

Diel feeding chronology of the skate *Raja Agassizii* (Müller & Henle) (Pisces, Elasmobranchii) on the continental shelf off Ubatuba, Southeastern Brazil

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ABSTRACT. The diet and diel feeding pattern of the skate *Raja agassizii* were investigated through analysis of stomach contents. A total of 280 stomachs were collected by a series of hauls during a daily cycle in three periods, 8-10 January 1987, 22-24 July and 2-4 December 1988, from the inner continental shelf of the coastal ecosystem of Ubatuba, São Paulo State, Brazil (25°35'S; 45°00'W). According to the results of the stomach fullness and of the number of fresh prey, it is suggested that this species presents continuity in the feeding activity during a day. The stomach contents were mainly composed of crustaceans. Nematodes, polychaetes and fishes also occurred. No changes were observed in dietary composition between day and night.

KEY WORDS. Rajidae, diel feeding, food habits, marine demersal fish, southwestern Atlantic

Raja agassizii (MÜLLER & HENLE 1841), a small skate Rajidae, has been reported for the western Atlantic from the south of Brazil to Argentina (FIGUEIREDO 1977) and has been considered as endemic species to the Argentinian zoogeographic province. It is one of the most abundant demersal fishes of the inner Brazilian continental shelf off Ubatuba and is commonly found until to 50m depth (ROSSI-WONGTSCHOWSKI & PAES 1993). According to the study developed by COMPAGNO (1990), *R. agassizii* is a Rajobenthic ecomorphotype, whose components are versatile colonizers of bottom habitat.

Very little is known on the ecology of *R. agassizii*. SOARES *et al.* (1992) made a brief study of its diet. Along this, although much work has been done on the feeding habits of skate species worldwide (HACUNDA 1981; SMALE & COWLEY 1992; PEDERSEN 1995), little attention has been given to diel feeding, which is the subject of this study.

With the increasing interest in multispecies management, it is essential to understanding of the trophic relationships within an ecosystem, of which feeding habits are an integral component.

The present study is part of the multidisciplinary project "Utilização Racional de Ecossistemas Costeiros da Região Tropical Brasileira, estado de São Paulo" (Rational Utilization of Coastal Ecosystems of the Brazilian Tropical Region, State of São Paulo), the purpose of which was to obtain a thorough knowledge of the

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structure and the basic features explaining the functioning of the platform ecosystem off Ubatuba.

This paper presents the first study of diel feeding pattern of *R. agassizii*, a key demersal fish of the Ubatuba ecosystem. It also examines the diel changes in food composition in summer and winter.

MATERIAL AND METHODS

Study area

The study area is located in the platform of the coastal system off Ubatuba (22°30'S, 45°00'W) (Fig. 1). During summer, there is a two-layer stratification water mass; the upper water (Coastal Water) is warmer and less saline than the bottom water layer (South Atlantic Central Water). During winter, the study area is filled with Coastal Water (CASTRO FILHO *et al.* 1987). Muddy sediments were found at the southern part of the area while a mixed sand type dominated at the others parts (PIRES-VANIN 1993). The euphotic zone thickness is variable and not dependent on season; the bottom of the euphotic zone can reach 10m depth or the bottom of the system (AIDAR *et al.* 1993). The sun rises between 05-06h (summer days) and 06-07h (winter days), and sets between 18-19h (summer days) and 17-18h (winter days).

Sampling and laboratory procedure

Sampling was conducted during 24-hour periods between 8-10 January 1987 (summer 1987), and 48-hour periods between 22-24 July (winter 1988) and between 2-4 December 1988 (summer condition 1988) at fixed stations, on the coastal area of Ubatuba (Fig. 1). Hauls of 30 min were carried out at approximately three hours intervals to cover the entire diel cycle. Hauls were conducted using an otter trawl and cod end lines with 25-mm mesh. Water temperature and salinity were recorded in each six hours interval.

Total length (± 1 mm) and total body mass (± 0.1 g) of skate were measured. Stomachs were removed, preserved in 10% buffered formalin, and weighed (± 0.01 g). The degree of stomach fullness was estimated using a scale of five levels from 0, for an empty stomach, to 4, for a full stomach, having three intermediate values (almost empty: >0 to 25%; half full: >25 to 50%; almost full: >50 to 75%). Fish with signs of regurgitation were discarded.

Stomach contents were sorted, identified to taxonomic groups and weighed to the nearest 0.001g. Digestive state of each prey item was recorded according to SCRIMGEOUR & WINTERBOURN (1987) and SOARES & APELBAUM (1994) in three levels (1-fresh, without signs of digestion; 2-partially digested; and 3-digested, unidentifiable remains or indigestible parts only).

Data analysis

Three types of data were used to investigate diel feeding activity: the relative frequency of stomach fullness degree; the wet mass of the stomach content, as percentage of fish body mass (stomach fullness index as %BM); and the number of fresh prey in each fish, in terms of total prey and of most abundant ones (SCRIMGEOUR & WINTERBOURN 1987; PARRISH & MARGRAF 1990).

