

**Macrobenthic fauna on intertidal mudflats in the Dutch Wadden Sea:
Species abundances, biomass and distributions in 2004 and 2006**

Casper Kraan, Anne Dekinga, Eelke O. Folmer, Henk W. van der Veer, and
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NIOZ-Report 2007-2

**Met een "Expert Judgement": veranderingen in de benthische macrofauna in de
Nederlandse Waddenzee tussen 2004 en 2006 en daarvoor**

This report was written at the request of NAM, Assen.

Royal Netherlands Institute for Sea Research (NIOZ),
Department of Marine Ecology

Expert judgement: veranderingen in de benthische macrofauna in de Nederlandse Waddenzee tussen 2004 en 2006 en daarvoor

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Texel*

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1. Inleiding

Ondanks het grote belang van benthos in de Waddenzee voor het functioneren als rust- en voedselgebied voor vogels, is onze kennis over diezelfde bodemfauna nog steeds beperkt. Kwantitatieve studies starten pas in begin 70-er jaren. Van voor die tijd is slechts anekdotische informatie bekend, naast productiegegevens van mosselkwekers. Voor een overzicht van het bodemfaunaonderzoek en -monitoring wordt verwezen naar het uitvoerige overzicht opgesteld door Essink voor RIKZ (Anon 2005). Voor inbedding van de huidige studie wordt volstaan met een overzicht op hoofdlijnen.

De eerste benthos-studies kwamen deels voort uit zuiver wetenschappelijke vragen, zoals het werk van Beukema (1982) op het Balgzand in de westelijke Waddenzee en deels uit toegepaste vraagstellingen, zoals het werk van Essink (Essink & Romeyn 1994) rond de effecten van lozingen uit een smeerpipeline in de oostelijke Waddenzee. Traditioneel was dit werk gebaseerd op de zogenaamde raaienmethode, waarbij niet het verkrijgen van een ruimtelijke dekking van belang is, maar de interacties tussen soorten. Deze interacties werden gevolgd in een aantal karakteristieke gebieden, waarbij bemonsteringen beperkt bleven tot de droogvallende wadplaten. In die tijd was er geen geschikte apparatuur om ook de diepere delen te bemonsteren. Dit werk is zowel in de oostelijke als de westelijke Waddenzee tot op heden voortgezet, waarbij de laatste jaren een uitbreiding heeft plaats gevonden met raaien in het subtidal. Incidenteel heeft hierbij ook een Waddenzeebrede raaienbemonstering plaatsgevonden (Beukema 1976).

Meer aandacht voor de rol van benthos in het Waddenzee-ecosysteem ontstond met het BOEDE (Biologisch Onderzoek Eems-Dollard Estuarium) project, geïnitieerd om de effecten van afvalwaterlozing in de Dollard te bepalen (BOEDE 1983). Dit project kreeg later een vervolg in het EMOWAD (Ecologische Modellering Waddenzee) project (EMOWAD 1988). Parallel hiermee kwam in 1983 een overzicht gereed van alle beschikbare wetenschappelijke kennis over de Waddenzee (Wolff 1983).

Een eerste inzicht in de ruimtelijke verspreiding van benthos dateert uit begin 90-er jaren. Onder de leiding van Piersma werd in delen van de Waddenzee voor de eerste keer een gridbemonstering uitgevoerd (Piersma 1994). Tot voor kort beperkte dit zich voornamelijk tot de westelijke Waddenzee en enkele plekken in het oostelijke deel: Simonszand en Engelmansplaat.

Momenteel kunnen een tweetal kennisbronnen geïdentificeerd worden die geen van beide gebiedsdekkend zijn: de raabemonsteringen lopend van 1970 tot op heden, en de grid-bemonsteringen vanaf 1988 (maar pas vanaf 1996 gebiedsdekkend in de westelijke Waddenzee). Opgemerkt moet worden dat deze bemonsteringen zich beide beperken tot de zogenaamde "soft-sediments". Onderzoek op harde substraten, zoals een dijkvoet of mosselbanken, vindt nauwelijks plaats. Toch is een recente invasive soort, de Japanse oester *Crassostrea gigas*, via hard substraat het systeem binnengekomen om nu in toenemende mate op de soft-sediments dominant aanwezig te zijn.

2. Functioneren van het Waddenzee systeem

Het functioneren van het Waddenzee ecosysteem is nog steeds een onderwerp van discussie. Retrospectief onderzoek wordt sterk beperkt door het gebrek aan kwantitatieve informatie van voor de 70-er jaren.

Op grond van hydrografisch werk van Postma (1954) wordt de Waddenzee gezien als accumulatiegebied van zand en slib met daaraan verbonden organisch materiaal. De afbraak van dit materiaal levert, samen met de aanvoer vanuit zoetwaterlozingen, de noodzakelijke nutriënten voor de primaire productie in het gebied. Deze, zowel pelagische als benthische primaire productie, wordt samen met het aangevoerde organisch materiaal gezien als de belangrijkste voedselbronnen voor het benthos (EMOWAD 1988; Lindeboom *et al.* 1989). Het functioneren van de Waddenzee vertoont grote overeenkomsten met een zuiveringsinstallatie: aangevoerd organisch materiaal wordt afgebroken. Voordat de eutrofiëring in de 70-er jaren plaatsvond, was de aanvoer en afbraak van organisch materiaal mogelijk de belangrijkste nutriëntenbron voor het gebied. Met het op gang komen van de eutrofiëring is de directe aanvoer van nutriënten met de zoetwaterlozingen een belangrijkere bron geworden.

Anekdotische informatie suggereert dat de Waddenzee in het verleden absoluut niet arm aan bodemdieren, vogels en vissen is geweest. Nog tijdens de Tweede Wereldoorlog moesten fuiken dagelijks gelegegd worden om te voorkomen dat de (dikke) houten steunpalen braken. Een dergelijke rijkdom is tegenwoordig niet meer aanwezig. Het is best mogelijk dat dit te maken heeft met grote veranderingen in de structuur van het Waddenecosysteem gedurende de laatste 70 jaar. In de loop van deze periode verdwenen voornamelijk de structuurvormende ecosysteembouwers zoals de zeegrassen en oesters en, recentelijk in de westelijke Waddenzee, ook de mossels. Daarmee gingen allerlei biologische feedbacksystemen verloren waarmee het ecosysteem mogelijk afhankelijker is gemaakt van externe nutriëntentoevoer (Norling *et al.* 2007; Olf *et al.* in prep.). Wat betreft het functioneren van het huidige systeem zou dit betekenen dat een groter deel van de primaire productie niet meer door de hogere trofische niveaus maar door het microbiële voedselweb in het systeem wordt gebruikt.

3. Het macrobenthos: top-down of bottom-up control?

Gezien de belangrijke rol die het macrobenthos speelt in het gebied, leidt dit al snel tot de vraag *wat* de aantallen en hoeveelheid benthos in het gebied bepaalt? "Bottom-up control" stelt dat het voedselaanbod de beperkende en controlerende factor is, terwijl bij "top-down control" de consumenten de bepalende en sturende factor zijn.

De sterke toename van macrobenthos in delen van het Balgzand in de 70-er jaren, parallel aan de toename van de nutriënten (zgn. eutrofiëring), suggereerde een sterke voedselbeperking en daarmee een bottom-up control: zowel aantallen organismen, als hun biomassa, namen toe parallel aan de eutrofiëring (Beukema & Cadée 1997). Dit signaal was niet overal aanwezig. In sommige delen van vooral de lagere wadplaten leken andere factoren bepalend te zijn. Verder is de Waddenzee in de 60-er jaren geteisterd door een aantal zware vervuilingen met vastgestelde effecten op in ieder geval vogels en zeezoogdieren (Wolff 1983), en het is de vraag of het macrobenthos bij het begin van de series van Beukema (1976) zich hierdoor niet op een historisch laag niveau bevond.

In de loop der tijd is het besef doorgedrongen dat andere factoren minstens zo belangrijk kunnen zijn. Een cruciale factor lijkt de vestiging van benthoslarven vanuit de watermassa op de bodem te zijn. In het verleden kenmerkte het gebied zich mede door een mozaïek van habitats (mosselbanken, zeegrasvelden, etc.). Hier is tegenwoordig weinig meer van over. Het verdwijnen van zeegrasvelden en de verwoesting van wadplaten door mechanische kokkelvisserij lijkt hier een rol in te spelen (Piersma *et al.* 2001; Piersma 2006; Van Gils *et al.* 2007; Kraan *et al.* 2007).

Hoewel in ieder geval het gebrek aan aanwas van jong broed een van de belangrijkste factoren lijkt te zijn (Van der Meer *et al.* 2001), zijn er nog veel zaken onduidelijk: hoe zijn de interacties tussen soorten?, wat bepaalt en welke factoren bepalen de verhouding tussen wormen en schelpdieren?, wat zijn "regime shifts" en onder welke omstandigheden treden ze op?, wat is de invloed van klimaatverandering?; kan het gebied zijn habitatdiversiteit weer terugkrijgen?, etc. Op dit moment is geen eenduidend antwoord op de vraag te geven of het macrobenthos top-down dan wel bottom-up gecontroleerd is.

4. Lange termijn veranderingen in het macrobenthos in de Waddenzee

De grote verschillen in morfologie en hydrografie zowel tussen als binnen de verschillende kombergings-gebieden in de Waddenzee betekenen dat op ieder moment ook grote ruimtelijke verschillen in macrobenthos aangetroffen kunnen worden, los van lange termijn verschillen.

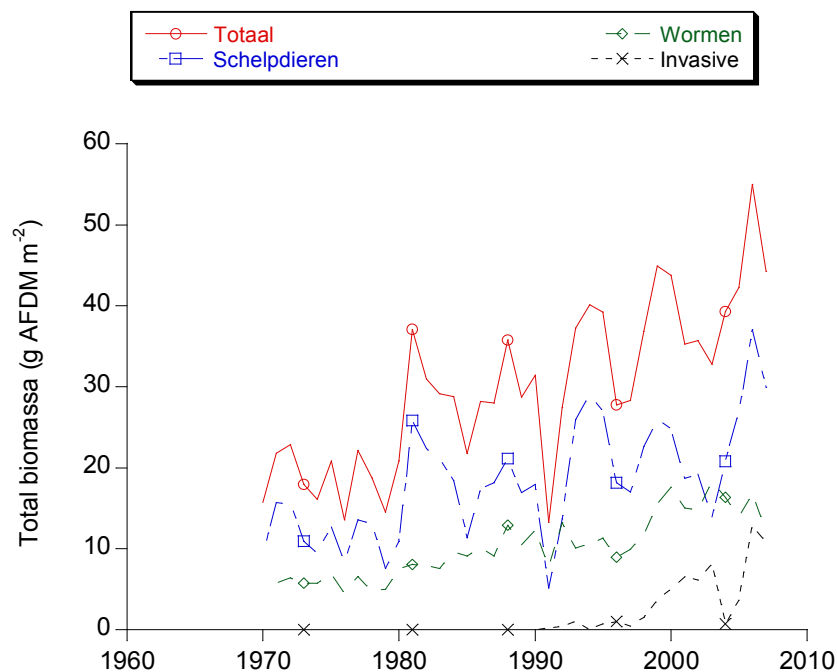
Lange termijn verschillen worden voor een belangrijk deel gedreven door de patronen in de jaarlijkse aanwas van jonge dieren (het recruitment succes). Het recruitment succes wordt in belangrijke mate bepaald door de natuurlijke variaties in vooral omgevingsfactoren zoals water temperatuur, zoutgehalte etc. die direct invloed hebben op de voortplanting zelf dan wel indirect werken d.m.v. effecten op de predatoren. Aangezien water temperatuur in belangrijke mate bepaald wordt door heersende klimatologische omstandigheden (strengere versus zwakke winters etc.) betekent dit dat identieke patronen in aanwas op een grote ruimtelijke schaal van meerdere kombergings-gebieden en zelfs de gehele Waddenzee gevonden kunnen worden. De nauwe verwantschap en sterke overeenkomst in levenswijze tussen diverse soorten kan er toe leiden dat dezelfde grootschalige patronen in meerdere soorten optreden (Beukema *et al.* 2000; Beukema *et al.* 2001).

Het feit dat de meeste soorten meerdere jaren dan wel zelfs langlevend (> 10 jaar) zijn betekent dat de jaarlijkse fluctuaties in aanwas nog meerdere jaren door kunnen werken in de biomassa. Fluctuaties dan wel veranderingen in voornamelijk temperatuur en saliniteit kunnen tot het plotsklaps verdwijnen van soorten en verschijnen van nieuwe soorten leiden (de invasieve soorten). Als deze veranderingen op grote schaal plaats vinden en in meerdere componenten van het systeem wordt zelfs van een regime shift gesproken (Weijermans *et al.* 2005).

De NIOZ Balgzand serie (1970-heden) is het meest geschikt om de lange termijn veranderingen in het macrobenthos te kunnen beschrijven (zie figuur 1). Vanaf het begin van de serie lijkt er sprake te zijn van een continue toename van het macrobenthos op het Balgzand. De eutrofiering in de 70-er jaren werd verantwoordelijk gehouden voor de

sterke toename rond 1980, hoewel de sanering van de lozingen in de 90-er jaren geen negatief effect op de biomassa lijkt te hebben gehad (Beukema *et al.* 2002; Dekker & Waasdorp 2007). De langzame trend van toenemende biomassa gaat gepaard met grote jaar op jaar fluctuaties en betekent niet dat omstandigheden zich alleen maar verbeteren voor soorten die van benthos afhankelijk zijn. Zo wordt de recente toename veroorzaakt door de introductie van de Japanse oester, een soort die door de dikke schelp niet of nauwelijks door vogels en vissen gegeten kan worden. De toename in schelpdieren weerspiegelt de sterke toename van twee geïntroduceerde soorten: het Amerikaans Mesheft *Ensis americanus* en de Strandgaper *Mya arenaria*. Het nonnetje, mossels, en de kokkel namen verder af; een trend die ingezet is in midden 90-er jaren (Dekker & Waasdorp 2007). Ondanks de toename in de totale biomassa, lijkt de hoeveelheid benthos dat geschikt is als voedsel voor vogels en vissen eerder achteruitgegaan te zijn.

Wat de aantallen betreft, lijkt er een verworming van de bodemfauna plaatsgevonden te hebben, dat wil zeggen dat wormachtigen (bijvoorbeeld Draadworm, Wapenworm, Zeeduizendpoot) in aantal toegenomen zijn ten opzichte van de schelpdieren (Beukema *et al.* 2002; Van Roomen *et al.* 2005; Piersma 2006). Deze verschuiving wordt ook weerspiegeld door de vogelgemeenschap die de Waddenzee bezoekt in het winter halfjaar. Schelpdiereters, zoals Kanoeten en Eiders, zijn in aantal afgenomen, terwijl wormeneters, zoals Bonte strandloper en Rosse grutto, juist in aantal toegenomen zijn (Van Roomen *et al.* 2005).



Figuur 1. Lange termijn veranderingen in het macrobenthos op het Balgzand, westelijke Waddenzee. Gegevens naar Dekker & Beukema (unpubl.).

5. Veranderingen Waddenzee 2004-2006

De huidige gegevensseries zijn sterk beperkt zowel in ruimte als in tijd. Voor veel van de kombergings-gebieden in de Waddenzee is geen informatie van het macrobenthos bekend. Dit maakt op dit moment het volgen dan wel het analyseren van veranderingen op het niveau van kombergings-gebieden onmogelijk. Door de beperkte hoeveelheid data kan slechts een vergelijking gemaakt worden tussen oostelijke en westelijke Waddenzee en daarbinnen tussen een paar kombergings-gebieden.

Het nonnetje (*Macoma balthica*) is in aantal afgenomen in de periode 2004-2006, waarbij dit in het westelijke deel van de Nederlandse Waddenzee al jaren speelt en het gaat om een reductie van 90% in aantallen sinds begin jaren 1990 (Van Gils *et al.* in prep.; Drent *et al.* in prep.). De afname lijkt zich nu ook uit te breiden naar het oostelijke deel van de Nederlandse Waddenzee, waarbij de afnames in de westelijke kombergingen van het oostelijke deel (Borndiep, Pinkegat, Zoutkamperlaag) het sterkst zijn. De oostelijke kombergingen (Eilanderbalg, Schild, Eems-Dollard) blijven op hetzelfde niveau. MON*BIOLOGIE laat precies dezelfde trends zien (Dekker & Waasdorp 2007).

Kokkels (*Cerastoderma edule*) geven een heel ander beeld: een lichte toename in de westelijke Waddenzee en een sterke toename in de oostelijke Waddenzee sinds 2004. Dit beeld wordt bevestigd door de bemonsteringen binnen MON*BIOLOGIE (Dekker & Waasdorp 2007).

Mossels (*Mytilus edulis*) nemen in de oostelijke Waddenzee licht toe, maar op het westwad daarentegen is en blijft het areaal met mossels tot een minimum beperkt.

Japanse Oester (*Crassostrea gigas*): deze geïntroduceerde soort is ondanks onheilspellende berichten in de media en wetenschappelijke literatuur, op de droogvallende platen nog steeds geen soort van betekenis. We zien een lichte toename in de oostelijke Waddenzee. Op het Balgzand (MON*BIOLOGIE) is het een soort van geringe, maar wel toenemende, betekenis. Deze indrukken van veranderingen zijn alleen gebaseerd op aantallen, omdat biomassa data niet compleet waren (zie rapport).

6. Vereiste sampling design

Het zal duidelijk zijn dat met de bestaande bemonsteringsmethodieken lokale veranderingen in benthos niet geanalyseerd kunnen worden. De huidige kwalitatief uiterst onvolkomen gegevensseries, zowel in ruimte als tijd, maken een eenduidende interpretatie van veranderingen onmogelijk. De raabemonsteringen verspreid over de Waddenzee zijn vooral bedoeld voor de analyse van interacties tussen soorten en voor de gridbemonsteringen ontbreken op dit moment een Waddenzee brede dekking. Noodzakelijk zijn spatiëel en temporeel gemultiplieerde waarnemingsreeksen.

Momenteel vindt in het verlengde van deze rapportage een door de NAM ondersteunde analyse plaats, om te komen tot een optimale benthos bemonstering van de Waddenzee om mogelijke veranderingen in bepaalde kombergingen als het gevolg van bepaalde ingrepen te kunnen traceren en te volgen. De eerste resultaten van de analyse suggereren een opzet waarbij in ieder kombergings-gebied random een aantal locaties, eventueel gestratificeerd, m.b.v. een gridbemonstering jaarlijks gevolg worden (Bijleveld *et al.* in prep.). De definitieve resultaten komen in het eerste kwartaal van 2008 beschikbaar.

Literatuur

- Anonymous (2005) Bodemfauna en beleid. Een overzicht van 35 jaar bodemfauna onderzoek en monitoring in Waddenzee en Noordzee. Rapport RIKZ/2005.028154 pp
- Beukema, J.J. (1976) Biomass and species richness of the macro-benthic animals living on the tidal flats of the Dutch Wadden Sea. *Journal of Sea Research*, 10, 236-261.
- Beukema, J.J. (1982) Annual variation in reproductive success and biomass of the major macrozoobenthic species living in a tidal flat area of the Wadden Sea. *Journal of Sea Research*, 16, 37-45.
- Beukema, J.J., & Cadée, G.C. (1997) Local differences in macrozoobenthic response to enhanced food supply caused by mild eutrophication in a Wadden Sea area: Food is only locally a limiting factor. *Limnology & Oceanography*, 42, 1424-1435.
- Beukema, J.J., Essink, K. & Dekker, R. (2000). Long-term observations on the dynamics of three species of polychaetes living on tidal flats of the Wadden Sea: the role of weather and predator-prey interactions. *Journal of Animal Ecology*, 69, 31-44.
- Beukema, J.J., Dekker, R., Essink, K., et al. (2001) Synchronized reproductive success of the main bivalve species in the Wadden Sea: causes and consequences. *Marine Ecology-Progress Series*, 211, 143-155.
- Beukema, J.J., Cadée, G.C., & Dekker, R. (2002) Zoobenthic biomass limited by phytoplankton abundance: evidence from parallel changes in two long-term data series in the Wadden Sea. *Journal of Sea Research*, 48, 111-125.
- BOEDE (1983) Biologisch onderzoek Eems-Dollard estuarium. BOEDE publicaties en verslagen, 1983, nr. 1. 267 pp.
- Dekker, R. & Waasdorp, D. (2007) Het macrozoobenthos op twaalf raaien in de Waddenzee en Eems-Dollard in 2006. *NIOZ-rapport 2007-1*.
- EMOWAD I (1988) Ecosysteemmodel van de westelijke Waddenzee. *NIOZ-rapport 1988-1*.

- Essink, K. & Romeyn, K. (1994) Estuarine nematodes as indicators of organic pollution; an example from the Ems estuary. *Netherlands Journal of Aquatic Ecology*, 28, 213-219.
- Kraan, C., Piersma, T., Dekinga, A., Koolhaas, A., & Van der Meer, J. (2007) Dredging for edible cockles *Cerastoderma edule* on intertidal flats: short-term consequences of fishermen's patch-choice decisions for target and non-target benthic fauna. *ICES Journal of Marine Science*, 64, 1735-1742.
- Lindeboom, H., Van Raaphorst, W., Ridderinkhof, H. & Van der Veer, H.W. (1989) Ecosystem model of the western Wadden Sea: a bridge between science and management? *Helgoländer Meeresuntersuchungen*, 43, 549-564.
- Norling K., Rosenberg R., Hulth S., Gremare A. & Bonsdorff E. (2007) Importance of functional biodiversity and species-specific traits of benthic fauna for ecosystem functions in marine sediment. *Marine Ecology-Progress Series*, 332, 11-23.
- Piersma, T. (2006) *Waarom nonnetjes samen klaarkomen en andere wonderen van het wad*. KNNV Uitgeverij, Utrecht.
- Piersma, T., Koolhaas, A., Dekinga, A., Beukema, J.J., Dekker, R., & Essink, K. (2001) Long-term indirect effects of mechanical cockle-dredging on intertidal bivalve stocks in the Wadden Sea. *Journal of Applied Ecology*, 38, 976-990.
- Postma, H. (1954) Hydrography of the Dutch Wadden Sea. *Archives Néerlandais de Zoology*, 10, 405-511.
- Van der Meer, J., Beukema, J.J., & Dekker, R. (2001) Long-term variability in secondary production of an intertidal bivalve population is primarily a matter of recruitment variability. *Journal of Animal Ecology*, 70, 159-169.
- Van Gils, J.A., Piersma, T., Dekinga, A., Spaans, B., & Kraan, C. (2007) Shellfish-dredging pushes a flexible avian toppredator out of a protected marine ecosystem. *Public Library of Science Biology*, 4, 2399-2404.
- Van Roomen, M., Van Turnhout, C., Van Winden, E., Koks, B., Goedhart, P., Leopold, M., & Smit, C. (2005) Trends van benthivore watervogels in de Nederlandse Waddenzee 1975-2002: grote verschillen tussen schelpdiereneters en wormeneters. *Limosa*, 78, 21-38.
- Wolff, W.J (Ed.) (1983) *Ecology of the Wadden Sea*. Balkema, Rotterdam.

