008^{**}$ ) (Fig. 12). This suggests that both samples belong to a different spawning group. It might be that adult sole come to the Belgian coast in late summer/autumn to feed and that the Belgian coasts presents a mixed feeding ground with sole from several spawning grounds. We are in the process of ageing the individual samples to check for any cohort effects and we will increase the number of genotyped individuals to confirm the pattern. In the next year 30 individuals per population will be sequenced to check for sex-biased dispersal. Genetic similarity of juvenile sole caught in the Scheldt estuary (Zandvliet) and adult sole caught along the Belgian coast suggests that there might be limited dispersal. This hypothesis needs to be further examined by increasing the number of samples and by complementary otolith microchemical analyses.



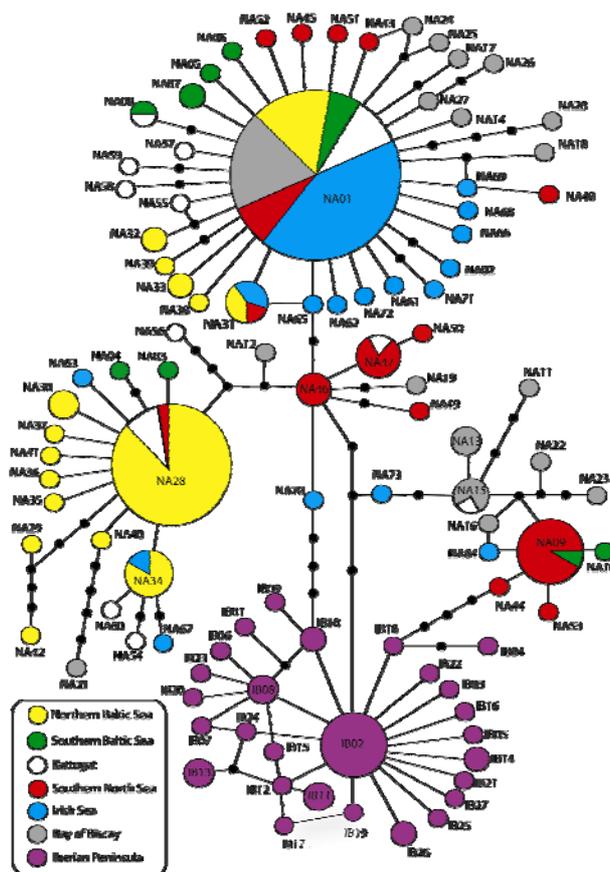
**Figure 12. MDS plot based on genetic distances (Nei 1972) of sampling populations genotyped with 12 microsatellite markers. (Bel: Belgian coast (adults); Zan: Zandvliet (juveniles); Nor: Norfolk Banks (adults); Bis: Bay of Biscay (adults); Tex: Texel (juveniles); Tha: Thames (adults); ThaJ: Thames (juveniles). The two numbers at the end refer to the sampling year).**

For the sand goby *Pomatoschistus minutus*, reciprocal monophyly was found between a Mediterranean Sea (MS) and an Atlantic Ocean (AO) Clade with a Middle-Pleistocene origin (Fig. 13).



**Figure 13.** Maximum likelihood tree of all *Pomatoschistus minutus* Cyt *b* haplotypes and three haplotypes of *P. lozanoi* as the genetic outgroup. Bootstrap values are indicated for statistically supported groupings ( $\geq 50\%$ ) for maximum likelihood (ML), maximum parsimony (MP) and neighbour-joining (NJ) (ML/MP/NJ). Because of the high number of haplotypes, the clades for which no supported groupings were detected, are comprised.

The AO-Clade contains two evolutionary significant units (ESUs): the Iberian Peninsula (IB) Group and the North Atlantic (NA) Group. These two groups diverged during Middle Pleistocene glacial cycles.



**Figure 14.** Statistical parsimony network of the Cyt *b* haplotypes of the sand goby’s AO-Clade. The size of the circles is proportional to the number of sand gobies sharing that haplotype

For the NA-Group there is evidence for geographic sorting of the ancestral haplotypes with recent radiations in the Baltic Sea, Irish Sea, North Sea and Bay of Biscay (Fig.14). Pre-LGM subdivision signals were not erased during the LGM. Middle Pleistocene glaciations yielded different historically isolated evolving sets of populations but in contrast to most other analyses, only the northern Atlantic group contributed to the postglacial recolonization. The demographic histories of the Mediterranean Clade and the two Atlantic ESUs were studied with Bayesian Skyline Plots (BSP). They were mainly influenced by expansions dated during the Middle Pleistocene glaciations and post-Eem respectively (plots of the analyses not shown). The historical demography of Mediterranean sand gobies was mainly influenced by Middle Pleistocene glaciations in contrast to the demography of the Atlantic that was shaped by Late Pleistocene expansions (Larmuseau et al. 2009).

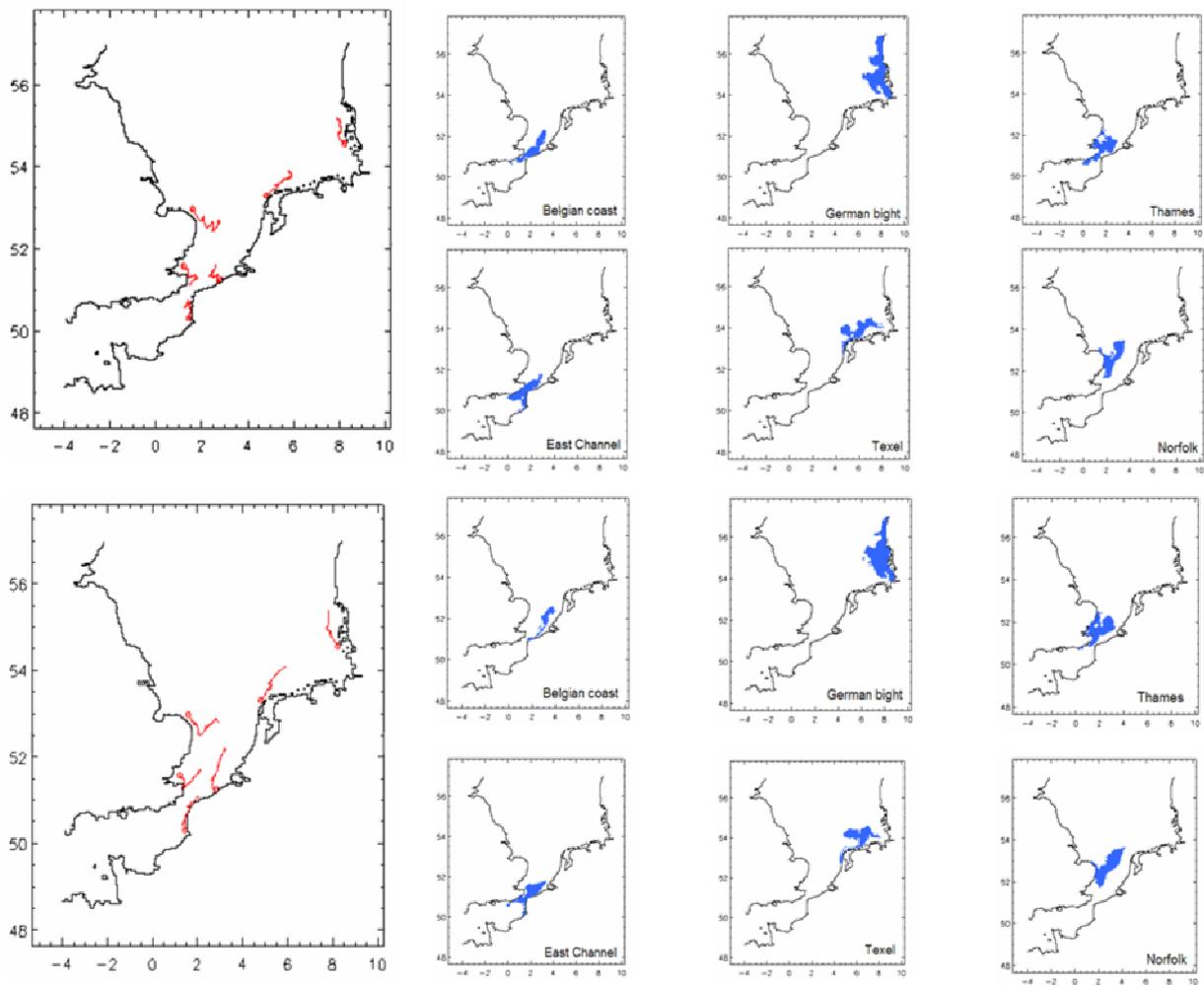
### **Dispersal dynamics: a modelling approach**

Fig. 15 shows the results obtained for two of the simulations performed. In both cases, passive particles are released from the main spawning grounds and transported during 40 days. Eggs are spawned on the 15/04 in the first simulation and on the 01/05 during the second one. For each spawning site, the mean trajectories of the larvae during 40 days as well as the depth-integrated distribution of larvae on the 40<sup>th</sup> day are displayed. Blue areas indicate concentrations above 0 larvae per square meter. The results demonstrate the great influence of variation in hydrodynamic conditions in itself on the distribution of larvae at the end of the pelagic stage. In particular, the distribution of larvae spawned off the Belgian coast suggests significant local recruitment in the first simulation but a very little local recruitment in the second simulation. Simulations with active behaviour (vertical migration, 2 scenarios described above) have been performed to see if active behaviour can somehow counteract offshore drifts.

