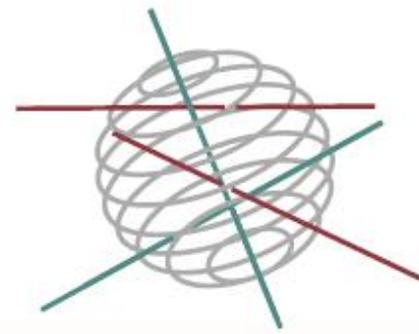


SSD

SCIENCE FOR A SUSTAINABLE DEVELOPMENT



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

"WESTBANKS"

J. Vanaverbeke, A. Braarup Cuykens, U. Braeckman, W. Courtens,
E. Cuveliers, K. Deneudt, A. Goffin, B. Hellemans, T. Huyse, G. Lacroix,
M. Larmuseau, J. Mees, P. Provoost, M. Rabaut, T. Remerie, M. Savina,
K. Soetaert, EWM. Stienen, H. Verstraete, F. Volckaert, M. Vincx



ENERGY 

TRANSPORT AND MOBILITY 

AGRO-FOOD 

HEALTH AND ENVIRONMENT 

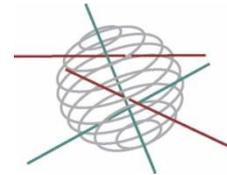
CLIMATE 

BIODIVERSITY   

ATMOSPHERE AND TERRESTRIAL AND MARINE ECOSYSTEMS   

TRANSVERSAL ACTIONS 

SCIENCE FOR A SUSTAINABLE DEVELOPMENT
(SSD)



North Sea



FINAL REPORT

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

“WESTBANKS”

SD/BN/01



Promotors
Magda Vincx/Jan Vanaverbeke
Ghent University (Ugent)
Biology Department, Marine Biology Research Group
Krijgslaan 281/S8, B-9000 Gent



Filip Volckaert
Katholieke Universiteit Leuven (KU Leuven)
Laboratory of Animal Diversity and Systematics
Ch. Deberiotstraat 32, B-3000 Leuven

Eric Stienen
Research Institute for Nature and Forest (INBO)
Kliniekstraat 25 – B-1070 Brussel

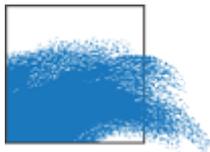


Jan Mees
Flanders Marine Institute (VLIZ)
InnovOcean Site
Wandelaarkaai 7, B-8400 Oostende



Authors
**Jan Vanaverbeke, Ulrike Braeckman, Marijn Rabaut, Thomas Remerie,
Magda Vincx**
Ugent

**Filip Volckaert, Els Cuveliers, Maarten Larmuseau, Bart Helleman,
Tine Huyse**
KU Leuven



**Eric WM Stienen, Ann Braarup Cuykens, Wouter Courtens, Hilbran
Verstraete**
INBO

Jan Mees, Annelies Goffin, Klaas Deneudt
VLIZ



Genéviève Lacroix, Marie Savina
MUMM

Karline Soetaert, Pieter Provoost
NIOO-CEME



D/2011/1191/34

Published in 2011 by the Belgian Science Policy Office

Avenue Louise 231

Louizalaan 231

B-1050 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 Office nor any person acting on behalf of the Belgian Science Policy Office 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, Braarup Cuykens A, Braeckman U, Courtens W, Cuveliers E, Deneudt K, Goffin A, Hellemans B, Huyse T, Lacroix G, Larmuseau M, Mees J, 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"***. Final Report. Brussels : Belgian Science Policy Office 2011 – 82 p. (Research Programme Science for a Sustainable Development)

TABLE OF CONTENTS

SUMMARY	5
1. INTRODUCTION	9
2. METHODOLOGY AND RESULTS	13
2.1 Benthic-pelagic coupling: effects of macrofauna on benthic ecosystem functioning.....	13
2.1.1 Material and Methods	13
2.1.2 Results.....	15
2.2 <i>Lanice conchilega</i> , fisheries and marine conservation	25
2.2.1. Material and Methods	25
2.2.2. Results.....	26
2.3 The role of dispersal for benthic organisms and demersal fish	34
2.3.1 Material and Methods	34
2.3.2 Results.....	38
2.4 Air-Sea biotic coupling	46
2.4.1 Material and Methods	46
2.4.2 Results.....	46
2.5 WestBanks integrative workshop	58
3. POLICY SUPPORT	59
3.1. Contribution of WestBanks results to policy development.....	59
3.2. Recommendations for a sustainable management of the North Sea, with emphasis on the BPNS	60
3.3. Recommendation on the designation of MPAs at a North Sea scale	63
4. DISSEMINATION AND VALORISATION	65
5. PUBLICATIONS	67
5.1 Peer reviewed	67
5.2 Others (only written contributions mentioned).....	69
6. ACKNOWLEDGEMENTS	73
7. REFERENCES	75

SUMMARY

It has now been widely accepted that human activities have a negative impact on marine ecosystems. Anthropogenic influences can be direct (i.e. through exploitation, pollution, and habitat destruction) or indirect (i.e. climate change). Overall, this results in declining biodiversity and impoverished ecosystem functioning, leading to a loss of ecosystem services provided by marine and coastal ecosystems. In the coastal zone, these human impacts triggered biodiversity loss, which resulted in negative impacts on important ecosystem services including food provision (fisheries), provision of nursery habitats, connectivity between habitats and filtering and detoxification services.

To protect the marine environment from further deterioration and initiate recovery where needed, the European Union implemented legislation that should lead to protection and management of important areas under the umbrella of the Natura 2000 network and aims to guarantee a good ecological status under the Water Framework Directive or Marine Strategy Framework Directive. Especially the Marine Strategy Framework directive advocates the implementation of the Ecosystem Approach to Management (EAM), which in turn should be based on "scientific understanding for assessing good environmental status in a coherent and holistic manner" (2010/477/EU).

Within the framework of the Belspo programme Science for a Sustainable Development, the WestBanks project took a holistic view on the coastal marine ecosystem, by focusing on the interactions between the benthic, pelagic and airborne realm at the species and population level. WestBanks built on the knowledge gathered on the structural, functional and genetic diversity and the understanding of the functioning of the coastal ecosystem of the Belgian Part of the North Sea (BPNS). The general objective of the WestBanks project was *to increase the understanding of the dynamic link between the benthic, pelagic and air-borne ecosystem*. Specific objectives included (1) studying the structuring role of key benthic organisms on the functioning of the benthic system and its impact on the benthic-pelagic coupling; (2) studying the structural and functional links between small-scale dispersal of key species and ecosystem units and (3) studying top predators (fish and birds) feeding at interfaces (benthic-pelagic and pelagic-air). This strategy ensures acquiring scientific knowledge that is of immediate use to support Belgium in implementing the European directives.

In a first work package, the link between the benthic and pelagic ecosystem was investigated. Through field measurements, experiments and modeling approaches, we investigated (1) *benthic* mineralisation processes of *pelagically* produced organic matter and (2) the effect of important macrofaunal organisms (i.e. ecosystem engineers) on benthic ecosystem functioning (including mineralisation processes and the dynamics of the lower food web).

Our results indicated that in the Westdiep area (western part of the Belgian Part of the North Sea), about 1% of the pelagically produced carbon is lost to the sediment every day, resulting in an annual carbon deposition of $72.9 \pm 6.2 \text{ g m}^{-2} \text{ d}^{-1}$.

Mineralisation of this organic matter is uncoupled from sedimentation: while two thirds of the modeled sedimentation occurs between late February and early June, only 25% of the annual benthic respiration and hence nutrient release occurs during this period. Mineralisation is retarded to late summer when high water temperatures prevail. This has important consequences, as the main nutrient release to the water column occurs when the pelagic system has moved back to its light-limited state when no further bloom events can be initiated. On the one hand, this reduces eutrophication-related problems; on the other hand it enables the development of rich benthic communities in the western part of the Belgian Part of the North Sea (BPNS).

These rich benthic communities do play an important role in the mineralisation processes as well. Our results clearly illustrate that bio-irrigation stimulates benthic respiration, nutrient release and denitrification (a key process counteracting eutrophication) while bioturbation activities withdraw organic matter from fast mineralisation through burial to deeper sediment layers. All of these processes are related to animal densities, and therefore a decrease in densities can possibly have implications for ecosystem functioning.

Macrofaunal ecosystem engineers did show temporal variations in their diet, depending on the timing relative to the phytoplankton bloom, and show assimilation of *Phaeocystis* derived material. In addition, our results show that both bioturbation and bio-irrigation were very important processes for the structure and dynamics of the lower benthic food web through the process of niche establishment.

Apart from being important for ecosystem functioning and the lower food web, we showed that ecosystem engineers are also of prime importance for the higher food web. Aggregations (i.e. reefs) of the bio-irrigating tubeworms *Lanice conchilega* create new habitats, thereby increasing macrofaunal diversity in general and providing food and shelter for juvenile flatfish species. However, physical disturbance (i.e. by beach trawling) of *Lanice* reefs results in decrease of the integrity of the reefs and may even lead to their collapse under high frequency physical disturbance. Research conducted along these lines resulted in for further policy-oriented research as the discussion of the classification of *Lanice conchilega* as a reef-building organism in a Habitat Directive context was ongoing during WestBanks.

Dispersal of juvenile fish was investigated by means of a combination of empirical and modeling studies. This combination is new for the area of the Southern Bight of the North Sea, and generates knowledge that contributes significantly to the understanding of connectivity on a North Sea scale. Models make it possible to take a dynamic approach and generate hypotheses on the short term, which can be validated by the field study. In addition, the field-based research allows for a multi-generational perspective (*versus* short time scale hypotheses from models).

The field based research suggested a limited dispersal of sole in the Southern Bight of the North Sea throughout its life time. However, this does not exclude the existence of links between spawning grounds. The modeling of larval sole dispersal over many years showed that some spawning grounds may be net exporters of larvae and some nursery grounds are net importers from spawning grounds further away.

The modeled variable exchange of larvae between nursery grounds (reflecting variation in dispersal, final larval abundance, larval origin and connectivity) is related to patterns and intensities of egg production, which is turn a yearly varying feature. The apparent lack of field results validating the modeling results can be caused by the ability of the markers to track dispersal and connectivity at a North Sea scale. Our results further suggest that more advanced markers, characterizing selective pressure, will be able to differentiate populations at a fine scale.

We showed that the Belgian sole nursery is one of the few areas in the North Sea where sole larvae are found during all years. Based on the modeled realized dispersal of sole larvae, this highlights the importance of the BPNS for the recruitment of sole. Hence, it is clear that deterioration of the habitats at the BPNS will have a negative influence on the sole populations on a North Sea scale.

Coupling the air-borne and pelagic ecosystem was achieved by investigating the feeding ecology of marine top predators (Sandwich and Common Tern) in an MPA context. Therefore, both the distribution of tern prey (i.e. pelagic fish) and foraging terns was investigated in a field study. We showed that the diet of breeding Common and Sandwich tern reflected the abundances of Clupeidae, Gobidae and Gadidae in the pelagic realm. Our results further indicate that the Wenduinebank should be recognized as an important area for seabirds. This sandbank holds high densities of prey fish during the breeding season and terns frequently used this area and its surroundings for foraging.

Since terns are highly specialized single-prey loaders feeding in the vicinity of their breeding colony in the upper water layers on a limited range of prey items, they serve as very good candidates as health indicators for the pelagic ecosystem. Within WestBanks, it was evaluated which tern-related parameter can be used for this purpose. The indicator must be relatively easy to measure and must reflect an explicit link between the pelagic ecosystem and the reproductive abilities of the terns in the breeding colonies. We found a significant correlative link between the proportion of clupeids in the faeces of adult Sandwich Tern and chick survival, while there was no relation between the adult diet and food presented to chicks. This suggests that a high availability of clupeids results in a good breeding success by directly influencing the parental condition or the composition of the breeding population (i.e. relatively higher number of "good breeders" in good clupeid years).

Further research showed that the composition of faecal samples of Sandwich Tern relates to the reproductive output of Common Terns. Investigating the parameters for reproductive success on a larger scale in the major breeding colonies of the Northwest European population of Common Tern, we showed that variation in reproductive output is largely determined by chick survival (and not by clutch size and hatching success). This suggests that chick survival can be used as a health indicator for the presence of food in the pelagic ecosystem, if non-intrinsic effects (i.e. adverse weather conditions, flooding events and excessive predation) are ruled out by monitoring research.

The WestBanks projects resulted in four finalized PhD's so far, one more PhD is in the writing phase. Now, 30 papers were published in the international peer reviewed literature and some more are under review or in preparation.

Apart from the scientific output, results obtained during WestBanks were used for policy advice in the framework of formal projects financed by Federal Public Service (FPS) Health, Food Chain Safety, and Environment - Belgian Marine Policy administration, or on an ad-hoc basis in Belgium and The Netherlands. In addition, the WestBanks projects resulted in the development of experimental and molecular techniques and modeling expertise that was not available in Belgian marine sciences as yet.

While some of the WestBanks results and expertise were of use in tackling direct policy related questions, not all of our results were translated into recommendations that can be used in an Ecosystem Approach to Management. Therefore, our recommendations and supporting results are summarised below:

(1) We recommend using important ecosystem engineers as conservation targets to come to a sustainable management of the North Sea.

- Coastal benthic ecosystems have an important buffer capacity against eutrophication processes.
- Eutrophication and physical disturbance by e.g. beam-trawl fisheries are interlinked through the biology and ecology of bottom dwelling organisms in general, and the presence of strong ecosystem engineers in particular.
- Ecosystem engineers have an important bottom up and top down effect on the marine ecosystem.
- Physical disturbance leading to decreasing densities of ecosystem engineers implies an important decline of the eutrophication-counteracting benthic processes in shallow coastal seas.

(2) We recommend the installation of sufficiently large protected areas to ensure the viability of sole populations.

- The Belgian Part of the North Sea is one of the few areas in the North Sea where sole larvae are found all years
- Sole populations are connected on evolutionary and life-cycle time scales

(3) We recommend the extension of the Bird Directive Area V3 for the protection of the breeding colonies of terns in Zeebrugge

- Zeebrugge holds one of the largest tern colonies of Europe
- Reproductive success depends on the presence of sufficient amounts of herring in the vicinity of the breeding colonies
- Areas including the Wenduinebank, the Scheur and the southern border of the Vlakte van de Raan are major foraging areas for terns due to the presence of a rich fish fauna and are not protected under the framework of Natura 2000.

KEYWORDS: benthic ecosystem functioning, ecosystem engineers, connectivity of fish populations, feeding ecology of terns

1. INTRODUCTION

It has been widely accepted that coastal seas are important ecosystems for humans, as they provide important goods (e.g. food, biomedical molecules and mineral resources) and services (e.g. climate regulation, storm protection and nutrient cycling) for society. Apart from these so-called production and regulation services, coastal systems provide opportunities for trade, recreation, tourism, research and education and have a considerable cultural, aesthetic and spiritual value (Lesly & McLeod 2007, Beaumont et al. 2007). However, the Millennium Ecosystem Assessment (MA 2005) clearly indicated that many ecosystem services provided by coastal and marine ecosystems are declining. Man-made direct (exploitation, pollution and habitat destruction) and indirect (climate change and related perturbations of ocean biogeochemistry) impacts caused measurable changes in marine biodiversity. In the coastal zone, these biodiversity losses impaired at least four critical ecosystem services: (1) fisheries; (2) provision of nursery habitats and (3) connectivity between habitats and (4) filtering and detoxification services (Worm et al. 2006). The negative impact on the latter service probably resulted in declining water quality increasing occurrences of harmful bloom and oxygen depletion (Dame et al. 2002).

The awareness that marine ecosystems need urgent protection was emerging at the UN Convention of Biological Diversity in 1992, where it was advocated that a system of Marine Protected Areas (MPAs) should be developed and effectively managed by 2010. At the European level, the EU Biological Diversity Plan (European Commission, 2006) stated that necessary conservation and management measures should be taken by 2012. The legal basis obliging the member states of the European Community to take protection measurements are the European Bird Directive (79/409/EEC) and the Habitat Directive (92/43/EEC), which will result in the designation of MPAs as part of the Natura 2000 network. The Bird Directive will result in the delineation of Special Protection Areas (SPAs), while Special Areas of Conservation will be implemented in response to the Habitat Directive.

While the designation of MPAs may lead to protective measures for limited areas, there is also a growing concern of the marine ecosystem in general. Objectives for a healthy ecosystem are formulated in the Water Framework Directive (WFD, 2006/60/EC) and the Marine Strategy Framework Directive (MSFD, 2008/56/EC). The WFD holds for lakes, rivers, transitional and coastal waters, while the MSFD is limited to marine waters. The ecological concept underlying both directives is relatively simple and consists of comparing the current state of an area with the expected state under minimal or sustainable human use, and in case of deterioration, intervening to bring it back to the desired good status (Van Hoey et al. 2010). The WFD aims at achieving Good Ecological Status (GES), which is evaluated by the integration of well-defined quality criteria per quality element. For biological quality of coastal sediments, the biological quality element consists of attributes of macrofaunal communities. The MSFD aims at achieving Good Environmental Status (GeNS) by 2020. GeNS take into account the structure, functioning and processes of the marine environment together with natural physiographic, geographic and climatic factors, as well as physical and chemical conditions including those resulting from human activities.

As such, the step from WFD to MSFD implies a better incorporation of an Ecosystem Approach to Management (EAM), as it requires a step forward from the structural community level to a functional ecosystem assessment (Van Hoey et al. 2010).

It is obvious that the designation and management of MPAs, and the implementation of EAM in the marine environment should be based on sound scientific knowledge. In the position paper on the EAM of the Marine Board of the European Science Foundation, Rice et al. (2010) clearly stated that productivity and the transfer and recycling of carbon and nutrients between the water column and the seabed is among the most pervasive processes acting on the diversity, structure and function of marine ecosystems and research on this topic is pivotal for the implementation of the EAM. On the other hand, knowledge on population genetics and demographic connectivity is urgently required to set up a successful network of MPAs (Palumbi 2003). Assessing the current status, and documenting the achievement of GEnS should be based on monitoring (Rice et al. 2010). The latest UN Convention on Biological Diversity (Nagoya, 2010) noted the slow progress in the establishment of MPAs (current 1%). and confirmed the need for protection of 10% of the ocean by 2012.

Therefore, research conducted within WestBank took a holistic view on the coastal marine ecosystem, by focusing on the interactions between the benthic, pelagic and airborne realm (Figure 1) at species and population level.

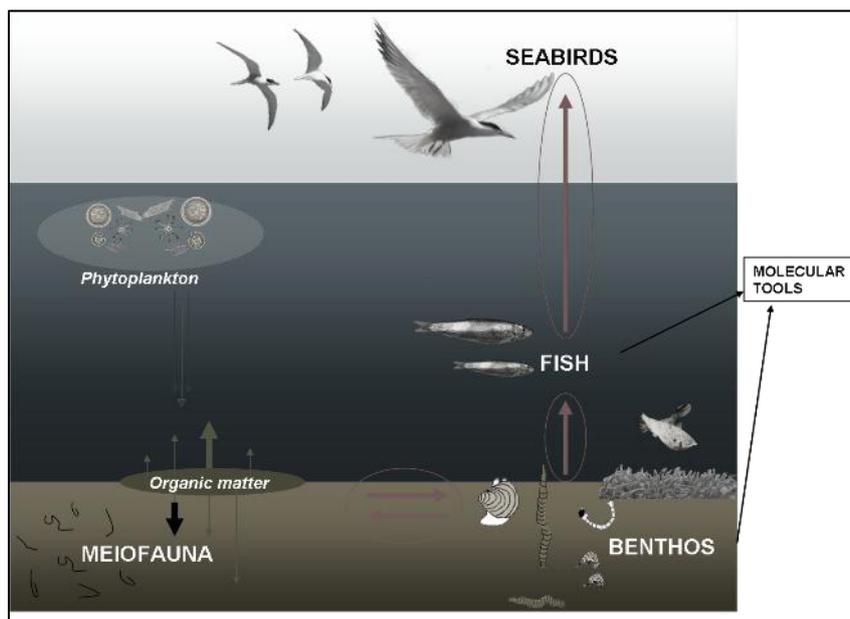


Figure 1. Research scheme of the WestBanks project

We wanted to obtain important knowledge on contemporary burning issues on the biodiversity-ecosystem functioning link, molecular and physical connectivity of fish populations, and developments of indicators for the health of the marine ecosystem by a combination of field observations, experiments and modeling efforts. This paves the road for elaborate, mechanistic models increasing the capacity for accurate predictions.

The **interaction between the water column and the sediment** was investigated by (1) studying the effect of the functional diversity of macrofaunal bio-engineers on the mineralisation of organic matter from the water column and the smaller components of the benthic food web (i.e. nematodes); (2) describing how pelagic primary production (including the harmful algae *Phaeocystis*) cascaded in animal biomass and (3) assessing the importance of reef-building polychaetes (*Lanice conchilega*) for the other macrofauna and fish and (4) evaluating the effects of man-made disturbance on ecosystem functioning and structure.

Connectivity between populations of flatfish was investigated to understand short- and long-term dispersal. It was done by combining original data from molecular approaches, otolith microchemical analyses and modeling. Otolith microchemistry reveals information about dispersal at the ecological time-scale (within the life cycle of an individual fish – ‘snapshot connectivity’) while molecular work is needed to provide information on connectivity at the evolutionary time scale (‘long-term connectivity’). Modeling the dispersal of sole larvae reveals the link between spawning locations and nursery grounds and provides information on the effect of external factors (temperature, hydrodynamics, food availability and predation) on this dispersal.

While the WFD resulted in the development of suitable biological indices to document the biological status of the seafloor (e.g. Grémare et al. 2009), this has not been realised for the pelagic environment so far. Within WestBanks, **health indicators** were developed to evaluate the functional link between the pelagic realm and top-predators by investigating the dietary preferences of key species and the ecology of forage fish in order to link changes in prey fish communities to fitness effects of top-predators.

By conducting the research as outlined above, the WestBanks objectives were set to tackle fundamental research questions in order to provide data, models and expertise that are of great value for a management level aiming at sustainable use of the Belgian Part of the North Sea.

2. METHODOLOGY AND RESULTS

2.1 Benthic-pelagic coupling: effects of macrofauna on benthic ecosystem functioning

As the benthic ecosystem is fuelled by sedimentation of pelagically produced organic matter, it is of high importance to understand fluxes across the sediment-water interface, and the fate of the organic matter in the benthic ecosystem. With WestBanks, these fluxes were quantified and the role of the macrofauna in structuring both processes and benthic communities was investigated (Task 1.1 and 1.2)

2.1.1 Material and Methods

The coupling between the benthic and pelagic compartments at station 115bis (51°09.10' N 02°37.10' E) in the Western Coastal Banks area was studied by analyzing a time series of benthic oxygen consumption measurements, and chlorophyll-a concentrations both in the water column and in the sediment.

The station was sampled on a monthly basis during one year. Sediment was collected with a 180 cm² Reineck box corer. Three subcores with a diameter of 36 mm were taken immediately after recovery of the samples, and sliced at 1 cm intervals for pigment analysis. 78.54 cm² subcores were taken for oxygen consumption measurements. Sediment slices were freeze-dried. After determination of the dry weight, acetone was added to extract the pigments and the fluid was filtered on a 0.2 µm nylon filter. Water samples were collected with a Niskin sampler on the CTD wire, approximately one meter above the bottom.

Phytopigment concentrations in the sediment and water column samples were determined using a Gilson high-performance liquid chromatography (HPLC) system, equipped with a Spherisorb C18 column, an Applied Biosystems 785A Programmable Variable Wavelength Detector, a Hewlett-Packard Diode Array Spectrophotometer and a Gilson 121 Fluorometer. HPLC solvents and gradients applied were slight modifications of the method of Jeffrey et al. (2003). Analysis of the chromatograms was performed with the UniPoint HPLC software package. Total sediment chlorophyll concentrations were determined by integrating the concentrations over the first ten centimeters. In case no values were available for some of the deeper layers, the lowest value encountered in that core was used instead.

Sediment community oxygen consumption (SCOC) measurements were performed in two 78.54 cm² cylindrical cores with a magnetic type of stirring in order to homogenize the water in the cores. The concentration of oxygen was monitored by means of an electrode which was subsequently calibrated in oxygen-saturated and oxygen-depleted water. Oxygen consumption rates were calculated as the slope of the regression of oxygen concentration versus time, and corrected for sediment surface area. For this regression, only the initial linear part of the time-series was used.

The assimilation of OM by macrobenthos was investigated by means of an experimental field monitoring from February to September 2008 at a sandy coastal station in front of Oostende (51°19.27'N, 2°52.09'E, 18 m depth, 9 km offshore).

The importance of benthic and pelagic food sources for macrobenthos was investigated by means of fatty acid (FA) biomarker analysis. We sampled the pelagic food sources by means of a Niskin bottle and filtered the water samples on pre-combusted GF/F-filters. The benthic food sources were sampled by means of 8 ml (4 cm depth) subsamples of a Reineck Box Corer. Macrobenthos was sampled using a Van Veen grab and brought back alive to the lab. Macrobenthic organisms were immediately dissected to remove the gut and its content. Remaining tissue was blended and this slurry was stored frozen until FA extraction. The FA from the polar and neutral lipid (PL and NL) fractions were extracted from the macrobenthic slurries, water and sediment using the modified Bligh and Dyer method (Boschker et al. 1999). The resulting FAMES (Fatty Acid Methyl Esters) were analyzed by means of a GC-c-IRMS at the NIOO-CEME using a small injection jet. **The extraction method for FA is new expertise for the Marine Biology section, gained from the collaboration with NIOO-CEME within the Westbanks consortium.**

In a next step, we investigated how macrofaunal functional diversity and densities influences (1) ecosystem functioning (i.e mineralisation) and (2) the structure (vertical distribution, density and diversity) and food web dynamics of the dominant members of the smaller benthic fauna: the nematodes.

The importance of different functional traits of macrofauna and corresponding densities for benthic processes of the Southern Bight of the North Sea was investigated by 2 laboratory experiments: before (winter, temperature = 10°C) and after (summer, temperature = 18°C) sedimentation of the spring phytoplankton bloom. Single species treatments of key species (*Abra alba*, *Lanice conchilega* and *Nephtys* sp.) with different functional traits were added to microcosms at 3 density levels (natural, lower, lowest) to account for possible density declines. Sediment–water exchanges of oxygen and nutrients, denitrification and bioturbation were measured and nitrification and total N mineralisation were modeled using a mass balance approach. More details about sampling are given in Braeckman et al. (2010). **These incubation experiments and modeling techniques are new expertise for UGent – MarBioI, gained from the collaboration with NIOO-CEME within the Westbanks consortium.**

In the next two series of experiments, the role of macrobenthic identity in nematode biodiversity, vertical distribution and food assimilation was assessed. To this aim, fine sandy sediment of coastal stations was collected by means of a Reineck Boxcorer. This sampling gear was chosen to maintain the original vertical distribution of nematodes. Macrofauna was removed from the different sediment sections and microcosmoi were reconstructed in their original vertical stratification. In the first experiment, the three macrofaunal key species (*A. alba*, *N. hombergii* and *L. conchilega*) were introduced to these microcosmoi in single species treatments according to their natural densities. We investigated how the biogeochemical environment typically created by the different macrobenthic species and the direct interactions (disturbance, competition and predation) would affect the vertical distribution of the nematodes.

In the second experiment, we tried to unravel the nematode dynamics after a simulated phytodetritus pulse under contrasting structuring factors. We repeated the previous set-up, but contrasted the macrobenthic effect of *A. alba* (bioturbator) and *L. conchilega* (bio-irrigator, both referred to as biological mixing) with a physical mixing effect. In addition, we added a labeled food source (^{13}C labeled non-axenic diatoms (*Skeletonema costatum*, a diatom naturally occurring during spring and autumn phytoplankton blooms (Rousseau et al. 2002)). The "physical mixing" treatment consisted of defaunated controls of which we thoroughly mixed the upper 2 cm of the sediment on a two-day basis, in order to simulate naturally occurring physical disturbance by wave action or storm events. Our treatments in this experiment consisted of: food addition to (1) *A. alba*, (2) *L. conchilega*, (3) physical disturbance and a (4) control. Two additional controls without food served respectively as a reconstruction control (5) (sliced before algae addition) and a food addition control (6). Oxygen penetration depth was measured at the end of the experiment (both experiments 1 and 2) and Sediment Community Oxygen Consumption (SCOC) was measured 3 days and 10 days after algae addition (experiment 2 only). After two weeks, the sediment from the microcosmoi was sliced in vertical sections and subsamples for grain size, pigments and nematode community analysis, stable isotopes of different compartments (sediment, nematodes, macrobenthos; only in experiment 2) were taken from homogenized sediment sections. Details on sampling and data analysis can be found in Braeckman et al. (in press). At the end of the experiment (i.e. after 14 d) on the role of macrofaunal identity in structuring nematode biodiversity and vertical distribution, the control treatment without macrobenthos was found to be detrimental to nematode density and diversity, which points to the importance of macrobenthic engineering to sustain the smaller components of the food web.

2.1.2 Results

Sedimentation and mineralisation of primary production

From January to mid-March, water temperatures were around 5°C. From April on, temperatures gradually increased until they reached 20°C from late July until late September. Between October and December, temperatures decreased again to 5°C (Fig. 2b).

Chlorophyll-a concentrations (Fig. 2a) in the water column varied between 2 and 45 mg m^{-3} . From mid-September through early February, concentrations remained fairly constant and below 6 mg m^{-3} . From late February on the chlorophyll-a concentration rose sharply, resulting in peak concentrations of 40 mg m^{-3} and above in late March and April. By mid-June, concentrations had dropped below 10 mg m^{-3} . In the sediment, depth-integrated chlorophyll-a concentrations ranged from 110 to 450 mg m^{-2} (Fig. 2c). Between early September and late February, the chlorophyll-a values stayed roughly between 100 and 200 mg m^{-2} . In March, the chlorophyll-a concentration rose to around 200 mg m^{-2} , and in May integrated concentrations of 450 mg m^{-2} were measured. Between late May and early September, the chlorophyll-a values gradually declined. Overall, the sediment chlorophyll-a concentration in the sediment lags behind the water column concentration by about one month. With temperatures peaking in late summer, there is a difference of about four months with the highest concentrations of phytopigments in the water column and sediment.

