The trophic role of the squid *Loligo plei* as a keystone species in the South Brazil Bight ecosystem

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Gasalla, M. A., Rodrigues, A. R., and Postuma, F. A. 2010. The trophic role of the squid *Loligo plei* as a keystone species in the South Brazil Bight ecosystem. – ICES Journal of Marine Science, 67: 1413–1424.

The issue of whether loliginid squid can influence the average structure of marine ecosystems in a keystone role, i.e. a strong effect with relatively low biomass, has not yet been examined. Here, the diet of *Loligo plei* in inner shelf waters of the South Brazil Bight was examined, as a first step, based on the stomach contents of 2200 squid hand-jigged in shallow water (<30 m) and taken as bycatch of shrimp trawlers in deeper water (30–100 m). Diet varied by size, season, and fishing zone. Stomachs were not empty in ~12%, with more empty during winter. The range of mantle lengths of squid caught by jigging (101–356 mm) appeared to differ from the squid trawled (30–236 mm), and the diet also differed. Food categories recorded in deeper water did not include amphipods or polychaetes, but in both fishing areas, fish were the most common prey. The fish prey identified included *Trachurus lathami*, small pelagic species, trichiurids, and *Merluccius hubbsi*. Demersal species, such as *Ctenosciaena gracilicirrhus*, and flatfish were also present. An ecosystem network model is updated through which a mixed-trophic impact matrix and "keystoneness" indicators were calculated. *Loligo plei* represents an important link between pelagic and demersal energy pathways, with high indices of keystoneness.

Keywords: diet, fisheries, foodweb, keystoneness, modelling, multispecies interactions.

Received 15 November 2009; accepted 10 June 2010; advance access publication 29 July 2010.

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Introduction

Loliginid squid play an important ecological role in coastal marine ecosystems worldwide, many species representing a significant link in foodwebs, as predators and prey (Pierce and Guerra, 1994; Santos and Haimovici, 2002; Boyle and Rodhouse, 2005; Pierrepont *et al.*, 2005; Rodhouse, 2005; Staudinger, 2006). Their role as prey can be of relevance to energy pathways and, in some regions, the consumption of squid by predatory fish can surpass the quantity of squid caught by the fishing fleet (Overholtz *et al.*, 2000; Daly *et al.*, 2001). Moreover, the increasing trends in some squid populations have been associated with top-down trophic control (i.e. the effect of predation on ecosystem dynamics) as a consequence of intense fishing pressure and the depletion of some of their common predators (Gasalla and Rossi-Wongtschowski, 2004; Rodhouse, 2005).

As predators, squid can impact fish communities (Boyle and Pierce, 1994; Guerra and Rocha, 1994; Pierce *et al.*, 1994; Santos and Haimovici, 1998; Hunsicker and Essington, 2008), with implications for energy flux and the temporal structure of ecosystems (Macy, 1982; Rodhouse and Nigmatullin, 1996). Moreover, squid populations can potentially impact the recruitment success and the natural mortality of commercially exploited species (Boyle and Rodhouse, 2005).

Knowledge of the trophic interactions of squid is basic to understanding their ecological role and its significance in marine ecosystems (Overholtz *et al.*, 2000; Hunsicker and Essington, 2008). Information on feeding habits and trophic position may be applied in a multispecies modelling context, which may also have utility for management and conservation (Gislason, 1999; Gasalla and Soares, 2001; Christensen and Walters, 2004; Gasalla and Rossi-Wongtschowski, 2004).

In Brazil, the long-finned squid *Loligo plei* is one of the dominant cephalopods on the continental shelf of the South Brazil Bight (SBB; 22–28°S) in the southwestern Atlantic Ocean. It is exploited commercially from Cape Frio (22°S) to Cape Santa Marta Grande (28°S) and is the most important loliginid in the fisheries of the coastal states of São Paulo and Santa Catarina (Perez *et al.*, 2005; Rodrigues and Gasalla, 2008). In São Paulo, *L. plei* is captured by shrimp trawlers as bycatch and as the target of small-scale hand-jigging within the SBB. In shallower water surrounding the islands, artisanal fishers catch squid mainly during summer, when the animals seem to aggregate to spawn (Rodrigues and Gasalla, 2008).

The diet of *L. plei* in the SBB was first described by Juanicó (1979). Recently, however, studies on the feeding habits of *L. plei* have focused on Santa Catarina Island (Martins *et al.*, 2006; Martins and Perez, 2007) and Ubatuba (Corbisier *et al.*, 2006) and have been based on stomach contents and stable isotope signatures, respectively. Studies indicate that *L. plei* is mostly piscivorous and probably opportunistic, with seasonal and ontogenetic shifts in diet.

The present study aimed to contribute to the understanding of the trophic relationships of *L. plei* in the SBB based on an analysis of a new set of stomach contents from squid of various sizes taken at different depths. A secondary objective was to apply the new diet information to updating an ecosystem model (Gasalla and Rossi-Wongtschowski, 2004; Gasalla, 2008) to evaluate the trophic impacts of squid and their "keystoneness" in the ecosystem.

Keystone species are defined as species that, despite being relatively less abundant, have a strong influence on ecosystem dynamics and on the abundance of other species, i.e. their effects are large and disproportionate to their abundance or biomass (Paine, 1995; Power *et al*., 1996; Libralato *et al*., 2006). Their presence seems to be crucial in maintaining community organization and biodiversity, often including many indirect effects, implying that such species are very important relative to the rest of the community (Mills *et al*., 1993; Paine, 1995). Although squid biomass can increase rapidly in an ecosystem, i.e. the relative importance can change seasonally, the critical trophic role of squid in an average community structure has also been highlighted, e.g. in the Southern Ocean (Rodhouse and White, 1995) and the Pacific Ocean (Zeidberg and Robison, 2007; Arancibia and Neira, 2008). However, the issue of whether loliginid squid have a keystone role in the structure of typical marine ecosystems, i.e. a strong effect relative to their biomass, has not yet been examined. Therefore, this study aimed to explore the trophic role of *L. plei* and to determine, through calculating quantitative indicators, whether it is a keystone species in a shelf ecosystem off southeastern Brazil.

Material and methods

Diet composition

The diet of *L. plei* was identified through stomach-content analysis of specimens obtained from fisheries. The samples were collected monthly or, when possible, weekly, at landing points along the coast of São Paulo, particularly at the ports of Santos and São Sebastião (Figure 1). Size-stratified random subsamples were collected and, when catches were small, all the squid landed were sampled. Skippers were interviewed to obtain information about the fishery, such as location and depth of capture. From August 2002 to July 2003, squid were sampled from trawlers targeting pink shrimp (*Farfantepenaeus* spp.) at depths of 30–100 m between southern Rio de Janeiro (23°S) and Itajai (27°S), referred to below as deeper or shelf samples. During summer (November–April) of the years 2003 and 2009, squid were sampled from hand-jiggers operating around São Sebastião Island in water <30 m deep, referred to below as nearshore or inshore samples.

In the laboratory, the mantle length (ML, mm), total body weight (BW, g), and sex were recorded. Stomachs containing food remains were examined under a stereomicroscope. The contents were sorted into four biological groups (fish, cephalopods, crustaceans, and polychaetes), and the weight and frequency of occurrence were recorded. Because of the level of digestion of the prey, fish were identified mainly by the presence of otoliths, scales, vertebrae, and eye lenses in the stomach contents. Crustaceans were identified from eyes, exoskeletal remains, and appendages, and cephalopods from beaks, eye lenses, arms, and sucker rings. Fish and cephalopods were identified to the lowest taxon possible, consulting local unpublished identification guides and an otolith reference collection. When the otoliths found in the stomachs were very small, it was difficult to compare them with the otoliths of adult fish available in the collections and guides. Therefore, otoliths taken from small fresh fish common in the region were used. In addition, some otoliths