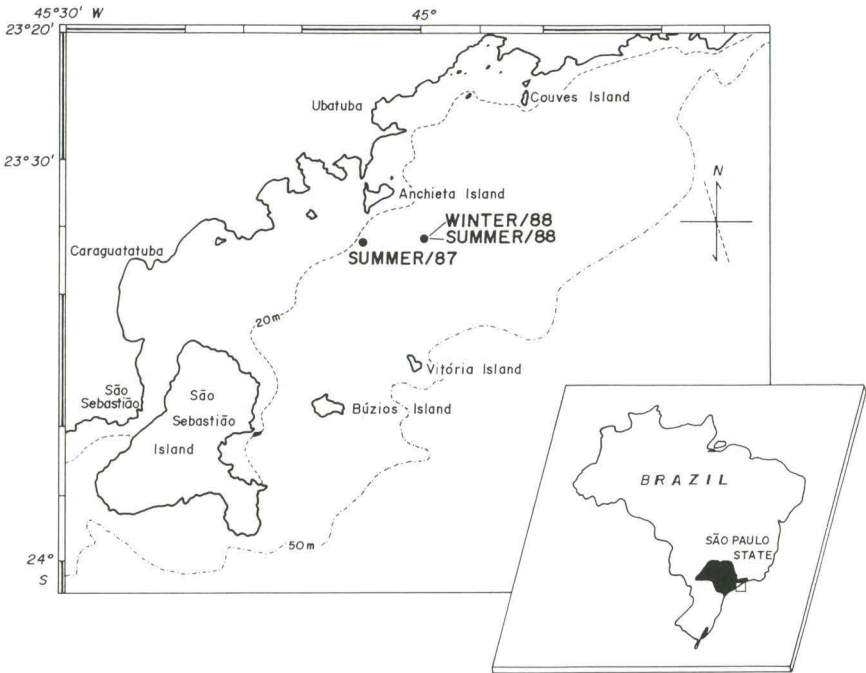


Fig. 1. Sampling sites on the Brazilian shelf off Ubatuba. Summer 1987: 8-10 January; summer condition 1988: 2-4 December and winter 1988: 22-24 July.

To test for discontinuity in feeding over time of day, the samples were firstly grouped into six periods of the daily cycle, dawn (05-06h in the summer and 06-07h in the winter), morning (06-12h in the summer and 07-12h in the winter), afternoon (12-18h in the summer and 12-17h in the winter), dusk (18-19h in the summer and 17-18h in the winter), evening (19-24h in the summer and 18-24h in the winter) and night (24-05h in the summer and 24-06h in the winter). They were then grouped to light and dark time for analyse of stomach fullness index and number of fresh prey.

As the distribution of %BM and of number of fresh prey usually failed the homoscedasticity tests, non-parametric Kruskal-Wallis and Mann-Whitney tests were used to test for significant difference (ZAR 1996).

Diet composition was analysed through frequency of occurrence (%O) and gravimetric index, based on wet mass (%M), of each prey item (BERG 1979; HYSLOP 1980). Dietary comparisons were made using the Schoener's index (LINTON *et al.* 1981): $PS = 1 - 0.5 (\sum P_{xi} - P_{yi})$, where, PS is the percent similarity, P_{xi} and P_{yi} are the proportions of food category *i* (prey category) in the diet for all pairs of samples. The index varies from 0 (no overlap) to 1 (complete overlap). Values equal to or greater than 0.6 were considered significant (HARMELIN-VIVIEN *et al.* 1989).

Table I contains sampling times, number and size ranges of *R. agassizii* during the three sampling periods.

Table I. Collection dates, number and size range of the skate, *Raja agassizii*, from the Brazilian shelf off Ubatuba during the three periods under analysis.

Summer 1987 (Depth - 30m)			Summer 1988 (Depth - 38m)			Winter 1988 (Depth - 38m)		
Date	Time of haul (Hour)	Sample size	Date	Time of haul (Hour)	Sample size	Date	Time of haul (Hour)	Sample size
08 January	05:32-06:02 ¹	18	02 December	14:00-14:30 ¹	8	22 July	15:13-15:43 ¹	10
	08:08-08:38 ¹	21		17:02-17:32 ¹	4		21:45-22:15	16
	11:20-11:50 ¹	22		21:21-21:51	14	00:10-00:40	16	
09 January	14:07-14:37 ¹	16	03 December	05:06-05:36 ¹	3	23 July	06:13-06:54 ¹	4
	17:05-17:35 ¹	10		08:10-08:40 ¹	2		10:46-11:16 ¹	9
	20:03-20:33	3		11:04-11:34 ¹	2		12:35-13:05 ¹	10
10 January	22:50-23:20	8	04 December	14:15-14:45 ¹	8	24 July	15:23-15:53 ¹	15
	02:03-02:28	4		17:20-17:50 ¹	2		18:40-19:10	5
				20:00-20:30	7		21:11-21:41	8
				23:00-23:30	4		03:02-03:32	5
				02:00-02:30	7		06:13-06:43 ¹	4
				08:00-08:30 ¹	3		09:13-09:43 ¹	7
							12:06-12:36 ¹	5
Length range (mm)	99.0-600.0		204.0-465.0		208.0-493.0			
Mean length (mm)	36.3±8.3		355.5±7.2		361.9±5.7			
Weight range (g)	4.1-800.3		25.4-479.5		33.7-663.6			
Mean weight (g)	275.7±17.3		222.6±13.3		247.8±12.5			

1) Daylight.

