Trophic relationships among cephalopod species along the water column inferred from stomach contents and stable isotope analyses

S. Keller*, A. Quetglas, M. Valls, F. Ordines, A. de Mesa and E. Massutí
Instituto Español de Oceanografía, Centre Oceanogràfic de les Balears, Moll de Ponent, s/n, 07015 Palma, Spain.
*Fax: +34971404945 *E–mail: stefanie.keller@ba.ieo.es*

Introduction

It is well known that cephalopods play a key role in the marine food webs, either as voracious predators or important prey of a large set of predators. In this study we investigated the trophic relationships among cephalopod species taken along the water column by means of stomach content and stable isotope analyses. With the main aim of determining if there are fluxes of matter between nectobenthic and pelagic domains mediated by cephalopods, we analysed different aspects such as diet composition, niche breadth, diet overlap, diet seasonal differences and day-night feeding rhythms from samplings conducted in the western Mediterranean during two seasons with contrasting oceanographic conditions.

Material and methods

Samples were collected on the shelf (200 m depth, bathymetric stratum 1) and slope (600-900 m, bathymetric stratum 2) during summer and autumn surveys. At the shelf bathymetric stratum, sampling was carried out at: 1) near surface (SUR1) from 0-60 m; 2) in the benthic boundary layer (BBL1), less than 50 m above the bottom; and 3) on the bottom (BOT1). At the slope bathymetric stratum, sampling was performed at: 1) near surface (SUR2) from 0-80 m depth; 2) in the 400-600 m deep scattering layers (DSL); 3) on the bottom (BOT2). For comparative purposes, a few hauls were also performed near the bottom in this slope bathymetric stratum (BBL2). In all cases, SUR, BBL and DSL samplings were performed using a mid-water trawl, while the BOT samplings using a bottom trawl. The stomachs of all cephalopod individuals caught in these samplings were analyzed, with the only exception of a few cases where random samples were taken owing to the large amount of available material. Whenever possible, a sample of three individuals per species was collected for carbon and nitrogen stable isotope analyses (SIA).

In all the diet analyses shown, only those species with a number of stomachs ≥10 were used. Diet overlap and niche breadth were obtained with Ecological Methodology software v7.0 (Krebs 1999), whereas similarity analysis (SIMPER) and dietary indexes were calculated using PRIMERv6.1.6 (Clarke & Gorley 2006).

Species composition

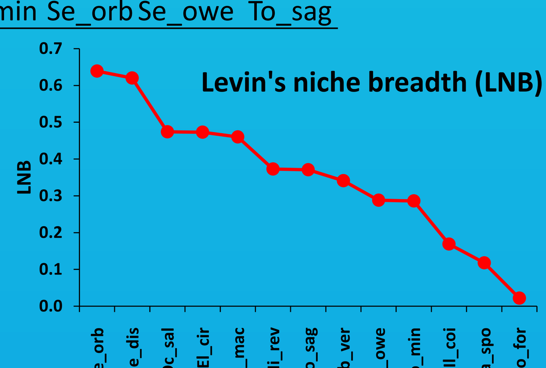
A total of 1286 stomachs from 26 cephalopod species belonging to 12 Families were analyzed.

	Species	Family	Nstomachs	Sprey	Nprey items
1	*Abralia veranyi*	Enoploteuthidae	192	11	61
2	*Alloteuthis media*	Loliginidae	10	3	9
3	*Ancistrocheirus lesueurii*	Ancistrocheiridae	1	0	0
4	*Ancistroteuthis lichtensteinii*	Onychoteuthidae	6	3	6
5	*Bathypolypus sponsalis*	Octopodidae	31	7	79
6	*Chiroteuthis veranii*	Chiroteuthidae	1	0	0
7	*Eledone cirrhosa*	Octopodidae	133	21	101
8	*Heteroteuthis dispar*	Sepiolidae	39	7	20
9	*Histioteuthis bonnellii*	Histioteuthidae	3	2	2
10	*Histioteuthis reversa*	Histioteuthidae	86	16	64
11	*Illex coindetii*	Ommastrephidae	264	28	516
12	*Loligo forbesi*	Loliginidae	110	30	1228
13	*Neorossia caroli*	Sepiolidae	2	2	2
14	*Octopus salutii*	Octopodidae	18	8	17
15	*Octopus vulgaris*	Octopodidae	1	1	2
16	*Onychoteuthis banksii*	Onychoteuthidae	1	0	0
17	*Opisthoteuthis calypso*	Opisthoteuthidae	4	2	3
18	*Pteroctopus tetracirrhus*	Octopodidae	8	9	13
19	*Rossia macrosoma*	Sepiolidae	72	19	45
20	*Rondeletiola minor*	Sepiolidae	51	5	19
21	*Scaeurgus unicirrhus*	Octopodidae	2	0	0
22	*Sepia orbignyana*	Sepiidae	20	17	29
23	*Sepietta oweniana*	Sepiolidae	172	13	101
24	*Taonius pavo*	Cranchiidae	1	1	1
25	*Todaropsis eblanae*	Ommastrephidae	1	0	0
26	*Todarodes sagittatus*	Ommastrephidae	57	28	101

