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Evidence for two sympatric species of snipefishes *Macroramphosus* spp. (Syngnathiformes, Centriscidae) on Great Meteor Seamount

Abstract About 202 specimens of snipefishes (*Macroramphosus* spp.) from Great Meteor Seamount (GMR, subtropical NE Atlantic, 30°N, 28.5°W) were analysed with respect to diet composition and morphology. Fifty specimens belonged to the deep-bodied benthos-feeding type (b-type) whose diet consisted of foraminifers, pteropods, decapods and polychaetes, whereas the slender planktivorous individuals (p-type, *n*=140) mainly fed on ostracods, copepods, pteropods and foraminifers. Twelve specimens showed no specialisation with respect to feeding (p/b-type). Both feeding types can be significantly distinguished from each other by means of bi- and multivariate morphological analysis considering the variables body depth, length of second dorsal spine, diameter of orbit and standard length. We discuss the hypothesis that *M. gracilis* represents a transient juvenile stage of *M. scolopax*. Since our specimens of the *M. gracilis* type were larger than specimens of the *M. scolopax*-type, such an ontogenetic shift is unlikely to occur. Our results support the hypothesis of Clarke for Australian snipefishes that for *Macroramphosus* spp. locally two distinct sympatric species must be anticipated, corresponding to *M. scolopax* and *M. gracilis* and the b- and p-types, respectively.

Keywords *Macroramphosus* · Great Meteor Seamount · Habitat partitioning · Sympatric species

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Introduction

(In all oceans, snipefishes of the genus *Macroramphosus* Lacepède, 1803 (Centriscidae, Macroramphosinae; nomenclature follows Eschmeyer (1998)) 444 abundantly inhabit shelf regions and seamounts, principally between 20 and 40° of latitude in both hemispheres (see Wilson and Kaufmann 1987; Parin et al. 1997).

Two vernacular names have been established for *Macroramphosus* spp. to account for the observed variability worldwide, i.e. longspine snipefish and slender snipefish. At present, the worldwide record of 13 species can be traced back to these two different types of species, i.e. the longspine snipefish *M. scolopax* (L., 1758, originally described as *Balistes scolopax*) and the slender snipefish *M. gracilis* (Lowe, 1839, originally described as *Centriscus gracilis*) (Eschmeyer 1998). Synonyms for *M. scolopax* are: *M. scolopax* var. *elevatus* Waite, 1899 (Habitat location: New South Wales, Australia), *M. lancifer* Ogilby, 1910 (Queensland, Australia), *Silurus cornutus* Forsskål, 1775 (Mediterranean Sea), *M. otteri* Fowler, 1934 (New Jersey, USA), *M. robustus* Ogilby, 1910 (Queensland, Australia) and *M. sagifue* Jordan & Starks, 1902 (Suruga, Japan). For *M. gracilis* the following synonyms were found: *Centriscus brevispinis* Kner & Steinbrechner, 1867 (Samoa), *M. hawaiiensis* Gilbert, 1905 (Hawaiian Is.), *Centriscus japonicus* Günther, 1861 (Japan), *M. molleri* Whitley, 1930 (New South Wales, Australia) and *Centriscus velitaris* Pallas, 1770 (Indonesia). However, for *M. gracilis* the taxonomic status is still unclear, since it is both treated as a genuine species and as a juvenile form of *M. scolopax* (see Froese and Pauly 2001). In turn, already the distribution of sampling locations of the type species indicates the co-existence of two types of snipefishes in every oceanic realm. Reviewing the genus Mohr (1937) concluded that there were only two valid species worldwide, *M. gracilis* and *M. scolopax*. However, he also considered the grey to blue, slender and short-spined *M. gracilis* likely to be a juvenile stage of the red-orange deep-bodied *M. scolopax*. Such shifts in morphology are known in other species. For

example, the seamount-associated armorhead *Pseudopentaceros wheeleri* (Humphreys and Tagami 1986; Koslow 1997) spends up to 2.5 years in the pelagic stage where it builds up large fat reserves ('fat' form) and takes a slender form ('lean' form) after settling on seamounts where the fat reserves are consumed during the remaining span of life. A further review of the status of *Macroramposus* by Ehrich and John (1973) continued to distinguish two distinct species in the North Atlantic, but the findings of intermediate specimens forced Ehrich (1976) to revise the status of *M. gracilis* so that it became a juvenile stage of *M. scolopax* again. Consequently, Ehrich (1976) subsumed all specimens of the genus under *M. scolopax*. In turn, Clarke (1984) investigated *Macroramphosus* spp. from near the edge of the continental shelf of SE Australia. Due to the occurrence of two distinct dietary types also significantly differing in morphological characters, he evidenced the existence of two separate species of *Macroramphosus* in SE Australia. He also suggested that this could resemble the variability observed in other parts of the world's oceans and referred to the necessity of further research in this respect.

The uncertain status of *M. gracilis* and the sympatric occurrence of the two types raises questions about radiation and co-existence of species. According to competition theory, sympatric members of a guild should vary in some decisive features by a ratio known as Hutchinson's rule in order to partition diet and habitat (Schoener 1974). In turn, selection pressure by means of competition promotes divergence in adaptive radiation (Schluter 1994). It aims at the exploitation of new resources, enforced by means of ecological character displacement as a tool for new exploitative capabilities and finally increasing reproductive isolation of populations (Schluter 1993). Thus, exploitation of new resource types and the development of accompanying differences in morphology are indicators of adaptive radiation (Futuyama 1990). This rationale paves the way for a multivariate investigation strategy considering both the exploitation of resources, i.e. diet, as well as differences in morphology.

Two such approaches have been applied to analyse the high variability in *Macroramphosus* spp.: while Ehrich (1976) carried out a morphological analysis with subsequent analysis of diet, Clarke (1984) analysed the diet with subsequent morphological analysis. We combined and compared both approaches and present new data supporting the hypothesis of Clarke (1984) that two sympatric species of *Macroramphosus* spp. exist.

