Marijn Rabaut

Lanice conchilega, fisheries and marine conservation

Towards an ecosystem approach to marine management

LANICE CONCHILEGA, FISHERIES AND MARINE CONSERVATION

Towards an ecosystem approach to marine management

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LANICE CONCHILEGA, FISHERIES AND MARINE CONSERVATION

Towards an ecosystem approach to marine management

LANICE CONCHILEGA, VISSERIJ EN MARIENE BESCHERMING

Naar een ecosysteembenadering voor het beheer van de zee

Marijn Rabaut

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DANKWOORD

Een doctoraat schrijven is je jong leven opofferen

Dit zijn de woorden waarmee Magda me over de streep trok om een doctoraat te beginnen. Ik beschouw mijn jong leven nog niet afgerond en als een opoffering heb ik het niet mogen ervaren. Wel heb ik de zogenaamde academische vrijheid mogen proeven. Ze bestaat dus echt.

Zoals ik echter op zee geen al te sterke deining kan verdragen - en dat is een eufemisme-, zo had ik absolute nood aan een duidelijke richting en die heb ik gekregen van mijn (co)promotoren Steven en Magda.

Magda, ik kan soms wel doordraven over koffie of tonijn, maar dat belette je niet om wetenschappelijk heel duidelijk achter me te blijven staan. Zonder die steun was het me nooit gelukt. Met zachte dwang leerde je me hoe om te gaan met experimenten en de daarmee gepaard gaande tegenslagen. Je toonde waarheen het kon gaan en opende deuren. Tenslotte leerde ik veel meer dan wetenschap alleen; je leerde me de complexiteit aanvoelen van 'wetenschap bedrijven', en dat gaat een stuk verder dan wetenschappelijke resultaten produceren. Ik heb een flink stuk naïviteit verloren (dus misschien heb je toch gelijk wat de opoffering van het jonge leven betreft).

Steven, toen ik aan het MPA-verhaal begon, heb jij concrete inhoud en richting gegeven voor mijn doctoraat. Je zette het 'Lanice-verhaal' op de sporen. Het vele overleggen en zoeken naar gepaste staalnametechnieken en benaderingen hebben me vooruit geholpen. Oprechte dank voor de begeleidende taak die je vastberaden op je hebt genomen.

Wormenadvocaat

Vóór mij was het pad al wat geëffend. '*Lanice conchilega* specialist' Gert van Hoey was zijn doctoraat aan het afronden toen ik begon. Gert, je doctoraat en je advies bleven ontzettend belangrijk tijdens het schrijven. Intussen weten we dat niet alleen de kokerworm maar ook een uitgebreid aperitief en avondmaal (om Oregon Pinot Gris niet te noemen) gedeelde interesses zijn.

Goed, ik wou dus iets gaan aanvangen met de schelpkokerworm, die zo interessant bleek, en onderzoeken hoe die zich verhoudt t.o.v. visserij en natuurbeheer. Hiervoor zouden niet alleen ecologisch onderzoek en experimenten nodig zijn, maar ook de juridische aspecten kwamen al snel boven drijven. Jan Schrijvers was de eerste die me hierin wegwijs maakte en algauw leerde ik op het Maritiem Instituut An Cliquet en Frank Maes kennen; en via hen ook Dirk Bogaert.

An, je nam altijd de tijd om de wettelijke puntjes op de 'i' te leren zetten en om te discussiëren over wat kan en/of moet. Daarnaast was er steeds tijd om een beetje bij te kletsen en zo kreeg de inhoud van een artikel en een boekhoofdstuk stilaan vorm.

Sofie Derous was diegene die me inwijdde in de wereld van de biologische waarderingskaarten en die de input heeft geleverd voor de discussie rond het MPA-proces waarin de juridische aspecten naast de ecologische en economische werden geplaatst.

Zand, modder, kokers en vis

Voor het sedimentologische aspect en vooral voor de akoestische waarnemingen van de schelpkokerworm was het bijzonder fijn om samen te werken met mijn studiegenote Isabelle Du Four onder begeleiding van Vera Van Lancker.

Vera, ik heb enorm veel opgestoken van de Belgica-campagnes en hoop dat we in de toekomst op hetzelfde elan verder kunnen!

Voor de zoektocht naar jonge platvis vaarde ik ook wel eens buiten de Belgische wateren. Zo kwam het dat ik mee kon met Jan van Dalfsen. Jan, de *drive* waarmee jij de zee op ging, je onderwatercamera testte, de stalen opspoelde etc. werkte heel aanstekelijk, zelfs al werd de deining op de ondiepe Waddenzee me al snel te veel. Het was een bijzonder mooie ervaring.

Des expériences avec un chalut

Mijn allereerste experimenten heb ik uitgevoerd in Boulogne-sur-mer. Voor de verstoringen waren we afhankelijke van een kleine Franse boot en dito schipper. De staalnames gebeurden in de winter, ook ’s nachts. Gelukkig was dit het moment waarop ik mijn eerste thesisstudenten ‘in dienst’ had. Kaat en Ulrike, jullie enthousiasme en werklust waren cruciaal om het experiment te laten slagen. Beide mastertheses droegen in belangrijke mate bij aan het doctoraat. Intussen zijn we niet alleen al een aantal jaren collega’s, maar is er een vriendschap ontstaan om te koesteren. Ook voor andere experimenten had ik het geluk te kunnen rekenen op de leergierigheid van masterstudenten. Achtereenvolgens werkte ik samen met Giorgos Nakas (uitwerken van de *Owenia*-stalen), Rocio Gamarra (subtidaal boomkorexperiment) en Liesbeth Van de Moortel (link *Lanice*-platvis).

GLMMs zijn hot

Statistiek is een vreemd beestje; ik heb er een haat-liefde verhouding mee. Frederik Hendrickx is de man die erin slaagt het boeiende aspect van veralgemeende lineaire gemengde modellen (GLMMs dus) te belichten. Frederik, statistiek is een uitdaging die je me met volle goesting hebt doen aangaan. Tot op het laatste moment kon ik je bellen om nog iets uitgelegd te krijgen.

De doctoraatsstudent schrijft alles zelf

Onjuist natuurlijk. Dat alle hoger genoemde mensen een duidelijke stempel op mijn werk hebben gedrukt bewijst dit doctoraat. Ik ben blij dat jullie namen in de auteurslijst van één of meerdere van mijn schrijfsels staan. De finale kwaliteitscontrole kwam natuurlijk van de jury, waarvoor dank.

Een doctorandus is een betaalde student

Dat klopt ongeveer. Als doctoraatsstudent bleef ik inderdaad wel tussen de studenten hangen, zij het steeds vaker als begeleider. Naast de vijf thesisstudenten die ik al heb vernoemd, bleek de kokerworm een ideaal onderzoeksobject om bachelofproeven aan te wijden (met dank aan Delphine, Tessa, Charlotte, Joke, Hans, Hannes, Lieven en Peter voor de geleverde input). Ook het begeleiden van practica was fijn. Vooral op de praktijkstages in Wimereux is het enthousiasme van biologen-in-spe bijzonder aanstekelijk.

Macrofiel?

Het is fijn werken op ons labo; ik vermoed dat zowat iedereen van de collega's ooit eens is meegeweest op één van mijn staalnames op zee of op het strand. Iedereéén wordt bij deze nog eens oprecht bedankt. Zelfs voor de heel intensieve staalnameperiodes stonden altijd snel enthousiaste collega's klaar. Ook toen ik de labowagen gezwind in het Franse zand plantte werd er niet gemord maar simpelweg naar een oplossing gezocht (dank aan Annick, Lies, Annelies, Bart, Carl, Jeroen en Veronique). Toen ik op een bepaald moment zelf kokerwormen begon te knutselen, beschikte ik in een mum van tijd over een leger creatieve vrijwilligers, zelfs uit het 'professorenkorps' (dank Ann Vanreusel). En altíjd had Dirk een lumineus idee om een technisch probleem op te lossen, altijd maakten Annick en Isolde me wegwijs in verschillende procedures en administraties, altijd stonden Danielle, Guy en Bart paraat om te helpen. Als ik weer eens een shape file nodig had of iets gemodelleerd wou zien dan deed Bea dat met de grootste vanzelfsprekendheid. Ook buiten het labo vond ik voor die shapefiles hulpvaardige mensen: dank u Els Verfaillie (UGent) en Klaas Deneudt (VLIZ)! Nog meer technische ondersteuning kwam van het VLIZ: Dré dacht actief mee over hoe de Zeeleeuw kon worden ingezet voor mijn onderzoek, Lies zette mijn data in propere databanken, Ward hielp me aan o.a. 'MarBEF-nummers' en Tjess bezorgde me de Zeeleeuwdata, bij Jan Seys en Jan Mees kan je altijd raad krijgen etc... . Dank zij verschillende projecten leerde ik ook de mensen van het ILVO kennen. Kris, Gert, Jochen, Karl, Hans, Annelies, Sofie, Daan,... ik hoop dat we nog vele projectjes en projecten samen kunnen aanpakken. Karl, ik bewonder je gave om beestjes te fotograferen; dank voor het mooie beeldmateriaal (en voor je eeuwig enthousiasme natuurlijk). Eric en Wouter (INBO) leerden me veel bij over zeevogels (al blijf ik een leek!). Eric bezorgde me de nodige referenties als ik toch eens iets over vogels wou schrijven. Ook Jan en Francis (BMM) wil ik vernoemen: zoals je weet hebben jullie mijn doctoraat beïnvloed tijdens de soms toch uitdagende discussies. Michael Fettweis (BMM) stuurde me heel snel de gevraagde 'turbiditeitsartikels' op in de drukke eindsprint. Voor mij was het uitzonderlijk dat ik niet alleen met wetenschappelijke instituten, maar ook met beleidsmensen in dialoog kon gaan. Voor 'strandaangelegenheden' was het een genoegen om Jean-Louis Herrier te leren kennen (met dank aan natuurwachter Koen om me telkens weer in het reservaat toe te laten). Voor de echte 'zee-zaken' kwam ik dan weer terecht bij de federale overheidsdiensten. Geert, Wendy, Steven (en later ook

Saskia): dank voor het luisterend oor; ik hoop dat dit doctoraat voor jullie effectief als ondersteunend wordt ervaren!

Geen marien onderzoek zonder zee. Het Belgische deel van de Noordzee leerde ik kennen vanop de Belgica en de Zeeleeuw. De bemanning op beide schepen toonde zich altijd heel hulpvaardig. Zonder jullie zou het niet gelukt zijn! Buiten de Belgische wateren kon ik rekenen op de de mensen van de Herman Simon (Nederland) en de Sepia II (Frankrijk) voor de logistieke steun.

Ik wil hier zeker ook onze relatief nieuwe 'denktank' van de macrobenthologen ('de macrofielen') danken (Carl, Joke, Karen, Ulrike, Jan, Delphine, Sarah, Bea, Liesbeth, Pieter maar ook de 'oudgedienden' Annick, *Backi* en Wouter) . Op onze Macrobiol-bijeenkomsten is gezellig discussiëren de norm, of het nu gaat over wormen, duikers, windmolens, mossels of strandvlooien. Af en toe moet een mens eens kunnen nakaarten. Voor een avondje uit was het soms moeilijk om geen bereidwillige collega's te vinden, niet waar Jeroen (Dr. Jos), Karl (TL), Kaat, Uli, ...?

Doctoreren is reizen

Dat lijkt inderdaad wel zo. In het kader van internationale netwerken, symposia, congresssen en workshops heb ik vaak interessante mensen mogen ontmoeten die mijn doctoraat in belangrijke mate hebben beïnvloed en waaraan ik leuke herinneringen en warme vriendschappen heb overgehouden. Voor ik het besefte maakten we een daguitstap rond Klaipeda met Karsten, Nils, Christian en Judith. Ook Tjeerd was daar en hij is diegene die me leerde op een andere manier nadenken over het concept van 'ecosysteemingenieur'. Gareth en Francesc, dank voor de gezellig avonden in Klaipeda (*pigs ears*) en in Valencia... Olivier, Sébastien en Caroline blijf ik me herinneren als een jolig Frans trio tijdens de plezante avonden in Sesimbra. Gregory, Els, Mari, Ana, Fien en vele anderen maakten er een warm platvissensymposium van. Ik kan onmogelijk iedereen noemen, maar de mensen van het CRESCO in Dinard wil ik hier toch heel expliciet danken. *Merci Laurent, Jérôme, Nicolas et tous les collègues!* Tijdens een workshop daar aan de Bretoense kust had ik het geluk om Ruth Callaway –dé *Lanice*-specialiste- te leren kennen. *Ruth, thanks for all your inspiring comments!* We beleefden een heel intensieve workshop met nog meer indrukwekkende mensen als

Stanislas Dubois, Matt Frost, Vicky Hendrick, etc. Het leverde me een pak ‘grondstof’ op voor de algemene discussie van het doctoraat. Dank!

De kokerworm enthousiasmeert

Zeg nooit dat mensen niet geïnteresseerd zijn in wormen. Vooral op het einde van mijn doctoraat, toen ik mijn vrienden vroeg om te helpen met dingen waar ik zelf niet bepaald goed in ben, sloeg de vlam over. Klaas begon prompt uren te werken aan de montage van een filmpje, Dirk las als een gek al mijn artikels om met die kennis in de huid van de schelpkokerworm te kruipen en zijn levensverhaal op te tekenen. Mijn zus Lore heeft uren, dagen en weekends gespendeerd om de kokerworm te schetsen zoals zij hem zag en de layout te krijgen tot wat het geworden is. Tim en Olivier grepen de kokerworm dan weer aan om er culinaire hapjes mee te verzinnen. Al dit enthousiasme is het mooiste geschenk dat ik kon krijgen.

De ‘BTC-vrienden’ dank ik voor het ontspannende weekend net voor het indienen. Quinten, dank voor je oprechte interesse in ‘mijn opstel’. Het ‘transitiegroepje’ van de Brugse Poort leverde enthousiasme en inspiratie. Merci! Dirk, Jeroen, Johanna, Charlotte, Evelien, Lore en Liesbeth: het ‘artalistatie-weekend’ midden in mijn doctoraatsstress was een vlucht uit tijd en ruimte om te blijven herinneren. En dank voor de leuke loopmomentjes, Elisabeth! Ine, Hannelore en Isabelle: onze ‘marelacdineetjes’ vind ik echt gezellig. Veerle en Maarten: de legendarische pelgrimtocht dwars door Frankrijk was zalig, net als alle culinaire fietsweekendjes in navolging hiervan. De duikreizen naar de Costa Brava, steevast met enthousiaste biologen leerden me veel bij over het onderwaterleven. Het tellen van slijmvisjes samen met Joke en Katja zal ik nooit vergeten!

En dan zeg ik vaneigens ook nog ‘danke’ aan Wowo, Els, Klaas, Elisabeth, Tim, Valérie, Loes, Jan, Lot, Pieter, Katrien, Jeroen, Evelien, Bert, Lies, Peter, Anke, Bert, Stijn, Wim, Manu, Maarten, Veerle, Sarah en Matthias voor jullie betrokkenheid van dichtbij of iets verderaf en voor jullie deugddoende aanwezigheid op menige feestelijkheid.

Ook mijn moetie is enthousiast geworden over mijn onderzoeksobject. Interessante disucussies rond visserij, visconsumptie etc. werden dan ook plots familiegesprekken. Jullie onvoorwaardelijke steun gaf me een enorm comfortabel gevoel. Dank u, moetie en Michael.

Steun van dezelfde grootteorde mocht ik ervaren van mijn schoonouders: merci, Patrick en Martine!

Nelle en Kim, Jeronte en Vlientje, Lore: jullie betekenden zoveel in de aanloop naar dit doctoraat. En Morris, vanaf nu maak ik massa's tijd voor je (en ja, je mag eens mee in 'mijn' vliegtuig).

Visserij, mariene bescherming en Lanices aan de ontbijttafel

Mijn lief, mijn vrouw. Heb ik van jou een bioloog gemaakt of jij van mij een 'goede wetenschapper *s.l.*'? Ieder experiment hebben we samen bediscussieerd, iedere letter van mijn doctoraat passeerde je kritische oog. Het is duidelijk dat we al jaren aan een visie timmeren. Het is even duidelijk dat dit een weerslag heeft op dit doctoraat. Je aandeel in dit werk kan niet overschat worden. Want zonder jou was ik ik niet. Ik kijk uit naar de rest van ons leven! Liefs,

Marijn

Gent, 25 november 2009

Het doctoraat kwam tot stand met de financiële steun van het Fonds Wetenschappelijk Onderzoek – Vlaanderen (FWO-Vlaanderen) en de Universiteit Gent (UGent)

PROLOOG

Een verhaal

Dirk Elst en Liesbeth Hiele

De Visser.

(Liesbeth)

'Godverdoms stierewere',

Ze waren gisterenavond rond *ten achten* vertrokken en sindsdien was het nog niet opgehouden met gieten. 't Goot evenveel als dat er oude wijven zijn in Oostende. Het water droop niet, het stroomde langs Pieres neus, op zijn gele jekker en via zijn *botten* het dek op. Daarbij was de wind nog naar 't noorden gekeerd en moesten ze de luwte van de Wenduinebank opzoeken om de garnalen te volgen.

'k gon godverdomme nog natter zin van die rène dan van t zèwater.'

Het was de laatste sleep en *subit* zouden ze het net binnenhalen. Piere schatte dat ze nu al 70 kilo *gèrnaars* in het koelruim hadden liggen van de de vorige twee slepen. Het gebeurt niet zo veel dat ze de garnalen in vier keer moesten koken.

't Is e bèrejoar vo de gèrnaars, atter van de joare ien durft piepn dam der te vele ut aln, ewe, e krigt e tettelokker achter ze kop'

Ollène spittig dat de prijs naar beneden gaat met de aanvoer, maar niet mee omhoog met de diesel.

Nog een keer binnenhalen, spoelen, sorteren, *'n overschot were t zètje in* en de *goeie gèrnaars* koken.

'An ze twie euro nalf aln, en ke me pintje verdiend vannuchtnt'

Piere begon *gereed* de diesel op te stoken, zodat de ketel pekel al *were e bitje* kon beginnen schuimen. De pekel *zelve* was al wat dik geworden.

'Nog eki zuk e noop en k gon me lepel drin kun rechte zetn'

De *moteur* pruttelde tegen. Van deze keer zat het gelijk wel heel zwaar.

Of...

Piere zette de machine *in hank* om het net op te halen.

Wanneer het net boven kwam, vielen Pieres schouders naar beneden.

'Me zin in de drèndels gesloan, chance nog dat de nette nie gescheurd is.'

't Is goed te weten dat de *gèrnoars* eten vinden tussen die *drèndels*, maar 't is verdomme ambetant als ze je netten verstoppen.

Lanice conchilega.

(Dirk)

Het lijkt buiten nogal grijs vandaag. Ik stak vanmorgen een tentakel uit en voelde onmiddellijk hoe het met het water was gesteld. Wisselvallig en somber overigens. Niet echt mijn ding. Ik leef op het ritme van het licht, de kleur ervan en grijs ontmoedigt me een beetje.

Vandaag gaat het stormen, neem dat gerust van mij aan. Tegen de middag zal de stroming zo fel zijn dat al het plankton me tussen de vingers -excuseer tentakels- zal glippen. Honger zal mijn deel worden. Ik blijf binnen vandaag, daar valt niets tegen in te brengen, indien je daartoe een poging zou ondernemen natuurlijk. Ga gerust je gang. Ik verroer me niet. Hoogstens zal ik wat bodemzand en keitjes oppoetsen, polieren en tegen de avond misschien als het niet te koud wordt, zal ik wat aan mijn koker prutsen.

Hij mag gerust wat langer, bedenk ik me plots.

'Er is onheil op komst', was mijn eerste gedachte vanochtend. In de hoop er op voorbereid te zijn nog voor het zijn afschuwelijke grijze kop toont, dacht ik dat. Dit keer speelde de afgelopen nacht -geen al te kwalijke overigens- me geen parten. Ik zweer het je: Het enige wat ik er aan overhield was een onbestemd gevoel in mijn darmkanalen alsof een kei op mijn naakte lijf lag en wat ik ook deed, ik kreeg hem er niet af.

Moet je nu eens kijken wat de buren doen? De sukkels zijn zich van geen kwaad bewust. Op dit vroege uur verliezen ze zich al in het voorlopige geluk van alledag. Alsof ze met hun diepwaterballet de tijding kunnen keren. Of oefenen ze al hun fameuze liefdespirouette? Dat is wat vroeg, niet? Tja, wie zal het zeggen, de laatste jaren kennen wij hier op de bodem enkel een langgerekt seizoen, niemand geraakt er nog wijs uit. Zolang er niemand nu al met zaad en eitjes begint rond te strooien is het wel oké. Wat moet je tijdens deze lange dagen en zo dicht op elkaar? Tijdens deze trage uren in het heerlijke niets? Lang zal het niet duren vooraleer iemand het in zijn kop haalt om in deze periode van het jaar de gebruikelijke vruchtbaarheidsriten werkelijk uit te voeren.

Wel mooi om naar te kijken. Ik word in ieder geval heel rustig van al dat gekronkel vanuit de ontelbare kokers, die hier opeengepakt staan. Typisch dat ik weer aan de kant sta en vanuit het kijkgat in mijn koker kijk naar het leven, dat zich binnen die kleine cirkel in slow motion voltrekt. Vandaag waag ik me niet aan een ruime blik -breedbeeld zo je wil. Het lijkt me te eng en het gevoel dat zich in mijn ranke lijf ophoudt is naar mijn wormenmening al bangelijk genoeg.

Wanneer je er zo naar kijkt, met een onbevangen blik van een niet-deelnemer, zou je kunnen zeggen dat wij kokerwormen, met ons sierlijk gladde lijf, overgeleverd zijn aan de grillen van de stroming, maar dat is niet zo. Wij zitten hier al te lang om de elementen slaafs te ondergaan. In feite duwen wij ons geluk in de richting die ons het zachtst lijkt. De rest gaat vanzelf, het water doet zijn werk en wij schuiven er op onze golven doorheen. Zoals de zeeslangen, maar dan niet zo lomp natuurlijk.

Als ik hier nu zo rondkijk dan valt het me op dat er al heel wat kokers zijn bijgebouwd. En ook dat vind ik oké. Zo palmen wij hier samen als een groot lijf de onmetelijke ruimte in, zo innen wij ze en richten ze in zoals wij ze zien. Het is ook veiliger voor onze bezoekers, de stroming euhm... stroomt dan minder en op die manier zijn zij meer op hun gemak. En als de gast tevreden is dan is de gastheer dat in een ruk toch ook, niet?

Ooit was dat wel anders.

Twee jaar geleden woonde ik op een andere plek op de zeebodem. Tot die rampzalige dag. Vandaar dat ik nogal gevoelig ben voor de gemoedswisselingen van de wijde zee.

Het begon allemaal op een grijze ochtend zoals vandaag. Ik deed mijn ochtenddans en zwierde enthousiast met mijn tentakels. Behoedzaamheid was me vreemd in die dagen.

Die dag begon echter stiller dan gewoonlijk, alsof er ergens iets op de loer lag dat ons petje te boven ging. Het water zat vol stofdeeltjes, glinsterend in het flauwe schijnsel van de zon. Het voelde ijzig aan en de platvissen die zich normaal gezien in het zand onderstoppen en daar uren stil liggen, zag ik die ochtend laag over de bodem wegschieten. Iets gaf het startschot die dag.

Kortom, het zat behoorlijk scheef. Ik volgde mijn gevoel en kronkelde door de glinsterende wolk stofdeeltjes en liet me terug in mijn koker zakken.

Nog voor ik me goed en wel geïnstalleerd had, hoorde ik een naderend gebrom. De bodem trilde en het onheilspellend geluid zwol aan. Boven mij schoof er een reusachtige schaduw voor de zon. Ik dacht eerst aan een rog of een haai maar die maken niet zo'n hels kabaal, in tegendeel: ze zijn meestal heel stil, wanneer ze jagen tenminste. Neen, de schaduw was veel groter en schoof traag over onze nederzetting en in de verte kwam er enorme stofwolk van op de bodem razendsnel dichterbij. Beiden -schaduw én stofwolk- stonden in een gek verband met elkaar: Wanneer de ene boven ons hoofd van ons weggleed dan kwam de andere op de bodem met dezelfde snelheid dichterbij. Ik werd bang, alles veranderde binnen enkele seconden: de smaak van het water, het geluid van de zee, haar schemerduisternis en haar zilte geur werd een mengeling van steen en gas, dat hier af en toe uit de bodem schiet.

Mijn koker schudde en beefde. Door de opening bovenaan zag ik al andere kokers als engelen in het schijnsel door het water voorbij tuimelen. Ondertussen kraakte en knarste alles rondom mij. Ik was in paniek en gelaten tegelijk. Ontredderd zou je kunnen zeggen. Een aal die denkt dat hij altijd al de jager was maar plots beseft dat hij op enkele seconden prooi geworden is. Zoiets.

Ik trok mijn tentakels in, tegen mijn lijf, op hetzelfde moment ontplofte mijn koker, als een te nauw kleedje rond mijn lijf. De kracht waarmee het gebeurde scheen -vreemd genoeg- van binnenuit te komen. Het was ijskoud, modder kolkte en schuurde tegen mijn vel. Terwijl ik tuimelde als een eitje uit een moederworm, verloor ik alle controle op de situatie: ik gaf me over. Je reageert enkel nog instinctief omdat elke cel in je lijf het zo dicteert. Je ondergaat het en dat is alles.

En dan werd alles in een knip rustig. Ik plooide me recht en zag de modderwolk verder over de bodem in de donkere diepte verdwijnen. Het gebrom en getril ebde langzaam weg. Het was voorbij en ik geloofde er niets van. Tot op de dag van vandaag herinner ik enkel wat fragmenten van de ramp, maar ik krijg ze nooit tot een geheel. Ik zie dan lange aaneengeknoopte slierten zeewier die het kolkende modder voortdrijven, uiteengereten platvissen en andere kokerwormen die slap als dode planten met de razernij mee draaien. Naar mijn gevoel stroken die verbrokkelde beelden niet helemaal met de realiteit die veel groter en vreemder was dan de mijne. Je ziet enkel wat je werkelijk kent, denk ik dan.

Achteraf lag ik languit op de bodem en sloeg voorzichtig met een tentakel naar het schijnsel van de zon, die flauw door de dikke glinsterende mist scheen. Hij viel onmiddellijk terug in het zand dat opwaaide en een bedje spreidde. Wat een geluk: Ik ben niet geraakt, suste ik mezelf. Ik hief nog een andere tentakel op en ook hij liet zich onmiddellijk vallen. De zee drukte nog te krachtig om rond te dansen. Mijn vermoeidheid was immens, mijn bewegingen nog nooit zo traag.

Tegen beter weten in testte ik toch al mijn tentakels op kneuzingen of breuken en ik had geluk: buiten die drukkende moeheid in mijn leden was ik heelhuids door die vreemde storm geraakt. Ik lag nog uren verlamd op de bodem van de zee, in het zachte zand, deels ook om van de schrik te bekomen. Toen ik mezelf voorzichtig van de bodem tilde en traag door het waterruim zweefde zag ik pas de omvang van de ramp. De tornado had niets ontzien, alles was grijs en overhoop, hier en daar zweefde stukken van planten door het flauwe zonlicht. Voor de rest was de bodem kaal. Zo grijs en eenzaam zag de zee er nog nooit uit.

Een koude verlamde me van binnenuit. Ik weet niet hoe lang ik daar zo verloren door de zee zweefde maar het voelde aan als een eeuwigheid. In het begin dacht ik vlug te sterven, ik had me daar al op ingesteld, maar mijn lijf bleef zich -vreemd genoeg- bewust van de koude, van de stroming, van de rommel die af en toe tegen me aan sloeg. Ik voelde me zoals de dode rog, die boven mijn hoofd als een plastic zak door het water tuimelde. Je zag het: Er was geen enkele weerstand meer in zijn gestroomlijnde lijf. Hij leek al te rotten. Wanneer alle gewaarwordingen uit mijn lijf getrokken zijn, valt me dat lot ongetwijfeld ook te beurt, dacht ik nog.

Na een tijdje keek ik zelfs niet meer rond, het kon me niet meer schelen, ik wou slapen als ik dat maar kon. Opeens -ik weet niet wanneer exact- verscherpte de wazige ruimte rondom mij. De nacht ging over in de ochtend en kleurde stilaan geel-oranje tot een zomermiddag onder een hoge zon. Er keerde zelfs een lauwe warmte in mijn lijf terug. Het glinsterende melkwegstelsel waarin ik zweefde zag ik nog nooit zo fel en ik zakte, bleef zakken alsof de stralen die door het water kliefden, me naar beneden drukte.

Al gauw bereikte ik de bodem zonder de geringste moeite. Hij lichtte schijnbaar van onderuit op. Aan mijn linkerkant stonden enkele kokers in een bosje bij elkaar. Er sliep een platvis in het zand en enkele soortgenoten wuifden met hun tentakels sierlijk boven hun sjofele kokers. Toen ik in hun midden neerdaalde, raakten enkele soortgenoten me aan en ik voelde me terug geleefd. Mijn leven was tot dat moment altijd een geweest van aanraken en aangeraakt worden. De uren of dagen dat ik door het waterruim zweefde waren doodse uren of dagen geweest. Mijn lijf had alle weerstand laten gaan, had zich in slaaptoestand gezet. Zoals de platvissen doen wanneer ze dutten op de bodem.

Toen ik die kleine nederzetting van mijn soortgenoten bereikte, hing ik me nog een tijdje op hun tentakels die me zacht in het schijnsel van de zon wiegden. Totdat ik besloot om tot daden over te gaan, met iedereen in het kleine wormendorp kennismaakte -bij ons gaat dat snel- en voor mezelf een nieuwe koker te bouwen. Ik groef me eerst een eind in de bodem in en graaide daar wat materiaal bij elkaar. Toen ik zwoegend de oppervlakte bereikte, zocht ik nog meer rommel bij elkaar: steentjes, stukjes mosselschaal, zand, korrels en zelfs plastic en stapelde alles tot een fijne, licht kronkelende koker, naar het beeld dat ik van mezelf heb, maar dan praktischer.

De volgende dag werd ik wakker in een kathedraal van licht. Terwijl ik sliep had de zee zich voor een tijdje teruggetrokken en onze kleine nederzetting bevond zich op een eindeloze vlakte van zand. De zee zat in kleine plasjes. Dat gebeurde wel vaker, vertelden de andere kokerwormen me. Mijn tentakels bleven wijselijk binnen want de stroming was hier heel anders, heel licht, te licht om je in te bewegen. Je krijgt er geen greep op. Gelukkig was mijn koker nog tot aan de rand gevuld met zeewater. Bovenaan, door de opening blonk het helste blauw dat ik ooit in mijn wormenleven zag, er dreven grote witte kwallen voor de zon en een frisse zucht zong door het zand. Af en toe schoot er een witte krijsende engel door het beeld dat ik van de omgeving had, door mijn kleine ronde kijkgat en ik wist onmiddellijk: deze vreemde zee is de hemel en de hel tegelijk.

De Wetenschapper.

(Dirk en Liesbeth)

Een kille novemberdag, 6.30. Ik stuur de veel te grote camionette de snelweg op. Naast me houden twee bereidwillige collega’s hun mokken in evenwicht, nippen af en toe aan de koffie, terwijl ze met glazuren vingers koffiekoeken naar binnen werken; de nacht is nog voelbaar.

Oostende nadert en we rijden de dag binnen.

De mannen van de Zeeleeuw staan al klaar. Veel wind. ‘Shit,’vloek ik bij mezelf. Dat belooft... Voortdurend eten en geen koffie is de boodschap... Te zuur. Tja, daarvoor is ’t nu te laat.

We laden het materiaal op de boot, MIDAS wordt wakker geschud. Nooit gesnapt waarom dat saai datasysteem zo'n naam kreeg.

Iedereen lijkt er klaar voor.

‘*Were zand scheppn, of is ’t korrn van deze kie*?’, vraagt een bemanningslid.

Het is niet mijn eerste keer. ‘Een beetje de twee', antwoord ik als een werfleider. 'Eerst stalen nemen met de Van Veen, daarna vissen met de boomkor om de bodem te verstoren en dan terug bodemstalen.’

De boodschap dat er echt gevist zal worden, zorgt voor lichte euforie .

‘Dat zijn de *tracks*; kan je de boot hierover heen laten drijven?’ vraag ik de schipper. ‘Intussen nemen we zoveel mogelijk Van Veen stalen om te checken of we wel goed zitten.’

‘Ik doe mijn best’, antwoordt de schipper, *‘maar tis wel gin otto é’*.

‘We zien wel waar we komen,’ knik ik.

De Van Veen grijper braakt zijn eerste staal uit. Wie kwam er ooit op het idee om zeebodemstalen te nemen met deze kruising van een mislukte slatang en een reuzenotenkraker? Meneer Van Veen wellicht. Dat is die zanger van ‘*opzij opzij opzij*‘, toch?

‘*We gaan toch nie heeln dag zand scheppn*?’ haalt één van de mannen me uit mijn dromerij.

‘Neenee’, zeg ik wakker en kordaat, om de gemoederen te bedaren.

‘Wat zoek je *misjien*?’, vraagt de immer hulpvaardigste van de bende. Hoe heette hij ook alweer?

‘Kokerwormen’.

De mannen blijken het te kennen, al wordt onder de term heel wat meer verstaan. De spanning stijgt. Ze gaan er volledig in op en willen graag veel ‘*puuptjes*’ vinden.

Even later wordt de verwachting ingelost; wanneer De Van Veen open valt, ligt heel de tafel vol brokken zeebodem, ditmaal zitten er veel kokers tussen.

‘*Das een goein é; je hebt een keer chance en een keer gin chance. Jah, die puuptjes da komt en gaat met ’t were é’*.

Ik staar in de verte, waar de zee de lucht raakt, er in overgaat en hoop dat we straks op de juiste plek zullen verstoren én dat het allemaal iets uithaalt.

De volgende Van Veen komt boven en wordt op de tafel gelost. Bovenop honderden kokertjes ligt een tong. Wat een toeval, een tong in de Van Veen grijper. Bovenop een *Lanice*-rif. Het lijkt wel de samenvatting van mijn hele onderzoek.

Het slepen kan beginnen. De mannen van de Zeeleeuw staan plots allemaal op het dek. De spanning stijgt. Meer deining. Op zee en in mijn hoofd. Het reispilletje werkt -weeral- niet.

Koeken en koffie worden visvoer. We doen drie slepen van telkens een half uur. De netten zitten vol: garnalen, pitvissen, slangsterren, een pieterman, harnasmannetjes; een zeenaald! En ook enkele commerciële vissen.

Alles wordt snel opgemeten en teruggegooid. De bemanning gaat even door zijn dak als de jonge kabeljauw snel weer over boord gaat.

'Smiet je gieder die gulle weg?'. Verontwaardiging alom. Een collega-onderzoekster doet een poging het uit te leggen, maar iedereen ziet dat het kabeljauwtje op zijn zij op de golven drijft.

Enkel de meeuwen vinden het tafereel amusant.

Onmiddellijk na de verstoring mag de Van Veen grijper weer bijten en braken. Dit zijn de stalen die de onmiddellijke schade moeten aantonen. Soms lijkt er weinig aan te zien, maar in andere gevallen zijn de kokers duidelijk vernield.

Ik vis een losgeslagen koker uit de hoop, speel er even mee en gooi hem dan bij de rest van het staal. Weet ik veel dat net die worm een nieuw rifje op het strand had gevonden.

CHAPTER 1

GENERAL INTRODUCTION

Includes:
Rabaut, M., Vincx, M. and 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 Fisheries: Management, economics and perspectives, Ed by N. F. McManus and D. S. Bellinghouse. 485-495.
Nova Science Publishers, New York.

*This chapter frames the thesis by picturing the broad range of marine conservation and fisheries to eventually come to a detailed review of the current state of the art. In the first part, the concept of marine protected areas is introduced with a focus on the close link between ecosystem functioning and human activities (*in casu *fisheries). Further, the macrobenthic ecosystem component is defined as well as possible conflicts with so-called mobile fishing gear. A sketch of the legal framework and marine conservation policies is provided. The second part explains what is understood by the concept of ecosystem engineers, how these organisms can create habitat complexity and where tensions with mobile fishing gear are expected. The third part introduces the central ecosystem engineer of this thesis -* Lanice conchilega *- through the review of what is known about the biology, the ecology and the vulnerability of this species. Finally, the thesis research is introduced with the objectives, a brief description of the Belgian part of the North Sea and an outline of the thesis to guide the reader through the different chapters of this thesis.*

Nature conservation at sea

Marine protected areas

Nature conservation is about the preservation of nature, that is the preservation of biodiversity and ecosystem functioning (Van Houtan, 2006). On a global scale, current rates of biodiversity loss exceed those of the historical past by several orders of magnitude and show no indication of slowing. Two of the most important direct drivers of biodiversity loss and ecosystem service changes are overexploitation of the ecosystem and habitat change (Millennium Ecosystem Assessment, 2005). On a European scale, a recent report from the European Environment Agency (EEA) (EEA, 2009) warns that most species and habitats across the continent are in poor condition and that the risk of extinction continues to rise. Politically, the European Union is failing to meet the pledge to halt biodiversity loss by 2010. The challenges are even greater in the marine environment, which are due to the specific features of the less accessible environment. This holds particularly true for the marine ecosystems focused on in this thesis which are the coastal marine areas of North-Western Europe that consist largely of sedimentary sand banks and swales. Management measures at sea are restricted to the management of the human activities, as active restoration measures are yet difficult to apply. Therefore, marine management is largely focused on the maintenance of the benefits that originate from exploitation of resources, *i.e.* the use of goods that are provided by the sea (Beaumont *et al.*, 2007). This utilitarian vision on the marine environment is obvious in marine conservation objectives, where the concept of conservation is often reduced to stocks rather than taking a wider interpretation such as the ecosystem. Costanza *et al*. (1997) estimate that marine ecosystems generate two-thirds of the total value provided by global ecosystems. Most of these goods and services are considered infinite relative to the scale of the economic subsystem (Daly, 1992) leading to a so-called externalization of environmental costs (Massarrat, 1997). This relates to a generally very low resource (*i.e.* goods, commodities) cost that more or less contains only the labour costs necessary to obtain them. This way of valuing resources (e.g. wild fish stocks) ignores the costs of repairing the damage resulting from resource use (Aubauer, 2006). This means that gains have been achieved at the expense of emergent costs in the form of losses in biodiversity and degradation of many ecosystem services (Millennium Ecosystem Assessment, 2005).

In response to these changes, the concept of 'marine protected areas' (MPAs) has been developed in an attempt to halt the deterioration of the sea. MPAs are recognized as a viable tool by conservationists, resource managers, scientists and coastal planners. According to the World Conservation Union (IUCN, 1988) an MPA is defined as: 'Any area of intertidal or subtidal terrain together with their overlying waters and associated flora, fauna, historical and cultural features, which has been reserved by law or other effective means to protect part or the entire enclosed environment'. One constraint, however, is that MPAs are often implemented without a firm understanding of the economic, social and ecological consequences. The rush to implement MPAs has set the stage for paradoxical differences of opinion in the marine conservation community (Agardy *et al.*, 2003).

The legal protection of marine habitats has developed only very recently. The need to designate Marine Protected Areas (MPAs) as a contribution to preserve and improve marine biodiversity and ecosystem functioning has been put forward in several international policy instruments and legislation. These generally consist of a mixture of specific marine instruments and mixed terrestrial/marine instruments (Cliquet *et al.*, 2008a). In the European seas which are heavily exploited, it is clear that pressure reduction will play a key role if one aims to reach sustainability through the application of the ecosystem approach to environmental management (EEA, 2009). The European Birds Directive[1] and the Habitats Directive[2] are the two international legal bases that oblige member states of the European Community to designate marine areas as part of the Natura 2000 network.

Of all human activities at sea, fishing marine species for human and animal consumption has been specified as one of the most significant (Salomon, 2009). As fisheries activities exist in nearly all marine habitats and problems in marine renewable resource management surface on a world-wide scale, the discussion to use MPAs as a means to restore fish populations or even to increase fisheries profits is still ongoing (Kaiser, 2005). However, the amount of information that is now available to manage systems sustainably is often perceived as insufficient, leading to policies where conservation strategies and fisheries plans are still managed separately.

Fisheries

Fisheries are generally recognized as the major critical factor for an MPA to succeed or to fail (Kelleher, 1999), most often linked to overexploitation (e.g. Myers and Worm (2003)). This relates to human fishing behaviour where fishing fleets do not shrink in response to diminishing fish resources, unlike natural predator populations that do respond to declines in their food sources (so called Ratchet effect, *sensu* Ludwig *et al.* (1993)). This behaviour is partly explained by a subsidy driven fisheries management (Sumaila and Pauly, 2007). Moreover, the selective targeting of too many large specimens leads to the accrement of a so-called 'Darwinian debt' (Walsh *et al.*, 2006), while the overexploitation itself leads to the well-known phenomenon of 'fishing down marine food webs', which will lead to the succession of local extirpation, followed by global extinctions (Pauly *et al.*, 1998). Ecosystems may potentially shift (a so-called 'regime shift') as a consequence of human overexploitation (Scheffer and van Nes, 2004). Finally, physical disturbance of the sea bottom by mobile fishing gear is considered to have a major impact on the ecosystem. This thesis will focus on

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[1] Directive 79/409/EEG of 2 April 1979 on the Conservation of Wild Birds, *PB L* 103, 25 April 1979 (hereafter: Birds Directive); text of the Directive, with later amendments, see http://eur-lex.europa.eu/LexUriServ/site/nl/consleg/1979/L/01979L0409-20070101-nl.pdf.

[2] Directive 92/43/EEG of 21 May 1992 on the Conservation of Natural Habitats and of Wild Fauna and Flora, *PB L* 206, 22 July 1992 (hereafter: Habitats Directive); text of the Directive, with later amendments, see http://ec.europa.eu/environment/nature/legislation/habitatsdirective/index_en.htm.

the last aspect of physical bottom disturbance by mobile fishing gear through the quantification of the impact on the bottom dwelling organisms, focusing on macrobenthos.

Macrobenthos (*i.e.* bottom fauna defined as invertebrate animals larger than 1 mm) is recognized as fundamentally important in the functioning of marine ecosystems as is reflected in their inclusion in metrics to calculate the intrinsic biological value (Derous *et al.*, 2007) or the environmental quality (Borja *et al.*, 2003). In soft-bottom ecosystems, benthic densities and species richness are heavily determined by the seabed characteristics (mainly sediment types) (Bergman *et al.*, 1991, Van Hoey *et al.*, 2004, Vanaverbeke *et al.*, 2000) and this benthic ecosystem component is important in determining the densities and species richness of higher trophic levels such as demersal fish (Cabral, 2000, Langton and Watling, 1990, Molinero and Flos, 1992, Rijnsdorp and Vingerhoed, 2001) and birds (Cramp and Simmons, 1977, Degraer *et al.*, 1999, Godet *et al.*, 2008, Van Waeyenberge *et al.*, 2001, Von Blotzheim and Bauer, 1968, 1969).

These benthic environments are often under threat as fishing with mobile fishing gear is known to be a major cause of habitat deterioration in soft-bottom ecosystems (Dayton *et al.*, 1995). Physical destruction of marine habitats has been reported as one of the main impacts of fisheries, with benthic communities particularly hard hit by trawling (Salomon, 2009). Kaiser *et al.* (2002) describe how macrobenthic productivity is decreasing as fishing intensity increases and high-biomass species are being removed from the benthic habitat. Jennings *et al.* (2001a) found that total biomass of infauna and epifauna significantly decreased with trawling disturbance. Moreover, there is plenty of evidence of damage and mortalities of invertebrates in trawl nets (Bergman and Hup, 1992, Brylinsky *et al.*, 1994, Kaiser and Spencer, 1996, Schratzberger *et al.*, 2002, Witbaard and Klein, 1994). Therefore, not only overexploitation is of concern, but also direct damage to benthic biota urgently needs to be addressed in areas where bottom gear is applied (Bergman and Hup, 1992, Kaiser and Spencer, 1996, Sparks-McConkey and Watling, 2001). However, the largely unknown temporal and spatial dynamics of target and non target species as well as of fishermen makes it difficult to find a link between species composition and fishing effort (Craeymeersch *et al.*, 2004).

Ecosystem engineers, habitat complexity and fisheries

Ecosystem engineers

The structurally complex framework provided by emergent features constitutes an important organizing aspect and is critical to the functioning of many ecosystems (Jones *et al.*, 1994). The relationship between structure and functioning owing to biotic-abiotic interactions was conceptualised in the idea of 'ecosystem engineering' (Jones *et al.*, 1994, 1997, Wright and Jones, 2006). Ecosystem engineers are organisms that directly or indirectly modulate the availability of resources to other species by causing state changes in biotic or abiotic materials. In doing so they modify, maintain and/or create habitats (Jones *et al.*, 1994). By reshaping the landscape, ecosystem engineers change the abiotic context upon which biotic interactions heavily depend (Byers *et al.*, 2006). Due to their functional characteristics, ecosystem engineers can exert a strong influence on ecosystem properties that exceeds what may be expected based on their relative abundance alone (Hooper *et al.*, 2005). The value of the ecosystem-engineering concept, therefore, lies in its ability to formalize interactions among organisms that are mediated by the physical environment (Wilby, 2002).

Emergent structures in marine ecosystems that reach a few centimetres into the water column can have a profound effect on the structure and functioning of marine ecosystems. The ecological effects of habitat structuring organisms lie in the increase of habitat complexity. They tend to dominate in stressful environments (Jones *et al.*, 1997) and therefore they are well described for all kinds of marine environments: coral reefs (e.g. Holbrook *et al.* (1990)), Darwin mounds (e.g. Van Gaever *et al.* (2004)), kelp forests (e.g. Steneck *et al.* (2003)), ascidians (e.g. Castilla *et al.* (2004)), sea grass meadows (e.g. Alfaro (2006), Hovel (2002)), mussel Banks (e.g. Hild and Günther (1999), People (2006), Ragnarsson and Raffaelli (1999)) , oyster beds (e.g. Lenihan (1999)) and polychaete tubes (e.g. Callaway (2006), Van Colen *et al.* (2008)). In many coastal sediments, they are known to have far reaching consequences (Bouma *et al.*, 2009). These systems provide habitat for a wide range of taxa, including post-settlement juveniles of commercially important fish species (Watling and Norse, 1998). They may provide refuge from predation, competition and physical as well as chemical stresses, or may represent important food resources and critical nursery or spawning habitats. In addition, these structures modify the hydrodynamic flow regime near the sea floor, with potentially significant ecological effects on sedimentation, food availability, larval and/or juvenile recruitment, growth and survival. As such, habitat structures and heterogeneity influence faunal abundance, species richness and species composition of invertebrate and fish communities (Koenig *et al.*, 2000, Turner *et al.*, 1999). This engineering template has received less ecological attention than the processes generating spatial and temporal patterns of organisms within engineered landscapes (Crain and Bertness, 2006).

As a proper management of important engineers can protect numerous associated species and functions by expanding distributional limits for numerous species, it has been advocated to use these organisms as conservation targets (Crain and Bertness, 2006). This will necessitate a shift towards a more process-based understanding of the functioning of systems; an important step towards ecosystem-based management (Byers *et al.*, 2006). These authors developed a conservation framework that uses the ecosystem engineer concept. Although their model emphasizes non-trophic engineering effects, they also stress on the important and often interacting role of trophic and other biological interactions in restoration. The ecosystem engineer concept should therefore be considered as a contributory process among those factors affecting the distribution and abundance of organisms and the functioning of ecosystems (Wright and Jones, 2006). In most habitats, regardless of environmental stress, ecosystem engineers provide the template for all other ecosystem processes, making these engineers essential to conservation and a valuable starting point to bring the ecosystem approach in practice.

Fisheries and habitat complexity

When looking specifically at soft-bottom areas, locations with ecosystem engineered emergent habitats are proven to be vulnerable to fishing impacts (e.g. *Pectinaria (Lagis) koreni* (Bergman and van Santbrink, 2000)). Trawling has the capability of altering, removing or destroying the complex, three-dimensional physical structure of benthic habitats by the direct removal of biological and topographic features (Turner *et al.*, 1999). Chronic fishing disturbance may be sufficient to severely reduce the complexity of such habitats by removing the fragile sessile fauna (Collie *et al.*, 1997, Thrush *et al.*, 1998) or by reducing the suitability of the area to species of commercial importance (Kaiser *et al.*, 1999b, Sainsbury, 1987). For epifauna, a general decrease in sessile larger bodied species was observed, while more resilient, mobile fauna increased along with increasing fishing disturbance (e.g. Kaiser *et al.* (2000a)). A conceptual model of Auster (1998) demonstrates that fishing gear significantly reduces habitat complexity for most habitats. In a long-term study (1906-2000) on the North Sea, the change in distribution and abundance of epibenthic species since the beginning of the 20th century was attributed to bottom fisheries (Callaway *et al.*, 2007).

Therefore, in the marine environment, ecosystem engineers are key species when it comes to the preservation of both the ecological functions and fishing activities. Removal of ecosystem engineers by mobile bottom gear could have devastating effects on local biodiversity and important water-sediment processes (Coleman and Williams, 2002). Identifying and preserving probable engineering species and responsive ecosystems should be a key priority for conservation which would result in a shift to a process-based understanding of the functioning of whole systems, which is a large and important step towards ecosystem-based management (Byers *et al.*, 2006).

Lanice conchilega

The tube dwelling polychaete *Lanice conchilega* (Terebellidae) is the target ecosystem engineer of this thesis (Figure 1). These bristle worms are thought to be almost cosmopolitan; in Europe, they colonize a wide range of intertidal and subtidal sediments down to about 1900 m (Hartmann-Schröder, 1996, Holthe, 1986, Ropert and Dauvin, 2000, Van Hoey *et al.*, 2008). A phylogeographic study in the North-eastern Atlantic Ocean suggests the presence of inter-specific genetic variation (*i.e.* cryptic species) (Depauw, 2007, Vanaverbeke *et al.*, 2009b), similar to some other sedentary polychaetes (Jolly *et al.*, 2006).

Figure 1. Lanice conchilega*. From left to right: close up of individual in Bay of Heist; patches of aggregations in the Bay of Heist; dense aggregation of living* L. conchilega *in an undisturbed aquarium set up;* L. conchilega *individuals in the Bay of Heist.*

Biology and general characteristics

The life cycle of *L. conchilega* starts with egg fertilization in the water column leading to a protrochophora and subsequent trochophora larva. This stage is followed by a metatrochophora phase (still pelagic) of a few days and eventually the aulophora larva originates (Bhaud, 1988). This aulophora larva is already characterized by a (transparent) tube and has the morphological characteristics of a juvenile. In this stage, the larva succeeds to an intermediate benthic stage for a few days and re-enters the water column afterwards (using its tube as a floating device) (Bhaud and Cazaux, 1990). This aulophora larva is able to feed in the water column where it stays for a prolonged period of time (up to 60 days) (Bhaud and Cazaux, 1990). Important factors which trigger benthic settling are the availability of habitat structures and effects of these on the local hydrodynamic regime, enhancing the settlement of larvae in areas already populated by adults (Callaway, 2003a). During settlement, tentacles glue the anterior end of the larval tube to the substratum and extend the tube (Heimler (1981) as cited in Van Hoey (2006)). Once settled, the larva turns to the juvenile and adult stage. In this benthic stage, *L. conchilega* builds a linear tube, which consists of mucus and particle lined walls. Cemented particles consist of calcium carbonate grains (60-80%) and the tube is built up as two to three concentric layers (Fournier *et al.*, 2009). The tube has a diameter of 5 mm and a length of up to 65 cm (but generally not longer than 20 cm) (Jones and Jago, 1993, Ziegelmeier, 1952) in which the worm can retreat very fast upon physical disturbance (Bergman and Hup, 1992). If an individual is completely washed out from the sediments, it is able to re-establish its tube within 24 h (Nicolaidou, 2003). The top end of the tube protrudes above the sediment some 1-4 cm and ends in a fringe of filaments of mucus-bound coarse sand grains (Jones and Jago, 1993). The polychaete is a suspension feeder when occurring in relatively high densities and turns to deposit feeding at low densities (Buhr, 1976, Buhr and Winter, 1977). The filtration rate is positively linearly related to body size while the relative daily food intake decreases with growth. The species has an assimilation efficiency between 70.6% and 77.2%, independent of body size (Buhr, 1976). The results show that *L. conchilega* is within the range of obligatory suspension feeding organisms. Denis *et al.* (2007) emphasize that the clearance rate capacity of *L. conchilega* is further influenced by the current flow velocity (with an optimum at 15 cm s^{-1}). The organic matter food source for *L. conchilega* consists of phytoplankton and microphytobenthos

(Dubois *et al.*, 2007b), the latter probably being more important –at least in intertidal areas- as discussed by Lefebvre *et al.* (2009). Nevertheless, large densities of juvenile *L. conchilega* can directly decrease food availability as they have recently been suggested to induce local 'biological shading' and may consequently reduce the gross microphytobenthos production (Denis and Desreumaux, 2009).

Patches of high abundance of the species not only attract the aulophora larvae but also hydrodynamically trap sediment (Dittmann, 1999, Eckman, 1983, Heuers *et al.*, 1998). It results in the occurrence of gentle mounds and shallow depressions (Carey, 1987, Féral, 1989, Hartmann-Schröder, 1996, Hertweck, 1995, Zühlke, 2001). A phenomenological model (*i.e.* integration of several phenomena without having detailed information on each phenomenon) showed that the prevailing velocity of the near-bottom flow determines whether high density patches originate or not (Grimm, 1999). Once aggregations are present, both tube building and sediment trapping have far reaching consequences on the local sedimentary and hydrodynamic environment. Modelling studies suggest that high flow velocities lead to a continuous growth of patches while a mosaic of patches originates at intermediate flow velocities (Heuers *et al.*, 1998). In addition, high density aggregations function as important carbonate traps (Fournier *et al.*, 2009, Jones and Jago, 1993). The volume represented by the tubes itself compacts the sediment framework and increases the rigidity. Furthermore, the mucopolysaccharide secretions coat the sediment grains and contribute to the rigidity (Jones and Jago, 1993). The increased sediment compaction explains the formation of the biogenic concretions.

The settlement strategy of the larvae plays a major role in determining the temporal stability of these *L. conchilega* aggregations (Strasser and Pieloth, 2001, Van Hoey, 2006). Mature *L. conchilega* individuals have an estimated maximum egg production of 90000-160000 oocytes (Bhaud, 1988). The release of gametes results in fertilization from where the life cycle restarts. The reproduction peak takes place in spring followed by two smaller peaks in summer and autumn (Van Hoey, 2006). The average life span of *L. conchilega* seems to differ between regions (Van Hoey, 2006). In France, they were reported to reach a life-span of three years (Ropert and Dauvin, 2000), in the Wadden Sea, the life span was estimated at 1-2 years (Beukema *et al.*, 1978) while in the Belgian part of the North Sea (BPNS) the life span of the *L.*

conchilega individuals was estimated to be one year, with variations of a few months (Van Hoey, 2006), though older specimens were occasionally found.

Ecology

In intertidal areas, the biogenic emergent structures affect the distribution and abundance of infaunal species by influencing the habitat structure. Carey (1987) created artificially high density *L. conchilega* aggregations by transplantation; infaunal abundance increased significantly. The effect on both abundance and species diversity was tested on natural *L. conchilega* aggregations in Germany on two sandflats of the East Frisian Wadden Sea (Callaway, 2003b, Dittmann, 1999, Zühlke, 2001, Zühlke *et al.*, 1998), in the UK on an exposed beach in South Wales (Callaway, 2006) and in France in the Bay of Mont-Saint-Michel (Jaffré, 2009). These studies show that *L. conchilega* alters the benthic community composition with a significantly higher species diversity and abundance among tube aggregations. Two bivalve species (juveniles of *Mya arenaria* and *Mytilus edulis*) and two polychaete species (*Phyllodoce (Anaitides) mucosa* and *Hediste diversicolor*) occurred in higher densities in the *L. conchilega* aggregations, while five species were found to be exclusively associated with the patches (*Sagartia troglodytes*, *Malmgreniella lunulata*, *Eumida sanguinea*, *Gammarus locusta* and *Microprotopus maculatus*). One species (*Aphelochaeta marioni*) was found in lower numbers in the patches (Zühlke, 2001). Similar results were found in the UK, where 27 out of 56 species were found exclusively in samples with *L. conchilega* (Callaway, 2006). This study emphasizes that not only groups of tubes, but also single polychaete tubes act as an ecosystem engineer. Furthermore, the author points out that *E. sanguinea* lives among the fringe filaments of the tube top while the haustorid amphipod *Urothoe poseidonis* inhabits areas deep in the sediment in close vicinity to the tube. In an experiment with metal sticks as mimics for *L. conchilega* tubes, mean individual abundances and species richness were found to be significantly higher in the artificial tubes plots than in untreated reference areas. Juveniles of *Mya arenaria* were found in higher numbers in the plots where they used the tube structure for attachment to their byssus threads (Zühlke *et al.*, 1998). In the longer run, Callaway (2003b) described how the juveniles of the blue mussel *M. edulis* used the artificial tubes to attach on, remained attached and turned the plots into fully developed intertidal mussel banks. The author suggests that under favourable conditions mussel banks may also develop on natural intertidal *L. conchilega* aggregations. Moreover, mussel banks have been reported centrally in the *L. conchilega* aggregations (Hertweck, 1995), suggesting that mussel bank development may indeed be favoured by the presence of high density *L. conchilega* patches. A recent study in the intertidal area of the Bay of the Mont-Saint-Michel shows that also there, species richness, abundance and total biomass production increases significantly with increasing *L. conchilega* densities (Jaffré, 2009). Finally, in the Dutch part of the North Sea, a surf zone study suggests that the observed localized high macrobenthic abundance and richness can be explained by the presence of dense aggregations of juvenile *L. conchilega* (Janssen *et al.*, 2008). Furthermore, not only macrobenthic species profit from the environment modulated by *L. conchilega* but also several nematode species (Linhomoeidae spp., Molgolaimidae spp. and Microlaimidae spp.) were found in considerable higher abundances at a distance of 5 mm from the tubes (Zühlke *et al.*, 1998). These authors suggest that there might be a link between predatory polychaetes and the distribution pattern of nematodes around the tubes. Moreover, preliminary results of an ongoing experimental study show that nematodes are vertically redistributed and have a higher survival when *L. conchilega* is present, as they occur in far higher densities deeper down in the sediment (Braeckman *et al.*, in prep.).

The influence on faunal abundance, species richness and species composition in subtidal areas has been described in the thesis of Van Hoey (2006) for the first time (see also Van Hoey *et al*. (2008), Addendum I). The implications of the presence of *L. conchilega* in different habitats were evaluated on a North Sea scale. In four habitats (shallow muddy sand, shallow fine sand, deep fine sand and shallow medium sand), the density of the surrounding benthos increased with increasing density of *L. conchilega*. The number of species, however, more or less reached an asymptotic value or even decreased after reaching a critical density (1000 ind m^{-2} in fine sands: *cf.* Addendum I). This research concluded that *L. conchilega* patches are responsible for an increased habitat quality in an otherwise uniform habitat, resulting in a higher survival of the surrounding benthic species.

These far reaching ecological consequences of (dense aggregations of) *L. conchilega* can be attributed to different mechanisms and its modulation capacity. The settlement of larvae and juveniles (Callaway, 2003a) and the stabilizing effect of the realized state changes of the abiotic environment (Jones and Jago, 1993) are important mechanisms that have been described above. The trapping of the sediment is a physical process by which dense tube aggregations change the hydrodynamics on a small geographical scale. This stabilization and formation of an emergent structure is probably the most important causative factor to attract the associated benthos as a consequence of a so-called skimming flow (*i.e.* a decrease of current velocity at the sediment-water interface). This effect was shown not only to be the direct implication of the tubes changing the local hydrodynamics, but reinforcing alternative processes caused by the production of mucus, presence of bacteria, benthic diatoms etc. may explain the stabilizing impact of relatively low density aggregations (Eckman *et al.*, 1981, Fager, 1964, Murray *et al.*, 2002).

Not only changing sediment characteristics explain the attraction of several species but also biogeochemical changes contribute to changes in species composition. Forster and Graf (1995) calculated O_2-fluxes into the sediment attributed to *L. conchilega* and suggest that it acts as a piston when moving in its tube (*i.e.* 'piston-pumping'), hereby introducing oxygen rich water deep into the sediment. This intermittent ventilation pattern has repercussions on various fluxes as Braeckman *et al*. (accepted) showed that, owing to its irrigation activity, *L. conchilega* has pronounced influences on benthic respiration, denitrification and nutrient release. The strong removal of ammonium might have favourable consequences for sediment inhabiting organisms. Finally, the biogenic structures are thought to function as a safe haven for several species that use the space in between the tubes to shelter.

In tidal sand flats, dense aggregations of *L. conchilega* were shown to be important feeding grounds for birds (Beukema *et al.*, 1993, Carey, 1987, Godet *et al.*, 2009b, Godet *et al.*, 2008, Jaffré, 2009, Petersen and Exo, 1999). Intertidal *L. conchilega* aggregations may also serve as an important shelter or feeding ground for juvenile flatfish; the surf zone of sandy beaches is intensively used by a number of epibenthic macro-crustaceans and flatfish species (Beyst *et al.*, 2001). Moreover, in the shallow subtidal, it has been suggested that flatfish species actively select for a tube mat biotope built up by *Chaetopterus* sp. and *L. conchilega* (Rees *et al.*, 2005, Shucksmith *et al.*, 2006) and clusters of *L. conchilega* constitute a large feeding area for 0-group flatfishes like *Pleuronectes platessa* and *Solea solea* (Amara *et al.*, 2001).

Lanice conchilega ***and the quantification of anthropogenic impacts***

Apart from studies on the natural implications and functioning of L. *conchilega*, the species has been used to quantify anthropogenic impacts. it is a bioaccumulator of pollutants and was found to be a suitable representative for measuring bioaccumulated organochlorine residues (Goerke and Weber, 1998, Mattig *et al.*, 1997). The species was found very suitable because the species is euryhaline, it is relatively widespread and in the intertidal it is easily identifiable by its characteristic tube. The PCB pattern is influenced by the geographical location reflecting environmental PCB changes from the English Channel towards the German Bight. Locally, the impacts of river mouths can be distinguished in the pollution load (Goerke and Weber, 1998).

Direct physical disturbance of *L. conchilega* aggregations has been shown in the intertidal where *Ruditapes philippinarum* (Manila clam) cultivation showed to cause significant effects through a drastic total abundance decrease, a modified spatial pattern and a strongly altered benthic assemblage. Closely associated benthic macrofauna is altered along the whole production cycle and the scraping of the superficial sediment during harvesting of *R. philippinarum* is the most negative practice (Toupoint *et al.*, 2008). These authors hypothesize that also in the subtidal, *L. conchilega* habitats may be more adversely affected by fishing than those on unconsolidated sediment. Kaiser *et al.* (1996) investigated the suction dredging impact of *R. phillippinarum* cultivation and found that *L. conchilega* densities decreased after harvesting. The overall suction dredging impact was found to be profound; these effects were, however, barely detectable after seven months. Moreover, the habitat alteration via *R. philippinarum* cultivation induces subsequent effects for higher trophic levels as was shown by a significant loss of attractiveness for the feeding *Haematopus ostralegus* specimens (Oystercatchers) (Godet *et al.*, 2009b).

Other anthropogenic impacts include sludge disposal of dredged material and aquaculture activities such as M. edulis farming. Although *L. conchilega* can survive repeated additions of settling material at the sea bed, through upward burrowing and tube-building activity (Rees *et al.* (1992) and references therein), the species shows a strong decline when covered by disposal sediments and the species is considered to be an indicator for disposal effects as they have a sensitive response to sludge disposal activities and show a slow recovery (Witt *et al.*, 2004).

Lanice conchilega was absent from the disposal area, as was the associated macrofauna, leading to a reduced benthic diversity. Another indirect impact is to be expected with large-scale introduction of bivalve species as they have the capacity to destroy pelagic larvae (Davenport *et al.*, 2000, Lehane and Davenport, 2002). Therefore, the development of *M. edulis* aquaculture in front of the coast may have far reaching consequences for the renewal of intertidal *L. conchilega* aggregations as well as for other macrofauna species with pelagic larval stages. This remains, however, highly speculative.

Physical disturbance by mobile fishing gear such as beam trawling has been hypothesized as an important factor determining the stability of *L. conchilega* aggregations (Van Hoey, 2006). A short reference to a potential impact was made in a study on direct effects of beam trawling on benthic fauna in which *L. conchilega* tubes were always damaged in comparison with intact specimens in the control area (Rumohr *et al.*, 1994). Degraer *et al.* (2009) suggest that it is possible that *L. conchilega* aggregations would possibly evolve to a system with a yet higher diversity if beam-trawling would be banned, as larger and longer living species would be able to settle and survive.

Lanice conchilega ***and nature conservation***

In recent years, the use of this particular ecosystem engineer in nature conservation has been advocated several times (Godet *et al.*, 2008, Janssen *et al.*, 2008, Toupoint *et al.*, 2008, Van Hoey, 2006), mainly because of the high functional value that is considered as an important conservation stake. However, direct suggestions on how to use this tube building polychaete as a proxy for nature conservation or as an indication of the ecosystem's resilience are scarce. Therefore, in the current thesis, this relatively well-described ecosystem engineer is investigated for its applicability as model species to test fisheries impacts and its use in marine conservation.

Thesis research

Aims

Concepts as 'integrative' and 'ecosystem approach' are often mentioned as key concepts to manage renewable marine resources sustainably. However, when policy decisions about the marine environment are made, nature conservation and fisheries management appear to be managed separately. This thesis explores possibilities for the integration of marine conservation and fisheries, as these two aspects of marine management are unarguably closely related. This integration should be based on scientific research that is cost-efficient and ready-to-use in marine ecosystem management. In the context of this thesis, high density *L. conchilega* aggregations will be further studied in depth and specific experiments are set up to generate insights that can support both conservation and fisheries management strategies (Figure 2). The investigation of knowledge gaps about a specific benthic ecosystem is considered a useful strategy to implement the ecosystem approach when it comes to benthic ecosystems. Furthermore, post-larvae and juveniles of commercially important flatfish species might be influenced by the presence of the biogenic habitats created by *L. conchilega*. The focus is on coastal zones, both intertidal and subtidal, as these are subject to a constant demand from a wide range of human activities, suggesting that the continued functioning of the natural communities in some areas may be under threat (Riou *et al.*, 2001).

Therefore, the present thesis starts from the following questions:

Is* L. conchilega *an important and useful ecosystem engineer within a conservation context?

- What are the benthic species-specific interactions in a *L. conchilega* dominated environment?
- Can *L. conchilega* qualify as reef builder?

How resilient are* L. conchilega *aggregations towards the impact of beam-trawling?

- How resilient is *L. conchilega* itself?
- How resilient is the associated fauna?

What is the functional value of* L. conchilega *aggregations for higher trophic levels?

- What is the function of intertidal *L. conchilega* aggregations for post-larval flatfish?
- What is the function of subtidal *L. conchilega* aggregations for juvenile flatfish?

How can* L. conchilega *be used in the framework of an ecosystem approach to marine management?

- How is an MPA-process generally evolving in temperate soft-bottom marine areas?
- How can dynamic marine environments be legally protected?
- How can *L. conchilega* be used in marine conservation to integrate science, policy and fisheries in an ecosystem approach?

The four 'subquestions' represent the core research of the thesis. The 'ecosystem funtions' investigated here are only those specified in the four questions above and we emphasize that the functionality of marine ecosystems is obviously much wider than the role played by macrobenthic diversity and the trophic role of predators. As indicated by e.g. Boero and Bonsdorff (2007), the functioning of ecosystems is based on an efficient circulation of matter and energy through various levels of biological organisation, involving primary, secondary (and higher) production and decomposition. Three basic cycles of matter and energy concur to the functioning of ecological systems: biogeochemical (extraspecific) cycles, life (intraspecific) cycles, and food webs (interspecific cycles). The first cycle would include potential functions as nitrogen remineralisation (*cf. supra*) but is not a subject of this thesis.

The final aim of this thesis is not only to answer the specific questions, but to demonstrate how these 'subquestions' can contribute to a more integrative approach in marine management. The information provided in this thesis on *L. conchilega*, fisheries and marine conservation aims at contributing to the implementation of the ecosystem approach in temperate soft-bottom marine environments (with a focus on North-Western Europe).

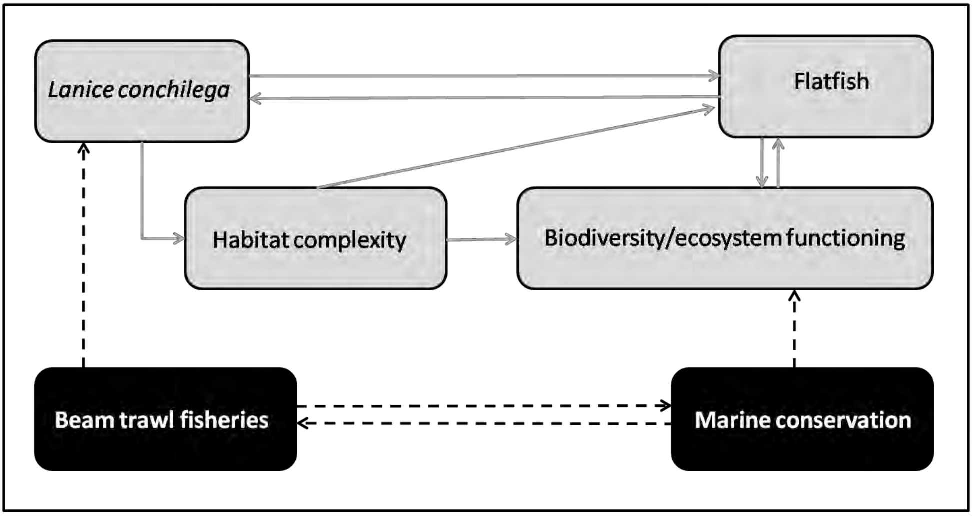

Figure 2. Schematic representation of the potential links within the benthic habitat created by dense aggregations of Lanice conchilega *and the use of these to quantify fisheries impacts and to underpin marine conservation and fisheries management strategies. The thesis aims at investigating how beam trawl fisheries and marine conservation relate (black boxes); the biotic interactions are represented in gray.* Lanice conchilega *is used as the basic ecosystem engineer to investigate habitat complexity, bioversity and ecosystem functioning. The relation between* L. conchilega *and flatfish is investigated. The link between beam trawl fisheries and flatfish is not represented here as this is beyond the scope of this thesis.*

Belgian part of the North Sea

This thesis focuses on temporal soft-bottom marine environments and uses the Belgian part of the North Sea (BPNS) as a case study area in several chapters. The BPNS (Figure 3) is a rather small and shallow shelf area (3600 km^2; max. 46 m depth), characterized by the presence of several sandbank systems, more or less oriented parallel to the coast (Figure 4). on a North Sea scale, the BPNS is a relatively rich and highly heterogeneous area within the group of habitats with mobile substrates (Rees *et al.*, 2007). The characteristic geomorphologic and sedimentological diversity of these soft-bottom habitats is directly responsible for the high biological diversity and species richness, reflected in a mosaic of several distinguishable macrobenthic communities (Degraer *et al.*, 2002, Van Hoey *et al.*, 2004). The area is hence a relatively diverse area in comparison with mobile substrates in other parts of the North Sea. In a simplified representation of the Belgian macrobenthic marine environment, four species communities are distinguished (Degraer *et al.*, 2009) (Figure 3). The most valuable areas for macrobenthos in the BPNS coincide with places where the *Abra alba* community is found (Derous, 2007).

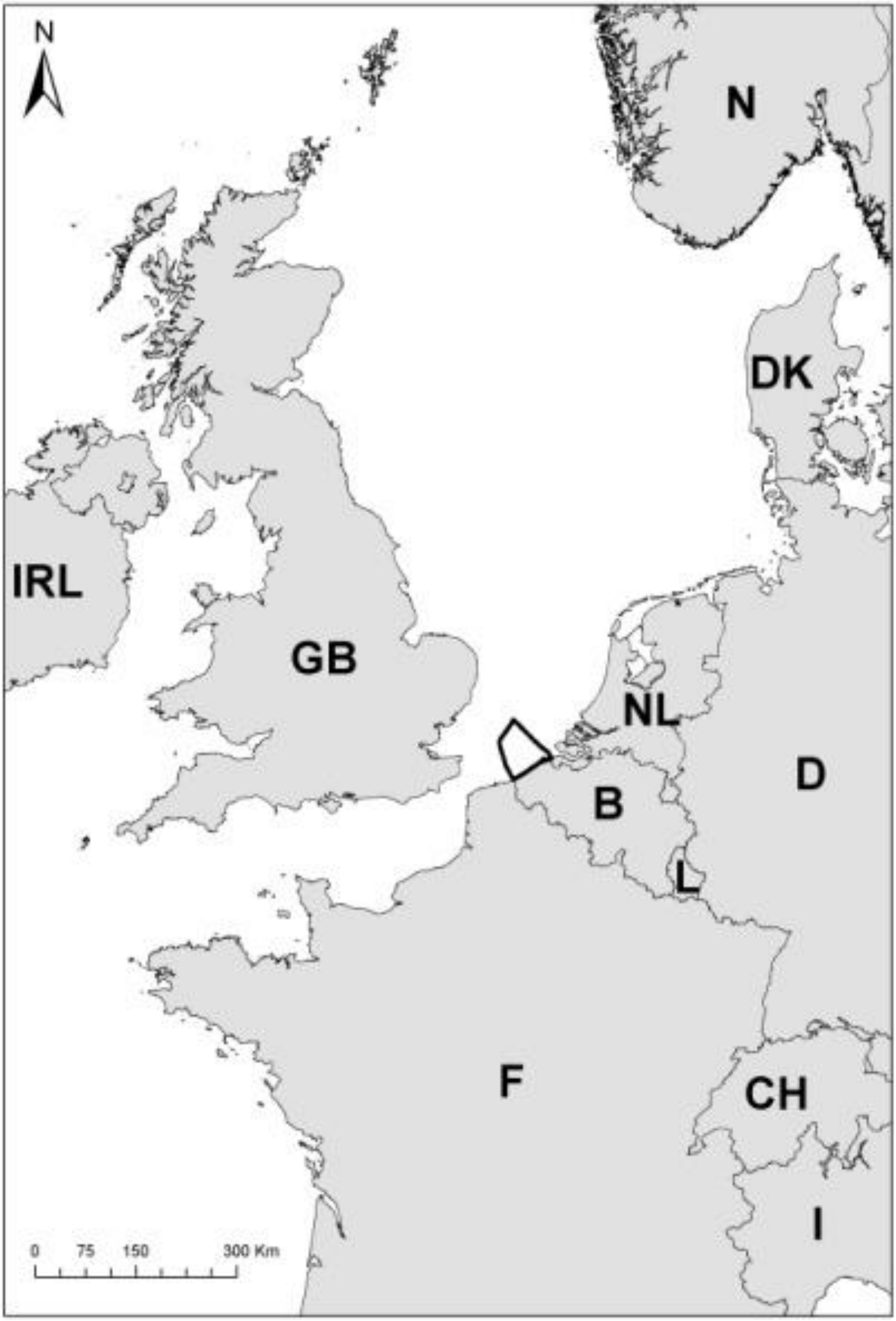

Figure 3. North-Western Europe and the position of the Belgian part of the North Sea (BPNS)

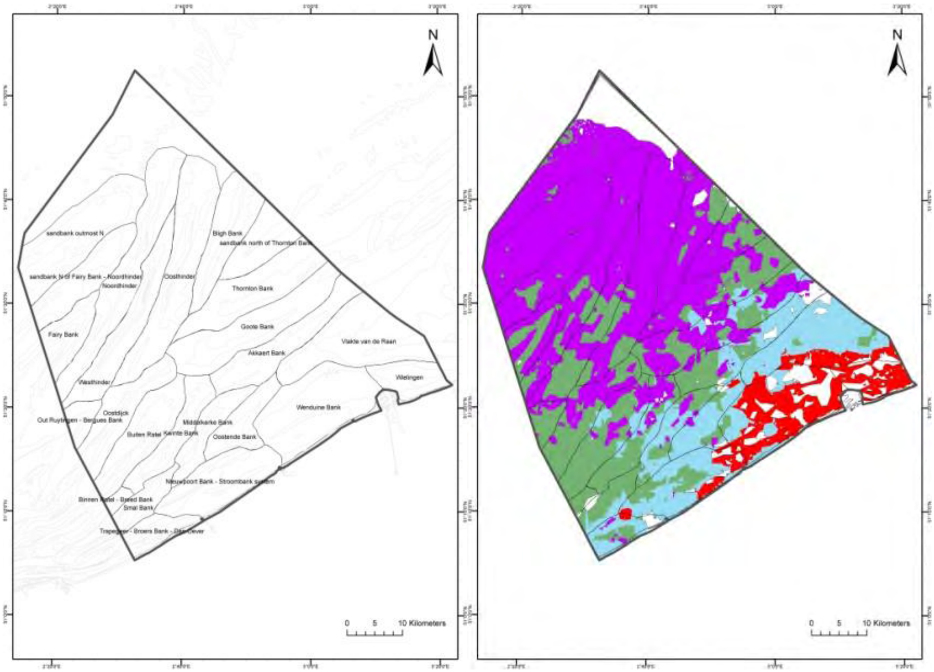

Figure 4. Left: Bathymetry of the BPNS, with indication of large sand bank systems (Degraer et al., 2009); right: Geographical distribution of the different macrobenthic communities in the BPNS as predicted from habitat suitability models (Degraer et al., 2009, Degraer et al., 2008b) (red: Macoma balthica*; blue:* Abra alba*; green:* Nephtys cirrosa *and purple:* Ophelia limacina *community; white: unpredictable).*

The BPNS is a well-known and particularly heavily used area (Figure 5). By far the commonest fishing technique in Belgium is beam trawl fisheries, mainly small beam trawlers for *S. solea* and *P. platessa* (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 (Goffin *et al.*, 2006). Existing restrictions on fisheries include amongst others the prohibition to fish within 3 nm off the coast with ships of more than 70 BT as well as a prohibition on bivalve fisheries within 12 nm. The area has a rich marine management history where an 'MPA-process' is evolving. Recently, a study on the potential Sites of Community Interest in the Belgian marine waters (*i.e.* within the framework of the EC Habitats Directive) was performed (Degraer *et al.*, 2009). In the BPNS, there is currently no no-take zone to protect the marine environment, where all fishing activities are prohibited.

