Associations between fish species of the Dutch coast and estuaries

Benthos-epibenthos interactions in the Dutch Wadden Sea

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Overzicht BEON habitatrapporten, verschenen in het kader van het project 'Kartering van habitats/ecotopen in de Nederlandse zoute wateren'

In het kader van BEON (Beleidsgericht Ecologisch Onderzoek in Noordzee/Waddenzee) worden een aantal speerpunten onderscheiden. Bij het speerpunt 'verstoring habitats' staat als prioriteit onder systeemkennis vermeld dat onderzocht moet worden welke ecotopen onderscheiden kunnen worden, waar ze zich bevinden en wat hun karakteristieken zijn. Het tweede prioritaire onderwerp stelt de vraag naar het belang van bepaalde ecotopen voor bepaalde soorten. Het uitgevoerde project sluit aan bij deze vragen.

Beleidsrelevantie

Het beleid in de kustwateren en de Waddenzee is gericht op het duurzaam functioneren en gebruiken van het systeem. Door het multifunctionele karakter van het gebruik wordt verweving van functies als uitgangspunt genomen. Indien dat niet mogelijk is, wordt zonering toegepast. Bij verweving van functies wordt uitgegaan van optimalisatie van de verschillende functies; bij scheiding wordt in de onderscheiden gebieden veelal gestreefd naar maximalisatie. Door indeling in ruimte en tijd wordt ernaar gestreefd de negatieve effecten op de overige functies zo klein mogelijk te houden, zowel bij verweving als scheiding. Voor beleid en beheer is het essentieel de habitatkarakteristieken te kennen waarop elke functie gebaseerd is. Bovendien is het noodzakelijk te weten waar de betreffende karakteristieken voorkomen. In een voorgaand BEON-project wordt voor een aantal organismengroepen aangegeven wat de belangrijkste habitatkarakteristieken zijn. Vooral fysische parameters blijken belangrijk. Deze zijn nog maar zeer ten dele op bestaande kaarten weergegeven.

Het project heeft eveneens als doel om door middel van een case-study een basis te leggen voor een generieke methodiek en ondersteunend instrumentarium om de geschiktheid van ruimtelijk inhomogene gebieden voor verschillende soorten en gebruiksfuncties te kunnen evalueren en presenteren.

Het in kaart brengen van ecotopen en habitats is essentieel voor de toepassing van de EU-Habitatrichtlijn en de regelingen die getroffen moeten gaan worden in het kader van het Biodiversiteitsverdrag van Rio.

Als afsluiting van het project zijn een viertal rapporten uitgebracht:
Omdat het voorkomen van organismen niet uitsluitend wordt bepaald door de duidelijk waarneembare fysische en biologische eigenschappen van de locatie is onderzocht of de microverspreiding van voedsel een belangrijke factor was. Hierover wordt gerapporteerd in de rapportage van NIOO-CEMO en WL (BEON rapport nr. 98-14: BEON Habitat. MICRO MACRO. A research project to the relation between physical parameters and the distribution of macro-benthos on a tidal flat (WL). Comparing patterns in macrofauna structure at different scales: within tidal flats, between tidal flats and between estuaries
(NIOO-CEMO)). Het onderzoek werd uitgevoerd in de Westerschelde

De tweede rapportage bevat twee onderdelen uitgevoerd door RIVO-DLO en NIOZ. In deze rapportage wordt de verspreiding van vissen in kustwateren en Waddenzee beschreven in relatie tot abiotische en biotische (voedsel) gegevens (BEON rapport nr. 98-16: Wetenschappelijke eindverantwoording en korte samenvatting van de RIVO-DLO bijdrage aan het BEON-project 'Kartering van habitats/ecotopen in de Nederlandse zoute wateren (RIVO-DLO). Benthos-Epibenthos interactions in the Dutch Wadden Sea (NIOZ).

In een rapportage van RIVM, IBN-DLO, en RIKZ wordt het gebruik van het habitat en ecotoopbegrip nader uitgewerkt (BEON rapport nr. 98-11: Naar een ecotopensysteem zoute wateren Nederland). Hiertoe is een hiërarchisch systeem ontwikkeld dat algemeen toepasbaar is in Kustwateren.

Voorgesteld wordt de term habitat te reserveren voor een benadering waarbij vanuit een organisme gedacht wordt. Een habitat kan dan gedefinieerd worden als **'het type omgeving waarin een organisme leeft'**; het wordt bepaald door de eisen die dat organisme aan zijn omgeving stelt. Deze benadering is belangrijk bij het beschermen van bedreigde organismen.

Bij een integraal beleid waarbij van een aantal functies wordt uitgegaan, heeft het meestal voordelen het ecotoopbegrip te hanteren. Binnen een bepaald ecotoop is ruimte voor een aantal organismen of een levensgemeenschap. Als definitie voor ecotoop wordt aangehouden **'een geografische eenheid die binnen bepaalde grenzen homogeen is wat betreft de belangrijkste hydraulische, morfologische en fysisch-chemische omgevingsfactoren die relevant zijn voor de biota'**.

In de vierde rapportage (RIKZ, IBN-DLO, RIVM) wordt op basis van de ontwikkelde theorie een voorbeeld gegeven van een ecotopenkaart van de Waddenzee (BEON rapport nr. 98-13: Naar ecologische kaarten van de Waddenzee). Door middel van overlays en door de gebruiker samen te stellen legenda's en klassegrenzen kunnen ecotoop en habitatkaarten gemaakt worden. Het inbrengen van informatie betreffende het voorkomen van organismen en het ontwikkelen van rekenmodules om optimale ontwikkelingsomstandigheden in kaart te brengen is onderdeel van projecten buiten BEON, en is voor de Waddenzee reeds uitgevoerd voor Zeegras en voor de Westerschelde voor de Kokkel. Een kaart die de optimale ontwikkelingsmogelijkheden voor mosselbanken wordt ontwikkeld door IBN-DLO, RIVO-DLO en RIKZ.

In opdracht van de HID-Noordzee werd gelijktijdig gewerkt aan de ontwikkeling van ecotopenkaarten voor de Noordzee waarbij gestreefd moest worden naar afstemming. De toegepaste methoden en ontwikkelde applicaties zijn in gezamenlijk overleg ontwikkeld. Het **'Ecotopen GIS Noordzee'** (Auteur J.G. Hartholt) is onlangs uitgebracht.

Inhoud

Wetenschappelijke eindverantwoording en korte samenvatting van de RIVO-DLO bijdrage aan het BEON-project 'Kartering van habitats/ecotopen in de Nederlandse zoute wateren' (RIVO-DLO)

Associations between fish species of the Dutch coast and estuaries

Benthos-Epibenthos interactions in the Dutch Wadden Sea (NIOZ)

Wetenschappelijke eindverantwoording en korte samenvatting van de RIVO-DLO bijdrage aan het BEON-project 'Kartering van habitats/ecotopen in de Nederlandse zoute wateren'

P.D de Jong, RIVO-DLO

Binnen het BEON-project 'Kartering van habitats/ecotopen in de Nederlandse zoute wateren' heeft RIVO-DLO de taak op zich genomen om de visfauna the analyseren. Hiertoe zijn de door het RIVO-DLO uitgevoerde boomkorsurveys geanalyseerd met het doel de ruimtelijke structuur in de visfauna vast te stellen. Met behulp van multivariate statische technieken is getracht soortsgroepen te onderscheiden en hun ruimtelijke verspreiding vast te stellen. Er is drie keer een wetenschappelijke verslaglegging geleverd met betrekking tot dit onderzoek:

(1) Hartgens, E.M. , P.D. de Jonge & A.D. Rijnsdorp, 1996. Spatial distribution of the North Sea fish assemblages with special reference to the coastal and estuarine waters of the Netherlands. In: Habitatkartering en beschrijving van Nederlandse kustwateren. BEON-rapport nr. 96-5

(2) de Jong, P.D., 1997. Analyse van de samenhang tussen vissoorten in de vangsten van een meerjarige survey met garnalennet in de Waddenzee, kustzone en Zeeuwse stromen. Tussentijds rapport, januari 1997. Niet door BEON gepubliceerd.

(3) de Jong, P.D., 1997. Associations between fish species of the Dutch coast and estuaries. Te publiceren als wetenschappelijk artikel, bijgevoegd.

Hieronder zal in het kort aan de hand van de drie rapportages de resultaten van het onderzoek worden samengevat. De drie rapportages worden aangeduid met (1),(2) en (3), zie hierboven.

In (1) worden de resultaten van cluster analyses besproken voor de survey gegevens van najaar 1990-1994. Er kunnen met de zogenaamde hiërarchische clusterings methodiek geen duidelijke soortsgroepen worden geïdentificeerd. De analyse levert de clustering op van 3 soorten die min of meer specifiek zijn voor ondiep water en van 10 soorten die min of meer specifiek zijn voor diep water. Verder is er een groot cluster van 46 soorten, met daarin zowel soorten die specifiek zijn voor ondiep water als die specifiek zijn voor diep water. De individuele trekken van de surveys worden met behulp van 'disjoint' clustering op grond van de vangstsamenstelling geclusterd in een van te voren vastgesteld aantal clusters. In de trekken die ver buiten de kust liggen, kon een duidelijk onderscheid gemaakt worden tussen een cluster van noordelijke trekken en een cluster van zuidelijke trekken. Voor de trekken langs de kust en in de estuaria echter werden geen ruimtelijk gescheiden clusters gevonden. De trekken langs de kust en in de estuaria zijn met een andere vangstmethode uitgevoerd dan de trekken ver buiten de kust en in de conclusies wordt dan ook aanbevolen om vergelijkend onderzoek te doen naar het effect van de vangstmethode op de vangst. Andere conclusies van (1) zijn: een opvallend verschil tussen de Zeeuwse delta en de Waddenzee, een geleidelijke overgang tussen zuidelijke en noordelijke kuststations en een overheersende invloed van zgn. 'nursery type' soorten zoals kleine schol (*Pleuronectes platessa*) op de cluster indeling.

In (2) wordt het onderzoek enerzijds uitgebreid naar de survey gegevens voor voorjaar en najaar 1980-1984, anderzijds beperkt tot de surveygegevens langs de Nederlandse kust, in de Waddenzee en in de Zeeuwse delta, aangezien binnen het gehele project de aandacht geconcentreerd wordt op de Nederlandse Waddenzee en dit bovendien als voordeel heeft dat de betrokken gegevens alle met dezelfde vangstmethode zijn verzameld. Met behulp van Multi Dimensonal Scaling zijn een soort 'landkaarten' van de soorten gemaakt, waarbij soorten die vaak tegelijk in vergelijkbare aantallen gevangen zijn, dichtbij elkaar liggen. Op deze kaarten konden geen duidelijke soortsgroepen worden onderscheiden. In (2) is tevens een begin gemaakt aan het gebruik van een eenvoudige statistische test voor associatie, dat in (3) verder is uitgewerkt.

