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Fish and cephalopods associated with the squid *Loligo vulgaris* Lamarck, 1798 in Portuguese waters*

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SUMMARY: Fish and cephalopod taxa occurring in association with *Loligo vulgaris*, in Portuguese waters between Lisbon and Vila Real de Santo António, were investigated by sampling with bottom trawling equipment between 1990-1991 and 1993-1995. The family Triglidae, the genera *Pagellus* and *Trachurus* and the four species *Alloteuthis subulata*, *Boops boops*, *Callionymus lyra*, and *Merluccius merluccius* were found, on average, in at least 75% of the trawls with *L. vulgaris*. Conversely, that cephalopod was found in at least 75% of the trawls with the family Trachinidae, the genera *Dentex*, *Diplodus*, *Liza* and *Torpedo* and the six species, *Hyperoplus lanceolatus*, *Pagrus pagrus*, *Pomatoschistus m. minutus*, *Psetta m. maxima*, *Scophthalmus rhombus* and *Spicara flexuosa*. An index of "affinity" (ranging from -∞ to 1) between *L. vulgaris* and the other taxa was used in order to highlight co-occurrences of an unlikely coincidental nature. Lists of taxa with high affinity index scores (0.5 to 1) are given for 5 different situations: all samples together; samples grouped by bottom depth; samples grouped by research cruise; research cruises grouped by season and by year. Pair wise comparisons between all taxa lists for each of the 5 situations were made, indicating a greater influence of depth than any other factor in the composition of the lists. The significance of the degree of similarity between lists of taxa, "preferred" under different circumstances and the reasons for those "preferences" are discussed.

Key words: Fishes, Cephalopods, *Loligo vulgaris*, species associations, Portugal.

RESUMEN: PECES Y CEFALÓPODOS ASOCIADOS CON EL CALAMAR *LOLIGO VULGARIS* LAMARCK, 1798 EN AGUAS DE PORTUGAL. – Se listan los peces y cefalópodos que se encuentran en asociación con *Loligo vulgaris* en aguas portuguesas entre Lisboa y Vila Real de Santo António, capturados con arrastre de fondo entre 1990-1991 y 1993-1995. La familia Tríglidos, los géneros *Pagellus* y *Trachurus* y las especies *Alloteuthis subulata*, *Boops boops*, *Callionymus lyra*, y *Merluccius merluccius* se encontraron, por término medio, como mínimo en el 75% de los arrastres junto con *L. vulgaris* y, por otra parte, este cefalópodo también estuvo presente al menos en el 75% de los arrastres con la familia Traquínidos, los géneros *Dentex*, *Diplodus*, *Liza*, *Torpedo*, y las especies *Hyperoplus lanceolatus*, *Pagrus pagrus*, *Pomatoschistus m. minutus*, *Psetta m. maxima*, *Scophthalmus rhombus* y *Spicara flexuosa*. Se utilizó un índice de afinidad (de -∞ a 1) entre *L. vulgaris* y los otros táxones para hacer sobresalir las cooccurrencias no coincidentales. Se dan listas de táxones con altos grados de afinidad (entre 0.5 y 1) para cada una de 5 situaciones diferentes: todas las muestras en conjunto, muestras agrupadas por profundidad, muestras agrupadas por crucero, cruceros agrupados por estación y por año. Se hacen comparaciones entre todas las listas de táxones, dos a dos, para cada una de las 5 situaciones descritas, que indican una influencia mayor de la profundidad que de cualquier otro factor en la determinación de la constitución de las listas. Se discute el significado de la variación de la composición de las listas de táxones "preferidos" por *L. vulgaris* en situacións distintas y las razones para estas "preferencias".

Palabras clave: Peces, cefalópodos, *Loligo vulgaris,* asociación de especies, Portugal.

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INTRODUCTION

The economic and social importance of the European squid (*Loligo vulgaris*, Lamarck 1798) in southern European countries, especially Portugal has frequently been documented (Cunha and Moreno, 1994; Shaw, 1994). From a situation in which there was little information available –possibly endangering the species in the face of an eager fishery– a more informed position has now been reached. Nevertheless, much is still to be known about this squid species in Portugal, and one area of particular interest is its interrelationships with the accompanying fauna and descriptions of the communities where it is found.

Communities are usually described in terms of their component species or physical structure (Smith, 1980), the latter sometimes dependent upon the former. In describing a community, apart from the physical description of the location (in marine communities the depth, for instance), species are usually first identified, and then quantified (Margalef, 1974). Mathematical calculations, of greater or lesser complexity, often under the form of multivariate analysis (Gauch, 1986), are performed on the data to determine similarities and dissimilarities between any number of samples taken from a single community or between a number of communities. These in turn may be analysed both from the point of view of the community as a whole or from the point of view of the species in the community (Margalef, 1974; Smith, 1980).

The present study aims at describing marine communities where they interact with *L. vulgaris*, and so the species approach, rather than the community approach, was taken.

When the community is analysed from the point of view of the species, indices of affinity between species may be employed as a way of describing that community. Two examples of this approach may be found in Margalef (1974) and Smith (1980). These two "affinity indices" both vary between -1 and 1 for a gradation between two species which display negative association (-1) or maximum positive association (1). The equations utilised do not, however, take into consideration other factors, which for the purposes of this work were considered important. Since sampling areas do not necessarily reflect the whole distribution area of either of the species being compared, simultaneous occurrence in most of the samples taken may reflect a very wide distribution of one of them, resulting in a necessary co-occurrence but not an affinity with the other. On the other hand, a small number of samples with one species may result from the species being on a fringe of its distribution or being rare but does not imply avoidance, and some affinity may exist. Another shortcoming of these equations is that they only reflect a "one sided" affinity, i.e. if species #1 co-occurs with species #2 in 100% of the samples with the former, they get an affinity score of 1, regardless of whether there are more samples with the latter or not. A different "affinity index" was thus considered necessary.