Methods

Sampling

Material from the Great Meteor Seamount (GMR, subtropical NE Atlantic, 30°N 28.5°W) was analysed, obtained during the M42/3-cruise of the RV Meteor in September 1998 (Pfannkuche et al. 2000). Sampling was conducted with a GOV-bottom trawl with 450 meshes opening width and 32 m wing span (Uiblein et al. 1999; detailed description in Fock et al. 2002). Stretched codend mesh size was about 15 mm. Sampling depth varied between 295 and 349 m. On Great Meteor Seamount *Macroramphosus* spp. and *Capros aper* were numerically dominant (Uiblein et al. 1999). For *Macroramphosus* spp. a total of 82,700 fishes were caught. For the extensive analyses of morphology and diet, 202 fishes were randomly drawn from deep-frozen subsamples in order to cover a diurnal cycle (Table 1).

Diet and morphometrics

Eleven morphometric characters were measured (Fig. 1). From these, morphometrics of the second dorsal spine (second ray of the first dorsal fin) were used to classify each specimen as *gracilis*-, *scolopax*- or intermediate morphotype, according to Ehrich (1976). This classification considers the location of the base of the spine in relation to the anus, the length of the spine in relation to body length, and the size of the second dorsal fin.

Due to lack of a well-defined stomach, the whole alimentary tract was examined for dietary analysis. According to Clarke (1984), the alimentary tract is separated into an anterior, mid- and posterior section and the rectum. Prey items were identified to major taxa by means of a dissection microscope. Items with fleshy tissue were counted as dietary items, items without any flesh were counted as remains, e.g. single echinoderm spines, single polychaete setae, calcareous deposits of unknown origin. With regard to the main diet, specimens were classified as either plankton feeders (p-type), benthic feeders (b-type) or mixed feeders (p/b-type) (after

Table 1 Specimens of *Macroramphosus* spp. selected; for the analysis of diet and morphology from Great Meteor Seamount in 1998; columns a, b and c indicate different types of analysis, a: analysis for feeding types and morphology, b: detailed analysis of food items (subsample of a), c: analysis of fullness index and the diurnal feeding pattern (subsample of a or b)

Station	Position[a]	Depth (m)[b]	Time of catch	Numbers of specimens analysed		
				a	b	c
488	30.05°N 28.54°W	291.5	00.40–00.55	36	21	19
495	30.09°N 28.44°W	327	05.23–05.39	16	–	15
469	30.07°N 28.54°W	298	10.15–11.00	19	–	19
470	30.08°N 28.56°W	299.5	12.51–13.37	33	19	16
482	29.91°N 28.40°W	321	15.43–16.01	40	20	20
483	30.08°N 28.45°W	326	18.15–18.31[c]	19	–	19
487	29.92°N 28.38°W	320	22.21–22.38	39	20	17
Total				202	80	125

[a] 'Position' is mid position of trawl
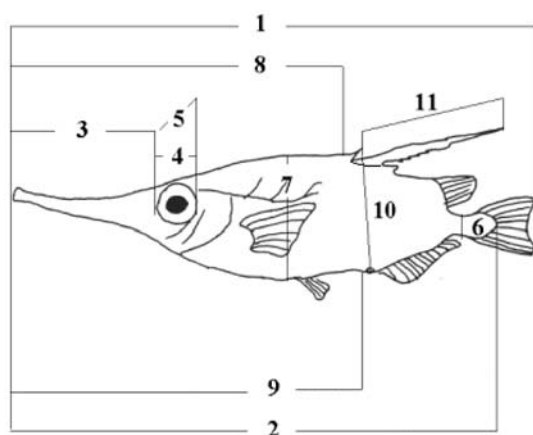[b] 'Depth' is mean depth
[c] Dusk

Fig. 1 Morphometric measurements for *Macroramphosus* spp. *1* Total length (*TL*), *2* standard length (*SL*), *3* snout length (*SnL*), *4* orbit diameter (*O*), *5* inter-orbital length (*IOL*), *6* smallest depth of tail (*DT*), *7* body depth (*BD*), *8* pre-dorsal length (*PdL*), *9* pre-anal length (*PaL*), *10* distance from anus to insertion of second dorsal spine (*AP*), *11* length of second dorsal spine (*DS*)

Clarke 1984). The numbers of identified food items were pooled with regard to the diet types. Similarly, the frequency of occurrence, defined as the number of fish with food item *i*, was determined for each diet type.

It is known from the literature that p-type and *gracilis*-type on the one side, and b-type and *scolopax*-type, on the other side, should be equivalent. Length frequency distributions were applied to check whether comparable size ranges of the fishes were obtained within different categories compared with the total population on the Great Meteor Seamount. Distributions were based on total length measurements, since total length was measured onboard during the 1998 cruise.

For each prey item, a 'relative importance index' (RI) was calculated after Hyslop (1980), based on numbers (*N*), frequencies (*F*) and weight (*W*):

$$RI_i[\%] = \frac{100A_i}{\sum\limits_{i}^{n} A_i} \qquad (1)$$

where $A_i = \%F_i + \%N_i + \%W_i$, and F_i (%) = 100/number of analysed guts × number of guts with food item *i*, N_i (%) = percentage of food item *i* of the total number of food items, W_i(%) = percentage of ash-free dry weight (AFDW) of food item *i* of the total AFDW, and *n* = number of different food items. Empty alimentary tracts were included in the calculation.

An index was developed to indicate the degree of fullness of the alimentary tract. Three levels of fullness were chosen: 2 = maximum fullness, conspicuously widened cross-sections; 1 = observable contents, but not completely filled; and 0 = no contents. Fullness index was analysed and displayed by means of bar charts.