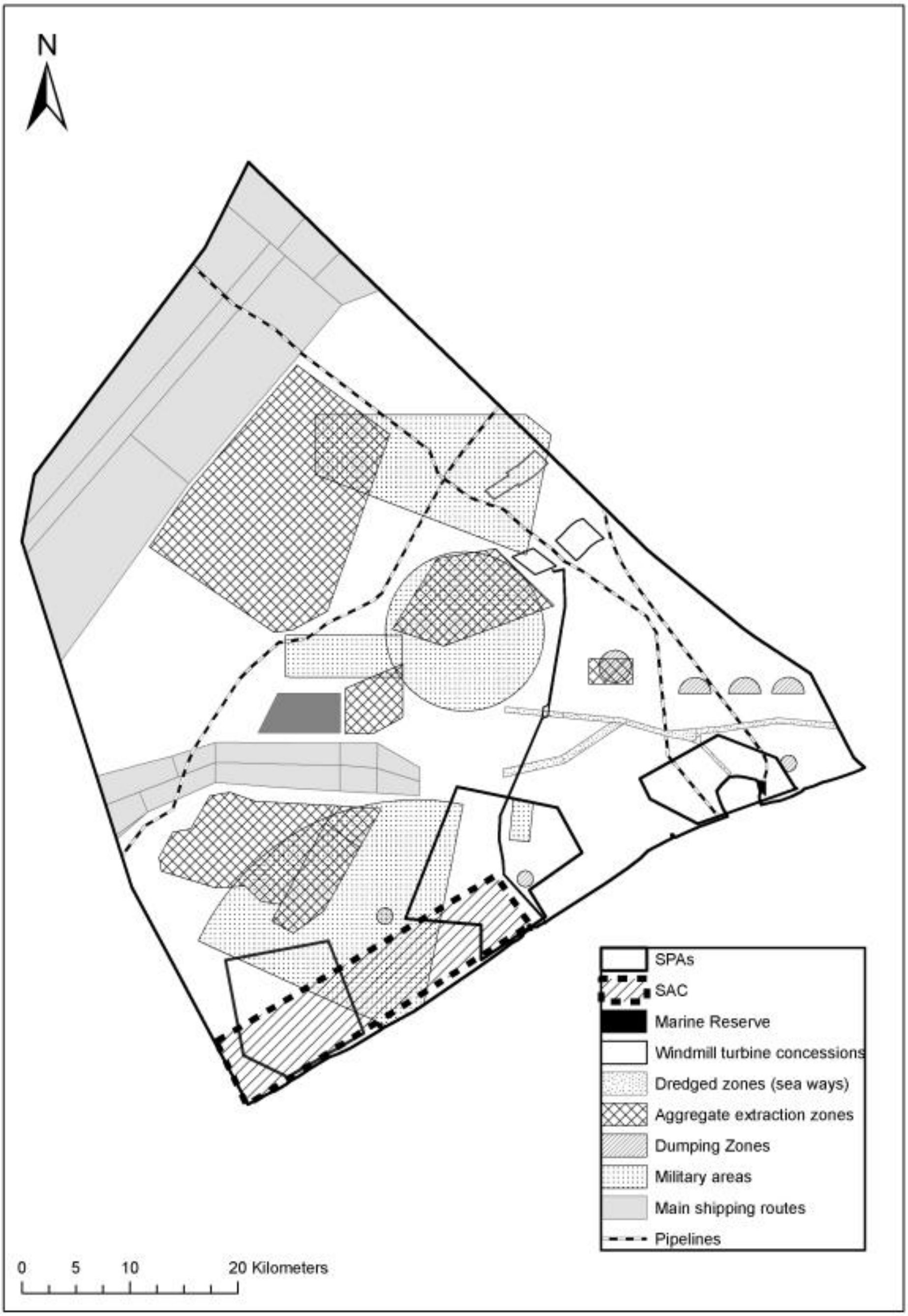

Figure 5. The Belgian part of the North Sea with indication of both the allocated areas for different human activities (adopted from Maes et al. (2005); updated) and the allocated MPAs.

In the BPNS, *L. conchilega* occurs along the coast and is part of the *A. alba* community (Van Hoey *et al.*, 2004). The *A. alba* community is one of the ecologically most important soft-sediment macrobenthic communities along the coastal areas of the English Channel and the Southern Bight of the North Sea (Van Hoey *et al.* (2005) and references therein). The most important species are *A. alba*, *Tellina fabula*, *Nephtys hombergii*, *P. (Lagis) koreni* and –as mentioned before- *L. conchilega* (Desroy *et al.*, 2003, Prygiel *et al.*, 1988, Van Hoey *et al.*, 2004). In the Belgian part of the North Sea, the presence of *L. conchilega* could be modelled on the basis of specific sediment characteristics (median grain size, mud content and coarse fraction content) (Willems *et al.*, 2008). The highest *L. conchilega* densities are found in shallow fine sands and the species has the capacity to double the biodiversity of the *A. alba* community (Van Hoey, 2006).

Outline

Apart from the general discussion, this thesis is a compilation of research articles (published, currently under review or in preparation). For that reason, the outline and output of the chapters resembles almost exactly the published or submitted papers. Each chapter is therefore intended to be an autonomous part, which can be read on its own. Inevitably, there may be some overlap between the introductions and material and methods of the different chapters. The chapters have been organized in four different parts. Part I focuses on the biological and physical characteristics of the benthic habitat that is produced by aggregations of L. conchilega. *Part II evaluates the impact of physical disturbance on the benthic part of this system. These studies aim at providing insight in the impact of beam-trawling, a wide spread physical disturbance. Part III leaves the exclusively benthic focus and investigates the importance of such ecosystem engineered habitats for higher trophic levels. Several flatfish species are chosen as these are target species of beam-trawl fisheries. Finally, Part IV investigates concepts of marine conservation, discusses the legal framework and ends with an integration of conceptual insights and results of the thesis. Results that did not belong to the candidate's core research are provided as supplemental information in the addenda. The cited literature is generalized and listed at the end of the thesis.*

The overall aim of this study is generating ecological insights that are directly of use in implementing the ecosystem approach in the management of temperate soft-bottom marine areas. The broader framework of this thesis is explained and the target ecosystem engineer is introduced in **Chapter 1**. This general introduction is based on the following published book chapter: *Rabaut, M., Vincx, M. and 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 Fisheries: Management, economics and perspectives, Ed by N. F. McManus and D. S. Bellinghouse. pp. 485-495. Nova Science Publishers, New York***.** The presentation of the original results of the thesis study starts with **Part I**, where *L. conchilega* is investigated in detail. **Chapter 2** guides the reader through the effect this tube building polychaete has on the benthic densities and on the community structure. Different ecosystem engineering implications are discussed and the gradual community shift according to increasing abundances of *L. conchilega* density was investigated based on a long term data set in Belgian coastal waters. These implications are explained on a species-specific basis. The chapter has been published as *Rabaut, M., Guilini, K., Van Hoey, G., Vincx, M. and Degraer, S. 2007. A bio-engineered soft-bottom environment: The impact of* Lanice conchilega *on the benthic species-specific densities and community structure. Estuarine Coastal and Shelf Science, 75: 525-536.* In **Chapter 3**, physical characteristics of high density aggregations of the tube worm were investigated to explain the modulation mechanisms that create the observed community shift. The characterization of these physical features together with the biological characteristics investigate whether dense aggregations classify as 'reefs' (referring to the guidelines to apply the definition of reefs as used within the EU Habitats Directive). The chapter has been published as *Rabaut, M., Vincx, M. and Degraer, S. 2009. Do* Lanice conchilega *(sandmason) aggregations classify as reefs? Quantifying habitat modifying effects. Helgoland Marine Research, 63: 37-46.*

To link this particular biogenic habitat with human activities, several short term experiments were set up to quantify the impact of physical disturbance (comparable to beam-trawl fisheries) (**Part II**). The study presented in **Chapter 4** quantifies the impact of physical disturbance on the survival of *L. conchilega* itself. This was studied with a specially designed sampling technique to bring undisturbed *L. conchilega* aggregations to the lab. Manipulations were done using a device to disturb at different intensities. The results of chapter 4 are being revised as *Rabaut, M., Vincx, M., Hendrickx, F. and Degraer, S. subm. The resistance of* Lanice conchilega *reefs to physical disturbance. ICES Journal of Marine Science.* After having quantified the impact on the ecosystem engineer itself, an *in situ* experiment (**Chapter 5**) was set up to test how vulnerable the species that live in close association with *L. conchilega* are. This chapter presents a one-off beam trawl disturbance experiment in the low intertidal. This experimental fishing event was followed by an intensive sampling during low tide of treatment and control areas. These results have been published as *Rabaut, M., Braeckman, U., Hendrickx, F., Vincx, M. and Degraer, S. 2008. Experimental beam-trawling in* Lanice conchilega *reefs: Impact on the associated fauna. Fisheries Research, 90: 209-216.*

The ecological value of the increased benthic diversity and abundance for flatfish seemed to be an important knowledge gap. Therefore, **Part III** investigates the ecological interactions between the benthic habitat created by *L. conchilega* and flatfish. More specifically, **Chapter 6** focuses on the distribution of post-larval plaice (*P. platessa*) in its nursery area (the intertidal zone) and the potential redistribution impact of *L. conchilega* reefs. This chapter will be published as *Rabaut, M., Van de Moortel, L., Vincx, M. and Degraer, S. accepted. Biogenic reefs as structuring factor in* Pleuronectes platessa *(Plaice) nursery. Journal of Sea Research (DOI 10.1016/j.seares.2009.10.009).* We turn to the subtidal in **Chapter 7**. Both the distribution and feeding behaviour of the two flatfish species *P. platessa* and *Limanda limanda* are studied in function of the presence of high densities of an ecosystem engineer. In this study two different ecosystem engineered habitats are tested for (*L. conchilega and Owenia fusiformis*) and sampling is done in two different coastal areas (the BPNS and the Dutch part of the Wadden Sea). This chapter has been submitted to *Estuarine, Coastal and Shelf Research* as: *Rabaut, M., Van de Moortel, L., van Dalfsen, J., Vincx, M. and Degraer, S. subm. Importance of eco-engineered inshore habitats for juvenile flatfish.*

Part IV reflects on the policy, objectives and legal aspects of marine conservation and discusses the potential use of the presented thesis results to apply the ecosystem approach in marine management. **Chapter 8** brings literature on marine conservation strategies in soft-bottom temperate areas together in one 'systems approach' that provides answers to the questions 'why?', 'how?' and 'what is the effectiveness?' of MPAs. The 'systems approach' was applied to the Belgian coastal environment and linked with the results found for *L.*

conchilega. This chapter has been published as *Rabaut, M., Degraer, S., Schrijvers, J., Derous, S., Bogaert, D., Maes, F., Vincx, M. and Cliquet, A. 2009. Policy analysis of the 'MPA-process' in temperate continental shelf areas. Aquatic Conservation: Marine and Freshwater Ecosystems, 19: 596-608.* In **Chapter 9**, the reader is introduced to the (international) legislative framework. The chapter evaluates whether and how ecosystem dynamics play a role in conservation strategies and investigates how this is implemented in a rather rigid legislative framework. The Belgian case is developed as an example of how international (EU) legislation has been interpreted until now. This chapter has been published as a book chapter: *Rabaut, M. and 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.* The last chapter of this part (**Chapter 10**) discusses the results of the thesis in the framework of marine policies concerning both conservation and fisheries issues. The potential use of *L. conchilega* to support, to underpin or to contribute to a more holistic approach in marine management is discussed. This general discussion of the thesis results ends with general conclusions and suggestions on where to go from here.

Finally, the **addenda** provide supplemental information to the thesis, but were not considered to belong to the core results for this thesis.

Addendum I complements Chapter 2 and describes the implications of the presence of *L. conchilega* in different habitats on a North Sea scale. The addendum has been published as: *Van Hoey, G., Guilini, K., Rabaut, M., Vincx, M. and Degraer, S. 2008. Ecological implications of the presence of the tube-building polychaete* Lanice conchilega *on soft-bottom benthic ecosystems. Marine Biology, 154: 1009-1019.* The candidate contributed to the discussion and partly to the analyses of results.

Addendum II describes the visualization of *L. conchilega* reefs using side scan sonar imagery and was published as *Degraer, S., Moerkerke, G., Rabaut, M., Van Hoey, G., Du Four, I., Vincx, M., Henriet, J.P. and Van Lancker, V. 2008. Very-high resolution side-scan sonar mapping of biogenic reefs of the tube-worm* Lanice conchilega. *Remote Sensing of Environment, 112: 3323-3328.* Contributions of the candidate include sampling and measurements in the Bay of Heist, writing of parts of the introduction, methodology and discussion.

Addendum III focuses on another tube building ecosystem engineer –*O. fusiformis*- for which the biological as well as the physical characteristics are investigated. The addendum points out which stabilizing effects biogenically created habitats can have, using a multibeam echosounder. The addendum will be submitted as: *Rabaut, M., Du Four, I., Van Lancker, V., Degraer, S. and Vincx, M. in prep. Ecosystem engineers stabilize sand bank systems:* Owenia fusiformis *aggregations as ecologically important microhabitat.*

PART I

THE ECOSYSTEM ENGINEER *LANICE CONCHILEGA*

CHAPTER 2

A Bio-engineered soft-bottom environment:

The impact of *Lanice conchilega* on the benthic species-specific densities and community structure

Published as:
Rabaut, M., Guilini, K., Van Hoey, G., Vincx, M. and Degraer, S. 2007.
A bio-engineered soft-bottom environment: The impact of *Lanice conchilega* on the benthic species-specific densities and community structure.
Estuarine Coastal and Shelf Science, 75: 525-536.

Abstract

This paper evaluates the effect of the tube building, habitat structuring polychaete *Lanice conchilega* on the macrobenthic community and on sediment characteristics of its habitat. To investigate which factors make species occur in a well-known bio-engineered habitat, macrofaunal and sedimentological data, gathered over a period of ten years in a shallow, fine sediment bottom of the Belgian Part of the North Sea, were submitted to analyses. Both sediment composition and community structure of the associated macrofaunal matrix were affected by the presence of *L. conchilega*. The effect of the protruding tubes on hydrodynamics clearly resulted in retention of fine sediment particles, while the increased coarse fraction was assumed to reflect a dynamic population build-up. This study confirmed that tube aggregations of *L. conchilega* expand the realized niche of several species without forming its own association. A species rank list was created according to each species' association with *L. conchilega*. This species rank list is extensively discussed based on all ecological knowledge available. Species are favoured by the habitat modifying ability of the polychaete tubes, which create and regulate refuge for species, alter the interactions between local species and change the physical factors of the environment. This descriptive and correlative data study examines the ecological importance of the bio-engineer *L. conchilega* on species level.

Key words

Lanice conchilega, tube dwellers, bio-engineers, community composition, species diversity, associated species, Europe, Belgium, BPNS

Introduction

Habitat structuring organisms are known to add or alter physical, chemical and biological factors and are therefore often referred to as bioengineers (Jones *et al.*, 1994). The ecological mechanisms behind the effect of habitat structuring organisms are well described for all kinds of environments: coral reefs (e.g. Holbrook *et al*. (1990)), Darwin mounds (Van Gaever *et al.*, 2004), kelp forests (Steneck *et al.*, 2002), ascidians (Castilla *et al.*, 2004)**,** sea grass meadows (Alfaro, 2006, Hovel *et al.*, 2002), mussel banks (Ragnarsson and Raffaelli, 1999), oyster beds (Lenihan, 1999) and polychaete tubes (Bolam and Fernandes, 2003, Callaway, 2006). The structural complex framework provided by these emergent features constitutes an important organizing aspect and is critical to the functioning of many ecosystems (Jones *et al.*, 1994). These structures represent important habitats for a variety of marine organisms. They may provide refuge from predation, competition and physical as well as chemical stresses, or may represent important food resources and critical nursery or spawning habitats. In addition, these structures modify the hydrodynamic flow regime near the sea floor, with potentially significant ecological effects on sedimentation, food availability, larval and/or juvenile recruitment, growth and survival. As such, habitat structures and heterogeneity influence faunal abundance, species richness and species composition of invertebrate and fish communities (Koenig *et al.*, 2000, Turner *et al.*, 1999). Though modulation mechanisms are understood quite well, there is often a lack of information on how species assemblages restructure themselves in bio-engineered systems. This study investigates which factors make species to occur in a well known bio-engineered habitat, based on the autecology of individual species.

The common tube dwelling polychaete *Lanice conchilega* (Terrebellidae) is the target bio-engineer in this paper. The physiology, tube structure (Jones and Jago, 1993, Ziegelmeier, 1952), hydrodynamic influence (Dittmann, 1999, Eckman, 1983, Heuers *et al.*, 1998), as well as the occurrence of *L. conchilega* patches (Hartmann-Schröder, 1996) has already been extensively described. In intertidal areas, the tube patches are known to have consequences for the distribution and abundance of infaunal species by influencing the habitat structure (Callaway, 2006, Carey, 1987, Dittmann, 1999, Féral, 1989, Zühlke, 2001, Zühlke *et al.*, 1998). This patchy distribution of tube aggregations within a specific habitat is useful to investigate the bio-engineering implications of this polychaete. Recently, bio-engineering influence on faunal abundance, species richness and species composition in subtidal areas has been proved (Van Hoey, 2006). These results indicate that effects on density and diversity are most pronounced in shallow fine sand. Besides, this study shows that rather than forming its own association, *L. conchilega* expands the realized niche of several species.

This study focuses on samples from the Belgian Part of the North Sea (BPNS), a shallow area with a sediment composition of mainly fine sand. The hypothesis that *L. conchilega* tube aggregations influence the benthic species assemblage by creating ecological optimal niches for species otherwise living in suboptimal conditions is tested for the specific study area analyzed here. This paper provides a species rank list by association degree with *L. conchilega*, based on community and species analyses. This ranking is extensively discussed on the basis of available ecological knowledge of all species. Furthermore, the influence of *L. conchilega* on sediment fractions was tested. In order to do so, macrobenthic data from samples taken in a restricted area of the North Sea, over a period of ten years, were selected on the basis of physico-chemical habitat characteristics (sedimentology and depth) and submitted to analyses. This allows an assessment of the natural variation in the abundance of *L. conchilega* and its associated community, independent of geographical and temporal variability. This approach enabled us to test for the impact an ecosystem engineer. However, this is a correlative data study and we are fully aware of the fact that causal relationships cannot be proved here.

Material and methods

Study area

The study area covers a transect of the BPNS situated in the Southern Bight of the North Sea, close to the Belgian coast (66 km in length) (Figure 1). This shallow area (max. 46 m depth) consists of several sandbank systems, more or less oriented parallel to the coast. The characteristic geomorphologic and sedimentological diversity of these soft-bottom habitats is directly responsible for the high biological diversity and species richness, reflected in a mosaic of several distinguishable macrobenthic communities (Degraer *et al.*, 2002, Van Hoey *et al.*, 2004).

Data origin

Data, gathered on the BPNS, over a period of ten years (October 1994 until March 2005), was selected on the basis of habitat classification, which takes into account sedimentological characteristics and bathymetrical information. A dataset of 657 macrobenthic samples was submitted to analysis. This subset of samples were selected from shallow locations (< 25 meter according to MLWS level) at which the fine sediment fraction was the largest. Sediment characteristics are known to determine macrobenthic species occurrence (Van Hoey *et al.*, 2004). To test the impact of *L. conchilega* as bio-engineer, samples were selected based on specific median grain size values (125-250 μm) because (1) a similar macrobenthic species assemblage is expected based on sedimentology and (2) different densities of *L. conchilega* are expected in these sediments (Willems *et al.*, 2008).

The benthos was sampled using a Van Veen grab of 0.1 m^2 surface area and sieved through a 1 mm mesh-sized sieve. Macrofauna was identified to the lowest possible taxonomic level (further referred to as species) and counted. Species abundance data were standardised to a total number of individuals per m^2. Organisms were classified into five trophic groups: (1) suspension feeders, (2) surface-deposit, facultative suspension and interface feeders (capable of alternative suspension- and surface-deposit feeding dependent on flow conditions), (3) subsurface deposit feeders and grazers and (4) omnivores, predators and scavengers. Species that forage by more than one feeding mode were classified by their most common feeding mechanism, while species for which information is lacking were grouped together in the category ‘unknown’. Parasites (5) occurred coincidentally; they were not adequately sampled and therefore excluded from this study. Information available on the autecology of particular species was also gathered and is considered in the discussion.

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: (0) samples without tubes and samples with *L. conchilega* densities ranging from (1) 1-50 ind m^{-2}, (2) 50-300 ind m^{-2}, (3) 300-1500 ind m^{-2} and (4) > 1500 ind m^{-2}. This division was based on the most significant results obtained by a one-way ANOSIM analysis.

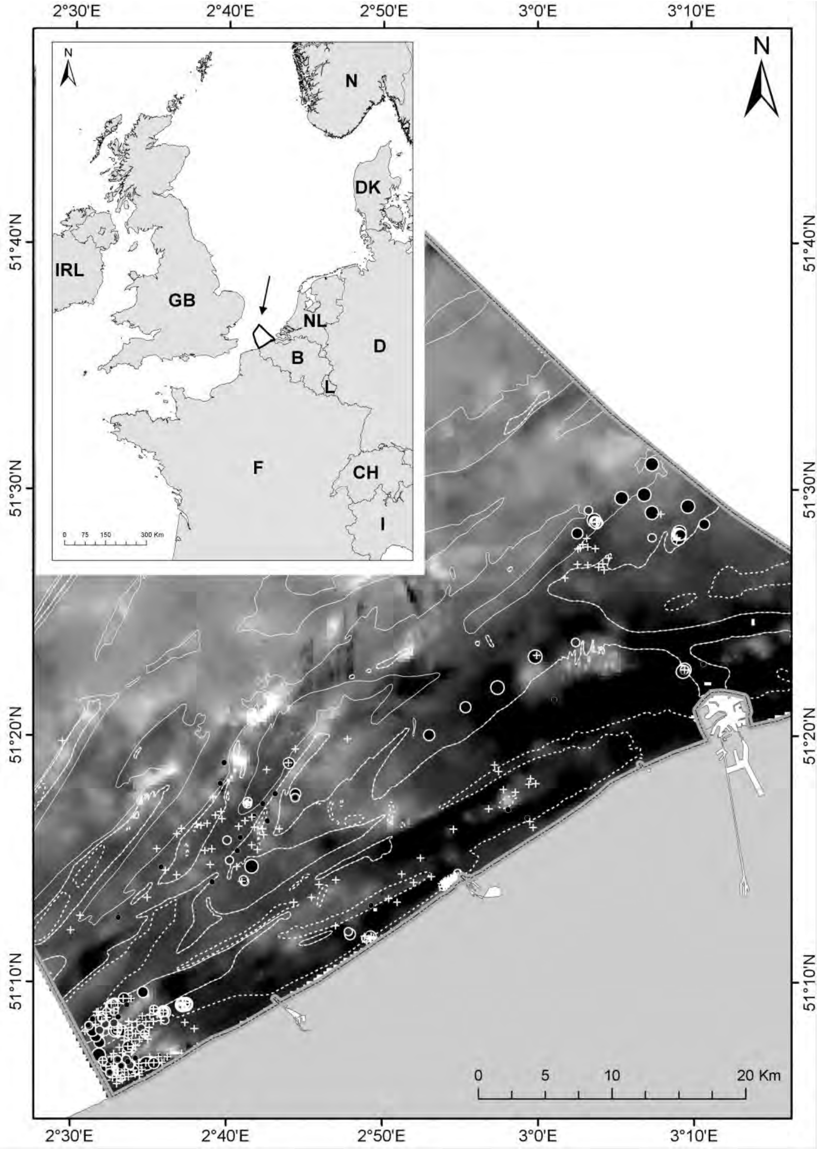

Figure 1. Distribution of the sample locations in the shallow subtidal and low intertidal areas of the Belgian Part of the North Sea (BPNS). Depth contours of 10 m (white dotted lines) and 20 m (white lines) are visualised. Modelled full coverage sediment characteristics are represented from light grey (coarse median grain size; max. 762 µm) to black (fine median grain size; min. 0.37 µm) (Verfaillie et al., 2006). The 657 samples were selected based on sediment characteristics. Each sample is represented according to Lanice conchilega *density class (white edged black dots, dimension of dots from small to large for classes 1-4 respectively);* L. conchilega*-free samples are represented by white crosses.*

Data analysis

To investigate potential effects of *L. conchilega* tube aggregations on the grain size composition in the patches, data on sediment fractions (according to the Udden-Wentworth logarithmic scale (Buchanan, 1984)) obtained by a Coulter LS particle size analyser, were examined. The Mann-Whitney U test was applied to check for differences in median grain size and in allocation of sediment fractions between the *L. conchilega* classes. This non-parametric test was used because the assumptions for parametric tests, even after transformation, were not fulfilled (Conover, 1999).

The quantitative faunistic data were analysed using a combination of multivariate and univariate methods. Zühlke (2001) and Callaway (2006) designated a species assemblage composed of *L. conchilega* tubes plus accompanying organisms as a '*L. conchilega* community'. We emphasise the fact that in our study area *L. conchilega* is part of the well defined *Abra alba - Kurtiella bidentata* community (Van Hoey *et al.*, 2004), in which it structures the habitat and thus influences the present species community. We therefore refer to the '*L. conchilega* community *s.s.*', when discussing its community structure. The benthic community structure was analysed with the PRIMER v5 statistical package (Clarke and Warwick, 2001). Non-parametric multidimensional scaling (MDS) and analysis of similarity (one-way ANOSIM) were used to describe (dis-)similarities between benthic faunal communities from *L. conchilega* communities and sites where *L. conchilega* did not occur. The MVDISP algorithm of the PRIMER v5 software was used to quantify the variability in each density class and to calculate the Index of Multivariate Dispersion (IMD). This comparative Index contrasts the average rank of the similarities among samples of a certain density class with the average rank of other density class sample groups (Clarke and Warwick, 2001). With the SIMPER program the (dis)similarity between the communities and the percentage contribution of each species to the similarity within and dissimilarity between communities was examined. Species richness for different *L. conchilega* density classes was calculated using the PRIMER v5 software package and is presented by total number of species (S) and Margalef's index (d) which takes into account the given number of individuals (Clarke and Warwick, 2001).

In order to identify species possibly associated with the presence of *L. conchilega,* four criteria were applied. The Indicator Species Analysis (ISA, Pcord4 programme) was carried out and an association degree (the percentage of occurrence of a species in samples with *L. conchilega* relative to the total presence of that species in all samples) was calculated. Besides this, the Mann-Whitney U test was used to compare abundances of these species between samples with and without *L. conchilega*. Finally, the correlation of the density of *L. conchilega* tubes with individual species abundances was tested with the Spearman Rank correlation analysis. A species was defined as positively associated with *L. conchilega* when (1) a significant indicator value was attributed, (2) the association degree was more than 50%, (3) species density significantly differed between samples with and without *L. conchilega* and if (4) a positive and significant correlation with the density of *L. conchilega* was found. Based on these results a species list was made in which species are ranked according to a summation of the indicator value and the association degree.

Results

Sediment characteristics

Fine sand (125 - 250 µm) was the major sediment fraction in all samples, with a contribution ranging from 49 - 65%. The median grain size ranged from 143 to 250 µm (mean ± SD: 206 µm ± 24 µm), but did not show significant differences according to the presence of *L. conchilega*. Comparing the contribution of sediment fractions in samples with and without *L. conchilega,* a significant difference ($p \leq 0.0001$) was found for every fraction, except for the fine and medium sand fractions (respectively $p = 0.062$ and $p = 0.184$). A comparison between the classes revealed that these differences were mainly caused by significant differences ($p \leq 0.01$) in clay and silt fractions between the *L. conchilega* class of > 1500 ind m^{-2} and all other classes, and by significant differences ($p \leq 0.02$) in clay, silt and very fine sand fractions between the *L. conchilega* classes of 1 - 50 ind m^{-2} and 50 - 300 ind m^{-2} and the tube-free patches, with the mentioned fractions always higher in the denser *L. conchilega* patches. The coarse fraction differed rather significantly ($p < 0.001$) between patches with > 300 ind m^{-2} (classes 3 and 4) and all other classes (Figure 2). Volume percentage of the three finest and the coarsest sediment fraction increased gradually, however not linearly, with increasing *L. conchilega* densities.

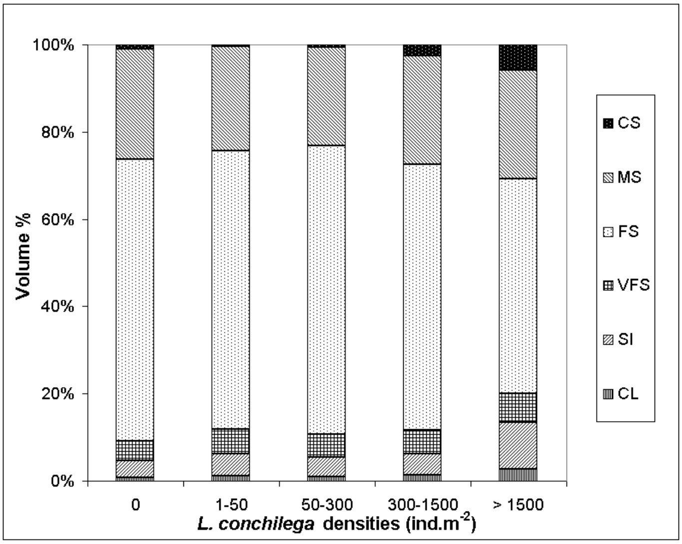

Figure 1. The grain size distribution (CS: coarse sand 500-1000 µm; MS medium sand 250-500 µm; FS fine sand 125-250 µm; VFS: very find sand 63-125 µm; SI: silt 3.9-63 µm; CL: clay 0.06-3.9 µm) versus the different Lanice conchilega *density classes. Clay and silt fractions are significantly larger in the highest density class. Coarse sand fraction is larger in samples with more than 300* L. conchilega *specimens.m^{-2}.*

Community analysis

The one-way ANOSIM analysis revealed that the species community around *L. conchilega* tubes could be distinguished from the species community in tube-free sediments (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). 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. These results are summarised in Table 1 and visualised in a 2-dimensional ordination graph constructed by the MDS-analysis (stress 0.22) (Figure 3). The benthos composition showed no clear grouping. Nevertheless communities differed gradually according to increasing abundances of *L. conchilega*, with the community of high *L. conchilega* density sharply defined as the inner circle, enlarging when *L. conchilega* densities are decreasing. 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 (IMDs) have negative values, implying that all similarities among samples of a *L. conchilega* density class were greater than the similarities of samples between different density classes. The further the density classes are separated, the closer the IMD is to -1 (Table 2).

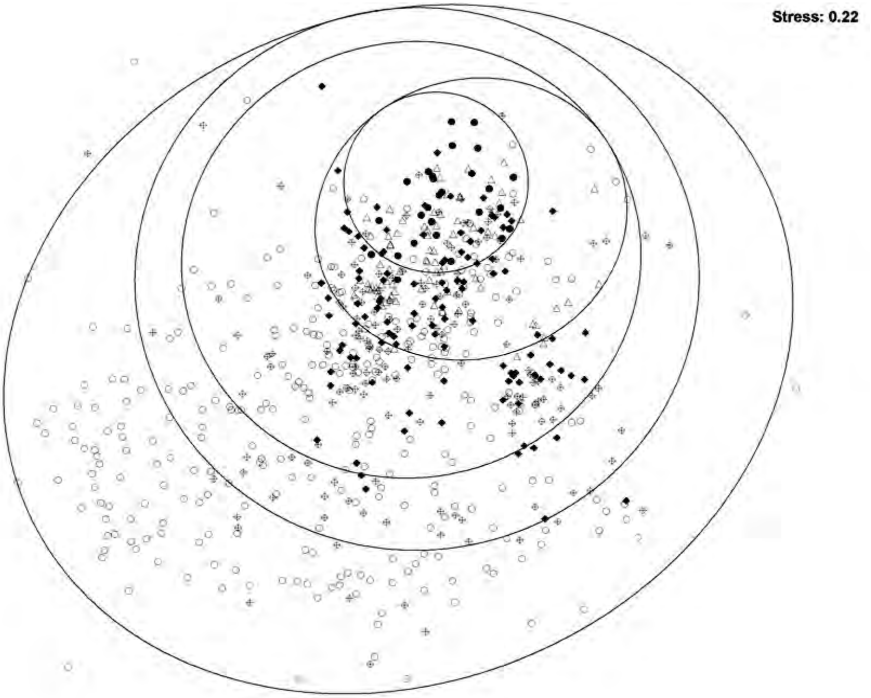

Figure 2. Two-dimensional MDS ordination plot of similarities between species assemblages of different density classes of Lanice conchilega *aggregations (classes 1-4, respectively crossed squares, filled gray squares, open triangles and black filled dots) and* L. conchilega*-free samples (open dots) (using Bray-Curtis similarity measure of square root transformed data). The „babushka" like organisation of the samples indicates that* L. conchilega *restructures the species assemblage by expanding the realized niche of several species.*

Species analyses

Associated species

Hundred and sixty-two macrobenthic species (*L. conchilega* excluded) were recorded in this study of which 66 were found to be positively associated with *L. conchilega* (*i.e.* 41%). Of these associated species, polychaetes counted the highest number of species (30 species or 45%), and were the most abundant taxonomic group (63%), followed by bivalves (25%), amphipods (7%), oligochaetes (2%), ophiuroids (1%) and others (2%). A ranking list of the positively and negatively associated species is given in Table 3. Positively associated bivalves were *Donax vittatus, Ensis* spp., *Kurtiella bidentata, Spisula subtruncata, Abra alba, Tellina fabula* and others.

Table 1. Results of the global and pairwise ANOSIM and SIMPER analysis for differences between the macrofauna community composition of Lanice conchilega *patches with different classes of densities (1-4) and* L. conchilega*-free patches (0).*

	R	*p*	Dissimilarity
L. conchilega presence/absence			
Global test	0.237	0.001	78.9
L. conchilega classes			
Global test	0.028	0.045	
Pairwise test			
1 - 0	0.029	0.025	78.2
2 - 0	0.054	0.016	78.4
2 - 1	0.002	0.420	70.6
3 - 0	0.095	0.002	80.0
3 - 1	0.047	0.030	71.2
3 - 2	0.033	0.027	63.2
4 - 0	0.207	0.001	83.3
4 - 1	0.129	0.013	76.2
4 - 2	0.113	0.010	67.9
4 - 3	0.090	0.043	57.5

Table 2. Indices of Multivariate Dispersion (IMDs) show that all similarities among samples of a Lanice conchilega density class were greater than the similarities of samples between different density classes. The further the density classes are separated, the closer the IMD is to -1.

Density class	Density class compared with	IMD value
1	0	-0.278
2	0	-0.608
2	1	-0.406
3	0	-0.802
3	1	-0.647
3	2	-0.29
4	0	-0.838
4	1	-0.694
4	2	-0.352
4	3	-0.057

For polychaetes, *Pygospio elegans, Eumida sanguinea, Harmothoe* spp., *Spiophanes bombyx* etc. were found to be strongly associated whereas some of the most associated amphipods were *Pariambus typicus, Urothoe poseidonis, Gammarus* spp., etc. Based on association degree only, eight species were exclusively associated (100%) with *L. conchilega* tubes: *Gattyana cirrhosa,* *Asterias rubens*, *Bodotria arenosa*, *Gammarus* spp., *Leucothoe lilljeborgii*, *Liocarcinus navigator*, *Amphilochus neapolitanus* and *Pagurus bernhardus*. However, due to their presence in a low number of samples (max. 19) and/or low densities, their indicator value never exceeded a value 5. Five species were found to be negatively associated with *L. conchilega* (Table 3). Besides the negative (significant) correlation values, these species were significantly more abundant in samples without *L. conchilega* ($p < 0.01$).

Average macrobenthos densities (mean ± SE) of 8080 ± 1032 ind m^{-2} were found in the presence of *L. conchilega*, while 1608 ± 146 ind m^{-2} were found in samples without *L. conchilega*. There was a positive correlation between the steadily increasing macrobenthic densities and densities of *L. conchilega* ($R = 0.59$; $p < 0.001$). Species richness was increasing with *L. conchilega* densities, except for the highest *L. conchilega* density class (Table 4).

Trophic composition

Trophic group analysis showed a gradual increase in density for every trophic group with increasing densities of *L. conchilega*, except for the suspension feeders. The suspension feeders reached their maximum density within the range of 1 - 50 *L. conchilega* ind m^{-2}. Yet their relative abundance did not strongly vary, as is also the case for subsurface deposit feeders. The overall most successful trophic groups were the groups of surface-deposit, facultative suspension and interface feeders, followed by the omnivores, predators and scavengers. They dominated both in *L. conchilega* patches and in *L. conchilega*-free patches; surface deposit feeders however dominated stronger in *L. conchilega*-free patches, while predators gained dominance in the vicinity of *L. conchilega*.

When considering density distributions of all macrobenthic species, in samples with >1500 *L. conchilega* ind m^{-2}, densities of other benthic species tended to decline; this trend was, however, not found to be statistically significant. Only 11 out of the 162 species, all polychaetes and decapods, seemed to bear the highest *L. conchilega* densities and are listed in Table 5. Their density increased significantly ($p \leq 0.032$) and contributed to the overall increase of macrobenthic density. Among these tolerant species, predators and scavengers were particularly numerous (8 species).

Table 3. Rank list of the associated species. Species are ranked based on the summation of the indicator value (ISA) and the association degree.

	ISA		Association	Mann-Whitney *U*-test	Spearman rank correlation	
	Indicator value	*p*	degree (%)	*p*	*R*	*p*
L. conchilega patches						
Eumida sanguinea	65	0.001	83	0.000	0.730	0.000
Spiophanes bombyx	72	0.001	63	0.000	0.558	0.000
Phyllodoce (A.) maculata- mucosa	59	0.001	76	0.000	0.614	0.000
Pariambus typicus	56	0.001	78	0.000	0.610	0.000
Tellina fabula	61	0.001	62	0.000	0.397	0.000
Capitella spp.	52	0.001	68	0.000	0.418	0.000
Pectinaria spp.	44	0.001	75	0.000	0.507	0.000
Nephtys hombergii	61	0.001	57	0.000	0.375	0.000
Ensis spp.	51	0.001	67	0.000	0.388	0.000
Oligochaeta spp.	49	0.001	69	0.000	0.401	0.000
Abra alba	52	0.001	65	0.000	0.441	0.000
Nereis spp.	41	0.001	72	0.000	0.417	0.000
Spisula subtruncata	53	0.001	55	0.000	0.124	0.001
Polydora spp.	10	0.001	97	0.000	0.296	0.000
Kurtiella bidentata	45	0.001	61	0.000	0.303	0.000
Magelona spp.	49	0.005	56	0.000	0.333	0.000
Gattyana cirrhosa	5	0.001	100	0.000	0.246	0.000
Microprotopus maculatus	19	0.001	86	0.000	0.370	0.000
Notomastus latericeus	34	0.001	70	0.000	0.372	0.000
Spio spp.	43	0.001	61	0.000	0.261	0.000
Liocarcinus navigator	3	0.004	100	0.002	0.178	0.000
Harmothoe spp.	22	0.001	82	0.000	0.354	0.000
Amphilochus neapolitanus	3	0.003	100	0.003	0.209	0.000
Leucothoe lilljeborgii	3	0.005	100	0.003	0.142	0.000
Abludomelita obtusata	21	0.001	82	0.000	0.361	0.000
Bodotria arenosa	3	0.011	100	0.005	0.108	0.005
Sigalion mathildae	32	0.001	71	0.000	0.270	0.000
Asterias rubens	3	0.014	100	0.007	0.148	0.000
Gammarus spp.	2	0.024	100	0.011	0.088	0.024
Cirratulidae spp.	38	0.001	64	0.000	0.324	0.000
Pagurus bernhardus	2	0.031	100	0.028	0.129	0.001
Leucothoe incisa	28	0.001	73	0.000	0.361	0.000
Bodotria scorpioides	12	0.001	88	0.000	0.321	0.000
Atylus swammerdami	13	0.001	87	0.000	0.284	0.000
Eteone longa	25	0.001	75	0.000	0.353	0.000
Nassarius reticulata	29	0.001	70	0.000	0.236	0.000
Liocarcinus pusillus	5	0.002	94	0.000	0.239	0.000
Stenothoe marina	7	0.002	91	0.000	0.252	0.000
Megaluropus agilis	6	0.001	91	0.000	0.226	0.000
Autolytus spp.	18	0.001	78	0.000	0.226	0.000

Owenia fusiformis	29	0.001	66	0.000	0.276	0.000
Scoloplos (S.) armiger	41	0.000	53	0.000	0.218	0.000
Ophiura spp.	30	0.001	64	0.000	0.214	0.000
Phtisica marina	3	0.020	91	0.007	0.174	0.000
Poecilochaetus serpens	18	0.001	75	0.000	0.230	0.000
Liocarcinus holsatus	16	0.001	77	0.000	0.316	0.000
Orchomene spp.	3	0.015	90	0.012	0.123	0.002
Sthenelais boa	20	0.001	72	0.000	0.253	0.000
Pseudocuma spp.	21	0.001	71	0.000	0.265	0.000
Perioculodes longimanus	17	0.001	76	0.000	0.241	0.000
Donax vittatus	19	0.001	72	0.000	0.186	0.000
Heteromastus filiformis	13	0.001	78	0.000	0.236	0.000
Diastylis bradyi	25	0.001	65	0.000	0.270	0.000
Ampelisca brevicornis	15	0.001	76	0.000	0.250	0.000
Actiniaria spp.	25	0.001	65	0.000	0.195	0.000
Arenicola marina	5	0.005	84	0.002	0.092	0.018
Pholoe minuta	15	0.001	73	0.000	0.248	0.000
Urothoe poseidonis	28	0.005	58	0.000	0.163	0.000
Glycera alba	17	0.001	67	0.000	0.199	0.000
Corophium spp.	3	0.045	81	0.034	0.118	0.002
Glycera convoluta	5	0.013	79	0.008	0.125	0.001
Phyllodoce (A.) rosea	4	0.020	77	0.017	0.156	0.000
Venerupis senegalensis	12	0.001	69	0.001	0.156	0.000
Eteone flava	4	0.026	75	0.019	0.155	0.000
Crangon crangon	8	0.003	70	0.004	0.181	0.000
Phyllodoce (A.) groenlandica	5	0.045	67	0.039	0.150	0.000

	ISA		Association degree (%)	Mann-Whitney *U*-test	Spearman rank correlation	
	Indicator value	*p*		*p*	*R*	*p*
L. conchilega-free patches						
Nephtys cirrosa	33	0.001	38	0.000	-0.198	0.000
Bathyporeia spp.	25	0.001	27	0.000	-0.218	0.000
Pontocrates altamarinus	10	0.001	20	0.000	-0.180	0.000
Urothoe brevicornis	4	0.027	17	0.002	-0.131	0.001
Scolelepis bonnieri	5	0.001	14	0.001	-0.127	0.001

Table 4. *Species richness for different* Lanice conchilega *density classes, represented by average number of species per sample in each density class (S) and by Margalef's index (d). Species richness increases with increasing* L. conchilega *densities, except for the highest* L. conchilega *density class*

Density class	*S*	*d*
0	12,80	1,71
1-50	17,66	2,15
51-150	22,89	2,65
151-300	25,76	2,95
301-500	29,23	3,27
501-1000	32,83	3,59
1001-1500	35,57	3,89
>1500	33,93	3,66

Table 5. *List of species found to be tolerant for the highest* Lanice conchilega *densities (> 1500 ind* m^{-2}*). (P: polychaete, D: decapod)*

Surface-deposit, facultative suspension and interface feeders (2)
Spiophanes bombyx (P)

Subsurface deposit feeders and grazers (3)
Pectinaria spp. (P)
Scoloplos (S.) armiger (P)

Omnivores, predators and scavengers (4)
Crangon crangon (D)
Eteone longa (P)
Eumida sanguinea (P)
Gattyana cirrosa (P)
Harmothoe spp. (P)
Liocarcinus holsatus (D)
Liocarcinus pusillus (D)
Phyllodoce (Anaitides) maculata-mucosa (P)

Discussion

Effect of Lanice conchilega *on sediment properties*

Lanice conchilega occurred with different population densities at the sample sites of the BPNS and small-scale density variations were recorded where replicates were taken. The distribution of different density classes is visualised in Figure 1. This indicates that mosaic distribution patterns in which patches of low and high density alternate on a scale of meters, are formed in a similar way to what is found in some parts of the intertidal areas (Carey, 1987, Heuers *et al.*, 1998), where dense aggregations of *L. conchilega* have been described as distinguishable mounds (Heuers *et al.*, 1998). These mounds are formed because high densities of *L. conchilega* locally influence the hydrodynamics (Eckman, 1983). In dense tube assemblages the velocity of the near-bottom flow is reduced and normal, laminar near-bottom flow is deflected around and across the assemblages (Heuers *et al.*, 1998). The reduced current velocities in the patches increase the residence time of particles (Friedrichs *et al.*, 2000) and thus facilitate the deposition of silt, clay and very fine sand particles as observed in this study. These findings were consistent with results from studies conducted on other tube-building polychaete patches (Bolam and Fernandes, 2003, Eckman *et al.*, 1981, Noji, 1994). As differences in hydrodynamics are related to tube density, sediment composition changed with a variation in density of *L. conchilega*. However, the significant though moderate increase in the finest sediment fractions in the *L. conchilega* patches might be limited due to the activity of burrowing and crawling infauna and predating epifauna. Their presence can lower the resistance of sediments to erosion (the stability of the sediment) and promote resuspension of the finest fractions into the water column (Rhoads and Young, 1970). Though our results support the current knowledge of sedimentation impact, we point out that this correlative data study cannot distinguish this effect from the preference of the worm for a certain sediment type.

A gradual increase in the coarse sand fraction with increasing densities of a tube-building polychaete has never been recorded before. Therefore it can only be hypothesised that this fraction is a residue of *L. conchilega* tubes, as this species is known to line the walls of its burrow with coarse particles, firmly incorporated into an elastic mucous membrane (Jones and Jago, 1993). The tubes could get buried and biodegraded underneath accumulating finer sediments, after the inhabiting polychaetes died or left their tubes due to growth or disturbance (Carey, 1987). As this fraction of coarser sand increases with increasing *L. conchilega* densities, this could reveal some information on the age and dynamics of these patches. It is known that *L. conchilega* aulophore larvae prefer the vicinity of tubes of conspecific adults for initial settlement (Callaway, 2006, Carey, 1987, Heuers *et al.*, 1998, Zühlke, 2001). Moreover it has been reported to be more successful in areas with adults present than areas without (Heuers and Jaklin, 1999). In environmental favourable and stable conditions, the interactions between adults and larvae could result in a successful build-up of a dense population, of which the succession process could be reflected in the sedimentary environment.

The parallel increase of the volume percentages of the finest and the coarsest sediment fraction might balance the median grain size, which possibly explains why there was no difference[3] between the *L. conchilega* classes.

Effect of **Lanice conchilega** *on the benthic community*

Results indicated that even low densities of 1 - 50 ind m^{-2} had a significant effect on the macrobenthic community. When all classes are taken into account, total density of the macrobenthic fauna significantly augmented with the presence of *L. conchilega*[4][5]. These findings support the results of previous studies on *L. conchilega* (Callaway, 2006, Dittmann, 1999, Zühlke, 2001, Zühlke *et al.*, 1998), other polychaete tube patches (Bolam and Fernandes, 2003, Luckenbach, 1987, Noji, 1994, Woodin, 1978) and even imitations of polychaete tubes (Callaway, 2003b, Dittmann, 1999, Zühlke *et al.*, 1998).

The MDS ordination clearly illustrates this shift in community composition and indicates that *L. conchilega* alters the community structure of the benthic fauna, even when present at low densities. Further the plot clearly shows that the structuring effect creates communities that consist entirely of species sampled out of the same species pool. Based on the enlarged difficulty to compress the relationship of this large quantity of data into two dimensions, we obtained a relatively high, though acceptable stress value of 0.22.

An explanation for the overall increase in species richness can be partially found in the fact that there is a greater chance to catch a species, when occurring in higher densities (Downes *et al.*, 2000). However, the driving force that allows these higher densities to evolve can be attributed to the capacity of *L. conchilega* to create or modify the habitat in a way that is favourable and generates good living conditions, for many species. The result is an increased habitat complexity and heterogeneity (niche diversification) that facilitates the evolution of a more diverse community (Bell *et al.* (1991) as cited in: Downes *et al.* (2000)). This confirms that *L. conchilega* not only alters the physical but also the biological factors and is therefore referred to as a bio-engineer (Jones *et al.*, 1994). The ability of *L. conchilega* to enhance the

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[3] Difference in median grain size

[4] Note: *L. conchilega* densities were excluded from the 'macrobenthic densities'.

[5] Note: there was no data available on the size-frequency-distribution; the highest densities class may include many young individuals. The implications of different size-frequency-distributions are not known. However, as most samples were taken in autumn (in the BPNS almost exclusively adults, *cf.* Chapter 1), the effect of juveniles is probably low. The long-term analysis on this autumn samples reduces the risk of biased conclusions.

survival of certain species in more optimal conditions is reflected in a gradual community shift, based on changes in relative abundances of macrobenthic species. However, the MDS results, as well as the indicator values (max. 72) clearly show that the species found to be positively associated with *L. conchilega*, belonged to the overall species-pool of the habitat. Though we selected samples from one habitat type (fine sediment) and hence worked within one macrobenthic community, significant ANOSIM results were found. The relatively low R value indicates that all samples belong to the same community. The structuring effect is shown in the decreasing Dispersion Factor Values with increasing *L. conchilega* densities which is visualised in the "Babushka" like pattern of the MDS. Furthermore, Indices of Multivariate Dispersion (IMDs) show that density classes differ, emphasising the structuring effect. These results confirm that this bio-engineer shapes the community structure considerably by expanding the realized niche of several species, without forming its own community *s.l.* (see also Dittmann (1999) and Zühlke *et al.* (1998)).

Effect of **Lanice conchilega** *on species' abundances*

All positively associated species obviously take advantage from the favourable conditions within the patches. This section explains the presence or absence of species, based on the available knowledge on the autecology and species interactions. In general, the presence or absence of associated species can be considered as a result of the habitat modifying ability of *L. conchilega* and/or direct interaction with the tubes, or as rather accidental.

All but one of the exclusively associated species have never been reported elsewhere as being exclusively found in the presence of *L. conchilega* tubes. Therefore their exclusive presence in the *L. conchilega* samples can be regarded as accidental[6], even more so as they are only found in a few samples (6 to max. 19 samples). Only the amphipod species *Gammarus locusta* has previously been reported as exclusively associated with *L. conchilega* in an intertidal area (Callaway, 2006). *Gammarus* is known as a genus of amphipods of which certain species actively enter the water column and have a high mobility on the scale of tens of meters (Ragnarsson and Raffaelli, 1999). Perhaps in this case the more stable *L. conchilega* beds are

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[6] It concerns species that are not adequately sampled in a quantitative way with a Van Veen grab. Other sampling techniques have to be used to sample these species. Therefore, the occurrence of these in our samples was considered accidental.

actively preferred and may facilitate the existence of this species that otherwise could not occur within that flow and sediment regime.

Direct interaction with the tubes includes the settlement of larval and postlarval benthic organisms (Qian *et al.*, 1999). Juvenile bivalves are known to settle on the worm tubes, as they provide attachment facilities in a relatively protected area. This settlement is a passive process facilitated by the hydrodynamic regime ("skimming flow") around the tubes (Eckman, 1983, Heuers *et al.*, 1998). Increasing densities of *L. conchilega* could provide more and secure settlement surface, which partially explains the increasing presence of positively associated bivalves in this study area. Based on a comparable phenomenon observed in patches of the tube-building polychaete *Pygospio elegans*, it is assumed that once established, the juvenile bivalves may have benefited from the indirect effects of the tubes slowing down the water flow across the beds, promoting the feeding and increasing protection from erosion and predation (Bolam and Fernandes, 2003). This increased protection may also favour the presence of species earlier observed in or attached to the tubes (Callaway, 2006, Zühlke, 2001) and found to be positively associated with *L. conchilega* in this study: *Eumida sanguinea* and *Harmothoe* spp. In previous studies, *E. sanguinea* (probably juveniles) was almost exclusively found among the sand fringes at the top-end of the tubes, where it may share its food source and profit from the shelter in these so called miniature hatcheries (Callaway, 2006, Zühlke, 2001). The scale worm *Harmothoe* spp. was found inside the tubes (Callaway, 2006). *Harmothoe* spp. are also known to live commensally with other species that construct burrows and cavities, such as the lugworm *Arenicola marina* (Reise, 2002).

Amphipods were abundantly represented among the positively associated species (16 species). Callaway (2006) suggests that all amphipods may benefit from the loosened sediment around single tubes, as this facilitates penetration of the sediment surface and could explain their success. Higher densities of bioturbating species might also contribute to a looser structure of the sediment in between the tubes. While most amphipod species migrate between the water column and the sediment and were exclusively found in the upper 0-2 cm surface layers of the sand, *Urothoe poseidonis* seemed to live (without migrating) at a depth of 4 cm or below, down to about 15 cm, in close proximity to the tubes (Callaway, 2006). The actual benefit for *U. poseidonis* may be an improved oxygen supply in the sediments surrounding the tubes, mediated by the mobility of *L. conchilega* in its tube. Forster & Graf (1995) found increased oxygen concentrations in the sediment along the whole length of the tube and suggested that *L. conchilega* acts as a piston, exchanging burrow water with the overlying water. Besides crawling over and in the sediment, two positively associated free-living amphipod species *Pariambus typicus* and *Phtisica marina* may also interact directly with the tubes. They have previously been observed to perform a clinging behaviour in which they attach to algae with adapted grasping appendages (Guerra-Garcia *et al.*, 2002). Aikins & Kikuchi (2001) showed that the preference of a tube-dwelling *Corophium* amphipod species for algal and artificial filamentous structure habitat, was explained by decreased current velocity, increased detritus trapping (and thus food availability) and increased shelter provision. Analogous phenomena are encountered in the *L. conchilega* reefs and may likewise facilitate the success of amphipods clinging to the tubes.

While the space between the tubes serves as a refuge from epibenthic predators or impact of physiological stress (Bolam and Fernandes, 2002, Woodin, 1978), infaunal predators are certainly not inhibited and seem on the contrary to be rather attracted to the species rich tube patches. Polychaetes and amphipods counted the highest numbers of predatory species positively associated with *L. conchilega*. Some of these species were at least found once in higher abundances in the presence of *L. conchilega* in previous studies: *Eumida sanguinea, Eteone longa, Phyllodoce (Anaitides) maculata-mucosa, Nephtys hombergii* (Callaway, 2006, Dittmann, 1999, Zühlke, 2001, Zühlke *et al.*, 1998). The fact that the three most positively associated species (*E. sanguinea, S. bombyx and P. maculata-mucosa*) also occurred as species tolerant to the highest *L. conchilega* densities, indicates a very close association with the tubes.

The five negatively associated species are part of the *Nephtys cirrosa* community which is characterised by clean mobile sands (Van Hoey *et al.*, 2004). Therefore, it can be assumed that sediment related factors are responsible for the habitat preference of these species in our study. As the presence of *L. conchilega* implies an increase in the finest sediment fractions, the absence of *N. cirrosa* and *Bathyporeia* spp. in the tube patches can be considered as a *L. conchilega* mediated effect. Moreover, in this study area, the *Nephtys cirrosa* community seems to border the *L. conchilega* communities *s.s.*, which is considered to be part of the *Abra alba - Kurtiella bidentata* community *s.l.* (Van Hoey *et al.*, 2004).

In general, the response pattern of a particular species to a factor induced by *L. conchilega*, e.g. potential refuge, will not only reflect the consequences of the exclusion of large predators or disturbers, but will also mirror the interactions with the assemblages around the refuge (Luckenbach, 1987). Beside the direct or indirect physical impact of the tubes' presence, interactions amongst species take place based on the activities of crawling, burrowing and irrigating, and providing or competing for habitat structures or food. In order to further explain the species interactions in this highly complicated coexistence, we analysed the trophic group composition of the *L. conchilega* community *s.s.*

Effect of trophic interactions on the **Lanice conchilega** *community* **s.s.**

Trophic interactions may at least equal habitat engineering in importance, and both are linked and affected by differential mobility of the organisms and by their physical environment (Reise, 2002). As protruding structures, the tubes reduce the near-bottom flow velocity which enhances particle settlement. This implies increased food availability, as clay particles tend to bind higher quantities of organic matter (Nichols, 1970). Prolonged sedimentation of relatively fresh organic matter will promote the growth of suspension and interface feeders in the first place, while extended deposition is beneficial to (sub)surface-deposit feeders as well and promotes a higher diversity of feeding types (Wieking and Kröncke, 2005). It is remarkable however that the abundance of associated suspension feeders remains relatively low and even declines when > 50 *L. conchilega* ind m^{-2} are present, while all other trophic groups increase in abundances with increasing *L. conchilega* densities. This observation can be explained by several factors.

Surface dwelling and burrowing polychaetes are known to have a direct and/or indirect negative effect on the survival of e.g. bivalve recruits (which make up the majority of the positively associated suspension feeders) by respectively predation and/or burial due to high resuspension of the sediment (Luckenbach, 1987). *Lanice conchilega* itself is less affected by predation and resuspended particles as it can withdraw within its tube and is known to be able to switch to deposit feeding when occurring in low densities. Moreover, tubes protrude up to 4 cm from the sediment surface and they have the ability to burrow through newly deposited sediment. They may also be less susceptible to suffocation by clogging of the filter apparatus than bivalves, a trend observed in areas subject to higher inputs of particulate organic matter (Pearson & Rosenberg, 1978). In addition, a potential competition for food and/or space between *L. conchilega* and other suspension feeders could result in favour of *L. conchilega*. The fact that no other positively associated suspension feeding polychaete was found possibly reflects the success of *L. conchilega* in competition.

The success of surface-deposit or facultative suspension feeders can be attributed to the higher deposition rate of detrital organic matter between the tubes and the increased bacterial biomass, due to enhanced nutrient fluxes occurring around the tubes (Eckman, 1985). They even may increase the own food supply by stimulation of microbial growth by feeding and irrigation ("microbial gardening") (Hylleberg, 1975; Miller *et al.*, 1984; Grossmann & Reichardt, 1991 as cited in: Snelgrove & Butman, 1994). Furthermore, their relative ability to resist lower oxygen tensions and higher acidities and sulphide concentrations favours them to withstand higher organic matter inputs (Pearson and Rosenberg, 1978), which co-occurs with increased sedimentation of the finest sediment fractions.

While tube structures provide shelter from large, mobile epibenthic predators/disturbers, endobenthic predators have access to abundant prey. The higher densities of infaunal predators in *L. conchilega* patches could primarily be a response to higher meio- and macrobenthic densities at these sites (Dittmann, 1999, Luckenbach, 1987, Zühlke, 2001). However, in accordance with the cage experiment studies of Ambrose (1984) and Sardá *et al.* (1998), an increased total density of infaunal predators and ratio of predatory to non-predatory infauna (Σ Predators / Σ non-predators ratio were for classes 0-4 respectively in percentages 15; 14; 18; 28 and 48) was found, following the presence and increased densities of L. conchilega tubes. This indicates that the tube aggregations can be considered as natural epibenthic predator/disturber exclusion structures, comparable to what Ambrose (1984) assumed for sea grass beds, with increasing refuge efficiency as densities of the tubes increase. As the ratio is notably higher in samples containing >1500 *L. conchilega* individuals per m^2, predation by infaunal predators on non-predatory infauna may be considered as a more important structuring force in these dense patches than in the less dense patches. This is based on the assumption that predatory infauna are preferentially preyed upon by epibenthic predators or that predatory and non-predatory infauna are preyed upon equally but predatory infauna reduce the abundance of other infauna (Ambrose, 1984).

The observed community shift to lower diversity and higher densities in the highest class could also be an effect of exclusion of epibenthic predation/disturbance according to the intermediate disturbance hypothesis, as proposed by Connell (1978). This hypothesis predicts that at low disturbance, in our case due to epibenthic predators/disturbers, diversity declines as competitive dominants monopolize the habitat (Peterson, 1982). These competitive dominants were identified as bearing the highest *L. conchilega* densities. They were mainly represented by relatively large-sized infaunal predators. In this study decapods were also considered as infaunal predators or scavengers since they are known to be an important food source for demersal fishes (e.g. Dauvin (1988) and Mauchline (1982), as cited in: Wang and Dauvin (1994)) and they or their juveniles can certainly profit from the tube reefs as a refuge. The increase of these relatively large-sized infaunal predators can be explained by the fact that shallow-dwelling species are more susceptible to epibenthic predation than deeper-dwelling species (Blundon and Kennedy (1982), Holland *et al.* (1980), Virnstein (1977) as cited in: Wilson (1990)). The increased survivorship of decapod crustaceans (shrimp and brachyuran crabs), which reduces infaunal abundances significantly, was also found in sea grass beds where fish were excluded (Wilson, 1990). In general, the dense polychaete tube reefs directly and positively increase the density of primarily predatory infauna by giving them shelter. At a certain density however, they also indirectly and negatively affect macroinfaunal organisms which are preyed upon by these predators, or excluded due to competition for food or space.

Conclusion

This study supports the findings of other studies on bio-engineering organisms. *Lanice conchilega* positively influences macrofaunal density, species richness and community composition. This paper provides information on the specific mechanisms that lead to species aggregation in a well defined bio-engineered habitat. A rank order of associated species was produced, based on an *in situ* sampling design. This rank list of associated species, combined with the available ecological knowledge, allows explaining functional group interactions. Nevertheless, we admit that the exact nature of the relationships between species, and with the tube patches remain uncertain in some cases. We conclude that knowledge on the autecology of species is crucial to reach full explanation of this particular system. This requires controlled experiments in which the influence of dynamic variables, e.g. recruitment success, competition for space, trophic interactions, inter-related variables as grain size, organic content, microbial content and food supply, is examined systematically, as it is unlikely that one of these factors alone can explain the presence of species in a particular habitat. We believe that this descriptive and correlative data study points out the ecological implications of *L. conchilega* on species level and serves as a solid basis for research on mechanistic relationships between the observed species.

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CHAPTER 3

Do *Lanice conchilega* aggregations classify as reefs? Quantifying habitat modifying effects

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Abstract

The positive effects of the tube dwelling polychaete *Lanice conchilega* for the associated benthic community emphasizes this bio-engineer's habitat structuring capacity (Rabaut *et al.* in Estuar Coastal Shelf Sci (2007)). Therefore, *L. conchilega* aggregations are often referred to as reefs. The reef building capacity of ecosystem engineers is important for marine management as the recognition as reef builder will increase the protected status of the concerned species. To classify as reefs however, bio-engineering activities need to significantly alter several habitat characteristics: elevation, sediment consolidation, spatial extent, patchiness, reef builder density, biodiversity, community structure, longevity and stability (guidelines to apply the EU reef-definition by Hendrick and Foster-Smith (J Mar Biol Assoc UK 86:665-677 (2006)). This study investigates the physical and temporal characteristics of high density aggregations of *L. conchilega*. Results show that the elevation and sediment consolidation of the biogenic mounds was significantly higher compared to the surrounding unstructured sediment. Areas with *L. conchilega* aggregations tend to be extensive and patchiness is high (coverage 5-18%). The discussion of present study evaluates whether *L. conchilega* aggregations can be considered as reefs (discussing physical, biological and temporal characteristics). Individual aggregations were found to persist for several years if yearly renewal of existing aggregations through juvenile settlement occurred. This renewal is enhanced by local hydrodynamic changes and availability of attaching structures (adult tubes). We conclude that the application of the EU definition for reefs provides evidence that all physical and biological characteristics are present to classify *L. conchilega* as a reef builder. For temporal characteristics, this study shows several mechanisms exist for reefs to persist for a longer period of time. However, a direct evidence of long-lived individual reefs does not exist. As a range of aggregation development exists, 'reefiness' is not equal for all aggregations and a scoring table to quantify *L. conchilega* reefiness is presented.

Key words

Lanice conchilega, reef characteristics, reefiness, tube dwelling polychaete

Introduction

Structures that reach only a few centimetres into the water column represent important habitats for a variety of marine organisms while dimensions of biogenic structures in marine ecosystems are generally of a lower order of magnitude than their terrestrial counterparts (e.g. forests) (Watling and Norse, 1998). They may provide refuge from predation, competition and physical as well as chemical stresses, or may represent important food resources and critical nursery or spawning habitats. Habitat structures and heterogeneity influence the faunal abundance, species richness and species composition of invertebrate and fish communities (Koenig *et al.*, 2000, Turner *et al.*, 1999). Emergent features provide a structural complex framework that constitutes an important organizing aspect and is critical to the functioning of many ecosystems (Jones *et al.*, 1994).

Persistent emergent structures in aquatic environments are often referred to as 'biogenic reefs'. Because of their important ecological functions, marine reefs have received considerable attention, both from scientists and policy makers. Though intuitively the concept is easily understood, several definitions are still being applied. In the framework of the EU Habitats Directive (EEC/92/43), a definition of reefs is provided by the Interpretation Manual of European Union Habitats and is as follows in the last updated version (EUR27): "Reefs can be either biogenic concretions or of geogenic origin. They are hard compact substrata on solid and soft bottoms, which arise from the sea floor in the sublittoral and littoral zone. Reefs may support a zonation of benthic communities of algae and animal species as well as concretions and corallogenic concretions." (European Commission DG Environment (2003, 2006, 2007)). Holt *et al*. (1998) refer to a broader definition of reefs (both rocky reefs as biogenically induced reefs) that was proposed by Brown *et al*. (1997) (as cited in Holt *et al.* (1998)). This definition was used to select Special Areas of Conservation in the UK in the framework of the Habitats Directive and was later altered by (Holt *et al*., 1998) by adding that the unit should be substantial in size and should create a substratum which is reasonably discrete and substantially different from the underlying or surrounding substratum.

The common tube-dwelling polychaete *Lanice conchilega* is a well-known and widely distributed bio-engineer in soft bottom environments (Rabaut *et al*., 2007). The physiology, tube structure (Jones and Jago, 1993, Ziegelmeier, 1952), hydrodynamic influence (Dittmann, 1999, Eckman, 1983, Heuers *et al.*, 1998), as well as the occurrence of *L. conchilega* aggregations (Carey, 1987, Hartmann-Schröder, 1996) have already been described at length. The tube aggregations are known to have positive consequences for the distribution and abundance of infaunal species in intertidal and subtidal areas by influencing the habitat structure (Callaway, 2006, Carey, 1987, Dittmann, 1999, Féral, 1989, Rabaut *et al.*, 2007, Van Hoey, 2006, Zühlke, 2001, Zühlke *et al.*, 1998). However, there is still uncertainty about the 'reef building' capacity of this ecosystem engineer. Holt *et al*. (1998), for instance, discuss benthic species as reef builders and state explicitly that they will not include aggregations of *L. conchilega* yet because it is not known how stable they are and whether they are sufficiently solid or altered to qualify as biogenic reefs. This indicates that it is still undecided whether *L. conchilega* classifies as a reef builder. It is, however, important to evaluate the reef building capacity of ecosystem engineers as the recognition as reef builder will increase the protected status of the concerned species (e.g. reefs are listed under Annex I of the EC Habitats Directive EEC/92/43 as a marine habitat to be protected by the designation of Special Areas of Conservation (SACs)).

This study evaluates the 'reef like' features of *L. conchilega* aggregations for which the recommendations on how to interpret and apply the EU reef definition are used (Hendrick and Foster-Smith, 2006). 'Reef-like' features fall in three characteristic groups, following Hendrick and Foster-Smith (2006): (1) physical characteristics: elevation, sediment consolidation, spatial extent and patchiness; (2) biological characteristics: biodiversity and community structure; and (3) temporal characteristics: longevity and stability. Few authors refer to the physical characteristics of *L. conchilega* aggregations (Carey, 1987), except for the change in sedimentary composition (Rabaut *et al.*, 2007, Van Hoey, 2006).This paper studies the habitat modifying capacity of the ecosystem engineer *L. conchilega* and aims to evaluate whether it classifies as a reef builder. This is done through the quantification of the physical properties and the temporal stability of aggregations of the species. The discussion evaluates whether *L. conchilega* aggregations exist that could qualify as reefs by bringing together all 'reef-like' characteristics. Moreover, this paper aims to design a scoring system for reef characteristics which allows evaluating the reefiness of *L. conchilega* aggregations in subtidal areas.

Material and methods

Aggregations of *L. conchilega* occur mainly in subtidal areas, but intertidal aggregations close to the MLWS line do exist. The physical characteristics of these intertidal aggregations are assumed to be comparable with the subtidal ones as remote sensing imagery of *L. conchilega* aggregations is very similar in both zones (Degraer *et al.*, 2008a). Therefore, field data was gathered in the intertidal zone. Measurements were done in the Bay of Heist, at the interface of the Flemish beach reserve and the adjacent Belgian integral marine reserve (Figure 2), where *L. conchilega* aggregations of approximately 1-12 m² alternate with tube-free areas in this intertidal zone, generating a surface structure of gentle mounds and shallow depressions (Figure 1). All measurements were done during May and June 2006 in eleven different delineated aggregations (replicates) that were randomly chosen and in *L. conchilega* free areas next to each aggregation.

Figure 1. Pictures of the low intertidal zone of the beach reserve Bay of Heist. Lanice conchilega *aggregations of approximately 1-12 m² alternate with tube-free areas in this intertidal zone, generating a surface structure of gentle mounds and shallow depressions.*

To test whether differences in physical characteristics exist, measurements were performed in aggregations of different tube worm densities. Densities were determined by counting tubes with visible fringes (Van Hoey *et al.*, 2006) in five replicate quadrants of 10 cm² in each replicate aggregation. These density measurements were used to link to the physical characteristics (either directly or through the use of density classes: 500 ind m^{-2}; 500-1500 ind m^{-2}; > 1500 ind m^{-2}). The physical characteristics measured are elevation, sediment consolidation, spatial extent and patchiness (based on Hendrick and Foster-Smith (2006)).

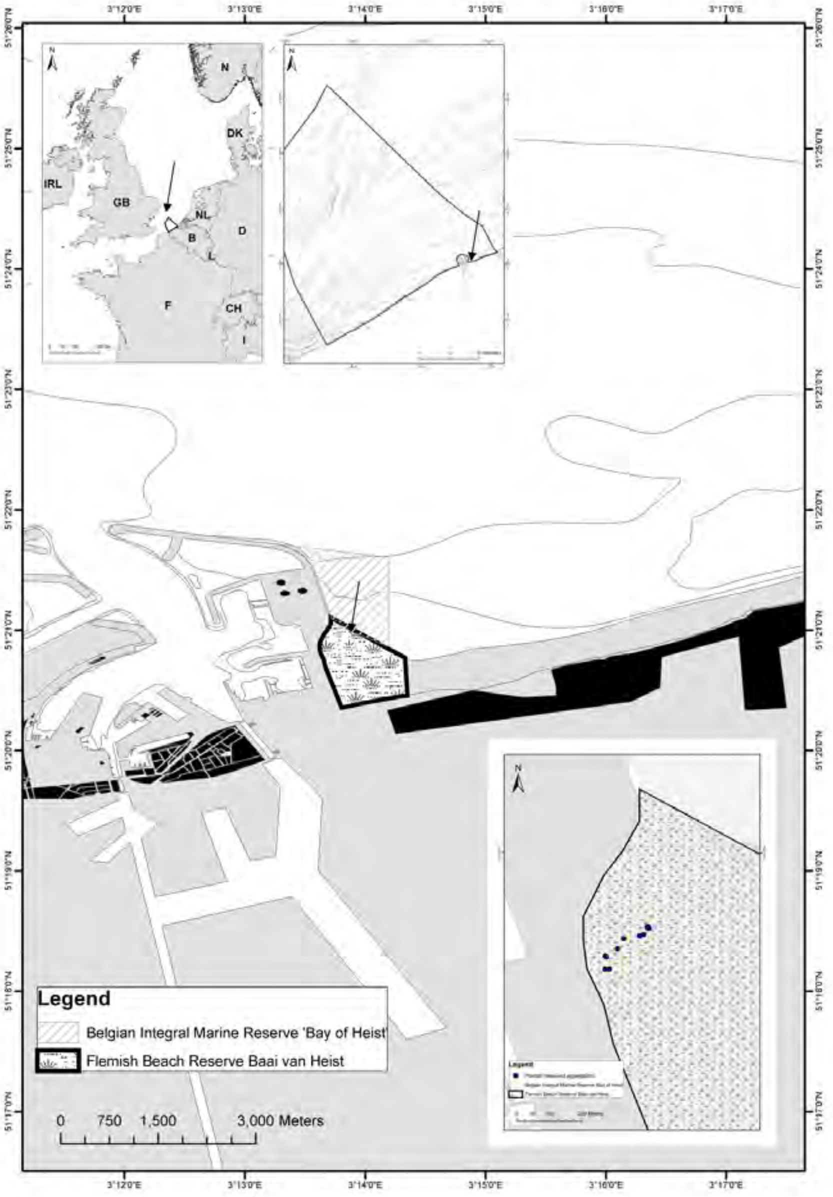

Figure 2. Location of the Belgian part of the North Sea (above left); location of the Flemish beach nature reserve Bay of Heist (above right); and location of beach area with high density aggregations of Lanice conchilega. *Indication of the 11 aggregations that were studied (below right).*

The elevation of the aggregations was measured in a relative manner, *i.e.* the elevation differences to the nearest 0.5 cm from one side of the reef to the other side (parallel to the water line) (Figure 3). In other words, height above the surrounding sediment surface level was measured. These measurements were also done in the same zone, but with no *L. conchilega* present. The difference between the elevation of the biogenic mounds and the elevation of the areas without *L. conchilega* was tested with a Mann-Whitney U test.

Figure 3. Methodology to determine the relative height differences of individual aggregations: the vertical distance to the horizontal conduit was measured every 10 cm.

The field vane test is commonly used for determination of undrained shear stress in fine-grained soils (Åhnberg *et al.*, 2004). A shear vane is developed to measure sediment stability rapidly in a way that enables repeated measures. The instrument is portable, hand deployed and consist of a vane attached to a torque meter (van Leeuwe *et al.*, 2005). In present study, a small portable shear vane with a diameter of 49 mm, a penetration depth of 5 mm and an accuracy of 0.01 kg cm^{-2} (*i.e.* 0.98 mbar) was used. In the eleven delineated aggregations, five replicate measurements were done. For each of these replicates, a measurement was done just outside each aggregation (*i.e. L. conchilega* free areas). Differences between the two groups of measurements (inside versus outside) were tested with a Mann-Whitney U test. The spatial extent of the *L. conchilega* zone was also measured in the Bay of Heist. The patchiness of the reefs occurring in the investigated zone was based on the delineation of individual aggregations of *L. conchilega* as detected through high resolution side scan sonar imagery (Klein 3000 series, 445 kHz). The imagery is a reflection of the acoustic energy that is backscattered from the seafloor and is displayed in different levels of grey. The differences in backscattering are in decreasing order determined by (1) the geometry of the sensor-target system, (2) the angle of incidence of each beam, local slope, etc., (3) the physical characteristics of the surface, such as the micro-scale roughness, and (4) the intrinsic nature of the surface (composition, density, relative importance of volume versus surface diffusion/scattering for the selected frequency) (Blondel and Murton, 1997). The imagery of a subzone of the total *L. conchilega* area of the Bay of Heist was analyzed using the geographical information system (GIS) ArcView 9.2. The surface of individual reefs was calculated as well as the surface of the subzone in which they occurred. The percentage coverage was calculated and provided together with the information on individual aggregation surface (average, minimum, maximum) an indication of patchiness.