RESULTS

Diel feeding

According to the Kruskal Wallis and Mann-Whitney tests, there were no significant differences in stomach content mass (%BM) among periods of the day (Tab. II) and between daylight and night (Tab. II, Fig. 2) in the three seasonal periods analysed.

Table II. Results of Kruskal-Wallis and Mann-Whitney tests comparing stomach content mass (expressed as %BM) and number of fresh prey of the skate, *Raja agassizii*, from Brazilian shelf off Ubatuba.

Variables	Six periods of day			Daylight / night	
	N	χ^2	P value	W	P value
Summer 1987	102				
Stomach content (%BM)		6.13	0.294	698.5	0.993
Total fresh prey		2.49	0.928	855.5	0.259
Penaeidean fresh prey		4.88	0.674	No night occurrence	
Caridean fresh prey		5.60	0.586	787.0	0.457
Summer 1988	64				
Stomach content (%BM)		5.63	0.344	560.0	0.167
Total fresh prey		9.58	0.088	533.5	0.311
Penaeidean fresh prey		8.08	0.151	No night occurrence	
Caridean fresh prey		7.19	0.207	550.5	0.034 ¹
Winter 1988	114				
Stomach content (%BM)		2.52	0.773	1312.0	0.945
Total fresh prey		24.65	<0.001 ²	1758.5	0.589
Penaeidean fresh prey		9.39	0.094	1578.0	0.430
Caridean fresh prey		24.78	<0.001 ²	1794.5	0.450

1) P values < 0.05; (2) P values < 0.001.

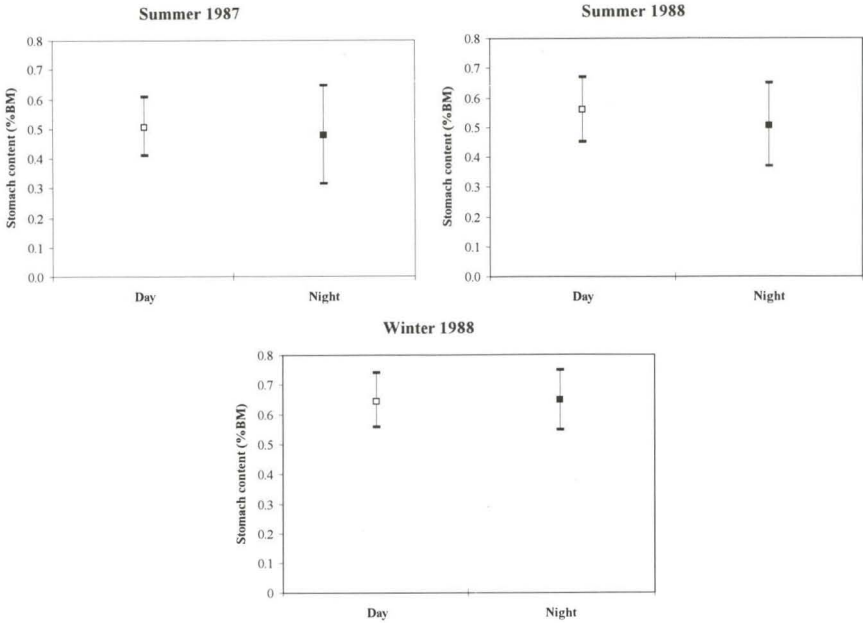


Fig. 2. Mean values of stomach content wet mass (as %body mass), with 95% confidence interval of the skate, *Raja agassizii*, collected during daylight and night in the three periods under analysis.

The stomachs of the skates collected during the daylight, as well as, during the night contained food in the three seasonal periods of the study (Fig. 3). Very low frequency of empty stomachs were registered at night, only during the summer of 1987. The majority of the stomachs were, at least, half full by day and by night, in the three seasonal periods.

In relation to the number of fresh prey, there was no significant difference in the total prey among six periods of a day and between daylight and night, during the summers of 1987 and 1988. Although low in number, fresh penaeidean shrimps were found only at daylight. The number of caridean shrimps collected during daylight was a little higher than that of the night during summer of 1988, but it is similar to the summer 1987 (Tab. II, Fig. 4). During the winter of 1988, although differences in the total and in the caridean shrimp fresh prey were observed among periods of day (highest number in the morning), no differences were observed between daylight and night (Tab. II, Fig. 4).

