Korte termijn effecten van de mechanische kokkelvisserij in de westelijke Waddenzee op bodemfauna

Casper Kraan, Theunis Piersma, Anne Dekinga, Jaap van der Meer,
Jan A. van Gils, Bernard Spaans, Anita Koolhaas en Ciska Raaijmakers

Koninklijk Nederlands Instituut voor Onderzoek der Zee

Foto: J. de Vlas

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   - 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.

   2:
   -Consequenties van schelpdiervisserij voor een kenmerkende predator, de kanoet (voorlopige analyses door J. van Gils, T. Piersma en B. Spaans).

1. Samenvatting

Algemeen werd aangenomen dat mechanische kokkelvisserij plaats vindt op delen van het wad met een lage biodiversiteit, de zogenaamde kokkelbanken. Uit meerjarig onderzoek van het NIOZ op gemiddeld 2700 monsterpunten in de westelijke Waddenzee tussen 1998 en 2001 blijkt echter dat deze visserij juist plaatsvond op plekken met de hoogste dichtheid aan bodemleven en de grootste soortenrijkdom.

Het probleem van een ontbreken van een experimentele proefopzet in ons onderzoek naar visserij effecten hebben we ondervangen door een gepaarde analyse van veranderingen in de dichtheden aan bodemfauna op beviste en onbeviste delen van verder vergelijkbare gebieden uit te voeren. Een jaar na bevissing zijn de meeste schelpdiersoorten in dichtheid achteruitgegaan terwijl de meeste kleine wormen en kleine kreeftachtigen (schaaldiertjes) in dichtheid zijn toegenomen.

Onze aanwijzingen dat mechanische kokkelvisserij plaats vindt op de ecologisch rijkste wadplaten en wordt gevolgd door een zekere ‘verworming’ van het wad is consistent met de resultaten in de EVA2 rapportage en de internationale literatuur. We hebben geen aanwijzingen kunnen vinden dat na vissererij een herstel van de bodemfauna in de richting van de oorspronkelijke schelpdiergemeenschappen plaats vindt.

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2. Inleiding

Grootschalige vormen van mechanische zeebodemvisserij zoals trawlen en dreggen worden in toenemende mate gezien als de grootste bedreiging voor marine biota (zie Roberts 1997, 2002; Watling & Norse 1998; Coleman & Williams 2002; Dayton 2003; Rosenberg 2003). Hoewel negatieve effecten van zeebodem-beroerende vismethoden voor vele gebieden uitvoerig gedocumenteerd zijn (Dayton et al. 1995; Jennings & Kaiser 1998; Collie et al. 2000; Piersma et al. 2001), is er nog steeds behoefte aan gegevens over dergelijke visserij-effecten voor het Waddenzee-ecosysteem. Met het beschikbaar komen van de resultaten van het onderzoek voor de tweede fase van de evaluatie van het schelpdiervisserijbeleid (EVA2), komt er beter zicht op de ecologische gevolgen van de schelpdiervisserij voor de Nederlandse Waddenzee. Losstaand van dit EVA2 onderzoek wordt er door het Koninklijk NIOZ vanwege haar fundamenteel natuurwetenschappelijk onderzoeksprogramma langjarig en op grote schaal onderzoek gedaan aan de bodemfauna van de Waddenzee. Vanwege een NWO-PIONIER project aan de trofische interacties tussen wadvogels en bodemfauna, met name de relatie tussen Kanoetstrandlopers *Calidris canutus* en Nonnetjes *Macoma balthica*, hebben NIOZ-medewerkers vanaf 1994 iedere nazomer een grid bestaande uit ca. 2700 monstermunten (170 km^2) tussen de Vlakte van Kerken bij Texel en het Schellinger Wantij bemonsterd.

De resultaten van dit onderzoek worden momenteel bewerkt voor publicatie in de gerefereerde wetenschappelijke literatuur. Dit is een langdurig proces, terwijl momenteel door de overheid veel beleid wordt voorbereid. Om bij de besluitvorming over het toekomstig beheer van wadplaten over zo veel mogelijk relevante wetenschappelijke informatie te kunnen beschikken, hebben wij gemeend de tijdens een voordracht op het CEES-RUG symposium over de ecologische effecten van de schelpdiervisserij in de Waddenzee (Haren, 29 januari 2004) gepresenteerde onderzoeksresultaten alvast beschikbaar te maken in voorlopige ‘rapport’-vorm. Achtereenvolgens bespreken wij de vraag of mechanische kokkelvisserij alleen plaats vindt op soortenarme ‘kokkelbanken’, hoe de dichtheden van verschillende bodemdieren een jaar na visserij veranderd zijn, en of bodemdieren die relatief sterk aan bevissing bloot staan verschillend ‘reageren’. In de discussie gaan we kort in op mogelijke lange-termijn effecten van de mechanische schelpdiervisserij, en bespreken we, eveneens heel kort, of, en hoe, onze resultaten overeenkomen met de bevindingen van het EVA2 onderzoek. In de twee Appendices bevinden zich een eerder verschenen wetenschappelijke publicatie, alsmede een voortgangsverslag over de mogelijke effecten van schelpdiervisserij op de aantallen kanoeten in de westelijke Waddenzee

3. Materiaal en methoden

ONDERZOEKSGEBIED EN MATE VAN BEVISSING

Het onderzoeksgebied (Fig. 1) ligt in het westelijke deel van de Nederlandse Waddenzee. Het getijverschil is 1.5 m bij doodtij en 2 m bij springtij. Het droogvallende deel is 890 km^2 groot. Het sediment bestaat uit zand en modderig zand met een gemiddelde partikelgrootte van 140 tot 200 ìm (Piersma et al. 2001; L. Zwarts mond. med.). Een grid van monsterpunten dekt een aanzienlijk deel van dit studiegebied (170 km^2).

Kokkelvisserij is toegestaan vanaf half augustus, maar vond in de praktijk plaats tussen begin september en eind december (of eind januari-februari zoals in 2002-2003). De positie en vis-aktiviteit wordt op elk schip geregistreerd met een “black-box” (GPS-logger), verkregen van het Productschap Kokkels (Kamermans & Smaal 2002). Data uit deze “black-boxes” worden door het Productschap verwerkt en geanalyseerd. Dit resulteert in kaarten met gekleurde blokken van 0.1 minuten lengtegraad bij 0.5 minuten breedtegraad. Blokken worden alleen getoond als meer dan 2% van het oppervlak daadwerkelijk geraakt is door de zuigkor. In 1998, 2000 en 2001 werden respektievelijk 14.9%, 11.5% en 15.4% van onze monsterpunten bevist (Fig. 2). In 1999 vond de kokkelvisserij hoofdzakelijk plaats in het oostelijk deel van de Waddenzee. De totale fractie van de hele Waddenzee die tussen 1992 tot 2001 bevist werd bedroeg 19%. Voor ons studiegebied bedroeg dit van 1998 tot 2001 21.6%.

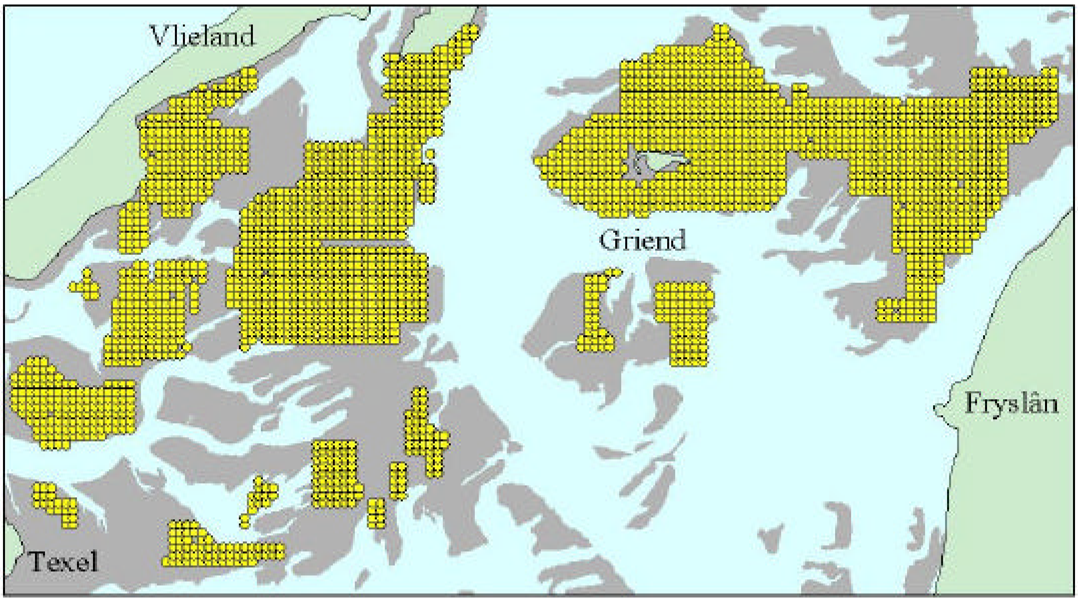

Fig. 1 : Het studiegebied, de Westelijke Waddenzee (wadplaten in grijs) met de bemonsteringsposities.

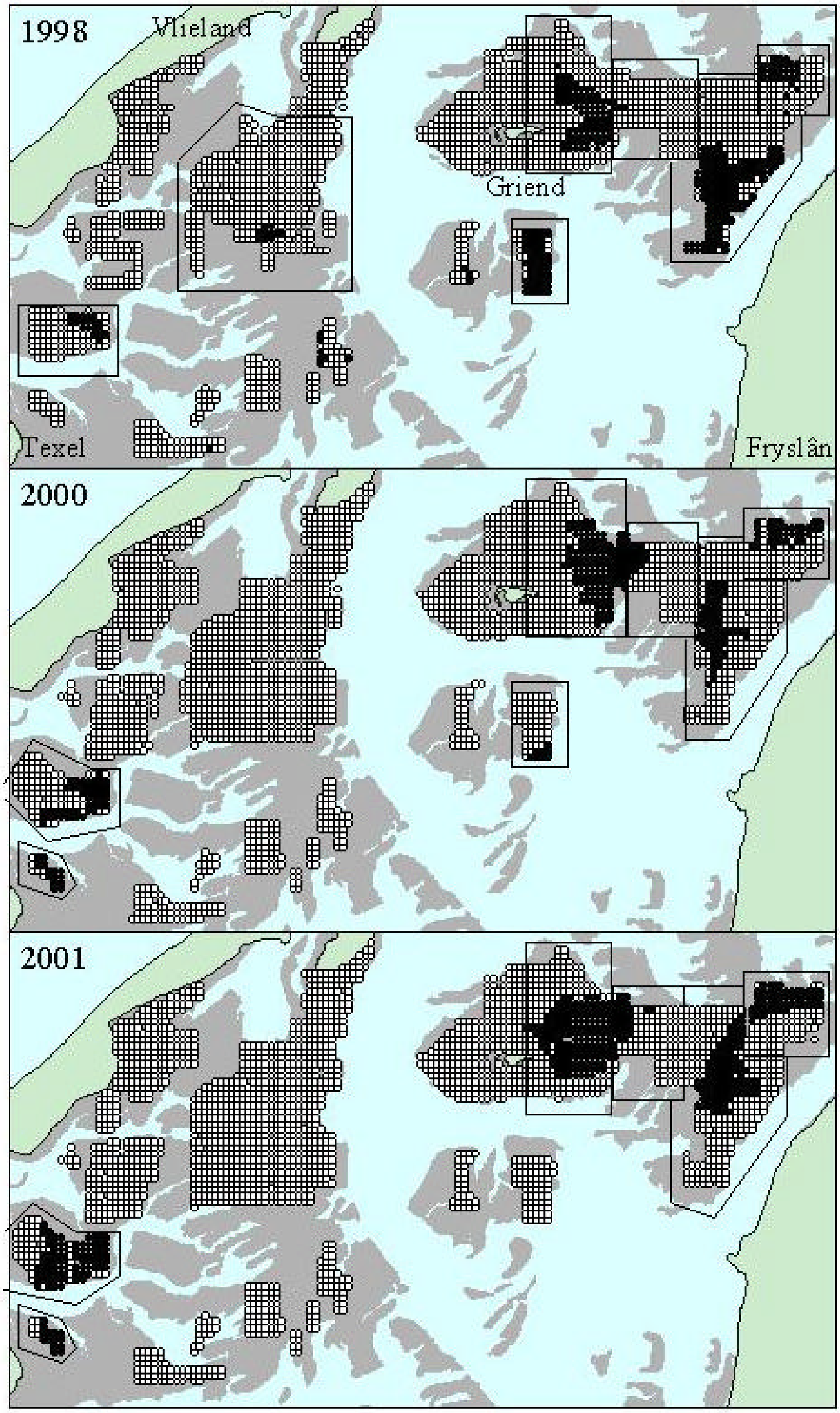

Fig. 2 : Beviste posities in ons onderzoeksgebied. Binnen de zwarte kaders worden de gebieden aangegeven waarbinnen zich (gepaard) de beviste en onbeviste delen bevinden waartussen de vergelijkingen worden gemaakt.

MONSTERMETHODEN

De ca. 2700 monsterpunten binnen het grid (Fig. 1) werden jaarlijks zowel lopend als vanuit een rubberboot (Fig. 3 en Fig. 4) bemonsterd tussen midden juli en begin september, altijd voordat de kokkelvisserij zijn aanvang nam. De monsterpunten liggen zowel in de noord-zuid als in de oost-west richting 250 meter uit elkaar. Posities werden gevonden m.b.v. GPS (Garmin 45 en 12, WGS 84). Op elk punt werd een sediment monster met een oppervlak van 1/56 m^2 en een diepte van 20-25 cm gestoken. De monsters werden ter plekke gezeefd door een 1 mm zeef, waarbij alle taxa werden geteld en op leeftijd gebracht. Alle kreeftachtigen en schelpdieren werden in een plastic zak bewaard in een –20 °C vriezer, zodat later de lengtes gemeten konden worden, en bij schelpdieren het vlees gescheiden kon worden van de schelp. As-vrij-droog-gewichten werden bepaald, na drogen van het vlees tot een konstant gewicht bij 60 °C, door verbranding bij 560 °C in een oven. Deze biomassa-gegevens worden hier niet gepresenteerd.

Al in 1998 bleek er een invasie te zijn van de exotische borstelworm *Marenzelleria wireni*, maar deze soort werd pas vanaf 2000 goed gekwantificeerd. Deze worm en andere zeldzame soorten zoals het Goudkammetje *Pectinaria koreni* werden daarom niet meegenomen in de analyse.

Fig. 3 : Lopend bemonsteren.

Fig. 4 : Bemonstering met rubberboot.

STATISTIEK

De statistische analyses zijn in twee groepen in te delen. Allereerst wordt de eenvoudige vraag gesteld of in een bepaald jaar de gebieden die bevist gingen worden verschillen (in termen van totale dichtheid aan bodemdieren, totaal aantal soorten en de kans op voorkomen van een afzonderlijke soort) van gebieden die onbevist bleven. Er is hier dus nog geen sprake van een (ongepland) veld-experiment waarin de vraag gesteld wordt of de behandeling ‘kokkelvisserij’ een effect heeft op de bodemfauna. Het is slechts een simpele vergelijking tussen twee typen gebieden (te bevissen en onbevist). Per gebied worden de gestoken individuele monsters beschouwd als een aselecte steekproef. Hoewel formeel niet helemaal correct (er zouden regelmatigheden op de ruimtelijke schaal van de afstand tussen gridpunten kunnen optreden), is dit een algemeen aanvaarde veronderstelling. De nulhypothese dat beide gebieden niet verschillen qua bodemfauna werd getoetst met behulp van een Student t-test (totale dichtheid aan bodemdieren, totaal aantal soorten anders dan de kokkel) of een C^2 toets, Yates gecorrigeerd (kans op voorkomen van een afzonderlijke soort).

