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Influence of upwelling conditions on feeding habits and trophic position of planktophagous fish

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INTRODUCTION

Food web relationships are essential in ecosystem studies. Coupling of stomach content analyses and isotopic data provide a comprehensive analysis of fish trophic relations by integrating an instantaneous record of diet with the isotopic information which reflects the food assimilated by an organism during an extended time preceding the sampling.

The importance of environmental phenomena in food web variability has been to date poorly documented. We analyze the effect of different upwelling conditions on the functioning of a planktonic food web. We hypothesize that differences in isotopic ratios under these contrasting upwelling intensities possibly originate from both changes in the isotopic signature of basal levels and shifts in the feeding habits of planktophagous fish species.

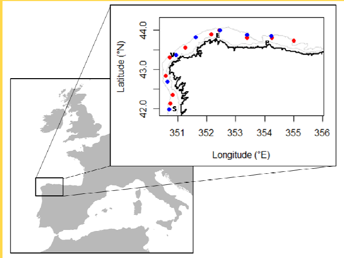

Figure 1. Map of the study area showing sampling points in 2012 (red) and 2013 (blue). Buoys measuring upwelling intensity are signalised by their first letter. Isobaths of 100 and 200 m are shown by grey lines.

MATERIAL & METHODS

The effect of upwelling conditions on the trophic level of four planktofagous fish (*Gadiculus argenteus*, *Capros aper* and juveniles of *Micromesistius poutassou* and *Merluccius merluccius*) on the continental shelf off Northwestern Spain was assessed by coupling stomach content analyses and isotopic data. Sampling was carried out in autumn along a transect parallel to the coast on the continental shelf at 130-180 m depth (Figure 1) along following the upwelling intensity gradient. In addition, the study was performed in two contrasting years: 2012 characterised by an intermittent and weak upwelling season and 2013 with an intense and extended upwelling period (Figure 2). In addition to stomach content and isotopic analyses of fish muscle, the isotopic signature of benthic detritus and sub-superficial phytoplankton were also identified to characterize the basal isotopic level.

