

Life cycles and feeding habits of *Syngnathus taenionotus* and *S. abaster* (Pisces, Syngnathidae) in a brackish bay of the Po River Delta (Adriatic Sea)

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ABSTRACT: We investigated the population structure, life cycles and gut contents of 2 species of pipefish, *Syngnathus taenionotus* and *S. abaster*, in a brackish embayment of the Po River Delta (North Adriatic Sea). These 2 species inhabit the nearshore environment of the bay where the sandy bottom is covered by macroalgae, and were sampled for 1 yr. The main differences in life history traits between *S. taenionotus* and *S. abaster* respectively can be summarized as follows: life span is about 24 vs 17 mo; reproductive season begins in February vs March, and lasts 5 vs 4 mo; average length of fingerlings at the time they hatch from the male brood pouch is 20.3 (± 1.2) vs 13.5 (± 1.0) mm; egg incubation period is 2 mo vs 1 mo; average number of ripe eggs per mature ovary is 46 (± 9) vs 104 (± 40); average number of embryos incubated by male is 84 (± 17) vs 109 (± 27). Finally, the sex ratio in the reproductive population is more male-biased in *S. taenionotus* than in *S. abaster*. The 2 species probably do not compete for food resources, remaining almost completely segregated in 2 different foraging micro-habitats during most of their life span. The new-born spring individuals of both species feed almost exclusively on harpacticoids of the genus *Tisbe*. As they mature, *S. abaster* continue to prey on phytal organisms while the larger *S. taenionotus* become zooplanktivorous.

INTRODUCTION

Shore fish communities are an important component of deltaic shallow water brackish environments. During the warm season this habitat is occupied by large numbers of small fishes, both juveniles of several migratory species, which use these brackish bays as nursery ground, and resident species (Quignard 1984). The latter are usually characterized by small size, short life cycle, one or few reproductive seasons, and increased parental care.

Pipefish of the Syngnathidae family are among the most typical representatives of these fish communities. During community studies (Ferrari & Chierigato 1981, Ferrari & Rossi 1983, Maccagnani et al. 1985, Rossi 1986, Franzoi et al. 1989) carried out on a brackish embayment of the Po River Delta, the Sacca di Scardovari, 2 species of pipefishes were often found together, both with relatively high abundance values: *Syngnathus*

taenionotus Canestrini, 1871 and *Syngnathus abaster* L., 1758. Characteristic of the Syngnathidae life cycle is the male parental care. Males develop 2 skin folds ventrally, which merge into a brood pouch. Here, eggs and embryos are first inseminated and then incubated until they reach independence. For this reason, syngnathids have been considered interesting and important subjects in the study of sex role reversal, mate choice, and parental energy investment (Berglund et al. 1986a, b, 1988, 1989, Svensson 1988, Steffe et al. 1989, Berglund 1991, Vincent et al. 1992).

Another extensively investigated aspect of the pipefishes' life history has been their foraging ecology. They are gape-limited pipette-feeders with specialised predatory strategies (sit-and-wait or slow-search behaviour) (Ryer & Boehlert 1983, Howard & Koehn 1985, Main 1985, Ryer & Orth 1987, Ryer 1988, Tipton & Bell 1988, Steffe et al. 1989). However, little is known about pipefish biology and ecology in the Adriatic. In this

study, population structures, life cycles and feeding habits of *Syngnathus taenionotus* and *S. abaster* have been investigated in order to describe differences in how these congeneric species exploit the same environment.

MATERIALS AND METHODS

Study area. The Sacca di Scardovari is a bay of about 32 km², located in the southern part of the Po Delta. It is connected southwards to the sea by a mouth barred by partly submerged sand banks. The embayment consisted of 2 zones with clear differences in hydrodynamic and trophic features (Colombo et al. 1979). Water renewal in the northern area is more sluggish than in the southern one, which is directly influenced by tidal currents and water flow from the terminal branches of the river. This pattern is also reflected by overall sediment distribution inside the bay, with finer particles covering the bottom of the inner part of the embayment.

Three sampling stations were chosen within the bay across the southern and northern basins. The bottom is sandy at all 3 stations as a consequence of their near-shore location, and is covered by thick macroalgae beds (*Ulva* sp., *Gracilaria* sp.), especially during the warm season.

As expected, both temperature and salinity were extremely variable in this environment. It is important to stress that the very low water temperatures during the winter months (from 4.0 to 5.5 °C in January 1982) may have caused fishes to find shelter in deeper, warmer waters.

Sampling and data analysis. From June 1981 to July 1982, sampling was carried out 19 times at almost monthly intervals (fortnightly in April, May, June and July) at the 3 stations.

Sampling was performed with a 60 m long beach seine, with a 6 m high central stretch, made of 2 mm mesh-size net. Maximum sampling depth was 1.5 m, i.e. the height of the poles keeping the seine's wings open when it was hand-trawled towards the beach, starting at about 40 to 50 m from the shore. Fishes were killed in a solution of chlorobutano and preserved in 10 % formalin. Back in the laboratory they were transferred into 5 % neutralized formalin for long-term preservation.