In (3) kunnen op basis van de statistische test voor associatie twee soortsgroepen worden onderscheiden met respectievelijk 20 en 36 soorten. Met dezelfde test konden ook de trekken op basis van hun soortssamenstelling in twee groepen verdeeld worden: 'inshore' trekken die voornamelijk in de Waddenzee en Zeeuwse delta liggen en 'kust' trekken die voornamelijk langs de kust liggen. Sommige trekken uit de groep van 'inshore' trekken liggen echter langs de kust en 'kust' trekken komen ook voor in Wadden zee en de Zeeuwse delta. In de Zeeuwse delta komen wel meer 'kust' trekken voor dan in de Waddenzee. De 'inshore' trekken worden geprefereerd door de kleinere soortsgroep, de 'kust' trekken door de grotere soortsgroep. Gemiddelde diepte en zoutgehalte is lager voor de de groep van 'inshore' trekken dan voor de 'kust' trekken, maar er is enorm veel overlap in de waarden voor deze abiotische factoren. Vertegenwoordigers van de groep van soorten met een voorkeur voor de 'inshore' trekken zijn: jonge haring (*Clupea harengus*), zeedonderpad (*Myoxocephalus scorpius*), spiering (*Osmerus eperlanus*), sprot (*Sprattus sprattus*), zeenaalden (*Syngnathidae*) en puitaal (*Zoarces viviparis*). Vertegenwoordigers van de groep van soorten met een voorkeur voor de 'kust' trekken zijn: schurftvis (*Arnoglossus laterna*), dwergtong (*Buglossidium luteum*), pitvis (*Callionymus lyra*), schar groter dan 10 cm (*Limanda limanda*), schol groter dan 25 cm, tong tussen 15 en 25 cm (*Solea solea*), kleine pieterman (*Trachinus vipera*) en horsmakreel (*Trachurus trachurus*). De soorten uit beide soortsgroepen worden vaak samen gevangen, hetgeen een geleidelijke overgang in de visfauna van 'inshore' naar de kust aangeeft. Sommige soorten, zoals dwergtong, die typisch zijn voor de 'kust' trekken, nemen in voorkomen af bij meer zuidelijke ligging van de trekken. De kleinste lengtegroepen van schol en schar worden in geen van beiden groepen ingedeeld, aangezien zij in praktisch alle vangsten aanwezig waren. In (1) speelt kleine schol wel een belangrijke rol in de cluster indeling van de trekken, maar het onderzochte gebied van (1) is groter en beslaat ook delen van de Noordzee, waar geen kleine schol voorkomt. De in (2) gevonden groepsindeling van soorten en trekken is globaal hetzelfde voor de voorjaarsgegevens uit de periode 1980-1984, de najaarsgegevens uit de periode 1980-1984 en de najaarsgegevens uit de periode 1990-1994.

De resultaten van de in (1),(2) en (3) uitgevoerde statistische analyses wijzen allen in dezelfde richting. Op basis van de gebruikte gegevens moet geconcludeerd worden, dat langs de Nederlandse kust, in de Waddenzee en in de Zeeuwse delta geen duidelijk gescheiden visgemeenschappen voorkomen. Het lijkt er meer op, dat er een geleidelijke overgang bestaat van estuariene soorten naar de soorten van de open Noord Zee. Daarnaast lijkt er ook een geleidelijke overgang te bestaan van noord naar zuid. In de overgang van estuariene soorten naar de soorten van de open Noord Zee kunnen twee losse soortsgroepen onderscheiden worden, die de extremen in deze overgang vertegenwoordigen. Geografisch gezien kunnen deze extreme groepen echter zeer dicht bij elkaar liggen en ook de bijbehorende abiotische factoren, zoals diepte en zoutgehalte, zijn sterk overlappend voor beide extreme groepen. De ruimtelijke verspreiding van deze extreme groepen en hun abiotische voorkeur is daardoor niet eenduidig vast te stellen. Estuaria en kusten vormen een zeer dynamische leefomgeving en de vissoorten die hier leven moeten een sterk aanpassingsvermogen hebben. Dit aanpassingsvermogen, in combinatie met hun mobiliteit, stelt deze vissoorten in staat om een breed scala aan overlappende habitats te bewonen.

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Associations between fish species of the Dutch coast and estuaries.

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Abstract

Catch data of a shrimp trawl survey in the Dutch coastal waters and estuaries were analysed to identify contrasting species groups, their geographical distribution and their relation with a limited number of environmental variables measured during the survey. A simple and objective method for the separate grouping of species and hauls was based on presence-absence contingency tables. Two contrasting species associations were found. The hauls could also be divided in two groups on the basis of their species composition: 'inshore' hauls that are mainly situated in the Wadden Seas and the Scheldt estuary and 'coastal' hauls, mainly found along the coast. However, the geographical separation between the two is not a sharp one. There is a close match between the two independent classifications. The 'inshore' hauls are preferred by one group of species, the 'coastal' hauls by the other. Not surprisingly, the average depth and salinity was lower in the 'inshore' hauls than in the 'coastal' hauls, but there was considerable overlap in the range of observations. Despite the significant differences in species composition, the species of both groups were often caught in variable mix, indicating a gradual transition between the species associations rather than a sharp distinction that might be related to major differences in habitat requirements.

Key words: fish, associations, coast, estuaries

Introduction

The Dutch coastal waters and estuaries are characterized by a fish fauna with more than 130 species (Nijssen & de Groot, 1987), which is about half the number of species identified from the North Sea (Ekman, 1953). In order to develop ecologically sound policies to conserve species diversity, there is a need for information on possible associations between fish species, the geographical distribution of such species assemblages, their relation with environmental factors, and also the ecological interactions between species within a group.

Recent studies of the association between fish species are roughly of two kinds. Firstly, the observations are subjected to cluster analysis and then the clusters are related to environmental factors (e.g. Riley et al., 1981; Colvocoresses & Musick, 1984; Overholtz & Tyler, 1985, Bergstad, 1990; Daan et al., 1990; Greenstreet & Hall,1996). Drawback of this approach is that most clustering methods involve an element of subjectivity (Manly, 1986; James & McCulloch, 1990; Clarke, 1993). Secondly, the distributions of individual species may be related to environmental variables and species with similar preferences are grouped together (e.g. Scott, 1982a,b; Murawski & Finn, 1988; Perry & Smith, 1993; Thiel et al., 1995). This approach can be easily flawed by the unbalanced distribution of the observations over relevant environmental factors (James & McCulloch, 1990).

In this study, the first approach is followed to analyse catch composition data of a shrimp trawl survey in the Dutch coast and estuaries. An objective method for species grouping is applied based on a simple statistical test for association. The aim is to identify contrasting species groups, their geographical distribution and their relation with a limited number of environmental variables measured during the survey. Detailed analysis of the environmental factors and species interactions involved falls outside the scope of this paper.

Materials and methods

Survey data

The catch data are derived from a long-term annual survey off the Dutch coast and in the estuaries using a shrimp trawl with 20 mm mesh size, a towing speed of 3 knots and 15 minutes haul duration. The Waddensea was sampled by RV 'Stern' and the Scheldt estuary by RV 'Schollevaar', both using a 3 m beam. The Dutch coast up till 12 nautic miles offshore was sampled by MV 'GO29' and RV 'ISIS' with a 6 meter beam. Details of the gear have been described by Boddeke et al. (1969). The minimum fishing depth is 2 meter and thus there are no data for tidal flats. Data from two periods have been used: 1980-1984 and 1990-1994. During the first period, the survey was performed in spring and in autumn, during the second one only in autumn. Around 230 hauls per survey have been made annually. Spring surveys were carried out between April 6th and May 18th, autumn surveys between September 6th and October 19th. During each haul, the following environmental variables are measured: depth, surface salinity (missing for the 1990-1994 period), surface temperature and turbidity (Secchi-disc reading). Since there is no stratification in the area, these data are considerd representative for the water column.

Gobies (*Pomatoschistus* sp.) and pipefish (*Syngnatidae*), except snake pipefish (*Entelurus aequoreus*), are treated as species groups because identification at the species level is missing or dubious. For plaice (*Pleuronectes platessa*), sole (*Solea solea*), dab (*Limanda limanda*), turbot (*Scophthalmus maximus*), brill (*Scophthalmus rhombus*), cod (*Gadus morhua*) and whiting (*Merlangius merlangus*), different length-groups were distinguished following Knijn et al. (1993). For these common species, individuals of different length may have completely different preferences regarding habitat and food. Therefore, these length groups are treated as separate 'species'.

Statistical analysis

The catch data were analysed on a presence-absence level using 2x2 contingency tables (table 1, Krebs, 1979). High values for *a* and *d* in combination with low values for *b* and *c* indicate positive association between two species, whereas low values for *a* and *d* in combination with high values for *b* and *c* indicate negative association. There is no association, if the presence of species A is independent of the presence of species B. The deviation from independence was tested for using a $\chi 2$–test. The strength of the association (V) between the two species is given by the coefficient of association (Krebs, 1979):

$$V = \frac{ad - bc}{\sqrt{(a+b)(c+d)(a+c)(b+d)}}$$

V may vary from -1 indicating complete negative association to 1 for complete positive association and is around zero in the absence of association.

Table 1 2x2 contingency table for species; a, b, c and d represent a number of hauls

	species A	
species B	present	absent
present	*a*	*b*
absent	*c*	*d*

The 2x2 contingency tables were constructed for all combinations of two species caught in one season during a five year period, and corresponding $\chi 2$–tests were done (p=0.05). Length groups of species were treated as individual species. The similarity in species composition of two hauls during one season in one year was analysed accordingly by counting the number of species present in both hauls etc.. The set up was essentially similar to table 1, but in this case species A and B were replaced by haul X and Y and *a* , *b* ,*c* and *d* represent a number of species. Structurally high values for *d* were avoided by using only species caught in more than 25 hauls. Due to computational limitations, it was necessary to do the analysis of the association between hauls on a yearly basis in order to reduce the number of combinations.

The contrast between groups was based on negative associations between species belonging to different groups. An heuristic approach was applied to form the largest possible groups in which the species have (1) no significant negative association with any other species in the same group and (2) a significant negative association with at least one species in every other group. Thus, only species with at least one significant negative association with another species can be placed in a group. The heuristic algorithm forms groups starting with species with several significant negative associations and combines groups to obtain the largest possible groups. Pairs, triplets and quadruplets of species with only significant negative association between themselves and not negatively associated with any species of the larger groups were excluded. The reason is that any assignment of these species to the larger groups would be arbitrary since it can be done in several valid ways, starting with incorporating any of the species in any of the contrasting groups. The same approach was used to form contrasting groups of hauls based on significant negative association between hauls.

In order to analyse the relation between species groups and groups of hauls, the occurrence of a species in a group of hauls was compared with its overall occurrence during the same season and year and deviation was tested for with the binomial test (p=0.05). A significantly higher occurrence than expected indicates preference of a species for that group of hauls, a significantly lower occurrence indicates avoidance.

Differences in environmental variables between contrasting groups of hauls were analysed with a t-test (p=0.05).

Results

For every season in a five-year period, the species with negative associations were divided in two contrasting groups (table 2). The negative associations observed were always rather weak, with V-values not lower than -0.2. Thus, the analysis identified contrasting but non-isolated groups of species. Two third of the total of 84 (length groups) of species caught in the survey area could be assigned to one of the two contrasting groups. The other species showed no significant negative association with any other species, either because they were too rarely represented in the catches, or because they were omnipresent in the survey area. For instance, the smallest length groups of dab (0-10 cm) and plaice (0-15 cm), both very abundant in the survey area and with a high catchability in the shrimp trawl net, did not show a negative association with any other species.