The relation between local hydrodynamic changes induced by the *L. conchilega* aggregations and the renewal of these aggregations by juveniles was tested with artificial *L. conchilega* aggregations in the study area. During the recruitment period of *L. conchilega*, five replicates of 1 m^2 with 1000 artificial tubes have been created in the Bay of Heist to mimic hydrodynamic impacts of the biogenic mounds. Wooden sticks with an inner diameter of three mm were used. The length of the tubes was 22 cm and they were place 18 cm deep into the sediment (*i.e.* four cm above the sediment surface). Plots were created on t_{-1} in zones with none or very few *L. conchilega* specimens. At next spring tide (t_0), a small scale hydrodynamic pattern was apparent: in each replicate plot several small areas could be identified with a higher sedimentation rate. In each artificial plot of 1 m^2, three replicate surface areas of 10 cm^2 were chosen as high sedimentation zones and three as low sedimentation zones. In these zones, density of newly settled juveniles was quantified for each defined area of 10 cm^2. These replicates remained the same within one plot during the experiment at later measurements[7]. In order to reduce time effects, t_{-1} was not the same spring tide date for all plots. As the monitored areas within each plot were the same, the data were analyzed using repeated measures ANOVA.

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[7] Measurements were performed two more spring tides after t_0 (*i.e.* on t_1 and t_2).

Results

Mean densities of 2104 +/- 219 SE individuals per m² were found (maximum 3640 +/- 323 SE; minimum 620 +/- 177 SE). Different measurements were done for all density classes, in order to link this with the other reef characteristics. The *L. conchilega* biogenic mounds in the Bay of Heist reached an average elevation of 8.4 +/- 1.8 cm. The highest elevation was 16.5 cm. There was a significant ($p < 0.0001$) difference in elevation when the aggregations were compared with zones outside the aggregations. No significant difference was, however, observed between aggregations of different densities ($p > 0.28$). Shear stress inside the aggregations is far higher than immediately outside the aggregations ($p < 0.0001$) (Figure 4). A clear correlation also appears between the shear stress and the densities of *L. conchilega* tubes (R = 0.82, $p < 0.0001$). Kruskal Wallis test for differences in shear stress between different density groups (< 500 ind m^{-1}, 500-1500 ind m^{-1}, > 1500 ind m^{-1}) reveals significant differences ($p < 0.01$) which mark the importance of high densities to locally consolidate the sediment.

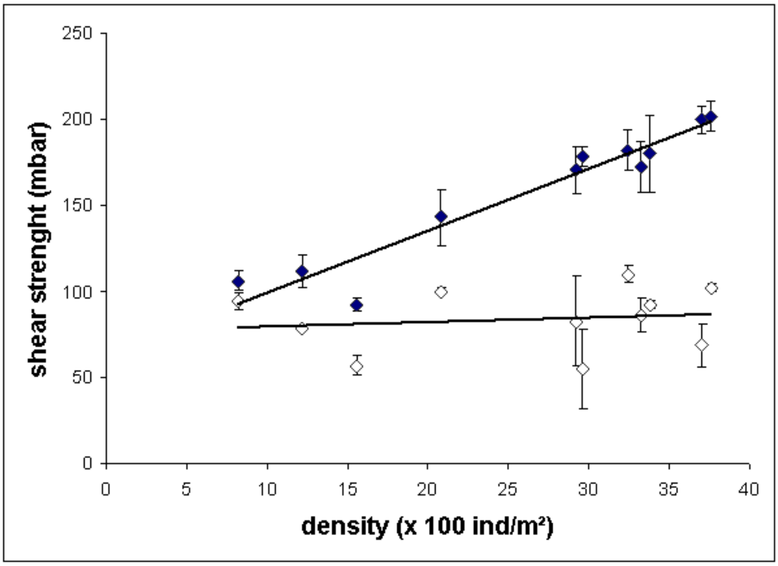

Figure 4. Shear stress. The shear stress of 11 aggregations of different densities was measured. Measurements were done inside the aggregation (filled diamond) as well as immediately beside each aggregation (open diamond). Shear stress is significantly higher inside the aggregation compared with shear stress outside the aggregation. The shear stress of high density aggregations is significantly higher than the shear stress of low density aggregations. Visualized error bars are standard errors, calculated on five replicate measurements per aggregation.

The spatial extent of the intertidal area in the Bay of Heist, where *L. conchilega* aggregations occur, was estimated to be 220000 m^2 and was found near the low water tide line (Figure 2). Based on the side scan sonar imagery the aggregations had an average surface of 1.37 m^2 (+/- 2.02 m^2 SD), the largest aggregation reached a surface of 12.31 m^2 whereas the smallest identifiable aggregation was only 0.05 m^2 (Figure 5). The coverage was calculated to be 18.4%.

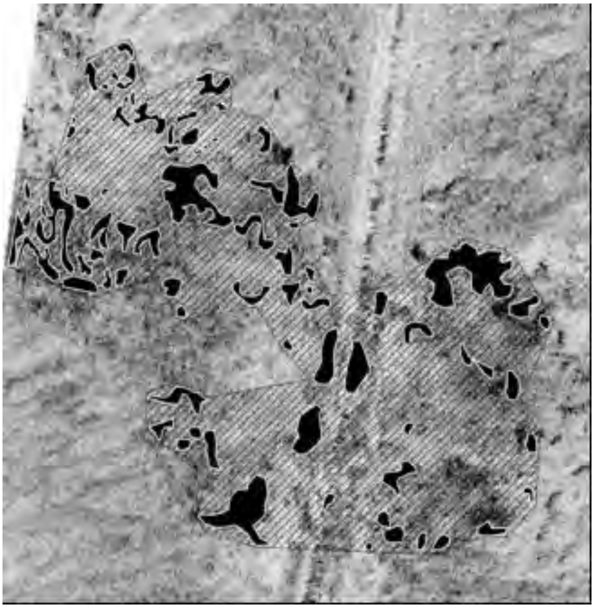

Figure 5. Patchiness. A subzone (shaded area) with identified Lanice conchilega *aggregations (black) as apparent from the side scan sonar imagery. The relative coverage area (ratio of* L. conchilega *aggregations over the total area in which they occur) is 18.4% and the average aggregation reaches an area of 1.37 m^2 (min 0.05 m^2; max 12.31 m^2)*

The artificial tube reef experiment in the intertidal zone shows that a changing hydrodynamic pattern on a very local scale occurs as a result of the presence of adult *L. conchilega*. This pattern leads to a settling advantage for juvenile *L. conchilega*, as is visible in Figure 6. Comparison between areas showing clear sedimentation and areas without sedimentation within each artificial plot shows a significantly higher settling ($p < 0.001$) in the areas with sedimentation shortly after t_0 (Figure 7). However, this initial settling advantage was not sustained during subsequent spring tides.

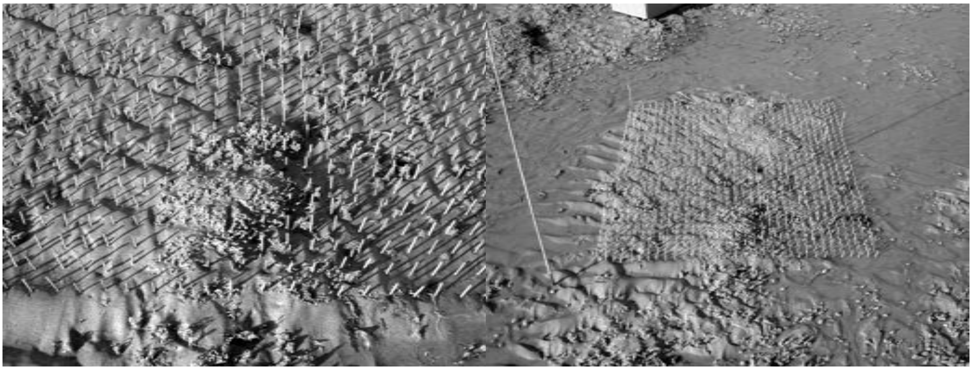

Figure 6. Artificial tube experiment. Pictures showing local sedimentation patches that proved to enhance settlement of juvenile Lanice conchilega significantly shortly after sedimentation.

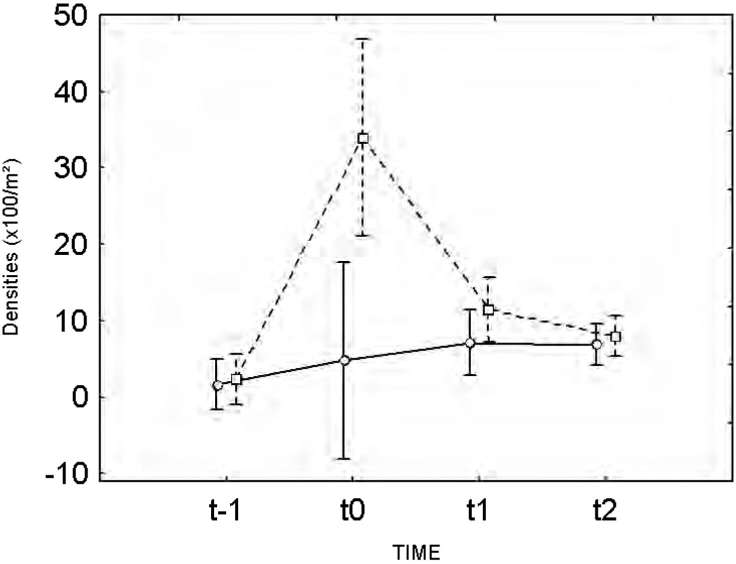

Figure 7. Juvenile settlement enhanced through changing hydrodynamics. Within artificial tube aggregations, densities are followed up during four spring low water tides both in areas were sedimentation occurred (square) and in areas without sedimentation (circle). Sedimentation zones enhance the settlement of juvenile Lanice conchilega *significantly shortly after sedimentation. This pattern was consistent as not all plots were placed at the same spring tide. This settlement enhancement was not sustained for a longer period of time as no real adult tubes to attach on were present in the artificial tube plots.*

Discussion

This paper quantified physical properties and studied mechanisms that enhance long term stability of *L. conchilega* aggregations. The habitat modifying capacity of the ecosystem engineer *L. conchilega* is discussed in this section. This information is used to evaluate whether this particular species classifies as a reef builder. Following the recommendations of Hendrick and Foster-Smith (2006) to interpret and apply the EU reef definition, the results presented in this paper will be discussed together with the existing literature on the physical, biological and temporal features of *L. conchilega* aggregations.

Recorded densities of *L. conchilega* vary widely and reach densities of around 5000 ind/m^2 (though occasionally higher densities can be found). Density is the characteristic that relates to many of the other reef characteristics. Information on the density of *L. conchilega* provides insight in the physical characteristics (e.g. the consolidation of the sediment), probably also in the temporal characteristics and in the other biological characteristics. Results on the quantification of the densities in the aggregations show that the normal density range is covered, except for the very high densities.

The elevations in the intertidal zone of the Bay of Heist are not very pronounced, but do differ significantly from the surrounding sediment. The report of Holt *et al*. (1998) refers to *L. conchilega* aggregations reaching elevations of 45 cm (intertidal area at North Norfolk coast) while Carey (1987) reports intertidal *L. conchilega* aggregations of up to 80 cm. However, more pronounced elevations could have been enhanced by other organisms, as the described cementation of the macroalgae *Enteromorpha* sp. and *Polysiphonia* sp. on Tentsmuir Beach (Carey, 1987). The results also suggested that this elevation occurs with relatively low *L. conchilega* densities (500 ind m^{-2}) and remains the same for increasing densities. There is currently no information available on the elevation of subtidal aggregation, though the very similar side scan sonar imagery of both intertidal and subtidal aggregations (Degraer *et al.*, 2008a) suggests that they are of the same order of magnitude.

The consolidation of the sediment by *L. conchilega* is reflected in the increased shear stress in *L. conchilega* aggregations. Moreover, there was a clear correlation with the density of *L. conchilega*. On the one hand, this effect could be related to the drainage effect of the tubes, which would explain the correlation; on the other hand the effect might be explained by the change in sedimentary composition (Rabaut *et al.*, 2007). The clear correlation with the tube density can possibly be used as a proxy for this consolidation in the future.

Concerning the spatial extent and patchiness, Ropert and Dauvin (2000) reported an estimated colonized subtidal area of more than 2000000 m² in the Bay of Veyst, whereas on the Gröniger plate in Germany several thousands of m² of colonized intertidal sand flat have been reported (Zühlke, 2001). Presented results show that the areas of occurrence of dense aggregations are generally extended. They are larger in subtidal than in intertidal areas (Degraer *et al.*, 2008a). The extensive areas in which *L. conchilega* aggregations occur is of importance as a more extensive area has a greater conservation significance than a smaller one (Hendrick and Foster-Smith, 2006).

Patchiness relates to the variation in individual aggregation surface and, more importantly, to the coverage percentage of reefs within a reef zone. Average, minimum and maximum aggregation surface provide insight in the variation of aggregations. This study showed that the variation is high and that it can be measured based on side scan sonar imagery. With this technique it was also relatively straightforward to calculate the coverage of the aggregations within a certain area. The same technique could be used in subtidal areas though to date, no such quantification has been performed.

Concerning the biological implications of *L. conchilega*, the impact of *L. conchilega* on the biodiversity was demonstrated by Zühlke (2001) (intertidal) as well as by Rabaut *et al*. (2007) and Van Hoey *et al*. (2008) (subtidal). Table 1 provides some (maximum) values as published by the respective authors. The impact of *L. conchilega* on the diversity indices was calculated by taking the ratio of the biodiversity value when *L. conchilega* is present over the value in the same region when *L. conchilega* is absent. For this relative impact, it is clear that the impact in the subtidal areas is higher.

Furthermore, in the study of Zühlke (2001) species richness was found to be generally higher in *L. conchilega* aggregations than in areas free of *L. conchilega* for data over several years. Diversity indices taking account of evenness indicated significantly higher diversity in *L. conchilega* aggregations than in references. However, no correlation was found between the density of *L. conchilega* tubes and species richness or individual abundances. The community structure of associated fauna was found to be significantly different from *L. conchilega*-free areas in three out of four investigated years when *L. conchilega* was actually present. Rabaut *et al*. (2007) found that species richness within the aggregations increased together with *L. conchilega* densities. In addition, a positive correlation between the steadily increasing macrobenthic densities and densities of *L. conchilega* could be found.

Table 1. Biological characteristics as taken from different authors. In order to compare different values, only data related to biological reef characteristics were extracted from the publications. Only maximums are presented here to illustrate that differences occur for different regions (figures are indicative as they are presented as round numbers, deduced from published graphs). The effect of Lanice conchilega *on the diversity indices (N0 total number of species; N1 exp (H'), with H' the Shannon diversity) was calculated by taking the ratio of the biodiversity value when* L. conchilega *is present over the value in the same region when* L. conchilega *is absent („reference', indicated as „ref').*

	Intertidal Zühlke (2001)	Subtidal Van Hoey *et al.* (2008)	Subtidal Rabaut *et al.* (2007)
L. conchilega density (max ind m^{-2})	4000	5000	5000
N0 (max)	10.5	29	35.6
*N0/N0*ref	1.2	2.4	2.8
N1	5.1	10	
*N1/N1*ref	1.3	1.7	
Abundance (max ind m^{-2})	72000	4500	8000
Abund/Abund ref	2	9	5
ANOSIM	$p < 0.001$		$R = 0.23$, $p < 0.001$

The study of Van Hoey *et al*. (2008) showed that the implications of subtidal *L. conchilega* were the same for a large geographic area and in different kinds of sediment types. In this study, a significant and positive correlation between the benthic density and the density of *L. conchilega* has been described as well as increasing species richness with increasing density of *L. conchilega*. However, this trend was found to be inconsistent: after reaching a certain density of *L. conchilega* the number of associated species no longer augmented, which is probably related to competition for space. This finding is an indication that very high density aggregations are of less value than intermediate density aggregations.

Also community structure was proved to change when *L. conchilega* was present. ANOSIM results prove this difference in community structure is highly significant (Table 1). Moreover, Rabaut *et al*. (2007) confirmed that communities differed gradually according to increasing abundances of *L. conchilega* density (a so called 'Babushka' type of community structure). This effect is related to the increasing structural complexity when the density of this tube builder increases which in turn creates more niches and consequently more food provision. The species-specific explanation for this general increase has been described for different densities of *L. conchilega* aggregations (Rabaut *et al.*, 2007).

Temporal characteristics of the aggregations are difficult to estimate without long-term monitoring of individual aggregations. Long-lived, stable biogenic concretions are expected to have a greater value in respect of the aims of the Habitats Directive than an otherwise comparable habitat of ephemeral nature (Hendrick and Foster-Smith, 2006, Holt *et al.*, 1998). In her long term analysis of intertidal aggregations, Zühlke (2001) suggested that *L. conchilega* aggregations are ephemeral in intertidal areas. This unsustainability of aggregations on tidal flats could be related to the dynamic characteristics of this environment and to freezing temperatures in winter (e.g. Strasser and Pieloth (2001); Zühlke (2001)). In the absence of storms or strong winters, *L. conchilega* aggregations could probably survive for several years. In subtidal environments, hydrodynamic stress is lower and the water layer protects this environment against steep drops in temperature. Moreover, individual mounds that are biogenically constructed by *L. conchilega* are described to persist for more than 1 year (Carey, 1987).

Because *L. conchilega* is a short living species (Van Hoey, 2006), the biogenic structures can only persist through efficient renewal of juveniles each year. One of the mechanisms of how juveniles settle more successfully on existing aggregations on adults was described in an intertidal study of Callaway (2003a).

Moreover, the results of the present study showed that hydrodynamic changes induced by biogenic mounds make the pelagic larvae to settle on existing aggregations. This significant settling effect was not sustained over time. We hypothesize that the artificial tubes used in the hydrodynamic experiment were too smooth and that no juveniles could attach to them. We reason that juveniles were able to settle on the hydrodynamic mounds, but could not settle into the sediment because of the absence of real adult tubes. We suggest that hydrodynamic changes induced by *L. conchilega* aggregations induce first settlement, while in a second phase adult tubes serve as an ideal surface to attach before they settle in the sediment. The initial settling effect was reproduced at different times during the recruitment period, which made the observed results reliable. Therefore, it is assumed that individual aggregations of high density aggregations can persist for several years, though the maximum lifespan is difficult to estimate. Large scale destruction because of storms or general degradation after a failed reproduction period is probable to occur in some years. This might lead to the conclusion that these structures are ephemeral in nature but it appears to be widely accepted that in that respect all reef building organisms are ephemeral by nature (Hendrick and Foster-Smith, 2006) as the vulnerability to natural (e.g. storms) or anthropogenic (e.g. fisheries) events increases with the emergent character.

The relation between the presence of adult tubes and the settling advantage of juveniles suggest that there is a relation between the density of the aggregations and the longevity, as the chance of being renewed with juveniles is higher for high density aggregations.

'Reefiness' of **Lanice conchilega** *aggregations*

Holt *et al*. (1998) disqualified *L. conchilega* aggregations as reefs because it is "unlikely that they are sufficiently solid or altered to qualify as biogenic reefs" and because it is "not known how seasonal/stable these features are". However, the application of the EU Habitats Directive definition of 'reefs' (habitat 1170 of Annex I) – using the guidelines provided by Hendrick and Foster-Smith (2006) - provided clear evidence that all characteristics needed to classify biogenic structures as reefs are present in the case of high density aggregations of *L. conchilega*.

We acknowledge, however, that a range of values exists for the different reef characteristics. The formation of so called *L. conchilega* reefs is a continuous process which starts from '*L. conchilega* bed' formation with a low value for the physical, biological and temporal reef criteria and ends with very pronounced biogenic structures that are very 'reefy'. Not all reef characteristics will increase at the same time and might in some cases even be adversary. In order to differentiate between *L. conchilega* aggregations or areas, we combined our findings in order to define the 'reefiness' (*sensu* Hendrick and Foster-Smith) of *L. conchilega* reefs wherever they are found in subtidal areas. Therefore, we have made a scoring system (Table 2) for a variety of reef characteristics. As aggregations mainly occur in subtidal areas, this scoring table is constructed for subtidal reefs.

In the first place the scoring system aims to provide insight in the range in which different reef characteristics for *L. conchilega* are to be situated. The values are based on the results presented in this paper[8]. This scoring system can be applied through the quantification of each characteristic for a given subtidal *L. conchilega* reef area. Some characteristics are difficult to quantify but several characteristics are correlated (as mentioned above). The *L. conchilega* density score relates positively to several other characteristics, though biodiversity score drops when aggregations reach very high densities (adversary reef characteristics). To combine these different scores in one overall 'reefiness' score for the area, the individual scores should be weighted for importance and reliability. The more data and accuracy is available for the value of a reef feature, the more weight it receives. It is also suggested by Hendrick and Foster-Smith (2006) to give the greatest weighting to elevation, area and temporal stability. The value of the scoring system lies in the possibility to compare different areas where *L. conchilega* occurs.

Conclusions and outlook

The physical characteristics of L. conchilega aggregations are presented in this study for intertidal systems. These results suggest that the characteristics as described by Hendrick and Foster-Smith (2006) are fulfilled. Besides, literature (e.g. Zühlke (2001), Rabaut *et al.* (2007), Van Hoey *et al.* (2008)) shows that the biological characteristics are well known and that the characteristics to classify *L. conchilega* aggregations as reefs are fulfilled. It is, however, still difficult to estimate what the spatial extent and patchiness is 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 (Zühlke, 2001). However, subtidal systems are expected to be more stable and some mechanisms exist for the aggregations to be replenished by juveniles.

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[8] The scoring system summarizes the biological, physical and temporal characteristics as presented in this study. The methodology used and the aims of the 'reefiness scoring table' is analogous to what has been proposed by Hendrick and Foster-Smith for *S. spinulosa*. As indicated by these authors, the importance of the approach lies in the structured consideration of all the reef characteristics and the scoring process itself. It is, therefore, more helpful as a means of comparing the relative values of two different areas of reef. Hendrick and Foster-Smith base their knowledge on the existing range that have been described or observed.

Table 2. Scoring system for a variety of reef characteristics, as adapted from the S. spinulusa scoring system, proposed by Hendrick and Foster-Smith (2006), p. 667

	Characteristic Score		
	Low	Medium	High
	0	50	100
Elevation score[9]	~ 5 cm	5 - 9 cm	> 9 cm
Relative height of the patch			
Sediment consolidation score[10]			
Shear vane stress	~ 1 kg cm^{-2}	~ 1.5 kg cm^{-2}	~ 2 kg cm^{-2}
Area score[11]			
Extent of total area	1000 m^2	50000 m^2	> 100000 m^2
Average area of individual reefs	~ 1 m^2	~ 2 m^2	2 - 10 m^2
Patchiness score[12]			
Percentage cover of patches within the total area	~ 5 %	5 - 10 %	> 10 %
Lanice conchilega *Density score*[13]			
Average density of L. conchilega (m^{-2})	~ 500 individuals	500 - 1500 individuals	> 1500 individuals
Biodiversity score[14]			
Species richness (S)	~ 18	~ 25	> 30
Margalef's index (d)	~2	~ 2.5	> 3
Longevity score[15]	1 year	2 years	> 2 years

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[9] Minimum is based on the Habitats Directive, maximum is based on what has been found in this study.

[10] 1 kg cm^{-2} appeared to be the minimum value to have significant differences with the surrounding bare fine sands (average 0.8 kg m^{-2}).

[11] Concerning the spatial extent and patchiness, Ropert and Dauvin (2000) reported an estimated colonized subtidal area of more than 2000000 m^2 in the Bay of Veyst, whereas on the Gröniger plate in Germany several thousands of m^2 of colonized intertidal sand flat have been reported (Zühlke, 2001). Presented results show that the areas of occurrence of dense aggregations are generally extended. They are larger in subtidal than in intertidal areas (Degraer *et al.*, 2008a). The extensive areas in which *L. conchilega* aggregations occur is of importance as a more extensive area has a greater conservation significance than a smaller one (Hendrick and Foster-Smith, 2006). Hendrick, V.J. and Foster-Smith, R.L. 2006. *Sabellaria spinulosa* reef: A scoring system for evaluating 'reefiness' in the context of the Habitats Directive. Journal of the Marine Biological Association of the United Kingdom, 86: 665-677. The spatial extent of the intertidal area in the Bay of Heist, where *L. conchilega* aggregations occur, was estimated to be 220000 m^2 and was found near the low water tide line (Figure 2). Based on the side scan sonar imagery the aggregations had an average surface of 1.37 m^2 (+/- 2.02 m^2 SD), the largest aggregation reached a surface of 12.31 m^2 whereas the smallest identifiable aggregation was only 0.05 m^2 (Figure 5).

[12] Patchiness relates to the variation in individual aggregation surface and, more importantly, to the coverage percentage of reefs within a reef zone. The coverage was calculated to be 18.4%.

[13] Recorded densities of *L. conchilega* vary widely and reach densities of around 5000 ind/m^2 (though occasionally higher densities can be found). Mean densities of 2104 +/- 219 SE individuals per m^2 were found in this study (maximum 3640 +/- 323 SE; minimum 620 +/- 177 SE).

[14] Based on Chapter 2 (S = 17.66) for lowest density class, which is different from *L. conchilega* free areas (S = 12.80). See Chapter 2 for more information.

[15] A one year survival of a reef system is perceived as a minimum to develop a structure that can be referred to as reef. A fully developed "high quality" reef is estimated to sustain for more than 2 years, though no data is available (*cf.* general discussion for elaborate discussion on this topic).

One of these mechanisms has been described in present study. Here also, only long-term monitoring with advanced remote sensing techniques will provide insights in the longevity of individual aggregations.

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PART II

BEAM-TRAWL IMPACTS ON *LANICE CONCHILEGA* REEFS

CHAPTER 4

The resistance of *Lanice conchilega* reefs to physical disturbance

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The resistance of *Lanice conchilega* reefs to physical disturbance.
Submitted to ICES Journal of Marine Science

Abstract

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

Key words

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

Introduction

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

The biogenic structures found here are produced by the ecosystem engineer *Lanice conchilega* (Polychaeta, Terebellidae). This species is a well-known and widely distributed tube dwelling polychaete in soft bottom marine environments (Rabaut *et al.*, 2007). The physiology, the tube structure (Jones and Jago, 1993, Ziegelmeier, 1952), the hydrodynamic influence (Dittmann, 1999, Eckman, 1983, Heuers *et al.*, 1998), the ecosystem-engineering influence on faunal abundance, the species richness and the species composition (Callaway, 2006, Rabaut *et al.*, 2007, Van Hoey *et al.*, 2008) as well as the occurrence of *L. conchilega* aggregations (Carey, 1987, Hartmann-Schröder, 1996) have been documented. The aggregations produce clearly defined microhabitats which alternate with areas without *L. conchilega*, generating a surface structure of gentle mounds and shallow depressions. This 'seascape' can be visualized using side scan sonar imagery (Degraer *et al.*, 2008a). Experiments show that *L. conchilega* pumps oxygen into the bottom (Braeckman *et al.*, accepted, Forster and Graf, 1995) which is important for the composition of the benthic community and for the presence of specific benthic species (Steyaert *et al.*, 2005). Furthermore, this habitat seems to be of importance for higher trophic levels such as juvenile flatfish (Van de Moortel, 2009, Vanaverbeke *et al.*, 2009a) and birds (Godet *et al.*, 2008). Rabaut *et al*. (2009b) demonstrated that the biogenic structures formed by dense aggregations of *L. conchilega* qualify as reefs. The good knowledge on this reef system show this species aggregations are particularly well suited as a proxy for measuring the impact of physical disturbance.

Therefore, this study hypothesizes that these biogenic structures are measurably affected by physical disturbance. Bergman and Hup (1992) found significant mortality after beam trawl disturbance for *L. conchilega*, especially for juveniles. Their study aimed at a general mapping of the fisheries impact on the benthos community of a soft bottom environment. However, no emergent *L. conchilega* reef structures (*sensu* Rabaut *et al*. 2009) occurred as there were no dense aggregations in their sampling area (355 individuals per m^2). Studies on the reef system as such do exist as field studies with the aim to quantify the impact of one beam trawl passage on the associated *L. conchilega* reef fauna, without focusing on *L. conchilega* as such (Gamarra, 2008, Rabaut *et al.*, 2008). There is, however, no information available on the mortality of individual *L. conchilega* specimens within one reef. Fully controlled laboratory experiments are needed to measure the physical disturbance on the patchy reef habitat with known pressures on exact locations and time. The aim of this study is therefore to quantify direct mortality of *L. conchilega* as a consequence of sustained physical disturbances of dense aggregation reefs with varying frequency, using an experimental laboratory set up. This information may contribute to the knowledge on the resistance of this particular reef system. Recently, it has been argued that experiments can provide valuable insights in systems that underpin ecological resilience (Thrush *et al.*, 2009). Therefore the results on the resistance of *L. conchilega* reefs will be discussed in the light of the general resilience of this system.

Methods

In order to measure mortality within a *L. conchilega* reef as a consequence of repeated fisheries disturbance with known pressures, a fully controlled laboratory set up has been designed. Four undisturbed reef blocks were sampled in the intertidal zone of Boulogne-sur-Mer, France (50°44.10′N 1°35.25′E) on 14 June 2006. The reef blocks were sampled to a depth of 25 cm with rectangular frames of 0.12 m^2 (width: 0.30 m; length: 0.40 m) (i.e. a sample volume of 0.03 m^3); sampling depth allowed to sample entire tubes. The bottom was sealed with a removable bottom plate (Figure 1). The four reef blocks were stored at a constant temperature (17° C) and the frames were replaced by aquariums to allow for continuous water circulation (Figure 1). The sea water was enriched with algae (*Isochrisis galbana*) (renewal every other 48 h) using a concentration of 40E+06 cells L^{-1}, i.e. 800 µg L^{-1} organic weight (Helm *et al.*, 2004), to avoid food limitation (based on Denis *et al.* (2007)). Each reef block was divided into four sectors. Four disturbance regimes were randomly applied in each reef block: disturbance with a frequency of one disturbance every 12, 24 and 48 h (Tr1, Tr2 and Tr3) and no disturbance (C) (Figure 1). Pressure was applied to the treatments as a single passage of a metal plate (6 cm^2 in contact with bottom) loaded with weights (1.41 kg) on top that protrude above the water column during deployment. This allowed applying a pressure of 2.31 $N.cm^{-2}$, coinciding with that of a four meter beam trawl (based on Lindeboom and De Groot 1998, Chapter 3).

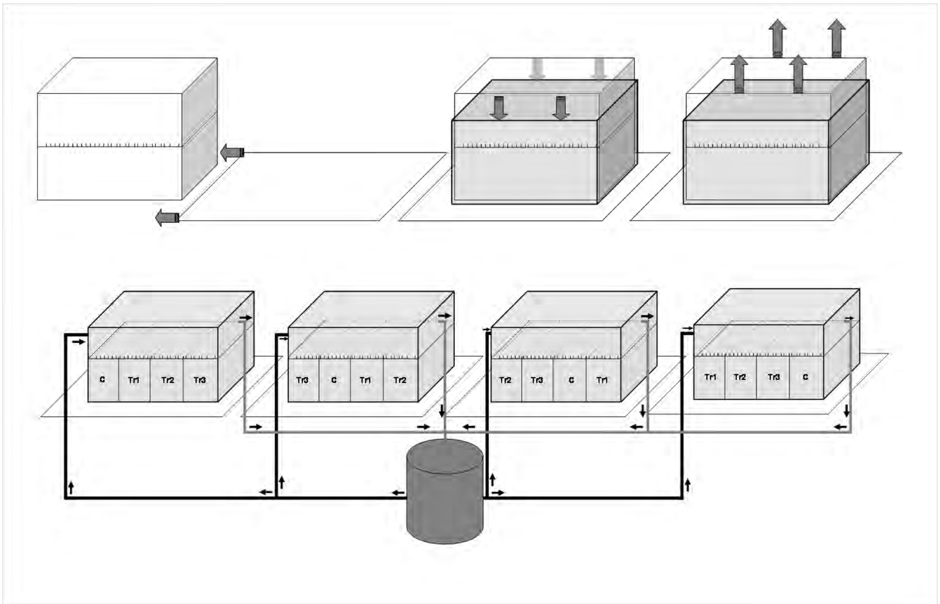

Figure 1. Experimental set up. Above: sampling of an undisturbed reef block; Below: experimental design: four undisturbed reef blocks, each with four treatment zones (C, Tr1, Tr2, Tr3); arrows indicate water circulation.

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

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

Results

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

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

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

Densities of *L. conchilega* dropped with time in all treatments (Figure 2), including the non-disturbed control sectors. Survival in the control sectors drops from 88.3% +/- 4.1% SE at 48 h to 5.6% +/- 2.0% SE at hour 624. The block effect is significant for all treatments (except for Tr1) (Table 2) and Tr2 and Tr3 show an interaction effect with time. This implies that there is an experimental 'cage effect'. Therefore, this reef block effect was incorporated as a random factor in the model that tests for the treatment effect.

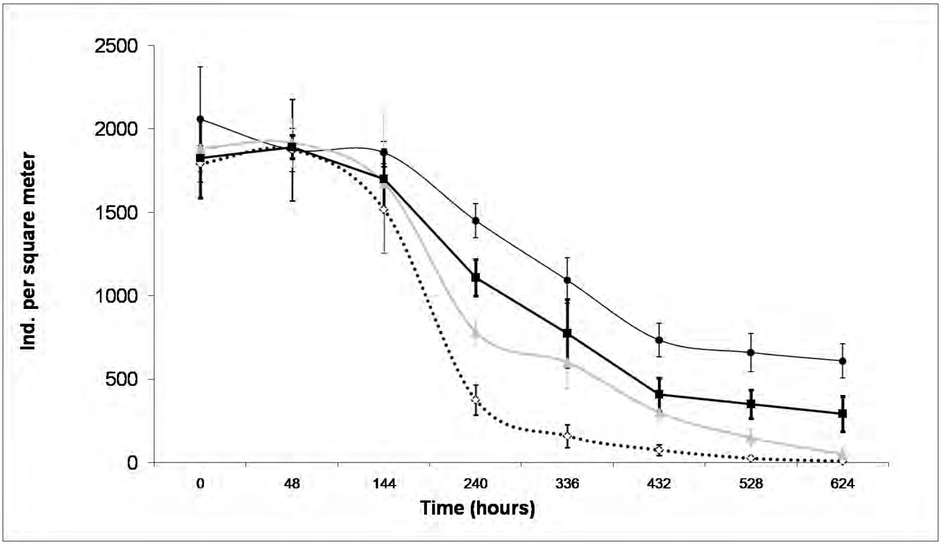

Figure 2. Density evolution of Lanice conchilega *for three treatments (dashed line: Tr1; grey line: Tr2; black square: Tr3; black bullet: control).*

Table 2. Significance levels for overall block and time effect per treatment. The block effect is significant for all treatments (except for Tr1) and therefore, results on treatment effects are based on a mixed model, taking the block effect into account. Significant differences (p < 0.05) are highlighted.

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

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

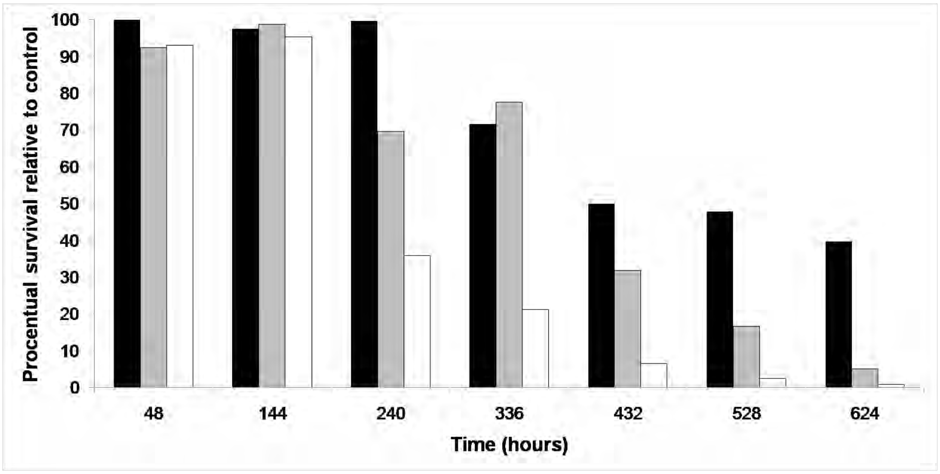

Figure 3. Survival proportions over time for the disturbed sectors (white: Tr1; grey: Tr2; black: Tr3). Proportions are visualized as a percentage of the control proportions for each time (i.e. survival proportions in control are set to 100%).

Discussion

Effects of the survival of *L. conchilega* emerged as a significant factor after 18 disturbances (in 18 days) and after 20 disturbances (in 10 days). These results indicate that the direct impact (i.e. mortality) of this ecosystem engineer occurs after several subsequent disturbances. The current experimental design allowed incorporating the block effect in the analyses while the level of replication allowed for detection of significant differences. The low survival levels in the control areas potentially lead to an underestimation of the physical disturbance applied, as the specimens may have been less resistant under the laboratory conditions. Nevertheless, the statistical analysis of proportions rather than absolute survival leads to correct estimation of the response. Survival under disturbance is relatively high when analyzed relative to the survival in controls. This relatively high survival proportions of *L. conchilega* after physical disturbance is attributed to the fact that the species builds tubes of about 20 cm length in which they can retreat very fast. Therefore, they are assumed to be able to escape from beam trawl disturbance (Bergman and Hup, 1992), although there is no information available on exact reaction times. This escape behavior is confirmed in our study. After the upper part of the tube has been destroyed, *L. conchilega* can rebuild the protruding part of the tube quickly, as was visible in our experiment, and can even re-establish its tube when washed out from the sediments within 24 h (Nicolaidou, 2003). The density evolution of *L. conchilega* (Figure 2) does show a drop in disturbed areas after six days, a trend that turned out not to be significant. This can be attributed to the high fluctuation and variation in the data during the first days which might be related to the use of only four replicates per treatment.

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

The aim of this experiment is to contribute to the knowledge on the resistance of *L. conchilega* reefs. The quantification of the resistance to physical disturbance relates to the capacity to sustain under certain exogenous disturbances. Therefore, this study contributes also to the knowledge of the resilience of this reef system as resilience is defined as the capacity of a system to renew and sustain specific conditions or processes in spite of exogenous disturbances or changes in driving forces (Carpenter and Folke, 2006). Ecological resilience assumes that an ecosystem can exist in alternative self-organized or "stable" states (Peterson *et al.*, 1998). The stability of an ecosystem's ecological functions is determined by the presence or absence of so-called driver species (Walker, 1995), which can take many forms such as ecosystem engineers (Peterson *et al.*, 1998). The present study quantifies the survival of the ecosystem engineer *L. conchilega* (i.e. a driver species of the *L. conchilega* reef habitat) under different physical disturbance regimes. Moreover, the *L. conchilega* reef ecosystem consists of several important (associated) species (Rabaut *et al.*, 2007), which are also vulnerable to physical disturbance, as demonstrated for beam trawl passage (Rabaut *et al.*, 2008). Thus, the resilience of the reef system is defined by several drivers (i.e. the tube builder and the closely associated species). This quantification is important for continental shelf areas such as the North Sea (Rabaut *et al.*, 2007, Van Hoey *et al.*, 2008), where *L. conchilega* reefs occupy areas with strong hydrodynamics (Lanckneus *et al.*, 2001) and intense trawling (Gislason, 1994, Jennings *et al.*, 1999, Rabaut *et al.*, 2009a). The high species richness and increased abundance in *L. conchilega* reefs (Rabaut *et al.*, 2007, Rabaut *et al.*, 2009b), together with the attraction of juvenile flatfish (Rabaut *et al.*, accepted, Van de Moortel, 2009), make the areas with *L. conchilega* reefs attractive for fisheries. Therefore, a high frequency of disturbance is expected, though exact figures are not yet available. This indicates that current physical disturbance does not have a great negative impact on the tube builder itself. In the longer run, the reefs are dependent on successful recruitment (Rabaut *et al.*, 2009b), a mechanism that was not taken into account in this study on short term impacts. However, results may also imply that some reefs are possibly disturbed at frequencies that are comparable to the the current study leading to local destruction of the reefs.

Conclusion

Lanice conchilega reefs consist of dense aggregations of the tube worm as well as of the associated fauna. The resilience of the reefs relates to the vulnerability of those two components. The impact on the associated fauna has been described before. The present study quantifies the survival of *L. conchilega,* a driver species of the reef habitat, under different physical disturbance regimes. The experimental approach allowed the disturbing specific reefs that naturally occur in a patchy habitat with known pressures on exact locations and times. Significant impacts on the survival of *L. conchilega* emerged in this study after several subsequent disturbances. This indicates that *L. conchilega* is relatively resistant to physical disturbance but that the reefs can collapse under continued high frequency fishing pressure. The relatively high survival proportions of *L. conchilega* after physical disturbance can be attributed to the escape behavior and the high capacity for tube regeneration.

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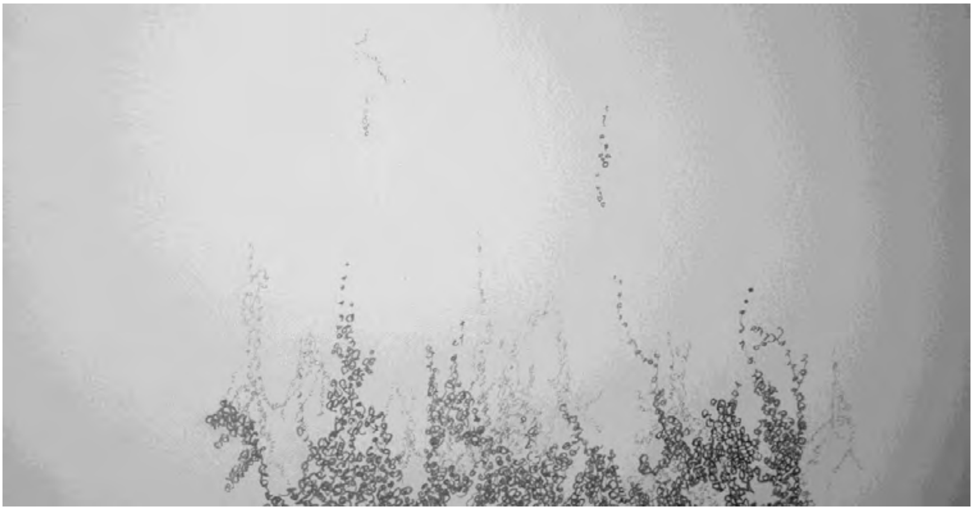
CHAPTER 5

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



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Experimental beam-trawling in Lanice conchilega reefs: Impact on the associated fauna.
Fisheries Research, 90: 209-216.

Abstract

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

Key words

Beam-trawl disturbance, associated fauna, *Lanice conchilega*, *Eumida sanguinea*, GLMM

Introduction

Fisheries impact on soft bottoms

Impact of fisheries on benthic ecosystems has been reported to vary substantially depending both on the type of gear used and on the nature of the impacted habitats (e.g. Brylinski *et al*. (1994), Kaiser *et al*., (2006)). The impact of beam trawling on soft-sediment systems has already triggered considerable attention (e.g. Bergman and Hup (1992), Kaiser and Spencer (1996), Sparks-McConkey and Watling, (2001)). However, the former studies did not focus on specific habitats or niches within these soft-sediment systems. Kaiser *et al*. (2002) mention that biogenically structured habitats are more adversely affected by fishing than unconsolidated sediment habitats. Moreover, biogenically structured habitats have the longest recovery trajectory in terms of recolonisation of the habitat by the associated fauna[16]. Yet, soft-sediment organisms that create structures reaching only a few centimetres into the water column have been described as an important habitat supporting a diversity of taxa (cf. ecosystem engineers: Jones *et al*. (1997), Coleman and Williams, (2002), including post-settlement juveniles of commercially important fish (Watling and Norse, 1998)). Quantifying the resilience of biogenically created habitats towards fisheries in soft sediments is therefore considered to be a key factor in assessing fisheries impact in the soft sediment environment.

Lanice conchilega

This study focuses on the habitat engineer (Rabaut *et al*., 2007) *Lanice conchilega* (Polychaeta). This tube worm can be found in elevated patches of high densities (Ropert and Dauvin, 2000), in which suspended material is trapped. The availability of habitat structures and their effect on the local hydrodynamic regime are important causal factors for polychaete larvae settling (Callaway, 2003a). As such, patches of high abundances trap sediment and evolve towards biogenic emergent structures. They are referred to as "*L. conchilega* reefs" and create a heterogeneous habitat, which attracts species from the surrounding unconsolidated environment, thus enhancing biodiversity (Ager, 2002, Dittmann, 1999, Zühlke, 2001). The fauna associated with *L. conchilega* reefs depends to some extent on the nature of the habitat and the species community but *L. conchilega* always has an effect on the benthos (Dittmann,

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[16] Kaiser *et al*., 2002.

1999, Rabaut *et al.*, 2007, Zühlke *et al.*, 1998). Some of these species live in commensal relationship with *L. conchilega*, such as *Eumida sanguinea* (Callaway, 2006), a predatory polychaete living between the fringes of the tubes. Besides the increased diversity, intertidal *L. conchilega* reefs harbour high benthic standing stocks and are considered to be highly productive (Callaway, 2006, Zühlke, 2001, Zühlke *et al.*, 1998). Also in subtidal areas, *L. conchilega* acts as a bio-engineer (Rabaut *et al.*, 2007). As enhanced standing stocks and productivity attract opportunistic demersal predators such as sole and plaice, the multitude of target species[17] makes these reefs attractive for fisheries (Rijnsdorp *et al.*, 2000).

Aims of the study

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

Methods

Intertidal study area

This impact study was carried out in the intertidal zone, which offered several advantages for a controlled field experiment. First of all, there was no interference with commercial fisheries. This was related to the limited depth and the location in a protected zone where fishermen are not allowed. Secondly, the substantial tidal range made it possible to disturb the plots at high water spring tide (HWST) and to look for evidence of gear passage at low water spring tide (LWST). Thirdly, it was possible to sample manually and to visually follow

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[17] Not only food, but also shelter may be an important factor. Higher habitat complexity can enhance both functions (*cf.* Chapter 1 and Chapter 2). The driving force that attracts flatfish is elaborated in Part III (*cf. infra*).

up the recovery. The experimental area was situated in the intertidal zone of the seashore of Boulogne-sur-mer, France (50°44.10′ N, 1°35.25′ E; figure 1), a pocket-beach sheltered by two harbour walls. The largest zone covers an area of about 45000 m^2 and is situated below the mean low waterline at spring tide. These lower reefs are only visible with extreme LWST conditions. The reef zones located higher on the beach were exposed at every low water: patches of the higher western zone occupied an area of about 4000 m^2, while the higher eastern zone has patches with a total area of 2500 m^2. The experiment was performed in the latter areas in which a treatment and control zone was delineated prior to disturbance (figure 1). *Lanice conchilega* patches in this study area reach on average densities of 3259 +/- 269.1 individuals per m^2 (+/- SE) and the maximum density observed was 8262 individuals per m^2. These densities however, differed at a small scale (*i.e.* within the same reefs). This is an inherent characteristic of the investigated system as has been recorded by Carey (1987) and Heuers *et al*. (1998). Novel statistical modelling techniques allowed inclusion of the *L. conchilega* densities and modelling of the error structure as such (cf. infra).

Disturbance and sampling

On February 13th 2006, during HWST, a one-off disturbance event was simulated with the *RV* Sepia 2. A beam trawl of 2.9 m width trawled the previously delineated treatment zone nine times. At the low tide (T0) following the experimental fishing, *L. conchilega* patches with evidence of beam-trawl passage were traced. Three treatment plots were defined (TR 1 - 3) and four control sites (C 1 - 4) were selected randomly and marked with star pickets to facilitate future tracing. Macrofauna samples were collected with an inox macrocorer of 15 cm diameter (*i.e.* 0.017 m^2), sampling to a depth of 40 cm. Each set of replicate samples was accompanied by an additional sample collected for sediment (diameter 3.6 cm; penetration depth 5cm).

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

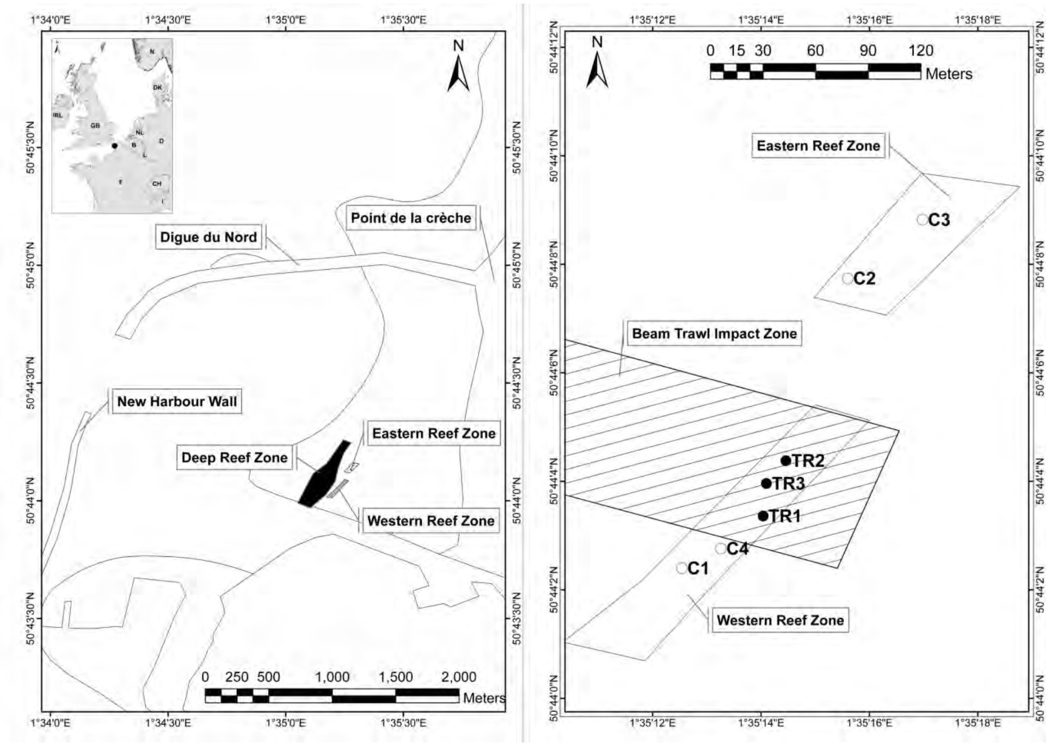

Figure 1. Sampling location. Location of Boulogne-sur-mer in France (●), Europe (inset), Location of the Lanice conchilega *reef zones at the „pocket beach' (left) and sampling positions for treatment (●) and control (○) samples (right).*

Table 1. Disturbance (D) and sampling times of the experiment. The hours are indicative and coincide in reality with the moment of lowest water level to be able to reach the study area.

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

Sample processing

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

Statistical analyses

The Primer v5 (Clarke and Warwick, 2001) statistical package was used for calculating diversity indices and carrying out SIMPER, ANOSIM and non-metric multidimensional scaling (MDS) analyses. Bray-Curtis dissimilarities were used to construct this MDS-diagram and averages of replicates were plotted. The recovery trajectory of treatment samples towards control samples was evaluated with a seriation test (calculating the index of multivariate seriation -IMS- with the RELATE routine of the Primer v5 software package). If the community changes exactly match the linear sequence, then the IMS takes the value one. If, on the other hand, there is no discernable biotic pattern along the transect, then the IMS will be close to zero. These near-zero values can be negative as well as positive but no particular significance is attached to this (Clarke and Warwick, 2001). To test for the effect of the treatment on densities of associated species, a generalized linear mixed model was used in which the fixed factors treatment, time, and their interaction effect, were related to the response variables of interest. The dependence of the response variables to the density of *L. conchilega* was incorporated by including it as a covariable in the statistical model. As the response variables are count data, the residual error structure was assumed to follow a Poisson distribution with the variance multiplied by an overdispersion parameter. Because the predictor and the mean response are not linearly related to each other, the relationship was specified by a log link function. The error structure of the model also incorporated dependency within replicates by including replicate setting as a random term. The fixed effects structure was reduced in a backward stepwise manner. The effect on associated species richness and on Pielou's evenness was analysed following a similar approach, but with the residual error structure assumed to follow a normal distribution.

Results

Sediment characteristics and species composition

The sediment of the Boulogne beach site is largely composed of fine sand (mean ± SE: 62.14 ± 3.00%) and medium sand (mean ± SE: 33.67 ± 2.48%). Silt and clay content show values between 0 and 3.20% (mean ± SE: 0.51 ± 1.08%), which classifies this type of sediment as clean sand[18]. No significant differences in sediment composition between sites[19], between sampling occasions, nor between treatments have been observed.

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

Beam-trawl impact on community composition

Three clusters of samples were distinguished. The first group consisted of only one element: the average of treatment replicates at T0 sampling. The second group comprised the averages of the treatment replicates of sampling times T1, T2 and T3. The third group was made up of all averages of control replicates and the average of treatment replicates of T5, the sampling time by which full recovery was observed. The second group is situated between the first group (impacted) and the third group (recovered and control). There is a shift of treatment samples towards control samples, which indicates the direction of recovery towards these control samples over time. This recovery trajectory has a significant IMS value

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[18] *cf.* Dernie, K.M., Kaiser, M.J. and Warwick, R.M. 2003. Recovery rates of benthic communities following physical disturbance. Journal of Animal Ecology, 72: 1043-1056.

[19] T-test on sediment differences

of 0.61 (p = 0.0003). For this IMS values all control samples were averaged, as there was no recovery trajectory within the C samples (IMS = -0.36; p = 0.85). The MDS-plot clearly demonstrates an impact at the community level, which is, however, not a long-lasting one. As indicated in Table 2, SIMPER analysis revealed diminishing dissimilarity between TR and C communities over time, with the exception of T4 (due to stormy weather). Samples of T5TR are more similar to the control samples than to the other treatment samples (TR excluding T5TR) and dissimilarity between control and treatment samples increases when T5TR is considered as belonging to the control samples (Table 2).

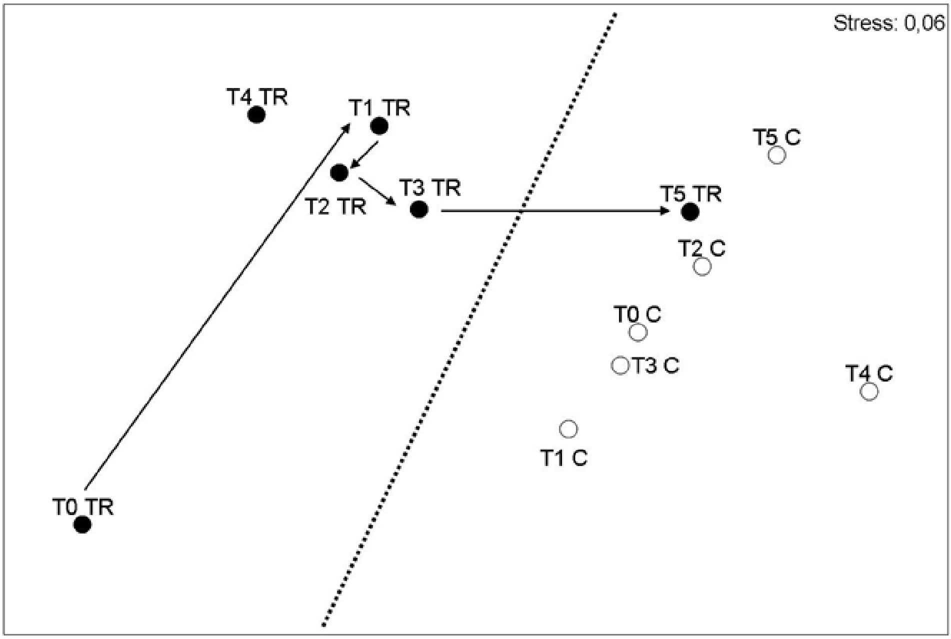

Figure 2. Two dimensional MDS ordination (stress = 0.06) of community data for each treatment and sampling occasion (means of replicates). Treatment (●) community composition evolves over time to the community composition of the control (○) samples (with the exception of T4: stormy weather). The recovery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

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

Table 2. SIMPER results showing differences between treatment samples (over time) and control samples (as one group). Dissimilarity is most pronounced between the treatment samples at T0 and the control samples; dissimilarities are decreasing over time (except for T4, storm effect). Samples of T5TR are more similar to the control samples than to the other treatment samples (TR-T5TR) and dissimilarity between control and treatment samples increases when T5TR is considered as belonging to the control samples.

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

Beam-trawl impact on total macrofauna density

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

Table 3. GLMM results for total number of individuals (i.e. summing up all macrofauna per sample). Treatment (tr) and Lanice conchilega *(nlan) densities describe the total number of individuals significantly. Neither time nor interaction effects (nlan x tr and time x tr) were significant and were left out of the final GLMM.*

Effect	F	DF	*p*
nlan	45.69	1	<0.0001
tr	7.34	1	0.0096
time	-	-	NS
nlan x tr	-	-	NS
time x tr	-	-	NS

Beam-trawl impact on community diversity

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

Beam-trawl impact on species level

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

Table 4. GLMM results E. sanguinea. Treatment (tr) and Lanice conchilega *(nlan) densities describe distribution of* Eumida sanguinea *significantly. Neither time nor interaction effects (nlan x tr and time x tr) were significant and were left out of the final GLMM.*

Effect	F	DF	*p*
nlan	30.49	1	<0.001
tr	11.92	1	0.0012
time	-	-	NS
nlan x tr	-	-	NS
time x tr	-	-	NS

The same model was used for *Urothoe poseidonis* densities. None of the explanatory factors explained the *U. poseidonis* densities in a significant way (p > 0.0544). Nevertheless, the study of multivariate results of community composition over time indicates an impact on *U. poseidonis*. At T0, SIMPER analysis showed that *U. poseidonis* was not present in the characteristic community of TR (not included in 95% of the community), whereas this species appeared in all other samples (TRs from T1 onwards and all Cs). SIMPER analysis indicated that two other species were important in community structure (*C. capitata* and *N. cirrosa*).

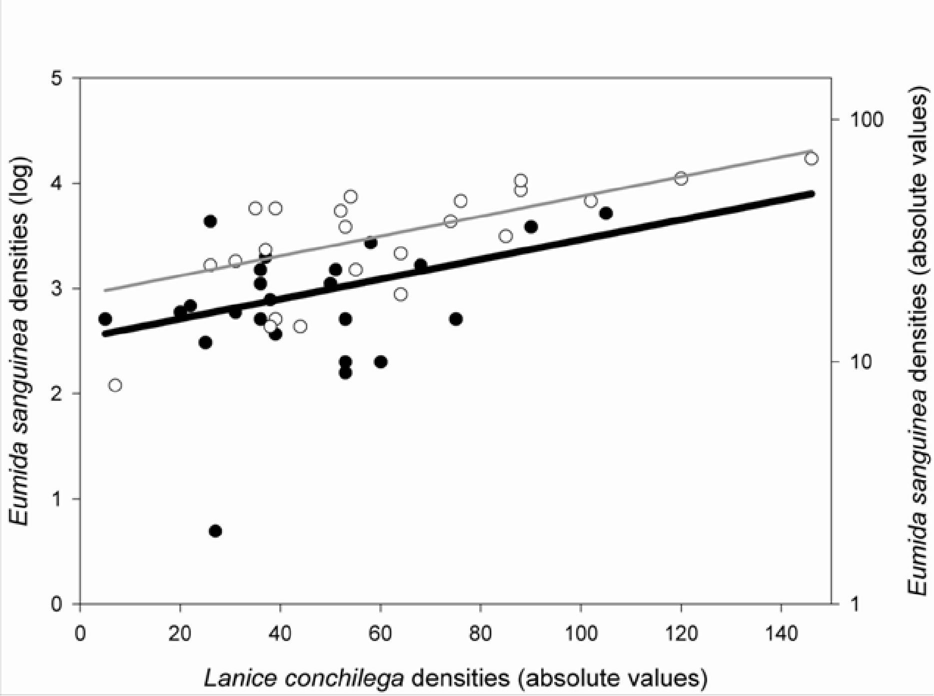

Figure 3. Impact on Eumida sanguinea. *Treatment values (●) and control values (○) are set out as a function of* Lanice conchilega *densities.* E. sanguinea *is always related with* L. conchilega *densities (same slope), but densities of* E. sanguinea *are significantly lower in treatment samples (lower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

The same generalized linear mixed model was used to test the explanatory factors for these two species. *Capitella capitata* densities could be described only through the densities of *L. conchilega*. No effect of treatment, time or interaction effects were observed for the two species. *L. conchilega* densities could not explain the densities of *N. cirrosa*.

As *E. sanguinea* and *U. poseidonis* showed a treatment effect, the community response on the treatment was tested without these species. The general recovery pattern as described for the whole community was largely maintained for the analyses where one of these species was excluded. Still, if a community with both species excluded is analyzed, the pattern largely disappears (figure 4). This proves that the community response was dictated by only two associated species. As *E. sanguinea* was the only species showing a significant treatment effect, it was verified whether the impact on total number of individuals was determined by this species or not. The tests performed for total number of individuals were repeated with *E.*

sanguinea excluded from the dataset. The results of the model runs show that the significant treatment effect disappears (p = 0.46). This species group was however still significantly described by *L. conchilega* densities (p < 0.0001).

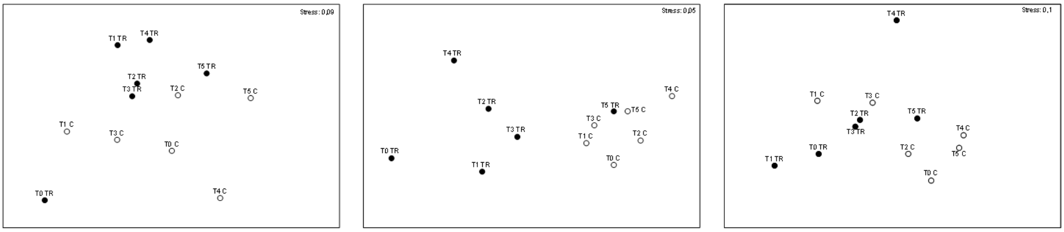

Figure 4. Two dimensional MDS ordinations with exclusion of Eumida sanguinea *(left),* Urothoe poseidonis *(middle) and both species (right). Only when both species are excluded from the dataset, the distinction between treatment (●) community and control (○) community is not visible anymore.*

Discussion

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

Eumida sanguinea

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

The high impact on this species can be explained by its high abundance and by its ecology. *Eumida sanguinea* lives in between the fringes of the *L. conchilega* tubes, which may serve as miniature hatcheries for *E. sanguinea*, providing food and possibly some shelter (Callaway, 2006). Moreover, during the sample treatment most *E. sanguinea* individuals were found inside the *L. conchilega* tubes and between the fringes. Hence, *E. sanguinea* is susceptible to being removed mechanically by the beam trawl. Olivier and Retière (1998) showed that *E. sanguinea* does not drift away during high tide, but stays at the sea bottom. This indicates that the low abundances are not merely due to differential removal during spring tide. The importance of *E. sanguinea* was confirmed by the disappearing treatment effect on the total number of individuals when this species was excluded from the dataset. However, analysing the recovery on community level as shown in the MDS plot could not be attributed to this most abundant species alone; Figure 4 shows clearly that the recovery trajectory is defined through the impact on *E. sanguinea* together with *U. poseidonis*.

Urothoe poseidonis

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

Recovery mechanism

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

The recovery pattern drawn in the MDS plot (Figure 2) was confirmed through the seriation test (RELATE analysis) and the SIMPER results (Table 2). This fast recovery is possibly related to the renewal of the population of *E. sanguinea* (with *L. conchilega* reefs close by, serving as a source). Negrello *et al*. (2006) emphasized the importance of this small-scale dispersal for infaunal recolonization on a tidal flat and noticed that recolonization can also occur through migration across the water column. This migration is suggested to be passive rather than active (Savidge and Taghon, 1988). We suggest that recovery from disturbance occurs gradually through adult migration from sediments surrounding the plots rather than by recruitment of juveniles as the timing and duration of the experiment excluded recruitment as a recovery mechanism. This dispersal may depend on sediment bed-load transport of large amounts of sediment and adult fauna into areas that have been trawled or because of exposure to wave action and currents, as suggested in Hall and Harding (1997) (mechanical harvesting of cockles) (as cited in Kaiser *et al*. (2001)). Intertidal *L. conchilega* reefs are probably more resilient to trawling because of (1) their adaptation to continuous natural disturbances (wave action and wind stress) and (2) the smaller number of associated species. Therefore, the recovery following a trawling disturbance is expected to happen faster in the intertidal, but with the same impact-recovery responses and mechanisms as in subtidal areas.

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

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

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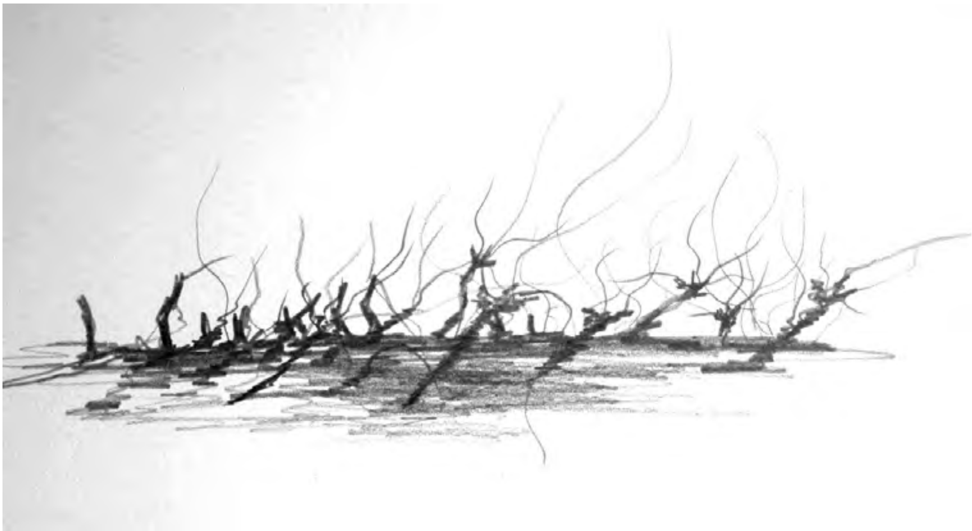
PART III

THE FUNCTIONAL VALUE OF *LANICE CONCHILEGA* REEFS FOR HIGHER TROPHIC LEVELS

CHAPTER 6

Biogenic reefs as structuring factor in *Pleuronectes platessa* nursery



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Abstract

The structural distribution of juvenile flatfish in nursery areas is generally studied on a larger scale on which the effects of abiotic factors such as sediment characteristics, beach profile, tides, and turbidity dominate. The biotic structuring factor has never before been investigated from a very small scale-perspective. The latter is the subject of the present study. In an *in situ* experimental sampling design, the structuring effect of biogenic reefs on the distribution of *Pleuronectes platessa* (Plaice) in an intertidal nursery area is investigated. The density distribution of this flatfish species is significantly ($p < 0.0001$) explained by the presence of reefs built up by the polychaete *Lanice conchilega*. The importance of this reef builder has been highlighted before in other studies but present study demonstrates that not only the benthic biodiversity is affected by *L. conchilega* reefs, but that the distribution pattern of *P. platessa* is structured by them as well. This structuring impact of small-scale benthic reefs creating a patchy environment in nursery areas potentially plays an important role in other marine environments and indicates the need for further research on the ecological function of benthic reef environments for several flatfish species. Further modification of these biogenic habitats may lead to a loss of one or more ecosystem functions which flatfish species depend on.

Key words

Polychaete reefs, *Lanice conchilega*, *Pleuronectes platessa*, flatfish nursery, marine conservation

Introduction

The surf zone of Belgian sandy beaches is intensively used by a number of epibenthic macro-crustaceans and flatfish species (Beyst *et al.*, 2001). Despite the structurally homogeneous environment, several authors suggest that fluctuations in physical variables (e.g. wave exposure, sediment particle size and turbidity) have a strong influence on the relative abundance of certain species and may alter the composition and species richness (Blaber and Blaber, 1980, Clark *et al.*, 1996, Pihl, 1986, Pihl and Vanderveer, 1992, Romer, 1990). However, local biological characteristics of the beaches might be of major importance (Nicolas *et al.*, 2007) and the need to estimate the quality (biologically) of habitats that are potentially important for juvenile flatfish has already been emphasized (Le Pape *et al.*, 2003b). The Belgian coastal waters have been acknowledged as nursery area which is explained by abiotic variables on the one hand and food availability on the other hand (Dewicke *et al.*, 1998). It is known that the mobile and relatively homogenous nature of the substratum on sandy shores implies that few refuges are available. However, habitat structuring organisms possibly signify another important small scale variable to explain the relative abundance of several species. Habitat structuring organisms are known to add or alter physical, chemical and biological factors and are therefore often referred to as ecosystem engineers (Jones *et al.*, 1994). These structures represent important habitats for a variety of marine organisms. In most habitats, regardless of environmental stress, ecosystem engineers provide the template for all other ecosystem processes, making these engineers essential to conservation. This engineering template has received relatively less ecological attention than the processes generating spatial and temporal patterns of organisms within engineered landscapes (Crain and Bertness, 2006).

The complex biogenic benthic habitats formed by sessile emergent tube dwelling polychaetes are of potential ecological importance. In some cases they act as refuges for juveniles of some commercial species (Auster *et al.*, 1997, Walters and Juanes, 1993) and are associated with a diverse assemblage of fauna that may be important prey (Kaiser *et al.*, 1999a, Peattie and Hoare, 1981). The common tube dwelling polychaete *Lanice conchilega* (Terrebellidae) is the target ecosystem engineer in present study. The physiology, tube structure (Jones and Jago, 1993, Ziegelmeier, 1952), hydrodynamic influence (Dittmann, 1999, Eckman, 1983, Heuers *et* *al.*, 1998), as well as the occurrence of *L. conchilega* patches (Hartmann-Schröder, 1996) has already been described extensively. The influence on faunal abundance, species richness and species composition has been proved based on a long-term dataset (Rabaut *et al.*, 2007), which shows that the species can be classified as an important ecosystem engineer. Recently, scientific evidence showed that *L. conchilega* qualifies as reef builder under the definition of the Habitats Directive (Rabaut *et al.*, 2009b). Moreover, it has been suggested that flatfish species actively select for a tube mat biotope build up by *Chaetopterus sp.* and *L. conchilega* (Rees *et al.*, 2005). In present study we hypothesize that post-larval flatfish (*incasu Pleuronectes platessa*) selects for small spatial scale variations in a reef environment within one beach.

Material and Methods

Study area

The investigated sandy beach is situated along the eastern part of the Belgian coast in the Flemish nature reserve “Bay of Heist” (51°20’N; 3°14’E) (Figure 1). The beach has an intertidal zone of c. 500 m with a tidal range of 5 m. According to the slope and fine median grain size, the beach classifies as a dissipative beach (Wright *et al.*, 1979). However, this particular beach is protected from strong hydrodynamic impacts by the harbour wall of Zeebrugge, built into the sea; therefore, the typically heavy wave action dissipated in a wide surf zone (McLachlan, 1990) is reduced in present study area. According to Short (1996), the study area rates as a ‘low-energy, dissipative beach’. The sheltered condition of the beach in the lee of the harbour wall together with the high turbidity makes the area favourable for the development of *L. conchilega* reefs. These reefs can be found below the mid-tidal level, with a maximum near lowest water level. As such, relatively small reefs (surface of c. 1-12 m^2) occur in an area with several other reefs, generating a ‘reef zone’ consisting of gentle mounds and shallow depressions, with about 20% coverage by reefs (Degraer *et al.*, 2008a, Rabaut *et al.*, 2009b). The location of the reef zones (*i.e.* zone consisting of patches of several reefs interspersed with small patches of bare sediment) could be marked during low tide. These reef areas were considered as treatment zone.

*Figure 1. Sampling area. Position of Belgian part of the North Sea (top left); Sampling zone in the Bay of Heist, protected by the harbour wall of Zeebrugge (top right and bottom left); Position of treatment (*i.e. *reef) and control (*i.e. *bare sand) zones (bottom right).*

Sampling design

The beach, in which the *L. conchilega* reefs were present, was divided into two different zones. One zone was classified as reef area (treatment zone; *i.e.* zone consisting of several reefs), whereas the other zone besides, at the same height on the beach with similar characteristics did not have the tube building polychaete (control zone; *i.e.* bare sediments without any reef). Within each zone, 2 to 4 samples were taken at each sampling event with the hyperbenthic sledge. This sledge samples the hyperbenthos from 0.5 to 45 cm above the bottom. The hyperbenthic sledge consists of two nets placed one above the other (3 m long; mesh size 1 mm) (Beyst *et al.*, 2002b). The results are only based on the contents of the lower net as no flatfish is caught in the higher net. For each sample, the sledge was towed by two persons during 2.5 minutes. Samples were taken on five different days in spring around spring tide events of March-April 2008 (10/3, 28/3, 3/4, 17/4, 25/4) (replication over time). Sampling was performed during ebbing with a water column of 1 to 0.3 m. Replication was done over time. The relatively small sample size combined with the time interval between sampling events justify the assumption of independent sampling.

Sampling treatment

Samples were stored in an 8% formaldehyde solution. Subsequently, all samples were sorted and juvenile flatfish specimens were identified to species level and counted. The length of all specimens was measured. Only individuals of age group 0 yr were used for further analysis as only two individuals of age group I yr were found.

Statistical analysis

To test for the effect of the presence of *L. conchilega* on the densities of juvenile flatfish, a generalized linear model was used in which the fixed factors treatment (*i.e.* presence/absence of *L. conchilega*), time and their interaction effect, were related to the densities of juvenile flatfish species. The SAS software package was used as modelling environment. As the response variables are count data, the residual error structure was tested against a Poisson distribution. When overdispersion became apparent in the model output, the model was rerun, taking the overdispersion into account in order to avoid underestimation of the standard errors. Because the predictor and the mean response are not linearly related to each other, the relationship was specified by a log link function. The fixed effects structure was reduced in a backward stepwise manner.

Results

Two flatfish species were found during this study: *Solea solea* (Sole) and *Pleuronectes platessa* (Plaice). We captured 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). 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 2). Comparison between control and treatment show significant differences in *P. platessa* densities ($p < 0.0001$) (Figure 2, 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.

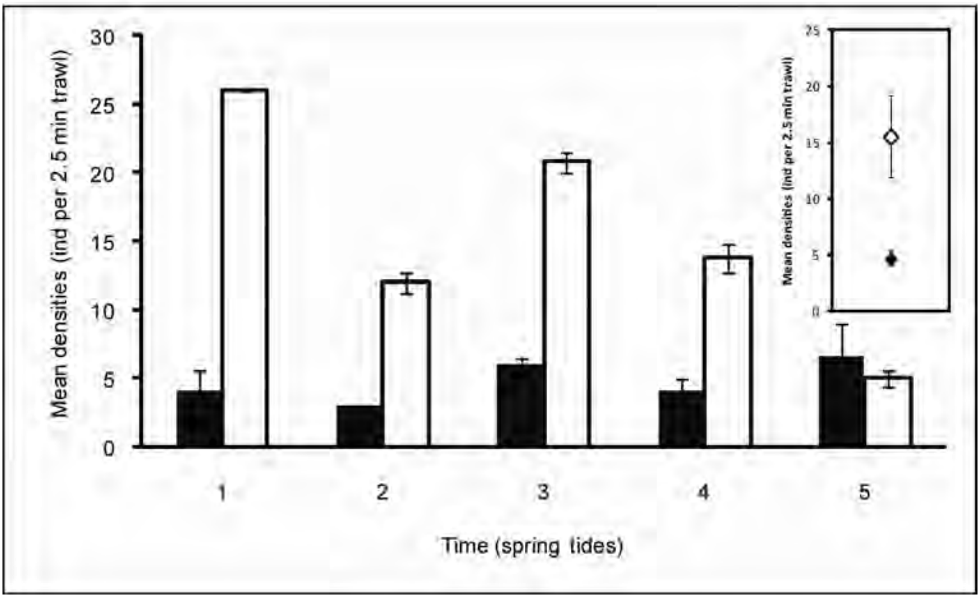

Figure 2. Density distribution of Pleuronectes platessa *(0-group); densities outside* Lanice conchilega *reefs (black) compared with densities inside* L. conchilega *reefs (white). Inset: Overall flatfish density differences between control zones without* L. conchilega *(black) and treatment zones with* L. conchilega *(white). These differences are significant ($p < 0.01$).*

Discussion

Results show that 0-group *P. platessa* densities are described by the presence of *L. conchilega*. On a large scale (hundreds of meters), structuring abiotic factors as the beach profile and turbidity has been highlighted in earlier studies (Beyst *et al.*, 2001, 2002a). Data shown here indicate that on a small scale (meters) habitat structuring organisms such as tube building polychaetes are able to influence the distribution of *P. platessa*. These findings contradict another study in the English Channel where no clear association was found between flatfish abundance, structuring epifauna, and prey availability (Hinz *et al.*, 2006). Nevertheless, it has been suggested that emergent structures, in otherwise low-relief benthic habitats, may play an important role in the ecology of some juvenile flatfishes (Ryer *et al.*, 2004). This study confirms these findings and suggests that aggregations of *L. conchilega* provide shelter for *P. platessa*. As burying in sand is only a partial refuge for juvenile flatfishes (Ansell and Gibson, 1993), reefs may be a good alternative to hide in.

