INTERNATIONAL COUNCIL FOR
THE EXPLORATION OF THE SEA

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Demersal Fish Committee
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CONSUMPTION OF BENTHOS BY NORTH SEA COD AND HADDOCK IN 1981

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Abstract.

Benthos-fish interactions were quantified for North Sea cod and haddock on the basis of stomach content data collected within the framework of the Stomach Sampling Project in 1981. For comparison available cod data for 1980 were also included.

Taking into account the density distribution of the predators and their absolute stock sizes according to VPA, consumption rates were calculated for major prey taxa in three different areas by season, indicating large regional and seasonal variations. However, interannual variations between the two sets of cod stomach content data appeared to be comparatively small and it is concluded that from a multispecies point of view the assumption of a constant quantity of available benthic food is as good as any.

Crustacea represent the dominant prey of cod and annelids, echinoderms and crustacea contribute approximately equal shares in the food of haddock. When comparing epibenthic species compositions in cod stomachs and trawl catches large incongruencies were observed. Some species frequently observed in stomachs do not occur in trawl catches, whereas for others it is the other way round. Not only are fish highly selective, but apparently also sampling gear does not catch benthic animals indiscriminantly. In the absence of reliable quantitative data on relative prey abundance, analysis of prey selection is hampered.

The estimated rate of consumption per unit area by the cod and haddock stocks combined decreases progressively from the southern (0.8 $g.C.m^2.y^{-1}$) to the northern North Sea (0.5). The results are compared with available production figures, indicating that either consumption is estimated too high or production figures are too low. One outstanding problem in such comparisons is that benthos represents a highly heterogeneous aggregate of organisms with very differenet positions in the food chain. Fish feed only on specific components, which are rarely singled out in benthos studies.

Introduction.

*) Present address: Netherlands Institute of Sea Research. P.O.Box 59, 1790 AB DEN BURG, Texel, The Netherlands.

Although multispecies assessment deals specifically with consumption of exploited fish species by exploited fish species, secondary interests have been aroused in quantitative aspects of benthos-fish interactions in the North Sea. Within Multispecies VPA predation mortalities are estimated taking into account varying prey densities over the years and assuming constant vulnerability indices of each prey category to each predator category (ANONYMOUS, 1986). However, to estimate the annual fractions eaten of each exploited prey some assumption must be made about the available amount of 'other' food, i.e. prey organisms not included in the exploited species array. So far three possibilities have been proposed: (1) other food represents a constant fraction of the total food (POPE, 1979); (2) other food provides a fixed amount from year tot year (HELGASON & GISLASON, 1979); (3) the total available food is constant, other food being calculated dynamically by subtraction of available exploited prey (SPARRE,1980). The model applied sofar by the ad hoc Multispecies Assessment Working Group (ANONYMOUS,1986) is capable of optionally treating other food according to either one of these three assumptions. Still, from the multispecies assessment point of view direct quantitative information on possible changes in the amount of other food available to the various predators is important in order to provide guidelines for further model development.

Other food includes unexploited fish species and benthic and pelagic evertebrates. For cod (DAAN, 1973), haddock (DE LA VILLEMARQUÉ, 1985) and whiting (HISLOP et al, 1983) epibenthic macrofauna species appear to represent the larger part of the other food component. Although some very broad estimates of production of benthos have been published in generalized ecosystem modelling studies (eg. STEELE, 1974), very little quantitative information is available that can be utilized to discriminate between 'edible' and 'non-edible' components of this highly heterogeneous assemblage of species. Therefore, to investigate aspects of benthos-fish interactions the food spectra of the predators deserve high priority, whereas benthos investigations should accordingly discriminate between various groups of animals with different vulnerabilities.

Although the Stomach Sampling Project in 1981 was primarily aimed at the collection of reliable information on quantities of exploited fish species in the food of the various predators, other prey have been routinely identified in the samples. This paper summarizes information on benthic evertebrates in the food of cod and haddock, with special emphasis on estimating rates of consumption per unit area by the total population. The haddock data were kindly made available by Mrs J. Hersart de la Villemarque (IFREMER, Nantes). Additional data on cod stomachs collected in 1980 were available to investigate interannual variations.