The sediment oxygen uptake rate ranged from 4 to 32 $\text{mmol m}^{-2} \text{d}^{-1}$ (Fig. 2d). The lowest values were measured from January to March, while peak values about one order of magnitude higher were observed in mid-June and mid-August.

As phytopigments are climaxing in spring in both the water column and the sediment, and highest temperatures are reached in late summer, benthic oxygen consumption peaked somewhere in between but generally showed a greater resemblance to temperature than to the phytopigment concentrations.

A simple box model was constructed describing the transfer of chlorophyll-a and bulk carbon to the sediment column and their subsequent remineralization. The model comprises five parameters: the net sinking velocity and the carbon-to-chlorophyll ratio of the water column organic matter, the degradation rates constants of chlorophyll-a and bulk carbon, and the Q_{10} temperature coefficient which is a measure for the sensitivity of the degradation rates to temperature. The model was subjected to sensitivity and identifiability analyses in order to identify a suitable selection of parameters to be estimated. Based on the results, all five parameters were retained.

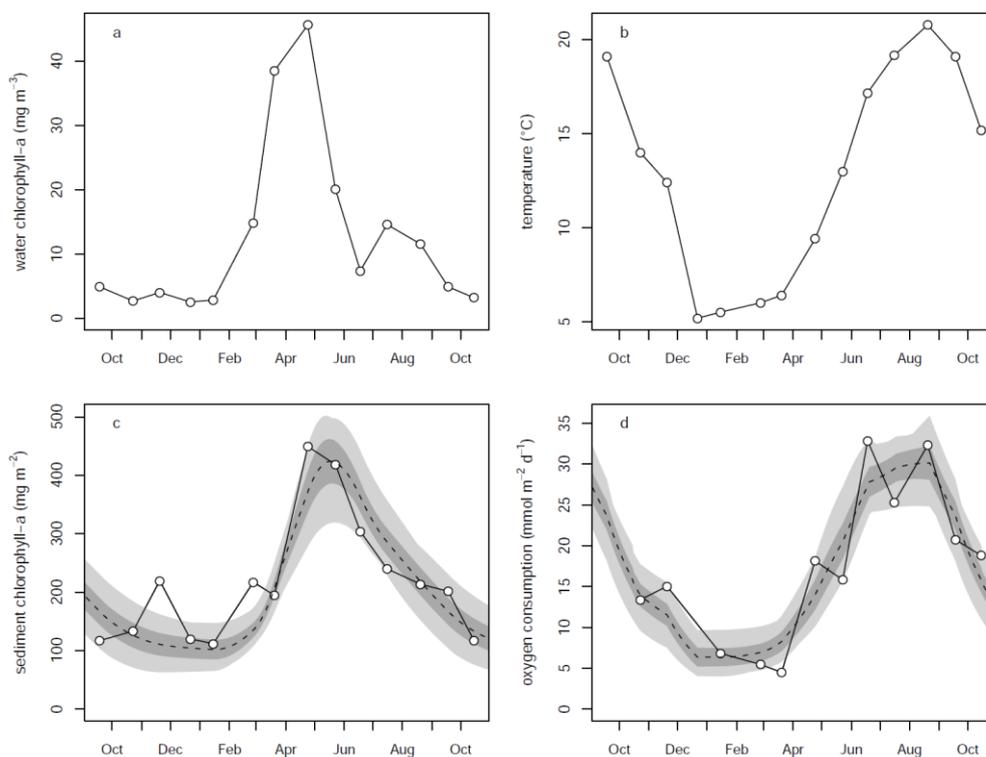


Figure 2: Measurements of water column chlorophyll-a (a), temperature (b), sediment chlorophyll-a (c) and benthic oxygen consumption (d). For (c) and (d) the global model sensitivity is given as well, with light gray indicating the range of model results and dark gray the standard deviation. The dashed line shows the median as well as the the best-fit model run, which cannot be distinguished visually.

After a first calibration which produced a set of optimal parameter values, a Markov Chain Monte Carlo (MCMC) was used to estimate probability distributions for each of the parameters (Fig. 3). The deposition velocity was constrained at $0.158 \pm 0.034 \text{ m d}^{-1}$ by the MCMC routine. This means that about 1% of all carbon in the water column is lost to the sediment every day.

Combining this with the obtained weight/weight carbon to chlorophyll-a ratio of 94.2 ± 21.9 , we can calculate a annual carbon deposition of $72.9 \pm 6.2 \text{ g m}^{-2} \text{ d}^{-1}$.

This figure is well constrained thanks to the collinearity between both parameters. Using the MIRO model and water column data, Lancelot et al. (2005) calculated a carbon export to the sediment of $51 \text{ gC m}^{-2} \text{ y}^{-1}$ or about one quarter of the annual net primary production ($213 \text{ gC m}^{-2} \text{ y}^{-1}$), which corresponds quite well to our estimate. Our estimate of the carbon to chlorophyll-a ratio is higher than the often assumed value of 50 for spring blooms, but measured ratios have been shown to vary widely and be quite high in *Phaeocystis* colonies.

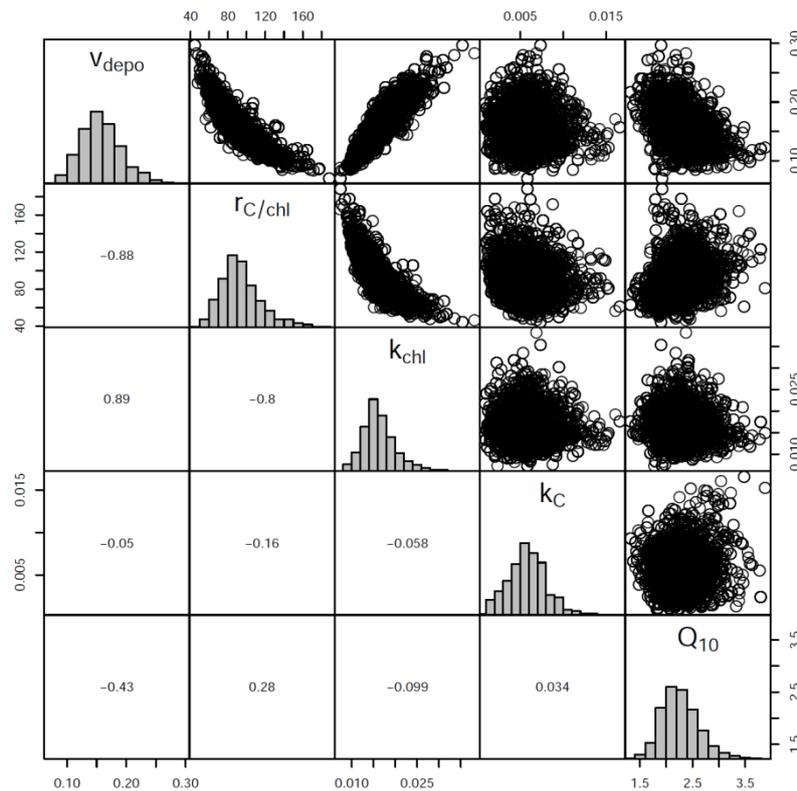


Figure 3: Results of the MCMC procedure. The top right panels show pair-wise plot of all accepted parameter sets. Probability distributions for each parameter are shown in the center panels, the bottom panels give the correlation for each parameter pair.

The mean chlorophyll degradation rate constant at 20°C of $0.0163 \pm 0.0038 \text{ d}^{-1}$ appears to be somewhat low when compared to literature. A value often used to derive particle reworking coefficients from chlorophyll-a sediment profiles is 0.03 d^{-1} (Josefson et al. 2002). Other studies (Boon and Duineveld 1998; Gerino et al. 1998; Green et al. 2002; Hagy et al. 2005) refer to the empirical relationship between temperature and the chlorophyll-a decay rate constant as determined by Sun et al. (1993). Based on this equation, the expected degradation rate constant is 0.022 d^{-1} at 5°C , 0.033 d^{-1} at 10°C and 0.068 d^{-1} at 20°C . However, it needs to be noted that this relationship was established using open oxic incubations with fresh diatom cells.

The MCMC procedure yielded a mean carbon degradation rate constant of $0.0058 \pm 0.0023 \text{ d}^{-1}$. This means that chlorophyll degradation is estimated to be roughly twice as fast as the overall carbon degradation.

TOC degradation rate constants have been studied using steady state (Boudreau 1998; Soetaert et al. 1998; Sauter et al. 2001) and dynamic (Soetaert et al. 1996; Herman et al. 2001) diagenetic modelling, and laboratory incubation experiments (Westrich and Berner 1984; Kristensen and Holmer 2001; Lehmann et al. 2002). The reported values span several orders of magnitude, which can be attributed to differences in source material, temperature, redox conditions, and modelling approach. The mean Q_{10} value resulting from our model is 2.27 ± 0.36 , which means that in our model the degradation rate constants of both chlorophyll-a and carbon in general are expected to double for a temperature increase of 10°C .

Our modelling results have confirmed the important role that temperature plays in the functioning of the benthic compartment in the Western Coastal Banks area. Organic matter degradation rates in the sediment will more than double for an increase in temperature of 10°C , which corresponds more or less to the water temperature difference between the peak of the spring bloom and late summer, when temperatures are at their highest. The resulting uncoupling between sedimentation and remineralisation has important consequences for the functioning of the pelagic compartment as well, as large quantities of nutrients will only be recycled after the system has moved back to its light-limited state. In fact, while two thirds of the sedimentation in our model takes place between the onset of the spring bloom in late February and its end in mid-June, only about one quarter of the annual benthic respiration, and therefore nutrient release, takes place during that same period. The prolonged presence of bloom material in the sediment column at station 115bis also enables a rich community and important biomass of meio- and macrofauna to develop between the onset of the spring bloom and late summer.

Assimilation of organic matter by macrobenthos

FA biomarkers in the suspended particulate matter mirrored phytoplankton dynamics in the water column, consisting of a small diatom dominance early spring, succeeded by a mass *Phaeocystis* peak followed by a mixed diatom-dinoflagellate bloom (Fig. 4). Deposition and subsequent bacterial degradation of the phytoplankton bloom were reflected in sediment PL FA biomarkers (Fig. 4).

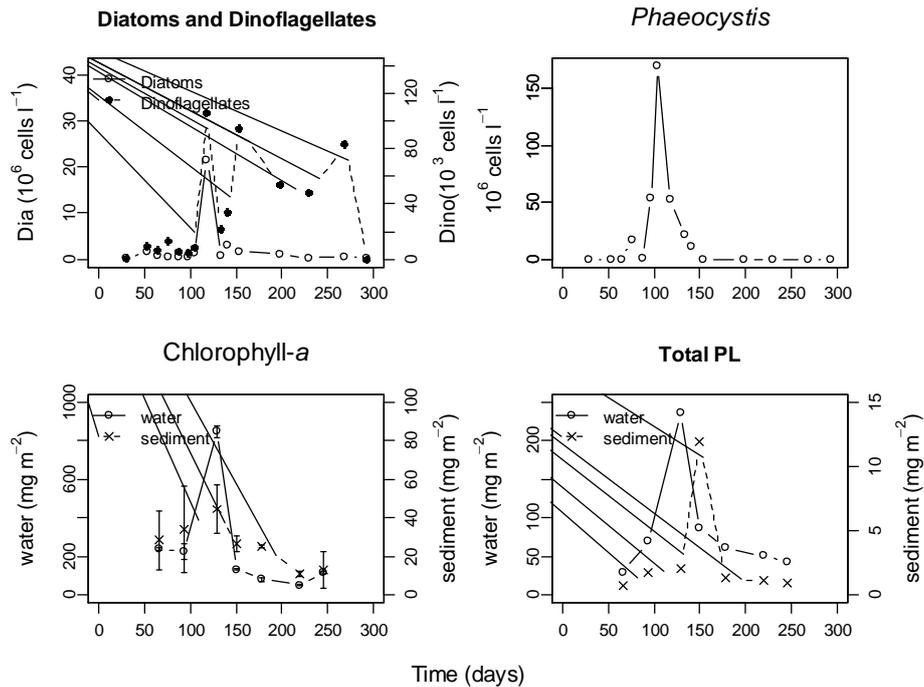


Figure 4: Microscopic counts of the major phytoplankton groups (upper panels) in the water column, average integrated average chlorophyll–a content of suspended matter \pm SE ($n = 3$) (18 m) and sediment \pm SD ($n = 2$) (4 cm) (3rd panel) and single values of Polar Lipids in suspended matter and sediment during the time course. Mind different scales on y-axes

Based on PL, the major planktonic groups within OM of water and sedimentary food sources can be distinguished (Sargent and Whittle 1981; Volkman et al. 1998; Dalsgaard et al. 2003).

The NL fraction of consumers is known to be a good reflection of their diet (Caramujo et al. 2008). The main distinction in FA biomarker concentration within macrobenthic tissue was observed at the species level (50% of variation), the diet of *L. conchilega* consisting of bacteria (18:1 ω 7c, i-17:0) and diatoms (16:1 ω 7c) and that of *N. hombergii* of diatoms (16:2 ω 4), and more dinoflagellates (22:6 ω 3, 18:5 ω 3(12-15)) and invertebrates (22:1 ω 11c) (Fig. 5). Temporal variation explained almost 20%: the two species retained more bacterial (10Me16:0) and *Phaeocystis* (18:1 ω 9c) markers before the bloom, while they accumulated more poly-unsaturated FA (20:5 ω 3) after the bloom

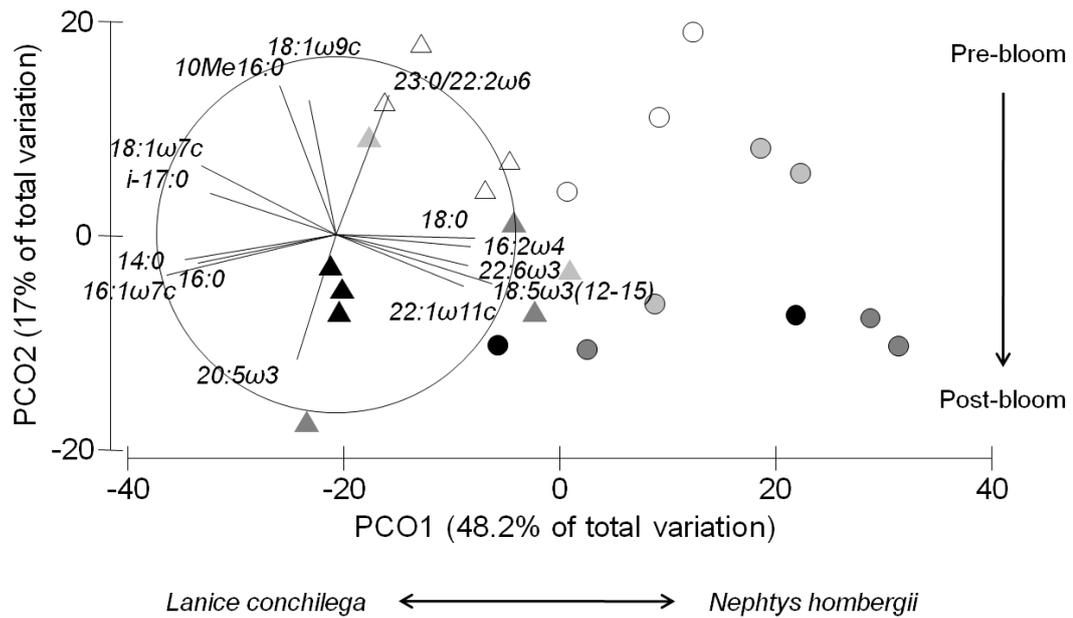


Figure 5: PCO analysis of relative abundance of Neutral Lipids in *Lanice conchilega* (Δ) and *Nephtys hombergii* (\circ) over the time course (April: \square – end of May: \blacksquare – end of the end of June: \blacktriangle – September: \blacksquare). Vectors represent specific FA biomarkers correlating > 70% with one of the first 2 PCO axes

Influence of macrobenthic functional identity and density on benthic ecosystem functioning

Our experiments revealed that summer mineralisation in the absence of fauna was 2 times higher than in winter. Fauna stimulated microbial respiration more in summer (up to 100% in *L. conchilega* treatments) than in winter (negligible fauna effect) (Fig. 6).

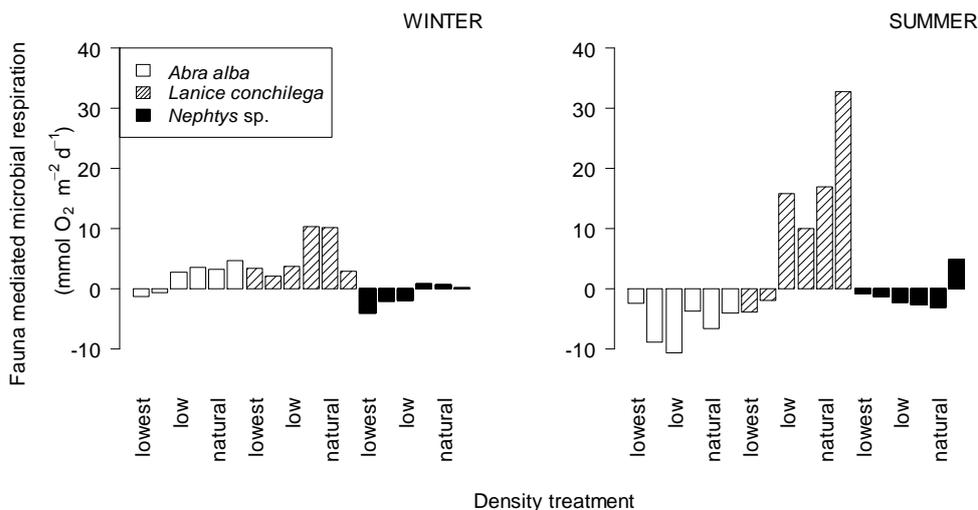


Figure 6: *Abra alba*, *Lanice conchilega* and *Nephtys* sp. Fauna mediated microbial respiration for winter (left); and summer (right) for increasing densities of all species in $\text{mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$. Values are calculated as measured sediment community oxygen consumption (SCOC) minus predicted SCOC

As chlorophyll a concentrations were similar in both seasons, the stronger fluxes in summer must be explained by a higher macrobenthic activity owing to the elevated temperature and better condition of the animals. Stimulation of mineralisation by the 3 species in the microcosms was different, as it was related to behavior. Owing to its irrigation activity, the tube dweller *L. conchilega* had more pronounced influences on benthic respiration, nutrient release and denitrification than did the biodiffusers, *A. alba* and *Nephtys* sp. *A. alba* appeared to be a more effective bioturbator than *Nephtys* sp (Fig. 7).

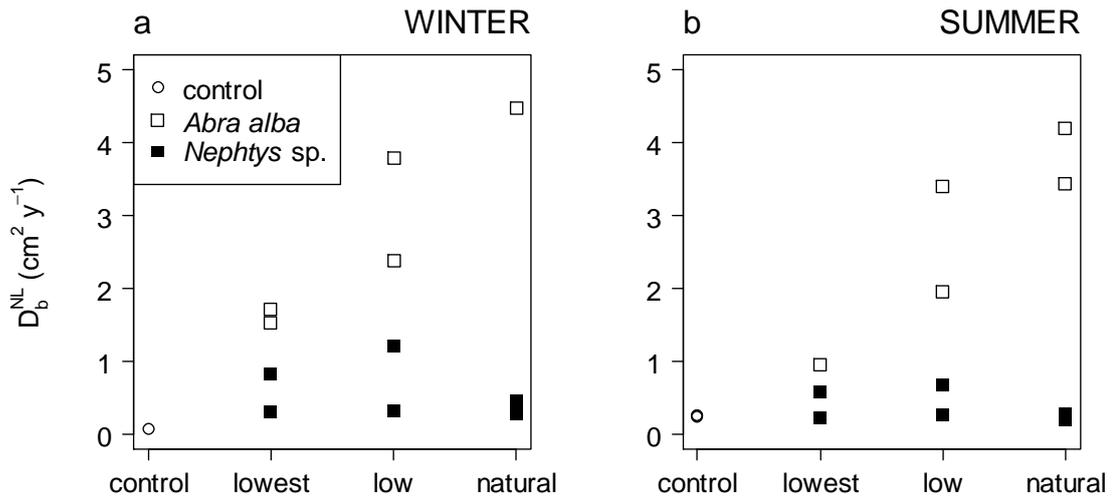


Figure 7: *Abra alba* and *Nephtys* sp. Bioturbation rate D_b^{NL} (as cm² of sediment reworked per year) per density level for each species for (a) winter and (b) summer

Processes such as benthic respiration, nutrient fluxes, denitrification and bioturbation seem to be related to animal densities and therefore decreases in densities can possibly have implications for ecosystem functioning.

At the end of the experiment (i.e. after 14 d) on the role of macrofaunal identity in structuring nematode biodiversity and vertical distribution, the control treatment without macrofauna was found to be detrimental to nematode density and diversity, which points to the importance of macrobenthic engineering to sustain the smaller components of the food web.

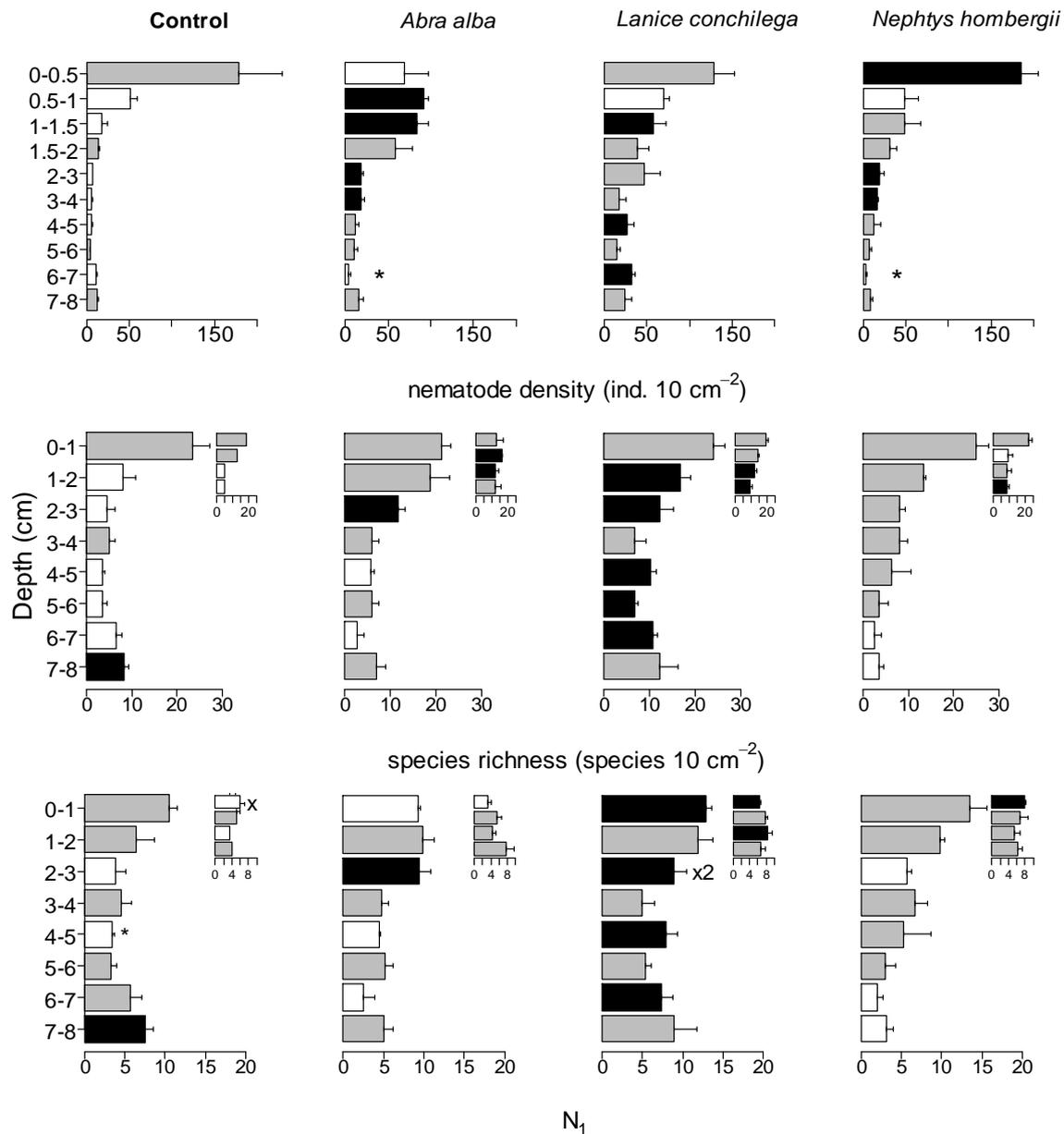


Figure 8. Nematode density (upper panel) and diversity (mid panel: species richness; lower panel: Hill's diversity index N_1) profiles in control, *Abra alba*, *Lanice conchilega* and *Nephtys hombergii* treatments (from left to right). Main graphs indicate analyses on whole core (cm scale); inset graphs show analyses on the upper 2 cm (0.5 cm scale). *Significantly lowest values. x: N_1 of the control 0–0.5 cm slice was only lower than the 0–0.5 cm slice of *N. hombergii*. x2: N_1 of the *L. conchilega* 2–3 cm layer was only higher than N_1 of the control 2–3 cm layer. The higher (black bar) and lower (white bar) nematode density of each pair according to pairwise tests and slices not significantly different from other slices (grey bar) are indicated. Error bars indicate SE.

Nematode densities were highest at the sediment surface in all treatments, but subsurface density peaks were observed in *A. alba* (to 3 cm depth) and *L. conchilega* (to 7 cm depth) microcosms (Fig. 8). In the *A. alba* treatment, the dominant non-selective deposit feeding and the epistrate feeding nematodes shifted downwards probably to avoid disturbance and exploitative competition by the bivalve siphons at the surface, while they might have benefited from the faecal pellets deposited in the subsurface

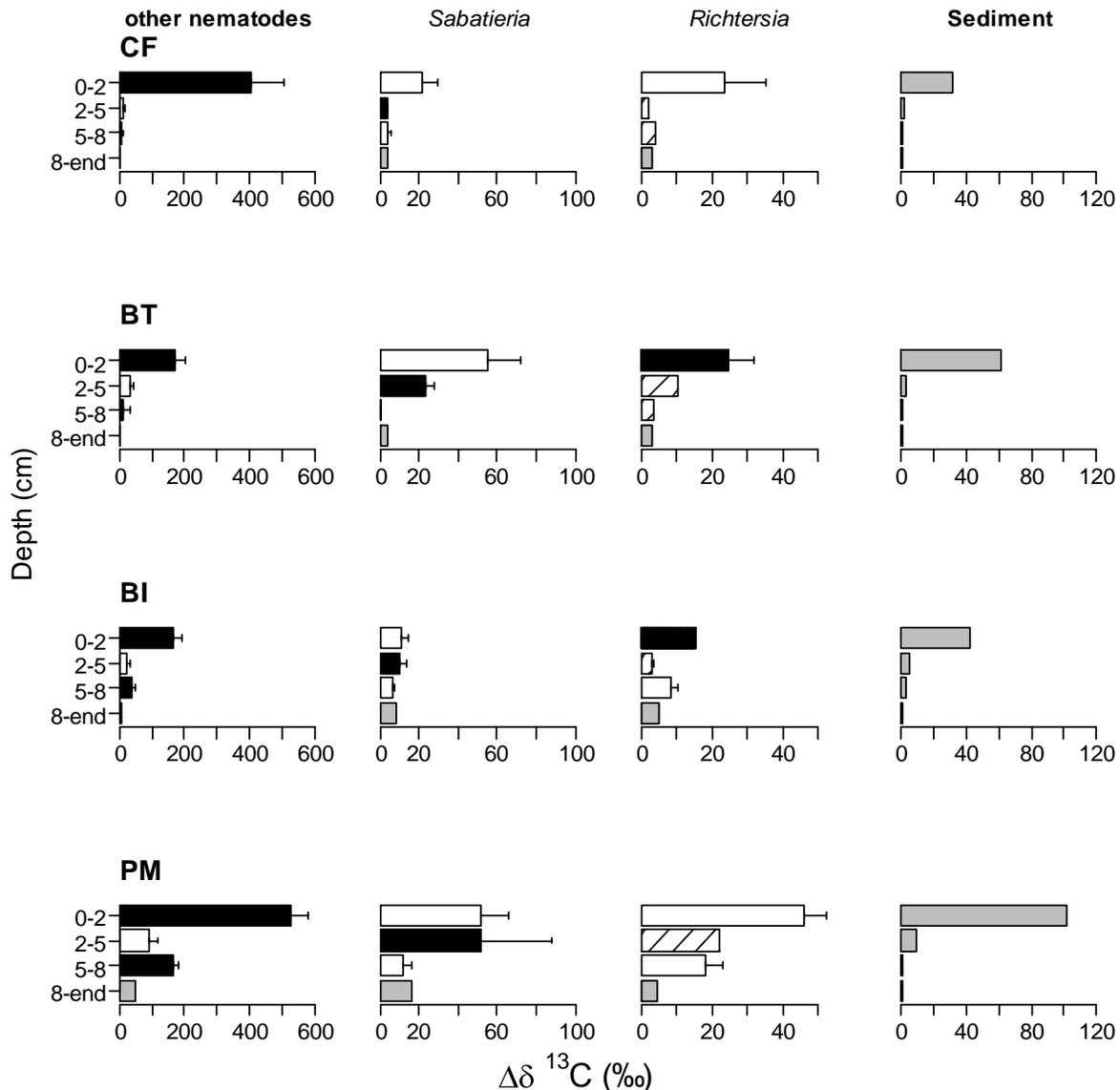


Figure 9: Specific uptake ($\Delta\delta^{13}\text{C}$) of labelled diatoms by 'other nematodes', *Sabatieria* and *Richtersia* and averaged TOC in the different depth layers in the control + food (CF), bioturbator (BT), bio-irrigator (BI) and physical mixing (PM) treatments (from left to right). Specific uptake differed among TR (PM > BI and BT) and among DxSp. Grey shades of nematode panels as in FIG 1. Coarse striped bars indicate < 3 replicates. Note different scaling of x-axes. Error bars indicate SE

In the *L. conchilega* treatment, the several dominant species were redistributed over depth layers, indicating polychaete-mediated habitat extension from surface into depth. Nematode communities seemed hardly affected by the presence of *N. hombergii*. These results reveal that functionally contrasting macrobenthic engineering effects shape nematode communities in different ways, which may maintain the role of nematodes in ecosystem functioning.