Vervolgens werd wel de vraag gesteld of de behandeling “kokkelvisserij” een effect heeft op veranderingen in de bodemfauna. Hoewel er geen formeel experiment heeft plaatsgevonden (de behandelingen “kokkelvisserij” en “geen kokkelvisserij” werden niet aselect toegewezen aan een van te voren goed gedefinieerde verzameling plots) is zoveel als mogelijk geprobeerd achteraf een experimentele opzet na te bootsen. Hiertoe werden 8 min of meer aaneengesloten beviste gebieden gepaard met een nabijgelegen onbevist gebied, dat wat betreft van belang geachte abiotische factoren als hoogteligging, overstromingsduur en sedimentsamenstelling overeenkwam (Figuur 3). Per paar werd vervolgens de volgende log-ratio uitgerekend:

$$\log\left(\frac{N_{b0}}{N_{c0}}\times\frac{N_{c1}}{N_{b1}}\right),$$

waarbij *N* staat voor de dichtheid aan een bepaalde soort, de eerste index de behandeling aanduidt (*b* is bevist, c is controle) en de tweede index de periode (0 vóór bevissing, 1 na bevissing). Onder de nulhypothese dat de relatieve veranderingen tussen perioden 0 en 1 gelijk zijn voor beide behandelingen is de verwachting voor deze log-ratio gelijk aan 0. De test van de nulhypothese is uitgevoerd met een één-steekproef t-test, gebruik makend van de 20 (3 combinaties van jaren, maximaal 8 locaties) waargenomen log-ratio’s.

4. Resultaten

RELATIEVE RIJKDOM AAN BODEMFAUNA VAN BEVISTE GEBIEDEN

In de drie jaren waarin er kokkelvisserij plaatsvond in ons studiegebied (1998, 2000 en 2001) is de totale dichtheid aan bodemdieren significant hoger in te bevissen gebieden dan op posities waar niet gevist gaat worden ($P<0.01$; Fig. 5).

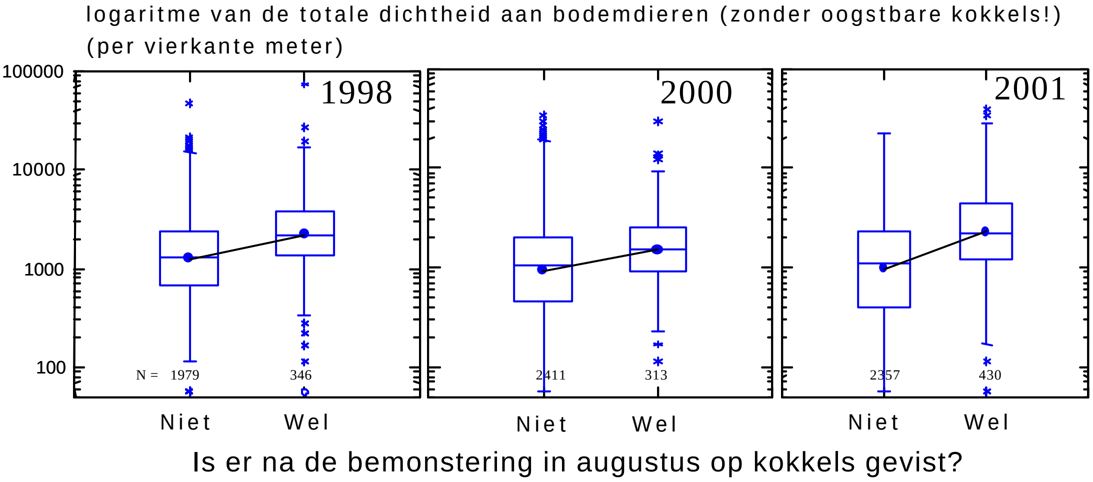

Fig. 5 : Totale dichtheid (minus “maatse” kokkels) aan benthos in wel of niet te bevissen posities. De oogstbare kokkels zijn niet in het totaal betrokken

Op de posities op de wadplaten die bevist gaan worden bevinden zich ook een significant groter aantal soorten vergeleken met de posities die niet bevist gaan worden (($P<0.01$; Fig. 6). We kunnen dus stellen dat kokkelvissers wadplaten bezoeken die relatief veel biomassa en veel soorten hebben, de meest biodiverse delen van het wad.

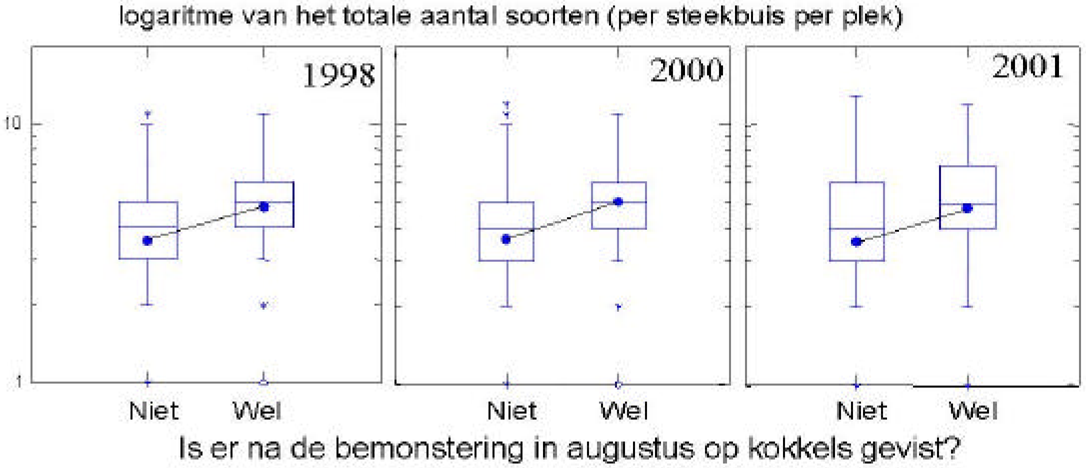

Fig. 6: Totaal aantal soorten in wel of niet te bevissen posities (n-waardes hetzelfde als fig. 5

Tabel 1: Relatieve dichtheden van bodemdieren op monsterpunten die later door kokkelvissers werden bezocht t.o.v. dichtheden op niet beviste posities. P-waardes waren altijd zeer klein ($p < 0.01$). * $p < 0.05$. De gestippelde lijn scheidt de soorten die relatief veel (met ratio's groter dan 1) dan wel relatief weinig (met ratio's kleiner dan 1) op te bevissen gebieden voorkwamen.

Soort	**Taxonomische groep**	**Gemiddelde ratio**	**1998**		**2000**		**2001**	
		Te bevissen / niet te bevissen	**Ratio**	**Test-statistiek**	**Ratio**	**Test-statistiek**	**Ratio**	**Test-statistiek**
Beviste soort & grootteklasse								
***Cerastoderma edule*, >20 mm**	**Bivalvia**	**4.28**	**4.26**	398.7	**3.76**	285.6	**4.83**	228
'Onbeviste' soorten								
Mytilus edulis	**Bivalvia**	**4.64**	**8.12**	12.19	**5.15**	6.96	**0.65**	4.1 *
Hediste diversicolor	**Polychaeta**	**3.03**	**2.73**	31.75	**4.30**	87.91	**2.05**	66.08
Heteromastis filiformis	**Polychaeta**	**2.91**	**3.17**	136.1	**2.56**	127.6	**3.01**	107.3
***Cerastoderma edule*, <20 mm**	**Bivalvia**	**2.82**	**3.26**	160.6	**1.79**	35.6	**3.40**	132.4
Mya arenaria	**Bivalvia**	**2.75**	**2.49**	80.5	**2.35**	73	**3.42**	110.3
Abra tenuis	**Bivalvia**	**2.73**	**0.79**	**0.23**	**1.02**	7.13	**6.39**	56.14
Macoma balthica	**Bivalvia**	**1.78**	**1.53**	123	**1.44**	87.9	**2.37**	48.7
Eteone longa	**Polychaeta**	**1.73**	**-**	-	**0.74**	**0.44**	**2.71**	56.65
Nephthys hombergii	**Polychaeta**	**1.71**	**2.87**	**0.07**	**2.01**	15.38	**0.25**	44.47
Carcinus maenas	**Decapoda**	**1.30**	**1.24**	**1.13**	**1.07**	**0.67**	**1.58**	10.84
Arenicola marina	**Polychaeta**	**1.08**	**0.36**	12.89	**1.62**	27.13	**1.27**	8.75
Ensis americanus	**Bivalvia**	**0.96**	**1.31**	**2.62**	**0.89**	**0.16**	**0.67**	**1.32**
Phyllodoce mucosa	**Polychaeta**	**0.80**	**0.20**	**3.43**	**0.55**	**1.03**	**1.66**	9.16
Corophium volutator	**Amphipoda**	**0.78**	**0.18**	**0.29**	**0.10**	**0.11**	**2.07**	85.45
Scoloplos armiger	**Polychaeta**	**0.76**	**0.58**	73.81	**0.72**	24.18	**0.99**	14.24
Gammarus locusta	**Amphipoda**	**0.71**	**1.41**	**0.03**	**0.49**	**2.4**	**0.24**	**2.36**
Lanice conchilega	**Polychaeta**	**0.59**	**0.76**	**1.6**	**0.54**	**2.31**	**0.64**	33.56
Tellina tenuis	**Bivalvia**	**0.23**	**-**	-	**0.30**	564.8	**0.15**	13.14
***Urothoë* sp.**	**Isopoda**	**0.17**	**0.08**	71.52	**0.22**	33.53	**0.21**	51.25

In plaats van het totale aantal bodemdieren per vierkante meter kunnen we natuurlijk ook voor iedere soort apart de dichtheden uitrekenen voor posities die later in het seizoen werden bevist en posities die niet werden bevist. In tabel 1 zijn deze gegevens samengevat. Uiteraard kwamen de oogstbare kokkels meer voor in te bevissen gebieden: de dichtheid was er gemiddeld 4,3 keer zo hoog als in gebieden die niet door kokkelvissers werden bezocht. Mosselen kwamen ook veel meer voor in te bevissen gebieden en hetzelfde geldt voor zeeduizendpoten *Hediste diversicolor*, draadwormen *Heteromastis filiformis*, kleine kokkels en de meeste andere schelpdieren. De organismen die relatief weinig voorkwamen op te bevissen posities zijn kleine wormen en kreeftachtigen.

IS ER EEN JAAR NA BEVISSING SPRAKE VAN VERANDERING?

Kokkelvisserij richt zich alleen op ‘maatse’ kokkels groter dan 20 mm. Als test voor de kracht van onze metingen zouden we verwachten dat de relatieve dichtheid van deze kokkels op beviste delen van onze proefvlakken een jaar na bevissing zouden zijn afgenomen ten opzichte van de niet beviste delen. Uit Fig. 7 blijkt dat dit inderdaad het geval is.

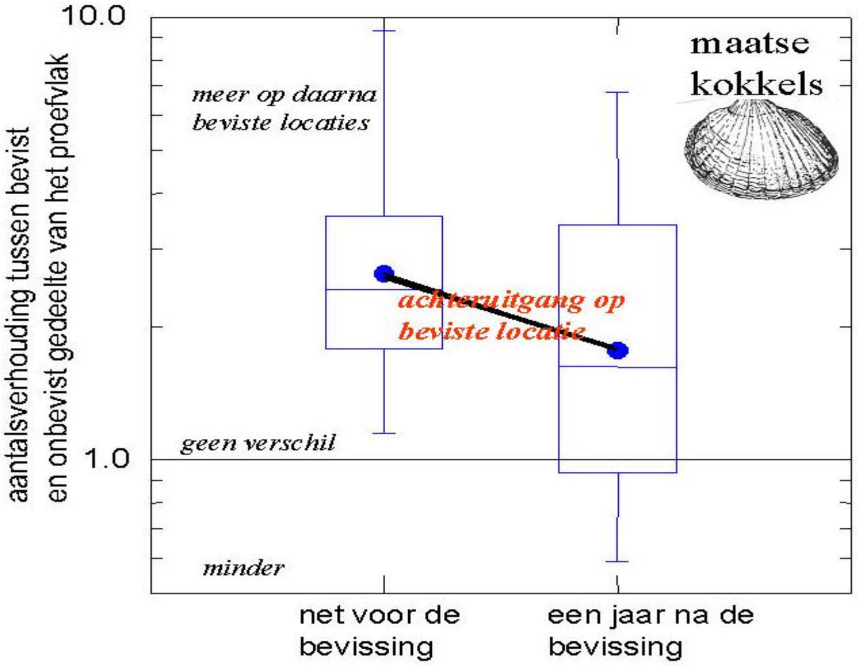

Fig. 7: Relatieve verandering van de dichtheden aan ‘maatse’ kokkels een jaar na bevissing. Dit verschil is significant ($P < 0.05$).

Uit een uitbreiding van de analyse naar een aantal andere karakteristieke soorten (Fig. 8), blijkt dat de meeste schelpdiersoorten een jaar na bevissing een achteruitgang in dichtheden laten zien, al zijn deze dichtheidsveranderingen alleen voor het nonnetje (bijna) statistisch significant. Een aantal kleine wormensoorten vertonen echter een toename in dichtheid (Fig. 8).

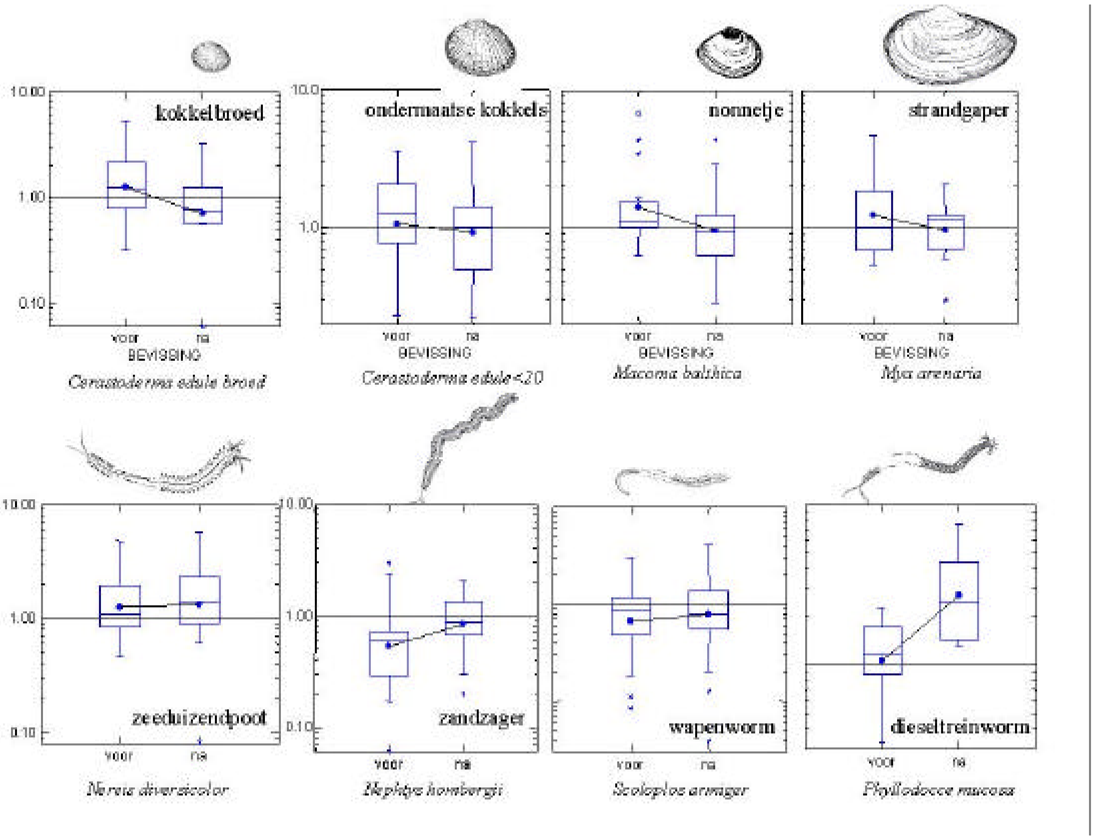

Fig. 8: Relatieve verandering een jaar na bevissing.
kokkelbroed: t = 1.317, df = 18, p = 0.2, ondermaatse kokkels: t = 1.363, df =11, P= 0.2, nonnetje: t = 2.025, df = 15, p = 0.061, strandgaper: t = 1.179, df = 12, p = 0.261, zeeduizendpoot: t = -0.204, df = 16, p = 0.841, zandzager: t = -0.362, df = 9, p = 0.726, wapenworm: t = -0.956, df = 18, p = 0.352, dieseltreinworm: t = -0.585, df = 5, p = 0.585

Hoewel vanwege de grote natuurlijke variatie de af- of toenamen per individuele soort niet significant zijn, blijkt dar wanneer we de schattingen voor de relatieve dichtheidsveranderingen van de verschillende bodemfaunasoorten koppelen aan het relatieve voorkomen van die soorten op de beviste posities (uit tabel 1) er een duidelijk en significant en negatief verband is tussen het relatieve voorkomen op te bevissen plaatsen en de dichtheidsverandering in het jaar na bevissing (Fig. 9). Juist de schelpdieren die samen met de oogstbare kokkels voorkomen op beviste plaatsen gaan, ondanks dat ze niet worden geoogst, relatief het meest achteruit in dichtheid. Dit betekent dat de zwaarst beviste soorten ook het kwetsbaarst zijn. Mosselen ontbreken in deze analyse omdat ze alleen in de te bevissen deelgebieden aanwezig waren en dus geen ratio’s berekend konden worden. Deze mosselen werden een jaar na bevissing nimmer terug gevonden.

