FEEDING PATTERN OF *SEPIA OFFICINALIS* (CEPHALOPODA: SEPIODIDEA) IN THE RIA DE VIGO (NW SPAIN)

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(Figures 1-3)

The feeding pattern of *Sepia officinalis* was studied from field data obtained in two 24 h sampling operations carried out in August and February. The August results showed a 24 h feeding pattern in which most feeding occurred during darkness. The increase in feeding coincided with dusk and the first hours of darkness. In February there was no clear discontinuity in the feeding pattern but, as in August, the greatest incidence of empty guts was between noon and dusk. The fullness index was 3% in August and 1.7% in February.

INTRODUCTION

The importance of feeding pattern is well documented in fish (Jenkins & Green, 1977; Simenstad & Cailliet, 1986) but there are not many reported studies in cephalopods. Feeding patterns, as defined by Jenkins & Green (1977) have been studied, to our knowledge, only in *Todarodes pacificus* (Okiyama, 1965), *Loligo pealei* (Vovk, 1972), *Loligo opalescens* (Karpov & Cailliet, 1978), *Illex illecebrosus* (Amaratunga *et al.*, 1979; Amaratunga, 1980) and *Nototodarus gouldi* (O'Sullivan & Cullen, 1983). Boyle (1983) dealt with aspects of feeding in several cephalopod species but not specifically with feeding pattern. Aspects of feeding in *Sepia officinalis* have been reviewed by Nixon (1987). The present work describes the daily feeding pattern in *Sepia officinalis* from data collected in the field.

MATERIAL AND METHODS

A total of 255 specimens of *Sepia officinalis* were collected from the Ria de Vigo in two 24 h sampling operations carried out on 7 August 1986 and 26 February 1987. Sampling sites in the Ria are shown in Figure 1. The principal characteristics of the hauls, time intervals and number of specimens collected are given in Table 1.

Two different types of gear were employed; in August a beach seine of the type described by Arnaiz & Coo (1977), and in February, a small otter trawl as described by Alonso-Allende & Guerra (1984). Each haul lasted 15 min. Bottom temperature was measured during each haul and is given in Table 1. Low tides were at 0943 and 2216 h GMT in August, and at 0753 and 2005 h in February. There was a new moon on both occasions. Times of sunrise and sunset are indicated in Figure 2.

Figure 1. Map of Ria de Vigo showing the location of sampling sites in August (a) and in February (f).

Table 1. Characteristics of the hauls, specimens captured and bottom temperatures

Date	Times (GMT)	Number of hauls	Depth initial	Depth final	Type of bottom	Bottom temp (°C)	Number captured	Conditions
7.8.86	0749-1034	6	3	8	sand,algae	18.0±1	15	sun, no wind
	1214-1631	7	3	8	sand,algae	18.0±1	26	sun, no wind
	1644-1908	7	2	6	sand,algae	18.0±1	22	sun, no wind
	2134-0030	6	2	5	sand,algae	18.0±1	28	clear sky, no wind
	0259-0521	7	3	5	sand,algae	18.0±1	24	clear sky, no wind
26.2.87	0749-1034	3	12	17	mud	12.0±1	29	cloud, wind
	1214-1631	5	13	26	mud	12.0±1	21	cloud, wind
	1644-1908	3	5	25	mud	12.0±1	19	cloud, wind
	2134-0030	4	12	18	mud	12.0±1	43	rain, wind
	0259-0521	3	15	22	mud	12.0±1	28	rain, wind

Figure 2. Weight Fullness Index (WFI) geometric mean variations in August specimens, ML≤40 mm (●), ML>40 mm (▲) and in February (O)

Specimens were preserved on board at 4°C in ice boxes and all samples were stored at -20°C in the laboratory. For analysis the individual blocks of frozen cuttlefish corresponding to each haul were thawed in tapwater at room temperature. Each specimen was numbered and the following parameters recorded.

- 1) Dorsal mantle length (ML) to the nearest mm
- 2) Total drained wet body weight (BW)
- 3) Sex
- 4) Maturation stage. Scale 1-5 (immature to post spawning) by criteria essentially similar to those of Richard (1971) and Allonso-Allende & Guerra (1984)
- 5) Gut fullness as subjective fullness index (SFI). Scale 0-4 (stomach empty to distended) by criteria similar to Amaratunga & Durward (1979) and Hyslop (1980).
- 6) Weight of stomach contents (WSC) to nearest mg.
- 7) Stomach contents. Prey items identified to lowest taxon possible.
- 8) Digestive state index (DSI). Scale 1-4 (most digested to least digested) by criteria similar to Karpov & Cailliet (1978).