In the third experiment, nematode survival and subsurface peaks in nematode density profiles were most pronounced in the *Lanice conchilega* treatment. However, nematode specific ($\Delta\delta^{13}\text{C}$) uptake of the added diatoms was highest in the physical mixing treatment, in absence of competition by macrobenthos and where the diatom ^{13}C was homogenized (Fig. 9). Nematodes fed clearly on bulk sedimentary organic material rather than selecting the added diatoms.

The total C budget ($\mu\text{g C m}^{-2}$) encompassing TO^{13}C remaining in the sediment, respiration, nematode and macrobenthic uptake highlighted the limited assimilation by the latter and the major role of bacterial respiration (Fig. 10). Bioturbation and especially bio-irrigation facilitated the lower food web mainly on the long term (niche establishment). Since the freshly added diatoms represent only a limited food source for nematodes, the macrobenthic effect was more pronounced in facilitating the lower food web than the negative structuring effects such as competition.

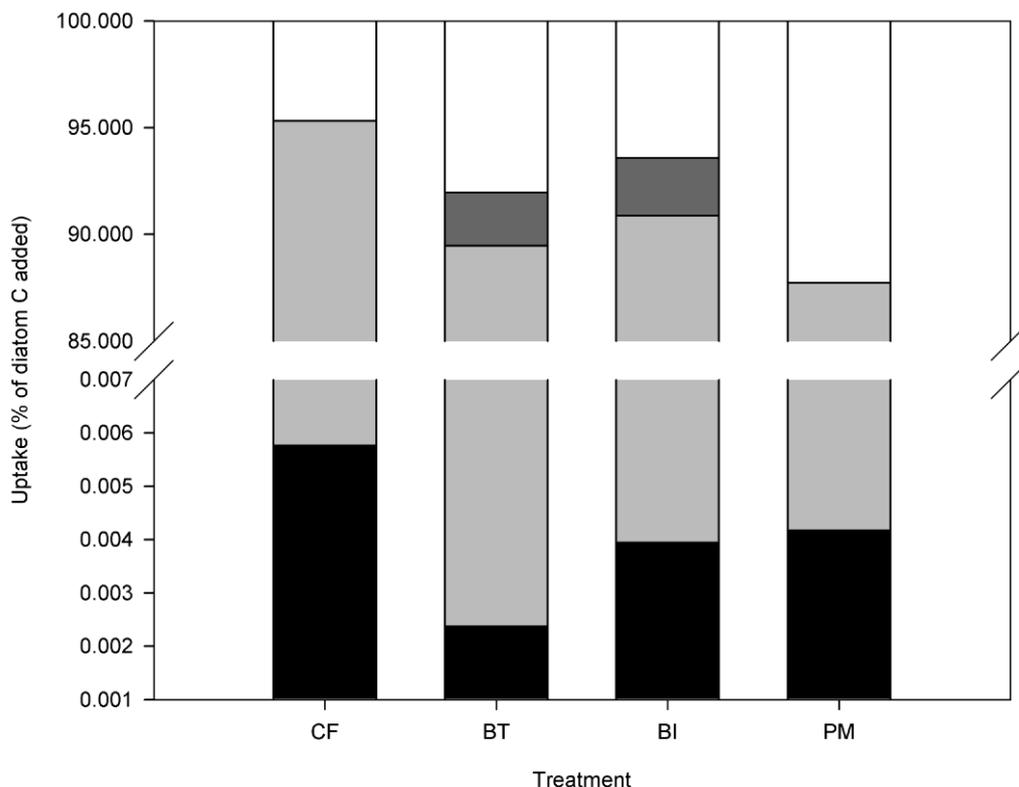


Figure 10: Mineralisation of the added diatom C in the control + food (CF), bioturbator (BT), bio-irrigator (BI) and physical mixing (PM) treatment (from left to right) by the nematode (■) and macrobenthic (■) compartments and due to respiration (■). Only "Remaining" algal C (□) differs significantly among treatments. Error bars not shown.

2.2 *Lanice conchilega*, fisheries and marine conservation

The trophic interactions at the sediment-water interface (Task 1.3) focused on the assessment of the importance of *Lanice conchilega* for the diversity of the macrofauna in general and for juvenile flatfish. Moreover, policy related research investigated whether *Lanice* aggregations can be classified as "reefs" according to the Habitat Directive, paving the road for true policy-related papers.

2.2.1. Material and Methods

The consequence of tube aggregation of *L. conchilega* for the ecosystem functioning in subtidal areas was investigated by means of data gathered over a period of 10 years (October 1994 – March 2005) on the BPNS. Data was selected on the basis of habitat classification taking into account sedimentological characteristics and bathymetrical information. A dataset of 657 macrobenthic samples was submitted to analysis. To test the impact of *L. conchilega* as bio-engineer, samples were selected based on specific median grain size values (125-250 μm). In order to study the possible change in benthic community composition due to the presence of *L. conchilega* tubes, samples were divided into 5 classes. We refer to Rabaut et al. (2007) for more details on the methodology.

After assessing the importance of *L. conchilega* aggregations for benthic diversity, it was investigated whether these aggregations can be considered to be "reefs" in the Habitat Directive context. Therefore, we quantified different characteristics of dense *L. conchilega*. Different methods were used to quantify the physical characteristics of intertidal aggregations: shear vane to measure shear stress, sederoplots to measure elevation, counting frames to estimate densities and artificial tube reefs to understand the temporal characteristics. This was combined with the existing knowledge on the biological characteristics. This 'reefiness' methodology was taken from Hendrick and Foster-Smith (2006). We refer to Rabaut et al. (2009b) for more details on the methodology.

In a next step, the vulnerability of *L. conchilega* to physical was investigated by means of laboratory experiment. The laboratory experiment served to assess the impact of sustained physical disturbance regimes at varying frequencies. Survival proportions were measured over time and tested with a generalized linear mixed model (GLMM). We refer to Rabaut (2009) for more details on the methodology.

As the *L. conchilega* aggregations harbour a rich associated community, it can be expected that physical disturbance (i.e. beam trawling) has an effect on this associated community as well. Survival proportions were measured over time and tested with a generalized linear mixed model (GLMM). We refer to Rabaut (2009) for more details on the methodology. Beam-trawl impact on the associated fauna of *L. conchilega* reefs has been studied in the field both in the intertidal and in the subtidal zone. At each location, a one-off beam trawl disturbance was performed followed by an intensive sampling of treatment and control areas. We refer to Rabaut et al. (2008) for more details on the methodology.

As the previous series of experiments and studies indeed indicated that the presence of *L. conchilega* increased benthic diversity (see below), the question rises if this increased diversity is of importance for juvenile flatfish. If this is indeed the case, the presence of *L. conchilega* aggregations could be taken into account in future modeling studies on sole connectivity, as pioneered in WestBanks and reported in Chapter 2.3. The relation between the ecological value of the observed increased benthic diversity and the abundance for flatfish has been tested in two different studies. A first study investigated the ecological interactions between the benthic habitat created by *L. conchilega* and postlarval *Pleuronectes platessa* (Plaice) in the intertidal zone (Bay of Heist). Samples were taken at each sampling event with the hyperbenthic sledge (mesh size 1 mm). For each sample, the sledge was towed by two spring tide events of March-April 2008. To test for the effect of the presence of *L. conchilega* on the densities of juvenile flatfish, a generalized linear model was used. We refer to Rabaut et al. (2010) for more details on the methodology. A second investigation aimed at evaluating whether juvenile flatfish species (such as Plaice and Dab) select for small scale engineered habitats built up by the tube dwelling polychaetes *L. conchilega* or *Owenia fusiformis*. The two benthic tube worm engineered habitats are investigated in two different geographical areas. Flatfish were collected with a beam trawl. Within each particular geographical area, the two habitats were sampled. A minimum of ten individuals per area (and in each habitat) of Plaice and Dab were selected for further stomach analyses. The biomass (mg AFDW) of each prey item present in the stomach as well as the flatfish biomass was measured. The relative importance of prey in the diet was expressed as percent of numerical abundance (N%), weight (G%) and fullness (FI%). Data was analyzed using generalized linear models. We refer to Rabaut (2009) for more details on the methodology.

Based on these results, and taking into account the literature on various aspects of MPAs, allowed the construction of a theoretical or 'systems approach' that is applicable to temperate soft-bottom marine areas. This analytical systems approach led to the identification of three chronological blocks: policy objectives, decision making and impacts. This systems approach was visualized in a flow chart, which made the general approach to MPAs easier to apply within a broader marine management framework.

Some aspects of this topic have been covered before, but this study seeks to integrate research (with emphasis on ecosystem engineers) and theory about the 'MPA-process' to build a systems approach which simplifies the complexity of many real-world scenarios. Within WestBanks, this concept has been tested with the Belgian case study (BPNS) of how MPAs are established, managed and have impacts. We refer to Rabaut et al. (2009a) for more details on the methodology.

2.2.2. Results

***Lanice conchilega* aggregation: importance, vulnerability, and resilience**

We showed that that the species community around *L. conchilega* tubes could be distinguished from the species community in tube-free sediments (One-way ANOSIM, $R = 0.237$, $p = 0.001$).

A dissimilarity-value of 78.9 was found between samples with and without *L. conchilega* tubes. A global test based on *L. conchilega* classes showed significant ($p = 0.045$) but only slightly distinguishable species communities ($R = 0.028$) coinciding with decreasing *L. conchilega* abundance (Fig. 11). The most pronounced community differences were found between samples with >1500 *L. conchilega* ind.m⁻² and samples without *L. conchilega* individuals ($R = 0.207$, $p = 0.001$), with a dissimilarity value of 83.6.

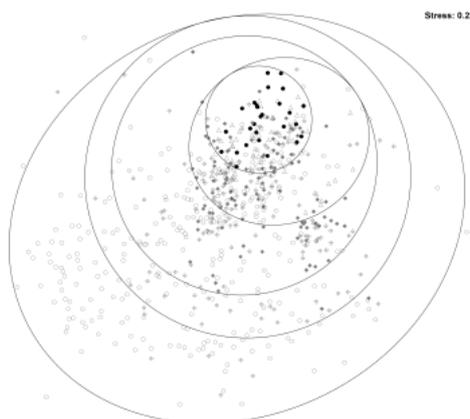


Figure 11. Two-dimensional MDS ordination plot of similarities between species assemblages of different density classes of *L. conchilega* aggregations (classes 1-4, respectively, crossed squares, filled grey squares, open triangles and black filled dots) and *L. conchilega*-free samples (open dots) (using Bray Curtis similarity measure of square root transformed data).

This "Babushka" type of community structure was further investigated using the MVDISP algorithm. The highest variability was found in the samples without *L. conchilega* (Dispersion Factor Value 1.135), while lowest variability occurred in the samples with highest *L. conchilega* densities (Dispersion Factor Value 0.242). The Indices of Multivariate Dispersion (IMD) have negative values, implying that all similarities among samples of concerned *L. conchilega* density class are higher than any similarities among samples of other density class. The further the density classes are separated, the closer the IMD is to -1. We refer to Rabaut et al. (2007) for more details on the results and an elaborated discussion on these.

Our investigation of the physical aspects of *L. conchilega* aggregations revealed that both elevation ($p < 0.001$) and shear strength ($p < 0.001$) were higher in *L. conchilega* patches than outside the patches. In addition, shear strength was positively correlated with *Lanice* densities, pointing to the importance of high densities for local sediment consolidation.

The artificial reef experiment in the intertidal zone of the Bay of Heist confirmed that changing hydrodynamic patterns on a very local scale, as a result of the presence of adult *L. conchilega*, leads to a settling advantage for juvenile *L. conchilega*. Comparison between areas with and without sedimentation within each artificial plot shows a significantly higher settling in the areas where sedimentation occurs. However, next spring tide, densities no longer show differences between the two areas and other mechanisms take over (Callaway, 2003).

This was combined with side scan sonar images of other research (Degraer et al. 2008), measurements on spatial extent and current biological knowledge (Zühlke (2001), Van Hoey (2006), Rabaut et al. (2007)). These results are summarized in a 'reefiness scoring table' (Rabaut et al. 2009b).

It is however still 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. Finally, reefs should be stable enough to persist for several years (temporal reef-characteristics). For the latter, it is known that aggregations can sometimes persist longer but that they are generally ephemeral in intertidal areas (Callaway et al. 2010). However, subtidal systems are expected to be more stable and some mechanisms exist for the aggregations to be replenished by juveniles. Again, only long-term monitoring with advanced remote sensing techniques will provide insights in the longevity of individual aggregations

When exposed to physical disturbance, survival of *L. conchilega* individuals dropped significantly after 10 and 18 days (with a disturbance frequency of every 12 and 24 h, respectively) (Fig. 12). The results indicate that *L. conchilega* is relatively resistant to physical disturbance but that reefs can potentially collapse under continuous high frequency disturbance. The results of this experiment are discussed in the light of beam trawl fisheries, a common physical disturbance in areas where *L. conchilega* reefs occur. **This experimental approach resulted in a quantification of the physical disturbance level a system can handle.** We refer to Rabaut (2009) for more details on the results and an elaborated discussion on these.

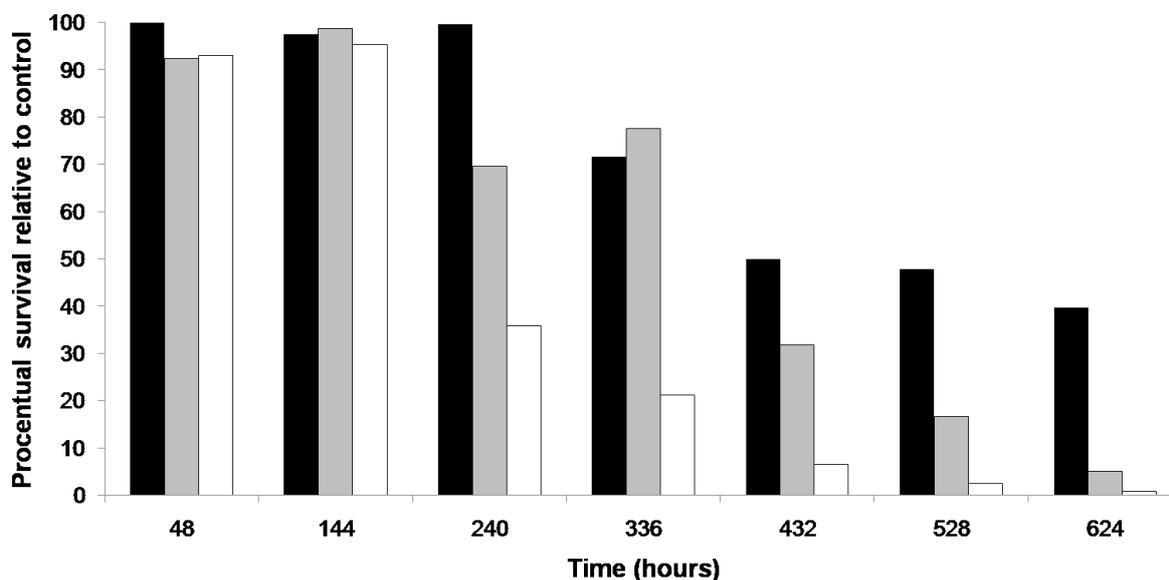


Figure 12. Survival proportions over time for the disturbed sectors (white: Tr1; grey: Tr2; black: Tr3). Proportions are visualized as a percentage of the control proportions for each time (i.e. survival proportions in control are set to 100%).

The beam-trawl experiment in the intertidal area showed an impact at the community level (Fig. 13). SIMPER analyses showed that 90 % of the communities in both treatment and control plots were characterized by a small number of species (*E. sanguinea*, *Capitalla capitata*, *U. poseidones*, *Nephtys cirrosa* and *S. filicornis*). The most pronounced impact was on *E. sanguinea* which was significantly impacted during the entire period of the experiment.

The same result appeared for the total macrofauna density. However, an overall quick recovery from disturbance was observed. We refer to Rabaut et al. (2008) for more details on the results and an elaborated discussion on these.

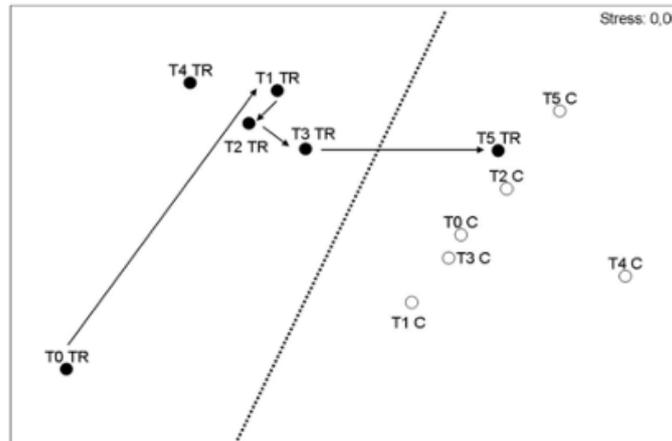


Figure 13. Two-dimensional MDS ordination (stress = 0.06) of community data for each treatment and sampling occasion (means of replicates). Treatment (●) community composition evolves over time to the community composition of the control (○) samples (with the exception of T4: stormy weather). The recovery trajectory plotted here has an IMS value of 0.61 ($p < 0.01$).

In the subtidal experiment with a similar set up, closely associated species (e.g. *Eumida sanguinea*, *Phyllodoce (Anaitides) mucosa*, *Eteone longa*) as well as some other co-occurring species (e.g. *Abra alba* and *Kurtiella bidentata*) were shown to be significantly impacted by the trawling disturbance. Opportunistic species as *Capitella* sp., *Heteromastus* sp. and *Notomastus* sp. were considered as negatively associated to *L. conchilega* and their density increased significantly shortly after beam trawl passage. We refer to Gamarra (2008) and Rabaut et al. (in prep.-b) for more details on the results and an elaborated discussion on these.

Generalizing, the effect of beam trawling on the associated fauna follows two main lines: we discerned on the one hand vulnerable species that are negatively affected and of which the recovery can either be fast or slow. On the other hand there is a group of negatively associated (opportunistic) species which increase in densities shortly after a beam trawl disturbance. This indicates that the reef structure itself can persist under intermediate beam trawl pressure but the integrity of the reef is hurt as the system as a whole degrades shortly after disturbance. **This indicates that the richest soft-bottom habitat of the BPNS is potentially under threat, but it also indicates that the physical structure of the reef can withstand current beam trawl regime.**

During the field sampling, conducted to investigate the effect of *Lanice* aggregations on juvenile flatfish, 269 *P. platessa*, ranging from 0.6 – 4.0 cm (average length 1.477, SD = 0.272) and 8 *S. solea* ranging from 0.9 – 1.4 cm (average length 1.250, SD = 0.151) were caught. Only for *P. platessa*, a representative amount of specimens was available to perform further analyses.

Overall, there were no differences in *P. platessa* densities over time within the control zone, nor within the treatment zone ($p > 0.7$) (Figure 14). Comparison between control and treatment show significant differences in *P. platessa* densities ($p < 0.0001$) (Figure 14, inset). The mean abundance of *P. platessa* in *L. conchilega* free zones (control) was 4.70 (± 0.66 SE) individuals per sample, while the abundance in the *L. conchilega* zones (treatment) was 15.50 (± 3.63 SE) individuals per sample. We refer to Rabaut et al. (2010) for more details on the results and an elaborated discussion on these.

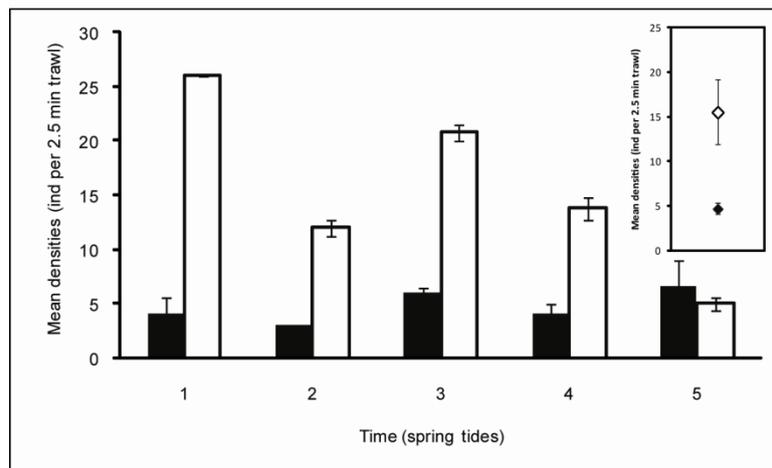


Figure 14. Density distribution of *Pleuronectes platessa* (0-group); densities outside *Lanice conchilega* reefs (black) compared with densities inside *L. conchilega* reefs (white). Inset: Overall flatfish density differences between control zones without *L. conchilega* (black) and treatment zones with *L. conchilega* (white). These differences are significant ($p < 0.01$).

For the second flatfish study within WestBanks, results show that the two flatfish species occur in significant higher densities in the ecosystem engineered subzones (Figure 15). Analyzing per age class reveals that for *L. limanda* only age class 0 occurs in significantly higher densities in the *O. fusiformis* area, while for *P. platessa* each age class occurs in higher densities in the *L. conchilega* areas, but no difference was found for age class 1 in the *O. fusiformis* areas (Area 1). No age effects or interaction effects were found.

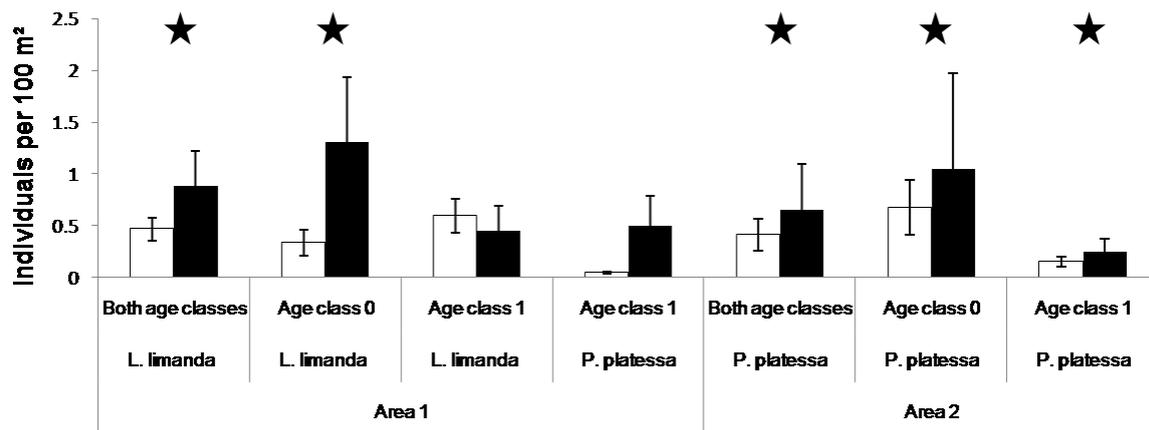


Figure 15. Flatfish densities. Both flatfish species are represented per geographical area and per age class. White bars represent flatfish densities in subzones without the ecosystem engineer; black bars represent flatfish densities in ecosystem engineered subzones. Significant differences between habitats are indicated with a star.

In the overall analyses per flatfish species (*i.e.* both study areas together), the fullness index (FI%) is significantly higher within ecosystem engineered areas for *P. platessa* of age class 0. For *L. limanda*, significantly lower FI% was found for age class 0 individuals caught within the ecosystem engineered subzone (Fig. 16).

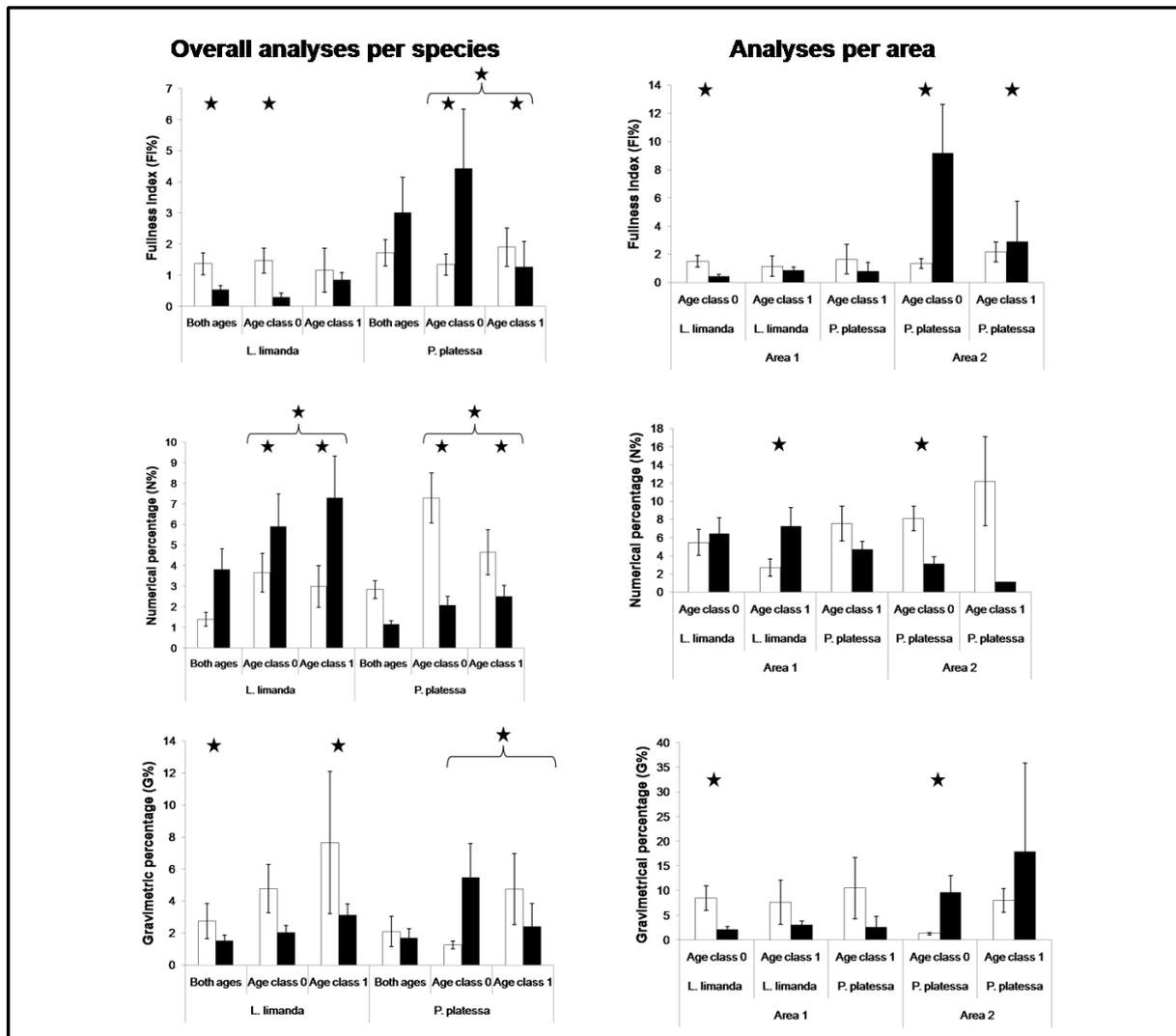


Figure 16. Overall stomach analysis per species (left) and per geographical area and species (right) of the fullness index (FI%), proportional numerical differences (N%) and proportional gravimetric differences (G%). Non-ecosystem engineered subzones are represented with white bars; ecosystem engineered subzones are visualized as black bars. Significant differences between subzones are indicated with a star. Interaction effects (habitat x age) are indicated with a brace.

Numerically, all responses turn out to be significant, with relatively more prey in the stomachs of *L. limanda* caught in the ecosystem engineered subzone and the opposite for *P. platessa*. Gravimetrically, the response is different with significantly more prey biomass in flatfish caught in the non-ecosystem engineered subzone (*L. limanda* age class one and *P. platessa*) (Fig. 16). Analyzing the same parameters per area, in Area 1, *L. limanda* age class 0 has a significantly higher fullness index and a gravimetrically higher stomach content outside the ecosystem engineered subzone as well, while the age 1 group caught within the ecosystem engineered subzone has numerically a higher stomach content (Fig. 16). In Area 2, both age classes of *P. platessa* have a higher fullness index and age class 0 has a gravimetrically higher stomach content within the ecosystem engineered subzone. Numerically, age class 0 of this flatfish species has a higher stomach content in the non-ecosystem engineered area. We refer to Rabaut (2009) for more details on the results (e.g. all significance levels) and an elaborated discussion on these.

Ecosystem engineers and MPA research

Integrative management is important within the MPA-process as is visualized in a simplified flow chart in Figure 17.