Since large regional differences exist in the benthic communities encountered within the North Sea and to allow subsequent comparison of rates of benthos consumption with standing prey stocks, as may ultimately emerge from the Benthic Mapping project planned for 1986 (ANONYMOUS, 1985), three areas were selected, which correspond largely with a subdivision proposed by GLEMAREC (1973) on the basis of features of both the hydrography and the benthic community of the North Sea (fig 1). He proposed an open sea area defined approximately by the 100 m isobath, an offshore area between 40 and 100 m depth and a coastal area within the 40 m isobath. Enclosed within these limits a northern, central and southern area were defined for the present analysis. Estimates given for the total North Sea are based on all samples taken within the survey boundaries also indicated in fig 1.

Material and methods.

Data on sampling intensity for cod stomachs in 1980 and 1981 have been given by DAAN (1981,1983) and for haddock by DE LA VILLEMARQUÉ (1985). Procedures of analysis have been extensively described in ANONYMOUS (1981). Species were identified according to the lowest possible taxonomic level, which was determined by the state of digestion or alternatively by our ready taxonomic knowledge. Both weights and numbers of organisms were recorded for each size class of each prey category identified within a sample.

Stomach samples by predator size class were first grouped by statistical rectangle. To obtain the average stomach contents within an area, the information within each rectangle was weighted according to the relative density of the predator size class. The densities were derived from the average catch per hour fishing in each rectangle during the survey. The stomach contents (wst) were then converted to daily consumption rates according to the model developed by DAAN (1973). The individual consumption rates for each size class were multiplied with the average density (RELN), summed over the size distribution and divided by total density to obtain the estimated daily consumption (CON) by an average individual predator in the area, irrespective of size. In mathematical terms:

$$\overline{CON}(A) = \left(\sum_{S} (2*wst(S,A) / D(S)) \right) / RELN(A) \qquad [1]$$

where S is the index for size class, A for area and D is the digestion time in days.

To obtain an estimate of the consumption per unit area transformation was required from the relative numbers per hour fishing to absolute densities. Therefore, the total number of fish (NVPA) older than 1 year in the population according to VPA (ANONYMOUS, 1984) on January 1st was split according to the relative survey density times the number of rectangles in each area divided by the relative survey density times the number of rectangles (NREC) in the total North Sea. Thus:

$$N(A) = NVPA*(NREC(A)*RELN(A) / \sum_{a} (NREC(a)*RELN(a))) \qquad [2]$$

where a is also an area index.

Sofar no effort was undertaken to take account of differences in catchability with increasing size, nor of changes in the predator population over the year.

Annual consumption figures for the absolute number of fish in each area were obtained by multiplying [1] and [2]. These were divided by the surface area and a conversion factor of 0.1 g carbon per g wet weight was applied to allow comparison of consumption per unit area with available production figures in the literature. These are sometimes given in ash free dry weight or energy equivalents and the following conversion factors were applied: 1 g AFDW ~ 0.4 g C; 13.5 kcal ~ 1 g C (KUIPERS, pers. comm).

Results.

Tables 1-3 provide estimated quarterly and annual consumption rates in g wet weight per square m by area for cod in 1980 and 1981 and for haddock in 1981. Since cod sampling was limited in 1980, estimates have only been made for the three areas in the first and third quarter. The estimated densities of predators, the consumption rates and the contribution of various benthos groups are graphically presented in fig 2. Consumption of benthos by cod is lowest in the northern and highest in the southern North Sea in both years. This is partly caused by higher densities in the latter area (fig 2.A.a, 2.B.a) but also by a higher proportion of benthos in the food (fig 2.A.d, 2.B.d). This difference can be ascribed to the prevailing presence of juvenile cod in the southern North Sea (eg. ANONYMUS, 1979), which rely more heavily on evertebrates for their food requirements than their larger brothers (DAAN, 1973);

Crustacea, particularly epibenthic decapods, represent consistently the larger part of benthic prey throughout the North Sea during all seasons (fig 2.B.e). Annelids, largely consisting of one single species (Aphrodite aculeata) may in some instances contribute up to 20% of the benthic prey, whereas molluscs are rather more variable. In general the contribution of the latter is very small, but in the southern North Sea during winter large numbers of Cyprina and Ensis have been recorded in the stomachs. At one occasion or another organisms of a wide variety of other groups have been identified, but the consumption rates on these groups are negligable and they have been omitted from the tables.

Haddock are known to depend much more on benthic evertebrates than cod (DE LA VILLEMARQUE (1985). The total impact of haddock on benthos is accordingly very much higher (table 3). Not surprisingly, predation is largely restricted to their main area of distribution in the northern and central North Sea (fig 2.C.a). The contributions of the 4 major groups vary considerably within areas and seasons, but overall Annelids, Crustaceans and Echinoderms appear to be approximately equally distributed among the food of haddock. The share of Molluscs is less than half of each of the other three major components.

