AN EVALUATION OF INTERTIDAL FEEDING HABITATS FROM A SHOREBIRD PERSPECTIVE: TOWARDS RELEVANT COMPARISONS BETWEEN TEMPERATE AND TROPICAL MUDFLATS

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ABSTRACT

Macrozoobenthic communities of intertidal soft sediments are reviewed worldwide from the perspective of a mollusc-eating shorebird species. Based on 19 sites, total biomass figures varied between 5 and 80 g AFDM per m^2 (average 24 g AFDM per m^2); no latitudinal trends are apparent. The contribution made by bivalves and gastropods varies between 1% and 99%, north-temperate intertidal flats having relatively more molluscs than tropical flats. Intertidal flats in the tropics contain a greater variety of taxa, with brachiopods in Indonesia and echinoderms in northwest Australia contributing significantly to biomass only there. Limits to the occurrence of avian predators of intertidal benthos are set by the harvestable fraction of the biomass on offer and the costs of living at a particular site. No systematic differences in the harvestable fraction of the total mollusc-biomass for a worldwide occurring shorebird species specializing on molluscs (knots *Calidris canutus*) were apparent between temperate and tropical intertidal areas, in spite of large differences in maintenance metabolism incurred by these birds. The harvestable fractions of bivalves in the two West African areas (Banc d'Arguin, Mauritania and Guinea-Bissau) tended to be high (23-84% of total biomass in six species), they were relatively low (2-52% in five species) in the temperate Wadden Sea and the tropical northwest Australian site. Harvestable biomass determines the intake rate of shorebirds, as illustrated by functional-response curves of knots feeding on two bivalves species. We argue that the collection of information on size-depth relationships along with faunal and biomass surveys at a range of sites is bound to greatly increase our understanding of both the biology of tidal-flat invertebrates and the resource base underpinning the spectacular seasonal migrations of shorebirds.

1. INTRODUCTION

Many species of shorebirds depend on coastal intertidal areas for their survival. They feed on macrobenthic invertebrates which become available during low water. Almost all shorebird species reproduce in the north temperate, boreal or arctic zones. However, during the nonbreeding season they reach the southern corners of the world in great numbers (MORRISON & ROSS, 1989; EVANS & DAVIDSON, 1990; HOCKEY *et al.*, 1992; PIERSMA, in press). Shorebirds travelling from one coastal area to another are likely to encounter a variety of intertidal sites containing an even greater variety of benthic faunal assemblages. Although species abundance and aspects of community structure have invited interesting comparisons between temperate and tropical areas in the subtidal (THORSON, 1957; SANDERS, 1968; WARWICK & RUSWAHYUNI, 1987; KENDALL & ASCHAN, 1993) and the intertidal (REISE, 1991) zones, the biomass figures of the intertidal macrozoobenthic fauna of soft sediments, the component of marine ecosystems that shorebirds rely on, have never been genuinely compared on a worldwide

basis (see WOLFF, 1983, 1991; REISE, 1985). Given the great variety of ways in which intertidal areas can be compared, and the problems involved in comparisons of variably collected data sets, this is no easy task. The comparison becomes easier from the viewpoint of one of the predators of macrozoobenthos, a shorebird species for example, since for such predators only part of the community characteristics are important. Quantifying the differences between intertidal sites from a shorebird perspective could also help towards understanding their nonbreeding distribution. Here we try to summarize the information available from the literature and unpublished sources, and to evaluate it in the light of the demands of a particular long-distance migrating shorebird species specializing on molluscs, the knot *Calidris canutus* (PIERSMA & DAVIDSON, 1992).

