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Trophic ecology of an Atlantic kelp forest fish assemblage (NW Spain) targeted by recreational fishers and implications for coastal management

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Although necessary for sustainable management of coastal ecosystems the understanding of trophic ecology of kelp fishes remains largely limited in the NE Atlantic. In this paper, stable isotope ratios of carbon (C) and nitrogen (N), complementarily with analyses of stomach contents, were used to investigate the trophic ecology of an Atlantic kelp forest fish assemblage targeted by spear fishers in Galicia (NW Spain). Trophic habits of the fishes were consistent across the species ranges and six trophic niches were identified. Chelon labrosus *was the only pelagic omnivore, while* Conger conger *and* Dicentrarchus labrax *were the principal predators, preying on benthic osteichthyes. The intermediate carnivorous* Diplodus sargus *mainly preyed on benthic molluscs, while* Labrus bergylta *exploited a wider range of prey. Although associated with different trophic niches, the two morphotypes of* L. bergylta *showed some degree of diet overlap, providing little support to the hypothesis of their separate management. Moreover,* L. bergylta *can be a keystone species whose adequate management has relevant implications for the sustainable use of the European kelp forest ecosystems.*

Keywords: Temperate rocky reefs, fish assemblages, kelp forests, recreational fisheries, stomach contents, stable isotope ratios

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INTRODUCTION

Kelp forests are highly valuable and complex ecosystems (Costanza *et al.*, 1997) with wide distribution over cold and temperate seas around the world (Dayton, 1985; Steneck *et al.*, 2002). Even though at large scales it is difficult to discern between natural and anthropogenic impacts (Dayton *et al.*, 1998), overfishing, global warming and other human-driven pressure have shown significant effects on kelp forests (Steneck *et al.*, 2002; Ling *et al.*, 2009; Connell & Russell, 2010; Wernberg *et al.*, 2010; Harley *et al.*, 2012).

European kelp forests currently are one of the most human-impacted coastal ecosystems, which might lead to an enormous loss of biodiversity and valuable resources (Airoldi *et al.*, 2008). This impoverished condition is deemed to hamper their resilience to global warming (Philippart *et al.*, 2011; Harley *et al.*, 2012) and other impacts (Ling *et al.*, 2009; Russell *et al.*, 2009; Wernberg *et al.*, 2011).

Among consumers putatively important in the ecosystem's functioning, kelp fishes deserve particular attention since they are key species that provide relevant commercial and recreational resources (Harvey *et al.*, 2001; Steneck *et al.*, 2002; Harley *et al.*, 2012). Moreover, there is growing concern about recreational fisheries worldwide (Schroeder & Love, 2002; Cooke & Cowx, 2006; Lewin *et al.*, 2006). Thus, the inclusion of recreational fisheries in the management of the coastal ecosystems has recently been encouraged by the EU (Council of the European Union, 2008a; European Parliament & Council of the European Union, 2013). However, there are few studies on the fish populations targeted by recreational fisheries (Kearney, 2001; Arlinghaus, 2006; Pawson *et al.*, 2008), especially in the case of recreational spear fishing (Jouvenel & Pollard, 2001; Morales-Nin *et al.*, 2005; Pita & Freire, 2014). Spear fishers mainly target top predators (Lloret *et al.*, 2008; Pita & Freire, 2016), ecologically and economically key components of marine ecosystems that are very vulnerable to fishing (Cheung *et al.*, 2005, 2007) and other anthropogenic impacts (Maxwell *et al.*, 2013). This situation is particularly perturbing in southern European countries, with a strong tradition of spear fishing (Pawson *et al.*, 2008), where spear fishers are competing for space and resources with commercial fishers (Coll *et al.*, 2004; Lloret *et al.*, 2008; Pita & Freire, 2016).