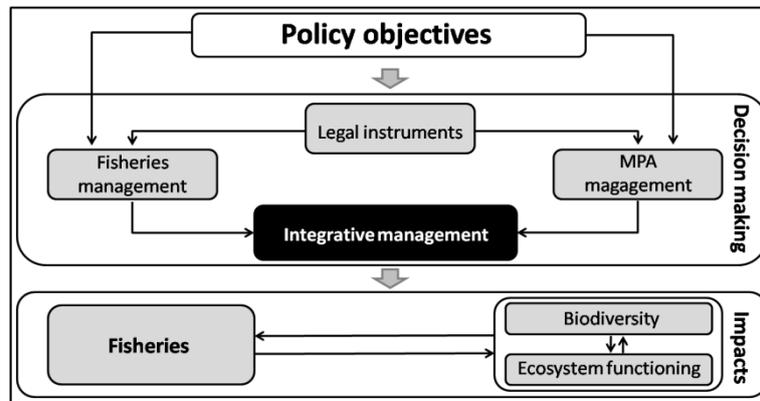


Figure 17. Simplified flow chart of the 'MPA-process'. The basic aim of the protected area must be clear from the beginning, as objectives for nature conservation may be well different from fisheries management objectives. To come to an ecosystem approach to marine management, no sectorial strategies should be applied but management measures from different sectors should be tuned in an integrative management.

The flow chart that was designed as a mental mapping exercise resulting from a literature review, illustrates (1) why MPAs originate, (2) how they are designated and (3) how they have various impacts in a temperate soft-bottom area. The relation between fisheries and MPA-management appears to be most challenging in soft-bottom temperate marine areas because of conflicting interests and institutional differences. Activities limited in space and not relying directly on ecosystem functions (e.g. offshore energy production and aggregate extraction) are generally easier to manage than fisheries. By far the commonest fishing technique in Belgium is beam trawl fisheries, mainly small beam trawlers for *Solea solea* (common sole) and *Pleuronectes platessa* (plaice) (45 thousand fishing hours per year) and shrimp fisheries for *Crangon crangon* (brown shrimp) (23 to 35 thousand fishing hours per year) in the coastal areas. The most valuable areas for macrobenthos in the BPNS coincide with places where the *Abra alba* community is found. This community hosts various bio-engineering species that form biogenic structures (e.g. *Lanice conchilega* (Callaway 2006, Van Hoey 2006, Rabaut et al. 2007) and *Owenia fusiformis* (Somaschini 1993, Rabaut 2009, Rabaut et al. in prep.-a) which are often referred to as hotspots of biodiversity. These ecologically valuable areas are often vulnerable to beam trawl disturbance as was proved in the case of *L. conchilega* in an experimental trawling study (Rabaut et al. 2008). We refer to Rabaut et al. (2009a) for more details on these results. Further discussion can further be found in Rabaut (2009).

We conclude that ecosystem engineers such as *L. conchilega* are model organisms for studying the sediment-animal-interactions, quantifying the strength of a benthic engineer in modifying its habitat and thereby affecting other species. Moreover, this study shows that ecosystem engineers are important within a conservation context.

As such, the ecological knowledge built up within the WestBanks project has the potential to contribute to the transition to more-resilient relationships between society and ecosystems. See Rabaut (2009). for elaborate discussion.

2.3 The role of dispersal for benthic organisms and demersal fish

Dispersal was investigated by means of (1) an empirical study on the dispersal of the economical fish sole *Solea solea* and the trash fish sand goby *Pomatoschistus minutes* (Task 2.1) and (2) a modeling study (Task 2.2) on the dispersal of sole larvae. The combination of both approaches is essential for understanding connectivity. Models make it possible to take a dynamic approach and generate hypotheses on the short term, while the field based research provides the necessary validation on a short term and allows for a multi-generational perspective. Such **approach is novel for the Southern Bight** of the North Sea and provides much needed answers for the organisation of Marine Protected Areas.

2.3.1 Material and Methods

In order to investigate the dispersal dynamics of **sole** (*Solea solea*), samples were collected by beam trawl along the Belgian Coast in May/June 2007 (BELs07), May 2008 (BELs08), August 2007 (BELf07) and August 2008 (BELf08). Fish caught in spring were in spawning condition, while the fish from August were spent. The total length of all fish was measured, a fin sample was taken and preserved in ethanol, and otoliths were collected. In the laboratory, DNA was purified with a commercial kit (Nucleospin Tissue extraction Kit) according to the manufacturer's conditions (Macherey-Nagel GmbH, Düren, Germany).

Samples were initially genotyped at 15 microsatellite loci (F8-ICA9, F8-ITG11, F13-II8/4/7, F8-IIGT15, F14-IIGT16 (Iyengar et al. 2000); (Sos(AC)6, Sos(AC)20, Sos(AC)40, Sos(AC)30, Sos(AC)45, (Garóia et al. 2006); SolCA13, SolGA12, Sol19A (Porta & Alvarez 2004); SseGATA26, SseCA28 (Funes et al. 2004)) on an automated capillary sequencer ABI 3130 AVANT (Applied Biosystems).

For some samples, mitochondrial DNA data have been generated; a total of 110 individuals from the Belgian Coast were sequenced at a 590 bp fragment of the mitochondrial cytochrome *b* (cyt *b*) locus (Table I). The cyt *b* gene was amplified by PCR using the primers CB1bis-F (5'-TACGTCCTCCCCTGAGGACAGATATC-3') and SolCytb1-R (5'-GGCGCTCTAACACTGAGCTAC-3'). Products were sequenced with the Forward primer only because of the unambiguous sequence results. Sequences of 590 bp were checked with SeqScape v. 2.1 (Applied Biosystems) and aligned with BIOEdit v.7.0.5 (Hall 1999). Results were compared with a larger dataset containing sole from a larger geographical range in the Northeast Atlantic.

Table I Sample code, sampling date, position, number of samples taken (N), number genotyped (G), number sequenced (S)

Sample Code	Date	Latitude	Longitude	N	G	S
BEL07S	May/2007	51°23'22"N	3°10'01"E	96	96	10
BEL07F	Aug/2007	51°21'14"N	2°55'45"E	80	75	3
BEL08S	May/2008	51°23'22"N	3°10'01"E	96	71	45
BEL08F	Aug/2008	51°21'14"N	2°55'45"E	60	58	52

To identify potential genotyping errors in the microsatellite data (i.e. stuttering, large allele dropout or null alleles), the software MICROCHECKER v.2.2.3 (van Oosterhout et al. 2006) was used. Null allele frequencies were also estimated for each locus and population using the Expectation Maximization algorithm of Dempster et al. (1977) carried out by the software FREENA (Chapuis & Estoup 2007).

For the microsatellite data, genetic diversity was estimated as the observed and unbiased expected heterozygosity with GENETIX v. 4.05 (Belkhir et al. 2004). Mean allelic richness (AR) over all loci (El Mousadik & Petit 1996) was calculated with FSTAT v.2.9.3 (Goudet 1995). Genetic differentiation was quantified with global and pairwise FST (Weir & Cockerham 1984) using GENETIX v. 4.05 (Belkhir et al. 2004) for the microsatellite data. Significance was tested using 1000 permutations.

Haplotype diversity (h), nucleotide diversity (π) and their standard deviation, and the number of polymorphic sites were calculated for the mitochondrial DNA sequences using DNAsp v.5 (Librado & Rozas 2009).

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 give new opportunities for current research in *Pomatoschistus* species (Larmuseau et al. 2008).

Next, an up-to-date phylogeographic analysis of *P. minutus* was realized by sequencing the mtDNA cytochrome *b* (Cyt *b*) gene and by genotyping eight microsatellite markers on sand gobies from 12 and eight locations respectively. Several phylogenetic and population genetic methods were used to explore the phylogeographic pattern of the sand goby. The historical demography of *P. minutus* was studied through a mismatch analysis and a Bayesian Skyline Plot (Larmuseau et al. 2009b; Larmuseau et al. 2010b).

Finally, a genetic analysis based on the SNP variation on the rhodopsin (*RH1*) gene was realized for *P. minutus*. First, we used a phylogenetic approach to determine the molecular evolution on the rhodopsin *RH1* gene among closely related 'sand goby' species (Teleostei, Gobiidae). Fragments of the *RH1* gene (868 bp) were sequenced and analyzed for nine 'sand goby' species that inhabit different photic environments (Larmuseau et al. 2010a). Next, the same fragment of the *RH1* gene was analyzed in 165 *Pomatoschistus minutus* individuals from seven populations across its whole distribution range (Larmuseau et al. 2009b). Finally, *RH1* sequences of 491 extra sand goby individuals from 15 locations in the Baltic Sea and the southern North Sea (including the Westbanks) were analysed to understand the possibility for local adaptation and the dispersal dynamics between and within both marine regions (Larmuseau et al. 2010c).

The **modeling** approach was tackled by coupling a module of a Lagrangian particle-tracking model to the NOS 3D hydrodynamical model of the Southern North Sea (Luyten et al., 1999) (Fig. 18) in order to track each particle individually.

This technique allows easy integration of biological properties dependent of larval history.

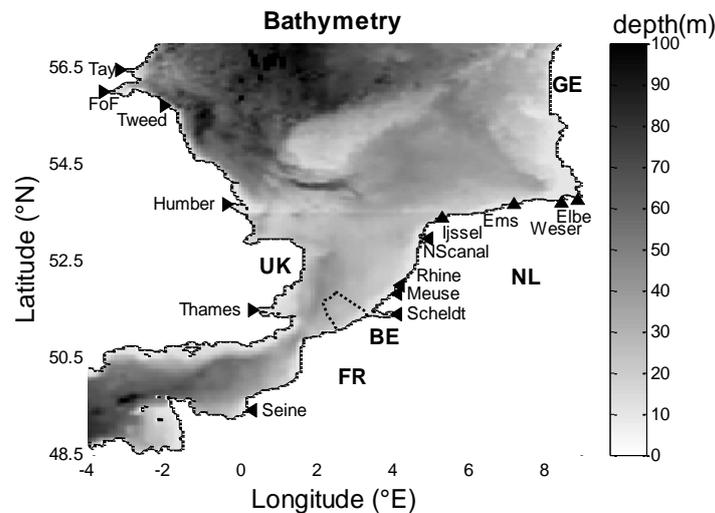


Figure. 18. Geographic implementation of the model with bathymetry (m).

Interannual variability. Twelve years of simulations (1995-2006) have been performed taking into account actual meteorological conditions and river discharges in order to assess the interannual variability.

Individual Based Model (IBM). The v1.0 of the sole larvae IBM detailed in Savina et al. (2010), has been used to study the impact of meteorological conditions (based on 2 years 1995 & 1996), spawning date (15 April & 1 May) and vertical active behaviours (3 different schemes) on the final dispersal of larvae [results have been presented in WestBanks annual reports 2007-2009 and are not repeated here]. In the next version (v2.0 currently under development), the impact of the environment is included by considering a temperature dependency of spawning date, larval stage duration and larval mortality. The results presented in this report have been obtained with the current version of the IBM (preliminary version of v2.0).

Larval stages: 4 larval stages are considered: (1) eggs, (2) 'Yolk' larvae, (3) 'First-Feeding' larvae and (4) 'Metamorphosing' larvae. For each stage, a proper duration and mortality is estimated by using a parameterization (not detailed here) taken from literature (Fig. 19).

Vertical migration: active vertical movements inspired from the literature have been implemented (Savina et al. 2010). Eggs and yolk larvae float in the surface waters, first-feeding larvae perform diel vertical migrations in the surface waters and metamorphosing larvae perform tidal vertical migrations in the bottom waters until the end of the simulation.

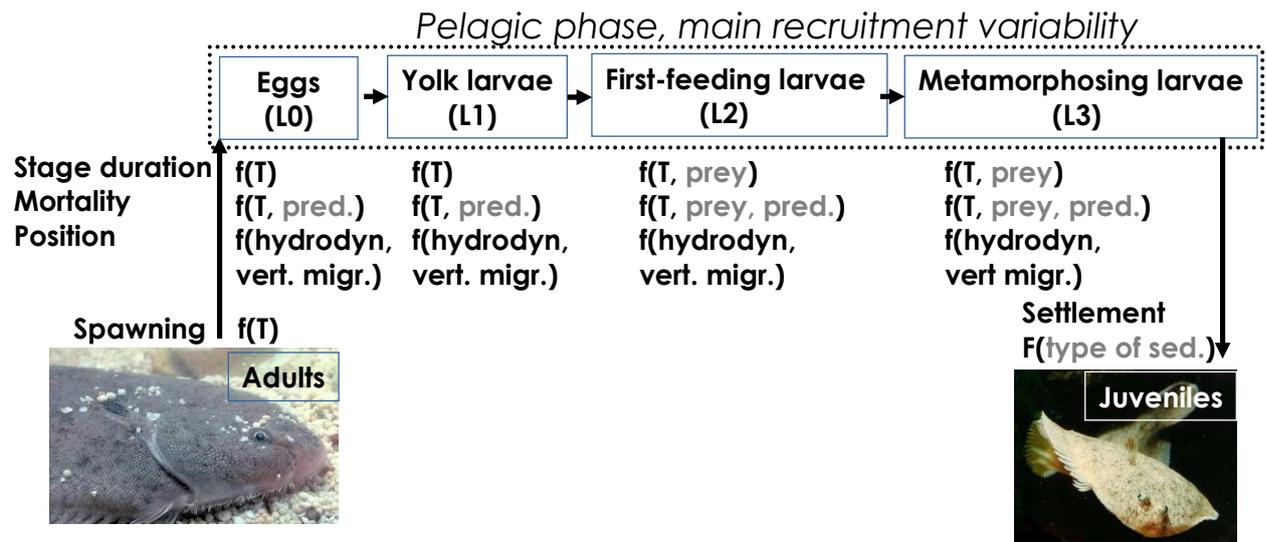


Figure. 19: Schematic representation of the sole larvae IBM model. The version 2.0 is still in development and the factors in gray are not parameterized yet.

Spawning areas: Six spawning areas have been identified (Fig. 20 left panel) from the literature (Rijnsdorp et al. 1992, Bolle et al. pers. comm.).

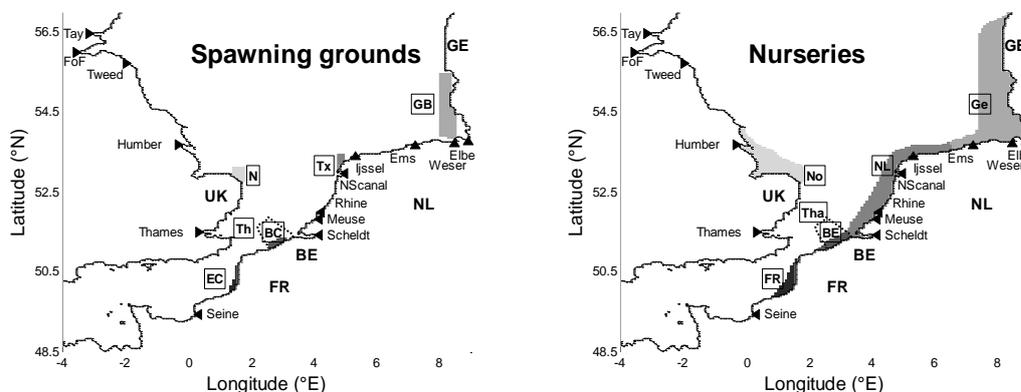


Figure. 20 Left panel: Spawning areas (EC: Eastern Channel, BC: Belgian coast, Tx: Texel, GB: German Bight, N: Norfolk banks, Th: Thames estuary). Right panel: Nurseries (FR: French coast, BE: Belgian coast, NL: Dutch coast, Ge: German coast, No: Norfolk area, Tha: Thames estuary area).

Number of eggs: The total number of particles released at the 6 spawning grounds is 368,000 (1000 per grid cell, Savina et al. 2010). Due to the low survival rate, a significant number of larvae die (99.99965 % on average); hence it is necessary to consider a number of eggs sufficiently large at the beginning of the simulation. For that purpose each particle is considered as a superindividual that represents 10^6 eggs.

Spawning period: The spawning date is estimated from temperature fields. Since the spawning peak occurs at around 10°C (van Beek 1989 in ICES-FishMap 2005), the spawning date is estimated by computing the first day where the temperature of 10°C is reached (on average for each spawning grounds) (Fig. 21).

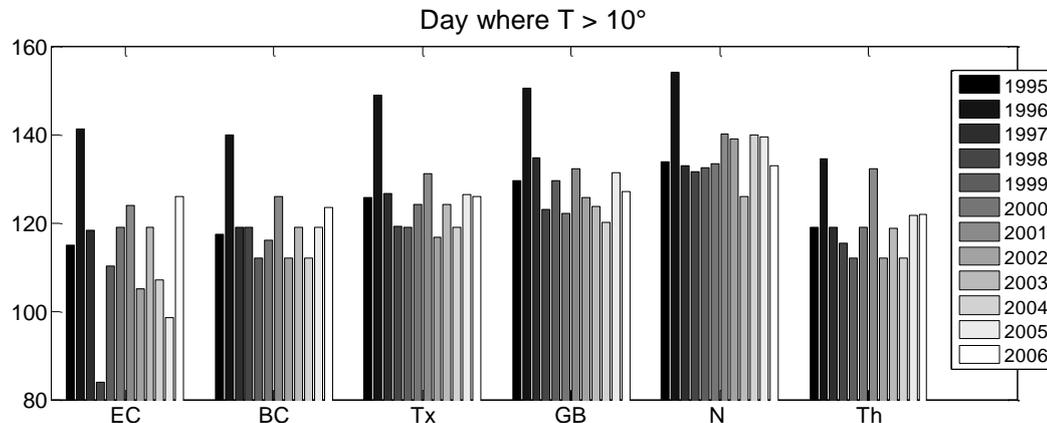


Figure. 21. First day where $T > 10^{\circ}\text{C}$. Average over the different spawning grounds

There is a significant variability between spawning grounds and years. On average over the whole period (1995-2006), the mean date where T reaches 10°C is respectively the 24th April (EC), the 30th April (BC and Th), the 6th May (Tx), the 9th May (GB) and the 16th May (N). The earliest and latest date of spawning estimated from temperature are respectively the 25/03 (EC) and the 03/06 (N).

Settlement: At the end of the pelagic phase, larvae settle in the nurseries. The nurseries are defined as the coastal areas whose depth is below 20m (Fig. 20, right panel).

2.3.2 Results

Genetic structure and adaptation of the sand goby

The phylogeographical analysis of the distribution pattern of the sand goby *Pomatoschistus minutus* showed reciprocal monophyly between a Mediterranean Sea (MS) and an Atlantic Ocean (AO) Clade with a Middle-Pleistocene origin. 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. 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. The demographic histories of the Mediterranean Clade and the two Atlantic ESUs were mainly influenced by expansions dated during the Middle Pleistocene and Late Pleistocene glaciations respectively (Larmuseau et al. 2009b).

Microsatellite loci confirmed the global phylogeographical pattern of *P. minutus* that was observed with mitochondrial DNA markers.

Three groups consistent with the mitochondrial lineages were defined (Mediterranean, Iberian and North Atlantic group) (Fig. 22) and indications for a recent founder-event in the northern Baltic Sea were found. No differentiation was observed within each marine system, including the southern North Sea. Moreover, differences in the degree of population differentiation between the nuclear and mitochondrial markers were large (global F_{ST} -values for microsatellites = 0.0121 and for mtDNA = 0.4293) (Larmuseau et al. 2010b).

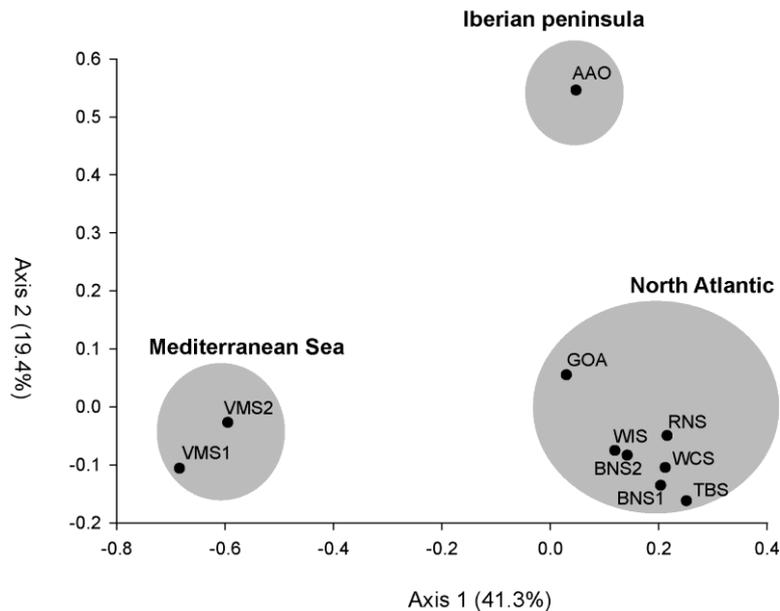


Figure 22. Factorial correspondence analysis plot based on microsatellite data of 10 samples of *Pomatoschistus minutus*.

A high level of interspecific polymorphism at the rhodopsin (*RH1*) gene was observed within the 'sand goby' group. Clear indications for positive Darwinian selection were provided by: (1) linking functional variation on the *RH1* gene to specific light environments of the different fish habitats; (2) constructing and comparing phylogenies based on *RH1* and the 'neutral' 12S and 16S mtDNA fragments; and (3) by performing statistical tests to detect signatures of directional selection on the *RH1* gene. These results suggest that also intraspecific variation on the rhodopsin gene within *P. minutus* can be influenced by natural selection. Therefore, *RH1* can be an interesting marker to understand local adaptation and the connectivity patterns between sand goby populations (Larmuseau et al. 2010a).

The population genetic analysis within *Pomatoschistus minutus* showed a high level of intraspecific polymorphism at the *RH1* gene, including functional mutations. A high and complex population differentiation was observed between samples. Analyses of d_N/d_S substitution rate ratios and likelihood ratio tests under site-specific models detected a significant signal of positive Darwinian selection on the *RH1* gene. A strong discrepancy in population differentiation was noticed between *RH1* gene variation and the presumably neutral microsatellites and mitochondrial data. Samples did not cluster according to geographical or historical proximity with regards to *RH1*, but according to the general photic conditions of the habitat environment of the sand goby (Larmuseau et al. 2009a).

We found that variation at the *RH1* gene in the Baltic populations showed signatures of diversifying selection, whereas *RH1* in the North Sea showed signatures of stabilizing selection. No significant differentiation was observed between samples of *P. minutus* within the southern North Sea based on rhodopsin variation (Fig. 23) (Larmuseau et al. 2010c).

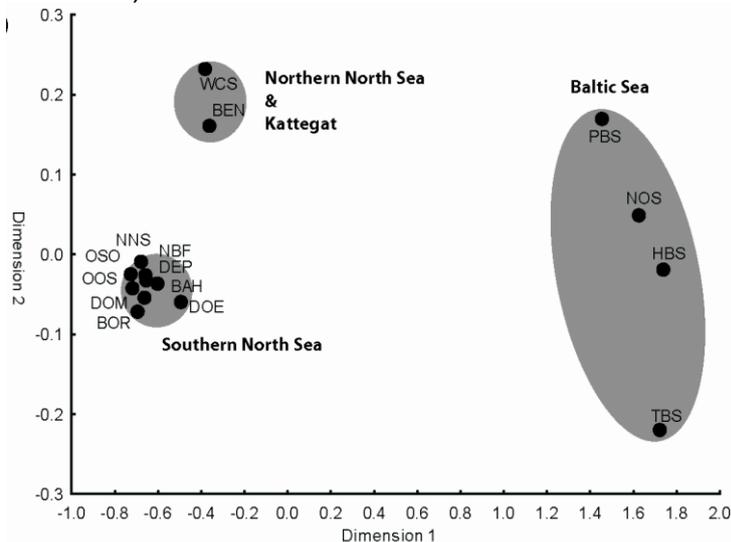


Figure 23. Non-metric multidimensional scaling plots of sand goby populations based on genetic distances (Cavalli-Sforza & Edwards 1967) of the rhodopsin variation of *Pomatoschistus minutus* samples from the Baltic and North Sea.

Connectivity of sole populations: empirical approach

The MICROCHECKER analysis indicated that loci F8-IIGT15, F14-IIGT16, Sos(AC)30 and Sos(AC)40 might be affected by null-alleles or stuttering in most samples. Therefore these loci were excluded from further statistical analyses. The average null allele frequency estimated by the EM algorithm in FREENA (DEMPSTER ET AL. 1977) was lower than 10 % in each of the 10 remaining loci.

Genetic diversity was very similar between all samples (Table II). There was no difference in expected or observed heterozygosity between the spring and autumn samples of both years. Allelic richness (based on 57 individuals) varied from 12.15 to 13.74.

Table II. *Solea solea*: number of genotyped soles (N), unbiased expected (He) and observed (Ho) heterozygosity and mean allelic richness across loci based on 57 individuals.

Sample Code	N	He	Ho	AR
BEL07s	96	0.769	0.718	13.11
BEL07f	75	0.767	0.710	12.15
BEL08s	71	0.771	0.691	13.74
BEL08f	58	0.771	0.691	12.48

There was no significant genetic differentiation (pairwise F_{ST}) between the Belgian samples of sole taken in 2007 and 2008. No significant differences could be observed between the spring and autumn samples of the same year.

Multi-locus F_{ST} was very low and not significant ($F_{ST} = 0.00056$), pointing to the absence of biologically relevant genetic differences.

Genetic diversity of the mitochondrial data, measured as the number of haplotypes and haplotype diversity was in general very high ($Hd > 0.7$). Differences in haplotype diversity in Table III might be explained by sample size, which was highly unbalanced.

Table III. Genetic diversity mitochondrial DNA sequences of *Solea solea*. Number of sequences (S), number of haplotypes (h), haplotype diversity (Hd) with standard deviation, nucleotide diversity (Π) with standard deviation.

Sample Code	S	h	Hd	Π
BEL07S	12	6	0.867 (0.0850)	0.0069 (0.00090)
BEL07F	7	3	1.000 (0.2720)	0.0079 (0.00324)
BEL08S	25	20	0.782 (0.0650)	0.0047 (0.00067)
BEL08F	30	25	0.853 (0.0440)	0.0055 (0.00051)

When more sampling locations across Europe are included, an isolation-by-distance pattern was observed; with increasing geographical distance, genetic differences increased. Within the Southern North Sea, the Belgian spawning population seemed genetically very similar to other North Sea populations (e.g. English Coast, German Bight). This could be either due to high gene flow among the sole aggregations in the North Sea or due to a lack of discrimination power. A high number of SNP markers could provide more power for resolving small scale spatial patterns. Gene flow among local sole populations is possible through larval drift or through active migration of juvenile or (sub)adult individuals. Tagging studies on sole have shown a limited movement of adults from the spawning grounds (Burt & Millner 2008). Furthermore, otolith microchemistry studies suggested limited movement of juvenile sole during their first years of life in the Northeast Atlantic (de Pontual et al. 2000; Vasconcelos 2007; Leakey et al. 2009; Cuveliers et al. 2010). This suggests that the highest dispersal happens during the larval stage.

As physical tracking, otolith microchemistry and genetic profiling show limited mixing between stocks in the WestBanks area, the question remains whether planktonic larvae do disperse and whether the dispersal pattern varies between cohorts and spawning stocks. It has been documented that recruitment may vary considerably between a year, which is not only related to parental recruitment but also to larval survival. Therefore an individual based model (IBM) was implemented on the planktonic life stage of sole.

Connectivity of sole populations: modeling approach

The average (1995-2006) *trajectories* of the centre of mass of sole larvae from each spawning ground obtained by the model are shown on Fig. 24 upper panel. The mean trajectories show a general advection of larvae towards the north-east, as a result of the residual current prevailing in this region.

The final dispersal pattern of sole larvae computed by the model is shown on Fig. 24 lower panel. There is a significant interannual variability of both the mean trajectories and the final larvae abundance (not shown). Hence, from a management perspective; it is interesting to estimate where the presence of larvae is recurrent or exceptional.

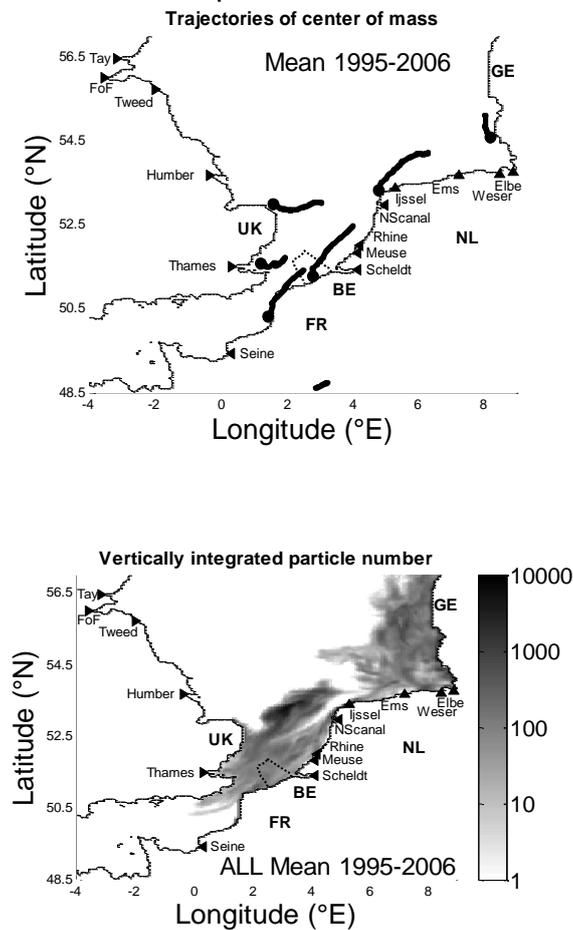


Figure 24: Upper panel: Trajectories of the center of mass of larvae from each spawning grounds. The big dot represents this origin. Lower panel: Final distribution of sole larvae at the end of pelagic phase (Nbr individuals/grid cell). Average over the whole period 1995-2006.

The frequency of larval presence has been estimated by computing the number of years where larvae are present in each grid cell (Fig. 25). There are only a few areas (very close to the coast and offshore from UK towards NE) where larvae are found in all years.