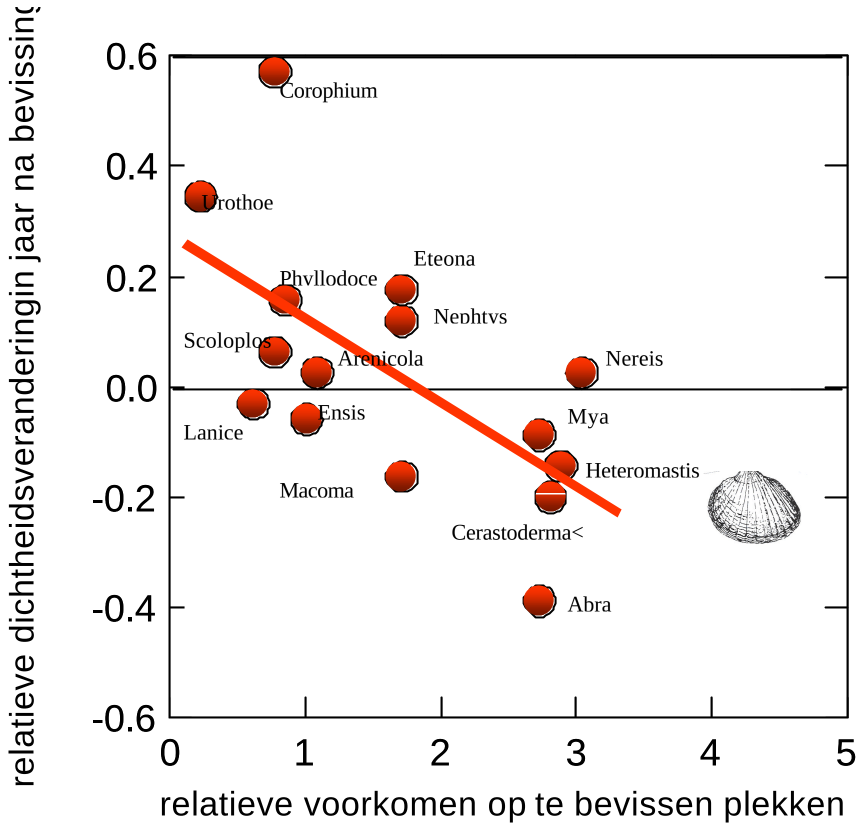

Fig. 9 : Relatieve dichtheidsverandering van verschillende soorten bodemdieren gekoppeld aan het voorkomen op te bevissen plekken (plaatje van kokkel is “maatse kokkel”, deze doet niet mee in de trendlijn). De trendlijn is significant negatief (Spearman rank correlation, $r = -0.368$, $p < 0.01$

5. Discussie

Het methodologische kernprobleem bij alle evaluatiestudies van de effecten van de mechanische kokkelvisserij, zowel wat betreft het onderzoek dat is uitgevoerd in het kader van EVA2 als het onze, is het ontbreken van experimenten waarbij op aanwijzing van onderzoekers op gerandomiseerde plekken al dan niet mechanisch werd gevist en waar de veranderingen in bodemfauna werden gevolgd. In de hier gepresenteerde analyses proberen we zo goed mogelijk aan dit probleem tegemoet te komen door de aantalsveranderingen van het benthos voorafgaand aan de bevissing op beviste delen van een gebied te vergelijken met de aantalsveranderingen op onbeviste delen van hetzelfde gebied. We probeerden de beviste en onbeviste delen van deze gebieden/proefvlakken zo goed mogelijk met elkaar te ‘matchen’ wat betreft locatie binnen de westelijke Waddenzee, hoogteligging en sedimentkarakteristieken.

Binnen de EVA2 rapportage hebben onderzoekers van het RIZA (2004) aannemelijk gemaakt dat de laatste decade de kokkelvisserij meer en meer plaats heeft gevonden op wadplaten met een hoogteligging waar volgens de literatuur de grootste bodemfaunabestanden werden gevonden. In de hier gepresenteerde analyse hebben we meer direct kunnen laten zien dat de mechanische kokkelvisserij inderdaad plaats vindt op wadplaten met relatief veel bodemfaunasoorten en hoge dichtheden. Deze voorkeur van kokkels en kokkelvissers voor de ecologisch rijkste wadplaten zou geen grote ecologische consequenties hebben als er een jaar na bevissing alleen een afname zou zijn in de stand van de beviste soort, de kokkels van meer dan 20 mm. Uit onze analyses blijkt echter dat juist de soorten die relatief veel op beviste plekken voorkomen een jaar na bevissing de grootste afnames laten zien. Het gaat hier voornamelijk om schelpdiersoorten anders dan ‘maatse’ kokkels (inclusief het nieuwgevestigde kokkelbroed). Een aantal kleine wormensoorten en kleine crustaceën nemen tijdens het jaar na bevissing relatief in aantal toe. Dergelijke verliezen aan schelpdieren en toenamen van kleine wormen worden ook gerapporteerd in de EVA2 deelstudie van Leopold et al. (2004). We hebben hier te maken met de door Reise et al. in 1982 onderkende ‘verworming’. Een geringere vestiging van kokkelbroed na bevissing wordt voor de Waddenzee ook gerapporteerd door Piersma et al. (2001) en in de EVA2 deelrapportage van Kamermans et al. (2004). Dit gegeven maakt duidelijk dat juist bodemverstoring, zelfs voor de doelsoort, het kernprobleem bij deze vorm van visserij is.

Hoewel we nu in samenhang met de EVA2 rapportages de korte-termijn effecten van mechanische kokkelvisserij op de dichtheden aan bodemfauna in kaart hebben gebracht, is het natuurlijk van belang om ook inzicht te hebben in de lange-termijn effecten. Is er na een toename van wormen en kleine crustaceën weer een toename van de schelpdieren die relatief veel op de beviste plekken voorkwamen? Uit de EVA2 rapportage van RIZA (2004) bleek dat de in kaart gebrachte kokkelbanken in de periode 1990-2002 vrijwel allemaal buiten de gebieden lagen waar kokkels voorkwamen in de periode 1960-1990. Dit suggereert dat 'herstel' van broedval van kokkels lange tijd uitblijft. Piersma et al. (2001) vonden pas na 8 jaar een toename in de relatieve broedval op beviste plekken ten opzichte van niet beviste plekken verspreid over de hele Nederlandse Waddenzee.

Tenslotte nog een opmerking over de jonge mosselen die wij steeds op de te bevissen plekken aantroffen. Aangezien we een jaar na bevissing nimmer mosselen konden vinden waar we ze het jaar daarvoor wel vonden, moeten we constateren dat het mechanisch kokkelvissen de vestiging van nieuwe mosselbanken in de westelijke Waddenzee ernstig heeft belemmerd.

6. Conclusies

1. **Tussen 1998 en 2001 selecteerden kokkelvissers in de westelijke Waddenzee de wadplaten met de grootste dichtheid aan kokkels, maar ook de grootste dichtheid aan andere bodemfaunasoorten. Bovendien is op de beviste plekken de diversiteit aan bodemfauna significant groter dan de biodiversiteit op niet beviste plekken.**

2. **Er bestaat een duidelijke trend dat een jaar na bevissing schelpdieren relatief achteruit gaan in dichtheid, terwijl kleine wormen en kleine schaaldiertjes relatief toenemen. Dit is de door Reise reeds in 1982 besproken 'verworming' van het wad.**

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9. Appendices

1:
- 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.

2:
-Consequenties van schelpdiervisserij voor een kenmerkende predator, de kanoet (voorlopige analyses door J. van Gils, T. Piersma en B. Spaans).

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Long-term indirect effects of mechanical cockle-dredging on intertidal bivalve stocks in the Wadden Sea

THEUNIS PIERSMA*†, ANITA KOOLHAAS*, ANNE DEKINGA*,
JAN J. BEUKEMA*, ROB DEKKER* and KAREL ESSINK‡

**Netherlands Institute for Sea Research (NIOZ), PO Box 59 1790 AB Den Burg, Texel, the Netherlands;*
†Centre for Ecological and Evolutionary Studies (CEES), University of Groningen, PO Box 14, 9750 AA Haren, the Netherlands; and ‡Rijkswaterstaat, National Institute for Coastal and Marine Management (RIKZ), PO Box 207, 9750 AE Haren, the Netherlands

Summary

1. There is world-wide concern about the effects of bottom-dredging on benthic communities in soft sediments. In autumn 1988, almost a third of the 50-km^2 intertidal system around the island of Griend in the western Dutch Wadden Sea was suction-dredged for edible cockles *Cerastoderma edule* and this study assessed subsequent effects. An adjacent area not directly touched by this fishery and an area from which the mussel *Mytilus edulis* beds were removed, served as reference areas.

2. Sediment characteristics, together with the total stock size and settlement densities of *Cerastoderma*, Baltic tellin *Macoma balthica* and soft-shelled clam *Mya arenaria*, were documented during 11 successive autumns before (August–September 1988) and after (August–September 1989–98) the suction-dredging event in fished and unfished areas. Four other areas in the Dutch Wadden Sea, where changes in densities of juvenile bivalves from 1992 to 1998 were measured, served as additional reference locations.

3. Between 1988 and 1994, median sediment grain size increased while silt was lost from sediments near Griend that were dredged for cockles. The initial sediment characteristics were re-attained by 1996.

4. After the removal of all *Mytilus* and most *Cerastoderma*, the abundance of *Macoma* declined for 8 years. From 1989 to 1998, stocks of *Cerastoderma*, *Macoma* and *Mytilus* did not recover to the 1988 levels, with the loss of *Cerastoderma* and *Macoma* being most pronounced in the area dredged for cockles. Declines of bivalve stocks were caused by particularly low rates of settlement in fished areas until 1996, i.e. 8 years after the dredging.

5. A comparison of settlement in the short (1992–94) and medium term (1996–98) after cockle-dredging in several fished and unfished areas spread over the entire Dutch Wadden Sea, showed a significant negative effect of dredging on subsequent settlement of *Cerastoderma*. *Macoma* also declined, but not significantly.

6. We conclude that suction-dredging of *Cerastoderma* had long-lasting negative effects on recruitment of bivalves, particularly the target species, in sandy parts of the Wadden Sea basin. Initially, sediment reworking by suction-dredging (especially during autumn storms) probably caused losses of fine silts. Negative feedback processes appeared to follow that prevented the accumulation of fine-grained sediments conducive to bivalve settlement.

Key-words: BACI, benthic communities, conservation, fishery, soft sediments, spatfall.

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Correspondence: Theunis Piersma, Netherlands Institute for Sea Research (NIOZ), PO Box 59, 1790 AB Den Burg, Texel, the Netherlands (fax 31 222 319674; e-mail theunis@nioz nl).

Introduction

There is widespread concern that many forms of bottom-fisheries damage the epi- and infaunal communities of intertidal and subtidal sediments (Dayton *et al.* 1995; Brown & Wilson 1997; Fogarty & Murawski 1998; Jennings & Kaiser 1998; Hall 1999; Kaiser *et al.* 2000). Bottom-fisheries not only remove the target species (Robinson & Richardson 1998) but also impact on associated flora and fauna (de Vlas 1987b; Bergman & Hup 1992; Brylinsky, Gibson & Gordon 1994; Beukema 1995; Ferns, Rostron & Siman 2000). In addition, trawling, dredging and digging usually remove biogenic structures on the surface that are not easily replaced, such as mussel beds or banks of tube-living polychaetes, even when such elements are not the target of the fisheries (Reise 1982; Roberts 1997; Service & Magorrian 1997; Hall 1999). Depending on the scale of the fisheries and the local hydrological conditions, these effects on non-target organisms or structures, often responsible for key benthic processes, may also lead to changes in sediment characteristics (Shand 1987; Churchill 1989; Hall 1994; Snelgrove & Butman 1994; Oost 1995; Newell, Seiderer & Hitchcock 1998). Recovery may be slow (Collie *et al.* 2000), with benthic communities substantially changed (Roberts 1997; Hall 1999).

Of the four common bivalves in the intertidal area of the Dutch Wadden Sea [blue mussel *Mytilis edulis* Linnaeus, edible cockle *Cerastoderma edule* (Linnaeus), Baltic tellin *Macoma balthica* (Linnaeus) and soft-shell clam *Mya arenaria* (Linnaeus)], the mussels and cockles are commercially exploited. These species overlap in their algal food and time of feeding (Kamermans 1994) and grow more slowly where conspecifics or other bivalves are at high density (Kristensen 1957; Jensen 1992). Given that suspension- and deposit-feeding bivalves can be regarded as food-competitors (Kamermans *et al.* 1992; Beukema & Cadée 1997), the commercial removal of the stocks of one or two of these species could relax competition for food. This might result in enhanced fecundity and greater stocks of the non-target species.

We compared changes in sediment characteristics and abundance of three bivalve species at different intertidal flats in the Dutch Wadden Sea. Most of the data were collected during a long-term study to determine the year-to-year variations in food supply at a stopover and a wintering area of a long-distance migrating shorebird, the red knot *Calidris canutus* (Linnaeus) (Piersma *et al.* 1993, 1995). Over 11 consecutive seasons, in late July–September 1988–98, the distribution and abundance of molluscs on the intertidal areas around Griend were mapped in relation to sediment characteristics. Early in the study, in late September 1988, the large stocks of cockles in the northern part of the study area were mechanically harvested. Over the subsequent two winter seasons, two complexes of mussel beds in the western parts were also removed for commercial reasons. By analysing changes in sediment characteristics and bivalve stocks in areas that were either exposed or not exposed to shellfishing activities, we evaluated the null hypothesis that mechanical shellfishing activities leave intertidal communities intact and that they do not decrease subsequent settlement of shellfish, especially the target species. If this could be confirmed, one might consider such a fishery 'sustainable' (Lélé & Norgaard 1996). Unlike most studies of fishing impact (Collie *et al.* 2000), we documented long-term patterns of recovery rather than quantifying direct impacts.

Materials and Methods

MAIN STUDY SITE AND FISHERY ACTIVITIES

Griend is a small uninhabited island in the western part of the Dutch Wadden Sea (53°14′N, 05°15′E; Fig. 1). The intertidal flats covered by our benthic surveys amount to about 50 km^2. They are exposed for 2–7 h per low-water period. Heights, and corresponding emersion times, are greatest to the east and north-east of the island. West and north-west, and south and south-west, of the island of Griend there were large mussel beds that must have been present at least since the early 1960s (Veen & van de Kam 1988). Also in the south-east, again at the boundary of the intertidal flat and the main tidal channel south of Griend, mussel banks occurred historically. From 1941, the western edge of the island of Griend has repeatedly been reshaped by various types of breakers and dikes. The last reconstructions were carried out during the summers of 1985 and 1988. A 2·5-km long sand dike was built west and north of the old circular island (Janssen *et al.* 1994). The central saltmarsh and creek were undisturbed.