Interannual variability of the larvae dispersion due to meteorological year-to-year variability has been analysed by comparing results for years 1995 and 1996. All these results are given in Savina et al. (subm.).

### **Discussion**

Understanding the genetic structure of contemporary populations requires a distinction between historical and contemporaneous patterns. The patterns are strongly intertwined in the polychaete *Lanice conchilega* in the North Sea and English Channel, but show a distinct pattern for the sand goby along the Atlantic and Mediterranean coasts. Such features are not atypical of marine organisms and reflect the dynamics of the glacial and interglacial periods during the second part of the Pleistocene. In a contemporaneous perspective, dispersal dynamics of marine organisms operate on large and small scales. A genetic analysis of *L. conchilega* reveals both patterns, with large scale dispersal in the North Sea and local dispersal off Brittany.



**Figure 15 Mean trajectories (left) and depth-integrated distribution (right) of the larvae spawned on the 15/04/1995 and the 01/05/1995 after 40 days of transport.**

The analysis of the sand goby is in progress; the pattern will be validated with a fine-scale population genetic analysis based on nine microsatellite markers and candidate genes. Research is progressing as planned. The fine-scale pattern of sole is interesting. First of all the markers discriminate between samples on a small temporal and spatial scale (a feat which was hard to reach a few years ago), and secondly there seems to be an exchange of populations throughout the year on the Belgian Continental Shelf. This observation is new, but requires additional validation. Samples collected in 2008 are being processed and they will be analyzed together with those from 2007 to check for temporal genetic patterns between sampling years. Sample size will be increased where ever necessary. Furthermore, sex-biased dispersal will be checked through genetic differentiation in males and females.

The modeling of larval transport results suggest that (1) for passive transport, the variations in the larval retention above spawning sites due to the varying hydrodynamic conditions are not consistent through space (i.e. not the same for all the spawning sites); (2) the effect of active vertical movements on larval transport is not consistent through space either; (3) effects of active vertical movements include decreased retention above spawning sites, decreased transport, decreased horizontal dispersion

of larvae through reduced vertical shear; (4) variability in larval retention due to environment is higher than variability due to differences in the behaviour of larvae. (5) In terms of connectivity, exchanges of larvae between the 6 areas considered are low. Most important it tends to confirm the presence of subpopulations of sole in the Eastern Channel and southern North Sea. These novel findings will be backed up with additional validations.

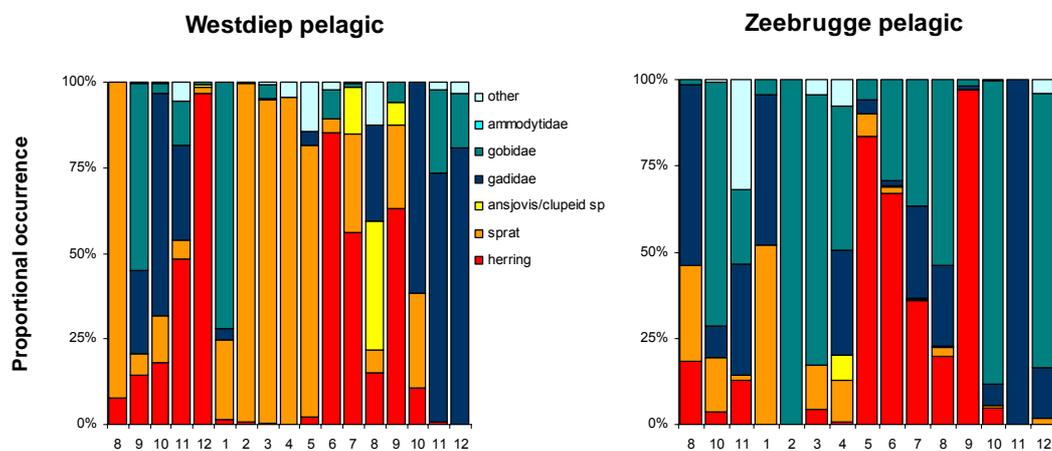
### WP 3: Air-Sea biotic coupling

Following the impact of a series of fish stock collapses on breeding performance and breeding numbers of seabirds in the North Sea, predator-prey relationships at the top of the marine food web became a focal point of attention (Barrett et al 1987, Monaghan et al 1989, Camphuysen 2005). Knowledge of the foraging ecology of top predators proved to be a crucial factor in determining the vulnerability of seabirds and marine mammals to anthropogenic pressure as well as natural ecosystem variation. So far, within the North Sea most attention has been given to ecosystems where sandeel is the dominating prey species for marine top predators (e.g. Furness & Tasker 2000, Camphuysen 2005, Wanless et al 2005). In the southern parts of the North Sea, the availability of prey species other than sandeel may play a more prominent role in the regulation of seabird populations (Stienen 2006). Previous research on the BCS revealed marked changes in breeding ecology of seabirds, abundance and distribution of wintering seabirds, as well as a strong increase in marine mammals during the past few years. Most likely some of these changes are related to local changes in prey fish availability whereas other events might be related to more widespread ecosystem changes. However, the underlying pelagic ecosystem has been insufficiently studied so that the causal links within these processes remain hidden. Consequently it is neither possible to predict the ecosystem effects of fish stock changes (whether or not caused by anthropogenic pressure such as eutrophication, fisheries and climate change) nor the impact of top predators on the underlying marine food web (top-down regulation studies conform recommendations by the EFS Marine Board 2003). Reductions of the amount of fishery offal may have disastrous and unexpected effects on seabird populations, even on those species that do not rely on discards (Votier et al 2004). Understanding the links between different units in the ecosystem is thus trivial for a sustainable use of our resources and to understand the human impact exerted on the ecosystem. Likewise, it is essential knowledge when setting up and maintaining a system for measuring the health of the ecosystem such as the OSPAR Ecological Quality Objectives (EcoQOs). The oil-rate in beached Common Guillemots *Uria aalge*, for example represents an EcoQO to monitor chronic oil pollution in the North Sea. Yet a recent drop in oil-rate on the BCS (winters 2004/05 and 2005/06) most likely reflects major food shortages among our wintering population and not a decrease in oil pollution. By measuring local food abundance this study will enhance our understanding of the underlying causes of ecosystem shifts and add to the usefulness of health indicators. The study aims at a better understanding of the resilience of the upper layer of the marine ecosystem at the BCS and to set up reliable methods to assess the health of the pelagic food web. Terns remain the key species for the development of health indicators for the pelagic food web, since these sensitive seabirds are indicators of the food situation par excellence (Furness & Tasker 2000, Stienen 2006) and because food ecology, reproductive parameters and the demography of their populations can be measured relatively easy. Other species will be added in order to better understand

the specific value of the Western Coastal Banks area for fish eating and benthivorous seabirds and the importance of the BCS for wintering seabirds. Great Crested Grebe *Podiceps cristatus*, Sandwich Tern *Sterna sandvicensis* and Common Tern *S. hirundo* are focal species in this study because of their protected status in Belgian marine waters (Haelters et al. 2004). Common Guillemot and Razorbill *Alca torda* are added to the list as wintering species of which preliminary knowledge on diet preferences exists. Although the latter two species are closely related, their spatial distribution patterns greatly differ in some parts of the Belgian coastal waters, whereas there is complete overlap in other areas. It is not known whether this is due to niche- or resource partitioning.

