FEEDING HABITS OF LOLIGO SANPAULENSIS
BRAKONIECKI, 1984 (CEPHALOPODA, LOLIGINIDAE)
IN SOUTHERN BRAZIL

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INTRODUCTION

Loligo sanpaulensis (= L. brasiiliensis) Brakoniecki, 1984 is distributed in the
Western South Atlantic along the coasts of Brazil, Uruguay and Argentina, approxi-
mately between latitudes 20°S and 42°S (Roper et al., 1984; Haimovicci & Perez,
1991a). The species is common from Buenos Aires Province in Argentina to Rio de
It is the most abundant coastal squid in southern Brazil, whereas Loligo plei (=
Doryteuthis plei) Blainville, 1823 occurs only in the warm season and on the outer shelf
(Juanicó, 1979; Haimovicci & Andriguettio,1986; Haimovicci & Perez, 1991b). The
fishery potential of both species along southern and southeastern Brazil is poorly known
but they have been increasingly exploited by artisanal fishermen as well as commercial
shrimpers. Landings for both species are reported together and attained 2,193 tons in
1986 (Costa & Haimovicci, 1990). The standing stock of L. sanpaulensis between
30°40’S and 34°20’S was estimated in 3,600 tons (+/- 44 %) in the spring of 1983
(Andriguettio & Haimovicci, 1991). Santos and Haimovicci (1997) studied predation on
L. sanpaulensis and found the species in the stomach contents of the La Plata dolphin
Pontoporia blainvillei, the penguin Spheniscus magellanicus, the fur seals Arcto-
cephalus spp, two species of squid and 24 fishes including demersal-pelagic and benthic

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ambush feeding species, and concluded that this squid occupy a intermediate level in
the shelf food webs of southern Brazil.

Few authors have studied the diet and feeding of *Loligo sanpaulensis*. Juanicó
(1979) studied the species distribution, population structure, reproductive cycle and
feeding from Rio de Janeiro to Mar del Plata. Costa (1994) studied food relations off
Cabo Frio, Rio de Janeiro (23°S).

In earlier papers, abundance, distribution, size and sex structures, and the repro-
ductive cycle of *Loligo sanpaulensis* were reported, with data from eight seasonal
groundfish cruises on the shelf and upper slope off southern Brazil (Andriguetto &
Haimovici, 1991, 1996). In this paper, data on stomach contents from the same surveys
are analyzed. Feeding habits and changes in food and feeding related to size, sex, season
and fishing grounds off southern Brazil are described and discussed.

MATERIALS AND METHODS

Samples of *L. sanpaulensis* were obtained at depths ranging from 10 to 220 m in
eight groundfish cruises of the RV Atlântico Sul, four on the inner shelf and four on
the outer shelf and upper slope off Rio Grande do Sul state between latitudes 28°35'S
and 34°S (Figure 1). Depth, latitude and bottom temperature ranges for all surveys are
given in Table 1. Additional shelf samples were taken from former cruises in January
1981 (summer) and April 1981 (fall).

Areas surveyed by the R/V Atlântico Sul on the continental shelf and upper slope off Rio Grande do Sul
State, southern Brazil, from 1981 to 1987. Latitudinal limits are approximate.
Table 1. Summary data of the cruises in which data on feeding of *Loligo sanpauleensis* were collected (frequency of occurrence, % of tows with *L. Sanpauleensis*: ML, dorsal mantle length; (*). Bottom temperature range between 100 and 200 m. from Haimovici and Perez, 1991b).