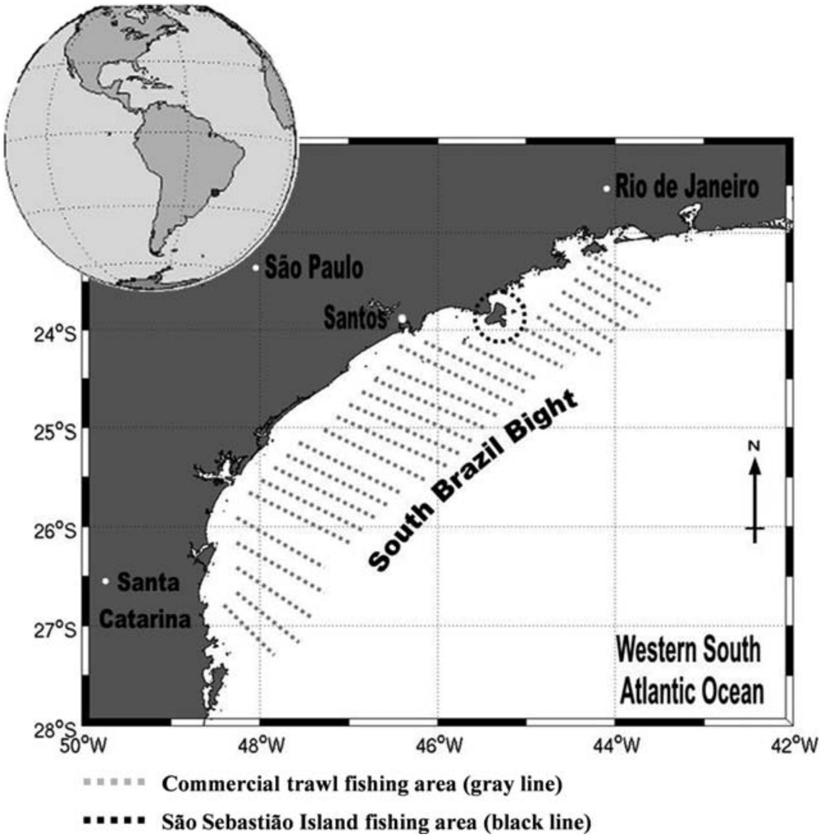

Figure 1. Location of squid fishing areas in the SBB, Southwest Atlantic.

were obtained from fixed material held by the Zoology Museum of the University of São Paulo (MZUSP), facilitating some species identification.

Four indices were adopted for the analysis of stomach contents:

(i) frequency of occurrence (Hyslop, 1980) $\%F = (N_i/N_t) \times 100$, where N_i is the number of stomachs containing a prey type and N_t the total number of non-empty stomachs;

(ii) percentage of total prey weight (Hyslop, 1980) $\%W = (W_i/W_t) \times 100$, where W_i is the weight of an individual certain prey and W_t the total weight of all prey;

(iii) percentage of prey total number $\%N = (N_j/N) \times 100$, where N_j is the total number of prey item j and N the total number of prey;

(iv) the index of relative importance (IRI; Pinkas *et al.*, 1971), which measures the importance of each prey item relative to other prey by taking into account the weight and the number of each prey item and the frequency at which each is found in the diet. IRI was calculated for prey items i using the equation: $\mathrm{IRI}_i = (\%N_i + \%W_i) \times \%F_i$. The IRI_i of each major group was then standardized to $\%\mathrm{IRI}_i$ (Hacunda, 1981), i.e. $\%\mathrm{IRI}_i = \left(\mathrm{IRI}_i / \sum_i^n \mathrm{IRI}\right) \times 100$, where n is the total number of groups identified.

Diet was compared by season and squid sex and size (30-mm ML classes). *Loligo plei* size-at-maturity (>150 mm ML) estimated from earlier studies (e.g. Perez *et al.*, 2005; Rodrigues and Gasalla, 2008) was used to compare diet results between juveniles and adults. Chi-squared tests (Zar, 1996) were used to compare the absolute values statistically.

Ecosystem modelling

The diet composition obtained from the stomach-content analysis was used to fill gaps in the diet matrix of an earlier ecosystem model of the SBB (Gasalla and Rossi-Wongtschowski, 2004; Gasalla, 2008), which was updated for the interactions of squid with "new" prey groups. The network model representing 2001 (Gasalla, 2008) was constructed with a mass-balance assumption using Ecopath with Ecosim 5.1 (www.ecopath.org; Christensen *et al.*, 2005), which allows for the end-to-end analysis of ecosystem structure in terms of average rates and states of the components, i.e. from the primary producers to the top predators. The model was constructed with 31 biological components (Bryde whales, dolphins, seabirds, large pelagic fish, sharks, rays, weakfish, other piscivorous fish, large benthic fish, flatfish, triggerfish, king weakfish, other benthic fish, octopus, cutlassfish, hake, croaker, other sciaenids, squid, mackerel, zooplanktivore carangids, carnivorous benthos, juvenile sardine, adult sardine, small pelagic fish, catfish, shrimps, mullet, zooplankton, detritivorous benthos, phytoplankton, discards, and detritus), 7 of which interacted with squid as prey and 14 as predator. The model estimated the biomass values for 21 of the 31 components, including squid.

The new diet matrix (including the new groups identified by the stomach contents analysis) was then used as the basis for calculating a mixed-trophic impact matrix (see below). The methodological approach followed the sequence illustrated in Figure 2.

Mixed-trophic impact matrix

The mixed-trophic impact matrix analysis was proposed by Ulanowicz and Puccia (1990) to assess the possible effect that changes in the biomass of one group would have on the biomass of others. The (i, j)th element represents the interaction between the impacting group i and the impacted group j, so $\mathrm{MTI}_{i,j} = \mathrm{DC}_{i,j} - \mathrm{FC}_{j,i}$, where $\mathrm{DC}_{i,j}$ expresses how much j contributes to the diet of i and to the fleet's catches and $\mathrm{FC}_{j,i}$ gives the proportion of the predation of j that is attributable to i as a predator.

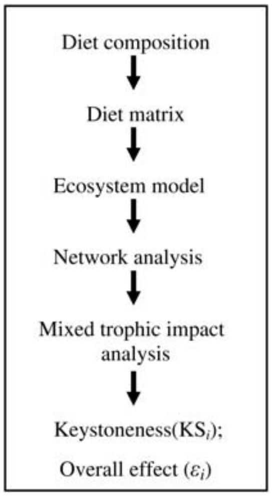

Figure 2. Methodological sequence for the diet matrix analysis and estimation of indices.

Given the mass-balance model of a trophic network, the mixed-trophic impact is estimated for each pair of functional groups (i, j) (directly interacting or not) of the trophic web by the net impact matrix. Each element of the matrix represents the relative change in biomass that would result from an infinitesimal increase in the biomass of the functional groups in the rows (Ulanowicz and Puccia, 1990; Christensen and Walters, 2004). Hence, the matrix can be used to estimate the total effect of one functional group on all the others in a given model (the overall effect). In this case, the values obtained for squid as both impacting (i) and impacted (j) groups (rows and columns of the matrix with respect to squid) were examined. Values were plotted as percentages separately. Negative elements indicate a prevalence of negative effects, i.e. the effects of the predator on the prey (top-down effects); analogously, positive elements indicate the prevailing effects of the prey on the predator (bottom-up effects).

"Keystoneness" index

The keystoneness index (KS_i) for squid was estimated using the method proposed by Libralato *et al.* (2006). The index is used for identifying the keystone species in an ecosystem. The modelling approach allows some of the difficulties in the experimental quantification of keystoneness to be overcome. Through a model, it is possible to estimate the strength of the interactions between model functional groups. Keystone species are defined as relatively low biomass species that have a relevant structuring role in their foodwebs. Therefore, the main elements to be measured are the overall effect shaped by the interaction strength of a group, and its relative biomass compared with the total biomass of a system.

The index was defined as $\mathrm{KS}_i = \log[\varepsilon_i(1 - p_i)]$, where p_i is the biomass component represented by the contribution of the functional group (B_i) to the total biomass of the foodweb $\left(\sum_\kappa B_\kappa\right)$, such that $p_i = B_i / \sum_\kappa B_\kappa$, and ε_i is the overall effect calculated from the mixed-trophic impact analysis, i.e. $\varepsilon_i = \sqrt{\sum_{j \neq i}^n m_{ij}^2}$, which relates to the maximum effect measured in each trophic web on a scale between 0 and 1 (Libralato *et al.*, 2006). The keystone functional groups are those ranking in terms of overall effect (ε_i closer to 1) and with the highest values of KS_i.

Results

Diet

From the 2200 *L. plei* stomachs examined, only 12% were not empty. The ML of squid caught in shallow water by hand-jigs was greater than that of those caught by the shelf-trawl fisheries, in which small immature squid dominated (88%; Table 1). The frequency of empty stomachs was lower in summer (Figure 3).

Table 2 lists the species found in the diet of *L. plei* by fishing season; a greater diversity of prey was found in summer. The frequency of occurrence (%*F*), number (%*N*), weight (%*W*), and the index of relative importance (%IRI) of each prey item in the diet of *L. plei* in the two fishing regions are listed in Table 3. According to the %IRI and the other indices, fish was the main food category in both regions, with values highest in shallow water (Table 3), followed by crustaceans (10.1 and 11.3%) and cephalopods (2.0 and 9.4%). Polychaetes were only found in the stomachs of squid caught nearshore (%IRI = 1.2).