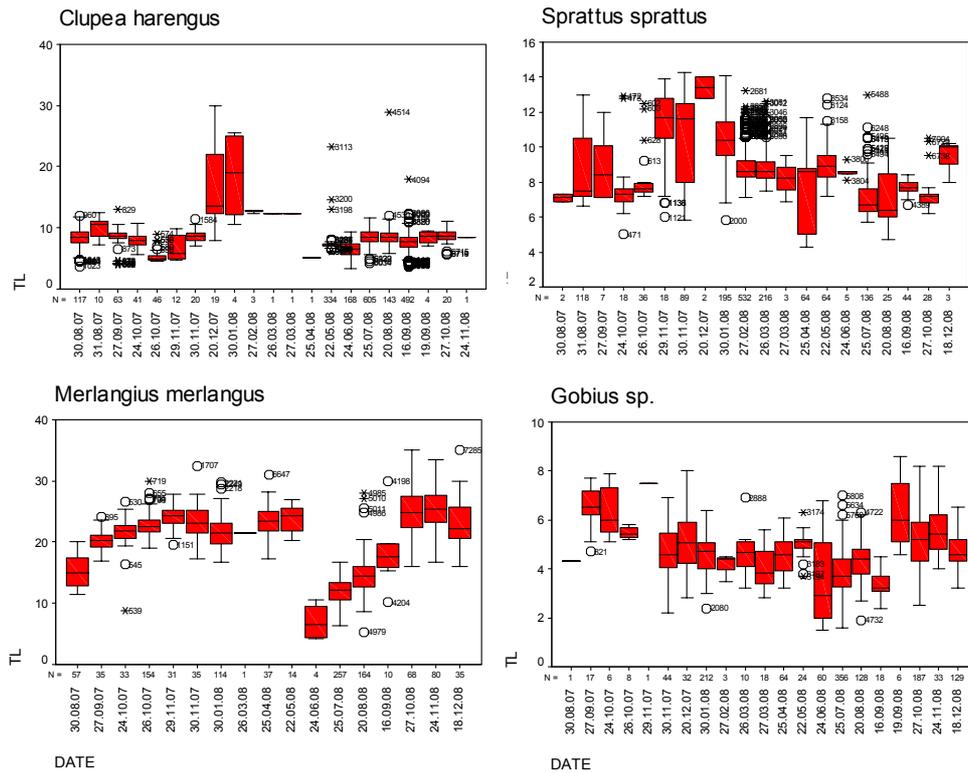
### Prey fish sampling

During the first phase of WESTBANKS, prey fish abundance was sampled monthly from August 2007 onwards at two key locations along the coast (Westdiep and Wenduinebank near Zeebrugge) using a pelagic MIK-net. The sampling locations greatly differ in the diversity and composition of the piscivorous avifauna. The Westdiep supports important wintering populations of Great Crested Grebe, whereas the Wenduinebank serves as a foraging area for Common and Sandwich Tern during the breeding season. Abundance and length distribution of pelagic fish species was measured on board the research vessel. The results indicate major differences in the composition of the fish community between the sampling sites, with the Westdiep supporting a pelagic fish fauna with more energy rich fish such as Clupeidae and Gadidae throughout the year (Fig. 16).



**Figure 16. Proportional importance of pelagic fish species caught with a MIK-net in the Westdiep and at the Wenduinebank near Zeebrugge during the period Aug 2007 (8) – December 2008 (12).**

The catches at the Wenduinebank were dominated by Gobidae. However, during the breeding season when seabirds concentrate in the port of Zeebrugge, the Wenduinebank holds a much higher density of prey fish than the Westdiep location. The mix of small Clupeidae, Gobidae and some Gadidae, perfectly matches the diet of the tern chicks and the adult diet of Common Terns (see below). Average prey fish size strongly fluctuated throughout the year (Fig. 17).

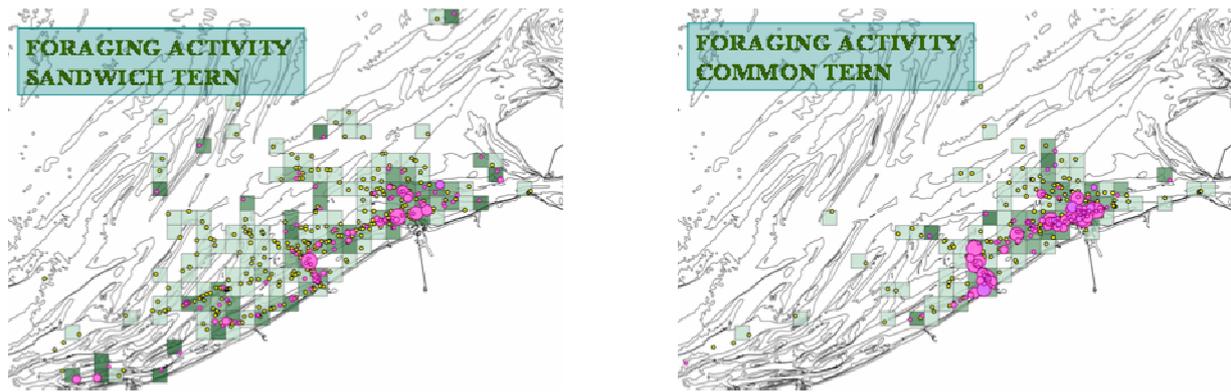


**Figure 17. Boxplots showing the seasonal variation in the standard length (TL in cm) of the four most numerous caught fish species/families during the fish sampling campaigns.**

During the breeding season (April-July) the size of the four most caught groups was smaller than during winter and better matches prey length that parent terns require to raise their chicks.

### Foraging activities of terns

During the fish sampling campaigns special attention was given to plunge diving terns (noting geographical position, foraging success and prey species). These findings were added to the existing INBO-database on seabird distribution (1992-2007) and were analysed in GIS. This reveals the hotspots of tern foraging activity at the BPNS (Fig. 18). The distribution of foraging individuals differs very much from that of non-foraging terns. During the breeding season, foraging activity was restricted to the near coastal zone at locations where strong gradients in depths occur (transition zones from gully to sandbank). Common Terns mainly foraged along the edges of the Wenduinebank, the port entrances of Ostend (Oostendebank and Nieuwpoortbank) and Zeebrugge, as well as along the gullies south and west of the Vlakte van de Raan. They largely avoided the Vlakte van de Raan itself for foraging. Sandwich Terns preferred the same areas but also travelled to the Westdiep and western Flemish Banks and more frequently used the Scheur near the Dutch border for foraging. Apparently, the Wenduinebank functions as an important foraging area for both species, but hitherto, this sandbank was not recognised as important for seabirds. This study shows that the Wenduinebank is of major importance for foraging terns and supports a rich fish fauna during the breeding season.



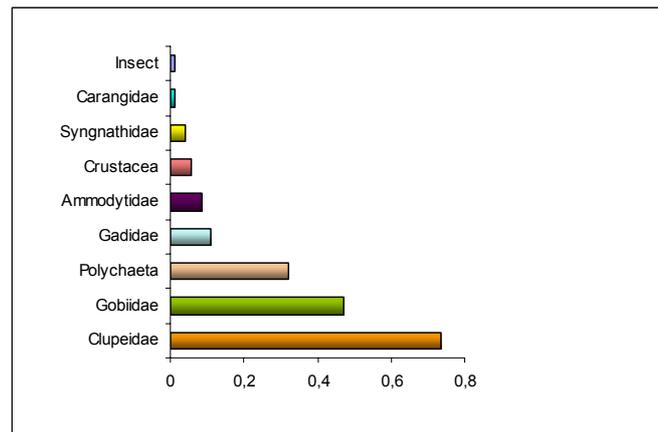
**Figure 18. Foraging activity of Sandwich Tern (left) and Common Tern (right) during the breeding season. Dots show the numerical occurrence of foraging terns and shaded grids represent foraging frequency ( i.e. number of actively foraging individuals/ total numbers).**

### Diet composition of terns

The foraging ecology of the terns was further studied in detail in the colony nesting in the port of Zeebrugge. Chick growth, mortality, diet composition and parental nest attendance was measured. Here only preliminary results on chick survival and diet will be presented. Diet of Common Tern chicks was based on 812 food remains found in the Zeebrugge colony during chick rearing in 2007-2008. Diet of adult Common Terns was based on prey remains found in 72 non-empty stomachs of adults found dead in the colony during period June 2004 – June 2008. These were mainly collision victims of the row of wind turbines situated between the breeding site and the foraging areas (Everaert & Stienen 2007, Stienen et al 2008). returning from a feeding trip and often having full stomachs. In both study years, the chicks’ diet was dominated by *Clupea harengus* and *Sprattus sprattus* (Table 3). Stomachs of adult terns also contained high proportions of Clupeidae (73.6% of all non-empty stomachs) but Also *Gobiidae* and polychaete worms were important prey items for adults (Fig. 19). The occurrence of nereid worms is consistent with the presence of *Nereis sp.* in faecal samples of adult Sandwich Terns (see below). Although these worms were not caught during our fish sampling campaigns, their presence in the diet of plunge diving seabirds that dive only a few decimetres deep strongly suggest that they are abundant in the pelagic system of the southern North Sea.