The reasons for some interactions between species in communities and ecosystems may be inferred from dietary studies. Several studies on cephalopod stomach contents (e.g. Castro and Guerra, 1990; Collins *et al.*, 1994; Guerra and Rocha, 1994; Rocha *et al.*, 1994), and others on the stomach contents of their predators, allowed a better understanding of trophic interactions. Prey items are generally fish, other cephalopods and annelids. Predators, as described by Summers (1983), include fish: sharks (Carrassón *et al.*, 1992; Dunning *et al.*, 1993); tuna and swordfish (Okutani and Tsukada, 1988; Rocha *et al.*, 1991; Dunning *et al.*, 1993; Guerra *et al.*, 1993; Seki, 1993); and an assortment of smaller fish (Yamamura *et al.*, 1993), seabirds and marine mammals. From these and other studies, a general consensus emerges on the overall important ecological role of cephalopods (Amaratunga, 1983; Nemoto *et al.*, 1985; Guerra, 1992; Boyle and Pierce, 1994). Squid in particular seem to establish complex trophic relations and other interactions with fish and cephalopods in the communities of the continental shelf.

In Portugal, marine communities have been classified and compared, with regard to the most abundant species (Serrão, 1989). The role of cephalopods in Portuguese communities has, however, not been described, except again for some trophic interactions deduced from dietary studies based on samples of Portuguese squid (Pierce *et al.*, 1994).

This study aims to assess: the degree of recurrence of each species or group of species of fish and cephalopods in samples with *L. vulgaris* in southern Portuguese waters, by providing a measure of the affinity between *L. vulgaris* and each one of those taxa; and the degree of variation of the fauna with the greatest affinity to *L. vulgaris* over time (between seasons and years) and with depth. These results will provide a better insight into the communities where *L. vulgaris* is found and thus, the extent of the role of this cephalopod species in the ecosystem. Partial attempts at explaining the associations observed are made by comparing the results obtained with known predator-prey interactions.

In addition, this study provides indicators of the presence of *L. vulgaris*.

MATERIAL AND METHODS

Data were collected over a period of five years, 1990 through 1995, except 1992, in 10 research cruises, comprising 301 bottom trawling stations, on board R/V "Mestre Costeiro", from Instituto de Investigação das Pescas e do Mar (IPIMAR). This vessel, a 27m long, 473HP, 147.7GT stern trawler is capable of operating in shallow waters, and, fitted with a crustacean–directed bottom–trawling net with a cod-end mesh size of 20mm, has proven to be an effective groundfish sampler. The sampling programme employed (Fig. 1), was aimed at obtaining information on the cephalopod species of the southern Portuguese coast, but all species of fish were also identified, counted and weighed. The pool of sampling stations considered was reduced to 267 from the total, reflecting the range of depths in which *L. vulgaris* occurs (up to 240 m).

The list obtained of all fish and cephalopod species on every valid trawl with at least one specimen of *L. vulgaris* was reduced in some families or genera in which the species are numerous and have similar habitats, or in cases where species identification in some cruises was not possible. Thus some families and genera were examined instead of their component species.

A percentage of co-occurrence between each of the taxa listed and *L. vulgaris* was obtained by:

$$Co_{(Lv)} = \frac{StLvA}{StLv} \times 100 \qquad (1)$$

where Co = Percentage co-occurrence, St = number of stations, A = taxum A, Lv = *L. vulgaris*, LvA = simultaneous occurrence of *L. vulgaris* and taxum A, StLv = total number of stations with at least one specimen of *L. vulgaris* (137).
Conversely, for each species compared to *L. vulgaris*:

$$Co_{(A)} = \frac{StLvA}{StA} \times 100 \qquad (2)$$

where StA = total number of stations with taxum A.

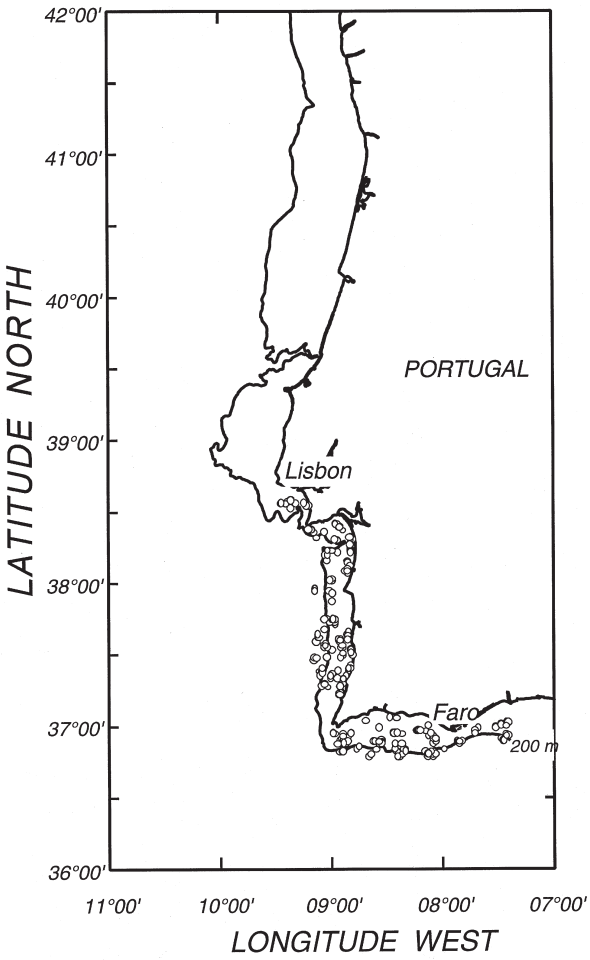

FIG. 1. – Distribution of the 301 trawling stations of the 5 year sampling programme. The coast line and the 200 m depth contour are represented.