The most frequently identified fish in both regions was the small scad *Trachurus lathami*. Engraulids (*Anchoa* spp.) were the second most common fish inshore, followed by the carangid *Selene* spp., centropomids, the small clupeid *Sardinella brasiliensis*, and flatfish. In the trawl catch, the second most common fish was cutlassfish (*Trichiurus lepturus*), followed by flatfish and *Merluccius hubbsi* (Table 3). Of these species, *T. lathami*, *M. hubbsi*, *S. brasiliensis*, *Selene* spp., centropomids, and flatfish had not been recorded previously in the diet of *L. plei* in the study area. Cephalopod prey was recorded, but only in the trawl samples, and all were loliginid squid, including *L. plei* and *L. sanpaulensis*. Crustaceans and polychaetes were generally too fragmented to permit further identification.

Table 1. Description of the squid (*L. plei*) sampled for stomach-content analysis.

Sampling area	SBB shelf (30–100 m)	São Sebastião Island (<30 m)
Squid ML range (mm)	30–236	101–356
Number of *L. plei* examined	862	1 338
Squid with stomach contents	125 (15%)	132 (10%)
Squid ≤150 mm ML with stomach contents	110 (88%)	49 (37%)

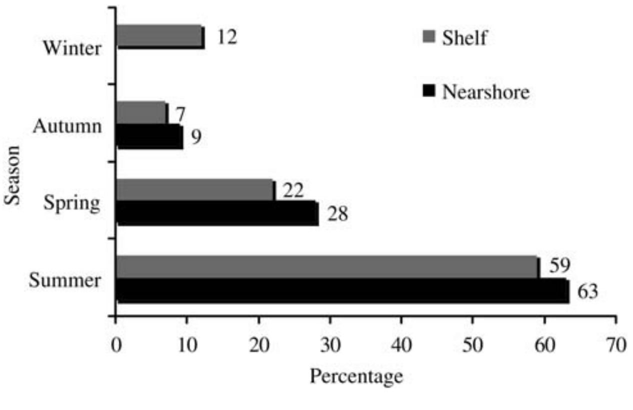

Figure 3. Percentage of squid with non-empty stomachs per season over the shelf (>30 m, grey bars) and nearshore (<30 m, black bars).

The %*F* of fish, cephalopods, crustaceans, and polychaetes in the stomach contents of *L. plei* of different ML classes are shown on Figure 4. Crustaceans in both areas, and polychaetes nearshore, were more commonly preyed on by smaller squid (Figure 4). Piscivory appeared to be greatest in the squid caught nearshore (Table 3). In both areas, though, the seasonal occurrence of fish in the diet in absolute numbers was significantly different between autumn/winter and spring/summer ($\chi^2_{\text{inshore}} = 41.2$ and $\chi^2_{\text{shelf}} = 22.5$; 2 d.f.; $p < 0.001$). However, within each season, the importance did not change significantly (Figure 5). There were no significant differences in the diet between sexes for the *L. plei* caught inshore. In deeper water, however, the %*F* of the prey groups (fish, cephalopods, and crustaceans) differed significantly between sexes ($\chi^2_{\text{shelf}} = 11.8$; 4 d.f.; $p < 0.05$), with significantly greater frequencies of cephalopods in the diet of males ($\chi^2_{\text{shelf}} = 9.0$; 1 d.f.; $p < 0.05$; Figure 6).

Trophic relationships, impacts, and keystoneness

Figure 7 synthesizes the energy links involving *L. plei* in the SBB ecosystem model by trophic level, based on the ecosystem modelling. Squid seem to link several trophic levels as well as demersal and pelagic pathways. Note that the model provided a broad picture of each prey or predator group interaction from which the squid-related data were extracted.

The results of the mixed-trophic impact analysis considering squid as an "impacting" group are shown in Figure 8. Positive and negative effects that squid can have on other groups (including biological and fishing compartments) are illustrated. Negative impacts are seen for several prey species, such as zooplanktivorous carangids (such as the scad) and small pelagic fish (Figure 7). Other groups seem to be impacted as a result of indirect effects or triangular interactions (e.g. hake, flatfish) and top-down effects on prey or on the fishing fleet's target species. The sum of the effects of these indirect interactions seems to reflect the complexity of the foodweb, and the effects also suggest or perhaps explain a potential strength of the group (*sensu* Menge *et al.*, 1994). In addition, the impact that other groups in the system can exert on squid can be extracted using the mixed-trophic impact matrix analysis (Figure 9). The predators of squid and other groups (and fishing fleets) that may impose an overall negative trophic impact on them are also represented in Figure 9. For example, weakfish, cutlassfish, whales, large pelagic fish, and mackerel seem negatively to impact squid as predators or via top-down, indirect effects (e.g. mackerel). Producers and plankton groups, small pelagic fish and carangids seem to impact squid positively via bottom-up processes (Figure 9).

Table 4 lists the results of the keystoneness index and overall effect analyses of *L. plei* in the system. Both indicators (KS_i and ε_i) for squid were high, showing that they are one of the keystone species in the SBB ecosystem network (the third highest group in the system in terms of the values of the indices).

Discussion

The trophic role of squid in marine ecosystems has been considered central to energy transfer from lower to higher trophic levels (Rodhouse and Nigmatullin, 1996; Boyle and Rodhouse, 2005). The overwhelming majority of information on prey has

Table 2. Species found in the stomach contents of *L. plei* in the present study and their seasonal occurrence.

			Fishing season			
Suborder or family	**Species**	**Common name**	**Summer**	**Autumn**	**Winter**	**Spring**
Fish						
Engraulidae	*Anchoa* spp.	Anchovy	X	X	–	X
Carangidae	*Selene* spp.[a]	Atlantic moonfish	X	X	–	–
Carangidae	*Trachurus lathami*[a]	Rough scad	X	X	–	X
Centropomidae	*Centropomus* spp.[a]	Snook	X	–	–	–
Clupeidae	*Sardinella brasiliensis*[a]	Brazilian sardine	–	–	–	X
Merlucciidae	*Merluccius hubbsi*[a]	Argentine hake	X	–	–	–
Sciaenidae	*Ctenosciaena gracilicirrhus*	Barbel drum	X	–	–	–
Trichiuridae	–	Cutlassfish	–	–	X	X
Cephalopods						
Loliginidae	*Loligo* spp.	Long-finned squid	X	X	X	X
Loliginidae	*Loligo sanpaulensis*	Sao Paulo squid	X	–	–	–
Loliginidae	*Loligo plei*	Slender inshore squid	X	X	–	X
Gammaridea (Crustacea)	–	Amphipod	X	–	–	X
Nereididae (Polychaeta)	–	–	X	X	–	X

[a] First record of this species in the diet of *L. plei*.

Table 3. Frequency of occurrence (%*F*), percentages by number (%*N*) and weight (%*W*), and the index of relative importance (%IRI) of the prey of the squid *L. plei* as determined by stomach-content analysis.

	Shelf (30–100 m)				Nearshore (<30 m)			
Prey type	**%*F***	**%*N***	**%*W***	**%IRI**	**%*F***	**%*N***	**%*W***	**%IRI**
Fish	72.8	45.0	62.4	79.3	78.8	48.1	82.8	86.7
Anchoa spp.	–	–	–	–	3.0	1.8	–	–
Ctenosciaena gracilicirrhus	–	–	–	–	0.8	0.3	–	–
Centropomidae	–	–	–	–	1.5	0.8	–	–
Flatfish	1.6	0.8	0.7	–	0.8	0.3	–	–
Merluccius hubbsi	0.8	0.4	0.9	–	–	–	–	–
Sardinella brasiliensis	–	–	–	–	0.8	0.3	–	–
Selene spp.	–	–	–	–	2.3	1.0	–	–
Trachurus lathami	10.4	10.4	9.6	–	3.8	1.6	–	–
Cutlassfish	3.2	1.5	1.6	–	–	–	–	–
Unidentified fish	56.8	32.0	49.6	–	65.8	42.3	–	–
Crustaceans	23.2	42.7	5.2	11.3	25.0	36.9	11.1	10.1
Amphipods	–	–	–	–	10.0	8.5	–	–
Cephalopods	20.8	12.3	32.4	9.4	18.9	7.5	4.9	2.0
Loligo plei	6.4	4.2	6.0	–	–	–	–	–
Loligo sanpaulensis	0.8	0.8	0.04	–	–	–	–	–
Unidentified cephalopods	13.6	7.3	26.4	–	–	–	–	–
Polychaetes	–	–	–	–	15.9	7.5	1.2	1.2