During 26 and 27 September 1988 (full moon spring tides, westerly gale of 7–8 Beaufort, causing high water levels), six suction-dredging cockle-fishing ships worked over the intertidal flats north of the island. No cockle-ships were seen fishing on 28 September, but during the following weeks, in situations with lower tides, cockle-fishing ships were observed north-east of the island. These ships are about 10 m wide and 40 m long, with a draft of 45–50 cm. They can fish with speeds of up to 8 km h^{-1} (Dijkema 1997), towing either one or two suction-dredges with a width from 50 cm to 115 cm. The upper layer of the sediment is first loosened by strong spouts in front of the suction-dredge. The loose upper layer is then sliced off at 2–3 cm according to the fishing companies. As this would not enable buried cockles with a diameter of 2–3 cm to be picked up, we regard 5 cm as a better estimate. The sliced material that does not 'escape' through a 15-mm bar mesh cage is sucked up and washed onboard over a sieve with a 15-mm mesh. The mussel beds near Griend were either dredged away or carried by hand.

By early October 1988 the sediments had been intensively reworked over a large area, with intact

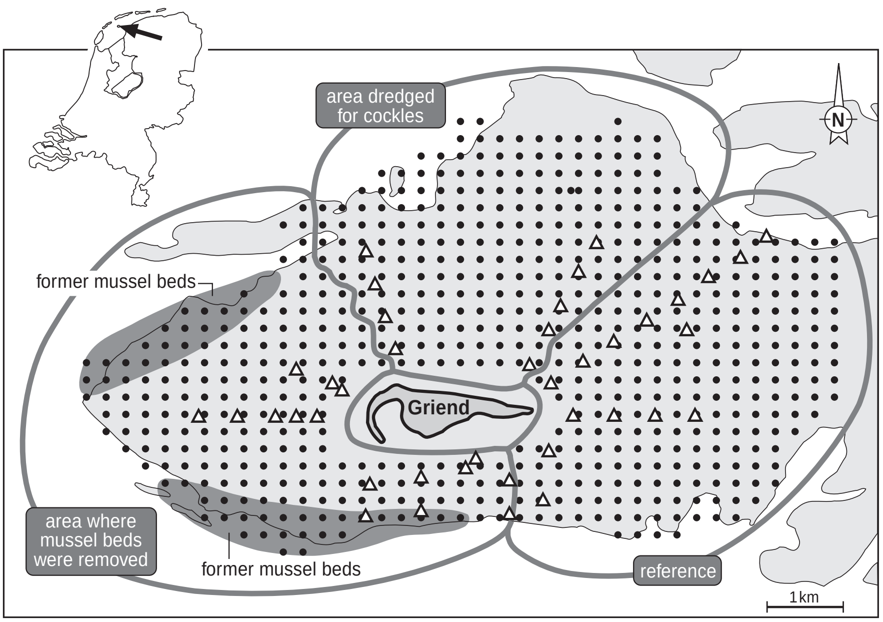

Fig. 1. Map of the study area in the western part of the Dutch Wadden Sea (see inset, map of the Netherlands) and the experimental 'design' to study fishery effects. The approximate extent of the intertidal areas north and north-east of the island of Griend that were mechanically fished for cockles in the 1988 season (from 26 September 1988 onwards) and the location of the beds of mussels *Mytilus edulis* that were removed over the winters 1989–91 are shown, as is the large unfished reference area in the east. The extent of the two benthos sampling strategies are shown by the triangles (indicating sampling stations along transects used in 1988–92) and by the dots (indicating the 250-m interval grid mapping method used from 1993 onwards), respectively. Sediment samples were collected at most of the locations indicated by triangles in 1988, 1992 and 1994, and at a larger number of sites thereafter (Piersma & Koolhaas 1997).

Macoma shells and shell fragments lying on the sediment surface. We estimated the extent of the cockle fishery based on these surface signs, further checked by deep cores to establish that sediment reworking took place (Fig. 1). During the following 9 years, cockle-fishing ships were not observed in the study area, but limited mechanical shellfishing took place along the eastern edge of the study area late in 1995 (J.D. Holstein, personal communication).

The mussel beds near Griend remained intact in late September 1988. During the following 2 years these beds disappeared but the precise timing is unknown. No mussel banks remained when we started fieldwork in late July 1991. As elsewhere in the Wadden Sea (Beukema 1993; Beukema & Cadée 1996; Beukema, Cadée & Dekker 1998; Smit *et al*. 1998), the beds had been fished out, mechanically or manually, when mussel stocks were exceptionally low after a succession of years with little recruitment. We did not see mussels near Griend until August 1994 when, on intertidal flats along the main channel south of the island, two 2-ha patches of summer-settled mussel spat were found. These small beds were affected by mechanical fisheries in the course of the autumn and had disappeared by the time we returned to Griend in early August 1995.

The intertidal area around Griend was divided into three areas on the basis of presence or absence and type of fishing activity. The western area had mussel beds that disappeared in 1989–91, the northern area was almost completely dredged for cockles in 1988 and the eastern area remained largely untouched and served as a reference (Fig. 1). Although the experimental and control sites were not chosen randomly, this study reflects the spatial scale of real fishing events (Hall 1999).

SEDIMENT ANALYSES

In early September 1988, i.e. before the cockle fishery took place, we took core samples for benthos and sediment at sites at 500-m intervals along transects around Griend (triangles in Fig. 1). In 1992 the same samples were taken, but in later years the survey was considerably extended (Piersma & Koolhaas 1997). At each location a sediment sample was taken with a 5-cm diameter core to a depth of 7–8 cm, and stored in a closed plastic bag at room temperature for 1–4 weeks, before freezing at –30 °C. Then the entire sample was first washed in fresh water, shaking the water–sediment mix, and sieved over a 50-µm mesh. The residue that passed through the 50-µm mesh was collected and weighed. After drying a part of the remainder of the sample to constant mass at 60 °C, the sediments were sieved over meshes of 63, 125, 250, 315, 500 and 1000 µm and weighed to the nearest mg. The fractions smaller than 50 µm and larger than 1000 µm (= 1 mm) were not used to calculate median grain size. The smallest fraction was analysed separately. Their removal hardly affected median grain size values. Median grain size was computed following Krumbein & Sloss (1963).

ABUNDANCE OF BIVALVES

All bivalve data were collected from late July to late September, and mostly in August. Earlier, we found no seasonal effects on abundance or biomass of bivalves over the period July–October (Piersma *et al.* 1993). Up to 1992 benthic abundances were monitored along a series of transects radiating from the island, starting 100 m offshore from the high-tide mark (triangles in Fig. 1). Along the transects cores were taken and sieved at 500-m intervals. In 1993 this system was replaced by a mapping method using a fixed grid at 250-m intervals, with sampling points at each grid intersection (dots in Fig. 1).

The bivalves in the western and northern areas at Griend were mapped in August–September 1988, just before the cockle-fishing in late September. After the cockle-dredging, due to the reworking of the sediments that led to the presence of large quantities of dead shells in the upper layer, sampling became difficult and sometimes impossible. Even in 1989 sieving and sorting the sediments at the fished transects was so difficult that we decided not to sample them that year.

Sampling locations along transects were found by pacing out the distance with a calibrated step-length and a hand-counter, using a compass to walk in the appropriate direction. Locations away from the transects were found by cross-reading the compass bearings on conspicuous landmarks. From 1993 the predetermined positions were found with a Philips AP-navigator (Philips, Eindhoven, the Netherlands), using the Europe-wide DECCA radio-beacon system (defunct since the mid-1990s), or using a hand-held Global Positioning System (GPS) (Garmin 45; Garmin Corporation, Lenexa, KS). To sample the bivalves, at each sampling station we took 20 sediment cores of 1/56 m^2 down to a depth of 20 cm and sieved each of them over a 1-mm mesh. The residue of each core was put into a separate identifiable plastic bag and stored frozen until laboratory treatment. In the more recent grid-mapping approach only one sediment core of 1/56 m^2 was taken at each point, but sampling depth did not change.

To compare the results of the benthic transects and the grid mapping, both methods were applied simultaneously in August 1993 (Piersma & Koolhaas 1997). For both *Cerastoderma* and *Macoma*, small individuals were better represented in the transect than the grid because samples on transects were numerically biased toward high flats where most settlement occurs. For *Macoma* the grid method yielded lower abundance and higher biomass values than transects. These contrasting effects were small and we refrained from adjusting the abundance measures for *Macoma*. As we sampled no deeper than 20 cm, only data for *Mya* smaller than 40 mm are presented, larger ones of this species living deeper in the sediment (Zwarts & Wanink 1984).

In the laboratory, the molluscs in each bag were counted and their maximum length measured to the nearest millimetre. In the case of bivalves, the flesh was removed from the shell and dried to constant mass at 55–60 °C and incinerated at 550 °C for 2 h to obtain species-, length-, site- and year-specific values of ash-free dry mass (AFDM) (Piersma *et al.* 1993). These data served as the basis for all abundance and biomass values presented here.

SETTLEMENT OF BIVALVE SPAT AT SITES OTHER THAN GRIEND

The settlement of small bivalves after their pelagic larval phase (spatfall) is widely studied (Beukema, de Bruin & Jansen 1978; Beukema 1989, 1992; Beukema *et al.* 1993). To evaluate the effect of cockle-dredging on juvenile bivalves we assembled data on post-settlement densities of *Cerastoderma* and *Macoma* for five different sites from much of the Dutch Wadden Sea. None of the sites was dredged for cockles in the 1990s up to 1998 (see Fig. 8a). Two of the sites (Griend and Balgzand) contained an area that had been affected by cockle-dredging in the late 1980s in addition to a non-impacted reference area. Another site (Hengst) had not experienced cockle-dredging in the late 1980s, and two sites (Piet Scheve Plaat and Groningen) were dredged for cockles in the late 1980s. Although the non-impacted reference sites were all in the west of the Dutch Wadden Sea and the treatment sites more spread out (cf. Fig. 8a), we would expect this to affect the analyses only if they showed congruent patterns in the degree of shelter from storms and wave action. In both the treatment and the reference group, two types of sites with respect to shelter were included. Some sites (Hengst and Griend) had little shelter from nearby dikes, islands or extensive intertidal areas and were thus exposed to winter storms and wave action, and some (Balgzand, Piet Scheve Plaat and Groningen) were relatively sheltered.

Bivalve abundances at the sites Piet Scheve Plaat and Groningen were obtained from a Rijkswaterstaat monitoring programme. For Groningen, data were used from location 54–1 (Essink 1978). At this location, each year in August–September 20 cores of 1/131 m^2 each were taken to a depth of 30 cm. At Piet Scheve Plaat core samples were taken along three transects. At each 760-m long transect 20 equidistant cores of 1/116 m^2 were taken (Dekker 1997). Samples were sieved in the field over a 1-mm mesh. The bivalves in the fraction that remained on the sieve were counted and measured soon afterwards in the laboratory. Although cockles were fished in the vicinity of the sampling location Groningen (between 1 and 15 September 1993, and in late August 1995), the site itself was not touched. In 1996–98 no cockles were fished at all in the vicinity of the Piet Scheve Plaat and Groningen (J.D. Holstein, personal communication).

At Hengst, sediment cores of 1/56 m^2 were taken at a variable number of locations evenly spaced according to a 250-m grid. Cores had a depth of 20 cm and were sieved over a 1-mm mesh. Samples were processed as described for Griend. The number of sampling stations used varied from 21 in 1992 to 100 in 1998.

At Balgzand, annually in August starting from 1973, 20-cm deep samples were taken at 15 stations (12 transects of 1 km length and three squares of 900 m^2) covering a total of about 0·45 m^2 per station (for details see Beukema 1974). Three of these stations were mechanically fished in autumn 1988 or in 1990, and served as a comparison for the 10 stations that were not subjected to shellfishing activities. Two low-lying stations where bivalves only rarely settled were left out of the comparison. Data from the entire Balgzand area were also used to assess whether standing stocks of *Cerastoderma* and *Macoma* were uniquely high in 1988, just before the fishery.

EXPERIMENTAL DESIGN AND STATISTICS

To test for the effects on sediment characteristics (median grain size and silt content) of area and fishing treatment, time (year, or combination of years) and the interactions between area and time, simple analyses of variance were applied, using individual sediment samples as replicates. The eastern segment of the flats served as the control for the two areas that were affected by either cockle-dredging or the removal of two mussel bed complexes (Fig. 1).

The geographical and temporal spread of the fishing effort around Griend allowed us to analyse statistically the effects on bivalve abundance as a single large-scale and long-term experiment according to a 'before/after and control/impact' (BACI) design (Schmitt & Osenberg 1996). More specifically, the BACI-variant of paired series (BACIPS) was used (Stewart-Oaten, Murdoch & Parker 1986; Schmitt & Osenberg 1996). As the experiment was unplanned, the abundance measures of bivalves in the 'before' situation were determined only once (in 1988). As outlined below, during 1990–95 the sediments of the cockle-dredged area were relatively coarse but fairly stable before returning (in 1996–98) to a state that resembled the initial situation. We thus had six annual average values from the period 1990–95 as replicates for the 'after' situation to compare with the single value from 'before'. There was no evidence of temporal autocorrelation in the measures of abundance during this period. As expected, only one of the 27 correlation coefficients was significantly different from zero under $P < 0·05$.

To ensure normality of the data on bivalve abundance, average numerical and biomass densities were log-transformed. We then calculated the differences in the log-transformed abundance measures for *Cerastoderma*, *Macoma* and *Mya* between reference and experimental areas. These differences equalled the log-transformed ratios of the untransformed abundance measures. Based on the six 'after' observations for the period 1990–95, the 95% prediction intervals for the log-transformed ratios were calculated based on the *t*-test (Sokal & Rohlf 1981). To test whether H_0: $\mu_1 = \mu_2$ can be falsified, it has to be determined whether the single 'before' observation falls in this predicted interval. If it does, there has been no significant change with respect to the difference between areas (i.e. H_0 is not rejected; there is no effect of treatment). If the single 'before' observation falls outside the predicted interval, it can be concluded that the specific treatment does have a significant effect on the abundance measure (with $P < 0·05$). The most insightful comparison was between the reference area and the area dredged for cockles, but we also compared the differences between the reference area and the area from where mussel beds were removed, as well as the differences between the two fished areas.

Although the design ensured that temporal fluctuations at the reference and experimental areas did not confound the detection of the fishery impact, any location-specific temporal difference would be interpreted as an impact (Underwood 1992, 1996). With regard to patterns in settlement of bivalves we extended the analysis 'beyond BACI' by also using data from locations other than Griend. It turned out that in 1995 one area (Hengst) was not well covered. We therefore averaged the spatfall densities for an early period (1992–94) and a late period (1996–98) and calculated the ratio of the two for each (sub) location. Log-transformed ratios are normally distributed and differences between fished and unfished areas were tested for significance by Student's *t*-tests. All statistical analyses were carried out in SYSTAT.

Results

SEDIMENT CHARACTERISTICS AROUND GRIEND

The first comprehensive assessment of sedimentary characteristics after the cockle-dredging in 1988 took place in 1992 (Fig. 2). Over all three areas, average median grain size increased from 166·2 μm (SD = 14·0, $n = 16$) to 174·2 μm (SD = 14·1, $n = 30$), with a further increase to 179·1 μm (SD = 16·3, $n = 28$) in 1994. A two-way analysis of variance showed that the difference between 1988 and 1992 was significant ($F_{1,40} = 6·614$, $P = 0·014$). There was also an important effect of area ($F_{2,40} = 12·071$, $P < 0·0001$) but no significant interaction between the two factors ($F_{2,40} = 1·482$, $P = 0·239$). This indicated that, although there were differences in median grain sizes between areas, there were no differences among areas in the changes in median grain size between 1988 and 1992.