Diet–morphology relationships

Relationships between diet and morphology were analysed with respect to classifications and to morphological measurements.

Classifications after Ehrich (1976) and Clarke (1984) were compared with each other by means of contingency tables. A χ^2 test was applied (Zar 1996). Results were considered significant at the $\alpha=0.05$ level.

Analysis of covariance (ANCOVA) was carried out to analyse differences in morphological characters between different feeding types (Backhaus et al. 1990; Underwood 1997). Multivariate analysis of morphological characters based on the classification of feeding types was carried out by means of discriminant analysis (Backhaus et al. 1990). Prior to ANCOVA, data were tested for normality and homogeneity of variances. The Bartlett's test on homogeneity of variances was applied since this test takes account of heterogeneous sample sizes (Zar 1996). Multivariate methods appear to be robust even if the homogeneity criterion is violated (Fock 2000). Results were considered significant at the $\alpha=0.05$ level for ANCOVA and at the $\alpha=0.01$ level for discriminant function analysis.

Results

Diet

Two major feeding types were identified, based on dietary composition. According to Clarke (1984), the first feeding type was classified as b-type, predominantly feeding on pelagic foraminifers and pteropods (Table 2). In terms of importance these two prey categories accounted for 48.4% of RI scores (Table 3). Although being of planktonic origin, these organisms were always found accompanied by sedimented particles such as calcareous deposits, grains of sand and remains of echinoderms. Further important prey items were polychaetes, decapods as well as already settled decapod larvae, indicated by the

Table 2 Numbers (*n*) and frequency of occurrence (*f*) of different food items in individuals of the p-type, b-type, and p/b-type of *Macroramphosus* spp. Feeding types defined after Clarke (1984)

No. of examined fish	b-type 26		p-type 46		p/b-type 8	
	n	*f*	*n*	*f*	*n*	*f*
Foraminifera	18,103	26	243	28	1,222	7
Pteropoda	8,239	22	241	38	1,164	6
Gastropoda	5,561	20	13	6	76	7
Ostracoda	4	3	971	45	75	4
Calanoida	18	11	854	46	59	4
Polychaeta	148	12	4	3	–	–
Decapod larvae	51	8	1	1	–	–
Decapoda	34	10	2	1	13	4
Amphipoda	21	4	4	1	10	1
Mysidacea	9	4	8	6	11	3
Cirripedia	5	2	–	–	–	–
Harpacticoidea	2	2	–	–	1	1
Isopoda	2	2	–	–	1	1
Bivalvia	2	2	–	–	–	1
Euphausiacea	–	–	–	–	2	–
Tanaidacea	2	2	–	–	–	–
Crustacea unidentified	46	15	103	33	23	7
Cephalopoda	–	–	–	–	1	1
Echinodermata	2	2	–	–	–	–
Fishes, unidentified pieces	–	–	1	1	–	–
Bryozoa	–	13		–		1
Unidentified items	25	9	48	21	5	3
Remains						
Echinoderm remains	219	11	2	2	26	2
Sponge remains	25	8	–	–	1	1
Calcareous deposits	–	19		2		2
Sand grains	–	17		1		3
Tube fragments	–	13		2		3
Polychaete remains	–	–		–		1
Total	**32,517**		**2,496**		**2,691**	

Table 3 Ash-free dry weight (AFDW) per item (mg ind^{-1}) and calculated 'relative importance index' (RI) of different prey taxa for b-, p- and p/b-type *Macroramphosus* spp. according to abundance and frequency data given in Table 2

	AFDW (mg ind^{-1})	RI		
		b	p	p/b
Foraminifera	0.040	28.3	12.8	25.0
Pteropoda	0.141	20.1	16.9	22.4
Polychaeta	1.026	9.9	3.6	1.5
Ostracoda	0.304	2.5	25.2	10.4
Calanoida	0.049	7.8	24.4	9.9
Euphausiacea	0.909	1.3	1.3	3.7
Decapoda	3.868	12.4	5.8	15.1
Decapod larvae	5.176	12.9	7.7	7.6
Amphipoda	1.362	4.7	2.3	4.4

metamorphosis of the thoracopods. Together, these groups of prey organisms accounted for 83.3% of RI scores. Individuals feeding on decapod larvae were found to exclusively feed on these items.

The second feeding type was classified as p-type after Clarke (1984). No bottom material was ingested. Main food items were ostracods and calanoid copepods, accounting for 49.6% of RI scores for this type. Pteropods and foraminifers still constituted a major portion of the diet, contributing 29.7% of RI scores.

Eight specimens belonged to a mixed feeding type (p/b-type, Table 2) mainly utilising foraminifers and pteropods. Decapods, calanoid copepods and ostracods appeared to be secondary items. Whereas copepods indicated prey of planktonic origin, occasional sediment particles also indicated a benthic feeding mode.

Diurnal feeding cycle

The time course of the fullness index (Fig. 2) indicated a well defined diurnal feeding cycle.

For p-type specimens, feeding activity started in the morning between 5 a.m. and 10 a.m. After 10.15 a.m. until the afternoon, the anterior part of the gut was filled with fresh and slightly digested prey items, and the majority of specimens had maximum fullness levels. In the evening and during the night, p-type specimens did not ingest much food, as indicated by zero values for fullness level 2 (Fig. 2A). For the middle section (Fig. 2B), maximum filling levels were reached in the afternoon and night, while the posterior part (Fig. 2C) showed maximum filling levels during the early morning hours just before the new feeding period started.

Despite the low numbers of available b-type specimens, a seemingly similar feeding cycle was observed as in p-type specimens. They also started to feed in the morning. Maximum filling level in the anterior part of the gut increased to 100% at noon (Fig. 2A). In contrast with the course for p-type specimens, considerable nocturnal feeding was found, with maximum fullness levels for the anterior section for about 40% of the investigated specimens even at 22.21 p.m. The degree of fullness for the middle section (Fig. 2B) increased steadily towards 22.21 p.m. However, only scarce data are available to indicate digestion in the early morning hours. Like p-type specimens, the only two specimens of the b-type caught between midnight and 5.23 a.m. had maximum filling levels at 4 and 5.23 a.m. in the posterior section (not shown).