In fig 3 the contribution of some major constituting species in the food of cod in 1981 is presented, indicating considerable regional differences, which undoubtedly reflect differences in geographical distribution of the prey. In general the seasonal differences are considerable as well. Not regarding possible sampling errors, such differences represent the combined effect of changes in the benthos population and the predator population, including effects of migration and changes in behaviour. Therefore, without considering details of the biology of both predator and prey interpretation of the variations is difficult.

In fig 4 a comparison of the food composition has been made with the numbers per hour fishing of various benthos species caught in English groundfish surveys as reported by DYER et al (1982, 1983). To facilitate comparison the numbers consumed per square m rather than weights consumed are presented in this case. By the nature of the sampling gear, the species caught belong largely to the epibenthos and therefore should also be available for predators like cod. Admittedly, the trawl data refer to surveys in august, whereas the stomach content data were summed over the year and therefore they are not strictly comparable. Still, from fig 4 it appears that both the trawl used and the cods take only a subset of the species, that are apparently available in each of these areas.

In table 4 the consumption rates over the year by the cod and haddock populations combined were converted to g carbon per square m. The summation has considerably reduced the variations between areas. Overall approximately 45% of the food requirements of these two predators is derived from benthic evertebrates. Crustaceans, Annelids, Echinoderms and Molluscs contribute roughly in the ratio of 3:2:2:1.

Discussion.

Considering the estimated consumption rates for cod in 1980 and 1981 (tables 1,2) , a rather similar pattern emerges in respect of the relative levels in different areas and in the contribution of major groups of benthic prey. The between year variations appear to be much smaller than the regional variations within seasons or the seasonal variations within regions. Because predation pressure by an individual predator varies so widely over the year and over the North Sea and because benthos dynamics in different regions are probably to a large extent independent of each other, it would seem unlikely that on the basis of stomach sampling schemes at a global North Sea scale significant annual differences in availability of benthic prey could be established, particularly because the predators may adapt their area of distribution according to prey availability. Moreover, since decreases in prey abundance in one area may be compensated by increases in another, overall the system should be strongly buffered against major overall changes. Therefore, for the time being from a multispecies modelling point of view the assumption of a constant amount of available benthic food would seem to be as good as any.

Within species consumption rates are even more variable than within major taxonomic groups. In some cases the differences may be related to shifts of predator and/or prey distributions. For instance, Brown shrimps (Crangon crangon) are preyed upon by cod most heavily in the southern North Sea during autumn and winter. At this time of year the shrimps migrate out of the shallow Waddensea areas (BODDEKE, 1971) and they are met by large numbers of cod moving south into the coastal zone. Similar features appear to apply to Macropipus holsatus. In contrast Nephrops is suffering largest losses in spring and summer, which may be related to a higher activity outside their burrows. Also Corystes is preyed upon more heavily in summer. Molluscs present a different set of problems, because it would seem highly unlikely that large Cyprina could be extracted by cod from the shells, which are rarely observed in the stomachs. When shells were found, they were crashed and this suggests that the animals had died before being eaten. ARNTZ & WEBER (1970) put forward the hypothesis that such prey have been killed by fishing gear, as has also been suggested for whelks (Buccinum) by DAAN (1973). Another feature of mollusc feeding is that stomachs packed with Ensis (also without any shells) have been recorded in Dutch coastal waters during severe winters (eg. in 1985) at the same time, when masses of dead Ensis were taken in trawl hauls. Apparently the cod take advantage of population kills caused by adverse hydrographical circumstances.

In conclusion, complex seasonal variations emerging from stomach sampling studies may be attributed to multiple causes and interpretation depends largely on knowledge of the biology of both predator and prey. The lack of congruency between the stomach content data and the survey data in respect of abundance of the various epibenthic prey species raises similar questions. Indeed, the conclusion here is that apparently abundant species in the survey are definitely not eaten by cod, but the reverse holds equally well. Only in depth studies of availabilty of prey and prey selection in restricted areas could possibly reveal the specific factors causing such discrepancies.

Benthos production estimates stem mainly from food chain modelling studies. STEELE (1974) estimated total production of North Sea benthos at 2-5 g $C.m^2y^{-1}$. Thus, only cod and haddock would already take care of 10-25% of the total benthos production. Taking into account (1) that only part of the benthos production is available for such predators, (2) that there must be a variety of other abundant predatory fishes utilizing benthos (partcularly other gadoids and flatfish) and (3) that benthos itself probably represents a complicated food web, in which a large part of the production is internally consumed, it would seem that these production and consumption figures do not match very well.