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Summary

The macrobenthic fauna on intertidal mudflats in the Dutch Wadden Sea is described based on an area-wide grid sampling in 2004 and 2006. This description serves as a so-called T_0 -assessment of the benthic fauna on intertidal mudflats before the onset of gas-retrieval in the eastern part of the Dutch Wadden Sea. For rare (present in less than 1% of the samples), common (present in less than 10% of the samples) and abundant (present in more than 10% of the samples), abundances, biomass and distribution patterns are presented. Next, an overview is presented of the other benthos monitoring programmes in the area. The existence of different benthos monitoring programmes in the Dutch Wadden reflects the fact that in such a highly dynamic and variable environment (intertidal, subtidal, sandy to muddy sediments) as the Dutch Wadden Sea, each research question requires its own specially designed, tailor-made, sampling programme. Finally, some suggestions are made about an optimal sampling design to monitor the macrobenthic community in the intertidal during gas-retrieval in the area.

1. Introduction

The international Wadden Sea is of major importance for waterbirds, e.g. ducks, geese, waders, gulls and terns. Not only for breeding, but also as wintering or stop-over area during their annual migration from and to the breeding grounds. In the Dutch part an estimated 2-3 million birds annually use the area in one way or another (van de Kam *et al.* 2004). For many species the available macrozoobenthos (all benthic fauna retained after sieving sediment with a 1-mm mesh), on flats exposed during low-tides, are of key-importance as a food-source.

In 1988 the Royal Netherlands Institute for Sea Research (NIOZ), in association with the University of Groningen, started a research-programme on an exemplar wader, the red Knot (*Calidris canutus*), combined with a benthic sampling programme (Piersma *et al.* 1993). This approach quickly resulted in knowledge on habitat use, diet, food detection and food availability of Knots (e.g. Dekinga and Piersma 1993; Piersma *et al.* 1993ab, 1995).

During the first years sampling was mainly done around the island Griend. From 1997 onwards, after a PIONIER-grant was awarded to T. Piersma by NWO, the benthic programme gradually expanded; nowadays the sampling area covers 225 km², mainly in the western Dutch Wadden Sea between Harlingen/Terschelling and Texel. By coincidence this scale matches the area needed for benthic monitoring as proposed by Armonies (2000). Occasionally, sampling is also done in more easterly areas, such as Engelmansplaat or Simonszand (van Leeuwe *et al.* 2008). Overall we actually are able to measure intertidal food-supplies at the scale used by foraging Knots, i.e. the whole western Dutch Wadden Sea.

The set-up of this research-effort, studying benthivorous waders and their benthic food-source on a large scale, is now also exported to other parts of the world that have migratory waders and intertidal mudflats, such as France, England, Germany and Australia (see Bocher *et al.* 2007; van Gils *et al.* 2005a). Currently, the design and methods of the benthic-sampling are being reviewed and compared with other sampling scheme's to optimize the design (Bijleveld *et al.* in prep.).

In 2004 and 2006 we undertook a major effort by sampling the western and eastern part of the Dutch Wadden Sea consecutively in both years. This

report summarizes abundance, biomass and distribution of all macrozoobenthic fauna encountered during these years. It should serve as a description of benthic fauna on intertidal mudflats before the onset of gas-retrieval in the eastern part of the Dutch Wadden Sea. This report thus represents a so-called T_0 -assessment.

2. Study area

The studied area comprises the intertidal part of the Dutch Wadden Sea. It has a tidal range between 1.5 m in the west and increasing amplitude further east, reaching a maximum of 4 m in the German part (van de Kam *et al.* 2004). The sediments exposed during low-tides can be characterised as sands and muddy sands, with a median grain-size ranging from 140 to 200 μm (Piersma *et al.* 2001; Zwarts *et al.* 2003). This area can be divided into 10 tidal-basins that get their saltwater input from different inlets (Fig. 1). In these different basins we sampled between 29 and 1929 stations, with a total of 3888 stations in 2006 and 3880 in 2004, respectively (Fig. 1; Table 1). Approximately 75% of the samples are taken in basins that are assigned to the western Wadden Sea area (Table 1).

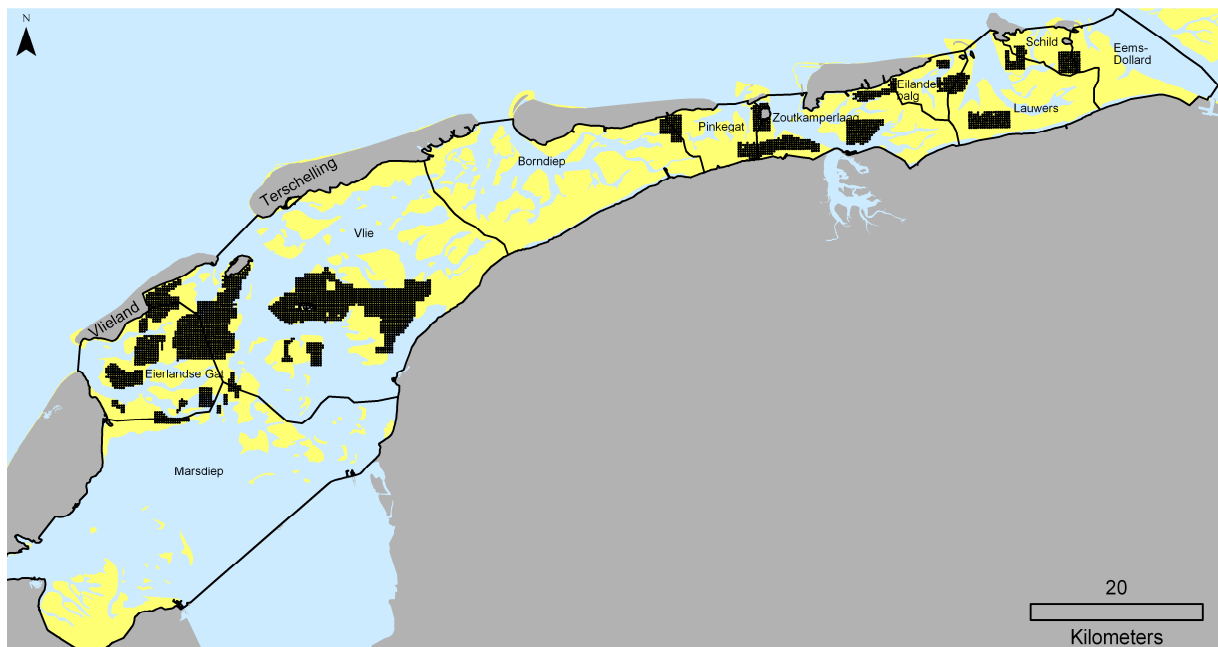


Figure 1: Map of the Wadden Sea, showing the sampling stations (2006) and the different tidal-basins.

Table 1: The number of samples taken in 2004 and 2006 in the different tidal-basins, divided over western and eastern Dutch Wadden Sea. Divisions in tidal-basins and east/west are based on a RIKZ-map called "Kombergingen", as provided by the NAM (G. Wintermans).

		2004	2006	
West	Marsdiep	67	67	
	Eierlandse Gat	778	783	
	Vlie	1887	1929	
East	Borndiep	51	57	
	Eems-Dollard	29	30	
	Eilanderbalg	94	92	
	Lauwers	275	250	
	Pinkegat	149	150	
	Schild	100	95	
	Zoutkamperlaag	450	435	
		2732	2779	West
		1148	1109	East
	3880	3888	Total	

3. Methods

Sampling

Sampling stations were visited once a year between mid July and early October either on foot during low tide or by boat during incoming, high, or outgoing tides. Sampling stations are arranged in a pre-determined grid, with a sampling-interval of 250 m. These sampling positions were assigned in the first year and revisited in the years after (Van der Meer 1997). Measured densities of benthic fauna did not demonstrably change over this 3-month sampling period (Piersma *et al.* 1993). There is no temporal effect on measured densities that would cause differences between tidal-basins. Sampling stations were found with handheld GPS (Garmin 45 and 12, using WGS84 as map datum). On foot, one sediment core of 0.018 m² down to a depth of 20 cm was taken and bottom (deeper than 4 cm) and top (upper 4 cm) were separately handled. By boat a total surface of 0.017 m² divided over 2 cores, also to a depth of 20 cm, was sampled. Maximum water coverage to allow boat-sampling was approximately 2

m, depending on weather conditions. The two methods, based on comparisons between benthos densities at 165 adjoining positions that were either sampled by boat or on foot between 1998 and 2004, did not yield different results (Kraan *et al.* 2007). The cores were sieved over a 1 mm mesh and of all species numbers were counted in the sieve and recorded; for bivalves age/size classes were also noted. To monitor the Mudsail *Hydrobia ulvea* an extra core was taken and sieved over a 0.5-mm mesh. Note that this is only for stations sampled on foot; Sampling by boat does not allow taking this extra sample, since it would be very difficult to obtain an undisturbed top-layer. All crustaceans and molluscs were collected in plastic bags and stored at -20 °C for later analyses.

In the laboratory the molluscs in each sample were measured to the nearest mm and the number of growth rings was counted. Additionally, for *Macoma balthica* also shell thickness and colour were noted. Then, the soft-parts, i.e. "meat", were separated from the shell and stored in crucibles. Both shells and meat were dried in a ventilated drying oven at 60 °C to constant mass. The next step was to weigh the dried shells and meat, followed by incineration of the meat in an oven at 550 °C for 5 hrs. After cooling in a desiccator the meats was reweighed, and after cleaning the empty crucibles were weighed again. In this way we determined the dry-mass of the meat and shells, and the ash mass and ash-free dry mass (AFDM). For more details see Piersma *et al.* (1993) and Van Gils *et al.* (2006ab).

To be able to relate benthic abundances, distributions and biomass to environmental variables we also collected sediment-samples. In every 1-km² block we took one sediment sample, which means that in total approximately 250 samples were collected for later analyses with the Coulter-Counter. The data obtained with this apparatus, median-grain size and silt %, display the most informative abiotic parameters, besides perhaps depth in relation to Dutch Ordinance Level (N.A.P.). Sediments are not included in this report (and not yet analyzed for 2006), but mentioned here to give a complete overview of the field- and lab-work. See Piersma *et al.* (2001) for details.

Note: Biomass-values for the eastern part of the Wadden Sea in 2004 have yet to be proceeded in the laboratory. Only abundance-data were used.

Taxonomic resolution

The grid-sampling, as noted before, was initialized to monitor the food for molluscivorous shorebirds. This starting point differs from most other monitoring series, like the Beukema/Dekker series on the Balgzand, who explicitly focus on benthos only (Beukema 1976). To focus on benthic macrozoobenthos from a bird's eye view, combined with high resolution sampling over a very large area, has a few consequences:

1. Polychaetes are counted in the field and no data on biomass are collected.
2. Taxonomic resolution of polychaetes is not always set at the species level. Counting them in the field means that no distinction can be made between *Heteromastus filiformis* and *Capitella capitella*, for example. Different *Nereids* are not separated, besides the obvious *Nereis virens* and *N. diversicolor*.
3. *Hydrobia ulvae* is only quantitatively sampled walking; by boot only presence/absence is noted.
4. Flesh and shell are not separated if bivalves were smaller than 7 mm. This is done to economize on the lab-work, but also for practical reasons (due to the small size the shells are likely to break during handling, and this will increase measurement errors)*. This problem is not only occurring in our analysis, but in others as well.

* To still be able to determine biomass of these small bivalves, conversion factors were applied (see van Gils *et al.* 2005b).

4. Results

This section will give an overview of every species encountered during sampling in 2004 and 2006. Species are split into three groups: Scarce, Common and Abundant. Scarce means that a species occurs in less than 1% of all stations that were sampled in 2006 (Appendix 1), thus present in less than 40 different stations. Common are those species that are present in less than 10% of all sampling stations, and abundant species are present in more than 10% of all stations. Maps are only shown for Common and Abundant species. All data on

distribution, presence, and biomass are presented in Appendix 1, 2, 3, 4, and 5. Appendix 6 contains the abundance/distribution maps.

4.1. Scarce Species

Abra alba

White Furrow shell, Witte Dunschaal (Scrobiculariidea) -

A very rare species only encountered twice in the Vlie tidal-basin in 2006 and absent in 2004 (in 2005 it appeared for the first time in our samples in the same tidal-basin as 2006). *A. alba* is very abundant in the coastal, subtidal zone in muddy sediments (Hayward and Ryland 1995; de Bruyne 2004).

Crassostrea gigas

Pacific Oyster, Japanse Oester (Ostreidea) -

This introduced species has permanently established itself over the last decade, as a follow-up species for the vanished native Flat Oyster (*Ostrea edulis*). First time recorded in the Wadden Sea in 1983, on the dykes of Texel (Wolff 2005a). Currently it is a common species of the subtidal parts of the Wadden Sea, whereas on the intertidal flats surveyed by us it has not (yet) been able to form permanent reefs. This species was encountered in very low abundances in three basins, Vlie, Zoutkamperlaag and Schild.

Mysella bidentata

NA, Tweetandmosseltje (Montacutidae) -

Presumed to be present in all parts of the Dutch Wadden Sea (Holtman *et al.* 1996), but this is not apparent from our data; it was only present in 4 tidal-basins (see Bocher *et al.* 2007, who also categorize *Mysella* as a rare species based on sampling in a number of tidal-systems in Northwest Europe). Where present, their densities were very low (maximum density 0.7 ind/m², Eierlandse Gat 2004). Present in 12 stations (0.3% of total number of stations) in 2006. The occurrence of *Mysella* is highly variable, and severely influenced by winter-temperature (Beukema 1979, 1989).

Petricola pholadiformis

American Piddock, Amerikaanse Boormossel (Petricolidae) –

Around 1890 introduced in waters around Great Britain and first observed in the Netherlands in 1905 (de Bruyne 2004). The introduction is probably related to import of Oysters from North-America (Wolff 2005a). This species bores into clay, peat or soft rocks substrates (Hayward and Ryland 1995). These substrates are rare or absent in the intertidal, which could explain the low abundances in the Wadden Sea. From the subtidal-area of the Wadden Sea it is known to occur in only 3% of all stations (total number of stations is 457) (Dekker 1989). Most “abundant” in the Eems-Dollard basin where 1.9 ind/m² were to be found in 2006.

Nereis virens

King Rag, Zager (Nereidae) –

Another introduced species from the North Atlantic or North Pacific that has established itself, after being recorded for the first time in 1915 (Wolff 2005a). A much wanted species as bait for angling and therefore also commercially harvested (Hayward and Ryland 1995). Data on annual take by fisherman, and scale of impact are virtually absent (Wolff 2005b). Only recorded on mudflats within the basins Zoutkamperlaag, Eierlands Gat and Vlie, with a maximum density of 0.3 ind/m². Overall, this species was present in 0.1 % of all stations in 2006.

Phyllodoce maculata

NA, Gestippelde Dieseltreinworm (Phyllodocidae) –

A beautiful species, characterized by a yellow body with black dots, that lives in muddy sand, under stones and in Mussel beds (Hayward and Ryland 1995). Present in 0.7% of all sampling stations in 2006, in almost all tidal-basins. Maximum density was 4.6 ind/m² in the Lauwers area 2004. Populations seem to be under control by the presence of the predatory polychaete *Nephtys hombergii* (Williams *et al.* 2004).

Scololepis foliosa

NA, NA (Spionidae) –

Highest recorded density is 0.6 ind/m² in 2006 (Eilanderbalg), but virtually absent from most other areas. This species is mentioned in Beukema (1989) as a

species that shows an increasing trend in abundance, as well as biomass. Prefers clean or slightly muddy sand, and usually is solitary (Hayward and Ryland 1995).

Littorina littorea

Periwinkle, Alikruik (Littorinidae) –

Common on intertidal rocky shores, but also makes feeding excursions on sheltered muddy flats (Hayward and Ryland 1995; de Bruyne 2004). Their food consists of algae. Mainly a species of the eastern Dutch Wadden Sea, where it is present in 1% of all samples, opposed to 0.1% in the western part.

Retusa obtusa

Mud Bubbleshell, Oubliehoren (Retusidae) -

Carnivore snail, that feeds on *Hydrobia ulvae* and diatoms. Occurs in the Wadden Sea on soft mudflats, rich in silt, especially areas that are not completely exposed during low-tides (de Bruyne 2004). It lives just below the sediment-surface. Due to its small size easily overlooked in the sieve. Only present in the eastern part of the sampling area in 2004 and 2006, but in other years also occurring in the Vlie area, especially close to the island Griend (own data). Found in 0.1% of all samples in 2006.

Palaemon sp.

NA, Steurgarnaal (Palaemonidae) –

Found once in the Eierlandse Gat basin in 2004. Occasionally found by Dekker/Waasdorp (pers. com.), but none were found in 2003 (Dekker and Waasdorp 2004).

Asterias rubens

Starfish, Zeester (Asteriidae) –

This is a species typically associated with hard-substrates, like rocks and shell-grid. It commonly occurs from the edge of the intertidal mudflats to deeper waters. Encountered in 2004 only in the Vlie and Eierlands Gat basin (0.1% of sampling stations in both areas), at stations close to the subtidal.

Leptochitona cinereus

Grey Coat-of-mail Chiton, Asgrauwe Keverslak (Ischnochitonidae) –

A species associated with hard-substrate, like rocks or shell-grid. Only found in 2004 and in the eastern part only. *Leptochitona* will probably increase, as it is commonly present on Oyster-beds.

Nemertine sp.

Flatworm, Platworm (Lineidae?) –

This peculiar species was only found in the western part of the sampling grid in 2006 (0.1% of all sampling stations), with a maximum density of 0.2 ind/m² in the Vlie area. According to Beukema (1989) this species is sensitive to low winter-temperatures, but information on other aspects of life-history are lacking.

4.2. Common Species

Abra tenuis

Triangular Peppershell, Tere Dunschaal (Scrobiculariidae) –

This small species is confined to intertidal mudflats with a soft substrate (Hayward and Ryland 1995). Within the intertidal it is distributed among the highest parts, where it is severely reduced after cold winters (Beukema 1979, 1989). The Dutch Wadden Sea is at the northern boundary of its distribution (Dekker and Beukema 1999). Besides cold winters, the mode of reproduction, e.g. direct development, also generates large fluctuations in population densities. Even local extinctions are occurring (Holmes *et al.* 2004). In our sampling grid it typically is most abundant in the western part (3.8% in the west, against 0.04% in the east); especially the Eierlandse Gat area boasts high densities (63.9 ind/m² in 2006). *Abra* also shows the importance of covering large areas with benthic monitoring. Basins in the west showed a density increase between 2004 and 2006, whereas in the east this is reversed. The contribution to the total biomass per m² is minimal with 0.11 gr AFDM/m² at most.

Ensis directus

Atlantic Jackknife Clam, Amerikaanse Zwaardschede (Solenidae) –

Exotic species that was first observed in the German Wadden Sea in the end of the seventies, and spread from there (de Bruyne 2004). Most likely this spread

was through larval transport (Wolff 2005a). The population expansion, at that time, was 75 km/year to the west and 125 km/year to the north (Armonies 2001). In 2004 still present in very low densities in the eastern part of the sampling area, but in 2006 it was only present in the west. Areas with high densities are very local and variable between years, usually a year with high recruitment is followed by years with a steadily decrease, until there is another successful recruitment (own data).

Mya arenaria

Sand Gaper, Strandgaper (Myacidae) –

Mya occurs in sandy sediments, often mixed with mud or gravel, up to a depth of 20 m (Hayward and Ryland 1995). Also an exotic species, most likely introduced through ballast water in Europe. Tentatively, this introduction is ascribed to the Vikings. First record in the Netherlands is from 1765 (Wolff 2005a). This species, due to its large size, generally contributes significantly to the total biomass (Beukema 1976). At the Balgzand area this species show a continuous increase in both average abundance and biomass in time (Dekker and Waasdorp 2007). Competitive interactions with *Macoma balthica*, *Cerastoderma edule*, as well as *Mytilus edulis* affect population dynamics (Williams *et al.* 2004). For the Vlie basin it actually is the species that ranks #1, when looking at bio-mass (3.52 g AFDM/m² max.). Numerically it is only an important species in the Vlie basin, although it also occurs in most other basins.

Mytilus edulis

Common Mussel, Gewone Mossel (Mytilidae) –

A bivalve that occurs in dense beds, mainly from the upper shore downwards into shallow sublittoral waters (Hayward and Ryland 1995). Once a very abundant species in the western part, but completely vanished. Only small patches remain/appear again, but no stable beds, as for now. Until recently heavily fished upon for consumption. More common in the eastern part (5.7% of all stations sampled), where protected areas were closed for fisheries and some musselbeds remained. Absent from the most westerly and easterly tidal basins. The biomass values show that it can be an influential species (max. 8.09 gr AFDM/m² Eilanderbalg). In a paper by Beukema (1976) it is the species that contributes most to the total biomass, based on transects scattered across the

whole Dutch Wadden Sea. Also in the subtidal it is very abundant (ranked 3rd) and contributes most to the total biomass (Dekker 1989)

Scrobicularia plana

Peppery Furrow Shell, Platte Slijkgaper (Scrobiculariidae) –

This species is also confined to the intertidal, where it occurs in soft sediments (Hayward and Ryland 1995). In the winter it buries twice as deep in the sediment as in summer (Zwarts and Wanink 1989). *Scrobicularia* reaches higher abundances in more southern areas, like Aiguillon Bay in France (Bocher *et al.* 2007). Within the Dutch Wadden Sea it is a widely distributed bivalve, that is only absent from the Marsdiep basin. Highest densities are found on the Eilanderbalg (21.1 ind/m² in 2004).

Tellina tenuis

Thin Tellin, Tere Platschelp (Tellinidae) –

Generally *Tellina* is distributed across sandy sediments (Hayward and Ryland 1995). This species is extremely sensitive to cold winter temperatures, expressed by decreased densities after a harsh winter (Beukema 1989; de Bruyne 2004). After the most extreme winters the population can periodically die out, followed by colonization from offshore North Sea populations (Dekker and Beukema 1999). Highest densities are found in the western part (4% of all samples, against 0.1% in the east), which most likely is due to the presence of more sandy sediments in this area.

Eteone longa

NA, NA (Phyllodoceidae) –

This species is apparently fairly tolerant to cold winter temperatures (Beukema 1979) and is becoming increasingly more abundant (Beukema 1989). In the subtidal parts of the Wadden Sea it already widespread and common (Dekker 1989). In our sampling area it is widespread, but not yet abundant (Appendix 1, 2, and 3). There is large variation in densities between 2004 and 2006, but almost always lower densities in 2006.