Fig. 1 illustrates the factors that shorebirds may take into account when evaluating the quality of an intertidal feeding area. Which pieces of information are necessary for a quantitative model of the quality of intertidal flats in different parts of the world? In addition to gaining sufficient food, discussed below, it
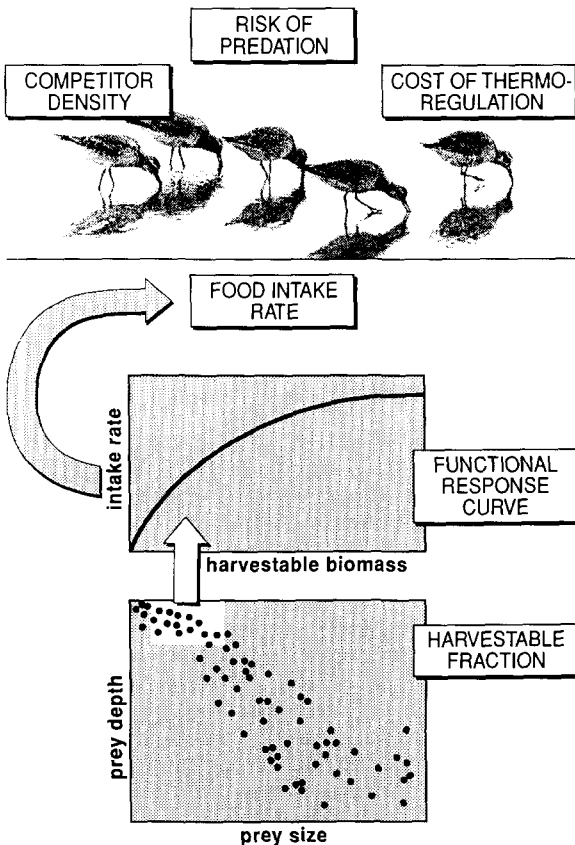
Fig. 1. Considerations of a shorebird (boxed) in its evaluation of the quality of feeding habitat. The quality of the feeding habitat is determined by the attainable intake rate, which is a function of the harvestable biomass (top graph). The latter consists of the prey with the appropriate size and within reach of the bill, the harvestable fraction (bottom graph).

is important not to die too easily at a site. Therefore, the risk of predation by predatory birds and mammals is something to consider (e.g. BIJLSMA, 1990; PIERSMA et al., 1993). Furthermore the cost of living, and especially the part related to thermoregulation, weighs heavily in northerly areas and affects the suitability of a site for shorebirds (EVANS, 1976; PIERSMA et al., 1991). The modelling tools to assess these costs from climatic and behavioural data are now available (WIERSMA & PIERSMA, in press). Food abundance is of obvious importance and usually the main factor considered in discussions of large scale patterns in shorebird distribution (e.g. PIENKOWSKI, 1981; EVANS & DUGAN, 1984; HOCKEY et al., 1992). However, it is not total food abundance that affects the suitability of an area, but rather the potential food-intake rate. Food-intake rate can be depressed by large numbers of feeding competitors through interference competition (SUTHERLAND & KOENE, 1982; ENS & GOSS-CUSTARD,

1984), and is related to the total benthic biomass by a complicated array of factors (e.g. PIERSMA, 1987). Not all prey of a kind are ingestible or profitable, because some are oversized or underweight, whilst others are inaccessible because they are buried too deeply in the sediment or are too slippery to be ingested easily and requiring excessive handling times (see ZWARTS & WANINK, 1984; ZWARTS et al., 1992; ZWARTS & WANINK, 1993). Those prey that are accessible, ingestible and profitable for a particular shorebird species are called harvestable (ZWARTS & WANINK, 1993). Intake rate is a function of the density of harvestable prey through species-specific functional-response curves (WANINK & ZWARTS, 1985).

ZWARTS & WANINK (1993) impressively document the seasonal and yearly variation in the abundance and harvestability of benthic invertebrate prey of shorebirds for a site in the Dutch Wadden Sea. In this contribution we provide a latitudinal axis to their story, albeit with much less detail. Comparative data on the size and depth distribution of some mollusc species fed upon by knots will be presented for a temperate intertidal area (the Dutch Wadden Sea) and three comparable tropical areas (the Banc d'Arguin in Mauritania, the Bijagos Archipélago in Guinea-Bissau and Roebuck Bay in northwest Australia).

2. REVIEW OF BENTHIC BIOMASS DATA FROM INTERTIDAL SOFT SEDIMENTS WORLDWIDE

In an attempt to approach completeness, we searched the computerized BIOSYS-archive on the key-words (intertidal) benthos, intertidal benthic fauna, macrozoobenthos, macrobenthos. This yielded 120 titles and abstracts. However, only two of these papers had sufficient detail and gave biomass data in proper currencies and taxonomic groupings to appear in the list (Table 1). Our personal libraries yielded data for 16 sites and the references listed in the examined sources yielded another two. As it turned out, for 11 of the 19 sites relevant data were collected by members of the same school (workers from the University of Groningen and NIOZ/RIN, Texel). Some good studies (e.g. ANSELL et al., 1978) present the data as wet weight rather than dry mass or ash-free dry mass, making it tricky to come to comparable figures in ash-free dry mass units, while others (e.g. MEIRE et al., 1991) do not allow the data to be split into the taxonomic categories used here.