Besides, it has also been demonstrated that food availability can be an important factor (Beyst *et al.*, 1999). An opportunistic utilization by flatfish of the available food resources in surf zone ecosystems has been shown (Lockwood, 1984, Molinero and Flos, 1992, Wyche and Shackley, 1986). The composition and quantity of juvenile *P. platessa* gut contents varies over a small spatial scale (meters) (De Raedemaecker *et al.*, submitted), while food availability in the nursery areas was not found to be related to *P. platessa* density (Pihl and Vanderveer, 1992). This apparent contradiction might be attributed to the spatial variability in condition, growth and diet of juvenile plaice (Beyst *et al.*, 1999). The present study shows that small scale variability of *P. platessa* density can be induced by biological factors and plays a significant role indeed. For age class 0, individuals smaller than 5 cm mainly feed on meiobenthos, while larger individuals shift to macrobenthos (Aarnio *et al.*, 1996).

Furthermore, this study is of interest for the protection of the intertidal environments if the ecosystems approach is to be applied within the framework of integrated coastal zone management. Habitat modification through the removal of emergent structure by anthropogenic and/or natural disturbance may influence patterns of distribution on a very small scale (*i.e.* within one beach), knowing that redistribution to less preferred habitat may decrease survival rates through increased losses to predation (Ryer *et al.*, 2004). Moreover, given the important nursery function of estuaries (Dolbeth *et al.*, 2008, Hampel *et al.*, 2005), these emergent structures contribute probably to survival of flatfish species in estuarine environments. The important conservation stake of these reef systems in intertidal environments has recently been advocated because of their particular functional value (Godet *et al.*, 2008), while it has been suggested that protection is possible under the EU Habitats Directive as habitat type 'reef' (Rabaut *et al.*, 2009b). Furthermore, the patchy environment created by *L. conchilega* is of potential importance for *P. platessa* in subtidal areas as well (as feeding ground, shelter, etc.), where patchy distribution of *P. platessa* has been reported before (Poos and Rijnsdorp, 2005). It has been suggested that relatively sparse elements of habitat structure can have important implications for resource management and conservation (Thrush *et al.*, 2001). Moreover, in the subtidal, severe habitat modification such as bottom trawling affect these reefs (Rabaut *et al.*, 2008).

Conclusion

This spatially small-scale research highlights that biogenic emergent structures such as *L. conchilega* reefs provide a patchy environment which ameliorates the nursery function of highly dynamic shores. Not only do the *L. conchilega* reefs affect the benthic biodiversity and ecosystem functioning (Callaway, 2006, Rabaut *et al.*, 2007, Van Hoey *et al.*, 2008), but they also influence the distribution pattern of *P. platessa*. The present study indicates the need for further research on the ecological function of emergent benthic ecosystem-engineered environments for *P. platessa* and other flatfish species.

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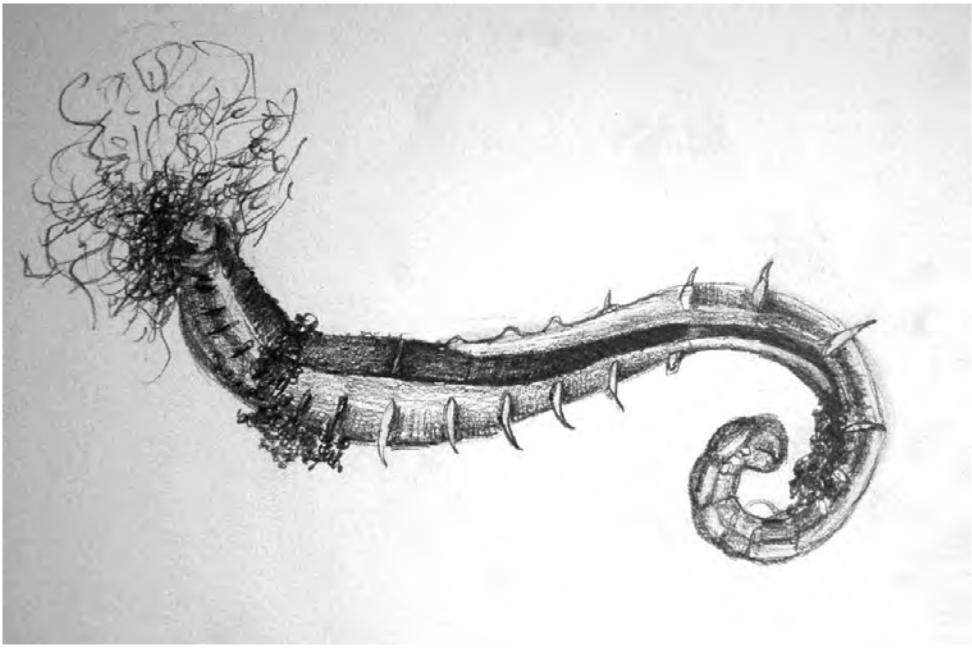
CHAPTER 7

Importance of eco-engineered inshore habitats for juvenile flatfish



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Abstract

Within coastal nurseries, the distribution of juvenile flatfish may depend on small-scale habitat variability. The present study investigates the relation between the distribution of two juvenile flatfish species (*Pleuronectes platessa* and *Limanda limanda*) with two sessile tube dwelling polychaetes that create specific habitats at high densities. Their modulating effects make them classify as ecosystem engineers. *Lanice conchilega* and *Owenia fusiformis*, both frequently occurring in the coastal zones of the North Sea are the studied ecosystem engineers. These two benthic tube worm systems are investigated for their function as 'essential juvenile habitat' (EJH) in two geographical areas (the Belgian part of North Sea and the Dutch part of the Wadden Sea). General responses were identified by comparing relative differences between ecosystem engineered habitats and adjacent bare sand (*i.e.* non-ecosystem engineered) habitats. Results show that both flatfish species select for the ecosystem engineered habitat. This behaviour was further investigated using stomach content analyses. For *P. platessa* occurring in *L. conchilega* habitat, this selection was explained as feeding behaviour. For the habitats created by *O. fusiformis*, no such a relation was found. For *L. limanda* higher densities within the ecosystem engineered habitats cannot be explained by feeding advantage but by the use of this habitat as a shelter. Therefore, higher flatfish densities could be explained by an antipredation behaviour. *Lanice conchilega* aggregations may be more important as feeding area for juvenile flatfish species in comparison with *O. fusiformis* aggregations. The indirect impacts of bottom trawling on benthic tube worm aggregations by reducing the suitability of the areas for juvenile flatfishes are discussed. We conclude that the emergent structures in the flatfish nursery area play an important role in the ecology of the juvenile flatfishes as feeding ground and/or as refuge from predation. These small-scale aspects of nursery grounds can be considered as EJH and merit attention in habitat suitability models as well as in marine conservation.

Key words

Pleuronectes platessa, Limanda limanda, Lanice conchilega, Owenia fusiformis, ecosystem engineers, flatfish, essential juvenile habitat, nursery area, North Sea

Introduction

Larger scale distribution patterns of juvenile flatfish are explained by temperature, depth, salinity and sediment characteristics (Gibson and Robb, 2000, McConnaughey and Smith, 2000, Moles and Norcross, 1995, Rijnsdorp *et al.*, 1990, Riou *et al.*, 2001, Rogers, 1992). The early life stages of many marine fishes migrate from the spawning grounds to the nursery areas and finally to the adult feeding ground (Harden Jones, 1968). For some flatfish species such as *Pleuronectes platessa*, no relation between age class and sediment-defined habitat is found (Gibson and Robb, 2000). For many species, nursery areas are characterized by few predators and high structural complexity (Wennhage, 2002). Moreover, emergent structures in otherwise low-relief benthic habitats, may play an important role in the ecology and population dynamics of some juvenile flatfishes (Pappal, 2006) as structurally complex benthic habitats reduce predation risk (Auster *et al.*, 1997, Joseph *et al.*, 2006, Ryer *et al.*, 2004).

Marine biogenic structures that reach a few centimetres into the water column can have a profound effect on the structure and functioning of marine ecosystems. These systems are heavily used by a variety of taxa, including post-settlement juveniles of commercially important fish species (Watling and Norse, 1998). Furthermore, food availability can be an important factor explaining flatfish distribution in the nursery (Beyst et al., 1999) and can even override abiotic habitat preferences (Phelan *et al.*, 2001). Flatfish nursery areas are generally characterized by higher densities and biomass of macrobenthic species in comparison with the adjacent non-nursery areas (Wouters and Cabral, 2009). It is, however, not always clear whether the preference for structured habitats is because of either the shelter or the feeding advantage, as was experimentally shown by Sogard (1992). Recently it has been recognized that in order to better understand patterns in habitat use of fish within nursery areas, a small-scale approach is desirable (Shucksmith *et al.*, 2006, Vinagre *et al.*, 2009).

The biogenic structures formed by sessile emergent tube dwelling polychaetes are of potential ecological importance because these act as refuge for juvenile fish (Auster *et al.*, 1997, Ryer *et al.*, 2004, Walters and Juanes, 1993). Moreover, these are associated with a diverse assemblage of fauna that provide important prey (Kaiser *et al.*, 1999a, Peattie and Hoare, 1981). The target biogenic structures of this study are those formed by *Lanice conchilega* and by *Owenia fusiformis.* These are sessile, tube dwelling polychaetes occurring at high density aggregations and well known from the coastal zones of the North Sea (Van Hoey *et al.*, 2008). These considerably increase abundance and diversity of the benthic community through their ecosystem engineering impact.

Lanice conchilega (Polychaeta, Terebellidae) builds a tube to a maximum of 5 mm in diameter and a length up to 65 cm, composed of grains and other solid particles. The top end protrudes above the sediment by 1-4 cm and ends in a fringe of filaments of mucus-bound sand grains, which traps suspended particles. For the macrobenthic community, the habitat modifying capacity of *L. conchilega* has been suggested to lie in the creation and regulation of safe havens for species, in influencing the interactions between local species and in changing the physical environment (Rabaut *et al.*, 2007, Van Hoey *et al.*, 2008). Therefore, the species has been described as an important ecosystem engineer. Its effect on biodiversity has been described extensively (Callaway, 2006, Carey, 1987, Dittmann, 1999, Féral, 1989, Rabaut *et al.*, 2007, Van Hoey, 2006, Zühlke *et al.*, 1998). *Lanice conchilega* has the capacity to double the biodiversity in the richest soft-sedimented macrobenthic habitat of the Belgian part of the North Sea (BPNS) (*i.e.* the *Abra alba – Kurtiella bidentata* community *sensu* Van Hoey *et al.* (2004)). Furthermore, several studies describe in detail how *L. conchilega* affects the abiotic environment (Braeckman *et al.*, accepted, Forster and Graf, 1995). Recently, the species has been defined as a true reef builder (Rabaut *et al.*, 2009b).

The tube building polychaete *O. fusiformis* (Polycaeta, Oweniidae) occurs in the same macrobenthic community (*Abra alba – Kurtiella bidentata*) as *L. conchilega*. *Owenia fusiformis* is a thin cylindrical, segmented worm, up to 10 cm long, that lives in a tough though flexible tube buried in the sand (Pinedo et al., 2000). The tube abruptly widens from the initial part towards the top end, increasing the external diameter from ca. 1 mm to 4 mm (Noffke *et al.*, 2009) and is composed of sand grains or shell fragments glued together in an overlapping, imbricate fashion. The tube is slightly longer than the worm and its top end may protrude to up to 2 cm from the surface. The species has an adult life span of three to four years (Menard et al., 1989), as opposed to *L. conchilega* which has a lifespan of about one year in Belgian waters (Van Hoey, 2006). The species is widely distributed in coastal regions throughout North-Western Europe, the Mediterranean, the Indian Ocean and the Pacific and occurs in fine to coarse sediments, reaching only high densities in finer sediments (Pinedo *et al.*, 2000, Somaschini, 1993). In a recent study *O. fusiformis* proves to be an ecosystem engineer that stabilizes sand bank systems (Rabaut *et al.*, in prep.). This has clear consequences for the biotic (benthic) community structure that profits from a stable small scale niche in an otherwise highly dynamic area.

Both ecosystem engineered habitats of *L. conchilega* and *O. fusiformis* have been extensively studied as for their macrobenthic species diversity and ecosystem functioning (Callaway, 2006, Carey, 1987, Dittmann, 1999, Féral, 1989, Rabaut *et al.*, in prep., Rabaut *et al.*, 2007, Somaschini, 1993, Van Hoey *et al.*, 2008, Zühlke *et al.*, 1998). It is, however, not clear whether these hotspots of biodiversity are important for juvenile flatfish dwelling in the nursery area. The areas of interest to this study are shallow coastal zones in the North Sea that serve as nursery grounds (Le Pape *et al.*, 2003a, Miller *et al.*, 1988, van der Veer *et al.*, 2001). Our study focuses on the juveniles of two flatfish species that occur in high densities (*Limanda limanda* and *P. platessa*). The general aim of this study is to investigate whether these juvenile flatfishes select for such small scale engineered habitats and whether this behaviour represents an antipredation and/or a feeding strategy. The two benthic tube worm engineered habitats are investigated in two different geographical areas. We hypothesize that general responses of these juvenile flatfish species to the presence of high densities of the two polychaetes can be identified when relative differences in abundance and stomach content between engineered habitats and adjacent non-engineered habitats are compared. The results are discussed int he framework of 'Effective Juvenile Habitats' (EJHs) (*sensu* Dahlgren *et al.* (2006)), together with the potential vulnerability towards mobile fishing gear.

Methodology

Sampling and sample treatment

One area of investigation was located in the Belgian part of the North Sea (BPNS) (51°21′N, 2°57′E), further referred to as Area 1 (Figure 1). A second area was located in the Dutch part of the Wadden Sea (DPWS) (54′00′N, 7°50′E), further referred to as Area 2 (Figure 1). In both areas two subzones were identified based on differences in density of the ecosystem engineer as quantified from Van Veen grab samples. Densities of the ecosystem engineer were averaged. Densities of > 150 ind m^{-2} were considered to be high and qualify as an ecosystem engineered habitat (Rabaut *et al.*, 2007, Rabaut *et al.*, 2009b), whereas averages < 50 ind m^{-2} where considered as non-engineered habitat. The densities of the ecosystem engineer in the different subzones (ecosystem engineered habitat versus non-ecosystem engineered habitat) were investigated for each area and differences between subzones were tested in generalized linear models with habitat as a fixed factor and the ecosystem engineer densities as the response variable. Both habitats in Area 1 differed significantly ($p < 0.0001$) with average *O. fusiformis* densities of 925 +/- 135 SE ind m^{-2} within the ecosystem engineered area and 31 +/- 21 SE ind m^{-2} outside. In Area 2, *L. conchilega* densities differed significantly ($p < 0.0001$) with average densities of 242 +/- 90 SE ind m^{-2} and 12 +/- 1 SE ind m^{-2} respectively. In Area 1, the dominant ecosystem engineer found was *O. fusiformis* (associated *L. conchilega* was on average only 16% of *O. fusiformis* densities) while in Area 2 it was *L. conchilega* (associated *O. fusiformis* was on average only 8% of *L. conchilega* densities). Both geographical areas were sampled for flatfish with a beam trawl, each time with sampling in both subzones (*i.e.* the ecosystem engineered subzone and the non-ecosystem engineered subzone; Figure 1). These subzones represent the fixed effect factor 'habitat'. Area 1 was sampled in October 2008 while Area 2 was sampled in June 2007. Sampling depths were respectively ca. 10 m and ca. 6 m. Flatfish were collected with a beam trawl. The beam trawl used in Area 1 had a width of 4 m and was deployed form the *RV* 'Zeeleeuw' while the trawl used in Area 2 was a 2 m beam trawl deployed from the *RV* 'WR76 Herman Simon'. Within each particular geographical area, the two habitats were sampled with exactly the same gear, to make flatfish density comparisons within the area possible (*cf.* sampling period and beam trawl used). Fish were identified, counted and measured on board. In the field, flatfish was anaesthetized in a benzocaïne (ethyl amino-4-benzoate) solution to prevent regurgitation of the stomach contents and preserved in an 8% buffered formalin solution. Flatfishes were divided in two age classes: age class 0, containing individuals between 5 and 9 cm and age class 1 containing individuals between 9.1 and 13 cm (Amara *et al.*, 2001, Beyst *et al.*, 1999). For age class 0, no individuals smaller than 5 cm were subjected to analysis as these small individuals are mainly feed on meiobenthos, while larger individuals shift to macrobenthos (Aarnio *et al.*, 1996). In the laboratory, a minimum of ten individuals, per area and in each habitat, of *P. platessa* and *L. limanda* was selected for further stomach analyses (Rijnsdorp and Vingerhoed, 2001). All prey items in the stomachs were counted and identified to the lowest possible taxonomic level (further referred to as species). The biomass (mg AFDW) of each prey item present in the stomach as well as the flatfish biomass was measured.

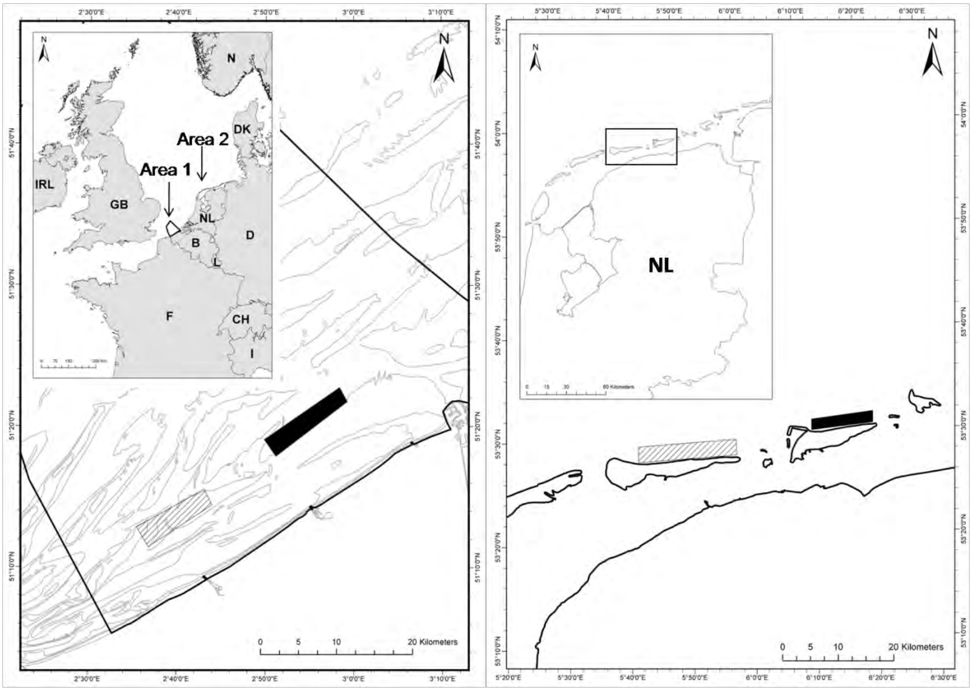

Figure 1. Study areas. Area 1 is located in the Belgian part of the North Sea, while Area 2 is located in the Dutch part of the Wadden Sea (in front of the islands Ameland and Schiermonnikoog). Non-ecosystem engineered subzones are shaded; black zones represent the ecosystem engineered subzones.

Data analysis

The relative importance of prey in the diet (*i.e.* stomach content) was expressed as percent of numerical abundance (N%), weight (G%), and fullness (FI%). N% and G% were calculated on non empty stomachs (Frid *et al.*, 1999), while FI% was calculated on all stomachs (including empty). Feeding activity was evaluated by the vacuity index (V%). These percentages were calculated for groups of samples as follows:

$$N\% = \frac{Number\ of\ food\ items\ in\ a\ stomach}{Total\ number\ of\ food\ items\ in\ group} \times 100$$

$$G\% = \frac{Total\ biomass\ in\ a\ stomach}{Total\ biomass\ in\ group} \times 100$$

$$FI\% = \frac{AFDW\ of\ stomach\ content}{AFDW\ of\ fish} \times 100$$

$$V\% = \frac{Number\ of\ empty\ stomachs\ in\ group}{Total\ number\ of\ analyzed\ stomachs\ in\ group} \times 100$$

To analyze more in detail prey selectivity, numerical, gravimetric percentages and the frequency of occurrence (FO%) were further calculated per species within each sampling group as:

$$N_i\% = \frac{Number\ of\ prey\ type\ i}{Total\ number\ of\ prey\ items\ in\ the\ stomach} \times 100$$

$$F_i\% = \frac{AFDW\ of\ prey\ type\ i}{Total\ AFDW\ of\ ingested\ food} \times 100$$

$$FO_i\% = \frac{Number\ of\ stomachs\ containing\ prey\ item\ i}{All\ stomachs} \times 100$$

Statistical analyses

Flatfish densities

Flatfish densities were compared between habitats within each geographical area, as different beam trawl types may have different catch efficiencies. All densities were recalculated to individuals per 100 m^2. Differences were calculated using a generalized linear model in which the fixed factors habitat, age and their interaction effect were related to the flatfish densities. As the response variables are count data, the residual error structure was assumed to follow a Poisson distribution with the variance multiplied by an overdispersion parameter. Because the predictor and the mean response are not linearly related to each other, the relationship was specified by a log link function. The fixed effects structure was reduced in a backward stepwise manner.

Stomach analyses

As the response variables are expressed as relative percentages, the residual error structure was assumed to follow a Binomial distribution. Hence, a generalized linear model was used to evaluate the significance of the fixed effect habitat, age and their interaction effect. The relationship was specified by a logit link function. In a first overall analysis all (non empty) stomachs of Area 1 and Area 2 were analyzed together. To account for the statistical dependence of observations from the same Area, this factor was included as a random effect (using a mixed model). In a second analysis, differences between habitats were analysed for each area and age separately (generalized linear model with habitat as a fixed effect). This analysis could only be performed for groups where stomachs of both habitats were present (*i.e.* for Area 1: both age classes of *L. limanda* and age class 1 of *P. platessa*; for Area 2: both age classes of *P. platessa*). For these groups, a detailed analysis on species composition was performed. Differences in prey species composition were analysed using multivariate ANOSIM and SIMPER analysis (Clarke and Warwick, 2001). When two factors (habitat and age) were analysed together, two way crossed ANOSIM and SIMPER routines were run (Primer v6).

The most important prey species were found on the basis of the frequency of occurrence (FO%) and the relative contribution of individual prey species to the dissimilarity between groups (SIMPER analysis; two way crossed when two factors involved). These analyses were performed both on numerical and gravimetric indices. Differences in diversity of prey species were based on differences in Shannon Wiener index (Hampel *et al.*, 2005), which was tested with a general linear model if there was homogeneity of variances (Levene's test) and if the residual error structure followed a Normal distribution (Shapiro-Wilk's test). If assumptions were not met, non parametric tests on Shannon Wiener index were performed (Wilcoxon).

Results

Flatfish densities

Where both age classes are analysed together, the two flatfish species occur in significant higher densities in the ecosystem engineered subzones (Figure 2; Table 1). 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 (Table 1).

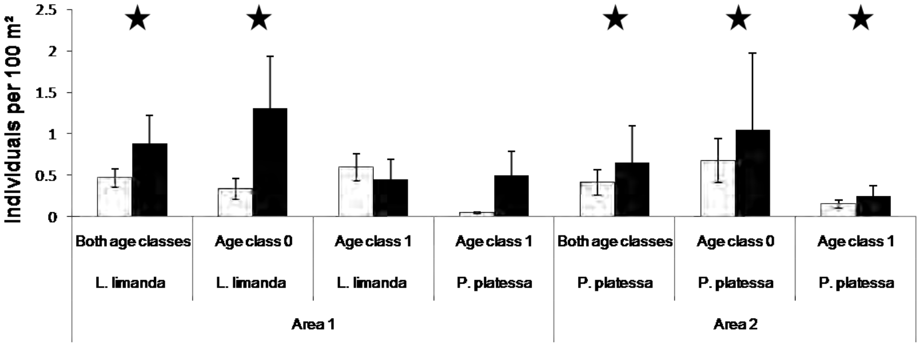

Figure 2. Flatfish densities. Both flatfish species are represented per geograpghical area and per age class. White bars represent flatfish densities in subzones without the ecosystem engineer; black bars represent flatfish densities in ecosystem engineered subzones.Significant differences between habitats are indicated with a star.

Table 1. Differences in flatfish densities between subzones, age and their interaction effect (p-values). Asterisks indicate significant differences. Differences between subzones represent differences between ecosystem engineered and non-ecosystem engineered habitats (referred to as the „Habitat' effect).

		Limanda limanda			*Pleuronectes platessa*		
		Habitat	Habitat x Age	Age	Habitat	Habitat x Age	Age
Area 1	Both age classes	0.0001*	0.5760	0.8368	-	-	-
	Age class 0	0.0002*	-	-	-	-	-
	Age class 1	0.1248	-	-	0.8428	-	-
Area 2	Both age classes	-	-	-	0.0001*	0.9699	0.1949
	Age class 0	-	-	-	0.0024*	-	-
	Age class 1	-	-	-	0.0076*	-	-

Stomach analyses

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 (Figure 3). 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*) (Figure 3, Table 2). 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 (Figure 3, Table 2). 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. Significance levels are summarized in Tables 2 and 3.

Table 2. Differences (expressed as p-values) in stomach contents between subzones, age and their interaction effect for numerical, gravimetric and fullness indices (independent of geographical area). Asterisks indicate significant differences. Differences between subzones represent differences between ecosystem engineered and non-ecosystem engineered habitats (referred to as the „Habitat' effect).In the analyses with both age classes, the results on individual factors „age' and „habitat' cannot further be interpreted when their interaction is significant (no asterisks).

		L. limanda			*P. platessa*		
		Habitat	Habitat x Age	Age	Habitat	Habitat x Age	Age
N%	Both age classes	<0.0001	0.0007*	<0.0001	<0.0001	0.0069*	0.134
	Age class 0	<0.0001*	-	-	<0.0001*	-	-
	Age class 1	<0.0001*	-	-	0.0002*	-	-
G%	Both age classes	0.0005*	0.9132	<0.0001*	0.0232	<0.0001*	<0.0001
	Age class 0	0.9995	-	-	0.9991	-	-
	Age class 1	0.0431*	-	-	0.8927	-	-
FI%	Both age classes	0.0019*	0.0892	0.6221	0.0732	<0.0001*	0.4691
	Age class 0	0.0069*	-	-	<0.0001*	-	-
	Age class 1	0.0746	-	-	<0.0001*	-	-

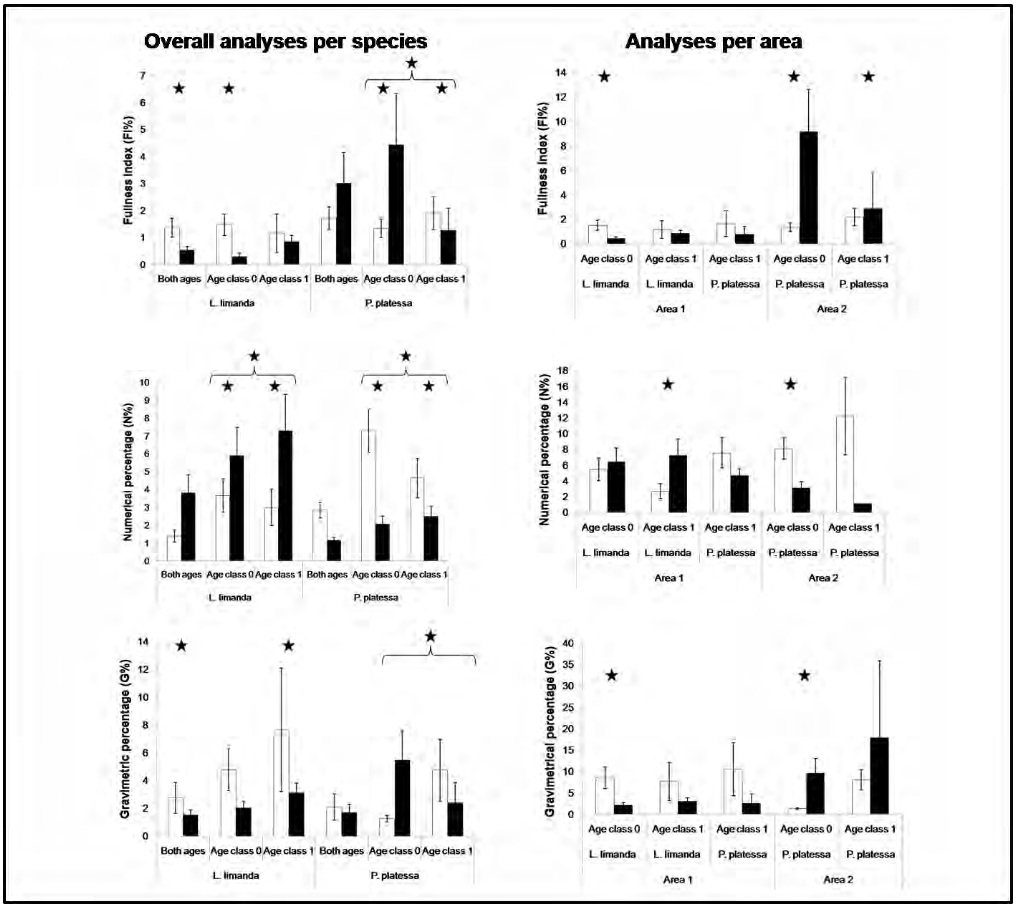

Figure 3. Overall stomach analysis per species (left) and per geographical area and species (right) of the fullness index (FI%), proportional numerical differences (N%) and proportional gravimetric differences (G%). Non-ecosystem engineered subzones are represented with white bars; ecosystem engineered 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.

Table 3. Differences (expressed as p-values) in stomach content per area and per age class. Differences for numerical, gravimetric and fullness indices are shown. Asterisks indicate significant differences.

			N%	G%	FI%
Area 1	*L. limanda*	Age class 0	0.6473	0.0030*	0.0018*
		Age class 1	0.0311*	0.1382	0.4483
	P. platessa	Age class 1	0.1317	0.0864	0.1723
Area 2	*P. platessa*	Age class 0	0.0030*	0.0005*	0.0002*
		Age class 1	0.1419	0.2806	0.0089*

The feeding activity was generally lower in ecosystem engineered habitats, as shown by the vacuity index (V%) (Table 4).

Table 4. Feeding activity (V%) within and outside ecosystem engineered subzones.

		Non-ecosystem engineered subzone	Ecosystem engineered subzone
L. limanda	Both age classes	10	29.16
	Age class 0	10	50
	Age class 1	10	0
P. platessa	Both age classes	16.67	24.32
	Age class 0	0	20
	Age class 1	25	29.41

In Area 1, two way crossed ANOSIM and SIMPER results for N% and G% show that there is a habitat effect when gravimetric percentages are used (table 5). Based on the frequency of occurrence (FO%) and on multivariate analyses on G% and N% data, the four most important prey species were selected: Caprellidea spec., *Microprotopus maculatus*, Hydrozoa and *L. conchilega* (Table 6).

Table 5. Prey species community composition. ANOSIM (R-values) and SIMPER dissimilarities between prey communities of flatfish caught inside ecosystem engineered subzones and those from outside and between age classes (two way crossed analyses when both ages are involved). ANOSIM R and correspondent p-values are given for numerical (N%) as well as for gravimetric (G%) percentages. SIMPER dissimilarities indicate differences in prey composition. Significant differences are indicated with an asterisk.

			N%			**G%**		
			R	***p***	**Dissimilarity**	**R**	***p***	**Dissimilarity**
Area 1	*L. limanda*	age	0.044	0.112	36.71	0.025	0.29	48.46
		habitat	0.009	0.375	36.55	0.362	0.001*	62.94
	P. platessa	habitat	0.15	0.072*	74.2	0.152	0.039*	82.65
Area 2	*P. platessa*	age	0.351	0.005*	71.46	0.311	0.001*	73.76
		habitat	0.581	0.001*	90.57	0.507	0.001*	94.12

Caprellidea spec. was gravimetrically more abundant as prey in *L. limanda* caught in areas with the ecosystem engineer, while *M. maculatus* was numerically more important as prey in areas without the ecosystem engineer. Hydrozoa seemed to be far more important as prey item in areas without ecosystem engineers. *Lanice conchilega* was found to be numerically more abundant as prey in *L. limanda* caught in the non-ecosystem engineered subzone (Figure 4). Differences linked to age class were found only for *M. maculatus* (%N, p = 0.0012) and for Hydrozoa (%G, p = 0.0417) (Table 6). There were no significant differences in Shannon Wiener index because of habitat (p = 0.6507) or age (p = 0.9627).

For *P. platessa* in Area 1 (age class 1 only), SIMPER results for N% and G% show a large dissimilarity between prey item assemblage of *P. platessa* caught in areas with and without ecosystem engineer (Table 5). Moreover, ANOSIM results show that there is a significant habitat effect when gravimetric percentages are used (Table 5). The four most important prey species are Caprellidea spec., *Phyllodoce (Anaitides) mucosa*, *L. conchilega* and Anthozoa spec. Caprellidea spec. was numerically more abundant as prey in *P. platessa* caught in the ecosystem engineered subzone, while *L. conchilega* was numerically more important as prey in non-ecosystem engineered subzones. Gravimetrically, only Anthozoa spec. differed significantly between habitats (more Anthozoa in areas without ecosystem engineer) (Figure 4, Table 6). There were no significant differences in Shannon Wiener index because of habitat (p = 0.1333).

In Area 2, two way crossed SIMPER results show a large dissimilarity between prey item assemblage of *P. platessa* (both age classes) caught in areas with and without ecosystem engineer (Table 5). Moreover, two way crossed ANOSIM results show that there is a significant habitat and age effect, both numerically and gravimetrically (Table 6). Based on frequency of occurrence (FO%) and on multivariate analyses on G% and N% data, the four most important preys are *Spio* spec., *L. conchilega*, *Pontocrates altamarinus* and *Nephtys hombergii* (Table 6).

Spio spec. is an important prey for *P. platessa* in the non-ecosystem engineered subzone (both numerically and gravimetrically), while *L. conchilega* seems to be an important prey in the ecosystem engineered subzones. No significant effects were found for *P. altamarinus* and *N. hombergii* (Figure 4, Table 6). Differences because of age classes were found for *Spio spec.*, which occurred in significantly higher densities in age class 0 (N%, p = 0.0266; G%, p= 0.002) and for *L. conchilega*, which was more frequently eaten by *P. platessa* of age class 1 (only gravimetrically, p = 0.0221). In terms of diversity of species, no significant differences were found between habitats (p = 0.2633) or ages (p = 0.5094).

Table 6. Most dominant prey items per species per area. Importance of prey items is based on frequency of occurrence (FO%), species contribution to the dissimilarity of community composition between subzones (SIMPER; two way crossed SIMPER when both ages are involved). Numerical and gravimetric differences of prey species between subzones is indicated with significance level (Asterisks indicate significant differences)

			FO%		SIMPER		*p* level	
		species	Non-ecosystem engineered subzones	Ecosystem engineered subzones	% contribution (N%)	% contribution (G%)	N%	G%
Area 1	*L. limanda*	Caprellidea sp.	100	87.86	28.03	22.47	0.0834	<0.0001*
		M. maculatus	32.2	42.14	19.24	6.69	0.0215*	0.1246
		Hydrozoa	95	15	-	30.18	-	<0.0001*
		L. conchilega	10.55	0	3.16	4.55	0.037*	0.0993
	P. platessa	Caprellidea sp.	14.24	50	18.89	13.15	0.0161*	0.2978
		L. conchilega	42.85	20	10.17	11.79	0.0323*	0.3885
		Anthozoa sp.	14.28	0	8.77	7.53	0.1016	0.0173*
Area 2	*P. platessa*	Spio sp.	68.75	25	39.51	39.56	<0.0001*	<0.0001*
		L. conchilega	6.25	16.67	33.43	24.75	<0.0001*	<0.0001*
		P. altamarinus	10	11.11	11.21	0.05	0.069	0.9828
		N. hombergii	21.25	0	3.27	2.8	0.2926	0.0501

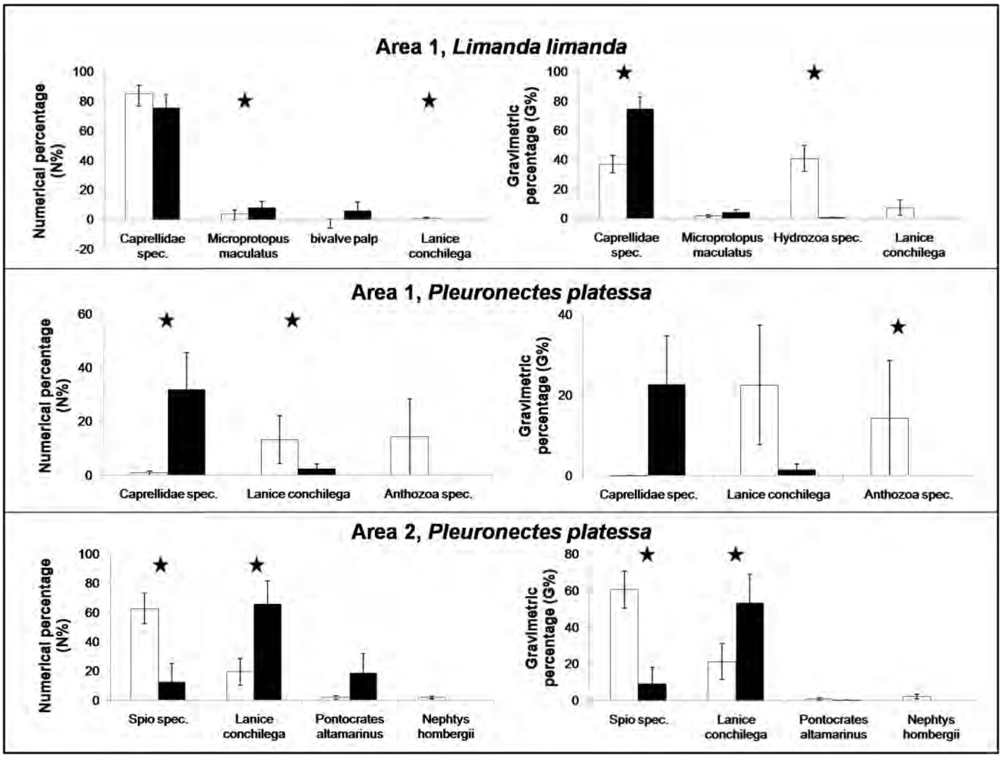

Figure 4. Prey species analyses per area and per flatfish species. Numerical (N%) and gravimetric (G%) differences for the most important prey species. Non-ecosystem engineered subzones are represented with white bars; ecosystem engineered subzones are visualized as black bars. Significant differences between habitats are indicated with a star.

Discussion

Flatfish densities and ecosystem engineered habitats

The ecosystem engineered habitats in this study attract juveniles of the flatfish species *L. limanda* and *P. platessa*. With *O. fusiformis* present as ecosystem engineer, *L. limanda* occurs at higher densities than outside the *O. fusiformis* area. The same pattern is found for *P. platessa* in *L. conchilega* habitat. Shucksmith *et al*. (2006) indicate that *P. platessa* densities correlate specifically with *L. conchilega* and *Chaetopterus* spec. Both *L. limanda* and *P. platessa* have been described before as being tightly associated with assemblages containing structuring epifauna such as hydroids, *Alcyonium digitum*, *A. diaphanum* and *Flustra foliacea* (Kaiser *et al.*, 1999b). However, no significantly higher densities of *P. platessa* age class 1 could be found in

O. fusiformis engineered areas. Flatfish species have a burial behavior to protect themselves against predation and therefore they generally avoid habitats that prevent burial (Phelan *et al.*, 2001), which suggest that the biogenic habitats investigated here provide enough refuge capacity. This is probably related to the sheltering function of the tubes itself. The generally higher densities of *P. platessa* and *L. limanda* suggest that the ecosystem engineered areas contribute with a greater proportion of individuals to the adult population than the mean level contributed by all habitats used by juveniles, regardless of area coverage. Therefore, these biogenic habitats may be considered as an 'Effective Juvenile Habitat (EJH)' (*sensu* Dahlgren *et al.* (2006)). However, the preference of juvenile flatfish for the biogenic habitats does not provide insight in the eventual survival of the juvenile flatfish species (*cf.* discussed below).

Pleuronectes platessa ***in and outside the biogenic habitat***

Whether analysed together or by geographical area (*i.e.* per ecosystem engineer), *P. platessa* has a higher fullness index within the ecosystem engineered areas. This is also reflected in the gravimetric percentage for age class 0 individuals of Area 2. The numerical percentage, however, shows a totally opposite trend. The higher gravimetric response of *P. platessa* in Area 2 is totally attributed to the predation on the ecosystem engineer concerned, *L. conchilega*. *Lanice conchilega* has previously been described as the predominant prey species of age class 0 *P. platessa* (Amara *et al.*, 2001). The higher number of prey items in areas without the ecosystem engineer was fully attributed to *Spio* spec. in Area 2. It seems that in the absence of the ecosystem engineer *L. conchilega*, *P. platessa* turns to *Spio* spec. as main prey item, which is an important item both numerically and gravimetrically. *Spio* spec. are described as positively associated with *L. conchilega* (Rabaut *et al.*, 2007), but it appears that *P. platessa* feed less on it when *L. conchilega* is available as prey. Although *Pontocrates altamarinus* is known to be negatively associated with *L. conchilega* (Rabaut *et al.*, 2007), it occurs more frequently as prey in flatfish caught in *L. conchilega* aggregations. In another study, *P. platessa* was found to be less vulnerable to predation in areas with filamentous green macroalgae in comparison with bare sand (Wennhage, 2002), suggesting that the biogenic habitats may be used as a refuge as well.

The *L. conchilega* aggregations in this study provide an important food source and relate to flatfish density. This might have consequences for growth rate as growth rate of *P. platessa* age class 0 was found to be influenced by food abundance and quality (van der Veer and Witte, 1993). These authors suggested that the differences in growth rate do not necessarily reflect competition for food, but might reflect differences in food composition and availability (searching and handling time). This particular feeding behaviour plays an important part in determining the distribution of flatfishes, though it remains unknown on which basis flatfishes select and subsequently maintain their position in their juvenile habitat (Gibson, 1997).

For *P. platessa* age class 1 of Area 1, there were no overall significant differences found, though there is an observation towards higher prey consumption in areas without the ecosystem engineer, *O. fusiformis*. Numerically, *L. conchilega* seems to be an important item outside the *O. fusiformis* engineered habitat while Caprellidea spec. were both numerically and gravimetrically much more important within the ecosystem engineered subzones. Although *L. conchilega* has been described as highly associated with *O. fusiformis* (Rabaut *et al.*, in prep.), it was not found to be important as prey item. This might be explained by the tube characteristics of this species. Hence, it is possible that juvenile *P. platessa* for reasons of food availability do select for biogenic structures created by *L. conchilega*, but not by *O. fusiformis*. On the contrary, the importance of Caprellidea spec. as prey is directly related to the presence of the *O. fusiformis* engineered habitat. These amphipod species have been observed to perform a clinging behaviour in which they attach to small-scale structures with adapted grasping appendages (Aikins and Kikuchi, 2001, Guerra-Garcia *et al.*, 2002). Therefore, they are probably easy to catch in biogenically structured habitats where there is plenty of structures to attach to. The importance of Anthozoa spec. for *P. platessa* is not very clear as the differences found are attributed to a high abundance of Anthozoan individuals in just one *P. platessa* individual.

Limanda limanda *in and outside the biogenic habitat*

Juveniles of *L. limanda* have a lower fullness index of the stomach when caught inside the ecosystem engineered habitats and a higher relative prey biomass outside the ecosystem engineered areas. The number of species in the stomach shows the inverse trend. Differences in food were mostly attributed Caprellidea spec. (higher pray biomass in ecosystem engineered subzone) and Hydrozoa spec. (higher prey biomass in non-ecosystem engineered subzone). *Microprotopus maculatus* is an important prey both inside and outside ecosystem engineered habitats, but was preyed on significantly more in the ecosystem engineered habitat. Amara *et al*. (2001) found polychaetes, hydrozoa and amphipods to be the most important prey items for *L. limanda*. They mention that in both *P. platessa* and *L. limanda* specimens, *L. conchilega* was consumed in high proportions.

Ecosystem engineer and juvenile flatfish

Overall, juveniles of both flatfish species select for ecosystem engineered habitats. This attraction can be partly explained by prey availability, which is certainly the case for *P. platessa* feeding in *L. conchilega* habitat. It has been suggested that prey availability might be the driving force for habitat selection of *P. platessa* within sandy habitats (Shucksmith *et al*., 2006). The composition and quantity of juvenile *P. platessa* gut contents varies over a small spatial scale (meters) (De Raedemaecker *et al*., pers. comm.), while food availability in the nursery areas was not found to be related to *P. platessa* densities (Pihl and Vanderveer, 1992). The intrinsic patchiness of *L. conchilega* reefs and the habitats formed by *O. fusiformis* (Rabaut *et al*., accepted, Rabaut *et al*., 2009b) is probably a key characteristic of these habitats as differences in nursery grounds could be a reflection of the spatial heterogeneity (Wouters and Cabral, 2009). For the habitats created by *O. fusiformis*, no such a relation could be found with *P. platessa*. The significantly higher densities of *L. limanda* in the *O. fusiformis* ecosystem engineered area were not explained by feeding advantage. The juveniles of this flatfish species might therefore enjoy other advantages in selecting the ecosystem engineered areas as preferred juvenile habitat. We hypothesize that juveniles of this flatfish species use the habitat as a shelter (refuge for predation) and prefer to feed outside these areas. Burying in sand provides only a partial refuge from predation (Ansell and Gibson, 1993) and the ecosystem engineering habitat may contribute to a reduced predation pressure. In this study, indications are found which suggest that *L. conchilega* aggregations are more important as feeding area for juvenile flatfish species than just proving shelter. However, as no feeding *L. limanda* juveniles have been caught in the *L. conchilega* habitat, it is not sure whether this flatfish species would profit from *L. conchilega* aggregations as food source. Surprisingly, the feeding activity of both flatfish species seems lower within the ecosystem engineered habitat, an effect that is more pronounced for *L. limanda* than for *P. platessa* which suggests there are probably multiple functions of the biogenic habitats.

Pleuronectes platessa generally prefers to consume common species and *L. limanda* utilizes any food source available (Lockwood, 1984, Wyche and Shackley, 1986). Therefore, we hypothesize in this study that the selectivity of juvenile flatfish to feed within biogenically created habitats is a result of their generally opportunistic feeding behaviour (Beyst *et al.*, 1999, Dolbeth *et al.*, 2008, Holmes and Gibson, 1983). Increasing abundances of relatively easy-to-catch prey attract these opportunistic feeders.

The present study demonstrates that biotic factors such as biogenically created habitats play an important role in juvenile flatfish distribution, being either a food source or providing shelter. These responses to biogenically created habitats only seem to occur for juveniles as in a study of different adult flatfish species (including *P. platessa*), no clear association was found between flatfish abundance, structuring epifauna, and prey availability (Hinz *et al.*, 2006).

Vulnerability towards beam trawling

Pleuronectes platessa and *L. limanda* are both commercial flatfishes that are exploited with bottom-fishing gear. These fisheries do not only have a direct impact on the adult flatfish stocks, but have also indirect effects. Bottom trawling can pose a significant threat to the integrity of complex benthic habitats, particularly those formed by sessile emergent fauna (Collie *et al.*, 1997, Kaiser *et al.*, 2000b, Rabaut *et al.*, 2008, Thrush *et al.*, 1998, Watling and Norse, 1998). For *L. conchilega* reefs, it has been demonstrated that the system degrades after one disturbance through the impact on the closely associated species (Gamarra, 2008, Rabaut *et al.*, 2008), while the whole reef system will collapse under continued high frequency disturbances (Rabaut *et al.*, subm.). The finding that bottom trawling may have a positive effect through an increase of small, soft-bodied organisms (as food for juvenile *P. platessa*) (Hiddink *et al.*, 2008b), does not hold for the ecosystem engineered habitats of this study, as it is the small bodied associated fauna that is removed by trawlers (Rabaut *et al.*, 2008). Thus, bottom trawling activities are able to reduce the suitability of the area as feeding and shelter zones to species of commercial importance (Sainsbury, 1987; Kaiser *et al.*, 1999).

The inclusion of the abundance of benthic fauna in habitat suitability models has been proven to be important in distribution predictions (Le Pape *et al.*, 2007, Nicolas *et al.*, 2007) and Ryer *et al*. (2004) suggest to incorporate considerations of emergent structures of low-relief benthic habitats that impart structural complexity into models for flatfish habitat-suitability. The important conservation stake of these biogenic systems has recently been advocated because of their particular functional value (Godet *et al.*, 2008), while it has been suggested that protection is possible under the EU Habitats Directive as habitat type 'reef' (Rabaut *et al.*, 2009b). Janssen *et al*. (2008) propose to include the surf zone in conservation management strategies, as these zones proved to be highly diverse, contains dense patches of *L. conchilega* and sustain juvenile flatfish populations. The availability of mostly less preferred habitat may decrease survival rates through increased losses to predation (Ryer *et al.*, 2004) or to suboptimal feeding. Therefore, a limitation in the extent of these emergent structures as nursery grounds could create a bottleneck in recruitment and determine the overall population size (Gibson, 1994) as mortality of late-larval and early-juvenile stages may affect year-class strength (Myers and Cadigan, 1993, van der Veer *et al.*, 1990). Competition for nursery grounds (or EJH) may therefore represent an important factor affecting the relative abundance of flatfish (Rijnsdorp *et al.*, 1990). The present study shows that small scale variability can be induced by biological factors and play indeed a significant role in the distribution of juveniles of *L. limanda* and *P. platessa*.

Conclusion

The ecosystem engineered habitats created by *O. fusiformis* and *L. conchilega* are found to be related to higher densities of juveniles of both the flatfish species *P. platessa* and *L. limanda*. These emergent structures in the flatfish nursery area are assumed to play an important role in the ecology of the juvenile flatfishes. The ecological role is explained by the provision of a food source and of shelter as refuge from predation. The ecosystem engineering shelter effect seems to be of more importance in comparison with the trophic interaction effect. The small-scale aspects of larger nursery grounds can be considered as EJH and merit attention in habitat suitability models as well as in marine conservation measures. The study confirms the particular functional value of these systems. Bottom trawling has been described to affect benthic tube worm aggregations and therefore the indirect impacts on the commercial flatfish stock need further study.

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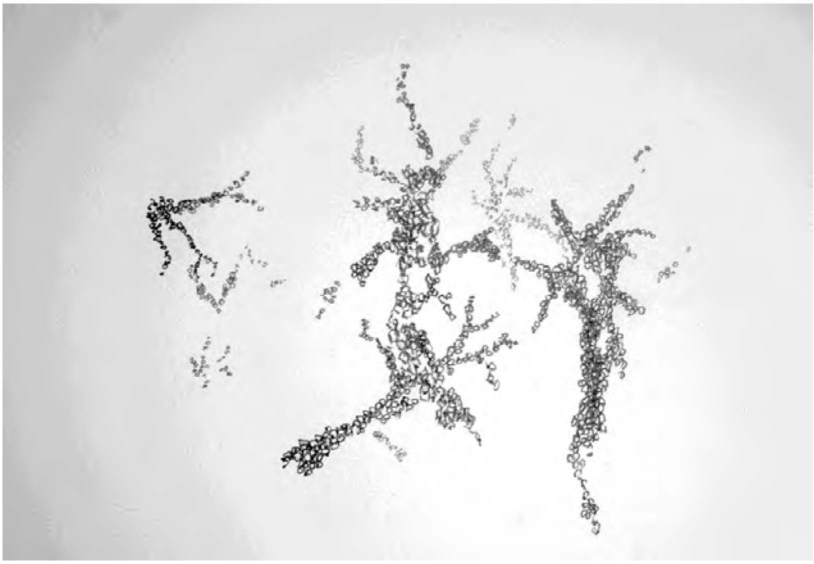
PART IV

LANICE CONCHILEGA, FISHERIES AND MARINE CONSERVATION

CHAPTER 8

Policy analysis of the 'MPA-process' in temperate continental shelf areas



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Abstract

1. The decision to designate, implement and manage marine protected areas (MPAs) is often made *ad hoc* without clear guiding procedures. This study evaluates the process of establishment and management of MPAs in temperate soft-bottom marine areas, including identification of objectives, site selection, designation, implementation, ecological effectiveness and socio-economic impacts.
2. For the first time, literature about marine conservation strategies in soft-bottom temperate areas is brought together in one 'systems approach', which is visualized in a flow chart including three phases: setting policy objectives, making decisions and evaluating the eventual effects of the MPA. Policy objectives are generally easy to identify and in most cases national policy objectives are driven by international and regional legal obligations. The decision making process is the most complex phase, as the acceptance of MPAs has to be balanced against the human activities that take place in the area.
3. 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.
4. The conceptual mapping exercise presented here serves as a basis for a systems approach for MPAs and has been tested for the Belgian coastal environment. In the Belgian 'MPA-process', the application of the systems approach proves to be useful in providing insight into the complex interactions of various authorities with scattered jurisdictions.
5. The unified and simplified representation of the various aspects is (1) a useful communication tool for policy makers and managers to inform other sectors and the public at large and (2) a valuable support system during the 'MPA-process' that considerably enhances the prospects for success.

Key words

MPA-process, policy, systems approach, fisheries, ecology, legalities, soft-bottom marine areas

Introduction

While the concept of marine protected areas has been around for centuries, the term Marine Protected Area (MPA) has been in use for only just over two decades. An MPA has come to mean different things to different people, primarily based on the level of protection provided by the MPA (NOAA, 2003). According to the World Conservation Union (IUCN, 1988) an MPA is defined as: 'Any area of intertidal or subtidal terrain together with their overlying waters and associated flora, fauna, historical and cultural features, which has been reserved by law or other effective means to protect part or the entire enclosed environment'. The level of protection of MPAs can vary from strictly protected areas to multiple use zones in which several fishing activities are still allowed. All MPAs can thus be fitted into one of the six IUCN categories of protected areas (IUCN, 1994), ranging from strictly protected areas (IUCN Category I) to multiple use zones (Category VI). However, the analysis from Wood of the MPA Global database (Wood, 2007) shows that there might be little correlation between actual protection levels and their IUCN Categories (MPA News, 2007). MPAs are one of the essential tools and approaches in the conservation and sustainable use of marine and coastal biodiversity. The designation and management of MPAs is an important objective for the parties to the 1992 Convention on Biological Diversity. A subtarget to the 2010 Biodiversity target requires that at least 10% of each of the world's ecological regions should be effectively conserved. Specifically on marine and coastal areas the parties adopted the target of developing a system of MPAs by 2012, which should be effectively managed. Moreover, MPAs are recognized as a viable tool for marine conservation by conservationists, resource managers, scientists and coastal planners. However, they are often implemented without a firm understanding of the economic, social and ecological consequences. The rush to implement MPAs has set the stage for paradoxical differences of opinion in the marine conservation community (Agardy *et al.*, 2003). Especially, the discussion to use MPAs as a mean to restore fish populations or even to increase fisheries profits is still going on and has recently been reviewed by Kaiser (2005).

MPAs have often been designated without clear guiding procedures and are too often allocated as an *ad hoc* decision in the framework of the management of natural resources, or because of international obligations. Although various MPA-studies may provide information on some significant attributes of individual MPAs, there is a lack of a simplified or unifying concept to follow during their establishment and operation. This study approaches the complex process of establishment and operation of MPAs (further referred to as the 'MPA-process') in an analytical way, including: identification of objectives, selection, designation, implementation, assessment of ecological effectiveness and socio-economic impacts. For the first time, literature on marine conservation strategies in soft-bottom temperate areas is brought together in one framework that provides answers to the questions 'why?', 'how?' and 'what is the effectiveness?' for MPAs.

Research strategy

Bringing together the available literature on various aspects of MPAs allowed 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 paper seeks to integrate research and theory about the 'MPA-process' to build a systems approach which simplifies the complexity of many real-world scenarios. This concept is tested with the inclusion of a case study of how MPAs are established, managed and have impacts in the Belgian part of the North Sea (BPNS). The BPNS is a shallow shelf area of 3600 km^2, characterized by the presence of several sandbank systems, in which a diversity in soft-bottom habitats is found (Van Hoey *et al.*, 2004). It is a well known and heavily exploited marine area with a rich marine management history where an 'MPA-process' is evolving. It is also characterized by a high institutional complexity and multi-level government. This makes it an ideal case to test the systems approach proposed here.

The current paper aims to combine the various aspects of the 'MPA-process' in temperate continental shelf areas. The first section presents the flow chart, while the various aspects of the concept are next explained in depth (for each block of the flow chart).

Table 1. Multi-level government in the BPNS and the coastal zone

<table>
<tr><td colspan="2">International obligations: conventions and commitments (2010 Target…)</td></tr>
<tr><td colspan="2">EU obligations: EU-directives (Habitats Directive…)</td></tr>
<tr><td colspan="2">Federal state</td></tr>
<tr><td>Federal competences at sea: nature conservation, protection of the marine environment, offshore windmill parks, shipping, military, etc.</td><td>Federal competences on land: contingency planning, etc.</td></tr>
<tr><td colspan="2">Flemish Region</td></tr>
<tr><td>Flemish competences at sea: fishing, dredging, etc.</td><td>Flemish competences on land: nature conservation, tourism, ports, etc.</td></tr>
<tr><td colspan="2">1 Province (West-Flanders)</td></tr>
<tr><td colspan="2">10 coastal municipalities</td></tr>
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The focus is on the legal and the ecological dimensions of the 'MPA-process' and the systems approach is tested through the application of each part of the flow chart to the Belgian coastal environment. Finally, potential bottlenecks in the systems approach are discussed as well as the value of such a flow chart for a marine management framework in temperate shelf areas.

Results

Flow chart

Based on the literature review, a flow chart (Figure 1) was built with three horizontal layers which coincide with three chronological blocks considered as phases in the 'MPA-process'. The first block on policy objectives serves as an answer to the question 'why?' and indicates that basically five different objectives exist to establish an MPA (*i.e.* commercial species conservation, reference site creation, species conservation, habitat conservation and international commitments). The second block reflects the decision making process. The number of MPAs needed, their location and size, as well as the degree of protection afforded, have all to be decided on in order to meet these objectives. The parameters for designation and the management measures need to be enshrined in a legal framework with compliance mechanisms. The establishment of an MPA always interacts with other sectors that make use of the marine environment, and consultations with other management organizations need to take place at this decision making phase. Monitoring of the established MPAs is an essential part of the MPA management, which is directly linked with the last block that evaluates the implications for both the ecology of the system and the socio-economic sectors related to the marine environment. Note that the effect of the measures implemented to reach policy objectives may require changes to (international) legislation and management strategy (dashed feedback arrows).

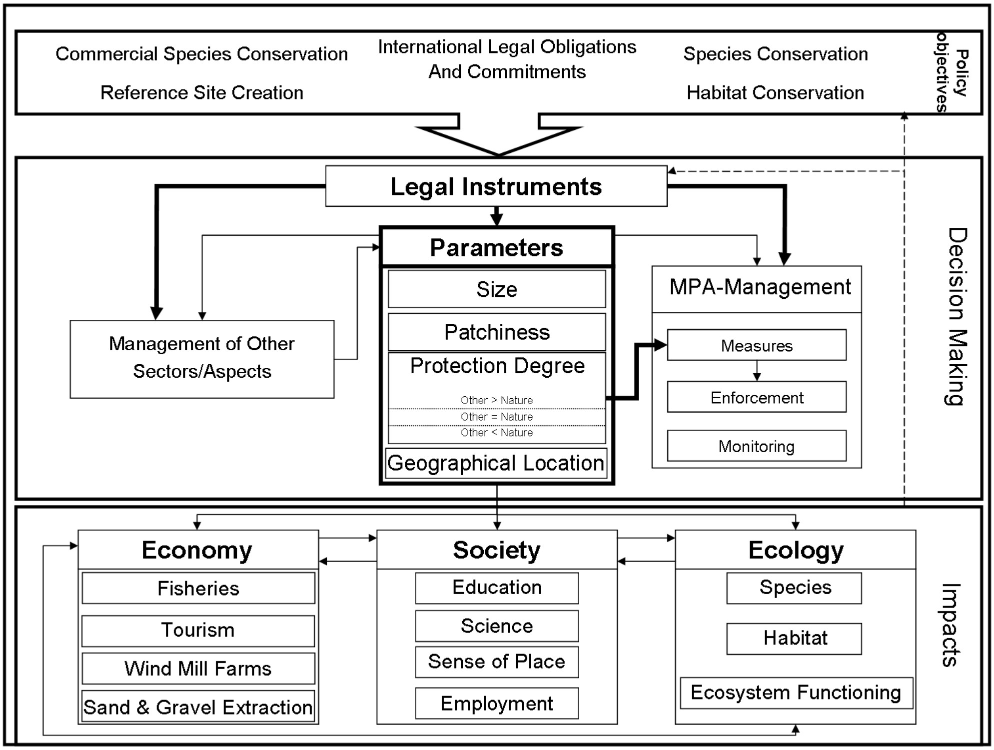

Figure 1. Flow chart as a visualization of the analytical systems approach. Three horizontal layers represent the „MPA-process' over time. This approach starts with the identification of the policy objectives (five different objectives exist). The designation and management scheme are settled during the decision making phase, in which there is also consultation with the management of other sectors. Established MPAs are expected to have an impact on the socio-economic activities of the concerned area as well as on the ecology of the system. This systems approach helps to analyse and evaluate the „MPA-process' in soft-bottom marine areas.

Systems approach and case study as test

Policy objectives

Concept

Policy objectives are commonly associated with habitat and species conservation. In such cases, indicator species are most often used (Kabuta and Laane, 2003). In general, surrogate species (*i.e.* flagship, focal, keystone, indicator and umbrella species) have been recognized as legitimate conservation targets on their own (Favreau *et al.*, 2006) as well as being effective in the selection of networks of areas for conservation (Larsen *et al.*, 2007), although this might cause some difficulties, especially in the marine environment (Rees *et al.*, 2006). A specific way of selecting species for conservation is valuing them according to their commercial value, although this has mostly no connection with their function within the ecosystem (Norton and Noonan, 2007). The policy objective of conserving a pristine environment is valuable in complex ecosystems with a low disturbance level (Pauly *et al.*, 2002), but is not very useful in temperate coastal shelf areas. Therefore, a policy objective that is feasible in these areas is to create a reference site. International legal obligations and commitments are considered here as policy objectives.

Belgian case

Belgian policy objectives are mainly the result of international obligations to protect and restore marine habitats, accepted in international and regional conventions such as the 1971 Ramsar Convention on Wetlands of International Importance, especially as Waterfowl Habitat, the 1992 OSPAR Convention for the Protection of the Marine Environment of the North-East Atlantic, the 1992 Convention on Biological Diversity and at the EU-level, the Directive 79/409/EEC on the conservation of wild birds, and the Directive 92/43/EEC on the conservation of natural habitats and of wild fauna and flora.

Belgium has to comply with international commitments on the designation and management of MPAs to establish a representative system of MPAs by 2012 (e.g. World Summit on Sustainable Development; Biodiversity Convention). At the EU level, several commitments have been made regarding conservation of marine biodiversity. The objective of the EU

Biodiversity Action Plan (European Commission, 2006) is to complete a network of marine Special Protection Areas (SPAs) by 2008 and Special Areas of Conservation (SACs) by 2012, for which management and conservation measures have to be established by 2012. The Belgian policy objectives focus on the protection of certain bird species and their habitats, obtaining a favourable conservation status of marine habitats, avoiding deterioration of habitats and disturbance of species and conserving the ecosystem function of the marine habitat. The objective to create a reference site was included in the first preparatory documents in the designation process (Vande Lanotte, 2004), but was eventually withheld from the legislation as a formal objective. The conservation of commercial species is not explicitly mentioned as a policy objective, although conservation of the marine habitat can include this as an implicit objective. Thus, four out of five policy objectives that were identified in the conceptual framework are included as Belgian policy objectives.

Decision making

Concept

After setting clear policy objectives, decisions to designate an appropriate area and to take appropriate management measures have to be made. The various aspects of this phase are based on legal instruments. Four basic parameters have to be decided on during the decision making phase: location, size, patchiness and degree of protection. As an MPA is a spatial management tool, the first three parameters are obvious and include a decision in the 'single large or several small' (SLOSS) dilemma (Baz and Garcia-Boyero, 1996, Simberloff and Abele, 1976). Site selection for a representative system of MPAs requires a biogeographic classification system (Hockey and Branch, 1997). This systematic selection of habitats starts with the abiotic environment, including morphological features, sediment conditions and water circulation. Afterwards, data generated with new research techniques can be supplemented (Rachor and Gunther, 2001), e.g. with side-scan sonar surveys (Degraer *et al.*, 2008a) and modelling exercises (Willems *et al.*, 2008). The size of an MPA has been discussed by several authors; according to Rachor and Günther (2001), a coherent network of MPAs in the German Bight could be achieved, if MPAs were not to be more than about 100 km apart. Furthermore, with a possible larval displacement of 10 km within 2-3 days, minimum areas of about 100 to 200 km^2 should be designated for successful protection. MPAs should be designed large enough to contain short-distance dispersing propagules and placed far enough apart so that long-distance dispersing propagules released from one reserve can settle in adjacent MPAs. A reserve of 4-6 km in diameter should be large enough to contain the larvae of short-distance disperses, and MPAs spaced 10-20 km apart should be close enough to capture propagules released from adjacent MPAs (Shanks *et al.*, 2003). The optimal size of MPAs should, however, be determined for each location by evaluating conservation needs and goals, quality and amount of critical habitat, levels of resource use, efficacy of other management tools, and characteristics of species or biological communities requiring protection (NRC, 2001). Hastings and Botsford's (2003) modelling exercise clearly shows the direct influence on the parameters to be chosen by decision makers. The model predicts that biodiversity goals will be reached with a single large reserve that is spacious enough to be self-sustaining. The required size is determined by the mean dispersal distance of the species and the required recruitment level. Then again, the model points out that MPAs as small as practically possible will meet the fisheries goals, because of enhanced larval export. A reserve network is a possible solution to these conflicting policy goals. Alongside the spatially defined parameters, the degree of protection must be settled during the decision making process. According to van der Meulen and de Haes (1996), three different degrees of protection are important: (i) areas primarily designated for other functions, where nature is 'supporting'; (ii) areas where nature conservation is equal to other functions; and (iii) areas primarily established for nature, including functions that are directly derived from this, such as ecotourism.

The setting of the parameters will influence the future management of the MPA itself as well as the management of other activities at sea. These activities may involve conflicting interests and include the following sectors or aspects: pollution (Jameson *et al.*, 2002), eutrophication (Ospar-Commission, 2000), dumping and dredging (Bergman *et al.*, 1991, Rachor and Gunther, 2001), oil/gas transport (Bergman *et al.*, 1991), navigation (Maes *et al.*, 2000), wind mill farms, fisheries effects (Lindeboom, 1995) and coastal defense (Kelleher, 1999).

The final part in the decision making process is the establishment of a management system for the MPA concerned. Wood (2007) estimates that MPAs cover about 0.6% of the world's oceans, of which 71% appear to have no active management (Pet and Mous, 2002). The management of an MPA should be based on several measures that are coupled to the degree of protection (as defined during the parameterisation). The period between reviews should be neither so short that lack of resources is a problem, nor so long that the management is not responsive (Kelleher, 1999). Restriction of (existing or potential) activities with a severe impact is the most applied way to improve or conserve the ecological value of a marine area. To carry through such restrictions, a business planning approach adapted to MPA-management has been proposed (Jameson *et al.*, 2002). With this approach, managers focus on the viability of the management system, *i.e.* the ability of the MPA to provide ecological goods and services to its target users over the long term. Besides, MPA-management should understand the participants involved in the management of other activities at sea. Collaborative management has been argued for as a possible model to use (*i.e.* stakeholders jointly manage the MPA with the conservation agency) (Kelleher, 1999), but Beem (2007) points out that the process of developing institutions for co-management is lengthy and time consuming. Chuenpagdee and Jentoft (2007) focus on what happens before the actual decision to implement a co-management system and they show that this 'step zero' is an important factor for ultimate success. They point out that this pre-implementation period can be very lengthy and that there is a certain degree of muddling through before successful co-management is achieved. It is clear that at least consultation with other interested parties at sea is necessary during the decision making process. The third aspect of MPA-management is monitoring (Figure 1). Out of 1306 MPAs surveyed world-wide by Kelleher *et al.* (1995), only in 31% of the areas did the managers think that they achieved their management objectives. To make MPA-management successful and adaptive, a periodic revision of the management is needed on the basis of ecological monitoring.

Belgian case

The federal Act on the protection of the marine environment (Act of 20 January 1999, amended by Act of 17 September 2005) is the basic legal instrument for the specific 'MPA-process'. This Act enables the designation of MPAs in Belgian marine waters (including the territorial sea and the exclusive economic zone). Five types of MPAs have been distinguished in the Act: integral marine MPAs, specific marine reserves, Special Protection Areas (SPAs) and Special Areas of Conservation (SACs), closed zones and buffer zones (Cliquet and Maes, 1998). Although the degree of protection of these MPAs might differ, all of them will probably fit into IUCN Category IV or VI. The requirements for IUCN Categrories I, II, III and V, such as size and ecological integrity, can probably never be met for Belgian MPAs. Only the marine reserves and SPAs/SACs are relevant for the focus of this paper. While marine reserves are, in principle, the areas most strictly protected, SPAs and SACs give implementation to the EU Birds and Habitats Directives respectively. After some failed attempts to designate marine reserves in the period 1999-2003 (Bogaert *et al.*, 2008, Bogaert *et al.*, 2009), several SPAs and SACs were designated by Royal Decree of 14 October 2005. A Royal Decree of 5 March 2006 designated the specific marine reserve the 'Baai van Heist'.

In the BPNS, different areas for marine protection have been designated implying that the geographical features (size, location, patchiness) were parameterized. Three areas along the coastline (Figure 2) were designated for the protection of birds (SPAs), with surface areas of 110.01 km², 144.8 km² and 50.95 km² respectively. Another two areas for the protection of habitats (SACs) were established: 'Trapegeer-Stroombank' (SAC 1), parallel along the West coast with a surface area of 181 km² and 'Vlakte van de Raan' (SAC 2) at the East coast with a surface area of19.17 km². These two SACs have the necessary surface and distance to each other (28 km) to be considered biologically linked (*cf. supra*). The specific marine reserve 'Baai van Heist' is a very small reserve of only 6,76 km² adjacent to a Flemish beach nature reserve (Figure 2).

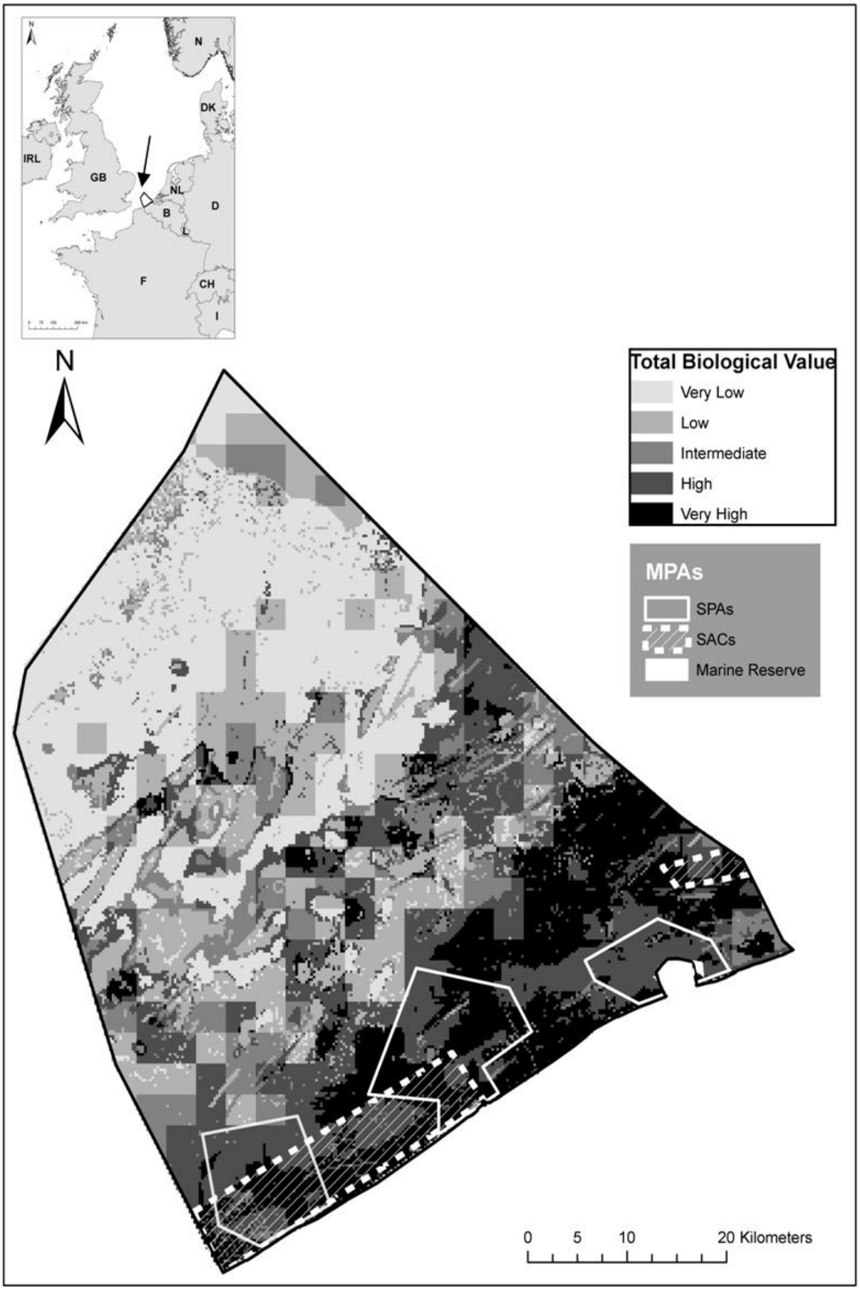

Figure 2. Location of the Belgian Part of the North Sea (BPNS) (left above); BPNS with indication of total biological value (adopted from Derous et al.*, 2007b) and the different MPAs (SACs, SPAs and the marine reserve „Baai van Heist').*

This parameterisation was based on the policy objectives of species and habitat conservation (which coincides with the fulfilment of international obligations). The present study evaluates whether the designated MPAs coincide with the areas hosting the most valuable species and habitats using the concept for biological valuation in marine environments proposed by Derous *et al*. (2007). This valuation strategy uses several valuation criteria other than the commercial value: namely rarity, aggregation, fitness consequences, biodiversity, naturalness and proportional importance. The strategy was subsequently tested for the BPNS (Derous, 2007) in which data of macrobenthos, sea birds, epibenthos and demersal fish were combined. The overall valuation map is shown in Figure 2, on which the different designated protected areas (SPAs and SACs) are superimposed. To evaluate the location of the SACs, the macrobenthos valuation map is used because this species group is most often used to typify temperate soft-bottom habitats (Van Hoey *et al.*, 2004). The highest biological value for macrobenthos was found near the coast, especially near shore in the western coastal area and diverging away from the shore line in the eastern coastal area. Other valuable areas for macrobenthos seem to be further offshore (Figure 3a). The high value of the coastal area mostly coincides with the presence of the *Abra alba* community. The most valuable areas for birds are represented in Figure 3b, with the three SPAs overlain the map. The valuation map clearly shows the high ornithological value of the coastal zone ('Vlaamse Banken', 'Zeelandbanken', 'Vlakte van de Raan'). This zone has long been recognized as being important for seabirds on the BPNS both as foraging area for breeding birds and for wintering birds (Haelters *et al.*, 2004, Seys, 2001, Seys *et al.*, 1999, Stienen and Kuijken, 2003).