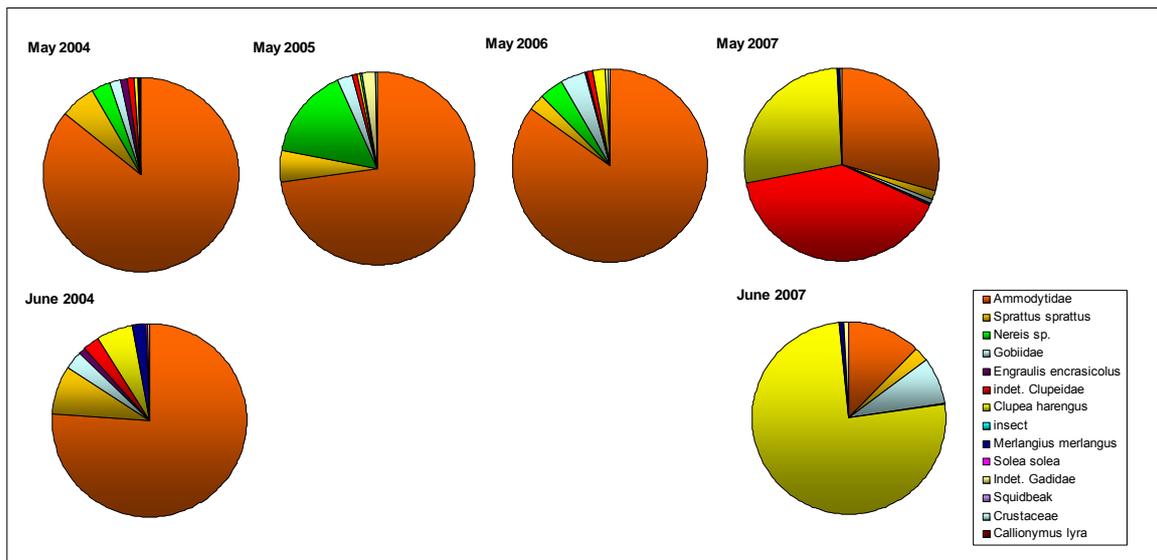
Prey taxon	Year	
	2007	2008
<i>Clupea harengus</i>	90,0	96,0
<i>Sprattus sprattus</i>	5,7	0,5
indet. Clupeidae	0,0	0,7
<i>Trisopterus luscus</i>	0,8	1,2
<i>Merlangius merlangus</i>	2,3	0,7
<i>Loligo sp.</i>	0,0	0,2
<i>Atherina presbyter</i>	0,5	0,2
Pleuronectidae	0,3	0,0
Syngnathidae	0,3	0,0
Ammodytidae	0,3	0,0
Gobiidae	0,0	0,5

**Table 3: Proportional composition of food remains found in the Common Tern colony in Zeebrugge during chick rearing. In total 389 and 423 preys were examined, respectively in 2007 and 2008.**



**Figure 19: Frequency of occurrence (FO) of prey types found in stomachs of adult Common Terns. FO = number of stomachs containing specific prey type/total number of non-empty stomachs.**

The preceding TROPOHOS study revealed that adult Sandwich Terns at least partly depend on non-piscivorous prey (Vanaverbeke et al 2007). Faecal samples taken in the breeding colony at Zeebrugge in 2001-2003 contained unexpected high numbers of nereid jaws, a benthic polychaete. It was hypothesised that the nereid worms were not taken from their benthic environment but that they were caught during the reproductive phase of the worms when they have a short period of pelagic occurrence. Since the worms reproduce in early spring (April), later samples should no longer contain nereid worms. Therefore, during the breeding seasons of 2004 and 2007 faecal samples were collected of both early breeders and late-laying terns. Sampling took place 1-2 days before hatching of the first egg in the focal (sub)colony. Since egg-laying is highly synchronised within subcolonies this ensures that the faeces originated from adults only. In each colony, 10 to 20 nests that were separated from species other than Sandwich Tern, were selected at random. The entire fresh guano layer surrounding the nest was removed and stored dry for later analysis. In the laboratory, the pooled material was carefully rinsed with water. Remains of animal material were extracted under a binocular and stored dry. Sagittal fish otoliths (identified to the lowest possible taxon using Härkönen (1986), Leopold et al. (2001) and our own reference collection), polychaete jaws, squid beaks and pincers of crustaceans were used to determine the terns' diet. Unfortunately, in the two years when seasonal changes in the adult diet were studied, the samples of early breeders contained low numbers of nereid jaws (Fig. 20). Only 11 and 2 jaws were found respectively in 2004 and 2007, representing 3.0% and 0.2% of the total number of prey items. Still none were found in the late samples, suggesting that reproductive swarming of these benthic species facilitates their availability for plunge diving seabirds.



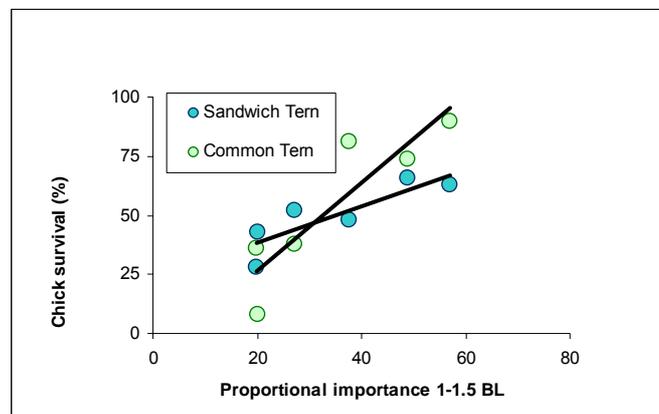
**Figure 20. Diet composition of self-feeding adult Sandwich Terns based on sagittal fish otoliths, polychaete jaws, squid beaks and pincers of crustaceans found in faecal samples collected in the Zeebrugge colony during the period 2004-2007.**

The results obtained during the preceding THROPHOS-study suggested that self-feeding adult Sandwich Terns strongly depended on *Ammodytidae*. During all study years (2001-2003) *Ammodytidae* dominated the faecal samples collected in Zeebrugge and this prey also dominated faecal samples collected at the Hirsholmene colony in Denmark and at Griend in the Netherlands (Vanaverbeke et al 2007). A very similar diet composition arose from the faecal samples collected in Zeebrugge during most of the recent years (Fig. 20). In 2007, however, we found a remarkable shift in the diet composition of adult Sandwich Terns in Zeebrugge. For the first time *Ammodytidae* appeared to be of minor importance, whereas small *Clupeidae* were found in high proportions in the faecal samples of both early and late breeders. This coincided with an exceptionally low chick mortality rate of Sandwich and Common Tern (Table 4). In contrast to the adults, chicks of Sandwich Terns largely depend on *Clupeidae*. A high abundance of small clupeids also seems crucial for the survival of Common Tern chicks.

Year	Clutch size (N eggs/nest)	Hatching success (%)	Fledging success (%)	Breeding success (N fledged young/pair)
1997	2.4	78	50	0.9
1998	2.5	77	61	1.2
1999	2.5	78	67	1.3
2000	2.3	91	37	0.8
2001	2.3	80	74	1.4
2002	2.2	79	8	0.1
2003	2.6	87	74	1.7
2004	2.1	81	38	0.7
2005	2.0	80	36	0.6
2006	2.0	50	81	0.8
2007	2.7	92	90	2.2
2008	2.4	88	86	1.8

**Table 4. Reproductive parameters of Common Tern in Zeebrugge during 1997-2008 measured within enclosures.**

During the breeding seasons 2002-2007, food delivery to Sandwich Tern chicks was observed from a hide placed in the vicinity of an enclosed part of the Zeebrugge colony (see Stienen et al 2000 and Vanaverbeke et al. 2007 for methodological details). The distribution of prey length offered to the tern chicks appeared crucial for their survival. In years when certain prey lengths were missing from the chicks’ diet, at a certain stage in the growing process parents could no longer satisfy the hunger of their chicks and many chicks that initially grew well starved to death (Vanaverbeke et al 2007). An examination of the prey length responsible for chick mortality revealed an important role of prey measuring 1-1.5 BL (where BL = 5.43 cm, corresponding to the average bill length of an adult Sandwich Tern). In years when the diet contained low proportions of small prey fish ranging in size between 5.4 – 8.2 cm (predominantly *Clupeidae*), chick mortality was much higher than in years when small prey was abundant (Fig. 21). Surprisingly, this relationship held for both Common and Sandwich Tern. Prey length distribution may thus be a good candidate to serve as indicator for the health of the pelagic ecosystem.

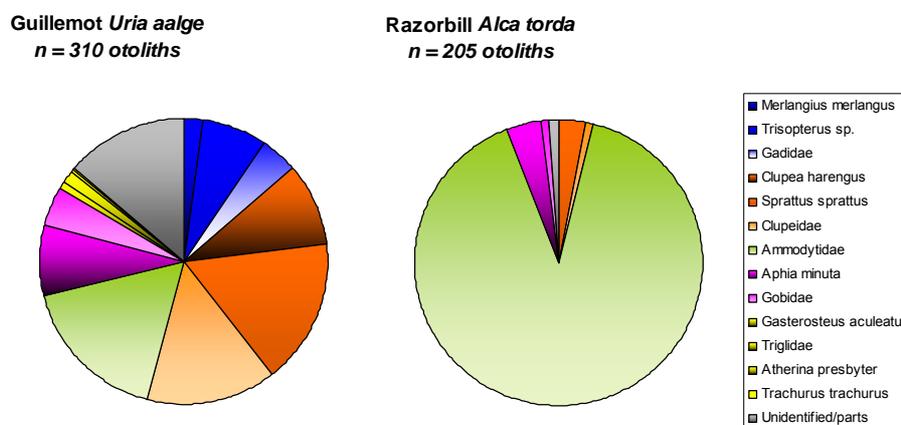


**Figure 21. Relation between the proportional importance of small prey fish in the diet of Sandwich Terns and the survival of Common and Sandwich Tern chicks in Zeebrugge during 2002-2007.**