The assembled data on the contribution to total biomass by gastropods, bivalves, polychaetes, oligochaetes, crustaceans, echinoderms and brachiopods are listed in Table 1 and summarized in Fig. 2. These taxonomic categories are of different systematic levels (MARGULIS & SCHWARTZ, 1988). Echinoderms and brachiopods are separate phyla, bivalves and gastropods are classes of the phylum mollusca, polychaetes and oligochaetes are classes of the phylum annelida, and crustaceans are a subphylum of

TABLE 1

Total biomass and taxonomic composition (both in g AFDM·m⁻²) of the benthic macrofauna of intertidal soft sediments around the world, based on a thorough literature search. For the Banc d'Arguin the results of an early (14a) and late survey (14) are given, but only the results of the most recent survey are presented in Fig. 2. Latitude is given in degrees north (+) or south (-). The depth to which sampling cores were pushed into the sediment is indicated as well as the mesh width of the sieves. Time of the year is indicated by month-numbers, 1-12 indicating a full year.

no	Area	Lat.	Sub-strate	Depth (cm)	Mesh (mm)	Time of year	Bi-valves	Gastro-pods	Mol-luscs	Poly-chaetes	Oligo-chae-tes	Crusta-ceans	Echino-derms	Brachio-pods	Total bio-mass
1	Firth of Clyde, Scotland, U.K.	57	sandy	15	0.5	10	4.37	0	-	0.47	0.25	0	0	0	5.10
2	Konigshafen, Germany	55	variable	?	?	1-12	1.06	15.36	-	2.33	0.75	0.07	0	0	19.57
3	Frisian coast, The Netherlands	54	muddy	40	1	8	62.40	7.29	-	10.50	0	0.24	0	0	81.00
4	Balgzand, The Netherlands	53	variable	30-40	1	3	19.29	0.43	-	9.95	0	0.68	0	0	30.35
5	Tamar Estuary, Cornwell, U.K.	50	muddy	25	0.5	1-12	8.87	0.00	-	4.44	0	0	0	0	13.31
6	Barnstable Harbor, Mass., U.S.A.	42	sandy	?	0.75	7	4.21	3.46	-	7.83	0	0.52	0.18	0	16.20
7	San Fransisco Bay, Ca., U.S.A.	38	muddy	?	0.5	2	15.68	0	-	0.58	0.08	0.29	0	0	16.63
8	Ria Formosa, Algarve, Portugal	37	variable	15	1	12-3	-	-	54.55	11.40	0	2.60	0	0	68.55
9	Merja Zerga, Morocco	35	muddy	25	1	3	22.52	0.03	-	0	0	0.03	0	0	22.57
10	Nakdong Estuary, South Korea	35	sandy	50	1	10-11	8.76	0.72	-	2.21	0	2.86	0	0	14.55
11	Gulf of Gabes, Tunisia	34	muddy	25	0.5	3	7.80	12.74	-	2.60	0	2.60	0.26	0	26.00
12	Sidi Moussa Estuary, Morocco	33	variable	25	1	3	0.97	9.31	-	1.87	0	0.05	0	0	12.21
13	Mai Po, Deep Bay, Hongkong	22	muddy	20	1	3,9	1.25	2.42	-	16.57	0.53	0.05	0.05	0	20.76
14	Banc d'Arguin, Mauritania	19	variable	40-45	0.6	2-4	11.00	1.90	-	3.90	0.10	0.10	0	0	17.00
-a	Banc d'Arguin, Mauritania	19	variable	25	1	2	5.36	0.19	-	1.78	0	0.26	0	0	7.59
15	Weg naar Zee, Surinam	6	muddy	35-40	1	9	0.05	0.00	-	0.09	0	6.25	0	0	6.45
16	Java, Indonesia	-6	muddy	30-40	1	3-4	4.56	0.03	-	0.74	0	1.38	0	4.09	10.80
17	Roebuck Bay, Australia	-18	muddy	20	0.5	3-5	4.49	0.92	-	4.01	0	0.42	6.17	0	16.01
18	Langebaan Lagoon, South Africa	-33	muddy	6	1	1-12	0.06	11.12	-	3.74	0	0.88	0	0	15.79
19	Swartskop Estuary, South Africa	-34	variable	30	3	6-7	0.94	0	-	0	0	42.76	0.15	0	43.85

data sources:

(1) from MCINTYRE, 1970: derived from fig. 4; AFDM estimated from dry mass figures with ratios given by PIERSMA, 1982: table 4.1.

(2) from ASMUS & ASMUS, 1986: computed from tables 1 (biomass values) and 3d (available surface area of each habitat).

(3) from ZWARTS, 1986: table 5.1.

(4) from BEUKEMA, 1991: table 1.

(5) from WARWICK & PRICE, 1975: table 1.

(6) from SANDERS et al., 1962: tables 3; AFDM estimated from dry mass figures with ratios given by PIERSMA 1982: table 4.1.

