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Diel and habitat-dependent resource utilisation by deep-sea fishes at the Great Meteor seamount: niche overlap and support for the sound scattering layer interception hypothesis

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ABSTRACT: Interspecific relationships of 4 dominant fish species of the Great Meteor seamount fish community (subtropical NE Atlantic, 30° N, 28.5° W), *Macroramphosus* spp. Lacépède 1803, *Capros aper* (L. 1758), *Antigonia capros* Lowe 1843 and *Zenopsis conchifer* (Lowe 1852) were analysed with respect to diet composition, habitat-dependent resource utilisation and niche overlap. For all 4 species, planktonic and micronektonic prey prevailed. In terms of the Relative Importance index (RI), the benthic share was 18.25% RI for *Macroramphosus* spp., 19% RI for *C. aper* and 20.38% RI for *A. capros*. Prey of *Z. conchifer* consisted of 48.57% RI mesopelagic and pelagic fishes and of 47.7% RI bentho-pelagic fishes. For all fishes, a permutation test revealed significant selection of prey in plateau margins of the seamount. Unweighted and novel-weighted overlap indices combining prey composition, habitat use and prey utilisation within habitats revealed high overlap between the boarfishes *A. capros* and *C. aper* and smaller overlap between other pairs. The results are in support of the sound scattering layer interception hypothesis (Isaacs & Schwartzlose 1965), which implies: (1) primarily pelagic food utilisation for bentho-pelagic fishes; (2) increased habitat-dependent utilisation rates at locations of interception with the sound-scattering layer; (3) diel changes in utilisation rates due to availability of prey; (4) sufficient resource partitioning among species in order to avoid competitive exclusion.

KEY WORDS: Permutation test · Hutchinson's rule · Sound-scattering layer · Bentho-pelagic fishes · Seamounts

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INTRODUCTION

Seamounts often maintain high standing stocks of micronekton and demersal fishes that are occasionally even of economical importance (Boehlert & Genin 1987, Koslow et al. 1994, Rogers 1994). Prominent representatives from subtropical seamounts with a summit depth range of 200 to 1000 m are armorheads (Pentacerotidae: *Pseudopentaceros*, *Pentaceros*), alfonsinos (Berycidae: *Beryx*), orange roughy (Trachichthyidae: *Hoplostethus*) and rockfishes (Sebastidae: *Sebastes*) both in the Pacific and Atlantic (Rogers 1994, Hareide & Garnes 2001). Taking account of the often impoverished nutritional conditions in the ambient oceanic regions, hypotheses have been developed to explain living conditions for seamount populations. Introduced by Isaacs & Schwartzlose (1965) and theoretically proven by Tseytlin (1985), interception with the advected and vertically migrating sound-scattering layer (SSL) has been suggested as providing a large enough prey source to maintain populations at seamounts (Hesthagen 1970, Rogers 1994, Parin et al. 1997). It has been shown that the SSL is a significant subsidy for continental slope fishes (Pereyra et al. 1969, Mauchline & Gordon 1991): In fact, vertical feeding migrations of seamount fishes in relation to the migration of the SSL have been observed (Lorz et al.

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1983, Boehlert & Genin 1987, Genin et al. 1988, Vinnichenko 1997, Vinnichenko 1998). In turn, SSL-seamount interactions have been indirectly evidenced through an increase in plankton patchiness over seamounts and increased diurnal predation on plankton over seamounts (Genin et al. 1988, 1994, Haury et al. 2000).

At the Great Meteor seamount (GMR, subtropical NE Atlantic, 30° N, 28.5° W), analysis of the horizontal distribution of seamount fishes over the plateau revealed that most of the populations were related to habitats at the edge of the plateau (Fock et al. 2002). At plateau margins the likelihood of interception with the horizontally advected SSL is increased. Vertically migrating SSL passes the marginal habitats twice a day during its ascent and descent, while the summit plateau is only supplied with advected prey during the descending phase of the SSL. Plateau margins are further affected by topographically induced circular currents around the summit and local upwelling phenomena caused by these current anomalies (Taylor-Column), which are also typical for GMR (Meincke 1971, Mourino et al. 2001). Thus, the availability of pelagic prey for fishes at plateau margins is likely to be further increased either directly through possible concentration effects (Olson & Backus 1985), retention effects (Mullineaux & Mills 1997) or augmentation of the food web through increased primary production (Comeau et al. 1995).

In terms of optimal foraging (Hart 1986), the SSL-interception hypothesis firstly implies reliance on pelagic prey. Secondly, it predicts an increased resource-utilisation rate because of the aggregation of fishes in plateau margins, i.e. locations of potential interceptions. Thirdly, the SSL-interception hypothesis predicts either cessation of feeding during periods of absence of migrating prey or a switch between diets depending on their diel availability. These features lead to a fourth implication; that of sufficient resource partitioning when the majority of a community prefers the same habitat due to optimal foraging in that particular habitat.

Differential horizontal habitat utilisation of fishes in sharply delimited biotopes such as reefs or seamounts is poorly understood, in spite of investigations on shelf-dwelling (Albert 1995) and shallow bank- and reef-dwelling fishes (Sogard et al. 1989, Burke 1995 McCormick 1995). Studies on deep-sea fishes have revealed changes of resource utilisation, in terms of diet composition, with depth (e.g. Bulman & Koslow 1992) or distribution with depth (e.g. Haedrich & Merrett 1988, Williams et al. 2001). Ontogenetically determined shifts in habitat utilisation, in terms of intraspecific competition, with corresponding spatial displacements have been analysed (e.g. Mueller et al. 1994, McCormick 1995).

Concerning the fourth tenet of the SSL-interception hypothesis, i.e. resource partitioning, the conceptual framework of Schoener (1974) allows prediction of patterns of niche overlap and ecological similarity for seamount fishes. Based on published data, Schoener (1974) concluded that in most cases 3 environmental niche dimensions were sufficient to explain the existing variability of niche performance for a given community. From the multitude of possible combinations of dimensions, habitat, prey and time proved to be most important in declining order. However, habitat quality is assumed to be less important than prey characteristics in environments with little spatial heterogeneity such as aquatic soft-bottom habitats (Schoener 1974, Piet et al. 1999). For marine hard-bottom habitats, substantial spatial niche partitioning in bentho-pelagic fishes can be found (Sala & Ballesteros 1997). Without partitioning, i.e. complete overlap in terms of habitat and diet preferences, compensatory mechanisms are required to provide territorial exclusion. Such founder-controlled communities are known for reef-fishes (Shpigel 1982, Townsend 1991).

For seamounts, analysis of time and habitat-dependent resource utilisation and resource partitioning of fishes has not yet been undertaken. These aspects are investigated in this paper with respect to the 4 implications from the SSL-hypothesis.

Four important inhabitants of the seamount bentho-pelagic fish community of the Great Meteor seamount were investigated: snipefish *Macroramphosus* spp., the boarfishes *Capros aper* and *Antigonia capros*, and the dory *Zenopsis conchifer*. These species account for 94.9% of total abundance and 71.4% of total fish biomass on GMR. The 2 boarfishes are morphologically very similar, but differ in size. In an analysis of habitat and diel preferences based on catch data from the 3 German cruises to GMR in 1968, 1970 and 1998, Fock et al. (2002) showed that *C. aper*, *A. capros* and *Z. conchifer* possessed a positive relationship to plateau margins, which was significant in the case of *C. aper*. In turn, *Macroramphosus* spp. showed a significant positive relationship to plateau habitats and daytime. These preferences were attributed to differential feeding modes with respect to the SSL-interception hypothesis.