The principal data of captured specimens is given in Table 2. For the August data the specimens are divided into two size groups (ML≤40 mm and ML>40 mm). The smaller specimens were not taken in the February hauls due to the selectivity of the trawl which had a mesh size of 30 mm.

Table 2. *Principal data of specimens captured*

Date	size (mm)	number	Mean ML ±SD (mm)	male	female	unsexed	percentage in maturation state			
							1	2	3	4
7.8.86	10-40	43	26.8(6.07)	17	10	16	100	0	0	0
	40-145	72	95.3(15.7)	29	43	0	15.4	60.3	16.6	7.7
26.2.87	40-205	140	84.2(36.8)	54	86	0	10.7	48.8	9.3	31.2

The weight fullness index (WFI= WSC x10000/BW) was taken to be a standardised measure of fullness and is given in Table 3 for each category in the different fishing intervals. The fact that the variance of WSC is not wholly independent of BW renders this ratio unsuitable for parametric tests (Sokal & Rohlf, 1969) and made it necessary to employ non-parametric tests (Siegel, 1959). The BW homogeneity of all specimens was tested using the Kruskal-Wallis test, adopting the significance level of $\alpha=0.05$ to reject the null hypothesis.

RESULTS

Table 3 summarizes the percentage of empty stomachs, those in the 1+2 and 3+4 digestive states and the values of weight fullness index for the five intervals considered for each date and the cuttlefish size classes. Figure 2 shows the variation of WFI geometric mean over 24 hours in August and February. Figure 3 shows the variation over 24 h in the percentage of empty stomachs and those in the different digestion states.

Table 3. Percentages of empty stomachs, digestive state index and weight fullness index of specimens captured

Date	Times (GMT)	Size class	No. of stomachs	Empty (%)	DSI 1&2	DSI 3&4	Arith. mean	WFI Variance	Geom. mean
7.8.86	0749-1034	≤40	no data	-	-	-	-	-	-
	1214-1631	≤40	10	70.0	30.0	0	19.33	3141.50	1.20
	1644-1908	≤40	12	83.33	08.33	08.33	09.58	703.66	0.91
	2134-0030	≤40	14	14.28	85.72	0	90.73	9108.83	37.22
	0259-0521	≤40	7	0	85.71	14.29	87.30	6607.46	62.04
	0749-1034	>40	15	26.67	60	13.33	23.85	786.71	9.86
	1214-1631	>40	16	62.50	31.25	06.25	06.25	153.01	1.69
	1644-1908	>40	10	70.50	20.00	10.00	08.62	441.31	1.45
	2134-0030	>40	14	0	57.14	42.86	73.18	2452.57	58.72
	0259-0521	>40	17	0	52.94	47.06	44.84	793.87	33.83
26.2.87	0749-1034	>40	29	62.06	24.14	13.08	22.93	2136.98	2.88
	1214-1631	>40	21	66.67	28.57	04.76	05.93	194.02	1.12
	1644-1908	>40	19	73.69	15.78	05.27	10.19	883.99	0.86
	2134-0030	>40	43	44.18	46.51	09.31	12.09	500.53	3.11
	0259-0521	>40	28	53.57	21.43	25.00	22.04	1781.72	3.11

Of the August catches, 44% of the smaller, and 28% of the larger animals had empty stomachs. The maximum value of WFI was 308 for the smaller, and 205 for the larger animals (or 3.08% and 2.05% of the body weight respectively), occurring in each case in the interval between 2134 and 0043 h. Of the February catches 40.2% had empty stomachs and the maximum WFI was 165 (1.65% of body weight) in the 0745-1043 h interval. In all cases where WFI was estimated the digestive state corresponded to DSI=4.

From the above there is a clear indication of a diurnal feeding pattern in which the onset of vigorous feeding activity occurs at dusk and may extend into the hours of darkness. This is seen most plainly in the graphs, except in the case of the weight fullness data for the February catches where the trend is only weak.