Dietary comparisons

Out of the 277 stomachs examined, 273 contained food and only seven (1.4%) were empty. The stomach contents of *R. agassizii* were mainly composed of crustaceans, nematodes, polychaetes, and teleostean fish. Crustaceans were clearly the most important food category by weight and frequency of occurrence and were represented by eight groups. Penaeidean, caridean and brachyuran were dominant groups (Tab. III).

Table III. Diet composition of the skate, *Raja agassizii* expressed by frequency of occurrence (O%) and percent mass (M%) in the daylight and night.

Food items	Summer 1987				Summer 1988				Winter 1988			
	Day N=87		Night N=15		Day N=32		Night N=29		Day N=64		Night N=50	
	O (%)	M (%)	O (%)	M (%)	O (%)	M (%)	O (%)	M (%)	O (%)	M (%)	O (%)	M (%)
Nematoda ¹	55.17	0.68	40.00	1.54	68.75	2.26	65.52	6.34	42.19	0.15	46.00	0.27
Polychaeta (Total) ¹	9.20	0.12	26.67	2.10	28.13	1.08	20.69	1.64	6.25	0.49	18.00	0.55
Polychaeta unidentified	9.20	0.12	26.67	2.10	28.13	1.08	20.69	1.64	6.25	0.49	18.00	0.55
Crustacea (Total)	90.80	89.94	100.00	88.69	100.00	91.22	93.10	88.78	98.44	97.33	100.00	98.52
Crustacea unidentified	9.20	7.28	13.33	0.15	9.00	6.39	3.45	0.30	96.72	90.33		99.12
Copepoda ¹	3.45	0.15	6.67	0.02	3.92	0.01			1.64	0.11		
Cirripedia ¹	1.15	*										
Stomatopoda ¹	17.24	0.60	6.67	0.07	9.38	0.64	24.14	1.66	21.88	0.15	2.00	0.13
Amphipoda ¹	3.45	0.01	6.67	0.02	40.63	1.49	27.59	0.60	90.63	69.36	6.00	0.11
Caridea (Total)	41.38	2.50	60.00	6.42	44.12	2.99	48.28	2.10	9.38	0.17	98.00	59.96
Caridea unidentified	9.20	0.29			3.13	0.04			76.56	68.69	20.00	0.81
Pasiphaeidae ¹	12.64	0.62	13.33	0.56	62.50	5.65	48.28	2.10	10.94	0.41	98.00	58.56
Processidae ¹	26.44	1.34	53.33	5.86							12.00	0.53
Alpheidae ¹	2.30	0.26			3.13	0.19			15.63	0.08	4.00	0.04
Ogyridae ¹	36.78	43.62	40.00	45.52	87.50	49.01	72.41	41.75	60.94	21.98	60.00	19.85
Penaeidea (Total)	9.20	1.29	6.67	0.64	12.50	1.32	10.34	0.95	32.81	4.05	18.00	1.82
Solenoceridae ¹	6.90	1.89	6.67	3.74	75.00	47.69	62.07	40.80	31.25	11.45	36.00	15.77
Sicyonidae unidentified ¹	8.05	8.47	26.67	24.13					10.94	6.47	6.00	0.22
<i>Sicyonia dorsalis</i> ¹	20.69	29.16	6.67	17.01							6.00	1.88
<i>Sicyonia typica</i> ¹	2.30	2.81									4.00	0.14
Shrimps unidentified	64.37	6.57	26.67	2.91	71.88	4.31	79.31	10.64	85.94	5.43	86.00	4.63
Brachyura (Total)	49.43	28.98	60.00	32.16	84.38	29.89	82.76	30.94	18.75	0.40	26.00	13.85
Brachyura unidentified	39.08	13.52	46.67	17.91	59.38	12.44	65.52	10.69	17.19	0.34	24.00	13.79
Portunidae ¹	11.49	5.75	13.33	1.18	15.63	4.18	31.03	19.27	22.95	9.69	2.00	0.06
Xanthidae ¹	1.15	0.04										
Majidae ¹	1.15	2.37			25.00	5.63	6.90	0.99	15.63	0.02		
Canceridae ¹	2.30	3.15	6.67	0.02	21.88	7.64	6.90	4.23	1.56	0.02		
Calappidae unidentified	5.75	4.04	6.67	12.92					1.56	0.04		
<i>Hepatus pudibundus</i>	1.15	0.11										
Parthenopidae ¹			6.67	0.13								
Leucosiidae ¹												
Anomura (Total)	10.34	0.96	40.00	1.44								
Albuneidae ¹	9.20	0.17	40.00	1.44								
Porcellanidae ¹	1.15	0.20										
Teleostei (Total)	27.59	9.27	53.33	7.67	15.63	5.44	31.03	3.25	4.69	2.04	12.00	0.65
Teleostei unidentified	26.44	7.72	53.33	7.67	15.63	5.44	31.03	3.25	4.69	2.04	12.00	0.65
<i>Porichthys porosissimus</i>	2.30	1.55										
Total ²	87.00	42.91	15.00	6.09	32.00	13.70	29.00	7.89	64.00	29.43	50.00	21.72
Percent Similarity (P.S.)					0.70	0.60			0.80	0.70		

(*) Values < 0.01%; (1) Prey items used for calculating P.S.; (2) Total are numbers of stomachs and prey wet mass (g).