The fourth parameter (degree of protection) was built on the reasoning that the designated areas have to be protected against potential impacts of future activities. Hence, current activities within the MPAs were not perceived as a threat to reaching the objectives. Specific conservation goals for each MPA have not yet been set, although several measures have been taken. Within the SPAs and SACs, the following activities are prohibited: all building activities, industrial activities and activities of commercial and advertising enterprises. In the SACs, the dumping of dredged material and inert materials of natural origin is also forbidden. In SPA 1 and SPA 2, common tern, sandwich tern, little gull and great crested grebe are protected.

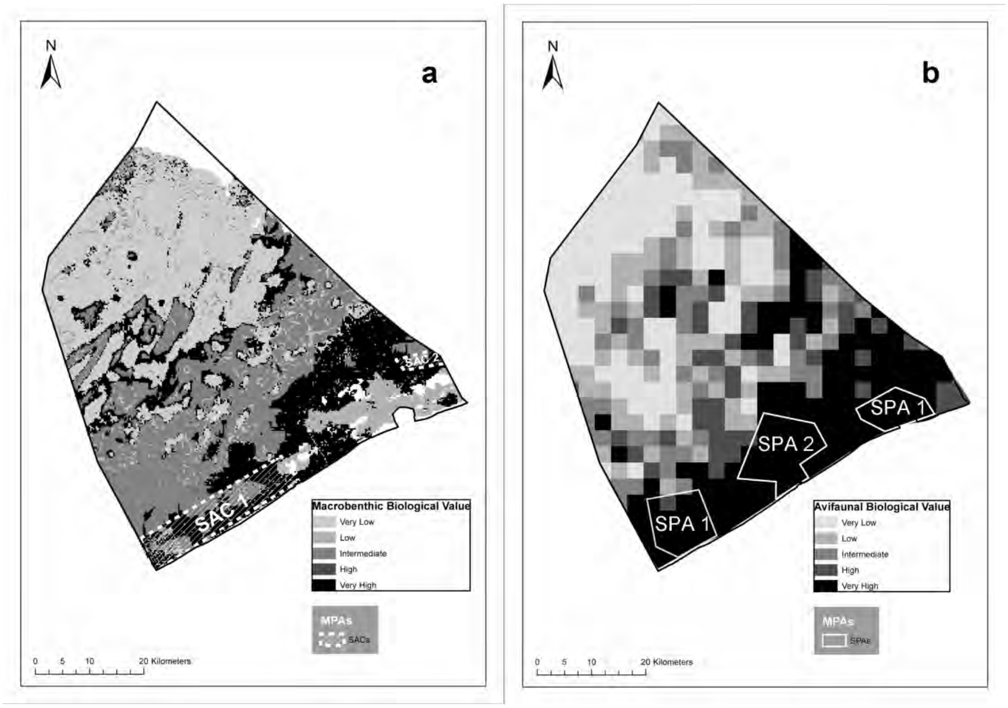

Figure 3. The BPNS with indication of the macrobenthic biological value (adopted from Derous et al.*, 2007b) and the Habitats Directive areas (SAC 1: „Trapegeer-Stroombank' and SAC 2: „Vlakte van de Raan') superimposed (a); the BPNS with indication of the avifaunal biological value (adopted from Derous et al., 2007b) and the Birds Directive areas (SPA 1, SPA 2 and SPA 3) superimposed (b).*

During winter, helicopter flights at altitudes of less than 500 ft and the passage of high speed vessels and offshore water sports are forbidden. The Minister of Environment can consult with the Minister of Defence on the planning of military firing exercises and other military activities. For the 'Baai van Heist', there is an in-principle, legal, strict protection regime forbidding all activities, except those explicitly allowed by Act or royal decree. This list of allowed activities, however, is rather extensive: surveillance and control, scientific research and monitoring, military activities, sea fisheries, pilotage, rescue and towing services, dredging, laying and maintaining of cables and pipelines, the digging of trenches and raising of the seabed, and those activities that are mentioned in the voluntary user agreements. Since all these different activities can still continue, the marine reserve and the SACs and SPAs in the Belgian marine environment can all be categorized as IUCN Category IV. For all MPAs, voluntary user agreements can be concluded with user groups such as sailing clubs, fishermen, etc., moreover, a policy plan must be formulated within three years after the designation of the site. Furthermore, an appropriate assessment has to be designed of all new plans and projects that are likely to have a significant effect on the site in view of the site's conservation objectives. A new plan or project can only be allowed if it does not adversely affect the integrity of the site concerned. In case of a negative assessment, the plan or project can only be allowed under certain strict conditions as provided in the royal decree (which implements Article 6 of the EU Habitats Directive).

Impacts

Concept

Once an MPA has been designated and implemented, this will have implications at the economic, social and ecological levels (Figure 1). In a simulation model, Martinet *et al*. (2007) examine the viability of fisheries and point out that economic, social and biological constraints have to be included to achieve sustainability. Ecological impacts relate to species gain/mortality and habitat recovery/destruction. These impacts depend greatly on the degree of protection and on the eventual measures taken. Within-MPA mechanisms might impact the outside-MPA area. This influence can be both on the ecosystem of the surrounding areas as well as on areas further off (Gell and Roberts, 2003). In temperate soft-bottom areas, the ecological status of benthic life is important. Benthic densities and species richness are heavily determined by the seabed characteristics (mainly sediment types) (Bergman *et al.*, 1991, Van Hoey *et al.*, 2004, Vanaverbeke *et al.*, 2000) and this benthic productivity is important in determining the densities and species richness of higher trophic levels such as demersal fish (Cabral, 2000, Langton and Watling, 1990, Molinero and Flos, 1992, Rijnsdorp and Vingerhoed, 2001) and birds (Cramp and Simmons, 1977, Degraer *et al.*, 1999, Van Waeyenberge *et al.*, 2001, Von Blotzheim and Bauer, 1968, 1969). Protection of keystone habitats and key species therefore leads to an enhanced settlement and recruitment of demersal fish, providing an increased biomass and spawning activity as well as changing age class structure. If the age/size of the stock residing within the protected areas increases and fecundity increases with age/size, then it is possible that the abundance of larvae in the system can increase dramatically after establishment of the MPA. The increased spawning activity leads to an enhanced reproductive output and could possibly end in a growth in larval export. Increasing densities and biomass ultimately can result in spill over to the adjacent fishing ground (Gell and Roberts, 2003, Kelleher, 1999, Pet and Mous, 2002, Pezzey *et al.*, 2000, Roberts *et al.*, 2001, Sainsbury and Sumaila, 2002, Sanchirico, 2000). The most important economic impacts of MPAs that can be expected in a soft-bottom temperate area are on sectors such as sand and gravel extraction (Rachor and Gunther, 2001), wind mill farms (Rachor and Gunther, 2001), tourism (Davis and Tisdell, 1996, Kelleher, 1999, UNEP, 2002) and fisheries (Hastings and Botsford, 2003, Pezzey *et al.*, 2000, Piet and Rijnsdorp, 1998, Sanchirico, 2000). Fisheries are generally recognized as the major critical factor for an MPA to succeed or fail (Kelleher, 1999). Kaiser *et al.* (2002) describe how productivity is decreasing as fishing intensity increases and high-biomass species are being removed from the benthic habitat. Moreover, the fishing industry is an economic sector that is active in large areas and is the basis for the strongest opposition to marine protection. This is attributed to people from the fisheries sector being anxious that reducing the area of fishing grounds will mean a decrease in catches.

Fishing with mobile fishing gear is known to be a major cause of habitat deterioration in many soft-bottom ecosystems (Dayton *et al.*, 1995). Jennings *et al.* (2001b) investigated the impact of trawling on benthic communities. They found that total biomass of infauna and epifauna significantly decreased with trawling disturbance. There is evidence of damage and mortalities in invertebrates in trawl nets (Bergman and Hup, 1992, Brylinsky *et al.*, 1994, Kaiser and Spencer, 1996, Schratzberger *et al.*, 2002, Witbaard and Klein, 1994).

Moreover, trawling has the capability of altering, removing or destroying the complex, three-dimensional physical structure of benthic habitats by the direct removal of biological and topographic features (Turner *et al.*, 1999). When looking specifically at soft-bottom areas, locations with biogenic structures are proven to be vulnerable to fishing impacts (e.g. *Pectinaria (Lagis) koreni* (Bergman and van Santbrink, 2000)). Chronic fishing disturbance may be sufficient to severely reduce the complexity of such habitats by removing the fragile sessile fauna (Collie *et al.*, 1997, Thrush *et al.*, 1998), reducing the suitability of the area to species of commercial importance (Kaiser *et al.*, 1999a, Sainsbury, 1987). For epifauna, a general decrease in sessile larger bodied species was observed, while more resilient, mobile fauna increased along with increasing fishing disturbance (e.g. Kaiser *et al.* (2000b)). A conceptual model of Auster (1998) demonstrates that fishing gear significantly reduces habitat complexity for most habitats, except for gravel areas with high current velocities where little settlement of epifauna occurs.

Belgian case

Figure 3 shows that the protected areas are allocated in areas that have a high biological value. The spatial parameters were chosen (i) to give the biologically most valuable areas a protected status (Figure 2 and 3) and (ii) to avoid some negative economic impacts (Figure 4). The areas where wind mills are allowed lie outside the protected areas and there has never been aggregate extraction in the protected areas as the grain size of the sediments in these areas is not valuable. The current protection measures inside the areas were explicitly chosen not to harm the only real economic activity taking place here, namely fisheries, which is the sector expressing the strongest opposition to marine protection. Reducing fishing effort is a decision that creates political difficulties as it has far-reaching, short term, social implications (Smith, 1995). Moreover, in Europe and North America, it is a sector that has been receiving significant public support, even when it is economically not significant (Steele and Hoagland, 2003), e.g. the fisheries sector in Belgium represented only 0.02% of the GNP in 2002 (National Bank of Belgium, Alex Hermans personal communication) and most fishing activities take place outside the BPNS.

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, Rabaut *et al.*, 2007, Van Hoey, 2006) and *Owenia fusiformis* (Rabaut *et al.*, in prep., Somaschini, 1993) 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).

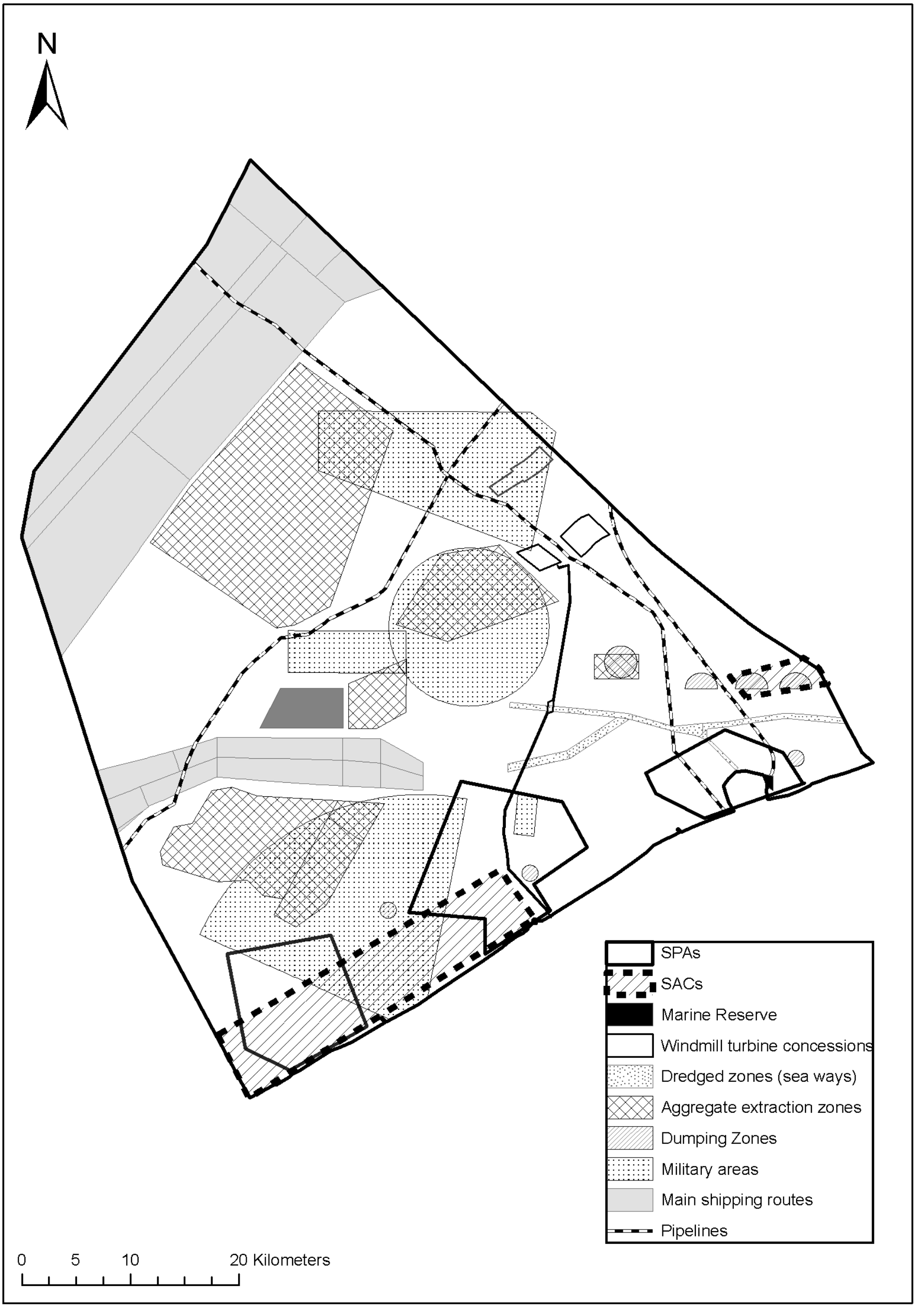

Figure 4. The BPNS with indication of both the allocated areas for different human activities (adopted from Maes et al., 2005; updated) and the allocated MPAs.

Discussion

Policy objectives

It is very likely that there would be far less interest in MPAs without current international legal obligations and commitments as demonstrated in Belgium where almost all designated areas have been established in the framework of the European Natura 2000 Network. This requires species and habitat conservation to be the fundamental objective of MPA establishment whilst the conservation of commercial species is considered a potentially indirect additional benefit, rather than a separate objective for MPA designation. The objective to create reference sites through MPAs was eventually not included in the Belgian legislation.

Decision making

The demarcation of MPAs in Belgian marine waters has been based on ecological information. Combining the biological valuation maps, produced by Derous (2007), with the designated Belgian MPAs, the parameterisation is concluded to be fairly well adapted to affect or conserve the ecology of the system in a potentially positive way. The main objective concerning the management of the MPAs uttered by the North Sea Minister (Vande Lanotte, 2004) was to safeguard them from future threatening activities (such as building of artificial islands etc.). The existing activities were considered to have no significant impact or belong to another level of competence, which cannot be dealt with within the framework of the Act on the protection of the marine environment (*cf. infra*). Nevertheless, consultation with the responsible authorities and stakeholders of other sectors took place. For sand extraction and offshore energy production demarcation zones outside the current MPAs were defined. In spite of this consultation, one energy firm (Electrabel) started a legal procedure for the Belgian Council of State to file a complaint against the designation of the 'Vlakte van de Raan' as SAC, because the withdrawal of an earlier environmental permit for building an offshore windmill farm in that area. The energy company asks for the annulment of the designation decision. In February 2008, the Belgian Council of State annulled the decision on the designation of the 'Vlakte van de Raan' as an SAC (*cf. post scriptum* below), because of insufficient motivation. Furthermore, the MPAs are not completely safeguarded against future activities as projects with a significant impact on the site can be allowed under certain conditions (in legal conformity with article six of the EU Habitats Directive and the Belgian legislation, *cf. supra*). Since absolute prohibition of only a few activities exists and certain activities can be allowed under limited circumstances, an inadequate protection regime might be the resulting practice.

Mobile fishing gear has a significant impact on the ecology of benthic systems (*cf. supra*). Therefore, it is surprising that there was no cooperation with the fisheries management, leading to the situation where none of the existing fishing activities have been restricted in the designated MPAs, not even within the two SACs. Social implications make it politically delicate to restrict fisheries and this probably explains in part why no fisheries restrictions currently exist for the Belgian MPAs. Furthermore, the federal government has only limited competence in this matter due to the state structure. The Belgian North Sea policy is divided over several institutional levels with the federal level and the regional level (Flemish Region) the most relevant. In this regard, the federal government has authority over environmental policy and protection of the marine environment, wind farms at sea, shipping, military activities, aggregate extraction, cables and pipelines. The Flemish Region is responsible for policy areas such as nature policy on the beach and the hinterland, recreation, ports, fishing, dredging, piloting and coastal defence. The Act on the protection of the marine environment states that the federal government cannot limit or restrict activities within the MPAs that are the competences of the Flemish Region. Thus, despite having competency over marine nature conservation, the federal government cannot deal with several activities affecting this competence (e.g. fisheries). Although the original Act of 1999 included the possibility to limit fisheries within marine reserves, the federal government amended the Act in 2005, excluding this option. This legal change was motivated on constitutional grounds, but is legally debatable (Cliquet and Bogaert, 2006). Consequently, if the conservation of the MPAs requires a limitation on fisheries, the Flemish government has to take decisions. As in Belgium no structural cooperation regarding marine issues exists (Cliquet *et al.*, 2004), solutions to this problem are more difficult.

Assuming that the political will exists to ban activities such as trawling in MPAs, the relation with the fisheries policy of the European Community (EC) is likely to cause additional problems. Fisheries belong exclusively to the competence of the EC, within the framework of the Common Fisheries Policy (CFP). The principal text is Council Regulation (EC) N° 2371/2002 of 20 December 2002 on the conservation and sustainable exploitation of fisheries resources under the CFP. Environmental issues on the other hand, are shared between the EU and the member states. Furthermore, the EC Treaty requires that environmental matters are integrated into other policy domains, such as fisheries. It is not clear to what extent the member states have legal authority to take measures for the restriction of fishing activities within the framework of marine nature conservation, and whether such measures can be taken through the CFP. Four possible options exist: 1. fisheries can only be restricted by the EC within the framework of the CFP; 2. fisheries can also be restricted by member states within the framework of the CFP; 3. restrictions to fisheries as a tool for MPA protection is seen as a nature conservation measure and is taken by the individual member state; 4. nature conservation measures are taken by the EC.

The European Commission's position is that fisheries management measures should be decided in the context of the CFP, given the fact that fisheries is an exclusive Community competence. This also applies to measures regulating fishing activities to protect a Natura 2000 site (European Commission, 2007). However, it could be argued that the limitation of fisheries, solely for the protection of a habitat or species, is an environmental regulation. In such a case, measures can be taken by either the EC or by member states as part of their environmental policy. The final decision of the appropriate legal basis will eventually have to be taken by the European Court of Justice. Until now, there is no clear case law that provides the appropriate legal basis for fisheries measures, as a nature conservation tool (Owen and Chambers, 2004).

If limitations of fisheries in MPAs have to be taken within the framework of the CFP, then the question remains whether member states have some competence to take those measures. According to the Fisheries Regulation, the member states have some powers to regulate fisheries, be it within the context of the CFP. These measures are, however, limited in time or space and are considered as being too limited to fulfil the requirements under the Birds and Habitats Directives (Owen, 2004). Moreover, it was stated recently that a development of a longer-term EU management view, including the reconciliation of fisheries and conservation objectives is necessary to reach sustainability in the marine environment (Hiddink *et al.*, 2008a).

Both MPA-management and management of other sectors (e.g. fisheries) are regulated at local as well as at international levels. The international character of marine areas together with the complex relationship between habitat deterioration and commercial fisheries make it difficult to define responsibilities in the broader framework of marine ecosystem management. The application of the systems approach for the Belgian coastal environment was useful to identify the difficulties in the decision making process, mainly because of competences that are scattered over the international, national and regional regulations.

MPA-management often lacks a thorough monitoring programme which makes it difficult to assess the effect of an MPA. Although in Belgium there is a legal obligation for permanent monitoring in the MPAs, there is no specific monitoring programme yet.

Impacts

The ecological impacts of an MPA are expected to be positive and evaluation should be coupled to the defined policy objective. This evaluation approach should be undertaken regularly based on a monitoring scheme. As fisheries appear to be an important issue with regard to both ecological impacts and at the decision making level, it is probable that the policy objectives –especially the habitat conservation objective- are difficult to comply with. On the one hand, some authors point out that habitat destruction might not be a major cause of decreasing fish populations, as they refer to the natural variability in fish populations that generally occurs on a time scale of decades, which is similar to that for technological improvements in fisheries (Steele and Hoagland, 2003, 2004). Overexploitation is then caused by the 'ratchet' effect described by Ludwig *et al.* (Ludwig *et al.*, 1993): unlike natural predator populations, which generally respond to declines in their food sources with rapid declines in population size, fishing fleets do not rapidly shrink in response to diminishing prey. This viewpoint is still under discussion (Zeller and Russ, 2004). On the other hand, beam trawl impacts on habitats have been observed and areas with a more complex biogenic structure and higher biodiversity, such as high density patches of tube dwelling polychaetes, are known to suffer from beam trawl activities.

Certain stakeholders such as fishermen may perceive economic impacts of MPA implementation to be negative. Nevertheless, the real economic impact on fisheries in Belgium would probably be low, as the economic value of the sector is very low. It is, however, important to mention that after a closure for fisheries inside an MPA, congestion on the remaining areas may occur (which can lead to gear conflicts and shifts to other target species), in the search to regain the economic loss for reduced fishing grounds. This may lead to sweeping environmental degradation outside the MPAs. Direct social implications relate to the restricted economic activities and its effects on employment, be it on a very local scale. Other social aspects relate to the opportunities that arise for scientific and educational purposes and to non-use values such as sense of place. These social impacts of MPAs are important for the public support for measures and require due attention. This debate, however, is beyond the scope of this article.

Conclusion

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. Policy objectives are easy to identify and relate in many cases to international legal obligations and commitments. The decision making process is the most complex phase during the MPA-process, as management of the MPA and that of other sectors are regulated both at a local and on an international level. Most difficulties arise because of the relation between fisheries and MPA-management. Not only conflicting interests, but also institutional differences are important bottlenecks in most cases. Although legal instruments are often established as a basis for the decision making process, they are generally weak as several competences are located in other sectors and/or other (international or regional) administrations. Monitoring programmes are necessary to evaluate the effectiveness of MPAs, but are often non-existing (‘paper MPA’). The ecological impacts are a measure to quantify the effectiveness of the MPAs, while economic impacts have to be managed through consultation during the decision making phase. Activities limited in space and reliant less on biological production are easier to manage (e.g. offshore energy production and aggregate extraction) than fisheries. Social implications for MPAs are generally important to create a public support for MPA-measures. The ‘MPA-process’ in the

Belgian coastal environment proves to be very difficult, such that reaching the policy objectives with the current (legal) system is highly unlikely. In Belgium, difficulties occur with the integration of fisheries management into the MPA-management. Not only the more common challenges such as social implications of fisheries restrictions and the international fisheries regulations, but also the complicated system with dispersed competences between the different authorities fuels conflict. Therefore, MPAs designated in the Belgian waters can, at best, be considered as 'structural paper MPAs' in which it will be difficult to implement an MPA-management regime that has the desired impacts at socio-economic and ecological level. However, the application of the systems approach proved to be useful in providing insight into the complex interactions during the 'MPA-process', especially during the decision making phase. The conceptual flow chart visualizes a systems approach for the complex 'MPA-process'. This unifying concept is useful for policy makers and managers (1) as a communication tool to inform other sectors and the public at large and (2) as a backing during the 'MPA-process' that considerably enhances the prospects for success.

Post scriptum. The MPA-process is a very dynamic process. This is again shown in the Belgian case in which very recently the Belgian council of State annulled the designation of the SAC 'Vlakte van de Raan' following the complaint of Electrabel (see discussion). Currently, it is unclear what the consequences of this decision will be and if and when the federal government will re-designate this area as an MPA.

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CHAPTER 9

The dynamics of the marine environment versus the rigid interpretation of nature conservation law

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Abstract

Dynamics in the marine environment tend to be orders of magnitude higher than their terrestrial counterparts. The functioning of marine ecosystems depends on these high dynamics and takes therefore place at vast geographical scales. Furthermore, oceans and seas seem to be quite prone to be affected by global climate change. As marine ecosystems are threatened, conservation strategies are set out in international policy to face the large scale of the ecosystem. However, not only the scale is important to manage marine ecosystems, also ecosystem dynamics should have a prominent place in the strategies. Present chapter points out the risk of applying an (international) environmental law system in a narrow way, leading to a slow decision making process and the inflexibility of management programs. This strict interpretation of international legislation is therefore expected to fail in its aim of implementing a sustainable use of the sea. The Belgian case is developed as an example, pointing out that international (EU) legislation is too rigidly interpreted and decelerates the implementation rate. During the policy process of MPA-designation, objection was given to the protection of particular tube worm aggregations. The reluctance of protecting important reef structures is amongst others due to the fact that interpretation of nature conservation law is related to difficulties in adapting to natural developments that are not easy to predict or to model. So far, application of nature conservation law has been rather static. This is well illustrated in this chapter with the case study on the Belgian part of the North Sea. Nonetheless, in the case of the EU Habitats Directive, a more flexible approach is possible and needed. We therefore advocate a robust though flexible interpretation of environmental legislation in the marine environment, especially because a changing climate is altering the environment in an even more profound and more unpredictable way. We acknowledge this is a difficult exercise, as there is a risk of undermining the final goal of environmental legislation if increasing flexibility would be translated into looser protection.

Key words

Marine ecosystem, environmental legislation, dynamics, Habitats Directive, reef, 1170, *Lanice conchilega*

Introduction

Dynamics of the marine environment

The marine environment is defined by different marine ecosystems in which physical, chemical and biological components are equally important in defining total system properties. Far more pronounced than in terrestrial systems, physical processes create the conditions for many important biological processes. The dynamics of the marine environment are therefore defined by a subtle and complex interplay between physical and biological processes. The geographical scale at which biota can act and range from microns to thousands of kilometres is defined by the physical processes. Nonetheless, the temporal scale of most processes seems much more determined by biota rather than by physical features. Interactions between physics and biology, however, do not entirely, or even mainly, take place in one direction (Mann and Lazier, 1991). It is particularly difficult to develop concepts and models that span this enormous range of scales and possibilities. Ecological succession is still a theme that is poorly documented in many marine ecosystems, while it is probably of far higher importance for the biodiversity and the ecosystem functioning than in terrestrial systems. The Intermediate Disturbance Hypothesis was originally developed for tropical forests by Connell (1978) but has also been tested in aquatic environments (Padisák *et al.*, 1993). It predicts a decrease in diversity along succession. Ecological succession is a fundamental concept in ecology and refers to more-or-less predictable and orderly changes in the composition or structure of an ecological community, resulting from (1) the ability of species to recruit and (2) interactions between early and later colonists (Clements, 1916, Connell and Slatyer, 1977).

Need for protection of the marine environment

International law does not always have a very compelling status as a recent report from the European Environment Agency (EEA, 2009) sounds the alarm that most species and habitats across the continent are in poor condition and the risk of extinction continues to rise. The European Commission is failing to meet a pledge to halt biodiversity loss by 2010. Individual states are often reluctant to embrace a sound conservation strategy and are not really concerned about ecological networks. They rather implement the international obligations in a vague and/or a rigid manner. The focus is most often on the protection of the human activities and there seems to be no willingness to work with the ecosystem approach. Most national legislations prefer species lists rather than 'ecosystems'. Therefore, it is difficult to apply scientific insights on how ecosystems work. The use of own definitions or popular perceptions about nature often overrules the academic advices. Furthermore, the legislative strategies itself are often too rigid to allow for a sustainable management of the environment. Ecosystem dynamics do not have a prominent place in the legislative strategies. The biophysical interactions on very different scales and the ecological succession mechanisms in the marine environment plead for more flexibility in interpretation and implementation of (international) environmental law.

Ecological restoration in the marine environment is a relatively recent concept, a delay which is clearly related to the specific features of this less accessible environment. This is even more pronounced in turbid marine areas that consist largely of sand banks and swales. Management measures at sea are restricted to the management of the human activities as active restoration measures are impossible to apply. Therefore, marine management is largely focused on the maintenance of the benefits that come from exploitation of resources, *i.e.* the use of goods that are provided by the sea (Beaumont *et al.*, 2007). The idea of viewing the environment as a producer of goods and services is relatively new, especially for the marine environment (Beaumont *et al.*, 2007). The same authors state that if environmental, social and economic concerns are to be integrated into an ecosystem approach, policy makers need to be able to quantify the provision of goods and services, on a before and after, site specific basis to get a true idea of the impact of a development or human activity. One problem that occurs is that provision of goods is often given priority over the provision of services, as services cannot be seen or held. They often do not yield an immediate market value, and are generally more difficult to quantify.

Also the legal protection of marine habitats has developed only very recently, compared to their terrestrial counterparts. The need to designate Marine Protected Areas (MPAs) as a contribution to preserve and improve marine biodiversity and ecosystem functioning has been put forward in several international policy instruments and legislation and consists generally of a mixture of specific marine instruments and mixed terrestrial/marine instruments (Cliquet *et al.*, 2008a). In the Plan of Implementation of the World Summit on Sustainable Development (2002)[20] governments accepted to establish a globally representative system of marine and coastal protected areas by 2012. At the 7th meeting of the parties (COP7) to the Convention on Biological Diversity (CBD-COP7)[21] it was decided to establish and maintain a network of marine and coastal protected areas by 2012. An example of a specific marine instrument, and relevant for the North Sea, is the OSPAR Convention[22]. A recommendation of 2003[23] aims at an ecologically coherent network of well-managed MPAs by 2010. In the mixed terrestrial/marine instruments, the most relevant for the protection of marine habitats are the Biodiversity Convention[24], the Ramsar Convention[25] and, for Europe, the EU Birds Directive[26] and the Habitats Directive[27]. These international legal obligations and commitments are a very important policy driver within the process of marine conservation (Rabaut *et al.*, 2009a).

The management and protection regime put forward in legislation often strives to keep habitat and species in a good conservation status within a protected area. Nature conservation law tends to be rather conservative, as it aims at the 'conservation' of certain habitats and species at a certain place. This goal is particularly difficult to achieve in a highly dynamic marine environment. Moreover, dynamic terrestrial ecosystems are facing similar challenges, especially with the rapidly changing climate. It has been stated that dynamics caused by climate change, such as rapid species migrations, will possibly pose problems to reach obligations put forward in 'static' nature conservation legislation (Cliquet *et al.*, 2009).

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[20] Plan of implementation of the World Summit on Sustainable Development, par. 32, c. In: United Nations. Report of the World Summit on Sustainable Development. Johannesburg, South Africa, 26 August- 4 September 2002. A/Conf.199/20; http://www.unmillenniumproject.org/documents/131302_wssd_report_reissued.pdf .

[21] *COP 7, Decision VII/5, Kuala Lumpur, 9 - 20 February 2004, Marine and coastal biological diversity. Review of the programme of work on marine and coastal biodiversity, par. 19; http://www.cbd.int/decisions/?dec=VII/5; COP 7 Decision VII/28, Kuala Lumpur, 9 - 20 February 2004, Protected areas (Articles 8 (a) to (e)), par. 18; http://www.cbd.int/decisions/?m=COP-07&id=7765&lg=0.*

[22] Convention on the Protection of the Marine Environment of the North-Eastern Atlantic, Paris, 22 September 1992; in force since 25 March 1998; http://www.ospar.org

[23] *OSPAR Recommendation 2003/3 on a Network of Marine Protected Areas.*

[24] Convention on Biological Diversity, Rio de Janeiro, 5 June 1992; in force since 29 December 1993; http://www.cbd.int

[25] Convention on Wetlands of International Importance especially as Waterfowl Habitat, Iran, 2 February 1971; http://www.ramsar.org

[26] Directive 79/409/EEG of 2 April 1979 on the Conservation of Wild Birds, *PB L* 103, 25 April 1979 (hereafter: Birds Directive); text of the Directive, with later amendments, see http://eur-lex.europa.eu/LexUriServ/site/nl/consleg/1979/L/01979L0409-20070101-nl.pdf.

[27] Directive 92/43/EEG of 21 May 1992 on the Conservation of Natural Habitats and of Wild Fauna and Flora, *PB L* 206, 22 July 1992 (hereafter: Habitats Directive); text of the Directive, with later amendments, see http://ec.europa.eu/environment/nature/legislation/habitatsdirective/index_en.htm.

Moreover, it has already been suggested to change (terrestrial) nature conservation policy in order to adapt to climate change (van Leeuwen and Opdam, 2003). Therefore, adaptation to climate change requires a more flexible approach (Verschuuren, 2007, Woldendorp, 2009). The same can be advocated for highly dynamic environments such as marine environments.

In the European seas which are heavily used, it is clear that pressure reduction will play a key role if one aims to reach sustainability through the application of the ecosystem approach to environmental management (EEA, 2009). The European Birds Directive and the Habitats Directive are the two international legal bases that oblige member states of the European Community to designate marine areas as part of the Natura 2000 network. The Natura 2000 network consists of Special Protection Areas (SPAs) for birds and Special Areas of Conservation (SACs) for certain habitats and species. This chapter will focus on marine habitats protection.

Within the European context it is therefore important to analyze how habitat-types have been described and how environmental managers should apply the ecosystem approach for the different marine habitats they need to restore or to protect. For the designation of the Natura 2000 network in the marine environment, the Commission has issued guidelines for both the designation and the management of those areas (European Commission, 2007) and has provided an interpretation manual of European Union habitats[28].

In this chapter, we will limit our analysis to the EU Habitats Directive and use marine habitat protection issues in the Belgian part of the North Sea as a case study. In what follows, we will screen the Habitats Directive and see if it is adapted to the dynamic character of the marine environment. A similar exercise was done for adaptation to climate change (Cliquet *et al.*, 2009). Similar problems can be detected for dynamic changes in the marine environment.

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[28] http://ec.europa.eu/environment/nature/natura2000/marine/docs/appendix_1_habitat.pdf

Legislative framework

Application of the Habitats Directive to the marine environment

The Habitats Directives clearly applies to the marine environment (Cliquet *et al.*, 2008a). In the definition of natural habitats, the Directive explicitly speaks of terrestrial and aquatic areas (article 1, b, Habitats Directive). The annexes of the Habitats Directive include marine habitats and marine species: nine marine habitat types in Annex I (European Commission, 2007) and 18 species in Annex II (European Commission, 2005). Examples of marine habitats are sandbanks which are slightly covered with sea water all the time (habitat 1110) and reefs (habitat 1170). The marine and coastal habitat categories mentioned in Annex I of the Directive are broadly defined and may allow for more than one interpretation by member states in the identification of areas to be designated (Mitchell, 1998). This could lead to the selection of different habitat sub-types (European Commission, 2007). Annex II also includes various marine species for which Special Areas of Conservation must be designated. Marine habitats and species are underrepresented in the annexes of the Directive. However, before the annexes are reviewed in order to add new marine habitats and species, the Commission thinks that member states should first fully implement the existing obligations, in particular with respect to the Natura 2000 network (European Commission, 2007, O'Briain, 1998).

In addition to being applicable in the territorial sea, the Directive also applies to the continental shelf and in the EEZ. This is confirmed in scientific literature (Backes *et al.*, 2001, Cliquet, 2001, Owen, 2001), in national jurisdiction[29], in jurisdiction by the Court of Justice[30], by the Council of the European Union[31] and the European Commission (European Commission, 2007).

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[29] R v. Secretary of State for Trade and Industry vs. Greenpeace, Queen's Bench Division (Crown Office List), CO/1336/99, 5 November 1999; http://web.uct.ac.za/depts/pbl/jgibson/iczm/cases/greenp.htm.

[30] Court of Justice, 20 October 2005, Case 6/04, Commission vs. Great Britain.

[31] Annex to Council Conclusions on the Strategy for the Integration of Environmental Concerns and Sustainable Development into the Common Fisheries Policy, Luxembourg, 25 April 2001, point 15; http://ue.eu.int/ueDocs/cms_Data/docs/pressData/en/agricult/ACF20DE.html.

Designation of protected areas under the Habitats Directive

The Habitats Directive of 1992 provides for the establishment of specific protected areas. Together with the Special Protection Areas, designated under the Birds Directive, these areas form a European ecological network, the 'Natura 2000 network'[32].

The Habitats Directive aims to designate areas for the natural habitats and habitats of species of community importance described in Annexes I and II, in order to reach a favourable conservation status and if necessary restore them. Member States contribute to the establishment of Natura 2000 by designating areas as Special Areas of Conservation (SACs). The procedure for the establishment of the SACs is described in article 4 and consists of various stages. First of all each Member State shall propose a list of sites indicating which natural habitat types in Annex I and which species in Annex II that are native to its territory the site currently hosts. The designation must take place on the basis of the criteria in Annex III (Stage 1) and relevant scientific data. Annex III includes the ecological criteria on which the designation should be based. Member States should not take into account economic and social criteria in the designation of SACs[33]. A second stage in the establishment of the Natura 2000 network consists in the Commission establishing a list of Sites of Community Importance (SCIs), drawn from the Member States' lists identifying those which host one or more priority natural habitat types or priority species and based on the criteria in Annex III (Stage 2). The decisions of the Commission for the establishment of the list are divided up according to biogeographical region. For most of these regions community lists have been established[34]. Once an area has been declared to be a Site of Community Importance, the Member State involved designates that area as soon as possible (and within six years at the most) as an SAC.

According to the EU Biological Diversity Plan (European Commission, 2006) final designation of SACs have to be done by 2010 (terrestrial) and 2012 (marine). The necessary management and conservation measures should be taken by 2010 (terrestrial) and 2012 (marine) for the SACs under the Habitats Directive.

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[32] Art. 3 (1), Habitats Directive.

[33] Confirmed in Case C-371/98 (Severn estuary).

[34] http://ec.europa.eu/environment/nature/natura2000/sites_hab/biogeog_regions/index_en.htm

In most EU countries the process of designating Natura 2000 sites is well underway, including those in the marine environment (as can be seen on the EU barometer[35]). The criteria for selecting the SACs are set forth in Annex III of the Habitats Directive. The selection of sites for habitats types of Annex I should be based on:

(a) The degree of representativity of the natural habitat type on the site;

(b) Area of the site covered by the natural habitat type in relation to the total area covered by that natural habitat type within national territory;

(c) The degree of conservation of the structure and functions of the natural habitat type concerned and restoration possibilities;

(d) A global assessment of the value of the site for conservation of the natural habitat type concerned.

For the habitats of species mentioned in Annex II, criteria for selection are:

(a) The size and density of the population of the species present on the site in relation to the populations present within national territory;

(b) The degree of conservation of the features of the habitat which are important for the species concerned and restoration possibilities;

(c) The degree of isolation of the population present on the site in relation to the natural range of the species;

(d) A global assessment of the value of the site for conservation of the species concerned.

Thus, in the Habitats Directive the size of habitats and number of species at a certain moment are important factors for the duty to designate conservation sites.

In the second phase of the designation of SACs, a community list is established. The criteria for the selection of these sites include:

(a) The relative value of the site at national level;

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[35] http://ec.europa.eu/environment/nature/natura2000/barometer/index_en.htm

(b) the geographical situation of the site in relation to migration routes of species in Annex II and whether it belongs to a continuous ecosystem situated on both sides of one or more internal Community frontiers;

(c) The total area of the site;

(d) The number of natural habitat types in Annex I and species in Annex II present on the site;

(e) The global ecological value of the site for the biogeographical regions concerned and/or for the whole of the European territory of Member States, as regards both the characteristic of unique aspect of its features and the way they are combined.

Also here most criteria in the second phase are aimed at selecting sites based on the actual presence of habitats and sites. In view of the dynamic nature of the marine environment it is necessary to take into account adaptation to both natural and climate driven changes. Protected sites may have an important role in providing locations where the full range of potential species association within each habitat type can develop. The transitional stages of habitats should be recognised, as ecosystems typically tend to evolve as a result of natural succession or due to changing climate (Hossell *et al.*, 2003). All of this should be explicitly taken into account when evaluating the designation of sites. Ideally, the criteria of Annex III of the Habitats Directive should be expanded and include specifically criteria that allow for adaptation to natural developments.

Conservation objectives

According to the preamble of the Habitats Directive, the necessary measures have to be implemented in each area, having regard to the conservation objectives pursued. Conservation objectives are also important when assessing the impact of plans and projects on the site. Article 6 (3) states that any plan or project likely to have a significant effect thereon, shall be subject to appropriate assessment of its implications for the site in view of the site's conservation objectives. In the case by the Court of Justice on the *cockle fisheries in* *the Wadden Sea*[36], the importance of conservation objectives was confirmed: where a plan or project is likely to undermine the site's conservation objectives, it must be considered likely to have a significant effect on that site.

Conservation objectives thus have to be set for those species and habitats that have been identified in the Standard Data Form that member states send to the Commission when proposing sites of community importance. Most EU Member States are still in the process of defining those objectives. Conservation objectives can be defined in quantitative parameters (e.g. for the conservation of a certain habitat type we need 40 % of the available habitat on the territory, sample species richness (S) of 26, 5 typical or associated species). However, it is not necessary to define the conservation objectives with quantitative criteria. Qualitative criteria can serve as objectives, too. If for example the capability of an area to serve as a habitat for a certain species is the conservation objective, this objective is still met even when the species concerned has left the area because of effects of natural dynamics or climate change[37].

Conservation objectives are defined both on a national/regional level and on site level. This is necessary, in order to make an appropriate assessment of the conservation status of the habitats and species, and on the impact of human activities on the site. However, at site level, the loss of a species as a result of natural or climate change dynamics, may have significant implication for achieving the conservation objectives, especially if the species concerned is the prime reason for the site’s designation. The loss of such species could have serious implications with respect to judging if the Member State is meeting the obligations under the Habitats Directive (Hossell 2003). In some cases a change in conservation objectives or an adjustment of the boundaries of an area may be justified (see further on case study).

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[36] Case C-127/02, concerning a request for prejudicial decision under Art. 234 EG, submitted by the Council of State (Netherlands) by decision of 27 March 2002, recorded on 8 April 2002, in the procedure 'Landelijke Vereniging tot Behoud van de Waddenzee' (National Association for the Protection of the Wadden Sea), 'Nederlandse Vereniging tot Bescherming van Vogels' (Dutch Association for the Protection of Birds) against the Secretary of State for Agriculture, Nature Management and Fisheries, in the presence of the Coöperatieve Producentenorganisatie van de Nederlandse Kokkelvisserij (Cooperative Producers' Organisation of the Dutch Cockle Fisheries) UA.

[37] The Dutch Council of State, acting as administrative judge, has ruled that such qualitative criteria are sufficient, Council of State November 6th 2008, 200802545/1, 2009 *Tijdschrift voor Milieu en Recht* , no. 29.

However, we face a possible conflict between the need for legal certainties and the reality of scientific uncertainties: stakeholders want conservation objectives to be set for a long term and be permanent. This is difficult, if not impossible, in the marine environment where there is a combined effect of natural succession and climate change: species will disappear, other species will occur, for which new conservation objectives will have to be set.

Natural as well as climate driven dynamics influence the succession and make the dynamics unpredictable. However, they can be taken into account to some extent by formulating more qualitative rather than quantitative conservation objectives and by allowing changing these objectives after a certain time (*i.e.* increased flexibility). However, both these solutions face the disadvantage of a loss of legal certainty when applying the legal regime (Cliquet *et al.*, 2009).

Conservation measures and management of the sites

For the sites protected under the Habitats Directive, Member States must take necessary conservation measures (article 6 (1), Habitats Directive). According to the Habitats Directive 'conservation' means a series of measures required to maintain or restore natural habitats and the populations of species of wild fauna and flora at a favourable status (article 1 (a)). The conservation status of a natural habitat will be taken as favourable when:

- Its natural range and areas it covers within that range are stable or increasing,

- The specific structure and functions which are necessary for its long-term maintenance exist and are likely to continue to exist for the foreseeable future, and

- The conservation status of its typical species is favourable as defined further in the Habitats Directive (article 1 (e)).

The conservation status for species will be taken as favourable when:

- Population dynamics data of the species concerned indicate that it is maintaining itself on a long-term basis as a viable component of its natural habitats,

- The natural range of the species is neither being reduced nor is likely to be reduced for the foreseeable future, and

- There is, and will probably continue to be, a sufficiently large habitat to maintain its populations on a long-term basis (article 1 (i)).

The conservation measures mentioned in article 6 (1) include, where necessary, the establishment of appropriate management plans and appropriate statutory, administrative or contractual measures which correspond to the ecological requirements of the Annex I habitats and Annex II species on the sites. According to the Commission guidelines management plans are a useful tool in managing the marine sites and facilitating the achievement of the objectives of Natura 2000 (European Commission, 2007). In light of the dynamic character of the marine environment, management plans will have to be revised or updated in an appropriate time scale, taking account of changes that have occurred in the site. Those changes could be caused by nature, external forces acting on nature, development of scientific knowledge and conservation management techniques (European Commission, 2007).

Besides the positive conservation measures Member States must take appropriate action for the SACs to avoid the deterioration of natural habitats and of habitats of species and to avoid disturbance of the species for which the areas have been designated (article 6 (2), Habitats Directive).

In the light of the effects of natural dynamics and climate change, this raises a couple of questions. The definitions of a favourable conservation status as mentioned above, might cause problems for certain habitats and species in the marine environment, because these requirements again are formulated in a rather static way. The population data of the existing species present or the habitat distribution at a certain moment may not diminish. However, as a consequence of natural dynamics or climate change, the predictability of the occurrence of the protected habitat (or species) becomes more difficult.

It is clear that deterioration, when this is the consequence of insufficient measures against human activities, has to be avoided according to article 6 (2). In the marine environment this could for instance include limitation of fishing or certain types of fisheries (see below on Belgian case). However, what happens when species disappear or habitats change, as a consequence of natural or climate induced changes?

In a case against the UK on the transposition of article 6 (2), Habitats Directive in Gibraltar, the Court seems to be very restrictive. In that case the United Kingdom held as an argument that only non-natural deterioration is to be avoided. The Advocate General on the contrary held that the examples brought forward by the UK, changes in sea level and climate change, relate less to nature in general than to structural environmental changes that jeopardise the conditions for the continued existence of the protected habitats and species in the Natura 2000 sites concerned. The Court did decide that at least to some extent the Member States are obliged to take measures to react to natural changes to avoid deterioration of the habitats and species which the areas have been designated for. 'It may be necessary to adopt both measures intended to avoid external man-caused impairment and disturbance and measures to prevent natural developments that may cause the conservation status of species and habitats in SACs to deteriorate.' [38] However, in the marine environment natural dynamics might just lead to a change in species and habitats. Again, if the conservation objectives have been formulated in such a way that natural dynamics are included as a feature of the habitat, than those natural developments will probably not be considered as 'deteriorating'.

It has to be seen whether and how the Court itself will accept 'natural changes' as a reason for a decline of a certain habitat type or species in a protected area. Guidance by the EU is needed on how to assess the conservation status of each species and habitat type with respect to succession or complete alteration due to combined effects of natural dynamics and climate change (Hossell 2003). Even if you could consider climate change as a situation over which you have no influence (as an individual state), than still, the burden of proof is for the Member State to show that the deterioration is the direct consequence of climate change. According to the Advocate General only if a Member State can show that deterioration in quality is due to objective circumstances over which it has no influence, it may justify the reduction in the extent of a protected area. It might be very difficult for Member States to provide the required necessary proof (Woldendorp 2007).

Furthermore, the deterioration of a habitat will often be caused by more than just climate change, but will already have been influenced by other human induced causes as well (Woldendorp 2007). For those factors Member States should take appropriate steps to avoid

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[38] Case C-6/04, Commission v. United Kingdom, par. 34.

deterioration and cannot rely on the exception of natural developments or objective circumstances.

Whereas art. 6 (2) is mainly concerned with deterioration by human induced activities, the Habitats Directive deals explicitly with natural developments in art. 9: an SAC may be considered for declassification where this is warranted by natural developments noted as a result of the surveillance provided for in article 11 of the Habitats Directive. We can take the viewpoint that only negative natural developments are meant here. Although a declassification because of positive developments could be possible, it is considered unlikely due to ongoing threats to fauna and flora (Thomas, 2008). A declassification will not be necessary when a dynamic system evolves towards an equally valuable system that is also in need of further protection measures. Declassification should in any case be considered as an exceptional measure, in light of the conservation and restoration obligations provided for in the Directive (see also Thomas 2008).

Assessment of plans and projects

An assessment framework for the implementation of (new) activities is determined in article 6 (3)-(4) of the Habitats Directive: any plan or project that is not directly connected with or necessary to the management of an SAC, but likely to have a significant effect thereon, shall be subject to an appropriate assessment of its implications for the site in view of the site's conservation objectives. The national authorities can only agree to the plan or project after having ascertained that it will not adversely affect the natural features of the site concerned and after having provided opportunities for participation if necessary (article 6 (3), Habitats Directive). A possible exception is provided for in article 6 (4) of the Habitats Directive: a plan or project may nevertheless be carried out, in spite of a negative assessment of the implications for the site, if certain conditions are met. No alternative solutions should be available; it should concern imperative reasons of overriding public importance, including reasons of a social or economic nature; and the Member State should take all compensatory measures necessary to ensure that the overall coherence of Natura 2000 is protected. The Commission should be informed of the compensatory measures adopted.

Given the importance of article 6 (3)-(4) a further concretization of concepts such as *significant consequence* and *appropriate assessment* is very important. The Court of Justice has made some conclusions about those concepts in a preliminary ruling about the *cockle fisheries in the Wadden Sea*[39]. In this case, the Court stated the importance of the conservation objectives (see above). As it is more complex to define conservation objectives in the dynamic marine environment and in the light of climate change, the appropriate assessment becomes more difficult, as conservation objectives might evolve.

Conservation of Belgian marine habitats

Habitats in the Belgian marine environment

The protection of marine habitats in Belgium is to be implemented within the framework of international and European legislation such as the Habitats Directive. As mentioned above, the Habitats Directive states that on the basis of relevant scientific information and on the basis of the criteria set out in Annex III, each Member State should propose a list of sites indicating which natural habitat types in Annex I and which species in Annex II are native to its territory. For animal species ranging over wide areas these sites shall correspond to the places within the natural range of such species which present the physical or biological factors essential to their life and reproduction (article 4).

For a good interpretation of the habitats that are listed under Annex I of the Habitats Directive, the European Commission has provided an interpretation manual of European Union habitats, of which the latest version was published in July 2007 (EUR 27). In present case for the Belgian part of the North Sea (BPNS), we focus on the habitats that fall under the 'coastal and halophytic habitats – Open sea and tidal areas'. For the Belgian marine areas, three different habitat types occur:

Sandbanks which are slightly covered by sea water all the time (1110)

Sandbanks are elevated, elongated, rounded or irregular topographic features, permanently submerged and predominantly surrounded by deeper water. They consist mainly of sandy sediments, but larger grain sizes, including boulders and cobbles, or smaller grain sizes

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[39] Case C-127/02 (cockle fisheries).

including mud may also be present on a sandbank. Banks where sandy sediments occur in a layer over hard substrate are classified as sandbanks if the associated biota are dependent on the sand rather than on the underlying hard substratum. "Slightly covered by sea water all the time" means that above a sandbank the water depth is seldom more than 20m below chart datum. Sandbanks can, however, extend beneath 20m below chart datum. It can therefore be appropriate to include in designations, such areas where they are part of the feature and host its biological assemblages. Besides, the guidelines indicate that for the North Atlantic and North Sea invertebrate and demersal fish, communities of sandy sublittoral should be included. It is clear that the current SAC Trapegeer-Stroombank in the BPNS (see below) was designated for the occurrence of habitat 1110 (as well as for the occurrence of high diversity of Bivalves and for its importance as a resting place for seals). However, more scientific research will be necessary to define the favourable conservation status of this specific area as the current definition is too generic for direct application. Almost the entire Belgian part of the North Sea can be considered as an area consisting of sandbank systems which are slightly covered by sea water all the time and more potential SCIs will be proposed. Note that not only the top of a sandbank, but also the slope and the swale are an inherent part of the sandbank system and hence, this complex falls under the 1110-habitat.

Mudflats and sandflats not covered by seawater at low tide (1140)

Habitat type 1140 is defined as 'sands and mud of the coasts of the oceans, their connected seas and associated lagoons, not covered by sea water at low tide, devoid of vascular plants, usually coated by blue algae and diatoms'. They are of particular importance as feeding grounds for wildfowl and waders. The BPNS has areas that fall under this definition, as sandy beaches fulfil the criteria of the definition. Moreover, a subtidal sand bank in front of the coast of Heist is currently growing as a consequence of sedimentation leading to periods in the tidal cycle during which the sandflat is not covered by water. Hence, this area currently classifies as 1140-habitat. This sandflat has not been proposed as an SCI yet.

Reefs (1170)

Reefs can be either biogenic concretions or of geogenic origin. They are hard compact substrata on solid and soft bottoms, which arise from the sea floor in the sublittoral and littoral zone. Reefs may support a zonation of benthic communities of algae and animal species as well as concretions and corallogenic concretions. Reef forming animal species in the North Atlantic and North Sea include polychaetes, bivalves and cold water corals. For each species group some examples are provided which should be taken into account when deciding whether a certain habitat type is present or not, but such lists of examples should not be considered as being exhaustive (pers. comm. F. Kremer, European Commission, DG Environment, Nature and Biodiversity Unit).

In the Belgian part of the North Sea, both patches of gravel (may classify as geogenic reefs; more off shore) and high density patches of a tube building polychaete (may classify as biogenic reefs; more in shore) occur. This chapter will only elaborate on the latter. In intertidal areas, the tube patches are known to have consequences for the distribution and abundance of infaunal species by influencing the habitat structure (Callaway, 2006, Carey, 1987, Dittmann, 1999, Féral, 1989, Zühlke, 2001, Zühlke *et al.*, 1998). The patchy distribution of tube aggregations within a specific habitat is useful to investigate the ecosystem engineering implications of this polychaete. Recently, ecosystem engineering influence on faunal abundance, species richness and species composition in subtidal areas has been proved (Rabaut *et al.*, 2007, Van Hoey *et al.*, 2008). These results indicate that effects on density and diversity are most pronounced in shallow fine sand. The aggregations form clearly defined microhabitats which alternate with areas without *L. conchilega*, generating a surface structure of gentle mounds and shallow depressions. This 'seascape' can be visualized using side scan sonar imagery (Degraer *et al.*, 2008a). Experiments show that *L. conchilega* is able to pump oxygen into the bottom (Braeckman *et al.*, accepted, Forster and Graf, 1995) which is important for the benthic community composition and for specific benthic species (Steyaert *et al.*, 2005). This pumping stimulates further the mineralization processes in the bottom (Braeckman *et al.*, accepted), which is important for the ecosystem functioning. Furthermore, this reef habitat seems to be of importance for higher trophic levels such as juvenile flatfish (Rabaut *et al.*, accepted, Van de Moortel, 2009, Vanaverbeke *et al.*, 2009a) and birds (Godet *et al.*, 2008). Besides, Rabaut *et al.* (2007) and Van Hoey *et al.* (2008) show that rather than forming its own association, *L. conchilega* expands the realized niche of several species. A recent scientific study (Rabaut *et al.*, 2009b) investigated the habitat modifying effects of this tube dwelling polychaete. To classify as reefs however, ecosystem engineering activities need to significantly alter several habitat characteristics: elevation, sediment consolidation, spatial extent, patchiness, reef builder density, biodiversity, community structure, longevity and stability (guidelines to apply the mentioned definition are provided by Hendrick and Foster-Smith (2006)). Rabaut *et al.* (2009b) show that the elevation and sediment consolidation of the biogenic mounds was significantly higher compared to the surrounding unstructured sediment. Areas with *L. conchilega* aggregations tend to be extensive and patchiness is high. Rabaut et al (2009b) combine these results with previous studies on the biological implications of this species. The impact of *L. conchilega* on the biodiversity was demonstrated by Zühlke (2001), Rabaut *et al*. (2007) and Van Hoey *et al.* (2008). The authors evaluate the different physical and biological aspects of the tube worm aggregation and conclude, based on scientific evidence, that *L. conchilega* qualifies as a reef builder (Rabaut *et al.*, 2009b).

Associations

The interpretation manual (EUR27) provides also a listing of the habitat types that can be associated in the field (European Commission, 2007). Sandbanks (1110) can be found in association with the two other habitats that are found in the BPNS: mudflats and sandflats not covered by seawater at low tide (1140) and reefs (1170). Reefs (1170) can in their turn be found in association with sandbanks (1110).

Because of only recent scientific appreciation of *L. conchilega* as reef builder, ‘reefs’ (1170) are not considered, at this moment, as a habitat for the Special Area of Conservation in the Belgian coastal waters. It is, however, clear that the reef builder *L. conchilega* will be important for the allocation of potential SCIs in Belgian marine waters as well as for the evaluation of the favourable conservation status of the habitats in the eventual SACs.

As Member States have to propose a list of sites indicating which natural habitat types in Annex I are native to its territory the sites host on the basis of relevant scientific information and reefs are mentioned as a possible associated habitat to that of sandbanks (1110), there is a clear need to integrate these biogenic reefs in formal regulation and measures. Moreover, the species is a proxy for biodiversity and for the provision of goods and services. The ecological restoration of the particular sandbank habitats in the BPNS will also be related to reducing existing human pressure. There is general scientific evidence that beam trawl fisheries have a far reaching impact on sandbank systems and more specifically, there is evidence of decreasing biodiversity of the polychaete reefs after fishing disturbance (Rabaut *et al.*, 2008).

Annex III of the Habitats Directive provides criteria for selecting sites eligible for identification as sites of community importance and designation as SAC. We evaluate the site assessment criteria for the polychaete reef habitat that occurs in the BPNS (as an association of the habitat type sandbank):

(a) Degree of representativity of the natural habitat type on the site: it is known from literature that the tube building polychaete is a key species for the rich macrobenthic sandbank community in which it occurs and the biological implications of the species are far reaching.

(b) Area of the site covered by the natural habitat type in relation to the total area covered by that natural habitat type within national territory. The exact percentage of reefs that occur within the SAC is difficult to estimate. This relates to the specific characteristics of the marine environment. A modelling approach of Willems et al. (2008) shows that the occurrence is strongly related with the sediment grain size. It will be possible in the future to make more accurate estimations of the total area that is covered, because remote sensing can be used to visualize reefs (Degraer *et al.*, 2008b).

(c) Degree of conservation of the structure and functions of the natural habitat type concerned and restoration possibilities. It concerns an exceptional habitat which locally increases the biodiversity in a significant way and it has an important ecosystem function in the BPNS (importance for other trophic levels and for mineralization processes: see above). Furthermore, research showed that beam trawl fisheries affect the ecological function of the reefs (Rabaut *et al.*, 2008). The ecological restoration possibilities lie in a prohibition for bottom fisheries to be active within the SAC.

(d) Global assessment of the value of the site for conservation of the natural habitat type concerned. The ecological implications of this reef building polychaete have been described above. Besides, ecological restoration and protection of the reefs will support the goods and services and will help managers to reach sustainability through the application of the ecosystem approach.

Policy process

There would be far less interest in MPAs in Belgium without current international legal obligations and commitments and most designated areas have been established in the framework of the European Natura 2000 Network (Rabaut *et al.*, 2009a). All other marine management initiatives have largely focused on the maintenance of the benefits that come from exploitation of resources.

As of now, two areas in the Belgian marine environment have been proposed to the Commission and have been included in the list of sites of community importance. The areas were designated in Belgian legislation by Royal Decree of 14 October 2005 (Bogaert *et al.*, 2008, Cliquet, 2008, Cliquet *et al.*, 2008a, Cliquet and Decleer, 2007).

Additional areas also qualify as SCIs and a list of other SCIs is currently being built and is expected end 2009, while the list had to be adopted by 2008. This delay will probably jeopardize the deadline of final SAC designation (2012) and might influence the agreement taken in the framework of the Biodiversity Convention to establish a system of MPAs by 2012 (which confirmed the target that had been included in the Plan of Implementation plan of the World Summit on Sustainable Development (2002)).

The protection of marine habitats in Belgium is basically done through designation of SACs within the framework of the Habitats Directive. The interpretation of this international environmental law has been rather conservative until now, rendering it more difficult to adopt the management strategy to both natural and climate driven changes. These quite unpredictable changes do indeed create difficulties to develop concepts and models that span the enormous range of scales and possibilities. Therefore, some flexibility to allow for ecological succession should be built in as soon as protected areas are designated. This chapter showed that from a legal (EU) perspective, three marine habitat types occur in Belgian marine waters (1110, 1140 and 1170). An evaluation process to identify potential SACs in the BPNS took place during Spring 2009. Both scientists and policy makers were involved in the process. During this process, a rather narrow interpretation of the EU Habitats Directive was especially clear for the designation of areas to protect the habitat type 1170 ('Reefs'), particularly when referring to *L. conchilega* reefs. Scientific research, however, classifies *L. conchilega* as a reef builder and is occurring in the BPNS, especially in the shallow sandbank areas (Rabaut *et al.*, 2009b). Article 4 of the Habitats Directive indicates that Member States should use relevant scientific information as well as criteria set out in Annex III to propose a list of sites indicating which natural habitat types in Annex I are native to its territory the sites host. It has been shown earlier in this chapter that the reef habitat type can easily be assessed as important using the criteria of Annex III of the Habitats Directive. Nevertheless, *L. conchilega* reef systems are thought to be an intermediate succession state. Without external (natural or anthropogenic) disturbance, the reefs may be colonized by juvenile mussels (*Mytilus edulis*), which can under certain circumstances take over the system from *L. conchilega* (Callaway, 2003b). Protection measures for *L. conchilega* might therefore lead to the development of mussel or oyster beds (which have totally disappeared in the Belgian part of the North Sea). The dynamics as a consequence of biological and physical actors make it necessary to allow natural ecosystems to evolve. From a legal perspective the Habitats Directive only provides a possibility in article 9: an SAC may be considered for declassification where this is warranted by natural developments noted as a result of the surveillance provided for in article 11 of the Habitats Directive. This will, however, only take place if there is a significant deterioration in quality of the habitat (see above). In current case where a *L. conchilega* reef evolves towards a mussel or oyster reef there would be no reason to declassify the SAC because of article 9.

The Interpretation Manual (EUR27) is a helpful instrument, with lists of examples of species and/or habitat. However, the Interpretation Manual did not mention *L. conchilega* as a reef builder, leading to the argumentation that these reefs cannot be protected in the framework of the Habitats Directive. Nonetheless, the list provided in the manual is not exhaustive and scientific evidence should be used (article 4) to evaluate whether a species is a reef builder, taking the definition of the directive into account. There is however still debate on how to interpret the rather vague definition of the Interpretation Manual. The criteria to qualify *L. conchilega* were based on those of *Sabellaria spinulosa*, a tube building polychaete that apparently classifies under the latest definition as it is listed in the example list of the Interpretation manual (EUR27).

Despite the similarities in approach, it was argued not to use sediment consolidation as a measure in the case of *L. conchilega*. This argument was more of a strategic nature, as it was argued that users of the marine environment that are restricted in their activity because of conservation measures within Natura 2000, would go to court. However, only scientific evidence should be used (article 4) to evaluate a habitat designation. Moreover, as we saw above, the Commission guidelines provide for the possibility for sub-habitat types, because of the wide categories of marine habitat types in Annex I.

The policy process for marine conservation in Belgium shows a rather conservative interpretation of international environmental law until now. It is not clear whether all relevant scientific evidence will be used by the authorities for the final SAC designation though the evaluation process made already clear that there is some reluctance to allocate 1170 SACs for *L. conchilega*.

Conclusion

The final aim of marine conservation strategies is to stop deterioration of the marine environment in terms of biodiversity and ecosystem functioning. However, natural environments generally develop in ways that are not easy to predict and even less so in the marine environment. Implementation of EU nature conservation legislation demonstrates that there is a rigid interpretation of international environmental law. The Belgian case study evaluates the different habitat types that are listed in the Habitats Directive and described in the interpretation manual of European Union habitats (EUR27). Scientific research classifies *L. conchilega* as a reef builder and is occurring in the BPNS, especially in the shallow sandbank areas. Article 4 of the Habitats Directive indicates that Member States should use relevant scientific information as well as criteria set out in Annex III. This study shows that the reef habitat type can easily be assessed as important using scientific information and the criteria of Annex III of the Habitats Directive. Moreover, the interpretation manual describes reefs (1170) as possible associated habitat type to that of sandbanks (1110). During an evaluation process to identify potential SACs in the BPNS marine habitats with scientists and policy makers it became clear that there is some reluctance to allocate SACs for 1170-*L. conchilega* habitat. Although the Habitats Directive leaves some room for flexibility, interpretation has so far been rather conservative. As the impact of beam trawl fisheries on these reefs is known (Rabaut *et al.*, 2008), we speak out to classify SACs as a sandbank habitat type (1110), with an associated reef habitat type (1170) and suggest a ban of bottom fisheries in this area. This comes down to the application of the ecosystem approach and will lead to ecological restoration and protection of this marine area.

This chapter illustrates that there is an urgent need to develop more flexible interpretation of international environmental legislation for the marine environment, taking into account the unpredictability of biological features, physical characteristics and the subsequent ecological succession. These unpredictable changes become of greater importance as global warming alters most ecosystems, including oceans and seas. Moreover, the case study demonstrates that international law is sometimes interpreted more conservative than it is supposed to be or is interpreted in such a way that it hampers a sound marine conservation strategy. We emphasize, however, that misuse of increased flexibility is a dangerous pitfall when it is interpreted as weaker protection.

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CHAPTER 10

General discussion

Towards an ecosystem approach to marine management

If a transition towards a more-resilient relationship between society and ecosystems is what we want then it should be based on ecological knowledge (Carpenter and Folke, 2006). This holds particularly true when the sea is used as a natural resource (e.g. fish) and society (e.g. the fisheries community) depends on the marine ecosystem. The results of this thesis on Lanice conchilega*, fisheries and marine conservation are therefore discussed in the light of their potential value for the application of the ecosystem approach to marine management. The chapter starts discussing the marine conservation issues of the previous two chapters and underlines the importance of ecosystem engineers in fisheries management. The discussion goes on by highlighting how ecosystem engineers can be used within the framework of integrative management. The use of ecosystem engineers as a way to apply the ecosystem approach is then developed as a case study for* L. conchilega*.*

Marine conservation and fisheries

The final aim of marine conservation strategies is to stop deterioration of the marine environment in terms of biodiversity and ecosystem functioning. Overexploitation and degradation of habitats are considered to be the most important drivers of biodiversity loss and ecosystem changes, especially in oceans and seas (*cf.* Chapter 1). In the European seas which are heavily used, it is clear that pressure reduction will play a key role if one aims to reach sustainability through the application of the ecosystem approach to environmental management (EEA, 2009). The North Sea is one of the most exploited marine areas in the world, with the BPNS (Chapter 1) lying in the centre of these activities (Douvere *et al.*, 2007, Maes *et al.*, 2005). Therefore, management of human activities at sea through a thorough marine spatial planning (MSP) is urgently needed (Douvere *et al.*, 2007). Within this MSP framework, MPA-networks should be developed to attain nature conservation targets. However, natural environments generally develop in ways that are not easy to predict (see Chapter 9) and nature conservation measures basically come down to a reduction of anthropogenic pressure. Therefore, restriction of (existing or potential) activities with a severe impact is the most common way to improve or conserve the ecological value of a marine area (Chapter 8). These activities may involve conflicting interests and include a lot of sectors (for full list check Chapter 8). For *Sabellaria alveolata*, another reef building polychaete (*cf. infra*) several drivers of change were suggested such as water temperature (climate change), sediment supply, water quality and coastal defense practices (Frost *et al.*, 2004). The dynamics of such systems are not fully understood and more investigation is needed to understand the interplay of different drivers. A more flexible nature conservation strategy should therefore be adapted (Chapter 9). This interpretation has still to be robust as there is a risk of undermining the final goal of environmental legislation if increasing flexibility would be translated into looser protection.

The impact of omnipresent fisheries on the marine biodiversity and on the functioning of the ecosystem has been identified as a key concern in marine conservation strategies (Chapter 1 and 8). In temperate continental shelf areas, where often mobile fishing gear is used, the link between fisheries and MPA-management is challenging (Chapter 8). Policy objectives for an MPA are generally easy to identify and in most cases national policy objectives are driven by international and regional legal obligations. However, MPAs often have the additional (generally implicit) objective of being directly beneficial for fisheries (Cudney-Bueno *et al.*, 2009). Selecting fish species for conservation because of their commercial value mostly has no connection at all to their function within the ecosystem (Norton and Noonan, 2007). Nevertheless, MPAs can potentially provide a number of (indirect) benefits for fisheries, e.g. protection of target stocks, 'spill-over' to adjacent fisheries and strengthening trophic cascades (Eklöf *et al*. (2009) and references therein), though the recovery time of exploited fish communities is often slow (Stobart *et al.*, 2009). A fishing ban within an MPA may further lead to an export of impacts to the adjacent 'unprotected' areas, potentially leading to gear conflicts and shifts to other target species and further degradation outside the MPA (*cf.* Chapter 8). It is clear that the mutual relation between ecosystem functioning and exploitation of the goods and services thereof is complicated. From a fisheries management point of view, a proper application of fishing effort controls is probably more efficient than installing no-take zones (Kaiser, 2005). From a nature conservation perspective on the contrary, habitats and species conservation is the main focus. Therefore, when commercial fisheries are identified as causes of habitat degradation or species loss, a reduction or a ban of (certain) fishing activities imposes itself. Although restoration of the ecosystem's integrity can theoretically increase fish stock sizes, it has been shown that this may not always be the case (Kaiser, 2005) or may even have opposite outcomes (Hiddink *et al.*, 2008b). This illustrates that the first step in the MPA-process (*i.e.* policy objectives, *cf.* Chapter 8) is of utmost importance; the purpose of MPAs to conserve habitats and biodiversity of non-target species is not necessarily consistent with the maintenance of sustainable fish stocks. The debate on the usefulness of MPAs is otherwise confused by the lack of goals and objectives of such systems (Kaiser, 2005). Even if both objectives can possibly be reached within one MPA, it must be clear from the start what the basic aim of the protected area is. A reserve network is a possible solution to these conflicting policy goals. The policy objectives for each area within the network should be formulated for a geographical area rather than in a sectorial way. Therefore, both MPA-management and fisheries management must support the management strategies for a specific area. Integrative management is important within the MPA-process as is visualized in a simplified flow chart in Figure 1. Chapter 8 discussed that this is generally not the case in reality where management is sectorial at local as well as at international levels. The international character of marine areas together with the complex relationship between habitat deterioration and commercial fisheries make it difficult to define responsibilities in the broader framework of marine ecosystem management. Moreover, reducing fishing effort is a decision that creates political difficulties as it has far-reaching, short term, social implications (Smith, 1995).

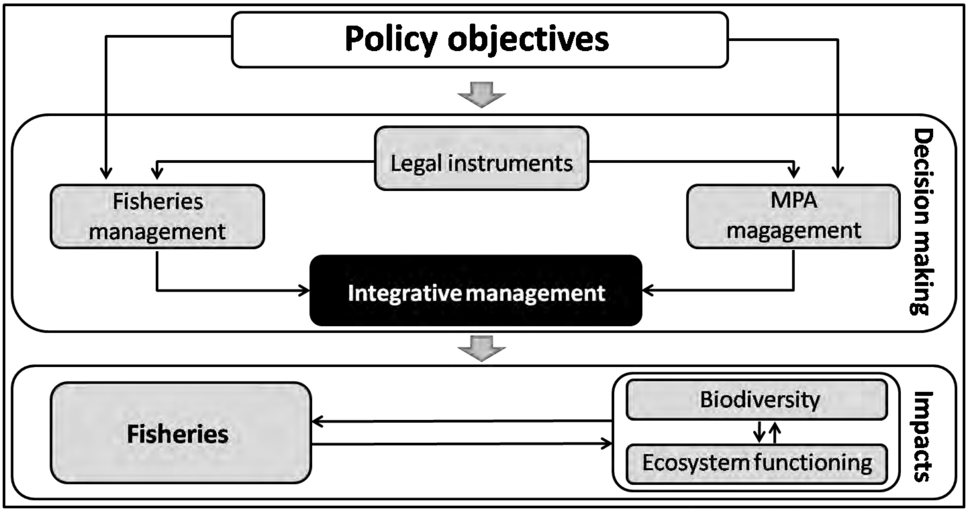

Figure 1. Simplified flow chart of the ‚MPA-process'. The basic aim of the protected area must be clear from the beginning, as objectives for nature conservation may be well different from fisheries management objectives. To come to an ecosystem approach to marine management, no sectorial strategies should be applied but management measures from different sectors should be tuned in an integrative management. Besides fisheries, also other sectors will need to be included: cf. *Chapter 8.*

The political need to appease a desperate fishing industry has tended to push management decisions towards, and often beyond, the upper confidence limits for future allowable catches. Such behaviour is not surprising given the typical short life-span of the average government, for whom the shadow of the future does not apply (Kaiser, 2005 and references therein).

Fisheries management and ecosystem engineers

During the past 25 years of attention paid to the consequences of fishing, there have been significant lags between descriptive and empirical studies on the one hand, and public awareness on the other, while political responses to important issues have been small (Coleman and Williams, 2002). The authors provide an overview of how the impact of fisheries on the ecosystem has evolved in the recent years rather than the direct impact on the fish stock. They identify three 'lines of study'. The impact of bycatch for non-targeted species was addressed first because high-profile marine species were involved. Secondly, the awareness expanded to include incidental effect of bottom trawling to epibenthic communities, with a strong focus on the physical destruction or bioconstructions rather than on the functional losses resulting from species removal. The third and final line of study is about cascading effects and complex feedback mechanisms as a result of species interactions, with studies on trophic cascades and fishing down food webs (Coleman and Susan (2002) and references therein). These authors point out that the phenomenon of ecosystem engineers in relation to fisheries activities is largely understudied, given the importance of structure (both abiotic and biotic) to fisheries productivity and the declines of so many species resulting from fishing pressure. The loss of habitat structure generally leads to lower abundances (biomasses) and often to declines in species richness (Airoldi *et al.*, 2008). Therefore, the impact of fisheries on marine ecosystem engineers is considered as a potentially serious problem because engineering activity influences both biological diversity and ecosystem functioning. It is not only necessary to value the function of ecosystem engineers in their environment but also to recognize the consequences of their anthropogenically induced degradation. Therefore, ecosystem engineers merit increased scientific and conservation emphasis, because of the fundamental role that they play in shaping habitat and the dependent communities from microbes to predators (Coleman and Williams, 2002).

From ecosystem engineer to ecosystem approach

The framework within which the results are further discussed is visualised in a flow chart (Figure 2). The functioning of ecosystems and its biodiversity takes place in the wider natural marine environment. Most ecosystems are exploited by man. Management strategies on how to exploit the available resources are in progress. When this management is integrative, management measures can reach sustainable exploitation and certain conservation objectives (Figure 2). The challenge is to accumulate ecological knowledge of the system and to have a true integration of the multi-sectoral management. When this challenge is tackled, ecosystem engineers can be used to reach integrative management as they are critical for the ecosystem integrity and functioning.

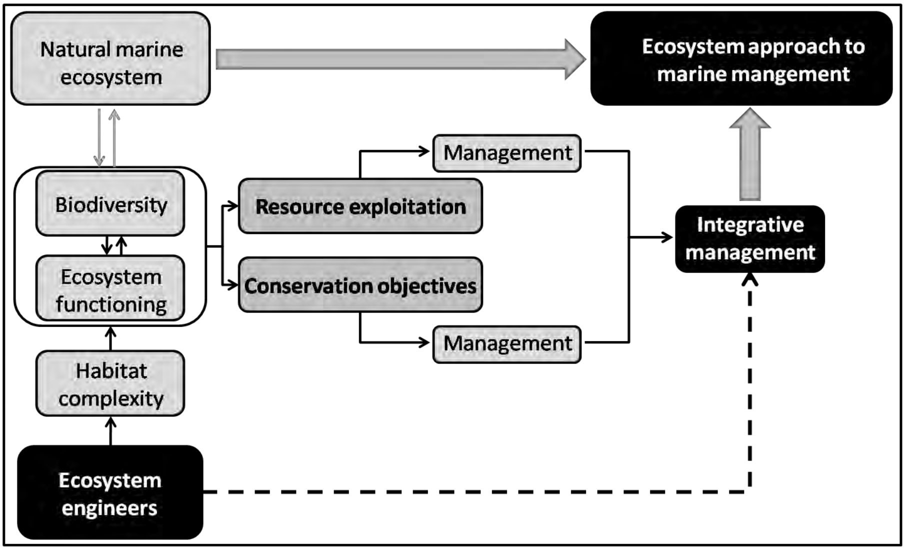

Figure 2. Flow chart visualising how ecosystem engineers may be useful within a marine nature conservation context and may lead to the application of the ecosystem approach to marine management

The possibility to generate knowledge on the biodiversity, ecosystem functioning as well as on the resilience of a particular ecosystem -starting from an ecosystem engineer- is discussed in this chapter for *L. conchilega*. The potential of this ecosystem engineer is visualised in Figure 3. We will start by discussing the effects of the presence of *L. conchilega* aggregations on their environment. Both horizontal and vertical links will be discussed. The effect on biodiversity will further be assessed against the original niche theory. We continue by discussing the resilience towards beam trawling. Information on both the functioning of the ecosystem and the impact of anthropogenic activities can serve as a basis to rethink management strategies and to start to integrate nature conservation and fisheries management. When the potential of the ecosystem engineer has been elaborated, this chapter discusses the 'label' under which the ecosystem engineered habitat may be protected. Different labels are discussed and the potential of applying the 'reef label' to *L. conchilega* is discussed with the characteristics of other tube worm reefs. Finally, some aspects on mapping these habitats will be discussed. The opportunities these newly acquired ecological insights provide are presented as general conclusions.