In this scenario, a European legal framework for the protection of coastal rocky reefs hosting kelp forests and associated flora and fauna has been developed (Council of the European Union, 2008b). Some of the measures designed to improve the conservation of these ecosystems include the creation of Marine Protected Areas (MPAs) in Europe (European Parliament & Council of the European Union, 2008). Marine Protected Areas are valuable management tools for conservation purposes (Willis *et al.*, 2003), that also provide benefits to fishery management (Roberts *et al.*, 2005), especially to

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sedentary fishes (Hilborn *et al.*, 2004). However, the design of MPAs has not always been entirely based on scientific advice (Allison *et al.*, 1998; Roberts, 2000; Hilborn *et al.*, 2004). In this context, deeper knowledge of kelp ecosystems functioning is needed to set up effective ecosystem-based management measures like MPAs (Steneck *et al.*, 2002; Schiel & Foster, 2015).

In particular, information about the functional role of kelp fish species, including their trophic relationships, is important for the understanding of how their removal impacts other species in the ecosystems, thus improving effective long-term management (Fantle *et al.*, 1999; Steneck *et al.*, 2002; Madin *et al.*, 2010). In addition, knowledge on trophic relationships informs MPA managers by determining if these species are appropriate for that approach, and helps in the identification of ecologically significant species that should be monitored to evaluate how effective any management approach is (Steneck *et al.*, 2002; Schiel & Foster, 2015; Wernberg *et al.*, 2016). Unfortunately, the trophic ecology of kelp fish assemblages remains largely unknown in many regions of the North-east Atlantic.

Among these regions, Galicia (NW Spain) is a paradigmatic case because it is in the southern range margin of European kelp forests (Bárbara *et al.*, 2005). Ecological information about range margin populations is especially valuable to understand the influence of global threats, to which they are particularly vulnerable (Travis & Dytham, 2004).

In Galicia, global warming has already reduced the intensity of the up-welling system governing large-scale macro-ecological processes of the coastal ecosystems (Bode *et al.*, 2009). Consequently, the dominant kelp communities of this region, mainly constituted by algae of the families Phyllariaceae and Laminariaceae (Bárbara *et al.*, 2005) and that serve as foundation species by creating habitat for other organisms (Orland *et al.*, 2016), are being progressively replaced by smaller warm-temperate species (Fernández, 2016). Furthermore, Galician kelp fishes have greatly reduced their abundances in recent decades (Pita & Freire, 2014). Habitat degradation and destruction (Pita *et al.*, 2008; Doldán-Garcia *et al.*, 2011), combined with extensive pollution (Beiras *et al.*, 2003; Franco *et al.*, 2006; Bellas *et al.*, 2008) may have played their part in a scenario where climate change is an added challenge (O'Brien *et al.*, 2000; Attrill & Power, 2002; Baudron *et al.*, 2014; Montero-Serra *et al.*, 2015). Moreover, a powerful fishing sector is operating in Galicia (Villasante, 2012), where kelp forest fishes has been traditionally targeted by both artisanal (Freire & García-Allut, 2000) and recreational fisheries, which include spear fishing and rod and line fishing (Pita & Freire, 2016). To cope with this situation, in recent years three MPAs have been created in Galicia: The Maritime-Terrestrial National Park of the Atlantic Islands of Galicia, aimed at conservation (Jefatura del Estado de España, 2002) and two MPAs with partial restrictions on fishing, the marine reserve of fishing interest 'Los Miñarzos' (Xunta de Galicia, 2007) and the marine reserve of fishing interest 'Ría de Cedeira' (Xunta de Galicia, 2009). However, the three MPAs are facing management difficulties and doubts about their effectiveness have arisen (Velando & Munilla, 2011; Perez de Oliveira, 2013; Fernández-Vidal & Muiño, 2014).

In order to describe for the first time food habits of a coastal kelp fish assemblage targeted by spear fishers in Galicia, the ratio between the stable isotopes of nitrogen ($^{15}N/^{14}N$, expressed as $\delta^{15}N$) and of carbon ($^{13}C/^{12}C$, expressed as $\delta^{13}C$) have been used in this paper. Since the use of stable isotopes does not allow assessment of the relative contribution of prey with similar stable isotope compositions, fish stomach content analyses were also used to assess their concordance with the results of the stable isotopes analyses. Furthermore, to assess if trophic habits are consistent across the species' geographic ranges, a comparison with other studies on the same fish species was performed. Therefore, the information on the trophic ecology of the investigated fish assemblage can be used to assess potential effects of fishing, among other impacts on fish communities and kelp ecosystems. Therefore, the results of this paper will contribute to the conservation of the NE Atlantic kelp forest ecosystems by facilitating decision-making procedures.