Diet overlap

Percentage diet overlap (Schoener index)

	Ab_ver	Ba_spo	El_cir	He_dis	Hi_rev	Il_coi	Lo_for	Oc_sal	Ro_mac	Ro_min	Se_orb	Se_owe	To_sag
Ab_ver	100.0												
Ba_spo	6.0	100.0											
El_cir	11.5	20.1	100.0										
He_dis	56.6	6.0	15.4	100.0									
Hi_rev	65.7	11.7	18.2	53.1	100.0								
Il_coi	33.7	3.3	9.3	17.2	49.0	100.0							
Lo_for	8.1	0.5	2.4	10.4	17.4	49.1	100.0						
Oc_sal	1.4	15.3	46.7	0.0	5.7	7.0	0.3	100.0					
Ro_mac	44.6	10.3	23.3	27.6	39.9	26.3	3.6	11.8	100.0				
Ro_min	49.1	6.0	15.4	59.7	39.1	4.8	2.0	0.0	27.3	100.0			
Se_orb	25.0	1.2	26.9	22.3	30.4	23.4	6.1	10.3	54.5	14.6	100.0		
Se_owe	68.6	7.1	13.4	40.1	62.3	37.7	6.1	0.0	47.4	34.2	34.0	100.0	
To_sag	36.8	3.0	18.4	21.9	46.2	43.9	4.1	10.8	34.4	11.8	33.0	47.0	100.0



Significant diet overlap (Schoener index>0.6) was only found for a reduced number of species (*Abralia veranyi* vs *Histioteuthis reversa* vs *Sepietta oweniana;* and *Heteroteuthis dispar* vs *Rondeletiola minor*). *Loligo forbesi* displayed the most specialized diet (LNB=0.02), whereas *Sepia orbinyiana* and *H. dispar* were the most generalist (LNB=0.6); for all other species this index ranged from 0.12 to 0.47.

Prey composition along the water column

Pelagic hauls were carried out in the strongest and widest acoustic sound layers of the water column, using a Simrad EK60 echosounder at 18, 38, 70, 120 and 200 kHz. The images (echograms) are only two examples from the continental shelf and slope showing the different layers analyzed.

CONTINENTAL SHELF

SUR1

Average similarity: 26.36	SIMPER				
Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Teleost unidentified	4.9	21.3	0.6	80.7	80.7
Natantia unidentified	2.4	4.6	0.3	17.3	98.0

Sprey	Nprey items	Species richness (d)	Pielou's evenness (J')	Shannon diversity (H')	EMI
9	36	2.23	0.81	1.77	48.7

BBL1

Average similarity: 56.06	SIMPER				
Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Teleost unidentified	7.5	54.6	1.1	97.3	97.3

Sprey	Nprey items	Species richness (d)	Pielou's evenness (J')	Shannon diversity (H')	EMI
3	15	0.74	0.57	0.63	76.5

BOT1 — 200 m

Average similarity: 12.28	SIMPER				
Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Teleost unidentified	2.9	7.7	0.3	62.9	62.9
Meganyctiphanes norvegica	1.3	1.5	0.2	12.2	75.1
Maurolicus muelleri	1.2	1.2	0.1	9.6	84.6
Natantia unidentified	1.0	1.0	0.1	8.3	92.9

Sprey	Nprey items	Species richness (d)	Pielou's evenness (J')	Shannon diversity (H')	EMI
64	2035	8.27	0.47	1.94	40.4

CONTINENTAL SLOPE

SUR2 — 200 m

Average similarity: 16.27	SIMPER				
Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Natantia unidentified	3.2	9.3	0.4	57.0	57.0
Teleost unidentified	1.7	2.4	0.2	14.7	71.6
Meganyctiphanes norvegica	1.6	2.1	0.2	13.2	84.8
Nematoscelis megalops	1.4	1.5	0.1	9.1	93.9

Sprey	Nprey items	Species richness (d)	Pielou's evenness (J')	Shannon diversity (H')	EMI
15	69	3.31	0.86	2.34	36.5

Both on the shelf and the slope, the diversity was highest on the bottom and lowest on the BBL.