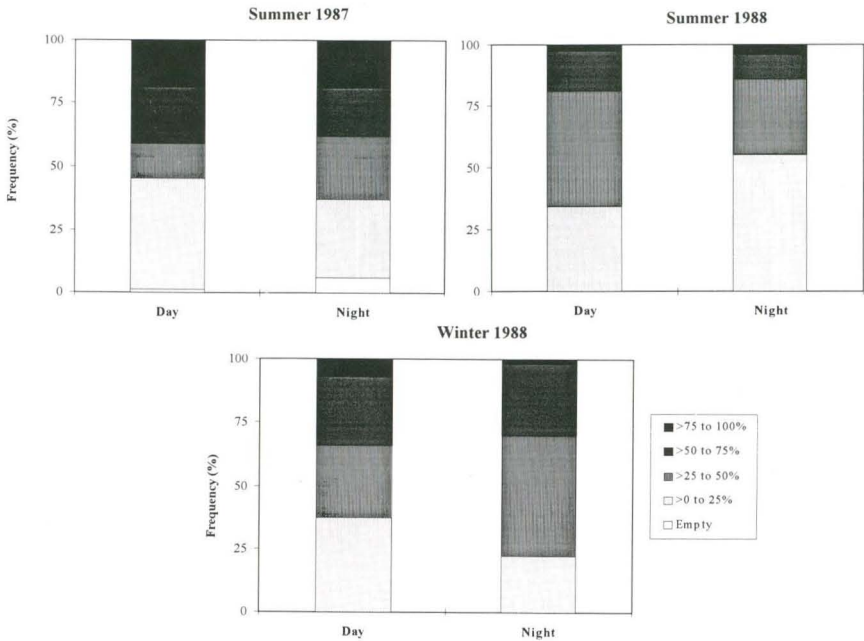


Fig. 3. Relative frequency of stomach fullness of the skate, *Raja agassizii*, collected during daylight and night in the three periods under analysis.

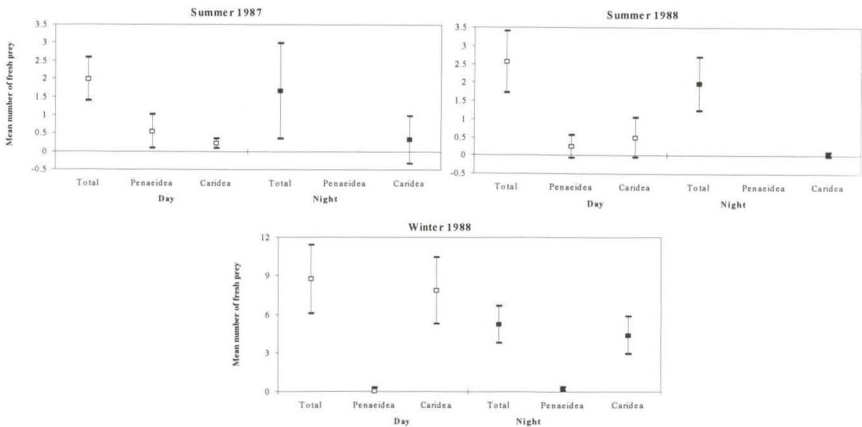


Fig. 4. Mean number of fresh prey and 95% confidence interval of the stomach content of the skate, *Raja agassizii*, collected during daylight and night in the three periods under analysis.

Diet composition was similar between daylight and night for both summers and winter, according to the percent of similarity analysis (Tab. III).

During the summers of 1987 and 1988, the main identified items were penaeidean shrimps and brachyuran crabs. On an occurrence basis, nematodes, caridean shrimps and teleostean fishes were also important. The main penaeidean

prey in the summer of 1987 was *Sicyona dorsalis* (Sicyonidae) and in the summer of 1988 was *Pleoticus mulleri* (Solenoceridae). Brachyuran crabs were represented by Portunidae in the summer of 1987 and by Portunidae, Majidae and Calappidae in the summer of 1988 (Tab. III).

During winter of 1988, stomach contents were comprised mainly of caridean and penaeidean shrimps. Nematode preys were important in terms of occurrence. *Leptocheila serratorbita* (Pasiphaeidae) was the main caridean prey and *Pleoticus mulleri* (Solenoceridae) the main penaeidean prey (Tab. III).

Hydrography

The bottom water mass in the summers of 1987 and 1988 was colder and more saline and in the winter of 1988 was warmer and less saline. During the summer, both the temperature and the salinity were constant along the day. During the winter, both the temperature and the salinity fluctuated along the day, but did not show a cycle (Fig. 5).