Length distribution

The unimodal distribution of the total population of *Macroramphosus* spp. had a peak length of 130 mm and a range of 100–170 mm (Fig. 3). The same length range was covered by both major feeding types, i.e. b-type and p-type specimens (Fig. 4). Whereas the p-type specimens fairly well represented the unimodal distribution of the total population, with a maximum at 130 mm, two modes appeared for the b-type specimens (Fig. 4B). The main
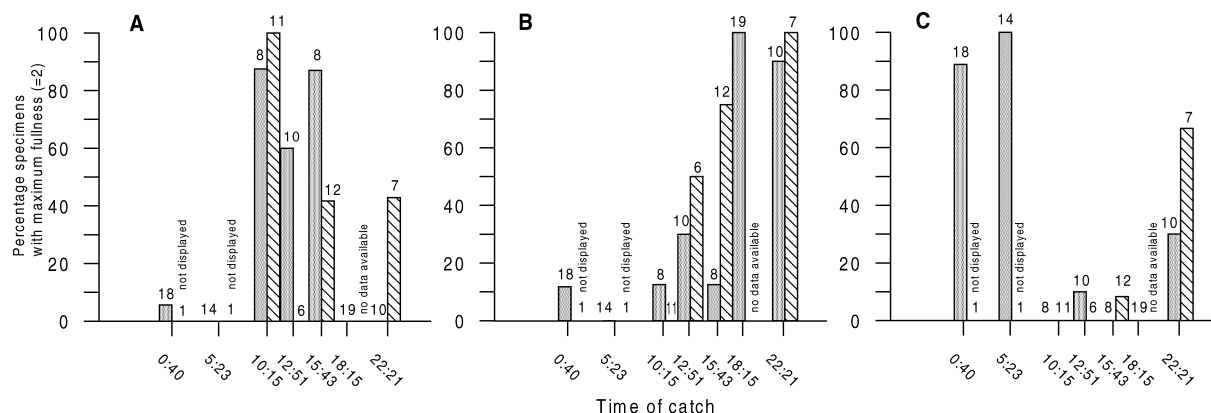

Fig. 2A–C Diurnally varying levels of fullness index of different parts of the alimentary tract of p- and b-type *Macroramphosus* spp. *Grey bars* p-type specimens, *hatched bars* b-type specimens. *Numbers* indicate numbers of examined specimens. In certain cases numbers for available b-type specimens were either very small ('*not displayed*') or lacking ('*no data available*'). **A**, **B**, **C** refer to anterior, mid-, and posterior parts, respectively, of the alimentary tract. '*Time of catch*' refers to starting time (see Table 1)
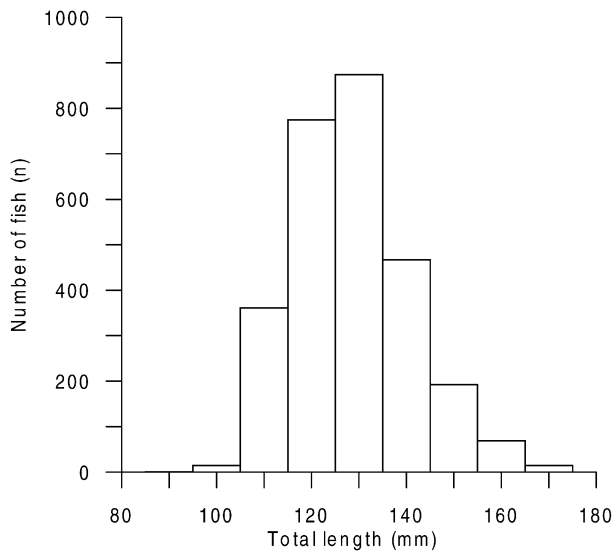
mode was again at 130 mm, accompanied by a minor mode at 110 mm. However, the number of specimens analysed for length was much smaller for the b-type group, so that the minor mode may be an artefact. From the entire group of 202 specimens, 140 were classified as p-type, 50 as b-type and 12 as p/b-type. The subgroups of specimens for the b- and p-types drawn for detailed analysis of diet fitted into the same size ranges, i.e. 106–152 mm length for the b-type, and 112–166 mm length for the p-type specimens, indicating that the p-type specimens were slightly larger.

The morphological classification of specimens after Ehrich (1976) yielded different proportions of slender to robust specimens as compared with the classification of feeding types. Whereas the major group p-type specimens corresponded to only 68 specimens of the slender *gracilis* type, the intermediate group was dominant, with 108 specimens, compared with only 12 mixed feeders of the p/b group. Common to both classifications was the small proportion of robust b-type and *scolopax*-type specimens. The length distributions of Ehrich-classified specimens (Fig. 5) show that *gracilis*-type and intermediate speci-

Fig. 3 Frequency distribution of the total catch of *Macroramphosus* (*n*=2,769). Length classes of total length indicated