Between 1994 and 1998 there was a decline in median grain size in the area previously dredged for cockles (Fig. 2), and values seemed to return to the prefisheries level. A two-way analysis of variance indeed showed a significant difference between 1994 and 1998 ($F_{1,39} = 7·010$, $P = 0·012$) and an effect of area ($F_{2,39} = 7·138$, $P = 0·002$), but again no significant interaction between the two factors ($F_{2,39} = 1·784$, $P = 0·181$). A two-way

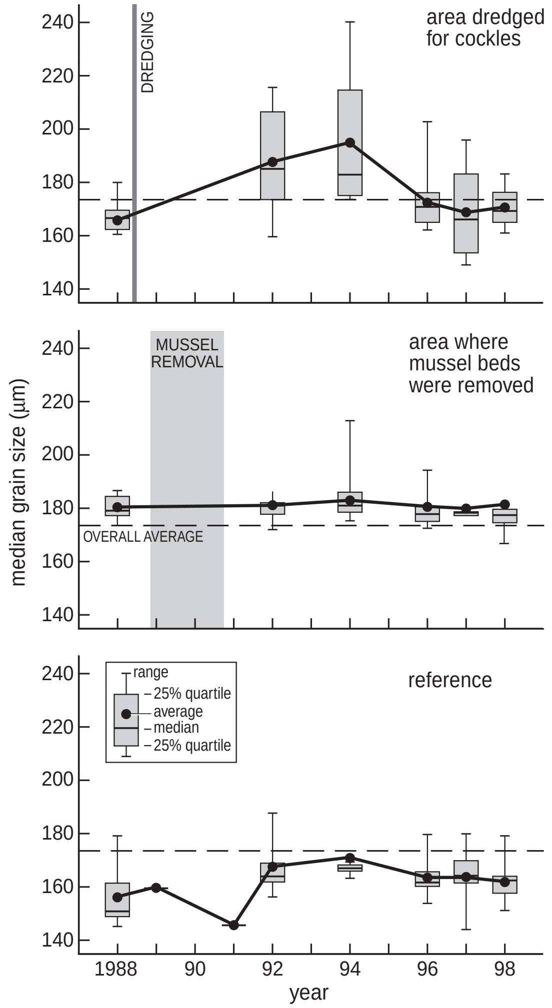

Fig. 2. Changes in median grain size of the sediments in the three experimental areas around Griend in the period 1988–98. Data are presented as box-plots (boxes indicating medians ±25% quartiles, vertical bars indicating ranges, and large dots average values, as indicated). The boxes are based on samples from four to 16 different stations per area per year. For reference the dashed horizontal lines indicate the average value based on all samples from all areas from all years.

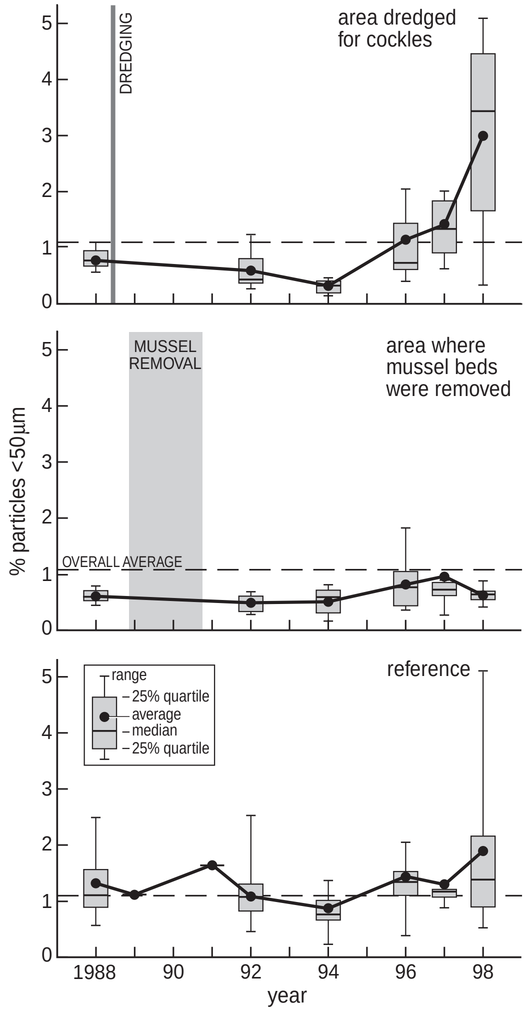

Fig. 3. Changes in silt content of the sediments in the three experimental areas around Griend in the period 1988–98. Data are presented as box-plots (boxes indicating medians ±25% quartiles, vertical bars indicating ranges, and large dots average values, as indicated). The boxes are based on samples from four to 16 different stations per area per year. For reference the dashed horizontal lines indicate the average value based on all samples from all areas from all years.

analysis of variance, assuming that sediment samples collected in the periods 1992–94 and 1996–98 yield two sets of independent data points, confirmed a significant difference between the first and second period ($F_{1,153} = 5{\cdot}687$, $P = 0{\cdot}018$), a large effect of area ($F_{2,153} = 22{\cdot}456$, $P < 0{\cdot}0001$), and a significant interaction term between the time and place ($F_{2,153} = 4{\cdot}499$, $P = 0{\cdot}013$).

A similar analysis was carried out for silt content (Fig. 3), a sediment characteristic that tends to be much more variable as a consequence of surface perturbations (van Straaten 1965). A two-way analysis of variance for the differences between 1988 and 1992 showed a strong effect of area ($F_{2,40} = 10{\cdot}031$, $P < 0{\cdot}0001$) but no effect of year ($F_{1,40} = 1{\cdot}233$, $P = 0{\cdot}273$), nor of interactions between area and year ($F_{2,40} = 0{\cdot}009$, $P = 0{\cdot}991$). A comparison between 1988 and 1994 did not show significant effects or interaction terms either. The low silt content in 1988–94 was followed by a steep increase up to 1998, especially in the area previously dredged for cockles (Fig. 3). A comparison between 1994 and 1998 indeed showed a significant effect of year ($F_{1,38} = 10{\cdot}556$, $P = 0{\cdot}002$), no effect of area ($F_{2,38} = 2{\cdot}168$, $P = 0{\cdot}128$) and a significant interaction term between area and year ($F_{2,38} = 4{\cdot}957$, $P = 0{\cdot}012$). So the increase in silt content after 1994 was significant, and so were differences in the extent of the increase between areas.

In summary, there were significant temporal changes in the two sediment characteristics over the period 1988–98, and in several cases the magnitude of these changes differed significantly between the three areas around Griend. The sedimentary changes were most pronounced in the area dredged for cockles (Figs 2 and 3), with an increase in median grain size and a reduction in silt content from 1988 to 1994 being followed by a return to pre-impact conditions 8–11 years after the fishery.

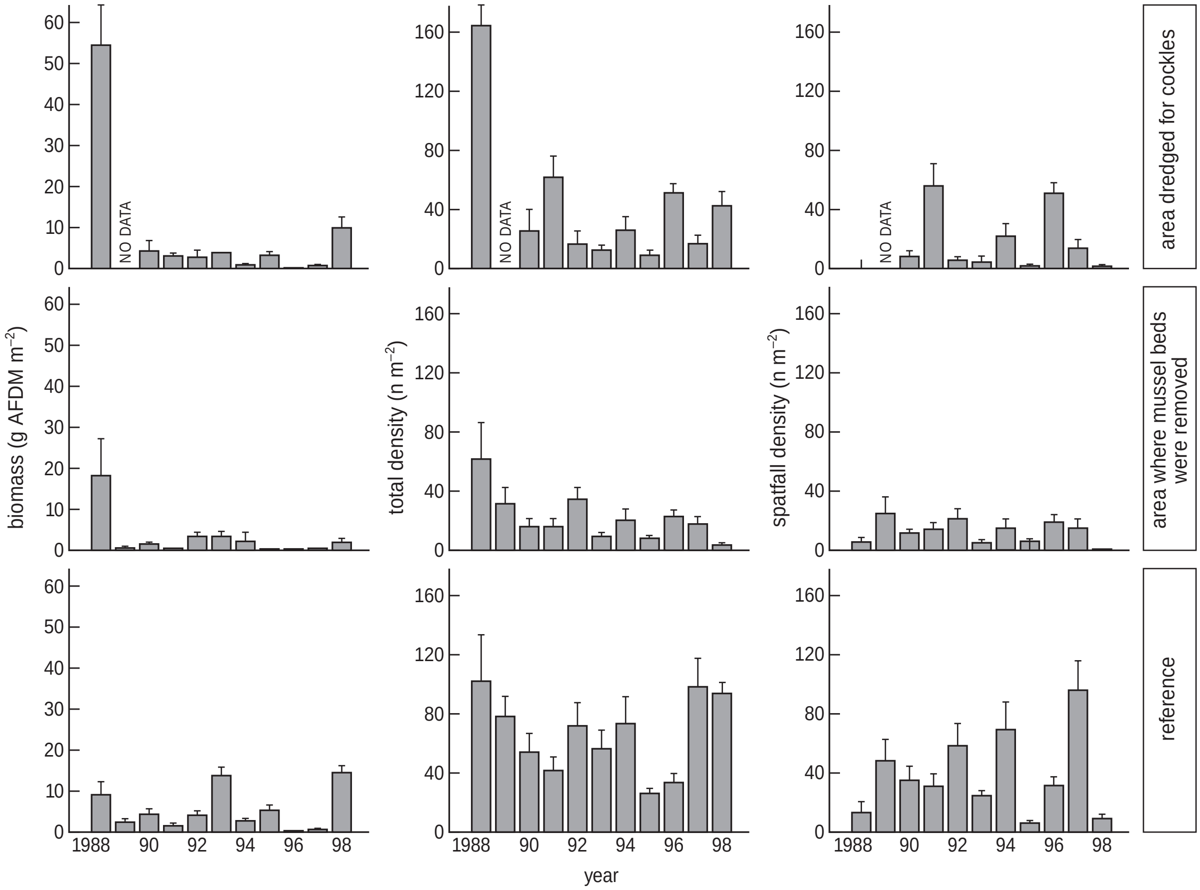

Fig. 4. Changes in biomass (left panels), numerical density (middle panels) and the density of spatfall (right panels) of edible cockles *Cerastoderma edule* in the three experimental areas around Griend from 1988 to 1998. The error bars indicate 1 SE.

CHANGES IN STOCKS OF BENTHIC BIVALVES AROUND GRIEND

The dredging of cockles in September and October 1988 took place in an area where cockle biomass and total density were higher than in the other two areas (Fig. 4 and Table 1). The limited extent of mechanical cockle-dredging carried out along the eastern edge of the reference area in 1995 was reflected by the low biomass of *Cerastoderma* in 1996. In the area dredged for cockles in 1988, peaks in settlement occurred in 1991 and 1996, whereas in the reference area settlement showed peaks of increasing height in 1990, 1992, 1994 and 1997 (Fig. 4). There was a significant treatment effect on the differences in abundance of *Cerastoderma* between the reference area and the area dredged for cockles (Table 1). Whereas biomass and total density were lowest in the reference area before the fishery incident, these abundance measures were significantly higher afterwards. The same difference occurred between the reference and the 'mussel' area; there were no differences between the experimental 'cockle' and 'mussel' areas (Table 1). We found no spatfall in the area dredged for cockles in 1988 (Fig. 1), and therefore it is not so surprising that after dredging spatfall densities of *Cerastoderma* actually increased in the cockle-dredged area relative to the reference area (Table 1).

Biomass of *Macoma* was higher in the area dredged for cockles than in the reference and mussel areas before the fisheries in 1988 (Fig. 5 and Table 1). As with *Cerastoderma*, before the cockle fishery the biomass of *Macoma* was lowest in the reference area compared with the area dredged for cockles but significantly higher afterwards (Table 1). The same differences were found between the reference and the mussel area, and between the mussel and cockle area, indicating that the mechanical cockle harvest negatively affected the standing stocks of *Macoma*. Nevertheless, a reverse pattern was shown by total and spatfall density of *Macoma* (Table 1; note that, particularly in this species, total densities are almost entirely comprised of spatfall). This indicated that spatfall densities in the reference and mussel areas, relative to the cockle area, decreased after the fishery events.

Soft-shelled clams *Mya* < 40 mm in length were rarely encountered on the intertidal flats around Griend until there was strong recruitment, especially in the reference area, in 1991, 1994 and 1996 (Fig. 6). For *Mya*, differences in density between the reference area on the one hand and the cockle and mussel areas on the other became significantly larger after the fishery events (Table 1).

Thus, on the basis of either the biomass or the density measures, for all three species there was evidence

Table 1. Multiple comparisons of the abundance measures for the three bivalve species *Cerastoderma*, *Macoma* and *Mya* between different 'treatments/areas' at Griend (Figs 4–6) relative to the occurrence of fishery activities (Before = 1988 and After = 1990–95). 'Cockle' is a shorthand for 'area dredged for cockles' and 'mussel' means 'area where mussel beds were removed' (Fig. 1). The factorial difference in abundance between two treatments T_1 and T_2 is indicated by the T_1/T_2 ratios presented (these were all back-transformed from the logarithms used in calculations). A statistically significant difference ($P < 0{\cdot}05$) between the ratio before (R_B) and the ratio after the fishery activities (R_A) (i.e. if H_0: $\mu_1 \neq \mu_2$, indicated in the last column by $R_B <> R_A$), means that the difference in abundance between the treatment areas has changed. If $R_B < R_A$ then the abundance in T_1 compared with T_2 has significantly decreased. If $R_B > R_A$ then the abundance in T_1 compared with T_2 has increased

Comparison (T_1 vs. T_2)	Species	Category	Abundance measure	Average ratio (T_1/T_2) After (R_A)	Prediction interval ratio (T_1/T_2) After	Ratio (T_1/T_2) Before (R_B)	Outcome *t*-test
Reference vs. cockle	*Cerastoderma*	All ages	Biomass	1·65	0·93–2·94	0·23	$R_B < R_A$
	Cerastoderma	All ages	Density	2·38	1·35–4·17	0·82	$R_B < R_A$
	Cerastoderma	Spatfall	Density	3·02	0·99–9·19	13·37	$R_B > R_A$
	Macoma	All ages	Biomass	1·36	1·18–1·58	0·65	$R_B < R_A$
	Macoma	All ages	Density	2·77	2·36–3·25	4·47	$R_B > R_A$
	Macoma	Spatfall	Density	5·47	3·06–9·79	54·27	$R_B > R_A$
	Mya	All ages	Biomass	0·50	0·00–46·95	1·00	NS
	Mya	All ages	Density	2·75	2·17–3·48	1·00	$R_B < R_A$
	Mya	Spatfall	Density	3·99	0·40–39·37	1·00	NS
Reference vs. mussel	*Cerastoderma*	All ages	Biomass	2·98	1·11–8·02	0·51	$R_B < R_A$
	Cerastoderma	All ages	Density	3·21	2·85–3·63	1·63	$R_B < R_A$
	Cerastoderma	Spatfall	Density	2·65	1·76–3·99	2·23	NS
	Macoma	All ages	Biomass	1·61	1·45–1·80	1·19	$R_B < R_A$
	Macoma	All ages	Density	3·75	3·47–4·05	4·25	$R_B > R_A$
	Macoma	Spatfall	Density	7·24	6·54–8·02	7·91	NS
	Mya	All ages	Biomass	4·04	0·54–30·45	1·00	NS
	Mya	All ages	Density	5·35	1·78–16·06	1·00	$R_B < R_A$
	Mya	Spatfall	Density	2·88	0·47–17·69	1·00	NS
Mussel vs. cockle	*Cerastoderma*	All ages	Biomass	0·56	0·09–3·29	0·45	NS
	Cerastoderma	All ages	Density	0·74	0·42–1·31	0·50	NS
	Cerastoderma	Spatfall	Density	1·14	0·34–3·84	5·98	$R_B > R_A$
	Macoma	All ages	Biomass	0·84	0·67–1·05	0·55	$R_B < R_A$
	Macoma	All ages	Density	0·74	0·64–0·85	1·05	$R_B > R_A$
	Macoma	Spatfall	Density	0·76	0·44–1·28	6·86	$R_B > R_A$
	Mya	All ages	Biomass	0·12	0·01–1·19	1·00	NS
	Mya	All ages	Density	0·51	0·12–2·28	1·00	NS
	Mya	Spatfall	Density	1·39	0·05–42·16	1·00	NS

for statistically significant negative effects of shellfishing (especially cockle-dredging) on overall bivalve abundance (Table 1). Perhaps surprisingly, in none of the three bivalve species was there statistical evidence that juvenile settlement was reduced as a consequence of the fishery (significant positive trends even occurring in *Cerastoderma* and *Macoma*). These slightly confusing results could have resulted from competitive adult–juvenile interactions (Hancock 1973; Beukema 1982; Ólafsson, Peterson & Ambrose 1994) contributing to the particularly low spatfall densities in the highly cockle-rich dredged area in 1988. Nevertheless, especially in the area dredged for cockles (Figs 4–6), densities of spatfall of all three species were noticeably higher in 1996–98 (years with small median grain sizes, high silt content) compared with 1990–95 (years when sediments were relatively coarse). The increase equalled a factor of 1·8 in *Cerastoderma*, 3·8 in *Macoma* and 2·3 in *Mya*. That none of the differences based on log-transformed annual averages reached significance (Student's *t*-tests, $P \geq 0{\cdot}1$) was not surprising given the short period (3 years) over which the reversed sediment characteristics occurred and the response of the settling bivalves could be studied.