Harmothoe sp.

NA, Zeerups (Polynoinae) –

Once again a species with a very wide distribution, combined with low densities. As in some other species, like *Tellina tenuis* and *Abra tenuis*, it is also sensitive to low winter temperatures (Beukema 1989). In 2006 it was present in 2% of all samples.

Marenzelleria viridis

NA, NA (Spionidae) –

A permanently established exotic species, introduced via ballast water into the Wadden Sea. It was observed for the first time in Dutch waters in 1983 (Wolff 2005a). Predominantly occurs in the western part, but can be found as far east as well. If present, the densities can be very high, e.g. 207 ind/m² (Vlie basin 2004). This species apparently filled an empty niche, since there are no interactions between original macrobenthic species and this newcomer (see Essink *et al.* 1998). Based on sampling in previous years we have the impression that it is a winter-sensitive species that is enormously reduced in abundance after a cold winter (own data).

Pygospio elegans

NA, Zandpijp (Spionidae) –

A small tube-building Spionidae, that makes the tubes out of fine sand grains embedded in mucus (Hayward and Ryland 1995). *Pygospio*, a short-lived species, is able to quickly colonize available habitat, after removing all standing stock before-hand (Beukema *et al.* 1999). Its population-size is density-dependent on Cockles, which means that populations are negatively influenced by high Cocker-densities (Flach 1996). One of the more abundant species in subtidal areas of the Dutch Wadden Sea (Dekker 1989). In the intertidal parts it is widely distributed, but its centre of occurrence is in the eastern part. This is a very difficult species to assess, since all the little tubes have to be checked on occupancy. Therefore, all the zero-values in Appendix 2 and 3 for the year 2004 most likely indicate that the species was unseen, not that it was absent.

Crangon crangon

Brown Shrimp, Garnaal (Crangonidae) –

The common ingredient of shrimp-cocktails, therefore heavy industrial fisheries are targeting this species. Occurs on sandy sediments in the intertidal, and further down to a depth of 50 m (Hayward and Ryland 1995). In the winter-season they migrate to deeper, warmer waters, whereas in early spring they start moving up in the intertidal zone again (Beukema 1979). The western part of the Wadden Sea has a higher presence of Shrimp than the eastern part (6.6% against 0.8% in 2006). Densities in the western part stayed equal more or less, but in the east a large reduction in abundance between 2004 and 2006 is noticeable.

Carcinus maenas

Shore Crab, Strandkrab (Portunidae) –

This species is very abundant from pools at the beach to a depth of 200 m (Hayward and Ryland 1995). In the subtidal Wadden Sea it is one of the important species, regarding total biomass (Dekker 1989). Again a species that is sensitive to low temperatures in winter (Beukema 1989; Beukema et al. 1993). As with the Common Shrimp, also presence in the western part is much higher. The peak of abundance is in the Eierlandse Gat basin, with densities of 12.8 ind/m², but this species is also present in all other basins.

Corophium volutator

NA, Slijkgarnaal (Corophiidae) –

Only found in the intertidal parts of the Wadden Sea, where it builds semi-permanent burrows in mud (Hayward and Ryland 1995). Shellducks (*Tadorna tadorna*) moulting in the Wadden Sea, based on dropping analyses, includes *Corophium* in their diet (Kraan et al. 2006). Populations are negatively influenced by high *Cerastoderma* densities, since these disturb their burrows (Flach 1996). This species is almost ten times more abundant in the western part than in the eastern part. The Vlie basin inhabits densities of 432 ind/m² in 2006. This means that it is the runner-up after the winner *Hydrobia*. Eight out of ten basins have *Corophium* in varying densities.

Gammarus locusta

Hopper, Vlokreeft (Gammaridae) –

The Hopper occurs from the middle shore to the subtidal, often in high abundances under stones or amongst algae (Hayward and Ryland 1995). It is a widely-distributed species, although never in very high densities. Highest densities are found on the Eilanderbalg (34.3 ind/m² in 2004). In general densities in 2006 were always below densities from 2004.

4.3. Abundant Species

Cerastoderma edule

Common Cockle, Gewone Kokkel (Cardiidae) -

A widely distributed species that occurs in sandy mud, sand, and fine gravel sediments (Hayward and Ryland 1995). Also in the subtidal it is a species of importance (Dekker 1989). The population is characterized by large fluctuations, as a result from high variability in success of spatfall and recruitment. Cockles are sensitive to severe winters, as well as winters that are colder than average (Beukema 1979, 1989). Nevertheless, their depth of living in the sediment remains the same, regardless of season (Zwarts and Wanink 1989). In general, but with exceptions, there is successful recruitment after a cold winter (Beukema 1989). Mechanical harvesting of this species has recently been banned from the Dutch Wadden Sea (see Piersma *et al.* 2001; Van Gils *et al.* 2006b, Kraan *et al.* 2007). Every tidal-basin has Cockles in varying densities, but its centre of occurrence is in the east. 41% of all stations have Cockles, against 16% in the western part in 2006. Densities in 2006 were minimally equal to 2004 or higher, with a maximum of 527 ind/m² on the Eilanderbalg. Overall it is the species that contributes most to the total biomass, for example 51 g AFDM/m² in the Eems-Dollard basin.

Macoma balthica

Baltic Tellin, Nonnetje (Tellinidae) –

This is the best studied bivalve in the Netherlands. Over the last 19-years much research has been done, ranging from molecular ecology (Luttikhuizen 2003), life history variation (Drent 2004), anti-predation traits in an evolutionary framework (De Goeij and Luttikhuizen 1998; Edelaar 2002), and recruitment studies

(Hiddink 2002; Bos 2005). *Macoma* is a mostly intertidal species with preference for soft sediments (Hayward and Ryland 1995). It has not been recorded at depths over 25 m (Holtman *et al.* 1996). At the time Dekker (1989) did his research, it still was the most common bivalve in the subtidal area and Beukema (1989) noticed an increase in density in the intertidal areas. Since then, it has markedly declined in the intertidal (Drent *et al.* in prep.). 0-group class *Macoma* is commonly preyed upon by *Crangon crangon*, *Carcinus maenas*, Gobies *Pomatoschistus*, and juvenile flatfish (Hiddink *et al.* 2002). This species also was negatively influenced by mechanical cockle-dredging. Not so much the current standing stock, but more the recruitment in the years after dredging (Piersma *et al.* 2001). The Baltic Tellin occurs in 24% of all sampling stations in 2006, with the same division between east and west as the Cocker (more common in the east). Highest densities are now found in the Lauwers basin.

Arenicola marina

Lugworm, Wadpier (Arenicolidae) –

An important bait species that occurs in clean to muddy sand (Hayward and Ryland 1995), and lives in burrows. Populations are generally stable and not limited by cold winters (Beukema 1979). High levels of biomass and density are dependent on high recruitment rates of young lugworms (Beukema 1978). Population trends between intertidal flats can be very different or even opposite to each other, due to migration of juveniles that escape unfavourable conditions (Beukema and Essink 1986). *Arenicola* is evenly distributed between east and west (18% and 20%), and present in all basins in comparable densities between 2004 and 2006.

Heteromastus filiformis

NA, Draadworm (Capitellidae) –

It should be noted that *Heteromastus*-numbers are a composite of *Heteromastus* and *Capitella capitata*, since we are not able to distinguish the two in the field. 40% of all samples in 2006 had at least one individual, with increasing densities towards the east. Also in subtidal waters it is a very common and abundant species (Dekker 1989). In the intertidal it is increasing (Beukema 1989). Its numbers are mainly controlled by two factors: predator-abundance (i.e. *Nephtys*

hombergii) and food-abundance (Schubert and Reise 1986; Beukema *et al.* 2000).

Lanice conchilega

Sand Mason, Zandkokerworm (Terebellidae) –

A tube-building worm, that builds tubes out of sand grains and shell fragments. The tubes have a ragged fringe at the mouth end (Hayward and Ryland 1995).

Lanice mainly live in sandy sediments and rarely in more muddy bottoms (Holtman *et al.* 1996). Survival strongly depends on winter-temperatures, and is higher after warmer winters (Beukema *et al.* 1978; Beukema 1979). *Lanice* is twice as common in the west, as in the east, based on presence/absence in 2006. This is not unexpected, as this species prefers more sandy sediments. Densities were in general much higher in 2004 than in 2006.

Nephtys hombergii

White Catworm, Zandzager (Nephtyidae) –

This predatory species is highly sensitive to temperatures in winter (Beukema 1989, Beukema *et al.* 1996). Population developments are mainly influenced by conditions in winter (Beukema *et al.* 1978; Beukema *et al.* 2000). *Nephtys* is equally distributed in its presence; east and west are the same with figures of 25-26% presence. Densities in both years (2004 and 2006) are comparable, which implies that there was a balance between recruitment and mortality.

Nereis diversicolor

Ragworm, Zeeduizendpoot (Nereidae) –

This species lives in burrows, made in muddy sand (Hayward and Ryland 1995). Unlike some other species its presence is not influenced by winter temperature, although it burrows deeper into the sediment in more severe winters (Beukema 1979). The presence of *Nereis* is evenly distributed, with in both parts a presence of ~38%. Every tidal-basin shows a different density pattern between 2004 and 2006; it ranges between equal densities, lower and higher densities. In general the eastern basins have slightly higher densities.

Scoloplos armiger

NA, Wapenworm (Orbiniidae) –

A widely distributed worm that occurs almost in all sediment types, including almost anoxic sediments and sea grass beds (Holtmann *et al.* 1996). In the subtidal it is also common (Dekker 1989). In intertidal areas it showed a sharp increase in numbers from the middle of the 1980's (Fig. 4, Beukema 1989). Population dynamics are closely linked to food-abundance and predator-abundance (i.e. *Nephtys hombergii*) (Schubert and Reise 1986; Beukema *et al.* 2000). Based on an elegant analysis by Armonies and Reise (2003) it could be shown that this polychaete is the only macrobenthic species that actually occupies all suitable habitat. Although *Scoloplos* is assumed to be a species without sediment preferences (Armonies and Reise 2003), it was twice as common in the west, as in the east, based on presence/absence data 2006. The western part generally has coarser sediments than the eastern part. Also densities were higher in the western basins, although only marginally.

Hydrobia ulvae

Mudsnail, Wadslakje (Hydrobiidae) –

A species, which favors firm mud and muddy sediments, and can be found up to a depth of 20 m (Hayward and Ryland 1995). Severe winters do not seem to influence its population dynamics (Beukema 1979), but migratory behaviour can give opposite trends in abundances between intertidal areas (Beukema and Essink 1986). The time-scale in which these migrations take place is in the order of some hours to a couple of days (Armonies and Hartke 1995), and they are assumed to be an adaptation to escape crowded conditions (Levinton 1979). In the subtidal it is the most abundant species with an average density of 12967 ind/m² (Dekker 1989). Based on presence/absence for all stations in 2006 *Hydrobia* is more common in the eastern part of the Dutch Wadden Sea than in the western part. The variation in average density is high, e.g. the Lauwers had 28 ind/m² in 2004 and 13333 ind/m² in 2006. Note that the densities are only based on points that were sampled on foot.

Urothoe sp.

NA, Buldozerkreeftje (Haustoriidae) –

Twice as common in the three most western basins, compared to the other, more eastern basins. Densities in 2006 were lower than in 2004, especially in the eastern part. This species is a commensal with *Arenicola marina*; it lives inside the feeding pocket of *Arenicola* (Reise 2002).

5. Overview of other existing monitoring series

At present a number of other benthos monitoring programmes exist in the Dutch Wadden Sea, carried out under the responsibility of different agencies: MON*BIOLOGIE, RIVO schelpdier-monitoring and the NIOZ Balgzand series.

5.1. MON*BIOLOGIE

This is the oldest benthic monitoring series in the Netherlands. It already started in 1968 on the Balgzand near Den Helder, followed by the Groninger wad at Noord-polderzijk (1969) and was expanded with the Heringsplaat (Dollard) in 1978 and the Piet Scheveplaat (Ameland) in 1978 (Dekker and Waasdorp 2004) and Noordpolderzijk. These monitoring-series are grouped under MON*BIOLOGIE and are funded by Rijkswaterstaat, Rijksinstituut voor Kust en Zee (RIKZ).

Balgzand - Sampling is done via 3 transects twice every year in late winter and late summer. The length of each transect is 980 m with an inter-sample distance of 20 m, which means that each transect consists of 50 sampling points. 5 consecutive samples are grouped into one; so every transect has 10 combined samples. Samples are taken to a depth of 35 cm, with a sediment-core of 190 cm² in winter or 90 cm² in summer, and sieved with a 1-mm mesh sieve.

Piet Scheveplaat and Heringsplaat - Again sampling is done along transects (three transects on both mudflats) twice a year, with a sampling depth of 35 cm and a core with a surface of 90 cm². The length of transects is 760 m at the Piet Scheveplaat and 870 m at the Herings-plaat; one transect contains 20 sampling points.

Noordpolderzijk - Benthos is sampled in 5 square plots, with 16 to 20 samples per plot. Sampling is done twice per year in February/March and again between July

and end of September. Total area covered is 5 km², with a distance of 1 to 2 km between the plots. A plot is 30 x 30m.

For more details see: Beukema 1976, 1989; Beukema and Essink 1986; Beukema *et al.* 1993, 2001; Strasser *et al.* 2003.

5.2. RIVO-schelpdier monitoring

This commercial monitoring focuses on Edible Mussels *Mytilus edulis* and Cockles *Cerastoderma edule*. Sampling is done in spring with a stratified grid, which means that in areas with high expected densities sampling is done with a higher intensity. The distance between North-South transects is approximately 2220 m, with a sampling-interval of around 463 m. Both decrease when stratification is applied (Bult *et al.* 2004; Kamermans *et al.* 2004; Steenbergen *et al.* 2005).

Mussel- and Cockle-beds were visited based on occurrence in previous years, fisher-men's information and aerial surveys. Depending on the location in the intertidal a wide array of methods were applied for sampling (Steenbergen *et al.* 2005). Sampling-depth was 10 cm at most and collected sediment was sieved through a 4- to 5-mm mesh (Kamermans *et al.* 2004). Normally samples are analyzed in the field and discarded. Information on other bivalves is not reported, but noted in the field (no information on other taxa).

The data on macrozoobenthos used within the EVA-2 project were collected within the RIVO-series; samples that normally were only handled in the field were taken back to the lab for analyses. Specifically, the data collected in 1998 (1800 stations), 2000 (~1900 stations) and 2001 (~1900 stations) were used. Also some extra autumn sampling was done (2000, 2001 and 2002) to validate interpolation methods that calculate stocks in autumn, based on stocks present in spring (Kamermans *et al.* 2004). The EVA-2 project ended in 2004. Only bivalves and some common polychaetes were taken into account. Measured variables on bivalves are length, year-rings and different forms of fresh-weight (Bult *et al.* 2004).

5.3. NIOZ Balgzand series

The Balgzand-area is 50 km² in total, with 14 transects scattered across the area. Three of these transects are included in MON*BIOLOGIE, the others are sampled outside this framework by NIOZ. The NIOZ Balgzand series started in 1968 by Beukema and is funded by NIOZ. Sampling is done via transects twice every year in late winter and late summer. The length of each transect is 980 m with an inter-sample distance of 20 m, which means that each transect consists of 50 sampling points. 5 consecutive samples are grouped into one; so every transect has 10 combined samples. Samples are taken to a depth of 35 cm, with a sediment-core of 190 cm² in winter or 90 cm² in summer, and sieved with a 1-mm mesh sieve.

5.4. Why different monitoring programmes

The existence of different benthos monitoring programmes in the Dutch Wadden reflects the fact that in such a highly dynamic and variable environment (intertidal, subtidal, sandy to muddy) as the Dutch Wadden Sea each research question requires its own specially designed tailor-made sampling programme.

In this respect, the RIVO-sampling, only focuses and reports Mussel- and Cockle-densities, based on stratified sampling. The applied sampling-depth (max. 10 cm) and used mesh-size (4-5 mm) result in lack of information on deep burying species and small bivalves that are washed through the sieve, as well as smaller polychaetes that are washed out. This means that this monitoring is limited in scope. EVA-2 is not considered here, because they used data from RIVO, and lasted a couple of years only.

This leaves us with MON*BIOLOGIE and the Wader-Benthos research programme, which each have their own strong-points and weaknesses. See Figure 2 for an overview of sampling sites within these monitoring-series. Compared to the Wader-Benthos series, MON*BIOLOGIE has a much more restricted sampling area, although all points are visited twice per year. The data are limited to three tidal-basins, which would limit any statistical comparison to these basins. More detailed information on biomasses is gathered, with a slightly higher taxonomic resolution, due to the fact that everything is collected and analyzed in the lab.

The advantage of the Wader-Benthos programme is that it covers the complete Dutch Wadden Sea with a high-resolution sampling grid. In every tidal-basin we sample between 29 and 1929 stations, which would allow comparisons at the tidal-basin level. Some limitations are already discussed in the Methods-section.

Probably a mix of both programmes would be the most beneficial set-up for monitoring changes in the whole Wadden Sea. A workable solution could be to extend the Wader-Benthos programme by collecting polychaetes from every 16th sample. This means that for every square-km one sampling-station is completely analyzed in high detail the lab. In practice the extra sampling-time is not the bottle-neck, but the extra time that has to be devoted to labwork. Another modification of the Wader-Benthos programme could involve a more evenly spread sampling set-up. Now the sampling stations are very unevenly divided across the basins and this could be improved.

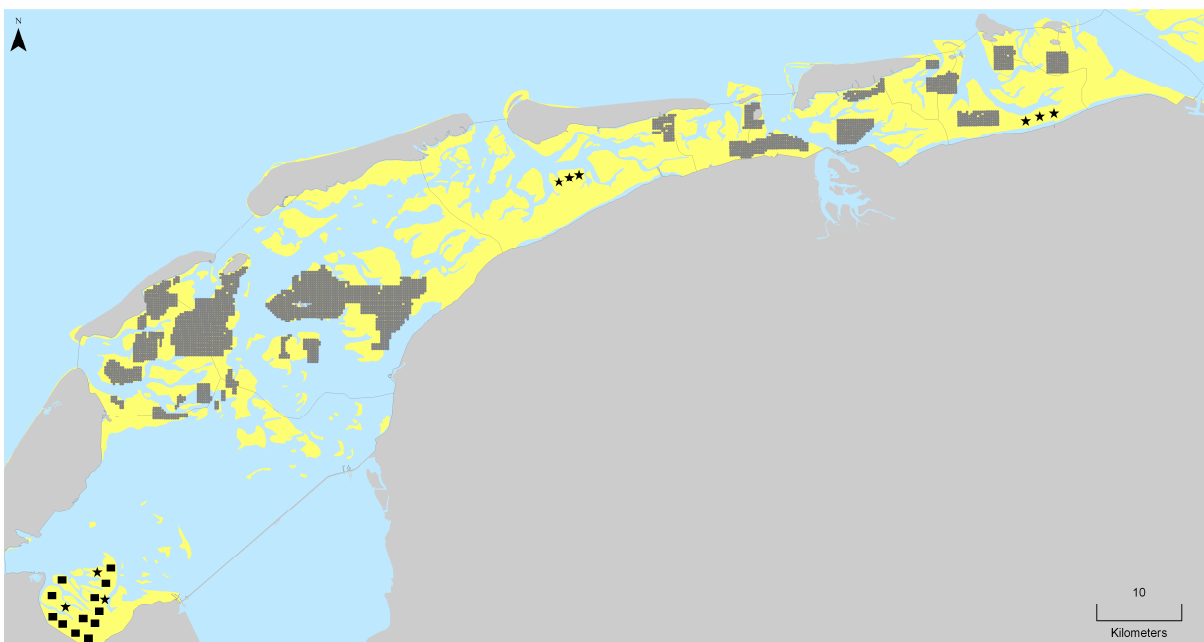


Figure 2: Map showing all sampling done within the Bird-Benthos monitoring (dots), and MON*BIOLOGIE (crosses), and transects monitored by NIOZ (squares).

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7. References

- Armonies, W. 2000. On the spatial scale needed for the benthos community monitoring in the coastal North Sea. *Journal of Sea Research* **43**:121-133.
- Armonies, W. 2001. What an introduced species can tell about the spatial extension of benthic populations. *Marine Ecology Progress Series* **209**:289-294.
- Armonies, W., and D. Hartke. 1995. Floating of mud snails *Hydrobia ulvae* in tidal waters of the Wadden Sea, and its applications in distribution patterns. *Helgolander Marine Research* **49**:529-538.
- Armonies, W., and K. Reise. 2003. Empty habitat in coastal sediments for populations of macrozoobenthos. *Helgolander Marine Research* **56**:279-287.
- Beukema, J. J. 1976. Biomass and species richness of the macro-benthic animals living on the tidal flats of the dutch wadden sea. *Journal of Sea Research* **10**:236-261.
- Beukema, J. J. 1989. Long-term changes in macrozoobenthic abundance on the tidal flats of the western part of the Dutch Wadden Sea. *Helgolander Marine Research* **43**:405-415.
- Beukema, J. J., and K. Essink. 1986. Common patterns in the fluctuations of macrozoobenthic species living at different places on tidal flats in the wadden sea. *Hydrobiologia* **142**:199-207.
- Beukema, J. J., Dekker, R., Essink, K., and H. Michaelis. 2001. Synchronized reproductive success of the main bivalve species in the wadden sea: causes and consequences. *Marine Ecology Progress Series* **211**:143-155.
- Beukema, J. J., Essink, K., and H. Michaelis. 1996. The geographic scale of synchronized fluctuation patterns in zoobenthos populations as a key to underlying factors: climatic or man-induced. *ICES Journal of Marine Science* **53**:964-971.
- Beukema, J. J., Essink, K., Michaelis, H., and L. Zwarts. 1993. Year-to-year variability in the biomass of macrobenthic animals on tidal flats of the wadden Sea: how predictable is this food source for birds? *Journal of Sea Research* **31**:319-330.
- Beukema, J.J. 1979. Biomass and species richness of the macrobenthic animals living on a tidal flat area in the Dutch Wadden Sea: effects of a severe winter. *Journal of Sea Research* **13**:203-223.
- Beukema, J.J., de Bruin, W., and J.J.M. Jansen. 1978. Biomass and species richness of the macrobenthic animals living on the tidal flats of the Dutch Wadden Sea: long-term changes during a period with mild winters. *Journal of Sea Research* **12**:58-77.
- Beukema, J.J., Essink, K., and R. Dekker. 2000. Long-term observations on the dynamics of three species of polychaetes living on tidal flats of the Wadden Sea: the role of weather and predator-prey interactions. *Journal of Animal Ecology* **69**:31-44.
- Beukema, J.J., Flach, E.C., Dekker, R., and M. Starink. 1999. A long-term study of the recovery of the macrozoobenthos on large defaunated plots on a tidal flat in the Wadden Sea. *Journal of Sea Research* **42**:235-254.