MATERIALS AND METHODS

Sampling and morphometrics. Material from the M42/3-cruise of the RV 'Meteor' to GMR in 1998 was used (Pfannkuche et al. 2000). During the cruise, sampling was conducted with a GOV-bottom trawl with a wing span of 32 m (Uiblein et al. 1999, detailed description in Fock et al. 2002). Basic information on fish species and samples is provided in Table 1. Mor-

Table 1. Investigated fishes and degree of stomach emptiness. Stomach emptiness is expressed as Vacuity Index VI (see text). Spatio-temporal habitat categories in order are Day-a, Day-b, Day-c, Night-a, Night-b, Night-c (See Table 2). Nominal total catch refers to estimated total catch in 12 hauls at GMR (Uiblein et al. 1999). Due to the small number of hauls in habitat category c, no specimens from night hauls were available for this habitat (values in parentheses)

Parameter	*Macroramphosus* spp.	*Capros aper*	*Antigonia capros*	*Zenopsis conchifer*
Weight (mean, g wet wt)	13	25	273	1066
Size ranges (cm standard length)	10–15	8–14	14–20	32–53
No. stomachs examined	42[a]	97	39	61
No. stomachs containing prey	42	93	39	40
VI_i (%)	0	4.1	0	34.4
No. of stomachs by spatio-temporal habitat category	22, 20, 0, 0, 0, (0)	14, 28, 14, 15, 25, (0)	3, 12, 3, 7, 14, (0)	6, 10, 14, 11, 20, (0)
Nominal total catch (n)	82775[b]	25104[b]	81[b]	95[b]

[a]Only samples with mixed populations consisting of *M. scolopax*-type and *M. gracilis*-type fishes considered
[b]Specimens partly discarded

phometrical measurements presented for *Capros aper* and *Antigonia capros* follow Ehrich (1977).

Analysis of fish diets. For prey, either stomach contents (*Capros aper*, *Antigonia capros*, *Zenopsis conchifer*) or gut contents (*Macroramphosus* spp., see Clarke 1984) were analysed. Specimens were omitted from analysis when advanced digestion prevented analysis of the prey items. In *Macroramphosus* spp., 2 feeding types with either predominantly benthic or pelagic diet are to be discerned (Ehrich & John 1973, Ehrich 1976, Clarke 1984). Only stations with mixed population samples were included.

Stomach emptiness was expressed as Vacuity Index VI_i, i.e. as percentage number of empty stomachs or stomachs with only hard-structured remains (needles, single scales, setae etc.) compared to the number of all stomachs for fish species *i* (see Gomes et al. 1998). For each fish species *i*, the frequency of occurrence of each prey item *j* ($\%F_j$), its percentage by number ($\%A_j$) and its percentage by weight ($\%W_j$) were calculated (Hyslop 1980, Amundsen et al. 1996). $\%F_j$ was determined as number of stomachs of fish species *i* with prey item *j* compared to all non-empty stomachs of *i*. $\%A_j$ was calculated as number of prey item *j* (N_j) compared to the total abundance of all prey items for fish species *i* (N_{tot}). $\%W_j$ was calculated similarly. Reference weights for each prey item were obtained from more or less undigested specimens.

For overall comparisons of prey utilisation the compound 'Relative Importance index' (RI, %) was calculated for each prey item *j* (George & Holiday 1979, Hyslop 1980):

$$\%RI_j = (\%F_j + \%A_j + \%W_j) \times 100 / \sum_j (\%F_j + \%A_j + \%W_j) \quad (1)$$

As a ternary index, RI is qualitatively comparable to the likewise ternary 'Index of Relative Importance' (IRI; for calculation see Hyslop 1980), since with both indices the same ranking of prey items is obtained (Rosecchi & Nouaze 1987). Compound indices are highly sensitive to errors from imprecise estimates of $\%F_j$, $\%A_j$ and $\%W_j$ (Tirasin & Jörgensen 1999), so in this paper only primary data, not compound indices, were subjected to statistical analysis.

Statistical analysis of habitat-dependent resource utilisation. Accounting for variation in time and habitat of the fish assemblage (Fock et al. 2002), samples were assigned to 2 time (day and night) and 3 spatial categories (Fig. 1, Table 2). As opposed to an analysis of prey selection as the disproportionate utilisation of a prey item compared to prey concentration in the ambient environment (e.g. Bremset 2000), we investigated

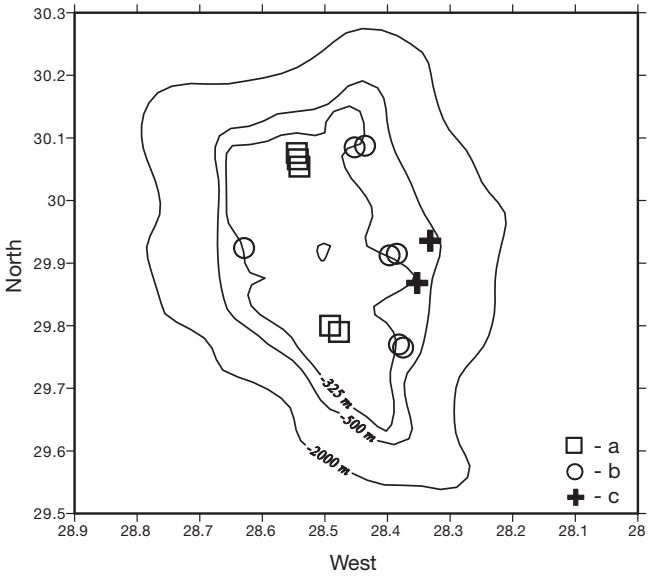

Fig. 1. Investigation area and location of trawling stations and spatial habitat categories a, b and c (see Table 2)

Table 2. Definition of spatio-temporal habitat categories. Respective locations for spatial categories depicted in Fig. 1

Factor	Category	Definition
Daytime	Night	19:00 to 6:00 h
	Day	6:00 to 19:00 h
Habitat	a	Plateau, mean catching depth 290 m, depth range 285 to 310 m
	b	Inner margin, mean catching depth 310 m, depth range 302 to 365 m
	c	Outer margin, mean catching depth 355 m, depth range 358 to 470 m

whether a certain prey item was disproportionately utilised within different environmental categories relative to the number of fish specimens caught in these environmental categories. This is achieved with a permutation test, reassigning prey data randomly to fish specimens. Randomisations are required when test distributions are unknown (Crowley 1992, Rice 2000). In this case, as for all kinds of stomach analyses, the uncertainty in counting prey demands a data-dependent approach to assess significance. In order to take account of daytime effects apparent in the uneven availability of specimens for the investigation (Table 1), the re-assignment of prey data to fish specimens in spatial categories was permuted separately for the 2 temporal categories, i.e. the test had a nested design. For each data set 250 permutations were conducted.

For each fish species i, the percentage by number per category for each prey item j was calculated. We called this percentage by distribution, indicated by the lower-case letters of the respective habitat. For habitat category b this is:

$$\%b_j = b_j/N_j \times 100 = b_j/(a_j + b_j + c_j) \times 100 \quad (2)$$

where b_j is the proportion of N_j in habitat b.