WERE BIVALVE STOCKS EXCEPTIONALLY HIGH IN 1988?

During the first 6 years after the fishing in 1988, median grain sizes were high (Fig. 2), silt content was low (Fig. 3) and spatfall densities of bivalves were also quite low (Figs 4–6). Probably as a consequence, the overall biomass of *Cerastoderma* failed to recover from the fishing in late 1988 and there was a steady decline in overall standing stock of *Macoma* (Fig. 7; for biomass on year the Spearman rank correlation coefficient $= -0{\cdot}905$, $P < 0{\cdot}05$). One could argue that these patterns were entirely due to *Cerastoderma* and *Macoma* stocks having reached uniquely high levels in the year 1988. No long-term data are available for the intertidal flats around Griend to examine this possibility, but such data do exist for Balgzand, *c.* 60 km to the southwest in the Wadden Sea. Such a comparison is valid not only because of the proximity of the two intertidal flat systems, but also because changes in macrobenthic abundance tend to be synchronized over large parts of the Wadden Sea (Beukema *et al.* 1993; Beukema, Essink & Michaelis 1996).

Cerastoderma stocks at Balgzand were high in 1988, as they were around Griend, but even higher stocks

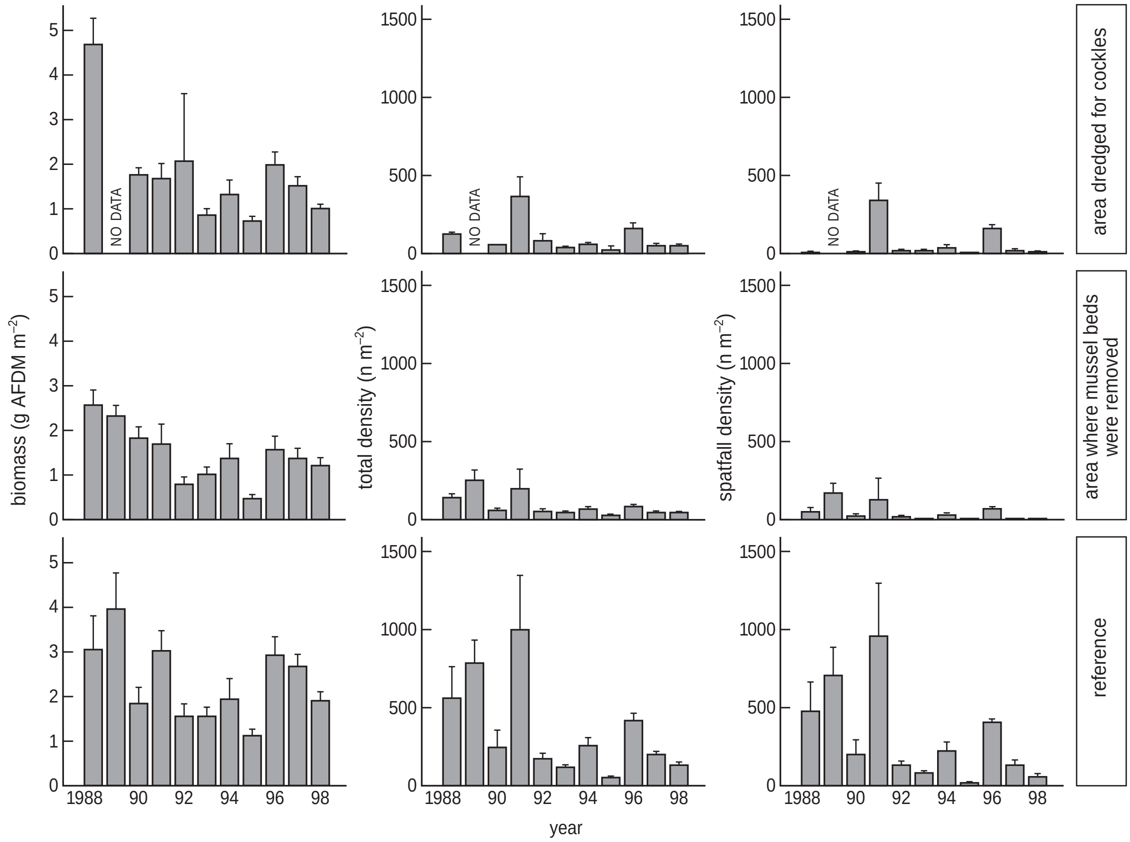

Fig. 5. Changes in biomass (left panels), numerical density (middle panels) and the density of spatfall (right panels) of Baltic tellins *Macoma balthica* in the three experimental areas around Griend from 1988 to 1998. The error bars indicate 1 SE.

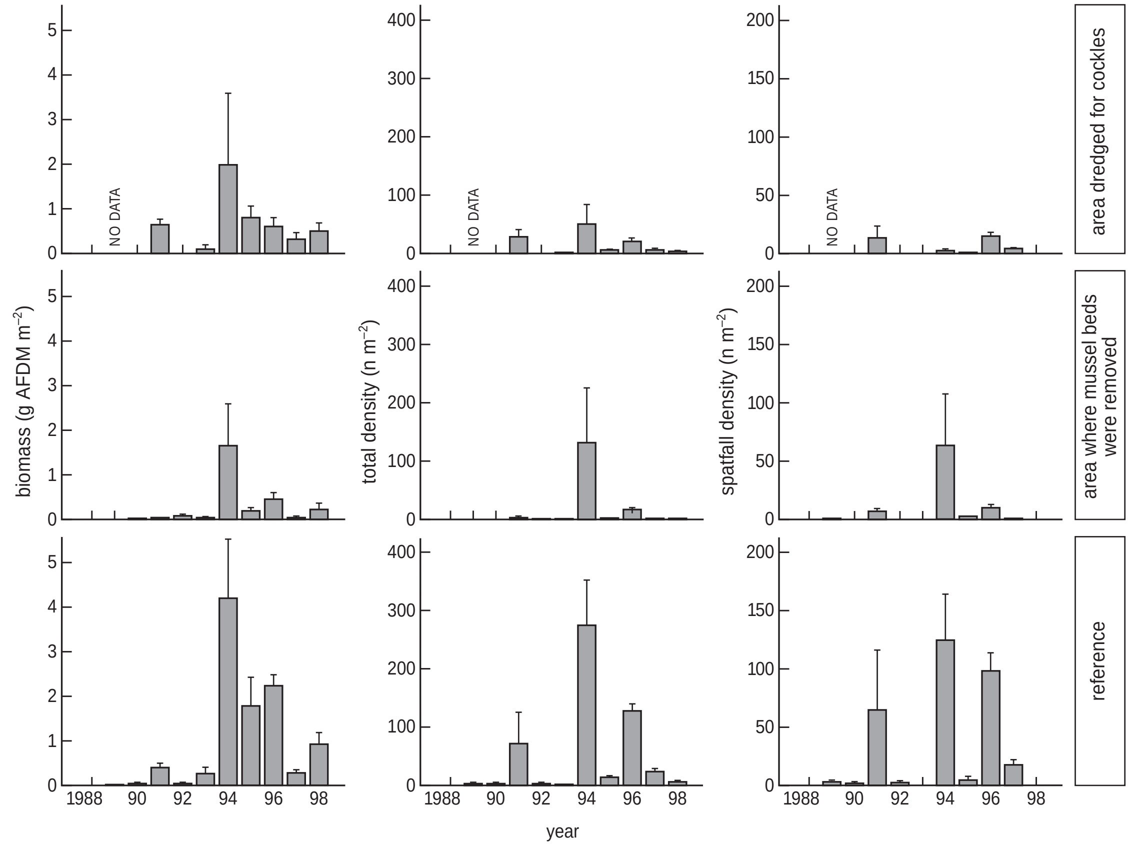

Fig. 6. Changes in biomass (left panels), numerical density (middle panels) and the density of spatfall (right panels) of soft-shelled clams *Mya arenaria* in the three experimental areas around Griend from 1988 to 1998. The error bars indicate 1 SE.

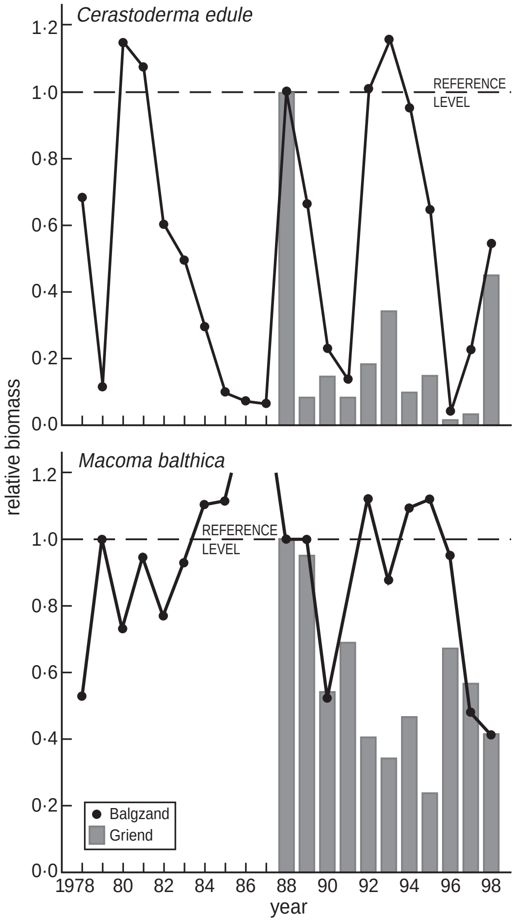

Fig. 7. Comparison of the long-term changes in the index of overall average biomass of *Cerastoderma edule* (top) and *Macoma balthica* (bottom) around Griend (1988–98, histogram) and at Balgzand (1978–98, dots connected by line) scaled to the site-specific average biomass in 1988. For Griend we have used overall average biomass rather than biomass in the unfished reference area in view of the fact that *Cerastoderma* was abundant on the dredged area in 1988 but almost absent for a long time afterwards.

were found in 1980, 1981, 1991 and 1994 (Fig. 7, top). In view of the published evidence for macrobenthic synchronization in the Wadden Sea, cockle stocks at Griend in 1988 were unlikely to be exceptional. For *Macoma* the picture for Balgzand told an even clearer story (Fig. 7, bottom). Between 1978 and 1998 there were 7 years when stocks exceeded those of 1988 and 9 years when stocks were smaller.

'BEYOND-BACI': TESTING LONG-TERM INDIRECT EFFECTS ON SETTLEMENT

The evidence presented so far demonstrates significant negative effects of mechanical shellfishing on overall bivalve abundance, but is less clear about the role of recruitment in causing the strong relative decline of bivalves in the dredged area. The BACIPS comparisons (Table 1) provided no evidence for negative effects of mechanical shellfishing on bivalve settlement within the first 8 years after fishing (in fact, sometimes the contrary). However, the strong recruitment of *Cerastoderma* and *Macoma* in the subsequent 3 years, especially in the dredged area where sediment characteristics returned to initial values, suggested that dredging may indirectly affect bivalve recruitment through its impact on the sedimentary environment. It was possible to examine further the effect of this fishery on bivalve settlement using the log-transformed ratios of spatfall densities for an early period (1992–94) and a late period (1996–98) for five areas that did or did not experience cockle-dredging in the 1988–90 period (Fig. 8a).

For *Cerastoderma* (Fig. 8b), the difference in log-ratios of fished and unfished areas was highly significant (separate-variance model, $t = 5{\cdot}720$, d.f. = 4·4, $P = 0{\cdot}003$). The initial failure of *Cerastoderma* stocks to recover in the area dredged for cockles near Griend may thus have been a consequence of reduced recruitment and not due to some odd local phenomenon other than mechanical fisheries. The long-term absence of high cockle densities appeared to be a genuine effect of the mechanical cockle fishery.

For the non-target species *Macoma* (Fig. 8c), a difference in settlement between fished and unfished areas could not be confirmed statistically. The direction of the difference was the same as for *Cerastoderma*, but the power of our test was not large enough to show that the ratios for fished areas were significantly lower than ratios for unfished areas ($t = 2{\cdot}053$, d.f. = 3·7, $P = 0{\cdot}116$).

Discussion

SPATIAL SCALES AND THE LIKELIHOOD OF DETECTING EFFECTS

The strengths of this study are, first, its spatial scale, comparing adjacent treatment and reference areas of 10–15 km^2 and also comparing sampling areas of varying in size from less than 1 km^2 to 15 km^2 that are up to 100 km apart. Secondly, we followed the recovery process over 10 years. Its weaknesses are inevitably the lack of treatment replication for the Griend example, in the limited run of pretreatment data, and in the non-random allocation of treatment or reference areas in the overall Wadden Sea comparison. The value of the comparison between the cockle-dredged and reference area near Griend may have been limited by the fact that the reference area consisted of relatively high and sheltered intertidal flats, whereas most of the dredged area was lower and more exposed to storms and wave action. Nevertheless, the comparisons involve realistic manipulations and the problems are partly compensated by the internally time-paired comparisons between treatment and reference (Stewart-Oaten, Murdoch & Parker 1986). In addition, the contrasts that we found in the long term trends in recruitment of *Cerastoderma* and *Macoma* were confirmed for similarly contrasting recruitment patterns at sites far away from the core study area near Griend (Fig. 8).