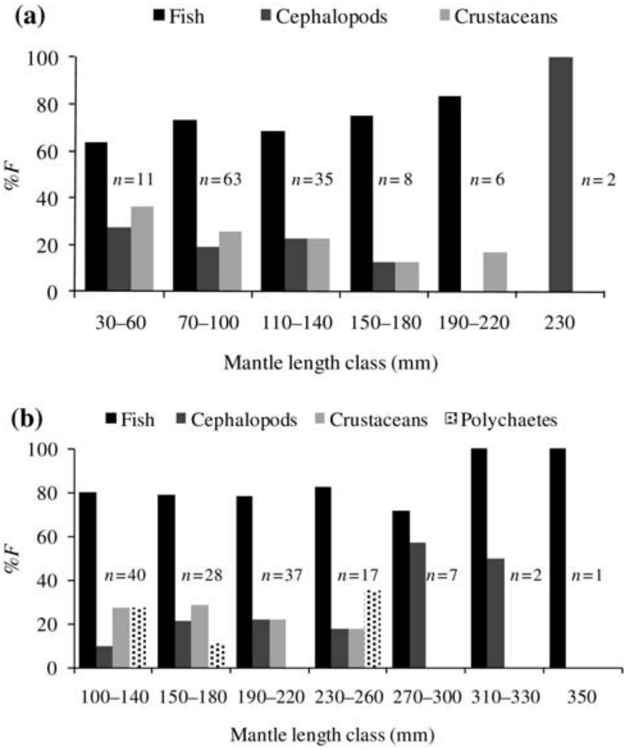

Figure 4. Frequency of occurrence of fish, cephalopods, crustaceans, and polychaetes in the stomach contents of squid by size (in squid ML classes) from (a) the shelf and (b) nearshore. *n* is the number of stomachs analysed.

been produced by studying stomach contents (Nigmatullin, 2005), but more feeding studies of squid and stomach-content analysis of their predators are still required to explore empirical relationships, which can be quite complex. Older squid can consume fish species that were their natural predators when they were young (Hanlon and Messenger, 1996). Also, when considering the diet in the complex context of multispecies interactions in a marine system, each piece of improved knowledge can represent an important and novel input, contributing to an understanding of the trophic ecology of various species in the system. In terms of ecosystem modelling, trophic links should ideally be expressed in terms of multivariate functional responses, but to do this requires more information on trophic interactions than is generally available.

We have here generated four main findings. First, differences in feeding habits between areas tend to be associated mainly with the different sizes of squid caught. Daily, vertical, and seasonal inshore–offshore migration and exposure to different spatial

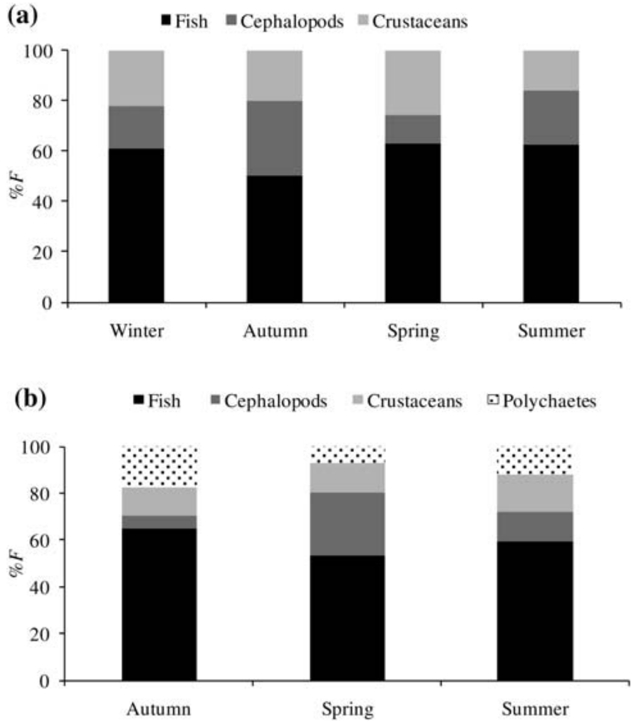

Figure 5. Frequency of occurrence of fish, cephalopods, crustaceans, and polychaetes in the stomach contents of squid by season in (a) shelf, and (b) nearshore samples.

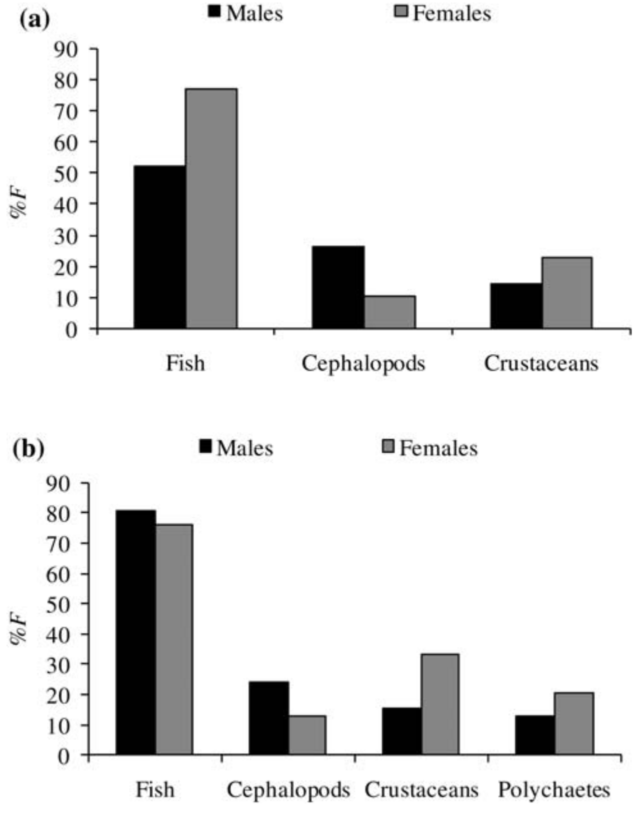

Figure 6. Frequency of occurrence of prey groups by sex of *L. plei* in (a) shelf waters, and (b) nearshore.

and temporal variations in marine production systems and prey populations during the lifespan of squid (Hatfield and Cadrin, 2002; Buresch *et al.*, 2006; Olyott *et al.*, 2006) can probably explain such findings. Second, the size at the onset of piscivory (the size at which the organisms start to feed on fish) for individual squid seems to be lower than thought previously. Third, the results here appear to confirm the hypothesis that *L. plei* feeding habits in the SBB are associated with a favourable environment shaped by the fertilizing, cold, nutrient-rich water masses forming the lower layer of the Brazil Current. Finally, the findings suggest that *L. plei* may potentially be a keystone species in the SBB ecosystem, something not considered previously.

In terms of diet composition, fish were the dominant prey in the diet of *L. plei* in this study, and crustaceans, cephalopods, and polychaetes showed different importance in each spatial (shelf and inshore) and seasonal (summer and winter) case. Similar results have been found in other studies of loliginids (Pierce *et al.*, 1994; Andriguetto and Haimovici, 1997; Santos and Haimovici, 1998; Hunsicker and Essington, 2006; Martins and Perez, 2007), along with an observed ontogenetic change, i.e. an increase in piscivory with growth. Also, access to a greater diversity of prey by inshore schools of *L. plei* seems to be demonstrated by the results here, i.e. prey that were not reported previously in the diet of *L. plei* have now been identified here.

The presence of off-bottom demersal (e.g. *M. hubbsi*, *T. lathami*, and *Ctenosciaenna gracilicirrhus*), benthic (flatfish), and pelagic fish (e.g. *Anchoa* spp. and *S. brasiliensis*) in the diet of *L. plei* indicates that it feeds throughout the water column. The fish prey items consumed by *L. plei* in both areas are consistent with the general view of loliginid feeding in southern Brazil (Santos and Haimovici, 1998; Martins *et al.*, 2006; Martins and Perez, 2007). *Trachurus* and *Merluccius* spp. have also been reported in the diet of loliginids elsewhere, such as *L. forbesi*, *L. vulgaris*, and *L. pealeii* (Sauer and Lipiński, 1991; Boyle and Pierce, 1994; Guerra and Rocha, 1994; Rocha *et al.*, 1994; Hunsicker and Essington, 2006). Martins and Perez (2007) also found that crustaceans were important prey, principally in the diet of small squid, similar to the results here. However, *S. brasiliensis*, *Selene* spp., centropomids, and flatfish were found in the diet of *L. plei* for the first time here. In addition, *L. plei* and *L. sanpaulensis* were identified as the cephalopod species found in the stomachs, suggesting cannibalism and that squid do feed on other species of squid.

The incidence of cannibalism was higher in the shelf samples (9.4%) than inshore (2%), contrary to the findings of Ibáñez and Keyl (2010), who reported a greater incidence in squid captured by jigs than in those captured by nets. Nevertheless, the results of cannibalism in squid caught in commercial samples need to be analysed with caution because the behaviour of squid entrapped in nets may be atypical (Ibáñez *et al.*, 2008). Perhaps cannibalism may be more frequent when squid density is greater (Agnew *et al.*, 2000) or food scarcer (Pecl and Jackson, 2006).