- Bocher, P., Piersma, T., Dekinga, A., Kraan, C., Yates, M.G., Guyot, T., Folmer, E.O., and G. Radenac. 2007. Site- and species-specific distribution patterns of molluscs at five intertidal soft-sediment areas in northwest Europe during a single winter. *Marine Biology* **151**:577-594.
- Bos, O.G. 2005. Recruitment variation of *Macoma balthica* (L.). Is there a role for larval food limitation? PhD Thesis, University of Groningen.
- Bult, T.P., Ens, B.J., Baars, D., Kats, R., and M. Leopold. 2004. Evaluatie van de meting van het beschikbare voedselaanbod voor vogels die grote schelpdieren eten. Eindrapport EVA-2, deelrapport B3, RIVO rapport nummer C018/04.
- de Bruyne, R.H. 2004. Veldgids Schelpen. KNNV Uitgeverij, Utrecht.
- de Goeij, P., and P. Luttikhuisen. 1998. Deep-burying reduces growth in intertidal bivalves: field and mesocosm experiments with *Macoma balthica*. *Journal of Experimental Marine Biology and Ecology* **228**:227-237.
- Dekinga, A., and T. Piersma. 1993. Reconstructing diet composition on the basis of faeces in a mollusc-eating wader, the Knot *Calidris canutus*. *Bird study* **40**:144-156.
- Dekker, R. 1989. The macrozoobenthos of the subtidal western Dutch Wadden Sea. 1. Biomass and species richness. *Journal of Sea Research* **23**:57-68.
- Dekker, R., and D. Waasdorp. 2004. Het macrozoobenthos in de Waddenzee in 2003. NIOZ-rapport 2004-3.
- Dekker, R., and D. Waasdorp. 2004. Het macrozoobenthos op twaalf raaien in de Waddenzee en de Eems-Dollard in 2004. NIOZ-rapport 2005-1.
- Dekker, R., and D. Waasdorp. 2007. Het macrozoobenthos op twaalf raaien in de Waddenzee en de Eems-Dollard in 2006. NIOZ-rapport 2007-1.
- Dekker, R., and J.J. Beukema. 1999. Relations of summer and winter temperatures with dynamics and growth of two bivalves, *Tellina tenuis* and *Abra tenuis*, on the northern edge of their intertidal distribution. *Journal of Sea Research* **42**:207-220.
- Drent, J. 2004. Life history variation of a marine bivalve (*Macoma balthica*) in a changing world. PhD Thesis, University of Groningen.
- Edelaar, P. 2002. The ecology and evolution of anti-predation traits in a burrowing bivalve, *Macoma balthica*. PhD Thesis, University of Groningen.
- Essink, K, Eppinga, J., and R. Dekker. 1998. Long-term changes (1977-1994) in intertidal macrozoobenthos of the Dollard (Ems estuary) and effects of introduction of the North American spionid polychaete *Marenzelleria* cf. *wireni*. *Senckenbergiana Maritima* **28**:211-225.
- Flach, E.C. 1996. The influence of the Cockle, *Cerastoderma edule*, on the macrozoobenthic community of tidal flats in the Wadden Sea. *Marine Ecology* **17**:87-98.
- Hayward, P.J., and J.S. Ryland (eds.). 1995. Handbook of the Marine fauna of North-West Europe. Oxford University Press, New York.
- Hiddink, J.G. 2002. The adaptive value of migrations for the bivalve *Macoma balthica*. PhD Thesis, Rijksuniversiteit Groningen.
- Hiddink, J.G., Marijnissen, S.A.E., Troost, K., and W.J. Wolff. 2002. Predation on 0-group and older year classes of the bivalve *Macoma balthica*: interaction of size selection and intertidal distribution of epibenthic predators. *Journal of Experimental Marine Biology and Ecology* **269**:223-248.
- Holmes, S.P., Dekker, R., and I.D., Williams. 2004. Population dynamics and genetic differentiation in the bivalve mollusc *Abra tenuis*: aplanic dispersal. *Marine Ecology Progress Series* **268**:131-140.
- Kamermans, P., Bult, T., Kater, B., Baars, D., Kesteloo, J., Perdon, J., and E. Schuiling. 2004. Invloed van natuurlijke factoren en kokkelvisserij op de dynamiek van bestanden van kokkels (*Cerastoderma edule*) en nonnen (*Macoma balthica*) in de Waddenzee, Ooster- en Westerschelde. Eindrapport EVA-2, deelrapport H4, RIVO rapport nummer C058/03.
- Kraan, C., Piersma, T., Dekinga, A., and B. Fey. 2006. Bergeenden vinden Slijkgarnaaltjes en rust op nieuwe ruiplaats bij Harlingen. *Limosa* **79**:19-24.
- Kraan, C., T. Piersma, A. Dekinga, A. Koolhaas, and J. van der Meer. 2007. Dredging for edible cockles *Cerastoderma edule* on intertidal flats: short-term consequences of fishermen's patch-choice decisions for target and non-target benthic fauna. *ICES Journal of Marine Science* **64**:1735-1742.

- Levinton, J.S. 1979. The effect of density upon deposit-feeding populations: movement, feeding and floating of *Hydrobia ventrosa* Montagu (Gastropoda: Prosobranchia). *Oecologia* **43**:27-39.
- Luttikhuizen, P.C. 2003. Spatial arrangement of genetic variation in the marine bivalve *Macoma balthica* (L.). PhD Thesis, University of Groningen.
- Piersma, T., de Goeij, P. and Tulp, I. 1993. An evaluation of intertidal feeding habitats from a shorebird perspective: towards relevant comparisons between temperate and tropical mudflats. *Netherlands Journal of Sea Research* **31**:503-512.
- Piersma, T., Hoekstra, R., Dekinga, A., Koolhaas, A., Wolf, P., Battley, P., and P. Wiersma. 1993. Scale and intensity of intertidal habitat use by knots *Calidris canutus* in the western wadden sea in relation to food, friends and foes. *Journal of Sea Research* **31**:331-357.
- Piersma, T., Koolhaas, A., Dekinga, A., Beukema, J.J., Dekker, R., and K. Essink. 2001. Long-term indirect effects of mechanical cockle-dredging on intertidal bivalve stocks in the Wadden Sea. *Journal of Applied Ecology* **38**:976-990.
- Piersma, T., van Aelst, R., Kurk, K., Berkhoudt, H., and L.R.M. Maas. 1998. A new pressure sensory mechanism for prey detection in birds: the use of principles of seabed dynamics? *Proceedings of the London Royal Society B* **265**:1377-1383.
- Piersma, T., van Gils, J., de Goeij, P., and J. van der Meer. 1995. Holling's functional response model as a tool to link the food-finding mechanism of a probing shorebird with its spatial distribution. *Journal of Animal Ecology* **64**:493-504.
- Reise, K. 2002. Sediment mediated species interactions in coastal waters. *Journal of Sea Research* **48**:127-141.
- Schubert, A., and K. Reise. 1986. Predatory effects of *Nephtys hombergii* on other polychaetes in tidal flat sediments. *Marine Ecology Progress Series* **34**:117-124.
- Steenbergen, J., Baars, J.M.D.D., Kesteloo, J.J., van Stralen, M.R., and J.A. Craymeersch. 2005. Het mosselbestand en het areaal aan mosselbanken op de droogvallende platen in de Waddenzee in het voorjaar van 2005. RIVO-rapport C065/05.
- Strasser, M., Dekker, R., Essink, K., Günther, C.-P., Jaklin, S., Kroncke, I., Madsen, P.B., Michaelis, H., and G. Vedel. 2003. How predictable is high bivalve recruitment in the Wadden Sea after a severe winter? *Journal of Sea Research* **49**:47-57.
- van de Kam, J., Ens, B., and T. Piersma. 2004. Shorebirds. An illustrated behavioural ecology. KNNV Publishers, Utrecht.
- van der Meer, J. 1997. Sampling design of monitoring programmes for marine benthos: a comparison between the use of fixed versus randomly selected stations. *Journal of Sea Research* **37**:167-179.
- van Gils, J. A., and T. Piersma. 1999. Day-and night-time movements of radiomarked Red Knots staging in the Western Wadden Sea in July-August 1995. *Wader Study Group Bulletin* **89**:36-44.
- van Gils, J. A., Battley, P.F., Piersma, T., and R. Drent. 2005a. Reinterpretation of gizzard sizes of red knots worldwide emphasises overriding importance of prey quality at migratory stopover sites. *Proceedings of the London Royal Society B* **272**:2609-2618.
- van Gils, J. A., Piersma, T., Dekinga, A., Spaans, B., and C. Kraan. 2006b. Shellfish-dredging pushes a flexible avian top predator out of a protected marine ecosystem. *Public Library of Science – Biology* **12**, 2399-2404.
- van Gils, J. A., Spaans, B., Dekinga, A., and T. Piersma. 2006a. Foraging in a tidally structured environment by red Knots (*Calidris canutus*): ideal, but not free. *Ecology* **87**:1189-1202.
- van Gils, J., de Rooij, S.R., van Belle, J., van der Meer, J., Dekinga, A., Piersma, T., and R. Drent. 2005b. Digestive bottleneck affects foraging decisions in red knots *Calidris canutus*. I. Prey choice. *Journal of Animal Ecology* **74**:105-119.
- van Leeuwe, M., E. O. Folmer, A. Dekinga, C. Kraan, K. Meijer, and T. Piersma. 2008. Staat handkokkelvisserij op gespannen voet met behoud biodiversiteit in de Waddenzee? *De Levende Natuur* **109**:15-19.

- Williams, I.D., van der Meer, J., Dekker, R., Beukema, J.J., and S.P. Holmes. 2004. Exploring interactions among intertidal macrozoobenthos of the Dutch Wadden Sea using population growth models. *Journal of Sea Research* **52**:307-319.
- Wolff, W.J. 2005a. Non-indigenous marine and estuarine species in the Netherlands. *Zoologische Mededelingen* **79**:1-116.
- Wolff, W.J. 2005b. The exploitation of living resources in the Dutch Wadden Sea. *Helgolander Marine Research* **59**:31-38.
- Zwarts, L., and J. Wanink. 1989. Siphon size and burying depth in deposit- and suspension-feeding benthic bivalves. *Marine Biology* **100**:227-240.
- Zwarts, L., Dubbeldam, W., van den Heuvel, H., van de Laar, E., Menke, U., Hazelhoff, L., and C. J. Smit. 2003. Bodemgesteldheid en mechanische kokkelvisserij in de Waddenzee. RIZA, Lelystad.

8. Appendix

Appendix 1: Species-list, with occurrence in %, based on 2004

Species	Taxonomic Group	% present											West	East	Total	
		Marsdiep	Eierlandse Gat	Vlie	Bom-Diep	Pink-gat	Zoutkamper-laag	Eilander-balg	Lauwers	Schild	Eems-Dollard					
<i>Atrypa alba</i>	Bivalvia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Atrypa tenuis</i>	Bivalvia	0	1.7	1.4	0	0	0	0	0.7	1	0	1.5	0.3	1.1		
<i>Cerastodema edule</i>	Bivalvia	1.5	9.4	18.3	17.7	26.2	26.7	21.3	36.7	19	13.8	15.3	27.2	18.8		
<i>Crassostrea gigas</i>	Bivalvia	0	0	0.2	0	0	0	0	0	0	0	0.11	0	0.08		
<i>Euis directus</i>	Bivalvia	1.5	3.3	3.5	3.9	0	1.3	2.1	2.5	0	3.5	3.4	1.6	2.9		
<i>Macoma balthica</i>	Bivalvia	0	22.9	30.4	31.4	36.2	46.2	32.98	59.23	29	27.6	27.5	44.3	32.5		
<i>Mya arenaria</i>	Bivalvia	0	2.8	12.4	9.8	6.7	5.6	6.4	8.4	3	6.9	9.3	6.5	8.5		
<i>Mytella bidentata</i>	Bivalvia	0	1.3	0.2	0	0	0	0	0	0	0	0.5	0	0.4		
<i>Mytilus edulis</i>	Bivalvia	0	0	0.4	0	0	2.7	1.1	1.5	4	0	0.3	1.8	0.7		
<i>Petricola pholadiformis</i>	Bivalvia	0	0	0.05	0	0	0	0	0.4	0	0	0.04	0.09	0.05		
<i>Sorobactaria plana</i>	Bivalvia	0	0.6	1.2	11.8	5.4	6	3.2	7.6	2	3.5	0.99	5.9	2.5		
<i>Tellina tenuis</i>	Bivalvia	0	3.7	2.2	0	0.7	1.3	1.1	2.2	0	3.5	2.6	1.3	2.2		
<i>Arenicola marina</i>	Polychaeta	3	19.8	13.7	5.9	18.8	18.9	26.6	21.1	20	6.9	15.2	19.3	16.4		
<i>Eteone longa</i>	Polychaeta	3	5	4.6	1.96	4.03	2.4	6.4	11.3	4	3.5	4.7	5.2	4.6		
<i>Harmothoe</i> sp.	Polychaeta	0	0.9	1.5	1.96	0.7	0.7	1.1	5.8	2	3.5	1.3	2.2	1.6		
<i>Heteromastus filiformis</i>	Polychaeta	11.9	33.4	51.2	31.4	46.3	48.4	61.7	51.6	39	55.2	45.5	48.6	46.2		
<i>Laeonereis acanthodes</i>	Polychaeta	17.9	38.7	20.5	35.3	32.2	37.8	34.04	45.5	36	55.2	25.6	38.8	29.5		
<i>Marenzelleria viridis</i>	Polychaeta	6	6.81	21.4	7.8	6.7	6	18.1	6.6	28	10.3	16.9	9.3	14.6		
<i>Neptys hombergii</i>	Polychaeta	37.3	22.4	20.6	15.7	26.2	24.9	13.8	34.6	21	24.1	21.5	25.7	22.8		
<i>Nereis diversicolor</i>	Polychaeta	17.9	42.2	43.2	43.1	51.7	45.1	51.1	42.9	29	51.7	42.3	44.6	43		
<i>Nereis virens</i>	Polychaeta	0	0.5	0.2	0	0	0	0	0	0	0	0.3	0	0.2		
<i>Phyllodoce maculata</i>	Polychaeta	1.5	1.3	1.5	0	1.3	1.3	1.1	8	3	0	1.4	3	1.9		
<i>Pygospio elegans</i>	Polychaeta	0	0.3	0.2	0	0	0	0	0	0	0	0.2	0	0.13		
<i>Scoloplos armiger</i>	Polychaeta	43.3	75.5	63.4	29.4	36.9	32.9	46.8	26.9	34	17.2	66.4	32.7	56.4		
<i>Scololepis foliosa</i>	Polychaeta	0	0	0.05	0	0	0	0	0	0	0	0.04	0	0.03		
<i>Hydrobia ulvae</i> *	Gastropoda	0	2.4	10.4	1.96	5.4	7.8	14.9	18.9	18	3.5	7.9	12.7	8.9		
<i>Littorina littorea</i>	Gastropoda	0	0.1	0	0	0	0.2	0	0	1	0	0.04	0.2	0.08		
<i>Retusa obtusa</i>	Gastropoda	0	0	0	0	0	0.4	0	0	0	0	0	0.2	0.05		
<i>Crangon crangon</i>	Crustacea	1.5	6.4	6.3	5.9	4.7	4	2.1	7.6	0	0	6.2	4.4	5.7		
<i>Praunus</i> sp.	Crustacea	0	0.1	0	0	0	0	0	0	0	0	0.04	0	0.02		
<i>Carcinus maenas</i>	Decapoda	4.5	12.1	6.1	1.96	5.4	5.8	5.3	9.8	3	3.5	7.8	6.2	7.9		
<i>Corophium volutator</i>	Amphipoda	0	3.6	14	0	0.7	3.3	3.2	2.2	3	3.5	10.7	2.5	8.3		
<i>Gammarus locusta</i>	Amphipoda	7.5	7.6	3.02	0	1.3	1.1	4.3	3.6	6	0	4.4	2.4	3.9		
<i>Urothoe</i> sp.	Isopoda	9	51.5	16.6	1.96	12.1	14.2	17	15.3	17	24.1	23.5	14.4	20.8		
<i>Asterias rubens</i>	Asteroida	0	0.1	0.11	0	0	0	0	0	0	0	0.1	0	0.08		
<i>Leptochitona cinerea</i>	Polyplocophora	0	0	0	0	0	0	1.1	0	0	0	0	0.09	0.03		
<i>Nemertea</i> sp.	Nemertea	0	0.1	0.05	0	0	0	0	0	0	0	0.07	0	0.05		

* Presence/absence is used, based on all sampling stations

Appendix 2: Species-list, with occurrence in %, based on 2006

Species	Taxonomic Group	% present											West	East	Total
		Marsdiep	Eierlandse Gat	Vlie	Born-diep	Pinke-gat	Zoutkamper-laag	Eilander-balg	Lauwers	Schild	Eems-Dollard				
<i>Abra alba</i>	Bivalvia	0	0	0.1	0	0	0	0	0	0	0	0	0.1	0	0.1
<i>Abra tenuis</i>	Bivalvia	0	5.4	3.8	0	0	0.2	0	0	0	0	0	3.8	0.04	2.7
<i>Cerastoderma edule</i>	Bivalvia	4.5	13.8	17.7	45.6	38	27.4	63	55.2	24.6	76.7	0	16.3	41	23.4
<i>Crassostrea gigas</i>	Bivalvia	0	0	0.1	0	0	1.6	0	0	1.1	0	0	0.04	0.7	0.2
<i>Ensis directus</i>	Bivalvia	7.5	6	1	0	0	0	0	0	0	0	0	2.6	0	1.8
<i>Macoma balthica</i>	Bivalvia	1.5	14.1	18.3	17.5	31.3	39.5	55.4	51.6	29.5	40	0	16.7	40.5	23.5
<i>Mya arenaria</i>	Bivalvia	0	4.1	10.6	3.5	2	1.4	2.2	1.2	2.1	0	0	8.5	1.6	6.6
<i>Mysella bidentata</i>	Bivalvia	0	0.8	0.2	0	0.7	0.2	0	0	0	0	0	0.3	0.2	0.3
<i>Mytilus edulis</i>	Bivalvia	0	1.3	0.3	8.8	1.3	6.2	2.2	2	2.1	0	0	0.6	5.7	1.5
<i>Petricola pholadiformis</i>	Bivalvia	0	0	0.1	0	0	0	0	0	0	3.3	0	0.04	0.1	0.1
<i>Scrobicularia plana</i>	Bivalvia	0	0.4	1.3	0	6	4.6	12	9.6	6.3	13.3	0	1	6.7	2.6
<i>Tellina tenuis</i>	Bivalvia	4.5	7.5	2.6	0	0	0.2	0	0	0	0	0	4	0.1	2.9
<i>Arenicola marina</i>	Polychaeta	1.5	22.7	19.5	5.3	20.7	18.9	14.1	21.6	9.5	10	0	20	17.6	19.3
<i>Eteone longa</i>	Polychaeta	1.5	6.5	3.1	0	0.7	0.7	0.8	2.8	1.1	0	0	4	1.4	3.3
<i>Harmothoe</i> sp.	Polychaeta	0	2.7	2.3	3.5	2	1.2	1.1	2	0	3.3	0	2.3	1.5	2.1
<i>Heteromastus filiformis</i>	Polychaeta	10.5	24.1	46.1	42.1	38.7	49	53.3	47.2	48.4	76.7	0	39.1	47.9	41.6
<i>Lamice conchilega</i>	Polychaeta	19.4	31.4	8.9	8.8	12	4.6	2.2	4	22.1	10	0	15.5	7.1	13.1
<i>Marenzelleria viridis</i>	Polychaeta	0	1.2	11.2	0	2	0.7	1.1	1.2	1.1	3.3	0	8.1	1.1	6.1
<i>Nephtys hombergii</i>	Polychaeta	41.8	26.2	25.5	24.6	24.7	24.6	17.4	26.8	39	30	0	26.1	25.4	25.9
<i>Nereis diversicolor</i>	Polychaeta	10.5	36.7	38.8	35.1	45.3	36.3	40.2	43.6	28.4	46.7	0	37.5	39	38
<i>Nereis virens</i>	Polychaeta	0	0	0.2	0	0	0.5	0	0	0	0	0	0.1	0.2	0.1
<i>Phyllodoce maculata</i>	Polychaeta	0	1.9	0.3	1.8	0.7	0.2	0	1.6	0	0	0	0.7	0.6	0.7
<i>Pygospio elegans</i>	Polychaeta	0	0	1.7	0	3.3	7.1	5.4	2	6.3	13.3	0	1.2	5.1	2.3
<i>Scoloplos armiger</i>	Polychaeta	52.2	64.9	46.2	10.5	38	24.6	25	22.8	36.8	26.7	0	51.6	26.4	44.4
<i>Scololepis foliosa</i>	Polychaeta	0	0.1	0.2	0	0	0	0	0.4	0	0	0	0.1	0.2	0.2
<i>Hydrobia ulvae</i> *	Gastropoda	1.5	3.1	11.4	1.8	12.7	10.8	40.2	22.4	21.1	23.3	0	8.8	16.9	11.1
<i>Littorina littorea</i>	Gastropoda	0	0	0.4	0	0	1.4	2.2	0	1.1	6.7	0	0.1	1	0.4
<i>Retusa obtusa</i>	Gastropoda	0	0	0	0	0	0	1.1	0.4	1.1	0	0	0	0.3	0.1
<i>Crangon crangon</i>	Crustacea	1.5	0	7	0	2.7	0.2	1.1	0.4	2.1	0	0	6.6	0.8	5
<i>Palaemon</i> sp.	Crustacea	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Carcinus maenas</i>	Decapoda	3	13.9	5.6	0	1.3	5.1	4.4	2.4	0	0	0	7.8	3.1	6.5
<i>Corophium volutator</i>	Amphipoda	0	4.5	16.9	0	0	0.5	1.1	1.6	6.3	0	0	13	1.2	9.6
<i>Gammarus locusta</i>	Amphipoda	3	0	1.6	0	0	1.2	5.4	1.2	2.1	0	0	2.9	1.4	2.5
<i>Urothoe</i> sp.	Isopoda	14.9	40.9	15.9	1.8	10	11.5	13	9.6	7.4	10	0	22.9	10	19.3
<i>Asterias rubens</i>	Asterioidea	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Leptochitona cinereus</i>	Polyplocophora	0	0	0	0	0	0	0	0	1.1	0	0	0	0.1	0.03
<i>Nemertine</i> sp.	Nemertea	0	0.1	0.2	0	0	0	0	0	0	0	0	0.1	0	0.1

* Presence/absence is used, based on all sampling stations

Appendix 3: Density (n/m²) per tidal-basin in the western Dutch Wadden Sea.