### Diet composition of auks

During the period January 2003 – March 2008, respectively 133 and 48 beach washed corpses of Common Guillemot *Uria aalge* and Razorbill *Alca torda* were collected from the Belgian beaches and stored in the freezer. After dissection, stomachs of the birds were opened and carefully rinsed with cold water over a 125 µm sieve. Remains of animal material were retained under a binocular and stored dry. Respectively 49.6% and 58.3% of the examined stomachs of Common Guillemot and Razorbill actually contained food remains. The 470 sagittal otoliths of fish were later identified using Härkönen 1986, Leopold et al 2001 and our own reference collection. Otolith width (OW in 0.01 mm) and length (OL in 0.01 mm) were measured using a microscope fitted with a digital Leica DFC290 camera and Leica IM50 software (version 5). The data will be analysed in detail during the second phase of the Westbanks-project, but a preliminary analyses of numerical occurrence of fish otoliths already revealed striking dietary differences between the two study species (Fig. 22). Apparently resource

partitioning explains why wintering areas of Guillemot and Razorbill can overlap and why the two species often occur in mixed flocks. Razorbill diet was largely restricted to Ammodytidae, while that of Guillemot was dominated by Clupeidae and contained various other prey species as well. This held true in all three years for which a reliable number of stomachs was collected (winters 2005, 2006 and 2007). A pronounced prey specialism in Razorbills and a more opportunistic feeding behaviour of Common Guillemots was also found in a comparative diet study of birds killed during the Tricolor oil spill in the south-eastern North Sea in January 2003 (Ouweland et al 2004). In fact, Ouweland et al (2004) found a similar broad diet preference of Common Guillemot but with slightly lower proportions of *Clupeidae* (28 % vs. 47% in our study) and higher proportions of Ammodytidae (31% vs. 20%).

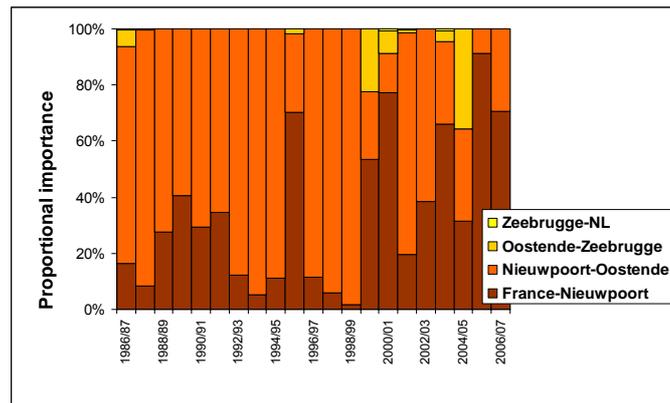


**Figure 22. Diet composition based on sagittal fish otoliths found in the stomachs of 133 and 48 beached washed corpses of Common Guillemot *Uria aalge* and Razorbill *Alca torda* collected on the Belgian beaches during the period January 2003 – March 2008.**

The most striking difference is that for Razorbills found during the Tricolor incident, clupeids were of prime importance (72%), whereas this study found that sandeels predominated the diet (91%). In a second stage of the WESTBANKS project, prey size will be examined as well as effects of age and sex of on the birds' diet preferences.

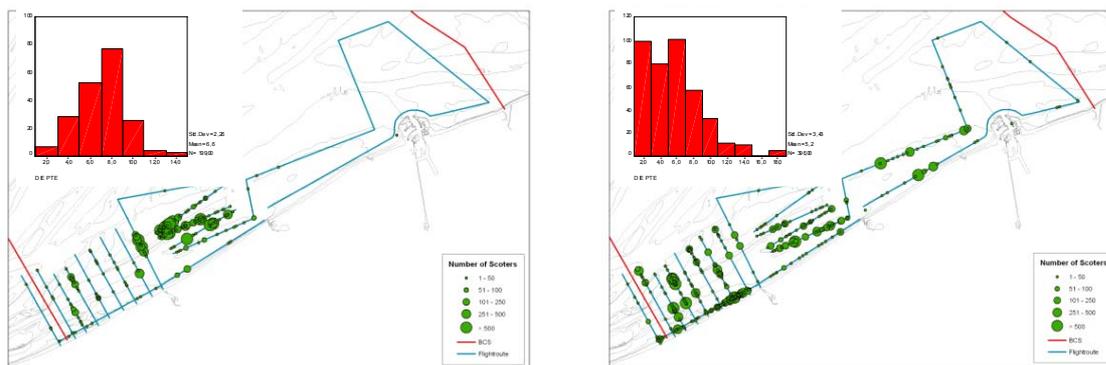
### Benthivorous seabirds

An analysis of standardised aerial surveys of Scoters (Black Scoter *Melanitta nigra* and Velvet Scoter *Melanitta fusca*) performed along the Belgian coast revealed a major change in wintering areas (Fig. 23 and 24).



**Figure 23. Proportions of the wintering populations of Scoters residing in different parts of the Belgian marine waters in 1986/87-2006/07 based on aerial surveys.**

The wintering sites historically occupied by Scoters encompasses the Nieuwpoortbank, Middelkerkebank and Kwintebank, an area that supported high densities of *Spisula* sp. (Degraer et al 2006), one of the preferred prey species of Scoters. The distributional shift occurred around the winter 1999/2000 and coincided with a strong reduction in *Spisula* sp. (Van Hoey et al 2007).



**Figure 24. Distribution of Scoters *Melanitta* sp. between December 1996 and March 1999 (left figure) vs. the distribution between October 1999 and February 2008 (right figure). The top left insets show the depth distribution of Scoters in the two periods.**

The current wintering areas are situated much closer to the coast at shallower depth and proportionally more Scoters winter in the southwestern part of the BPNZ. Visual observations suggested that in this area Scoters prey upon *Ensis* sp., but this has to be further confirmed by analysis of stomach contents of beach washed Scoters.

## GENERAL CONCLUSIONS AND RECOMMENDATIONS

Research conducted within the WestBanks project clearly showed **the tight ecological links between the benthic, pelagic and air-borne ecosystems. Integrated research** on all aspects of the marine ecosystem is not only a conceptually appealing approach but is indeed practicable to support sustainable management strategies for the Belgian Part of the North Sea.

Furthermore, our results clearly demonstrate the **need for the implementation of management plans** aiming at saving the seafloor from further damage in order **to sustain the high diversity and ecosystem functioning rates**, while we could also point out the **need for an expansion of the MPAs** on the BPNS.

The benthic ecosystem is an important area for the mineralisation of pelagically produced organic matter. Mineralisation provides the water column with the necessary nutrients for the phytoplankton bloom. Three macrobenthic species (*Lanice conchilega*, *Abra alba* and *Nephtys* sp.), present in high densities in the Western Coastal Bank area were shown to be important for the sustainability of the ecosystem processes. When densities of these species in laboratory manipulations dropped below *in situ* densities, a decrease in sediment reworking, fluxes of oxygen and nutrients across the sediment-water interface and lower denitrification rates were observed. Our work further suggests that the key species chosen have a different impact on the ecosystem functioning and hence a decrease of one functional group will not be counteracted for by another functional group. **This shows that human activities having a negative impact on the occurrence of benthic key species lead to a loss of the efficiency of the functioning of the benthic ecosystem.** It is beyond doubt that human activities indeed have a negative impact on the occurrence of important macrobenthic species on the BPNS. We provided evidence for the vulnerability of *L. conchilega* and its associated fauna to beam trawling. **The perception of this habitat being resilient to beam-trawling is explained while the vulnerability of the associated fauna provide a warning measure for habitat deterioration.**

Macrobenthic species are not only important for maintaining ecosystem function. The modulation effects *Lanice conchilega* has on the abiotic environment does have far reaching consequences for the species abundance and diversity (creating the so-called *L. conchilega* community *s.s.*). Therefore, this tube dwelling polychaete have been described as an important ‘ecosystem engineer’. It can be used as an indication for biodiversity and bioproductivity and is present in high densities near the coast (< 12 nm). Therefore, both for implementation of current management plans within the SAC and for the sustainable management conservation of habitats in the BPNS this species needs attention. Within the WestBanks projects, it was shown that **high density aggregations should be considered as reefs.** This is important in the framework of the Habitats Directive, as reefs are listed under Annex I and

must be protected in the SACs. **We therefore advocate to classify the SAC as a sandbank habitat-type (1110), associated with the reef habitat-type (1170).** This would also allow for better criteria for the ecological restoration in the area as the reefs represent a higher biological value.