In both areas studied (the shelf and inshore), the most frequently identified fish species eaten was the scad *T. lathami*, especially during spring and summer. Saccardo *et al.* (2005) recorded the concentrations of this species inshore for spawning and feeding, principally in spring and summer. In addition, *T. lathami* shows the same pattern of daily vertical migration as *L. plei*, moving up through the water column at night and descending during the early morning (Saccardo, 1987; Martins and Perez, 2006). The daily pattern of *L. plei* feeding close to the surface by night is also verified by the greater frequency at which small

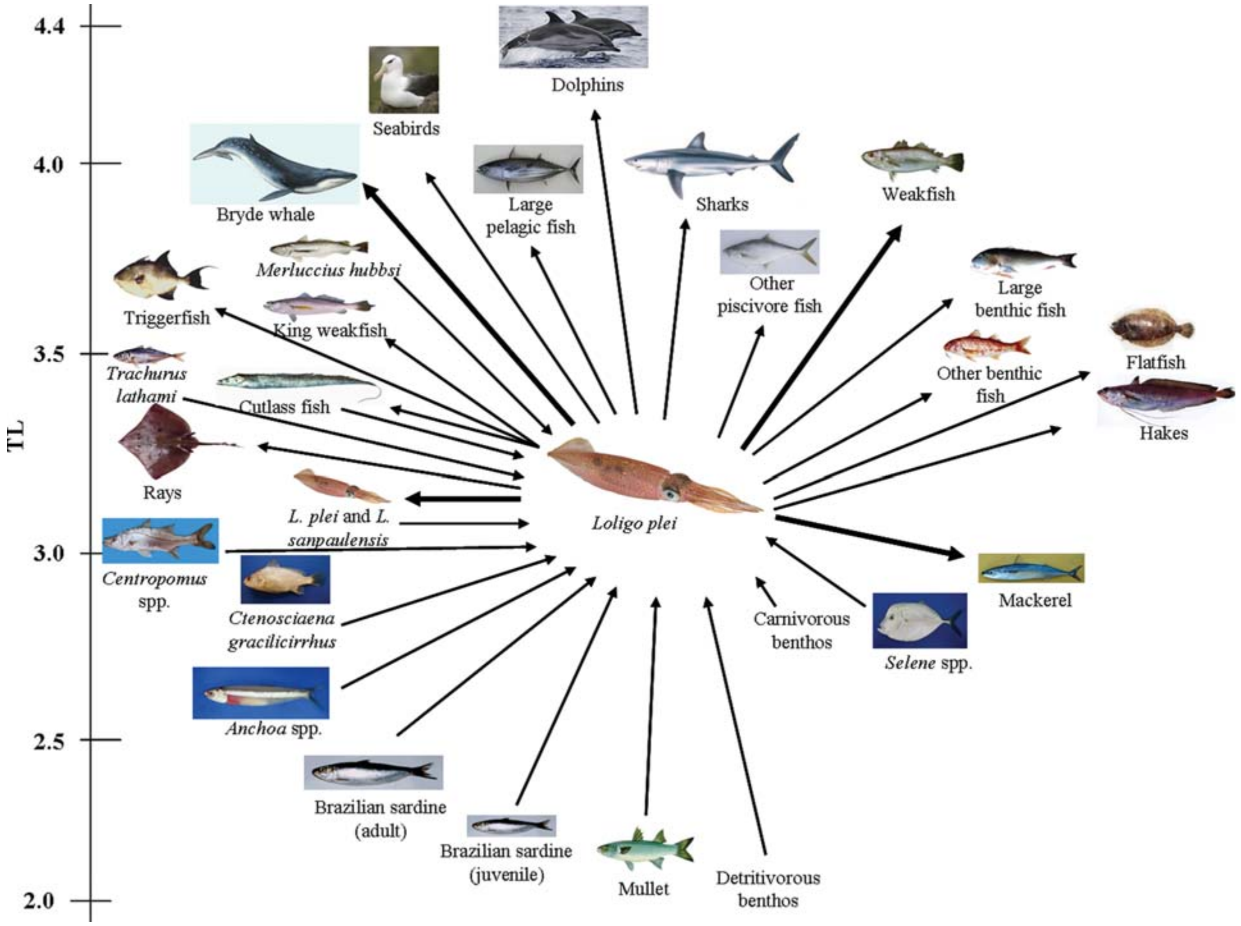

Figure 7. A *Loligo*-centred overview of trophic interactions in the SBB. The *y*-axis is the trophic level (TL) and arrow width illustrates importance in the diet.

pelagic fish (*Anchoa* spp., but also *T. lathami*) are recorded in the stomachs of squid caught at night (Postuma, 2010), and it seems to be a common behaviour of loliginids (Arkhipkin and Nigmatullin, 2008).

In general, the feeding activity was most intense in summer, when there seems to be greater availability of food as a consequence of the intrusion then of nutrient-rich South Atlantic Central Water (SACW), which supports the recruitment of pelagic fish (Matsuura, 1995). However, the fact that fewer empty stomachs were found in summer could also mean that squid feed less actively or that there is a different diurnal cycle of feeding. In summer, mature *L. plei* aggregate inshore to spawn (Rodrigues and Gasalla, 2008), and it is expected that the timing of spawning permits the young to hatch at the peak of productivity. During summer, the vertical stratification of the water column caused by the seasonal thermocline provides an upper layer of warmer, less saline water and a layer beneath of the colder SACW (Castro and Miranda, 1998). The scad *T. lathami* as well as some other squid prey are found between 50 and 100 m deep at temperatures between 15 and 17°C (Mello *et al*., 1992; Saccardo and Katsuragawa, 1995), typical of the SACW, and it is likely that squid take advantage of such an enriched environment.

The incidence of empty stomachs found was greater in winter, perhaps associated with less food availability then. The nutrient cycle and productivity of the SBB often change in winter related to the offshore retreat of the SACW, which does not have such a strong influence then on the middle and the inner shelves. This, resulting in a decline in plankton biomass and larval fish abundance, also seems to affect the upper trophic levels during winter (Lopes *et al*., 2006).

The percentage of empty stomachs we found seems to be higher than in temperate regions where the water is cooler (Pierce *et al*., 1994; Santos and Haimovici, 1998; Hunsicker and Essington, 2006). Higher temperatures can increase the metabolic rate and the need for prey ingestion (Hunsicker and Essington, 2008), resulting in rapid digestion and making it more difficult to identify prey, and it is likely too that the time that food remains in the stomach is less.

Piscivory of *L. plei* in the SBB has been shown previously in the quantifications of regional ecosystem models (Gasalla, 2004; Gasalla and Rossi-Wongtschowski, 2004) and by isotope analysis in the central region of Ubatuba (Corbisier *et al*., 2006). There, squid seem to feed close to the seabed and in the water column, making them an important link between pelagic and demersal realms.

An important contribution of this study was the inclusion of new groups into an existing ecosystem model, which allowed for a new, more-balanced model of the ecosystem and a rather different picture of the system. Comparing the results with the diet matrix of the preliminary model in Gasalla and Rossi-Wongtschowski (2004), new interactions with prey were included