Syngnathus taenionotus and *S. abaster* were easily distinguished by the shapes of their snouts (Fig. 1): in *S. taenionotus* it is longer than in *S. abaster* (Dawson 1986). *S. taenionotus* was classified based on characters such as the head dorsolateral profile, which, in

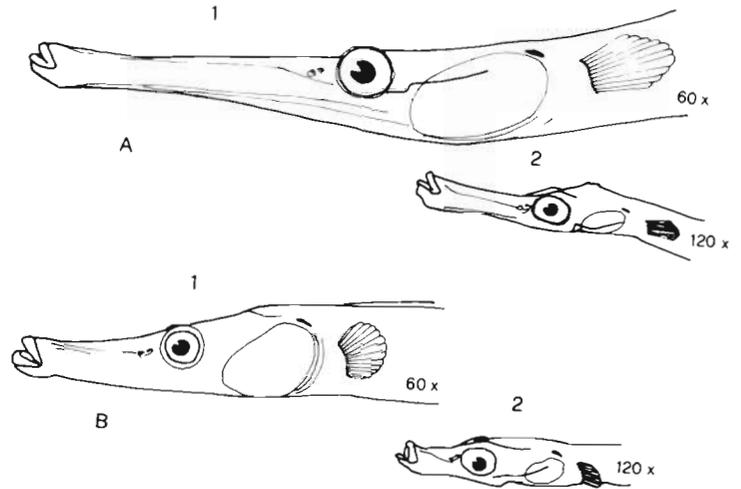


Fig. 1. (A) *Syngnathus taenionotus*. Detail of the heads of adult (1: SL = 174.5 mm) and young (2: SL = 27.0 mm). (B) *Syngnathus abaster*. Detail of the heads of adult (1: SL = 124.0 mm) and young (2: SL = 24.5 mm)

contrast to *S. acus*, is not markedly elevated in the post-orbital part (D'Ancona 1934, Dawson 1986) (Fig. 1), the number of subdorsal rings, the number of pre-anal rings and especially the number of post-anal rings. Indeed, all these are the main characters which distinguish *Syngnathus taenionotus* from *S. acus* (Table 1), a species that could be misclassified as *S. taenionotus*.

The standard length (SL \pm 1 mm) of every specimen was measured by an ichthyometer when the sample involved less than 500 specimens; otherwise stratified random subsamples of 500 individuals were used.

The number of ripe eggs in the ovaries were counted in a sample of 60 fully mature females per species. In these females, the whole gonad was also checked to assess the eggs' ripening. Diameters of a total of 60 eggs from 3 females per species were measured. In a sample of 60 males with full brood pouches from each species, the eggs or embryos they were carrying were counted. The total lengths of 35 newly hatched juveniles per species were measured.

For each species, the standard length range and proportion of individuals per cohort were obtained by resolving each monthly polymodal length frequency distribution of measured specimens in the single gaussian components (Abramson 1971).

Gut content analysis. Analysis of the contents of the digestive tract was performed on 12 subsamples, grouping specimens of the 2 species into 3 seasons (spring: from June 1981 and 1982; summer: from July and August 1981; autumn: from September and October 1981) and 2 age-groups (0-age and 1-age cohorts). Each subsample consisted of 30 full-gut contents (empty guts occasionally found were replaced by others), except in the case of autumn subsamples of

Table 1. *Syngnathus taenionotus*. Some meristic measurements of specimens from Sacca di Scardovari compared with those for the same species from Venice Lagoon by D'Ancona (1934) and for *S. acus* (a species which could be misclassified as *S. taenionotus*) reported both by D'Ancona (1934) and Dawson (1986) ({}: modal class). TL: total length

	<i>S. taenionotus</i>		<i>S. acus</i>	
	(this study) n = 60	(D'Ancona) n = 13	(D'Ancona) n = 44	(Dawson)
TL range (cm)	2.4–19.0	13.7–18.6	15.1–29.9	to 46
No. of subdorsal rings				
Range	9–10	8–10	7–9	8–10
$\bar{x} \pm SD$	9.38 \pm 0.49	[9]	[8]	
No. of pre-anal rings				
Range	16–18	16–18	18–20	17–21
$\bar{x} \pm SD$	17.11 \pm 0.49	[17]	[19]	
No. of post-anal rings				
Range	34–38	33–39	38–42	38–43
$\bar{x} \pm SD$	35.90 \pm 0.97	[38]		

Syngnathus taenionotus, in which only 6 full guts of 0-age and 11 of 1-age groups were found. Food items were classified at species level when possible, and counted. Prey species were pooled into 'guilds', corresponding to the microhabitats in which they dwell. Moreover, food items within each guild were kept discrete in 2 arbitrary size categories.

We recognized the following guilds and size categories:

SED = small-sized species living in the sediments (e.g. harpacticoids)

SED + = large-sized species living in the sediments (e.g. corophids)

PHT = small-sized phytal animals (mainly harpacticoids)

PHT + = large-sized phytal animals (e.g. gammarids, isopods)

MIX = small-sized epibenthic organisms living on the bottom but able to migrate transitorily into the water column (e.g. harpacticoids)

MIX + = large-sized epibenthic organisms (e.g. palemonids)

PLN = small-sized planktonic organisms (e.g. calanoids, zoeae)

PLN + = large-sized planktonic organisms (mainly mysids)

PSC = occasionally found post-larval stages of fish.

Average abundance values and the corresponding relative abundances per guild (p_{ij}) were then calculated. A cluster analysis of the age/season subsamples of both pipefish species was performed, calculating a Horn's overlap index similarity matrix between paired subsamples. Horn (1966) proposed his measurement of overlap, R_0 , derived from information theory, as the appropriate index when one is more interested in the overlap in foraging habitat than the overlap in exploi-

tation of alternative food items from within the same habitat. The computational formula is as follows:

$$R_0 = [\sum(p_{ij} + p_{ik})\ln(p_{ij} + p_{ik}) - \sum p_{ij}\ln p_{ij} - \sum p_{ik}\ln p_{ik}]/2\ln 2$$

where p_{ij} = proportion prey guild i is of the total prey guilds of subsample j ; p_{ik} = proportion prey guild i is of the total prey guilds of subsample k .