In order to determine the degree of affinity between each of the taxa and *L. vulgaris*, an equation was developed, aiming at producing a numeric value (affinity index) increasing with the decreasing likelihood of accidental co-occurrence between the two, in the form:

$$AI = \frac{1 - \dfrac{StAxStLv}{StTxStLvA}}{1 - \dfrac{StLv}{StT}} \qquad (3)$$

where AI = affinity index and T = total number of stations considered (267). Equation (3) yielded numeric values between negative infinity and 0 for taxa which co-occurred with *L. vulgaris* in fewer occasions than expected for random encounters; between 0 and 1 for taxa which co-occurred with *L. vulgaris* more frequently than expected for random encounters; and 0 for a number of co-occurrences expected for random encounters.

This equation: underestimates the instances of a high percentage of co-occurrence between the two species if one of them is very common in the samples; overestimates the instances in which percentages of co-occurrence are low and one species is rare in the samples but seldom or never occurs without the other; and finally, produces a "two-sided" score (the result is equal whether the comparison is made from species #1 to species #2 or vice-versa).

For comparisons, taxa with AI scores between 0.5 and 1 were selected as those with high affinity to *L. vulgaris,* and no implications were made as to the meaning of the difference between an affinity of 0.5 and an affinity of 1.

Lists of taxa with AI of 0.5 and above were produced for the complete pool of samples: samples grouped by research cruise; samples grouped by four depth strata (0 to 50 m, 51 to 100 m, 101 to 150 m and 151 to 240 m), research cruises grouped by season of the year and research cruises grouped by year.

Pair-wise comparisons between lists of taxa (Mood *et al.,* 1974) were made by determining proportions of similarity:

$$p = \frac{x}{n} \qquad (4)$$

where p = proportion, x = number of matches (taxa occurring in either list in the pair) and n = total number of taxa in both lists. Then an average of the similarities between the pairs constituted by each list and every other list was calculated by:

$$\text{average} = \frac{x_1 + x_2 + \ldots + x_N}{n_1 + n_2 + \ldots + n_N} \qquad (5)$$

where subscripts represent each pair in comparison and N = total of pairs of lists being compared. The respective standard deviation was obtained from

$$\text{standard deviation} = \frac{\sqrt{n_1 p_1 q_1 + n_2 p_2 q_2 + \ldots + n_N p_N q_N}}{n_1 + n_2 + \ldots + n_N} \qquad (6)$$

where q=1-p.

Finally, the results of the comparisons of every pair of lists were plotted on graphs to provide a visual estimate of the degree of variation obtained.

RESULTS

A total of 87 taxa comprising 136 fish and 16 cephalopods were collected throughout the sampling period, corresponding to a Shannon-Wiener Index (Shannon and Weaver, 1949) score of 0.95. An average of 16 fish and 4 cephalopod taxa per trawling operation was obtained from the sampling programme.

Table 1 lists the 40 species, 17 genera and three fish families. Table 2 lists the 10 species, one genus and one cephalopod subfamily considered.

In the survey area overall, the community was dominated in frequency of occurrence (% occur) by the family Triglidae and species of the genus *Trachurus*, followed by: *Merluccius merluccius, Boops boops, Callyonimus lyra,* the genera *Pagellus, Microchirus,* and *Serranus, Scyliorhinus canicula* and the cephalopods *Alloteuthis subulata, Octopus vulgaris* and the genus *Eledone*. *L. vulgaris* was found in approximately half of the sampling stations

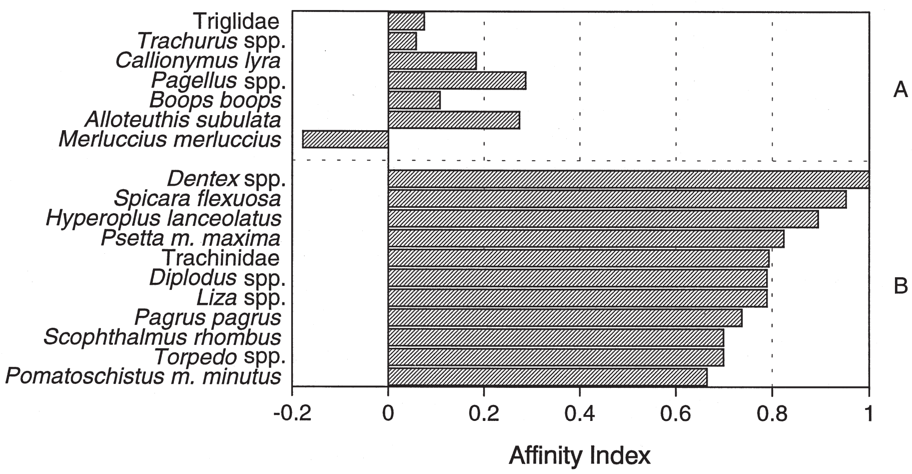

FIG. 2. – Affinity Index scores for (A) taxa occurring in at least 75% of the stations with *L. vulgaris* and (B) taxa within which stations of occurrence *L. vulgaris* was present at least 75% of the times. Taxa are ordered according to Co, equations (1) in A and (2) in B.