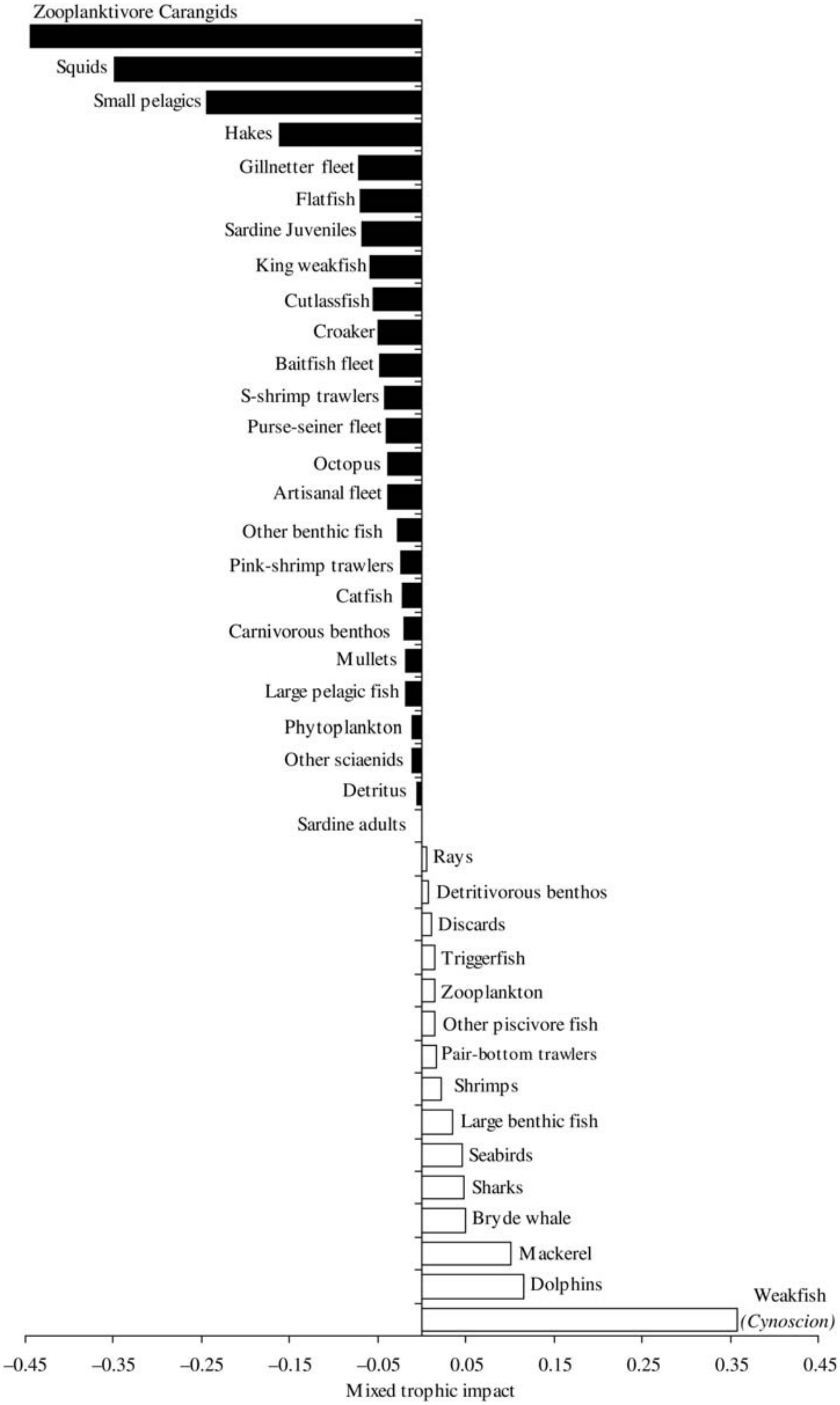

Figure 8. Mixed-trophic impact of squid as an impacting group in the SBB ecosystem.

in the updated model (e.g. small pelagic fish, zooplanktivorous carangids, sardine, hake, small sciaenids, and cutlassfish), increasing the complexity of squid interactions in the network analysis and providing a different mass-balance output. In this context, one might suggest that if the model changes substantially through including more detailed data on squid, it could imply that similar changes would be seen if more detailed data on another component of the model became available. However, the mass-balanced model was robust to changes in the diet of most of the groups except squid and sardine.

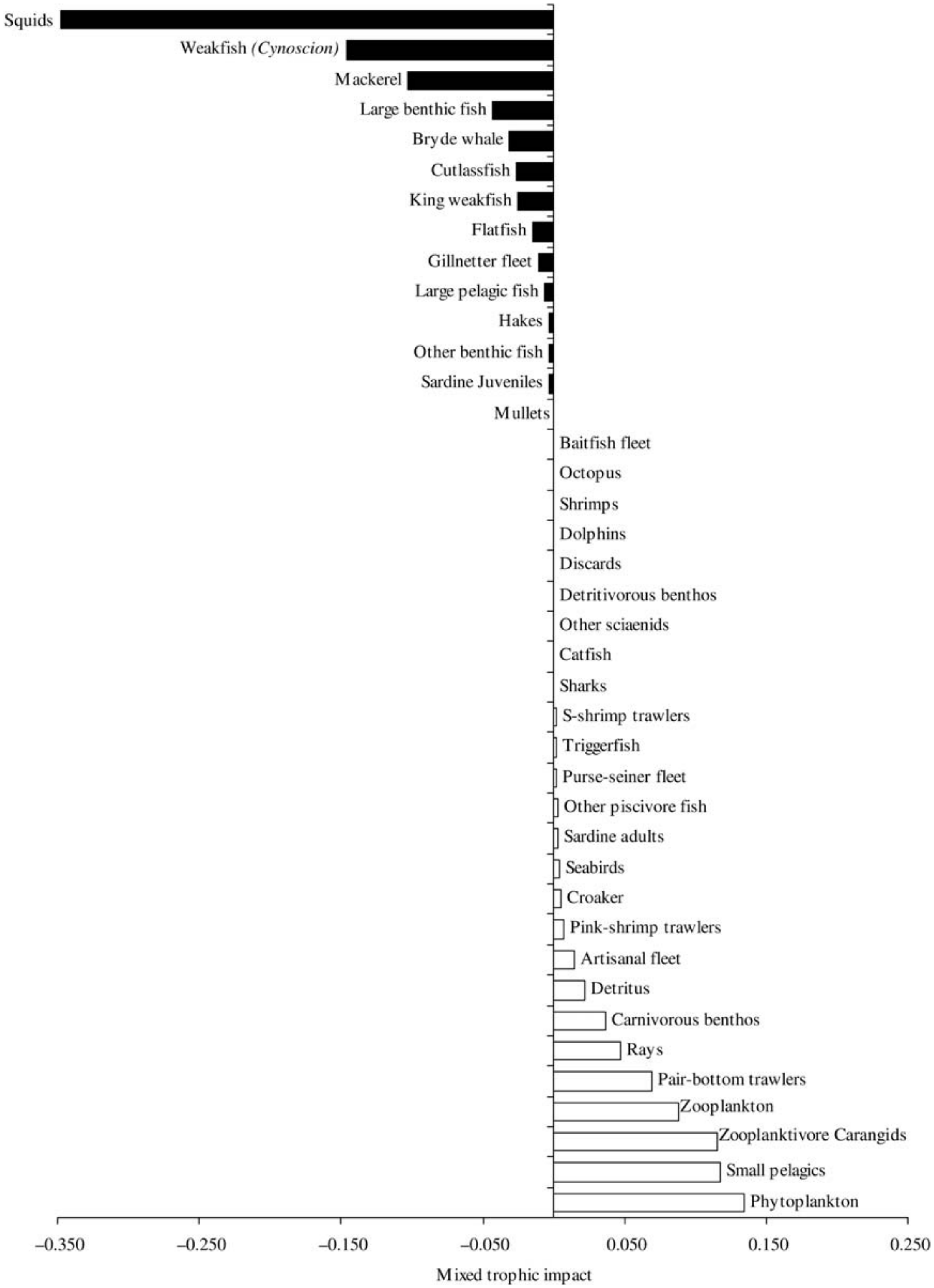

Figure 9. Mixed-trophic impact of squid as an impacted group in the SBB ecosystem.

Another important contribution is the quantification of the keystoneness indicators for the squid component, for which values were high and indeed scored third. These findings on the potential keystone role of squid in the SBB coastal ecosystem can be particularly useful in guiding future empirical studies of the ecosystem, and especially in establishing conservation priorities, e.g. in defining critical or key species that deserve special attention or effective action in terms of conservation and monitoring. Since the first definition of keystone species by Paine (1969), their importance for conservation purposes has been widely

Table 4. Indices of keystoneness and overall effect for the squid *L. plei* from the SBB ecosystem model.

Index	Value (squid)	Value range
KS_i (keystoneness)	−0.0189	0.0 to −2.0
ϵ_i (overall effect)	0.82	0.0 to 1.0

recognized, although common difficulties in experimental approach do exist. Additionally, the constraints imposed by the different roles assumed by species in time and space (Menge *et al.*, 1994; Paine, 1994; Estes *et al.*, 1998) might raise scepticism about the original definition of the keystone species concept, given the lack of an approach for quantifying keystoneness in an ecosystem perspective (Libralato *et al.*, 2006).

In that respect, testing the different roles of cephalopods in different marine ecosystems may be problematic. However, the mixed-trophic matrix upon which the methodology adopted here relied allows for considering direct and indirect effects of squid trophic interactions, so it can be useful in studying cephalopod ecology in a multispecies context, e.g. considering the known range of predator–prey relationships and both top-down and bottom-up processes in the foodweb. In that context, the strong interaction found for *L. plei* indicates that even a small change to their biomass could impact several elements of an ecosystem.

Keystone species do not always exert a great impact through top-down effects, a feature initially suggested to be a defining characteristic of keystone species (Paine, 1969) and hence proposed for identifying keystones (Davic, 2003; Libralato *et al.*, 2006). Considering that squid in the SBB seem to affect both types of trophic controls (Gasalla and Rossi-Wongtschowski, 2004), our results seem to support the concept that both top-down (Paine, 1969; Menge *et al.*, 1994; Estes *et al.*, 1998) and bottom-up effects in keystoneness are important (Bustamante *et al.*, 1995; Menge, 1995; Libralato *et al.*, 2006). It is hoped that further studies on the trophic ecology, population dynamics, and stock assessment of squid may allow more-accurate quantification of their keystone role in marine systems worldwide in future. As noted by Nigmatullin (2005), the level of our knowledge is too low to elucidate real and detailed schemes describing the role of cephalopod trophic relationships. However, the analyses conducted here can be reproduced in other systems to compare the different trophic roles and impact that squid can exert in foodwebs.