Fig. 4 Frequency distribution of the subsamples of **A** p-type and **B** b-type snipefish (p-type *n*=140, b-type *n*=50). Length classes of total length indicated
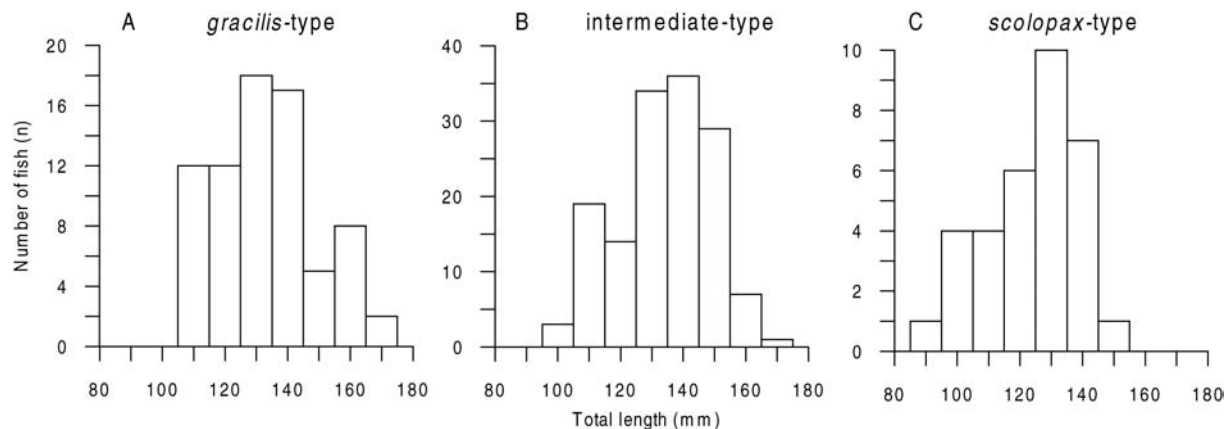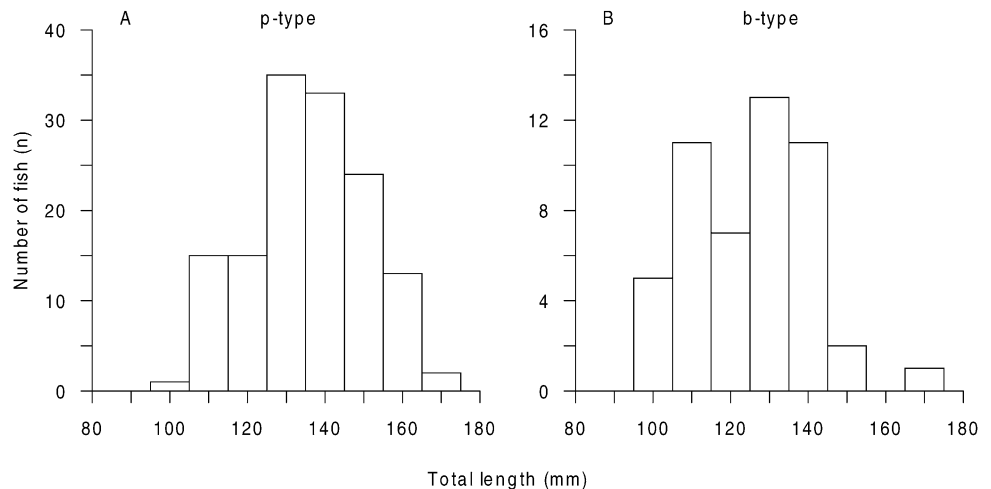

Fig. 5 Frequency distribution of total length of *Macroramphosus* morphotypes classified after Ehrich (1976) as **A** *gracilis*-type, **B** intermediate type and **C** *scolopax*-type snipefish (morphotype *gracilis* *n*=68, morphotype intermediate *n*=109, morphotype *scolopax* *n*=25)
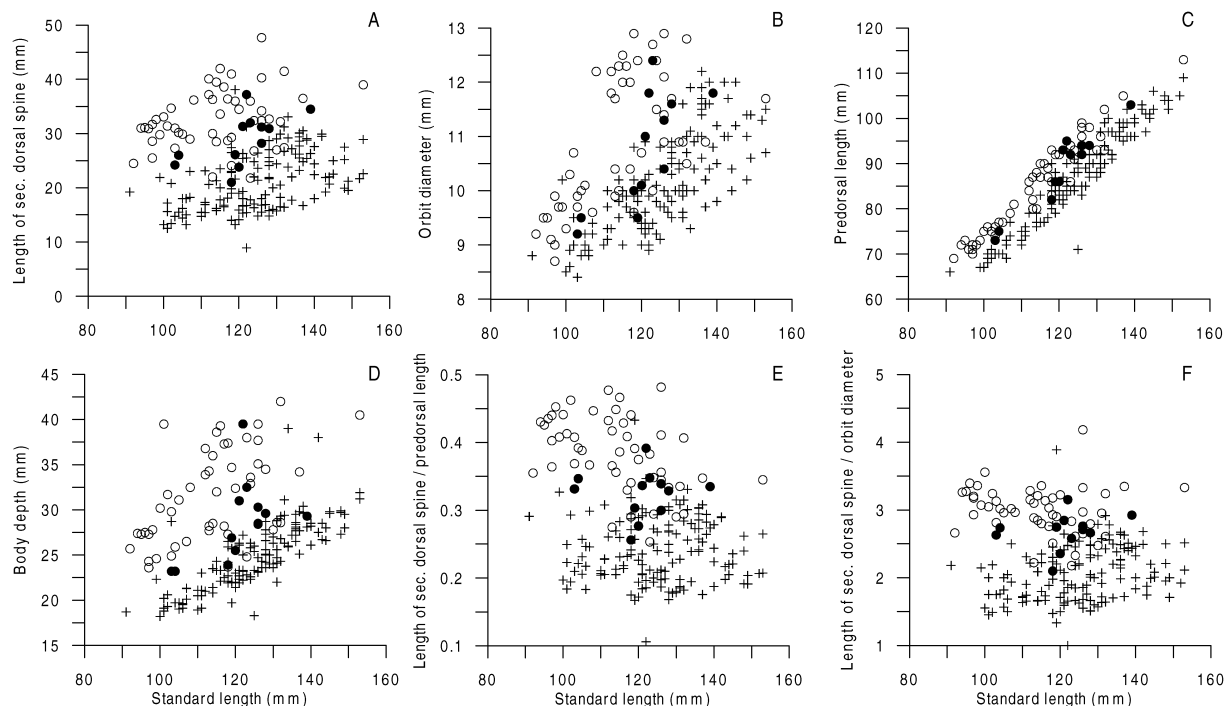
Fig. 6 Bivariate scatterplots of morphological characters versus standard length for different feeding types. **A** Length of second dorsal spine (*DS*), **B** orbit diameter (*O*), **C** pre-dorsal length (*PdL*), **D** body depth (*BD*), **E** ratio of length of second dorsal spine to pre- dorsal length, and **F** ratio of length of sec. dorsal spine to orbit diameter vs standard length of *Macroramphosus*. *Open circles* b- types (*n*=50), *solid circles* p/b-types (*n*=12), *crosses* p-types (*n*=140)