MATERIALS AND METHODS

Study area and sample collection

Kelp forests are mainly constituted in Galicia by *Laminaria hyperborea* (Gunnerus) Foslie, 1884, *L. ochroleuca* Bachelot de la Pylaie, 1824 and *Saccorhiza polyschides* (Lightfoot) Batters, 1902 (Bárbara *et al.*, 2005), while fish species that inhabit these ecosystems are dominated by the families Gadidae, Sparidae and Labridae (Pita *et al.*, 2014; Pita & Freire, 2016). Moreover, spear fishers tend to catch abundant species like *Dicentrarchus labrax* (Linnaeus, 1758), *Diplodus sargus* (Linnaeus, 1758) and *Labrus bergylta* (Ascanius, 1767) (Pita & Freire, 2014).

In June 2005, two recreational fishing competitions lasting 5 h each were held in the rocky reefs of the Ártabro Gulf, an open, oceanic bay located in the NW of Galicia with extensive kelp forests (Figure 1). Recreational fishers (29 fishers in each competition) caught 275 fishes with spear guns, at depths not exceeding 30 m. During the subsequent process of identification and weighing of catches, and to avoid interference with the normal progress of the competitions, the organization allowed the researchers to take a limited number of fish samples. Within these limitations, fish samples were taken of the widest possible range of sizes of each of the available species.

Since it has been suggested that there are two morphotypes of *L. bergylta* (Almada *et al.*, 2016; Quintela *et al.*, 2016), that differ in their colour (i.e. 'Pinto', a spotted and reddish form, and 'Maragota', plain greenish or brown; Villegas-Ríos *et al.*, 2013), they were treated separately in this paper.

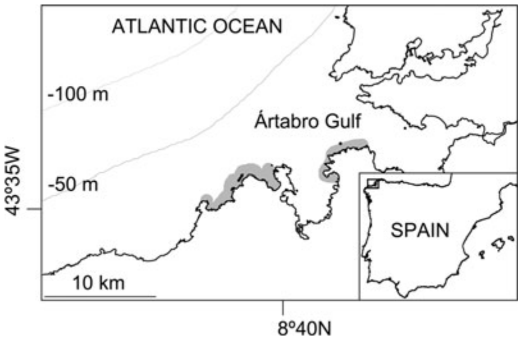

Fig. 1. Map of the study area in the Ártabro Gulf showing in grey shade the coastal rocky reefs where the sampled fishes were caught by spear fishers.

Fishes were measured (total length to the nearest mm) and weighed, stomachs were preserved in 70% alcohol, while ~1 cm^3 of dorsal muscle of each fish was collected and, following Carabel *et al.* (2009), refrigerated for less than 3 h, frozen and stored at −30 °C.

STOMACH CONTENTS

Stomach contents were analysed macroscopically under a binocular microscope and identified to the lowest possible taxonomic level. Thereafter, a per cent index of relative abundance for prey was estimated (McComish, 1967; Klarberg & Benson, 1975), based on an assessment of the percentage contribution by volume of each food category to the total contents (Pillay, 1952), and corrected by the degree of filling of the stomach (Frost, 1943):

$$\mathrm{RA}_{ij} = V_i \times F_j\,(\%),$$

where RA$_{ij}$ is the relative abundance of prey i in stomach j, V_i is the estimated percentage of the stomach j volume occupied by prey item i and F is an index of the filling of the stomach j; full ($F_j = 1$), mid ($F_j = 0.5$) and empty ($F_j = 0$). Thereafter, the RA per prey item and species was obtained and scaled down to a percentage basis (RA$_{\mathrm{sp}}$). Parasites and inorganic items were excluded.