A dendrogram was drawn using the flexible classification algorithm of Lance & Williams (1967) with $\beta = -0.25$.

RESULTS

A total of 13 898 specimens of *Syngnathus taenionotus* and 3924 of *Syngnathus abaster* were caught (Table 2). Populations of both species were far more abundant during the warm season, when they reproduce. The low figures recorded in autumn and winter are likely due to fishes having migrated to warmer, deeper water

Length frequency distributions

Fig. 2 shows the monthly size frequency distribution of both species. Months in which the number of specimens was less than 10 are not reported. For both species, the occurrence of 2 cohorts per year is evident. By analysis of length frequency distributions, it was possible to distinguish the recruit's cohorts (0-age) and the parent's cohorts (1-age and probably 2-age). In accordance, specimens of *Syngnathus taenionotus* with a standard length (SL) less than 10.5 cm have been considered 0-age, as have those of *S. abaster* with SL less than 8.0 cm.

Table 2. Number of specimens of *Syngnathus* species caught at each station in the Sacca di Scardovari. '(2)' means 2 samples per month

	<i>S. taenionotus</i>				<i>S. abaster</i>			
	Stn 1	Stn 2	Stn 3	Total	Stn 1	Stn 2	Stn 3	Total
Jun 1981 (2)	247	6357	134	6738	63	186	27	276
Jul 1981 (2)	520	3511	2394	6425	336	467	352	1155
Aug 1981	19	14	42	75	4	2	25	31
Sep 1981	0	2	13	15	204	2	8	214
Oct 1981	2	6	0	8	6	16	0	22
Nov 1981	0	0	0	0	0	0	1	1
Dec 1981	0	0	0	0	0	0	0	0
Jan 1982	0	0	1	1	0	0	0	0
Feb 1982	0	0	1	1	0	2	0	2
Mar 1982	0	0	2	2	0	0	2	2
Apr 1982 (2)	21	0	31	52	4	1	4	9
May 1982 (2)	346	13	81	440	20	20	7	47
Jun 1982 (2)	57	2	72	131	32	863	217	1112
Jul 1982	1	4	5	10	394	613	46	1053
Total	1213	9909	2776	13898	1063	2172	689	3924

The 0-age cohorts of both species first occurred in May. Recruitment of *Syngnathus taenionotus* continued until the end of September (although 2 specimens out of 8 sampled in October were of about 2 cm in length). Recruitment terminated in August for *S. abaster*.

The largest specimens (from 17.5 to 19 cm) of *Syngnathus taenionotus* were found in April 1982. The following month (May 1982), no individual exceeding 17.5 cm was found. On the other hand, specimens up to 21.4 cm SL were caught in shore water off the Po Delta in July 1991 (Franzoi pers. obs.). Probably, the above-mentioned April 1982 specimens had survived the winter twice. This suggests a life span of at least 24 mo.

In *Syngnathus abaster* the parental cohort seemed to disappear almost completely after September, thus indicating a life span of about 17 mo.

Life cycles

Life history parameters inferred from both direct observation and the above analysis of population structures are summarized separately for each species (Table 3). Their life cycles are as follows:

***Syngnathus taenionotus*.** The reproductive season begins in February. In fact, the only specimen sampled that month (Table 2) was a female with ripe ovaries. Similarly, the only 2 specimens caught in March (Table 2) were males with brood pouches containing eggs. Mature females disappeared from samples after July, while breeding males disappeared after August. Newly-born fish appeared in the population in May, and were still present in September (also October).

Hence, the reproductive season appears to last about 5 mo. The time lag from both the first occurrence of breeding males (March) to the first occurrence of juveniles (May) and the last occurrence of mature females (July) to the last occurrence of juveniles (September) suggest an incubation time of about 2 mo. Peak abundance of the 0-age cohort occurred in June-July, however.

The average percentage of females in the adult population (> 10.5 cm SL) was 46.4 % and the sex ratio did not significantly differ from a 50:50 ratio ($\chi^2 = 0.852$, not significant at 1 df). However, during the peak of reproductive activity, in April-May, *Syngnathus taenionotus* showed a sex ratio favouring males (April: 5.4 males per female, $\chi^2 = 19.34$, $p < 0.001$ at 1 df; May: 7.8 males per female, $\chi^2 = 40.19$, $p < 0.001$ at 1 df).

The average number of embryos per male was about twice that of ripe eggs per female. Theoretically, each male is able to simultaneously incubate the eggs from at least 2 females.

Microscopical observation of the ovaries showed that, besides the relatively small number of actually ripe eggs, there was also a continuous series of oocytes and eggs at several different ripening stages.

***Syngnathus abaster*.** The reproductive season begins in March; the 2 adults caught in February were not sexually mature, while the 2 specimens sampled in March were mature females (Table 3); males with brood pouches containing eggs/embryos were caught from the beginning of April. Mature females and breeding males disappeared from the samples after July. Newly hatched fishes appeared in the population in May and were present until August. The reproduc-