(7) from NICHOLS, 1977: table 4.

(8) from RUFINO et al., 1985: computed from table 2, combining two types of intertidal flat, weighting equally.

(9) from PIERSMA, 1983: table 5.9.

(10) from DOORNBOS et al., 1986: computed from table 2.

(11) from VAN DIJK, 1986: table 3.7.

(12) from PIERSMA, 1983: computed from tables 5.2, 5.6 and 5.7, weighting each area equally.

(13) S. McChesney, pers. comm.; means of extensive sampling in March and September 1992

(14) from WOLFF et al., 1993: computed from table 4 (with 8.1 g AFDM·m⁻² for Anadara senilis included in the figure for bivalves).

(14a) from PIERSMA, 1982: computed from table 4.4, weighted for surface area of habitat types according to table 3.5.

(15) from SWENNEN et al., 1982: table 1.

(16) from ERFTEMEIJER & SWENNEN, 1990: computed from tables 1-4 (mean of 4 areas).

(17) from TULP & DE GOEIJ, in press: table 2.

(18) from PUTTICK, 1977: computed from appendix 1, means calculated for period March 1974-March 1975 for Bottelary site; AFDM estimated from dry mass figures with ratios given by PIERSMA,1982: table 4.1.

(19) from HANEKOM et al., 1988: computed from appendix 1, weighting for surface area of different transects.

the phylum arthropoda. Oligochaetes never contributed much to biomass and were lumped with polychaetes in Fig. 2. Total biomass varied between 5 and 80 g AFDM per m², with an overall average of 24 g AFDM per m². No latitudinal trend was apparent in total biomass (Fig. 2B). The contribution made by molluscs varied between 1% and 99% (Figs 2A and 2C), north temperate intertidal flats having relatively more molluscs than tropical flats. Intertidal flats in the tropics contained a greater variety of the major taxonomic groups. Brachiopods were only found on intertidal flats on Java, Indonesia (ERFTEMEIJER & SWENNEN, 1990). Echinoderms such as brittle stars and sea cucumbers (while also present at other sites such as
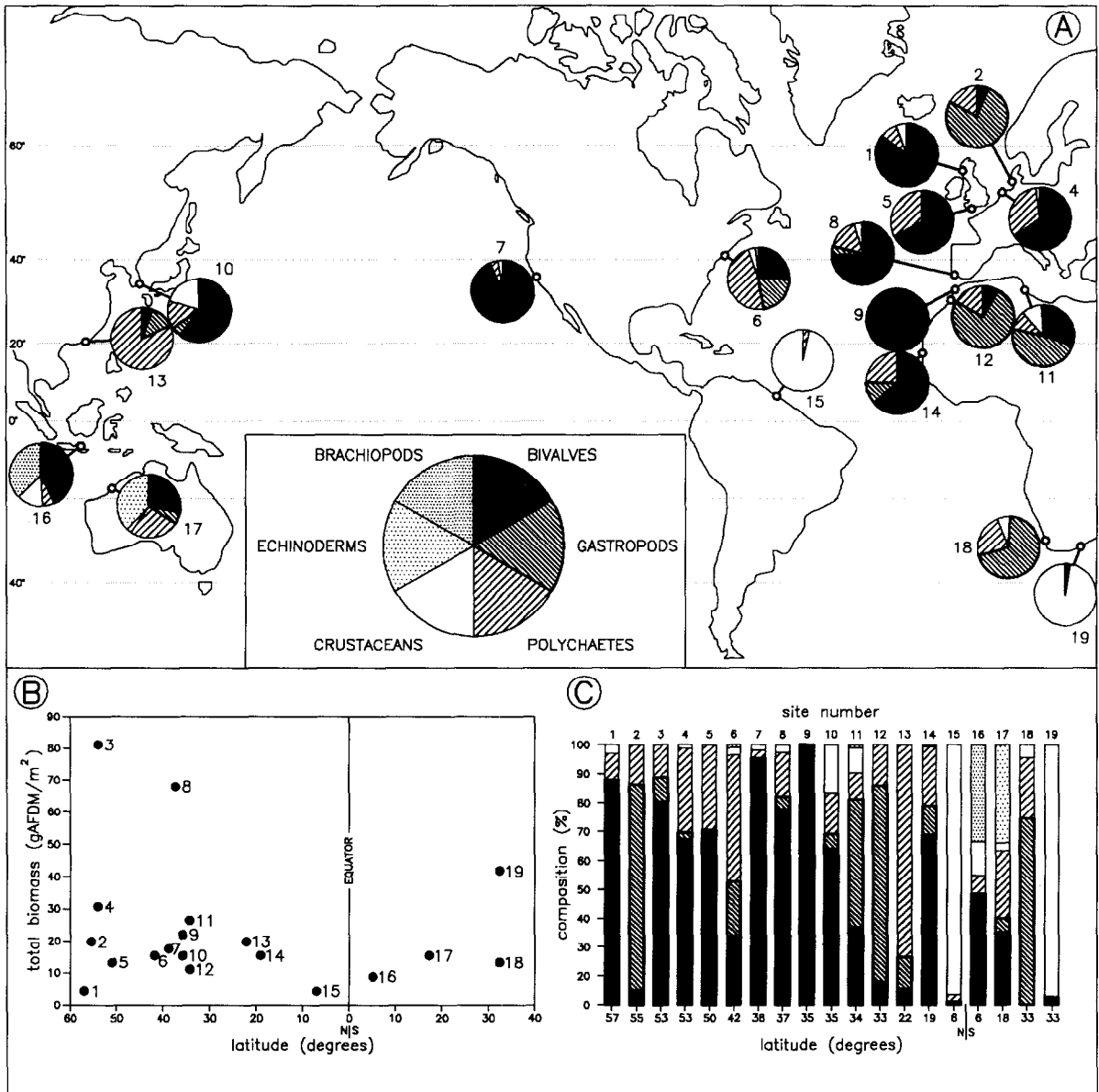
Fig. 2. Biomass and composition in terms of major taxonomic groupings of macrozoobenthos of soft intertidal sediments around the world. This Figure is based on the data presented in Table 1. The pies in the map (A) give the mass-specific composition of the macrozoobenthic community at most of the sites. The numbers refer to those in Table 1. Panel (B) shows the variation in total-biomass figures on a latitudinal axis. (C) gives the trends in taxonomic composition, again on a latitudinal axis. Oligochaetes never contributed much to biomass and were lumped with the polychaetes.