RACHOR (1982), using different P/B ratios for different areas, made separate production estimates for various North Sea regions and arrived at values (converted to g C) of 5.0, 0.4 and 0.3 for the southern, central and northern North Sea respectively. Apparently there is scope for considerable regional variation in benthos production. Taking these values at face value the discrepancies for the northern and central North Sea would be even worse. Also it contrasts the result that benthos consumption by these two predators is fairly equally spread throughout the region (table 4). However, RACHOR's values refer specifically to macro-endofauna species not consumed by cod and haddock and therefore are not directly comparable. DE WILDE et al (1984) estimated community respiration of a local benthic community in the southern North Sea at 46 g C m^2y^{-1}, which on the assumption of 20% transfer efficiency would result in a rather higher production value of approximately 10. However, the Oystergrounds selected for this study represent a highly productive front area and cannot be considered as representative for the total southern North Sea.

JONES (1982,1984) estimated total consumption by the cod and haddock population at 0.24 and 0.4 g C m^2y^{-1} respectively, which is only about 50% of the value obtained in this study. He inferred that benthos production when converted to g carbon would be only 0.8 g C m^2y^{-1}. Apparently there is considerable uncertainty about the level of benthos production. The common problem characteristic of all modelling approaches is that between actual basic observation and global North Sea estimate lie a vast number of untestable assumptions and hardly justifiable extrapolations. Indeed, generally one has to play around a great deal with available values, before one can make the ends of a food chain meet. However, similar objections do certainly apply to the present contribution to benthos-fish interactions. In progressing from observed stomach contents to consumption by total North Sea predator populations the assumption of a constant catchability for all size classes in the survey and linking everything to VPA population estimates as if these provide the ultimate truth may easily introduce bias of unknown magnitude. Since we have taken the traditional VPA estimates for the predator stocks, one would expect to make an underestimate of consumption, because Multispecies VPA runs indicate that allowing for predation mortalities among exploited fish species results in even larger stock sizes (ANONYMOUS, 1986). Thus, actually the discrepancy is even worse than indicated by our figures.

Because it is impossible to evaluate the error terms around our estimation procedures, one might rightly question whether such consumption estimates are worth at all preparing. Hopefully, however, this paper does help to stress the fact that quantitative benthos-fish interactions represent a major hole in our knowledge about the North Sea ecosystem.

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Table 1.
Total consumption and consumption of benthos by the cod population in 1980 in g wet weight per square m per quarter for three areas.

Area	Quarter	Total	Annelida	Mollusca	Crustacea	Echinoderm.	Total Benthos
North	1	1.27	0.01	0.01	0.08	.	0.10
	3	0.91	0.00	.	0.13	.	0.13
Central	1	0.29	0.01	.	0.05	.	0.06
	3	2.30	0.02	0.00	0.26	.	0.31
South	1	4.23	0.64	0.04	1.28	.	2.74
	3	1.86	0.32	0.06	1.04	.	1.42

Table 2.
Total consumption and consumption of benthos by the cod population in 1981 in g wet weight per square m per quarter and per year for three areas and for the total North Sea.

Area	Quarter	Total	Annelida	Mollusca	Crustacea	Echinoderm.	Total Benthos
North	1	1.79	0.04	0.01	0.23	.	0.28
	2	0.87	0.02	0.01	0.10	.	0.13
	3	3.79	0.02	0.00	0.20	.	0.22
	4	0.56	0.01	0.00	0.06	.	0.06
	Total	7.01	0.09	0.02	0.59	.	0.69
Central	1	1.32	0.08	0.02	0.20	.	0.30
	2	1.52	0.07	0.00	0.15	.	0.22
	3	1.29	0.00	0.01	0.17	.	0.20
	4	0.70	0.04	0.01	0.16	.	0.21
	Total	4.82	0.18	0.05	0.67	.	0.94
South	1	4.90	0.44	0.29	1.40	.	2.43
	2	2.34	0.31	0.04	0.90	.	1.28
	3	1.26	0.22	0.02	0.59	.	0.84
	4	2.72	0.13	0.01	1.69	.	1.85
	Total	11.22	1.10	0.37	4.66	.	7.84
Total	1	1.21	0.07	0.05	0.26	.	0.41
	2	1.17	0.08	0.03	0.33	.	0.48
	3	0.60	0.03	0.01	0.19	.	0.23
	4	0.17	0.01	0.00	0.07	.	0.09
	Total	3.14	0.19	0.09	0.86	.	1.21

Table 3.
Total consumption and consumption of benthos by the haddock population in 1981 in g wet weight per square m per quarter and per year for three areas and for the total North Sea.