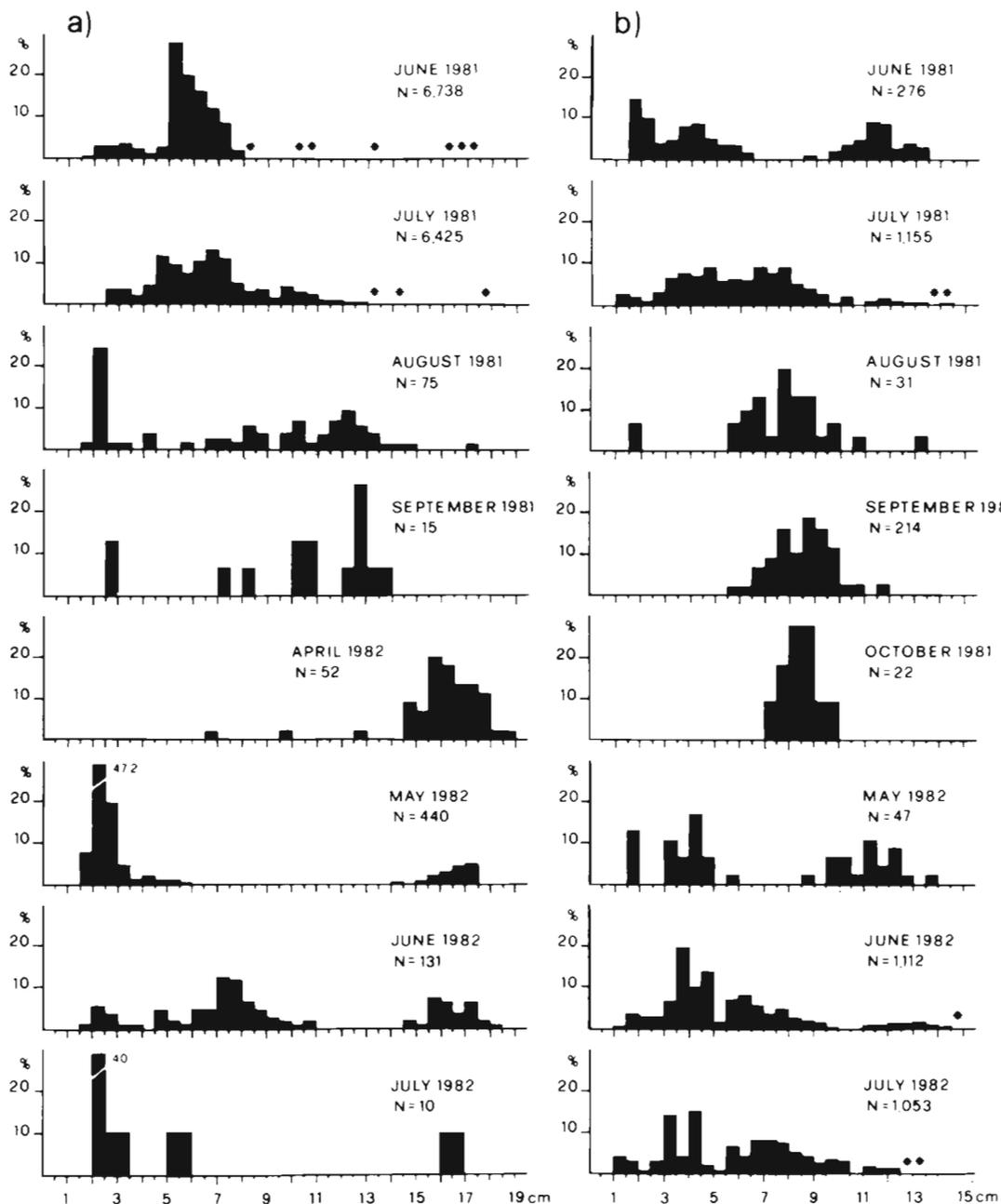


Fig. 2. Monthly per cent frequency distributions of standard lengths of (a) *Syngnathus taenionotus* and (b) *S. abaster*. N: number of specimens caught; * values less than 1 %

tive season and incubation period, estimated in the same way as for *S. taenionotus*, last about 4 mo and 1 mo respectively. Again, the highest abundance of recruits occurred in June–July.

The average percentage of females in the adult population (>8 cm SL) was 47.5 %, and the sex ratio was not significantly different from 50:50 ($\chi^2 = 1.183$, not significant at 1 df). During May and June (1 mo before the recruitment peaks) the percentage of females in the adult population was 38.2 % ($\chi^2 = 0.747$, not signif-

icant at 1 df) and 45.0 % ($\chi^2 = 2.09$, not significant at 1 df).

Unlike the other species, each male seems potentially capable of receiving eggs from only one female.

Ovaries of *Syngnathus abaster*, contrary to those of *S. taenionotus*, take up most of the abdominal cavity when they are mature, containing nearly exclusively ripe eggs, except a few thin layers of small oocytes lining the ovary wall.

Table 3. Comparison between some life-history traits of *Syngnathus* species from Sacca di Scardovari

	<i>S. taenionotus</i>	<i>S. abaster</i>
Ovigerous females	Feb–end Jul	Mar–end Jul
No. of eggs/female (mean ± SD; n = 60)	46 ± 9	104 ± 40
Egg diameter (mm) (mean ± SD; n = 60)	1.4 ± 0.2	1.2 ± 0.2
Female percentages during reproductive peak ^a	Apr: 15.7 – May: 11.4	May: 38.2 – Jun: 45.0
Males with brood pouch	Mar–Aug	beg. Apr–end Jul
No. of male broods per reproductive season	2	4
No. of eggs/male (mean ± SD; n = 60)	84 ± 17	109 ± 27
Occurrence of juveniles	May–Sep (Oct)	May–Aug
Egg incubation	2 mo	1 mo
SL at birth (mm) (mean ± SD; n = 35)	20.3 ± 1.2	13.5 ± 1.0
Life span	~ 20–24 mo	~ 13–17 mo
No. of reproductive seasons per lifetime	2	1

^a See text

Feeding habits

***Syngnathus taenionotus*.** Results from the gut content analysis of *S. taenionotus* subsamples are shown in Tables 4 & 5.