For every season in a year, the hauls with negative associations were always divided in two contrasting groups. The negative association between hauls was never complete, V-values being at minimum -0.6. Thus, the analysis identified also contrasting but non-isolated groups of hauls. Only a fifth of all the hauls used in the analysis could be assigned to one of the two contrasting groups. The other hauls belonged to pairs or triplets showing negative association only among themselves or, more commonly, showed no negative association at all and were thus of intermediate species composition.

One group of hauls was mainly situated in the Waddensea and the more inland part of the Scheldt estuary, the other group was mainly coastal (figure 1). Hauls from one group were often very close to hauls of the other group, especially in the Scheldt estuary. A few 'inshore' hauls were located along the coast, whereas 'coastal' hauls were sometimes found in the Wadden Sea and, more frequently, in the Scheldt estuary. Several sampling positions yield hauls, that in one year belong to the group of coastal hauls and in another year to the group of inshore hauls. As the grouping of hauls from one season was rather consistent for every year in a 5-year period, groups of hauls from every year were combined to form groups of hauls for a season in the whole 5-year period. The results discussed below are based on those combined groups of hauls.

The results of the binomial test show, that the group of inshore hauls was preferred by species from group I and avoided by species from group II and the other way round for the group of coastal hauls (table 2). However, the pattern of preference and avoidance is not straightforward for every species in both groups.

Representatives of group I with a clear preference for the 'inshore' hauls were: herring (*Clupea harengus*), bull rout (*Myoxocephalus scorpius*), smelt (*Osmerus eperlanus*), sprat (*Sprattus sprattus*), pipefish and eelpout (*Zoarces viviparis*). Representatives of the group II with a clear preference for the 'coastal' hauls were: scaldfish (*Arnoglossus laterna*), solenette (*Buglossidium luteum*), dragonet (*Callionymus lyra*), dab larger than 10 cm, plaice larger than 25 cm, sole between 15 and 25 cm, lesser weever (*Trachinus vipera*) and scad (*Trachurus trachurus*). Despite a clear preference, this does not mean, that these species are present in all the hauls within 'their' group. For instance, solenette and lesser weever were absent in the 'coastal' hauls in the Scheldt estuary and scaldfish was present in only one.

The pattern of grouping in species groups and groups of hauls is the essentially the same for spring 1980-1984, autumn 1980-1984 and autumn 1990-1994. There are differences between the three periods in the exact species composition within a group and the exact geographical location of the hauls within a group, but there is no indication of seasonal differences or a shift in grouping over the years.

For corresponding periods, the average depth and surface salinity of hauls was significantly lower for the 'inshore' hauls than for the 'coastal' hauls (table 3). However, hauls as deep as 25 meter were found in the group of inshore hauls and the group of coastal hauls contained hauls as shallow as 3 meter. Also for salinity, there was a large overlap between the two groups: in the group of inshore hauls, the maximum was 33.5 %, while in the group of coastal hauls, the minimum was 9.2 %. The average surface salinity was higher for the group of inshore hauls for autumn 1980-1984 than for the group of coastal hauls for spring 1980-1984. Consistent with the faster warming and cooling of the shallower inshore waters, the average surface temperature of the inshore hauls was significantly higher than of the coastal hauls in spring and lower in autumn. Average Secchi disc reading of the inshore hauls was significantly higher than of the coastal hauls during autumn 1980-1984, but significantly lower during autumn 1990-1994. Higher Secchi disc readings mean lower turbidity.

Table 2 Species in the two groups of species, their overall abundance and their occurrence in the groups of hauls; **+:** preference, **-:** avoidance, 0: neutral (bionomial test, two-sided, p=0.05), np: species is not present in species group

	nr. of positive hauls			inshore hauls			coastal hauls		
	spring 80-84	autumn 80-84	autumn 90-94	spring 80-84	autumn 80-84	autumn 90-94	spring 80-84	autumn 80-84	autumn 90-94
total number of hauls	1118	1126	1187						
number of hauls in group				186	51	133	188	57	167
species group I									
Agonus cataphractus	475	425	306	0	0	+	0	0	0
Alosa fallax	11	68	22	np	0	+	np	0	0
Anguilla anguilla	186	458	82	0	0	0	0	0	0
Ciliata mustela	191	295	345	np	+	+	np	-	-
Clupea harengus	461	568	558	+	+	+	-	-	-
Dicentrarchus labrax	8	13	26	np	np	0	np	np	0
Gadus morhua 0-25 cm	322	303	112	-	+	+	+	0	-
Gasterosteus aculeatus	76	9	12	+	np	np	0	np	np
Liparis liparis	33	381	235	np	+	+	np	-	-
Merlangius merlangus 0-15 cm	329	676	490	np	np	+	np	np	-
Myoxocephalus scorpius	491	486	234	+	+	+	-	-	0
Osmerus eperlanus	182	255	190	+	+	+	-	-	-
Pholis gunnellus	74	113	75	+	+	0	-	-	0
Platichthys flesus	683	513	440	np	+	+	np	-	-
Pomatoschistus	336	600	848	np	np	0	np	np	-
Scophthalmus rhombus 0-15 cm	56	68	58	0	np	np	0	np	np
Solea solea 0-15 cm	793	932	665	np	np	-	np	np	0
Sprattus sprattus	384	444	256	+	+	+	-	0	-
Syngnathidae	219	361	378	+	+	+	0	-	-
Zoarces viviparis	424	477	345	+	+	+	-	-	0
species group II									
Ammodytidae	164	166	163	0	0	-	0	0	+
Arnoglossus laterna	76	16	117	-	0	-	+	+	+
Atherina presbyter	70	35	6	0	0	np	-	0	np
Belone belone	4	9	5	np	0	np	np	0	np
Buglossidium luteum	137	64	110	-	0	-	+	+	+
Callionymus lyra	299	192	333	-	-	-	+	+	+
Callionymus reticulatus	0	0	8	np	np	0	np	np	+
Entelurus aequoreus	25	4	4	0	np	np	0	np	np
Eutrigla gurnardus	87	51	14	0	np	np	+	np	np
Gadus morhua > 25 cm	217	82	27	-	0	np	+	+	np
Hyperoplus lanceolatus	51	67	80	0	0	0	+	0	+
Limanda limanda 10 -15 cm	473	740	470	0	-	-	+	+	+
Limanda limanda 15 -20 cm	482	280	283	-	0	-	+	+	+
Limanda limanda 20 -25 cm	255	127	178	-	0	-	+	+	+
Limanda limanda > 25 cm	141	48	58	-	0	-	+	+	+
Merlangius merlangus 15-25 cm	464	542	392	-	0	np	+	0	np
Merlangius merlangus > 25 cm	109	163	78	-	0	-	+	+	0
Microstomus kitt	3	10	26	np	np	0	np	np	+
Mugilidae	6	10	1	np	0	np	np	0	np
Mullus surmuletus	0	11	26	np	0	0	np	0	+

Table 2 continued

Pleuronectes platessa 15-25 cm	720	803	623	np	np	-	np	np	+
Pleuronectes platessa > 25 cm	199	221	165	0	-	-	+	+	+
Pomatoschistus	336	600	848	0	-	np	+	+	np
Scomber scomber	2	13	5	np	0	np	np	0	np
Scophthalmus maximus 15-25 cm	66	98	64	0	0	0	0	0	+
Scophthalmus maximus > 25 cm	42	12	21	0	0	np	+	+	np
Scophthalmus rhombus 0-15 cm	56	68	58	np	0	np	np	0	np
Scophthalmus rhombus 15-25 cm	48	31	39	np	0	0	np	0	+
Scophthalmus rhombus > 25 cm	28	33	20	-	0	0	0	+	+
Solea solea 15- 25 cm	433	456	219	-	-	-	+	+	+
Solea solea > 25 cm	219	159	76	-	-	0	+	+	0
Trachinus vipera	28	36	120	0	0	-	+	+	+
Trachurus trachurus	16	138	109	0	-	-	+	+	+
Trigla lucerna	112	98	126	-	np	0	+	np	+
Trisopterus luscus	334	583	379	-	-	0	+	0	0
Trisopterus minutus	67	46	50	-	np	0	+	np	0

Table 3 Averages of environmental variables measured during the survey for the contrasting groups of hauls. Bold figures are significantly different from the average in the other group of hauls for the corresponding season and years (t-test, two-sided, p=0.05)

	inshore hauls			coastal hauls		
	spring 80-84	autumn 80-84	autumn 90-94	spring 80-84	autumn 80-84	autumn 90-94
depth (m below surface)	**7.8**	**7.2**	**7.9**	**12.6**	**13.6**	**14.7**
surface salinity (%)	**25.8**	**28.9**	missing	**27.3**	**29.7**	missing
surface temperature (^{O}C)	**9.3**	**14.9**	**14.4**	**9.0**	**15.6**	**14.9**
Secchi disc reading (m bel. surface)	1.0	**0.9**	**0.8**	1.1	**0.6**	**1.1**

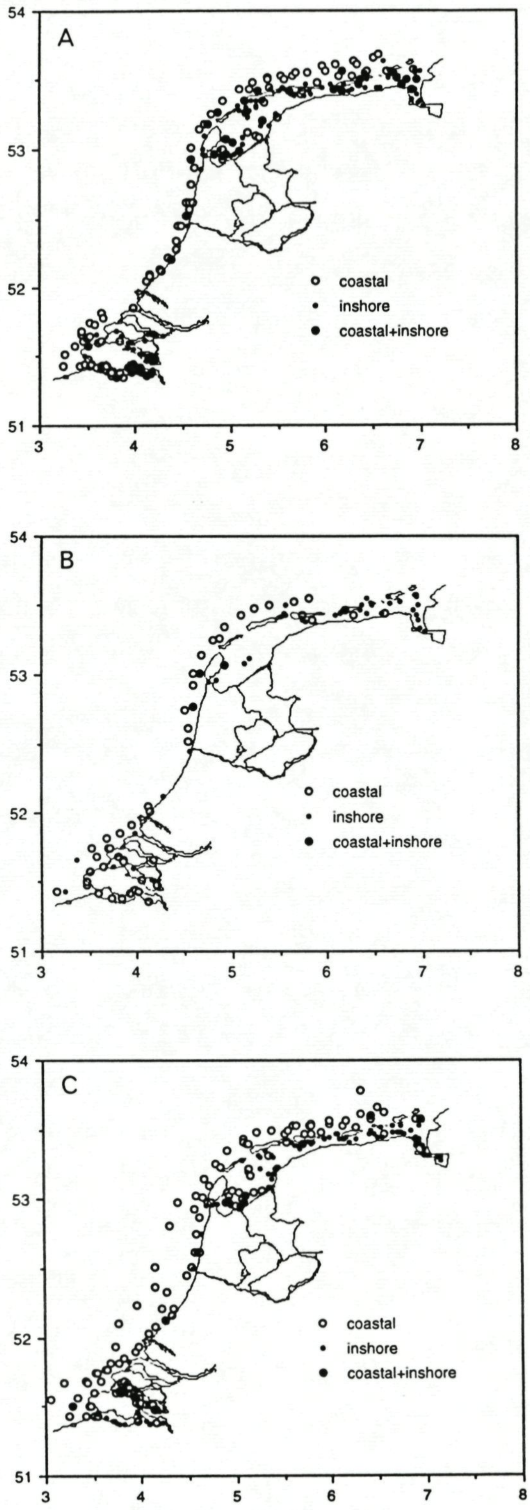

Figure 1 The geographical distribution the group of 'inshore' hauls and the group of 'coastal' hauls combined per 5-year period and season; A. spring 1980-1984, B. autumn 1980-1984, C. autumn 1990-1994

Discussion

Because the use of positive associations generally does not lead to contrasting groups (Krebs, 1979), negative associations were used. The grouping of species and hauls is based on the simultaneous presence of many of such negative associations. Several hundred times, the hypothesis of no association was rejected at a confidence level of 0.05 for every individual test. Thus, there is a high probability, that several of the negative associations observed are spurious. The problem of simultaneous statistical inference can be dealt with by using adjusted, much lower confidence levels. This would result in a strong reduction in the power of the tests and the identification of fewer negative associations. In this study, the identification of the largest possible contrasting groups of fish species was given priority above exact statistical results.