Two different tests were applied. A test on tendency determined whether the differences of resource utilisation between 2 habitat types were drawn from a random distribution. The difference between 2 habitats (Fig. 2) is described as:

$$diff_{ba,\,j} = \%b_j - \%a_j \quad (3)$$

where $\%a_j$ and $\%b_j$ are the percentages by distribution for prey item j in habitat categories a and b respectively and $diff_{ba}$ is the difference between them. This difference is calculated for both types of plateau margin vs the plateau, i.e. b – a and c – a. The actual $diff_{ba,\,j}$ from Eq. (3) is compared to a distribution of randomised $diff_{ba}$'s obtained from permutations of the original data matrix.

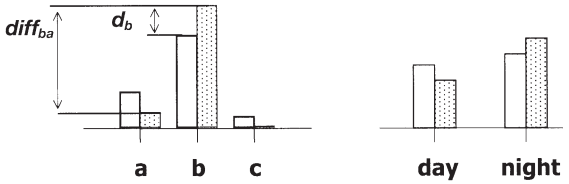

Fig. 2. Template for graphical display of diet utilisation within spatio-temporal categories (habitats a, b, c; day/night) and descriptions of test statistics $diff_{ba}$ and d_b. The percentage by distribution of specific prey items in habitats and time of day, respectively (shaded bar) is contrasted with the percentage by distribution of the predatory fish species in habitats and time of day, respectively (empty bar). Statistic d is calculated as within-category difference between empty and shaded bars, statistic $diff$ is calculated as between-category difference between shaded bars only. (Note: The elements of the matrices $\mathbf{H}_i$ [feeding use] are obtained by multiplying the percentages by distribution for time [shaded bars in 'day' or 'night'] by the respective percentages by distribution for Habitats [shaded bars in a, b and c] for each prey item)

A test on quantitative selection simultaneously takes into account differences within all 3 habitats. For this a squared statistic d^2 is derived (Eq. 4), which is calculated from the sum of squares of differences of percentages by distribution between fish species i and prey item j for each habitat category:

$$d_a = \%a_i - \%a_j; \quad d_b = \%b_i - \%b_j; \quad d_c = \%c_i - \%c_j$$
$$d^2 = d_a^2 + d_b^2 + d_c^2 \quad (4)$$

Here $\%b_i$ is the percentage by distribution of the investigated specimens of fish species i and $\%b_j$ the respective measure of prey item j (Eq. 2). The outcome depends on the variation of $\%a_j$ since $\%a_i$ (the proportion of fish specimens i in habitat a) is invariant. The test is rooted in Ivlev's foraging index E (Ivlev 1961) and its derived form, Jacobs' index (Jacobs 1974), since both indices deploy differences in the nominator to describe the degree of selection. For E, a translation of the indices into the context of habitat-dependent resource utilisation would be $(\%a_i - \%a_j)/(\%a_i + \%a_j)$. This approach is different to Hurlbert's approach (Hurlbert 1978) of calculating a utilisation proportion from the ratio of actual to potentially possible utilisation, i.e. $\%a_j/\%a_i$.

Three types of spatial resource utilisation are discerned, analogous to the analysis of spatial distribution patterns (see Elliott 1983, p 37–49): (1) Regular, non-selective utilisation. The distribution of utilised prey items matches the distribution of investigated fishes. (2) Random, non-selective utilisation. The distribution of prey items differs from the distribution of investigated fishes, but the deviations are within random bounds. (3) Selective utilisation. The distribution of utilised prey items differs significantly from the distribution of investigated fishes.

Treated as 1-tailed test (Zar 1996), regular utilisation in terms of tendency or quantitative selection is found when the actual statistic is smaller than the 5-percentile of the random distribution. In turn, selective utilisation is found when the actual statistic is bigger than the 95th percentile of the random distribution. From the 2 tests applied, the test on tendency is more sensitive since it considers both the direction and the amount of deviation, whereas the test on quantitative selection through squaring of differences puts emphasis on the amounts of deviations.

Power analysis (Erdfelder et al. 1996) yielded sufficient power values of >0.99 in all significant cases. This is in line with findings from Zoschke & Lüdin (2001) that power is sufficiently high, even though measurements are inaccurate, when the sample size is large enough (here n = 250).

Niche overlap. In the analysis of resource partitioning, 2 rationales have to be taken into account. One considers the resources actually used, which requires knowledge on abundances of resource states; the other considers the principle of partitioning, i.e. the overlap in resource use when no constraints in resource availability are considered (Hurlbert 1978). We refer to the latter since we have no estimates of abundance of habitat types or of diets in the ambient environment. In this case, overlap similarity α is appropriate, which was introduced and originally performed for community analysis as Renkonen index (Hurlbert 1978, Loman 1986):

$$\alpha = \sum_i \min(p_{1,j}, p_{2,j}) \quad (5)$$

where $p_{1,j}$ and $p_{2,j}$ denote proportions of category j (measure of diet composition) in classes 1 and 2 (fish species i with $i = 1,2,3,...,k$), respectively. This is equivalent to Schoener's overlap equation (Schoener 1968), which has been frequently applied to other topics such as trend analyses in fisheries (Macpherson & Gordoa 1992) and dietary overlap (e.g. Blaber & Bulman 1987, Pedersen 1999):

$$\alpha = 1 - 0.5\left(\sum_i |p_{1,j} - p_{2,j}|\right) \quad (6)$$

Since

$$\alpha = \sum_i \min(p_{1,j}, p_{2,j})$$

and

$$\beta = \sum_i \max(p_{1,j}, p_{2,j}) = \sum_i \min(p_{1,j}, p_{2,j}) + \sum_i |p_{1,j} - p_{2,j}|$$

and

$$\alpha + \beta = 2$$

then

$$2\alpha + \sum_i |p_{1,j} - p_{2,j}| = 2$$

After re-arranging, Eq. (6) is obtained.

Three different matrices describe the utilisation of resources for fish species i (e.g. Sala & Ballesteros 1997). $\mathbf{F}_i$ is the $(j,1)$-matrix of proportions of dietary composition of prey items j in terms of RI (see Table 3), $\mathbf{H}_i$, i.e. feeding use (Sala & Ballesteros 1997), is the respective habitat utilisation (j,k)-matrix for fish species i within k combinations of habitat categories for all prey items j (see Fig. 2), and $\mathbf{A}_i$ is the $(k,1)$-matrix of abundance proportions for i in all k spatio-temporal categories (Table 1). Considering that niche space is inherently multidimensional, through multiplication of the matrices $\mathbf{F}_i$, $\mathbf{H}_i$ and $\mathbf{A}_i$ weighted utilisation matrices are obtained. The calculations and dimensions of the resulting matrix determine its interpretation. For example, multiplying $\mathbf{F}_i^{\mathrm{T}}$ and $\mathbf{H}_i$ (Eq. 8) results in an interim matrix where each element contains the sum of the habitat utilisation coefficients of the prey items times their respective proportions in the diet, thus a diet weighted matrix with k elements describing habitat use for k spatio-temporal categories.