Area	Quarter	Total	Annelida	Mollusca	Crustacea	Echinoderm.	Total Benthos
North	1	2.30	0.21	0.03	0.19	0.11	0.58
	2	1.70	0.12	0.15	0.03	0.38	0.71
	3	5.27	0.38	0.06	0.06	0.03	1.39
	4	3.36	0.13	0.00	0.15	0.00	2.02
	Total	12.63	0.84	0.25	0.43	0.53	4.71
Central	1	0.56	0.22	0.07	0.03	0.15	0.49
	2	3.79	0.16	0.01	0.11	0.20	0.49
	3	4.39	0.22	0.28	0.15	0.60	1.76
	4	2.16	0.59	0.06	1.16	0.19	2.04
	Total	10.90	1.19	0.41	1.46	1.15	4.78
South	1	0.11	0.03	0.00	0.01	0.04	0.08
	2	0.18	0.10	0.02	0.08	0.02	0.15
	3	0.21	0.01	0.00	0.07	0.04	0.13
	4	0.31	0.08	0.05	0.07	0.06	0.26
	Total	0.81	0.22	0.07	0.23	0.16	0.63
Total	1	1.22	0.23	0.08	0.12	0.20	0.65
	2	2.94	0.22	0.11	0.18	0.39	0.93
	3	2.46	0.18	0.07	0.11	0.22	1.04
	4	1.91	0.26	0.06	0.33	0.16	1.30
	Total	8.54	0.90	0.32	0.75	0.89	3.92

Table 4.
Total consumption and consumption of benthos in 1981 by the cod and haddock populations combined in g carbon per square m per year for three areas and for the total North Sea.

Area	Total	Annelida	Mollusca	Crustacea	Echinoderm.	Total Benthos
North	1.96	0.09	0.03	0.10	0.05	0.54
Central	1.57	0.14	0.05	0.21	0.12	0.57
South	1.20	0.13	0.04	0.48	0.02	0.80
Total North Sea	1.17	0.11	0.06	0.16	0.09	0.51