The weakness of the negative associations indicates that the groups are not entirely mutually exclusive. Even clear representatives of the two contrasting groups, like smelt and dragonet, were not seldom caught together. Also, the hauls with the sharpest contrast have species in common, like the omnipresent smallest length group of dab and plaice.

The catch data used came from a routine sampling program with standardised gear. Thus it is unlikely that the groups represent an artefact caused by the use of different sampling methodologies in different areas. However, the use of a single gear also has its drawbacks. The shrimp trawl net only samples a narrow layer above the bottom and is selective for bottom-dwelling species. Catchability of species exploiting the whole column of water like herring, sprat and grey mullets (*Mugilidae*) is low (Breckling & Neudecker, 1994) and may vary with water depth. Although, in this study, herring and sprat are strongly connected to inshore hauls, they are generally not considered to be typically inshore species (Knijn et al., 1993). With the survey gear, a considerable stretch of the bottom has to be fished to collect a sample that is sufficiently large from a research-efficiency point of view. A 15 minute haul covers a distance between 1500 and 2000 m. The possible presence of more subtle species associations occurring over shorter distances may thus be obscured. Moreover, a variety of important habitats in the survey area can not be fished with the shrimp trawl net: tidal flats, stony areas and mussel beds. In conclusion, the pattern of distribution found in this study is strongly influenced by the gear used in the survey program, but the existence of more clear-cut patterns of associations remains to be proven.

The results have been analysed on a presence-absence basis and therefore information on abundance is lost. However, it can be argued that, due to the gear selectivity and the known patchiness in the distribution of many fish species, the catch numbers are generally a poor estimate of their abundance on the site of sampling.

Many fish species from the species groups are not resident along the Dutch coast or in the estuaries, but show migration towards the open sea dependent on season or life stage (Zijlstra, 1978; Fonds, 1978). Examples are flounder (*Platichthys flesus*) and five-bearded rockling (*Ciliata mustela*), which leave the estuaries in winter for spawning in the North Sea, and herring and sprat, which inhabit coastal and estuarine waters only as juveniles during a rather short period. The seasonal migration of individual fish species, e.g. flounder and five-bearded rockling, sometimes caused differences between their presence in a species group for spring and for autumn data. Seasonality did not affect the overall grouping of species, because the groups were formed around resident species, such as eelpout, bull rout and smelt for the group with preference for the 'inshore' hauls and scaldfish, solenette, dragonet and lesser weever for the group with preference for the 'coastal' hauls. The preference of an individual species for a group of hauls gives only a poor indication of its exact distribution in the survey area. This is illustrated by the example of solenette and lesser weever, which both have a preference for the 'coastal' hauls, but are absent in the 'coastal' hauls in the Scheldt estuary.

Despite the significant differences in the average values for depth and salinity between the two groups of hauls, there is a large overlap between their ranges. Also, several sampling positions yield hauls that were grouped on the basis of their species composition with 'coastal' hauls in one year and with 'inshore' hauls in another. Fish species living in estuaries and coastal regions often show a high degree of tolerance for fluctuations in environmental variables such as temperature and salinity (Miller et al., 1983). This tolerance, together with their mobility, enables these species to explore a wide range of overlapping habitats.

The Scheldt estuary appears to have a relatively 'coastal' character compared to the Wadden Sea. In the Scheldt estuary, there are steep gradients from the tidal flats to deep channels and pits, whereas the Wadden Sea is mainly very shallow with only a few locations deeper than 15 m.

The results are to be interpreted as a general tendency in the distribution of fish species along the Dutch coast and in the estuaries. They do not provide a proof that there are two different communities. Neither are the results statistically exact, nor are the associations identified mutually exclusive. Moreover, there are not necessarily only two. Rather, the results suggest, that there is a gradual transition in the survey area from estuarine species, via coastal species, towards the fish community of the Southern and Eastern North Sea as identified by Daan et al. (1990). Within this transition, two rather loose species associations can be distinguished, representing the extremes within the survey area. Geographically, these extremes can be very close. To reveal, whether these species associations are hold together by feeding interactions, further research is needed along the line of the study by Daan et al. (1990).

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BENTHOS-EPIBENTHOS INTERACTIONS IN THE DUTCH WADDEN SEA

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CONTENTS

ABSTRACT

In this paper, the 'distribution hypothesis' is studied for the common epibenthic species in the Dutch Wadden Sea area. A total of 38 sampling stations, distributed over the intertidal and subtidal of the Dutch Wadden Sea, were visited in August - September 1987 and simultaneously sampled for benthic infauna and epibenthic predators. The benthic fauna consisted of in total 26 different species, of which 15 belonged to the Polychaetes, 6 to the Molluscs and 5 to the group of Crustaceans. No clear difference between intertidal and subtidal areas could be observed. All species were found in the intertidal and only *Corophium volutator* did not occur in the sublittoral. Biomass values were on average higher in the intertidal than in the sublittoral. The mean biomass in the intertidal amounted about 75 g AFDW.m^{-2}, while in the sublittoral values were on average about 28 g AFDW.m^{-2}. Most biomass consisted of bivalves and the very high values were mainly caused by mussel beds in the intertidal. At all stations, crustaceans hardly contributed to the total biomass figure. In the epibenthic survey, in total 21 epibenthic species were caught among which 18 fish species. Almost all species did occur in the sublittoral, except for the butterfish *Pholis gunellus*. The sea-snail *Liparis liparis* and the scad *Trachurus trachurus* were only found in the sublittoral and did not occur in the intertidal. With respect to the relative frequency of occurrence and biomass of a species, 5 species could be considered as characteristic for the intertidal. The sand goby *Pomatoschistus minutus*, the brown shrimp *Crangon crangon* and the shore crab *Carcinus maenas* were present at all stations, and also the plaice *Pleuronectes platessa* and the Nilsson's pipefish *Syngnathus rostellatus* could be found at more than 75% of the stations. In the sublittoral, two other species were common: the sandeel *Ammodytes tobianus* and the bull rout *Myoxocephalus scorpius*. Also the starfish *Asterias rubens* and the dab *Limanda limanda* were more frequently observed in the sublittoral. A few significant relationships between epibenthic and benthic species were found. The dab *Limanda limanda* showed a negative relationship with the bivalve *Macoma balthica*. The abundance of the whiting *Merlangius merlangius* was positively related to the biomass of the polychaete *Magelone papilliformis*. The sand goby *Pomatoschistus minutus* showed a positive relationship to the biomass of *Capitella capitata* and the brown shrimp *Crangon crangon* showed a relationship with *Heteromastus filiformis*. In the present analysis this 'distribution hypothesis' could not be validated. The main reason was a too low number of sampling stations. The validation should be repeated with a much larger number of sampling stations, including very muddy areas. Another improvement would be a more frequent sampling in time, instead of August-September only.

1. INTRODUCTION

In a previous paper the habitat characteristics for the functional groups of the fish fauna of the Dutch coastal zone were analysed based on survey data of the western Wadden Sea (Van der Veer & Witte, 1996). The various functional groups showed a different pattern of relative use of the different habitat types. For all four functional groups (resident, non-spawning, nursery-type and seasonal visitors) the intensity in using various habitats increased from intertidal to subtidal and tidal channel. Species richness was lowest at the tidal flats and highest in the tidal channels. For both the resident species and the nursery-type species growth appeared to be maximal and only determined by the prevailing water temperature. This supports the 'carrying capacity' hypothesis which states that the various predatory fish species are not food limited, and that no density-dependent growth occurs. The 'distribution hypothesis', predicting a relationship between the distribution of both predator and its main prey species was falsified for the resident species studied. Their distribution did not correspond to that of their main prey items, the crustaceans. However, in the nursery-type species the distribution was related to that of their prey items, the infauna. It was concluded that the distribution of the various fish species will only follow that of their main prey species in case of sessile infaunal prey. In case the main prey items consist of mobile epibentic species, no relationships will be present.

So far, the 'distribution hypothesis' has only be studied in a restricted area, the western part of the Dutch Wadden Sea and for a small number of fish species (Van der Veer & Witte, 1996). In this paper, the 'distribution hypothesis' will be studied for the other common epibenthic species, including crustaceans. Furthermore, the analysis of the benthos-epibenthos interactions will be expanded to the whole Dutch Wadden Sea area. Based on simultaneous sampling of infauna and epibenthic fauna, the benthos-epibenthic relationships will be analysed in relation to the 'distribution hypothesis'.

2. MATERIAL AND METHODS

The survey was carried out in August and early September 1987 and covered the Dutch Wadden Sea. In total 38 stations were visited and sampled at low water for macrozoobenthos and at high water for the epibenthic community (Table 1). 20 stations were located in the intertidal zone and 18 stations were situated in the sublittoral. The intertidal is defined as the area with drained tidal flats at low-low-water spring (LLWS). Sublittoral or subtidal areas are areas between LLWS and LLWS - 5 m. Tidal channels are areas deeper than 5 m below LLWS. The position of the stations was located with a Philips AP Navigator (accuracy ± 50 m).

2.1. Macrozoobenthic sampling

At each intertidal station 50 samples were taken, at 20 m distance along a transect of 1000 m at low water. A PVC core of 86.5 cm^2 was used up to a depth of 30 cm. In total, a surface area of 0.42 m^2 was sampled. In the sublittoral 5 samples were collected with a 0.06 m^2 box core at a depth of at least 15 cm. Macrobenthic animals were collected by sieving the sediment in the field through a 1 x 1 mm sieve. They were preserved in a 4% formalin-seawater solution and sorted out in the laboratory into species and if possible into different year classes.

Ash-free dry weights (AFDW) were determined for all animals or of subsamples by drying at 60°C for 2 h. The weight loss at 560°C was considered to represent the AFDW. All numbers and biomass values were converted into numbers or g AFDW per m^2 ($n.m^{-2}$ and g $AFDW.m^{-2}$). For each station the arithmetic mean value was computed.