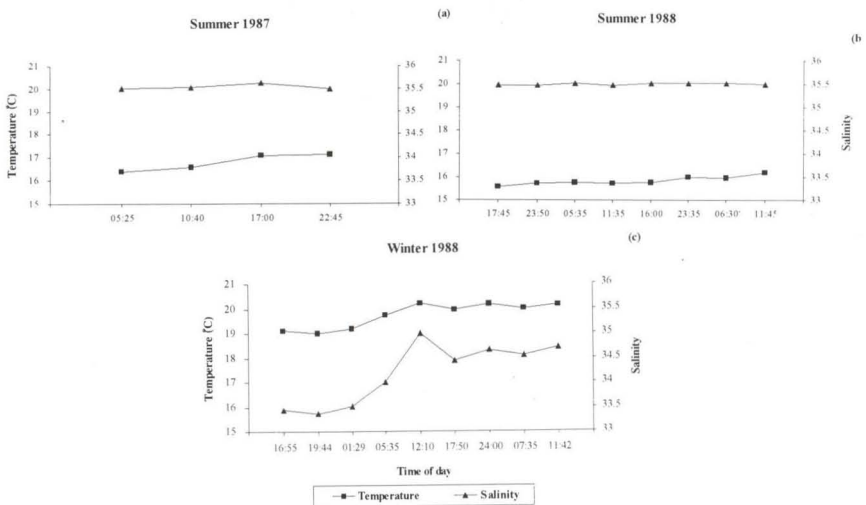


Fig. 5. Fluctuations of the bottom water temperature and salinity during a 24-hour period, in January 1987 (8-10), December 1988 (2-4) and July 1988 (22-24). Summer: sunrise (05-06h), sunset (18-19h); Winter: sunrise (06-07h), sunset (17-18h).

DISCUSSION

Raja agassizii showed no significant variation in feeding activity during 24-period of a day. Nevertheless, as JENKINS & GREEN (1977) argued, it is possible that major diel differences do exist in diel feeding, but not reflected by stomach content mass. They referred to fishes with low stomach evacuation rate that could regularly feed during specific periods, but still maintain a relatively full stomach.

That could be the case for the skate *R. agassizii*, because stomachs contained food by daylight, as well as, by night, and the proportion of empty stomachs found

was very low. Furthermore, it is known that complete gastric evacuation takes substantially longer for elamobranchs than for teleosts (MEDVED 1985; SCHURDAK & GRUBER 1989), although very few evacuation rates have been estimated for skate species (NELSON & ROSS 1995).

The stomach fullness indexes can lead to misinterpretation of daily periodicity in feeding. But the occurrence of fresh prey would provide a good measure of the time of day when fish feed, as has been noted by BOWMAN & BOWMAN (1980). However these results did not show feeding discontinuity in *R. agassizii*. The absence of fresh penaeidean shrimps at night can be considered a weak indication of temporal discontinuity during summer, although there existed no significant differences in the overall number of total fresh prey present in stomachs.

Continuity of feeding in demersal fish has been observed by some researchers, based on field data. Many species feed continuously throughout the day, as was shown for Atlantic cod (*Gadus morhua*) and small silver hake (*Merluccius bilinearis*) of the west North Atlantic (DURBIN *et al.* 1983), and for *Hyporhamphus melanochir* (ROBERTSON & KLUMMP 1983). Similar results were found for *Coe-lorhynchus fasciatus* from the coast of Namibia (MACPHERSON 1985) and for the hakes *Merluccius capensis* and *M. paradoxus* of South Africa's west coast (PAYNE *et al.* 1987). Three scorpionfishes were observed by HARMELIN-VIVIEN *et al.* (1989) to feed preferentially during night, although they were active during daylight.

Continuous feeding activity during day could be related to food availability as well as to dietary requirements as proposed by ROBERTSON & KLUMMP (1983). HARMELIN-VIVIEN *et al.* (1989) related this diel feeding pattern directly to the diurnal fluctuation in prey availability, which could be synchronized with diel dietary shift. DALGOV & YARAGINA (1990) observed daily feeding rhythms of the Barents sea cod and haddock only when they were feeding on stable concentrations of euphausiids.

Based on fresh prey, *R. agassizii* showed a weak tendency for diurnal feeding, which could be related to prey availability, but did not exhibit feeding periodicity in relation to light and dark periods of the day, both in summer and winter. This species did, however, exhibit seasonal changes in prey species consumed, which were probably related to seasonal food availability.

We propose that the feeding strategy exhibited by *R. agassizii* can be related to behaviour and to digestion rate. This skate feeds mainly on small benthic shrimps and crabs and also on tubicolous gammarids. We believe that, although these prey organisms show mainly nocturnal activity (PIRES-VANIN *et al.* 1995), *R. agassizii* can detect them by using their chemical sensory receptors either during day or night (ZAVALA-CAMIN 1996).

BLABER & BULMAN (1987) argued that epibenthic or benthopelagic feeders, which remain close to the bottom, might not exhibit a diel pattern related to day length because they are below the depth of light penetration. The authors studied the diel feeding chronology of 15 species of the upper continental slope of eastern Tasmania and only three of those species showed significant diel feeding pattern, which results are similar to those of the Mediterranean slope fish studied by MACPHERSON (1981).