Western Dutch Wadden Sea

	Marsdiep		Eierlandse Gat		Vlie	
	2004	2006	2004	2006	2004	2006
Bivalvia						
<i>A. alba</i>	0	0	0	0	0	0.1
<i>A. tenuis</i>	0	0	17.6	63.9	5.0	33.0
<i>C. edule</i>	0.9	2.6	8.6	17.3	23.4	23.4
<i>C. gigas</i>	0	0	0	0	0.1	0.1
<i>E. directus</i>	0.9	4.3	2.1	4.2	5.1	0.6
<i>M. balthica</i>	0	0.9	20.5	15.5	27.3	15.7
<i>M. arenaria</i>	0	0	1.8	3.4	20.0	13.4
<i>M. bidentata</i>	0	0	0.7	0.5	0.1	0.1
<i>M. edulis</i>	0	0	0	2.5	0.3	0.3
<i>P. pholadiformis</i>	0	0	0	0	0.03	0.03
<i>S. plana</i>	0	0	0.5	0.2	1.1	0.8
<i>T. tenuis</i>	0	2.6	2.4	5.2	1.4	1.7
Polychaeta						
<i>A. marina</i>	1.7	0.9	14.1	18.2	10.7	16.9
<i>E. longa</i>	1.7	0.9	3.3	4.8	3.1	2.2
<i>Harmathoe</i> sp.	0	0	0.5	1.7	0.9	1.4
<i>H. filiformis</i>	12.1	9.5	120.6	57.8	190.2	119.0
<i>L. conchilega</i>	12.9	13.8	74.4	72.2	54.8	13.6
<i>M. viridis</i>	4.3	0	11.2	0.8	207.2	17.9
<i>N. hombergii</i>	29.3	29.3	16.6	26.9	15.3	27.0
<i>N. virens</i>	0	0	0.3	0	0.1	0.1
<i>N. diversicolor</i>	12.9	6.0	61.3	97.4	108.6	73.7
<i>P. maculata</i>	0.9	0	0.8	1.2	1.0	0.1
<i>P. elegans</i>	0	0	0.1	0	0.1	4.3
<i>S. foliosa</i>	0	0	0	0.1	0	0.1
<i>S. armiger</i>	66.4	66.4	218.8	154.9	218.2	83.8
Gastropoda						
<i>H. ulvae</i> *			274.5	284.25	300.75	2507.93
<i>L. littorea</i>	0	0	0.1	0	0	0.1
<i>R. obtusa</i>	0	0	0	0	0	0
Crustacea						
<i>C. crangon</i>	0.9	0.9	5.2	4.9	5.2	6.1
<i>Palaemon</i> sp.	0	0	0.1	0	0	0
Decapoda						
<i>C. maenas</i>	2.6	1.7	12.8	10.2	4.5	4.4
Amphipoda						
<i>C. volutator</i>	0	0	5.3	4.4	230.1	432.1
<i>G. locusta</i>	4.3	1.7	8.4	6.7	4.6	1.5
Isopoda						
<i>Urothoe</i> sp.	28.4	40.5	301.4	267.2	127.0	130.3
Astroidea						
<i>A. rubens</i>	0	0	0.1	0	0.1	0
Polyplocophora						
<i>L. cinereus</i>	0	0	0	0	0	0
Nemertea						
<i>Nemertine</i> sp.	0	0	0.1	0.1	0	0.2

* Densities are only based on points sampled walking

Appendix 4: Density per m², per tidal-basin, in the eastern Dutch Wadden Sea.

Eastern Dutch Wadden Sea

	Bom-diep		Pinke-gat		Zoutkamper-laag		Eilander-balg		Lauwers		Schild		Eems-Dollard	
	2004	2006	2004	2006	2004	2006	2004	2006	2004	2006	2004	2006	2004	2006
Bivalvia														
<i>A. alba</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>A. tenuis</i>	0	0	0	0	0	0.1	0	0	0.4	0	3.4	0	0	0
<i>C. edule</i>	79.3	420.4	77.9	247.8	60.4	114.4	75.3	527.2	86.2	307.3	61.1	122.6	43.8	579.4
<i>C. gigas</i>	0	0	0	0	0	1.3	0	0	0	0	0	1.2	0	0
<i>E. directus</i>	2.3	0	0	0	0.9	0	1.2	0	1.7	0	0	0	2.0	0
<i>M. balthica</i>	57.7	13.2	51.1	31.4	72.5	38.3	91.0	105.4	122.1	71.0	40.2	44.0	39.8	48.1
<i>M. arenaria</i>	6.8	3.0	5.0	1.2	4.2	0.8	4.2	7.5	5.8	0.7	2.3	1.2	4.0	0
<i>M. bidentata</i>	0	0	0	0.4	0	0.1	0	0	0	0	0	0	0	0
<i>M. edulis</i>	0	13.2	0	0.8	9.6	19.2	1.2	30.2	2.5	5.1	8.7	1.8	0	0
<i>P. pholadiformis</i>	0	0	0	0	0	0	0	0	0.2	0	0	0	0	1.9
<i>S. plana</i>	6.8	0	3.4	4.2	6.3	2.9	21.1	11.2	5.6	7.8	1.2	4.3	2.0	7.7
<i>T. tenuis</i>	0	0	0.4	0	0.8	0.1	0.6	0	1.7	0	0	0	2.0	0
Polychaeta														
<i>A. marina</i>	4.5	3.0	14.2	14.2	14.1	14.0	19.5	13.6	16.2	15.1	13.2	6.6	4.0	7.7
<i>E. longa</i>	1.1	0	2.7	0.4	2.6	0.4	8.0	1.9	12.8	1.8	3.5	0.6	2.0	0
<i>Harmathoe</i> sp.	1.1	2.0	0.4	1.2	0.4	0.7	0.6	0.6	3.5	1.2	1.2	0	2.0	1.9
<i>H. filiformis</i>	75.9	108.4	141.9	110.1	122.2	151.0	138.1	223.2	165.2	272.5	84.7	142.7	242.9	421.5
<i>L. conchilega</i>	231.0	29.4	128.3	14.2	141.5	4.1	121.8	1.2	290.8	2.5	128.8	43.2	452.0	13.5
<i>M. viridis</i>	10.2	0	7.3	1.2	5.8	0.7	19.6	0.6	10.3	0.7	158.8	0.6	15.9	1.9
<i>N. hombergii</i>	10.2	17.2	20.5	16.9	17.8	19.6	8.5	13.1	25.2	22.6	13.3	26.1	25.9	17.3
<i>N. virens</i>	0	0	0	0	0	0.3	0	0	0	0	0	0	0	0
<i>N. diversicolor</i>	100.8	67.9	138.1	132.1	99.5	64.6	82.6	57.4	62.2	118.4	33.3	40.5	99.6	63.5
<i>P. maculata</i>	0	1.0	1.1	0.4	0.8	0.1	0.6	0	4.6	0.9	2.3	0	0	0
<i>P. elegans</i>	0	0	0	3.8	0	9.7	0	9.4	0	4.9	0	30.4	0	19.2
<i>S. foliosa</i>	0	0	0	0	0	0	0	0.6	0	0.2	0	0	0	0
<i>S. armiger</i>	41.9	14.2	96.7	72.7	70.0	41.6	56.7	42.7	37.8	25.7	46.2	49.2	15.9	34.6
Gastropoda														
<i>H. ulvae</i> *			89.1	6058.3	357.3	4044.9	615.9	8947.5	27.9	13333.4	148.6	25495.1		
<i>L. littorea</i>	0	0	0	0	0.1	2.4	0	2.5	0	0	0.6	1.2	0	3.8
<i>R. obtusa</i>	0	0	0	0	0.5	0	0	0.6	0	0.2	0	1.2	0	0
Crustacea														
<i>C. crangon</i>	6.8	0	4.6	1.5	5.6	0.1	1.8	0.6	9.3	0.2	0	1.2	0	0
<i>Palaemon</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Decapoda														
<i>C. maenas</i>	1.1	0	4.2	0.8	4.7	4.5	3.6	10.5	7.2	2.1	1.7	0	2.0	0
Amphipoda														
<i>C. volutator</i>	0	0	0.4	0	3.5	0.3	21.7	0.6	5.7	1.1	1.7	4.2	2.0	0
<i>G. locusta</i>	0	0	1.5	0	1.1	1.2	34.3	11.1	3.1	1.1	5.2	1.2	0	0
Isopoda														
<i>Urothoe</i> sp.	3.4	2.0	118.6	70.3	54.5	39.7	42.3	35.3	80.4	27.7	65.2	35.8	167.3	13.5
Asteroidea														
<i>A. rubens</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polyplacophora														
<i>L. cinereus</i>	0	0	0	0	0	0	0.6	0	0	0	0	1.2	0	0
Nemertea														
<i>Nemertine</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0

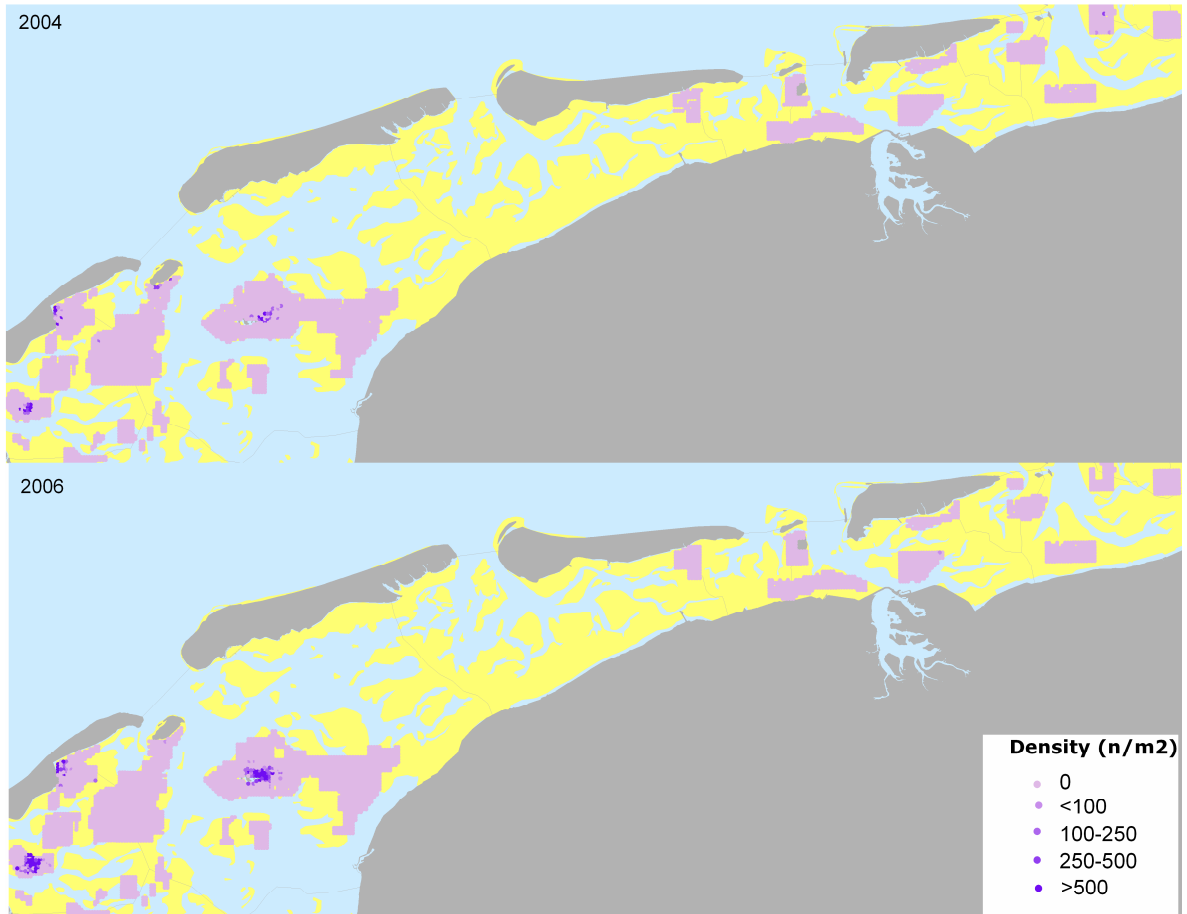
* Densities are only based on points sampled walking

	Western Dutch Wadden Sea						Eastern Dutch Wadden Sea													
	Marsdiep		Eierlandse Gat		Vlie		Borndiep		Pinkegat		Zoutkamperlaag		Eilanderbalg		Lauwers		Schild		Eems-Dollard	
	2004	2006	2004	2006	2004	2006	2004	2006	2004	2006	2004	2006	2004	2006	2004	2006	2004	2006	2004	2006
<i>A. alba</i>	0	0	0	0	0	0.0001	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>A. tenuis</i>	0	0	0.02	0.11	0.01	0.03	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>C. maenas</i>	0	0.26	0.04	0.13	0.01	0.17	0	0	0.08	0.144	0.05	0	0	0	0	0	0	0	0	0
<i>C. edule</i>	0.5	0.001	1.78	1.66	2.81	4.05	56.17	20.75	17.32	43.01	38.29	14.03	51.27							
<i>C. crangon</i>	0	0	0.001	0.02	0	0.03	0	0	0.002	0.002	0	0	0	0	0	0	0	0	0	0
<i>E. directus</i>	0.001	0.86	0.84	0.84	0.17	0.15	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>C. gigas</i>	0	0	0	0	0.24	0.12	0	0	2.16	0	0	0.69	0	0	0	0.69	0	0	0	0
<i>L. littorea</i>	0	0	0.006	0	0	0.006	0	0	0.11	0.07	0	0.04	0.29							
<i>M. balthica</i>	0	0.07	0.82	0.31	0.86	0.35	0.65	0.67	0.74	1.159	1.10	0.39	0.99							
<i>M. arenaria</i>	0	0	0.24	0.05	3.52	1.73	0.58	0.28	0.30	0.02	0.39	0.09	0	0	0	0.09	0	0	0	0
<i>M. bidentata</i>	0	0	0.001	0.001	0.0002	0.0002	0	0.001	0	0	0	0	0	0	0	0	0	0	0	0
<i>M. edulis</i>	0	0	0	0.003	0.04	0	2.99	0.50	6.06	8.09	0.67	0.44	0	0	0	0.44	0	0	0	0
<i>P. pholadiformis</i>	0	0	0	0	0.002	0.012	0	0	0	0	0	0	0.12							
<i>S. plana</i>	0	0	0.05	0.04	0.05	0.08	0	0.59	0.46	1.13	0.71	0.26	0.804							
<i>T. tenuis</i>	0	0.03	0.04	0.11	0.02	0.05	0	0	0.001	0	0	0	0	0	0	0	0	0	0	0
<i>H. ulvae*</i>			0.27	0.67	0.5	2.1			3.41	1.92			4.92			26.13				

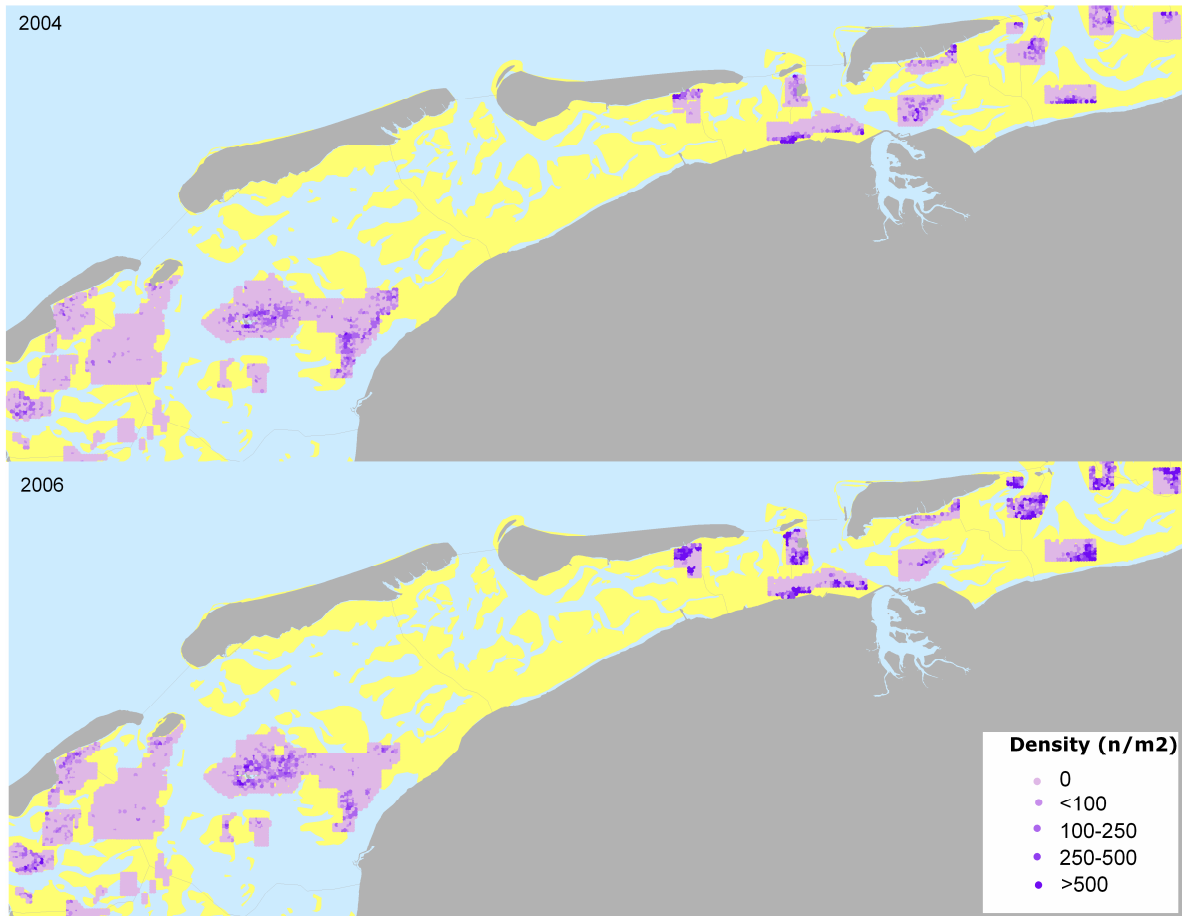
*Biomass only based on *Hydrobia ulvae* found in walking samples

Appendix 6: Distributional maps of Common and Abundant macrozoobenthic species.