PREY GROUP / SPECIES	*Capros aper*		*Gadiculus argenteus*		*Merluccius merluccius*		*Micromesistius poutassou*	
Year	2012	2013	2012	2013	2012	2013	2012	2013
Decapoda natantia	0.00	0.00	0.00	0.00	0.63	0.00	0.00	0.00
Processa sp.	0.00	0.00	0.00	0.00	0.31	0.00	0.00	0.00
Solenocera membranacea	0.00	0.00	0.00	0.00	0.10	0.00	0.00	0.00
Epibenthos	0.00	1.32	0.00	0.00	0.00	0.00	0.00	0.00
Hydroidea	0.00	0.44	0.00	0.00	0.00	0.00	0.00	0.00
Ophiuroidea	0.00	0.88	0.00	0.00	0.00	0.00	0.00	0.00
Gelatinous zooplankton	5.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chaetognata	0.28	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Jellyfish	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Salpidae	2.74	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Siphonophora	2.55	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Macrozooplankton	14.93	0.00	39.27	0.00	0.84	60.38	2.46	48.34
Eucarida	5.39	0.00	70.73	88.32	96.76	87.74	97.42	46.36
Euphausiid	0.00	0.00	55.12	56.07	96.76	87.74	97.42	46.36
Meganyctiphanes norvegica	0.00	0.00	0.00	0.00	0.00	59.43	0.00	13.91
Nyctiphanes couchii	0.00	0.00	37.68	0.00	0.00	0.00	0.00	0.00
Calyptopis	0.00	0.00	0.12	0.00	0.00	0.00	0.00	0.00
Furcilia	0.00	0.00	0.12	0.00	0.00	0.00	0.00	0.00
Mysidacea	5.39	0.00	0.85	0.00	0.00	0.00	0.00	0.00
Hypperiidae	8.79	0.00	0.49	0.00	0.84	0.94	2.46	34.44
Crustacean megalopa	0.57	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Crustacean zoea	0.19	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mesozooplankton	49.05	6.37	26.34	9.81	0.00	0.00	0.00	0.00
Copepod	24.10	3.08	26.83	9.66	0.00	0.00	0.00	0.00
Aechaetus sp.	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Aetidius sp.	3.69	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Calanus helgolandicus	0.76	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Caligus sp.	1.04	1.76	0.00	0.00	0.00	0.00	0.00	0.00
Calocalanus sp.	0.00	0.00	0.24	0.00	0.00	0.00	0.00	0.00
Candacia armata	3.97	0.22	3.90	0.16	0.00	0.00	0.00	0.00
Ditrichius sp.	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Macrosetella rosea	0.38	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Metridia lucens	1.61	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Paracalanus sp.	0.00	0.00	0.24	0.00	0.00	0.00	0.00	0.00
Paraeuchaeta sp.	1.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Pleuromamma sp.	0.28	0.00	0.37	0.00	0.00	0.00	0.00	0.00
Pseudocalanus sp.	0.00	0.00	0.49	0.00	0.00	0.00	0.00	0.00
Temora sp.	0.09	0.00	0.12	0.16	0.00	0.00	0.00	0.00
Copepod nauplii	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Unidentified calanoid <0.7 mm	0.09	0.66	0.00	0.00	0.00	0.00	0.00	0.00
Unidentified calanoid >1.5 mm	2.36	0.00	0.00	0.47	0.00	0.00	0.00	0.00
Unidentified calanoid 0.7- 1 mm	1.61	0.22	0.00	3.43	0.00	0.00	0.00	0.00
Unidentified calanoid 1- 1.5 mm	6.90	0.22	20.73	5.45	0.00	0.00	0.00	0.00
Harpacticoide	0.28	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Meroplankton	19.09	3.30	0.00	0.16	0.00	0.00	0.00	0.00
Cirripeda larvae	0.00	0.22	0.00	0.00	0.00	0.00	0.00	0.00
Decapoda larvae	7.37	2.86	0.00	0.16	0.00	0.00	0.00	0.00
Polychaete larvae	0.57	0.22	0.00	0.00	0.00	0.00	0.00	0.00
Veliger larvae	11.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cladocero	0.28	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ostracoda	5.29	0.00	0.24	0.00	0.00	0.00	0.00	0.00
Suprabenthos	6.62	43.08	0.61	0.00	0.31	2.83	0.00	0.00
Lophogaster typicus	0.00	0.00	0.00	0.00	0.31	2.83	0.00	0.00
Amphipoda	6.14	39.56	0.61	0.00	0.00	0.00	0.00	0.00
Caprellidae	3.88	24.18	0.00	0.00	0.00	0.00	0.00	0.00
Gammaridae	2.27	15.16	0.12	0.00	0.00	0.00	0.00	0.00
Isopoda	0.38	3.52	0.00	0.00	0.00	0.00	0.00	0.00
Gnatidae	0.28	3.52	0.00	0.00	0.00	0.00	0.00	0.00
Tanaidacea	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Teleost fish	0.00	0.00	0.12	0.31	1.36	7.55	0.12	17.22
Arnoglossus sp.	0.00	0.00	0.00	0.00	0.10	0.00	0.00	0.00
Gadiculus argenteus	0.00	0.00	0.00	0.00	0.42	0.00	0.00	0.00
Maurolicus muelleri	0.00	0.00	0.00	0.00	0.00	0.00	0.00	13.91
Micromesistius poutassou	0.00	0.00	0.00	0.00	0.10	0.00	0.00	0.00
Unidentified Gobidae	0.00	0.00	0.00	0.00	0.10	0.00	0.00	0.00
Other prey	23.72	49.23	0.98	1.56	0.10	0.94	0.00	1.99
Fish scales	0.57	9.45	0.00	0.00	0.00	0.00	0.00	0.00
Unidentified Cephalopoda	0.00	0.00	0.00	0.00	0.10	0.00	0.00	0.00
Unidentified prey	0.76	15.60	0.98	1.56	0.00	0.94	0.00	1.99
Foraminifera	9.36	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Colonial diatoms	2.84	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Invertebrate eggs	9.45	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Sand/ Stones	0.76	24.18	0.00	0.00	0.00	0.00	0.00	0.00

Table 2. Prey identified in the diet of the four fish species in 2012 and 2013. The importance of each prey taxa in the diet is quantified as the percentage of occurrence using number of prey.