Meanwhile, the finding that *L. plei* play a keystone role in the SBB ecosystem needs to be taken into account in the future development of more advanced ecosystem models and policy for the study area, e.g. in defining priorities for both local biodiversity hotspots conservation and fishery management plans.

Acknowledgements

We thank the Instituto Oceanografico of the University of São Paulo for providing the infrastructure for the research, the EU INCOFISH Project (Contract No. 003739), CNPq (the Brazilian National Research Council/Universal No. 485558/2007-6 and Productivity Grant to MAG), and FAPESP (São Paulo Research Foundation) for support. Fruitful early discussions with H. Arancibia (Universidad de Concepción, Chile) and colleagues stimulated the thought processes. We also acknowledge the participation of the local fishers during fieldwork and of several colleagues that helped with otolith identification, and Graham Pierce, Vladimir Laptikhovsky, and an anonymous reviewer for useful input. The contribution was presented during the CIAC ’09 symposium, and we thank the University of Vigo (Spain) and FAPESP (Brazil) for travel support.

References

Agnew, D. J., Hill, S., and Beddington, J. R. 2000. Predicting the recruitment strength of an annual squid stock: *Loligo gahi* around the Falkland Islands. Canadian Journal of Fisheries and Aquatic Sciences, 57: 2479–2487.

Andriguetto, J. M., and Haimovici, M. 1997. Feeding habits of *Loligo sanpaulensis* Brakoniecki, 1984 (Cephalopoda: Loliginidae) in southern Brazil. Nerítica, 11: 63–76.

Arancibia, H., and Neira, S. 2008. Overview of the stock of hake (*Merluccius gayi*) and forecast of its biomass including jumbo squid (*Dosidicus gigas*) prey–predator relationship in central Chile (33°S–39°S). California Cooperative Oceanic Fisheries Investigation Report, 49: 104–115.

Arkhipkin, A. I., and Nigmatullin, Ch. M. 2008. Ecological role of squid migrations. *In* Proceedings of the 4th International Symposium on Pacific Squids and the 3rd International Workshop on Squids, pp. 36–38 Universidad Catolica del Norte, Coquimbo.

Boyle, P. R., and Pierce, G. J. 1994. Fishery biology of Northeast Atlantic squid: an overview. Fisheries Research, 21: 1–16.

Boyle, P. R., and Rodhouse, P. 2005. Cephalopods: Ecology and Fisheries. Blackwell Science, Oxford. 452 pp.

Buresch, K. C., Gerlach, G., and Hanlon, R. T. 2006. Multiple genetic stocks of longfin squid *Loligo pealeii* in the NW Atlantic: stocks segregate inshore in summer, but aggregate offshore in winter. Marine Ecology Progress Series, 310: 263–270.

Bustamante, R. H., Branch, G. M., and Eekhout, S. 1995. Maintenance of an exceptional intertidal grazer biomass in South Africa—subsidy by subtidal kelps. Ecology, 76: 2314–2329.

Castro, B. M., and Miranda, L. B. 1998. Physical oceanography of the western Atlantic continental shelf located between 4°N and 34°S. *In* The Sea, 11, pp. 209–251. Ed. by A. R. Robinson, and K. H. Brink. John Wiley, New York.

Christensen, V., and Walters, C. 2004. Ecopath with Ecosim: methods, capabilities and limitations. Ecological Modelling, 172: 109–139.

Christensen, V., Walters, C., and Pauly, D. 2005. Ecopath with Ecosim: a User’s Guide. Fisheries Centre of the University of British Columbia, Vancouver, Canada. 154 pp.

Corbisier, T. N., Soares, L. S. H., Petti, M. A. V., Muto, E. Y., Silva, M. H. C., McClelland, J., and Valiela, I. 2006. Use of isotopic signatures to assess the food web in a tropical shallow marine ecosystem of southeastern Brazil. Aquatic Ecology, 40: 381–390.

Daly, H. I., Pierce, G. J., Santos, M. B., Royer, J., Cho, S. K., Stowasser, G., Robin, J-P., *et al.* 2001. Cephalopod consumption by trawl-caught fish in Scottish and English Channel waters. Fisheries Research, 52: 51–64.

Davic, R. D. 2003. Linking keystone species and functional groups: a new operational definition of the keystone species concept. Conservation Ecology, 7(1): r11. http://www.consecol.org/vol17/iss1/resp11.

Estes, J. A., Tinker, M. T., Williams, T. M., and Doak, D. F. 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. Science, 282: 473–476.

Gasalla, M. A. 2004. Impactos da pesca industrial no ecossistema da plataforma continental interna do Sudeste do Brasil: a abordagem ecosistêmica e a integração do conhecimento. PhD thesis, University of São Paulo, São Paulo.

Gasalla, M. A. 2008. Ecosystem-based fisheries modelling of the South Brazil Bight ecosystem. EU-INCOFISH (Integrating Multiple Demands on Coastal Zones with Emphasis on Aquatic Ecosystems and Fisheries) Project Final Report. http://www.incofish.org/Workpackages/WP4/ModelsWP4.php.

Gasalla, M. A., and Rossi-Wongtschowski, C. L. D. B. 2004. Contribution of ecosystem analysis to investigating the effects of changes in fishing strategies in the South Brazil Bight coastal ecosystem. Ecological Modelling, 172: 283–306.

Gasalla, M. A., and Soares, L. S. H. 2001. Comentários sobre os estudos tróficos de peixes marinhos no processo histórico da ciência pesqueira e modelagem ecológica. Boletim do Instituto de Pesca, 27: 243–259.

Gislason, H. 1999. Single and multispecies reference points for Baltic fish stocks. ICES Journal of Marine Science, 56: 571–583.

Guerra, Á., and Rocha, F. 1994. The life history of *Loligo vulgaris* and *Loligo forbesi* (Cephalopoda: Loliginidae) in Galician waters (NW Spain). Fisheries Research, 21: 43–69.

Hacunda, J. S. 1981. Trophic relationships among demersal fishes in a coastal area of the Gulf of Maine. Fishery Bulletin US, 79: 775–788.

Hanlon, R. T., and Messenger, J. B. 1996. Cephalopod Behaviour. University of Cambridge, Cambridge, UK.

Hatfield, E. M. C., and Cadrin, S. X. 2002. Geographic and temporal patterns in size and maturity of the longfin inshore squid (*Loligo pealeii*) off the northeastern United States. Fishery Bulletin US, 100: 200–213.

Hunsicker, M. E., and Essington, T. E. 2006. Size-structured patterns of piscivory of the longfin inshore squid (*Loligo pealeii*) in the mid-Atlantic continental shelf ecosystem. Canadian Journal of Fisheries and Aquatic Sciences, 63: 754–765.

Hunsicker, M. E., and Essington, T. E. 2008. Evaluating the potential for trophodynamic control of fish by the longfin inshore squid (*Loligo pealeii*) in the Northwest Atlantic Ocean. Canadian Journal of Fisheries and Aquatic Sciences, 65: 2524–2535.

Hyslop, E. J. 1980. Stomach contents analysis—a review of methods and their applications. Journal of Fish Biology, 17: 411–429.

Ibáñez, C. M., Arancibia, H., and Cubillos, L. A. 2008. Biases in determining the diet of jumbo squid *Dosidicus gigas* (D'Orbigny 1835) (Cephalopoda: Ommastrephidae) off southern–central Chile (34°S–40°S). Helgoland Marine Research, 62: 331–338.

Ibáñez, C. M., and Keyl, F. 2010. Cannibalism in cephalopods. Reviews in Fish Biology and Fisheries, 20: 123–136.

Juanicó, M. 1979. Contribuição ao estudo da biologia de Cephalopoda Loliginidae do Atlântico Sul Ocidental entre Rio de Janeiro e Mar del Plata. PhD thesis, Instituto Oceanográfico da Universidade de São Paulo, São Paulo. 102 pp.

Libralato, S., Christensen, V., and Pauly, D. 2006. A method for identifying keystone species in food web models. Ecological Modelling, 195: 153–171.

Lopes, R. M., Katsuragawa, M., Dias, J. F., Montú, M. A., Muelbert, J. H., Gorri, C., and Brandini, F. P. 2006. Zooplankton and ichthyoplankton distribution on the southern Brazilian shelf: an overview. Scientia Marina, 70: 189–202.