This was unlikely to have occurred in this study. The skate *R. agassizii* is a versatile colonizer of bottom habitat (COMPAGNO 1990), and the studied specimens were sampled within or below the euphotic zone according to AIDAR *et al.* (1993), where the hydrographic conditions measured by temperature and salinity did not have a strong diel shift during a day cycle. So no synchronizer related to diel feeding activity was identified.

According to the diel feeding pattern studies by BOUJARD & LEATHERLAND (1992), *R. agassizii* can be classified as a diurnal and nocturnal feeder, showing constant feeding activity. Although there is strong evidence that feeding by *R. agassizii* may occur of any period, daylight or night, one must be aware that results of feeding activity based on field data, are, to some extent, circumstantial as already suggested by GORDOA & MACPHERSON (1991). Therefore, additional work is required in order to improve our knowledge of the diel feeding in the skate *R. agassizii*.

CONCLUSIONS

The results of this study show absence of feeding discontinuity with the time of day in the skate *Raja agassizii*. Nevertheless because diel feeding activity is a process resulting from interactions among biotic and abiotic factors, additional study is suggested.

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REFERENCES

- AIDAR, E.; S.A. GAETA; S.M.F. GIANESSELLA-GALVÃO; M.B.B. KUTNER & C. TEIXEIRA. 1993. Ecosistema costeiro subtropical: nutrientes dissolvidos, fitoplâncton e clorofila-*a* e suas relações com as condições oceanográficas na região de Ubatuba, SP (Coastal subtropical ecosystem: dissolved nutrients, phytoplankton and chlorophyll-*a* relationships to oceanographical conditions in Ubatuba region, SP, Brazil). **Publicação esp. Inst. oceanogr.**, São Paulo, (10): 9-43.
- BERG, J. 1979. Discussion of methods of investigating the food of fishes, with reference to a preliminary study of prey of *Gobiomusculus flavescens* (Gobiidae). **Mar. Biol.** **50**: 263-273.
- BLABER, S.J.M. & C.M. BULMAN. 1987. Diets of fishes of upper continental slope of eastern Tasmania: content, calorific values, dietary overlap and trophic relationships. **Mar. Biol.** **95**: 345-356
- BOUJARD, T. & J.F. LEATHERLAND. 1992. Circadian rhythms and feeding time in fishes. **Env. Biol. Fish.** **35**: 109-131.

- BOWMAN, R.E. & E.W. BOWMAN. 1980. Diurnal variation in the feeding intensity and catchability of the Silver hake (*Merluccius bilinearis*). **Can. Jour. Fish. Aquat. Sci.** **37**: 1565-1572.
- CASTRO FILHO, B.M.; L.B. DE MIRANDA & S.Y. MIYAO. 1987. Condições oceanográficas na plataforma continental ao largo de Ubatuba: variações sazonais e em média escala (Hydrographic conditions on the continental shelf off Ubatuba: seasonal and meso-scale variability). **Bolm Inst. oceanogr.**, São Paulo, **35**: 135-151.
- COMPAGNO, L.J.V. 1990. Alternative life-history styles of cartilaginous fishes in time and space. **Env. Biol. Fish.** **28**: 33-75.
- DALGOV, A.V. & N.A. YARAGINA. 1990. **Daily feeding rhythms and food intake of Barents Sea cod and haddock in summer of 1989**. Netherlands, ICES, C.M. 1990/G.6., 22p.
- DURBIN, E.G.; A.G. DURBIN; R.W. LANGTON & R.E. BOWMAN. 1983. Stomach contents of silver hake, *Merluccius bilinearis* and Atlantic cod, *Gadus morhua*, and estimation of their daily ration. **Fish. Bull. U.S.** **81**: 437-454.
- FIGUEIREDO, J.L. 1977. **Manual de peixes marinhos do sudeste do Brasil. I. Introdução. Cações, raias e quimeras (Manual of marine fish from southeastern Brazil)**. São Paulo, Universidade de São Paulo, Museu de Zoologia, 104p.
- GORDOA, A. & E. MACPHERSON. 1991. Diurnal variation in the feeding activity and catch rate of cape hake (*Merluccius capensis* and *M. paradoxus*) off Namibia. **Fish. Res.** **12**: 299-305.
- HACUNDA, J.S. 1981. Trophic relationships among demersal fishes in a coastal area of the Gulf of Maine. **Fish. Bull.** **79**: 775-788.
- HARMELIN-VIVIEN, M.L.; R.A. KAIM-MALKA; M. LEDOYER & S.S. JACOB-ABRAHAM. 1989. Food partitioning among scorpaenid fishes in the Mediterranean seagrass beds. **Jour. Fish Biol.**, **34**: 715-734.
- HYSLOP, E.J. 1980. Stomach content analysis: a review of methods and their application. **Jour. Fish Biol.** **17**: 411-430.
- JENKINS, B.W. & J.M. GREEN. 1977. A critique of field methodology for determining fish feeding periodicity. **Env. Biol. Fish.** **1**: 209-214.
- LINTON, L.R.; R.W. DAVIES & F.J. WRONA. 1981. Resource utilization indices: an assesment. **Jour. Anim. Ecol.** **50**: 283-292.
- MACPHERSON, E. 1981. Resource partitioning in a Mediterranean demersal community. **Mar. Ecol. Prog. Ser.** **4**: 193-193.
- . 1985. Daily ration and feeding periodicity of some fishes off coast of Namibia. **Mar. Ecol. Prog. Ser.** **26**: 253-260.
- MEDVED, R.J. 1985. Gastric evacuation in the sandbar shark, *Carcharinus plumbeus*. **Jour. Fish Biol.** **26**: 238-253.
- NELSON, G.A. & M.R. ROSS. 1995. Gastric evacuation in the little skate. **Jour. Fish Biol.** **46**: 977-986.
- PARRISH, D.L. & F.J. MARGRAF. 1990. Gastric evacuation rates of white perch, *Morone americana*, determined from laboratory and field data. **Env. Biol. Fish.** **29**: 155-158.
- PAYNE, A.I.L.; B. ROSE & R.W. LESLIE. 1987. Feeding of hake and a first attempt