TABLE 1. – List of fish taxa considered. % Occur. (number of stations with each taxum divided by the total number of stations, in percentage), $Co_{(Lv)}$ (percentage of co-occurrence with *L. vulgaris*, from equation (1)), AI=Affinity Index; (–)=negative AI. AI calculations are based on all samples.

Family	Species	Common name	%Occur.	$Co_{(Lv)}$	AI
Ammodytidae	*Hyperoplus lanceolatus*	Greater sandeel	4.1	7.3	0.89
Apogonidae	*Epigonus telescopus*	Bigeye	0.7	0.7	(-)
Argentinidae	*Argentina sphyraena*	Argentine	50.9	37.2	(-)
Blenniidae	*Blennius ocellaris*	Butterfly blenny	8.6	7.3	(-)
Bothidae	*Arnoglossus* spp.	Scald fish	54.3	55.5	0.04
Callionymidae	*Callionymus lyra*	Common dragonet	71.2	78.1	0.18
Caproidae	*Capros aper*	Boarfish	50.6	27.7	(-)
Carangidae	*Trachurus* spp.	Jack, horse mackerels	86.5	89.1	0.06
Centracanthidae	*Spicara flexuosa*	Picarel	8.6	16.1	0.95
Cepolidae	*Cepola rubescens*	Redband fish	12.7	10.9	(-)
Chlorophthalmidae	*Chlorophthalmus agassizii*	Green eye	1.9	0.7	(-)
Citharidae	*Citharus linguatula*	Spotted flounder	40.1	35.8	(-)
Clupeidae	*Sardina pilchardus*	European sardine	37.8	48.9	0.47
“	*Sardinella aurita*	Round sardinella	0.7	1.5	1.00
“	*Sprattus sprattus*	Sprat	0.4	0.7	1.00
Congridae	*Conger conger*	European conger	43.1	39.4	(-)
Cynoglossidae	*Symphurus nigrescens*	Tongue sole	2.2	2.2	(-)
Engraulidae	*Engraulis encrasicholus*	European anchovy	10.1	13.1	0.47
Gadidae	*Gadiculus a. argenteus*	Silvery pout	10.9	5.1	(-)
“	*Micromesistius poutassou*	Blue whiting	21.7	13.9	(-)
“	*Phycis* spp.	Forkbeards	5.6	3.6	(-)
“	*Trisopterus luscus*	Pouting	7.1	9.5	0.51
Gobiidae	*Pomatoschistus m. minutus*	Spotted goby	10.9	16.1	0.66
Labridae	------------	Wrasses	2.6	2.2	(-)
Lophiidae	*Lophius* spp.	Angler fishes	24.7	14.6	(-)
Macrorhamphosidae	*Macrorhamphosus scolopax*	Longspine snipefish	51.3	37.2	(-)
Merlucciidae	*Merluccius merluccius*	European hake	81.0	74.5	(-)
Molidae	*Mola mola*	Sunfish	0.4	0.0	----
Mugilidae	*Liza* spp.	Mullets	2.2	3.6	0.79
Mullidae	*Mullus* spp.	Red mullets	58.1	65.7	0.24
Muraenidae	*Muraena helena*	Moray	0.4	0.7	1.00
Myliobatidae	*Myliobatis aquila*	Common eagle ray	1.1	1.5	0.47
Peristediidae	*Peristedion cataphractum*	Armed gurnard	2.6	2.2	(-)
Pleuronectidae	*Platichthys f. flesus*	European flounder	0.4	0.7	1.00
“	*Pleuronectes platessa*	European plaice	0.4	0.7	1.00
Rajidae	*Raja* spp.	Skates	53.9	56.2	0.08
Scombridae	*Scomber* spp.	“Scomber” mackerels	47.2	50.4	0.13
Scophthalmidae	*Lepidorhombus* spp.	Megrins	43.1	38.0	(-)
“	*Psetta m. maxima*	Turbot	2.6	4.4	0.82
“	*Scophthalmus rhombus*	Brill	3.4	5.1	0.70
Scorpaenidae	exc. *Helicolenus*	Scorpion fishes	20.2	22.6	0.22
“	*Helicolenus d. dactylopterus*	Rockfish	7.5	3.6	(-)
Scyliorhinidae	*Galeus melastomus*	Blackmouth catshark	0.7	0.7	(-)
“	*Scyliorhinus* spp.	Spotted dogfishes	61.8	54.7	(-)
Serranidae	*Anthias anthias*	Sea perch	3.7	4.4	0.30
“	*Serranus* spp.	Combers	62.9	66.4	0.11
Soleidae	*Dicologoglossa cuneata*	Little sole	6.7	7.3	0.16
“	*Microchirus* spp.	Thickback soles	64.0	65.0	0.03
“	*Solea* spp.	Soles	42.3	56.2	0.51
Sparidae	*Boops boops*	Bogue	71.9	75.9	0.11
“	*Dentex* spp.	Dentex	2.2	4.4	1.00
“	*Diplodus* spp.	Sargo breams	27.0	43.8	0.79
“	*Pagellus* spp.	Pandoras	65.9	76.6	0.29
“	*Pagrus pagrus*	Common seabream	7.5	11.7	0.74
“	*Spondyliosoma cantharus*	Black seabream	44.2	61.0	0.56
Torpedinidae	*Torpedo* spp.	Electric rays	3.4	5.1	0.70
Trachinidae	------------	Weevers	27.3	44.5	0.79
Trichiuridae	*Lepidopus caudatus*	Silver scabbardfish	27.3	16.8	(-)
Triglidae	------------	Gurnards	86.5	89.8	0.07
Uranoscopidae	*Uranoscopus scaber*	Stargazer	0.4	0.7	1.00
Zeidae	*Zeus faber*	Atlantic John dory	30.3	27.7	(-)