We now re-define the dietary component of resource utilisation as weighted by the abundance distribution of species i within habitats k and the utilisation of diet within the k habitats:

$$(\mathbf{H}_i\mathbf{A}_i)\mathbf{F}_i^{\mathrm{T}} = \mathbf{D}_i \quad (7)$$

where $\mathbf{D}_i$ is a (j,j)-matrix.

For spatio-temporal habitat utilisation weighted by abundance and dietary composition we obtain:

$$\mathbf{A}_i\,(\mathbf{F}_i^{\mathrm{T}}\mathbf{H}_i) = \mathbf{R}_i \quad (8)$$

where $\mathbf{R}_i$ is a (k,k)-matrix. $\mathbf{T}$ denotes the respective transposed matrix.

Overlap for $\mathbf{D}_i$ is then calculated as:

$$\alpha_{\mathrm{D}} = \sum_{j^2} \min(d_{1,.}, d_{2,.}) \quad (9)$$

where $d_{1,.}$ are the elements of respective matrices $\mathbf{D}_i$. α_{R} for $\mathbf{R}_i$, α_{F} for $\mathbf{F}_i$ and α_{A} for $\mathbf{A}_i$ are calculated similarly.

Due to inequality of matrices when the order of multiplication is changed, the $\mathbf{D}_i$'s and $\mathbf{R}_i$'s and thus α_{D}'s and α_{R}'s are different and considered independent.

For the purpose of comparison with published data we apply unweighted overlap indices concerning $\mathbf{F}_i$ and $\mathbf{A}_i$ and further weighted overlaps concerning $\mathbf{R}_i$ and $\mathbf{D}_i$ in order to describe spatio-temporal habitat and dietary overlap.

RESULTS

Prey items and diet composition

Prey items were aggregated into prey groups. In many cases the pre-digested remains did not allow for

Table 3. Major diet groups and dietary importance in terms of 'Relative Importance index'. The pelagic origin of foraminifers was proven by P. Heinz (pers. comm.). Note: the values for the matrix $\mathbf{F}_i$ are calculated from $\%RI_j/100$. $\%RI_j$ = percentage by Relative Importance index for prey item *j*. AFDW = ash-free dry weight

Prey group	Prey item	*Macroramphosus* spp.				*Capros aper*				*Antigonia capros*				*Zenopsis conchifer*			
		No. of stomachs with prey	No. of items	Biomass (mg AFDW)	$\%RI_j$	No. of stomachs with prey	No. of items	Biomass (mg AFDW)	$\%RI_j$	No. of stomachs with prey	No. of items	Biomass (mg AFDW)	$\%RI_j$	No. of stomachs with prey	No. of items	Biomass (mg AFDW)	$\%RI_j$
Foraminifera	Foraminifera, pelagic	38	12367	494.68	25.28	11	127	5.08	4.4								
Porifera	Spiculae[a]	3	5							1	1						
Hydrozoa	Pieces of colonies					6	16	0.64	1.76								
Echinodermata	Pedicellariae[a]	6	69														
Annelida	Polychaeta	11	141	144.67	4.96	8	8	8.21	2.82	2	2	2.05	0.82				
	Polychaete remains	1	1	1.03	0.36												
Crustacea	Amphipoda, benthic	6	35	47.67	2.46	7	10	13.62	3.01								
	Amphipoda, pelagic									27	80	88.12	11.83				
	Cirripedia	2	5	0.50	0.71												
	Cladocera					1	2	0.07	0.28								
	Copepoda, Calanoida	29	465	22.79	10.69	61	2297	112.55	45.15	22	518	25.38	15.10				
	Copepoda, Harpacticoidea	2	2	0.07	0.7												
	Decapoda	10	39	105.03	4.26	10	47	126.58	13.17	35	306	824.08	19.56				
	Decapoda, larvae	8	30	79.30	3.38												
	Euphausiacea	1	2	1.82	0.37	8	10	9.09	2.91								
	Isopoda	3	3	1.04	1.07	1	3	1.04	0.37								
	Mysidacea	8	20	6.95	2.88												
	Nauplius					10	12	0.24	2.74								
	Non-identified pieces[a]	42	332			70	140										
	Ostracoda	22	421	127.98	8.91	20	29	8.82	6.18	1	1	0.30	0.41				
	Tanaidacea	2	2	0.20	0.7												
Mollusca	Bivalvia	1	1	0.05	0.35												
	Cephalopoda	1	1	17.27	0.47	1	1	17.27	1.65	37	241	4161.78	27.71	3	3	51.81	2.59
	Gastropoda, pelagic	42	7924	1117.28	32.45	20	40	5.64	6.03	18	23	3.24	7.38				
Pisces	*Capros aper*													6	7	7434	9.27
	Chauliodus sp.									9	24	951.16	6.17	2	6	237.79	2.93
	Fish remains[a]	2	2			12	20										
	Macroramphosus spp.													26	58	14261	38.43
	Myctophidae					1	1	4.46	0.63	17	45	200.84	7.74	9	48	214.23	18.54
	Non identified[a]													10	20		
	Trachurus sp.													4	4	45474	27.10
	Vinciguerria sp.									2	2	20.23	0.86	1	2	20.23	1.14
Misc.	Eggs					24	276	2.76	8.92	1	1	0.05	0.24				
	Non-identified pieces[a]	42	166			35	70										

[a]Not included in calculations of indices

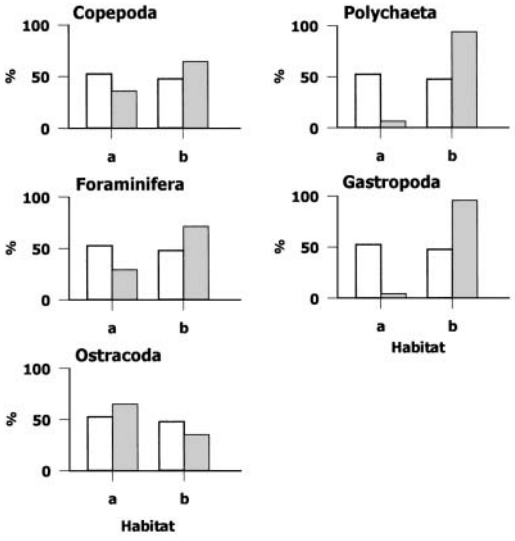

Fig. 3. *Macroramphosus* spp. Habitat-dependent resource utilisation of selected prey items. Percentage distribution of prey (shaded bar) and fish species (empty bar), see Fig. 2. No data available for nighttime and habitat c

further determination. Gastropoda consisted mainly of needle pteropods (e.g. Cavolinidae) and round-shelled species (e.g. Limacinidae). Among the copepods the genera *Scolethrix*, *Calanus*, *Pleuromamma* and *Arietellus* were identified. Hyperiid amphipods contributed mainly to the diet of *Antigonia capros* (e.g. genus *Vibilia*), whereas benthic gammaridean amphipods were found in *Macroramphosus* spp. Myctophid genera found in stomachs of *A. capros* and *Zenopsis conchifer* were *Lampanyctus*, *Lepidophanes*, *Diaphus*, and *Ceratoscopelus*. Euphausiids identified in *Capros aper* belonged to the genus *Thysanopoda*.

Almost no empty stomachs were found for *Macroramphosus* spp., *Capros aper* and *Antigonia capros* (VI ~ 0, Table 1). For *Zenopsis conchifer* a third of the stomachs were found empty (VI = 34.4%).