in the Gulf of Gabes, Tunisia, in low numbers), contributed 39% to the macrozoobenthic biomass in Roebuck Bay, northwest Australia (TULP & DE GOEIJ, in press). Crustaceans dominated the benthic fauna along the Surinam coast (SWENNEN *et al.*, 1982), and Swartskop Estuary, South Africa (thalassinid mudprawns *Upogebia*; HANEKOM *et al.* 1988).

Our worldwide survey of intertidal macrozoobenthos therefore yields few predictions about what to expect at different latitudes in terms of biomass and kinds of prey for shorebirds. But the number of taxa and variety of intertidal organisms to be encountered will be higher in the tropics (REISE, 1991), parallel to patterns in subtidal communities of soft

sediments (THORSON, 1957; SANDERS, 1968).

3. HARVESTABLE FOOD FOR KNOTS: A COMPARISON BETWEEN WADDEN SEA, BANC D'ARGUIN, BIJAGOS AND ROEBUCK BAY

Since nonbreeding knots only occur in coastal intertidal areas (PIERSMA & DAVIDSON, 1992) and feed almost uniquely on molluscs (e.g. PRATER, 1972; PIERSMA, 1991; ALERSTAM et al., 1992; DEKINGA & PIERSMA, 1993), they provide a good predator species from which to examine patterns in the harvestability of the mollusc resources at intertidal areas worldwide. Although there is great variability in biomass values of molluscs (Table 1), there is even greater variability in the size and depth distribution at the different sites, enhancing the variability in the mollusc biomass harvestable by knots. For example, most of the average bivalve biomass of 11 g AFDM·m^{-2} on the Banc d'Arguin is made up of the large-shelled giant bloody cockle Anadara senilis (8.1 g AFDM·m^{-2}), which can only be fed upon by oystercatchers Haematopus ostralegus (SWENNEN, 1990).

Based on work carried out in April 1988 in the Baie d'Aouatif, Banc d'Arguin, Mauritania, in March 1990 on the Vlakte van Kerken, Texel, Dutch Wadden Sea (see TULP & VERKUIL, 1993), in March-May 1991 in Roebuck Bay, northwest Australia (see TULP & DE GOEIJ, in press) and in February 1993 on intertidal flats east of Ilha de Maio, Archipélago dos Bijagos, Guinea-Bissau, all using the same methods, Fig. 3 gives the size-depth relationships for 11 mollusc species in this late-winter/early-spring period. All these species are known to be important prey for the locally occurring knots (TULP & VERKUIL, 1993; TULP & DE GOEIJ, in press; unpubl. data). The Figure also shows the harvestable fraction, the window in the size-depth plot for which the molluscs are both accessible and ingestible. Given the low intake rates and the high rates of ingestion of individual prey items reported for the tropical Banc d'Arguin (ZWARTS et al., 1990), we assume that even the smallest molluscs retained on 0.5- to 1-mm sieves in the tropics are profitable for knots. Hence we have not indicated a lower size threshold (cf. ZWARTS & WANINK, 1984).