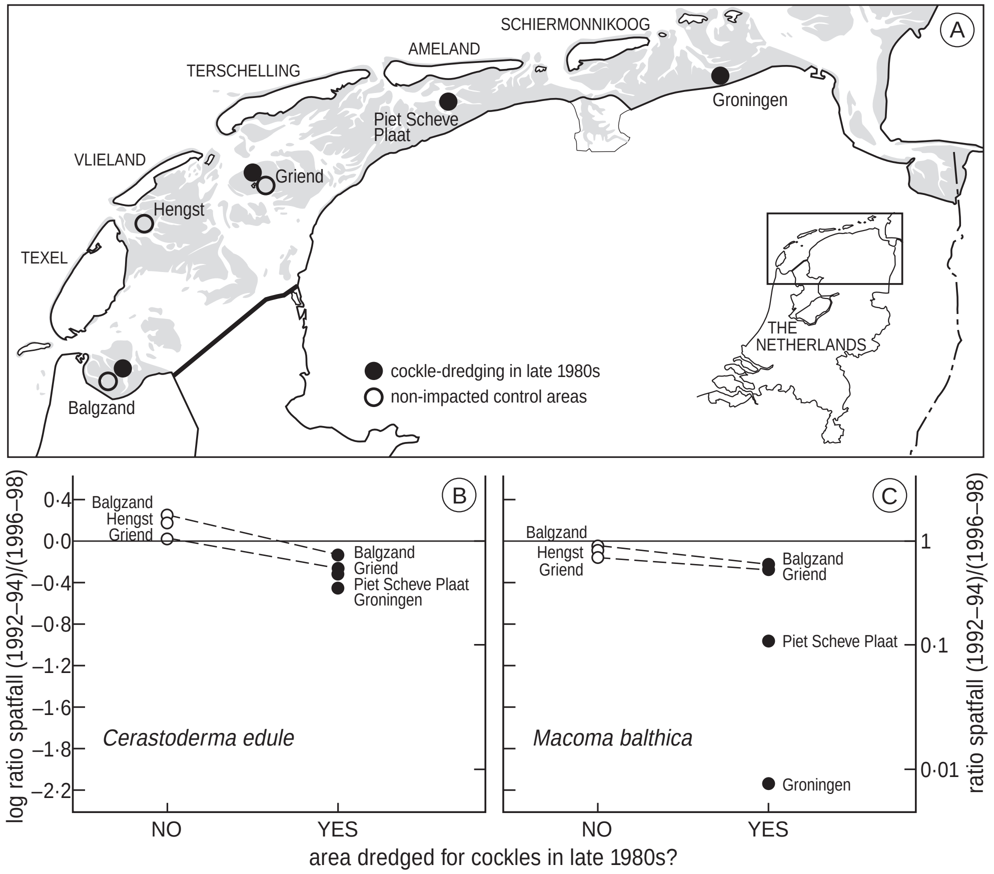

Fig. 8. Comparison of spatfall of *Cerastoderma edule* (b) and *Macoma balthica* (c) just after the cockle-dredging events in the 1988–90 period (average spatfall densities in 1992–94) and somewhat later in time (1996–98) on five different intertidal flat areas in the Dutch Wadden Sea (a) that were either exposed or not exposed to cockle-dredging. None of the areas was dredged for cockles after 1990. Two of the areas (Griend and Balgzand) contained a fished and a non-fished part and these data points are connected by dashed lines.

Variations in local geomorphology are therefore unlikely to have biased the conclusions with respect to the long-term effects of cockle-dredging.

On the basis of experiments to study the effects of cockle-dredging on non-target species in an intertidal area in Scotland, Hall & Harding (1997) concluded that, although the non-target benthic fauna may suffer high levels of mortality, ‘recovery is rapid and the overall effect on populations is probably low’ (but see Ferns, Rostron & Siman 2000). Hall & Harding (1997) also suggest that effects might vary with plot size. Their experimental plots varied in size between 0·02 ha (the smallest tractor-dredged surfaces) and a maximum of 0·5 ha (suction-dredged plots), with the total fished area covering 7 ha out of a total of over 100 ha (Hall & Harding 1997, fig. 3). This may explain why our conclusion differs from theirs: mechanical cockle-dredging at the scale at which it normally takes place, in our case covering about 1500 ha of a total of 5000 ha of intertidal flats (Fig. 1), appears from our data to have considerable effects on the target and non-target species. Also, their study took place in an area that had long been exposed to fishing and may have adjusted to such disturbances (Roberts 1997; Norris, Bannister & Walker 1998; Hall 1999). As is clear from a recent meta-analysis of fishing impacts on benthic communities (Collie *et al.* 2000), the disturbance caused by cockle-dredging needs qualification.

SEDIMENT CHARACTERISTICS AND THE SETTLEMENT OF BIVALVES

Reduced settlement explained the 8-year long decline in shellfish stocks around Griend after 1988. Dredging, especially in stormy conditions, causes the loss of fine silts (Churchill 1989; Hall 1994), which may explain why the sediments became somewhat coarser in the dredged area and attracted smaller densities of bivalve spat than after the reversal to initial conditions (Butman 1987; Thrush *et al.* 1996, 1997). We did not find clear differences in sediment characteristics between the reference area and the area where the mussel beds disappeared, but the loss of habitat complexity and sediment trapping by the nearby mussel beds may have aggravated the effects of cockle-dredging (Oost 1995; Meadows *et al.* 1998). The loss of adult shellfish stocks may have had the added effect that faeces and pseudofaeces were no longer produced, the lack of which could also have contributed to the loss of silt (Verwey 1952; Hertweck & Liebezeit 1996).

Especially in unconsolidated sediments, physical disturbances from natural (storms) and unnatural causes (dredging) can greatly affect the benthic fauna (Hall 1994; Wildish & Kristmanson 1997; Newell, Seiderer & Hitchcock 1998). As benthic organisms can substantially alter the properties of sediments by influencing interparticle adhesion, grain size distribution through the formation of faecal pellets (biodeposition), sorting of grain sizes, water content and the formation of structures, all of which relate to the stability of sediments with respect to fluid forces and geotechnical properties (Gray 1974; Rhoads 1974; Grant, Boyer & Sanford 1982; Probert 1984; Hall 1994; Paterson & Black 1999), interactions between animals and sediments work in both directions (Snelgrove & Butman 1994; Giblin, Foreman & Banta 1995). In soft sediments, anything affecting the benthic fauna is likely to change sediment characteristics, and vice versa. Physical disturbances that take place on a large scale, even if they occur only once, thus have cascading effects throughout the benthic community, including those of nearby areas, as animals and sediments move around to some degree (Hewitt *et al.* 1997; Turner *et al.* 1997; Hall 1999).

Winter storms may be the prime source of large-scale disturbances in open and exposed intertidal areas that are free from ice-scouring. Yet, we do not believe that winter storms were the causal agent of the cascade of effects that for a period of 8 years led to more sandy sediments around the island of Griend. This is rather longer than the recovery period after intense dredging of about 1 year that is thought to be typical of estuarine muds and sands (Newell, Seiderer & Hitchcock 1998). We suggest that storms merely increase the strength of a negative feedback that has its beginning in human perturbations of the sedimentary systems. According to this hypothesis, the mechanical removal of the large filter-feeding bivalves initiates sedimentary changes that lead to the disappearance of other filter-feeders such as *Macoma*. At that point these filter feeders can no longer produce the faecal pellets that play such an important role in the build-up of fine-grained sediments (Risk & Moffat 1977) that, in turn, attract settling bivalve larvae. The strength of such a negative feedback loop can be increased by winter storms that churn up the upper layer of sediments.

The intertidal flats examined in this study showed recovery with respect to spatfall of *Cerastoderma* and *Macoma* within a period of 10 years, perhaps reflecting a change from one ‘stable’ state to another (van de Koppel *et al.* 2001). The reversal of sedimentary characteristics occurred between 1994 and 1996. The winter of 1995–96 was cold, and calm in terms of wind conditions (data of Royal Dutch Meteorological Service, KNMI, De Bilt, the Netherlands). Therefore, the absence of major storms may have triggered this reversal. If this were true, not only would the recovery of mechanically fished areas greatly depend on chance conditions such as the incidence of winter storms, but repeated mechanical shellfisheries (especially in combination with stormy winters) could well compromise this reversibility.

We believe that the large intertidal flat system south of Richel and Vlieland (Waardgronden) provides a case in point. Historically, these flats were quite muddy (Postma 1957) and rich in cockle and mussel beds (Kreger 1939, 1940; Kristensen 1957). Now the beds are no longer present and the flats have turned into a large expanse of sandy flats low in silt where bivalves are few and far between (unpublished data from 1996 to 1999; Piersma & Koolhaas 1997). The closure in the 1930s of the nearby Zuiderzee may further have affected local hydrodynamics 30 years later. Yet this particular flat system historically comprised the main fishing grounds for cocklers (including the ones using mechanical harvesting methods) in the Dutch Wadden Sea until the 1990s (de Vlas 1982). Does this tell us that repeated mechanical disturbance of intertidal flats can lead to permanently altered systems?

Conclusions

After extensive experimentation on a New Zealand sandflat, Thrush *et al.* (1996) concluded that large-scale disturbances that destroy organisms with a role in maintaining habitat stability, such as the mussel and cockle beds in the Wadden Sea, are likely to result in very slow recovery dynamics, particularly in wave-disturbed soft-sediment habitats. In line with this, we propose that cockle-dredging of large areas of intertidal flat in the Dutch Wadden Sea in the late 1980s, perhaps in combination with the destruction of nearly all intertidal mussel beds, temporarily transformed relatively unstressed mid-shore communities living under relatively mild abiotic conditions into benthic communities typical of mobile sands low in silt and organic matter (Beukema & Cadée 1997; Newell, Seiderer & Hitchcock 1998; Hall 1999). Due to the many stress factors, the latter type of communities have low secondary productivity (Emerson 1989); much primary productivity remains unused by the benthic consumers (Beukema & Cadée 1997). Impact studies commissioned by the Dutch government (de Vlas 1982; 1987a,b) and reviews commissioned by the shellfishing industry (de Haan 1991) concluded that the ecological effects of suction-dredging are minor and of short-term duration. Our conclusion, that cockle-dredging leads to a significant long-term reduction in settlement and stocks of the target species, is therefore at variance with advice previously given to the Dutch government.

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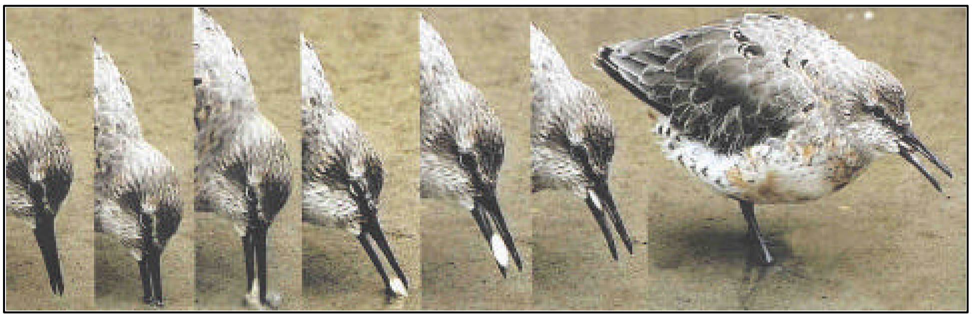
Consequenties van schelpdiervisserij voor een kenmerkende predator, de kanoet *Calidris canutus*

Voorlopige analyses door J. van Gils, T. Piersma en B. spaans

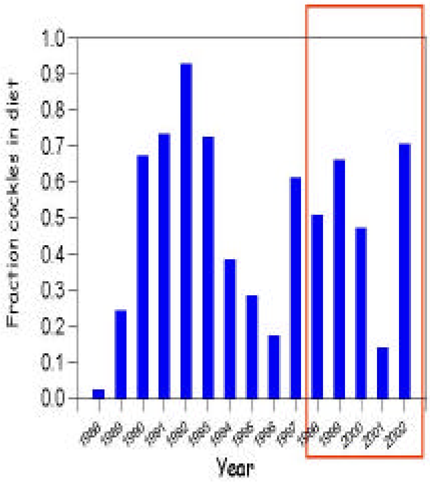
De mogelijke invloed van mechanische schelpdiervisserij op de kleine schelpdieretende vogels is tot nu toe een onderbelicht onderwerp gebleven. Alleen de gevolgen voor eiders en scholeksters, o.a. massale sterftes door voedselgebrek, zijn aangetoond en gepubliceerd (bijv. Camphuysen *et al*. 2002; EVA-II rapporten). Een soort die model staat voor deze “vergeten” groep, waartoe ook de meeuwen behoren, is de kanoetstrandloper *Calidris canutus*.

Het voedsel van de kanoet bestaat bij voorkeur uit nonnetjes en andere dunschalige schelpdieren (Piersma *et al*. 1993). Bij gebrek aan beter, worden kleine, eerstejaars kokkeltjes gegeten; deze zijn echter minder favoriet daar ze relatief veel onverteerbaar schelpmateriaal bevatten. Kanoeten hebben een afkeur voor dikschalige prooien omdat ze hun prooien in het geheel inslikken (Fig. 1), die vervolgens kraken in de spiermaag, en vervolgens al het verteerbare vlees van het onverteerbare schelpmateriaal scheiden in het darmkanaal. Hoe meer schelp per gram vlees, hoe trager dit verteringsproces verloopt, des te lager de energie opname-snelheid (Van Gils *et al*. 2003). Vanaf nu zullen we het omgekeerde van die schelp/vlees-verhouding, namelijk de vlees/schelp-verhouding, aanduiden met prooi-kwaliteit.



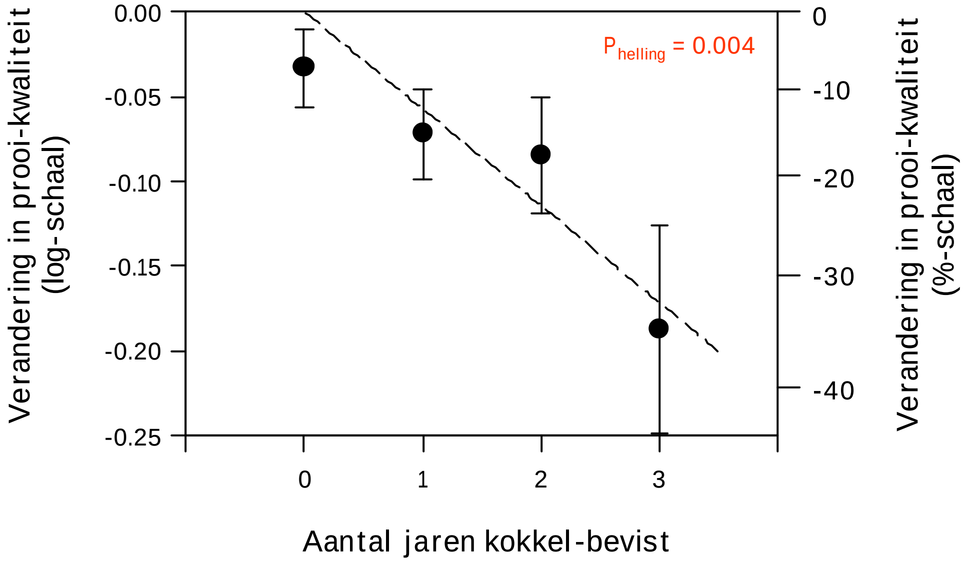
Figuur 1. Kanoeten slikken hun prooien in het geheel door.

Gezien het belang van prooi-kwaliteit voor de energiebalans van de kanoet (Van Gils *et al*. 2003), analyseren we hier het eventuele effect van kokkelvisserij op de prooi-kwaliteit. We toetsen daarbij de nulhypothese dat visserij geen schadelijke effecten heeft op kokkel-kwaliteit. Mogelijke negatieve effecten zouden kunnen lopen via slechtere vleesgroei, veroorzaakt door de gedocumenteerde verzanding van wadplaten na intensieve visserij (Piersma et al. 2001). De analyse beperkt zich tot de belangrijkste prooi van de kanoet in de afgelopen jaren, de kokkel. Ondanks de bovengenoemde afkeur voor zulke dikschalige prooien als kokkels, bleek het dieet van kanoeten de afgelopen jaren vaak te bestaan uit (eerstejaars) kokkels (Fig. 2). Dit is met name zo in jaren dat dunschalige soorten zoals het nonnetje en de strandgaper grotendeels afwezig zijn. Het dieet is gereconstrueerd aan de hand van het op soort brengen van herkenbare schelpresten in de faeces (Dekinga & Piersma 1993).



Figuur 2. Het aandeel kokkels in het dieet van kanoeten in de westelijke Waddenzee over de afgelopen 15 jaar. De jaren binnen het kader worden in dit rapport behandeld.