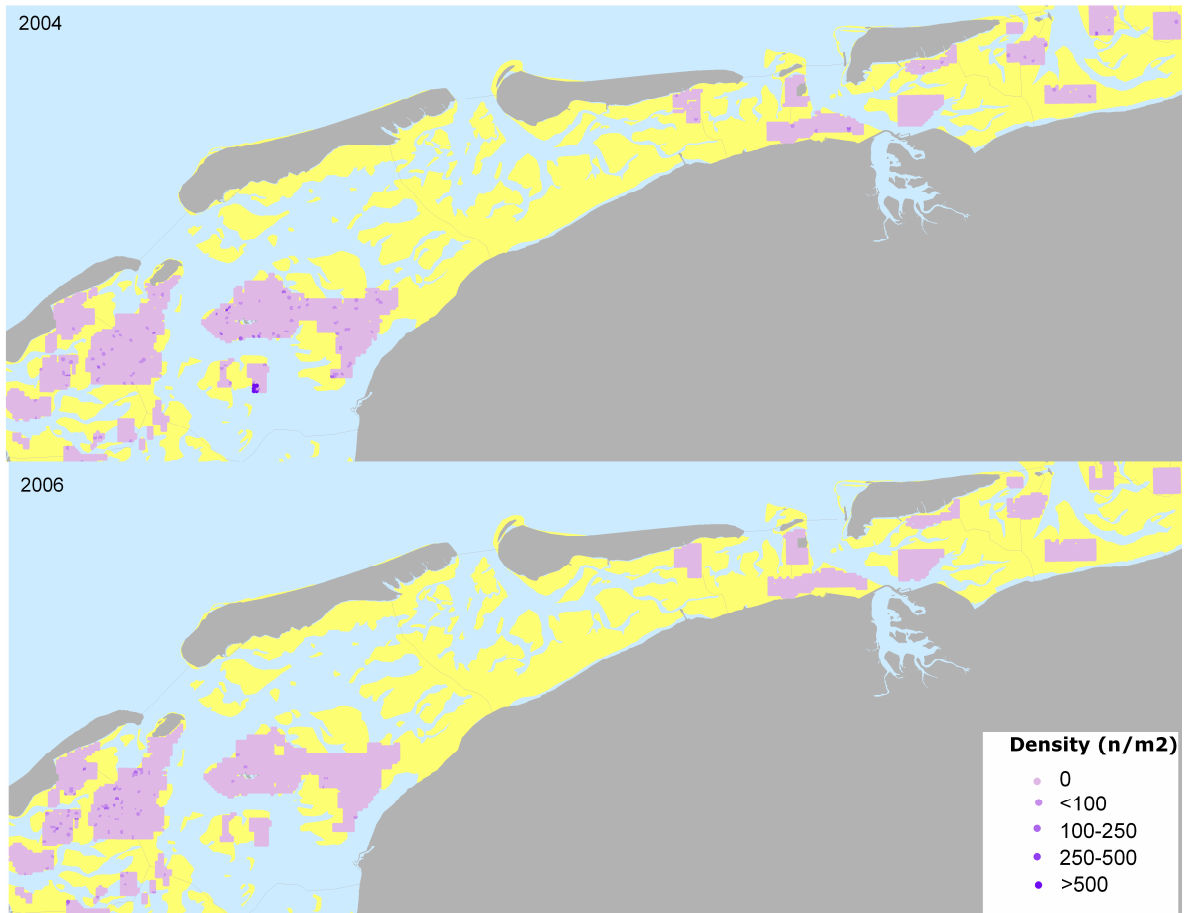
-Abra tenuis



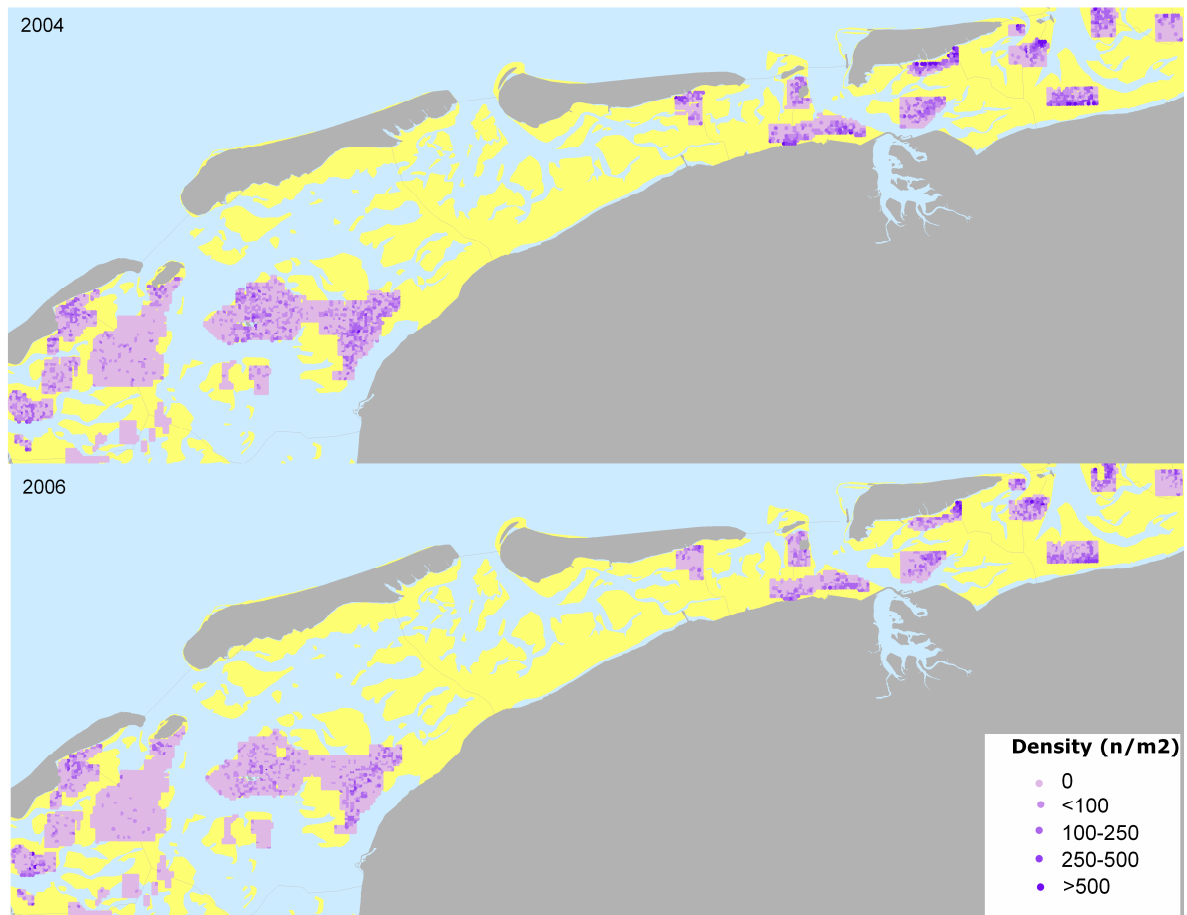
-*Cerastoderma edule*



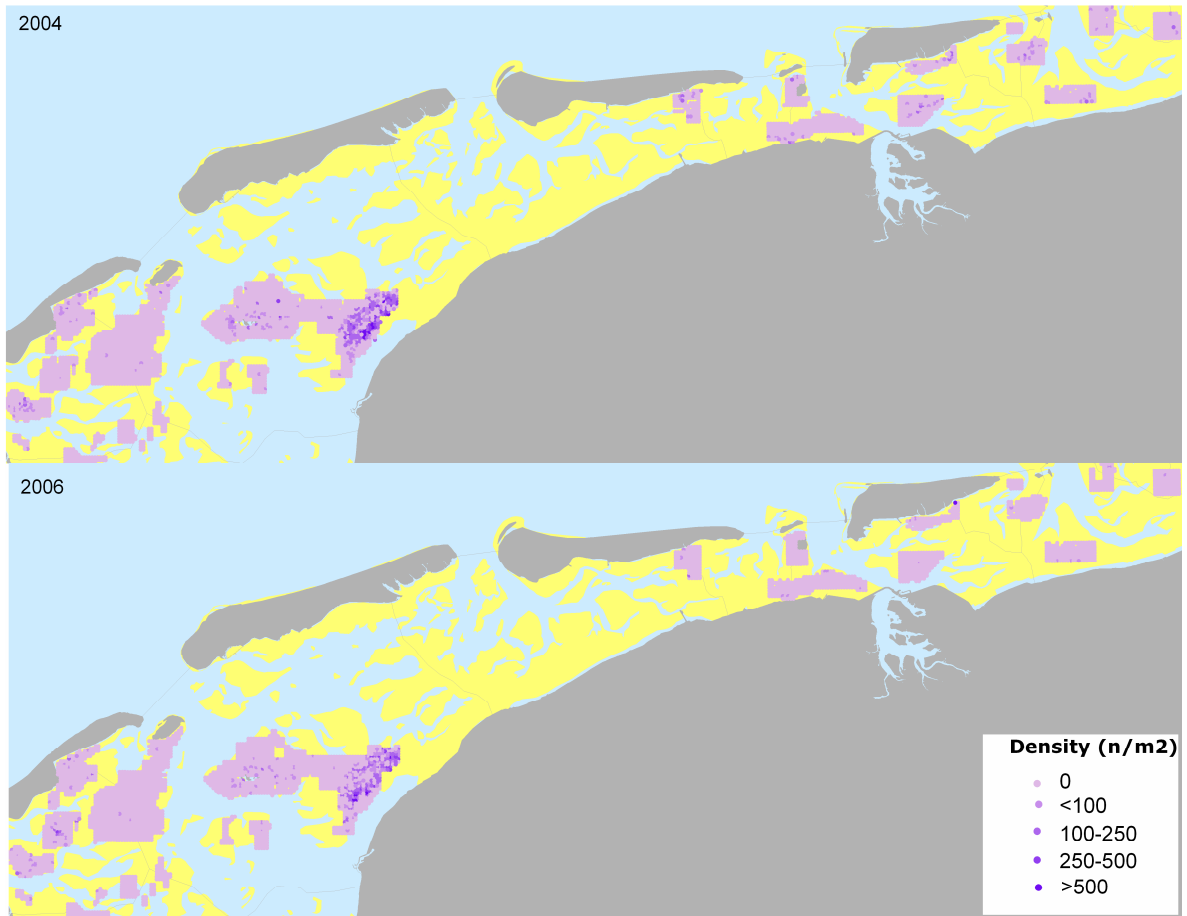
-*Ensis directus*



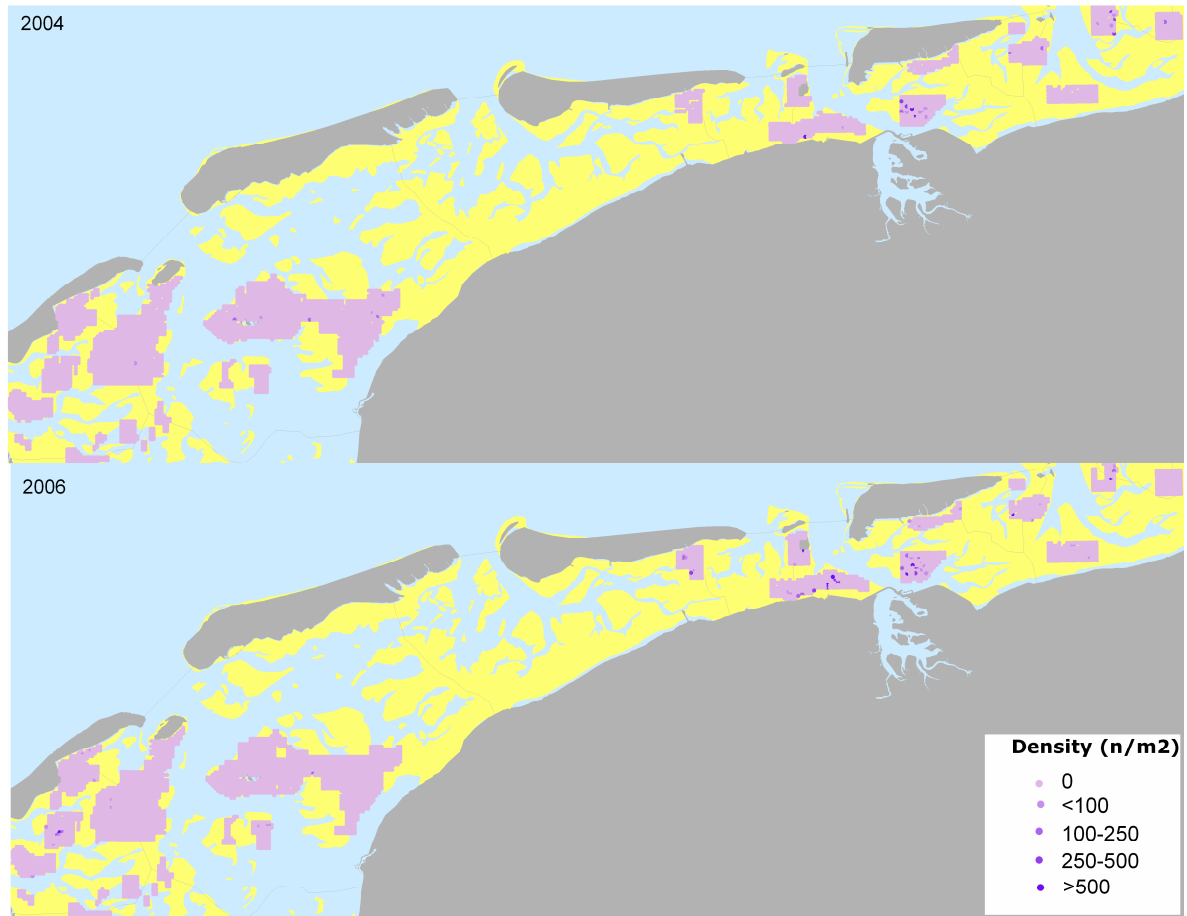
-*Macoma balthica*



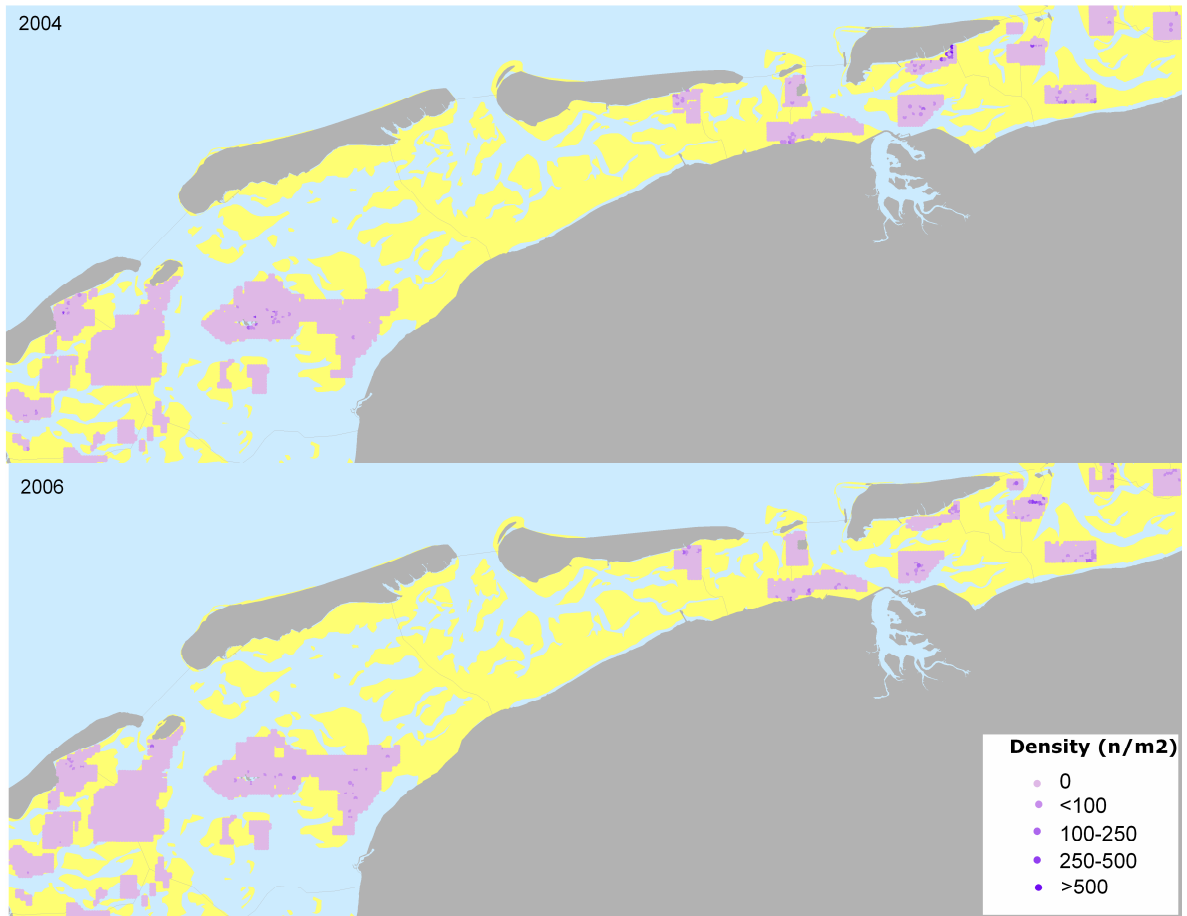
-*Mya arenaria*



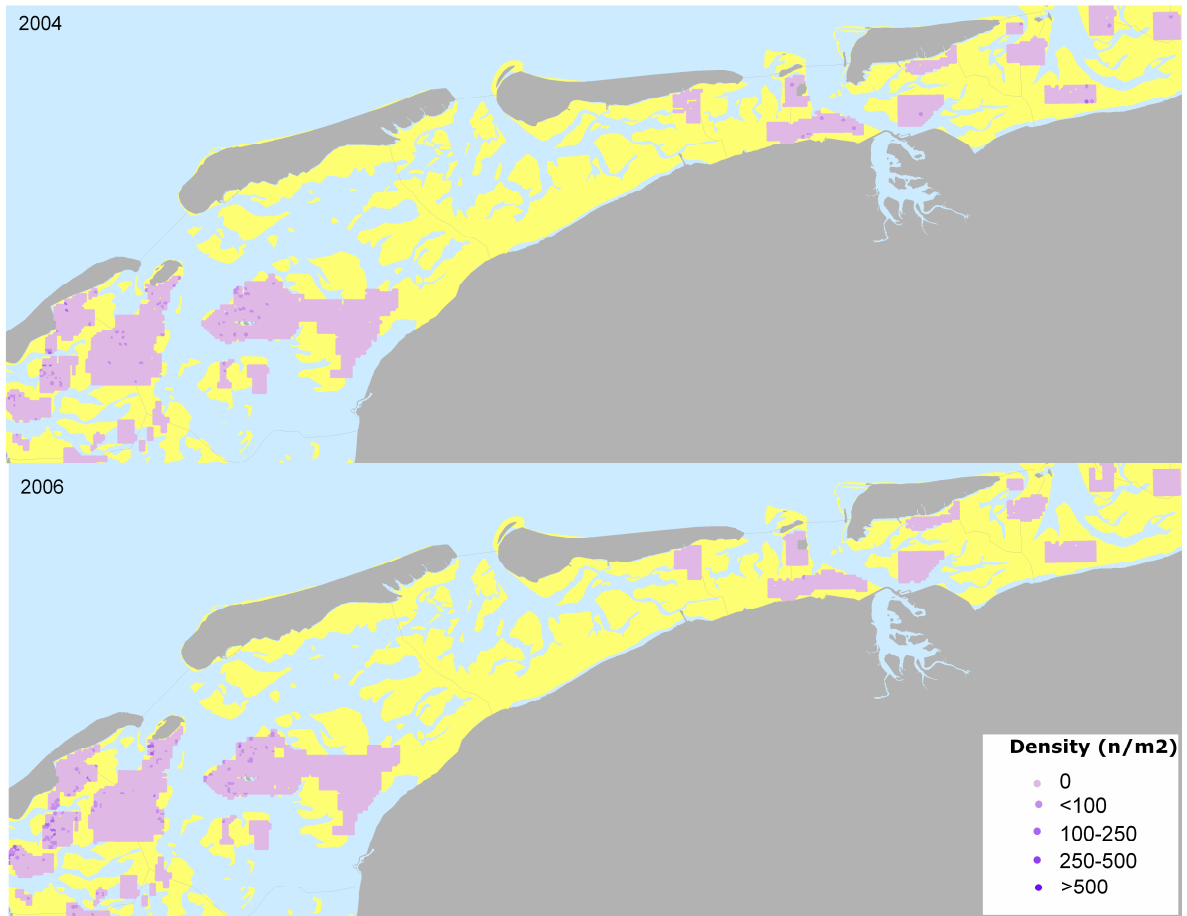