Common to all species was the low share of genuine benthic prey. The major benthic contributions were decapods to the diet of *Capros aper* and *Antigonia capros* with % RI values of 13.2 and 19.6 respectively (Table 3). For *Macroramphosus* spp., the benthic components mainly consisted of polychaetes, amphipods and decapods and decapod larvae, with a total 18.25% RI. For *C. aper* and *A. capros*, benthic contributions added up to 19 and 20.38% RI. No benthic prey was found for *Zenopsis conchifer*. *Macroramphosus* spp. predominantly fed on foraminifers, gastropods and calanoids, adding up to 68.42% RI. Calanoid copepods were the major fraction for *C. aper* with 45.15% RI. For *A. capros*, cephalopods prevailed with 27.71% RI. Mesopelagic fishes constituted a bigger portion of diet with 13.91% RI. For *Z. conchifer*, mesopelagic and pelagic fishes contributed 48.57% RI and bentho-pelagic fishes 47.7% RI. Fish remains were found in all 4 species.

Diel and habitat-dependent resource utilisation

Macroramphosus spp. No specimens from habitat type c were available. Due to constraints on sample composition, only daytime samples were analysed. From the 5 major prey items only ostracods were disproportionately more utilised in the plateau habitat type a (Fig. 3), though not significantly (Table 4). The other 4 items were more intensively utilised in plateau margin type b. For polychaetes and gastropods selection was significant (Table 4).

Capros aper. A diel change in resource utilisation appeared (Fig. 4). Whereas copepods and euphausiids were predominantly eaten diurnally, decapods were preferred nocturnally. Foraminifers and pteropods also showed a slightly increased utilisation rate during nighttime. For the utilisation of copepods and

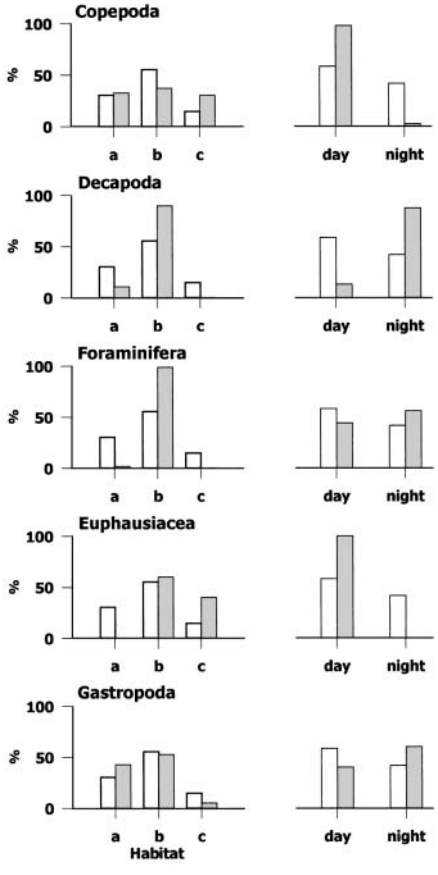

Fig. 4. *Capros aper*. Habitat-dependent resource utilisation of selected prey items. Percentage distribution of prey (shaded bar) and fish species (empty bar), see Fig. 2

Table 4. Statistical analysis of habitat-dependent resource utilisation from permutation tests. Only significant p-levels indicated ($p < 0.05$ indicates regular utilisation, $p > 0.95$ indicates selective utilisation of prey within a given habitat). For calculation of p, see text. Results with marginal significance levels in parentheses, nd = not determined

Predator	Prey item	Test on tendency				Test on quantitiative selection
		Regular utilisation	Preference of plateau vs margin	Preference of inner margin vs plateau (b vs a)	Preference of outer margin vs plateau (c vs a)	
Macroramphosus spp.	Copepoda				nd	
	Foraminifera				nd	
	Ostracoda				nd	
	Polychaeta			p = 0.99	nd	p = 0.99
	Gastropoda			p = 0.99	nd	p = 0.99
Capros aper	Copepoda				p = 0.99	
	Decapoda	p = 0.004[a] (a vs c)				
	Foraminifera			p = 0.99		p = 0.96
	Euphausiacea				p = 0.99	
	Pteropoda	p = 0.004 (a vs c), p = 0.01 (a vs b)				
Antigonia capros	Myctophidae					
	Total mesopelagic Fishes			p = 0.97		
	Copepoda					p = 0.01[a]
	Decapoda			p = 0.99		p = 0.98
	Cephalopoda					
Zenopsis conchifer	Myctophidae			p = 0.98	(p = 0.92)	
	Total mesopelagic Fishes			p = 0.97	p = 0.95	
	Macroramphosus spp.		(p = 0.93) (a vs b)			
	Capros aper					

[a]Spurious result, discussed in text

euphausiids a significant tendency was indicated for the preference of habitat type c, the outer margin. A preference for habitat type b was indicated for the utilisation of foraminifers both for tendency and quantitative selection. In turn, pteropods appeared to be regularly utilised. The significant result of regular utilisation obtained for decapods between habitats a and c is spurious, since in c night catches were underrepresented and thus the result is biased due to unbalanced sample design, because decapods were fed on during nighttime.

Antigonia capros. The small number of specimens available from habitat type c prevented thorough analysis of the outer margin habitat. Only 7% of the specimens analysed represented the outer reach of GMR (Table 1). Except for copepods, no diel effects were found (Fig. 5). Copepods were preferentially utilised during daytime. However, this result was due to 1 *A. capros*-specimen eating 433 copepods. Thus, the result of the statistical test on quantitative habitat-dependent selection is biased. Decapods and myctophids showed a tendency towards being utilised nocturnally. Except for cephalopods, all major prey items showed a tendency towards more intensive utilisation in habitat type b. This was significant for mesopelagic fishes (sum of myctophids and the stomiiform fishes *Chauliodus* sp. and *Vinciguerria* sp.) and decapods. For the latter the test on quantitative selection was also significant.

Zenopsis conchifer. A marked diel effect was found. Mesopelagic fishes were utilised during the night, whereas the bentho-pelagic fishes *Capros aper* and *Macroramphosus* spp. were predominantly eaten during the day (Fig. 6). Except for *Macroramphosus* spp., plateau margins showed an increased utilisation rate of prey items, significant in terms of tendency for the mesopelagic fishes (Table 4). For *Macroramphosus* spp., a weak opposite tendency in favour of the plateau habitat type a was found.