There are no latitudinal differences in the harvestable fraction for mollusc-eating knots. Whereas harvestable fractions of bivalves in the two West African areas (Banc d'Arguin and Guinea-Bissau) tended to be high (23-84% of total biomass in six species), they were relatively low (2-52% in five species) in the temperate Wadden Sea and the tropical Australian site. At the latter two sites harvestability was low because of the large sizes of the molluscs present (greater than the size threshold) and because of their great burying depth (deeper than bill length).

If we take the Balgzand figure (BEUKEMA, 1991) as a representative biomass value for the Wadden Sea, we can work out absolute harvestable mollusc-bio-

mass values for Wadden Sea, Banc d'Arguin and Roebuck Bay on the basis of Table 1 and Fig. 3. Assuming an overall harvestability of 15% in the Wadden Sea, the harvestable mollusc-biomass works out at 0.15·19.7= 2.96 g AFDM·m^{-2}. For the Banc d'Arguin this is 0.7·4.8= 3.4 g AFDM·m^{-2}, and for Roebuck Bay this is 0.5·5.4= 2.1 g AFDM·m^{-2}. Although these figures are still very rough approximations, they suggest that harvestable mollusc-biomass values are less different between areas at different latitudes than the maintenance costs incurred by knots over this range of sites. According to WIERSMA & PIERSMA (in press), maintenance costs in midwinter on the Banc d'Arguin are a factor 1.44/2.57=0.56 of those in the Wadden Sea, the harvestable mollusc-biomass being of the same order of size in the two areas.

An examination of the functional-response curves (HOLLING, 1959), relating intake rate of a predator to the abundance of its prey, can be illuminating to understand the decisive importance of the harvestable fraction of total biomass for feeding shorebirds. Examples for oystercatchers feeding on Macoma balthica and Scrobicularia plana are presented by HULSCHER (1982) and WANINK & ZWARTS (1985) respectively, and for knots feeding on Cerastoderma edule and Macoma balthica in Fig. 4. These are the normal prey species fed upon by oystercatchers (HULSCHER, 1982) and knots (ZWARTS & BLOMERT, 1992; PIERSMA et al., 1993) in the Wadden Sea. Good estimates of the functional-response equations not only allow a conversion of harvestable biomass in shorebird-intake rates, but they also allow comparisons between different kinds of prey. In Fig. 4 we have illustrated this by examining the absolute minimum-harvestable-biomass thresholds for knots expending a minimum of energy in the Wadden Sea (2.8 W, see WIERSMA & PIERSMA, in press), foraging for 12 h on prey with an energy value of 21 kJ per g AFDM and a digestive efficiency of 75%. Shallow-living Cerastoderma allow for lower harvestable biomass values than 3-cm-deep living Macoma. There is yet theoretical work to be done to find out how intake rates of a shorebird could sensibly be reconstructed from data on harvestable biomass of a range of prey species and prey choices.