-*Mytilus edulis*



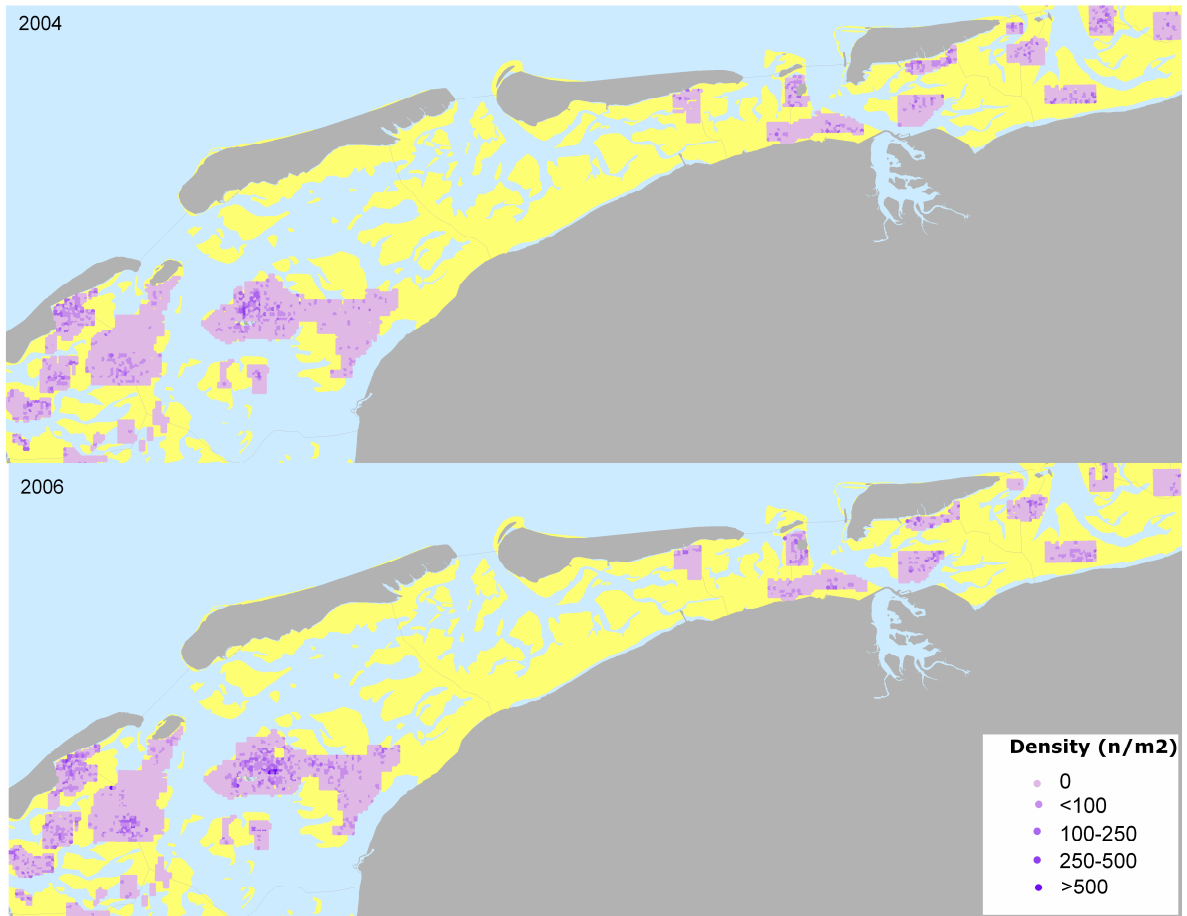
-Scrobicularia plana



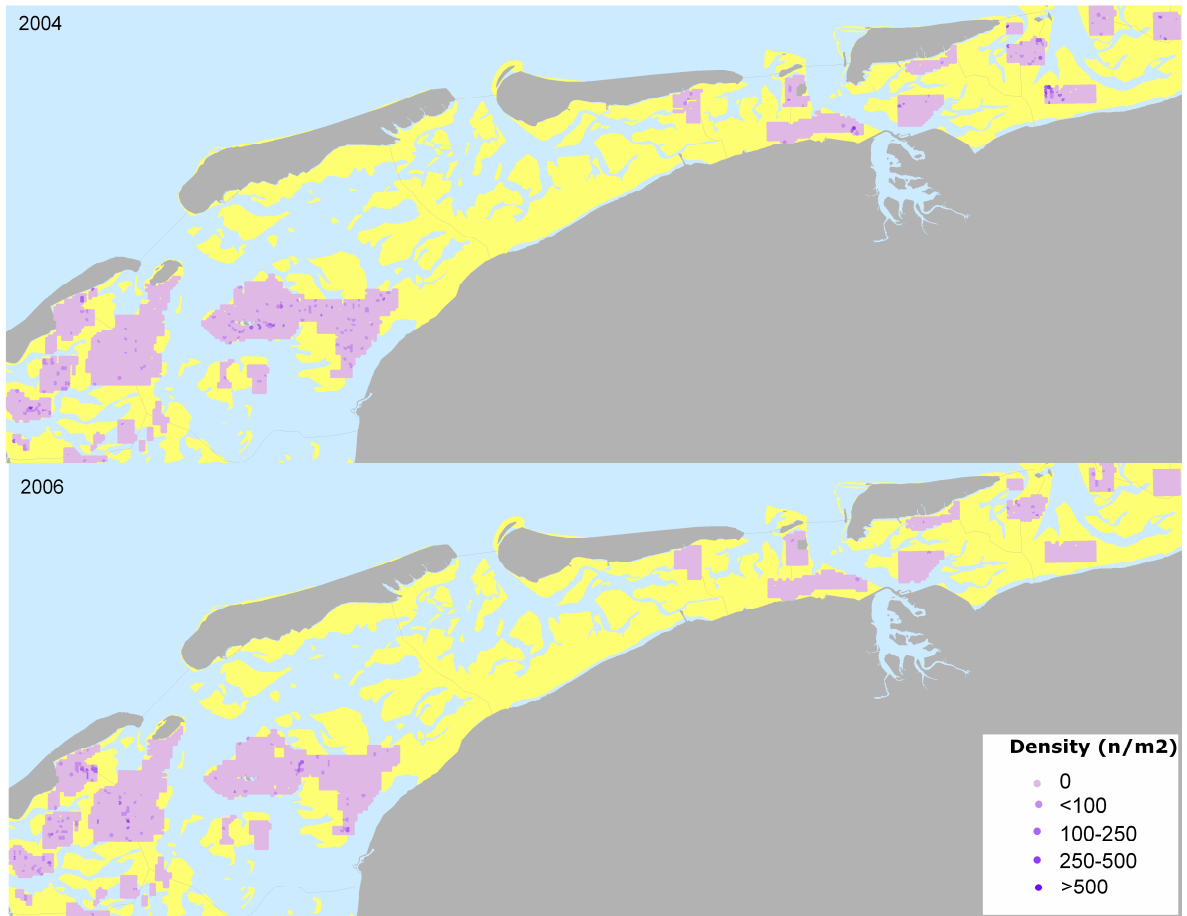
-Tellina tenuis



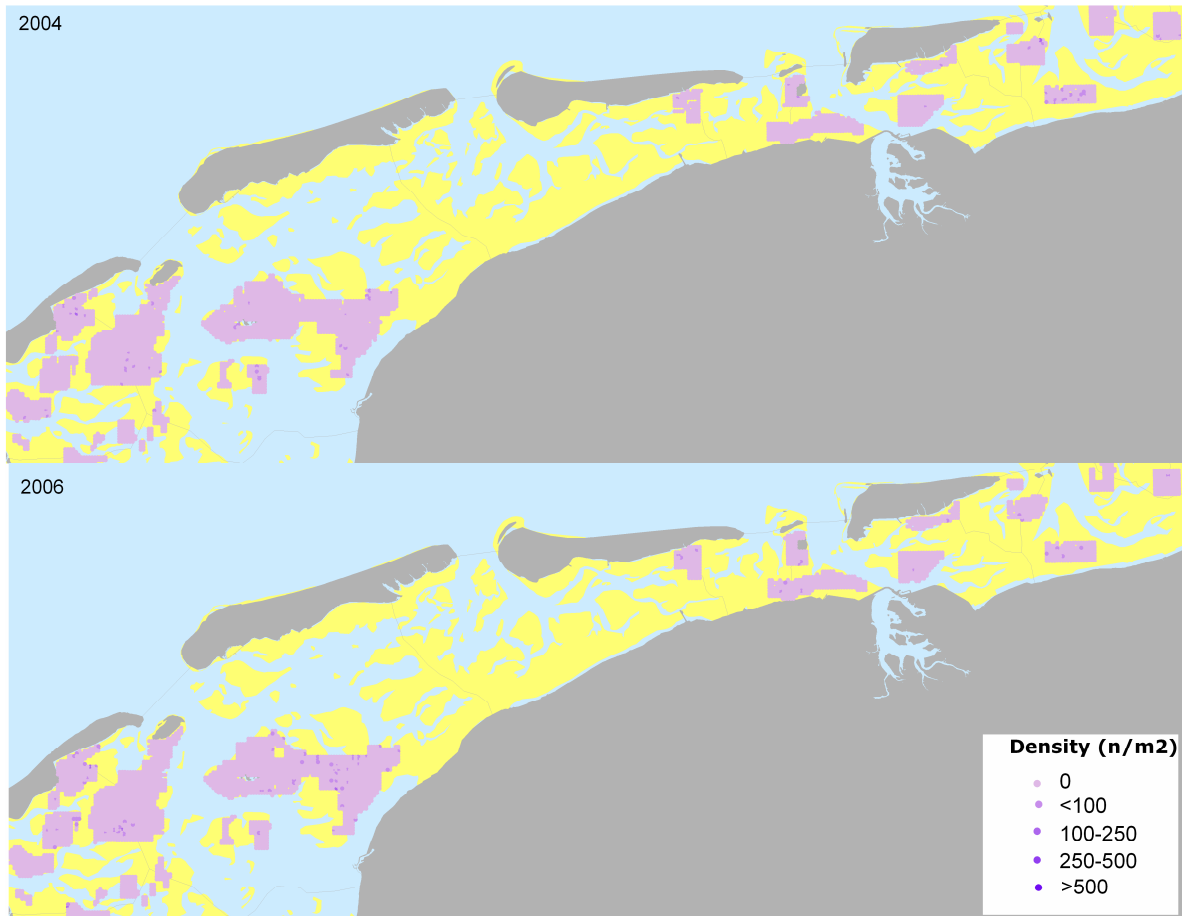
-*Arenicola marina*



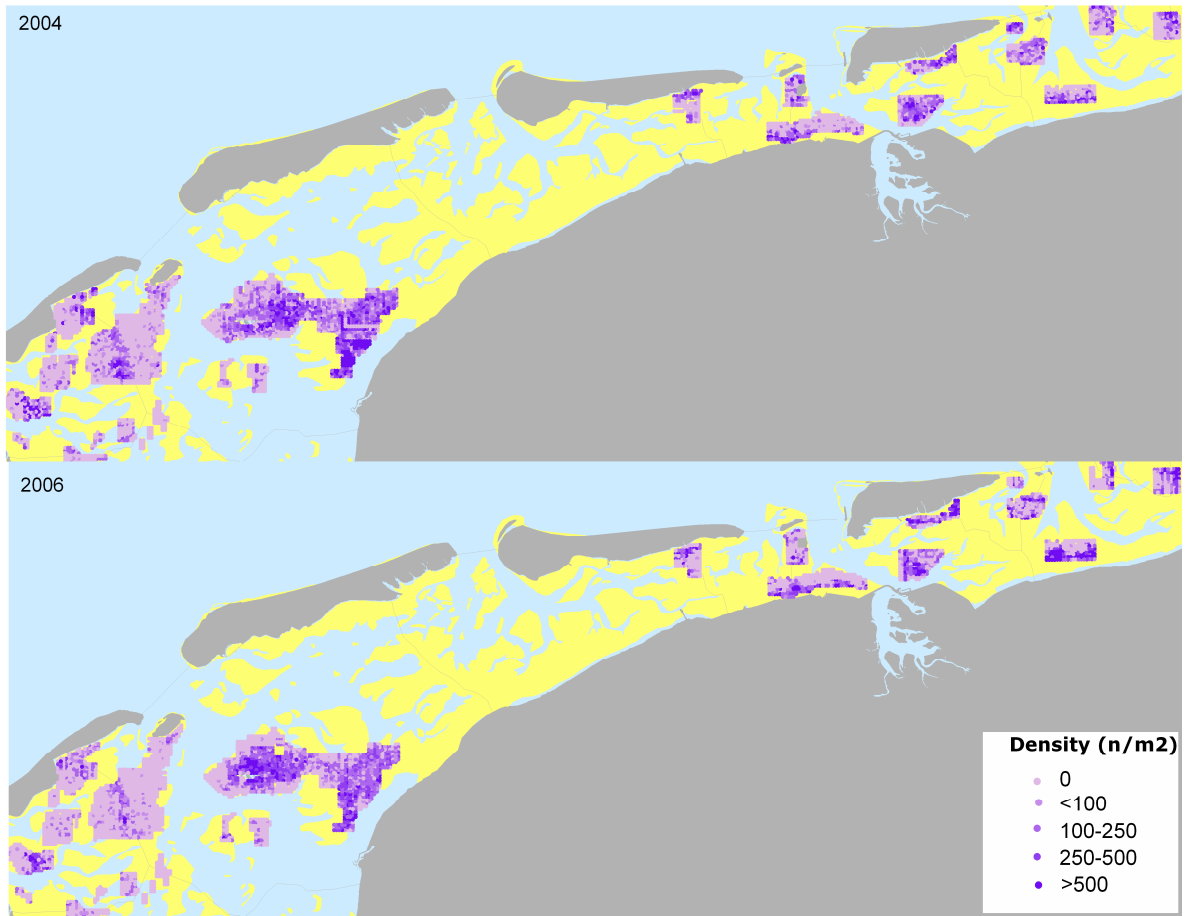
-Eteone longa



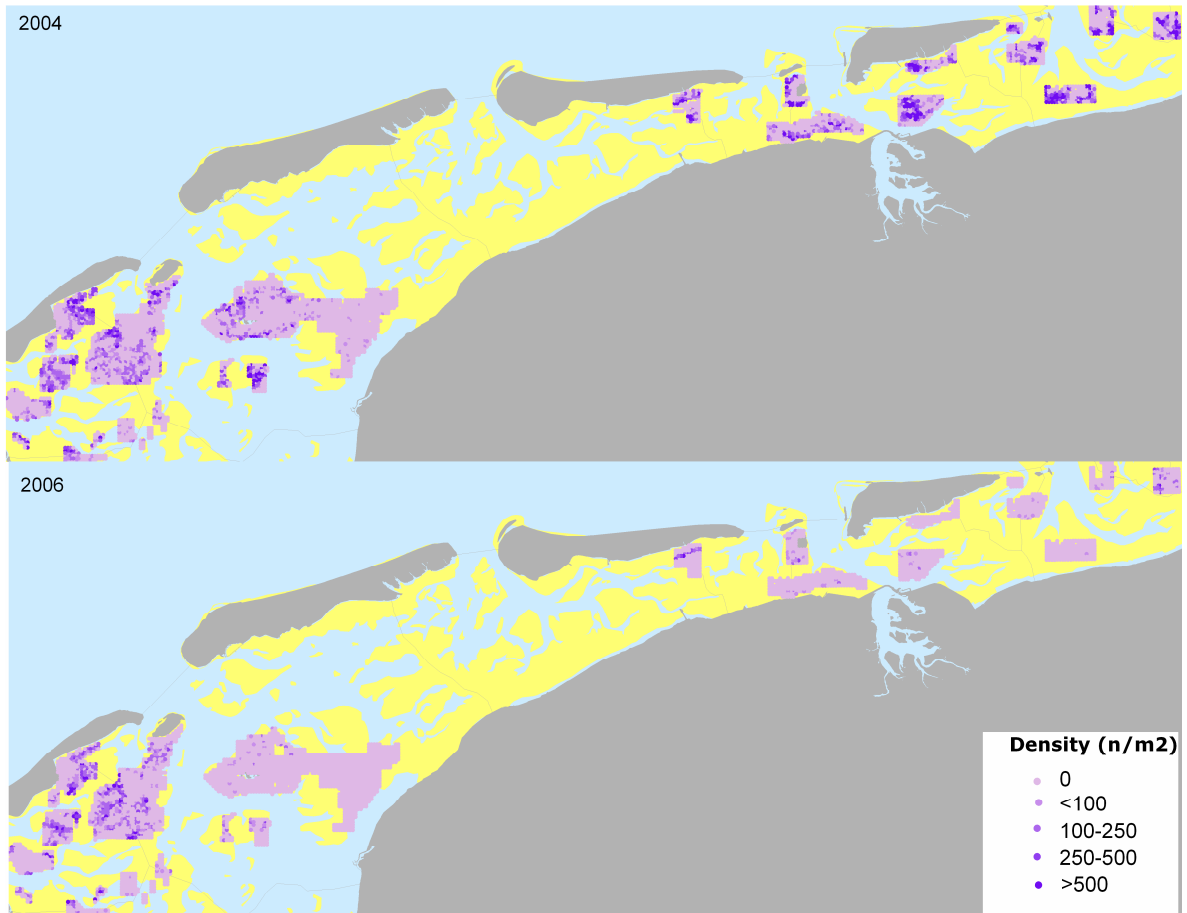
-Harmothoe sp.