<table>
<thead>
<tr>
<th>Cruise period</th>
<th>Latitude range (south)</th>
<th>Depth range (m)</th>
<th>Bottom temp. range (°C)</th>
<th>Number of tows and frequency of occurrence</th>
<th>Mantle length (mm) minimum, mean and maximum</th>
</tr>
</thead>
<tbody>
<tr>
<td>14 to 22/01/82</td>
<td>30°46' - 34°14'</td>
<td>12-119</td>
<td>12.8 - 22.9</td>
<td>42</td>
<td>20 58.4 160</td>
</tr>
<tr>
<td>16 to 26/04/83</td>
<td>30°51' - 34°18'</td>
<td>13-122</td>
<td>15.5 - 22.6</td>
<td>41</td>
<td>20 52.5 110</td>
</tr>
<tr>
<td>09 to 30/08/83</td>
<td>30°54' - 34°19'</td>
<td>12-160</td>
<td>11.3 - 17.8</td>
<td>54</td>
<td>10 76.2 190</td>
</tr>
<tr>
<td>08 to 19/11/83</td>
<td>30°46' - 33°36'</td>
<td>10-100</td>
<td>12.6 - 20.2</td>
<td>34</td>
<td>20 80.5 170</td>
</tr>
<tr>
<td>19/07 to 02/08/86</td>
<td>31°58' - 34°33'</td>
<td>130-504</td>
<td>14.0 - 16.0 *</td>
<td>17</td>
<td>20 50.1 90</td>
</tr>
<tr>
<td>06 to 15/09/86</td>
<td>28°35' - 31°11'</td>
<td>128-510</td>
<td>14.5 - 17.3 *</td>
<td>19</td>
<td>30 47.3 70</td>
</tr>
<tr>
<td>14 to 21/03/87</td>
<td>30°47' - 34°31'</td>
<td>128-498</td>
<td>14.7 - 17.5 *</td>
<td>18</td>
<td>20 45.4 80</td>
</tr>
<tr>
<td>14 to 19/05/87</td>
<td>28°53' - 31°15'</td>
<td>140-575</td>
<td>15.0 - 19.0 *</td>
<td>12</td>
<td>20 33.0 40</td>
</tr>
</tbody>
</table>
Samples were collected with bottom tows in tows 30 to 60 minutes long at a speed of three knots, both on the slope and on the shelf. All tows were carried between dawn and dusk. Bottom and surface temperatures were recorded after each trawl. A total of 2,340 specimens from all cruises and representative of different fishing depths and latitudes were fixed in 10% buffered formalin sea water and transferred into 70% ethanol after no less than 24 hours. In the home laboratory, the dorsal mantle length (ML) was measured in millimeters, and sex, maturity stage, and stomach and digestive caecum fullness (empty, partially full, full) were also recorded. Total weight and stomach contents were recorded in at least ten individuals per 10-mm mantle length (ML) class in each sample.

Stomach contents were analyzed under a binocular microscope with magnifications up to 30X. Food items were recognized only as fish, crustaceans or squid. Further detail was not possible in most cases because contents were highly fragmented by the beak while identifiable hard parts were uncommon. Percentages of occurrence of prey types were compared by season, sex, dorsal mantle length, and location. Feeding activity was inferred by comparing the proportion of stomachs and caeca with or without contents. Significance of differences was tested in all comparisons by chi-square tests and contingency tables, always at a significance level of 5%.

RESULTS

Stomach contents

Contents were examined for 624 specimens on the inner shelf and 122 from the outer shelf (Table 2). Most stomachs had only one kind of food, although 48 stomachs of shelf animals presented a second category, mostly sand and fish remains. Sand does not seem representative of natural feeding but it is consistent with feeding in the cod-end of a bottom trawl. Fish otoliths were conspicuously rare, suggesting that such items were not adequately preserved. Vertebrae and vertebral column sections were not uncommon. Two females with ML of 78 mm presented respectively two and one section of vertebral column, averaging 25 mm in length. Up to seven crustacean eyes and ten eyeballs were found in the same stomach. Suckers, and squid arms and tentacles were common, sometimes fairly undigested, suggesting they could have been ingested during capture. Typical loliginid beaks and chitinous sucker rings gave evidence of cannibalism as Loligo plei, the only other congeneric species in the area, was not caught in most surveys.

Diets differed between sexes, season and time of day, but not between sizes. Preference for fish was higher among squid females. Relative frequencies of food types in stomachs of females were 69% fish, 24% crustaceans and 7% squid, while figures for males were 54%, 31% and 15%, respectively. Fish was the most frequent item throughout the year for all mantle lengths, but squid and crustaceans increased signifi-

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cantly in summer and fall (Figure 2). Squid remains were found in 40% of the stomach contents from the summer cruise of 1981, although that could be an artifact due to the small number of samples on that cruise. In spring, only animals caught deeper than 60 m contained squid and crustaceans. Also, crustaceans were more frequent on the northern shelf in spring and winter. Proportions of food items changed also during the day, crustaceans decreasing and cannibalism increasing (Figure 3).

![Graph showing stomach fullness and food items by season](image)

**Fig. 2**

Proportions (%) of stomach fullness (upper) and food items (lower) in the stomachs of *Loligo sanpaulensis* per season on the inner shelf off southern Brazil.

The large proportion of stomachs with unidentified contents in slope samples prevented similar comparisons. More than 85% of all stomachs examined showed whitish, soft, amorphous material as the only item. Nevertheless, crustaceans were evidently absent.