4. SCOPE FOR FUTURE WORK

A snapshot for one time period (late-winter/early-spring) for four sites does not do justice to the enormous seasonal and long-term variability which we know to exist in the size and depth distribution of intertidal bivalves (PIERSMA et al., 1993; ZWARTS & WANINK, 1993). However, it is data of this kind that might allow us to outline broad-scale patterns in food availability for shorebirds (e.g. PIERSMA, 1987), and relate it to migratory phenomena in a proper way (cf. SCHNEIDER, 1981; HOCKEY et al., 1992). The measurements are not difficult to obtain; a little persistence in
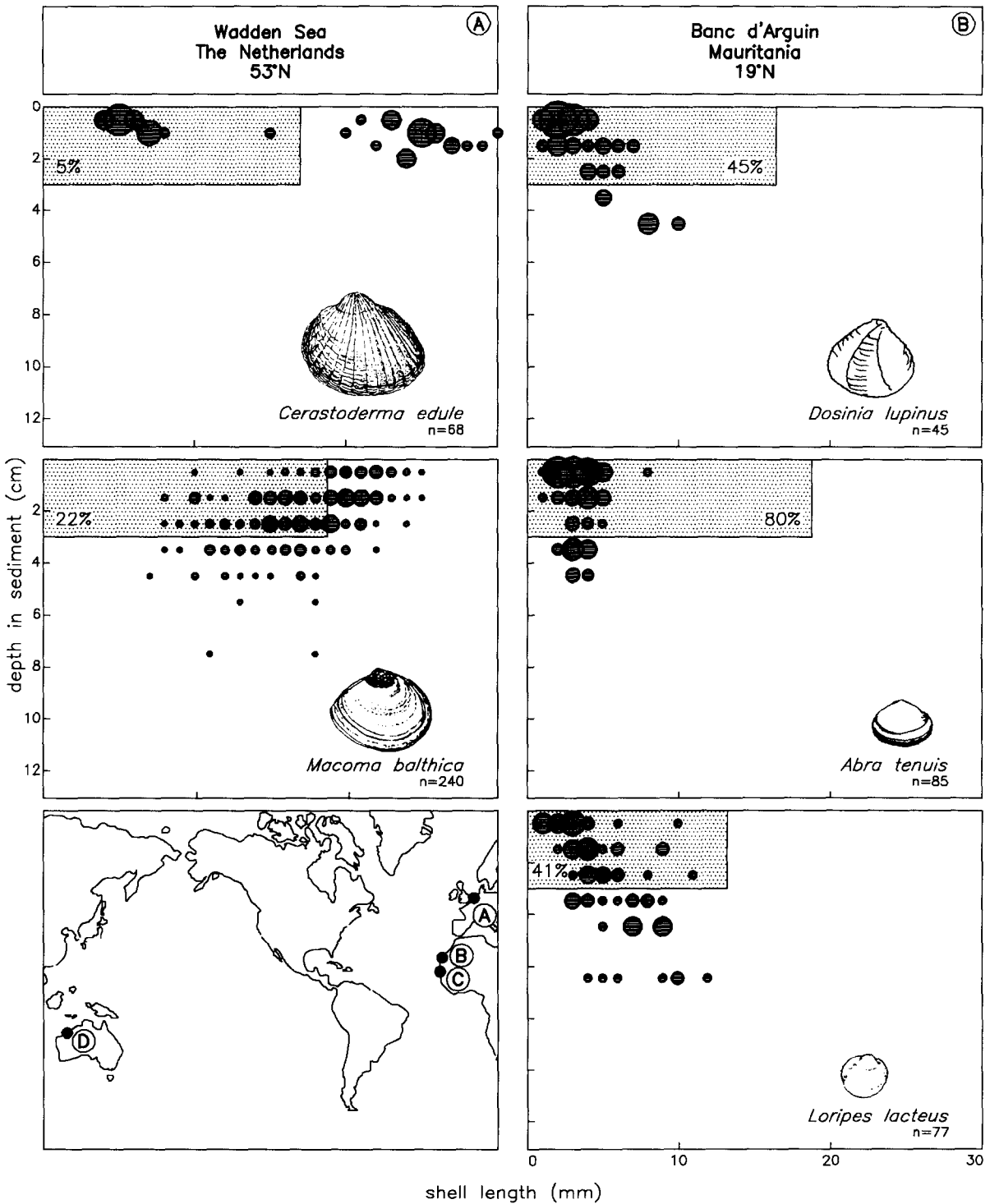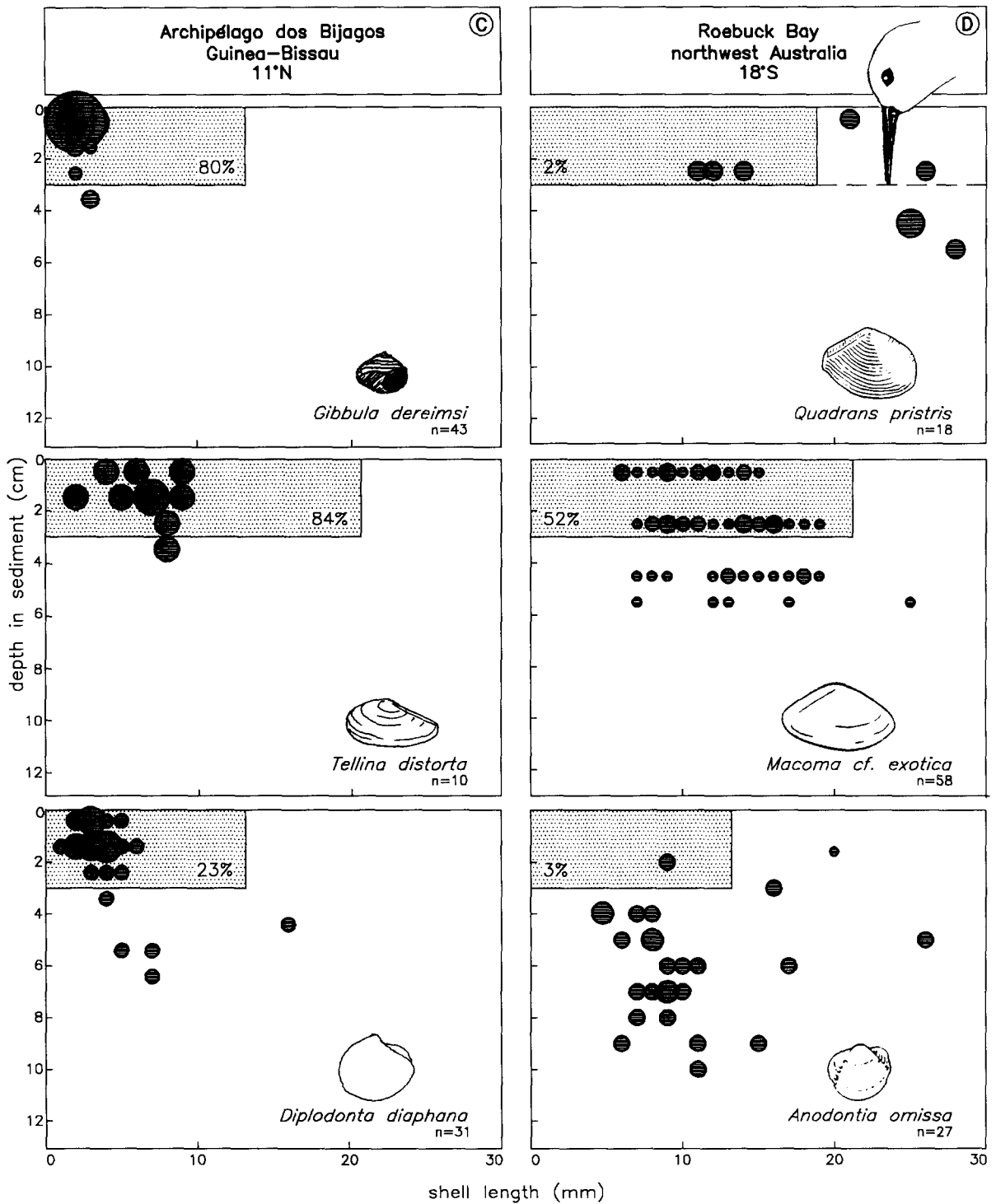
Fig. 3. Size-depth relationships for molluscs from the Wadden Sea (A) and from three comparable tropical intertidal areas, the Banc d'Arguin in Mauritania (B), the Bijagos Archipélago in Guinea-Bissau (C) and Roebuck Bay near Broome in north-west Australia (D). All measurements were made in the period February-April. Top row are miscellaneous species, middle row are tellinid-like bivalves and bottom row are all members of the family Lucinidae. The surface areas of the dots (given