A clear pattern evolves for the utilisation of prey items. In terms of significant non-spurious relationships, 11 relationships for plateau margins (either b or c) were found. One item was regularly utilised (gastropods by *Capros aper*). One relationship was significant for plateau habitats: that of *Zenopsis conchifer* to *Macroramphosus* spp., corresponding to the habitat preferences of *Macroramphosus* spp. (Table 5). At plateau margins, generally increased utilisation was

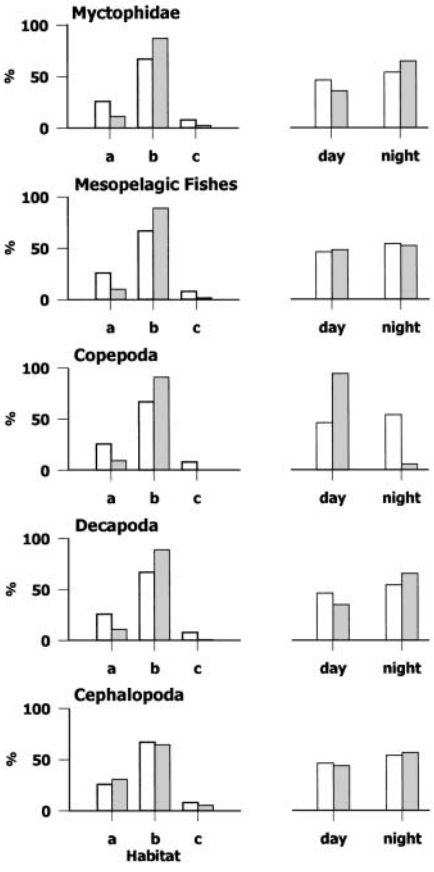

Fig. 5. *Antigonia capros*. Habitat-dependent resource utilisation of selected prey items. Percentage distribution of prey (shaded bar) and fish species (empty bar), see Fig. 2. Mesopelagic fishes comprise myctophids and the stomiiform fishes *Chauliodus* sp. and *Vinciguerria* sp.

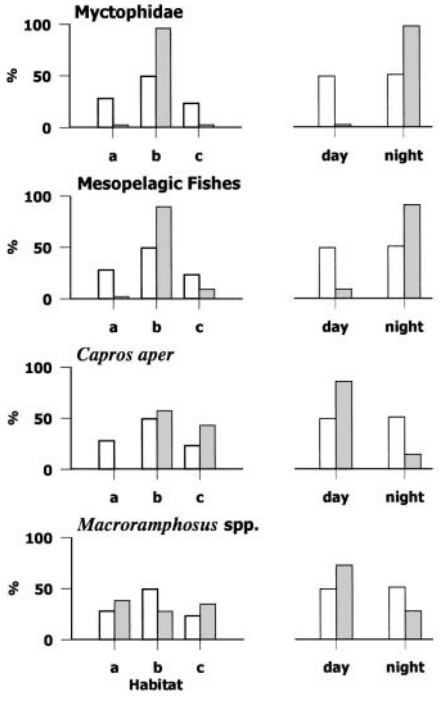

Fig. 6, *Zenopsis conchifer*. Habitat-dependent resource utilisation of selected prey items. Percentage distribution of prey (shaded bar) and fish species (empty bar), see Fig. 2. Mesopelagic fishes comprise myctophids and the stomiiform fishes *Chauliodus* sp. and *Vinciguerria* sp.

found for mesopelagic fishes, copepods, euphausiids and decapods. For the 4 fishes considered, prey items with significant habitat-dependent selection were also most important in terms of RI. The only non-significant case were foraminifers for *Macroramphosus* spp. Next to habitatdependent selection, a pattern of diel utilisation can be deduced. Except for *Antigonia capros*, mesopelagic fishes were preferably utilised during nighttime, with an opposite pattern for copepods and euphausiids. Benthic diet or pelagic objects that probably impinge on the seafloor after descent are preferably eaten at night, i.e. decapods, foraminifers and gastropods. Following the above-mentioned pattern for mesopelagic fishes, *Z. conchifer* consequently utilised bentho-pelagic fishes (*Macroramphosus* spp. and *C. aper*) during daytime. *A. capros* showed an almost even temporal utilisation pattern for cephalopods and mesopelagic fishes, indicating that these important prey items, comprising 42.5% RI, are more actively sought irrespective of their possible diel migrations.

Niche overlap

The preferences of plateau margins for 3 of the 4 fishes and partly similar patterns of habitat-dependent prey utilisation suggest that especially spatio-temporal niche overlap can be expected. In fact, unweighted habitat utilisation overlaps (from $\mathbf{A}_i$, Table 5) were

Table 5. Spatio-temporal habitat utilisation. Each entry represents the proportional abundance of the species within the spatial and temporal categories defined in Table 1. The values for the matrices $\mathbf{A}_i$ are represented by the respective column entries (see text)

Spatio-temporal category	*Macroramphosus* spp.	*Capros aper*	*Antigonia capros*	*Zenopsis conchifer*
Day-a	0.442	0.116	0.067	0.186
Day-b	0.452	0.428	0.490	0.305
Day-c	0.010	0.041	0.023	0.106
Night-a	0.047	0.082	0.048	0.126
Night-b	0.048	0.303	0.355	0.206
Night-c	0.001	0.029	0.016	0.072

Table 6. Weighted and unweighted dietary and habitat overlaps for GMR fishes. For calculation see text. ANT = *Antigonia capros*, CAP = *Capros aper*, MAC = *Macroramphosus* spp., ZEN = *Zenopsis conchifer*, nd = not determined, due to missing data for night-time and habitat type c

Type	Index	Species 1 Species 2	MAC CAP	MAC ANT	MAC ZEN	CAP ANT	CAP ZEN	ANT ZEN
Unweighted dietary overlap	α_F		0.380	0.240	0.005[a]	0.402	0.023[a]	0.135
Unweighted habitat overlap	α_A		0.650	0.625	0.597	0.885	0.780	0.666
Weighted dietary overlap	α_D		nd	nd	nd	0.961	0.014	0.135
Weighted habitat overlap	α_R		nd	nd	nd	0.699	0.683	0.544

[a]*Macroramphosus* spp. and *C. aper* serve as prey for *Z. conchifer*, RI values are 0.384 and 0.093 respectively

larger than the corresponding unweighted dietary overlaps (from $\mathbf{F}_i$, Table 3). Habitat utilisation overlaps were similar and ranged between 0.885 and 0.597 (Table 6). Smallest habitat overlaps were obtained in relationship to *Macroramphosus* spp. Unweighted dietary overlaps were more diverse. The order of unweighted overlaps with the largest values between fishes of neighbouring sizes, i.e. for *Macroramphosus* spp. and *Capros aper*, for *C. aper* and *Antigonia capros* and for *A. capros* and *Zenopsis conchifer*, indicates that size similarity leads to high overlap. In quantitative terms, the primarily nektonic diet of *Z. conchifer* separated this species from the others so that the lowest values were obtained in relation to this species ranging from 0.005 to 0.135. With 1 exception, weighting yielded smaller overlaps compared to unweighted overlaps. Only for the species pair *A. capros*/*C. aper* was the weighted dietary overlap considerably larger than the unweighted overlap, reaching 0.961. The generally smaller values for dietary overlap indicate that trophic separation is stronger than habitat separation.

In turn, the low overlap values obtained for *Zenopsis conchifer* in relation to *Macroramphosus* spp. and *Capros aper* must be modified with regard to the fact that these species not only compete with *Z. conchifer*, but also serve as prey.

DISCUSSION

Diet composition

Vacuity Index was found to be almost zero for the 3 smaller fishes investigated and was 34.4% for *Zenopsis conchifer*. Similarly, Clarke (1984) found no specimens of *Macroramphosus* spp. with empty guts off Australia. Ehrich (1971, 1974) determined VI estimates of 2.3% for *Antigonia capros* and 1.3% for *Macroramphosus* spp. at GMR, but comparably higher values for *Capros aper* (VI = 54.8%) and for *Z. conchifer* (VI = 100%, n = 4). Our value for *Z. conchifer* is within the range given by Macpherson (1983) for larger shelf fishes off Namibia (mean VI = 42.2%) and by Gomes et al. (1998) for fishes off the Azores (mean VI = 74.03%). Similarly, VI values for *Sebastes caurinus* and *S. maliger* off British Columbia varied between 20 and 60%, depending on season (Murie 1995). These species are comparable to *Z. conchifer* in terms of trophic level and size.