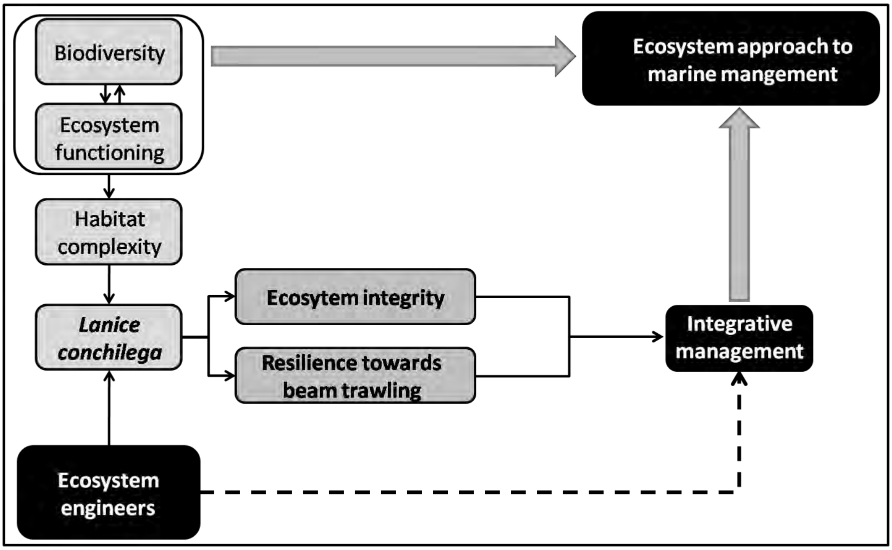

Figure 3. The use of Lanice conchilega *within an ecosystem approach to marine management*

The ecosystem engineer in its ecosystem

General patterns - both in intertidal and subtidal environments – of the implications of the presence of *L. conchilega* are increasingly obvious. Implications for the (macro)benthic environment were found to be far reaching (Chapter 1 and 2; Addendum I). *Lanice conchilega* has been studied on a North Sea scale and was shown to have a wide geographical distribution and a relatively low habitat specialization, but it appears to optimally occur in shallow fine sands (*cf.* Addendum I). The species was shown to have a consistent potential to positively affect the surrounding benthos, as was reflected in the significant and positive correlation between the benthic density and the density of *L. conchilega*. The detailed study on a large data set selected from the shallow fine sand fraction of the BPNS (*cf.* Chapter 2) and added considerable insight in how this species structures the community and which species-specific interactions determine the organization of this biogenic habitat. The driving force behind the structuring effect has been attributed to the capacity of *L. conchilega* to create or modify the habitat in a way that is favourable for many species. The result is an increased habitat complexity and heterogeneity that facilitates the evolution of a more diverse community. The community shift to lower diversity and higher densities in the highest class may be explained as a competition (for space) effect and could also be an effect of exclusion of epibenthic predation/disturbance according to the intermediate disturbance hypothesis, as proposed by Connell (1978). This hypothesis predicts that at low disturbance, in our case due to epibenthic predators/disturbers, diversity declines as competitive dominants monopolize the habitat (Peterson, 1982). These competitive dominants were identified as bearing the highest *L. conchilega* densities. This means that reefs that reach very high densities will have a lower 'reefiness' score (*cf.* Chapter 3) and intermediate density reefs can therefore be considered as more valuable.

Besides these horizontal effects on the macrobenthic species community, also top down effects - to other species groups (as meiofauna) and to the biogeochemical characteristics of the abiotic environment– have been reported (*cf.* Chapter 1 for detailed overview and references). This thesis shows that *L. conchilega* reefs also have bottom up effects on juvenile flatfishes. *Lanice conchilega* reefs were shown to affect habitat preference of post-larval *P. platessa* in intertidal nursery areas (Chapter 6). This proves that emergent structures, in otherwise low-relief benthic habitats, may play an important role in the ecology of some juvenile flatfishes. Nevertheless, effects on habitat preferences of flatfish within nursery areas are thought to be related to food availability as well (Beyst *et al.*, 1999, Phelan *et al.*, 2001, Wouters and Cabral, 2009). Therefore, Chapter 7 evaluates the importance of biogenic habitats as a feeding ground for juvenile flatfish species (*P. platessa* and *L. limanda*). These emergent structures in the nursery area played an important role in the ecology of these juvenile flatfishes. The significant attraction towards these habitats is partly explained as feeding behaviour. This is certainly the case for *P. platessa* feeding in *L. conchilega* reefs. 'Habitat structure-food density' interactions may be added to abiotic variables as factors influencing the use of resources by fishes (Crowder and Cooper, 1982). The challenge here is to find out whether the preference for structured habitats is because of the shelter or the feeding advantage (or both). The ecosystem engineered habitat in this study confirms that food abundance influences flatfish density. The significantly higher densities of *L. limanda* in the *Owenia fusiformis* ecosystem engineered area were not explained by feeding advantage.

The studies on the horizontal and vertical links with different ecosystem components and functions is important within the framework of the ecosystem approach (Figure 3) as information on the ecosystem's integrity is an important step towards integrative management.

Niche theory and *Lanice conchilega*

The apparent general ecosystem engineering effect of *L. conchilega* was visualised for the benthic community in the so-called 'Babushka-like pattern'. In Chapter 2, one possible explanation was found by applying niche theory and the effects of *L. conchilega* were described as an expansion of the realized niche of several macrobenthic species. However, an elaborate interpretation of the ecosystem engineer's implications for other species within the original concepts of niche theory still remains to be done. Therefore, a first attempt to re-evaluate the impact of the ecosystem engineer *L. conchilega* on the realized and fundamental niche of several associated species is presented here.

The niche theory origin and the evolution of the concept's meaning has been summarized by Vandermeer (1972). He points out that the concept was first introduced by Grinnell (1924), with 'niche' having two significant aspects: (1) the distributional nature and (2) the potential nature. The potential area in which a species can live (*i.e.* in the absence of their interactions with other species) was considered to define the niche while the distributional nature aspect defines the area in which one actually finds it. This is referred to as the pre-interactive conception of niche, later called the 'fundamental niche' (Hutchinson, 1957) or 'virtual niche' (Colwell and Futuyma, 1971). According to Vandermeer (1972), Elton (1927) interpreted the niche concept in terms of food habits and species interactions and therefore defined niche primarily as an organism's actual place in nature as opposed to its potential place in nature. This is referred to as the post-interactive conception of niche, later to be equated to the so-called 'realized niche' (Hutchinson, 1957) or 'actual niche' (Colwell and Futuyma, 1971). The niche breadth is defined as a set of habitats used by a species (Vandermeer, 1972). The distinctness of habitats within a niche can be based on the relative abundance of all species in the community to estimate the degree to which a given habitat contributed to the heterogeneity of the distribution of all species over all habitats (Colwell and Futuyma, 1971). Therefore, besides the presence of a species, also its (relative) abundance is important in the niche concept.

In this perspective, the density of *L. conchilega* can be viewed as an important factor determining niche breadth of associated species. As such, *L. conchilega* is expanding niche breadth rather than expanding the realized or actual niche. Elaborating further on the niche concept, the virtual or fundamental niche is defined by a multidimensional space built up by all relevant environmental ranges which the species can live in (Hutchinson, 1957). If we apply this hypervolume idea of the niche concept to the 'babushka-like' community pattern, then *L. conchilega* is adding another environmental variable (through its ecosystem engineering effects) to the multidimensional space that will define the fundamental niche of associated species. In other words, *L. conchilega* is then to be considered as an essential variable to map the fundamental niche of several species, *i.e.* the multidimensional space of an associated species is larger when taking the presence of this ecosystem engineer into account. However, it is still the realized niche that defines the actual distribution of the associated species. The realized niche is most often seen as a subset of the fundamental niche and this subset is defined by the interactions between species (Colwell and Futuyma, 1971, Hutchinson, 1957). Therefore, the species-specific interactions described in Chapter 2 define the realized niche within the enlarged multidimensional space an associated species can potentially occur. Finally, the eventual diversity and relative abundances in the reefs can potentially be interpreted with stochastic niche theory (Tilman, 2004). Within this framework, (1) community structure results from the success or failure of propagules of potential associated reef species; (2) the successful settlers must be able to grow and survive long enough to become reproductively successful adults while using the resources left unconsumed by established species and (3) the probability of successful settlement depends on how different a potential settler is from established species. Based on the insights in the ecological implications of ecosystem engineered habitats for demersal fish, biogenic habitats should also be included as a factor that shapes the multidimensional niche space of these fishes. This is of potential importance to integrate in species distribution models (SDMs) (*cf. infra*).

Resilience and resistance

Resilience is defined as the capacity of a system to renew and sustain specified conditions or processes in spite of exogenous disturbances or changes in driving forces (Carpenter and Folke, 2006). Ecological resilience assumes that an ecosystem can exist in alternative self-organized or "stable" states (Peterson *et al.*, 1998). The stability of an ecosystem's ecological functions is determined by the presence or absence of so-called driver species (Walker, 1995), which can take many forms such as ecosystem engineers (Peterson *et al.*, 1998). As shown in Part I and Addendum I, the *L. conchilega* system is defined by several drivers in the system: *L. conchilega* itself as well as the closely associated species. In part II, Chapter 4 quantifies the impact of physical disturbance for *L. conchilega* in a fully controlled experimental approach. Results indicate that the direct impact (*i.e.* mortality) of this particular ecosystem engineer occurs only after several subsequent disturbances. The impact of a one-off experimental beam trawl disturbance of fauna associated with intertidal reefs was studied in Chapter 5. It confirmed that closely associated species of *L. conchilega* reefs are impacted by beam-trawl fisheries. The intertidal study hypothesizes that the tightly associated species are impacted when subtidal reefs are beam-trawled. It was later confirmed in a subtidal experiment with a similar set up (Gamarra, 2008, Vanaverbeke *et al.*, 2009b). 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. Generalizing, the effect of beam trawling on the associated fauna follows two main lines: on the one hand you find vulnerable species that are negatively affected and of which the recovery can either be fast or slow. On the other hand you find 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. We emphasize here that the experimental studies to quantify physical disturbances (Chapter 4 and 5) remain difficult to translate to real-world scenarios as different chains, nets, weights and velocities are often applied (Fonteyne, 2000). The impact on the associated fauna is significant and it can be hypothesized that the reefs would as well be a good precursor for the settlement of longer living and slower growing epifauna. Translating experimental results from the intertidal to the subtidal is not always straightforward, but general patterns have emerged during this thesis. The settlement of longer living epifauna has been suggested for *M. edulis* (*cf. Infra* and Chapter 1) but may be true for several other species that are not able to maintain a healthy population under the current beam trawl activities. There is currently no information available on the further development of *L. conchilega* reefs under undisturbed conditions. Physical disturbances of beam trawl fisheries may have consequences for the functioning of the ecosystem.

The quantification of the resistance towards human activities (*in casu* fisheries) contributes to the knowledge on its resilience is an important step to progress to the ecosystem approach (*cf.* Figure 2). These activities can potentially be managed in such way to maintain the ecosystem's integrity.

The value of an important ecosystem engineer

The use of single species in conservation strategies has been proposed earlier by labelling them as 'surrogate species' (e.g. umbrella or flagship species). They have been defined as species whose requirements for persistence are believed to encapsulate those of an array of additional species (Lambeck, 1997). As discussed in Chapter 8, surrogate species can be considered legitimate conservation targets on their own (Favreau *et al.*, 2006) as well as being effective in the selection of networks of areas for conservation (Larsen *et al.*, 2007). However, application proves difficult, especially in the marine environment (Rees *et al.*, 2006). Moreover, umbrella and flagship species are popularly used in conservation strategies as surrogates for regional biota whose spatial distributions are poorly known. The choice of surrogates is often *ad hoc* and assumptions underlying those choices are usually not explicit and it has been argued that the utility of umbrella and flagship species as surrogates for regional biodiversity may therefore be limited (Andelman and Fagan, 2000). Therefore, *L. conchilega* cannot serve as a 'surrogate species'.

Appointing a species as an 'indicator' for nature value is another option, though the 'indicator label' has been brought under question as well, as ambiguous selection criteria and the use of inappropriate taxa is often the case. Moreover, taxa at high taxonomic levels are often suggested as indicator, especially for invertebrate taxa, including many unnecessary or even inappropriate species. Therefore, if indicators are to be chosen at species level, vertebrate species are often chosen as indicator, but they lack generally established tolerance levels and are not always directly impacted by ecosystem changes. Most suggested vertebrates serve other agendas while they lack characteristics desirable for indicator taxa (Hilty and Merenlender, 2000). Nevertheless, while traditional conservation efforts are focusing on charismatic species, the species that are the most critical in retaining community and ecosystem integrity and function are the ecosystem engineers that provide stress amelioration and associational defenses, and these should be the primary target of modern conservation efforts (Crain and Bertness, 2006). Therefore, *L. conchilega* should rather be viewed as an important ecosystem engineer that does not need to be protected as a species but because of its value in the functioning of the ecosystem. Labelling it as an 'indicator' does not seem the ideal way to protect the engineered 'reefy' habitat.

The value of *L. conchilega* lies in its numerous links to different ecosystem levels, in its apparently important function in the ecosystem and in its implications for biodiversity (*i.e.* its effect on the niche breadth of several species). Bouma *et al.* (2009) indicate that coastal sediments in temperate locations are strongly modified by ecosystem engineers that shape the coastal sea and landscape and control particulate and dissolved material fluxes. The modifying effect is often most pronounced if several individuals manage to establish together and as such synergistically succeed in modifying the environment (Bouma *et al.*, 2009). These authors divide coastal ecosystem engineers into two groups; either creating autogenic structures (epibenthic engineers achieving high diversity at the expense of endobenthos) or realizing allogenic sediment reworking (endobenthic engineers facilitating infauna but inhibiting epibenthos). This division is based on whether they spend most of their lifetime above or below the sediment. The most dominant epibenthic ecosystem engineers inhabiting temperate coastal sediments are reef building filter feeders or dense vegetations of sea grasses, macroalgae or salt marsh species. The epibenthic ecosystem engineers modify the sedimentary habitat mainly through their physical structures (Bouma *et al.*, 2009). The modulation effects of *L. conchilega* as described in this thesis (Chapter 1, 2, 3, 6 and 7) suggest that this ecosystem engineer acts primarily as a true autogenic ecosystem engineer. However, the increase in epibenthic associates does not seem to be at the expense of endobenthic associates. This is attributed to the fact that it is not possible to conclude whether *L. conchilega* spends most of its lifetime above or below the sediment. The protruding part of the tube above the sediment modifies the sedimentary habitat mainly through the creation of distinct physical structures (Chapter 2, 3) while the buried part influences the local physical and biogeochemical environment (Chapter 1, 2, 3). A habitat dominated by a principal autogenic or allogenic ecosystem engineer is expected to create a highly diverse benthic assemblage (Bouma *et al.*, 2009). This is confirmed in this thesis for *L. conchilega* which acts both as an autogenic and an allogenic ecosystem engineer (Godet *et al.*, 2008).

Lanice conchilega is considered an important ecosystem engineer, and provides the template for other ecosystem processes, making *L. conchilega* useful within a conservation context. Therefore, it is necessary to investigate under which status this ecosystem engineered habitat can potentially be used within marine management strategies and conservation policies.

Labelling the ecosystem engineer *Lanice conchilega*

Persistent emergent structures in aquatic environments are often referred to as ‘biogenic reefs’, rather than appointing surrogate or indicator species (*cf. supra*). Because of their ecological functions, marine reefs have received considerable attention, both from scientists and policy makers and they are a good proxy for MPA-design. As *L. conchilega* aggregations show similarities to structures that have been qualified as reefs before, this thesis tested whether aggregations of the species can theoretically qualify as reefs (Chapter 3) and discussed what the possible implications are for MPA-design (Part IV). Though the concept is easy to understand intuitively, several definitions are still being applied to the reef-concept. The danger now exists that the necessary shift from charismatic species protection to a more holistic ecosystem based preservation approach is evolving towards the protection of 'charismatic habitats'. Chapter 3 therefore evaluates the different reef criteria, starting from the reef definition of the EU Habitats Directive (Interpretation Manual EUR27). However, as is discussed in Chapter 9, when it comes to real policy making, there has been some reluctance to protect *L. conchilega* aggregations as reefs, even though there is sufficient scientific evidence to state that (1) *L. conchilega* aggregations have considerable reef characteristics and (2) the label 'reef' will lead to a more successful protection of the habitat of concern. The protection of *L. conchilega* habitats can never downgrade the protection of other more charismatic or rarer habitats. As indicated above, flagship species do have an important conservation value, and 'charismatic habitats' certainly do have too. The thesis aims at providing the information upon which it is possible to use a common ecosystem engineer as complementary target in modern conservation efforts as the reefs are shown to be important in retaining community and ecosystem integrity and function. The scientific interpretations provided in the thesis may therefore not be considered as an obligation to protect these systems in all European Member States. On the contrary, the solid scientific basis can be used as an opportunity to evolve towards the ecosystem approach (Figure 4), fully complementary to the protection of other habitats and species. The effective implementation of measures based on this information is up to decisions makers. Although the EU Habitats Directive leaves some room for flexibility, the interpretation of the Directive proofed conservative in the case of *L. conchilega* until now. In other words, the application of the ecosystem approach to marine management is possible but it is not an explicit requirement within the Habitats Directive. However, in the future, this ecosystem approach will become necessary and will be applied through the Marine Strategy Framework Directive. Meanwhile, the use of the recent insights in *L. conchilega* reefs in conservation strategies will not lead to downgrading the reef label or the protection of other habitats and a more flexible interpretation of environmental law is needed (Chapter 9). This interpretation has still to be robust as there is a risk of undermining the final goal of environmental legislation if increasing flexibility would be translated into looser protection.

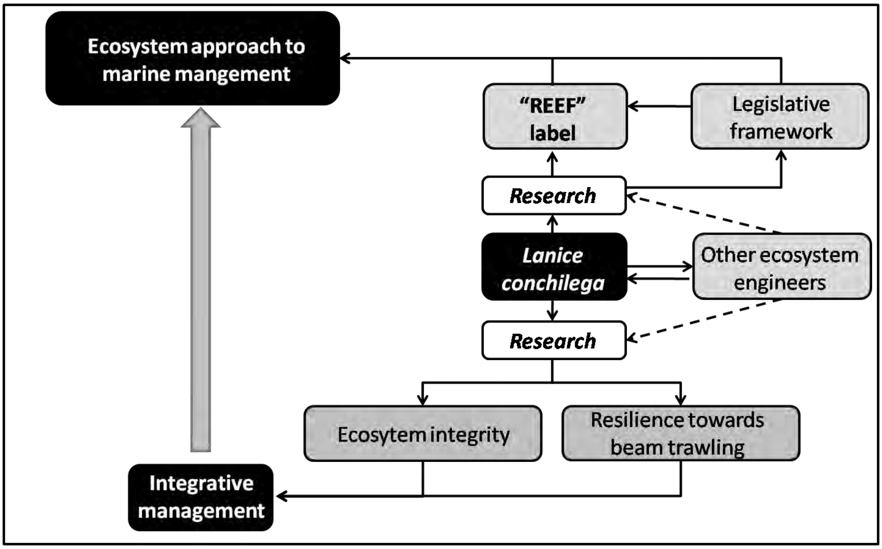

Figure 4. Flow chart representing the use of Lanice conchilega *within the context of an ecosystem approach to marine management, using the „reef label' to indicate and protect the functional value of the habitat created by* L. conchilega *aggregations rather than protecting the ecosystem engineer itself.*

Tube worm reefs

The preservation of bioconstructions created by tube worms is not new. Throughout Europe, several examples exist of tube worm aggregations that are protected under the 'reef label' (*cf.* Interpretation Manual of European Union (EUR27) of the EU Habitats Directive (EEC/92/43)). These examples are considered here as important cases against which the results of this thesis can be discussed. Therefore, the characteristics of the common reef building polychaetes *Sabellaria alveolata* and *Sabellaria spinulosa* (already listed in the Interpretation Manual) are discussed in detail together with those of *L. conchilega.*

Sabellaria alveolata is a filter feeding species commonly occurring along the European coasts (Dubois *et al.*, 2009, Dubois *et al.*, 2006, Dubois *et al.*, 2002). Reefs occur mainly on the bottom third of the shoreline and in the shallow subtidal (Holt *et al.*, 1998). *Sabellaria spinulosa*, on the contrary, is found almost entirely in the subtidal (Holt *et al.*, 1998).

The unique nature of the diverse assemblages found on bioconstructions of the ecosystem engineer *S. alveolata* is not related to the presence of particular species but it is rather owing to the juxtaposition of species belonging to surrounding communities (Dubois *et al.*, 2002). Moreover, biodiversity decreases again when very high densities are reached (so called 'platform-reefs') (Dubois *et al.*, 2002, Porras *et al.*, 1996). More or less the same structuring function on the benthic species composition was found for *S. spinulosa*, where no unique species have been found (Hendrick and Foster-Smith, 2006), though the reefs can have a considerable influence on the benthic community structure (Holt *et al.* (1998) and references therein). It has been suggested, however, to use biodiversity measures to distinguish the reef, as it is exactly this biodiversity aspect that made reefs listed under the Annex I of the Habitats Directive (Hendrick and Foster-Smith, 2006). The same authors suggest using multivariate analyses of the infaunal data to have a better indication of the distinctness of reef community. An analysis from the southern North Sea indicated significant community differences, where the similarity in community structure was found to be highest amongst the grabs with the highest density of *S. spinulosa*. This structuring effect is very much the same as the one described for *L. conchilega* in Chapter 2, and as found by several other authors (see Chapter 1). As such, *Sabellaria* species aggregations seem to expand the niche breadth of several species of the benthic community of the surroundings. For the demersal flatfish species *P. platessa* and *S. solea*, the most important polychaete prey species are *Owenia* sp., *Pectinaria* sp., *Lanice* sp. and *Nephtys* sp. while *Sabellaria* sp. was less frequently as prey (Rijnsdorp and Vingerhoed, 2001). Moreover, *M. edulis* and *S. alveolata* often occur together, and in many areas one or the other may be dominant at different times. It has been suggested that as both species depend on very heavy recruitment to form dense beds, stochastic factors affecting larval recruitment contribute to the dominance of one or the other species (Holt *et al.*, 1998). The settlement of larvae and juveniles may be enhanced by the adults of both species, but once settled they appear to use the same niche and become competitors. This competition is probably basically for space and to a lesser extent for food as competition for food between filter feeders is limited owing to differences in particle capture and selection (Lefebvre *et al.*, 2009). This relation is very similar to what have been found with *L. conchilega* reefs and *M. edulis* in the intertidal (for details: *cf.* Chapter 1). The influence of large polychaete populations in shallow coastal waters is often underestimated and further investigations are needed to determine their ecological role in the coastal food web (Dubois *et al.*, 2009).

Both *Sabellaria* species are able to considerably modify the physical environment. The elevations created by dense aggregations are significant and reach large dimensions (*S.*

spinulosa was found to reach 10-15 cm (Hendrick and Foster-Smith, 2006) and has been reported to grow up to 60 cm high (Holt *et al.*, 1998); *S. alveolata* is reported to reach regularly 50 cm thickness (Holt *et al.*, 1998)). *Sabellaria alveolata* builds its tube of selected inorganic particles (Gruet (1984) as cited in Dubois *et al*. (2005)) and the tube of S. *spinulosa* is constructed out of sand-sized particles (tube sediment mean = 297.8 μm) which the species actively selects for (Davies et al., 2009). The *S. alveolata* tube is built up as two to three concentric layers (Fournier *et al.*, 2009). The concretion is formed by the biogenic matrix of the worms that induce a coalescence of substratum that is different from the surrounding unconsolidated sediment. For *L. conchilega*, Jones and Jago (1993) already reported that the rigidity modulus increased by up to 88% as a consequence of aggregations of *L. conchilega*. They suggest that *L. conchilega* tubes act to increase sediment rigidity as do rigid steel rods to reinforce concrete. The strength of the tube walls clearly compensates for the weakness of the hollow burrows. In Chapter 3, the consolidation of the sediment was directly measured in the field showing that reefs are different from the surrounding unconsolidated sediment. The same chapter also points out that *L. conchilega* reefs show a significant elevation (generally +/- 10 cm and they can reach 45 cm (Carey, 1987) and even up to 80 cm (Holt *et al.*, 1998)). Furthermore, intertidal reefs of *S. alveolata* and *L. conchilega* have both far reaching consequences on the texture and distribution of intertidal sands (Figure 5) (Fournier *et al.*, 2009). The reef systems create a barrier effect in a very similar way, leading to the formation of a sand sheet in the fore-reef and mobile (mud rich) sand bars in the back reef. The position and orientation of the sand sheets and bars is slightly different and *L. conchilega* acts as a more efficient carbonate trapper (*cf*. tube build up).

Concerning the procreation, *S. alveolata* is spawning semi-continuously with 2 peak periods (May and September), though very high interannual variation in the reproductive effort has been reported. The larger scale distribution of the pelagic larvae is highly dependent on the local abiotic conditions (Dubois *et al.*, 2007a). Larval supply is considered very important for the maintenance of reefs (Ayata *et al*. (2009) Holt *et al.* (1998) and references therein) as they show a preferential settling on tubes of conspecific adults (Dubois *et al*. (2002) and references therein). They will, however, also settle on other calcareous and non calcareous substrata (Holt *et al.*, 1998).

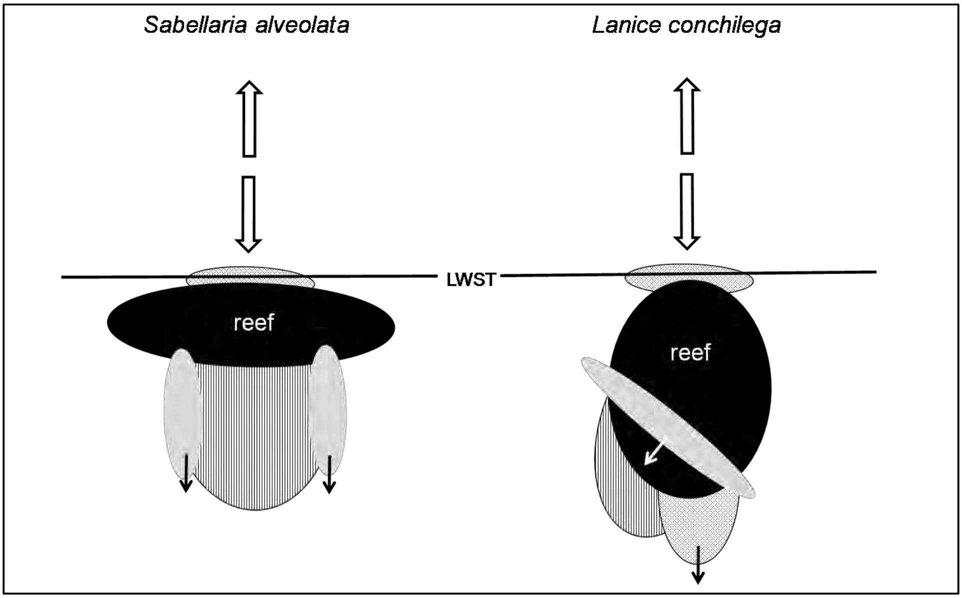

Figure 5. Sedimentary diagrams of Sabellaria alveolata *reef (left) and* Lanice conchilega *reef (right). The line represents the low water spring tide level (LWST) with the white block arrows indicating tidal directions; both reefs (in black) have a sand sheet in the fore reef (dotted grey) while mobile sand originate in the back reef (light grey, grow direction indicated with arrow) together with an organic rich mud flat (striped grey). Diagrams taken with permission from Fournier et al. (2009).*

Analogously, the reproduction peak of *L. conchilega* takes place in spring followed by two smaller peaks in summer and autumn (Van Hoey, 2006). A high interannual variation of larval supply exist (Strasser and Pieloth, 2001) and there is a preferential settling on conspecific adult tubes (Callaway, 2003a) (*cf.* Chapter 1). It has been suggested that, in some cases, there is a link between the settlement of *Sabellaria sp.* and *L. conchilega* as the latter is thought to stabilize sand sufficiently to allow subsequent colonization by *S. alveolata* (Larsonneur (1994) as cited in Holt et al. (1998)). It was speculated by Holt *et al.* (1998) that the same process might be possible with *S. spinulosa* too, since *L. conchilega* and *S. spinulosa* are sometimes found together. In the intertidal area of the Bay Mont-Saint-Michel *S. alveolata* and *L. conchilega* do co-occur, but reach high abundances in distinct geographical locations within the Bay (pers. obs.). Co-occurrence of high density aggregations of both species is uncommon, but does exist.

Larval transport and potential distribution is determined by abiotic factors as hydrodynamic forces and sedimentological characteristics while the occurrence of adults and a strong recruitment seem to be of importance for the continuity of the reef structure. Swift degradation of reefs can therefore be expected in some locations. A broad-scale UK-wide study showed that *S. alveolata* can appear and disappear from one year to another (Frost *et al.*, 2004). The authors indicate that more research is needed to have an idea on the natural cycles of variation in abundance and to understand how various (natural and anthropogenic) factors interact in controlling the distribution of *S. alveolata*. Episodic events of massive settlement are known to alternate with poor larval supply (Dubois *et al.*, 2007a), but in the longer run reefs can reoriginate at the same spot as evidenced for the Bay of Mont-Saint-Michel (Audouin and Milne-Edwards, 1832). Little is known about the stability of *Sabellaria spinulosa* reefs though Holt *et al.* (1998) state that it is likely that stability of the reefs is to some degree a function of stability of the substratum and they hypothesize that reefs will last longer in firm mixed sediments than in mobile sands. In the UK, extensive reef formations that were previously localized seem to have disappeared from year to year (pers. comm. V. Hendrick). Visualization of the reefs is possible with high resolution side scan sonar imagery (Hendrick and Foster-Smith, 2006), though it is not as useful as previously expected as the technique sometimes fails to distinguish reefs that are built up from sand-sized particles (pers. comm. V. Hendrick). For *L. conchilega,* the lack of knowledge on the stability and longevity of the features - together with the lack of evidence at that time about the consolidation impact of the features – was the main reason why Holt *et al*. (1998) did not evaluate *L. conchilega* in their reef review. The lack on long term data to estimate the temporal reef characteristics has been discussed in Chapter 3. However, in the Bay of Mont-Saint-Michel, Godet *et al*. (2009b) evidenced that the most abundant areas remained stable over the last two decades. Moreover, historical records showed that in the longer run reefs occur at the same location in the Chausey archipelago (chronologically in Audouin and Milne-Edwards (1828) than in De Beauchamp (1923) as cited in Godet *et al*. (2009b) and finally in the thesis of Godet (2008)). Different mechanisms that allow for reef renewal are discussed in Chapter 1 and Chapter 3 and we hypothesize that subtidal systems are more stable. However, only long-term monitoring will provide direct explanation of the longevity of individual aggregations for which in the subtidal advanced remote sensing techniques can be used (e.g. for *S. spinulosa* reefs and *cf. infra* and Addendum II for *L. conchilega* reefs).

Despite the fact that *S. alveolata* (Dubois et al., 2009), *S. spinulosa* (Davies *et al.*, 2009, Holt *et al.*, 1998) and *L. conchilega* occur in turbid marine waters, there seems to be an upper tolerance limit of particulate matter in suspension above which the reef builders weaken. Although more individuals of the reef are filter feeding with increasing suspended particulate matter, the clearance rates of individual *S. alveolata* are adversely affected (Dubois *et al.*, 2009). As far as *S. spinulosa* is concerned, damage due to sediment plumes is less clear, since there is no knowledge of the effects of different particle size although the impact is assumed to be rather low (Holt *et al.*, 1998). Nevertheless, burial of reef-building Sabellariid worms –tested on *Phragmatomoma lapidosa* - induces significant mortality (Sloan and Irlandi, 2008). On the other hand *S. spinulosa* may also act as an important driving factor during recovery of previously dredged areas through the settlement in large numbers (Cooper *et al.*, 2007). In intertidal areas, *L. conchilega* is assumed to be impacted by very high concentrations of particulate suspended matter, especially when relatively large mud quantities are present (pers. obs. Bay of Heist). This can potentially be the result of sludge disposal in front of the coast. The same effects have been described for the subtidal (Witt *et al.*, 2004), where *L. conchilega* was absent from the disposal area, as were the associated macrofauna, leading to a loss of diversity and a decline in abundances. Although the species can survive repeated additions of settling material at the sea bed (Rees *et al.* (1992) and references therein), *L. conchilega* proofed to be very sensitive to disposal activities and only a slow recovery was to be observed. The zone North of the Vlakte van de Raan in the BPNS shows low *L. conchilega* densities but much higher *O. fusiformis* densities (Addendum III) which is possibly related to the very high turbidity. The high turbidity is attributed to both the vicinity of the Scheldt estuary and the Sierra Ventana sludge disposal site (Fettweis *et al.*, 2007, Fettweis and Van den Eynde, 2003, Van den Eynde and Fettweis, 2006).

In general, anthropogenic influences can strongly modify the engineering community by removing autogenic ecosystem engineers through e.g. bottom trawling (Bouma *et al.*, 2009). Dubois *et al.* (2002) state that degraded areas are more and more widespread in *S. alveolata* reefs either directly because of destructive manual fishing methods or indirectly through the impact of shellfish aquaculture. The anthropogenic activities cause a reduction in new recruit densities leading to significant damage to both the structure and the associated fauna of the system (Dubois *et al.*, 2006, Dubois *et al.*, 2007a). Holt *et al*. (1998) review the impact of bottom fisheries on *S. spinulosa*. The disappearance of the species in some areas in the Wadden Sea has been suggested as a good indicator for fishing intensity. Large areas in the North Sea with *S. spinulosa* reefs have been reported to disappear due to fisheries activities and commercial shrimp fisheries are known to search for *S. spinulosa* upon which they trawl for shrimps (Holt *et al*. (1998) and references therein). Vorberg (2000) found in a one-off experimental disturbance with a shrimp beam trawl that in the short-run, the reef structure itself does not disappear as the natural growth and capacity for repair is such that they can rebuild destroyed parts of their dwellings within a few days. The author indicates, however, that trawling in the medium to long-term can have consequences for the integrity of the reefs in the event of intensive fishing. It is also stated that fishermen try to avoid reef contact, because entanglement could damage their gear. This kind of attraction and repulsion towards reefs have been mentioned for shrimp fisheries and *L. conchilega* reefs too, where shrimpers on the one hand aim at fishing upon the reefs (*cf*. Versluys, pers. comm. in Degraer *et al*. (2009)) but on the other hand experience gear damage or loss because of cementation of nets (pers. comm. M. Van Elslande). The same shrimper attitude exists in the UK (pers. comm. R. Callaway). Furthermore, the impact of physical disturbance on *L. conchilega* reefs has been described in Part II of this thesis. The reef structure itself appears to be relatively resistant to fisheries impact (Chapter 4) while the associated reef fauna experience an immediate impact (Chapter 5). In the event of intensive beam-trawling, the reef structure will eventually disappear (Chapter 4). As such, beam trawl impacts on subtidal reefs seem to be similar. However, for both reef systems there is not enough detailed knowledge on the natural development processes in the reef to interpret the significance of the various abiotic and biotic factors and it is therefore still difficult to predict the recovery capacity (*i.e.* the elasticity) of the different reef systems.

Several specific characteristics of individual *S. alveolata*, *S. spinulosa* and *L. conchilega* seem to be very different, and the visual appearance of intertidal *S. alveolata* reefs appears to be more charismatic. The characteristics of aggregations of the tube dwelling polychaetes, however, are strikingly similar. They all significantly change the benthic community without hosting unique species, they build elevated bioconstructions, generate a biogenic concretion through an increased consolidation, change the sedimentary environment and they can appear and disappear very fast but they do all have similar mechanisms that enhance stability and longevity. Differences are certainly there when a reef of one location is compared with another and differences will also occur between different reef building species. The criteria to make the comparison are at hand and it is perfectly possible to rank specific reefs and to rank even the different reef builders (or interaction reef builder x location). The qualification as reef as such lies in the relative difference to the direct surroundings (*i.e.* 'what is locally gained?'). However, there is enough evidence to include *L. conchilega* aggregations in conservation strategies under the 'reef label', as it adds specific reef like features to the natural environment. It is clear that the occurrence of an opportunistic tube building polychaete should not always lead to conservation measures. Where high density aggregations contribute to the local ecosystem's integrity, however, preservation measures would effectively contribute to the ecosystem functioning. Prioritization between different habitats is possible and needed.

Other benthic tube building ecosystem engineers that occur in high density aggregations also proved to have habitat modifying effects (Eckman *et al.*, 1981, Fager, 1964, Gallagher *et al.*, 1983). An important ecosystem engineer will classify as reef builder if the biological and physical features of the aggregations are significantly different from the adjacent habitat and if there is some indication of stability. Different aggregating ecosystem engineers should therefore be evaluated in the same way as *S. alveolata*, *S. spinulosa* and *L. conchilega*. It is, however, still unclear what is the ideal scale to do so (e.g. biodiversity manifests itself on different levels). These questions arise when species as *Pygospio elegans* are considered. This small tube building polychaete is able to structure the local environment on a rather small short-term scale. The sediment was shown to be affected directly or indirectly by the amount of tubes present (Brey, 1991, Montserrat *et al.*, 2008). In a defaunation experiment, elevated structures were reported and attributed to the tubes that 'root down' the sediment, entrain mud particles and prevent it from eroding (Montserrat *et al.*, 2008). The impact on biodiversity is significant and relates generally to facilitation of bivalve spat settlement (Bolam and Fernandes, 2003, Van Colen *et al.*, 2008). The subsequent enhanced bivalve competition, however, leads to a rapid decrease in *P. elegans* and a disappearance of the physical structure (Bolam and Fernandes, 2003, Montserrat *et al.*, 2008, Van Colen *et al.*, 2008). Another investigated tube building ecosystem engineer in this thesis is *O. fusiformis* (Addendum III and Chapter 7). This species seems to create in some cases physical structures. The species is able to shape the macrobenthic community, though the effect is limited and not related to the density of the ecosystem engineer. Although a thorough analysis has not been done on all potentially important ecosystem engineers, it is clear that but a few will classify as true reef builders. Research on the functioning of these systems as well as research on different criteria will be important to use the right legal framework to come to an ecosystem approach to marine management (*cf.* Figure 3).

Mapping *Lanice conchilega*

One of the major problems in subtidal marine ecosystems is the relatively poor accessibility which is even more pronounced in coastal marine areas that consist largely of sedimentary sand banks and swales (Chapter 1), due to low visibility. Remote sensing plays an important role in the investigation of marine biodiversity patterns. The localization of distinct features is important both for further research of the structures and for monitoring purposes within an ecosystem based management strategy. As such, remote sensing can map marine biodiversity in a relatively rapid and cost-effective manner (Newman *et al.*, 2006). However, although small-scale patchiness in a soft-sediment environment is ecologically highly significant (Schlacher *et al.*, 1998), the resolution of remote sensing often fails to describe this small-scale patchiness. The first study in which there was an indication that subtidal *L. conchilega* could be visualized with advanced remote sensing techniques was performed northeast of the island of Helgoland in the German part of the North Sea (Bartholomä, 2006). This study used a two-frequency, two-channel side-scan sonar system (Klein 595 100/500 kHz) deployed at a vessel speed of 4 knots with a sonar range of 150 m. This author found on specific locations a slight increase in signal roughness, which was attributed to the presence of *L. conchilega*, as proven from ground truth samples (Bartholomä, 2006). The visualization of *L. conchilega* reefs has been done by Degraer *et al.* (2008a) with the use of a side scan sonar (frequency 410 KHz, tow speed 4 knots and sonar range 50 m), a study that is included in this thesis (Addendum II). This study showed that areas with higher reflectivity, and a patchy and grainy acoustic facies coincided 'with reefs of the tube-worm *L. conchilega*'. The cemented sand grains and shell breccias in tubes (Ziegelmeier, 1952), the increased coarse sand fraction (Chapter 2), and the positive correlation between shear wave velocity and burrow density (Jones and Jago, 1993) are responsible for an increased sediment rigidity within *L. conchilega* reefs. This higher rigidity is believed to cause its higher reflectivity, as detected by side-scan sonar. We conclude that there are no major technical restrictions to use side scan sonar technology to map *L. conchilega* reefs. Multibeam technology did not detect the *L. conchilega* reefs (Addendum II) but patches of *O. fusiformis* could easily be identified with the use of multibeam imagery (Addendum III). In this addendum, repeated multibeam images over time were able to demonstrate the physical engineering capacity of tube building polychaetes. *Owenia fusiformis* is able to stabilize sand dunes that normally migrate 12 m a year (*cf*. Addendum III).

A complementary way to map an environment with patchy habitat characteristics is the relation with abiotic characteristics. If the habitat preference of a species can be modelled, the spatial distribution can be predicted on a full coverage scale from the environmental variables. However, Godet *et al.* (2009a) use 'Direct Field Observation' to map the intertidal zone and they show that a bias may exist when benthic habitats are mapped only using abiotic characteristics such as sediments and bathymetry. Nevertheless, the technique proved useful and the predictive power of the model will depend on the modelling techniques applied (Willems *et al.*, 2008) as well as on the quality of the full coverage environmental data that feed the model. This kind of species distribution modelling (SDM) can be done using generalized linear model techniques (GLMs), artificial neural networks (ANN) (Willems et al., 2008) or with model techniques based on maximum entropy (MaxEnt). This last technique generates 'maximum entropy models' and is a widely applicable technique to make predictions on the basis of incomplete information. This technique has been used to predict the spatial distribution of *L. conchilega* reefs in the BPNS (*i.e.* density threshold for 'reef presence' is 500 ind m^{-2}) (Degraer et al., 2009). The environmental variables that best predicted the distribution of *L. conchilega* reefs were silt content, maximum bottom current velocity, sea bottom slope, mean shear stress, the bathymetric position index and the rugosity. The area where reefs can be expected (Figure 6) coincides largely with the geographical position of the *A. alba* community (see Chapter 1). Therefore, according to this model, reefs can potentially occur in a large area, which is considered as an important insight to underpin potential conservation strategies (Degraer et al., 2009). The validation of such models with the real distribution of *L. conchilega* reefs may be done with side scan sonar imagery. This gives more insight in the driving forces behind the distribution of *L. conchilega* reefs in coastal areas. As such, the use of SDMs will allow us to potentially forecast anthropogenic effects on patterns of biodiversity at different spatial scales (Guisan and Thuiller, 2005), especially when validated with remote sensing data. An important remark here is that ecosystem engineers determine in part the niche breadth (*cf. supra*) and thus may be important in the prediction of the distribution of a species because SDMs are *de facto* quantifying the realized niche (Guisan and Thuiller, 2005). In other words, ecosystem engineers such as *L. conchilega* may become an important 'environmental variable' to predict the distribution of associated species. It has already been mentioned above that *L. conchilega* could be considered as an essential variable to map the fundamental niche of several species (*i.e.* the multidimensional space of an associated species is larger when taking the presence of this ecosystem engineer into account: *cf.* niche theory). This was tested in a preliminary MaxEnt model where *L. conchilega* has been used as an environmental parameter to predict the distribution of juvenile *S. solea* for which *L. conchilega* turned out to be the most important parameter (Vanaverbeke *et al.*, 2009a).

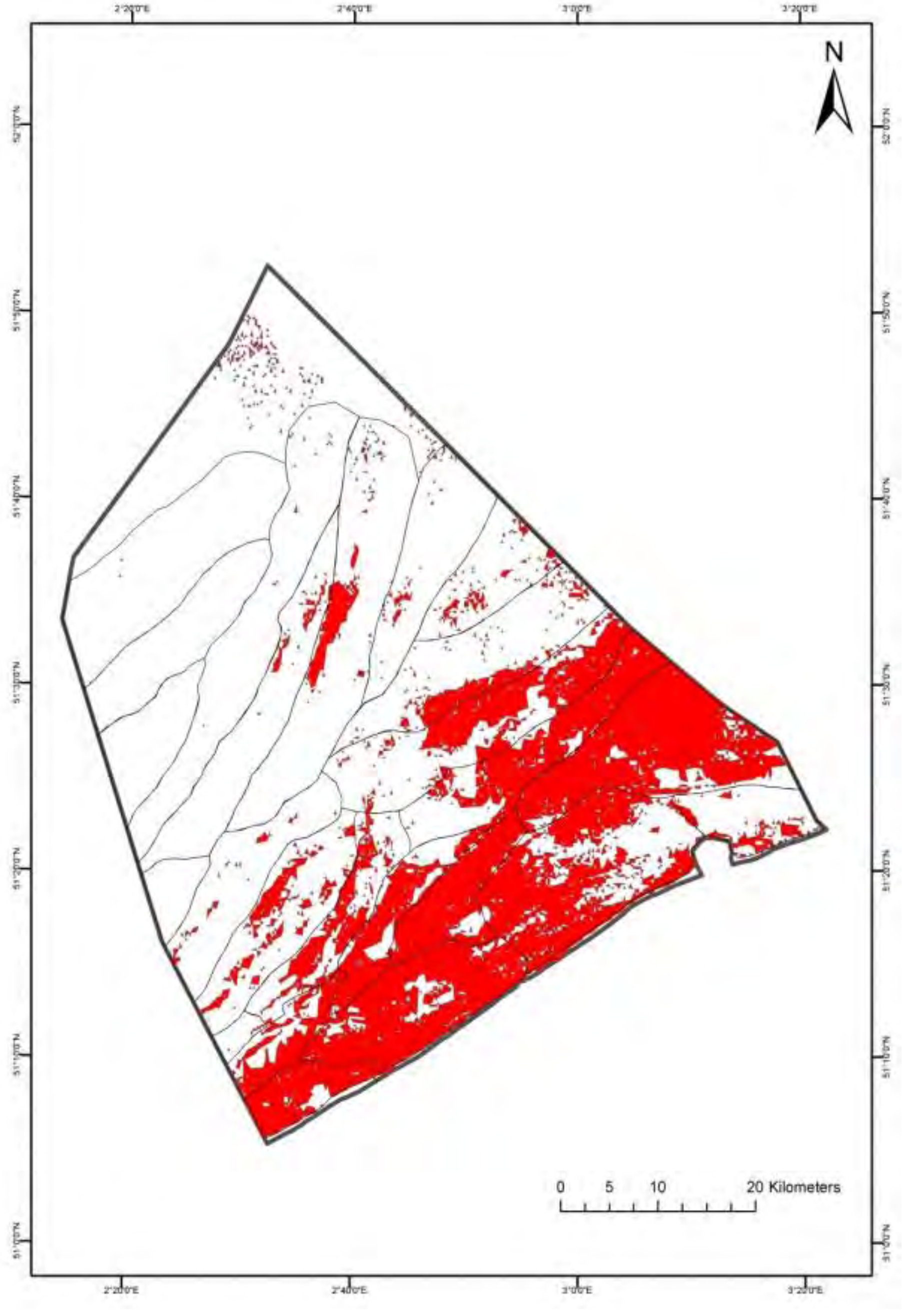

Figure 6. Predicted presence of Lanice conchilega *reefs (here defined as >500 ind m*$^{-2}$*) in the BPNS (based on MaxEnt habitat suitability model). The suitable area for* L. conchilega *reefs coincides with the geographical distribution of the* A. alba *community on the BPNS (see Chapter 1) (Degraer et al., 2009)*

Conclusions and outlook

The thesis addressed both ecological and conservation related questions in the framework of marine conservation strategies in soft-bottom temperate marine areas, focusing on a specific ecosystem engineer. The functioning of *L. conchilega* aggregations has been valued both for macrobenthic as well as for the demersal fish species and the consequences of anthropogenically induced degradations have been quantified. This thesis further elaborated its usefulness in a conservation context and proofs that this ecosystem engineer can be labelled as a reef building species for which a conservation framework is at hand.

The knowledge on the links between fisheries, marine conservation and *L. conchilega* is a useful basis to bring the ecosystem approach into practice in temperate soft-bottom marine areas such as the Belgian part of the North Sea. Quantitative results obtained in experiments and field work provided useful insights. Experimental results, however, are never easily translated to realistic systems where more factors play a role. This holds true for several experiments performed in this thesis (*cf.* mimicking fisheries disturbance, translating intertidal results to the subtidal, etc.). The impacts quantified in the theses are to be considered as an underestimation of the real-world impact. Dense aggregations of *L. conchilega* lose their high reef value when physically disturbed. As juvenile flatfishes make use of the reefs, habitat degradation is expected to result in effects on these flatfishes. These are –once grown to adults- target species of beam trawl fisheries.

Returning to the statement of Carpenter and Folke (2006), we conclude that *L. conchilega* is not only a model organism for studying the sediment-animal-interactions contributing to the strength of a benthic engineer in modifying its habitat and thereby affecting other species (Reise *et al.*, 2009), but it is also a useful ecosystem engineer within a conservation context. As such, the ecological knowledge built up in this thesis has the potential to contribute to the transition to more-resilient relationships between society and ecosystems.

Some answers generated during this thesis:

- *Lanice conchilega* is expanding the niche breadth of several species that otherwise only occur in very low abundances; *L. conchilega* is then to be considered as an important variable to map the fundamental niche of several species;

- Not only horizontal ecosystem effects on the macrobenthic species community exist, also positive vertical bottom up effects on juvenile flatfishes have been found in this work;
- The strategy of using small scale, short term studies on a limited number of species makes it possible to study a well defined area in a cost-efficient way;
- This thesis provides the information upon which it is possible to use a common ecosystem engineer as complementary target in modern conservation efforts as the reefs are shown to be important in retaining community and ecosystem integrity and function;
- The use of the common tube building polychaete *L. conchilega* within a conservation target lies in its value in the functioning of the ecosystem as an important ecosystem engineer rather than in protecting it merely as a species;
- *Lanice conchilega* can persist under intermediate beam trawl pressure but the integrity of a reef is hurt as the system as a whole degrades shortly after disturbance. Reduction of beam trawl fisheries to preserve this reef system is considered a valuable option. Furthermore, the reefs may serve as a precursor for longer living epifauna if physical disturbance decreases.
- Human activities that do not disturb the sea bottom (such as passive fishing techniques) are expected not to harm the integrity of the reef system.
- Fisheries management and marine conservation policy need to be fully integrated and decisions should be based on the insights in the marine ecosystem (*i.e.* ecosystem based);
- The information gathered in the case of *L. conchilega* is an example of ready-to-use information for the marine renewable resource management of the soft-bottom area of concern, taking the ecosystem approach into account;
- MPA-management and fisheries management show a sectorial approach at local as well as at international levels. A broader marine ecosystem management framework which addresses the complex relationship between habitat deterioration and

commercial fisheries is needed. In this framework, the results of this thesis underscore that a robust though flexible interpretation of environmental legislation in the marine environment is needed.

Some questions and hypotheses generated during this thesis:

- Current knowledge on reef development (Heuers *et al.*, 1998) use 'flow velocity' in a wide sense without being specific about mean velocity of near-bottom flow, maximum velocities, submersion time, wave impact and near-bottom turbulence. In the future, only empirical tests that are able to involve small-scale hydrodynamic measurements within the mosaic pattern together with experimental modifications of the local flow regime will provide the necessary insight in the formation of reefs. Comparison with more literature on the mechanisms described for other biota is undispensible;

- Single and multispecies laboratory flume experiments will provide more insight in the shelter function of the reefs for flatfishes;

- Knowledge on the autecology of associated macrobenthic species is crucial to have an idea on the exact nature of the relationships between species. This requires controlled experiments in which the influence of dynamic variables, e.g. recruitment success, competition for space, trophic interactions, inter-related variables as grain size, organic content, microbial content and food supply, is examined systematically.

- Full comparison with other reef building annelids as different *Sabellaria* species is needed (biological, physical, temporal characteristics) together with further study on their potential within nature conservation strategies;

- More research is needed to define what determines the recruitment success. Within future conservation strategies to protect the reefs, this aspect will be of high importance.

- Sludge disposal of dredged material is known to influence *L. conchilega*. Recent increase in mud content in the Flemish nature reserve Bay of Heist should be evaluated against disposal activities, together with the development of the reefs in the area;

- Further development of distribution models of *L. conchilega* through inclusion of ecological insights in the system and system dynamics (natural as well as anthropogenic). Moreover, a closer cooperation between spatial modellers, biogeographers, community ecologists, population biologists and ecophysiologists has been urged for in the terrestrial environment (Guisan and Thuiller, 2005), which should definitely be the case for the marine environment too, and more particular for the *L. conchilega* reef systems;

- More research is needed to quantify the economic trade-off of beam-trawling the reefs versus no bottom disturbance. Both fisheries data (geographical distribution of fishing activities) and a protocol to translate the results of impact studies in economic costs are needed.

- Repeated use of side scan sonar and multibeam imagery should be done to fine-tune their use in monitoring strategies and to create long term data to test for temporal stability of individual reefs;

- Following up the reef characteristics over time would provide insight in the seasonal and year-to-year variation of these reefy features. Ranges of biological, physical and temporal characteristics could subsequently be fine-tuned. This is also of importance for the conservation strategies to protect the reefs.

- Because the reefs may serve as a precursor for longer living epifauna if physical disturbance decreases, the necessary insights in the natural succession of this particular system can only be acquired through investigation of *in situ* natural reef development in the subtidal under reduced anthropogenic pressure (e.g. beam trawl ban).

ADDENDA

ADDENDUM I

Ecological implications of the presence of the tube building polychaete *Lanice conchilega* on soft-bottom benthic ecosystems

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Abstract

The common tube building polychaete *Lanice conchilega* is known as a habitat structuring species and can form dense aggregations. The effects of *L. conchilega* on the surrounding benthic community have received little attention, especially in subtidal areas. Therefore, the presence of *L. conchilega* in different habitats in the North Sea and its effect on the abundance, species richness, diversity and community structure in these habitats are evaluated in the present paper, based on data from the ICES North Sea Benthos Survey of 2000.

Lanice conchilega has a wide geographical distribution and a low habitat specialization, but optimally occurs in shallow fine sands. In the present study, the presence of *L. conchilega* resulted in a density increase and a significant (positive) correlation of the benthos density with the density of *L. conchilega*. Furthermore, the species richness (number of species) increased with increasing density of *L. conchilega*. This trend was, however, not consistent: the number of species reached more or less an asymptotic value or even decreased after reaching a critical density of *L. conchilega* (> 500 - 1000 ind/m^2), as observed in shallow fine sands. The same overall pattern was detected concerning the expected number of species. The N_1 - diversity index showed similar or slightly higher values in *L. conchilega* patches compared to patches without *L. conchilega*. From the results of the community analysis, it can be concluded that the species, which were responsible for the increase of the diversity, belonged to the overall species-pool of that habitat. The effects on density and diversity differed between the four discerned habitats (shallow muddy sand, shallow fine sand, shallow medium sand and deep fine sand), and were most pronounced in shallow fine sands. These patterns can be attributed to the habitat structuring capacity of *L. conchilega*. The mechanisms responsible for the increase of the habitat quality in patches of *L. conchilega* can be summarized as (1) changes in the hydrodynamics, (2) increases of the habitat stability and oxygen supply, and (3) a creation of habitat heterogeneity in a uniform environment. In this way, *L. conchilega* alters the habitat characteristics and affects other organisms, and can therefore even be considered as an ecosystem engineer. In other words, *L. conchilega* patches are responsible for an increased habitat quality in an otherwise uniform habitat, which results in a higher survival of the surrounding benthic species.

Key words

Lanice conchilega, geographical distribution, species diversity, benthos, habitat improvement, soft-bottom sediments, North Sea

Introduction

Biogenic habitat structures play a major role in structuring the distribution pattern of benthic fauna by modifying the sediment (Carey, 1987, Eckman *et al.*, 1981) and hydrodynamic parameters (Eckman, 1983), or by changing interactions between species (Woodin, 1978). Some tube-building polychaetes provide considerable structures in the otherwise relatively unstructured soft-bottom sediments (Bolam and Fernandes, 2002, Callaway, 2003b, Rees *et al.*, 2005, Woodin, 1978, Zühlke, 2001, Zühlke *et al.*, 1998). An example of a structuring tube-building polychaete is the sand mason, *Lanice conchilega*, which lives in a tube of sand or shell breccias attached to an inner thin organic layer. The tube itself is crowned with a sand-fringe, which protrudes 1 - 4 cm above the sediment surface (Ziegelmeier, 1952). This species can reach densities of several thousands of individuals per square meter (Buhr and Winter, 1977, Ropert and Dauvin, 2000, Van Hoey *et al.*, 2006), is found on all European coasts and colonizes a wide variety of intertidal and subtidal sediments down to about 1900m (Hartmann-Schröder, 1996, Ropert and Dauvin, 2000).

Despite its wide distribution and the formation of sometimes dense aggregations, the effects of the presence of *L. conchilega* on the surrounding benthic community have received little attention. The interaction between *L. conchilega* and the benthos was previously described by Zühlke *et al*. (1998), Dittmann (1999) and Zühlke (2001) on two sandflats of the East Frisian Wadden Sea (the Gröninger Plate and the Dornumer Nacken). These studies also described some experiments on the effect of artificial tubes on the benthos. Both studies concluded that the benthos in tidal flats has a temporary and optional association with the tubes of *L. conchilega* and that the presence of such structures enriched the *Arenicola*-dominated sandflat association in abundance and species numbers. This indicates that *L. conchilega* is a habitat structuring species, which affects the surrounding benthic community. In the study of Callaway (2006), on an exposed beach in South Wales, it was concluded that not only groups of tubes, but also single polychaete tubes affect the environment. This ability can be attributed to the following mechanisms (Callaway, 2006): (1) the tubes provide a settlement surface for larval and post-larval benthic organisms (Qian, 1999), (2) there is an improved oxygen supply in the sediments surrounding *L. conchilega* tubes (Forster and Graf, 1995), (3) the tubes affect the current velocities in the benthic boundary layer (Eckman *et al.*, 1981, Heuers *et al.*, 1998, Hild and Günther, 1999), (4) the tubes have a stabilizing effect on the sediment, and (5) the space between tubes can serve as a refuge from predation (Woodin, 1978).

Nevertheless, these conclusions were not confirmed for other habitats, especially in subtidal areas, where *L. conchilega* is widespread. A large-scale benthos survey, performed in the subtidal of the North Sea in 2000-2001 under the guidance of the Benthos Ecology Working group of ICES (Rees *et al.*, 2002, Rees *et al.*, 2007), provided an opportunity to focus on subtidal areas. The resulting dataset formed the basis of the description of the ecological implication of the presence of *L. conchilega* on some soft-bottom benthic ecosystems in the North Sea. In other words, the present study aimed to investigate the effects of the presence of *L. conchilega* on the abundance, species richness, diversity and community structure in different soft-bottom habitats in the North Sea, in view of the ecosystem engineering function of *L. conchilega*.

Material and Methods

Study area

The study area covers most of the English Channel and the North Sea (delimited by Norway and Denmark in the east, the UK in the west and Germany, the Netherlands, Belgium and northern France in the south). The North Sea (51° to 61° N, 3° W to 9° E) is divided into a number of loosely defined areas: a relatively shallow southern North Sea (Southern Bight and German Bight), the central North Sea (Doggerbank, Oysterground), the Northern North Sea, the Norwegian Trench and the Skaggerak, from which the last two areas were not included in the present study (Figure 1).

Data origin

Under the guidance of the Benthos Ecology Working group of ICES, a total of 2227 macrobenthic samples (1405 stations) were gathered in the North Sea and English Channel in the years 2000 or 2001. These data originate from various projects, including national monitoring surveys (Rees *et al*., 2002, Rees *et al*., 2007). The total dataset was used to describe the spatial distribution of *L. conchilega* in the North Sea. To enable detailed analyses on the effect of *L. conchilega* on the benthos, a uniform dataset was selected with only samples taken with a 0.1 m^2 Van Veen or Day grab and sieved alive on a 1 mm sieve. This resulted in a final dataset of 1098 samples (comprising 513 different stations).

All data was incorporated into a database, and taxonomic inter-comparisons were performed (Rees *et al*., 2002, Rees *et al*., 2007). These data modifications were executed during several workshops of the ICES study group on the North Sea Benthos Project 2000. After taxonomic clearance, a dataset consisting of 717 taxa (further referred to as species) was obtained. The density of *L. conchilega* in the present study is based on individual counts, rather than tube counts and should thus be considered as minimum counts (Van Hoey *et al*., 2006).

The sedimentological characteristics of the different samples were coded according to the following sediment classes: (a) mud, (b) muddy sand, (c) fine to medium sand, (d) medium to coarse sand, (e) sand and gravel, and (f) mixed sediments (Report ICES CM 2004/E:05). Additionally, water depth at each sampling station was recorded. The different habitat types were distinguished by sediment classes and bathymetrical information (shallow (< 70 meter) and deep (> 70 meter)) (following the benthic community analyses of Künitzer *et al*. (1992) and Rees *et al*., (2007)).

Data analysis

The effects of *L. conchilega* on the benthos were investigated for every habitat type in which the species was found and for which a representative number of samples (> 100) was available (Figure 2). This number of samples was chosen to exclude uncertainties in the results. The following univariate indices were used to describe the benthos (excluding *L. conchilega*) in each sample: (1) density N, (2) species richness S, expressed as number of species per sample (*i.e.* per 0.1 m^2), (3) the exponential form of the Shannon – Wiener index

N_1 (Hill, 1973) and (4) expected number of species (ES 50) (Hurlbert, 1971). The relations between those univariate indices and the density of *L. conchilega* in the different habitats were visualized based on different density classes of *L. conchilega* (defined in such way that they give the best reflection of the observed patterns). A Mann-Whitney U test was used to test for differences in the univariate indices between samples with and without *L. conchilega* and a Spearman rank correlation analysis was done to describe the correlation between the univariate indices and the density of *L. conchilega*. Non-parametric tests were used because the assumptions for parametric tests, even after transformation, were not fulfilled (Conover, 1971).

The benthic community structure within the different habitats was analyzed with non-parametric multidimensional scaling (MDS) on the fourth-root transformed dataset, in which the samples containing *L. conchilega* (group 1) and the samples without *L. conchilega* (group 2) were labelled *a priori*. Analysis of similarity (one-way ANOSIM) was used to test for differences between the two groups and SIMPER was used to investigate which species contributed most to the dissimilarity between the groups. These calculations were done with the Primer 5.2.9 software package (Clarke and Warwick, 2001).

Results

Distribution pattern

In 2000 - 2001, *Lanice conchilega* was found in the entire North Sea and English Channel (Figure 1) (25% of the stations). In the central English Channel, *L. conchilega* was seldom found (< 5% of the samples), whereas the species occurred frequently in the entire North Sea (42% of the samples). The areas with the highest frequency of occurrence and densities were the German Bight, the central part of the North Sea (east of the Dogger Bank) and along the French, Belgian and Dutch coast. In the deeper northern part of the North Sea, *L. conchilega* was frequently found, but in low densities (< 100 ind/m^2), whereas in the western North Sea, *L. conchilega* was seldom found and only in very low densities (< 100 ind/m^2).

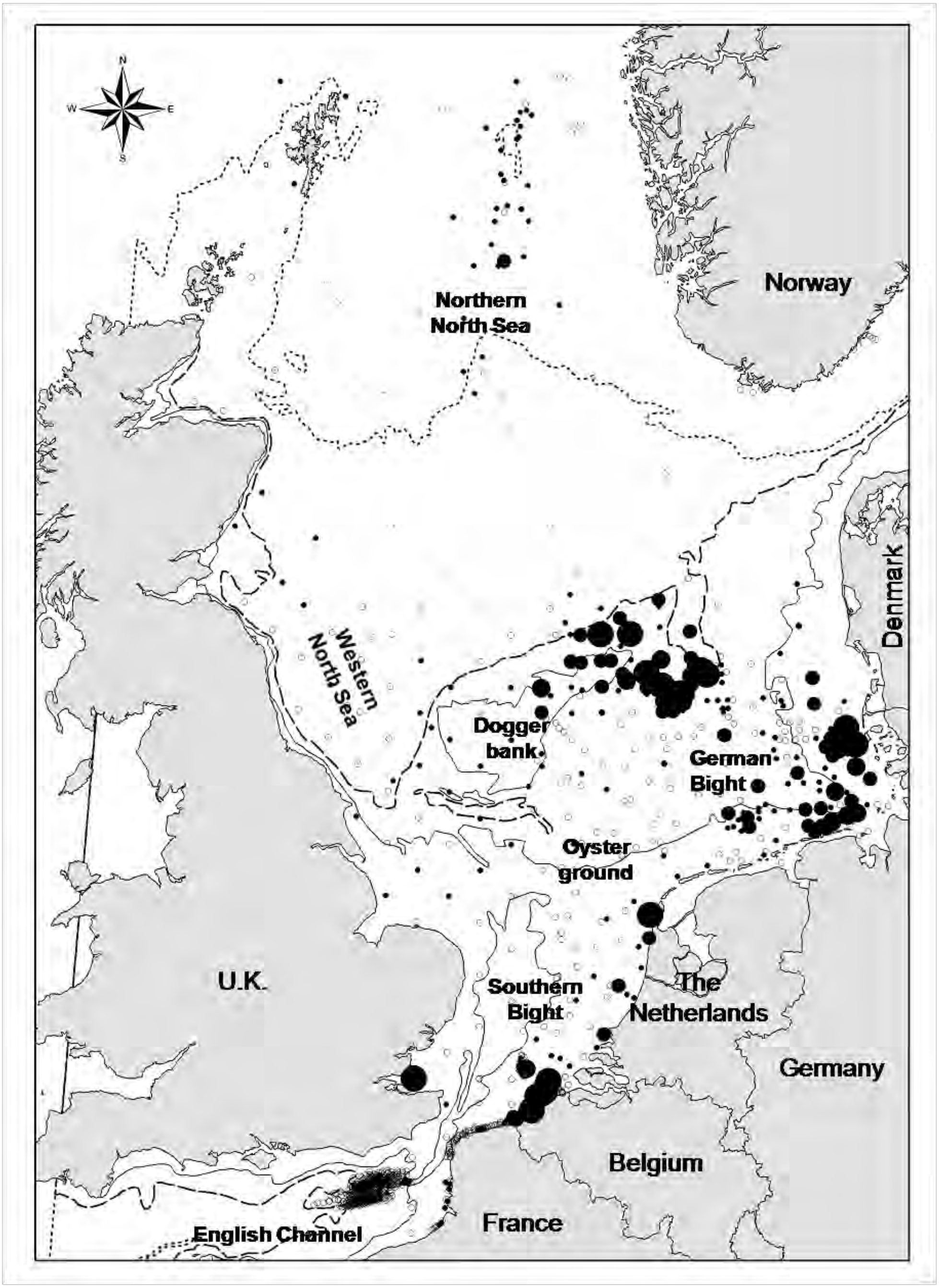

***Figure 1**. Density distribution of* Lanice conchilega *in the entire North Sea and English Channel. 0 ind/m^2: (○); 1-100 ind/m^2 (•); 100-500 ind/m^2 (●); 500-1000 ind/m^2 (⬤); > 1000 ind/m^2 (⬤)*

Habitat preferences

Lanice conchilega was found in most soft-bottom sediment types in the North Sea, with differences in frequency of occurrence and average densities between the discerned habitat types (Figure 2). No definitive conclusion of the occurrence of *L. conchilega* in shallow mud, deep muddy sands and deep medium sands could be made, due to the low number of samples in these habitat types (< 30 samples). As for the other habitats, the highest percentages of occurrence (41 - 51 %) and highest average densities (138 – 419 ind/m²) of *L. conchilega* in shallow areas were observed in mixed sediments, muddy and fine sand. In shallow medium and coarse sediments, the frequencies of occurrence (24 and 30%, respectively) and average densities (17 and 12 ind/m², respectively) were much lower. In deep muds and fine sands (> 70 meter), *L. conchilega* occurred frequently (53 and 45%, respectively), but in low average densities (32 and 14 ind/m², respectively). Although *L. conchilega* was found in all habitat types, for reasons of representativeness further detailed analyses were only done for habitats containing more than 100 samples (deep fine sand, shallow muddy sand, shallow fine sand and shallow medium sand).

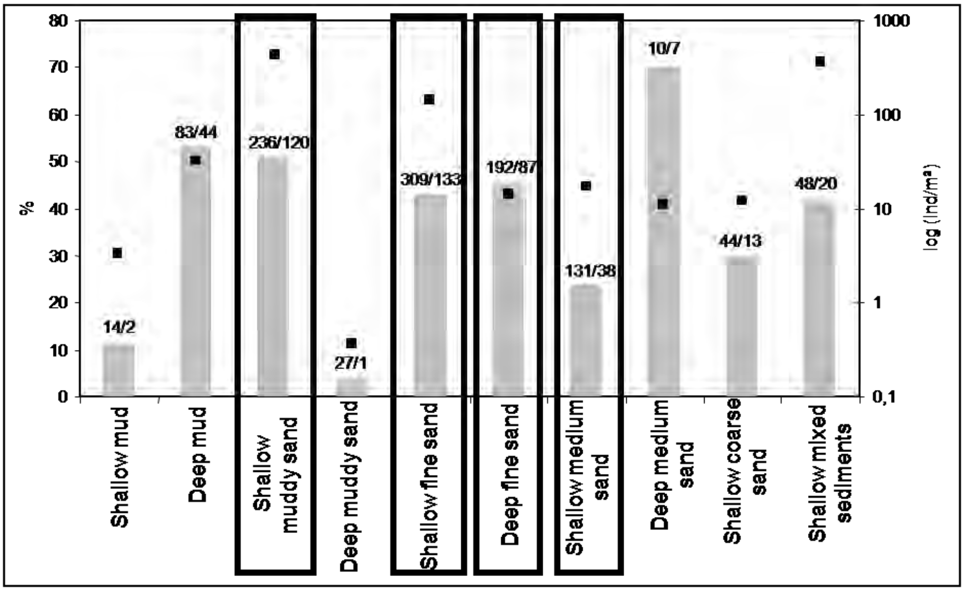

Figure 2. Percentage of occurrence (bars, left axis) and average density (log ind/m²) (squares, right axis) of Lanice conchilega *in the different habitat types (with indication of the total number of samples) versus samples with* L. conchilega*. The four habitats, which were represented by more than 100 samples in the database, were encircled.*

Effect of **Lanice conchilega** *on the benthic characteristics*

Presence / absence of **Lanice conchilega**

A highly significant difference ($p < 0.0001$) in benthic density and species richness (excluding *L. conchilega*) was found between *L. conchilega* samples and samples without *L. conchilega* in shallow muddy sands, fine sands and medium sands (Table 1). Those differences in density and species richness were significant in deep fine sands ($p = 0.0115$ and $p = 0.0027$). The N_1 - diversity index in *L. conchilega* samples differed significantly in shallow fine sands ($p < 0.0001$), medium sands ($p = 0.0012$) and deep fine sands ($p = 0.0225$). Only in shallow muddy sands, no significant difference was found ($p = 0.1299$). The ES(50) was only significantly different in shallow fine sands and medium sands ($p < 0.0001$).

Table 1. First, the differences tested in benthic density, species richness, N_1 -diversity and ES (50) by Mann-Whitney U test, between samples with and without Lanice conchilega *for the different habitats. Second, the Spearman rank correlation between the benthic density, species richness, N_1 -diversity and ES (50) and the density of* L. conchilega *for the different habitats. The number of observations (n) within each habitat where 236 for shallow muddy sand, 309 for shallow fine sand, 192 for deep fine sand and 131 for shallow medium sand.*

Habitats	Mann-Whitney *U*- test	Spearman rank correlation	
Density	*p*	R	*p*
shallow muddy sand	< 0.0001	0.45	< 0.0001
shallow fine sand	< 0.0001	0.63	< 0.0001
deep fine sand	0.011500	0.23	0.0013
shallow medium sand	< 0.0001	0.39	< 0.0001
Species richness			
shallow muddy sand	< 0.0001	0.4	< 0.0001
shallow fine sand	< 0.0001	0.65	< 0.0001
deep fine sand	0.002700	0.27	0.0001
shallow medium sand	< 0.0001	0.5	< 0.0001
N_1			
shallow muddy sand	0.129900	0.08	0.22
shallow fine sand	< 0.0001	0.39	< 0.0001
deep fine sand	0.022500	0.158	0.028
shallow medium sand	0.001200	0.36	< 0.0001
ES (50)			
shallow muddy sand	0.070000	0.08	0.22
shallow fine sand	< 0.0001	0.39	< 0.0001
deep fine sand	0.160000	0.17	0.17
shallow medium sand	< 0.0001	0.34	< 0.0001

Correlation between benthic univariate indices and density of **Lanice conchilega**

In the four habitats, the density of the surrounding benthos increased with increasing density of *L. conchilega* (Figure 3a). The increasing trend of the density was comparable in the four habitats. The correlation between the density of the benthic fauna and the density of *L. conchilega* was positive and significant in all habitats, but was strongest in shallow fine sands (Spearman R: 0.63) and was lowest in deep fine sands (Spearman R: 0.23) (Table 1).

Although species richness differed strongly between habitats, a significant positive correlation was found between the species richness and the density of *L. conchilega* in all habitats, with the highest value in shallow fine sands (Spearman R: 0.65) and the lowest in deep fine sands (Spearman R: 0.27) (Table 1). In shallow muddy sands, the correlation was atypical: the species richness decreased with higher densities of *L. conchilega.* In shallow muddy sands, the species richness decreased when the density of *L. conchilega* exceeded 1000 ind/m^2, while in shallow fine sands, the species richness levelled off at 500 ind/m^2 of *L. conchilega* (Figure 3b).

The N_1 -diversity index and its relation with *L. conchilega* density differed between the habitats (Figure 4a). In shallow muddy sands, the N_1 -diversity index did not increase with the *L. conchilega* density and did not show a significant correlation (Spearman R: 0.08; p = 0.22) (Table 1), whereas a minor, through significant to very high significant correlation was observed in the other three habitats. The strongest correlation was found in shallow fine sands (Spearman R: 0.39) (Table 1).

The trend in the ES(50) was comparable with that of the species richness (Figure 4b), with some small differences: (1) in shallow muddy sands and deep fine sand no increase and no significant correlation in ES(50) with the *L. conchilega* density was observed, (2) in shallow fine and medium sands an increase and a significant correlation (Spearman R: 0.39 – 0.34, respectively) was found, but the curve levelled off at 100 ind/m^2 in medium sands and decreased in fine sands when the density of *L. conchilega* exceeded 1000 ind/m^2.