DSL — 400 m

Average similarity: 18.58	SIMPER				
Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Natantia unidentified	3.5	11.0	0.4	59.2	59.2
Teleost unidentified	2.7	6.0	0.3	32.3	91.5

Sprey	Nprey items	Species richness (d)	Pielou's evenness (J')	Shannon diversity (H')	EMI
14	65	3.11	0.82	2.17	42.9

Along the water column, cephalopod trophic chains were based on fishes on the shelf but on crustaceans on the slope.

600 m

BBL2

Average similarity: 26.67	SIMPER				
Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Natantia unidentified	5.0	20.0	0.5	75.0	75.0
Ceratoscopelus maderensis	3.3	6.7	0.3	25.0	100.0

Sprey	Nprey items	Species richness (d)	Pielou's evenness (J')	Shannon diversity (H')	EMI
3	6	1.12	0.92	1.01	20.0

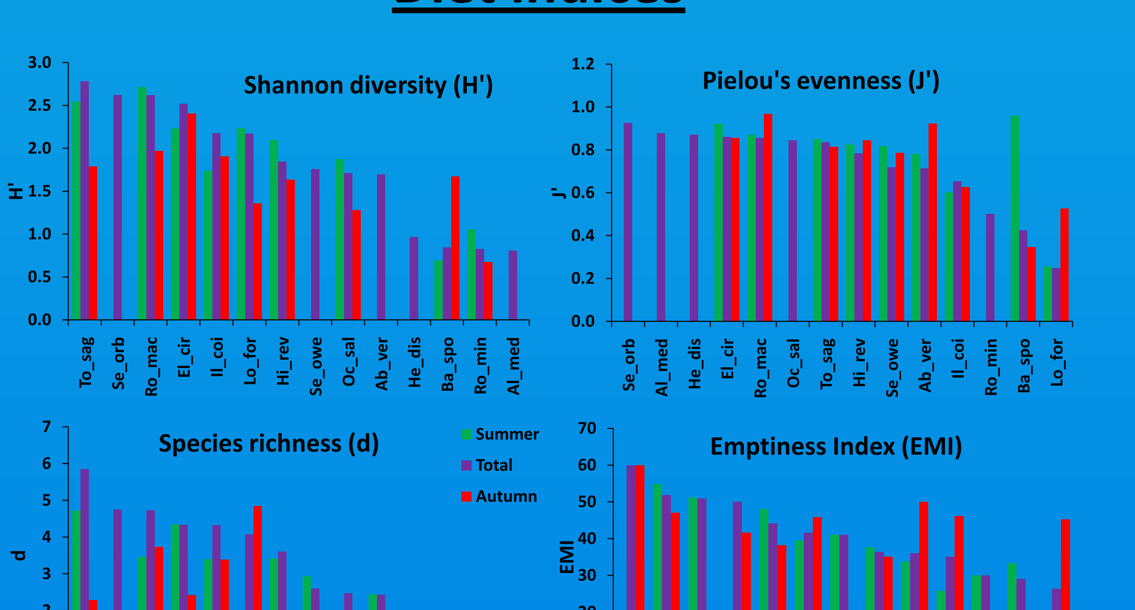
800 m

BOT2

Average similarity: 14.47	SIMPER				
Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Teleost undetermined	2.8	7.0	0.3	48.1	48.1
Crustacean undetermined	2.6	6.3	0.3	43.3	91.3