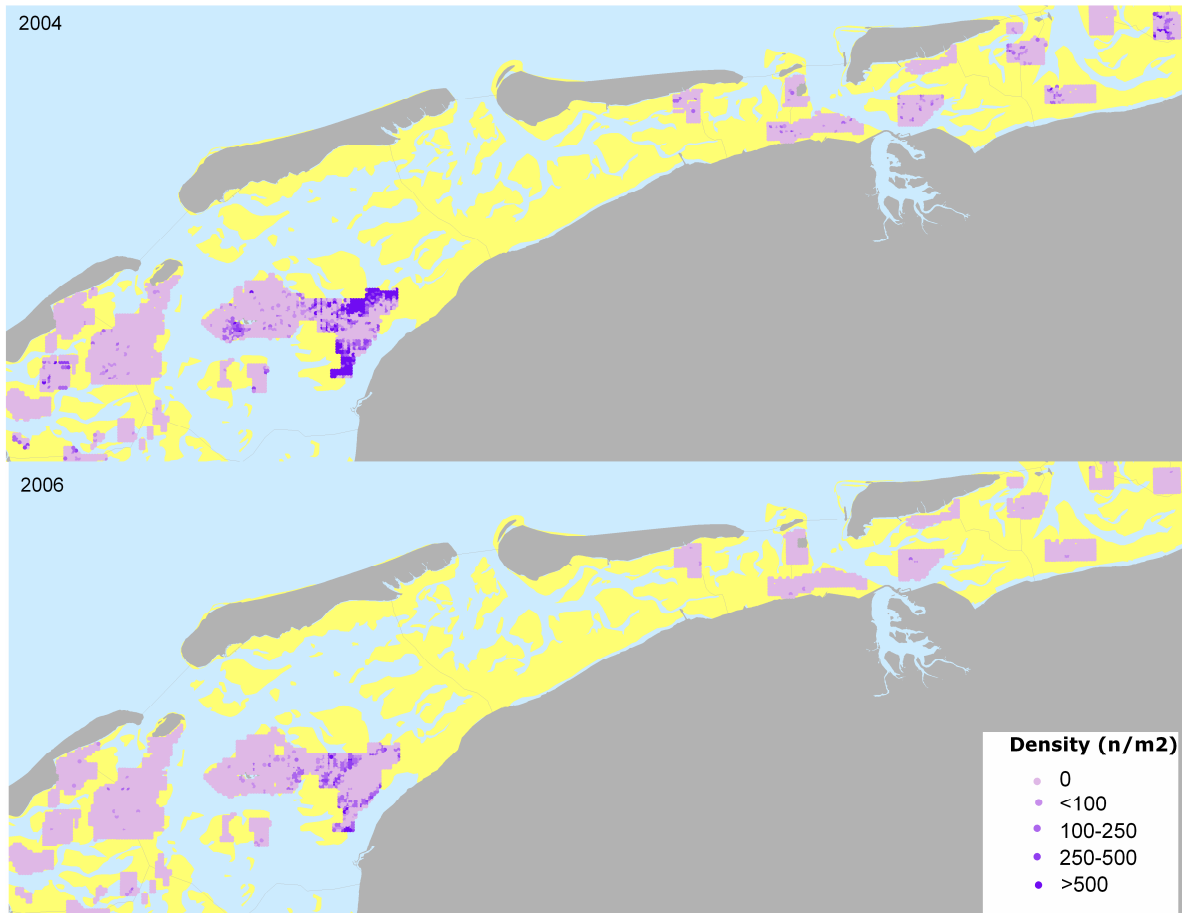
-Heteromastus filiformis



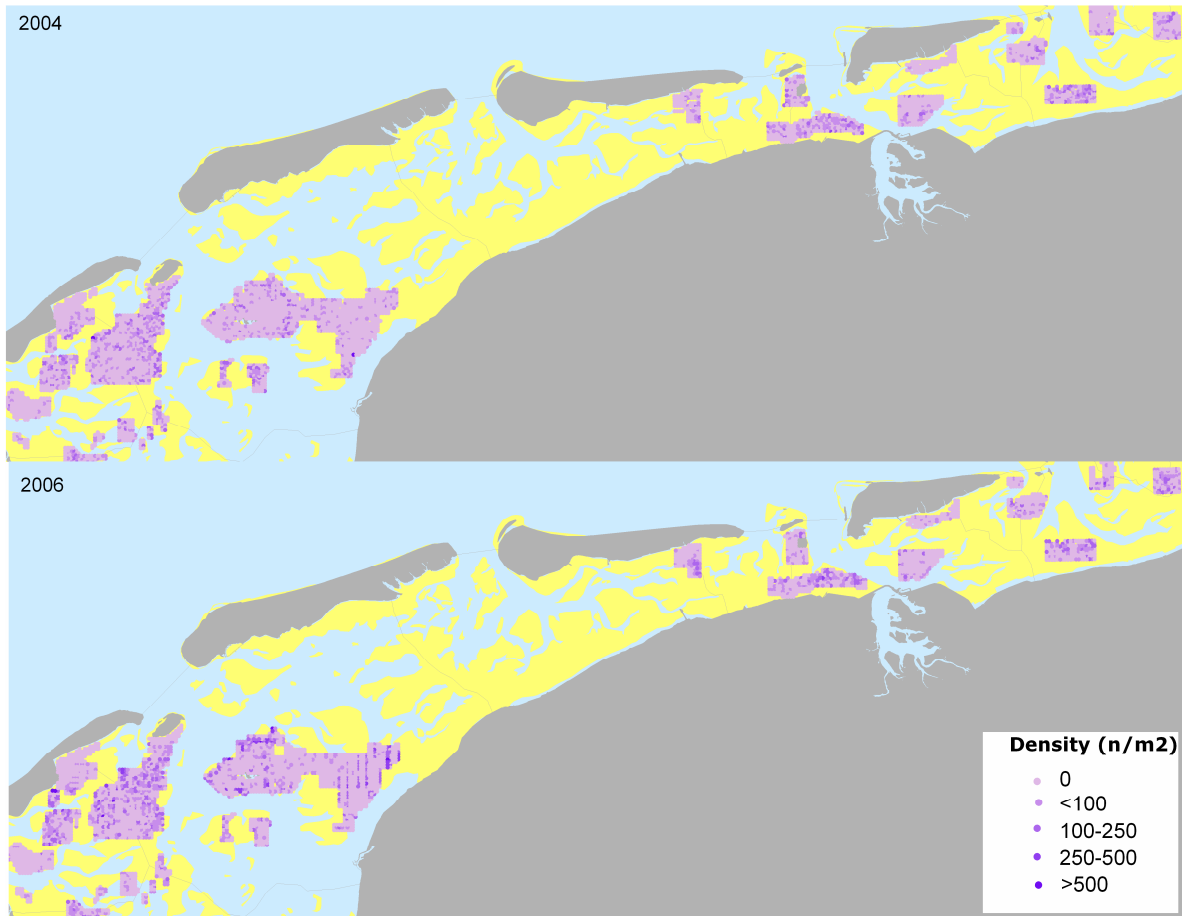
-Lanice conchilega



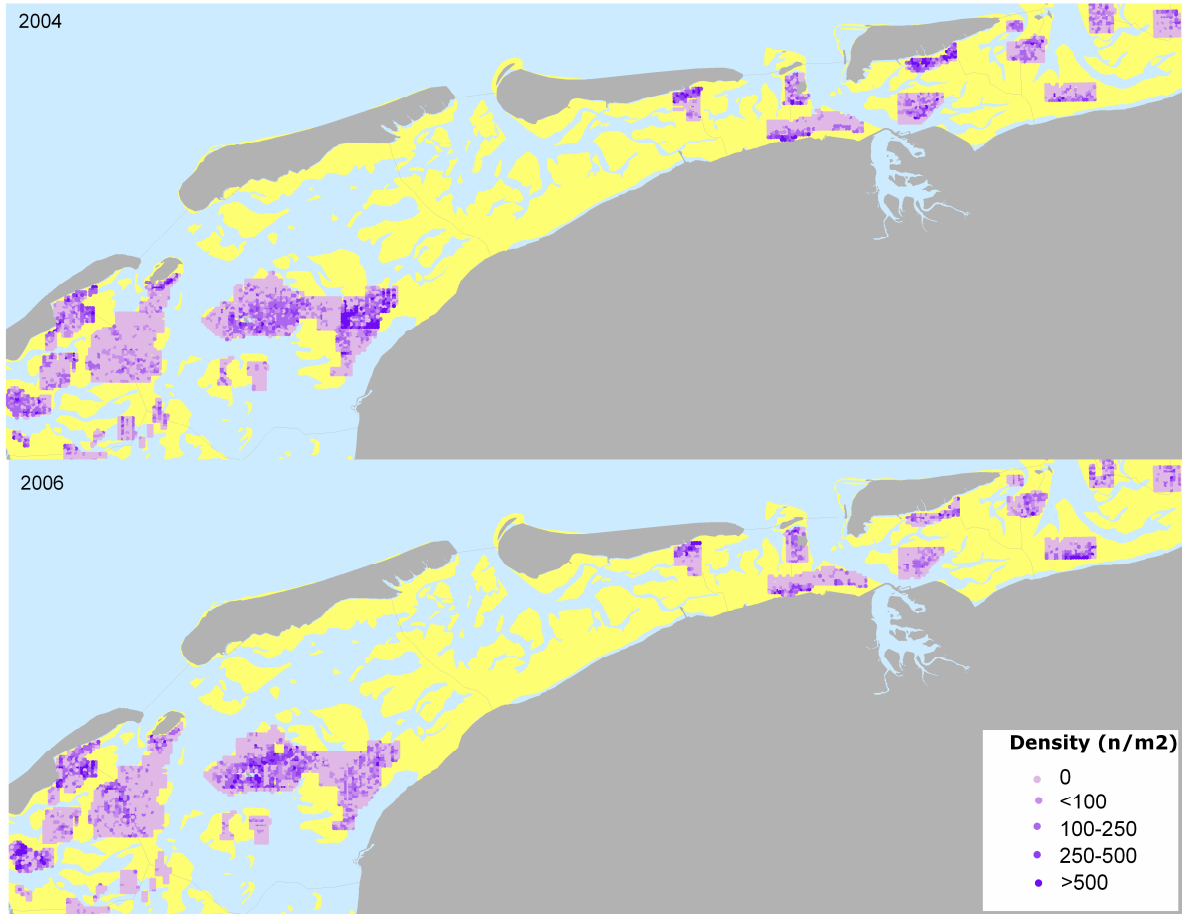
Marenzelleria viridis



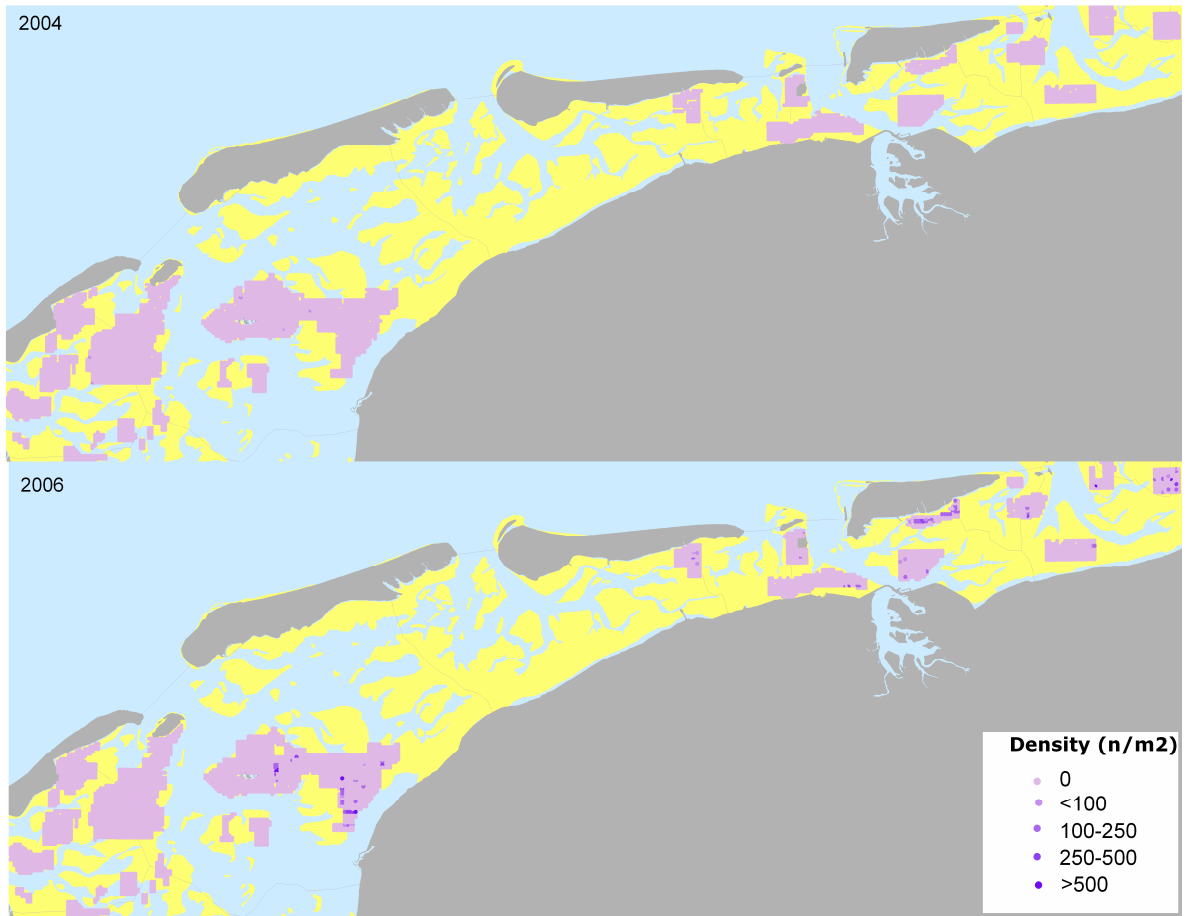
-Nephtys hombergii



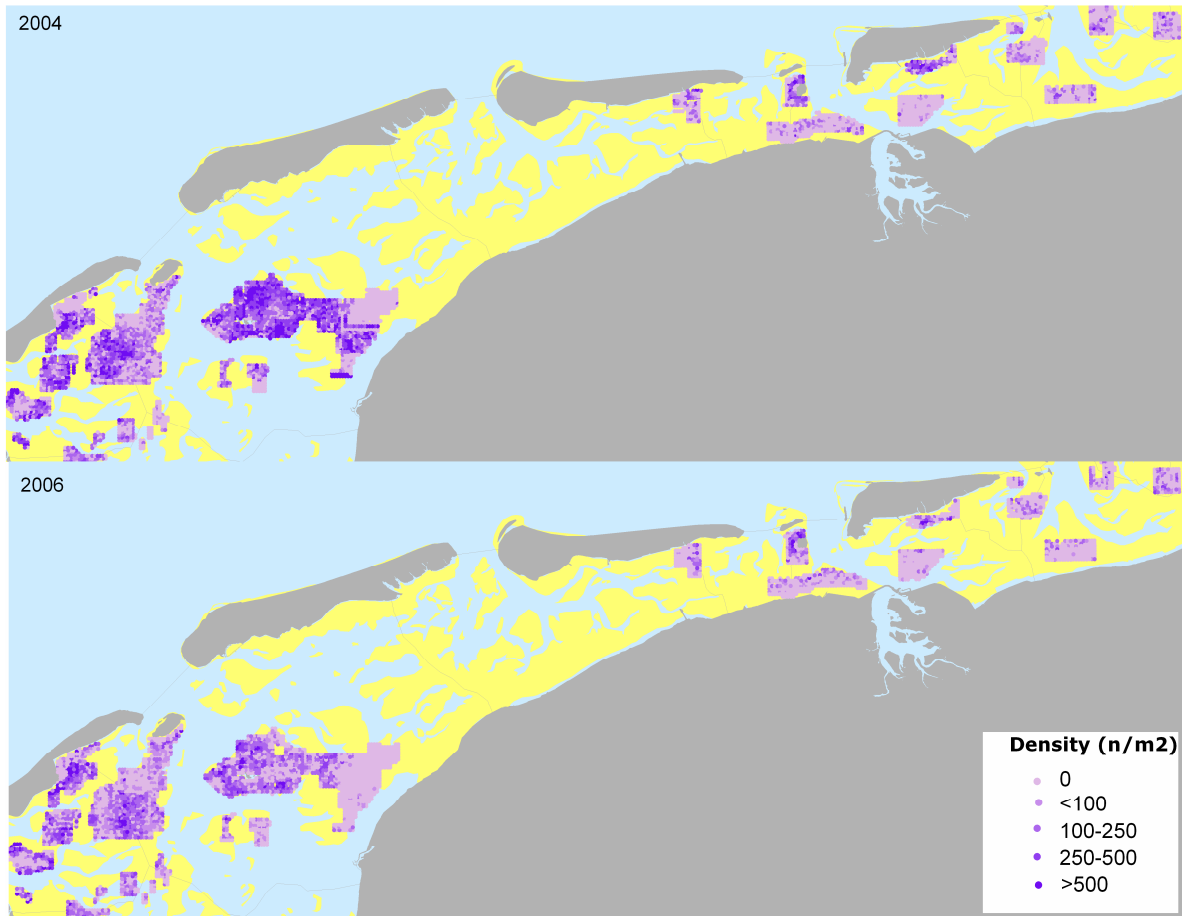
-Nereis diversicolor



-Pygospio elegans

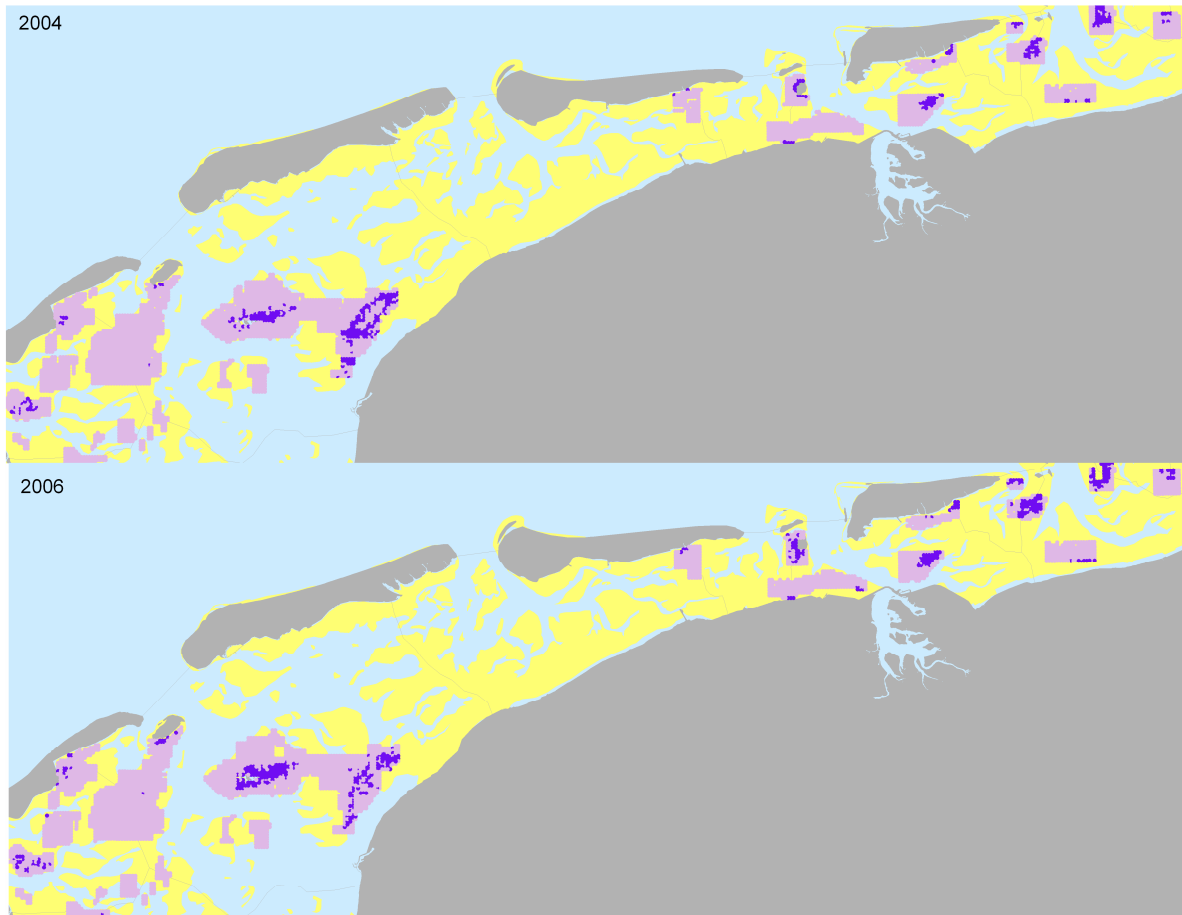


-Scoloplos armiger

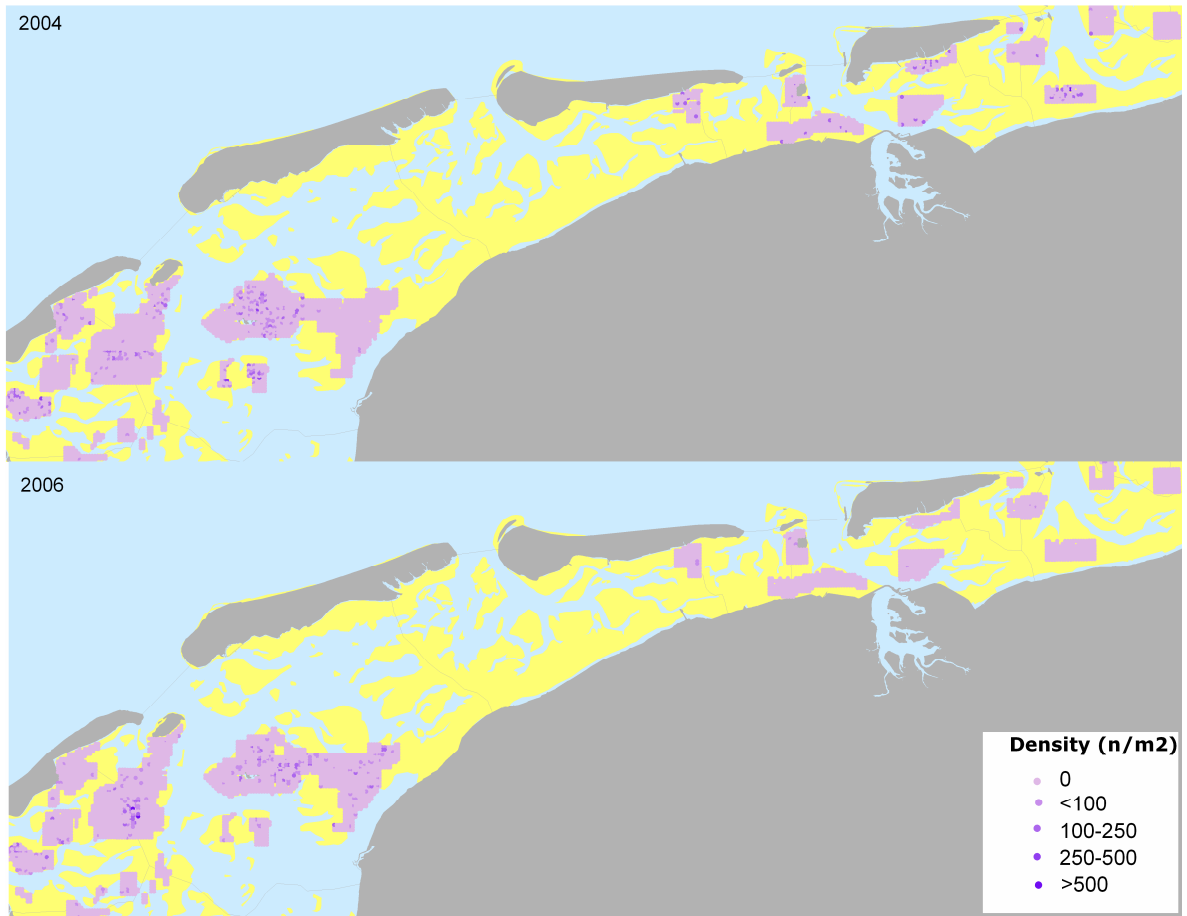


-*Hydrobia ulvae**

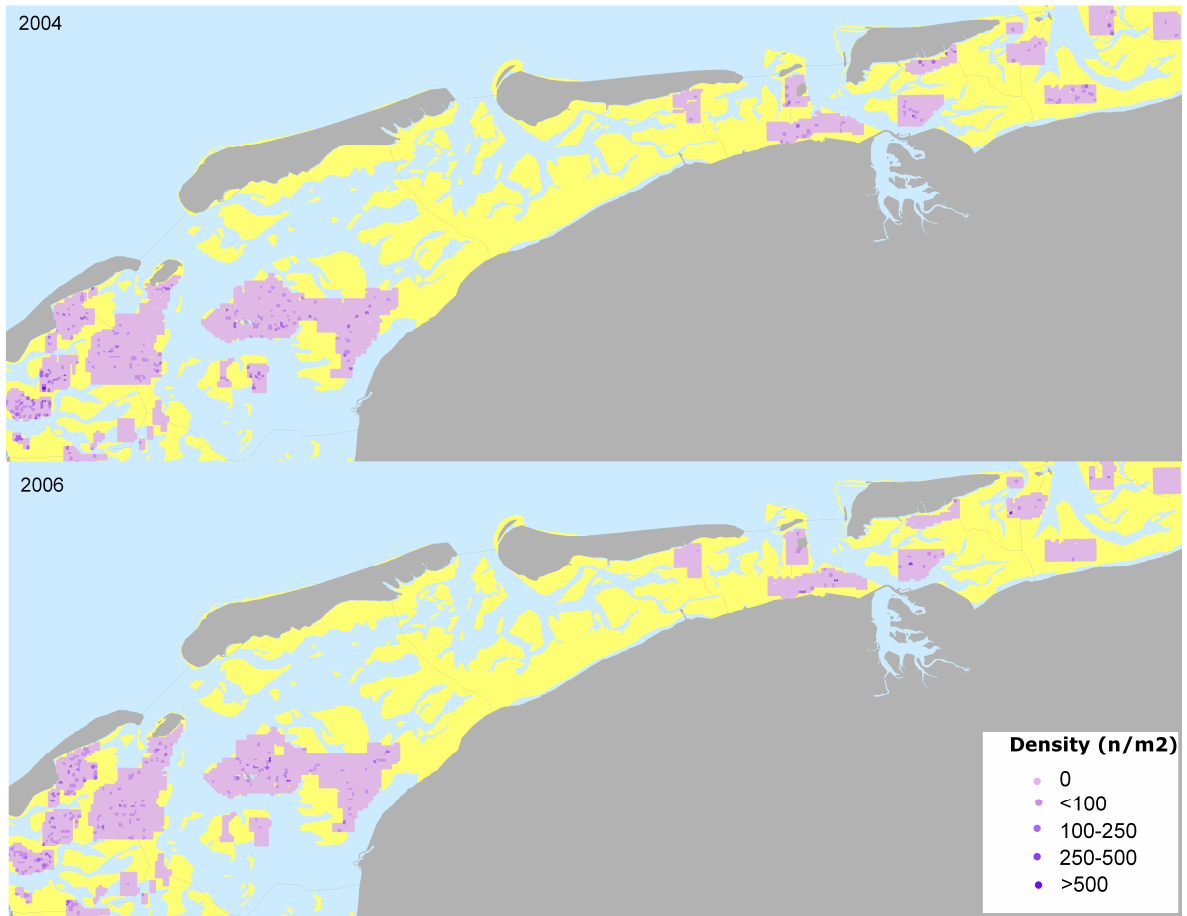
* presence (dark dots)/absence (light dots) is shown



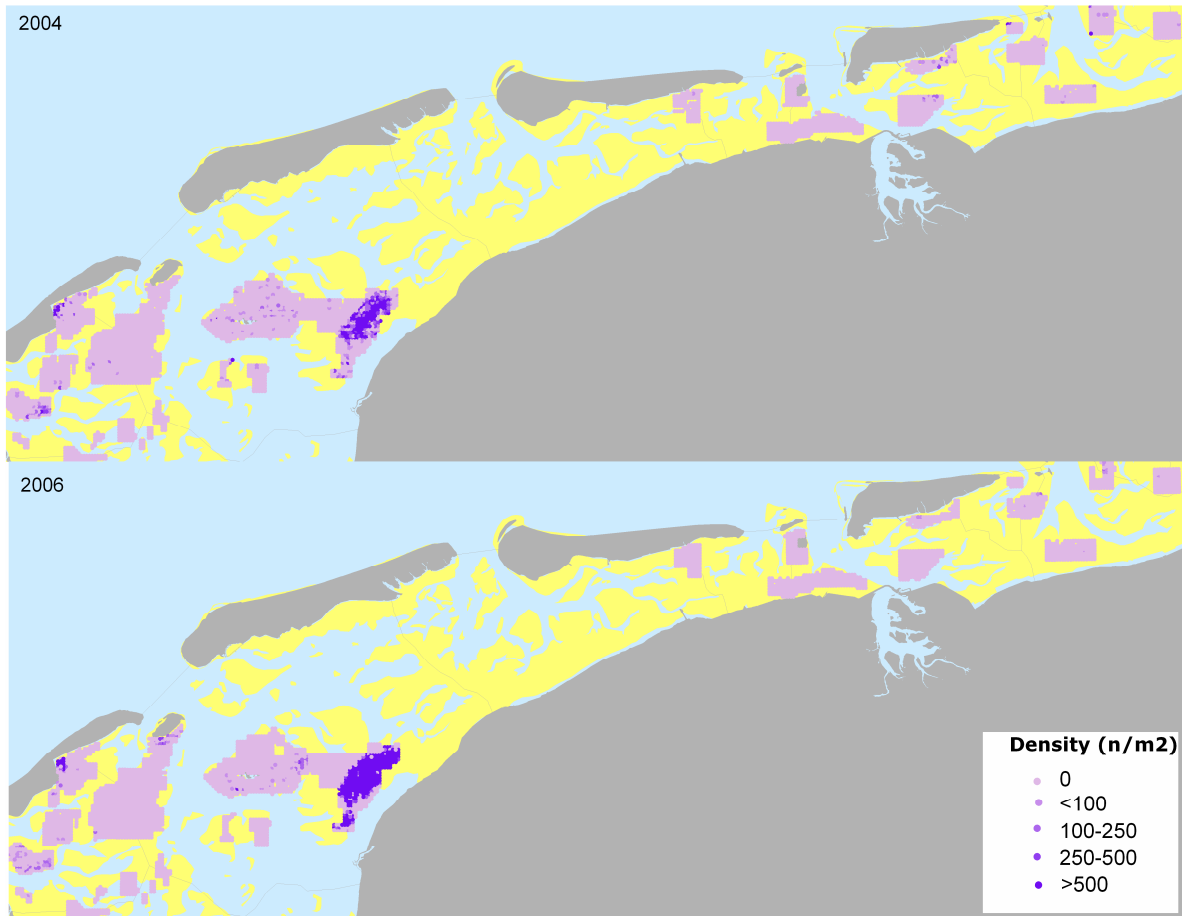
-*Crangon crangon*



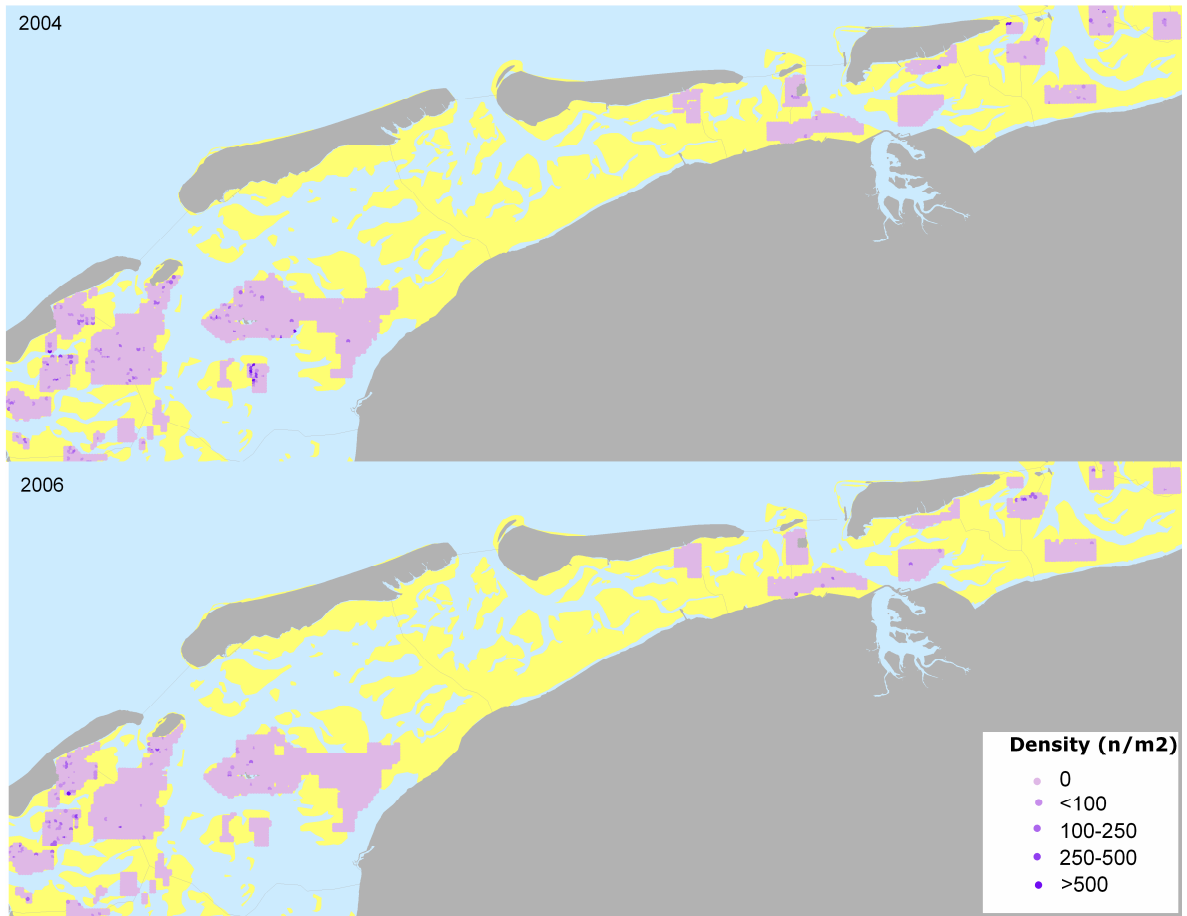
-*Carcinus maenas*



-Corophium volutator



-Gammarus locusta



-*Urothoe* sp.