2.2. Epibenthic survey

Sampling was carried out for a period of 3 h around high water during daytime following Kuipers (1973, 1977), since during this period the migrating part of flatfish populations is distributed randomly over the tidal flats, and consequently the migrating intertidal and the resident sublittoral populations will be split up.

In the intertidal, fishing was done from a rubber dinghy powered by a 25 Hp outboard motor using a 2 m beam trawl with 1 tickler chain in front and a 5 x 5 mm mesh size knotless nylon net. The distance covered by the hauls was registered by a meter wheel fitted to the frame. At each location 2 or 3 hauls of about 300 m were made, covering a total area of at least 1200 m^2. In the sublittoral and tidal channels fishing was done by RV 'Navicula' using a heavier 3 m beam trawl with 1 tickler chain and a 1 x 1 cm mesh size. For more information see Bergman *et al.* (1989). At each station 1 to 3 hauls were made of at least 600 m, covering at least 1800 m^2.

After sorting of the sample within a few hours, all epibenthic animals were identified and measured in 0.5 cm total length classes. Of each species numbers caught were converted into densities per 1000 m^2. Flatfishes were corrected for net efficiency according to the data of plaice of Kuipers (1975) and Dapper (1978) for the 2 m beam trawl and Bergman *et al.* (1989) for the 3 m beam trawl. For all other species, an average efficiency of 35% was assumed. For each station arithmetic-mean abundance and length were estimated. All statistical analyses were done with SYSTAT (Wilkinson, 1989) with adjustment (Bonferroni correction) to the probability for multiple testing (Rice, 1989).

3. RESULTS

3.1. Macrozoobenthic sampling

3.1.1. Species composition

In total 26 different species were found, of which 15 belonged to the group of Polychaetes, 6 to the Molluscs and 5 to the Crustaceans (Table 2). No clear difference between intertidal and subtidal areas could be observed. All species were found in the intertidal and except for *Corophium volutator* they did also occur in the sublittoral. Between stations, a difference in number of species present could be seen, however, both in the intertidal and the sublittoral the minimum number of species was more than 7.

With respect to relative frequency of occurrence of a species, most species appeared to be rather common (Fig. 1). In the intertidal *Macoma balthica* did occur at all station and also 7 more species did occur at more than 75% of the stations. Only 5 species were found at less than 25% of the stations in the intertidal: *Magelone papillicornis*, *Gammarus locusta*, *Tharyx marioni*, *Spiophanes bombyx* and *Corophium volutator*. All other species were present at between 25 and 75% of the stations. In general, species were less common in the sublittoral than in the intertidal. Only *Macoma balthica*, *Heteromastus filiformis* and *Scoloplos armiger* were also present at almost all stations in the sublittoral. Some species occurred much less frequently in the sublittoral and they could be considered more as intertidal species: the polychaete species *Eteone longa* and *Phyllodoce maculata* and the bivalves *Ensis americanus, Mytilus edulis*, *Cerastoderma edule* and *Mya arenaria*. *Corophium volutator* did not occur in the sublittoral at all.

3.1.2. Abundance

Biomass values were on average higher in the intertidal than in the sublittoral (Fig. 2). The mean biomass in the intertidal amounted about 75 g AFDW.m^{-2}, while in the sublittoral values were on average about 28 g AFDW.m^{-2}. Most biomass consisted of bivalves and the very high values were mainly caused by mussel beds in the intertidal. At all stations, crustaceans hardly contributed to the total biomass figure.

On species level, a few species formed the major part of the total biomass (Fig. 3). In the intertidal, *Mytilus edulis*, *Mya arenaria* and *Cerastoderma edule* occurred in mean biomasses of over 10 g AFDW.m^{-2}. Together with *Macoma balthica*, *Hydrobia ulvae* and *Arenicola marina* they formed up to 80 % of the total biomass. In the sublittoral also *Mytilus edulis* was most important in terms of biomass, followed by *Mya* *arenaria*. Together with *Nereis virens*, *Heteromastus filiformis* and *Carcinus maenas* they formed the major part of the total biomass in the sublittoral.

3.1.3. Interspecies relationships

Spearman's rank correlation test revealed a number of significant relationships between the biomasses of the various species (Table 3).

The lugworm *Arenicola marina* showed a significant positive relationship with *Harmothoe* sp and with the bivalves *Macoma balthica* and *Mya arenaria*. Also the biomass of *M. arenaria* was positively related to that of *Harmothoe* sp. and that of *M. balthica*. Another group of related biomasses was formed by the polychaete species *Nereis virens*, *Lanice conchilega* and *Phyllodoce maculata*. They all showed significant relationships with the two other species. The biomass of *L. conchilega* was also positively related to that of *Pectinaria koreni* and the bivalve *Ensis ensis*. Finally, *Eteone longa* showed a positive relationship with *Macoma balthica* and *Phyllodoce maculata*.

3.2. Epibenthic survey

3.2.1. Species composition

In total 21 epibenthic species were caught in the beam trawl catches (Table 4) among which 18 fish species. Almost all species did occur in the sublittoral, except for the butterfish *Pholis gunellus*. The sea-snail *Liparis liparis* and the scad *Trachurus trachurus* were only found in the sublittoral and did not occur in the intertidal.

With respect to the relative frequency of occurrence of a species, 5 species could be considered as characteristic for the intertidal (Fig. 4). The sand goby *Pomatoschistus minutus*, the brown shrimp *Crangon crangon* and the shore crab *Carcinus maenas* were present at all stations, and also the plaice *Pleuronectes platessa* and the Nilsson's pipefish *Syngnathus rostellatus* could be found at more than 75% of the stations. Together with 6 other species that occurred in a frequency of between 30 and 50% (flounder, dab, sole, herring, viviparous blenny and starfish), these species formed the major part of the intertidal epibenthic community. In addition in the sublittoral two other species were common: the sandeel *Ammodytes tobianus* and the bull rout *Myoxocephalus scorpius*. Also the starfish *Asterias rubens* and the dab *Limanda limanda* were more frequently observed in the sublittoral.

3.2.2. Abundance

Of all species found, only a few did occur in high densities. Both the mean and the median density resulted in about the same pattern (Fig. 5). The most abundant species were the sand goby *Pomatoschistus minutus*, the brown shrimp *Crangon crangon* and the shore crab *Carcinus maenas*. These species were also present at almost all stations. On average, densities in the intertidal appeared to be higher than those in the subtidal.

The other species of importance with respect to their density were the plaice, both in the intertidal and the subtidal, dab and sole in the subtidal, flounder in the intertidal, the viviparous blenny in the subtidal and Nilsson's pipefish in both the inter- and subtidal.

3.2.3. Relationship between species

Only 3 significant relationships between the abundance of species were found (Table 5). The shore crab *Carcinus maenas* showed a significant positive relationship with the brown shrimp *Crangon crangon* and with the sand goby *Pomatoschistus minutus.* The other significant relationship did occur between the dab *Limanda limanda* and the swimming crab *Liocarcinus holsatus.* This relationship was mainly caused by the stations in the subtidal.

3.3. Benthos-epibenthos interactions

A few significant relationships between the abundance of epibenthic and the biomass of benthic species was found (Table 6). The dab *Limanda limanda* showed a negative relationship with the bivalve *Macoma balthica.* The abundance of the whiting *Merlangius merlangius* was positively related to the biomass of the polychaete *Magelone papilliformis.* The sand goby *Pomatoschistus minutus* showed a positive relationship to the biomass of *Capitella capitata* and the brown shrimp *Crangon crangon* showed a relationship with *Heteromastus filiformis.*

4. DISCUSSION

4.1. Sampling strategy

The study of benthos-epibenthos interactions in the Wadden Sea automatically implies the combination of two completely different sampling strategies.

The benthic organisms are mostly sessile and can be collected in a rather easy straightforward manner; see for instance Beukema (1976). Core samples are sieved either directly at the tidal flats or on board in case of box core samples from subtidal stations. In the case of benthic samples, there is no real problem with respect to sampling efficiency. Only the mesh size of the sieve is influencing the size range of the organisms that can be collected. However, this size range is constant for all samples, irrespectively of sediment type or in other words sampling station. The main limitation in sampling the sessile benthic community is the small sampling area. Both for the intertidal stations and for the subtidal stations, the total area sampled is less than 1 m^2. This means that despite the high densities and biomasses of most benthic organisms, the data obtained are not representative for a large area.

The potential biases in sampling the epibenthic mobile organisms are different. All species are sampled with one sampling gear with a different efficiency for each species. For most species the exact efficiency is even unknown. Only in a few cases, such as for plaice *Pleuronectes platessa*, the net efficiency has been studied in detail and related to fish size (Kuipers, 1975).

Temporal variability is another potential source of bias. Kuipers & Dapper (1984) showed that at the tidal flats a clear seasonal pattern in abundance of epibenthic predators can be observed (Fig. 6). However, each species has its own timing and as a consequence a sequence of peak abundance of the various species can be observed between June and August. Therefore, densities observed in catches will depend on the timing of the sampling programme. The sampling window in this study (August-beginning of September) corresponds with a time period in which all species are still present in relatively high densities.

4.2. Relationship between species

4.2.1 Benthos

In terms of biomass only a few species account for most of the biomass. In the intertidal *Mytilus edulis, Mya arenaria* and *Cerastoderma edule*, together with *Macoma balthica, Hydrobia ulvae* and *Arenicola marina* formed up to 80 % of the total biomass. In the sublittoral also *Mytilus edule* was most important in terms of biomass, followed by *Mya arenaria*. Together with *Nereis virens, Heteromastus filiformis* and *Carcinus maenas* they formed the major part of the total biomass in the sublittoral. This means that in terms of biomass in the Wadden Sea, only a few species are characteristic. In total 26 species were found, however of most species biomass values were too low and their occurrence was too infrequent to permit an analysis of relationships and interactions.

Dankers & Beukema (1981) presented an overview of the distribution patterns of macrozoobenthic species in the Wadden Sea in relation to environmental factors. In their detailed analysis they concentrate on the most important abiotic factors, such as tide and water movements, sediment type, salinity and temperature. They excluded in their analysis the biotic factors and furthermore interactions between species were also not taken into account.

In our study, a number of significant relationships between the biomasses of species was found. The significant relationship between the lugworm *Arenicola marina* and *Harmothoe* sp illustrated the fact that *Harmothoe* is living in the hollows of *A. marina*. However, the relationships between *A. marina* and the bivalves *Macoma balthica* and *Mya arenaria* suggests that they might be considered as a community. The data further suggest that most probably the cockle *Cerastoderma edule* also belongs to this community. This *Arenicola*-bivalve community is especially important and abundant at the intertidal. From the information on the individual species as presented by Dankers & Beukema (1981) it appears that these three species do occur in the same range of abiotic conditions.

Another group of related biomasses was formed by the polychaete species *Nereis virens, Lanice conchilega* and *Phyllodoce maculata*. They all showed significant relationships with the two other species. Maybe *Heteromastus filiformis* also belongs to this group, however the relationships were not statistically significant. This *Nereis* group shows partly different requirements from that of the *Arenicola*-bivalve community: no significant relationships between species of both groups did occur.

4.2.2. Epibenthos

Although in total 21 epibenthic species were caught in the beam trawl catches, hardly any specific difference could be found between intertidal and subtidal. The butterfish *Pholis gunellus* did only occur in the intertidal and the sea-snail *Liparis liparis* and the scad *Trachurus trachurus* were only found in the sublittoral.