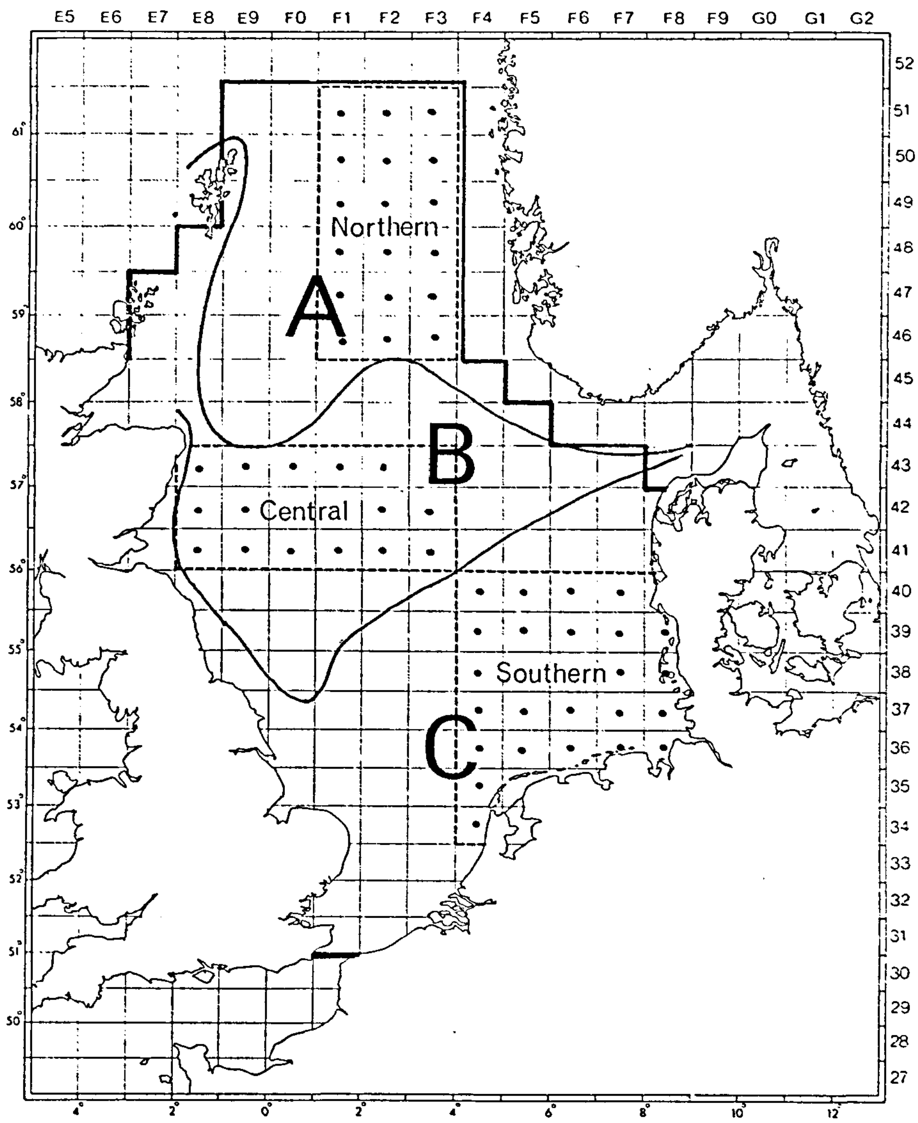


Figure 1.

Subdivision of the North Sea according to GLEMAREC (1973) in an open sea etage (A), an offshore etage (B) and a coastal etage (C). The position of the northern, central and southern areas considered in the present analysis is also indicated. The heavy lines border the total area sampled for cod and haddock stomachs and define the total North Sea as used in this paper.