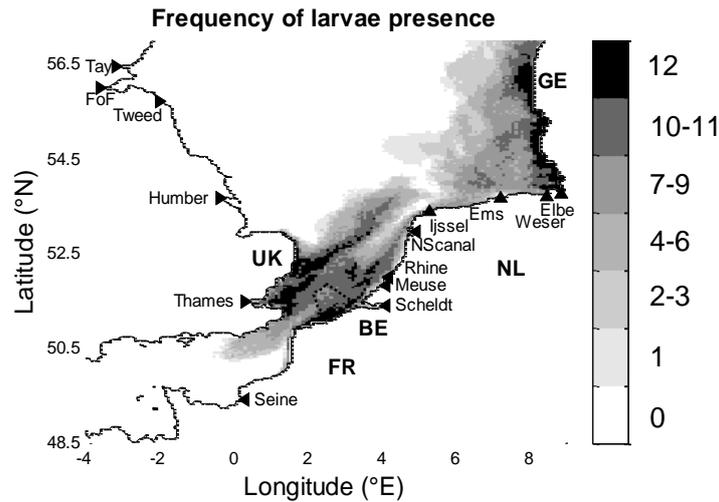


Figure 25: Frequency of presence of larvae at the end of pelagic phase over 12 years (1995-2006).

An estimation of the *origin of larvae* in each nursery was obtained by computing the percentage of larvae in the nursery originating from each spawning ground separately.

Fig. 26 shows this estimation on average for the whole period 1995-2006. It appears that on average, the French nursery is fed by eggs spawned in the EC spawning grounds; the Belgian nursery contains larvae originating mainly from EC and from BC; the larvae in The Netherlands nursery come in majority from BC and from EC and Tx; the German nursery contains larvae that have been spawned in the GB and Tx with a significant proportion of larvae coming from Tx; the Norfolk nursery is only fed by the associated spawning grounds; and finally the Thames nursery receives larvae spawned in the Thames, the Norfolk and the EC spawning grounds. The interannual variability of the larvae origin is nevertheless very high (not shown) in term of both: the relative origin of the larvae and the abundance of larvae reaching the nursery.

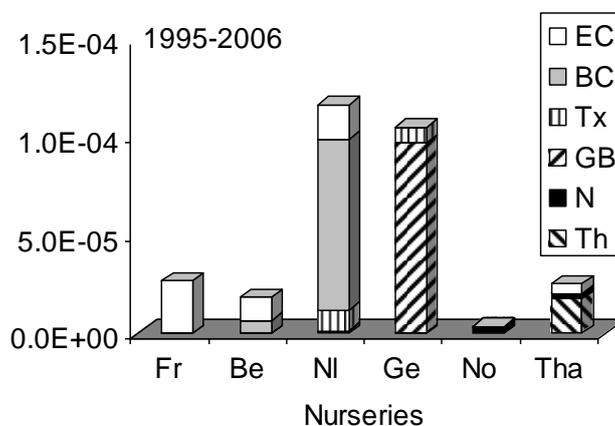


Figure. 26: Percentage of larvae (%) found in each nursery (at the end of pelagic phase) originating from each spawning

The exchange of larvae between the spawning grounds and the nurseries has been computed for all years. Fig. 27 (upper panel) shows the probability for larvae originating from a spawning site to recruit in a nursery after the pelagic stages (connectivity matrix).

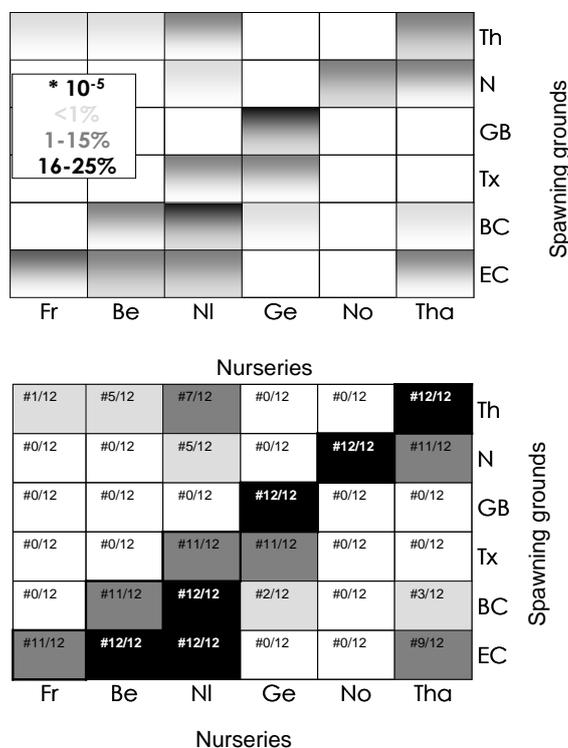


Figure 27: Upper panel: Connectivity matrix. The gray scale is proportional to the percentage of larvae exchanged (scale in %). The upper and lower colors correspond respectively to the maximum and the minimum found within the 12 years. Lower Panel: Frequency of connections between nurseries and spawning grounds. The gray scale gives an indication on how often connection/retention has been observed. Black: always, dark gray: frequent, light gray: sometimes and white: never. The numbers of years where connections have been found as possible over 12 years (#N/12) are indicated for each connection/retention.

Results show that the *exchanges of larvae* (i.e. connectivity) between the 6 areas considered are moderate: 12 connections happened out of 30 possibilities. The amount of larvae exchanged is much lower than the amount of larvae retained (self-recruitment) except in a few cases (ex. NI). This is not incompatible with the possible existence of subpopulations of sole in the Eastern Channel and southern North Sea.

From a management perspective, it is interesting to estimate the frequency of connections between spawning grounds and nurseries (Fig. 27 lower panel). This can be done by calculating the number of years where a connection has been found. It appears that the self-recruitment is a permanent feature for 3 nurseries: GE, No and Tha and almost a permanent feature (11 times over the 12 years) for the 3 other nurseries: FR, BE and NL (Fig. 27 lower panel). That means that in particularly exceptional years, these nurseries are not fed by the associated spawning area. Amongst the 12 connections that happen out of the 30 possible, only 3 are always found (EC spawning grounds that feeds Be and NI nurseries and the BC spawning ground that feeds the NI nursery), 4 are often found (at least 7 times over 12 years) and 5 are sometimes found (maximum 5 times over 12 years).

From field based research, the dispersal of sole throughout its life-cycle seems limited in the Southern Bight of the North Sea. Fish live largely in the (wide) neighbourhood of the spawning ground they were born in. However, this does not exclude any link between spawning grounds. Some spawning grounds may be net exporters of larvae and some nursery grounds net importers of larvae from spawning grounds further away. This was confirmed through the modeling of larval dispersal over many years. Patterns and intensities of egg production do vary between years and hence lead to the variable exchange of larvae between nursery grounds (with variation in dispersal, final larval abundance, larval origin and connectivity).

The modeling output provides a likely explanation for the locally weak genetic signal between the spawning grounds and stocks. It is accepted that at <1% of exchange (gene flow) of adults, distinct genetic patterns should be traceable. However, between 1 and 10% only advanced approaches making use of many markers of which a number have adaptive information are able to make the distinction (see EU FP7 project FishPopTrace). The rhodopsin gene (although studied in another fish than sole) clearly makes the point that a gene under selective pressure (in this case turbidity of the water column) is able to differentiate populations at a fine scale. Some fish seem to prefer turbid coastal zones while others aim for offshore clear waters, all based on allelic variation at a single gene. That's **remarkable and a novel finding**. At values > 10% exchange, populations are considered panmictic. Such situation does not seem to be present here.

However, the **very original modeling results** should be further analyzed to assess the main causes of variability. Do single, protracted or chronic weather and oceanographic events affect recruitment? Also the model itself requires further optimization. For example, larval mortality should be improved by including the prey fields and by assessing the mortality due to lack of food (Match – mismatch hypothesis of Hjort).

Field patterns of dispersal and connectivity should be further analysed through detailed genetic profiling of larvae, postlarvae and adults at the spawning and feeding grounds over several cohorts. The question remains open how sole populations function in a metapopulation context and to what degree human impact (e.g. fishing, climate and habitat change) affects the functioning. If just one connection between sole habitats is interrupted, a measurable impact on stock size is anticipated.

In order to have a useful tool for management, it is necessary to ensure the ecological significance of recruitment. This implies an accurate estimate of the number of eggs spawned during the full season. It also implies the characterization of the habitat throughout the full life cycle. In brief, the modeling output makes it feasible to point to the causes of the observed field patterns.

2.4 Air-Sea biotic coupling

In order to develop health indicators for the pelagic realm, we investigated the feeding ecology of the top predators in our study area: the Sandwich Tern and the Common Tern (WP3).

2.4.1 Material and Methods

Prey fish sampling and tern foraging activity at sea

From August 2007 until December 2009, prey fish abundance was sampled on a monthly basis at two key locations along the Belgian coast (the Westdiep area at the west coast and the Wenduinebank near Zeebrugge). In 2007 and 2008, a pelagic MIK-net was used. Due to logistic problems with the MIK-net, in 2009 the sampling was done with an otter trawl. The sampling locations greatly differ in the diversity and composition of the piscivorous avifauna. The Westdiep supports important wintering populations of Great Crested Grebe *Podiceps cristatus*, whereas the Wenduinebank serves as a foraging area for Common *Sterna hirundo* and Sandwich Tern *S. Sandvicensis* during the breeding season. Abundance and length distribution of pelagic fish species was measured on board of the research vessel.

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. All data from 1992-2010 and were analysed in GIS to acquire the distribution of terns during the breeding seasons as well as the foraging activity of terns in 3x3 km-grids (i.e. number of foraging terns/total number of terns). This reveals the hotspots of tern foraging activity at the BPNS.

Diet composition of terns

The foraging ecology of Sandwich and Common Terns was studied in detail in the breeding colony in the port of Zeebrugge. In this colony, each year chick growth, chick mortality, diet composition of chicks and parents and parental nest attendance was measured. In a first phase of Westbanks (Vanaverbeke et al. 2009) only preliminary results were presented. Here we report on the entire study period (2006-2010), using updated dietary data (faecal samples were re-analysed after detection of extremely small otoliths in one of the most recent samples) and supplementing the results with data gathered in subsequent years and in other colonies (Denmark and the Netherlands).

2.4.2 Results

Prey fish sampling and tern foraging activity at sea

Our field study indicates major differences in the composition of the fish community between the sampling sites. The Westdiep supports a pelagic fish fauna with more energy rich fish such as Clupeidae and Gadidae throughout the year (Fig. 28). The catches with the MIK-net at the Wenduinebank were dominated by Gobidae, catches with the otter trawl in 2009 were dominated by Gadidae and Clupeidae. Probably, this indicates a difference in catchability of certain groups between the net-types (the otter trawl samples close to the bottom, whereas the MIK-net truly samples pelagic) rather than a shift in species composition. Abundances of prey fish in the Westdiep were

rather low throughout the year except for some erratic high counts. A clear seasonal pattern in abundance is difficult to detect. The Wenduinebank however, held high densities of forage fish during the breeding season (April – July) when seabirds concentrate in the port of Zeebrugge and indeed frequently use the Wenduinebank and its surroundings for foraging.

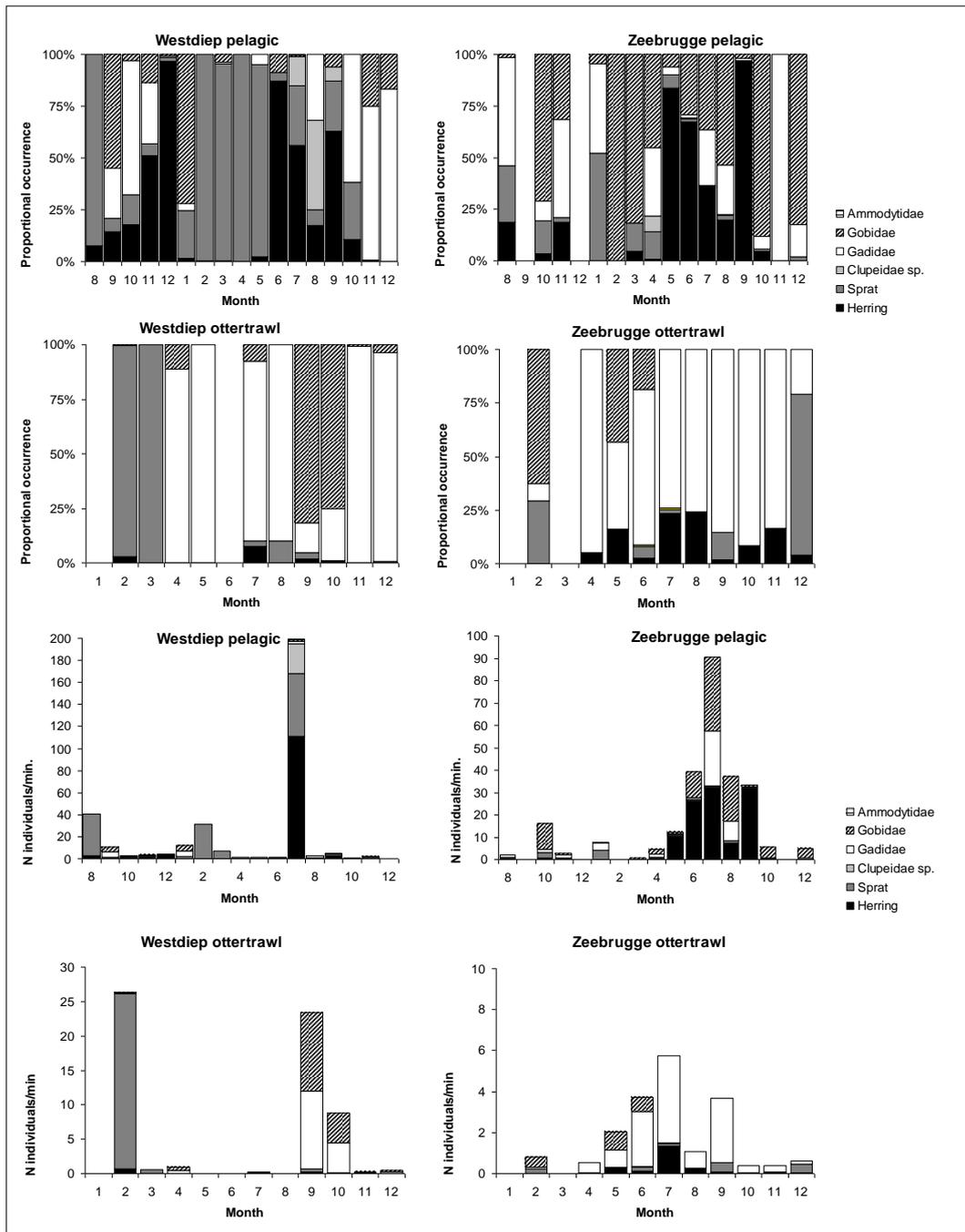


Figure 28.: Proportional importance (upper graphs) and the number of individuals caught per minute of pelagic fish species (lower graphs) caught with a MIK-net in the Westdiep and at the Wenduinebank near Zeebrugge during the period August 2007 (8) – December 2008 (12) and with an ottertrawl in 2009.

During this period, the mix of small Clupeidae, Gobidae and Gadidae, perfectly matches the diet of both adult and chicks of the breeding Common en Sandwich Terns (see below). Furthermore the shift from Sprat *Sprattus sprattus* during January – April to Herring *Clupea harengus* during May – August (especially visible in pelagic samples taken in the Westdiep area) and a mixture of these two species during the remaining part of the year, perfectly matches a similar shift in the diet of wintering auks in the Belgian part of the north sea.

Average size of the various sampled fish species strongly fluctuated throughout the year (Fig. 29). During the breeding season (April-July) the size of the five most caught species/families was generally smaller than during winter and therefore better matches the required prey length of terns to raise their chicks.

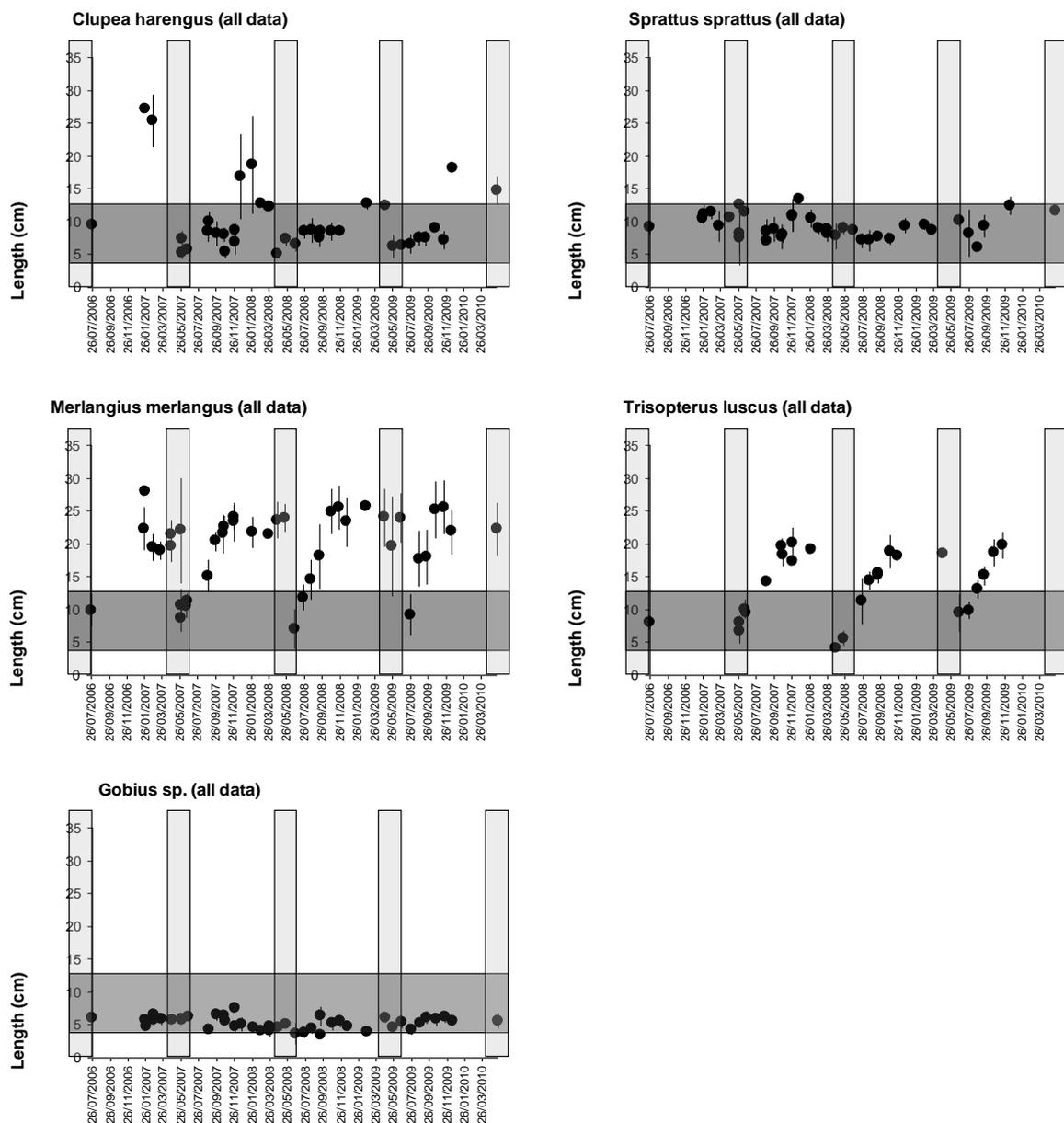


Figure 29. Seasonal variation in the standard length (TL in cm ± SD) of the five most numerous caught fish species/families during the fish sampling campaigns. The vertical bars indicate the breeding period of terns in Zeebrugge and the horizontal bars roughly outline the preferred prey range of the terns.

Our field study further revealed that the distribution of foraging individuals differs strongly from that of non-foraging terns (Fig. 30). During the breeding season, foraging activity was very much restricted to the near coastal zone mainly at locations where strong gradients in depths occur (transition zones from gully to sandbank). Common Terns predominantly foraged along the edges of the Wenduinebank, the port entrances of Ostend (Oostendebank and Nieuwpoortbank) and of Zeebrugge, as well as along the gullies south and west of the Vlakte van de Raan. Sandwich Terns preferred the same areas but also travelled to the Westdiep and western Flemish Banks and more frequently used the Goote Bank and the Thornton Bank 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.

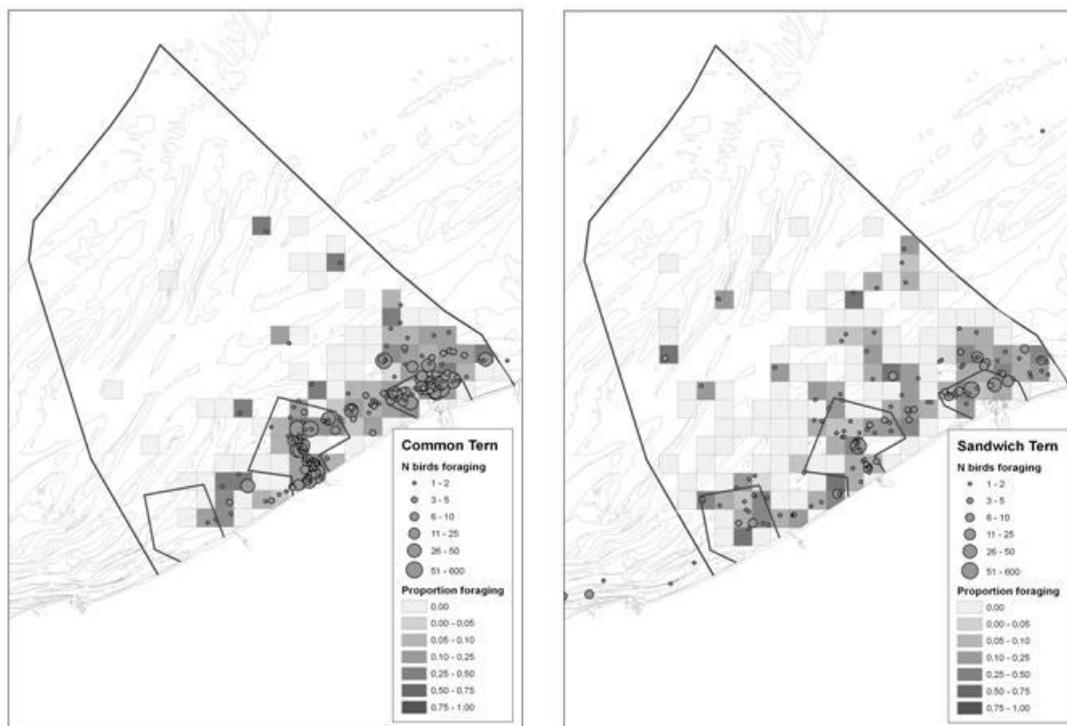


Figure 30: Foraging activity of Common Tern (left) and Sandwich Tern (right) during the breeding season in 1992-2010. Dots show the numerical occurrence of foraging terns and shaded grids represent foraging frequency (i.e. number of actively foraging individuals/ total numbers). Drawn lines indicate the border of the BPN and the three Natura-2000 sites.

Diet composition of terns

Diet composition of Common Tern chicks was based on 812 food remains found in the Zeebrugge colony during chick rearing in 2007-2008 as well as on protocols recorded from a hide in 2010. Diet of adult Common Terns was based on prey remains found in 75 food-containing stomachs of birds found dead in the Zeebrugge colony during period June 2004 – June 2008. These were mainly victims that collided with the row of wind turbines situated between the breeding site and the foraging areas (Everaert & Stienen 2007, Stienen et al 2008) often returning from a feeding trip. Stomachs of adult Common Terns contained high proportions of Clupeidae (72.0% of all stomachs and 63.5% of all otoliths/jaws), but also Gobiidae (45.3% and 9.4%) and polychaete worms (30.7% and 24.2%) were important prey items for adult Common Terns (Fig. 31).

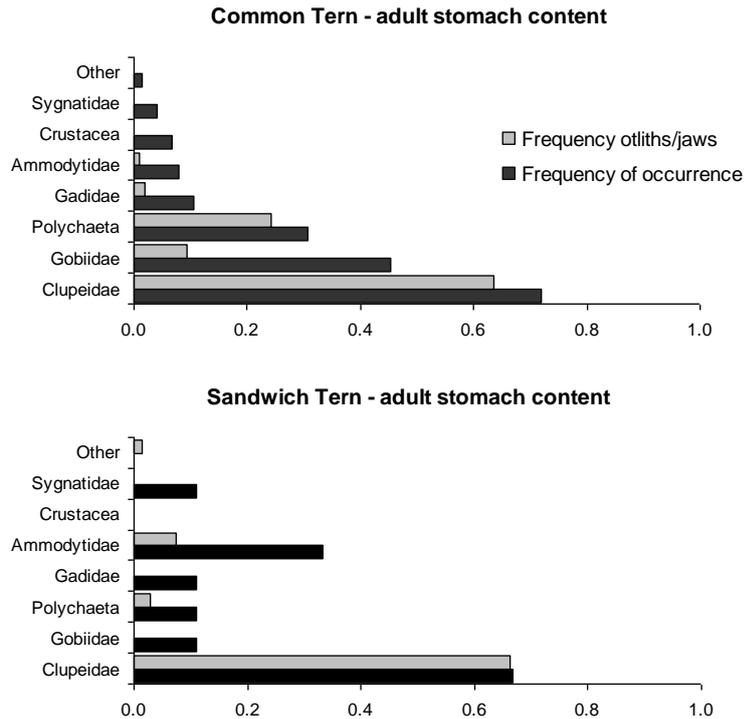


Figure 31. Stomach content of adult Common (N = 75 individuals) and Sandwich Terns (N = 9) found dead in the vicinity of the Zeebrugge colony in 2004-2008.

The diet of Common Tern chicks consisted of even higher proportions of Clupeidae (on average 92.1% of all prey items) than that of adults, whereas other prey items were only of minor importance for chicks (Fig. 32). Note that visual observation of chick feedings may give more reliable results as Gobiidae and other small prey (mainly larval fishes) are probably underestimated when diet composition is based on food remains found in the colony.

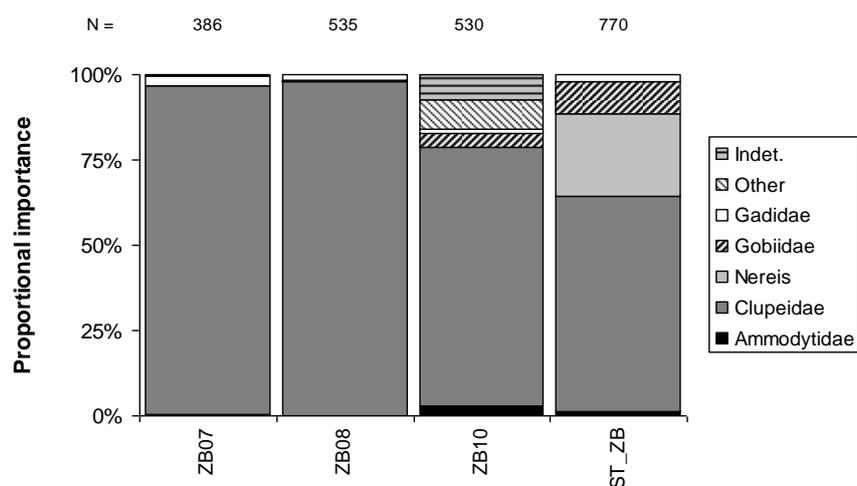


Figure 32. Differences between the diet fed to Common Tern chicks in Zeebrugge (ZB07, ZB08 and ZB10) and the species composition of otoliths/jaws in stomachs of self-feeding adults (ST_ZB). In 2007 and 2008 chicks diet was based on food remains found in the colony, whereas in 2010 visual observations of chick feedings were performed from a hide.

The preceding TROPHOS study revealed that adults of the presumed strictly piscivorous Sandwich Tern at least partly depend on prey items other than fish (Vanaverbeke et al. 2007). The TROPHOS study was based on faecal samples collected in the breeding colony in Zeebrugge. Here we complete the TROPHOS samples with Zeebrugge data of later years, reanalyse the older data and compare it with other colonies within the same biogeographic population. Furthermore, the faecal samples are compared with the stomach-content of 9 adult Sandwich Terns that were found dead in the vicinity of the Zeebrugge colony between 2004 and 2007 to evaluate the different sampling techniques. All faecal samples show a dominance of Clupeidae and Ammodytidae as forage fish for adult Sandwich Terns, but with the proportion of Clupeidae strongly varying between 9 and 79% (Fig. 33).