Common names from Sanches (1989)

(51.3%). The first six of the above mentioned taxa, together with *Alloteuthis subulata,* showed the highest percentages of co-occurrence with *L. vulgaris*.

AI scores for taxa occurring in at least 75% of the stations with *L. vulgaris* are generally low (Fig. 2A). These are taxa which are very common and do not

TABLE 2. – List of cephalopod taxa considered. % Occur. (number of stations with each taxum divided by the total number of stations, in percentage); $Co_{(Lv)}$ (percentage of co-occurrence with *L. vulgaris*, from equation (1)); AI=Affinity Index; (–)=negative AI. AI calculations are based on all samples.

Family (sub-Family)	Species	Common name	%Occur.	% Oc. with Lv	AI
Loliginidae	*Alloteuthis subulata*	European common squid	65.2	75.2	0.27
"	*Loligo forbesi*	Veined squid	15.4	14.6	(-)
Octopodidae	*Eledone* spp.	Horned and musky octopus	60.3	54.7	(-)
"	*Octopus defilippi*	Lilliput longarm octopus	0.7	0.7	(-)
"	*Octopus vulgaris*	Common octopus	62.5	65.7	0.10
Ommastrephidae	*Illex coindetii*	Broadtail shortfin squid	21	14.6	(-)
"	*Todaropsis eblanae*	Lesser flying squid	3.7	2.2	(-)
Sepiidae	*Sepia elegans*	Elegant cuttlefish	59.2	52.6	(-)
"	*Sepia officinalis*	Common cuttlefish	31.5	40.1	0.44
"	*Sepia orbignyana*	Pink cuttlefish	24	19.7	(-)
Sepiolidae (Rossinae)	*Rossia macrosoma*	Stout bobtail	3.4	0.7	(-)
" (Sepiolinae)	------------	Bobtail squids	23.6	19.0	(-)

Common names from Roper *et al*. (1984) and Sanches (1989).

occur with only *L. vulgaris*. On the other hand, those taxa within which stations of occurrence *L. vulgaris* was present at least 75% of the times, have AI scores closer to 1 (Fig. 2B). These are generally less abundant than *L. vulgaris* itself but co-occur with it in nearly every station where they were collected.

The list of 14 taxa which obtained AI scores with *L. vulgaris* between 1 and 0.5 for the complete pool

TABLE 3. – List of taxa with Affinity Index (AI) scores between 0.5 and 1 for stations grouped by depth strata. Gaps mean respective AI scores were inferior to 0.50.

Taxa	Depth strata (m)			
	0-50	51-100	101-150	151-240
Alloteuthis subulata				0.57
Anthias anthias	1.00	1.00		
Argentina sphyraena	1.00			
Blennius ocellaris	1.00			
Boops boops				0.50
Capros aper	1.00			
Dentex spp.	1.00	1.00		
Dicologoglossa cuneata	1.00	1.00		
Engraulis encrasicholus			0.86	
Helicolenus d. dactylopterus		1.00		
Hyperoplus lanceolatus	1.00			
Illex coindetii	1.00			
Labridae	1.00			
Lepidopus caudatus	1.00			
Lepidorhombus spp.		0.75		
Liza spp.	1.00			
Loligo forbesi	1.00		0.52	0.81
Lophius spp.	1.00			
Microchirus spp.	0.69			
Micromesistius poutassou	1.00			
Mullus spp.	0.50			
Octopus vulgaris				0.50
Pagrus pagrus		1.00		
Peristedion cataphractum			0.83	0.57
Phycis spp.		1.00		0.64
Pomatoschistus minutus	1.00		0.89	
Psetta m. maxima	1.00			
Scophthalmus rhombus			1.00	
Sepia orbignyana	1.00		0.53	
Sepiolinae	1.00			
Serranus spp.				0.57
Solea spp.			0.65	
Spicara flexuosa	0.59	1.00		
Symphurus nigrescens		1.00		
Torpedo spp.			1.00	0.86
Trisopterus luscus		1.00		1.00
Zeus faber	1.00			0.71

TABLE 4. – List of taxa with Affinity Index (AI) scores between 0.5 and 1 for the complete pool of stations.

Taxa	AI
Dentex spp.	1.00
Spicara flexuosa	0.95
Hyperoplus lanceolatus	0.89
Psetta m. maxima	0.82
Diplodus spp.	0.79
Liza spp.	0.79
Trachinidae	0.79
Pagrus pagrus	0.74
Scophthalmus rhombus	0.70
Torpedo spp.	0.70
Pomatoschistus m. minutus	0.66
Spondyliosoma cantharus	0.56
Solea spp.	0.51
Trisopterus luscus	0.51

of stations considered is given in Table 4. Eleven taxa correspond to the group in which stations of occurrence, *L. vulgaris* is present 75% or more of the times.