Figure 3. Percentage of empty stomachs (▲), stomachs with DSI 1&2 (●), and 3&4 (x). (A) August specimens ML ≤ 40 mm. (B) August specimens ML > 40 mm. (C) February specimens (ML > 40 mm).

Statistical tests

Tables 4-7 show the results of non-parametric statistical tests made on the different sets of data to clarify the inference drawn above.

Table 4 shows the results of the Kruskal-Wallis test used to test for homogeneity in weight between fishing intervals for all specimens. Homogeneity was the null hypothesis. The results show that the specimens were homogeneous in weight, the required condition for valid comparison between the samples in different weight ranges.

Table 5 shows the results of the Kruskal-Wallis test applied to the WFI data as a test for feeding continuity. Feeding continuity was the null hypothesis. The results show discontinuous feeding in August but continuous feeding in February. Similar results were obtained using the SFI and DSI data.

Table 4. *Values and significance of the Kruskal-Wallis test for homogeneity in weight of all specimens*

Date	Size class (mm)	FD	H	P
7.8.86	≤40	3	0.36	>0.05*
	>40	4	6.88	>0.05*
26.2.87	>40	4	3.04	>0.05*

* not significant

Table 5. *Values and significance of the Kruskal-Wallis test for feeding continuity*

Date	Size class (mm)	FD	H	P
7.8.86	≤40	3	16.83	<0.001
	>40	4	43.49	<0.001
26.2.87	>40	4	5.14	>0.05*

* not significant

Table 6. *Results of χ^2 test for feeding continuity based on DSI*

Date	Size class (mm)	FD	P
7.8.86	≤40	1	<0.01
	>40	4	<0.001
26.2.87	>40	3	>0.05*

* not significant

Table 6 shows the result of a χ^2 test to 'n' independent samples using the digestive state index. For the test the data were grouped in the following way. Each size class of the August catches was divided into two groups comprising, (a) empty stomachs with DSI 1, and (b) DSI 2, 3 and 4. All five time intervals (Table 1) were used for specimens > 40 mm. Only two time intervals (day and night) were considered in the case of the small specimens ≤ 40 mm. The February catches were similarly grouped but the 2nd and 3rd time intervals were combined to give only four intervals.

Table 7 shows the results of the Mann-Whitney test used to test for significant difference of WFI between time intervals. For the small August specimens there was no significant difference between the two afternoon periods or between the two night

Table 7. Results of Mann-Whitney test for differences in WFI between time intervals

Date	Size class (mm)	Time intervals (GMT)	Time intervals (GMT)			
			1214-1631	1644-1908	2134-0030	0259-0521
7.8.86	≤40	0749-1034	0	0	0	0
		1214-1631		p>0.05*	p<0.01	p<0.01
		1644-1908			p<0.01	p<0.01
		2134-0030				p>0.05*
7.8.86	>40	0749-1034	p<0.01	p<0.05	p<0.001	p<0.01
		1214-1631		p>0.05*	p<0.001	p<0.001
		1644-1908			p<0.001	p<0.001
		2134-0030				p<0.05

* not significant

periods. All other combinations showed a significant difference. In the case of the large specimens, only between the two afternoon periods was there no significant difference. For the February catches there was no significant difference between any of the time intervals. The same result was obtained when this test was applied to the subjective fullness index. Table 8 is a list of the prey species identified in the stomach contents by date and size class.

Table 8. Food items identified from stomachs of *S. officinalis*

7.8.86	7.8.86	26.2.87
ML≤40	ML>40	ML>40
Amphipoda	<i>Palaemon serratus</i>	<i>Processa edulis</i>
<i>Processa</i> sp.	<i>Carcinus maenas</i>	<i>Crangon crangon</i>
<i>Palaemon</i> sp.	<i>Liocarcinus marmoreus</i>	<i>Palaemon</i> sp.
<i>Crangon crangon</i>	<i>Pomatoschistus pictus</i>	<i>Pisidia longicornis</i>
Portunidae	<i>Aphia minuta</i>	<i>Asthenognathus atlanticus</i>
<i>Pomatoschistus pictus</i>	<i>Lesuerigobius friesii</i>	<i>Liocarcinus</i> sp.
<i>Aphia minuta</i>	<i>Gobius paganellus</i>	<i>Polybius henslowi</i>
Sygnathidae	<i>Sygnathus typhle</i>	<i>Pomatoschistus pictus</i>
	<i>Symphodus</i> sp.	<i>Pomatoschistus minutus</i>
	Ammodytidae	<i>Lesuerigobius friesii</i>
	<i>Trachinus vipera</i>	<i>Aphia minuta</i>
	<i>Sepia officinalis</i>	Labriidae
		<i>Buglossidium luteum</i>
		<i>Sepia</i> sp.