**Feeding activity**

Stomach fullness was determined for 1,254 animals on the shelf and 328 on the slope. In total, 28.7% were empty. Proportions of empty stomachs and caeca on the shelf were significantly higher in fall (Figure 2). An analysis of frequencies by classes of bottom temperatures showed higher frequency of full caeca and stomachs in spring...
and summer, suggesting more intense feeding activity in those seasons. Feeding activity on the slope seems to be more intense than on the shelf, but no evidence was found for seasonal variations (Table 2). The proportion of full stomachs was significantly higher on the southern part of the shelf, specially in winter and spring (Figure 4).

Fig. 3
Relative frequencies (%) of food items in the stomachs of Loligo sanpaulensis per period of the day on the inner shelf off southern Brazil. Periods are defined by starting times of tows, as follows: I, first hour after dawn; II, second hour after dawn; III, full day; IV, two hours before sunset.

Fig. 4
Relative frequencies (%) of full and partially full stomachs of Loligo sanpaulensis by latitude zone and season on the inner shelf off southern Brazil.
Proportion of full stomachs was higher for females and for larger specimens. Mature animals, regardless of size, also had stomachs more frequently full. Frequency of occurrence of empty caeca was high for mature females, for which the developed reproductive system seems to leave no room for the caecum (Table 3, Figure 5). Feeding activity also changed during the day, being more intense in full day and late afternoon (Figure 6).

Table 2 - Analysis of feeding habits of *Loligo sanpaulensis* in southern Brazil. Number of individuals examined for feeding habits, proportion of specimens with stomach contents and proportion of identifiable food items.

<table>
<thead>
<tr>
<th>Specimens examined for digestive fulness</th>
<th>Inner shelf</th>
<th>Upper shelf and slope</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1254</td>
<td>328</td>
</tr>
<tr>
<td>Specimens with food in the stomach</td>
<td>837 (67%)</td>
<td>291 (89%)</td>
</tr>
<tr>
<td>Specimens examined for prey type</td>
<td>624</td>
<td>122</td>
</tr>
<tr>
<td>Specimens with identifiable food items</td>
<td>287 (46%)</td>
<td>17 (14%)</td>
</tr>
</tbody>
</table>

Table 3 - Relative frequencies (%) of stomach and caecum fullness by stage of sexual maturity of *Loligo sanpaulensis* on the inner shelf off southern Brazil (n=sample size; NA=not applicable; definitions of stages of maturity according to Andriguetto and Haimovici, 1997).

<table>
<thead>
<tr>
<th>STAGE OF SEXUAL MATURITY</th>
<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Stomach fullness</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Males (n=607)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Empty</td>
<td>46</td>
<td>45</td>
<td>26</td>
<td>26</td>
</tr>
<tr>
<td>Partially full</td>
<td>43</td>
<td>40</td>
<td>54</td>
<td>61</td>
</tr>
<tr>
<td>Full</td>
<td>11</td>
<td>15</td>
<td>20</td>
<td>13</td>
</tr>
<tr>
<td>Females (n=647)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Empty</td>
<td>49</td>
<td>23</td>
<td>15</td>
<td>NA</td>
</tr>
<tr>
<td>Partially full</td>
<td>42</td>
<td>56</td>
<td>60</td>
<td>NA</td>
</tr>
<tr>
<td>Full</td>
<td>9</td>
<td>21</td>
<td>25</td>
<td>NA</td>
</tr>
<tr>
<td><strong>Caecum fullness</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Males (n=645)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Empty</td>
<td>24</td>
<td>37</td>
<td>18</td>
<td>33</td>
</tr>
<tr>
<td>Partially full</td>
<td>48</td>
<td>46</td>
<td>46</td>
<td>33</td>
</tr>
<tr>
<td>Full</td>
<td>28</td>
<td>17</td>
<td>36</td>
<td>33</td>
</tr>
<tr>
<td>Females (n=647)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Empty</td>
<td>26</td>
<td>27</td>
<td>71</td>
<td>NA</td>
</tr>
</tbody>
</table>
DISCUSSION