mens were slightly larger than *scolopax*-type specimens, which is in accordance with the differences in length distributions found for different feeding types. The sexes occurred in a ratio of 1:1.

Relationships between morphology and diet

The length distributions already showed discrepancies in the allocations of specimens to the *gracilis*-/p-type and the intermediate-/p/b-type categories. But despite these discrepancies, the two classification schemes were, to some extent, congruent. All 68 *gracilis*-type specimens belonged to the p-type, and nearly all individuals of the *scolopax*-type belonged to the b-type. However, the 109 individuals of the intermediate type were split up into all feeding types. In turn, specimens of the p-type were split between the corresponding *gracilis*-type and the interme- diate type. In almost the same way individuals of the b- type were subdivided in the corresponding *scolopax*-type and the intermediate type. Nearly all specimens of the p/ b-type belonged to the intermediate type.

A main contingency table was generated (Table 4) to investigate two hypotheses: (1) both classifications are the same, and (2) one classification scheme is better in describing or forecasting its counterpart than the other.

In the contingency table, considerable deviations in either direction appear. This is confirmed by the analysis of the whole master table. Both classification schemes

Table 4 Main contingency table for the analysis of classifications

Morphotype	Feeding type Classified after Clarke (1984)			Total
Classified after Ehrich (1976)	p-type	p/b-type	b-type	
gracilis	**68**			68
intermediate	72	**11**	26	109
scolopax		1	**24**	25
total	140	12	50	202

diverge significantly (χ^2=102.2, *df*=7, *P*<0.001). To answer the second hypothesis, subunits were extracted from the main contingency table. For both perspectives, i.e. the morphotype classification predicting the feeding types and vice versa, the distribution of diagonal elements of the table serves as reference data, since these values were correct predictions in both directions. The prediction of morphotypes from feeding type concept (Table 5a) is fairly successful, and no significant difference is obtained (χ^2=4.02, *df*=2, *P*=0.13). In turn, the prediction of feeding types from morphotype concept fails, indicating a signif- icant difference (Table 5b, χ^2=75.46, *df*=2, *P*<0.001).

Thus, the classification scheme according to feeding types was sufficient to describe both morphological and ecological variability within the populations.

Morphological characters between feeding types were significantly different in four cases (Fig. 6). In relation to standard length, b-type specimens had significantly longer

Table 5 Relation between morphotype and feeding type concept. (a) Observed numbers of morphotypes and expected numbers of feeding types for χ^2-test. (b) Observed numbers of feeding types and expected numbers of morphotypes for χ^2-test. Values were transformed to percentages (in parentheses) in order to preserve column totals

a	Morphotype classified after Ehrich (1976)	Numbers of observed morphotypes with consistent feeding type	Corresponding numbers of feeding types
	gracilis-type	68 (66.0%)	140 (p-type: 69.3%)
	intermediate type	11 (10.7%)	12 (p/b-type: 5.9%)
	scolopax-type	24 (23.3%)	50 (b-type: 24.8%)
b	Feeding type classified after Clarke (1984)	Number of observed feeding types with consistent morphotype	Corresponding numbers of morphotypes
	p-type	68 (66.0%)	68 (*gracilis*-type: 33.7%)
	p/b-type	11 (10.7%)	109 (intermediate: 54.0%)
	b-type	24 (23.3%)	25 (*scolopax*-type: 12.4%)

Table 6 Eigenvalues and standardised canonical discriminant function coefficients for morphological characters and canonical discriminant scores for associated feeding types. Eigenvalues indicate the variance explained by the respective discriminant function

	Function 1	Function 2
Statistics		
Eigenvalue	2.11	0.010
Cumulative eigenvalues	0.995	1.00000
Coefficients for morphological characters		
Standard length	0.918	0.444
Orbit diameter	0.341	0.726
Body depth	−0.914	−1.632
Length of second dorsal spine	−0.629	1.095
Scores for feeding types		
p-type (group means)	0.94	−0.02
b-type (group means)	−2.38	−0.52

Table 7 Re-classification matrix after discriminant analysis. Rows refer to observed classification, columns to predicted classification

Observed feeding types	% correctly classified	Specimens classified as		
		p-type	b-type	p/b-type
p-type	96.8	135	5	0
b-type	86.00	7	43	0
p/b-type	0.00	9	3	0
total		151	51	0

dorsal spines (Fig. 6A; $F=235{,}04$; $P<0.05$), bigger eyes (Fig. 6B; $F=115{,}04$; $P<0.05$), longer pre-dorsal lengths (Fig. 6C; $F=173{,}2$, $P<0.05$) and deeper bodies (Fig. 6D; $F=290.65$; $P<0.05$) than p-type snipefish. P/b-type specimens ranged between both groups. All variables except body depth (character 7 in Fig. 1) possessed homogeneously distributed variances between categories. However, the strongest separation of groups was obtained according to body depth, and the p-type specimens showed smaller variability within this character than b-type specimens. This was an important observation with respect to the commonly accepted distinction between slender and longspine snipefish. The significant differences between b- and p-type specimens were preserved, when combinations, i.e. ratios of variables, were deployed (Fig. 6E, F).