The phytal harpacticoid *Tisbe holothuriae* and, to a lesser extent, *T. histriana* and *T. bulbisetosa*, dominated the diet of the 0-cohort during spring, representing 95 % of food items (Table 5). Subsequently, *Syngnathus taenionotus* appears to have fed on zooplanktonic organisms (Table 5). Calanoids such as *Acartia clausi*, *A. latisetosa* and, to a lesser extent, *A. margalefi* were particularly important in the diet of the 0-cohort during summer, but also in that of the 1-cohort during both spring and summer. Decapod larvae (zoea) were also intensively preyed on by juveniles in summer, and were the dominant prey of adults in spring and especially summer. As the seasons progressed and size increased, *S. taenionotus* (both cohorts) fed on larger zooplanktonic organisms. In autumn the diet was almost exclusively made up of the mysid *Mesopodopsis slabberi* (Table 5). This may have been a consequence of the low number of individuals with full gut found in the autumn samples. However, this prey-species was also well-represented at other ages/seasons, except in the 0-age cohort during spring (Table 5).

***Syngnathus abaster*.** The most important food items in the diet of *S. abaster* were harpacticoids of the genus *Tisbe* (Tables 4 & 6). These are the most common representatives of the phytal meiofauna, chiefly associated with the *Ulva* thalli in the Sacca di Scardovari (Ceccherelli et al. 1982). *Tisbe holothuriae* and *T. bulbisetosa* were alternatively dominant prey in all seasons and in both cohorts, except the autumn 1-age specimens. A third species, *T. histriana*, was also well represented. Other meiobenthic harpacticoid species, as well as zooplanktonic copepods, occurred only sporadically, with the exception of *Canuella perplexa*, the most common benthic harpacticoid in the bay (Ceccherelli et al. 1982). This species was moderately preyed on by the 0-cohort specimens in summer (Table 6). Amphipods, such as the phytal *Gammarus insensibilis* and *Melita palmata* and the mucous tube-dweller *Corophium insidiosum*, contributed to the diet of the larger-sized specimens (1-cohort), especially in autumn (Table 6). The remarkable amounts of eggs found in the gut contents of 1-age specimens (Table 6) probably stemmed from gravid female gammarids. In *S. abaster* the corneous opercola of the polychaete *Ficopomatus enigmaticus* was recognized.

Table 4. General gut content composition from subsamples of *Syngnathus* species of the Sacca di Scardovari. Tn: *S. taenionotus*; Ab: *S. abaster*; Sp: spring; Su: summer; Au: autumn; 0 and 1. age-cohorts

Age/season subsamples	No. of fishes	Average no. of prey per gut (± SD)	No. of food items
TnSp0	30	117.73 ± 56.94	13
TnSp1	30	16.13 ± 6.80	15
TnSu0	30	81.13 ± 21.20	16
TnSu1	30	205.47 ± 139.09	14
TnAu0	6	2.67 ± 0.75	2
TnAu1	11	8.45 ± 0.50	1
AbSp0	30	42.40 ± 11.37	17
AbSp1	30	59.73 ± 38.69	19
AbSu0	30	62.20 ± 24.61	16
AbSu1	30	21.17 ± 23.16	15
AbAu0	30	27.93 ± 18.47	17
AbAu1	30	9.80 ± 5.88	21

Table 5. *Syngnathus taenionotus*. Average numbers (SD) per gut and corresponding relative abundances of food items in each subsample. Percentages more than 1 % (underlined) and 5 % (bold print) are highlighted. Subsample legends as in Table 4; food items are listed according to microhabitat guilds; for guild denominations see 'Materials and methods'