When calculations are based upon different sets of stations, the results are somewhat different, particularly where depths are concerned. Table 3 lists the 37 taxa in which at least one of the depth strata considered obtained an AI score equal to or greater than 0.5. It is perceivable that there is a minimal degree of overlap between the taxa occurring in each of the strata.

If each research cruise is considered a separate sample, AI scores between 1 and 0.5 reflect a greater degree of overlap between taxa lists (Table 5) than what was shown before. Thirty seven taxa are listed for comparisons between depth strata, but the individual taxa represented are not the same as before.

The greatest overlap in taxa lists is observed when research cruises are grouped by season and year (Tables 6 and 7, respectively). The lists of taxa with a high affinity to *L. vulgaris* are relatively stable throughout the year between 1990 and 1995,

TABLE 5. – List of taxa with Affinity Index (AI) scores between 0.5 and 1 for stations grouped by research cruise. Gaps mean respective AI scores were inferior to 0.50.

Taxa	Research cruises									
	Jan. 1990	Aug. 1990	Nov. 1990	Feb. 1991	May 1991	Jun. 1993	Nov. 1993	Feb. 1994	May 1994	May 1995
Alloteuthis subulata							0.50	0.51	1.00	
Anthias anthias		1.00	1.00			1.00				
Arnoglossus spp.	1.00									
Blennius ocellaris	1.00					1.00		1.00		
Cepola rubescens			0.54			0.50		1.00		
Citharus linguatula			0.67							
Dentex spp.	1.00	1.00	1.00		1.00		1.00			1.00
Dicologoglossa cuneata								1.00	1.00	1.00
Diplodus spp.	0.62	1.00	1.00	1.00	1.00	0.67		0.67	0.63	0.87
Engraulis encrasicholus			0.54		1.00	1.00				
Hyperoplus lanceolatus					1.00	0.50	1.00	1.00	1.00	1.00
Illex coindetii									1.00	
Labridae	1.00									1.00
Liza spp.			1.00			1.00				1.00
Loligo forbesi					1.00					
Lophius spp.										1.00
Microchirus spp.	0.59									
Micromesistius poutassou						1.00		1.00		
Mullus spp.										0.65
Pagellus spp.				0.73						
Pagrus pagrus		0.75			1.00	1.00	1.00		0.50	
Pomatoschistus m. minutus		1.00	1.00		0.64		1.00	0.61		
Psetta m. maxima			1.00		1.00		1.00	1.00		
Sardina pilchardus		0.58				0.75	0.71		0.78	0.84
Scomber spp.		0.64			0.82				0.60	
Scophthalmus rhombus			1.00				1.00	1.00		1.00
Scorpaena spp.				1.00				0.53	0.50	
Sepia officinalis		0.83			0.64	0.67				1.00
Sepiolinae			0.69				0.50	1.00		
Serranus spp.	0.67									
Solea spp.	0.71	0.71		0.68			0.50		0.57	
Spicara flexuosa	1.00		1.00	1.00	1.00	1.00	1.00	0.71	1.00	1.00
Spondyliosoma cantharus	1.00	0.79	0.74	1.00	0.64					0.79
Torpedo spp.		1.00		1.00						
Trachinidae	1.00	0.75	0.63	1.00	1.00		0.67	0.71	0.89	0.80
Trisopterus luscus		0.75			1.00	1.00		0.77		
Zeus faber							0.50			

TABLE 6. – List of taxa with affinity Index (AI) scores between 0.5 and 1 for research cruises grouped by season. Gaps mean respective AI scores were inferior to 0.50.

Taxa	Season			
	Winter	Spring	Summer	Autumn
Anthias anthias		0.50	1.00	
Dentex spp.	1.00	1.00	1.00	1.00
Dicologoglossa cuneata	1.00			
Diplodus spp.	0.78	0.77	1.00	0.74
Engraulis encrasicholus		0.83		
Hyperoplus lanceolatus	1.00	0.86		1.00
Labridae	1.00	0.50		
Liza spp.		1.00		
Pagellus spp.	0.53			
Pagrus pagrus	0.69	0.78	0.75	1.00
Pomatoschistus m. minutus			1.00	1.00
Psetta m. maxima	1.00	0.50		1.00
Sardina pilchardus		0.73	0.58	0.58
Scomber spp.			0.64	
Scophthalmus rhombus	1.00			1.00
Sepia officinalis		0.64	0.83	
Sepiolinae				0.69
Solea spp.			0.71	
Spicara flexuosa	0.84	1.00		1.00
Spondyliosoma cantharus	0.72	0.51	0.79	
Symphurus nigrescens				0.52
Torpedo spp.	0.75		1.00	
Trachinidae	0.87	0.82	0.75	0.61
Trisopterus luscus	0.58	0.50	0.75	

TABLE 7. – List of taxa with Affinity Index (AI) scores between 0.5 and 1 for research cruises grouped by year. Gaps mean respective AI scores were inferior to 0.50.