per depth/size category) are relative to the percentage of total biomass of that species. For *Cerastoderma edule* (A) and *Quadrans pristis* (D) part of the shells were larger than 30 mm and are not included. The windows in the upper-left corners indicate the harvestable fraction, *i.e.* molluscs with a depth and size that are both accessible and ingestible by knots. The indicated percentage gives the percentage of total biomass of the particular species that is harvestable by knots.

Fig. 4. Repercussions on intake rates by knots, of differences in harvestable biomass for two bivalve species living at different depths (0.5 cm deep *Cerastoderma edule* and 1-3 cm deep *Macoma balthica*: shaded area). This Figure is based on extensive laboratory trials with eight individual knots feeding on trays with soft sediment (J. van Gils, P. de Goeij and T. Piersma, unpubl. data).

kneeling on or in mud, sorting, measuring and counting is all that there is to it. As the size and depth distributions of prey are fitness-related functions critical to the life-history of the prey species (*e.g.* DILL, 1987; ENS *et al.*, 1993), comparative data will also shed light on behavioural adaptations allowing tidal-flat invertebrates to coexist with shorebirds and other epibenthic predators.

Future analytic endeavours will be greatly helped if we take up ZWARTS & WANINK's (1993) challenge and come up with sound data on seasonal changes in the availability of tidal-flat invertebrates from other areas than the Frisian foreshore. The survival of spatfall determines the eventual harvestable biomass to a large extent, but is known to vary enormously from year to year at temperate latitudes (BEUKEMA *et al.*, 1993. We do not know whether this is so in other areas as well. Therefore, measurements of the availability of benthic prey organisms have preferably to be carried out on a year-round basis, so that the persistence of a harvestable food resource can be explained from seasonality in recruitment, growth and

survival strategies of the tidal-flat invertebrates.

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