Concerning diet composition, a relatively low contribution of non-copepod crustaceans was found in the diet of the GMR fishes compared to those in other shelf areas. In shelf areas, decapods and amphipods constituted the dominant prey for *Macroramphosus* spp. (88% by weight, Matallanas 1982; 35% by frequency Clarke 1984), whereas foraminifers and gastropods were the most important prey items in this study. In the size class >9 cm standard length, major prey for *Capros aper* comprised euphausiids and amphipods in the Mediterranean and off Portugal (Macpherson 1979, Santos & Borges 2001), whereas copepods were the most important item in this study. For *Antigonia capros* at the Brazilian shelf, diet primarily comprised euphausiids and amphipods (Haimovici et al. 1994), whereas we found fishes and cephalopods to be major items. Even to some degree for *Zenopsis conchifer*, a crustacean diet was found (Macpherson 1983, Haimovici et al. 1994), whereas we observed a mostly nektonic diet. The predominant choice of myctophid prey and *Trachurus* spp. for *Z. conchifer* was similar in all studies (Macpherson 1983, Haimovici et al. 1994).

The shift in diet composition for *Capros aper* and *Macroramphosus* spp. from items with high individual biomass towards low biomass items of the plankton indicates that their diet quality at GMR is diminished compared to other shelf areas. In turn, at GMR *Antigonia capros* and *Zenopsis conchifer* were apparently able to substitute crustacean prey by cephalopods and by fish diet. This accentuates the capability of the fish species to adapt to the prevailing conditions with regard to presumed prey availability. The VI values further indicate that this adaptation is accomplished successfully and that the reduced nutritional value of the diet is counterbalanced by the amount eaten.

Habitat-dependent resource utilisation and the SSL-hypothesis

For the subtropical NE Atlantic, the sound-scattering layers undertake diel migrations from ca. 600 to 900 m to the surface (Kinzer 1969, Mozgovoy & Bekker 1991). This covers the depth range of plateau, marginal and even upper-slope habitats at GMR. The SSL consists of different layers inhabited by different groups of crustacean plankton at depths <600 m (Kinzer 1969) and mesopelagic fishes such as myctophids down to 900 m (Mozgovoy & Bekker 1991). Further non-migratory layers in subtropical waters are known, attributed to siphonophores and gonostomatids (Conte et al. 1986). Under the SSL-interception hypothesis, those predators that prey upon components from the upper SSL (preferably pelagic crustaceans) follow the SSL to the surface during night and descend at dawn with a significant positive relationship to the factor 'day'. For seamount fishes interception probability with a diel-moving SSL is likely to be highest at plateau margins, especially if deeper reaches, i.e. slope habitats, are also utilised and a circular current concentrates part of the prey field from the SSL around the seamount.

The SSL-interception hypothesis (Isaacs & Schwartzlose 1965, Rogers 1994) accounts for both the observed diel and spatial patterns of resource utilisation to explain the sustained fish populations at GMR. Our study authenticated the first 3 tenets: (1) reliance on prey of pelagic origin in terms of %RI, (2) increased utilisation rates of prey in plateau margins, (3) diurnally changing feeding due to changing availability of components of the SSL. Effects were evident for euphausiids, copepods and myctophids as pelagic prey items. For euphausiids and copepods, the diurnally changing mode of availability can be related to interactions between descending zooplankton and predators over shallow topography, as conceptually developed in Haury et al. (2000) and earlier works (Hesthagen 1970, Genin et al. 1988, 1994). The nocturnal predation on myctophids at GMR is in accordance with their migration. Migrating myctophids are nocturnally present in depths of 150 to 500 m, where they prey on euphausiids, amphipods and copepods and are themselves subject to predation (Clarke 1978, Watanabe et al. 1999, Moku et al. 2000, Butler et al. 2001). Thus, the daytime descent takes them below the reach of bentho-pelagic fishes at the top of shallow topography like GMR.

Minor exceptions from this scheme appeared for *Macroramphosus* spp. and *Antigonia capros*. *Macroramphosus* spp. were subject to diel predation in plateau habitats. This can be explained by an increased abundance of the genus in plateau habitats during the day (Table 5). *A. capros* showed an almost regular though not significant pattern for the utilisation of its main prey, i.e. cephalopods, in relation to time of day and choice of habitat. This probably indicates an active pursuit of prey irrespective of its near-bottom availability. Both exceptions from the SSL-interception hypothesis can be regarded as behavioural adaptation. Behaviourally modified utilisation of habitats is known from reef fishes (e.g. Eggleston et al. 1998).

Anticipating a more active pursuit of favourite prey by *Antigonia capros* contrasts the diel switch in prey utilisation observed for *Macroramphosus* spp., *Capros aper* and *Zenopsis conchifer*. The diel switch can be conceived as a switch from primary prey, in terms of RI, to secondary items when primary prey gets scarce due to diel migrations, and can be understood as capability of complementary feeding. For *C. aper*, this means switching from diel feeding on copepods (45.2% RI) to nocturnal feeding on decapods and gastropods (19.2% RI). *Z. conchifer* switches between nocturnal predation on pelagic and mesopelagic fishes (48.3% RI) and diurnal predation on *Macroramphosus* spp. (38.4% RI).

Limiting similarity and resource partitioning

In this paper we applied overlap indices to indicate ecological similarity of species. In an early review of overlap measurements, Hurlbert (1978) argued against the overlap index α since the calculation of overlap according to Eqs. (5) & (6) does not account for the variation of resource state abundance. With known abundances of resource states, this can be met by calculating encounter probabilities for 2 species within a given resource state (Hurlbert 1978). With unknown resource state abundances, we developed weighted overlap measures, where encounter probabilities can be seen to be substituted by feeding use ($\mathbf{H}_i$) and abundance distribution ($\mathbf{A}_i$) matrices, so that the major concern of Hurlberg is met. As already presented by Sala & Ballesteros (1997), we chose 3 different matrices to describe weighted resource utilisation. It appeared that weighted overlaps were generally smaller than the unweighted overlaps, and only in 1 case a higher value was obtained. The same phenomenon can be found by comparing weighted and unweighted overlaps (Piet et al. 1999). Piet et al., as well as Gladfleter & Johnson (1983), applied weighting by size structure, and concluded that unweighted overlaps tend to misinterpret community structure. The very high weighted dietary overlap for *Capros aper*/*Antigonia capros* of 0.961 resembles the values in Sala & Ballesteros (1997) for feeding use overlap observed for species of sea bream *Diplodus* spp. (0.8 to 0.99). We suggest that due to inherent multidimensionality of niche space,