In the intertidal, 5 species could be considered as characteristic. The sand goby *Pomatoschistus minutus*, the brown shrimp *Crangon crangon* and the shore crab *Carcinus maenas* were present at all stations, and also the plaice *Pleuronectes platessa* and the Nilsson's pipefish *Syngnathus rostellatus* could be found at more than 75% of the stations. Together with 6 other species that occurred in a frequency of between 30 and 50% (flounder, dab, sole, herring, viviparous blenny and starfish), these species formed the major part of the intertidal and the subtidal epibenthic community. In the sublittoral the sandeel *Ammodytes tobianus* and the bull rout *Myoxocephalus scorpius* were also common.

Despite the relative frequent occurrence of about 10 species, only a few relationships could be found. The significant positive relationships between the shore crab *Carcinus maenas* and the brown shrimp *Crangon crangon* and the sand goby *Pomatoschistus minutus* illustrates the fact that these three species occupy the same type of habitat. All three belong to the small group of very abundant species in the Wadden Sea, especially in the intertidal. The other significant relationship between the dab *Limanda limanda* and the swimming crab *Liocarcinus holsatus* reflects the fact that both species are mainly found in the subtidal.

These few relationships between epibenthic species might suggest that interactions between epibenthic species are absent or at least not strong.

4.3. Benthos-epibenthos interactions

Only a few significant relationships between epibenthic and benthic species were found. However, in case of a significant relationship this does not automatically imply a causal relationship. In the case of the dab *Limanda limanda* the negative relationship with the bivalve *Macoma balthica* more likely reflects the preference of the dab for subtidal areas and the preference for *Macoma* for the intertidal. Also it is doubtful whether the positive relationship between the abundance of the whiting *Merlangius merlangius* and the biomass of the polychaete *Magelone papilliformis* really reflects a causal relationship. Only the positive relationships between the sand goby *Pomatoschistus minutus* and the biomass of *Capitella capitata* and between the brown shrimp *Crangon crangon* and the biomass of *Heteromastus filiformis*, might reflect a causal relationship. For both species the benthic species forms an important prey item (Muus, 1966).

One of the aims of this paper was to expand the study of the 'distribution hypothesis' from the eel pout and bull rout to other common epibenthic species, including crustaceans and also to expand the analysis of the benthos - epibenthos interactions to the whole Dutch Wadden Sea area. In a previous study (Van der Veer & Witte, 1996) it was concluded that the 'distribution hypothesis', predicting a relationship between the distribution of predator and its main prey species would only be valid in the case of sessile infaunal prey items. For instance, the distribution of plaice in the western Wadden Sea corresponded to that of its main prey items (Van der Veer & Witte, 1996). However, in the present analysis this relationship is not validated. Moreover, hardly any significant relationships at all are observed. The lack of relationship cannot be caused by an inferior sampling design. The sampling programme in this studies is similar to that in the previous one. Therefore, in our opinion, the main reason is a too low number of sampling stations. This means that this validation should be repeated with a much larger number of sampling stations, including very muddy areas. Another improvement would be a more frequent sampling in time, as has been done in the previous study (Van der Veer & Witte, 1996).

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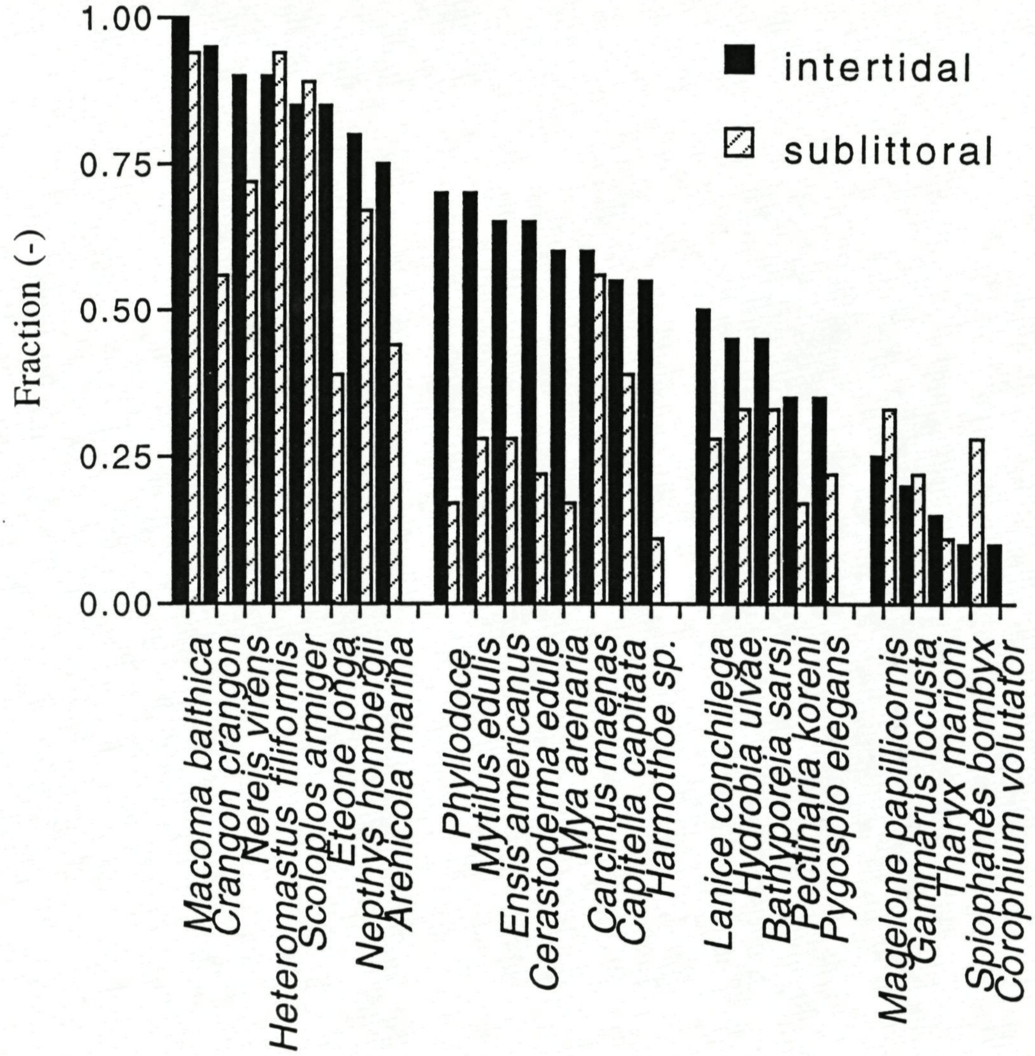

Fig. 1. Relative frequency of occurrence of a benthic species in the intertidal and the subtidal, expressed as fraction (-). 1 means present at all station, 0 present at no stations.

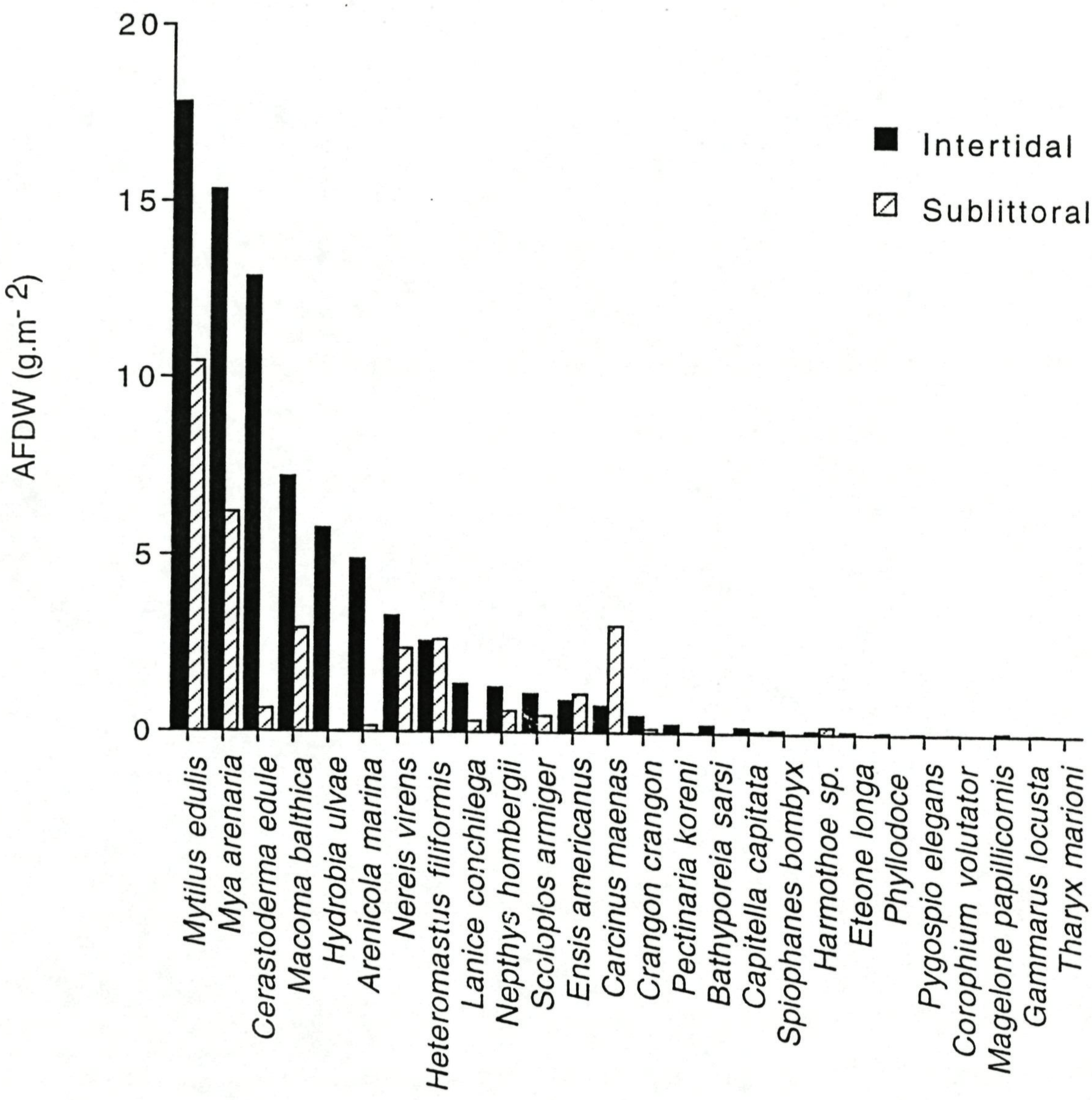

Fig. 2. Mean biomass (g AFDW.m^{-2}) of the various benthic species in the intertidal and subtidal.