Analyses of the WestBanks database (Vanaverbeke et al. 2009) suggest a clear spatial link between the occurrence of *L. conchilega* and larval/juvenile stages of sole (*Solea solea*). *L. conchilega* was persistent in the Western coastal zone for about 30 years. Though it is still not possible to analyse individual reefs over time, several mechanisms have been described showing how individual reefs are being renewed (Callaway, 2003; Rabaut *et al.*, in press) and remote sensing techniques can be used in the future to monitor the species’ reefs (Degraer *et al.*, 2008). **The results of the WestBanks project point out the possibilities to use this polychaete species as a proxy if a ‘science based, sustainable management’ is to be implemented in the Belgian coastal waters.**

Summarising, the results of the WestBanks project suggest that **all activities damaging the macrobenthic communities (commercial harvesting and beam trawling) should be minimized or ideally stopped in areas where a healthy sandbank system is aimed for (such as the SAC area Trapegeer-Stroombank).**

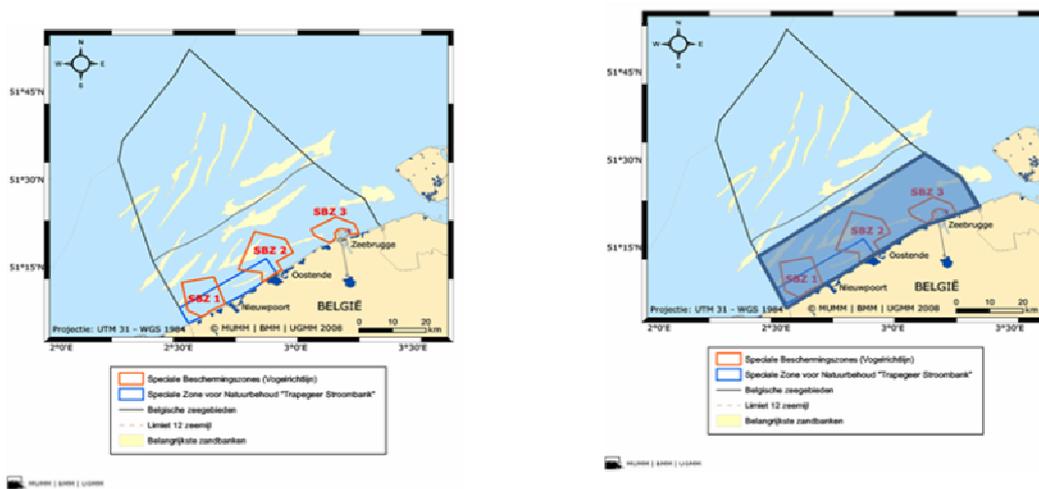
The genetic pattern of marine organisms in the Southern Bight of the North Sea is shaped by the glacial/ interglacial history of the NE Atlantic. This pattern is characteristic for the marine organisms inhabiting the whole North Atlantic Ocean, including the worm *L. conchilega* and the fishes *Solea solea* and *Pomatoschistus minutus*. It also means that populations inhabiting the Eastern Channel and the North Sea have only appeared after the last rise in sea level (Holocene) and thus show indications of a sudden population expansion and in some cases mixing of clades.

In addition, life history traits and dispersal potential of the organisms, in combination with the regional hydrodynamic patterns and dynamics, contributed to the contemporaneous patterns. Since the periodical tidal and aperiodical wind advection patterns are so influential in the WestBanks area, they are forces to be reckoned with in structuring populations (and the communities they are associated with). Accurate genetic tracking of populations of sole has made appear fine-scaled patterns never noticed before on the BPNS. There are for example indications that over a year cycle populations of sole are exchanged. The populations of the BPNS are distinguishable from most neighbouring regions. The outcome may **be important in terms of fisheries management.**

The modeling results of larval dispersion suggest that vertical movement does not have an effect on the variability of the retention of larvae above spawning sites. The variability in larval retention due to environment seems to be higher than due to differences in the behaviour of larvae. The application of the models further pointed to a low exchange of larvae between areas. The amount of larval exchange is lower than the amount of larvae retained in an area. This tends to confirm the possibility of the

presence of subpopulations of sole in the Eastern English Channel and Southern Bight of the North Sea. From these data we learn that the **interaction dynamics between spawning, nursery and feeding grounds of organisms have to be included in management plans for fisheries and marine protected areas.**

The research on birds highlighted the **link between seabirds and the pelagic realm.** Breeding success of terns and spatial distribution of seabirds is clearly linked with food availability. A large amount of information on the prey selection of marine top predators was collected during the first phase of WestBanks. This research will be continued along the same line since sudden changes were observed. **The factors underlying the breeding success of terns at the harbour of Zeebrugge (prey length distribution) are candidates to serve as an indicator for the health of the pelagic ecosystem.**



**Figure 25. Map of the BPNS with delineation of current SPA's (left) and suggested MPA (right panel, purple overlay).**

The updated knowledge of the distribution of seabirds at sea suggests that the **spatial delineation of the current Special Protected Areas on the BPNS of the North Sea should be largely extended** to fully protect the wintering and breeding bird populations at the Belgian coast. The current SPA's (ZB1 – ZB 3) are shown in Fig. 25 (left panel). A full coverage of the Terns' feeding grounds implies (1) including areas located more offshore; (2) including areas closer to the Dutch border and (3) connecting the existing SPA's. (Figure 1, right panel). In addition, (1) this area would encompass all major foraging grounds of seaducks, (2) it would be better geared to the delineation in BWZee, (3) it would be easier to manage and control, and (4) it would better fit with the SPA's along the Dutch coast.

## PERSPECTIVES for future WestBanks RESEARCH

The research conducted within the first phase of WestBanks sets the priorities for WestBanks Phase II. During this second phase, results obtained during the first phase will be used as basis for research for the following two years. The general outline of the project remains the same, since investigations will be targeted towards the benthic-pelagic coupling, the role of dispersal for benthic organisms and fish, and the air-sea biotic coupling.

The **benthic** work will focus on the role of macrobenthic organisms in the marine food web. This will be investigated from two points of view: (1) the influence of the macrobenthic activities on the meiobenthic food web and (2) the role of *L. conchilega* patches as food source for demersal fish.

Our results indeed indicate that activities of macrobenthic organisms alter the biogeochemical properties of the sediment and the distribution of food particles in the benthic environment. During TROPHOS, the meiobenthic food web was investigated both in the field and the lab (Franco et al. 2008 a,b). This showed that vertically segregated food webs exist in fine-grained sediment shortly after the phytoplankton bloom. It was hypothesised that macrobenthic activities were responsible for the mixing of the sediment and the uniform distribution of food sources in the sediment. This would explain the observed differences in reproductive response of the dominant nematode species (Steyaert 2003). We will further investigate the role of macro- and meiofauna in the benthic food web by means of lab incubations with labeled food in the presence of the various species (functional groups) of the macrobenthos. This will be combined with a field study to further investigate how diatoms and *Phaeocystis* cascades in the benthic food web. It will lead to an increased understanding of the role of the macrobenthos in the functioning of the benthic ecosystem and indirectly it will allow to assess the effects of eutrophication, via the proliferation of *Phaeocystis* and its consequent deposition on the trophic functioning of the sediment.

The second part of this topic is based on the fact that *L. conchilega* indeed is a reef-building organism which increases habitat heterogeneity and structure. We hypothesise a positive influence of these reefs on populations of common sole (*Solea solea*) due to (1) the increased habitat quality and structure and (2) evidence that common sole feeds on *L. conchilega* (Rijnsdorp & Vingerhoed 2001) and other polychaetes. We will compare the diet of common sole in areas where *L. conchilega* reefs are present or absent. This will make it possible to estimate the carrying capacity of the tube reefs towards common sole. In addition, lab experiment will be conducted to evaluate the attraction of juvenile sole to artificial biogenic reefs.

The work on the **dispersal dynamics of marine organisms** during the second phase of WestBanks will continue to focus on molecular research and modeling. Modeling reveals dispersal on the short

term, while genetics reveal patterns on the mid- and long-term. This combination is very suitable for understanding the dispersal dynamics and merits a close follow-up for fisheries and coastal zone management. The ecohydrodynamical dispersal model represents the first step in the development of an individual-based ecological model for sole larvae in the North Sea. So far the possibility to model individual life histories (Hinckley et al. 1996) has not been fully exploited. Interesting developments include: (1) interindividual variability in the biological responses; (2) explicit modeling of larval mortality and duration of egg and larval stages as a function of spatially varying parameters such as temperature and potentially food resources. Larval mortality is a key component to understand recruitment variability and to estimate connectivity. Molecular genotyping with neutral and progressively also adaptive markers will reveal stock structure and dispersal dynamics at a resolution never observed before. Promising is the embedding of these dispersal patterns and dynamics in a community/ecosystem based metapopulation concept.

The research on **seabirds** will further elaborate on the link between the airborne and the pelagic ecosystem. Further knowledge on the diet composition of the seabirds will be gathered in combination with the assessment of the spatial distribution of pelagic fish on the BPNS. On the one hand, this will increase our knowledge on the trophic interactions at the air-sea interface, but at the same moment it will produce indicators for measuring the health of the pelagic ecosystem.

During the first phase of WestBanks, all data collected since the start of the SPSD programmes by the WestBanks consortium were collected in single database. A first analyses of this database resulted in knowledge immediately transferable to the policy level while it generated scientific hypotheses as well (Vanaverbeke et al. 2008). During WestBanks II, a follow-up workshop will be organised in order to further test these hypotheses.