Food item	Guild	TnSp0		TnSp1		TnSu0		TnSu1		TnAu0		TnAu1	
		N	%	N	%	N	%	N	%	N	%	N	%
<i>Canuella perplexa</i>	(SED)			0.7 (0.9)	<u>4.1</u>					0.1 (0.3)			
Ostracoda	(SED)	0.2 (0.4)	0.2	0.1 (0.3)	0.4								
Nematoda	(SED)					0.1 (0.3)	0.1						
<i>Harpacticus flexuosus</i>	(PHT)			0.1 (0.3)	0.4	0.1 (0.3)	0.1						
<i>Tisbe holothuriae</i>	(PHT)	68.3 (35.1)	58.0	0.1 (0.3)	0.4	0.3 (0.4)	0.3						
<i>Tisbe histriana</i>	(PHT)	9.7 (5.0)	8.3	0.2 (0.4)	<u>1.2</u>	0.3 (0.4)	0.3						
<i>Tisbe bulbisetosa</i>	(PHT)	34.8 (15.4)	29.6	0.5 (0.6)	<u>2.9</u>	0.1 (0.3)	0.1						
<i>Cyclopina gracilis</i>	(MIX)					0.1 (0.3)	0.1						
<i>Acartia clausi</i>	(PLN)	3.5 (4.9)	<u>3.0</u>	4.3 (5.6)	26.8	25.8 (21.4)	31.8	14.6 (9.1)	7.1				
<i>Acartia margalefi</i>	(PLN)			1.2 (0.4)	7.4	2.2 (2.0)	<u>2.7</u>						
<i>Acartia latisetosa</i>	(PLN)					23.9 (16.0)	29.4	46.4 (56.4)	22.6				
<i>Calanipeda acquadulcis</i>	(PLN)					0.1 (0.3)	0.2						
<i>Paracalanus parvus</i>	(PLN)					0.1 (0.3)	0.1						
<i>Palaemon</i> sp. zoea	(PLN)	0.1 (0.3)	0.1	4.7 (3.8)	28.9	24.4 (19.6)	30.1	138.5 (104.9)	67.4				
<i>Carcinus</i> sp. zoea	(PLN)					1.1 (0.9)	<u>1.4</u>	0.2 (0.4)	0.1				
<i>Cirripedia nauplii</i>	(PLN)							0.1 (0.3)	<0.1				
<i>Corophium insidiosum</i>	(SED+)			0.1 (0.3)	0.4			0.1 (0.3)	<0.1				
<i>Gammarus insensibilis</i>	(PHT+)	0.5 (0.6)	0.4	0.1 (0.3)	0.8	0.1 (0.3)	0.1	0.1 (0.3)	<0.1				
<i>Melita palmata</i>	(PHT+)			0.1 (0.3)	0.4			0.1 (0.3)	<0.1				
<i>Idotea</i> sp.	(PHT+)	0.1 (0.3)	0.1										
<i>Sphaeroma</i> sp.	(PHT+)	0.1 (0.3)	0.1										
<i>Palaemon</i> sp. ad.	(MIX+)												
<i>Crangon crangon</i>	(MIX+)	0.1 (0.3)	0.1					0.1 (0.3)	<0.1				
<i>Hydrobia</i> sp.	(MIX+)			0.6 (0.9)	<u>3.7</u>								
<i>Mesopodopsis slabberi</i>	(PLN+)	0.1 (0.3)	0.1	3.3 (1.7)	20.6	2.3 (0.6)	<u>2.9</u>	4.5 (0.7)	<u>2.2</u>	2.5 (0.5)	93.6	8.5 (0.5)	100.0
Eggs	(PLN+)	0.2 (0.4)	0.2					0.3 (0.4)	0.1	0.2 (0.4)	6.4		
Insecta	(PLN+)	0.1 (0.3)	0.1	0.2 (0.4)	1.2	0.3 (0.5)	0.4	0.1 (0.3)	<0.1				
Pisces sp. juv.	(PSC)							0.3 (0.5)	0.2				
<i>S. taenionotus</i> juv.	(PSC)							0.2 (0.4)	0.1				

Table 6. *Syngnathus abaster*. Average numbers (SD) per gut and corresponding relative abundances of food items in each subsample. Percentages more than 1% (underlined) and 5% (bold print) are highlighted. Subsample legends as in Table 4; food items are listed according to microhabitat guilds; for guild denominations see 'Materials and methods'

Food item	Guild	AbSp0		AbSp1		AbSu0		AbSu1		AbAu0		AbAu1	
		N	%	N	%	N	%	N	%	N	%	N	%
<i>Canuella perplexa</i>	(SED)	0.1 (0.3)	0.2	0.1 (0.3)	0.1	4.5 (6.3)	7.2					0.1 (0.3)	0.7
<i>Microarthridon tailax</i>	(SED)	0.5 (0.8)	<u>1.1</u>										
<i>Ostracoda</i>	(SED)	0.3 (0.4)	0.6			1.0 (0.8)	<u>1.6</u>	0.1 (0.3)	0.3	0.6 (0.6)	<u>2.1</u>	0.5 (0.6)	<u>4.8</u>
Nematoda	(SED)	0.1 (0.3)	0.2										
<i>Harpacticus flexulosus</i>	(PHT)	1.8 (2.6)	<u>4.2</u>	0.1 (0.3)	0.1					0.2 (0.4)	0.7		
<i>Harpacticus littoralis</i>	(PHT)	0.4 (0.9)	0.9	0.1 (0.3)	0.2								
<i>Tisbe holothuriae</i>	(PHT)	26.7 (1.8)	63.0	3.8 (2.7)	6.4	17.3 (8.9)	27.8	15.4 (21.6)	72.4	15.9 (14.5)	57.0	1.0 (0.6)	10.2
<i>Tisbe histriana</i>	(PHT)	5.3 (3.6)	12.4	4.2 (3.0)	7.0	4.2 (3.6)	6.8			0.3 (0.6)	<u>1.0</u>	0.1 (0.3)	0.7
<i>Tisbe burbisetosa</i>	(PHT)	5.1 (3.0)	12.1	32.3 (22.9)	54.0	30.2 (20.3)	48.5	1.1 (1.7)	5.3	4.1 (1.3)	14.8	1.3 (1.5)	13.6
<i>Amphiascus parvus</i>	(PHT)											0.1 (0.3)	<u>1.3</u>
<i>Ameira parvula</i>	(PHT)	0.1 (0.5)	0.3										
<i>Pseudonychocamptus colomboi</i>	(PHT)	0.1 (0.3)	0.2										
<i>Ectinosoma dentatum</i>	(MIX)					0.2 (0.5)	0.3			0.1 (0.3)	0.5	0.1 (0.5)	<u>1.3</u>
<i>Mesochra portica</i>	(MIX)					0.1 (0.3)	0.1						
<i>Mesochra pygmaea</i>	(MIX)	0.2 (0.8)	0.5										
<i>Cyclopina gracilis</i>	(MIX)	0.2 (0.4)	0.5	0.1 (0.3)	0.2					0.2 (0.4)	0.7	0.1 (0.3)	<u>1.3</u>
<i>Acartia clausi</i>	(PLN)	0.1 (0.3)	0.2	0.3 (0.4)	0.5			0.1 (0.3)	0.6	0.3 (0.4)	<u>1.0</u>	0.1 (0.3)	0.7
<i>Calanipeda acquaedulcis</i>	(PLN)	0.6 (1.0)	<u>1.4</u>	1.1 (1.5)	<u>1.8</u>								
<i>Palaemon</i> sp. zoea	(PLN)			0.1 (0.3)	0.1					0.2 (0.4)	0.7		
<i>Corophium insidiosum</i>	(SED+)	0.5 (0.8)	<u>1.2</u>	2.2 (2.9)	<u>3.7</u>	1.1 (0.4)	<u>1.7</u>	0.1 (0.3)	0.6	1.6 (1.4)	5.7	0.1 (0.3)	<u>1.3</u>
<i>Corophium acherusicum</i>	(SED+)			0.7 (0.8)	<u>1.1</u>	0.3 (0.5)	0.5	0.1 (0.3)	0.3	0.7 (0.5)	<u>2.4</u>	0.9 (0.9)	9.5
<i>Ficopomatus enigmaticus</i>	(SED+)			0.1 (0.3)	0.1	1.7 (1.1)	<u>2.7</u>	0.1 (0.3)	0.3	2.0 (2.5)	7.2	0.3 (0.4)	<u>2.8</u>
<i>Gammarus insensibilis</i>	(PHT+)			0.1 (0.3)	0.1	0.8 (0.7)	<u>1.3</u>	0.1 (0.3)	0.6	0.5 (0.5)	<u>1.7</u>	1.9 (1.0)	19.1
<i>Gammarus aequicauda</i>	(PHT+)	0.4 (0.6)	0.9	3.5 (1.9)	5.9			0.4 (0.6)	<u>1.9</u>	0.6 (0.8)	<u>2.1</u>	0.5 (0.5)	<u>4.8</u>
<i>Melita palmata</i>	(PHT+)			1.5 (1.3)	<u>2.5</u>	0.3 (0.5)	0.5	0.6 (0.5)	<u>2.8</u>	0.4 (0.5)	<u>1.4</u>	0.5 (0.7)	<u>4.8</u>
<i>Idotea</i> sp.	(PHT+)			0.5 (0.6)	0.9			0.1 (0.3)	0.3	0.1 (0.3)	0.5	0.2 (0.4)	<u>2.0</u>
<i>Spheroma</i> sp.	(PHT+)					0.1 (0.3)	0.1					0.1 (0.3)	<u>1.3</u>
<i>Palaemon</i> sp. ad.	(MIX+)							0.4 (0.5)	<u>1.9</u>			0.1 (0.3)	0.7
<i>Palaemon elegans</i>	(MIX+)							0.7 (1.1)	<u>3.4</u>			0.1 (0.3)	<u>1.3</u>
<i>Mesopodopsis slabberi</i>	(PLN+)			0.1 (0.3)	0.2	0.1 (0.3)	0.1	0.3 (0.4)	<u>1.3</u>			1.7 (2.1)	17.0
Eggs	(PLN+)			9.0 (6.2)	15.1			1.7 (1.5)	7.9	0.1 (0.3)	0.5	0.1 (0.3)	0.7
Insecta	(PLN+)			0.1 (0.3)	0.1	0.1 (0.3)	0.1					0.1 (0.3)	0.7