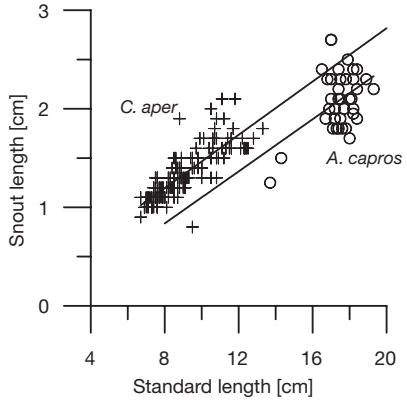

Fig. 7. *Capros aper* and *Antigonia capros*. Difference in snout length. Size-difference ratio is 1.55, of benefit to *A. capros*. The almost parallel regression lines with $r^2_{C.aper}$ = 0.68 and $r^2_{A.capros}$ = 0.2 indicate a size-difference ratio of 1.34, relative to standard length, of benefit to *C. aper*

weighting generally leads to better resolution of interspecies relationships. Since only little overlap in size classes appeared for GMR data (see Table 2), weighting by size structure can be neglected for the GMR fishes considered. In turn, in the presence of overlapping size classes, competition and thus overlap is likely to be much higher than indicated by our values of overlap. Competition between overlapping juvenile size classes of species can be avoided when juveniles undertake extended pelagic life stages in environments remote from seamounts. Such pelagic life stages are known for *Macroramphosus* (Badcock & Merrett 1976) and *Pseudopentaceros wheeleri* (Humphreys & Tagami 1986, Koslow 1997). *P. wheeleri* spends up to 2.5 yr in the pelagic stage before settling on seamounts. Strong intraspecific competition was also indicated for orange roughy at Australian seamounts (Koslow 1997).

Overlap measures provide the opportunity to analyse the fourth tenet of the SSL-interception hypothesis, i.e. understanding of co-existence of ecologically similar species. Schoener (1974) linked the concepts of limiting similarity with that of resource partitioning in order to describe diversity and regulation in competitively organised communities. Limiting similarity can be either expressed as overlap in terms of maximum allowable similarity or in terms of minimum necessary difference. Intuitively, both approaches are linked as one being the reciprocal of the other. For the analysis of minimum necessary differences, Hutchinson (1958) explored morphological differences in sympatrically living species where competition is assumed and discovered size difference ratios from 1.2 to 1.4. Mainly terrestrial studies since then have supported Hutchinson's rule, providing average difference ratios in the range 1.15 to 1.9 (Giller 1984, Schoener 1984), together with a few in aquatic environments (Berglund 1981, Morri & Bianchi 1995). Simberloff & Boecklen questioned the mere size-dependent approach and argued that morphologically similar species might differ with respect to other characteristics as well. This is exemplified by comparing the morphologically similar boarfishes *Capros aper* and *Antigonia capros*. In terms of weight, the size-difference ratio is >10, considering the length ratio the difference between the means is 1.85. However, the actual size difference in snout length, probably the most decisive factor in capturing prey, is 1.55 (Fig. 7), which is close to Hutchinson's rule. The highest degree of overlap was indicated for this pair of species, both for weighted and unweighted indices (Table 6). Thus, following the rationale of Schoener (1974) in linking overlap values and Hutchinson's rule, we employ the numerical minimum difference values as a starting point to further investigating the observed overlaps in terms of total allowable overlap. Considering 2 main dimensions of niche space, i.e. habitat and food separation (Schoener 1974), overall overlap has been considered as habitat overlap times dietary overlap (see also Gladfelter & Johnson 1983, Hansson 1984). This requires independent niche dimensions (Gladfelter &

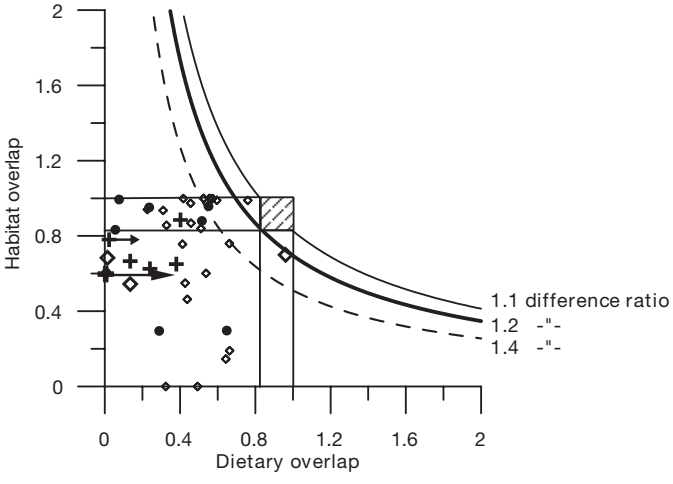

Fig. 8. Schematic representation of total overlap, i.e. conjoint dietary and habitat overlap, for GMR fishes (unweighted overlaps +, weighted overlaps ◆) and reference data from Thiel et al. (1996, ◇) and Naesje et al. (1991, ●) compared to isograms of maximum allowable niche overlap derived from Hutchinson's rule for difference ratios of 1.1, 1.2 and 1.4. Isograms are drawn as 2-D, i.e. squared, reciprocal difference ratios. Rectangles indicate maximum allowable overlap with a value = 1 for one of the niche dimensions and the corresponding value for the other dimension according to a 2-D 1.1-overlap isogram. Arrows indicate dietary overlap plus predatory effect for the species pairs *Zenopsis conchifer*/*Macroramphosus* spp. and *Zenopsis conchifer*/*Capros aper*. Hatched area indicates forbidden zone of high habitat overlap with high dietary overlap

Johnson 1983). For convenience we consider both the unweighted and weighted indices by pairs to be independent. Formally, we suggest that the exact relationship, i.e. dependency for the weighted overlaps between $\mathbf{D}_i$ and $\mathbf{R}_i$, can be described as the angle between the first eigenvectors both for $\mathbf{D}_i$ and $\mathbf{R}_i$ for the number of dimensions they have in common. Total weighted overlap is determined as the product of habitat and dietary overlaps $\alpha_R \times \alpha_D$. Further predatory impacts as indicated for *Zenopsis conchifer* on *Macroramphosus* spp. and *C. aper* should also be taken into account (Fig. 8). The reciprocals of difference ratios in a 2-D space of 1.21 (1.1^2), 1.44 (1.2^2) to 1.96 (1.4^2) are presented as isograms of maximum allowable total overlap (Fig. 8). The data fit well into the theoretically determined bounds. Compared to reference data from estuarine and limnetic habitats (Naesje et al. 1991, Thiel et al. 1996), the isogram of 1.44 is a good approximation of maximum allowable overlap and minimum necessary distance in the fish communities considered.

In all cases considered in this paper, dietary overlaps were more diverse (larger number of cases to be calculated) and numerically smaller than habitat overlaps. This stresses the prominent role of dietary resource partitioning in structuring the bentho-pelagic community, which was also emphasised by Piet et al. (1999). However, this cannot be generally extended, since data in the literature (Hopkins & Gartner 1992, Thiel et al. 1996, Sala & Ballesteros 1997) suggest a rather ambivalent relationship, i.e. in cases of closely related pairs of species, either dietary or spatial overlap may be pronounced, but not simultaneously. In analysing lizard and bird communities, Schoener (1974) came to the same either/or conclusion for interspecific pairs of species, indicating the complementarity of niche dimensions. This is reflected by no overlap data being in the forbidden zone outside the rectangles, which would indicate extreme values both for habitat and dietary overlap (Fig. 8, hatched area).

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