DISCUSSION

From the literature it appears that there is no common feeding pattern among the cephalopods. Some species feed mainly during the daylight hours and others at sunset and during the night. The present results suggest that sunset is the principal exogenous stimulus to feeding in *Sepia officinalis*. This is in line with the observations of Denton & Gilpin-Brown (1961) who showed that this species increases its buoyancy and is more active at night than in the day. Other benthic species show a similar behaviour. Johnson (1942) found that foraging is crepuscular or nocturnal in *Octopus dofleini*, Bergström (1985) observed that *Sepietta oweniana* feeds mainly at night and Shears (1988), from

laboratory observations and from stomach contents of field specimens, found that *Euprymna scolopes* also feeds mainly at night.

There are some striking differences between the August and February results. We do not think that the different sampling methods used on the two occasions can have contributed to this because they affect only the size of the specimens captured. In the August results it is possible to examine the effect of size and it is apparent that there is no marked difference between the size groups. Spawning is another factor that might be expected to affect seasonal feeding activity but again we think that this was not a significant factor in the present investigation. Very few of the animals captured were close to spawning and, furthermore, from our own observations both in the field and with captive animals there is no reduction in feeding activity of *Sepia officinalis* before spawning. It is well known that in some inshore species the feeding rhythm is affected by the tides (cf. Wolff *et al.*, 1980; Lagardère, 1987) but in the present data there is no indication of twelve hour peaks that would indicate a tidal effect.

It is likely that the results reflect a difference of prey availability between the two sampling occasions. Both the season and the different bottom substrate types could have contributed to differences in prey availability but it is not possible to separate the effects of these two factors in the present data. The bottom temperature in February was 6°C below that in August and would certainly have caused a reduction in activity and metabolic rate (Wolf *et al.*, 1985) which may account for the greater number of empty stomachs and the smaller values for maximum WFI found in the winter catches. If the maximum WFI in the summer catches (3% and 2% for the smaller and larger size groups) represents the daily feeding ration, it is low compared with the 4-8% we have found in tank experiments at the same temperature with similar animals in the >40 mm size range. It is possible that very rapid digestion and absorption immediately after prey capture (Jobling, 1985) may lead to an underestimate of the daily food intake in the field samples.

The method of prey capture by *Sepia officinalis* is well known (Nixon, 1987). The species is a visual predator and Messenger (1977) found that attacks were not initiated in darkness or in dim red light. Nevertheless some of our specimens taken at 20 m depth in moonless and overcast conditions contained very recent prey in the stomach, which indicates that their night vision is very sensitive. Young (1963) described retinal dark adaptation in several cephalopod species including *Sepia officinalis*. In the case of *Todarodes pacificus* dark adaption is well documented (Suzuki *et al.*, 1985). It occurs at about 1 lux, approximately the light intensity at the sea surface under a full moon, and *T. pacificus* will attack jiggs at 0.5 lux. *Sepia officinalis* may also detect prey such as prawns (*Palaemon* spp.) by light emitted from their light organs (Guerra, 1985). Finally, detection by chemoreception (Wells, 1966; Chase & Wells, 1986) or by mechanoreception (Hanlon & Budelmann, 1986) cannot be ruled out.

There are differences to be seen in Table 8 in the prey species taken by the >40 mm samples in August and February. This is most likely due to the difference in bottom type at the two sampling sites. Some of the February prey species such as *Carcinus meaeas*, *Liocarcinus marmoreus*, *Syngnathus typhle* and *Trachinus vipera* do not occur in the deep muddy bottoms in the Ria de Vigo (Guerra *et al.*, 1986)

From the limited data set presented here there is a strong indication of a feeding pattern but more sampling would be needed to establish a true feeding pattern chronology (Jenkins & Green, 1977).

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