ISOTOPIC COMPOSITION

The ratio between the stable isotopes of nitrogen (δ^{15}N) increases on average by 3.4 ± 1‰ (SD) with each of trophic transfer, while the ratio between the isotopes of carbon (δ^{13}C) increases only by 0.4 ± 1.3‰ (Minagawa & Wada, 1984; Post, 2002). Therefore, δ^{15}N can be used to determine the number of trophic levels between a consumer and the base of the food web, while δ^{13}C is commonly used to evaluate the source of the carbon, e.g. to distinguish carbon fixed by benthic or planktonic primary producers (Pinnegar & Polunin, 2000). Moreover, isotopic enrichment can be affected by the different rates of renewal of organic tissues (Tieszen *et al.*, 1983; Lee-Thorp *et al.*, 1989). Thus, tissues with low turnover rates, such as muscle, integrate isotopes accumulated over long periods of time (months) of the animal's life (Raikow & Hamilton, 2001) enabling greater accuracy in the inference of feeding habits than conventional analysis of stomach content.

Muscle samples were lyophilized by a Telstar Cryodos −50 for 48 h, and subsequently reduced to a fine powder using an agate mortar. To analyse the stable isotopic composition (C and N) in the tissues, three replicates per fish sample were processed, although only the mean isotopic composition of the replicates was used in the analyses. The samples were processed by a Thermo Finnigan Flash EA 1112 elemental analyser, coupled to a Thermo Finnigan Delta$^{\mathrm{plus}}$ mass spectrometer of isotope ratios. Isotopic ratio of C (δ^{13}C) and N (δ^{15}N) were calculated as:

$$\delta X = \left[\left(\frac{R_{\mathrm{Sample}}}{R_{\mathrm{Standard}}}\right) - 1\right] \times 10^3,$$

where X is ^{13}C or ^{15}N and R is the ratio ^{12}C/^{13}C or ^{14}N/^{15}N. R standard was the Pee Dee belemnite for C and atmospheric air for N. No corrections were made in relation to the presence of lipids in the samples due to the low lipid content in fish muscle tissues (Freire *et al.*, 2009).

The trophic level of each species was estimated according to the model developed by Hobson & Welch (1992):

$$\mathrm{TL} = 1 + \frac{\left(\delta^{15}N_{\mathrm{Sample}} - \delta^{15}N_{\mathrm{Reference}}\right)}{3.4},$$

where TL is the trophic level of the sampled fish using as reference the average δ^{15}N of potential available sources of food in the studied ecosystem, i.e. 6.3‰ in this case, estimated from mean values of benthic algae, sedimentary organic matter and pelagic suspended particulate organic matter obtained from Carabel *et al.* (2006). Following Post (2002) the average enrichment by trophic level used in the formula was 3.4‰. A TL close to 2 corresponds to an herbivore, a TL close to 3 to a carnivorous diet, and a TL close 4 to carnivores that eat other carnivores. Apex predators have a TL close to 5.

Data analyses

The δ^{13}C and δ^{15}N values obtained for the studied fish species were compared using the non-parametric rank sum Kruskal–Wallis test. In the case of a significant difference with the Kruskal–Wallis test, a post-hoc analysis was conducted using pairwise Mann–Whitney U tests. Adjusted P-values for multiple comparisons were estimated with the Holm adjustment method (Holm, 1979). Tests and calculations were obtained with the statistical software R v3.3.2 (R Core Team, 2016).

The trophic components of niche space can be quantified by using stable isotopic ratios (Bearhop *et al.*, 2004). Thus, Newsome *et al.* (2007) defined isotopic niche as an area (in δ-space) with isotopic values (δ-values) as coordinates. Although isotopic niche and trophic niche are not the same, they are likely to be tightly correlated (Jackson *et al.*, 2011). Therefore, in this paper trophic niches of fish species were identified by using the EM (Expectation-Maximization) algorithm initialized by model-based hierarchical clustering for parameterized Gaussian mixture models of the δ^{13}C and δ^{15}N paired values with the *Mclust* tool of the *mclust* package (Fraley *et al.*, 2012) of R v3.3.2 (R Core Team, 2016). Best model (between six and nine clusters) was selected by using Bayesian Information Criterion (BIC), and the species' centroids and their confidence interval ellipse were obtained (Fraley & Raftery, 2002).