Consequently, multivariate discriminant analysis provided a successful separation with respect to feeding types. The resulting discriminant function 1 yielded an eigenvalue of 2.11 and contributed more than 99% to the overall variance (Table 6). Thus, function 2 could be ignored. Morphological characters and feeding types could be grouped in the following way: (1) for b-type specimens, body depth and length of second dorsal spine were correlated, (2) for p-type specimens, orbit diameter and standard length were correlated. This takes into account that on average p-type specimens appeared to be slightly longer than b-type specimens (Fig. 4) and that 'slenderness' was the decisive character in separating the specimens.

The re-classification (Table 7) showed that a high proportion of p- and b-type specimens were correctly classified. However, none of the p/b-type specimens were correctly classified. Splitting this group up into either p- or b-type specimens indicated that the recognition of a transient type was probably a misperception.

Discussion

Little is known about the ecology and life history of *Macroramphosus* spp. The *M. gracilis*-like forms are known from both pelagic and bottom captures and feed mainly or exclusively on plankton (Ehrich and John 1973; Clarke 1984). The *M. scolopax*-like forms are described as being associated with the bottom and feed on both planktonic and benthic prey (Mohr 1937; Ehrich and John 1973). Clarke (1984) showed apparent differences in depth distributions among planktivorous and benthivorous specimens. Depth-dependent distribution could not be proved for the Great Meteor Seamount, since only samples from the seamount plateau were available.

In this paper we have shown that for *Macroramphosus* spp. at GMR two types of specimens can be distinguished, differing in terms of diet composition and morphology. The analysis of the feeding cycle revealed a further difference between b- and p-type specimens, indicating that b-type specimens were also feeding nocturnally. A comparison of classification schemes for morphotypes after Ehrich (1976) and feeding types after Clarke (1984)

showed that the feeding type concept was significantly better in predicting morphotype than vice versa. This was confirmed by further multivariate analysis revealing clear morphological differences with respect to feeding types. In the multivariate analysis, only one discriminant function was necessary to separate the categories, indicating a very strong separation of already distinct groups.

Diet and feeding cycle

In line with Clarke's (1984) investigations from SE Australia, specimens could be easily distinguished, either in slender p- or deep-bodied b-types. Additionally, a few mixed feeding individuals (p/b-type) were found. This is in agreement with results from Ehrich (1976) with the slender and short-spined *gracilis* type feeding on plankton and the deep-bodied and long-spined *scolopax* type feeding on plankton and benthos as well.

The benthic origin of prey for the b-type specimens was indicated by associated non-living bottom material such as grains of sand. The high amount of non-living matter also corresponds with the observations of Ehrich (1976). On Great Meteor Seamount, *scolopax* morphotypes contained benthic material including foraminifers and sand in their guts.

For b-type specimens, the spectrum of diet differed between SE Australia and the Great Meteor Seamount. Whereas foraminifers, pteropods, decapods and polychaetes constituted the main prey for b-type specimens in this study, gammaridean amphipods and bryozoans were consumed in SE Australia (Clarke 1984). Notwithstanding unknown stocks of prey organisms, different utilisation of prey items for b-type specimens is likely to be related to the different availability of food items in their respective habitats rather than to selective feeding.

In turn, diet composition for p-type and *gracilis*-type specimens, respectively, is consistent in all three studies (this study; Clarke 1984; Ehrich 1976).

Mainly daytime feeding was also observed in SE Australia (Clarke 1984). This feeding mode was explained by interception feeding with the sound scattering layer-interception, suggesting that maintenance of bentho-pelagic fish populations is provided through feeding on the advected plankton components in the vicinity of seamounts and shallow topography (Fock et al. 2002; Genin et al. 1988; Isaacs and Schwartzlose 1965; Rogers 1994). Being trapped, this plankton is vulnerable to predation by visual predators such as fish. The entrapment and feeding on diel migrators is expected to be most significant on seamounts with a top at depths between 100 and 300 m (Pearcy et al. 1977). Correspondingly, *Macroramphosus* spp. started feeding early in the morning when trapped organisms of the sound scattering layer were likely to be available.

Morphology

As for *Macroramphosus* spp. in SE Australia (Clarke 1984), high morphological variability can be significantly linked to the occurrence of two feeding types. Significant morphological differences were found for the characters length of second dorsal spine, body depth, orbit diameter, pre-dorsal length and standard length. Clarke (1984) concluded that, since no single character could provide full discrimination between p- and b-type specimens, the distinction should be based on four characters in multivariate analysis. Consistent with our results, Clarke (1984) found only a few specimens of the p/b-type. In turn, the morphological classification after Ehrich (1976) yielded a major fraction of intermediate specimens, consistent with Ehrichs's (1976) results: 118 out of 205 specimens were classified as intermediate. However, the morphological classification scheme was incapable of predicting any ecological difference in terms of diet composition, but not so the feeding type concept. Due to this imprecision, the morphological classification scheme must be treated with caution.

Apart from classification schemes, there appear to be morphological differences between populations from SE Australia and the Great Meteor Seamount. Whereas the Australian specimens differed significantly in snout length and body depth, the Meteor specimens differed significantly in terms of length of second dorsal spine and body depth, but not in snout length. These differences indicate that beyond the p- and b-type and *scolopax*- and *gracilis*-type distinctions, respectively, further differentiation might be necessary to distinguish world populations of *Macroramphosus* spp. (Kuranaga and Sasaki 2000) were able to distinguish between larval stages of Japanese *scolopax*-type specimens, Mediterranean *scolopax*-type and Californian *gracilis*-type specimens. However, the existence of two types of fishes in all habitats must be considered.