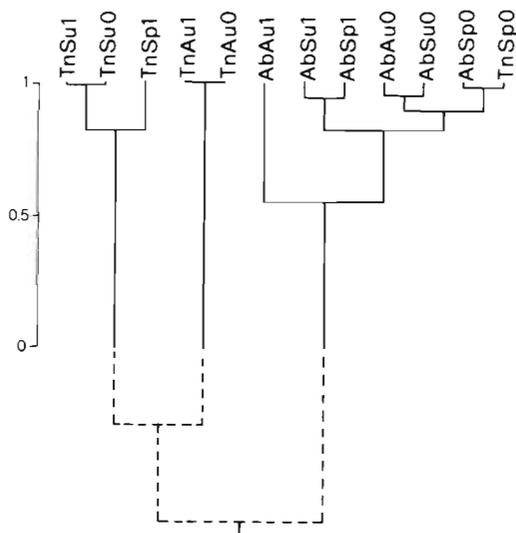


Fig. 3. Classification dendrogram of gut content subsamples of *Syngnathus* species based on the abundances of the preys grouped in microhabitat guilds. Tn: *S. taenionotus*; Ab: *S. abaster*; Sp: spring; Su: summer; Au: autumn; 0 and 1: age-cohorts

Foraging habitat comparison

When food items were grouped by microhabitat 'guilds' as shown in Tables 5 & 6, 2 species-specific clusters resulted (Fig. 3). The only exceptions were the spring subsamples of 0-age specimens of both *Syngnathus taenionotus* (TnSp0) and *S. abaster* (AbSp0), which show a very high similarity value. On the whole, the *S. taenionotus* cluster tended to be hierarchically ordered, first by season and then by age, whereas the reverse seemed to occur in the *S. abaster* cluster, suggesting the existence of some ontogenetic shifting in the diet of the latter species.

DISCUSSION

Life cycle differences

Syngnathus taenionotus and *S. abaster* can be found together in the nearshore phytal habitat of the Sacca di Scardovari during their reproductive season. For both species reproduction begins in the spring of the first year. *S. taenionotus* probably reproduce twice in its lifetime, while *S. abaster* reproduce once. The 2 species appear to have somewhat different reproductive strategies. *S. taenionotus* produces a smaller number of large young while *S. abaster* produces more, but smaller young. Production of larger young in *S. taenionotus*, possibly to escape predation and favour feed-

ing (Balon 1984), may necessitate its prolonged incubation period.