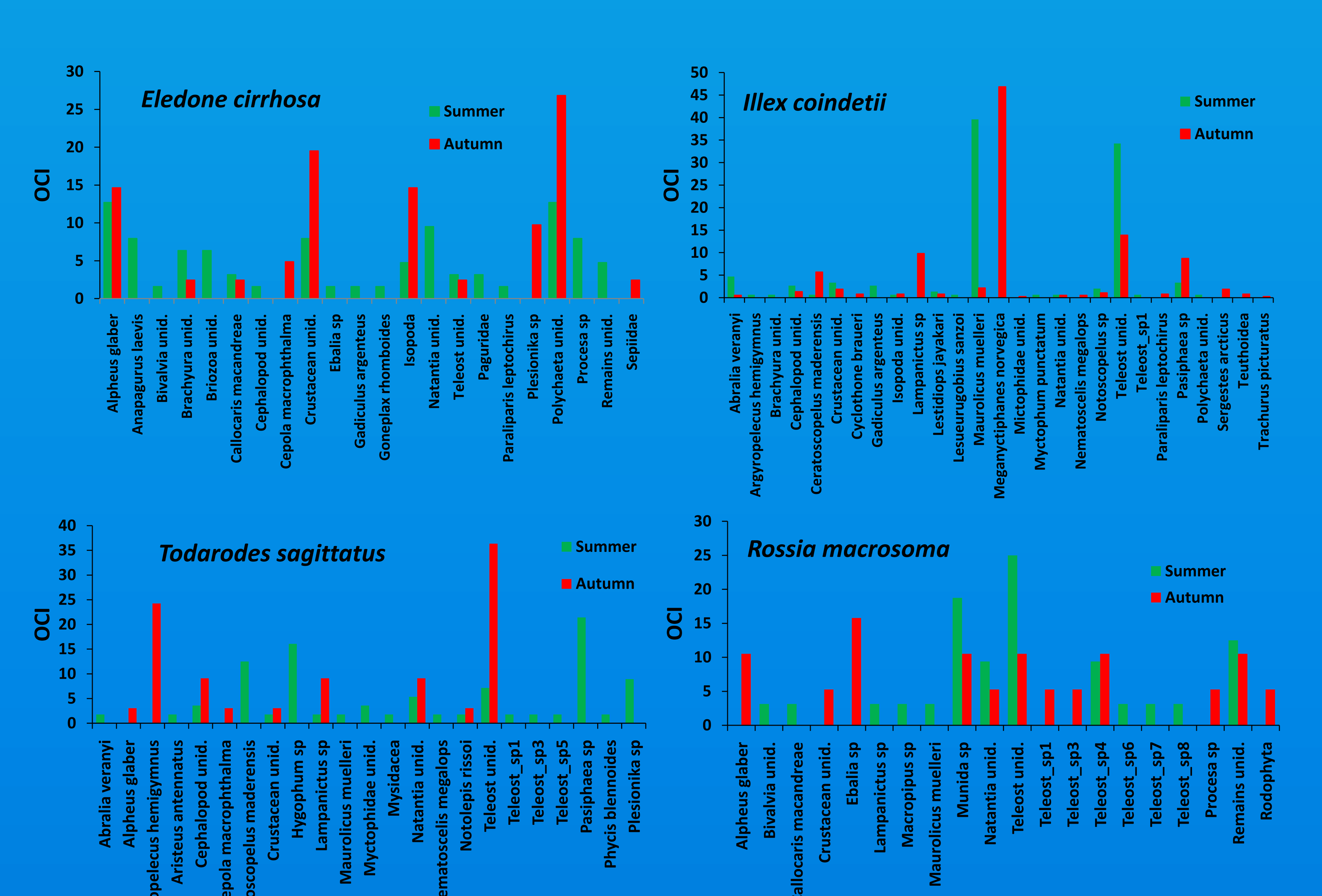
Sprey	Nprey items	Species richness (d)	Pielou's evenness (J')	Shannon diversity (H')	EMI
35	193	6.46	0.72	2.56	51.5

Diet indices



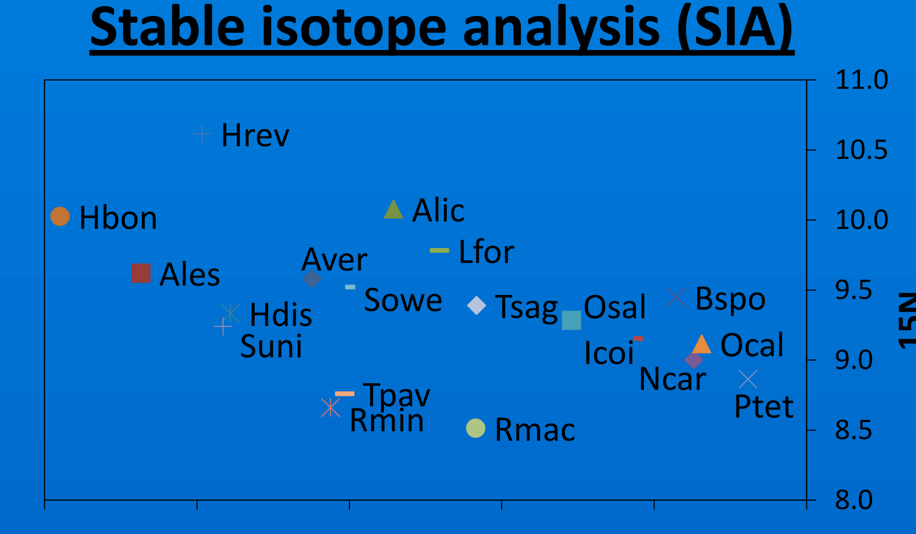
There were not clear homogeneous seasonal trends for the diet indexes shown. However, most species had higher H' values in summer than in autumn (6 vs 3). Although EMI did not display important seasonal differences, autumn values were notoriously higher than summer values in some species (*Histioteuthis reversa, Todarodes sagittatus* and *Loligo forbesi*).