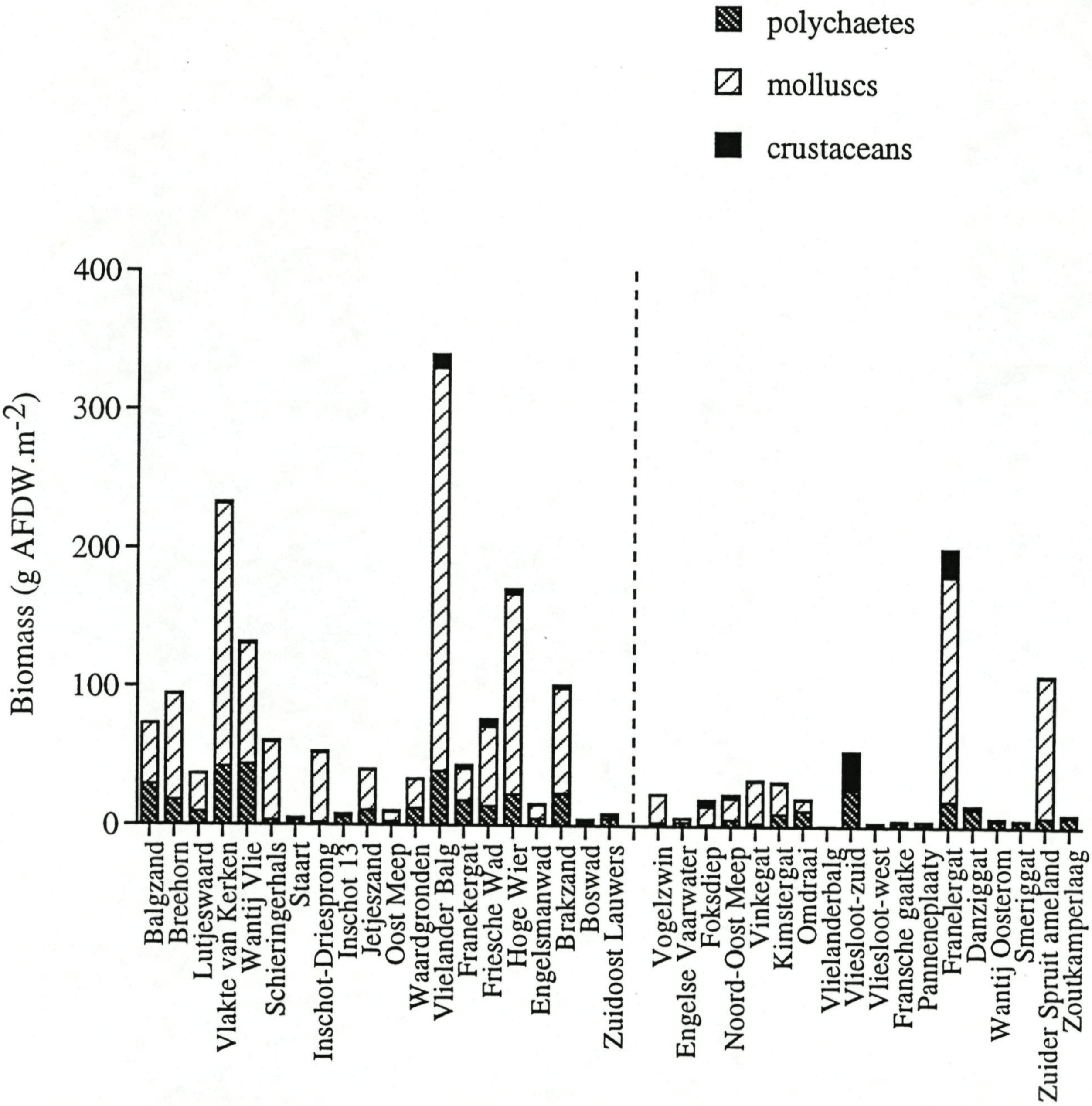

Fig. 3. Mean biomass (g AFDW.m^{-2}) of the benthos at the various sampling stations in the intertidal and subtidal, separated for polychaetes, molluscs and crustaceans.

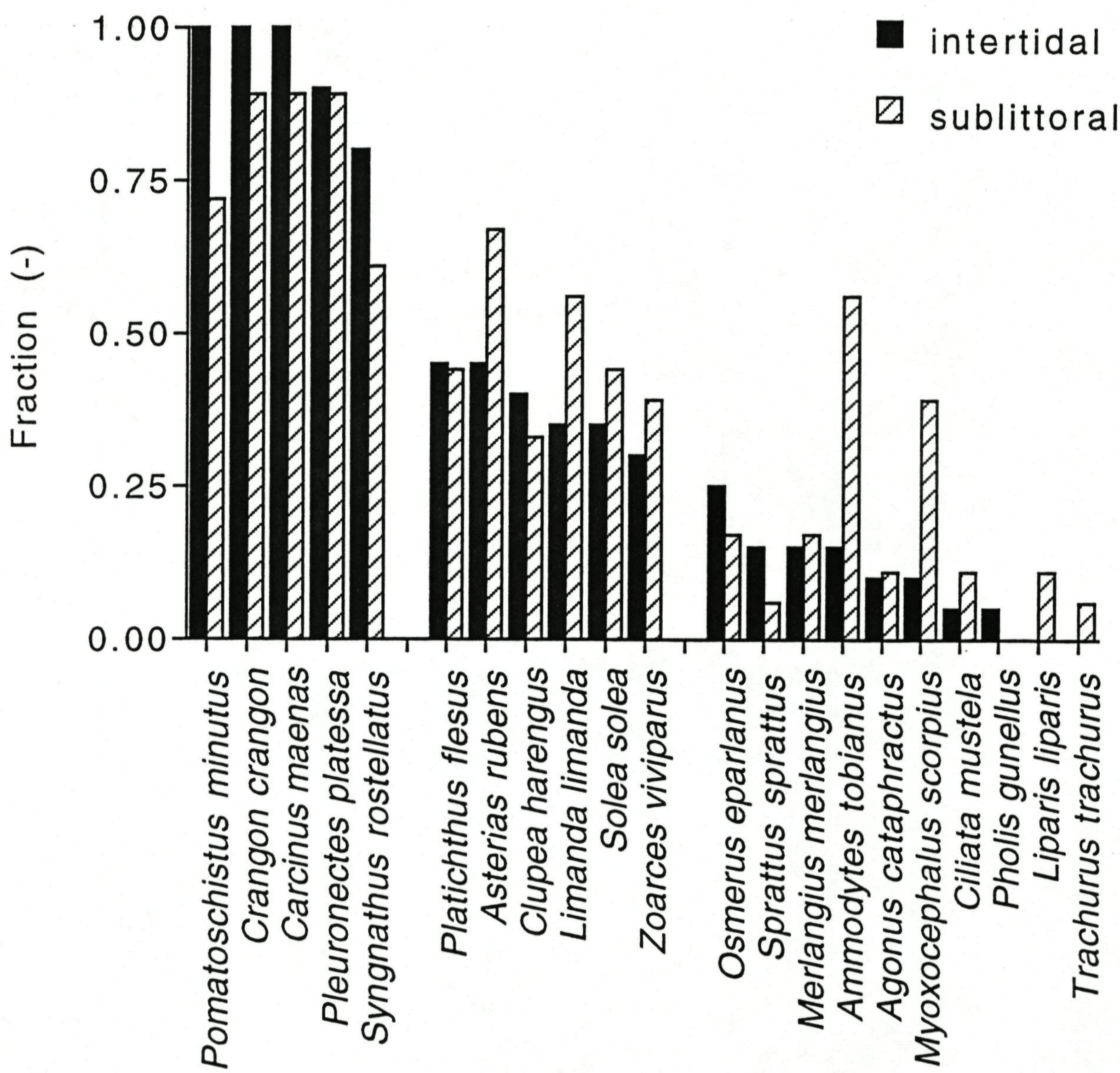

Fig. 4. Relative frequency of occurrence of a epibenthic species in the intertidal and the subtidal, expressed as fraction (-). 1 means present at all station, 0 present at no stations.

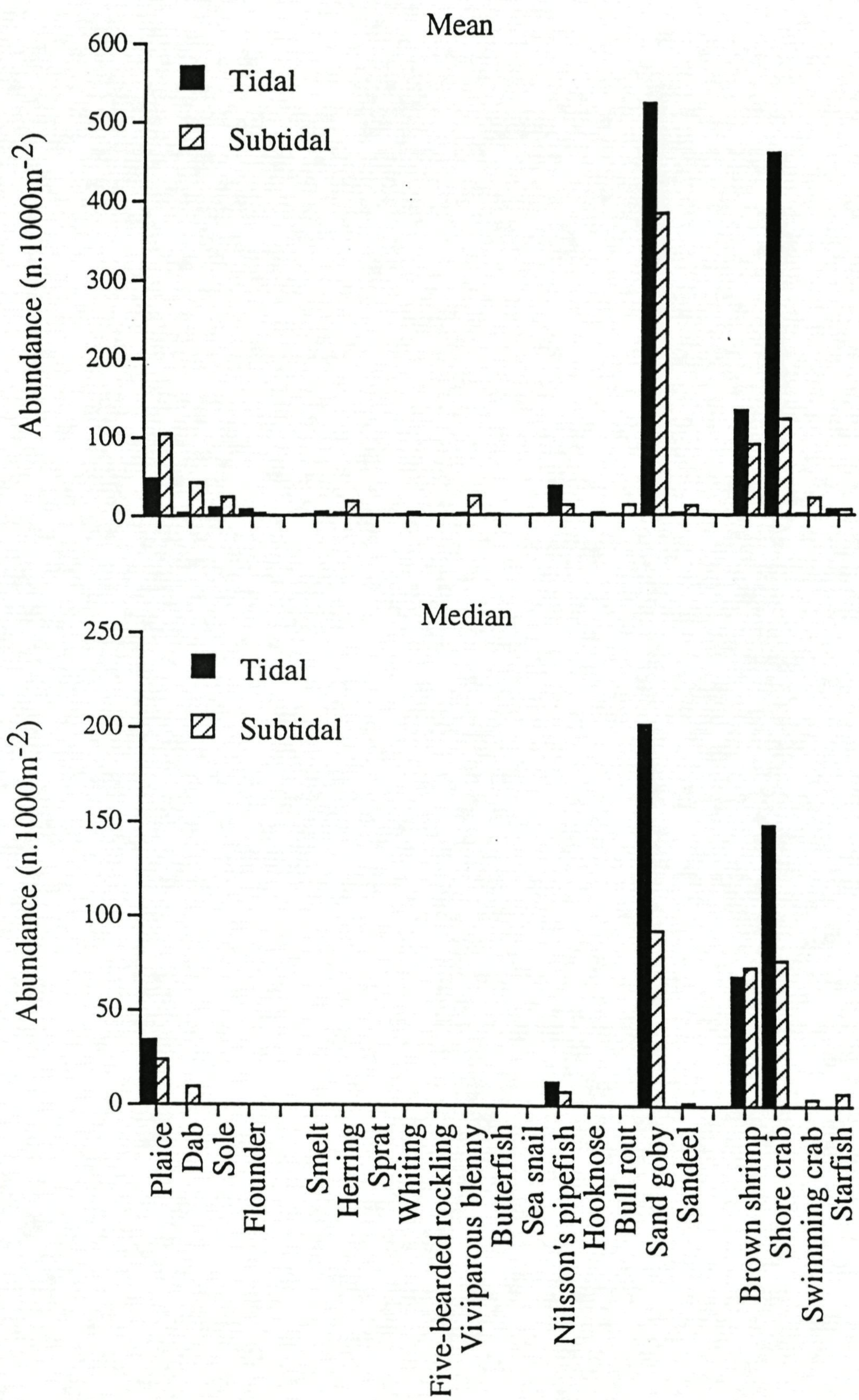

Fig. 5. Mean and median abundance (n. 1000 m^{-2}) of the epibenthic species at the various sampling stations in the intertidal and subtidal