Taxa	Year				
	1990	1991	1992	1994	1995
Anthias anthias	0.69			1.00	
Blennius ocellaris			1.00		
Dentex spp.	1.00	1.00	1.00		1.00
Dicologoglossa cuneata				1.00	1.00
Diplodus spp.	0.92	1.00	0.58	0.64	0.87
Engraulis encrasicholus		0.79	0.67		
Hyperoplus lanceolatus		1.00	0.67	1.00	1.00
Labridae					1.00
Liza spp.	1.00		0.50		1.00
Loligo forbesi		0.69			
Lophius spp.					1.00
Mullus spp.					0.65
Pagrus pagrus	0.59	1.00	1.00		
Pomatoschistus m. minutus	1.00	0.58	1.00		
Psetta m. maxima	1.00	1.00	0.50	1.00	
Sardina pilchardus			0.73		0.84
Scophthalmus rhombus	1.00		1.00		1.00
Scorpaena spp.		0.62		0.52	
Sepia officinalis	0.59		0.50		1.00
Sepiolinae				0.57	
Solea spp.	0.59	0.58			
Spicara flexuosa	1.00	1.00	1.00	0.88	1.00
Spondyliosoma cantharus	0.74	0.81			0.79
Torpedo spp.	0.75	0.69			
Trachinidae	0.75	1.00	0.50	0.81	0.80
Trisopterus luscus		1.00	1.00	0.57	

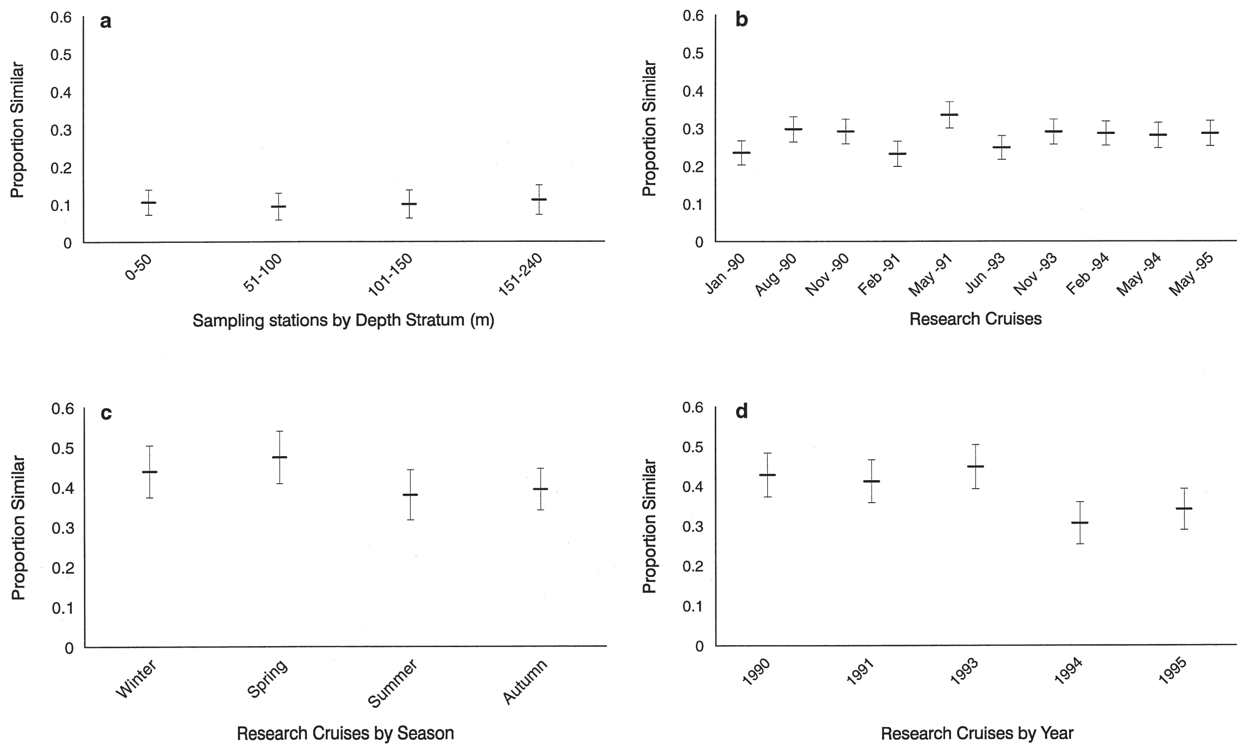

FIG. 3. – Multiple pair-wise comparisons between taxa lists. Each point in each graph represents a comparison between the list of taxa for that situation and every other list for the other situations represented in the same graph.

with proportions of similarity in either case of approximately 0.40. The two lists together represent 28 different taxa.

Overall, 47 taxa (77% of the total considered) displayed affinity indices of 0.5 or more in at least one of the factors assayed.

Figure 3 depicts multiple comparisons between every list of taxa and every other for each of the four situations described previously: (a) sampling stations by depth stratum; (b) sampling stations by research cruise; (c) research cruises by season; and (d) by year. From this figure it is possible to quickly visualise which of the analysed factors results in greater similarities between the lists of taxa and, conversely, which are the most important in determining variations.

DISCUSSION

The 136 fish species collected represent the benthic and benthopelagic communities associated with *L. vulgaris* in the south and southwest coasts of Portugal. These species correspond to the range characteristic of subtropical demersal fish communities: 140 in the Alboran Sea (Simarro, 1993); 93 in southern Brazil (Haimovici *et al.*,1994); 98 in Mississippi/Alabama (Brooks and Wolf, 1991); 141 in the Pacific coast of Mexico (Coronado-Molina and Amezcua-Linares, 1988); and 105 (Rodriguez-Capetillo *et al.*, 1987) to 152 (Yanez-Arancibia and Sanchez-Gil, 1986) in the southern Gulf of Mexico. References to counts of cephalopod species were only encountered for tropical Australia, where Dunning *et al.* (1994) recorded 21, a number comparable to that (16) in this study. These taxa lists are not constant in number or composition of species from study to study, as is evident from the two studies referenced above from the southern Gulf of Mexico. Nevertheless one would expect greater similarities between neighbouring communities than between those further apart, and thus a set of species lists representing a certain community or ecosystem in a relatively restricted area, such as the southwestern and southern coasts of Portugal, may be a valuable descriptor and more so if there can be an evaluation of which species preferentially occur with which others.