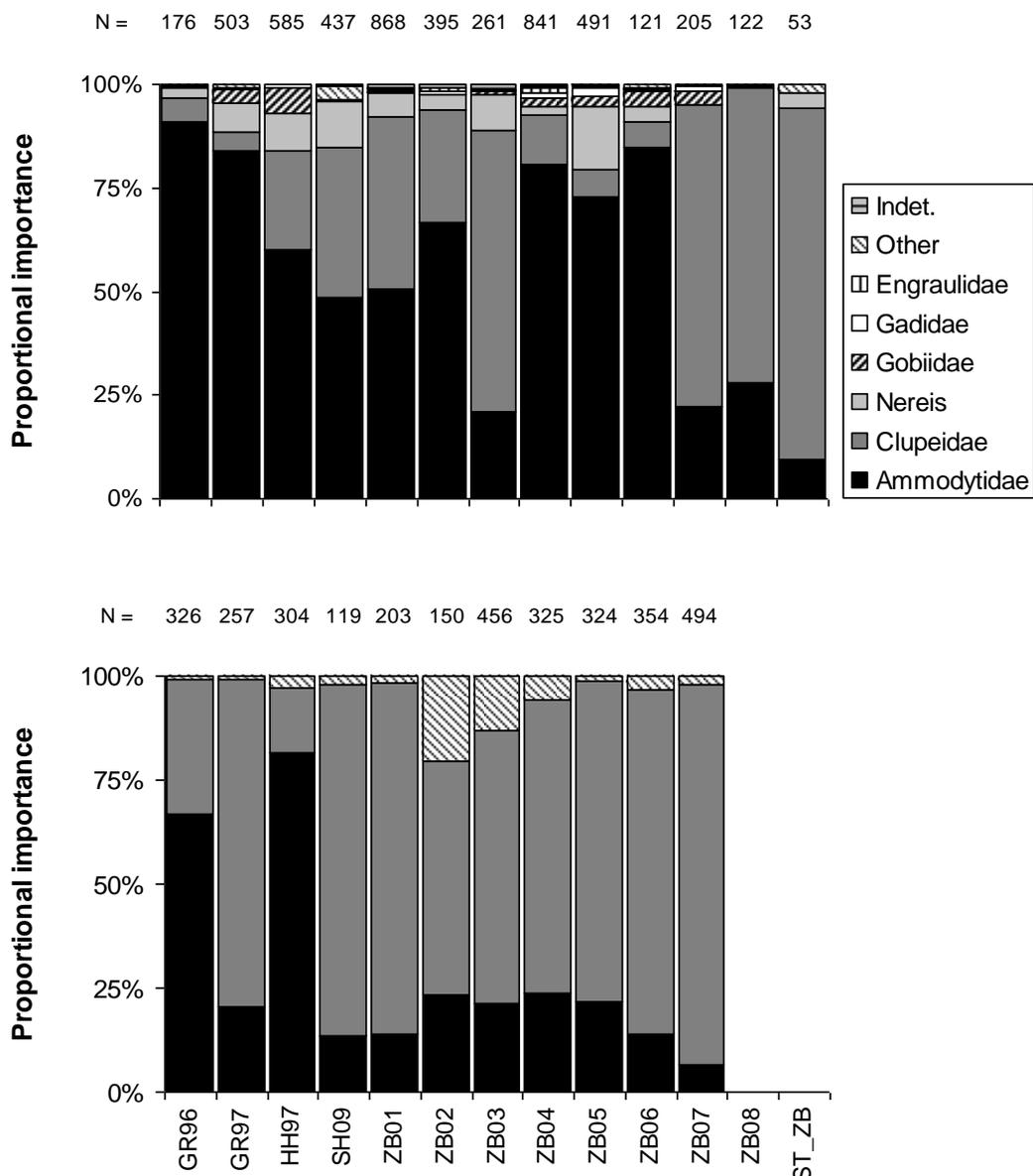


Figure 33. The upper graph compares the species composition found in faecal samples of adult Sandwich Terns at Griend, the Netherlands (GR96, GR97), Hisrholmene, Denmark (HH97), Scheelhoek, the Netherlands (SH09) and Zeebrugge, Belgium (ZB07 to ZB08) to the species composition of otoliths/jaws in stomachs of self-feeding adults in Zeebrugge (ST_ZB). The lower graph shows the diet composition of chicks based on visual observations in the colony.

The stomach content of adult Sandwich Terns shows a similar dominance of Clupeidae and Ammodytidae (Fig. 31), suggesting that both sampling techniques might be useful to evaluate the diet of Sandwich Terns.

Still, the relatively high proportion of clupeids (66.2% of all stomachs and 66.7% of all otoliths/jaws) in stomachs of adult Sandwich Terns is remarkable given the fact that seven birds out of nine were found in 2004-2006 when faecal samples suggested a high abundance of Ammodytidae. However, one must realise that in the case of Sandwich Terns the sample size of dead individuals was very small ($N = 9$) and the results are strongly biased (e.g. one bird found in 2006 contained all but one otoliths of clupeids, although vertebrae of clupeids were found in five other birds). Probably faecal sampling gives a more reliable and general view of the diet of adult Sandwich Terns than the analysis of the stomach contents of only a few individuals. Faecal sampling was performed around various nests and the samples contained food remains of the three weeks prior to hatching.

The results obtained during the preceding TROPHOS-study suggested that self-feeding adult Sandwich Terns strongly depend on Ammodytidae. After a thorough reanalysis of the rest fraction of the TROPHOS samples (ZB01- ZB03) however, we found many small otoliths of mainly clupeids. Therefore, in the current study the proportional importance of Ammodytidae for self-feeding adults is lower than earlier reported in the TROPHOS-study. This holds especially for 2003. The current WESTBANKS study reveals that the proportion of Ammodytidae in the adult diet strongly varies between years (Fig. 33), probably reflecting yearly variations in the abundance of either Ammodytidae or Clupeidae during the early breeding season. Except for the Hirsholmene colony in the Danish Kattegat and Zeebrugge in 2003, the diet of sandwich Tern chicks contained proportionally more clupeids than that of adults, while nereid worms make up an important part of the diet of adult Sandwich Terns but are never fed to their offspring (Fig. 33).

When looking in detail at the length distribution of the fishes (back-calculated from the size of the otoliths¹) found in the faecal samples of adult Sandwich Terns in Zeebrugge (Fig. 34), it shows that the smaller prey taken by self-feeding adults were all Clupeidae. The majority of the smallest otoliths (corresponding to fishes of 3.5-4.5 cm) could however not be determined to the species level since they lacked distinguishable features. The vast majority of the larger clupeids were *Clupea harengus* whereas *Sprattus sprattus* were of minor importance for adult terns. Most *Clupea harengus* were 0-group individuals ranging from 4.5 to 6.5 cm, whereas *Sprattus sprattus* generally were somewhat larger. The largest fish eaten by the Sandwich Tern parents in Zeebrugge was a sandeel sp. that measured 22.5 cm. Prey fed to the chicks followed a similar length distribution, except that the smallest specimens were almost not fed to the chicks so that average prey length of adults slightly shifted to larger fishes. The latter probably reflects a combination of seasonal growth of the forage fishes as well as wear of otoliths in the digestive track of adults.

¹ Note that no correction for otolith wear was applied and that biometric equations relating otolith size to fish length were taken from Depooter 2010 since the equations given by Leopold et al 2001 give unrealistic values for the smaller specimens

Adult Common Terns selected a narrow range of prey length, with 66.9% of the fishes measuring 4-4.5 cm (Fig. 34). Their chicks were offered somewhat larger prey (68.4% of the clupeids presented to the Common Tern chicks in 2010 measured 5.5-6.5 cm. Smaller fishes that were fed to the chicks comprised of a mixture of clupeids, Gobidae and larvae that could not be determined to the species level.

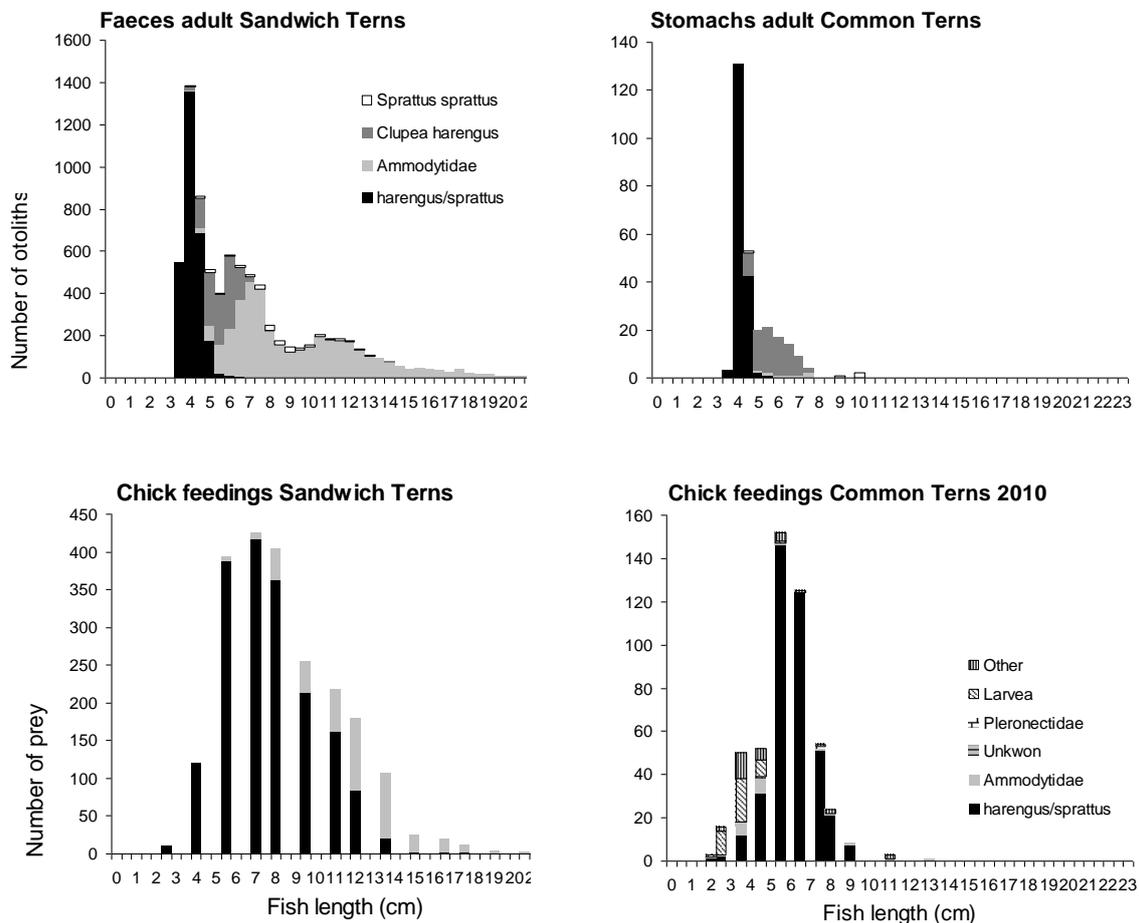


Figure 34. Distribution of back-calculated fish length from otoliths found in the faecal samples of Sandwich Terns in Zeebrugge during 2001-2008 (left upper graph) compared to the length distribution of Clupeidae and Ammodytidae fed to their chicks in 2001-2007 (lower graph left). The right graphs show the distribution of fish length in stomachs of adult Common Terns in Zeebrugge in 2004-2008 (upper graph) and of fish fed to the chicks in 2010.

In search of health indicators

Being highly specialised single-prey loaders that restrictively feed near the colony in the upper water layer on only a few prey species, terns are very good candidates to serve as indicators for the health of the pelagic ecosystem. In the WESTBANKS project we evaluate which parameter is the most suitable to act as an indicator. The indicator must be relatively easy to measure and must form an explicit link between the pelagic ecosystem and the reproductive abilities of the terns. Therefore we used long-term datasets on standardised measurements of reproductive parameters (clutch size, hatching success, chick survival and reproductive output) of both Common and Sandwich Tern breeding in Zeebrugge and compared those with several reputed indicators of food availability.

Most obvious relations that can be expected are intra-specific effects of the yearly variation in the diet of either adults or chicks on reproductive parameters and fitness. Proportionally more clupeids in the chicks' diet, for example, can have a positive effect on chick growth and survival as was found in the Dutch Wadden Sea (Stienen & Brenninkmeijer 2002). In this study, a single significant correlative connection between the adult diet and the various breeding parameters was found between the proportion of clupeids in the faeces of self-feeding adult Sandwich Terns and the survival of their chicks (Fig. 35). Since we found no significant correlation between the composition of the adult diet and that presented to their chicks, this result suggests that years with high proportions of clupeids in the adult diet, which probably reflects an early arrival of clupeids in Belgian coastal waters, either directly influences parental condition or indirectly affects the composition of the breeding population (more 'good' adults in good clupeid years).

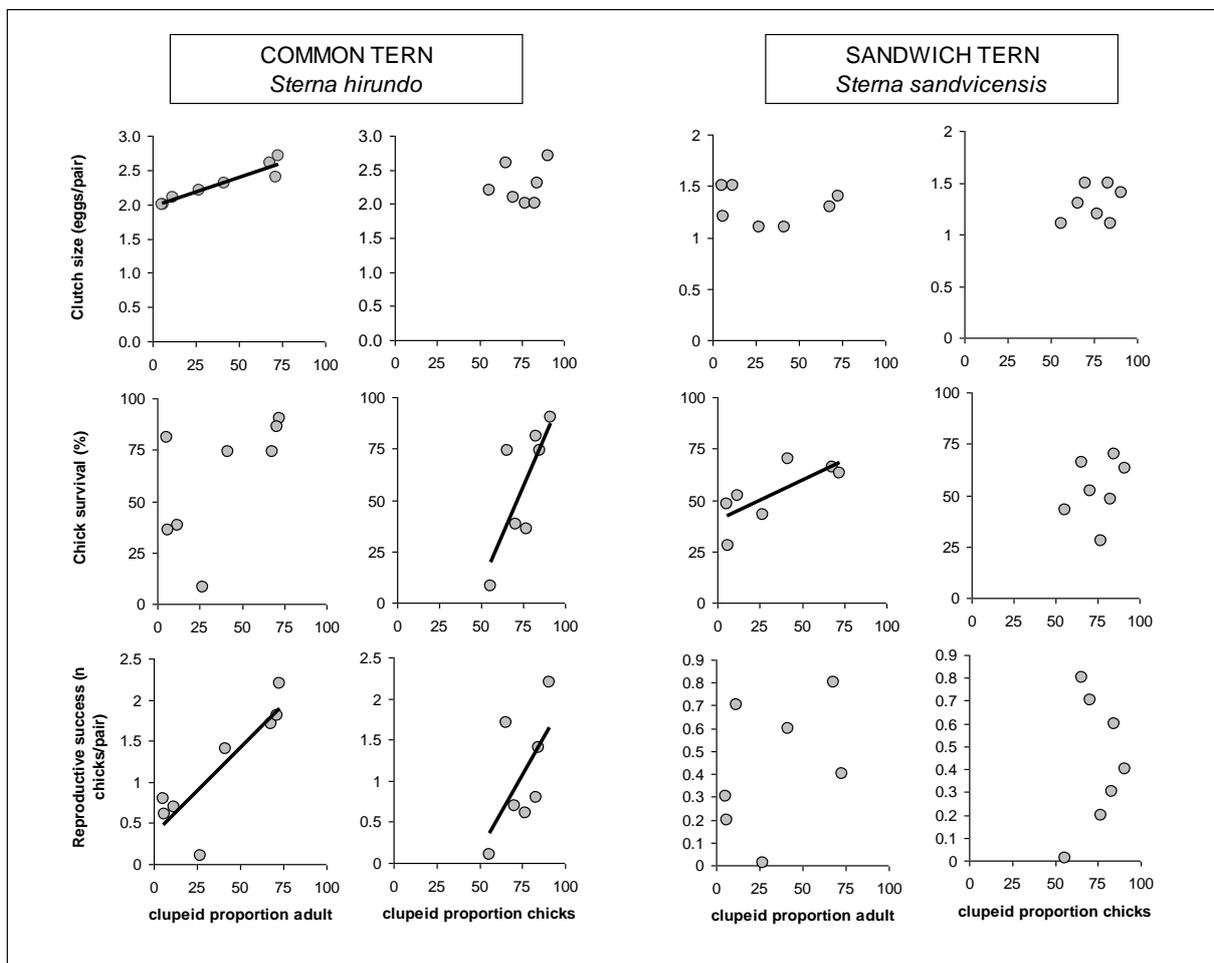


Figure 35. Correlation between the diet composition of adults/chicks of Sandwich Terns and the breeding parameters (clutch size, chick survival and reproductive success) of Common Tern (left panels) and Sandwich Tern (right panels) in Zeebrugge during the period 2001-2008.

In Belgium, the breeding season of Sandwich Terns normally precedes that of Common Terns with about 2 weeks. Therefore one would expect that the diet composition of Sandwich Terns might also be indicative for the food availability of Common Terns.

Indeed, the composition of the faecal samples of Sandwich Terns correlated strongly with the clutch size of Common Terns and ultimately with the reproductive output of Common Terns. Apparently Common Terns adjust clutch size to the prevailing food situation, leading to larger clutches in years with a higher abundance of clupeids during the settling phase. Subsequently, chick survival of Common Terns correlated well with the diet composition of Sandwich Tern chicks (here serving as a proxy for food availability/quality during early chick rearing).

As already shortly mentioned above, the timing of the arrival of young Herring might play a crucial role in this. In years that the 0-group Herring arrives early, food availability better matches the breeding rhythm of the terns. It appears that Common Terns (laying maximum clutches of 3 eggs) but not Sandwich Terns (maximum 2 eggs) adjust clutch size accordingly and that chick survival of both species is positively influenced by a high availability of clupeids early in the breeding season. The strong correlation between diet composition and reproductive parameters fits well the strong dependency on clupeids of both species and especially of Common Terns (see paragraph above).

It remains puzzling why the survival of Sandwich Tern chicks is not directly linked to the proportion of clupeids in their diet, as this is the case in the Dutch Wadden Sea (Stienen & Brenninkmeijer 2002). It appears that apart from availability and timing of prey, also length distribution of the forage fish is crucial for the survival of the Sandwich Tern chicks in Zeebrugge. The length distribution of clupeids strongly differed between years (Fig. 36), but without a clear link between prey length distribution in the diet of adults and chicks. Apparently small clupeids were lacking in 2004, 2005 and 2006 because of which adults were forced to consume larger clupeids and proportionally more Ammodytidae. In 2002 and 2003 relatively high proportions of small clupeids were found in the faeces of adult Sandwich Terns, indicating an early arrival of Herring in our coastal waters. Still in 2002, parents were apparently forced to switch to Ammodytidae (compare Figure 6) indicating that although size distribution of the prey fitted the terns' requirements the abundance of clupeids was low in this year.

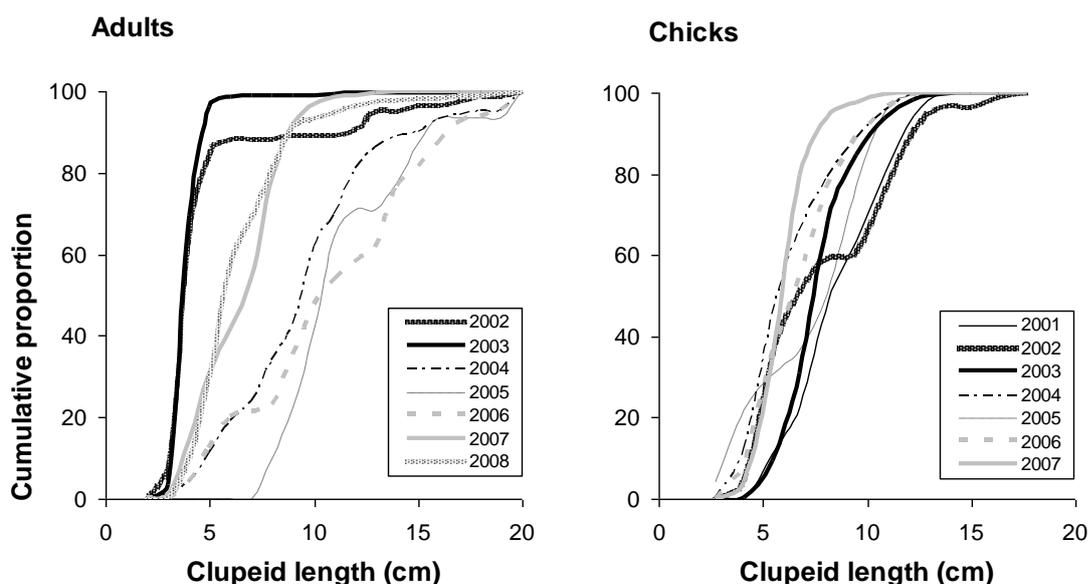


Figure 36. Yearly variation in the length distribution of Clupeidae found in adult faeces (left graph) and fed to the chicks (right graph) of Sandwich Terns in Zeebrugge during the period 2001-2008

It is known that Sandwich Terns adjust prey to the size of their growing chicks (Stienen et al 2000), which is also the case in the Zeebrugge colony (Fig. 37). Small chicks of less than 5 days old received clupeids averaging less than 5.4 cm in size. During linear growth when the chicks are between 5–15 days old and when energy needs sharply increase (Klaassen et al 1992), average prey size increased to more than 8 cm.

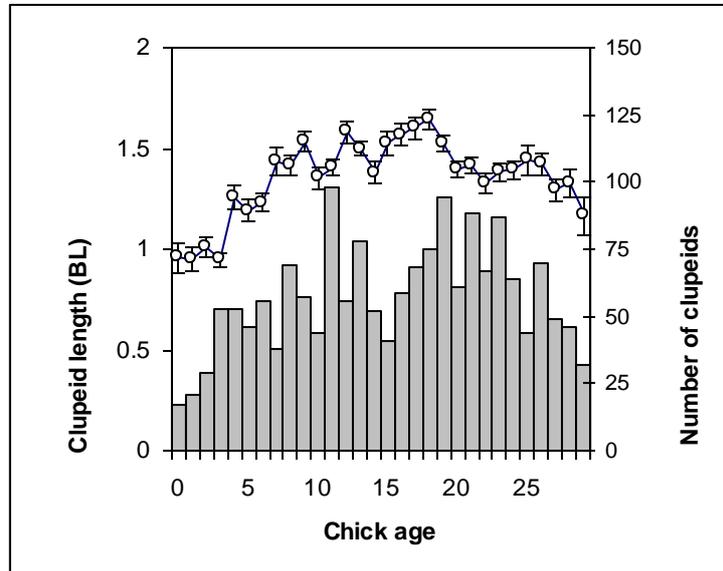


Figure 37. Relationship between the age of the chicks and the average size of clupeids (dots \pm SE) brought to Sandwich Terns in Zeebrugge the period 2001-2007 (left axis). The bars denote the sample size (right axis)

Particularly during this stage the availability of clupeids seems critical for Sandwich Terns as we found a strong correlation between the proportional importance of clupeids measuring 1-1.5 BL (corresponding to 5.4 – 8.2 cm) in the diet of Sandwich Tern chicks and their survival probabilities (Fig. 38). As this particular size of clupeids is even more important for Common Tern chicks, it is not surprising that also the survival of chicks of this species strongly correlates with the proportional importance of this size class in the diet of Sandwich Tern chicks.

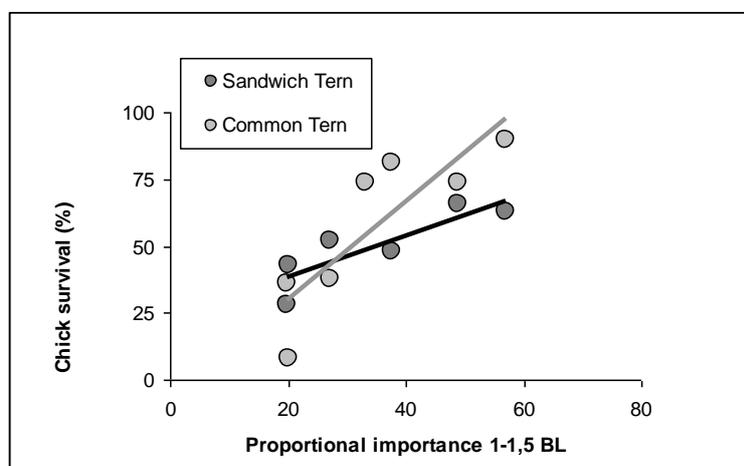


Figure 38. Relationship between the yearly proportion of clupeids measuring 1-1.5 BL (i.e. 5.4-8.2 cm) in the diet of Sandwich Tern chicks and the survival probabilities of Sandwich and Common Tern chicks in Zeebrugge in 2001-2007.

For a further generalisation of a possible health indicator we collected standardised measurements of reproductive parameters conducted in three major colonies within the Northwest European population of Common Terns (all measurements were conducted in enclosed parts of the colony: Banter See 1985 – 2010, Griend 1993 – 2007, Zeebrugge 1997 – 2010). In all three colonies variation in reproductive output was largely determined by variation in chick survival and not so much by variation in clutch size or hatching success (Fig. 39).

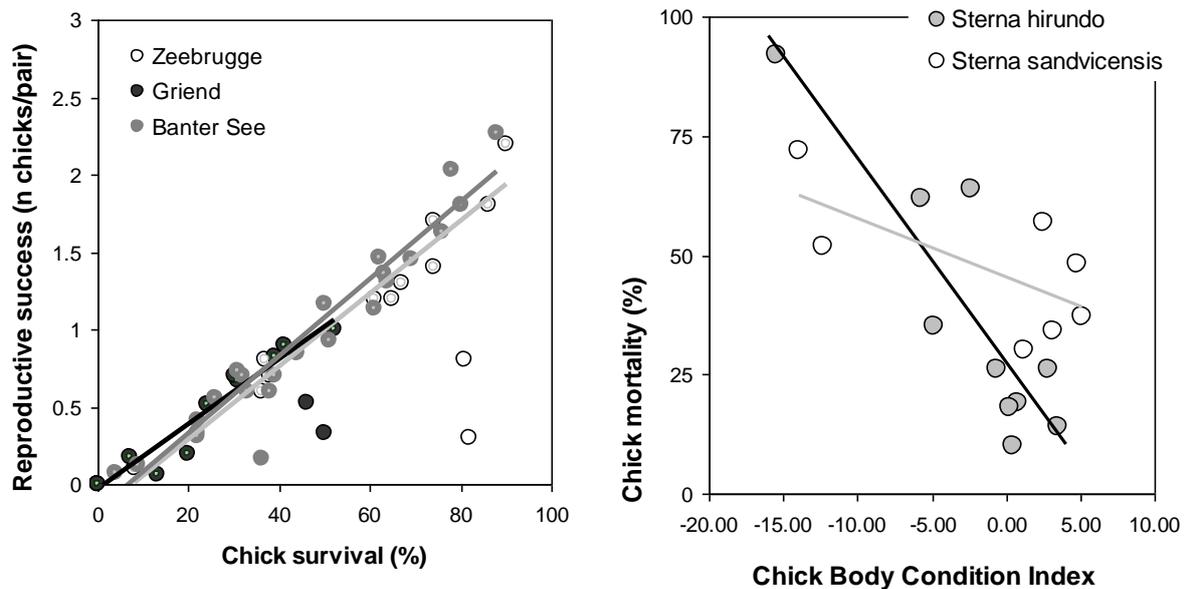


Figure 39. Except for five outliers there is strong linear relationship between chick survival and reproductive success of Common Terns in Zeebrugge (BE), at Griend (NL) and in the Banter See (DE) (left graph). In the Zeebrugge colony, chick body condition is indicative for mortality chances both in Common and Sandwich Tern (right graph).

Only five exceptions spread over the three colonies were found that did not fit this general picture. In all five cases either clutch size was markedly low (probably indicating early predation) or hatching success was unusually low because of mammalian predation or flooding events. This implies that in general chick survival is a good candidate to serve as a health indicator. Since we are searching for an indicator of the prevailing food conditions, chick survival should further show a causal link with food abundance. The above results already showed that in Zeebrugge chick survival is indeed linked to the feeding conditions, but on the other hand non-intrinsic effects such as adverse weather conditions, flooding events and excessive predation should be ruled out. This can partly be done by monitoring the causes of chick losses and by measuring body condition of the tern chicks. This is especially the case for Sandwich Terns where the brood size is normally reduced to one soon after hatching of the second chick (Stienen & Brenninkmeijer 2006). As a consequence, there will be almost no interaction between chick condition and brood size - chick body condition will most likely reflect the prevailing food conditions. Indeed in both species

the chick mortality correlated with the body condition of chicks (Fig. 39), but deviations from this pattern were unexpectedly large.

2.5 WestBanks integrative workshop

All of the above results are based on newly collected data or new experiments performed within WestBanks. However, it should be noted that the research groups involved in WestBanks have a long tradition of cooperation in Belspo funded projects (since SPSS I), and as such, collected many data on the BPNS. These data, together with supporting data from the open domain, were integrated in a single WestBanks database by VLIZ. This integrated WestBanks database consists of 730132 records on sediment related variables (biology and environmental variables) and 72107 records on water column derived data. The bulk of the biological data holds information on the abundance of macrobenthos, hyperbenthos and meiobenthos. Seabird data is stored as geographical grid files for the BPNS in order to allow easy spatial linking to the other biological data. The database was set up as a MS Access database, allowing easy access, transport and data operations and is similar to other databases built in the framework of the FP6 NoE MarBEF.

The compilation of this database created a basis for tackling relevant scientific and/or policy related questions that can never be answered by a single scientist alone. Therefore, scientists and end-users associated with the WestBanks project were invited to bring forward scientific issues that possible could be tackled using the WestBanks database. Most questions were submitted by the Federal Public Service – Marine Environment. During a workshop (Oostende, 29-31/10/2008), attempts were made to provide answers to these questions. Policy-related questions related to eutrophication problems and aspects of the reef-building polychaete *Lanice conchilega*. Scientific driven analyses targeted a global analysis of the diversity of the meio-and macrofauna of the BPNS, and the link between seabird distribution and the distribution of the macrofaunal prey. Results of this workshop were summarized in a report (Vanaverbeke et al. 2009, available at <http://www.vliz.be/imisdocs/publications/143615.pdf>) that was distributed among the end-users and interested parties in Belgium, France and the Netherlands. Results obtained during this workshop lead to the initiation of the Belspo targeted action ENSIS (Belspo SD/NS/09A) and a peer-reviewed scientific paper (Vanaverbeke et al. 2011).

3. POLICY SUPPORT

3.1. Contribution of WestBanks results to policy development

While WestBanks results were obtained from fundamental research, care was taken to translate the results to policy-relevant documents and or presentations during the project. A first step in communicating scientific results to federal and regional policy/management offices was done by setting up the annual WestBanks end-user meetings. These meetings were meant to inform both scientists and end-users about the scientific progress. In addition, every presentation ended with a *translation of the results into policy relevant information*. This information was included in the reports of these meetings that were sent out to all end-users of WestBanks. Presentations and reports were available for scientists and end-users on the restricted WestBanks website. It should be noted that for the WestBanks consortium, it is not clear how this information is actually being used in the North Sea policy/management decision tree.