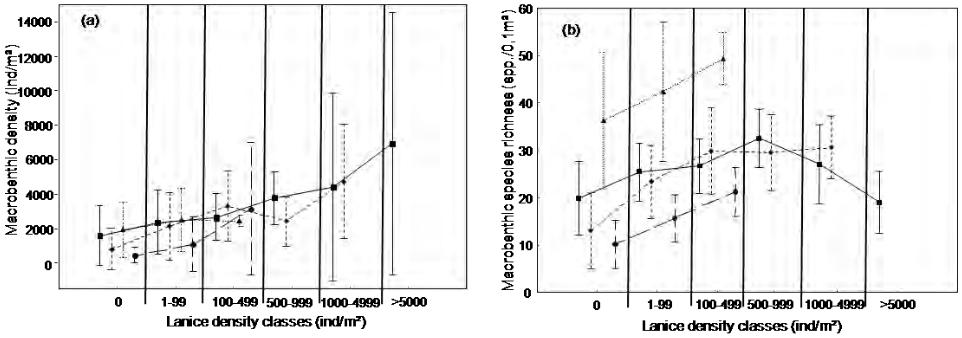

Figure 3. (a) The density (with exclusion of Lanice conchilega*) of the benthic species, versus the different* L. conchilega *density classes with indication of the standard deviation, and (b) the species richness (with exclusion of* L. conchilega*) of the benthic species, versus the different* L. conchilega *density classes with indication of the standard deviation. Shallow muddy sand: square; shallow fine sand: rhombus; deep fine sand: triangle; shallow medium sand: circle.*

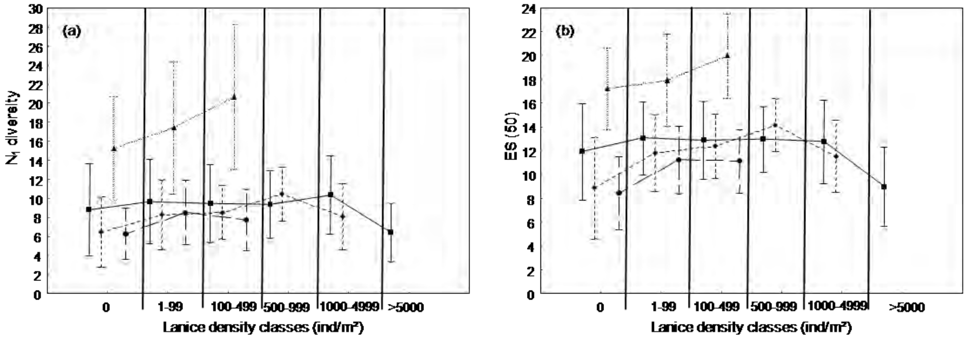

Figure 4. (a) The N_1*-diversity (with exclusion of* Lanice conchilega*) of the benthic species, versus the different* L. conchilega *density classes with indication of the standard deviation, and (b) the ES(50) (with exclusion of* L. conchilega*) of the benthic species, versus the different* L. conchilega *density classes with indication of the standard deviation. Shallow muddy sand: square; shallow fine sand: rhombus; deep fine sand: triangle; shallow medium sand: circle.*

Effect of **Lanice conchilega** *on the community structure*

When the community structure in the different habitats was visualized by MDS, it was clear that the samples containing *L. conchilega* individuals (group 1) were not clearly separated from the samples without *L. conchilega* (group 2), due to their central position in the MDS (Figure 5). The one-way ANOSIM analysis revealed that, for the four habitats, the two groups could be significantly distinguished ($p<0.05$). The R value was low, indicating a high overlap between the groups in all habitats (R = 0.125 for shallow fine sands [p = 0.001], R= 0.098 for shallow medium sands [p = 0.039], R = 0.097 for shallow muddy sands [p = 0.001] and R = 0.018 for deep fine sands [p = 0.048]). Based on the SIMPER results (Table 2), it became clear that the two groups were dominated by the same species, but with differences in their densities between the two groups. For most species their density was higher in the samples containing *L. conchilega* individuals. The average density of the species was 3 to 10 times higher in the samples with *L. conchilega* compared to the samples without *L. conchilega*, except in deep fine sand where the density differences were much lower (1.4 times) (Table 2).

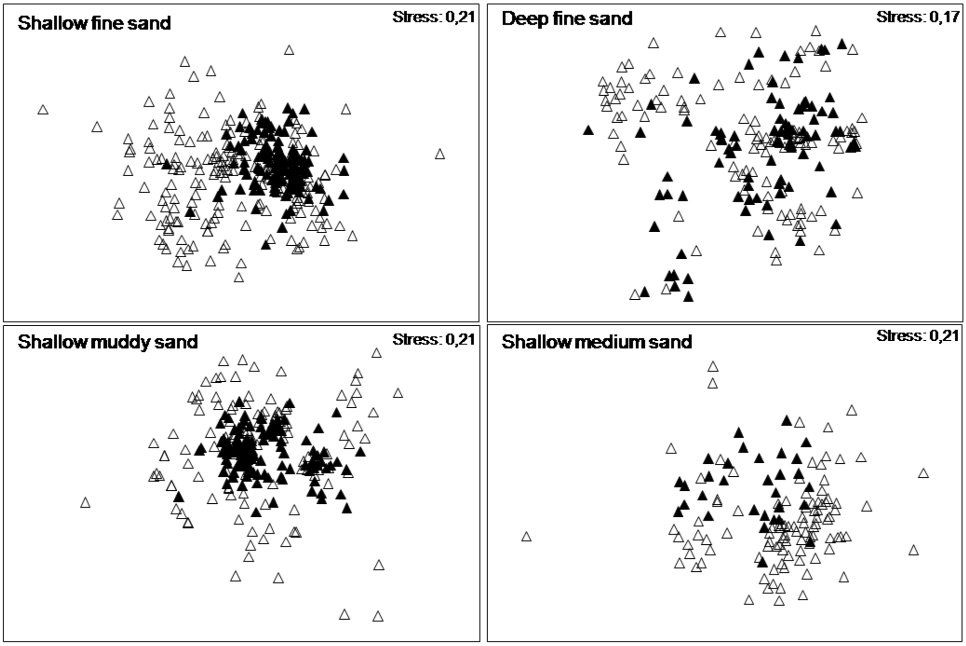

Figure 5. Two-dimensional MDS (Multi dimensional scaling) plot of similarities for the four habitats between samples with Lanice conchilega *individuals (black triangles) and samples without* L. conchilega *individuals (open triangles), with exclusion of the* L. conchilega *individuals.*

Table 2. SIMPER analysis: The first 25 species of the SIMPER species list, which contribute to the dissimilarity between group 1 (samples with Lanice conchilega*) and group 2 (samples without* L. conchilega*) for each habitat with indication of their average abundance (ind/m²) per group.*

Shallow fine sand			Deep fine sand			Shallow muddy sand			Shallow medium sand		
	Group 1	Group 2		Group 1	Group 2		Group 1	Group 2		Group 1	Group 2
Species	Av.Abund	Av.Abund	Species	Av.Abund	Av.Abund		Av.Abund	Av.Abund	Species	Av.Abund	Av.Abund
Spiophanes	601.01	66.15	*Myriochele*	497.47	452.76	*Amphicteis gunneri*	484.5	222.07	*Spiophanes*	651.06	51.23
Magelona	246.42	117.13	*Owenia fusiformis*	335.06	231.43	*Spiophanes*	388.08	102.4	*Gastrosaccus spinifer*	49.35	57.22
Bathyporeia	150.47	68.4	Pectinidae	279.66	220.38	*Mysella*	331.86	127.61	*Aonides paucibranchiata*	76.71	8.78
Tellina	145.6	29.2	*Spiophanes*	252.3	172.95	*Nucula nitidosa*	125.08	234.05	*Bathyporeia*	45.1	27.71
Ensis directus	263.18	23.73	*Amphicteis gunneri*	138.05	102.19	*Abra alba*	130.5	102.69	*Nephtys cirrosa*	35.58	51.51
Phoronida	115.49	124.32	Phoronida	100	44.95	*Corbula gibba*	75.5	92.59	*Scoloplos*	33.61	27.08
Echiurida	34.14	47.9	*Paramphinome jeffreysii*	42.07	28.57	Phoronida	136.17	32.84	*Spio*	30.48	13.28
Urothoe poseidonis	72.29	19.02	*Axinulus croulinensis*	32.87	23.9	Pectinidae	109.12	29.01	*Urothoe brevicornis*	14.13	12.35
Mysella	105.03	11.44	*Chaetozone*	33.1	24.1	*Magelona*	49.37	48.13	*Tellina*	9.26	20.8
Amphicteis gunneri	71.2	26.93	Hexacorallia	29.89	12	*Myriochele*	54.25	48.79	*Ophelia rathkei*	17.77	8.96
Scoloplos	33.32	14.07	*Thyasira*	32.3	23.9	*Pholoe baltica*	78.88	11.47	*Goniadella*	14.84	4.73
Pectinidae	45.2	12.05	*Aonides paucibranchiata*	22.64	14.38	*Tellina*	62.98	25.13	*Hydroides norvegicus*	20.32	0.1
Acrocnida brachiata	64.96	3.58	*Mugga wahrbergi*	38.62	13.24	*Scoloplos*	82.81	11.07	Echiurida	15.71	3.99
Nephtys cirrosa	15.61	18.07	*Prionospio*	29.77	20.86	*Chaetozone*	22.27	37.6	*Thracia*	15.48	0.81
Corbula gibba	72.33	7.84	*Laonice sarsi*	28.05	17.71	*Montacuta*	45.64	10.05	*Magelona*	18.55	13.42
Nemertina	36.32	4.33	Nemertina	33.91	27.05	*Phaxas pellucidus*	95.58	10.69	*Spisula*	11.77	5.56
Abra alba	45.79	15.01	*Mysella*	5.98	14.19	*Nephtys hombergii*	42.83	32.71	*Abra alba*	13.84	17.16
Nephtys hombergii	20.61	12.77	*Pseudomystides limbata*	21.49	19.81	*Owenia fusiformis*	31.63	14.18	*Urothoe poseidonis*	11.23	6.13
Hexacorallia	31.2	5.99	*Urothoe elegans*	19.2	18.86	*Harpinia antennaria*	27.58	8.71	*Stenothoe marina*	21.06	0
Polinices	19.49	3.02	Goniada	12.76	18	*Scalibregma*	12.25	21.72	*Notomastus*	15.06	1.48
Chaetozone	24.9	7.24	*Abra prismatica*	16.09	17.14	Hexacorallia	16.94	17.94	*Glycera lapidum*	8.9	3.16
Montacuta	18.65	5.86	*Scoloplos*	15.63	15.52	*Bathyporeia*	19.58	8.18	*Pisione remota*	4.81	5.94
Ophelia rathkei	8.14	7.24	*Aricidea (A.) wassi*	7.36	14.67	*Notomastus*	18.65	20.27	Hexacorallia	9.65	8.11
Goniada	17.97	5.28	*Timoclea ovata*	15.98	11.62	*Eudorella emarginata*	20	4.48	*Poecilochaetus serpens*	10.71	4.59
Spio	13.63	6.9	*Eudorella emarginata*	4.48	8.48	*Chamelea gallina*	21.17	3.88	*Branchiostoma lanceolatum*	6.06	3.11
Density of species at average 5 times higher in group 1 compared to group 2			Density of species at average 1.4 times higher in group 1 compared to group 2			Density of species at average 3 times higher in group 1 compared to group 2			Density of species at average 10 times higher in group 1 compared to group 2		

Discussion

Distribution and habitat preferences

Lanice conchilega has a cosmopolitan distribution, as it is found from the Arctic to the Mediterranean, in the Arabian Gulf and the Pacific, from the low water neap tide mark down to 1900 m (Hartmann-Schröder, 1996). In our survey, *L. conchilega* was found in the entire North Sea down to a depth of 180 meter (deepest record in the dataset was 380 meter). This tube–building polychaete is known to live mainly in sandy sediments from mud to coarse sand (Degraer *et al.*, 2006, Hartmann-Schröder, 1996), as was confirmed by the present study. Yet, shallow muddy and fine sands were strongly preferred: *Lanice conchilega* showed its highest frequencies of occurrence and densities in those sediments (more than 1000 individuals per m² compared to maximal 575 ind/m² in shallow medium sands). In the deeper habitats, *L.* conchilega was frequently encountered but only in low abundance (max. 170 ind/m² in deep fine sand).

The distribution of *L. conchilega* is mainly determined by the sedimentology as was shown in Willems *et al*. (2008). This study tried to model the habitat preferences of *L. conchilega* based on several types of environmental variables (granulometrics, hydrodynamics, pigments and nutrients), and only granulometric variables were selected in the final model. However, the hydrodynamics were assumed to be more important following the study of Buhr (1976) and Heuers *et al*. (1998), but sedimentology and hydrodynamics were more or less related. From the distribution map of *L. conchilega* (Figure 1), it can be deduced that the highest densities and percentages of occurrence were observed in the coastal areas of the North Sea (German Bight, French, Belgian and Dutch coast) and in the central part of the North Sea (east of the Dogger Bank). Those areas were characterized as zones with very high primary production in the North Sea (McGlade, 2002, Peters *et al.*, 2005). Next to physical factors (sediment type, flow regime), which mainly determine the distribution of benthic species, the availability of food might also have a positive influence on the abundance and occurrence of *L. conchilega*. Additionally, the occurrence of *L. conchilega* also depends on the recruitment success, which is highly variable (Van Hoey, 2006), but seemed to be successful in 2000 - 2001.

Hence, it can be concluded that *L. conchilega* has a wide geographical distribution and a low habitat specialization (*i.e.* eurytopic species), but optimally occurs in shallow fine sands and shallow muddy sands in the subtidal.

Ecological implications of the presence of **Lanice conchilega**

The results of the present study clearly show that *L. conchilega* has the potential to positively affect the surrounding benthos, which is reflected in the significant and positive correlation between the benthic density and the density of *L. conchilega*. Furthermore, the species richness increased with increasing density of *L. conchilega*. This trend was however not consistent: the number of species no longer increased or even decreased after reaching a critical density of *L. conchilega* (> 500 - 1000 ind/m²), as observed in shallow fine sands. A similar, but weaker trend was observed concerning the expected number of species and indicated an enrichment of species in *L. conchilega* patches. The N_1 -diversity index, which takes into account species dominance and richness, showed similar or slightly higher values in *L. conchilega* patches compared to patches without *L. conchilega*. These diversity patterns imply that mainly species with low abundance contribute to the higher species richness in samples containing *L. conchilega*. In other words, the chance to encounter a certain species increases in *L. conchilega* patches, due to the higher density of a lot of benthic species in those patches (see SIMPER results, Table 2), compared to the surroundings. The observed increases in species richness and abundances recorded in *L. conchilega* patches have also been discerned around the tubes of other polychaetes (Luckenbach, 1986, Woodin, 1978), in *L. conchilega* patches in intertidal areas (Callaway, 2003a, 2003b, 2006, Zühlke, 2001, Zühlke *et al.*, 1998) and even around artificial tubes (Dittmann, 1999, Zühlke *et al.*, 1998).

The MDS results visualized that in every investigated habitat the two groups (samples with (group 1) and without (group 2) *L. conchilega*) consisted mostly of species from the same species pool. This was confirmed by the ANOSIM and SIMPER results, where a significant difference between the two groups was found, but with a very low R value and a similar species dominance in the two groups. This indicates that there was a high overlap in species composition between the two groups, but the density of the species differed. These results confirmed the hypothesis that the species, which are affected by *L. conchilega* belong to the overall species pool of that habitat. This aspect is described more elaborately in Rabaut *et al*.

(2007). It was thus demonstrated that *L. conchilega* is affecting the benthos present in a particular habitat in the subtidal, rather than forming its own community (see also Zühlke *et al*. (1998) and Dittmann (1999)). In this way, it seems that the effect of *L. conchilega* tubes on the benthic fauna is highly dependent on the native species present in the surrounding sands at any moment and on their susceptibility to tube effects. This could be a reason why species richness and diversity levelled off in some habitats: almost no new species for that habitat were attracted. *Lanice conchilega* was considered to improve the habitat quality (e.g. habitat heterogeneity, food availability, flow velocity reduction), which led to increases of the densities of otherwise rare species in that habitat. In contrast, the decrease in species richness and diversity from a critical density of *L. conchilega* can be related to the competition for space and food in the *L. conchilega* patches.

It can also be argued that underlying factors (e.g. food availability) determine the densities of *L. conchilega* and therefore also the densities of other benthic species. However, the results of the present study, the studies of Rabaut *et al*. (2007), Zühlke *et al*. (1998) and Callaway (2003a, 2003b, 2006) clearly show that *L. conchilega* has the potential to affect the surrounding benthic species.

Nevertheless, differences in the effect of the presence of *L. conchilega* on the surrounding benthic species in the trends of density, species richness and diversity were observed between the investigated soft-bottom habitats in the North Sea. The strongest expression of the trend was observed in shallow fine sands, and the weakest in deep fine sands. The positive trend in shallow fine sands, can be attributed to the fact (1) that fine sands were the optimal habitat for *L. conchilega* and (2) that many species can profit from the habitat structuring capacity of *L. conchilega* in that environment. Shallow coastal areas were characterized by strong dynamics and a lot of disturbance and it can be hypothesized that *L. conchilega* patches create a certain stability that increases the survival of other benthic species. In deep fine sands, the effect of *L. conchilega* on benthic species was minimal. This might relate to the naturally higher benthic diversity (Künitzer *et al*., 1992) and the lower impact of the habitat modifying capacity of *L. conchilega* on the other benthic species in deep soft-bottoms. It has to be mentioned that *L. conchilega* was found in low densities, which make it impossible to predict the effect of dense patches (not yet found in those areas). *Lanice* *conchilega* had an effect on the density of some benthic species in shallow muddy sands, but no real increases of the species richness and diversity were observed. On the contrary, very high densities of *L. conchilega* (> 1000 ind/m²) had a negative effect. The reasons for this were not clear and further investigation is needed to draw conclusions for this habitat. In contrary, the habitat structuring capacity is more effective in shallow medium sands, where the benthic density and diversity increased even by lower densities of *L. conchilega*. This can be attributed to the fact that the occurrence of *L. conchilega* creates a 3D structure in the otherwise poor sandy environment.

It can be concluded that the presence of *L. conchilega* has ecological implications on the benthos in soft-bottom sediments, expressed in an increase of density and diversity of the benthos in the nearness of *L. conchilega*.

Lanice conchilega *as ecosystem engineer?*

The mechanisms responsible for the increase of the habitat quality in patches of *L. conchilega* can be summarized as (1) changes in the hydrodynamics, (2) increases of the habitat stability and oxygen supply, and (3) a creation of habitat heterogeneity in a uniform environment.

High densities of *L. conchilega* can influence the hydrodynamics, as has been shown in flume experiments, in which dense assemblages of tubes significantly reduced the current velocity of the near-bottom flow and in which normal, laminar near-bottom flow was deflected around and across the assemblages (turbulence effect) (Heuers *et al.*, 1998). These hydrodyamic changes have an effect on the sedimentation of particles, detrital food (Degraer *et al.*, 2002, Féral, 1989, Heuers *et al.*, 1998, Seys and Musschoot, 2001) and on the settling of larvae and benthic species (Callaway, 2003a, 2003b, Heuers *et al.*, 1998, Qian, 1999, Zühlke, 2001). The patches of *L. conchilega* caused sedimentation, sometimes leading to elevations of the sediment surface and to an increase of the bottom roughness. These processes indicate that dense aggregations cause a "skimming flow" (Morris, 1955) with reduced shear stress near the bottom (Heuers *et al.*, 1998) leading to a higher stability in the soft-bottom sediments. Tube building species are also known to control the pumping of water into and out of the bottom, by "piston pumping" in the case of *L. conchilega*, and provide oxygen to the adjacent sediment along the whole length of the tube (Forster and Graf, 1995).

Consequently, some species might benefit from an improved oxygen supply in the sediment surrounding *L. conchilega* tubes (Callaway, 2006). Due to the creation of tubes, extending out of the sediment, the habitat heterogeneity of the environment will increase, which leads to more niches for a wider variety of species. Specific species will not only interact with the tubes, but some species (predators) will be attracted by the higher food availability.

In this way (changing hydrodynamics, increasing the habitat stability and oxygen supply, habitat heterogeneity), *L. conchilega* alters the habitat characteristics and affects other organisms. Therefore, the species can be considered as an ecosystem engineer (Jones *et al.*, 1994). *Lanice conchilega* patches can even be considered as `biogenic reefs`, because *L. conchilega* is sometimes found in patches, which rise from the sea bed (10-40cm), in both intertidal and subtidal areas (Van Hoey, 2006). 'Biogenic reefs' were defined as biological concretions that rise from the sea bed and were created by the animals themselves (Holt *et al.*, 1998). The *L. conchilega* reefs were formed by sediment trapping in dense aggregations of *L. conchilega* tubes, which is a different mechanism than, for example, in *Sabellaria alveolata* reefs (real concretions of animal tubes) (Holt *et al.*, 1998). *Lanice conchilega* aggregations were also characterized by a constant renewal of the population due to the high turn-over of *L. conchilega* (Van Hoey, 2006). This is different from the real biogenic reef builders where the reef increases with settling juveniles on the older static structures. However, the biogenic structures of *L. conchilega* affect the density and species richness of the surrounding benthos, even at low densities (few individuals per m^2) (this study; Callaway (2006)). Although, in many cases, it is probably more realistic to refer to these aggregations as *L. conchilega* beds rather than reefs, their characteristics and effects are likely to be very similar to those of really protruding 'biogenic reefs'. Consequently, *L. conchilega* beds can be considered as important habitat structuring features in the soft – bottom sediments of the North Sea. In other words, *L. conchilega* patches were responsible for the increased habitat quality in an otherwise uniform habitat and result in a higher survival of the surrounding benthic species.

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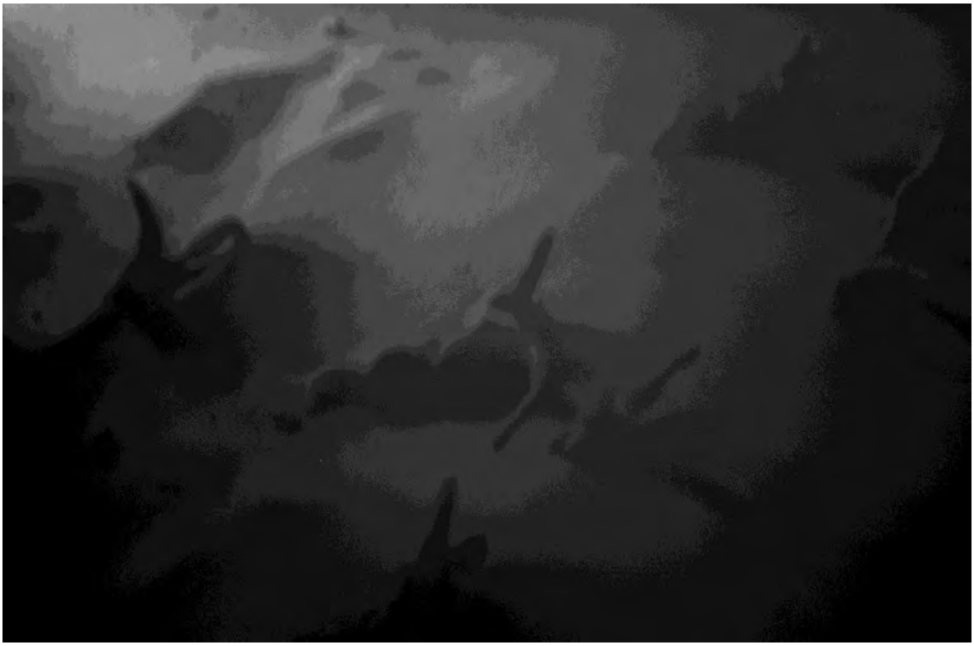
ADDENDUM II

Very-high resolution side-scan sonar mapping of biogenic reefs of the tube-worm *Lanice conchilega*



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Remote Sensing of Environment, 112: 3323-3328.

Abstract

Reefs of the tube-building polychaete *Lanice conchilega* are known to represent hotspots of biodiversity within inter- and subtidal soft sediments of the North Sea. However, because of their patchy distribution, point sampling does not appropriately map their subtidal spatial distribution. This study evaluated the feasibility to detect *L. conchilega* reefs by very-high resolution side-scan sonar imagery. A subtidal very-high resolution (410 kHz) side-scan survey, combined with grab sampling, revealed high densities of *L. conchilega* (up to 1979 ind m^{-2}) to coincide with a higher reflectivity, patchy and grainy acoustic facies. From the side-scan sonar imagery, individual reefs were estimated to reach a maximum size of 15 m^2. To ground truth the acoustic facies, the distribution of intertidal *L. conchilega* reefs was mapped at low tide and side-scan sonar imagery was recorded during the following high tide. Intertidal *L. conchilega* reefs had a patch size of 0.8 m^2 up to 11.6 m^2, elevated 7.5 to 11.5 cm above the surrounding seafloor and covered approximately 10 % of the selected area. The very-high (445 kHz) resolution side-scan sonar imagery revealed a similar acoustic facies as in the subtidal. Lower resolution (132 kHz) side-scan sonar imagery was less efficient to detect physically less developed *L. conchilega* reefs. We conclude that (1) there are no major technical restrictions to map *L. conchilega* reefs using side-scan sonar, (2) the developmental stage of *L. conchilega* reefs impacts the detectability of the reefs, and (3) very-high resolution side-scan sonar imagery is considered a necessity when mapping small-scale structures, such as *L. conchilega* reefs.

Key words

Remote sensing, side-scan sonar, biogenic reefs, *Lanice conchilega*, macrobenthos

Introduction

Remote sensing plays an important role in the investigation of marine biodiversity patterns. For example, satellite data provides information on phytoplankton productivity (Joint *et al.*, 2002), aerial hyperspectrometry is used for the ecological characterization of the intertidal habitat (Kromkamp *et al.*, 2006), and multibeam backscatter interpretation distinguishes between ecologically meaningful subtidal zones (Nasby-Lucas *et al.*, 2002). As such, remote sensing can map marine biodiversity in a rapid and cost-effective manner (Newman *et al.*, 2006). However, although small-scale patchiness is ecologically highly significant in a soft-sediment environment (Schlacher *et al.*, 1998), the resolution of remote sensing often fails to describe this small-scale patchiness.

The soft-sediment macrobenthic habitat of the Belgian part of the North Sea (BPNS) is an intensively investigated area (Van Hoey *et al.*, 2004). The soft sediments of the BPNS host no less than four distinct macrobenthic communities (Degraer *et al.*, 2003, Van Hoey *et al.*, 2004). The biodiversity of the *Abra alba* community is on average an order of magnitude higher (species richness: x 4 – x 6 and macrobenthic density: x 7 – x 34) (Van Hoey *et al.*, 2004) compared to the other communities. Within the fine sands, dominated by this *A. alba* community, biogenic reef structures constructed by the tube-building polychaete *Lanice conchilega*, may further enhance its biodiversity (species richness: x 2.8; average: 36 spp. 0.1 m^{-2} and macrobenthic density: x 7; average: 10985 ind m^{-2}) (Rabaut *et al.*, 2007). This relatively higher biodiversity can be attributed to (1) *Lanice*'s ability to stabilize the sediment, (2) the increase of surface area for larval settlement of benthic organisms created by its protruding tubes (Qian, 1999), (3) the enhancement of oxygen supply into the sediment (Forster and Graf, 1995), (4) the creation of benign hydrodynamic micro-habitat (Hild and Günther, 1999), and (5) the increase of habitat complexity (Woodin, 1978). High densities of *L. conchilega* are found throughout the major southern part of the North Sea (Van Hoey *et al.*, 2008).

Dense patches of *L. conchilega*, further called *L. conchilega* reefs (*cf.* elevation relative to the surrounding sediment, patchiness and enhanced biodiversity; *cf.* Hendrick and Foster-Smith (2006)), typically rise 10 – 40 cm from the sea bed as a consequence of sediment trapping in between the protruding tubes (Hild and Günther, 1999) and are further known to compact and slightly coarsen the sediment (Carey, 1987, Van Hoey, 2006). Remote sensing of the surface sediment, such as by side-scan sonar imagery, might thus be expected to pick up the distinct facies, created by the *L. conchilega* reefs. However, because the surface area, covered by an individual *L. conchilega* reef, generally does not exceed the order of square metres (Holt *et al.*, 1998), the resolution of the remote sensing technique used will determine whether the reefs will be detected or not. Our objective was therefore to investigate the feasibility of detecting the highly biodiverse *L. conchilega* reefs by very-high resolution side-scan sonar imagery.

Materials and methods

To explore the effectiveness of very-high resolution side-scan sonar imagery in detecting *L. conchilega* patches, a subtidal as well as an intertidal survey were performed. The subtidal sonar survey was compared with grab samples for macrobenthos. While these data allowed to search for aberrant acoustic facies within the side-scan sonar imagery of a typical subtidal *L. conchilega* reef environment, a direct ground truthing of the side-scan sonar imagery remained biased, mainly due to (1) scale issues, related to the randomness of point observations in a patchy *L. conchilega* reef area, and (2) small-scale georeferencing problems, related to the uncertainty in the samples' exact geographic positioning (e.g. grab sample position always deviates from the position of the ship due to e.g. prevailing currents). Further ground truthing in the subtidal, using diver or ROV observations, was impossible because of the low visibility (suspended particulate matter: 2-31 g m^{-3}, average: 7 g m^{-3}; www.mumm.ac.be/BELCOLOUR) in the area. The ground truthing problem was therefore tackled by an intertidal survey, during which the full coverage distribution of *L. conchilega* reefs was measured and mapped at low tide and side-scan sonar imagery was recorded during the following high tide.

Study areas

The subtidal survey was focused on the Trapegeer – Potje area (51°7'N, 2°33'E), a region known for its patches of high densities of *L. conchilega* (Degraer et al., 1999; Degraer et al., 2002) and part of the Belgian EU Habitat Directive Special Protection Area "Trapegeer Stroombank". The intertidal survey was conducted on the sandy beach of the Flemish nature reserve "Baai van Heist" (51°20'N, 3°14'E). Because of (1) the sheltered condition of the beach in the lee of the harbour wall of Zeebrugge, and (2) the high turbidity, several *L. conchilega* reefs could typically be found below the mid tidal level, with a maximum nearby the low water level (Figure 1). The focal reef area could thus be accessed for direct measurements at low tide.

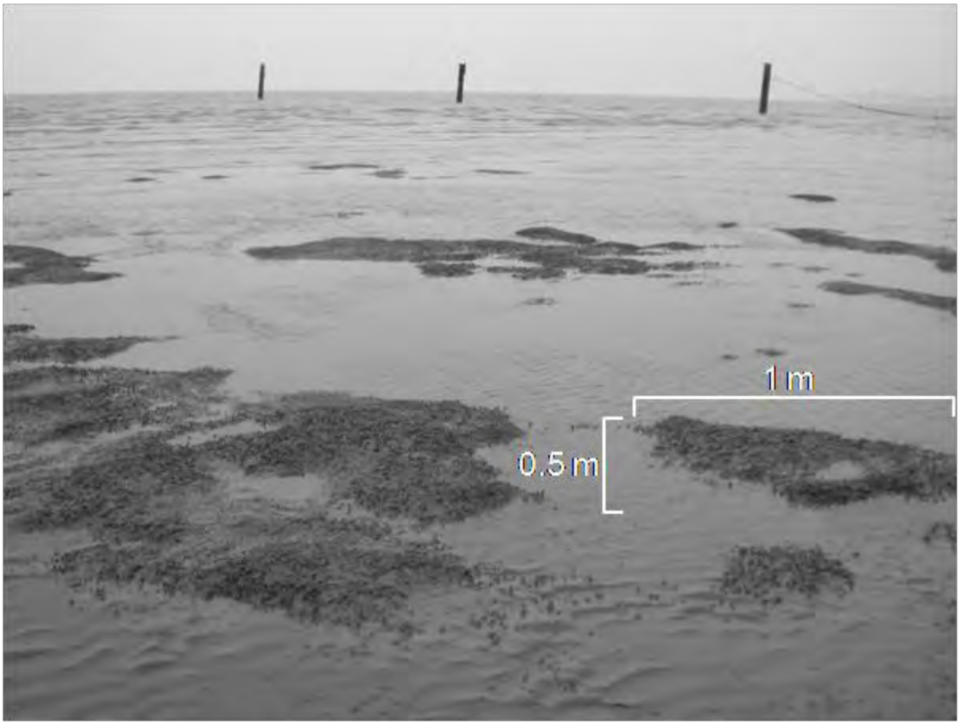

Figure 1. Picture of the patchy Lanice conchilega *reefs at the sandy beach of the Flemish nature reserve "Baai van Heist" (Belgium) at low tide.*

Lanice conchilega *reef characterisation*

In the subtidal, *L. conchilega* was sampled at five stations, evenly distributed across the bathymetric gradient from the Trapegeer sandbank down to the Potje swale and at a distance of approximately 350 m from each other. At each station, one Van Veen grab sample (sampling surface area: 0.1 m^2) was sampled in October 1999. After sieving over a 1 mm mesh-sized sieve, the individuals of *L. conchilega* were counted to estimate the species' density. Further direct characterization of the *L. conchilega* reefs in the subtidal study site was impossible, because – being a 0.1 m² snapshot – grab samples did not allow determining other physical properties, such as relative elevation or surface area of the individual reefs.

More detailed, physical *L. conchilega* reef characteristics were measured within the intertidal *L. conchilega* reef area at low tide (February 2007). The geographic position of the reef area was delineated by DGPS (Omnistar; accuracy: 0.5 – 1 m). *Lanice conchilega* density was estimated for seven randomly selected reefs by pooling the number of tubes within five randomly placed 10 cm² quadrants per reef (Van Hoey *et al.*, 2006). The elevation of the selected reefs, relative to the surrounding unstructured sediment, was quantified to the nearest 0.5 cm, while their surface area was estimated based on measurements of length and width of the individual reefs, assuming that the surface area can be described by an ellipsoid. Estimates of the total coverage within the *L. conchilega* reef area were based on *in situ* DGPS measurements.

Very-high resolution side scan sonar survey

Side-scan sonar was selected to demonstrate the feasibility of detecting small-scale *L. conchilega* reefs in the subtidal. The imagery is a reflection of the acoustic energy that is backscattered from the seafloor and is displayed in different levels of grey. The differences in backscattering are in decreasing order determined by (1) the geometry of the sensor-target system, (2) the angle of incidence of each beam, local slope, etc., (3) the physical characteristics of the surface, such as the micro-scale roughness, and (4) the intrinsic nature of the surface (composition, density, relative importance of volume versus surface diffusion/scattering for the selected frequency) (Blondel and Murton, 1997). For the operational procedures and constraints of side-scan sonar technology we refer to Blondel and Murton (1997).

Very-high resolution side-scan sonar imaging was performed in both the subtidal (October 1999) and intertidal area (February 2007). In the subtidal, a GeoAcoustics side-scan sonar was deployed at a frequency of 410 kHz (beam width 40°x0.3°). The sonar was towed at a speed of 4 knots and an altitude of 3-4 m above the sea bottom (MV *OostendeXI*). The sonar range was set at 50 m. Positioning was done using DGPS (Sercel NR103) at an accuracy of 1-3 m. All the data were recorded digitally using ISIS acquisition software (Triton-ELICS). The processing (at 10 cm resolution) and mosaicing were performed with ISIS and Delphmap. Corrections for the distance of the fish to the seabed (the slant range), lay-back/offset and the vessel speed were taken into account. In the intertidal, a Klein 3000 series was deployed both at a lower frequency of 132 kHz (beam width of 40°x0.7°) and at a very-high frequency of 445 kHz (beam width of 40°x0.21°), allowing the comparison of low and very-high resolution side-scan sonar imagery in detecting the *L. conchilega* reefs. The side-scan sonar was deployed from a rigid inflatable boat (RIB *Zeekat*), at an altitude of 1 m on average and a mean towing speed of 2.5 knots. The sonar range was set at 25 m. DGPS positioning was done using an Omnistar with an accuracy of 0.5 - 1 m. The data was processed at a grid resolution of 5 cm. All information was spatially referenced in ArcGIS 9.1. Finally, the images were exported as Geotiffs to allow importation to other software programmes.

Multibeam bathymetry

In the subtidal area, multibeam bathymetry was recorded using an Atlas Fansweep 20, 100 kHz (beam width 1.3°). The track spacing was chosen as a function of the side-scan sonar recordings. A tidal correction was performed (Van Cauwenberghe *et al.* (1993): M2 Reduction Model). The data was gridded (1 x 1 m and 5 x 5 m) using the Kriging algorithm. Bathymetric contour maps were generated from the gridded data. All information was spatially referenced in ArcGIS 9.1.

Results

Subtidal survey

Within the Trapegeer – Potje area, *L. conchilega* densities varied between 0 and 1979 ind m^{-2}: four stations were characterized by the absence or low densities (maximum 107 ind m^{-2}) of *L. conchilega*, while only one station revealed high densities (1979 ind m^{-2}) (Figure 2). The high density station was positioned on the upper part of the flank of the Trapegeer sandbank.

In the subtidal area, an aberrant acoustic facies of circular to elongated patches with a distinct medium to a high reflectivity was detected in the high density area of *L. conchilega* (Figures 2, 3). The texture was slightly grainy to grainy.

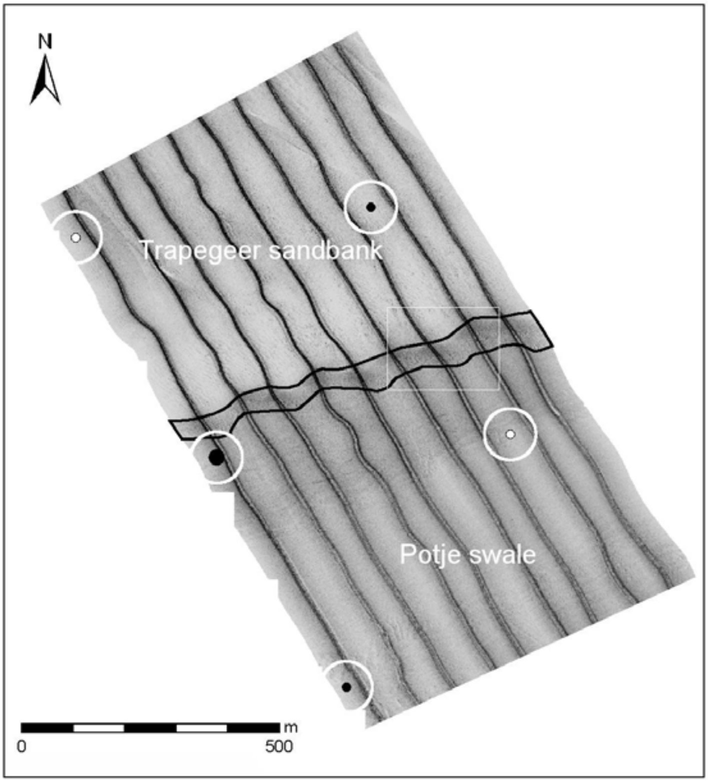

Figure 2. Side-scan sonar imagery of the subtidal Trapegeer – Potje study area, overlayed with the density distribution of Lanice conchilega. *O, 0* ind m^{-2} *(small circle) , 10 – 107* ind m^{-2} *(large circle) , 1979* ind m^{-2}*. The elongated band indicates the distribution of the* L. conchilega *acoustic facies, of which the inset is enlarged in Figure 3. The sampling points are encircled with a circle with a 50 m radius to depict the uncertainty in exact geographic positioning of the samples.*

The patchy texture was observed along an elongated band of approximately 60 m wide, following the overall bathymetry of the landward slope of the Trapegeer sandbank. Previously, the facies was considered aberrant, because it could not be attributed to bedforms that are typically expected in nearshore areas (Thornton *et al.*, 1998, Van Lancker *et al.*, 2004). As deducted from the georeferenced imagery, the patches had a maximum surface area of 15 m^2. The elevation could not be deduced, as the patches could not be distinguished from the 100 kHz multibeam imagery.

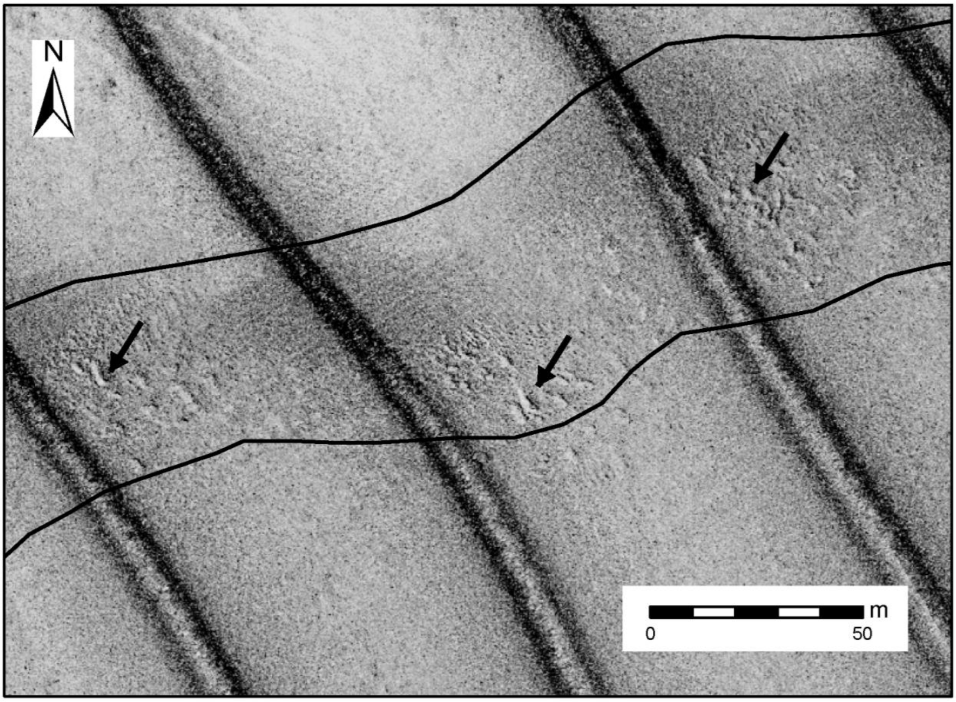

Figure 3. Detail of the acoustic facies of the subtidal Lanice conchilega *reef area (demarcated by the black lines) by very-high resolution (410 kHz) side-scan sonar imagery. The arrows point towards a selection of individual* L. conchilega *reefs.*

Intertidal survey

In a well delineated part of the beach, several *L. conchilega* reefs were found (Figures 1, 5). Tube densities within the reefs were on average 2813 ± SD 880 ind m^{-2}. Surface area of the reefs varied substantially and ranged from 0.8 m^2 up to 11.6 m^2 (average: 4.4 m^2). Individual reefs covered about 10 % of the selected *L. conchilega* reef area. The elevation of the reefs, relative to the surrounding sediment, was between 7.5 cm and 11.5 cm (average 9.3 ± SD 1.6 cm) (Figure 4).

The area with high densities of *L. conchilega* had high reflectivity and a patchy and grainy texture. This deviated acoustically from the megaripple fields and the surrounding low relief muddy areas (Figure 5).

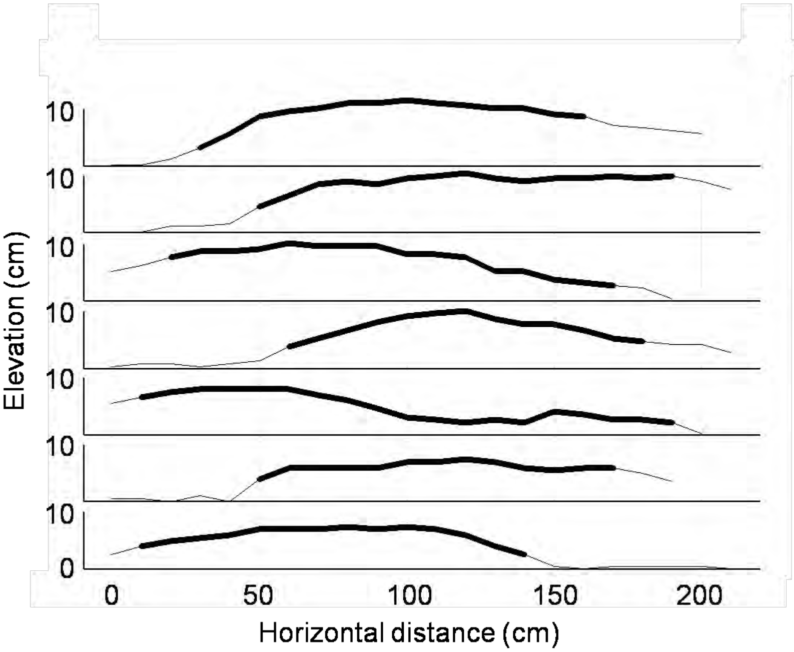

Figure 4. Elevation profile of seven selected Lanice conchilega *reefs in the intertidal survey area, relative to the surrounding sediment surface. For each profile, the position of the* L. conchilega *reef is indicated by the bold line.*

The few high reflectivity patches outside of the delineated area were most probably isolated individual *L. conchilega* reefs, scattered throughout the major part of the lower intertidal of the investigated sandy beach.

High versus lower-resolution side scan sonar imagery

In the intertidal area, the Klein 3000 side-scan sonar allowed to simultaneously acquire low resolution 132 kHz and very-high resolution 445 kHz side-scan sonar data from *L. conchilega* reefs (Figure 6). The typical high reflectivity, patchy and grainy texture, provided by the very-high resolution side-scan sonar image, was less pronounced in the low resolution side-scan sonar image. As a consequence, only the most developed *L. conchilega* reefs remained detectable using low resolution side-scan sonar imagery.

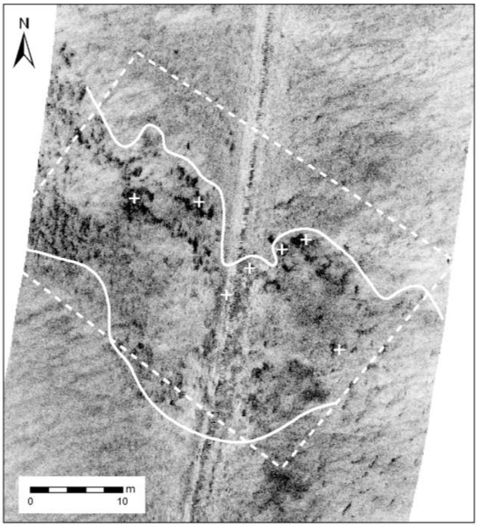

Figure 5. Very-high resolution (445 kHz) side-scan sonar image of the selected intertidal Lanice conchilega *reef area. Superimposed are (1) the selected study area (dotted white quadrangle), (2) the lower and upper limit of the* L. conchilega *reef area, as measured with DGPS in the field (full white lines) and (3) the indication of the seven reefs, where profile measurements were performed (white crosses).*

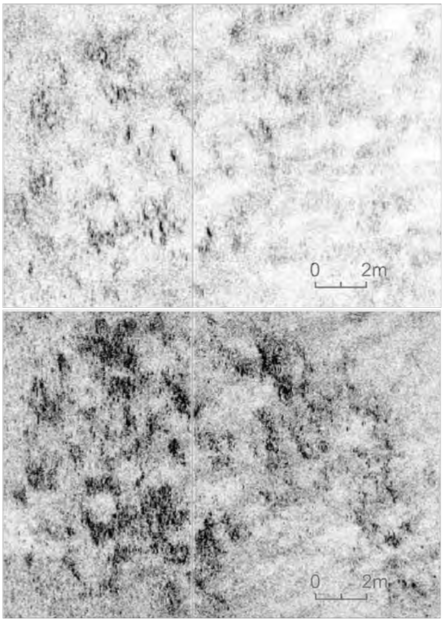

Figure 6. Lower resolution 132 kHz (top) and very-high resolution 445 kHz (bottom) side-scan sonar snapshot image of a selected intertidal area with Lanice conchilega *reefs (Klein 3000 series).*

Discussion

Side-scan sonar imagery

Despite the increasing use of multibeam technology in seabed habitat mapping, side-scan sonar technology is favourable for the detection of small-scale features, such as *L. conchilega* reefs, and for the discrimination of (small-scale) textural differences on the seafloor (Blondel and Murton, 1997, Thornton *et al.*, 1998, Van Lancker *et al.*, 2004). This was also demonstrated in this study where, contrary to side-scan sonar imagery, multibeam technology did not detect the *L. conchilega* reefs in the subtidal survey area. However, only a 100 kHz system was available. Very-high resolution (e.g. 300 kHz) multibeam systems may also be capable of detecting the reefs, but are likely to be less efficient because (1) side-scan sonar remains superior in the formation of narrow acoustic bundles under low grazing angles, leading to distinct shadows on the seafloor and (2) side-scan sonar has a more efficient band width sampling compared to multibeam. For an objective comparison of both systems, reference is made to Brisette and Clarke (1999). Furthermore, side-scan sonar is much easier to deploy and does not require an extensive calibration as would be needed for very-high resolution multibeam systems. Finally, the side-scan sonar swath width can be independent of the water depth, which is a big advantage in shallow waters, where *L. conchilega* prevails (Van Hoey *et al.*, 2008).

Although *L. conchilega* reefs could clearly be detected using very-high resolution side-scan sonar technology, the interpretation of their acoustic facies may not always be straightforward. The ability to discriminate the patchy texture is highly dependent on the system specifications (*i.e.* frequency and beam widths), the survey specifications (parallel versus longitudinal track lines, gain settings and altitude above the bottom), but above all weather conditions (e.g. wave action). The first two technical aspects can easily be dealt with adequately, based on the current knowledge of *L. conchilega* reef features (e.g. surface area and elevation). However, bad weather conditions cannot be controlled and may drastically deteriorate the image quality.

The cemented sand grains and shell breccias in tubes (Ziegelmeier, 1952), the increased coarse sand fraction (Rabaut *et al.*, 2007), and the positive correlation between shear wave velocity and burrow density (Jones and Jago, 1993) are responsible for an increased sediment rigidity within *L. conchilega* reefs. This higher rigidity is believed to cause its higher reflectivity, as detected by side-scan sonar. Furthermore, when the reefs were physically well developed (e.g. size and elevation), the more distinct shadows enhance the detectability by side scan sonar. This developmental stage of *L. conchilega* reefs is known to show a cyclic pattern, related to the seasonality in natality and mortality of the species (Van Hoey, 2006) . *Lanice conchilega* populations in the BPNS show a recruitment period from Spring to late Autumn, after which the adult population starts to die off. Because juveniles preferably settle onto adult tubes (Callaway, 2003a), juvenile settlement tends to fortify the reefs, leading to an increase of size and elevation as a consequence of sediment stabilization (*i.e.* accretion) (Carey, 1987). Following this period of reef fortification, mortality then starts to weaken the sediment stability, leading to a decrease of size and elevation (*i.e.* erosion). It is especially during this last period that less developed reefs might be encountered. This lower level of development was illustrated by the relatively low elevation levels of the *L. conchilega* reefs (maximum: 11.5 cm), measured during our intertidal survey in late winter (February). However, during the side-scan sonar survey in the intertidal zone we were able to detect even these less developed reefs, indicating the high sensitivity of very-high resolution side-scan sonar to *L. conchilega* reefs. Lower-resolution side-scan sonar proved less efficient in the detection of the reefs, mainly because of its larger beam width. Although, the low resolution data still weakly detected the *L. conchilega* reefs, one should be aware that the altitude of the sonar fish above the seafloor was only 1 m. In the subtidal area, where the fish was on average 3 to 4 m above the seafloor, the footprint was much larger and it became unlikely to observe these less developed reefs with low resolution data. Yet, if – for example as a consequence of recruitment failure – reefs further erode below a critical size and elevation, they will eventually become undetectable even with very-high resolution side-scan sonar. Whether such deteriorated *L. conchilega* reefs should still be considered biodiversity hotspots is doubtful, since both macrobenthic species richness and density are positively correlated to *L. conchilega* densities (Rabaut *et al.*, 2007, Van Hoey *et al.*, 2008). This size detection limit of the sonar systems has not been verified and would require extensive experiments, including visual ground truthing (Foote *et al.*, 2006).

Differences in technical specifications of both side-scan sonar surveys (e.g. different sonar systems, height of the fish above the seabed, scale issues and resolution) were believed to cause the differences in reflectivity of the *L. conchilega* reefs in the subtidal versus the intertidal. However, it is clear that in both cases the imagery of the area, in which *L. conchilega* reefs prevailed, was characterized by a higher reflectivity, patchy and grainy acoustic facies.

New insights in the spatial distribution of **Lanice conchilega** *reefs*

In addition to demonstrating the performance of very-high resolution side-scan sonar imagery in detecting *L. conchilega* reefs, our study further provides new insights in the small- and large-scale spatial distribution of these biogenic reefs.

While detailed knowledge on the habitat preferences of *L. conchilega* was already available and even modelled (Willems *et al.*, 2008), we still had a poor knowledge of the small-scale spatial distribution of *L. conchilega*. Grab samples often revealed its absence or low densities although the site was predicted perfectly suitable for *L. conchilega*. Part of this bias might be linked to the pronounced small-scale patchiness within the distribution of *L. conchilega* reefs as demonstrated by the full coverage side-scan sonar imagery. At the intertidal study site, *L. conchilega* reefs only covered 10 % of the total surface area. Hence, although some variability around this estimate might be expected, direct grab sampling of a *L. conchilega* reef area leads to a chance of only 10 % of hitting a *L. conchilega* reef in a suitable habitat. Small-scale and even large-scale distribution patterns of *L. conchilega* reefs are thus very unlikely to be retrieved through point sampling. This aspect is particularly critical when aiming at the identification of biodiversity hotspots, such as *L. conchilega* reefs. Remote sensing, such as very-high resolution side-scan sonar imagery, should thus be considered superior in the detection of patchy distributed structures, such as small-scale reefs, compared to direct point sampling. Visual observation through sediment profile imaging (SPI) (Birchenough *et al.*, 2006) might further be possible in the turbid waters. However, being spatially restricted, its ability to detect the patchy *L. conchilega* reefs is considered similar to point sampling, but it may allow (1) determining the density of tubes in the upper 10 to 20 cm of the seabed and (2) estimating the surface boundary roughness.

Our study sheds new light on the large-scale distribution of *L. conchilega* reefs. Whereas individuals can be found in a wide range of fine to medium muddy sands throughout the North Sea (Van Hoey *et al.*, 2008, Willems *et al.*, 2008), dense aggregations or reefs obviously do not. From the side-scan sonar survey we can deduce that *L. conchilega* reefs were found particularly along strips, following the overall seabed bathymetry and morphology. Because reefs were at the lee side of the Trapegeer sandbank and in the sheltered conditions of the intertidal survey area, shelter should be considered highly important in defining the distribution of *L. conchilega* reefs. This pattern has also been noticed on more exposed sandy beaches along the Belgian coast, where *L. conchilega* reefs are typically positioned at the lee side of bedforms within the ridge and runnel morphology.

Conclusions

- There are no major technical restrictions to map biodiverse *L. conchilega* reefs using side-scan sonar in various water depths, including the intertidal with the fish at an altitude of only 1 m above the seafloor. It is high time- and cost-efficiency will only improve with ongoing technological developments.
- On the side-scan sonar images, *L. conchilega* reefs were detected as a high reflectivity, patchy and grainy acoustic facies.
- The height of the *L. conchilega* reefs determines the reflectivity and thus the detectability of the reefs by acoustics. As such, very-high resolution side-scan sonar imagery is advised when aiming at the detection of small-scale structures, such as biogenic *L. conchilega* reefs.
- Given the patchy distribution of *L. conchilega* reefs, remote sensing (e.g. side-scan sonar imagery) is considered a necessity when mapping their distribution.
- This study should be considered a plea for using very-high resolution remote sensing in the soft-sediment environment.

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ADDENDUM III

Ecosystem engineers stabilize sand bank systems: *Owenia fusiformis* aggregations as ecologically important microhabitat

In preparation:
Rabaut, M., Du Four, I., Nakas, G., Van Lancker, V., Degraer, S. and Vincx, M. in prep.
Ecosystem engineers stabilize sand bank systems: *Owenia fusiformis* aggregations as ecologically important microhabitat.

Abstract

Ecosystem engineers modify the physical environment and have profound effects on ecosystem functioning and on local biodiversity. Yet, in soft bottom marine environments, they have rarely been included in hydrodynamic studies or in management strategies. The lack of quantified stabilization potential and ecological impact are, respectively, the main reasons for not including ecosystem engineers. The present study evaluates the ecosystem engineering capacity of the tube dwelling polychaete *Owenia fusiformis*. The ecological implications of aggregations of this species are investigated using a long term dataset (1994-2006). Results show that its presence has significant implications for species richness and species density. These aggregations are further investigated with different remote sensing tools. *Owenia fusiformis* is able to stabilize sand dunes that normally migrate 12 m a year. Specific biological characteristics explain the stabilizing effects in a highly dynamic environment. Our results confirm the need to pay attention to biota in sediment transport modelling. We conclude that *O. fusiformis* creates an important marine system which can be investigated with sensing techniques. These techniques can therefore be used to visualize hotspots of biodiversity, to quantify their biogeomorphological impacts and to underpin ecosystems based management in the marine environment.

Key words

Ecosystem engineer, remote sensing, sediment stability, side scan sonar, multibeam sonar, *Owenia fusiformis*, ecosystem management

Introduction

The relationship between structure and functioning is fundamental in ecosystem science (Levin, 1998). The structural complex framework provided by emergent features constitutes an important organizing aspect and is critical to the functioning of many ecosystems (Jones et al., 1994). Biogenic structures in marine ecosystems that reach a few centimetres into the water column can therefore have a profound effect on the structure and functioning of marine ecosystems. These systems are heavily used by a variety of taxa, including post-settlement juveniles of commercially important fish species (Watling and Norse, 1998). Anthropogenic activities can cause deleterious impacts on the seabed environment, which identifies the need to identify and map different types of benthic habitats and their associated biological communities. As the protection of vulnerable, rare or ecologically important areas is now widely recognized (Pickrill and Todd, 2003), there is a growing need for improved understanding of seafloor ecosystems to facilitate sustainable marine management and environmental monitoring.

The relationship between structure and functioning owing to biotic-abiotic interactions was conceptualised in the idea of 'ecosystem engineering' (Jones *et al.*, 1994, 1997, Wright and Jones, 2006). Ecosystem engineers are organisms that directly or indirectly modulate the availability of resources to other species by causing state changes in biotic or abiotic materials. In doing so they modify, maintain and/or create habitats (Jones et al., 1994). By reshaping the landscape, ecosystem engineers change the abiotic context upon which biotic interactions heavily depend (Byers et al., 2006). The value of the ecosystem-engineering concept, therefore, lies in its ability to formalize interactions among organisms that are mediated by the physical environment (Wilby, 2002).

The ecological effects of habitat structuring organisms are well described for all kinds of marine environments: coral reefs (e.g. (Holbrook et al., 1990), Darwin mounds (Van Gaever et al., 2004), kelp forests (e.g. (Steneck et al., 2003), ascidians (Castilla et al., 2004)**,** sea grass meadows (e.g. (Alfaro, 2006, Hovel *et al.*, 2002), mussel banks (Ragnarsson and Raffaelli, 1999), oyster beds (Lenihan, 1999) and polychaete tubes (Callaway, 2006, Van Colen *et al.*, 2008). Recently, a descriptive and correlative data study (Rabaut et al., 2007) illustrated the ecological importance of the ecosystem engineer *L. conchilega* in shallow soft-bottom areas.

The habitat modifying ability of this tube building polychaete creates and regulates refuge for species, alters the interactions between local species and changes the physical environment. This species has the capacity to double the biodiversity in the richest soft-sedimented macrobenthic habitat of the Belgian part of the North Sea (BPNS) (*i.e.* the *Abra alba* community) (Van Hoey et al., 2004). The effect of this species on biodiversity has been described extensively (Callaway, 2006, Carey, 1987, Dittmann, 1999, Féral, 1989, Rabaut *et al.*, 2007, Van Hoey, 2006, Zühlke *et al.*, 1998) and the species was recently defined as a reef builder (Rabaut *et al.*, 2009b). Furthermore, several studies describe in detail how *L. conchilega* affects the abiotic environment (Braeckman *et al.*, accepted, Forster and Graf, 1995).

The tube building polychaete, *Owenia fusiformis*, occurs in the same macrobenthic community (*Abra alba – Kurtiella bidentata*). *Owenia fusiformis* is a thin cylindrical, segmented worm, up to 10 cm long, that lives in a tough though flexible tube buried in the sand (Pinedo et al., 2000). The tube is composed of sand grains or shell fragments glued together in an overlapping, imbricate fashion. The tube is slightly longer than the worm and its top can protrude to up to two centimetres from the surface. Although several authors suggest that tubes of *O. fusiformis* mostly protrude above the sediment surface (Eckman *et al.*, 1981, Fager, 1964), there is, in some cases, still some uncertainty on the position of the tubes in the sediment, as recently discussed by Noffke et al. (2009). The species has an adult life span of three to four years (Menard et al., 1989), as opposed to *L. conchilega* which has a lifespan of about one year (Van Hoey, 2006). The species is widely distributed in coastal regions throughout North-Western Europe, the Mediterranean, the Indian Ocean and the Pacific and occurs in fine to coarse sediments, reaching only high densities in finer sediments (Pinedo *et al.*, 2000, Somaschini, 1993). There is little known about the formation of high density patches and their physical characteristics. The mechanisms of physical patch formation are certainly different compared to *L. conchilega*, as the tube is shorter and the organisms have a longer lifespan. Despite its wide distribution and the formation of aggregations, the ecological effects of this species have received little attention until now. Furthermore, the biotope seems to occur in sheltered areas with a high load of organic matter (pers. obs.).

As the marine environment proves difficult to access, remote sensing is taking up an ever more important role in the investigation of the structure and functioning of marine landscapes (Diaz *et al.*, 2004, Kenny *et al.*, 2003, Mayer, 2006). Remote sensing techniques permit to improve the knowledge of the marine biodiversity and more specifically, its spatial distribution in a cost-effective manner (Larsen et al., 2007). Side-scan sonar still remains the undisputed remote sensing tool for small object detection (Blondel and Murton, 1997, Brissette and Clarke, 1999) and has been used to detect emergent biota and to characterise small-scale patchiness within ecological valuable areas (Degraer *et al.*, 2008a). These authors departed from the existing ecological knowledge on *L. conchilega* aggregations and provide evidence that the biogenic mounds created by this species can be visualised using side-scan sonar techniques. Nevertheless, the technology of multibeam sonar systems has rapidly evolved since the last decade. These systems make it possible to map backscattering strength, together with detailed bathymetry, substantially improving the capability of sonars to discriminate different types of seafloor habitats (Dartnell and Gardner, 2004, Kostylev *et al.*, 2003, Wilson *et al.*, 2007).

Furthermore, biota can affect local sediment transportation and stabilize or destabilize the environment. Individual structures on an otherwise smooth sea bed ('isolated roughness elements', in hydrodynamic terms) are known to cause local scour by deflecting fluid of relatively high momentum toward the bed. Such scour is seen around animal tubes (Gage, 1977). It is widely believed that animal tubes stabilize sediments by altering the character of near-bed flow. In some cases, the region of maximum turbulent kinetic energy and shear stress production occurs away from the bed (this is the so-called "skimming flow") (Morris, 1950). "Skimming flow" may therefore occur above the tops of *O. fusiformis* tubes and have a stabilizing effect on the dynamic sand bank system.

In the present study we hypothesize that *O. fusiformis* reshapes the marine environment by profoundly changing the abiotic context. The aim of this study is to investigate the effect on the abiotic sand bank system as well as the consequences of this stabilizing effect for the associated species community. The combination of different remote sensing techniques and biological samples makes it possible to study the relationship between the structure and functioning of a specific ecosystem engineered habitat.

Material and Methods

Study area

The study area covers a transect of the BPNS situated in the Southern Bight of the North Sea, close to the Belgian coast (Fig. 1). This shallow area (max. 35 m depth) consists of several sandbank systems, oriented more or less parallel to the coast. The characteristic geomorphologic and sedimentological diversity of these soft-bottom habitats is directly responsible for the high biological diversity and richness, reflected in a mosaic of several distinguishable macrobenthic communities (Degraer *et al.*, 2008b, Van Hoey *et al.*, 2004). For the remote sensing measurements, the area north of the Vlakte van de Raan within the Belgian coastal zone (51° 30′N , 3° 6′E) (Fig. 1: rectangular area) has been targeted for this investigation. The location is about 16 km offshore from the harbour of Zeebrugge, close to the Belgian-Dutch border. Depth ranges between 15 and 24 m relative to Mean Lowest Low Water at Spring tide (MLLWS). The area encompasses a tidal swale and the landward slope of a sandbank (Fig. 1). Hydrodynamics are mainly tidally-driven; nevertheless, wind and density currents can be important. The average current velocity in the study area is 0.3 m/s during ebbing tide, increasing to 0.8 m/s during flood tide (Lanckneus et al., 2001). In this area, the residual current is flood-dominated (Fettweis and Van den Eynde, 2003) while the bedload transport is ebb-dominated (Du Four and Van Lancker, 2008). Very-large dunes *sensu* Ashley (1990) of 2 to 3 m occur in this area, with wave lengths of 100 to 500 m.

Biological data and analyses

Data, gathered on the BPNS, over a period of 11 years (October 1994 until November 2006), were selected on the basis of habitat classification, which takes into account sedimentological characteristics and bathymetrical information. A data set of 314 macrobenthic samples was submitted to analysis (Figure 1). This subset of samples was selected from shallow locations (<25 m according to MLLWS level) at which the fine sediment fraction was the largest, as sediment characteristics are known to determine macrobenthic species occurrence (Van Hoey et al., 2004).

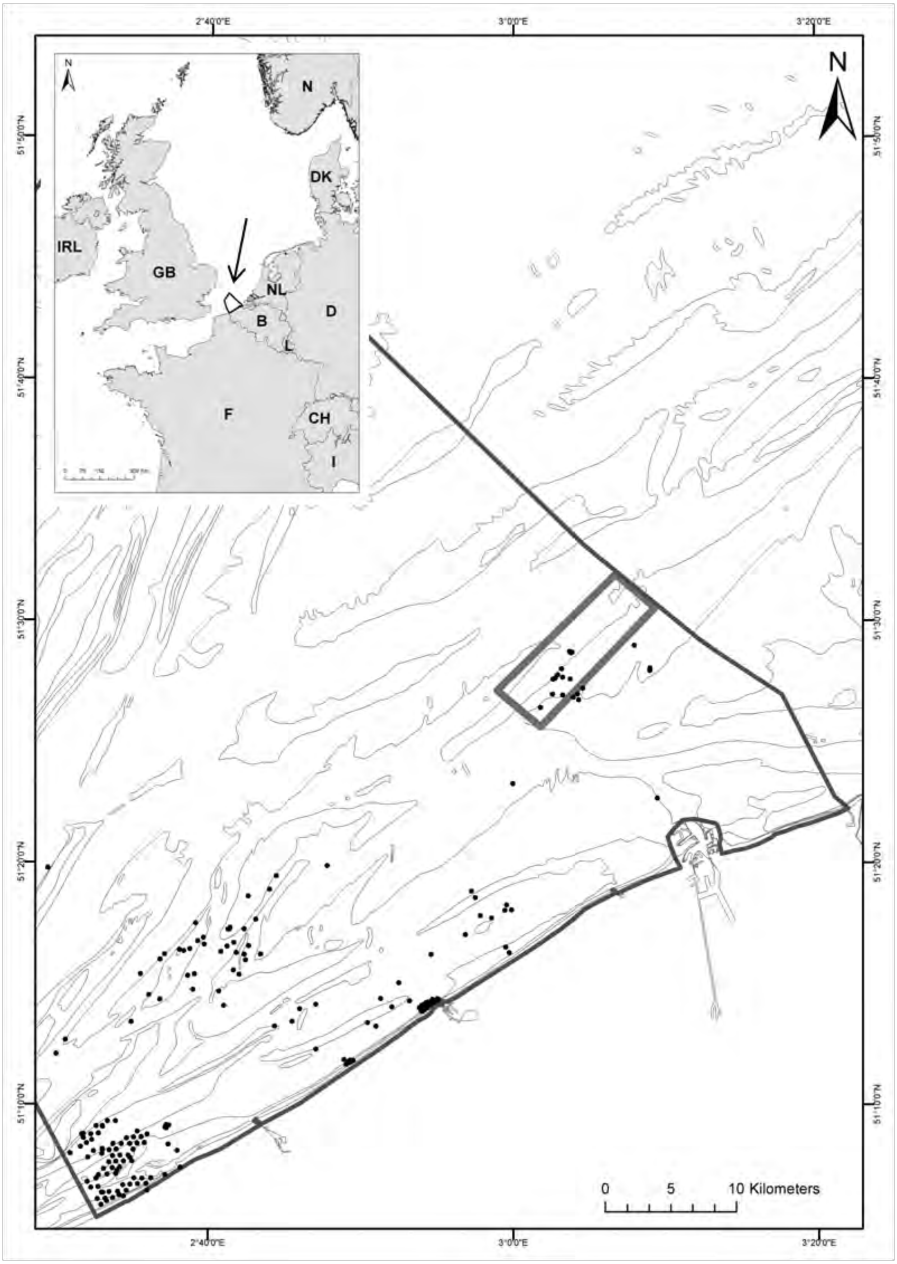

Figure 1. Position of the Belgian part of the North Sea (BPNS) (inset); Coastal zone of the BPNS with the 314 sample locations for biological analyses. Depth contours of 10 m and 20 m are visualised. Indication of the location where remote sensing measurements were performed (area North of Vlakte van de Raan; rectangle).

To test the impact of *O. fusiformis* as a ecosystem engineer, samples were selected based on specific median grain size values (125-250 µm); furthermore, samples with *L. conchilega* densities exceeding 10% of the *O. fusiformis* density, were removed in order to exclude the bias of the known bio-engineering *L. conchilega* (Rabaut *et al.*, 2007, Van Hoey *et al.*, 2008). All samples were collected with a Van Veen grab of 0.1 m^2 surface area and sieved alive through a 1 mm mesh-sized sieve. Macrofauna was identified to the lowest possible taxonomic level (further referred to as species) and subsequently counted. Species abundance data were standardised to a total number of individuals per m^2.

In order to study the possible change in benthic community composition as a consequence of the presence of *O. fusiformis* tubes, samples were divided into 4 classes: (0) samples without tubes and samples with *O. fusiformis* densities ranging from (1) 1-30 ind m^{-2}, (2) 31-150 ind m^{-2}, and (3) > 150 ind m^{-2}, further referred to as density groups.

The quantitative faunistic data were analysed using a combination of multivariate and univariate methods. The benthic community structure was analysed with the PRIMER v6 statistical package (Clarke and Warwick, 2001). Non-parametric multidimensional scaling (MDS) and analysis of similarity (one-way ANOSIM) were used to describe (dis)similarities between benthic faunal communities of *O. fusiformis* sites and sites where *O. fusiformis* did not occur. The MVDISP algorithm of the PRIMER v6 software was used to quantify the variability in each density class and to calculate the Index of Multivariate Dispersion (IMD). This comparative Index contrasts the average rank of the similarities among samples of a certain density class with the average rank of other density class sample groups (Clarke and Warwick, 2001). With the SIMPER program the (dis)similarity between the communities and the percentage contribution of each species to the similarity within and dissimilarity between communities was examined. Species richness for different *O. fusiformis* density classes was calculated and presented by total number of species (S) and Margalef's index (d) which takes into account the given number of individuals (Clarke and Warwick, 2001). Differences between density groups regarding the number of individuals (N), species richness (S) and Margalef's index (d) were tested with a general linear model (SAS software). Homogeneity of variances was tested (Levene's test) and differences between different density classes were tested with the post hoc Tukey test.

In order to identify species possibly associated with the presence of *O. fusiformis,* four criteria were applied (Rabaut et al., 2007). The Indicator Species Analysis (ISA, Pcord4 programme) was carried out and an association degree (the percentage of occurrence of a species in samples with *O. fusiformis,* relative to the total presence of that species in all samples) was calculated. Apart from this, the Mann-Whitney U test was used to compare abundances of these species between samples with and without *O. fusiformis*. Finally, the correlation of the density of *O. fusiformis* tubes with individual species abundances was tested with the Spearman Rank correlation analysis. A species was defined as positively associated with *O. fusiformis* when (1) a significant indicator value was attributed, (2) the association degree was more than 50%, (3) species density significantly differed between samples with and without *O. fusiformis* and if (4) a positive and significant correlation with the density of *O. fusiformis* was found. Based on these results species were ranked according to a summation of the indicator value and the association degree.

Multibeam bathymetry

Multibeam sonar was selected to detect small-scale *O. fusiformis* patches, to define their spatial extent and to show the influence of *O. fusiformis* aggregations on bedform stability.

Multibeam imagery was acquired in February and November 2006 and in February, October and November 2007, using a Kongsberg Simrad EM1002 multibeam echosounder (*RV Belgica*) (Fig. 2). In total, 33 km^2 was surveyed. The EM1002 provides high-resolution bathymetric data, with up to 111 receive beams of 2° (athwart) x 3.3° (fore-aft) width. It works at a nominal frequency of 95 kHz with a ping-rate of around 4 to 6 Hz. The data are real-time corrected for the roll and heave using a Seatex MRU 5 motion sensor and for the heading using an Anschütz Standard 20 gyrocompas. The geographic co-ordinates are provided by a Thales Aquarius 02 GPS positioning system with a theoretical precision of 10 mm. The soundings are tide-corrected using the specific M2 tidal reduction method for the Belgian coastal zone (Van Cauwenberghe et al., 1993) and referenced to the level of MLLWS. In water depths less than 30 m, the depth measurement accuracy is estimated to be around 10 cm RMS or 0.2 % of the depth (Kongsberg-Simrad, 1999-2001a). Post-processing was done using the software packages Neptune (Kongsberg-Simrad, 1999-2001b) and Fledermaus and resulted in digital terrain models (DTM) with a 1-m or 2-m grid resolution. All information was spatially referenced in ArcGIS 9.3.

To define the elevation of the individual patches, cross-sections aligned in a NW-SE direction were generated from the October 2007 DTM (Fig. 2). To investigate bed form migration, changes in the crest positions of the dunes were determined based on cross-sections aligned in a SW-NE direction (transverse to the dunes) and generated from all DTMs.

To validate the multibeam imagery, 117 ground truth samples were taken in within the study area (Fig. 2) of which *Owenia fusiformis* densities were determined.

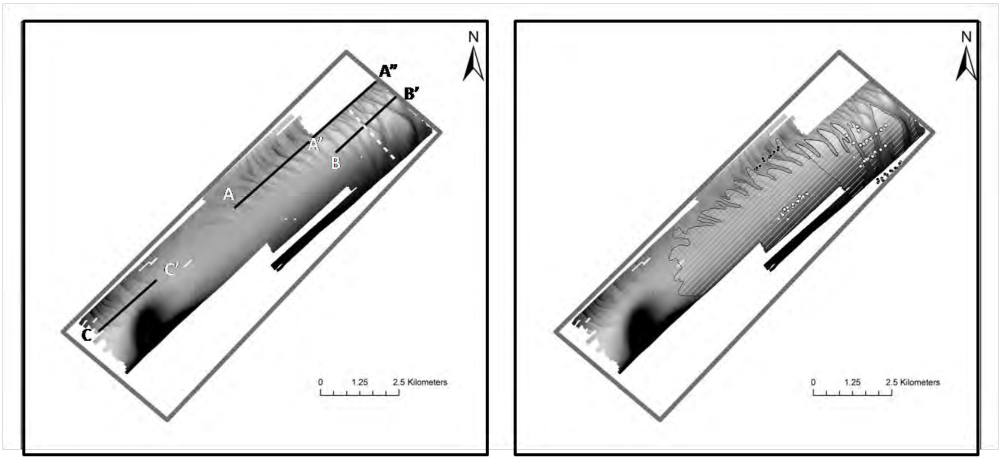

Figure 2. Study area north of the Vlakte van de Raan, where remote sensing imagery was acquired. Left: area with multibeam echosounder measurement, indication of investigated transects (black lines) and indication of a side scan sonar trackline (white dotted line); Right: delineation of the zone where Owenia fusiformis *is observed (dashed area) and position of ground truth samples inside (white dots) and outside (black dots) the* O. fusiformis *area.*

Side-scan sonar imagery

Side-scan sonar was selected to obtain a detailed view of the individual *O. fusiformis* patches. The imagery is a reflection of the acoustic energy that is backscattered from the seafloor and is displayed in different grey levels. Blondel and Murton (1997) explain the operational procedures and technical constraints of side-scan sonar technology.

Very high resolution side-scan sonar imagery was acquired in November 2007, using a Klein 3000 series, which was deployed at a frequency of 445 kHz. The sonar was towed at a speed of 4 knots with an altitude of 3-4 m above the sea bottom along a NW-SE transect (Fig. 2). The sonar range was set at 50 m. Positioning was done using CSI Wireless Inc. DGPS. All data were recorded digitally using ISIS acquisition software (Triton-ELICS). The processing (at 25 cm resolution) and mosaicing was performed with ISIS and Delphmap. Corrections for the distance of the fish to the seabed (the slant range), lay-back/offset and vessel speed were taken into account.

Finally, the images were exported as Geotiffs for further interpretation. All information was spatially referenced in ArcGIS 9.3.

Results

Biological implications of Owenia fusiformis

According to the one-way ANOSIM analysis, the macrobenthic community around *O. fusiformis* tubes is significantly different from the community in *O. fusiformis* free areas (R= 0.198; p = 0.001) (Table 1). A dissimilarity value of 82.3 was found between samples with and without *O. fusiformis*. Dissimilarities between density classes are relatively high, with the 0-density class being most distinguishable from all other classes. ANOSIM results reveal significant differences between all classes except between class 1 and class 2 (Table 1).

Differences in dispersion were investigated using the MVDISP algorithm. The highest variability was found in the samples without *O. fusiformis* (Dispersion Factor Value 1.019) while lowest variability occurred in the samples with highest *O. fusiformis* densities (Dispersion Factor Value 0.354). For each density class, the indices of multivariate dispersion (IMD values) show that similarities among samples of the concerned class are higher than the similarities among samples of a lower density class. The community structure is visualized in a 2-dimensional ordination graph constructed by the MDS-analysis (stress 0.24) (Fig. 3) and shows how the different density groups are organized. IMD values and MDS-analysis indicate that *O. fusiformis* expands the realized niche of several species and creates a so-called “Babushka” type of community structure (sensu Rabaut et al, 2007).