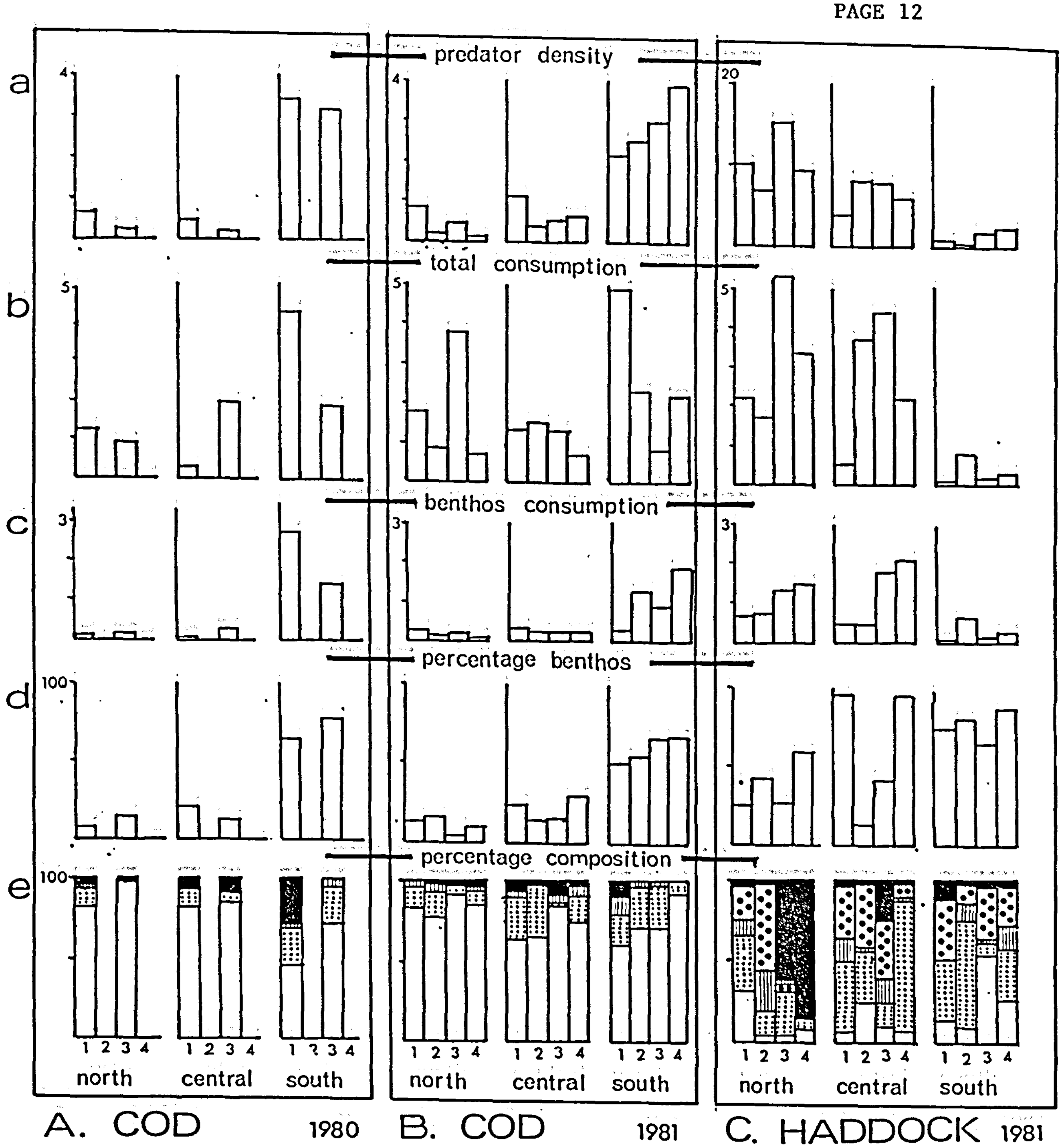


Figure 2.

Feeding data of cod in 1980 (A) and 1981 (B) and haddock in 1981 (C) by area quarter.

a. Predator density in numbers x 10^3 per square km.
b. Total consumption in g wet weight per square m per quarter.
c. Consumption of benthos in g wet weight per square m per quarter.
d. Percentage contribution of benthos to total consumption.
e. Percentage composition of benthic food by major taxa.