Macy, W. K. 1982. Feeding patterns of the long-finned squid, *Loligo pealei*, in New England waters. Biological Bulletin, 162: 28–38.

Martins, R. S., and Perez, J. A. A. 2006. Cephalopods and fish attracted by night lights in coastal shallow-waters, off southern Brazil, with the description of squid and fish behaviour. Revista de Etologia, 8: 27–34.

Martins, R. S., and Perez, J. A. A. 2007. The ecology of loliginid squid in shallow waters around Santa Catarina Island, southern Brazil. Bulletin of Marine Science, 80: 125–145.

Martins, R. S., Perez, J. A. A., and Schettini, C. A. F. 2006. The squid *Loligo plei* around Santa Catarina Island, southern Brazil: ecology and interactions with the coastal oceanographic environment. Journal of Coastal Research, Special Issue 39: 1285–1290.

Matsuura, Y. 1995. Exploração pesqueira: ambiente marinho no litoral brasileiro. *In* Ecossistemas brasileiros e os principais macrovetores de desenvolvimento: subsídios ao planejamento da gestão ambiental, pp. 42–48. Ministério do Meio Ambiente dos Recursos Hídricos e da Amazônia Legal, Brasília. 104 pp.

Mello, R. M., Castello, J. P., and Freire, K. M. 1992. Asociacion de especies pelagicas en el sur de Brasil durante inverno y primavera. Frente Maritimo, 11: 63–69.

Menge, B. A. 1995. Joint 'bottom-up' and 'top-down' regulation of rocky intertidal algal beds in South Africa. Trends in Ecology and Evolution, 10: 431–432.

Menge, B. A., Berlow, E. L., Balchette, C. A., Navarrete, S. A., and Yamada, S. B. 1994. The keystone species concept: variation in interaction strength in a rocky intertidal habitat. Ecological Monographs, 64: 249–286.

Mills, L. S., Soule, M. E., and Doak, D. F. 1993. The keystone-species concept in ecology and conservation. BioScience, 43: 219–224.

Nigmatullin, Ch. M. 2005. Towards the correct methodology of cephalopod feeding study: review of some neglected problems. Paper presented at the Proceedings of the Third International Symposium on Pacific Calamares and the second Taller Internacional sobre Calamares, November/December 2005. IMARPE, Callao, Perú. 3 pp.

Olyott, L. J. H., Sauer, W. H. H., and Booth, A. J. 2006. Spatio-temporal patterns in maturation of the chokka squid (*Loligo vulgaris reynaudii*) off the coast of South Africa. ICES Journal of Marine Science, 63: 1649–1664.

Overholtz, W. J., Link, J. S., and Suslowicz, L. E. 2000. Consumption of important pelagic fish and squid by predatory fish in the northeastern USA shelf ecosystem with some fishery comparisons. ICES Journal of Marine Science, 57: 1147–1159.

Paine, R. T. 1969. A note on trophic complexity and community stability. American Naturalist, 103: 91–93.

Paine, R. T. 1994. Marine Rocky Shores and Community Ecology: an Experimentalists Perspective. Excellence in Ecology, 4. International Ecology Institute, Oldendorf/Luhe, Germany. 152 pp.

Paine, R. T. 1995. A conversation on refining the concept of keystone species. Conservation Biology, 9: 962–964.

Pecl, G., and Jackson, G. 2006. How climate change may influence loliginid squid populations. *In* The Role of Squid in Pelagic Marine Ecosystems, pp. 28–30. Ed. by R. J. Olson, and J. W. Young. GLOBEC-CLIOTOP WG3 Workshop, University of Hawaii, Manoa.

Perez, J. A. A., Gasalla, M. A., Aguiar, D. C., Oliveira, U. C., Marques, C. A., and Tomás, A. R. G. 2005. *Loligo plei*. *In* Análise das Principais Pescarias Comerciais da Região Sudeste-Sul do Brasil: Dinâmica Populacional das Espécies em Explotação, pp. 62–68. Ed. by M. C. Cergole, A. O. Ávila-da-Silva, and C. L. B. Rossi-Wongtschowski. Instituto Oceanográfico—USP, São Paulo.

Pierce, G. J., Boyle, P. R., Hastie, L. C., and Key, L. 1994. The life history of *Loligo forbesi* (Cephalopoda: Loliginidae) in Scottish waters. Fisheries Research, 21: 17–41.

Pierce, G. J., and Guerra, Á. 1994. Stock assessment methods used for cephalopod fisheries. Fisheries Research, 21: 255–285.

Pierrepont, J. F., Dubois, B., Desormonts, S., Santos, M. B., and Robin, J.-P. 2005. Stomach contents of English Channel cetaceans stranded on the coast of Normandy. Journal of the Marine Biological Association of the UK, 85: 1539–1546.

Pinkas, L., Oliphant, M. S., and Iverson, I. L. K. 1971. Food habits of albacore, bluefin tuna, and bonito in California waters. California Department of Fish and Game Fish Bulletin, 152: 1–105.

Postuma, F. A. 2010. Biologia pesqueira da lula *Loligo plei* capturada na Ilha de São Sebastião (SP) e dinâmica da atividade pesqueira associada. Masters thesis, Instituto de Pesca de São Paulo, São Paulo.

Power, M. E., Tilman, D., Estes, J. A., Menge, B. A., Bond, W. J., Mills, L. S., Daily, G., *et al.* 1996. Challenges in the quest for keystones. Bioscience, 46: 609–620.

Rocha, F., Castro, B. G., Gil, M. S., and Guerra, Á. 1994. The diets of *Loligo vulgaris* and *Loligo forbesi* (Cephalopoda: Loliginidae) in Northwestern Spain Atlantic waters. Sarsia, 79: 119–126.

Rodhouse, P. G. 2005. World squid resources. *In* Review of the State of World Marine Fishery Resources, pp. 175–187. FAO Fisheries Technical Paper, 457.

Rodhouse, P. G., and Nigmatullin, Ch. M. 1996. Role as consumers. Philosophical Transactions of the Royal Society of London, 351: 1003–1022.

Rodhouse, P. G., and White, M. G. 1995. Cephalopods occupy the ecological niche of epipelagic fish in the Antarctic Polar Frontal Zone. Biological Bulletin, 189: 77–80.

Rodrigues, A. R., and Gasalla, M. A. 2008. Spatial and temporal patterns in size and maturation of *Loligo plei* and *Loligo sanpaulensis* (Cephalopoda:Loliginidae) in southeastern Brazilian waters, between 23°S and 27°S. Scientia Marina, 72: 631–643.

Saccardo, S. A. 1987. Morfologia, distribuição e abundância de *Trachurus lathami* Nichols, 1920 (Teleostei: Carangidae) na região sudeste-sul do Brasil. Boletim do Instituto Oceanográfico, Universidade de São Paulo, São Paulo, 35: 65–95.

Saccardo, S. A., Cergole, M. C., and Masumoto, C. 2005. *Trachurus lathami*. *In* Análise das Principais Pescarias Comerciais da Região Sudeste-Sul do Brasil: Dinâmica Populacional das Espécies em Explotação, pp. 156–161. Ed. by M. C. Cergole, A. O. Ávila-da-Silva, and C. L. B. Rossi-Wongtschowski. Instituto Oceanográfico—USP, São Paulo.

Saccardo, S. A., and Katsuragawa, M. 1995. Biology of the rough scad *Trachurus lathami*, on the southeastern coast of Brazil. Scientia Marina, 59: 265–277.

Santos, R. A., and Haimovici, M. 1998. Trophic relationships of the long-finned squid *Loligo sanpaulensis* on the southern Brazilian shelf. South African Journal of Marine Science, 20: 81–91.

Santos, R. A., and Haimovici, M. 2002. Cephalopods in the trophic relations off southern Brazil. Bulletin of Marine Science, 71: 753–770.

Sauer, W. H. H., and Lipiński, M. R. 1991. Food of squid *Loligo vulgaris reynaudii* (Cephalopoda: Loliginidae) on their spawning grounds off the Eastern Cape, South Africa. South African Journal of Marine Science, 10: 193–201.

Staudinger, M. D. 2006. Seasonal and size-based predation on two species of squid by four fish predators on the Northwest Atlantic continental shelf. Fishery Bulletin US, 104: 605–615.

Ulanowicz, R. E., and Puccia, C. J. 1990. Mixed trophic impacts in ecosystems. Coenoses, 5: 7–16.

Zar, J. H. 1996. Biostatistical Analysis. Prentice-Hall, New Jersey. 662 pp.

Zeidberg, L. D., and Robison, B. H. 2007. Invasive range expansion by the Humboldt squid, *Dosidicus gigas*, in the eastern north Pacific. Proceedings of the National Academy of Sciences of the USA, 104: 12948–12950.

doi:10.1093/icesjms/fsq106