On the other hand, each single male of *Syngnathus taenionotus* can simultaneously take care of eggs from more than 1 female (in theory, at least 2) whereas the male brood pouch of *S. abaster* only has room for as many eggs as a female seems to produce at each spawning. However, in pipefishes, mating may not be on a 1 female:1 male basis (Bayer 1980). In species of *Syngnathus*, females may parcel out the same batch of contemporary ripe eggs among many males, and embryos/postlarvae at different stages of development can be found in the pouch of a single male (Breder & Rosen 1966, Bayer 1980, Berglund et al. 1988).

In pipefish populations the parental investment is also elevated for males, in many cases to the extent of causing a sex role reversal: i.e. males limit species reproduction (Bayer 1980, Berglund et al. 1986a, b, 1989, Svensson 1988, Steffe et al. 1989, Berglund 1991). In fact, in many syngnathid species, females appear to produce more eggs, or produce them at a faster rate, than naturally available males could care for. Moreover, there is an apparent association between mating pattern (polygamous or monogamous) and the sex roles in syngnathids (Vincent et al. 1992). The longer incubation period and more distinct polygamy of *Syngnathus taenionotus* compared to *S. abaster* might suggest a more pronounced sex role reversal in the former species.

During the breeding season, *Syngnathus taenionotus* males are more numerous than females; this is less pronounced in *S. abaster* (Table 3). It is possible that *S. taenionotus* females might have avoided sampling since they occupy habitats other than the phytal one close to the shore (Steffe et al. 1989). Svensson (1988) demonstrated in the laboratory that reproducing females of *Syngnathus typhle* had increased activity and a higher food intake compared with reproducing males. *S. taenionotus* females feeding mainly on planktonic prey may prefer to forage in deeper less vegetated habitats. In contrast, incubating males seem to seek shelter preferentially in the dense phytal habitat.

Feeding habits

Syngnathus taenionotus and *S. abaster* in the Sacca di Scardovari seem to feed on different prey. The only strong dietary overlap between the 2 species is during spring, when the newly born feed exclusively on phytal harpacticoids of the genus *Tisbe*. The importance of meiofaunal harpacticoids as a food source is well known for syngnathids (Tipton & Bell 1988) as well as other small and/or juvenile fishes (Alheit & Scheibel 1982, Gee 1989, Coull 1990). Harpacticoid dominance

in the diet is not surprising, since harpacticoids are normally the dominant meiofaunal organisms in the phytal habitat of the Sacca di Scardovari (Ceccherelli et al. 1982).

Except for the newly born, individuals of the 2 species appear to occupy different foraging micro-habitats for most of their life span: *Syngnathus abaster* preys on phytal organisms whereas *S. taenionotus* becomes mainly zooplanktivorous. This suggests that *S. abaster* may remain within, or under, the phytal bed (*Ulva thalli*), whereas *S. taenionotus* may remain on top of the phytal canopy feeding on plankton that float by. Differential use of microhabitats in phytal environment has been demonstrated in syngnathid species by Howard & Koehn (1985).

Both cohorts of *Syngnathus taenionotus* preyed mainly on calanoids and on decapod larvae during summer but exclusively on mysids during autumn. Concurrent zooplankton investigations carried out at the same stations (Ferrari unpubl.) showed that zoeae disappeared from plankton in September 1981 whereas calanoids, on average, reached the relative minimum (1.7 %) of their yearly density trend in October 1981. Mysids may be a less desirable prey, utilized only when other preferred prey was not abundant during autumn. A similar occurrence was described by Ryer & Orth (1987) for *Syngnathus fuscus*. Other studies on species of *Syngnathus* (Main 1985, Ryer 1988) indicate that the abundance of prey types in the diet depends on the accessibility, or vulnerability, of the prey itself, as well as on abundance in the environment.

Both pipefish species investigated here are slow-moving suction feeders. We suggest that snout structure is related to their respective foraging strategies. Hyatt (1979) pointed out that, in general, the development of a long, tubular mouth, as in Syngnathidae and Fistularidae, serves as an adequate substitute to gill-rakers for zooplankton feeding. According to Muller & Osse (1984), who studied fish suction feeding thoroughly, the accuracy of aim required to catch a prey depends upon the total volume of the parcel of water sucked in as well as the length of the snout. In Syngnathids, the very rapid dorso-rotation of the head and the long snout allow a rapid acceleration of the snout tip towards the prey (Muller 1987). The velocity and acceleration of the water relative to the mouth aperture increase when the snout is longer (Muller & Osse 1984), so it is advantageous to increase the snout length when very rapid swimming prey are to be captured. *Syngnathus taenionotus* has a long and terminally cylindrical snout, whereas that of *S. abaster* is shorter and conical (Fig. 1). These characteristics of the *S. taenionotus* snout suggest this species has a greater aiming ability. In a less complex habitat, such as the

water column above the phytal canopy, free-swimming prey may escape more easily than prey crawling on substrates, such as algal leaves. A better aiming ability on the part of the predator is, then, an advantage in the former habitat. On the contrary, the shorter snout of *S. abaster* may be fitter on preying in a high-complexity habitat.

These considerations may explain why the new-born specimens of both species, with snout sizes not yet well-differentiated (Fig. 1), thrive well in the complex, phytal microhabitat foraging on the same kinds of prey.

Occurrence of dietary shifting to progressively larger prey has been described in syngnathid species (Livingston 1982, Ryer & Orth 1987, Tipton & Bell 1988), *Syngnathus abaster* shows a moderate change of its diet with increasing body size but this does not involve any ontogenetic change of foraging microhabitat. On the other hand, *S. taenionotus* specimens, as they mature, switch to the less complex microhabitat of the water column above algal beds, where they are probably more successful at capturing fast swimming prey. This switch from epiphytal to plankton feeding is accompanied by a morphological change: the snout elongates.

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