A second mechanism translating WestBanks results to policy is achieved through the participation of WestBanks partners in ad-hoc projects issued by the federal government during which direct, policy-relevant questions need to be answered. WestBanks scientists used WestBanks results to advise the federal government on the delineation of areas on the BPNS that fulfill the criteria of the Habitat Directive (HABITAT project -Degraer et al. 2009) and to define the favourable conservation status of protected species and habitats in the Belgian part of the North Sea, especially in marine protected areas (Degraer et al. 2010). WestBanks scientist advised the federal government on the vulnerability of seabirds to disturbance by kite-surfing activities along the Belgian coast (Stienen & Courtens 2010). During the EUTROF project (Van Hoey et al. 2009), WestBanks scientists contributed results and expertise to an assessment of the eutrophication status of the sediments of the BPNS in the framework of the OSPAR eutrophication assessment. This project also resulted in recommendation for the improvement of ongoing monitoring programmes. Most of the research on the modeling of the early life stages of sole was embedded in the SoleMod project (BELSPO).

Thirdly, communication of WestBanks results to the policy/management level was done on own initiative of the WestBanks consortium or individual WestBanks scientist. We already mentioned the organization of the WestBanks integrative workshop, during which question from the end users were answered in a formal report. Many questions were forwarded by the Federal Public Service (FPS) Health, Food Chain Safety and Environment - Belgian Marine Policy administration, and answered in a formal report (Vanaverbeke et al. 2009). In addition, advice and/or comments on federal management plans for MPAs (Rabaut & Cliquet 2008, Rabaut et al. 2008) and regional (i.e. Flemish) fisheries policies plans (Rabaut & Vincx 2008) were formulated. WestBanks scientists were invited to participate in a workshop on 'Use and Cost of Degradation of the Belgian Part of the North Sea: a socio-economical analysis (Oostende, 24 May 2011), organized by the the Federal Public Service (FPS) Health, Food Chain Safety and Environment - Belgian Marine Policy administration in the framework of the implementation of the Marine Strategy Framework Directive.

Within the WestBanks project, a one day symposium "The North Sea, field lab for marine protection" was organized in collaboration with Belspo and The Marine Board of the European Science Foundation (Leuven, 22 March 2011, see below for details).

This symposium offered the opportunity to review the state of MPA-related processes in North Sea countries. On request of the OSPAR Biodiversity Committee, this review, together with key recommendations was summarized in an information document (<http://www.vliz.be/projects/westbanks/symposium/downloads/WestBanksSymposiumLeuven22032011final.pdf>) authored by WestBanks scientists and the ESF-Marine Board, and submitted to OSPAR (on 1 April 2011), MUMM and the the Federal Public Service (FPS) Health, Food Chain Safety and Environment - Belgian Marine Policy administration. The outcome of the symposium is also taken up in the Working Group on Marine Protected Areas of the ESF-Marine Board. The task of this working group is to prepare a position paper on the implementation of a coherent network of MPAs in Europe in the framework of the Marine Strategy Framework Directive.

Again at the international level, WestBanks participants translate the expertise and results partly obtained during WestBanks in working groups of international organization. At the moment, Marijn Rabaut (Ghent University, Marine Biology Research Group) is the Belgian delegate of the Working Group on Marine Protected Areas of the Marine Board (European Science Fund), paving the road for an integrated MPA policy on the European Level. Filip Volckaert (KULeuven) was member of the ESF-Marine Board Working Group on "Science Dimensions of an Ecosystem Approach to Management of Biotic Ocean Resources (SEAMBOR)". The report of this working group (Rice et al. 2010) formulates actions and recommendations to ensure progress of the implementation of the Ecosystem Approach to Management and the Marine Strategy Framework Directive. Jan Vanaverbeke was invited to participate in the Joint Fact Finding working group in the Netherlands, a working group established within the implementation of a Natura 2000 management plan for the Dutch part of the Vlakte van de Raan. In addition, WestBanks participants are also active in several ICES study or working groups: Jan Vanaverbeke is member of the Working Group on Biodiversity Science; Filip Volckaert is a member of the ICES Working Group on the Application of Genetics in Fisheries and Mariculture, where he has been appointed to evaluate the evolutionary implications of MPAs. Geneviève Lacroix is a member of the ICES Working Group on modeling of the Physical/Biological Interactions (WGPBI). Eric Stienen represents Belgium in the ICES Working Group on Seabird Ecology (WGSE) and participates in data transfer to be used in the evaluation or the development of OSPAR ecological quality objectives (EcoQO) on oiled Guillemots, plastic particles in seabird stomachs and contaminants in seabird eggs. The data on seabird distribution gathered in WestBanks were made available to Eurobis and the EMODnet biological data portal where they can be consulted by the public at large.

3.2. Recommendations for a sustainable management of the North Sea, with emphasis on the BPNS

To come to a sustainable management, the WestBanks project indicates that two major threats resulting from human activities have to be managed in the shallow soft-bottom environment of the BPNS.

On the one hand, **the benthic ecosystem was proven to create an important buffer capacity for eutrophication** through the behavior of the bottom dwelling organisms while on the other hand physical disturbance of these organisms leads not only to a reduction of this buffer capacity but also to decreased biodiversity.

Eutrophication and physical disturbance by e.g. beam-trawl fisheries are interlinked through the biology and ecology of bottom dwelling organisms in general and the presence of strong ecosystem engineers in particular.

The WestBanks project was able to link different ecosystem components through an analysis of the functional diversity. Besides temperature, it is the biological activity (macrobenthic burial) that is responsible for the mineralization (during late summer) of the organic matter produced by the annual phytoplankton bloom (during spring). It was shown that both bioturbation and bio-irrigation are of paramount importance for ecosystem functioning in fine sandy sediments receiving high loadings of organic matter.

The 'ecosystem engineers' responsible for these processes were shown to be important in structuring the ecosystem both top down and bottom up.

Deeper down in the food web both the bivalve *Abra alba* and tubeworm *Lanice conchilega* deepened the habitat of the very small bottom animals (meiofauna), and especially *Lanice conchilega* was important for nematode survival. As far as the larger bottom organisms (macrofauna) are concerned, *Lanice conchilega* seems to be a very important ecosystem engineer that creates a new habitat that attracts many species. Going further up in the food web, the results of this project showed that juvenile flatfish makes use of the reef habitats created by the tubeworm. Therefore, the reef habitat is important both for its modulating impact on the physical environment and for the local biodiversity. Physical disturbance experiments indicate that the reef structure itself can persist under intermediate beam trawl pressure but the integrity of the reef is hurt as the system as a whole degrades shortly after disturbance.

Physical disturbance leading to decreasing densities of ecosystem engineers implies an important decline of the eutrophication-counteracting process in shallow coastal seas.

The detailed physical, biological and biogeochemical studies on these particular ecosystem engineers show the sediment-animal-interactions of the Western Coastal Banks and quantify the strength of benthic engineers within a conservation context. As such, the ecological knowledge built up within the WestBanks project form a solid basis to come to a true ecosystems approach to management for the Western Coastal Banks, the BPNS and even for the North Sea as a whole.

We recommend using important ecosystem engineers as conservation targets to come to a sustainable management of the North Sea.

Because of the activity of the bottom living organism, the Western Coastal Banks of the BPNS are a highly diverse ecosystem and form an important buffer against eutrophication.

Therefore, the level of eutrophication has to be managed not to trespass a threshold at which the important ecosystem engineers decline and bottom disturbing fisheries need to be reduced to a minimum and banned in dedicated areas (e.g. protection of reefs).

The work on the distribution of the juvenile sole showed that the Belgian sole nursery is one of the few areas in the North Sea where sole larvae are found during all years, highlighting the importance of the Belgian Part of the North Sea for the recruitment of sole at the scale of the entire North Sea.

As such, it is clear that deterioration of the habitats at the Belgian Part of the North Sea will have a negative influence of the sole populations on the North Sea scale

Given the connectivity of the sole populations in the North Sea, both on evolutionary and life-cycle time scales, it is clear that **transnational networks of sufficiently large protected areas are needed to ensure the viability of sole populations.**

Therefore, we recommend to effective installation of MPAs covering at least 10% of the BPNS, as required by the recent Convention on Biological Diversity. This should results in the installation of exclusive zones, restricted zones and open zones on the BPNS. Open zones can have continuous access to fisheries, exclusive zones should be managed under a **recovery plan and should function as source area for recruits**. The restricted area needs to be **tightly managed under gear and time restrictions**. Furthermore, including important **benthic ecosystem engineers (i.e. *Lanice conchilega*) as a variable in the dispersal model** of sole could improve our understanding of the factors inducing settlement of sole larvae.

The work on seabirds showed that the survival of tern chicks in Zeebrugge delicately depends on the early arrival and the survival of 0-group herring. A high presence of this age group during the first half of the chick rearing period ensures a high reproductive output. **As Zeebrugge holds one of Europe's largest tern colonies**, it is clear that **the nursery function for herring and the linked foraging function for terns need proper protection to ensure the favorable conservation of this ternery**. Especially the Wenduinebank, the Scheur and the southern border of the Vlakte van de Raan prove to be of major importance for foraging terns and supports a rich fish fauna during the breeding season. Only a part of this key foraging area is now protected within the framework of Natura-2000 which **urges for the extension of the Bird Directive Area V3** .

3.3. Recommendation on the designation of MPAs at a North Sea scale

The WestBanks-Belspo-ESF Marine Board symposium "The North Sea, field lab for marine protection" (Leuven, 22 March 2011) resulted in recommendations for the establishment of a coherent MPA network in the North Sea. Key recommendations were:

1. The Marine Strategy Framework Directive is a major driver towards implementation of the Ecosystem Approach in the North Sea as it will facilitate to better planning and management of existing and future uses and activities (e.g. North Sea fisheries are still a major driver of regional ecosystem changes);
2. Protecting ecosystem functioning (e.g. as a buffer against eutrophication) in the North Sea is of high importance. This could be achieved through the protection of key ecosystem engineers (e.g. tube worm reefs) and the progressive resettlement of lost indigenous species (e.g. the native oyster *Ostrea edulis*);
3. A coherent network of MPAs in the North Sea should:
4. Be represented by a system of no-take zones and MPAs with different levels of protection;
5. Be used to facilitate the achievement of Good Environmental Status;
6. Be used as an operational tool to better manage multiple and interacting human activities together in a sustainable way;
7. The North Sea MPAs network can only be coherent if a common (and trans-boundary) North Sea Marine Spatial Planning initiative is implemented;
8. To determine sustainability thresholds in the North Sea, the research community should develop scenarios for fishery closures in tandem with adequate percentages of different types of MPAs

4. DISSEMINATION AND VALORISATION

Dissemination of WestBanks results and activities was mainly channeled through scientific output (oral and poster contributions on international conferences, the WestBanks website and the public at large.

So far, 30 WestBanks papers were published in the peer-reviewed international literature (see below for an overview), and four PhD's (Marijn Rabaut – UGent, Maarten Larmuseau – KULeuven, Els Cuveliers – KULeuven and Ulrike Braeckman – UGent, PhD submitted) were finalized based on WestBanks research. A fifth PhD still needs to be submitted (Pieter Provoost, NIOO-CEME). Given the amount of scientific output, there is no doubt that WestBanks scientists provided important contributions to marine sciences.

The WestBanks website (<http://www.vliz.be/projects/westbanks/>) was online since May 2007, and received 330854 hits by the end of December 2010. A large interest in the WestBanks website was observed during the first (2007: 161758 hits) and last year (2010: 154929 hits). The website served as portal to information on WestBanks activities, data, and provided links to reports and papers. Given the large amount of visits on a scientific website, we consider our website a successful dissemination tool.

WestBanks was also visible on international websites. The webpage on *Lanice conchilega* of the Encyclopedia of Life (<http://www.eol.org/pages/614469>) specifically refers to WestBanks reports and scientific papers. The Dutch website "Zee in Zicht (Sea at Sight) refers to WestBanks on its page dedicated to *Lanice conchilega* (http://www.zeeinzicht.nl/vleet/index.php?item=schelpkokerworm&pageid=schelpkokerworm.htm&use_template=vleet_template.html).

All teams participated in events targeting the public at large (e.g. Wetenschapsweek, Nacht van de Onderzoeker, Planeet Zee, Het Jaar van de Dolfijn and UGent aan Zee). Besides, several lectures were given to the public at large during the "International year of Biodiversity"). Scientific knowledge gathered during the WestBanks projects was translated into a popularizing publication edited by several NGOs ("Nature Reserves in the North Sea, for the environment and for the people", Natuurpunt, Bond Beter Leefmilieu & WWF 2008 - http://www.natuurpunt.be/uploads/natuurbehoud/kustwerkgroep/documenten/rapport_noordzee.pdf). WestBanks results were noted in local, national and international press.

Valorisation can mainly be judged from the success of the WestBanks partners to use WestBanks expertise to participate in other national or international projects. Through its participation, scientists from the Marine Biology Research Group (Ghent University) participated in nationally funded projects by the Federal Public Service (FPS) Health, Food Chain Safety and Environment - Belgian Marine Policy administration (EUTROF, HABITAT) and Belspo (ENSIS, WAKO-II). We were successful in obtaining funding from FWO Vlaanderen ("National Science Fund") for 2 projects which were directly related to WestBanks research ('The functional role of marine macrobenthos in the metabolism of the sea floor (2008-2011) and 'The structuring role of biotic interactions between different size classes for benthic ecosystem functioning (2011-2013). Scientist from the Research Institute for Nature and Forest (INBO) participated in nationally funded projects by the Federal Public

Service (FPS) Health, Food Chain Safety and Environment - Belgian Marine Policy administration (HABITAT, Favorable Conservation Status) and Belspo (AsMade, ENSIS, WAKO-II). Under the authority of MUMM, INBO evaluates the effects of offshore wind farms on seabirds. INBO participates in a Dutch consortium to evaluate the effectiveness of measures taken to compensate for the impact of the extension of the Rotterdam Port on seabirds. Regularly INBO advises the Federal Government as well as the Flemish authorities on seabird-related issues.

At the international level, WestBanks results were integrated in the EU FP6 NoE MarBEF and EMODNET and WestBanks expertise allow the participation in the FP7 project MESMA and the FP7 proposal EcoBOS. The population genetic research on sole has been embedded in the EU FP6 project *Fisheries induced evolution* (FinE) <http://www.iiasa.ac.at/Research/EEP/FinE/> and the FP7 project FishPopTrace <http://fishpoptrace.jrc.ec.europa.eu/>. The focus of these studies relates to a European perspective on the evolutionary impact of overfishing and the tracing of the origin of caught fish.

A major WestBanks valorisation and dissemination work was achieved through the organisation of the symposium "The North Sea, field lab for marine protection", organised in collaboration with Belspo and the Marine Board, in Leuven at 22 March 2011. For this symposium, 182 participants from different nationalities gathered to get an overview of the MPA process in different North Sea countries (Belgium, The Netherlands, Germany, Norway, UK and France). We aimed at reaching multiple users of the sea, a goal that was achieved since participants were active in research, policy (at the Flemish, Belgian and European level), industry, consultancy and NGOs. Students participated as well. Invited experts from North Sea countries provided an overview of the state of the art of the MPA process in their own country, before highlighting the recent advances in their field of work. Topics included the Ecosystem Approach to Management, connectivity and representativity of MPAs, design and monitoring of MPAs, resolving conflicts between users of the sea, tools to implement management strategies in MPAs and socio-economic valuation of ecosystem services in an MPA context, with emphasis on the science-policy nexus (i.e. how do scientific data find their way to actual marine policy). This series of presentation was followed by a debate, during which scientists, NGOs and policy makers (Belgian and European level) discussed a number of topics that were chosen by the audience, in order to maximise the relevance of this debate.

The outcome of this symposium was of immediate use for the Working Group on Marine Protected Areas of the Marine Board, and a summary document was requested by the OSPAR Biodiversity Committee.

All information, presentations and the summary report are available online (<http://www.vliz.be/projects/westbanks/symposium/>)

5. PUBLICATIONS

5.1 Peer reviewed

2007

- Everaert J, Stienen EWM (2007). Impact of wind turbines on birds in Zeebrugge (Belgium): significant effect on the breeding tern colony due to collision. *Biodivers Conserv* 16: 3345-3359.
- 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* 48: 241-254
- Rabaut M, Guilini K, Van Hoey G, Vincx M, Degraer S (2007) A bio-engineered soft-bottom environment: The impact of *Lanice conchilega* on the benthic species-specific densities and community structure. *Estuar Coast Shelf Sci* 75:525-536
- Vandendriesche S, Stienen EWM, Vincx M, Degraer S (2007). Seabirds foraging at floating seaweeds in the Northeast Atlantic. *Ardea* 95: 289-298..

2008

- Larmuseau MHD, Guelinckx J, Hellemans B, Van Houdt JKJ, Volckaert FAM (2008). Fast PCR-RFLP method facilitates identification of *Pomatoschistus* species from the North Atlantic. *Journal of Applied Ichthyology* 24:342-344.
- Franco MA, Soetaert K, Van Oevelen D, Van Gansbeke D, Costa MJ, Vincx M, Vanaverbeke J (2008) Density, vertical distribution and trophic responses of metazoan meiobenthos to phytoplankton deposition in contrasting sediment types. *Mar Ecol Prog Ser* 358:51-62
- Franco MA, Soetaert K, Costa MJ, Vincx M, Vanaverbeke J (2008). Uptake of phytodetritus by meiobenthos using ¹³C labeled diatoms and *Phaeocystis* in two contrasting sediments from the North Sea. *J Exp Mar Biol Ecol* 362:1-8
- 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
- Stienen EWM, Brenninkmeijer A, Klaassen M (2008). Why do Gull-billed Terns *Gelochelidon nilotica* feed on fiddler crabs *Uca tangeri*? *Ardea* 96: 243-250.
- 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.

2009

- Larmuseau MHD, Raeymaekers JAM, Ruddick KG, Van Houdt JKJ, Volckaert FAM (2009). To see in different seas: Spatial variation in the rhodopsin gene of the sand goby (*Pomatoschistus minutus*). *Molecular Ecology* 18:4227-4239.
- Larmuseau MHD, Van Houdt JKJ, Guelinckx J, Hellemans B, Volckaert FAM (2009). Distributional and demographic consequences of pleistocene climate fluctuations for a marine demersal fish in the North-Eastern Atlantic. *Journal of Biogeography* 36:1138-1151.
- Rabaut M, Degraer S, Schrijvers J, Derous S, Bogaert D, Maes F, Vincx M, Cliquet A (2009) Policy analysis of the 'MPA-process' in temperate continental shelf areas. *Aquat Conserv* 19:596-608

- Rabaut M, Vincx M, Degraer S (2009) Do *Lanice conchilega* (sandmason) aggregations classify as reefs? Quantifying habitat modifying effects. *Helgol Mar Res* 63:37-46
- Schippers P, Snep RPH, Schotman AGM, Jochem R, Stienen EWM, Slim PA (2009). Seabird metapopulations: searching for alternative breeding habitats. *Popul Ecol* 51: 459-470.
- Van Oevelen D, Franco MA, Soetaert K, Moodley L, van Ijzerloo L, Vincx M, Vanaverbeke J (2009) Organic matter input and processing in two contrasting North Sea sediments: insights from stable isotope and biomass data. *Mar Ecol Prog Ser* 380:19-32

2010

- Braeckman U, Provoost P, Gribsholt B, Van Gansbeke D, Middelburg JJ, Soetaert K, Vincx M, Vanaverbeke J (2010) Role of macrofauna functional traits and density in biogeochemical fluxes and bioturbation. *Mar Ecol Prog Ser* 399:173-186
- Cuveliers EL, Geffen AJ, Guelinckx J, Raeymaekers JAM, Skadal J, Volckaert FAM, Maes GE (2010) Microchemical variation in juvenile *Solea solea* otoliths as a powerful tool for studying connectivity in the North Sea. *Marine Ecology Progress Series* 401: 211-220.
- Franco MA, Vanaverbeke J, Van Oevelen D, Soetaert K, Costa MJ, Vincx M, Moens T (2010) Bacterial, nematode and macrobenthic activity following a phytoplankton bloom in two contrasting sediments in the North Sea. *Marine Ecology* 31,276-290
- Larmuseau MHD, Huyse T, Vancampenhout K, Van Houdt JKJ, Volckaert FAM (2010). High molecular diversity in the rhodopsin gene in closely related goby fishes: A role for visual pigments in adaptive speciation? *Molecular Phylogenetics and Evolution* 55:689-698.
- Larmuseau MHD, Raeymaekers JAM, Hellemans B, Van Houdt JKJ, Volckaert FAM (2010). Mito-nuclear discordance in the degree of population differentiation in a marine goby. *Heredity* 105:532-542.
- Larmuseau MHD, Vancampenhout K, Raeymaekers JAM, Van Houdt JKJ, Volckaert FAM (2010). Differential modes of selection on the rhodopsin gene in coastal baltic and North Sea populations of the sand goby, *Pomatoschistus minutus*. *Molecular Ecology* 19:2256-2268.
- Rabaut M, Van de Moortel L, Vincx M, Degraer S (2010) Biogenic reefs as structuring factor in *Pleuronectes platessa* (Plaice) nursery. *J Sea Res* 64:102-106
- Savina M, Lacroix G, Ruddick K (2010). Modelling the transport of common sole larvae in the Southern North Sea: influence of hydrodynamics and larval vertical movements. *Journal of Marine Systems* 81: 86-98

2011 – in press – submitted

- Braeckman U, Provoost P, Sabbe K, Middelburg JJ, Soetaert K, Vincx M, Vanaverbeke J (under review) Temporal variation in macrobenthic diet as inferred from fatty acid biomarkers. *Mar Biol*
- Braeckman U, Provoost P, Moens T, Middelburg J, Soetaert K, Vincx M, Vanaverbeke J (2011) Biological vs. physical mixing effects on benthic food web dynamics. *PLoS One* 6(3), e18078. Doi:10.371/journal.pone.0018078

- Braeckman U, Van Colen C, Soetaert K, Vincx M, Vanaverbeke J (2011) Contrasting macrobenthic activities differentially affect nematode density and diversity in a shallow subtidal marine sediment. *Mar Ecol Prog Ser* 422:179-191
- Schippers PA, Snep RPH, Schotman AGM, Jochem R, Stienen EWM & Slim PA. The consequences of being colonial: Allee effects and alternative stable equilibria in metapopulations of seabirds. *Ecological Modelling*
- Van Franeker JA, Blaize C, Danielsen J, Fairclough K, Gollan J, Guse N, Hansen PL, Heubeck M, Jensen J-K, Le Guillou G, Olsen B, Olsen KO, Pedersen J, Stienen EWM & Turner DM (in press). Monitoring plastic ingestion by the northern fulmar *Fulmarus glacialis* in the North Sea. *Environmental Pollution*
- Vanaverbeke J, Merckx B, Degraer S, Vincx M (2011). Sediment-related distribution patterns of nematodes and macrofauna: two sides of the benthic coin? *Mar Env Res.* 71: 31-40.

5.2 Others (only written contributions mentioned)

2007

- Adriaens P, Anselin A, Decler K, Devos K, Goethals V, Spanoghe G, Stienen E, Vermeersch G (2007). Vogels: Bijlage 1 vogelrichtlijn en belangrijke trekvogels, *in*: Decler, K. (Ed.) (2007). Europees beschermde natuur in Vlaanderen en het Belgisch deel van de Noordzee: habitattypen: dier- en plantensoorten. Mededelingen van het Instituut voor Natuur- en Bosonderzoek, 2007.01: pp. 421-519
- Decler K, Anselin A, Bauwens D, Ronse A, Van Landuyt W, Stieperaere H, Coeck J, Buysse D, Van Thuyne G, Belpaire C, Stienen E, Courtens W, Haelters J, Kerckhof F, Thomaes A, De Knijf G (2007). Dieren en planten: Bijlage 2 en 4 habitatrichtlijn, *in*: Decler, K. (Ed.) (2007). Europees beschermde natuur in Vlaanderen en het Belgisch deel van de Noordzee: habitattypen: dier- en plantensoorten. Mededelingen van het Instituut voor Natuur- en Bosonderzoek, 2007.01: pp. 361-419
- Stienen, E.; Brenninkmeijer, A. (2007). De grote stern komt aarzelend terug *Vogelnieuws* 3: 14-15
- Stienen, E.W.M.; Van Waeyenberge, J.; Kuijken, E.; Seys, J. (2007). Trapped within the corridor of the Southern North Sea: the potential impact of offshore wind farms on seabirds, *in*: de Lucas M et al. (Ed.) (2007). Birds and wind farms: risk assessment and mitigation. pp. 71-80

2008

- Braeckman U, Provoost P, Gribsholt B, Middelburg J, Soetaert K, Vincx M & Vanaverbeke J. (2008). The role of macrofauna in the functioning of the seafloor: is there any seasonal, density or functional identity effect? *VLIZ Special Publication, 40: 33*
- Courtens W, Stienen E, Van de walle M (2008). Stern en te Zeebrugge: broeden op een kunstmatig schiereiland *Mens en Vogel* 46: 30-37
- Courtens W, Stienen E, Van de walle M, Stienen EWM (2008). Nieuws van het Sternenschiereiland te Zeebrugge *Vogelnieuws* 11: 13-16
- Courtens W, Stienen EWM, Van de walle M, Verstraete H (2008). Gemengd broedpaar Dougalls stern met Dougalls X visdief-hybride in Zeebrugge (België) = Mixed breeding pair roseate tern and hybrid roseate X common tern in Zeebrugge, Belgium *Sula* 21: 123-131

- Rabaut M, Braeckman U, Kerckhof F (2008) Nieuwe riffen geen gevaar voor wandelaars De Spille. Natuurpunt, Brugge, p 16
- Rabaut M, Braeckman U, Rappé K, Degraer S, Kerckhof F (2008) Borstelwormen bedreigen Heist: een sciencefictionverhaal De Grote Rede. VLIZ, Oostende, p 31
- Rabaut M, Cliquet A (2008) Opmerkingen bij voorontwerp beleidsplannen mariene beschermde gebieden. Publieksbevraging voorontwerp beleidsplannen mariene beschermde gebieden, Brussels (Belgium)
- Rabaut M, Stienen E, Cliquet A (2008) Commentaar bij ontwerpbeleidsplannen mariene beschermde gebieden. Document ter ondersteuning van het overleg met het kabinet van de Minister van de Noordzee, Brussels (Belgium), p 4
- Rabaut M, Vincx M (2008) Advies en opmerkingen op 'Strategische milieubeoordeling national operationeel programma Belgische visserijsector', Brussels (Belgium)
- Stienen EWM (2009). Minder olievervuiling in onze kustwateren, in: INBO (2009). INBO jaarboek 2008. pp. 60-61
- Verstraete H, Stienen E, Van de walle M (2008). Beached birds on the Flemish beaches, in: Mees, J. et al. (Ed.) (2008). VLIZ Young Scientists' Day, Brugge, Belgium, 29 February 2008: book of abstracts. VLIZ Special Publication, 40: pp. 72
- Verstraete H, Stienen EWM, Van de walle M (2008). Monitoring Vlaamse stranden - winter 2007/08. Rapport van het Instituut voor Natuur- en Bosonderzoek, R.2008.38. Instituut voor Natuur- en Bosonderzoek: Brussel, Belgium. 52 pp

2009

- Braeckman U, Frickel J, Vincx M, Vanaverbeke J (2009): 'Macrobenthos alters nematode vertical distribution' VLIZ Special Publication 41: 29
- Courtens W, Stienen EWM, Van de walle M, Verbelen D (2009). Monitoring van de SBZ-V 'Kustbroedvogels te Zeebrugge-Heist' en de SBZ-V 'Poldercomplex': resultaten van het vierde jaar (2008-2009). Rapport van het Instituut voor Natuur- en Bosonderzoek, 2009.38. Research Institute for Nature and Forest
- Courtens W, Stienen E, Van de walle M, Vanermen N, Verstraete H (2009). Mammals of the 'deep': shipbased surveys of cetaceans in the Belgian part of the North Sea (1992-2008). In: Mees J et al. (Ed.) (2009). VLIZ Young Scientists' Day, Brugge, Belgium 6 March 2009: book of abstracts. VLIZ Special Publication, 41: pp. 32,
- Degraer S, Braeckman U, Haelters J, Hostens K, Jacques T, Kerckhof F, Merckx B, Rabaut M, Stienen E, Van Hoey G, Van Lancker V, Vincx M (2009). Studie betreffende het opstellen van een lijst met potentiële Habitatrichtlijn gebieden in het Belgische deel van de Noordzee. Eindrapport in opdracht van de Federale Overheidsdienst Volksgezondheid, Veiligheid van de Voedselketen en Leefmilieu, Directoraat-generaal Leefmilieu. Brussel, België. 93 pp
- Everaert J, Stienen E. (2009). Impact of wind turbines on terns in Zeebrugge, Belgium. In: Stienen E et al. (Ed.) (2009). Seabird Group 10th International Conference, Brugge, Belgium 27-30 March, 2009: Book of abstracts. VLIZ Special Publication, 42, Communications of the Research Institute for Nature and Forest, INBO.M.2009 Forest, INBO.M.2009.1 Forest INBO.M.2009.1: pp. 20