The diet of *Loligo sanpaulensis* did not differ from what is known for other loliginid species (Bidder, 1966; Nixon, 1987; Amaratunga, 1983). No evidence was found in stomach contents for groups other than crustaceans, fishes and squids, although many authors also mention items such as polychaete worms, gastropods and chaetognaths (Martins, 1982; Loukashkin, 1975; Karpov & Cailliet, 1978, 1979). However, Whitaker's description of chaetognath remains adjusts to the material found in the stomachs of slope animals in our study (Whitaker, 1978).
Loiliginid diets are known to change with season, geographic location and size, (Vovk, 1974; Macy, 1982; Lipinski, 1987; Amaratunga, 1983). In this study, differences were marked between seasons, but no differences related to ML in the frequency of occurrence of fish were detected. That is in contrast to the findings of the above mentioned authors as muscular squids usually increase the proportion of fish and cephalopods in their diet during growth as increased attack speed and grabbing capacity allow them to catch fast moving prey (Haefner, 1964; Packard, 1972). This change was not observed from the frequency of occurrence of fish in the diet of L. sanpaaulensis, as fish was the main food item in the stomach contents even for small squid. However, a feeding shift in prey items may have occurred at a smaller size than sampled in this study (Vecchione, 1987). On the other hand, almost all studies mentioned above grouped samples from different seasons or locations. This could have introduced some bias in their conclusions regarding diet changes related to length. One exception is the work of Maurer and Bowman (1985) who observed variations in the diet of L. pealei similar to those observed here for L. sanpaaulensis, with crustaceans predominating in spring, and fish in summer and fall. Therefore, despite a marked preference for fish, the diet of L. sanpaaulensis seemed to be more a reflection of seasonal and spatial variations in prey abundance and availability.
Although squid stomach content was not identified at species level, data on fish distributions and assemblages in southern Brazil match the results presented here. From our data, the abundance of fishes with total length smaller than the mantle length of _Loligo sanpaulensis_ would be expected to be low at intermediate depths on the shelf in summer and fall, and higher in winter. In fact, the anchovy _Engraulis anchoita_, which is the most abundant species in the pelagic nekton off Rio Grande do Sul, is found in summer only at depths less than 30 m (Lima & Castello, 1995), therefore becoming less available where the squid is more abundant. Also, in winter and spring _Loligo sanpaulensis_ forms a consistent pelagic association with the cutlassfish _Trichiurus lepturus_, juveniles of the weakfish _Cynoscion striatus_, the hake _Merluccius hubbsi_, and two small neritic fishes, the anchovy _E. anchoita_ and the jack mackerel _Trachurus lathami_ (Mello et al., 1992). Except for the hake, those fishes feed mostly on pelagic crustaceans (Schwingel & Castello, 1995).

There are other evidences for a flexible feeding strategy in _L. sanpaulensis_, such as the absence of crustaceans in the stomachs of slope animals as well as other location-related differences, and also the differences of food items between day periods. Animals resorted to cannibalism just before sunset, when the frequency of empty stomachs increased sharply. Feeding activity was higher from mid-morning to late afternoon, when fish was the major food item. Cephalopods are known to be opportunistic predators, easily changing prey types, including members of their own species (Mangold, 1983; Boucher-Rodoni et al., 1987). Cannibalism can be an alternative to the reduction of metabolic rate when there is no other food available (O’Dor & Wells, 1987). The more pronounced cannibalism in the cruise of April 1981 could therefore be a response to a decrease in the availability of prey, even as the density of squid decreases (Andriguetto & Haimovici, 1991), as pelagic production in summer and fall was found to be lower than in other seasons (Castello et al., 1997).

To compensate for the simplicity of the analysis made in this study, observations on other species were used as independent checks. Some fish species exhibit similar feeding patterns in the same area, corroborating changes in prey availability. On the basis of samples from the same cruises, Teixeira and Haimovici (1989) concluded that the searobin _Prionotus nudigula_ takes more fish in winter and turns to Euphausiacea in other seasons. Also, at the depths where _L. sanpaulensis_ concentrated, the relative importance of Euphausiacea as a food item for _P. nudigula_ was extremely high. Another useful comparison can be made with the diet of _Trichiurus lepturus_ collected during the same survey. That species can be a good indicator of prey availability since it is co-occurring with _L. sanpaulensis_, feeds on a wide range of prey types, and modal prey size in stomach contents is 25 mm even for larger specimens (Martins, 1992), which is quite accessible to the squid. Where distributions with the squid overlapped, major food items for both juvenile and adult _T. lepturus_ were “filter-feeding macrozooplankton” (Euphausiacea) and “omnivorous micronekton” (Engraulidae, _E. anchoita_), suggesting that those preys were available in large amounts.
Few authors report differences between sexes, with usually higher cannibalism in males on spawning grounds (Karpov & Cailliet, 1979; Macy, 1982). In *Loligo sanpaulensis*, the preference for fish observed in mature females was coupled with higher frequencies of full stomachs and empty caeca obliterated by the reproductive organs. Fields (1965) points out that females of *L. opalescens* on spawning grounds almost always have empty stomachs and caeca, the latter being contracted. According to Boucher-Rodoni et al. (1987), the obliteration of the caecum by the mature reproductive system can demand adjustments in the digestive physiology, such as an increase in the activity of the digestive gland and of the appendages of the digestive duct, to compensate for the diminished functions of the cecum. Hirtle et al. (1981) observed food conversion rates higher for fish than for crustaceans in *Illex illecebrosus*. If that holds true for loliginids, a higher preference for fish among mature females in *L. sanpaulensis* could also be an adjustment to functional loss of the caecum.