Integration of all detailed investigations carried out at the interface between compartments of the marine ecosystem of the BPNS will result in drastic increase of our understanding of the marine environment that can be used in the framework of a sustainable management of the North Sea.

## ACKNOWLEDGEMENTS

This research was funded by the Belgian Science Policy (BELSPO, contract nr SD/BN/1A) in the framework of the SSD programme. Additional funding was provided by grants provided by the Flemish Fund for Scientific Research (FWO Vlaanderen) to Ulrike Braeckman, Marijn Rabaut and Tine Huyse and by grants provided by the Institute for the Promotion of Innovation through Science and Technology in Flanders, Belgium (IWT Vlaanderen) to Els Cuveliers. Genevieve Lacroix acknowledges support from the Belspo funded SOLEMOD project.

We would like to thank the master and crew of RV Belgica and Zeeleeuw for their skilfull help. Many colleagues (Dirk Van Gansbeke, Bart Beuselinck, Jürgen Verstraete, Joke Van Tomme, Karl Van Ginderdeuren, Britta Gribsholt, Frederic Gazeau, Jan Peene, Bert Sincke) helped during field work, experimental work of sample processing. We also thank the conservators of the Flemish Nature Reserve “Baai van Heist” .

We are grateful to Steven Degraer, Annelies Goffin, Klaas Deneudt, Jan Mees, Simon Claus, Bea Merckx, Nathalie De Hauwere for their contribution to the WestBanks integrated workshop of October 2008. WestBanks papers were produced in cooperation with Steven Degraer, Frederick Hendrickx and Katja Guilini.

## LITERATURE

- Aller RC (1988). Benthic fauna and biogeochemical processes in marine sediments: the role of burrow structures. In Blackburn, T. H. & J. Sørensen (eds): Nitrogen Cycling in Coastal Marine Environments. John Wiley & Sons Ltd., Chichester: 1-338
- Amara R, Poulard JC, Lagardère F, Désaunay Y (1998). Comparison between the life cycles of two Soleidae, the common sole, *Solea solea*, and the thickback sole, *Microchirus variegatus*, in the Bay of Biscay (France). Environmental Biology of Fishes 53: 193-209.
- Banta GT, Giblin AE, Hobbie JE, Tucker J (1995). Benthic respiration and nitrogen release in Buzzards Bay, Massachusetts. J Mar Res 53, 107-135
- Barrett RT, Anker-Nilssen T, Rikardsen F, Valde K, Røv N, Vader W (1987) The food, growth and fledging success of Norwegian Puffin chicks *Fratercula arctica* in 1980-1983. Orn Scand 18:73-83.
- Blackburn TH (1988). Benthic mineralization and bacterial production. Nitrogen Cycling in Coastal Marine Environments SCOPE 175-190
- Borremans C (1987). North Sea spawning grounds of the sole (*Solea solea*) located from the 1984 Belgian plankton survey. Proceedings of the V Congress of European Ichthyologists, Stockholm, Sweden
- Cabral HN (2000). Comparative feeding ecology of sympatric *Solea solea* and *S. senegalensis*, within the nursery areas of the Tagus estuary, Portugal. J Fish Biol 57: 1550-1562.
- Camphuysen CJ (2005) Understanding marine foodweb processes: an ecosystem approach to sustainable sandeel fisheries in the North Sea. IMPRESS final report, NIOZ-report 2005-5. Royal Netherlands Institute for Sea Research, Texel pp 240.
- Caradec S, Grossi V, Hulth S, Stora G, Gilbert F (2004). Macrofaunal reworking activities and hydrocarbon redistribution in an experimental sediment system. J Sea Res 52 (3):199-210
- Davis WR & Miller DC (1979). Burrowing activities and sediment impact of *Nephtys incisa*. Advances in Marine Environmental Research, Proceedings of a Symposium. Jacoff FS (ed.) 303-319
- Degrear S, Wittoeck J, Appeltans W, Cooreman K, Deprez T, Hillewaert H, Hostens K, Mees J, Vanden Berghe E, Vincx M (2006) The macrobenthos atlas of the Belgian part of the North Sea. Belgian Science Policy: Brussel, Belgium.
- EFS Marine Board (2003) Navigating the Future II: summary of Integrating Marine Science in Europe. 26pp.
- Everaert J, Stienen EWM (2007) Impact of wind turbines on birds in Zeebrugge (Belgium). Biodivers Conserv 16: 3345-3359.

- Fonds M (1979). Laboratory observations on the influence of temperature and salinity on development of the eggs and growth of the larvae of *Solea solea* (Pisces). *Mar Ecol Prog Ser* 1: 91-99.
- Forster S, Graf G (1995). Impact of irrigation on oxygen flux into the sediment: intermittent pumping by *Callianassa subterranea* and “piston-pumping” by *Lanice conchilega*. *Mar Biol* 123 (2): 335-346
- Franco MA, De Mesel I, Demba Diallo M, Van der Gucht K, Van Gansbeke D, van Rijswijk P, Costa MJ, Vincx M, Vanaverbeke J (2007). Effect of phytoplankton bloom deposition on benthic bacterial communities in two contrasting sediments in the southern North Sea. *Aquat Micr Ecol*: 241-254
- Franco MA, Soetaert K, Costa MJ, Vincx M, Vanaverbeke J (2008a) Uptake of phytodetritus by meiobenthos using <sup>13</sup>C labeled diatoms and *Phaeocystis* in two contrasting sediments from the North Sea *J Exp Mar Biol Ecol* 362: 1-8.
- Franco MA, Soetaert K, van Oevelen D, Van Gansbeke D, Costa MJ, Vincx M, Vanaverbeke J (2008b) Density, vertical distribution and trophic responses of metazoan meiobenthos to phytoplankton deposition in contrasting sediments. *Mar Ecol Prog Ser* 358: 51-62.
- Furness RW, Tasker ML (2000) Seabird-fishery interactions: quantifying the sensitivity of seabirds to reductions in sandeel abundance and identification of key areas for sensitive seabirds in the North Sea. *Mar Ecol Prog Ser* 202: 253-264
- Gérino M, Stora G, François-Carcaillet F, Gilbert F, Poggiale JC, Mermillod-Blondin F, Desrosiers G, Vervier P (2003). Macro-invertebrate functional groups in freshwater and marine sediments: a common mechanistic classification. *Vie Milieu* 53 (4):221-231
- Gilbert F, Hulth S, Grossi V, Poggiale JC, Desrosiers G, Rosenberg R, Gérino M, François-Carcaillet F, Michaud E, Stora G (2007). Sediment reworking by marine benthic species from the Gullmar Fjord (Western Sweden): Importance of faunal biovolume. *J Exp Mar Biol Ecol* (348):133-144
- Haelters J, Vigin L, Stienen EWM, Scory S, Kuijken E, Jacques TG (2004) Ornithological importance of the Belgian marine areas: identification of areas qualifying as Special Protection Areas under the European Birds Directive. *Bull KBIN, Biol* 74 sup: 1-91
- Härkönen T (1986) Guide to the otoliths of the bony fishes of the Northeast Atlantic. Danbiu, Hellerup
- Hendrick VJ, Foster-Smith RL (2006) *Sabellaria spinulosa* reef: a scoring system for evaluating 'reefiness' in the context of the Habitats Directive. *J Mar Biol Ass UK* 86:665-677
- Jollivet D, Comtet T, Chevaldonne P, et al. (1998). Unexpected relationship between dispersal strategies and speciation within the association *Bathymodiolus* (Bivalvia) - *Branchiopolynoe* (Polychaeta) inferred from the rDNA neutral ITS2 marker. *Cahiers de Biologie Marine* 39: 359-362.
- Jolly MT, Jollivet D, Gentil F, Thiébaud E, Viard F (2005) Sharp genetic break between Atlantic and English Channel populations of the polychaete *Pectinaria koreni*, along the north coast of Brittany, France. *Heredity* 94: 23–32
- Knowlton N. (1993) Sibling species in the sea. *Annual Review of Ecology and Systematics* 24: 189-216

Kristensen E (1988). Benthic fauna and biogeochemical processes in marine sediments: microbial activities and fluxes. In Blackburn, T. H. & J. Sørensen (eds): Nitrogen Cycling in Coastal Marine Environments. John Wiley & Sons Ltd., Chichester: 275-299

Lagardère F, Amara R, Joassard L (1999). Vertical distribution and feeding activity of metamorphosing sole, *Solea solea*, before immigration to the Bay of Vilaine nursery (northern Bay of Biscay, France). Environmental Biology of Fishes 56: 213-228.