The “fidelity” with which sets of species remain together in marine communities seems to depend largely on physical factors, particularly bottom depth (Smith, 1980), which is noticeable in this study (Fig. 3a). The taxa which showed high affinities to *L. vulgaris* in each of the depth strata defined, varied more than in any of the other factors assayed (research cruises, seasons and years). Comparisons between lists of taxa with high affinities to *L. vulgaris* obtained from each research cruise (Fig. 3b), showed the next largest differences, followed by comparisons between seasons (Fig. 3c) (seasonality apparently has a small influence in the composition of the group of species with high affinities to *L. vulgaris*), and comparisons between years (Fig. 3d).

These results seem to suggest the hypothesis that under similar environmental conditions *L. vulgaris* remains close to a limited group of taxa, that group varying slightly in composition which may, perhaps, result from differences in the abundance of each species (probably independent of the abundance of others). Under slightly different environmental factors, the composition of the "preferred" taxa may vary and may be perceived as something progressive rather than abrupt, since it may also affect each species differently and independently. This may be what is being displayed by the proportions of similarity of around 0.40 in the comparisons between seasons and between years. Under greater changes, such as those resulting from greatly different depths, more of the taxa in the list would change, as may be seen in Figure 3d where proportions of similarity vary slightly around 0.10.

Another hypothesis may be that *L. vulgaris* has a “preferred” limited group of species with which it is usually found, but in no circumstances does the sampling method employed ever catch them all together, possibly because many are less abundant than itself and most of them are seldom with it at the same time. Thus its “preferences” may appear to change under slightly different conditions or from place to place, resulting in relatively large fluctuations between research cruises. On the other hand, and since it occurs over a wider depth range than many other taxa, the list of its “preferred” taxa over great depth ranges will effectively change and only those with similar or greater depth ranges of occurrence maintain high affinities to it throughout the depth strata.

The reasons why *L. vulgaris* should be associated with a group of other species are, and will probably remain, a mystery, at least for as long as the behaviour of marine species and their time-activity budgets remain largely inaccessible. It is possible, however, to speculate that the most important reasons may be related to trophic interactions. Therefore it seems logical to look for similarities between lists of predators and prey of *L. vulgaris* and the lists of taxa which were seen to display a high affinity to the species, although matches are merely indicative.

The diet of *L. vulgaris* (Pierce *et al*., 1994; Guerra and Rocha, 1994; Rocha *et al*. 1994) shows an extended feeding spectrum, including phytophages, zooplankton-eaters and predators. Loliginid squids in turn are a prey item for many predators of the third and fourth trophic level.

Among those taxa co-occurring in 75% or more of the samples with *L. vulgaris*, *Callionymus lyra* and *Alloteuthis* spp. are known prey (Pierce *et al*., 1994); *Trachurus trachurus* is prey (Guerra and Rocha, 1994) as well as predator (Murta *et al.,* 1993); and *Pagellus* spp., the family Triglidae and *Merluccius merluccius* are known predators (Macpherson, 1979; Domanevskaya and Patokina, 1985; González *et al.,* 1985). Some of the taxa with which *L. vulgaris* occurs in at least 75% of the samples are prey, such as *Diplodus* spp. (Pierce *et al.,* 1994), *Hyperoplus lanceolatus* (Pierce *et al.,* 1994; Guerra and Rocha, 1994; Rocha *et al*., 1994) and *Pomatoschistus minutus* (Pierce *et al.,* 1994) while others, such as *Echiitys vipera* (family Trachinidae) and *Torpedo* spp. are predators (Creutzberg and Duineveld, 1986; Abdel-Aziz, 1994). Other predators of Loliginid squid, such as *Micromesistius poutassou* (Macpherson, 1978), *Dicologoglossa cuneata, Citharus linguatula* (Belghyti *et al.,* 1993) and *Illex coindetii* (González, 1994), although displaying low co-occurrences with *L. vulgaris*, had affinity index scores of 0.5 and above in at least one of the factors assayed with the samples, the same being true for several taxa of its prey, such as *Argentina sphyraena, Blennius ocellaris, Cepola rubescens, Helicolenus d. dactylopterus, Loligo forbesi, Micromesistius poutassou, Octopus vulgaris, Sardina pilchardus,* the Sepiolidae and *Trisopterus luscus* (Guerra and Rocha, 1994; Pierce *et al.,* 1994; Rocha *et al.,* 1994).

These predator-prey relationships probably depend greatly upon circumstances and reflect the typical opportunistic feeding behaviour which has been described for loliginid squid. Many other explanations for the affinities encountered may be examined (and some others should be), many requiring techniques and materials not yet readily available.

The role of *L. vulgaris* in the marine communities of the south and southwestern Atlantic coasts of Portugal appears to be an important one, not just for the many and complicated trophic interactions which may be inferred from previous studies, but also for the high affinities which under one situation or another the species displays with a very large proportion of the list of taxa sampled during the five-year study reported here. *L. vulgaris* is a widespread and abundant species, which, from the results in this study, may be considered a key species in Portuguese coastal waters.

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