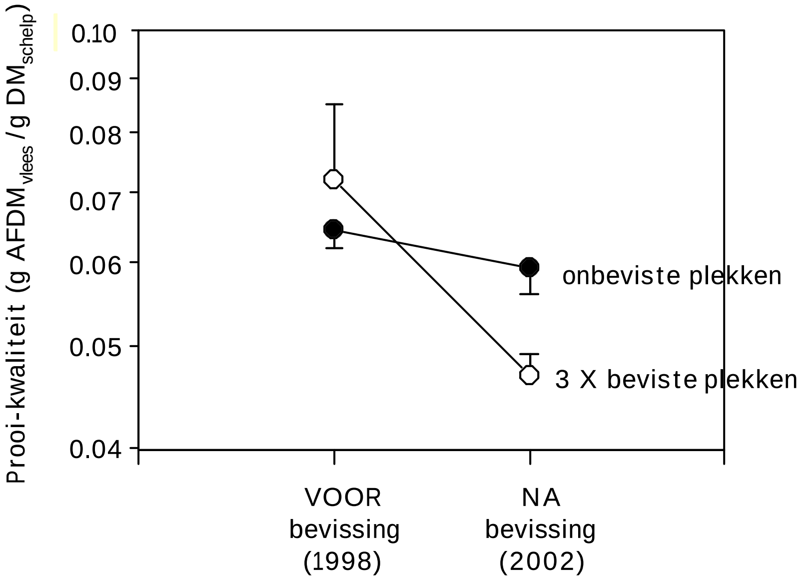
In de analyse kijken we naar de verandering in prooi-kwaliteit van voor kanoeten geschikte kokkels (16 mm). Binnen km^2-vakken (dus vakken met maximaal 16 monsterpunten) wordt de kokkelkwaliteit in één jaar (1998-2001) met de kokkelkwaliteit in een ander jaar vergeleken (1999-2002). Dit levert vakken op die in de tussentijd niet bevist zijn geweest (dit zijn meestal plekken met weinig kokkels), en vakken die in de tussentijd één, twee of drie jaren bevist zijn geweest. De analyse toont een verband tussen de mate van bevissing en kokkelkwaliteit (Fig. 3).



Figuur 3. Kokkel-kwaliteit neemt af in gebieden waar mechanische schelpdiervisserij heeft plaatsgevonden (± standaard fout). Deze afname is het sterkst in de vaakst beviste gebieden.

Uit verdere analyses blijkt bovendien dat vóór de bevissing (1998), de kokkels in de nog te bevissen vakken van een hogere kwaliteit waren dan de kokkels in de nimmer te bevissen vakken. Na drie jaren van bevissing blijkt de kwaliteit echter onder de kwaliteit van nimmer te bevissen vakken te liggen (Fig. 4).

Het blijkt dat deze effecten ook de kanoet treft. Dit komt vooral omdat de favoriete foerageergebieden van kanoeten in de westelijke Waddenzee in de kokkel-beviste gebieden liggen (Van Gils *et al.* in prep.). Buiten de beviste gebieden zijn er in de westelijke Waddenzee niet veel plekken waar kanoeten *voldoende* voedsel kunnen vinden om de winter te overleven. Daarnaast suggereert bovenstaande analyse dat de kwaliteit in de eerste jaren van bevissing (1998-2000) in zulke gebieden lager was dan in kokkel-beviste gebieden.

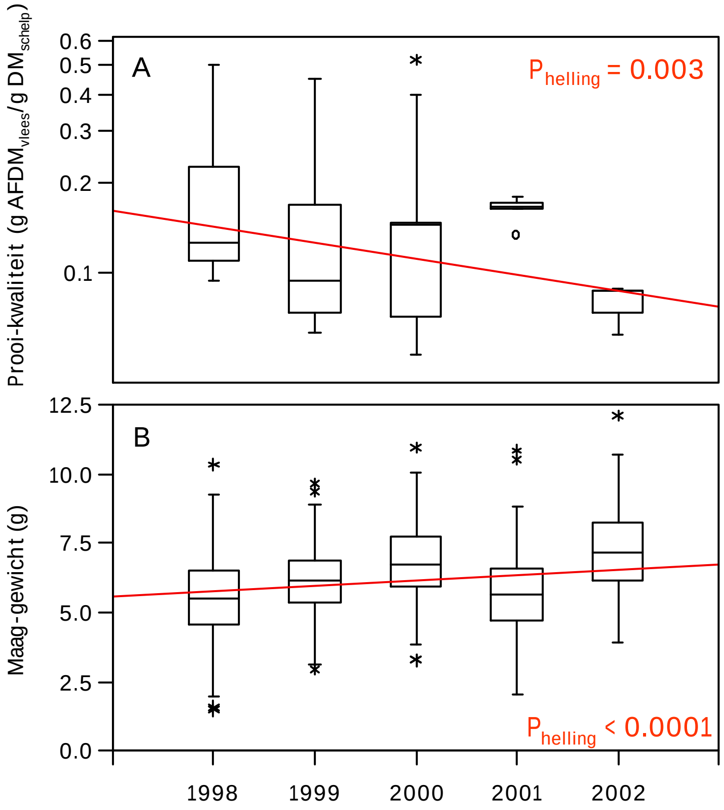


Figuur 4. Voor bevissing lag de absolute kwaliteit van kokkels hoger in nog te bevissen gebieden dan in nimmer te bevissen gebieden (± standaard fout). Na drie jaren van visserij is dit patroon omgekeerd.

Op grond van deze bevindingen zou je verwachten dat kanoeten dus steeds meer schelpmateriaal te verwerken krijgen per gram ingeslikt vlees. Dit idee hebben we voor de jaren 1998-2002 getoetst aan de hand van faeces-analyses. Hieruit blijkt inderdaad dat de gemiddelde ingeslikte prooikwaliteit (vlees per gram schelp) significant afnam (Fig. 5A; $P = 0.003$).

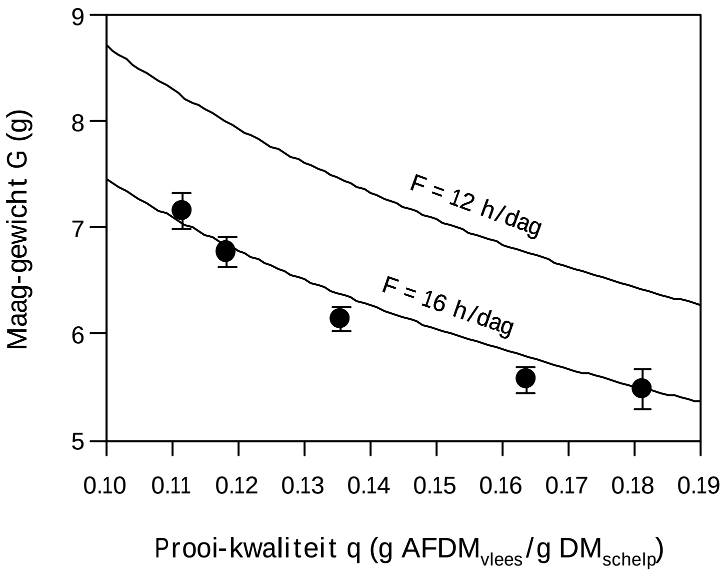
Uit experimenten met kanoeten in gevangenschap blijkt dat kanoeten zich kunnen wapenen tegen een daling in prooikwaliteit door hun spiermaag te vergroten (Dekinga *et al*. 2001; Van Gils *et al*. 2003). Het blijkt dat kanoeten met een vergrootte spiermaag onverteerbaar schelpmateriaal sneller verwerken (Van Gils *et al*. 2003), zodat de hoeveelheid opgenomen vlees in principe niet afneemt bij een daling in prooikwaliteit. Uit veldgegevens blijkt dat vrijlevende kanoeten in de Waddenzee ook inderdaad hun maaggrootte aanpassen aan seizoens-schommelingen in prooikwaliteit

(Van Gils *et al*. 2003). Hieruit volgt de verwachting dat in de jaren van intensieve visserij (1998-2002) kanoeten in de westelijke Waddenzee steeds grotere magen hadden om de daling in prooikwaliteit te compenseren.



Figuur 5. A. De kwaliteit van het dieet van kanoeten nam af in de loop der jaren. **B.** Als gevolg daarvan nam maaggrootte van kanoeten toe in de loop der jaren.

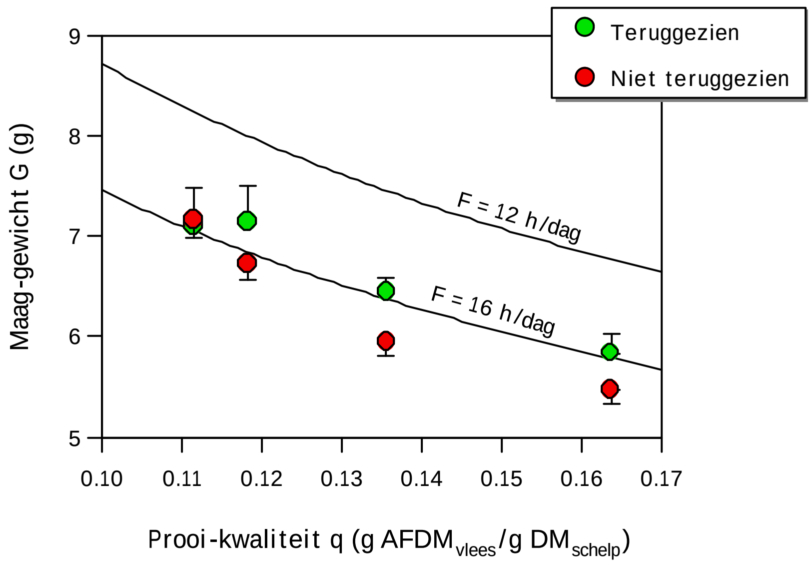
Door middel van echoscopie-metingen (Dietz *et al*. 1999) maten we jaarlijks de maaggrootte van enkele honderden kanoeten. Er bleek inderdaad een toename in maaggrootte te zijn opgetreden (Fig. 5B; $P < 0.0001$). Aan de hand van een energie-budget model konden we doorrekenen dat, gemiddeld gesproken, de waargenomen toename net voldoende was om het energie-budget rond te krijgen, m.a.w. om op gewicht te blijven (Fig. 6). Echter, omdat het hier gemiddelden betreft, betekent dit dat er jaarlijks toch vogels waren die een te kleine maag hadden om de lage prooi-kwaliteit aan te kunnen.



Figuur 6. Gemiddeld gesproken was maaggrootte jaarlijks precies voldoende om het energie-budget bij 16 uur foerageer in balans te houden (± standaard fout).

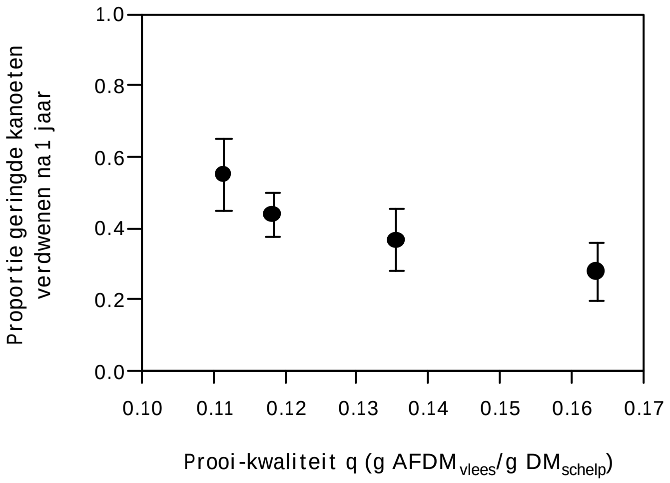
Een intensief kleurringen programma aan vrijlevende kanoeten (jaarlijks worden zo'n 500 individuen gemerkt) maakte het mogelijk het lot van deze vogels met 'ondermaatse magen' te volgen. Het bleek dat die vogels, die in het jaar van vangst niet meer werden teruggezien in de Waddenzee, gemiddeld gesproken een te kleine maag hadden (Fig. 7). Waarschijnlijk waren deze vogels uitgeweken naar elders in NW-Europa, hoewel intensieve waarnemingen in een van de belangrijkste overwinteringgebieden in de UK, de Wash (UK) dit niet bevestigden. Dit zou duiden op extra sterfte onder deze groep vogels. Daarentegen hadden vogels die in het jaar van vangst *wel* werden teruggezien een maaggrootte die voldeed aan de lokale omstandigheden (Fig. 7).

Hoewel kanoeten bekend staan om hun vermogen om verteringsorganen zoals spiermagen flexibel aan te passen aan lokale omstandigheden (Piersma & Lindström 1997), lijken bovenstaande analyses aan te geven dat beesten een afweging maken tussen enerzijds maaggrootte lokaal aan te passen en anderzijds het laag-kwalitatieve overwinteringsgebied te verlaten.



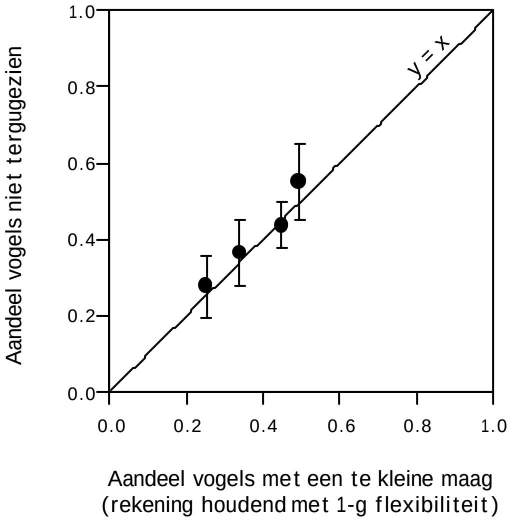
Figuur 7. In tegenstelling tot kanoeten die in het jaar van vangst werden teruggezien (groene symbolen), hadden kanoeten die in datzelfde jaar *niet* werden teruggezien (rode symbolen) magen die te klein waren om het energie-budget rond te krijgen (± standaard fout).

Dit idee wordt versterkt door de waarneming dat het aandeel vogels dat in het jaar na vangst niet wordt teruggezien afneemt met prooikwaliteit (Fig. 8), m.a.w. toeneemt met de vereiste maaggrootte. Aan de hand van de geschatte hoeveelheid vet bij aankomst uit de broedgebieden, hebben we berekend dat kanoeten hun maag hooguit één gram kunnen vergroten. Vogels die aankomen met een maag die meer dan één gram kleiner is dan lokaal vereist zouden dus moeten vertrekken.



Figuur 8. Het aandeel vogels dat niet werd teruggezien (± standaard fout) nam af met prooikwaliteit.

Dit idee konden we toetsen door gebruik te maken van een lange-termijn dataset aan maaggroottes bij aankomst in Waddenzee. Het blijkt dat het aandeel vogels dat in het jaar na vangst niet wordt teruggezien inderdaad gelijk is aan het aandeel vogels dat bij aankomst een maag heeft die meer dan één gram kleiner is dan lokaal vereist (Fig. 9).



Figuur 9. Het aandeel vogels dat niet werd teruggezien (± standaard fout) is gelijk aan het aandeel vogels dat bij aankomst een te kleine maag heeft (rekening houdend met de mogelijk voor 1-gram flexibiliteit).

Sommerend kunnen we zeggen dat mechanische schelpdiervisserij in de westelijke Waddenzee in de gebieden waar mechanisch naar kokkels is gevist de prooikwaliteit is afgenomen. Kanoeten konden dit deels ondervangen door maagvergroting. Echter, naarmate de prooikwaliteit verder afnam, werd het voor steeds meer individuen te moeilijk om hun maag adequaat ter vergroten. Deze vogels werden niet meer teruggezien in de Waddenzee. Dit betekent dat de vogels of naar elders uitgeweken zijn, hoewel daar geen aanwijzingen voor zijn vanuit de ringwaarnemingen, of doodgegaan zijn. In het geval dat de vogels naar elders uitgeweken zijn zou dit feit op zich ook tot een verhoogde sterfte geleid kunnen hebben.

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