Diet composition per species



In most species diet composition changed with season (summer, autumn). The figures show some examples in terms of occurrence index (OCI) for four different species.

Stable isotope analysis (SIA)



Stable isotope analysis (SIA) clearly separated typical pelagic species such as *Histioteuthis* sp (upper left-hand side) from typical benthic species such as *Pteroctopus tetracirrhus* (down right-hand side). Interestingly, species such as *Illex coindetii and Todarodes sagittatus,* which are considered important nictemeral migrators (Jereb & Roper 2010), were closer to the benthic than to the pelagic species.

Diet differences during day-night cycle

Todarodes sagittatus

DAY		
Average similarity: 17.77	SIMPER	
Species	Av.Abund	Contrib%
Teleost unidentified	4.3	84.8
Natantia unidentified	1.2	5.3

NIGHT		
Average similarity: 12.21	SIMPER	
Species	Av.Abund	Contrib%
Teleost unidentified	2.8	45.2
Hygophum sp	2.6	37.1
Plesionika sp	1.2	7.2
Natantia unidentified	1.11	6.59

Histioteuthis reversa

DAY		
Average similarity: 13.67	SIMPER	
Species	Av.Abund	Contrib%
Teleost unidentified	3.3	65.6
Natantia unidentified	2.2	29.1

NIGHT		
Average similarity: 19.26	SIMPER	
Species	Av.Abund	Contrib%
Natantia unidentified	3.5	55.5
Meganyctiphanes norvegica	2.2	20.0
Teleost unidentified	2.1	17.9

Abralia veranyi

DAY		
Average similarity: 28.92	SIMPER	
Species	Av.Abund	Contrib%
Natantia unidentified	4.4	61.8
Teleost unidentified	3.4	33.7

NIGHT		
Average similarity: 28.41	SIMPER	
Species	Av.Abund	Contrib%
Teleost unidentified	4.8	71.6
Natantia unidentified	2.9	24.8

Some species showed important differences in diet during the day-night cycle. *H. reversa*, for instance, consumed preferentially fishes (66%) during the day but natantian crustaceans (76%) during the night. The contrary is true for *A. veranyi*, which based its diet on natantians (62%) during daylight but on fishes (72%) at night. Other species, such as *T. sagittatus*, did not show important differences, preying mostly on fishes both at day (85%) and night (82%).

Diet changes along the water column

Histioteuthis reversa		SIMPER					
Layer	Av. Similarity	Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
SUR2	22.28	Natantia unidentified	4.2	14.9	0.5	66.7	66.7
		Meganyctiphanes norvegica	2.4	4.4	0.2	19.9	86.5
		Teleost unidentified	1.7	2.1	0.2	9.5	96.0
DSL	14.16	Teleost unidentified	3.1	7.2	0.3	50.9	50.9
		Natantia unidentified	2.5	4.6	0.2	32.1	83.0
		Cephalopod unidentified	1.7	1.5	0.1	10.7	93.7
BBL2	33.33	Natantia unidentified	6.7	33.3	0.6	100.0	100.0
BOT2	20.26	Teleost unidentified	4.7	18.4	0.6	91.0	91.0
		Crustacean unidentified	1.8	1.8	0.1	9.0	100.0

Diet changed depending on the position along the water column. In our case, this analysis was only possible for a single species, *H. reversa,* which is supposed to perform nictemeral migrations in our study area (Quetglas et al. 2010). Excluding the BBL2 case, which only contained 5 stomachs, the importance of fishes decreased and that of crustaceans increased from the bottom to the sea surface.

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