Table 1. Results of the global and pairwise ANOSIM and SIMPER analysis for differences between the macrofauna community composition of Owenia fusiformis *patches with different classes of densities (1-3) and* O. fusiformis*-free patches (0).*

	R	p	Dissimilarity
Presence/Absence	0.198	0.001	82.3
Density classes			
Global test	0.124	0.001	
Pairwise test			
0 - 1	0.12	0.002	81.24
0 - 2	0.098	0.034	80.89
0 - 3	0.283	0.001	85.14
1 - 2	0.004	0.401	67.77
1 - 3	0.286	0.001	73.78
2 - 3	0.336	0.001	67.74

Average macrobenthos densities (mean ± SE) of 2464 ± 289 ind m^{-2} were found in the presence of *O. fusiformis*, while significantly lower densities of 1335 ± 153 ind m^{-2} were found in samples without *O. fusiformis* ($p = 0.0056$). Species richness differed significantly ($p < 0.0001$) for presence-absence groups. The highest macrobenthic density was found in density class 1, while the highest species richness (as reflected in S and d) occurred in class 2 (Table 2). For density classes, the group of samples without *O. fusiformis* differed significantly from all other density classes. However, none of the density classes with *O. fusiformis* could be distinguished significantly on the basis of N, S or d.

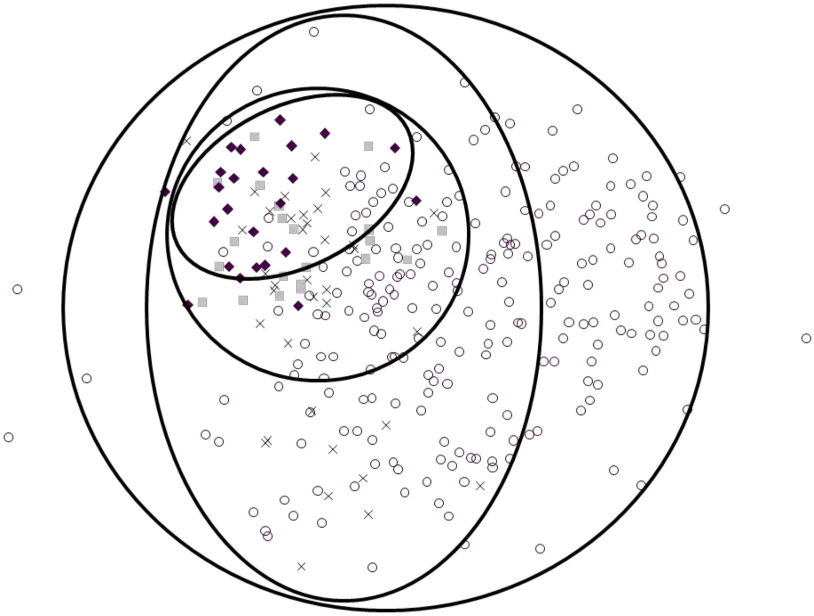

Figure 3. Two-dimensional MDS ordination plot of similarities between species assemblages of different density classes of Owenia fusiformis *aggregations (classes 1-3, respectively crosses, filled gray squares, filled diamonds) and* O. fusiformis *-free samples (open dots) (using Bray-Curtis similarity measure of square root transformed data). The „babushka" like organisation of the samples indicates that* O. fusiformis *restructures the species assemblage by expanding the realized niche of several species.*

Table 2. Abundance (N) and Species richness for presence/absence samples and for different Owenia fusiformis *density classes, represented by average number of species per sample in each density class (S) and by Margalef's index (d). Species richness increases with increasing* O. fusiformis *densities, except for the highest* O. fusiformis *density class. The highest macrobenthic density is found when* O. fusiformis *is present (maximum N within presence group found in class 1).*

Presence/Absence	**N**	**S**	**d**
0	1335	10.76	1.49
1	2464	19.10	2.40

Dens class	**N**	**S**	**d**
0	1335	10.76	1.49
1	3766	18.86	2.39
2	2216	21.62	2.71
3	2228	17.25	2.14

135 macrobenthic species (*O. fusiformis* excluded) were recorded in this study of which 19 were found to be positively associated with *O. fusiformis* (*i.e.* 14%) (Table 3). The three most associated polychaetes are *L. conchilega*, *Pholoe minuta*, *Notomastus latericeus*. For bivalves, *Abra alba* and *Kurtiella bidentata* seem to be clearly present in higher densities in areas with *O. fusiformis*. Relatively few amphipods appear in the list of positively associated species (e.g. *Ampelisca brevicornis* and *Melita sp*.). Echinoderms appear in the top ranking of associated species with *Ophiura sp*. on number one. Finally, the burrowing sea anemone *Edwardsia timida* is indicative for areas where *O. fusiformis* occurs. For each species, the relative contribution to the dissimilarity is indicated in the table (Table 3).

Abiotic implications of **Owenia fusiformis**

The digital terrain model, based on the multibeam echosounder recordings, reveals the presence of a patchy micro-habitat (Fig. 4). Ground truth samples were divided into two groups: 83 samples were taken in areas showing the patchy environment; 36 sampling locations were selected in an area without patches. In 93% of the samples of the first group, *O. fusiformis* was present, while for the ground truth samples outside the patches only 19% of the samples held *O. fusiformis*. Moreover, average densities (ind/m² +/- SE) were respectively 582.99 +/- 56.75 and 3.79 +/- 1.79. The patches are observed along an elongated band of approximately 2 km wide, following the overall bathymetry of the swale. On the landward slope of the sandbank, they occur in between the very-large dunes. Surface area of the patches varies substantially and ranges from 0.6 m² up to 12 m² (Fig. 5). The individual patches vary from circular to elongated and their elevation varies between 15 cm and 40 cm (Fig. 6). Side-scan sonar imagery also reveals the patchiness of the *O. fusiformis* aggregations (Fig. 4). Medium to relatively high reflectivity acoustic facies characterise the patches. The texture varies from slightly grainy to grainy.

The very large dunes, aligned in the NW-SE direction, have a wavelength between 150 and 450 m with an elevation ranging between 1.5 and 3 m. They exhibit an asymmetric cross-section with their steeper lee-slope mainly oriented towards the southwest, indicating net sand transport in that direction. Most of them have superposed small dunes on their stoss side. The wavelength of the small dunes varies between 0.10 and 0.15 m with an elevation ranging between 0.15 and 0.2 m.

Table 3. Rank list of the associated species. Species are ranked based on the summation of the indicator value (ISA) and the association degree. Mann-Whitney U indicates the significance level of differences in abundances of the species between samples with and without Owenia fusiformis. *The Spearmen Rank R-value indicates the correlation of the density of* O. fusiformis *tubes with individual species abundances. The last column represents SIMPER results, indicating the relative contribution of a species to the dissimilarity between samples with* O. fusiformis *and samples without.*

	ISA		Assoc degree	Mann-Whitney U-test	Spearman rank	SIMPER
Positively associated	indicator value	p	(%)	p	R (p<0.05))	% contribution
Ophiura sp.	63	0.001	57	0.000000	0.587396	4.72
Lanice conchilega	15	0.001	100	0.047012	0.409976	0.32
Pholoe minuta	32	0.001	82	0.000016	0.499130	0.88
Notomastus latericeus	49	0.001	63	0.000000	0.480938	2.15
Edwardsia timida	20	0.001	89	0.010635	0.424169	1.16
Acrocnida brachiata	16	0.001	93	0.035555	0.338578	0.4
Nereis sp.	45	0.001	62	0.000000	0.456615	1.21
Ampelisca brevicornis	21	0.001	82	0.005550	0.371184	0.51
Sthenelais boa	26	0.001	74	0.000360	0.384294	0.65
Actinaria sp	41	0.001	55	0.000002	0.351610	2.35
Oligochaeta sp	42	0.001	53	0.000001	0.341871	2.24
Melita sp	20	0.001	73	0.005924	0.354943	0.67
Pectinaria sp	35	0.001	55	0.000280	0.295016	1.04
Venerupis senegalensis	17	0.001	71	0.031815	0.259206	0.58
Phyllodoce (A.) maculata	32	0.001	50	0.000433	0.274872	1.26
Nassarius reticulatus	27	0.001	52	0.002206	0.235659	1.16
Eumida sanguinea	22	0.001	57	0.002270	0.293931	0.72
Glycera alba	21	0.001	56	0.018423	0.222493	0.61
Ophiura juv	22	0.001	53	0.014482	0.268687	1.5
Negatively associated						
Bathyporeia sp	1	0.002	11	0.002297	-0.225407	1.61
Urothoe poseidonis	3	0.006	11	0.001241	-0.229499	1.42
Nephtys cirrosa	4	0.001	12	0.000000	-0.362687	3.27
Spio sp.	3	0.002	18	0.016994	-0.174198	2.23

The very large dunes in the northern and central part, where the *O. fusiformis* aggregations occur, did not migrate during the two subsequent years (Fig 6, profiles A-A′-A′′, B-B′), while for the southern part of the study area, comparison of dune crests positions of the very-large dunes demonstrate that the dunes migrated 12 m towards the SW between February 2006 and November 2007 (Fig 6, profile C-C′).

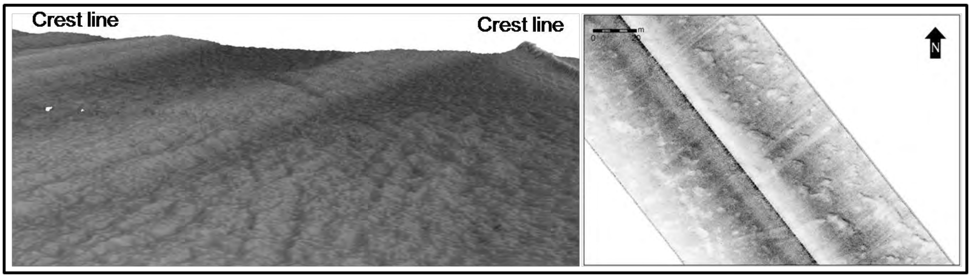

Figure 4. Visualisation of patches formed by Owenia fusiformis *aggregations, visualized with MBES (left, 3D), side scan sonar imagery (right, plan view).*

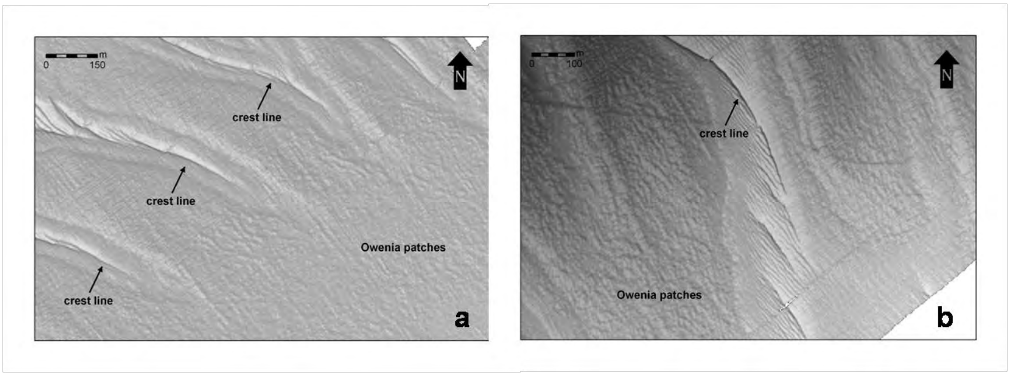

Figure 5. On the landward slope of the sandbank, Owenia fusiformis *patches occur in between the very-large dunes (in between crest lines): (a) general view and (b) detail. Surface area of the patches varies substantially and ranges from 0.6 m² up to 12 m².*

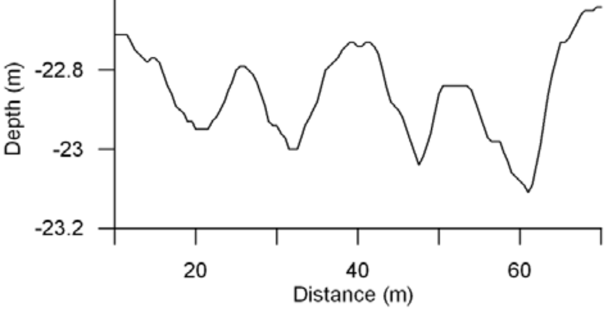

Figure 6. Cross section indicating heights. Small scale elevation differences represent Owenia fusiformis *patches. Their height varies between 15 cm and 40 cm.*

Finally, sediments accumulate over the whole dune area in the southern part, while in the other parts sediments accumulate only in the troughs, in-between the dunes (Fig. 7).

Discussion

Biotic implications of **Owenia fusiformis**

O. fusiformis is a strong ecosystem engineer. The two-dimensional ordination graph and the multivariate dispersion analysis demonstrate that *O. fusiformis* modulates its environment. The species does not create its own community, but structures the *A. alba – M. bidentata* community by expanding the realized niche of several species. This ecosystem engineering effect is very similar to the effect of *L. conchilega*, another tube dwelling polychaete of the same macrobenthic community (Rabaut et al., 2007). This kind of structuring the existing community is also referred to as the "babushka" like organization. The MVDISP results show an increasing dispersion of samples with decreasing *O. fusiformis* densities, which suggest a more stable environment when densities of *O. fusiformis* increase (Clarke and Warwick, 2001). However, *O. fusiformis* is not as strong an ecosystem engineer as *L. conchilega*. This is reflected in a lower relative increase of both average macrobenthic density (factor 5 for *L. conchilega*, factor 2 for *O. fusiformis*) and species richness (factor 3 versus factor 2). Moreover, the apparent "babushka" organization on community level is not reflected in a change of species richness and abundance over density classes of *O. fusiformis*. For these biological characteristics, the presence of *O. fusiformis* seems to be of importance, rather than the densities in which the species is present. The rank list of species shows species that prefer high to very high mud contents such as *Pholoe minuta* (Fauchald et al., 2009), *Notomastus latericeus* (Fauchald and Bellan, 2009) and *Ophiura sp.* (Stöhr and Hansson, 2009). The stable microhabitat created by *O. fusiformis* locally reduces currents (*cf.* "skimming flow"), which increases the mud content in this sheltered habitat. Other species like *Edwardsia timida* are known to occur in sheltered localities in shallow sublittoral areas (Wilson, 2007), which explains the high preference for the biogenically created habitat of *O. fusiformis*.

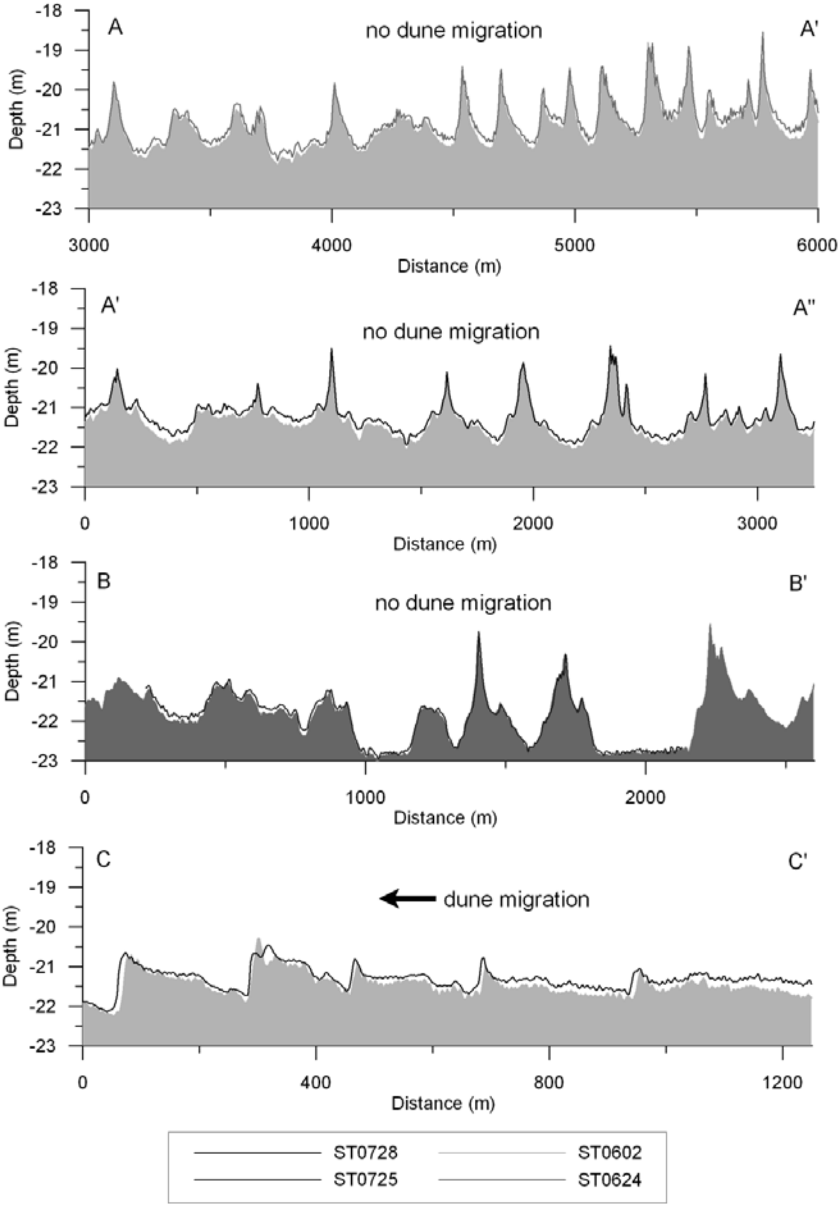

Figure 7. Dune migration. Dunes in the northern and central part, where the Owenia fusiformis *aggregations occur, did not move during the same time span (profiles A-A'-A'', B-B') while for the southern part of the study area, comparison of dune crests positions of the very-large dunes demonstrate that the dunes migrated 12 m towards the SW between February 2006 and November 2007 (profile C-C'). Note that sediments accumulate over the whole dune area in the southern part, while in the other parts sediments accumulate only in the troughs, in-between the dunes.*

Unlike *L. conchilega*, there are no species present that directly depend on the tubes of *O. fusiformis*. *Abra alba*, *M. bidentata* and *L. conchilega* are species that typically occur in shallow fine sand areas but occur more frequently and in higher abundances in areas were *O. fusiformis* is present (in whatever densities). This is similar to what has been found for the sponge *Halichondria panicea*, where the associated species were also found in other habitats (Peattie and Hoare, 1981) and species richness also seems to be higher in areas with this sponge. These emergent ecosystem engineers are able to trap (mostly juveniles of) species because of changing hydrodynamics rather than enrichment through active movement of organisms (Savidge and Taghon, 1988).

Owenia fusiformis *stabilizes dunes*

The results on the remote sensing imagery highlight the potential of using both multibeam and side-scan sonar to detect *O. fusiformis* aggregations. Both images show a patchy pattern. Degraer et al. (2008a) observed similar, though smaller patches on side-scan sonar images which corresponded with the occurrence of *L. conchilega* reefs (average surface of 4.4 m^2). The latter were, on the contrary, not detected with the 95 kHz multibeam sonar, probable due to their smaller surface area compared to *O. fusiformis* aggregations. However, under favourable circumstances, *L. conchilega* reefs can be detected also with very-high resolution multibeam systems (e.g. > 300 kHz systems). Still, the delineation of individual *O. fusiformis* patches is not straightforward using sonar systems of 95 kHz only. Even terrain analysis, allowing obtaining further quantitative descriptors of the bathymetry data, did not solve this problem (Wilson et al., 2007). Although its superior qualities in small object detection, the lack of depth information does not allow delineating the patches based on the very-high resolution side-scan sonar imagery.

Nonetheless, the remote sensing tools have demonstrated clearly the stabilizing effects *O. fusiformis* aggregations have on the geomorphology of sand dunes. The dunes in the northern and central part of the study area did not migrate between February 2006 and November 2007, while in the south-western part of the study area, dunes moved 12 m towards the SW. A dune migration of 12 m to the SW is expected in the whole study area (Besio *et al.*, 2004, Degrendele *et al.*, in prep., Nemeth *et al.*, 2002). The absence of dune migration in the northern and central part could only be attributed to the stabilizing effect of *O. fusiformis*.

Sediment stabilization by *O. fusiformis* has been hypothesized before as an explanation for the temporal stability of the *A. alba- Pectinaria (Lagis) koreni* community in the Bay of Seine (Thiebaut et al., 1997).

Borsje et al. (2009b) have discussed in detail the biophysical interactions between benthos and their sedimentary environment. They argue that biota are able to impact on hydrodynamics (e.g. adding roughness to the bottom) and may induce flow deceleration within epibenthic structures. Accounting for biota in both sediment dynamics and hydrodynamics may produce results of several orders of magnitude difference and can act on a large spatial and temporal scale. The same authors demonstrate the influence of ecosystem engineers on both the wavelength and presence of bedforms, hence having a direct effect on the morphodynamics also. From this, it is clear that biota form an inherent component of models predicting seabed dynamics. These are increasingly important with the expansion of human activities in coastal zones. Data from this study aid in the parameterisation of biological activity on sandbank systems. Monitoring this area (3-4 times a year) would provide insight into its temporal dynamics.

Biotic stabilization

The aggregations of *O. fusiformis* tubes might induce a "skimming flow", explaining the attraction of species preferring high mud content. However, Paarlberg et al. (2005) indicate that in general, stabilizing organisms can, but do not necessarily, cause an increase of mud content and additional sedimentation. Eckman et al. (1981) visualize the results of flume experiments (Nowell and Church, 1979) by representing the "critical" ratio between tube size and density that is critical to change from a destabilizing effect to a stabilizing one. In their experiments with *O. fusiformis*, they show that the maximum kinetic energy production and hence the maximum shear stress production occurs at the bed, which indicates that there is no skimming flow. Destabilization occurs at natural densities (as predicted from the produced ratio). They calculated that for *O. fusiformis* tube densities of below 13,000 ind /m^2 sediment destabilization will occur. However, a study with artificial tubes (Friedrichs et al., 2000) show a deceleration of current velocity with increasing tubes; they show that skimming flow conditions already occur at 8.8% surface coverage (*i.e.* 3836 tubes/m^2). Also Fager (1964) notes that stable patches occurred (*i.e.* absence of ripples) with relatively low densities.

Therefore, the presence of the tubes built by *O. fusiformis* cannot by itself explain the bed stability that is demonstrated in this study with the remote sensing imagery. Eckman et al. (1981) suggest that alternative processes compensate for the destabilizing effect of the *O. fusiformis* tubes: production of mucus by bacteria, benthic diatoms, filamentous algae and sea grasses. Fager (1964) described a diatom film within *O. fusiformis* aggregations that was uncommon at similar depths outside the aggregations. Murray et al. (2002) suggest that the mucus produced by the invertebrate itself may play a major role in the geophysical properties of the sediment through flocculation, drag reduction, pore blockage or cementation. Present study demonstrates the high stabilization potential of the species. This stabilization effect is most probably the result of subsequent effects after tube settlement as average tube density was around 600 ind m^{-2}. The biological characteristics of the species are of importance: the combination of the long lifespan and the rigid tube make that this ecosystem engineer is able to have far reaching stabilizing effects in a highly dynamic environment. Nevertheless, compared to the relatively low densities needed to detect the biological impact of the ecosystem engineer, higher densities of the species are a key to create detectable large scale stabilization. Moreover, large-scale effects of small-scale biological activity by stabilizing organisms are mainly responsible for the seasonal variation in suspended sediment concentrations (Borsje *et al.*, 2009a, Borsje *et al.*, 2008). Adults occur mainly as dense patches within fine and muddy sand (Barnay et al., 2003) and have been recorded off Helgoland Island in the North Sea (Noffke et al., 2009), in the English Channel (Dauvin and Gillet, 1991) and in the Mediterranean Sea (Pinedo et al., 2000). In present study, the influence of high nutrient supply of the Scheldt estuary is probably a driving force to have high density patches. Aggregations of *O. fusiformis* are generally stable but can disappear as a consequence of changing abiotic factors (such as harsh winters or reduced food supply) (Dauvin and Gillet, 1991, Noffke *et al.*, 2009).

Ground truth samples show average tube densities of over 500 ind/m^2, suggesting that relatively high densities are needed to have a clear stabilizing effect, compared to the relatively low densities needed to reach maximum biological effects.

Implications for management

Ecosystem engineers can extend a species range towards environments the species would otherwise physically have more difficulties to inhabit. Important ecosystem engineers alleviate limiting abiotic and biotic stresses, expanding distributional limits for numerous species, and often create the foundation for community development. As the management of important engineers can protect numerous associated species and functions, it has been advocated to use these organisms as conservation targets (Crain and Bertness, 2006). This will necessitate a shift towards a more process-based understanding of the functioning of systems; an important step towards ecosystem-based management (Byers et al., 2006). Present study demonstrates that for the marine environment, combining biological data analyses with remote sensing imagery provides more process-based insight in the benthic microhabitat that is created by *O. fusiformis*. Therefore, this study generates an opportunity to implement the ecosystems approach in this particular area.

Byers et al. (2006) developed a conservation framework that uses the ecosystem engineer concept. These authors argue that ecosystem engineers are often likely to be the causative agents, driving the transition between alternative system states. Although in their model they emphasize on non-trophic engineering effects, they also stress on the important and often interacting role of trophic and other biological interactions in restoration. The ecosystem engineer concept should therefore be considered as a contributory process among those factors affecting the distribution and abundance of organisms and the functioning of ecosystems (Wright and Jones, 2006). Present study qualifies the tube building polychaete *O. fusiformis* as an important ecosystem engineer. Results show that this species is able to modulate its environment in such a way that physical structures as large as sand dunes can be stabilized. The stabilizing function of benthic biota taken together with the increased ecological richness, make these environments of particular interest for future management schemes.

Anthropogenic impacts that affect benthic tube worm aggregations, such as towed bottom-fishing gear, can pose a significant threat to the integrity of complex benthic habitats, particularly those formed by sessile emergent fauna (Collie *et al.*, 1997, Kaiser *et al.*, 2000b, Rabaut *et al.*, 2008, Thrush *et al.*, 1998, Watling and Norse, 1998). Traditionally, fisheries managers have been preoccupied with the conservation of single stocks of target species, giving little or no consideration to the secondary effects of fishing on the marine ecosystem (Kaiser *et al.*, 2000b). Damage to the stabilized *O. fusiformis* habitat may not only cause reduced macrobenthic (prey) abundance (*cf.* e.g. possible effects on the associated species), but also an ecosystem change from a stabilized dune habitat towards a highly dynamic habitat with migrating dunes.

Moreover, the study area of present research (the "Vlakte van de Raan") is situated in the eastern side of the BPNS and constitutes an area of high biological value (Derous, 2007). The area was partially designated as a Special Area for Conservation in the framework of the EC Habitats Directive, but has been annulled by the Council of State because of insufficient motivation after a complaint against the designation by an energy firm (Cliquet *et al.*, 2008b). Present study emphasizes the ecological importance of this particular area and can serve as a motivation to reconsider this particular area. The identification and subsequent quantification of the value of specific ecosystem engineers are considered as important steps in the strategy to implement the ecosystems approach in the marine environment (Rabaut *et al.*, 2009c).

Conclusions

Owenia fusiformis proves to be an ecosystem engineer that stabilizes sand bank systems and has clear consequences for the biotic (benthic) community structure that profits form a stable small scale niche in an otherwise highly dynamic area. Aggregations of *O. fusiformis* can be mapped with both multibeam echosounder and side-scan sonar technology. The detectability of an enriched ecosystem engineered habitat provides opportunities to implement a sustainable management regime. Moreover, results emphasize that biota – especially ecosystem engineers- should be included in hydrodynamic sediment transport modelling. The present study proves that remote sensing techniques permit to improve the knowledge of marine biodiversity, its spatial distribution and its biophysical impact in a cost-effective way.

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SUMMARY – SAMENVATTING

SUMMARY

The oceans and coastal seas are heavily exploited, leading to biodiversity losses and degradation of the integrity of the ecosystems. Of all human activities at sea, fishing is considered one of the most intensive. The vision on the marine environment has been largely utilitarian untill now, which has lead to a focus on the maintenance of the benefits from the exploitation of resources. This approach did not prove to be efficient and in response to the continued degradation concepts as 'ecosystem approach' have now become the key concepts to manage the marine environment. In this respect, 'marine protected areas' (MPAs) have been installed in an attempt to halt the deterioration of the sea. The integration of marine conservation and fisheries management is therefore urgently needed and should be based on ecological knowledge to realize the transition to more-resilient relationships between society and ecosystems. The North Sea is one of the most exploited marine areas in the world, with the Belgian part of the North Sea (BPNS) representing the core of these activities. Therefore, the coastal marine areas that are situated in North-Western Europe and largely consist of sedimentary sand banks and swales are the focus of this thesis. Macrobenthos (*i.e.* invertebrate fauna larger than 1 mm) is recognized as fundamentally important in the functioning of marine ecosystems and this ecosystem component is the focal point of this thesis. High density aggregations of the ecosystem engineer *Lanice conchilega* (sandmason) are further studied in depth. *Lanice conchilega* is a tube dwelling bristle worm (Annelida, Polychaeta, Terribellidae). Experiments were designed to generate insights that can support conservation strategies and the relation with impacts of fisheries activities is investigated. As the management of important ecosystem engineers may protect numerous associated species and functions by expanding distributional limits for a lot of species, these organisms have been proposed as conservation targets in modern marine management. Therefore, proving the value of the ecosystem engineer *L. conchilega* within this framework is the basic aim of the thesis. **Chapter 1** pictured the broader context of conservation and fisheries management as well as what is the state of the art on the knowledge of *L. conchilega*.

Chapter 2 evaluated the effect of this species on the macrobenthic community and on sediment characteristics of its habitat based on a long term data set in Belgian coastal waters. Both sediment composition and community structure of the associated macrofaunal matrix were affected by the presence of *L. conchilega*. There was a positive correlation between the

steadily increasing macrobenthic densities and densities of *L. conchilega* (R = 0.59; p < 0.001). Species richness was increasing with *L. conchilega* densities, except for the highest *L. conchilega* density class. There from we can conclude that *L. conchilega* is able to restructure the macrobenthic community in a ''babushka" like organization, indicating that *L. conchilega* expands the niche breadth of several associated species. A species rank list was created according to each species' association with *L. conchilega*. This species rank list has been extensively discussed based on all ecological knowledge available. Species are favoured by the habitat modifying ability of the polychaete tubes, which create and regulate refuge for species, alter the interactions between local species and change the physical factors of the environment. **Addendum I** is fully complementary to Chapter 2 as it evaluated the ecosystem engineering consequences on a North Sea scale. The presence of *L. conchilega* in different habitats in the North Sea and its effect on the abundance, species richness, diversity and community structure in these habitats were evaluated. In four different habitats (shallow muddy sands, shallow fine sands, deep fine sands and shallow medium sands), the density of the surrounding benthos increased with increasing density of *L. conchilega* and were most pronounced in shallow fine sands. This addendum showed that *L. conchilega* patches are responsible for an increased habitat quality in an otherwise uniform habitat, resulting in a higher survival of the surrounding benthic species. **Chapter 3** characterized the physical features of dense aggregations and discussed this together with the biological characteristics in order to determine whether these dense aggregations can classify as 'reefs'. To classify as reefs, ecosystem engineering activities need to significantly alter several habitat characteristics. Results showed that the elevation and sediment consolidation of the biogenic mounds was significantly higher compared to the surrounding unstructured sediment. Areas with *L. conchilega* aggregations tend to be extensive and patchiness is high (coverage 5-18%). Individual aggregations were found to persist for several years if yearly renewal of existing aggregations through juvenile settlement occurred. This renewal is enhanced by local hydrodynamic changes and availability of attaching structures (adult tubes). This chapter concluded that the application of the definition for reefs as found in the Habitats Directive provides evidence that all physical and biological characteristics are present to classify *L. conchilega* as a reef builder. As a range of aggregation development exists, 'reefiness' is not equal for all aggregations and a scoring table to quantify *L. conchilega* 'reefiness' is presented.

The reef structures formed by *L. conchilega* were targeted in Part II to generate detailed knowledge on the impact of mobile fishing disturbance. **Chapter 4** described a laboratory experiment in which four disturbance regimes to *L. conchilega* reefs were applied. Survival dropped significantly after 10 days and after 18 days (with a disturbance frequency of every 12 and 24 hours, respectively). Besides the physical impact on *L. conchilega* itself, **Chapter 5** tests the vulnerability of the species that live in close association with *L. conchilega*. A treatment zone was exposed to a one-off experimental trawling during an intertidal *in situ* experiment. Subsequently, the impact on and recovery of the associated fauna was investigated for a period of nine days post-impact. Community analysis showed a clear impact followed by a relatively quick recovery. This impact and subsequent recovery was largely explained by two species: *Eumida sanguinea* and *Urothoe poseidonis*. Species analysis confirmed the beam-trawl passage significantly ($p = 0.001$) impacted *E. sanguinea* for the whole period of the experiment. The experiment confirmed that closely associated species of *L. conchilega* reefs are impacted by beam-trawl fisheries. Chapter 4 and 5 (*i.e.* Part II) provided insight in the resistance and therefore also in the resilience of the reef system and indicated 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 immediately after disturbance.

The relation between the ecological value of the observed increased benthic diversity and the abundance for flatfish seemed to be an important knowledge gap. Therefore, **Chapters 6 and 7** (*i.e.* Part III) investigated the ecological interactions between the benthic habitat created by *L. conchilega* and flatfish. The biotic structuring factor on flatfish' habitat preference was addressed for the first time. **Chapter 6** investigated in an *in situ* experimental sampling design, the structuring effect of biogenic reefs on the distribution of post-larval *Pleuronectes platessa* in an intertidal nursery area. The density distribution of this flatfish species was significantly ($p < 0.0001$) explained by the presence of *L. conchilega* reefs. As effects on habitat preferences of flatfish within nursery areas are thought to be related to food availability as well, **Chapter 7** evaluated the importance of biogenic habitats as a feeding ground for juvenile flatfish species (*P. platessa* and *Limanda limanda*). Both the distribution and feeding behaviour of the two flatfish species *P. platessa* and *L. limanda* was studied in function of the presence of high densities of an ecosystem engineer. In this chapter two different ecosystem engineered habitats are tested for (*L. conchilega* reefs and *Owenia fusiformis* aggregations) and sampling is done in two different coastal areas (the BPNS and the Dutch part of the Wadden Sea). General responses were identified by comparing relative differences between ecosystem engineered habitats and adjacent non-ecosystem engineered habitats. Results showed that both flatfish species select for the ecosystem engineered habitat. This behaviour was further investigated using stomach content analyses. For *P. platessa* occurring in *L. conchilega* reefs, this selection was explained as a feeding behaviour. For the habitats created by *O. fusiformis*, no such a relation was found. Therefore, Chapter 7 suggested that the juveniles use ecosystem engineered habitat both as a shelter (antipredation behaviour) and/or as feeding ground. These small-scale aspects of larger nursery grounds can be considered as 'Essential Juvenile Habitat' (EJH) and merit attention in habitat suitability models as well as in marine conservation measures. Part III showed that *L. conchilega* reefs also have bottom up effects on juvenile flatfishes. Linking these results to Part II pointed out that further modification of these biogenic habitats may lead to a loss of one or more ecosystem functions which flatfish species depend on.

In the last part of this thesis (Part IV), the results on *L. conchilega*, fisheries and marine conservation were discussed in the framework of their potential value in an application of the ecosystem approach supporting marine management. **Chapter 8** brought literature on marine conservation strategies in soft-bottom temperate areas together in one 'systems approach' that provided answers to the questions 'why?', 'how?' and 'what is the effectiveness?' of MPAs. This 'systems approach' was visualized in a flow chart and includes three phases: setting policy objectives, decision making and evaluating the eventual effects of the MPA. The analysis indicated that the relation between fisheries and MPA-management is the most challenging 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. The systems approach was applied to the Belgian case and proved useful in providing insight into the complex interactions of various authorities with scattered jurisdictions. **Chapter 9** further discussed the (international) legislative framework of marine protection. As marine ecosystems are threatened, conservation strategies are set out in international policy to face the large scale of the marine ecosystems. However, not only the scale is important to manage marine ecosystems, also ecosystem dynamics should have a prominent place in the strategies. The chapter pointed out the danger of interpreting and applying an (international) environmental law system in a narrow way, which leads to a slow decision making process and the inflexibility of management programs; this prevents the integration of dynamics of marine ecosystems. The strict interpretation of international legislation was therefore expected to fail in its aim of implementing a sustainable use of the sea. The Belgian case has been developed as an example, pointing out that international (EU) legislation is excessively strictly interpreted which decelerates the implementation rate. Nonetheless, in the case of the EU Habitats Directive, a more flexible approach is possible and needed. We therefore suggested applying a robust though flexible interpretation of environmental legislation in the marine environment. We acknowledged that there is a risk of undermining the final goal of environmental legislation if increasing flexibility is translated into looser protection. Finally, **Chapter 10** discussed the results of the present thesis. The restructuring capacity of *L. conchilega* through its effect on the niche of several associated species has been re-evaluated by revisiting the original and fundamental concepts of niche theory. Furthermore, the wider resilience of *L. conchilega* reefs was attributed to the ecosystem engineer itself as well as by the closely associated species (which define the biological features of the reefs). This resilience has been discussed with preliminary results of a one-off experimental beam-trawl study that has been performed on subtidal reefs. Chapter 10 continued by evaluating the conservation value of *L. conchilega* aggregations. From a general nature conservation perspective this particular tube builder is considered an important ecosystem engineer, and provides the template for other ecosystem processes, making *L. conchilega* useful within a conservation context. Therefore, the 'label' under which the aggregations may potentially be preserved has been discussed. Potential conservation under the 'reef label' was compared with other reef forming tube worms. These tube reefs all change the benthic community significantly without hosting unique species, they build elevated bioconstructions, generate a biogenic concretion through an increased consolidation, change the sedimentary environment and they can appear and disappear very fast but they all have similar mechanisms that enhance stability and longevity. However, prioritization between different habitats is possible and needed. The mapping of biogenic habitats within conservation strategies will be important and the use of remote sensing techniques (**Addendum II and III**) as well as species distribution models has been discussed. Finally, the potential use of marine protected areas and the relation to fisheries management have been discussed. This part provided an onset of how an ecosystem approach can be applied based on ecological insights and on focused research on anthropogenic impact. As ecosystem engineers merit increased scientific and conservation emphasis, the thesis results are to be interpreted as a first step towards the application of the ecosystem approach to marine management.

The thesis concludes that *L. conchilega* is not only a model organism for studying the sediment-animal-interactions contributing to the strength of a benthic engineer in modifying its habitat and thereby affecting other species, but it is also a useful ecosystem engineer within a conservation context. As such, the ecological knowledge built up in this thesis can potentially contribute to the transition to a more resilient relationship between society and ecosystems.

SAMENVATTING

Oceanen en zeeën zijn sterk geëxploiteerd, wat heeft geleid tot een ernstig verlies van biodiversiteit en de degradatie van het ecosysteem. Van alle menselijke activiteiten die op zee plaatsvinden, wordt visserij gezien als de meest significante. De sterk utilitaristische visie op het mariene milieu leidde tot een focus die vooral gericht is op het behoud van kortetermijnwinst door de exploitatie van de zee. Deze benadering bleek echter te kort te schieten en als antwoord op de voortschrijdende degradatie zijn concepten als 'ecosysteembenadering' intussen aanvaard als sleutelbegrippen voor het beheer van de zee. In dit opzicht worden 'mariene beschermde gebieden' (MBGs) aangelegd in een poging om de degradatie van de zee een halt toe te roepen. Een sterkere integratie van beleid rond mariene bescherming en visserij is dringend nodig en moet gesteund zijn op ecologische kennis willen we komen tot een transitie naar meer veerkrachtige ecoystemen. De Noordzee is één van de meest geëxploiteerde zeegebieden ter wereld en het Belgische deel van de Noordzee (BDNZ) ligt in het centrum van deze activiteiten. Daarom situeren de mariene ecosystemen in deze thesis zich in Noordwest Europa en gaat het vooral om kustwateren bestaande uit ondiepe zandbanken. Macrobenthos (*i.e.* ongewervelde fauna groter dan 1 mm) wordt erkend als een fundamentele ecosysteemcomponent voor het functioneren van mariene ecosystemen en deze component is de focus van deze thesis. Aggregaties van de 'ecosysteemingenieur' *Lanice conchilega* (de schelpkokerworm) worden in detail bestudeerd. *Lanice conchilega* is een kokerbouwende borstelworm (Annelida, Polychaeta, Terribellidae). Specifieke experimenten werden uitgevoerd om inzicht te verkrijgen in de mogelijkheid om deze soort in te schakelen in het beheer van de zee en in wat de relatie is tussen deze worm en de impact van visserij . Het beheer van belangrijke ecosysteemingenieurs wordt erkend als een manier om talrijke geassocieerde soorten en functies te beschermen omdat die de verspreidingslimieten van heel wat soorten uitbreiden. Het zijn dus soorten die een belangrijke plaats kunnen innemen in het hedendaags beheer van de zee. Daarom werd er geopteerd om met dit thesisonderzoek na te gaan wat in die context het belang kan zijn van de ecosysteem ingenieur *L. conchilega*. **Hoofdstuk 1** schetste de bredere context van natuurbeheer op zee en visserijbeheer alsook de huidige kennis van *L. conchilega*.

Hoofdstuk 2 evalueerde het effect van de soort op de macrobenthische gemeenschap en op het sediment van zijn habitat, dit op basis van gegevens uit een lange-termijn databank van de Belgische kustwateren. Zowel de sedimentsamenstelling als de gemeenschapstrucuur van de geassocieerde soortenmatrix bleek te zijn beïnvloed door de aanwezigheid van *L. conchilega*. Er was een positieve correlatie tussen de densiteiten van macrobenthos en van *L. conchilega* ($R = 0.59$; $p < 0.001$). De soortenrijkdom steeg samen met *L. conchilega* densiteiten, behalve voor de hoogste *L. conchilega* densiteitsklasse. Er kon dus geconcludeerd worden dat *L. conchilega* in staat is de macrobenthische gemeenschap te herstructureren en hij doet dat volgens een "babushka" -patroon, wat erop wijst dat *L. conchilega* de nichebreedte van verschillende geassocieerde soorten uitbreidt. In dit hoofdstuk werd ook een ranglijst opgesteld die de associatiegraad van de soorten met *L. conhilega* weergeeft. Deze soortenranglijst werd uitgebreid bediscussieerd op basis van de beschikbare ecologische kennis van de soorten. Geassocieerde soorten bleken bevoordeeld door het veranderend effect op de habitat van de kokers, die een schuilplaats creëren voor soorten, en die de interacties tussen soorten beïnvloeden en de abiotische omgeving veranderen. **Addendum I** is volledig complementair met hoofdstuk 2 omdat het de implicaties van *L. conchilega* onderzocht op Noordzeeschaal. De aanwezigheid van *L. conchilega* in verschillende habitats in de Noordzee en het effect op abundanties, soortenrijkdom en gemeenschapsstructuur in deze habitats werd geëvalueerd. De densiteit van het benthos steeg met die van *L. conchilega* in vier verschillende habitats (ondiep modderig zand, ondiep fijn zand, diep fijn zand en ondiep medium zand) en was het duidelijkst zichtbaar in ondiep fijn zand. Dit addendum toonde aan dat *L. conchilega* aggregaties verantwoordelijk zijn voor een verhoogde habitatkwaliteit in een habitat dat anders sterk gelijkvormig is. **Hoofdstuk 3** karakteriseerde de fysische kenmerken van dichte aggregaties en bediscussieerde dit samen met de biologische kenmerken om te bepalen of deze dense aggregaties als 'riffen' kunnen worden beschouwd. Om ze te classificeren als riffen moeten de activiteiten van de ecosysteemingenieur verschillende habitatkarakteristieken wijzigen. Resultaten toonden aan dat de verhoging en de consolidatie van biogene verhogingen significant hoger waren vergeleken met het omringende ongestructureerde sediment. Gebieden met *L. conchilega* aggregaties zijn vrij extensief en de *patchiness* is hoog (met een bedekking van 5-18%). Individuele aggregaties kunnen verschillende jaren blijven voortbestaan indien er sprake is van jaarlijkse hernieuwing van de bestaande aggregaties door middel van juveniele vestiging. Deze hernieuwing wordt bevorderd door locale hydrodynamische veranderingen en de beschikbaarheid van aanhechtingsstructuren (volwassen kokers). Uit dit hoofdstuk kunnen we besluiten dat de toepassing van de rifdefinitie zoals bepaald in de Habitatrichtlijn aanwijzingen verstrekt dat de fysische en biologische kenmerken om *L. conchilega* als rifbouwer te classificeren aanwezig zijn. Omdat er een scala van aggregatieontwikkelingen bestaat, vertonen niet alle aggregaties evenveel rifkenmerken. Hiervoor werd een zogenaamde *reefiness* tabel opgesteld om de rifkenmerken van een specifieke aggregatie te kunnen inschatten.

De rifstructuren gevormd door *L. conchilega* werden in **hoofdstuk 4** gebruikt om gedetailleerde effecten van fysische verstoring te onderzoeken. Dit hoofdstuk beschrijft een laboratoriumexperiment waarin vier verstoringsregimes op *L. conchilega* riffen werden toegepast. De overleving daalde significant na 10 en na 18 dagen (met een verstoringsfrequentie van iedere 12 en 24 uur, respectievelijk). Naast de impact van boomkorvisserij op de overleving van *L. conchilega* zelf, werd in **hoofdstuk 5** getest hoe kwetsbaar de soorten zijn die nauw met *L. conchilega* geassocieerd leven. Een behandelingszone werd blootgesteld aan een eenmalige experimentele boomkorverstoring tijdens een intertidaal *in situ* experiment. Daarna werd gedurende negen dagen de impact op (en het herstel van) de geassocieerde fauna onderzocht. De gemeenschapsanalyse toonde een duidelijke impact gevolgd door een relatief snel herstel. De impact en het daaropvolgend herstel had grotendeels te maken met twee soorten: *Eumida sanguinea* en *Urothoe poseidonis*. De soortenanalyse bevestigde dat de boomkorpassage *E. sanguinea* significant ($p = 0.001$) impacteerde voor de hele periode van het experiment. Het experiment bevestigde dat nauw geassocieerde soorten van *L. conchilega* riffen negatief beïnvloed worden door boomkorvisserij. Hoofdstukken 4 en 5 (*i.e.* deel II) verschaffen dus inzicht in de veerkracht van het riffensysteem en duidden aan dat de rifstructuren zelf kunnen blijven bestaan onder een bovenmatige boomkorvisserijdruk maar dat de integriteit van het rif aangetast wordt bij verstoring.

De relatie tussen de ecologische waarde van de waargenomen verhoogde benthische diversiteit en de abundanties voor platvis bleek een belangrijk hiaat in de huidige kennis.

Daarom werden de ecologische interacties tussen het benthische habitat van *L. conchilega* enerzijds en platvis anderzijds onderzocht in **hoofdstukken 6 en 7** (*i.e.* deel III). Het structurele effect van biota op de habitatvoorkeur van platvis werd voor de eerste keer onderzocht. **Hoofdstuk 6** onderzocht in een *in situ* experimentele staalnameopzet wat het structurerende effect is van biogene riffen op de verdeling van post-larvale *Pleuronectes platessa* in een intertidaal kraamkamergebied. De densiteitsdistributie van deze platvissoort werd significant ($p < 0.0001$) verklaard door de aanwezigheid van *L. conchilega* riffen. Omdat de effecten op de habitatpreferenties van platvissen in een kraamkamergebied ook gerelateerd kunnen zijn aan voedselbeschikbaarheid werd in **hoofdstuk 7** het belang van de biogene habitats als foerageergebied voor juveniele platvis geëvalueerd. Zowel de verspreiding als het foerageergedrag van de twee platvissoorten *P. platessa* and *Limanda limanda* werd bestudeerd in functie van de aanwezigheid van hoge densiteiten aan ecosysteemingenieurs. In dit hoofdstuk werden twee verschillende ecosysteemingenieurhabitats getest (*L. conchilega* en *Owenia fusiformis*) en staalname vond plaats in twee verschillende kustzones (het BDNZ en het Nederlandse deel van de Waddenzee). Algemene responsen werden onderzocht door relatieve verschillen tussen habitats met ecosysteemingenieurs te vergelijken met aangrenzende gebieden zonder de ecosysteemingenieur. De resultaten toonden aan dat beide platvissoorten een voorkeur hebben voor het habitat met ecosysteemingenieur. Dit gedrag werd verder onderzocht met behulp van maaganalyses. De voorkeur voor het habitat met ecosysteemingenieur kon worden verklaard als een foerageergedrag wat betreft de aanwezigheid van *P. platessa* in *L. conchilega* riffen. Er werd geen gelijkaardige link gevonden voor de habitats die gecreëerd werden door *O. fusiformis*. Daarom wordt in hoofdstuk 7 gesuggereerd dat de juvenielen de ecosysteemingenieurhabitats zowel als beschutting (antipredatiegedrag) en als foerageergebied gebruiken. De kleine biogene structuren die aanwezig zijn in de grotere kraamkamergebieden kunnen beschouwd worden als een 'essentieel juveniel habitat' (EJH) en verdienen aandacht in habitatgeschiktheidsmodellen alsook in maatregelen rond natuurbescherming op zee. Deel II toonde dat *L. conchilega* riffen ook *bottom up* effecten hebben op juveniele platvissen. Als we deze resultaten linken met die uit deel II, dan kunnen we stellen dat verdere modificatie van deze biogene habitats kan leiden tot verlies van één of meerdere ecosysteemfuncties waar platvissoorten afhankelijk van zijn.

De resultaten rond *L. conchilega*, visserij en mariene bescherming werden in het laatste deel van deze thesis (deel IV: hoofdstukken 8, 9 en 10) bediscussieerd in het licht van hun potentiële waarde in een toepassing van de ecosysteembenadering als ondersteuning van het beheer van de zee. **Hoofdstuk 8** evalueerde de literatuur rond mariene beschermingsstrategieën in gematigde gebieden met zachte substraten en bracht dit samen in een 'systeembenadering' die antwoord geeft op het waarom, het hoe en de effectiviteit van MBGs. Deze 'systeembenadering' werd gevisualiseerd in een flow-chart en omvat drie fasen: beleidsdoelstellingen vastleggen, beslissingen nemen en de uiteindelijke effecten van het MBG evalueren. De analyse toonde aan dat in de relatie tussen visserij en MBG-beheer de grootste uitdaging ligt omdat er conflicterende belangen zijn en grote institutionele verschillen bestaan. Andere activiteiten die plaatsvinden op een meer beperkte ruimtelijke schaal en die niet rechtstreeks afhankelijk zijn van het functioneren van het ecosysteem (bv. windmolens op zee en zandextractie) zijn over het algemeen gemakkelijker te beheren dan visserij. De systeembenadering werd toegepast op de Belgische situatie, wat aantoonde dat deze benadering hulp kan bieden bij het verwerven van inzicht in de ingewikkelde interacties tussen verschillende autoriteiten met versplinterde wetgeving. **Hoofdstuk 9** ging verder met het bediscussiëren van het (internationale) wetgevende kader van mariene bescherming. Omdat mariene ecosystemen bedreigd worden, werden er beschermingsstrategieën opgezet in een breder internationaal kader om te kunnen omgaan met de grote en grensoverschrijdende schaal van mariene ecosystemen. Ook ecosysteemdynamieken moeten een prominente plaats krijgen in de deze strategieën. Dit laatste werd in dit hoofdstuk geëvalueerd en het werd duidelijk dat een al te nauwe interpretatie van (internationaal) milieurecht risicovol kan zijn omdat het leidt tot een een traag beslissingsproces en inflexibiliteit in beheersprogramma's; op die manier kan niet worden ingespeeld op de dynamiek van mariene ecosystemen. De strikte interpretatie van internationale wetgeving wordt daarom geacht te falen in zijn doelstelling om tot een duurzaam gebruik van de zee te komen. Een Belgische gevalstudie werd uitgewerkt als voorbeeld en toonde aan dat internationale (EU) wetgeving te strikt geïnterpreteerd wordt en de implementatiesnelheid afremt. Nochtans is een flexibele benadering in het geval van de EU Habitatrichtlijn mogelijk en zelfs nodig. Daarom suggereerden we in dit hoofdstuk een degelijke doch flexibele interpretatie van milieuwetgeving in het mariene milieu.

Tenslotte worden in **hoofdstuk 10** de resultaten van deze thesis bediscussieerd. De capaciteit van *L. conchilega* om zijn biotische omgeving te herstructureren door zijn effect op de niche van verschillende geassocieerde soorten werd opnieuw geëvalueerd door terug te keren naar het originele concept van de nichetheorie. Verder werd de bredere veerkracht van *L. conchilega* riffen beschreven en werd die toegeschreven aan de gecombineerde veerkracht van de ecoysteemingenieur zelf en die van zijn nauw geassocieerde soorten. Deze veerkracht werd verder bediscussieerd met de preliminaire resultaten van een subtidaal boomkorexperiment. Hoofdstuk 10 zette de discussie verder met een evaluatie van de beschermingswaarde van *L. conchilega* aggregaties. Vanuit algemeen natuurbehoudstandpunt kan deze kokerbouwer als een belangrijke ecosysteemingenieur beschouwd worden die een sjabloon biedt voor andere ecosysteemprocessen, wat *L. conchilega* bruikbaar maakt binnen een context voor natuurbehoud. Daarom werd ook het 'label' bediscussieerd waaronder de aggregaties mogelijks kunnen worden beschermd. De mogelijke bescherming onder het 'riflabel' werd vergeleken met andere rifbouwende kokerwormen. Deze kokerriffen veranderen allemaal de benthische gemeenschap zonder unieke soorten te herbergen, ze bouwen verheven constructies, genereren biogene concreties door middel van een verhoogde consolidatie, ze veranderen de sedimentologische omgeving en ze verschijnen en verdwijnen vrij vlug al hebben ze allen gelijkaardige mechanismen om de stabiliteit en de levensduur te verhogen. Het is evenwel zo dat prioriteiten gesteld kunnen worden voor verschillende habitats. De kartering van biogene habitats binnen natuurbehoudsstrategieën zal belangrijk worden en het gebruik van *remote sensing* technieken (**addendum II en III**) alsook het gebruik van soortenverspreidingsmodellen werd bediscussieerd. Tot slot werd het mogelijke gebruik van mariene beschermde gebieden en de relatie tot visserijbeheer bediscussieerd. Dit deel verschafte dan ook een aanzet van hoe een ecosysteembenadering kan worden toegepast gebaseerd op ecologische inzichten en met een focus op onderzoek op antropogene impact. Ecosysteemingenieurs verdienen meer aandacht binnen het kader van mariene bescherming en daarom kunnen de resultaten van deze thesis geïnterpreteerd worden als een eerste stap naar de toepassing van de ecosysteembenadering voor het beheer van de zee.

Deze thesis besloot dat *L. conchilega* niet alleen een modelorganisme is voor het bestuderen van sediment-dier-interacties en als ecosysteemingenieur zijn habitat modificeert en daarbij ook andere soorten beïnvloedt, maar dat het ook een bruikbare ecosysteemingenieur is binnen het kader van mariene bescherming. De ecologische kennis die werd opgebouwd gedurende deze doctoraatsstudie kan daarom mogelijkerwijs bijdragen tot de transitie naar een meer veerkrachtige relatie tussen maatschappij en ecosysteem.

POPULAIRE SAMENVATTING

Vanaf het prille begin dat de mens begon te vissen met sleepnetten, was hij er zich van bewust dat dit tuig wel eens vernietigend kon zijn voor het bodemleven. De allereerste verwijzing naar het vistuig dat vermoedelijk heel sterk overeen stemt met wat we vandaag een boomkor noemen, komt voor in een 14de eeuws Brits document. Dit document verwijst naar het Nederlandse woord 'wonder-kuil', wat doet vermoeden dat de oorsprong van de boomkor zich in Vlaanderen situeert. Die allereerste verwijzing naar het bestaan van de boomkor is te vinden in een wettelijke tekst die handelt over de mogelijke vernietigende gevolgen van deze technieken en aanstuurt op het aan banden leggen van deze vorm van visserij.

Het eerste echte verbod op sleepnetvisserij kwam er in 1499 in Vlaanderen. De redenen luidden als volgt: "*het sleepnet schraapt en vernielt alles waar het over komt op een zodanige manier dat het wieren en structuren ontwortelt en wegveegt die dienen als beschutting voor de vis. Het ontneemt de zandbanken hun kuit wat de vissers ertoe verplicht in verder afgelegen wateren te vissen.*"

In de eeuwen die hierop volgden werd dit type vistuig vreemd genoeg niet aan banden gelegd maar werden steeds grotere schepen met zwaarder vistuig gebouwd om de visvangst op peil te houden. Anno 2009 blijft de boomkor een veelgebruikt vistuig. Het gebruik ervan wordt nog steeds in vraag gesteld. De uitdagingen van een (te) grote boomkorvloot zijn bekend: overbevissing, een 'darwiniaanse schuld' door het selectief wegvangen van grote vissen, waardoor steeds jongere vissen moeten instaan voor de voortplanting, het verdwijnen van toppredatoren (wat kan leiden tot het lokaal verdwijnen van soorten) en het vernietigen van het bodemleven.

Dit laatste is de focus van de thesis. Het onderzoek spitst zich toe op de effecten op dieren die in de zanderige zeebodem leven (schelpdieren, kreeftachtigen, wormen, ...). Er werd gekozen om dit onderzoek uit te voeren op de rifstructuren die gevormd worden door grote hoeveelheden schelpkokerwormen. De schelpkokerworm (*Lanice conchilega*) wordt in deze thesis dan ook in detail bestudeerd. Deze borstelworm leeft in het sediment en bouwt een lange koker uit zand en schelpstukjes en de koker heeft een een diameter van een halve centimeter. De top van de koker steekt zo'n vier centimeter uit het zand. Per vierkante meter kunnen er tot duizenden kokerwormen samen zitten. Door samen te pakken in hoge densiteiten creëren schelpkokerwormen als het ware oases in de zandwoestijn; door deze eigenschap om hun directe omgeving grondig te veranderen worden ze als belangrijke 'ecosysteemingenieur' beschouwd. De impact van boomkorvisserij op deze riffen werd onderzocht in het laboratorium en in natuurlijke omstandigheden. De verschillende experimenten tonen aan dat de schelpkokerworm zelf relatief goed bestand is tegen wat verstoring maar dat de soorten die in de riffen leven veel gevoeliger zijn. We krijgen m.a.w. een rif dat veel minder biologisch waardevol is.

Aangezien de boomkorvisserij jaagt op vis die op de bodem leeft (bv. platvis), werden voor deze thesis een aantal onderzoeken uitgevoerd op pladijs en schar. De hypothese waarrond werd gewerkt was dat deze platvissoorten profiteren van de riffen die gevormd worden door de schelpkokerworm. De resultaten tonen dat deze soorten een voorkeur vertonen om in de omgeving van de riffen te verblijven. Ze doen dit omdat daar meer voedsel beschikbaar is en de jonge platvis gebruikt de riffen ook als een soort schuilplaats. De riffen blijken dus een belangrijk aspect te zijn van het natuurlijke milieu van de (jonge) platvis. Het gebruik van de boomkor kan dus nadelig zijn voor platvis omdat ze een deel van hun voedsel en schuilplaats verliezen.

Een laatste deel van de thesis werkt rond het spanningsveld van mariene natuurbehoudsdoelstellingen en zeevisserij. Een literatuuranalyse rond strategieën voor mariene bescherming in gematigde gebieden met zanderige bodem beschrijft het hele proces van het aanleggen van een marien beschermd gebied. Deze analyse werd opgevat als een 'systeembenadering' en toont aan dat de grootste uitdaging ligt in de relatie tussen visserij en natuurbehoudsdoelstellingen omwille van conflicterende belangen en grote verschillen tussen de instellingen bevoegd voor visserij en bescherming van het mariene milieu. Daarom werden de resultaten van deze thesis omtrent de soortenrijke riffen van de schelpkokerworm bediscussieerd in het kader van de 'ecosysteembenadering'. De thesis benadrukt dat het gebruik van belangrijke 'ecosysteemingenieurs' aandacht verdient binnen het kader van mariene bescherming en dat ze ook kunnen gebruikt worden om de effecten van boomkorvisserij na te gaan. Daarenboven is voor de schelpkokerworm een duidelijk wettelijk kader aanwezig waarbinnen natuurbehoudsmaatregelen kunnen worden uitgevoerd (ze kunnen beschermd worden onder het ‘rif-label’ binnen het Europese Natura 2000 netwerk). De ecologische kennis die werd opgebouwd gedurende deze doctoraatsstudie kan daarom bijdragen tot een breder beheer van de zee. Vooral in het soortenrijke kustgebied van de Belgische Noordzee, met zijn ondiepe zandbanken, speelt de schelpkokerworm een belangrijke rol en verdient ze een plaats in de beleidsplannen rond duurzaam beheer van zowel de natuur als de visserij. De resultaten van deze thesis vormen daarom een belangrijke stap richting ‘ecosysteembenadering’ voor het beheer van de zee.

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CURRICULUM VITAE

PUBLICATION LIST & COMMUNICATIONS

CURRICULUM VITAE MARIJN RABAUT

After having obtained a Master in Biology (Zoology) and a Master in Marine and Lacustrine Sciences, the candidate started his scientific career in August 2004 at the Marine Biology Research Group of Ghent University. In October 2005, he continued his PhD research at the research group with the financial support of Research Foundation - Flanders (*FWO-Vlaanderen*) and the continued supervising support from Prof. Dr. S. Degraer (copromotor, supervisor) and Prof. Dr. M. Vincx (promotor). The doctoral research at Ghent University was embedded in the Westbanks project. This project aims to understand benthic, pelagic and air-borne ecosystem interaction in shallow coastal seas and is a cooperation project between different research institutes. This project is funded in the frame of the "Science for Sustainable Development" programme and is supported by the Belgian Science Policy. Furthermore, the candidate was involved in other research projects such as WaKo, BWZee, BBSea, Marebasse, Quest4D, Habitat (pSCI). Contributions to the EU Network of Excellence on marine biodiversity and ecosystem functioning (MarBEF) were made for Themes 2 and 3. Furthermore, the candidate is involved in the start up of a European project on monitoring and evaluation of spatially managed areas (MESMA), a project funded within the 7th framework programme of the EU (FP7).

The results presented in this thesis were communicated during several (national and international) conferences, symposia and workshops. Efforts to communicate results to decision makers as well as to the public at large are reflected in the advices and the national press citations. A list of oral and poster communications is provided below.

Upon submission of this thesis the candidate (co)authored 14 a1 papers (9 published/accepted, 3 under review and 2 to be submitted), 2 book chapters, 6 project reports and several advices. The publication list can be found below. The candidate has been peer reviewer for *Marine Ecology Progress Series*, *Helgoland Marine Research*, *Estuarine, Coastal and Shelf Science* and *Journal of Sea Research*.

PUBLICATION LIST

a1 journals (peer reviewed)

1. Degraer, S., Moerkerke, G., Rabaut, M., Van Hoey, G., Du Four, I., Vincx, M., Henriet, J.P. and Van Lancker, V. 2008. Very-high resolution side-scan sonar mapping of biogenic reefs of the tube-worm *Lanice conchilega*. Remote Sensing of Environment, 112: 3323-3328.
2. Derous, S., Agardy, T., Hillewaert, H., Hostens, K., Jamieson, G., Lieberknecht, L., Mees, J., Moulaert, I., Olenin, S., Paelinckx, D., Rabaut, M., Rachor, E., Roff, J., Stienen, E.W.M., van der Wal, J.T., van Lancker, V., Verfaillie, E., Vincx, M., Weslawski, J.M. and Degraer, S. 2007a. A concept for biological valuation in the marine environment. Oceanologia, 49: 99-128.
3. Derous, S., Austen, M., Claus, S., Daan, N., Dauvin, J.C., Deneudt, K., Depestele, J., Desroy, N., Heessen, H., Hostens, K., Marboe, A.H., Lescrauwaet, A.K., Moreno, M.P., Moulaert, I., Paelinckx, D., Rabaut, M., Rees, H., Ressurreicao, A., Roff, J., Santosi, P.T., Tatarek, A., Ter Hofstede, R., Vincx, M., Zarzycki, T., Degraer, S., Speybroeck, J. and Stienen, E.W.M. 2007b. Building on the concept of marine biological valuation with respect to translating it to a practical protocol: Viewpoints derived from a joint ENCORA-MARBEF initiative. Oceanologia, 49: 579-586.
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5. Rabaut, M., Degraer, S., Schrijvers, J., Derous, S., Bogaert, D., Maes, F., Vincx, M. and Cliquet, A. 2009a. Policy analysis of the 'MPA-process' in temperate continental shelf areas. Aquatic Conservation: Marine and Freshwater Ecosystems, 19: 596-608.
6. Rabaut, M., Du Four, I., Van Lancker, V., Degraer, S. and Vincx, M. in prep.-a. Ecosystem engineers stabilize sand bank systems: *Owenia fusiformis* aggregations as ecologically important microhabitat.
7. Rabaut, M., Gamarra, R., Vincx, M. and Degraer, S. in prep.-b. Experimental beam trawl effects on the subtidal macrobenthic community associated to *Lanice conchilega* reefs.
8. Rabaut, M., Guilini, K., Van Hoey, G., Vincx, M. and Degraer, S. 2007. A bio-engineered soft-bottom environment: The impact of *Lanice conchilega* on the benthic species-specific densities and community structure. Estuarine Coastal and Shelf Science, 75: 525-536.
9. Rabaut, M., Van de Moortel, L., van Dalfsen, J., Vincx, M. and Degraer, S. in prep.-c. Importance of eco-engineered inshore habitats for juvenile flatfish.
10. Rabaut, M., Van de Moortel, L., Vincx, M. and Degraer, S. accepted. Biogenic reefs as structuring factor in *Pleuronectes platessa* (Plaice) nursery. Journal of Sea Research.
11. Rabaut, M., Vincx, M. and Degraer, S. 2009b. Do *Lanice conchilega* (sandmason) aggregations classify as reefs? Quantifying habitat modifying effects. Helgoland Marine Research, 63: 37-46.
12. Rabaut, M., Vincx, M., Hendrickx, F. and Degraer, S. subm. The resistance of *Lanice conchilega* reefs to physical disturbance. ICES Journal of Marine Science.
13. Van Hoey, G., Guilini, K., Rabaut, M., Vincx, M. and Degraer, S. 2008. Ecological implications of the presence of the tube-building polychaete *Lanice conchilega* on soft-bottom benthic ecosystems. Marine Biology, 154: 1009-1019.
14. Verfaillie, E., Degraer, S., Du Four, I., Rabaut, M., Willems, W. and Van Lancker, V. subm. The relevance of ecogeographical variables for marine habitat suitability modelling of *Owenia fusiformis*. Estuarine, Coastal and Shelf Science.

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1. Rabaut, M. and Cliquet, A. in press. The dynamics of the marine environment versus the rigid interpretation of nature conservation law. *In:* Environmental Law Issues and Developments, Ed by. Nova Science Publishers, New York.
2. Rabaut, M., Vincx, M. and 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:* Fisheries: Management, economics and perspectives, Ed by N. F. McManus and D. S. Bellinghouse, pp. 485-495. Nova Science Publishers, New York.

Reports

1. Degraer, S., Braeckman, U., Haelters, J., Hostens, K., Jacques, T., Kerckhof, F., Merckx, B., Rabaut, M., Stienen, E., Van Hoey, G., Van Lancker, V. and Vincx, M. 2009. Studie betreffende het opstellen van een lijst met potentiële Habitatrichtlijn gebieden in het Belgische deel van de Noordzee, Brussels. 93 pp.
2. Depestele, J., Courtens, W., Degraer, S., Derous, S., Haelters, J., Hostens, K., Moulaert, I., Polet, H., Rabaut, M., Stienen, E. and Vincx, M. 2008. WaKo: Evaluation of the environmental impact of gill nets and beam-trawl fisheries on the Belgian part of the North Sea (End Report) [in Dutch]. VIS/02/B/05/DIV, ILVO-Fisheries, Ostend (Belgium). 253 pp.
3. Van Lancker, V., Du Four, I., Papili, S., Verfaillie, E., Schelfaut, K., Rabaut, M. and Degraer, S. 2007. Habitat signitare catalogue, Belgian part of the North Sea, Belgian Sicence Policy. 27 pp.
4. Vanaverbeke, J., Braeckman, U., Claus, S., Courtens, W., De Hauwere, N., Degraer, S., Deneudt, K., Goffin, A., Mees, J., Merckx, B., Provoost, P., Rabaut, M., Soetaert, K., Stienen, E. and Vincx, M. 2009. Long-term data from the Belgian Continental Shelf in the framework of science-based management of the coastal North Sea: Report of the WestBanks integrative workshop, Belgian Science Policy (Belspo), Brussels. 23 pp.
5. Vanaverbeke, J., Braeckman, U., Courtens, W., Cuveliers, E., Degraer, S., Huyse, T., Larmuseau, M., Provoost, P., Rabaut, M., Remerie, T., Savina, M., Soetaert, K., Stienen, E., Van den Eynde, D., Van de Walle, M., Vanreusel, A., Volckaert, F. and Vincx, M. 2007. Understanding benthic, pelagic and air-borne ecosystem interactions in shallow coastal seas: WestBanks, Belgian Science Policy (Belspo). 28 pp.
6. Vanaverbeke, J., Braeckman, U., Cuveliers, E., Courtens, W., Huyse, T., Lacroix, G., Larmuseau, M., Maes, G., Provoost, P., Rabaut, M., Remerie, T., Savina, M., Soetaert, K., Stienen, E., Verstraete, H., Volckaert, F. and Vincx, M. 2009. Understanding benthic, pelagic and air-borne ecosystem interactions in shallow coastal seas: WestBanks, Belgian Science Policy (Belspo), Brussels. 54 pp.

a4 journals (non-peer reviewed, national journals)

1. Rabaut, M., Braeckman, U. and Kerckhof, F. 2008. Nieuwe riffen geen gevaar voor wandelaars. De Spille: 3. p.16
2. Rabaut, M., Braeckman, U., Rappé, K., Degraer, S. and Kerckhof, F. 2008. Borstelwormen bedreigen Heist: een sciencefictionverhaal. De Grote Rede: 22. p.31

Advices

1. Rabaut, M. and Cliquet, A. 2008. Opmerkingen bij voorontwerp beleidsplannen mariene beschermde gebieden. Publieksbevraging voorontwerp beleidsplannen mariene beschermde gebieden. Federale Overheidsdienst Volksgezondheid, Veiligheid van de Voedselketen en Leefmilieu, DG Leefmilieu, dienst Marien Milieu. June 2008, Brussels (Belgium).
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3. Rabaut, M. and Vincx, M. 2008. Advies en opmerkingen op 'Strategische milieubeoordeling national operationeel programma Belgische visserijsector'. Landbouw- en visserijbeleid van de Vlaamse Overheid. July 2008, Brussels (Belgium).

COMMUNICATIONS

1. Cliquet, A., Bogaert, D. and Rabaut, M. 2008. Constraints for Natura 2000 in the marine environment. A Belgian case study. Littoral 2008. Oral presentation (A. Cliquet), November 2008, Venice (Italy).
2. Degraer, S., Derous, S., Rabaut, M., Vincx, M., Courtens, W., Stienen, E., Paelinckx, D., Deckers, P., Deneudt, K., Hostens, K., Moulaert, I., Roff, J., Van Lancker, V. and Verfaillie, E. 2008. Biological valuation: Guidelines for a transparent and generally applicable protocol for the marine environment. World Conference on Marine Biodiversity. Oral presentation (S. Degraer), November 2008, Valencia (Spain).
3. Rabaut, M., Cliquet, A., Vincx, M. and Degraer, S. 2008a. Ecological restoration in the Belgian Part of the North Sea. Sixth European Conference on Ecological Restoration (SER). Poster presentation, September 2008, Ghent (Belgium).
4. Rabaut, M., Degraer, S. and Vincx, M. 2008b. An update on beam trawling *Lanice* reefs: The subtidal experiment. Westbanks (End-user meeting). Oral presentation, April 2008,
5. Rabaut, M., Kerckhof, F., Vincx, M. and Degraer, S. 2007a. Wat betekent de zandbank voor het benthos? Studiedag 'De zandbank van Heist, een boeiend fenomeen'. Oral presentation, October 2007, Knokke-Heist (Belgium).
6. Rabaut, M., Vincx, M. and Degraer, S. 2005. Impacts of marine protected areas for ecosystem and fisheries. Third Marine Biology Section Symposium (ThiMBSS). Oral presentation, February 2005, Ghent (Belgium).
7. ---. 2006a. Ecological interactions in *Lanice* fields: An ecosystem approach for nature conservation in the North Sea. GOA-UGent Project BBSea. Oral presentation, December 2006, Ghent (Belgium).
8. ---. 2006b. Intertidal *Lanice conchilega* bioherms. Long lasting structures built up by short living species: How do they manage? Sandy Beach Symposium. Poster presentation, Vigo (Spain).
9. ---. 2007b. Beam-trawling bio-engineered habitats: Implications for homeless benthos and hungry sole. Fifth Marine Biology Section Symposium (FiMBSS). Oral presentation, February 2007, Ghent (Belgium).
10. ---. 2007c. Ecological importance of *Lanice conchilega* reefs and the resilience towards beam-trawling. WestBanks (End-user meeting). Oral presentation, November 2007,
11. ---. 2007d. Ecologische Interacties in Lanice-velden : een ecosysteembenadering voor natuurbeheer in de Noordzee. Overleg met FOD Leefmilieu in het kader van Natura2000. Oral presentation tijdens October 2007,
12. ---. 2007e. Het gebruik van een 'ecosysteemingenieur' om het beheer te ondersteunen (voorbeeldstudie 1). Jaar van de Dolfijn. Poster presentation, November 2007, Nieuwpoort (Belgium).
13. ---. 2007f. A strategy to generate ready-to-use ecological Information to manage marine soft-bottom areas. European Symposium on Marine Protected Areas as a Tool for Fisheries Management and Ecosystem Conservation. Poster presentation September 2007, Murcia (Spain).
14. ---. 2007g. Trophic interactions at the sediment-water interface. End-user meeting in the framework of the WestBanks project. Oral Presentation, March 2007,
15. ---. 2007h. The use of ecosystem engineers to underpin ecosystem management. The *Lanice conchilega* case. European Symposium on Marine Protected Areas as a Tool for Fisheries Management and Ecosystem Conservation. Poster presentation September 2007, Murcia (Spain).
16. ---. 2008c. Beam trawling, benthic diversity and ecosystem functioning in temperate soft-bottom habitats. World Conference on Marine Biodiversity. Oral presentation, November 2008, Valencia (Spain).
17. ---. 2008d. Trawling reefs: Impacts of habitat modifications on flatfishes. 7th International Flatfish Symposium (IFS). Oral presentation, November 2008, Sesimbra (Portugal).
18. ---. 2009a. Does *Lanice conchilega* classifies as reef builder? Workshop on the conservation of Annelid reefs (CAREEFS). Oral presentation, September 2009, Dinard (France).
19. ---. 2009b. The ecosystem engineer *Lanice conchilega*. Workshop on the conservation of Annelid reefs (CAREEFS). Oral presentation, September 2009, Dinard (France).
20. ---. 2009c. Tube worm reefs as important ecosystem engineers in the coastal zone: Biological hotspots stabilizing sand bank systems. Coasts and Estuaries in a Changing World, CERF2009. Oral presentation, November 2009, Portland (USA).
21. Rabaut, M., Vincx, M., Van Hoey, G., Remerie, T., Braeckman, U. and Degraer, S. 2007i. *Lanice conchilega*: The role of a native ecosystem engineer in explaining biodiversity. Workshop on native and invasive ecosystem engineers (MarBEF theme 2). Oral presentation, April 2007, Klaipeda (Lithuania).

This doctoral thesis bridges experimental research and policy issues in the marine environment. The focus is on the challenging relation between nature conservation and current fisheries practices. The study sites investigated consist largely of sedimentary sand banks and swales, situated in North-Western Europe. A particular biogenic habitat has been chosen to study both the ecological importance and the resilience towards the physical disturbance of beam-trawling. This habitat is *Lanice conchilega* reefs, which are distinct aggregations of tube dwelling polychaetes (bristle worms). The implications of these tube worm reefs for the benthic environment as well as for flatfish species are studied in depth and several experiments (in lab and field conditions) quantify the impact of beam trawl fisheries. The thesis finishes by integrating these results in legal policy options and discusses the process of MPA-implementation. The general discussion elaborates how this may contribute to the application of an ecosystem approach to support marine management .

This PhD research has been promoted by **Prof. Dr. M. Vincx** and **Prof. Dr. S. Degraer**. Marijn Rabaut is trained as biologist (MSc) and marine scientist (MSc) and carried out his research at the Marine Biology Research Group of Ghent University in Belgium. Financial support was provided by Research Foundation - Flanders (*FWO-Vlaanderen*) and Ghent University.

The thesis has been submitted in partial fulfilment of the requirements for the degree of Doctor in Science (Biology).

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