RESULTS & CONCLUSIONS

Stomach sampling evidenced that euphausiids constituted the majority of diet in *G. gadiculus* and juvenile *M. merluccius* and *M. poutassou* in both years (Table 1). Euphausiid species would act then rather as primary consumers than predators, as a preliminary analysis of their isotopic signature confirmed for the species *N. couchii* and *M. norvegica (*Figure 3). *C. aper* diet greatly differed between 2012 when it consumed mainly mesozooplankton and 2013 when it consumed more suprabenthos (Table 1)

The ratio of $\delta^{15}N$ indicated that the four fish species considered had a trophic level of two, standing approximately 6 points over the basal levels and probably predating on consumer species (Figure 3). Isotopic signature of the four species was significantly different among years but followed different patterns, only related to POM basal levels in the case of *C. aper*.

Basal ratios of C and N in benthic detritus showed neither interannual variability nor relation with the upwelling gradient. However, particulate organic matter (POM) had significantly higher $\delta^{15}N$ and $\delta^{13}C$ during the first year (Figures 4 and 5).

On the other hand, fish isotopic signatures were signifincantly different

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among years for most species, but the pattern was not consistent between species (figures 4 and 5). Regarding isotopic carbon a decreasing pattern along the upwelling gradient was found in all fish species in 2013 and in M. merluccius and M. poutassou in 2012 (Figure 4)

While basal differences in isotopic ratios exist, our analyses suggest that shifts in feeding habits may have a major role in determining species isotopic position, although not necessarily related to the upwelling index.

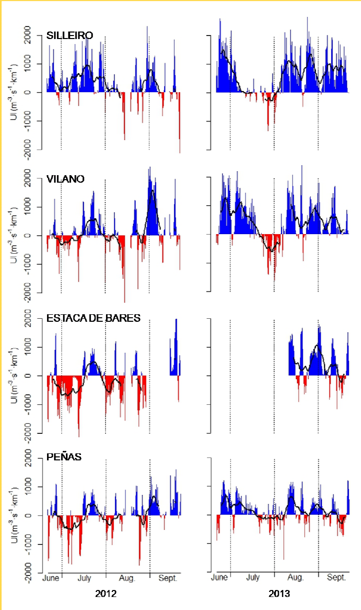

Figure 2. Upwelling index from buoys data [www.indicedeafloramiento.ieo.es] during the summer months preceding the study sampling. Weekly mean is superimposed as a solid line. See figure 1 for their locations on the map.

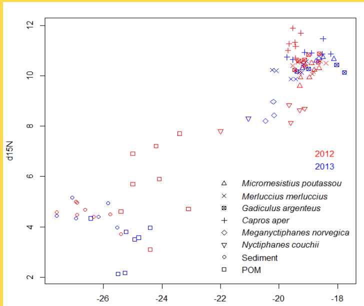

Figure 3. Scatterplot showing the isotopic composition of the four studied species, two of its prey (euphausiid species) and the isotopic baseline.

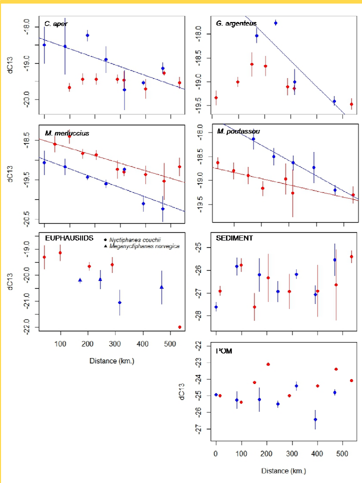

Figure 4. Isotopic carbon along the upwelling gradient. In 2012 (red) and 2013 (blue). When trends along the gradient were statistically significant ($p < 0.05$) the regression line is plotted.

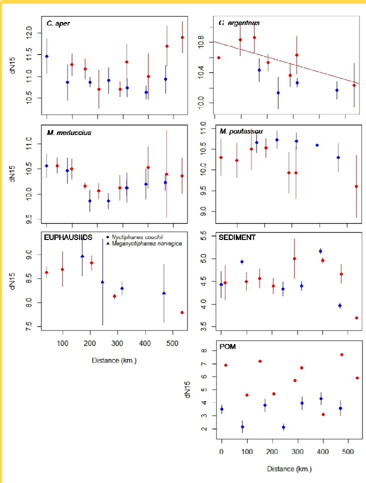

Figure 5. Isotopic nitrogen along the upwelling gradient. In 2012 (red) and 2013 (blue). When trends along the gradient were statistically significant ($p < 0.05$) the regression line is plotted.