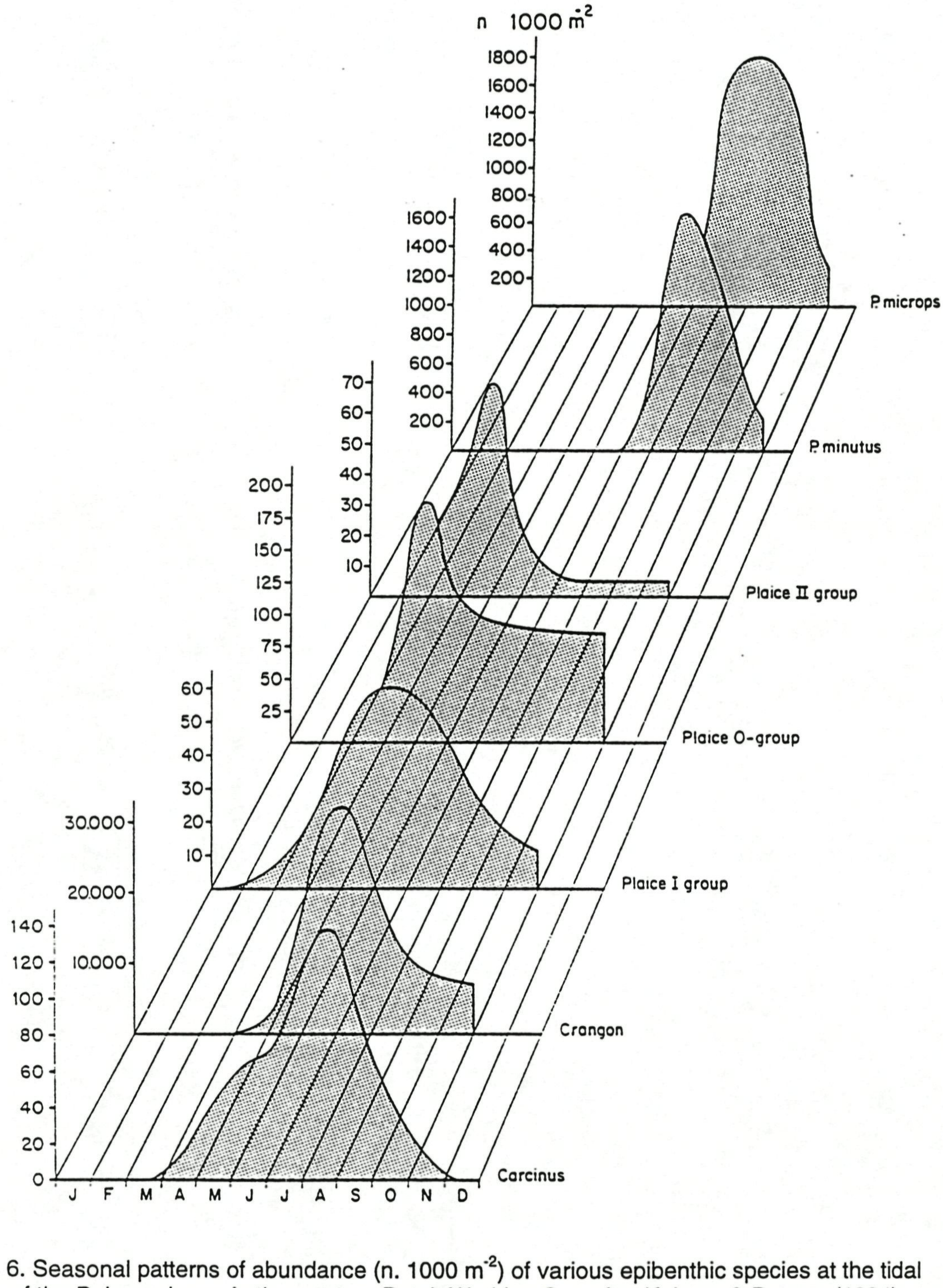

Fig. 6. Seasonal patterns of abundance (n. 1000 m^{-2}) of various epibenthic species at the tidal flats of the Balgzand area in the western Dutch Wadden Sea after Kuipers & Dapper (1984).

TABLE 1

Stations in the various tidal basins of the Dutch Wadden Sea, sampled for macrozoobenthos and epifauna. 200 code refers to intertidal stations; 300 code to subtidal areas. At each station 2-4 beam trawl samples and 5 macrozoobenthic samples were collected. Mean position, together with water depth (m) is given. For more information see text.

Station	Station	Benthos code	Epifauna code	Latitude (N)	Longitude (E)	Depth (m)
	Marsdiep					
1	Balgzand	L	294	52'56	4'54	0.6
2	Breehorn	1	295	52'57	4'59	1.1
3	Lutjeswaard	2	296	52'59	5'03	1.2
	Eierlandsche Gat					
4	Vlakte van Kerken	247	247	53'09	4'55	1.2
5	Vogelzwin	334	334	53'09	4'55	4.0
6	Engelsche Vaarwater	335	335	53'11	4'59	7.0
7	Foksdiep	336	336	53'09	5'00	7.5
	Vlie					
8	Wantij Vlie	19	252	53'16	5'01	2.3
9	Schieringerhals	20	253	53'15	5'09	1.5
10	Staart	21	253	53'14	5'08	1.5
11	Inschot-Driesprong	22	249	53'11	5'08	1.6
12	Inschot-13	23	249	53'11	5'09	1.6
13	Jetjeszand	33	259	53'18	5'17	1.0
14	Oost Meep	34	258	53'19	5'25	1.0
15	Waardgronden	254	254	53'12	5'06	0.9
16	Vlielander Balg	250	250	53'17	5'06	2.7
17	Franekergat	255	255	53'17	5'16	1.1
18	Noord Oost Meep	327	327	53'18	5'29	2.5
19	Vinkegat	329	329	53'19	5'33	1.0
20	Kimstergat	330	330	53'17	5'27	2.5
21	Omdraai	337	337	53'09	5'09	7.5
22	Vlielander Balg	338	338	53'16	5'06	8.5
23	Vliesloot-zuid	339	339	53'16	5'04	8.0
24	Vliesloot-west	340	340	53'16	5'02	4.5
25	Fransche Gaatje	341	341	53'17	5'08	3.5
26	Pannenplaat	342	342	53'17	5'13	1.5
27	Franekergat	343	343	53'17	5'18	3.0
	Borndiep					
28	Friesche Wad	48	235	53'24	5'50	1.0
29	Hoge Wier	237	237	53'23	5'42	1.6
30	Dantziggat	322	322	53'23	5'48	5.0
31	Wantij Oosterom	326	326	53'23	5'30	0.5
	Pinkegat					
32	Engelsmanplaat	54	231	53'26	6'02	1.8
33	Smeriggat	318	318	53'26	6'00	4.0
34	Zuider Spruit Ameland	321	321	53'25	5'55	1.0
	Friesche Zeegat					
35	Brakzand	59	229	53'26	6'11	1.9
36	Zoutkamperlaag	316	316	53'25	6'11	6.0
	Lauwers					
37	Boswad	217	217	53'29	6'29	2.3
38	Zuidoost Lauwers	218	218	53'29	6'27	-

TABLE 2

Taxonomic list of macrozobenthic species found in the various samples, latin names together with common Dutch names

Latin name	Dutch name
Polychaetes	
Arenicola marina	zeepier
Scoloplos armiger	wapenworm
Magelone papillicormis	
Nephtys hombergii	zandzager
Nereis virens	zager
Spiophanes bombyx	
Pectinaria koreni	goudkammetje
Heteromastus filiformis	draadworm
Lanice conchilega	schelpkokerworm
Eteone longa	
Phyllodoce maculata	gestippelde dieseltreinworm
Pygospio elegans	
Tharyx marioni	
Capitella capitata	
Harmothoe sp.	zeerupsachtigen
Molluscs	
Hydrobia ulvae	wadslakje
Ensis ensis	kleine zwaardschede
Macoma balthica	nonnetje
Cerastoderma edule	kokkel
Mya arenaria	strandgaper
Mytilus edule	mossel
Crustaceans	
Gammarus locusta	vlokreeftachtigen
Corophium volutator	slijkgarnaal
Carcinus maenas	strandkrab
Crangon crangon	gewone garnaal
Asterias rubens	zeester

TABLE 3

Significant Spearman's rank correlations (*) after Bonferroni correction (p<0.001) between the biomass of benthic species. For more information see text.

	A.m	N.v.	P.k.	L.c	E.l.	P.m.	H.	E.e.	M.b.	M.a.	G.l.	C.m.
Arenicola marina												
Nereis virens												
Pectinaria koreni												
Lanice conchilega		*	*									
Eteone longa												
Phyllodoce maculata		*		*	*							
Harmothoe sp.	*											
Ensis ensis				*								
Macoma balthica	*				*							
Mya arenaria	*						*		*			
Gammarus locusta												
Carcinus maenas				*							*	

TABLE 4

Latin name	English name	Dutch name
Pleuronectes platessa	plaice	schol
Limanda limanda	dab	schar
Solea solea	sole	tong
Platichthys flesus	flounder	bot
Osmerus eperlanus	smelt	spiering
Clupea harengus	herring	haring
Sprattus sprattus	sprat	sprot
Merlangius merlangus	whiting	wijting
Ciliata mustela	five-bearded rockling	vijfdradige meun
Zoarces viviparus	viviparous blenny	puitaal
Pholis gunnellus	butterfish	botervis
Liparis liparis	sea-snail	slakdolf
Agonus cataphractus	hooknose	harnasmannetje
Myoxocephalus scorpius	bull rout	zeedonderpad
Ammodytes tobianus	sandeel	zandspiering
Syngnathus rostellatus	Nilsson's pipefish	kleine zeenaald
Pomatoschistus minutus	sand goby	dikkopje
Crangon crangon	brown shrimp	garnaal
Carcinus maenas	shore crab	strandkrab
Liocarcinus holsatus		gewone zwemkrab
Asterias rubens	starfish	gewone zeester

TABLE 5

Significant Spearman's rank correlations (*) after Bonferroni correction (p<0.001) between the abundance of epibenthic species. For more information see text.

	L.l.	*P.m.*	*C.m.*	*C.c.*	*L.h.*
Limanda limanda					
Pomatoschistus minutus					
Carcinus maenas		*			
Crangon crangon			*		
Liocarcinus holsatus	*				

TABLE 6

Significant positive (+) and negative (-) Spearman's rank correlations after Bonferroni correction (p<0.001) between the abundance of epibenthic species and the biomass of benthic species. For more information see text.

Epibenthic species	Benthic species	
Limanda limanda	*Macoma balthica*	-
Merlangius merlangius	*Magelone papilliformis*	+
Pomatoschistus minutus	*Capitella capitata*	+
Crangon crangon	*Heteromastus filiformis*	+

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