Evidence for two sympatric species at GMR

Non-ambiguous evidence was presented for differences in morphology, diet composition, and feeding cycle between p- and b-type specimens. It was statistically proven that no true transient stage in terms of a p/b-type could be established. One of the strongest arguments in the *scolopax/gracilis* debate was the observed length distribution of *Macroramphosus* spp., with the *gracilis* type being smaller than the *scolopax* type (Ehrich 1976). This paved the way for the juvenile-stage hypothesis, suggesting that *gracilis*-type specimens were juvenile *scolopax*-type specimens. However, we have shown that under both classification schemes the p- and the *gracilis*-type specimens were actually larger than the corresponding b- and *scolopax*-type specimens. This brings into question the juvenile-stage hypothesis. Actually, small *scolopax*-morphotype specimens and thus juvenile specimens are known (e.g. Kuiter 2001). Larval morphology further
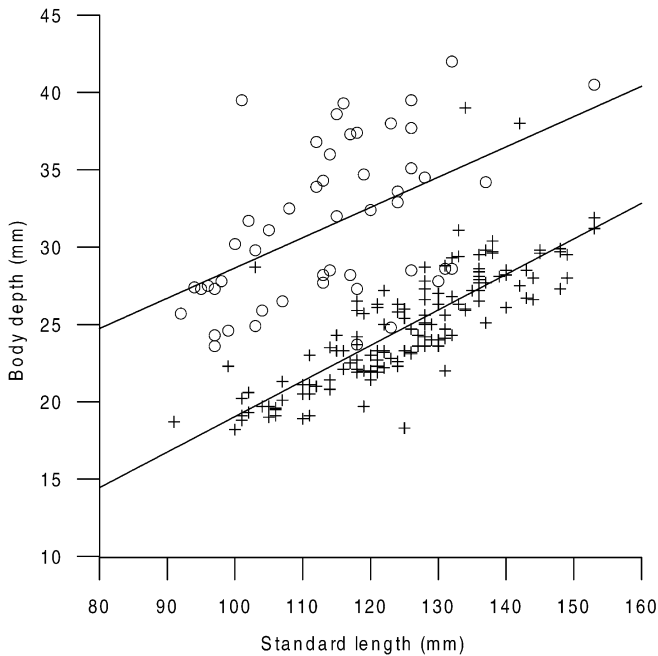
Fig. 7 Regressions of body depth vs standard length for p-type (*crosses*; R^2=0.63) and b-type (*squares*; R^2=0.25) specimens resembling part of Fig. 6D. Within the given size range the average ratio between the body depth of b- and p-type specimens is 1.38±0.15. The ratio was calculated from the regression graphs for either feeding type

confirms the existence of at least two species (Kuranaga and Sasaki 2000).

Sympatric species develop strategies for habitat and resource partitioning (Schoener 1974). It is assumed that ecological differences in diet composition and habitat use of sympatric species reflect corresponding morphological differences (Schluter 1993). Based on experimental work on different species of sticklebacks, Schluter (1994) showed that resource competition actually promotes morphological diversification. Similarly to *Macroramphosus* spp., sympatric sticklebacks differed in body depth and resource use between benthos and open-water species (Schluter 1993). The extent to which sympatric species must differ in practice is known as Hutchinson's rule (Hutchinson 1959; Schoener 1974). The rule says that in decisive morphological characters a minimum difference of 1.2–1.9 must be obtained to maintain a sufficient functional difference, i.e. ecological separation in the utilisation of a resource category, to permit coexistence under a given set of resource and consumer densities (Gladfelter and Johnson 1983). Actually, for *Macroramphosus* spp. the length-dependent difference in body depth between b- and p-types is 1.38 in the given size range (Fig. 7). However, this is only an indirect proof of the two-species hypothesis.

Further examples of character displacement within sympatric species are known (e.g. Brown and Wilson 1956; Fenchel 1975a, 1975b; Schluter and McPhail 1992). Frequency-dependent selection provides a mech-

anism for adaptive peak-shifts and has been implicated in the process of speciation itself (Schluter 1994).

The difference in body depth for *Macroramphosus* spp. is likely to be an important adaptation. Body depth and body shape are responsible for swimming capabilities. The slender pelagic p-type is probably a better swimmer and well adapted to prey in open waters whereas the deep-bodied benthos-associated b-type is able to manoeuvre near the bottom to detect benthic prey. Planktivorous pelagic fishes adapted to cruising have a compressed fusiform body, whereas slow-swimming epibenthic fishes that pick or suck their prey off the substrate are of gibbose form (Motta et al. 1995). Capture success in open water may be enhanced by the elongated body shape of pelagic individuals by providing reduced drag (Schluter 1993).

Studies on chaetotontid fish indicate that species with similar diets reach higher abundances when they show spatial separation on the reef (Bouchon-Navaro 1986) and, in a similar way, co-existing anemone-fishes with the same host anemone had different distribution patterns on the reef (Elliott and Mariscal 2001). Clarke (1984) reported apparent differences in depth distribution between p- and b-type specimens in south-east Australia. Resource partitioning by means of partitioning feeding habitat was postulated from differences in the diets of three estuarine sunfishes (*Lepomis* spp.; VanderKooy et al. 2000). In the same way, long-snouted morphologically similar reef fish of the genus *Forcipiger* from the same habitat showed dietary separation (Hobson 1974). In contrast to the omnivorous *F. flavissimus*, *F. longirostris* has a restricted diet consisting of small caridean decapods (Hobson 1974). These examples of speciation in limited habitats are comparable to the case of *Macroramphosus* spp. on seamounts and the open shelf. Actually, speciation was claimed to be a highly relevant process on seamounts (de Forges et al. 2000; Rogers 1994; Wilson and Kaufmann 1987). Based on the evidence from this study, we support Clarke's (1984) conclusion that two sympatric species exist locally, both at GMR and the Australian shelf. The question of whether two or more species exist on a worldwide scale still remains unresolved.

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