Larmuseau M.H.D., Guelinckx J., Hellemans B., Van Houdt J.K.J., Volckaert F.A.M. (2008) Fast PCR-RFLP method facilitates identification of *Pomatoschistus* species from the North Atlantic. J Appl Icht 24: 342-344

Larmuseau M., Volckaert F.A.M. (2009) Distributional and demographic consequences of Pleistocene climate fluctuations for a marine demersal fish in the North-Eastern Atlantic. Journal of Biogeography (in press)

Leopold MF, Van Damme CJG, Philippart CJM, Winter CJN (2001) Otoliths of North Sea fish: interactive guide of identification of fish from the SE North Sea, Wadden Sea and adjacent fresh waters by means of otoliths and other hard parts. CD-ROM, ETI, Amsterdam. .

Luyten P., Jones JE, Proctor R, Tabor A, Tett P, Wild-Allen K (1999). COHERENS - A Coupled Hydrodynamical-Ecological model for Regional and Shelf seas: User Documentation, MUMM Report, Management Unit of the Mathematical Models of the north Sea, Belgium: 911 p.

Mahaut M-L, Sibuet M, Shirayama Y (1995). Weight-dependent respiration rates in deep-sea organisms. Deep-Sea Res I 42 (9):1575-1582

Mermillod-Blondin F, Rosenberg R, Francois-Carcaillet F, Norling K, Mauclair L (2004). Influence of bioturbation by three benthic infaunal species on microbial communities and biogeochemical processes in marine sediment. Aquat Microb Ecol 36 (3):271-284

Michaud E, Desrosiers G, Mermillod-Blondin F, Sundby B, Stora G (2005). The functional group approach to bioturbation: II. The effects of the *Macoma balthica* community on fluxes of nutrients and dissolved organic carbon across the sediment--water interface. J Exp Mar Biol Ecol (326): 77-88

Michaud E, Desrosiers G, Mermillod-Blondin F, Sundby B, Stora G (2006). The functional group approach to bioturbation: The effects of biodiffusers and gallery-diffusers of the *Macoma balthica* community on sediment oxygen uptake. J Exp Mar Biol Ecol 337 (2):178-189

Molinero A, Flos R (1992) Influence of season on the feeding habits of the common sole *Solea solea*. Mar Biol 113: 499-507.

Monaghan P, Uttley,JD, Burns MD, Thaine C, Blackwood J (1989) The relationship between food supply, reproductive effort and breeding success in Arctic Terns *Sterna paradisae*. J Anim Ecol 58: 261-274.

Muths D, Davoult D, Gentil F, Jollivet D (2006) Incomplete cryptic speciation between intertidal and subtidal morphs of *Acrocnida brachiata* (Echinodermata: Ophiuroidea) in the Northeast Atlantic. Molecular Ecology 15: 3303-3318

Nei M (1972) Genetic distance between populations. American Naturalist 106:283

- Ouwehand J, Leopold MF, Camphuysen CJ (2004). A comparative study of the diet of Guillemots *Uria aalge* and Razorbills *Alca torda* killed during the Tricolor oil incident in the south-eastern North Sea in January 2003. *Atlantic Seabirds* 6: 147-164.
- Palumbi SR, Metz EC (1991) Strong reproductive isolation between closely related tropical sea urchins (genus *Echinometra*). *Molecular Biology and Evolution* 8:227-239
- Pingree RD, Pugh PR, Holligan PM, Forster GR (1975) Summer phytoplankton blooms and red tides along tidal fronts in the approaches to the English Channel. *Nature* 258: 672-677
- Rijnsdorp AD, Vingerhoed B (2001) Feeding of plaice *Pleuronectes platessa* (L.) and sole *Solea solea* (L.) in relation to the effects of bottom trawling. *J Sea Res* 45: 219-229.
- Rabaut M, Guilini K, Van Hoey G, Magda V, Degraer S (2007) A bio-engineered soft-bottom environment: The impact of *Lanice conchilega* on the benthic species-specific densities and community structure. *Est Coast Shelf Sci* 75:525-536
- Rabaut M, Braeckman U, Hendrickx F, Vincx M, Degraer S (2008) Experimental beam-trawling in *Lanice conchilega* reefs: Impact on the associated fauna. *Fish Res* 90:209-216
- Rabaut M, Degraer S, Schrijvers J, Deros S, Bogaert D, Maes F, Vincx M, Cliquet A (in press a) Policy analysis of the ‘MPA-process’ in temperate continental shelf areas. *Aquatic Conservation: Marine and Freshwater Ecosystems*
- Rabaut M, Vincx M, Degraer S (in press b) Do *Lanice conchilega* (sandmason) aggregations classify as reefs? Quantifying habitat modifying effects. *Helg Mar Res*
- Rijnsdorp A, Van Beek FA, Flatman S, et al. (1992). Recruitment of sole stocks, *Solea solea* (L.), in the North-east Atlantic. *Neth J Sea Res* 29: 173-192.
- Rijnsdorp AD, Vingerhoed B (2001). Feeding of plaice *Pleuronectes platessa* L. and sole *Solea solea* L. in relation to the effect of bottom trawling. *J Sea Res* 45(3-4): 219-229
- Russell, F. (1976). The eggs and planktonic stages of British marine fishes. London, Academic Press.
- Salomon J-C, Breton M (1993) An atlas of long-term currents in the Channel. *Oceanologica Acta* 16: 439-448
- Savina M, Lacroix G, Ruddick K (submitted) Influence of larval behaviour on the transport of sole larvae in the Southern North Sea: a modelling study.
- Seitzinger S (1988). Denitrification in freshwater and coastal marine ecosystems: ecological and geochemical significance. *Limnol.Oceanogr.* 33 702-724
- Sistmans WCH, Hummel H, Engelberts A, Markuse MM (2004). Inventarisatie macrofauna Westerschelde 2004 - Rapport Evaluatie van de verdieping van de Westerschelde. 39 pp
- Steyaert M (2003). Spatial and temporal scaled of nematode communities in the North Sea and Westerschelde. PhD thesis, Ghent University, 114 pp.
- Stienen EWM (2006) Living with gulls; trading off food and predation in the Sandwich tern *Sterna sandvicensis*. *Alterra Scientific Contribution* 15. Alterra, Wageningen pp 192

Stienen EWM, van Beers PWM, Brenninkmeijer A, Habraken JMPM, Raaijmakers MHJE, van Tienen PGM (2000) Reflections of a specialist: patterns in food provisioning and foraging conditions in Sandwich Terns *Sterna sandvicensis*. *Ardea* 88: 33-49.

Stienen EWM, Courtens W, Everaert J, Van de Walle M (2008). Sex-biased mortality of common terns in wind farm collisions. *Condor* 110: 154-157.

Thrush SF, Hewitt JE, Gibbs M, Lundquist C, Norkko A (2006). Functional Role of Large Organisms in Intertidal Communities: Community Effects and Ecosystem Function. *Ecosystems* 9: 1029–1040

Vanaverbeke J, Franco MA, Remerie T, Vanreusel A, Vincx M, Moodley L, Soetaert K, van Oevelen D, Courtens W, Stienen E, Van de Walle M, Deneudt K, Vanden Berghe E, Draisma S, Hellemans B, Huyse T, Volckaert F, Van den Eynde D (2007). Higher trophic levels in the southern North Sea “TROPHOS”: Final report EV/25. Belgian Science Policy: Brussel, Belgium. 89 pp

Vanaverbeke J, Braeckman U, Claus S, Courtens W, De Hauwere N, Degraer S, Deneudt K, Goffin A, Mees J, Merckx B, Provoost P, Rabaut M, Soetaert K, Vincx M (2009). Long-term data from the Belgian Continental Shelf in the framework of science-based management of the coastal North Sea. Report of the WestBanks integrative workshop, October 2008, 23 pp.

Van Hoey G (2006). Spatio-temporal variability within the macrobenthic *Abra alba* community, with emphasis on the structuring role of *Lanice conchilega* [Ruimtelijke en temporele variabiliteit binnen de macrobenthische *Abra alba* gemeenschap met nadruk op de structurende rol van *Lanice conchilega*]. PhD Thesis. Universiteit Gent. Faculteit Wetenschappen: Gent, Belgium. 187 pp.

Van Hoey et al 2007 G, Vincx M, Degraer S (2007). Temporal variability in the *Abra alba* community determined by global and local events. *J. Sea Res.* 58: 144-155.

Wanless S, Harris MP, Redman P, Speakman JR (2005) Low energy values of a fish as a probable cause of a major seabird breeding failure in the North Sea. *Mar Ecol Prog Ser* 294: 1-8.

Wegner, G., Damm, U, Purps, M (2003). Physical influences on the stock dynamics of plaice and sole in the North Sea. *Scientia Marina* 67(Suppl. 1): 219-234. Wikander B (1980). Biometry and behavior in *Abra nitida* (Müller) and *A. longicallus* (Scacchi) (Bivalvia, Tellinacea). *Sarsia* 65(4) 255-268

Zar JH (1995). *Biostatistical Analysis*. Prentice-Hall, Englewood Cliffs

Zuhlke R (2001) Polychaete tubes create ephemeral community patterns: *Lanice conchilega* (Pallas, 1766) associations studied over six years. *J Sea Res* 46:261-272