- Lacroix G, McCloghrie P, Huret M, North EW (2009) Hydrodynamic models. In Manual of Recommended Practices for Modelling Physical – Biological Interactions during Fish Early Life, pp. 3 – 8. Ed. by North E W, Gallego A, and Petitgas P. ICES Cooperative Research Report No. 295. 111 pp.
- Larmuseau MHD (2009). Sea (in)sight – From phylogeographical insights to visual local adaptation in marine gobies. Ph.D. thesis, K.U.Leuven, 258 pp. Advisor: Prof. dr. Filip A.M. Volckaert; Co-Advisor: Dr. Jeroen K.J. Van Houdt. ISBN 978-90-8649-272-5
- Larmuseau MHD (2009) Sea (in)sight – From phylogeographical insights to visual local adaptation in marine gobies. Pp. 212-214 in: Mees J. & Seys J. (Eds.) An overview of marine research in Belgium anno 2009. 10th VLIZ Young Scientists' Day. Special edition at the occasion of 10 years VLIZ. Oostende, Belgium, 27 November 2009: VLIZ Special Publication, 43. Vlaams Instituut voor de Zee (VLIZ): Oostende, Belgium.
- Paris CB, Irisson J-O, Lacroix G, Fiksen O, Leis JM, Mullon C, (2009) Application 2: Connectivity. In Manual of Recommended Practices for Modelling Physical – Biological Interactions during Fish Early Life, pp.63-76. Ed. by North E W, Gallego A, and Petitgas P. ICES Cooperative Research Report No. 295. 111 pp.
- Rabaut M (2009) *Lanice conchilega*, fisheries and marine conservation: Towards an ecosystem approach to marine management. PhD thesis, Ghent University (UGent)
- Rabaut M, Vincx M, Degraer S (2009) Fisheries and marine conservation: How to proceed in a knowledge-poor environment? On the need of interaction between ecological research and marine management. In: McManus NF, Bellinghouse DS (eds) Fisheries: Management, economics and perspectives. Nova Science Publishers, New York, p 485-495
- Stienen E, Courtens W (2009). 10 jaar Sternenschiereiland: een jubileum met gemengde gevoelens Vogelnieuws 13: 19-25
- Stienen EWM, Brenninkmeijer A, van der Winden J (2009). De achteruitgang van de visdief in de Nederlandse Waddenzee: exodus of langzame teloorgang? Limosa 82: 171-186
- Vancampenhout K (2008-2009). 'Adaptation at the rhodopsin gene in the 'sand goby' group on species and population level.' **M.Sc. thesis**, Biology, Katholieke Universiteit Leuven.; Promoter: Prof. dr. Filip A.M. Volckaert, Monitor: Dr. Maarten H.D. Larmuseau.
- van Dijk JGB, Stienen EWM, Gerritsen S, Majoor F (2009). Reproductie van de kokmeeuw in kust- en binnenlandkolonies Limosa 82: 13-22
- Vanermen N, Stienen EWM, Courtens W, Van de walle M, Verstraete H (2009). Monitoring van de effecten van offshore windmolenparken op zeevogels Vogelnieuws 12: 4-9
- Verstraete H, Stienen EWM, Van de walle M (2009). Vogelstrandingen op de Vlaamse stranden - winter 2008/09. Rapport van het Instituut voor Natuur- en Bosonderzoek, R.2009.60. Instituut voor Natuur en Bosonderzoek (INBO): Brussel, Belgium. 43 pp

2010

- Braeckman U, Provoost P, Soetaert K, Middelburg J, Vincx M, Vanaverbeke J (2010) Influence of macrobenthos on nematode dynamics after a phytoplankton bloom. VLIZ Special Publication 44: 22

- Courtens W, Stienen EWM, Van de walle M, Verbelen D, De Bie J, Adams Y (2010). Eindrapport monitoring van de SBZ-V 'Kustbroedvogels te Zeebrugge-Heist' en de SBZ-V 'Poldercomplex': resultaten van het vijfde jaar (2009-2010). Broedseizoen 2009. Winterhalfjaar 2009/'10. Rapport van het Instituut voor Natuur- en Bosonderzoek, R.2010.59. Instituut voor Natuur en Bosonderzoek (INBO): Brussel. 41 pp
- Fijn RC, Courtens W, Verstraete H, Poot MJM, Stienen EWM (2010). Radio telemetry as an additional tool to study feeding behaviour of breeding Sandwich Tern and Common Tern in the shallow coastal zone of the Netherlands. Bureau Waardenburg/INBO: Culemborg, Brussel
- Stienen EWM, Van de walle M (2010). Vogelstrandings op de Vlaamse stranden winter 2009/10. Rapport van het Instituut voor Natuur- en Bosonderzoek, R.2010.55. Instituut voor Natuur en Bosonderzoek (INBO): Brussel. 38 pp.,
- Stienen E, Courtens W, Van de Walle M (2009). Why sandwich terns *Sterna sandvicensis* work hard in The Netherlands and live leisurely in Belgium. In: Stienen E et al (Ed.) (2009). Seabird Group 10th International Conference, Brugge, Belgium 27-30 March, 2009: Book of abstracts. VLIZ Special Publication, 42, Communications of the Research Institute for Nature and Forest, INBO.M.2009 Forest, INBO.M.2009.1 Forest INBO.M.2009.1: pp. 60
- Stienen E, Ratcliffe N, Seys J, Tack J, Mees J, Dobbelaere I (2009). Seabird Group 10th International Conference, Brugge, Belgium 27-30 March, 2009: Book of abstracts. VLIZ Special Publication, 42, Communications of the Research Institute for Nature and Forest, INBO.M.2009 Forest, INBO.M.2009.1 Forest INBO.M.2009.1. Flanders Marine Institute (VLIZ)/Research Institute for Nature and Forest (INBO): Brussels, Belgium. viii, 68 pp
- Vanaverbeke J, Merckx, B, Degraer S, Vincx M (2010) Sediment-related distribution patterns of the nematodes and macrofauna: two sides of the benthic coin? VLIZ Special Publication 44:77
- Vanermen N, Stienen EWM, Onkelinx T, Courtens W, Van de walle M, Verstraete H (2010). Monitoring seabird displacement effects by offshore wind farms: a modeling approach, in: Degraer, S. et al. (Ed.) (2010). Offshore wind farms in the Belgian part of the North Sea: Early environmental impact assessment and spatio-temporal variability. pp. 133-152,

2011 – in press

- Braeckman U (2011). Macrobenthos structuring the sea floor: importance of its functional biodiversity for the benthic ecosystem. PhD thesis, 182 pp.
- Cuveliers EL (2011). Connectivity and genetic stability in sole (*Solea solea*). Ph.D. thesis, K.U.Leuven, 256 pp. Advisor Prof. Dr. F.A.M. Volckaert; Co-Advisor G.E.Maes. ISBN 978-90-8649-389-0.
- Rabaut M, Cliquet A (in press) The dynamics of the marine environment versus the rigid interpretation of nature conservation law. In: Environmental Law Issues and Developments. Nova Science Publishers, New York

6. ACKNOWLEDGEMENTS

The Westbanks project was funded by the Belgian Science Policy Office (BELSPO) in the frame of the Science for Sustainable Development programme.

We would like to thank the master and crew of RV Belgica and RV Zeeleeuw for their skillfull and patient help during sampling occasions at sea. Conservators of the marine reserve "Baai van Heist" are acknowledged for granting permission to enter the reserve. Annick Van Kenhove, Dirk Van Gansbeke, Annelien Rigaux, Bart Beuselinck, Peter van Breugel, Marco Houtekamer and Pieter Van Rijswijk provided technical help and logistical support. The Institute for the Promotion of Innovation through Science and Technology in Flanders (IWT-Vlaanderen) provided additional funding to Els Cuveliers and Maarten Larmuseau. The Flemish Fund for Scientific Research (FWO Vlaanderen) provided funding for Marijn Rabaut and Ulrike Braeckman.

7. REFERENCES

- Beaumont N, Austen MC, Atkins JP, Burdon D, Degraer S, Dentinho TP, Deros S, Holm P, Horton T, Van Ierland E, Marboe AH, Starkey DJ, Townend M, Zarzycki T (2007) Identification, definition and quantification of goods and services provided by marine biodiversity: Implications for the ecosystem approach. *Mar Poll Bull* 54(3): 253-265
- Belkhir K, Borsa P, Goudet J, Chickhi L, Bonhomme F (2004). Genetix v. 4.01, logiciel sous windowstm pour la génétique des populations *Laboratoire Génome et Population, Université Montpellier 2, Montpellier*
- Boschker HTS, De Brouwer JFC, Cappenberg TE (1999) The contribution of macrophyte-derived organic matter to microbial biomass in salt-marsh sediments: stable carbon isotope analysis of microbial biomarkers. *Limnol Oceanogr* 44:309–319
- Boon AR, Duineveld GCA, Berghuis EM, van der Weele J (1998). Relationships between benthic activity and the annual phytopigment cycle in near-bottom water and sediments in the Southern North sea. *Est Coast Shelf Sci* 46: 1-13.
- Boudreau, B.P., 1998. Mean mixed depth of sediments: The wherefore and the why. *Limnol Oceanogr* 43, 524-526
- Bouma TJ, Olenin S, Reise K, Ysebaert T (2009) Ecosystem engineering and biodiversity in coastal sediments: posing hypotheses. *Helv Mar Res* 63:95–106
- Braeckman U, Van Colen C, Soetaert K, Vincx M, Vanaverbeke J (in press) Contrasting macrobenthic activities differentially affect nematode density and diversity in a shallow subtidal marine sediment. *Mar Ecol Prog Ser* doi: 10.3354/MEPS08910
- Braeckman U, Provoost P, Gribsholt B, Van Gansbeke D, Middelburg JJ, Soetaert K, Vincx M, Vanaverbeke J (2010) Role of macrofauna functional traits and density in biogeochemical fluxes and bioturbation. *Mar Ecol Prog Ser* 399:173-186
- Braeckman U, Provoost P, Moens T, Middelburg J, Soetaert K, Vincx M, Vanaverbeke J (under review) Biological vs. physical mixing effects on benthic food web dynamics. *PLoS One*
- Burt GJ, Millner RS (2008). Movement of sole in the southern North Sea and eastern English Channel from tagging studies (1955-2004). *Science Series Technical Report*:44.
- Byers JE, Cuddington K, Jones CG, Talley TS, Hastings A, Lambrinos JG, Crooks JA, Wilson WG (2006) Using ecosystem engineers to restore ecological systems. *Trends Ecol & Evol* 21:493–500
- Callaway R (2006) Tube worms promote community change. *Mar Ecol Prog Ser* 308:49-60
- Callaway R, Desroy N, Dubois S, Fournier J, Frost MT, Godet L, Hendrick VJ, Rabaut M (2010) Ephemeral bio-engineers or reef building polychaetes: how stable are aggregations of the tube worm *Lanice conchilega* (Pallas, 1766)? *Integrative and Comparative Biology* 50:237-250
- Caramujo M, Boschker HTS, Admiraal W (2008) Fatty acid profiles of algae mark the development and composition of harpacticoid copepods. *Fresh Biol* 53:77-90.

- Caron A, Desrosiers G, Olive PJW, Retière C, Nozais C (2004) Comparison of diet and feeding activity of two polychaetes, *Nephtys caeca* (Fabricius) and *Nereis virens* (Sars), in an estuarine intertidal environment in Québec, Canada. *J Exp Mar Biol Ecol* 304:225–242
- Cavalli-Sforza LL, Edwards AWF (1967). Phylogenetic analysis models and estimation procedures. *Am J Hum Genet* 19:233-257.
- Chapuis MP, Estoup A (2007). Microsatellite null alleles and estimation of population differentiation. *Mol Biol Evol* 24:621-631.
- Coleman FC, Williams SL (2002) Overexploiting marine ecosystem engineers: potential consequences for biodiversity. *Trends Ecol & Evol* 17:40-44
- Cuveliers EL, Geffen AJ, Guelinckx J, Raeymaekers JAM, Skadal J, Volckaert FAM, Maes GE (2010). Microchemical variation in juvenile *Solea solea* otoliths as a powerful tool for studying connectivity in the North Sea. *Mar Ecol Prog Ser* 401:211-220.
- de Pontual H, Lagardere F, Troadec H, Batel A, Desaunay Y, Koutsikopoulos C (2000). Otoliths imprinting of sole (*Solea solea*) from the bay of Biscay: A tool to discriminate individuals from nursery origins? *Ocean Acta* 23:497-513.
- Dalsgaard J, St. John M, Kattner G, Müller-Navarra D, Hagen W (2003) Fatty acid trophic markers in the pelagic marine environment. In: Academic Press, pp 225-340
- Dame R, Bushek D, Allen D, Lewitus A, Edwards D, Koepfler E, Gregory L (2002) Ecosystem response to bivalve density reduction: management implications. *Aquatic Ecology* 36:51-65
- Degraer S, Adriaens P, Courtens W, Haelters J, Hostens K, Jacques T, Kerckhof F, Stienen E, Vanermen N, Van Hoey G (2010). Bepalen van instandhoudingsdoelstellingen voor de beschermde soorten en habitats in het Belgische deel van de Noordzee, in het bijzonder in beschermde mariene gebieden. Eindrapport in opdracht van de Federale Overheidsdienst Volksgezondheid, Veiligheid van de Voedselketen en Leefmilieu, Directoraat-generaal Leefmilieu. Brussel, België. 132 pp.
- Degraer S, Braeckman U, Haelters J, Hostens K, Jacques TG, Kerckhof F, Merckx B, Rabaut M, Stienen EWM, Van Hoey G, others (2009) Studie betreffende het opstellen van een lijst met potentiële Habitatrichtlijngebieden in het Belgische deel van de Noordzee. Eindrapport, 93 pp
- Degraer 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. ISBN 90-810081-6-1. 164 pp
- Degraer S, Vincx M, Meire P, Offringa H (1999) The Macrozoobenthos of an Important Wintering Area of the Common Scoter (*Melanitta nigra*). *J Mar Biol Ass UK* 79:243-251
- Dempster AP, Laird NM, Rubin DB (1977). Maximum likelihood from incomplete data via the em algorithm. *Journal of the Royal Statistical Society Series B* 39:1-38.
- Depooter D (2010). Comparative study of the diet of common guillemots *Uria aalge* and razorbills *Alca torda*, collected during beached bird surveys along the Belgian coast between 2002 and 2010. MSc Thesis. University Gent/INBO.
- El Mousadik A, Petit RJ (1996). High level of genetic differentiation for allelic richness among populations of the argan tree *Argania spinosa* (L. Skeels) endemic to Morocco. *Theor Appl Gen* 92:832-836.

- Everaert J, Stienen EWM (2007) Impact of wind turbines on birds in Zeebrugge (Belgium). *Biodivers Conserv* 16: 3345-3359.
- Funes V, Zuasti E, Catanese G, Infante C, Machado M (2004). Isolation and characterization of ten microsatellite loci for senegal sole (*Solea senegalensis* kaup). *Mol Ecol Notes* 4:339-341.
- Gamarra R (2008) Experimental beam trawl effect on subtidal macrobenthic community associated to *Lanice conchilega* reefs. MSc thesis, Ghent University (UGent)
- Garoia F, Marzola S, Guarniero I, Trentini M, Tinti F (2006). Isolation of polymorphic DNA microsatellites in the common sole *Solea vulgaris*. *Mol Ecol Notes* 6:144-146.
- Gerino, M., Aller, R.C., Lee, C., Cochran, J.K., Aller, J.Y., Green, M.A., Hirschberg, D.(1998). Comparison of different tracers and methods used to quantify bioturbation during a spring bloom: 234-thorium, luminophores and chlorophyll a. *Est, Coast Shelf Sci* 46: 531-547.
- Godet L, Toupoint N, Olivier F, Fournier J, Retiere C (2008) Considering the Functional Value of Common Marine Species as a Conservation Stake: The Case of Sandmason Worm *Lanice conchilega* (Pallas 1766) (Annelida, Polychaeta) Beds. *Ambio* 37:347-355
- Goudet J (1995). Fstat (version 1.2): A computer program to calculate f-statistics. *Journal of Heredity* 86:485-486.
- Green MA, Aller RC, Cochran JK, Lee C, Aller JY (2002). Bioturbation in shelf/slope sediments off Cape Hatteras, North Carolina: the use of Th-234, Chl-a, and Br- to evaluate rates of particle and solute transport. *Deep Sea Res II: Topical Studies in Oceanography* 49, 4627-4644.
- Grémare A, Labrune C, Berghe V, Amouroux JM, Bachelet G, Zettler ML, Vanaverbeke J, Fleischer D, Bigot L, Maire O (2009) Comparison of the performances of two biotic indices based on the MacroBen database. *Mar Ecol ProgrSer* 382:297
- Hagy JD, Boynton WR, Jasinski DA (2005). Modelling phytoplankton deposition to Chesapeake Bay sediments during winter-spring: interannual variability in relation to river flow. *Est Coast Shelf Sci* 62: 25-40.
- Hall TA (1999). Bioedit: A user-friendly biological sequence alignment editor and analysis program for windows 95/98/nt. *Nucleid Acids Symposium Series* 41:95-98.
- Halpern BS, Selkoe KA, Micheli F, Kappel CV (2007) Evaluating and ranking the vulnerability of global marine ecosystems to anthropogenic threats. *Cons Biol* 21:1301–1315
- Hansen LS, Blackburn TH (1992) Mineralization budgets in sediment microcosms: Effect of the infauna and anoxic conditions. *FEMS Microbiol Letters* 102:33-43
- 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 Assoc U K* 86:665-677
- Herman PMJ, Soetaert K., Middelburg JJ, Heip C, Lohse L, Epping E, Helder W, Antia AN, Peinert R (2001). The sea floor as the ultimate sediment trap - using sediment properties to constrain benthic-pelagic exchange processes at the Goban Spur. *Deep Sea Res II: Topical Studies in Oceanography* 48, 3245-3264.

ICES-FishMap, 2005. *Solea solea*.

Iyengar A, Piyapattanakorn S, Stone DM, Heipel DA, Howell BR, Baynes SM, Maclean N (2000). Identification of microsatellite repeats in turbot (*Scophthalmus maximus*) and dover sole (*Solea solea*) using a RAPD-based technique: Characterization of microsatellite markers in dover sole. *Mar Biotechnol* 2:49-56.

Jeffrey SW, Mantoura RFC, Wright SW (2003). *Phytoplankton Pigments in Oceanography: Guidelines to Modern Methods*. UNESCO.

Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. *Oikos* 69:373-386

Josefson AB, Forbes TL, Rosenberg R (2002). Fate of phytodetritus in marine sediments: functional importance of macrofaunal community. *Mar Ecol Prog Ser* 230, 71-85

Kristensen E, Holmer M (2001) Decomposition of plant materials in marine sediment exposed to different electron acceptors (O₂, NO₃⁻, and SO₄²⁻), with emphasis on substrate origin, degradation kinetics, and the role of bioturbation. *Geoch Cosmochim Acta* 56(3): 419-433.

Lancelot C, Spitz Y, Gypens N, Ruddick K, Becquevort S, Rousseau V, Lacroix G, Billen G (2005). Modelling diatom and Phaeocystis blooms and nutrient cycles in the Southern Bight of the North Sea: the MIRO model. *Mar Ecol Prog Ser* 289: 63-78

Larmuseau MHD, Guelinckx J, Hellemans B, Van Houdt JKJ, Volckaert FAM (2008). Fast PCR-RFLP method facilitates identification of *Pomatoschistus* species from the North Atlantic. *J Appl Ichthyol* 24:342-344.

Larmuseau MHD, Huyse T, Vancampenhout K, Van Houdt JKJ, Volckaert FAM (2010a). High molecular diversity in the rhodopsin gene in closely related goby fishes: A role for visual pigments in adaptive speciation? *Mol Phylogenet Evol* 55:689-698.

Larmuseau MHD, Raeymaekers JAM, Hellemans B, Van Houdt JKJ, Volckaert FAM (2010b). Mito-nuclear discordance in the degree of population differentiation in a marine goby. *Heredity* 105:532-542.

Larmuseau MHD, Raeymaekers JAM, Ruddick KG, Van Houdt JKJ, Volckaert FAM (2009a). To see in different seas: Spatial variation in the rhodopsin gene of the sand goby (*Pomatoschistus minutus*). *Mol Ecol* 18:4227-4239.

Larmuseau MHD, Van Houdt JKJ, Guelinckx J, Hellemans B, Volckaert FAM (2009b). Distributional and demographic consequences of Pleistocene climate fluctuations for a marine demersal fish in the north-eastern Atlantic. *J Biogeogr* 36:1138-1151.

Larmuseau MHD, Vancampenhout K, Raeymaekers JAM, Van Houdt JKJ, Volckaert FAM (2010c). Differential modes of selection on the rhodopsin gene in coastal baltic and north sea populations of the sand goby, *Pomatoschistus minutus*. *Mol Ecol* 19:2256-2268.

Leakey CDB, Attrill MJ, Fitzsimons MF (2009). Multi-element otolith chemistry of juvenile sole (*Solea solea*), whiting (*Merlangius merlangus*) and european seabass (*Dicentrarchus labrax*) in the Thames estuary and adjacent coastal regions. *J Sea Res* 61:268-274.

Lehmann MF, Bernasconi SM, Barbieri A, McKenzie JA (2002) Preservation of organic matter and alteration of its carbon and nitrogen isotope composition during simulated and in situ early sedimentary diagenesis. *Geochim Cosmochim Acta* 66: 3573-3584

- 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.
- Lesley HM, McLead KL (2007) Confronting the challenges of implementing marine ecosystem-based management. *Front Ecol Environ* 5(10): 540-548
- Lindqvist S, Norling K, Hulth S (2009) Biogeochemistry in highly reduced mussel farm sediments during macrofaunal recolonization by *Amphiura filiformis* and *Nephtys* sp. *Mar Env Res* 67:136-145
- Librado P, Rozas J (2009). Dnasp v5: A software for comprehensive analysis of DNA polymorphism data. *Bioinformatics* 25:1451-1452.
- Loreau M, Naeem S, Inchausti P, Bengtsson J, Grime JP, Hector A, Hooper DU, Huston MA, Raffaelli D, Schmid B, Tilman D, Wardle DA (2001) Ecology - Biodiversity and ecosystem functioning: Current knowledge and future challenges. *Science* 294:804-808
- Luyten P, Jones J E, 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.
- Maire O, Duchene JC, Gremare A, Malyuga VS, Meysman FJR (2007) A comparison of sediment reworking rates by the surface deposit-feeding bivalve *Abra ovata* during summertime and wintertime, with a comparison between two models of sediment reworking. *J Exp Mar Biol Ecol* 343:21-36
- 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. *Aq Microb Ecol* 36:271-284
- MA (Millennium Ecosystem Assessment) (2005) Ecosystems and human well-being: current state and trends. Washington DC, Island Press
- Molnar JL, Gamboa RL, Revenga C, Spalding MD (2008) Assessing the global threat of invasive species to marine biodiversity. *Frontiers Ecol Environ* 6:485-492
- O'Brien K, Keegan BF (2004) Size-related reproductive biology of the infaunal bivalve *Abra alba* (Bivalvia) in Kinsale Harbour (south coast of Ireland). *Mar Biol* 146:65-77
- O'Reilly R, Kennedy R, Patterson A (2006) Destruction of conspecific bioturbation structures by *Amphiura filiformis* (Ophiuroidea): evidence from luminophore tracers and in situ time-lapse sediment-profile imagery. *Mar Ecol Prog Ser* 315:99-111.
- 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.
- Porta J, Alvarez MC (2004). Development and characterization of microsatellites from senegal sole (*Solea senegalensis*). *Molecular Ecology Notes* 4:277-279.
- Rabaut M (2009) *Lanice conchilega*, fisheries and marine conservation: towards an ecosystem approach to marine management. PhD Thesis Ghent University, Ghent, Belgium:354 p
- 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 (2009a) Policy analysis of the 'MPA-process' in temperate continental shelf areas. *Aquat Conserv* 19:596-608
- Rabaut M, Du Four I, Nakas G, Van Lancker V, Degraer S, Vincx M (in prep.-a) Ecosystem engineers stabilize sand bank systems: *Owenia fusiformis* aggregations as ecologically important microhabitat.
- Rabaut M, Gamarra R, Vincx M, Degraer S (in prep.-b) Experimental beam trawl effects on the subtidal macrobenthic community associated to *Lanice conchilega* reefs.
- Rabaut M, Guilini K, Van Hoey G, Vincx M, Degraer S (2007) A bio-engineered soft-bottom environment: The impact of *Lanice conchilega* on the benthic species-specific densities and community structure. *Estuar Coast Shelf Sci* 75:525-536
- Rabaut M, Van de Moortel L, Vincx M, Degraer S (2010) Biogenic reefs as structuring factor in *Pleuronectes platessa* (Plaice) nursery. *J Sea Res* 64:102–106
- Rabaut M, Vincx M, Degraer S (2009) Do *Lanice conchilega* (sandmason) aggregations classify as reefs? Quantifying habitat modifying effects. *Helg Mar Res* 63:37-46
- Rice J, Fátima Borges M, Grehan A, Kennedy A, Loeng H, Maynou F, Serraõ Santos R, Skjoldal HR, Thébaud O, Vassilopoulou V, Volckaert F (2010) Science dimensions of an Ecosystem Approach to Management of Biotic Ocean Resources (SEAMBOR). ESF Marine Board Position Paper 14
- Rijnsdorp AD, van Beek FA, Flatman S, Millner RM, Riley JD, Giret M, Declerck R (1992). Recruitment of sole stocks, *Solea solea* (L) in the northeast 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 effects of bottom trawling. *J Sea Res* 45:219–229
- Rousseau V, Leynaert A, Daoud N, Lancelot C (2002) Diatom succession, silicification and silicic acid availability in Belgian coastal waters (Southern North Sea). *Mar Ecol Prog Ser* 236:61-73
- Sargent JR, Whittle KJ (1981) Lipids and hydrocarbons in the marine food web. In: Longhurst, A.R. (Ed.) (1981). *Analysis of marine ecosystems*:491-533
- Sauter EJ, Schluter M, Suess E (2001). Organic carbon flux and remineralization in surface sediments from the northern North Atlantic derived from porewater oxygen microprofiles. *Deep Sea Res I: Oceanographic Research Papers* 48: 529-553.
- Savina M, Lacroix G, Ruddick K (2010). Modelling the transport of common sole larvae in the Southern North Sea: Influence of hydrodynamics and larval vertical movements. *J Mar Sys* 81:86-98.
- Soetaert K, Herman PMJ, Middelburg JJ (1996). Dynamic response of deep-sea sediments to seasonal variations: A model. *Limnol Oceanogr* 41(8): 1651-1668
- Soetaert K, Herman PMJ, Middelburg JJ, Heip C (1998). Assessing organic matter mineralization, degradability and mixing rate in an ocean margin sediment (Northeast Atlantic) by diagenetic modeling. *J Mar Res* 56: 519-534.
- Somaschini A (1993) A mediterranean fine-sand polychaete community and the effect of the tube-dwelling *Owenia fusiformis* Delle Chiaje on community structure. *Int Rev Ges Hydrobio* 78:219-233

- 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, Brenninkmeijer A, (2002). Foraging decisions of Sandwich Terns in the presence of kleptoparasitising gulls. *Auk* 119: 473-486
- Stienen EWM, Courtens W (2010). Advies betreffende de effecten van kite-surfen op zeevogels. Advies van het instituut voor Natuur- en Bosonderzoek (INBO), INBO.A.2010.215, Brussel.
- 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.
- Sun MY, Lee C, Aller RC (1993) Laboratory studies of oxic and anoxic degradation of chlorophyll-a in Long-Island Sound sediments. *Geochim CosmochimActa* 57: 147-157
- Vanaverbeke J, Braeckman U, Cuveliers EL, Courtens W, Huyse T, Lacroix G, Larmuseau MHD, Maes GE, Provoost P, Rabaut M, Remerie T, Savina M, Soetaert K, Stienen EWM, Verstraete H, Volckaert FAMJ, Vincx M (2009). Understanding benthic, pelagic and airborne ecosystem interactions in shallow coastal seas "WestBanks": Final Report Phase 1. Belgian Science Policy: Brussel, Belgium
- 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.
- Van Hoey G (2006) Spatio-temporal variability within the macrobenthic *Abra alba* community, with the emphasis on the structuring role of *Lanice conchilega*. PhD thesis, Ghent University (UGent)
- Van Hoey G, Borja A, Birchenough S, Buhl-Mortensen L, Degraer S, Fleischer D, Kerckhof F, Magni P, Muxika I, Reiss H, Schröder A, Zettler ML (2010) The use of benthic indicators in Europe: From the Water Framework Directive to the Marine Strategy Framework Directive. *Marine Pollution Bulletin* 60:2187-2196
- Van Hoey G, Guilini K, Rabaut M, Vincx M, Degraer S (2008) Ecological implications of the presence of the tube-building polychaete *Lanice conchilega* on soft-bottom benthic ecosystems. *Mar Biol* 154:1009-1019
- van Oevelen D, Soetaert K, Franco MA, Moodley L, van IJzerloo L, Vincx M, Vanaverbeke J (2009) Organic matter input and processing in two contrasting North Sea sediments: insights from stable isotope and biomass data. *Mar Ecol Prog Ser* 380:19-32
- van Oosterhout C, Weetman D, Hutchinson WF (2006). Estimation and adjustment of microsatellite null alleles in nonequilibrium populations. *Mol EcolNotes* 6:255-256.
- Vasconcelos RP (2007). Discriminating estuarine nurseries for five fish species through otolith elemental fingerprints. *Mar Ecol Prog Ser* 350:117-126.
- Vitousek PM, Aber JD, Howarth RW, Likens GE, Matson PA, Schindler DW, Schlesinger WH, Tilman DG (1997) Human alteration of the global nitrogen cycle: sources and consequences. *Ecol Appl* 7:737-750
- Volkman JK, Barrett SM, Blackburn SI, Mansour MP, Sikes EL, Gelin F (1998) Microalgal biomarkers: a review of recent research developments. *Org*

- Geochem 29:1163–1179 Zühlke R (2001) Polychaete tubes create ephemeral community patterns: *Lanice conchilega* (Pallas, 1766) associations studied over six years. J Sea Res 46:261–272
- Worm B, Barbier EB, Beaumont N, Duffy JE, Folke C, Halpern BS, Jackson JBC, Lotze HK, Micheli F, Palumbi SR (2006) Impacts of biodiversity loss on ocean ecosystem services. Science 314:787
- Zühlke R, Blome D, van Bernem KH, Dittmann S (1998) Effects of the tube-building polychaete *Lanice conchilega* (Pallas) on benthic macrofauna and nematodes in an intertidal sandflat. Senckenb Marit 29:131-138
- Weir BS, Cockerham CC (1984). Estimating F-statistics for the analysis of population structure. Evolution 38:1358-1370.
- Westrich JT, Berner RA (1984) The role of sedimentary organic matter in bacterial sulfate reduction: The g-model tested. Limnol Oceanogr 29(2): 236-249.