Legend:
= Crustacea
= Annelida
= Echinodermata
= Mollusca
= Others

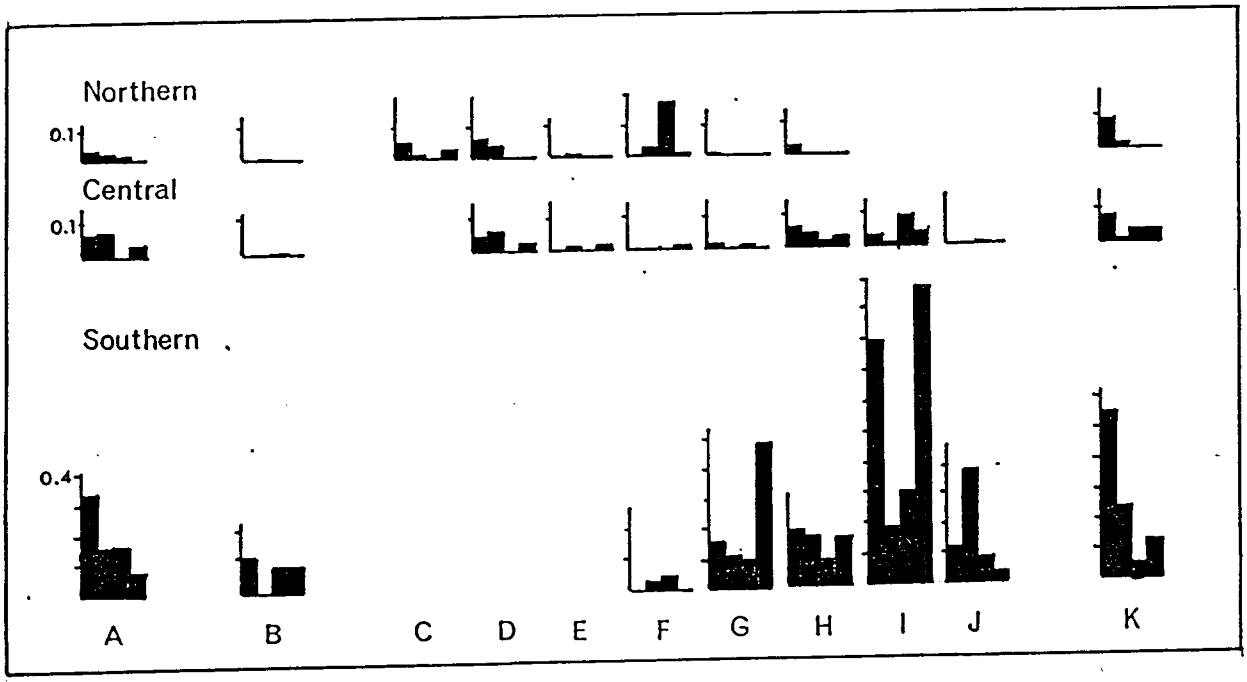
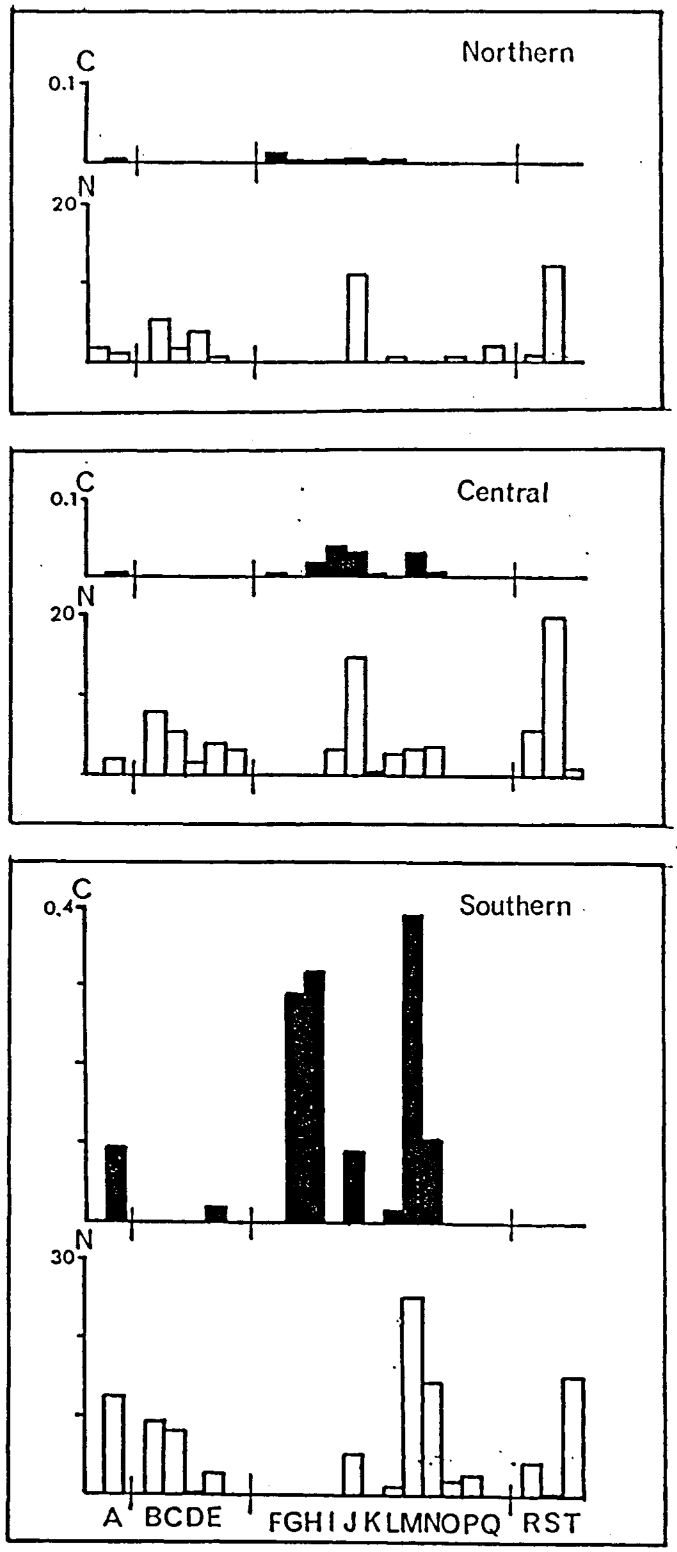


Figure 3.

Consumption in g wet weight per square m per quarter of various prey species by the cod population in 1981 by area.

A: Aphrodite aculeata
B: Cyprina islandica
C: Munida
D: Geryon tridens
E: Pandalus spec.
F: Nephrops norvegicus
G: Crangon spec.
H: Paguridae
I: Macropipus holsatus
J: Corystes cassivelaunus
K: others



A: Hyalinoecia tubicola
B: Aphrodite aculeata
C: Neptunea antiqua
D: Buccinum undatum
E: Colus gracilis
F: Cyprina islandica
G: Modiolus modiolus
H: Munidae
I: Crangon crangon
J: Crangon allmanni
K: Pandalus borealis
L: Pagurus bernhardus
M: Geryon tridens
N: Nephrops norvegicus
O: Macropipus holsatus
P: Corystes cassivelaunus
Q: Hyas coarctatus
R: Cancer pagurus
S: Lithodes maja
T: Ophiura texturata
U: Spatangus purpureus
V: Psammechinus miliaris

Figure 4.

Comparison of estimated consumption rates in numbers per square m per year (C) with estimated densities in numbers per hour fishing (N) of major epibenthic species (from DYER et al, 1982, 1983).