The proportion of *Loligo sanpaulensis* individuals with food in the stomach (67% on the inner shelf, 89% on the outer shelf) can be considered high when compared with values reported in the literature, which range roughly between 30% and 60%. For example, Macy (1982) reports values of 46.8% inshore and 45.4% offshore for *Loligo pealei*; from the review by Nixon (1987) the following values can be calculated: 33% for *Loligo opalescens*, 49% for *Loligo forbesi*, 60% for *Lolliguncula panamensis*, and 77% for *Sepioteuthis arcticus*. In this study, proportions were even higher for large, mature individuals. The survey area, including the upper slope, could therefore be an important feeding ground, specially prior to spawning, extending to the Argentinian shelf (Vigliano, 1985; Andriguetto & Haimovicci, 1996). From the distribution patterns for the species we have described (Andriguetto & Haimovicci, 1991), one observes that, throughout the year, highest frequencies of full stomachs coincided spatially with the highest population densities. The stock concentration south of the western boundary of the Subtropical Convergence, where productivity is greater, specially in winter and spring, suggests then that food availability is a major factor limiting distribution off Southern Brazil. In particular, our observations on reproduction (Andriguetto & Haimovicci, 1996) suggest that summer spawners may find adequate feeding grounds in winter in the outer shelf while winter spawners may recruit in part to the southern range of the species in northern Argentina in spring, feeding along the cold, rich waters of the Malvinas Current, close to the Subtropical Convergence.

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ABSTRACT

*Loiglo sanpaulensis* is the most abundant coastal squid in southern Brazil. This paper analyzes its feeding habits on the continental shelf and upper slope off Rio Grande do Sul state. Samples were taken during groundfish cruises from 1981 to 1987, covering an area from 28°35'S to 34°40'S at depths from 10 to 587 m. Stomach contents of over 2,300 specimens representing all seasons were examined. Fish was the most frequent prey in all seasons, followed by crustaceans and squid (*Loiglo sanpaulensis*), both more frequent in summer and fall. Prey composition varied with sex, season and time of day, but not with size. Feeding activity was higher in summer and spring, on the slope and the southern part of the shelf. *Loiglo sanpaulensis* is shown to feed opportunistically, depending on the availability of prey. Food availability is also a major distribution factor. The species migrates along the shelf, taking advantage of the Brazil and Malvinas Currents system to reach suitable spawning and feeding grounds.

Key-words: *Loiglo*, squid, fishing resources, feeding, food habits, Subtropical Convergence, Brazil.

RESUMO

*Loiglo sanpaulensis* é a lula mais abundante no região costeira do sul do Brasil. Este artigo analisa seus hábitos alimentares na plataforma costeira e talude superior do Rio Grande do Sul. As amostras foram obtidas em cruzeiros de pesca de arrasto de fundo do N/Pq Atlântico Sul realizados de 1981 a 1987 entre 28°35'S e 34°40'S, a profundidades de 10 a 587 m. Examinaram-se os conteúdos esôstomacais de mais de 2300 exemplares, capturados em diferentes épocas do ano. Os peixes foram as presas mais frequentes em todas as estações, seguidas de crustáceos e lulas (*Loiglo sanpaulensis*), ambos mais frequentes no verão e outono. A proporção de presas variou com sexo, estação do ano e hora do dia, mas não com tamanho. A atividade alimentar foi mais intensa no verão e primavera, no talude superior e na metade sul da plataforma. *Loiglo sanpaulensis* mostrou-se um predador oportunista, com sua distribuição dependendo da disponibilidade de alimento. A plataforma e o talude gaúchos parecem ser uma área de alimentação importante, especialmente antes da desova. A espécie migra ao longo da plataforma, aproveitando o sistema formado pelas Correntes do Brasil e das Malvinas para situar-se em locais adequados para a desova, provavelmente ao norte da área de estudo, e para a alimentação, nas águas mais produtivas ao sul da margem ocidental da Convergência Subtropical.


REFERENCES