- at determining their trophic role in the south African west coast marine environment. *In*: A.I.L. PAYNE, J.A. GULLAND & K.H. BRINK (Ed.). The Benguela and Comparable Ecosystems. **S. Afr. Jour. mar. Sci.** **5**: 471-501.
- PEDERSEN, S.A. 1995. Feedings habits of starry ray (*Raja radiata*) in West Greenland waters. **ICES Jour. mar. Sci.** **52**: 43-53.
- PIRES-VANIN, A.M.S. 1993. A macrofauna bêntica da plataforma continental ao largo de Ubatuba, São Paulo, Brasil. **Publicação esp. Inst. oceanogr.**, São Paulo, (10): 137-158.
- PIRES-VANIN, A.M.S.; J.P.S. JORGE & S. SARTOR. 1995. Variação diária e sazonal da fauna bêntica de plataforma continental no litoral norte do estado de São Paulo (The diel variation of the benthic fauna from São Paulo State northern coast, Brazil.). **Publicação esp. Inst. oceanogr.**, São Paulo, (11): 107-114.
- ROBERTSON, A.I. & D.W. KLUMMP. 1983. Feeding habits of the southern Australian garfish *Hyporhamphus melanochir*: a diurnal herbivory and a nocturnal carnivore. **Mar. Ecol. Prog. Ser.** **10**: 197-201.
- ROSSI-WONGTSCHOWSKI, C.L.D. & E.T. PAES. 1993. Padrões espaciais e temporais da comunidade de peixes demersais do litoral norte do Estado de São Paulo (Demersal fish community at Ubatuba region, southeastern Atlantic, Brazil: spatial and temporal patterns). **Publicação esp. Inst. oceanogr.**, São Paulo, (10): 169-188.
- SCHURDAK, M.E. & S.H. GRUBER. 1989. Gastric evacuation of the lemon shark *Negaprion brevirostris* (Poey) under controlled conditions. **Exp. Biol.** **48**: 77-82.
- SCRIMGEUR, G.J. & M.J. WINTERBOURN. 1987. Diet, food resource partitioning and feeding periodicity of two riffle-dwelling fish species in a New Zealand river. **Jour. Fish Biol.** **31**: 309-324.
- SMALE, M.J. & P.D. COWLEY. 1992. The feeding ecology of skates (Batoidea: Rajidae) off the Cape South Coast, South Africa. *In*: A.I.L. PAYNE; K.H. BRINK; K.H. MANN; R. HILBORN (Ed.). Benguela Trophic Functioning. **S. Afr. Jour. mar. Sci.** **12**: 823-834.
- SOARES, L.S.H. & R. APELBAUM. 1994. Atividade alimentar diária da cabrinha *Prionotus punctatus* (Teleostei: Triglidae) do litoral de Ubatuba, Brasil (Diel feeding of searobin *Prionotus punctatus* from Brazilian southeastern coast.). **Bolm Inst. oceanogr.**, São Paulo, **42**: 85-98.
- SOARES, L.S.H.; C.L.D.B. ROSSI-WONGTSCHOWSKI; L.M.C. ALVARES; E.Y. MUTO & M.A. GASALLA. 1992. Grupos tróficos de peixes demersais da plataforma continental interna de Ubatuba, Brasil. I. Chondrichthyes (Trophic groups of demersal fish community from the continental shelf, Ubatuba, Brazil.). **Bolm Inst. oceanogr.**, São Paulo, **40**: 79-85.
- ZAR, J.H. 1996. **Biostatistical analysis**. New Jersey, Prentice-Hall, 622p.
- ZAVALA-CAMIN, L.A. 1996. **Introdução aos estudos sobre alimentação natural em peixes**. Maringá, Eduem, 129p.