RESULTS

Stomach content

Stomach contents of 52 fishes of four different species were analysed: *Conger conger* (Linnaeus, 1758) (N = 5), *Dicentrarchus labrax* (N = 5), *Diplodus sargus* (N = 6) and *Labrus bergylta* (N = 36). The two morphotypes of *L. bergylta* were analysed separately: Pinto (N = 18) and Maragota (N = 18) (Table 1).

Only three fish stomachs were completely empty, seven stomachs contained parasites (Platyhelminthes, mainly Digenea), while inorganic items, like plastics or small stones were present in five stomachs. A total of 21 different preyed

Table 1. Percentage of relative abundance by species (RA_{sp}) of the prey items present in the stomach content of the kelp fish species, identified to the lowest possible taxonomic level.

Prey		RA_{sp} (%)				
		Conger conger (N = 5)	*Dicentrarchus labrax* (N = 5)	*Diplodus sargus* (N = 6)	*Labrus bergylta* (Maragota) (N = 18)	*Labrus bergylta* (Pinto) (N = 18)
Algae		0.0	0.0	3.17	2.36	0.65
Rhodophyceae	*Corallina* spp.	0.0	0.0	1.84	0.24	1.36
Liliopsida	*Zostera noltii*	0.0	0.0	0.0	0.06	0.0
Polychaeta		0.0	0.0	0.50	0.59	0.88
Maxillopoda	Balanidae	0.0	0.0	0.83	6.07	0.82
Maxillopoda	*Pollicipes pollicipes*	0.0	0.0	0.50	0.0	0.0
Malacostraca	Eumalacostraca	0.0	0.0	0.33	0.0	0.0
Malacostraca	Amphipoda	0.0	0.0	0.17	8.66	1.83
Malacostraca	Isopoda	0.0	0.0	0.0	4.48	19.86
Malacostraca	Cumacea	0.0	0.0	0.0	0.06	0.0
Malacostraca	Caridea	0.0	0.0	0.0	0.24	0.0
Malacostraca	Paguridae	0.0	0.0	0.0	0.0	1.41
Malacostraca	Brachyura	0.0	0.0	0.0	2.71	6.54
Gastropoda		0.0	0.0	0.17	1.53	0.47
Bivalvia		0.0	0.0	0.33	0.18	0.06
Bivalvia	*Mytilus galloprovincialis*	0.0	0.0	89.98	57.95	31.94
Echinoidea	Echinidae	0.0	0.0	0.17	0.0	0.06
Echinoidea	*Paracentrotus lividus*	0.0	0.0	0.0	0.0	0.35
Echinoidea	*Psammechinus miliaris*	0.0	0.0	0.0	3.30	6.31
Ophiuroidea		0.0	0.0	0.0	2.47	4.30
Actinopterygii		50.66	1.00	0.67	0.0	0.29
Undetermined		49.34	99.00	1.34	9.13	22.86

For comparison purposes, taxonomic level class was provided when possible. Sample size for each fish species is identified (N).

taxa were identified in the stomachs. *Mytilus galloprovincialis* (Lamark, 1819) was the prey with the higher mean relative abundance (RA = 66.61 ± 36.85%), followed by Isopoda (RA = 27.53 ± 33.95%), *Psammechinus miliaris* (P.L.S. Müller, 1771) (RA = 18.11 ± 19.10%) and Brachyura (RA = 11.21 ± 13.20%). The remaining prey accounted for 7.04 ± 16.42%, while undetermined items accounted for 25.13 ± 27.42%.

Fishes were the only identified prey for *C. conger* (RA_{sp} = 50.66%) and *D. labrax* (RA_{sp} = 1.0%), probably because of the high incidence of unidentified prey in their stomachs (49.3% and 99.0%, respectively). *Mytilus galloprovincialis* was the

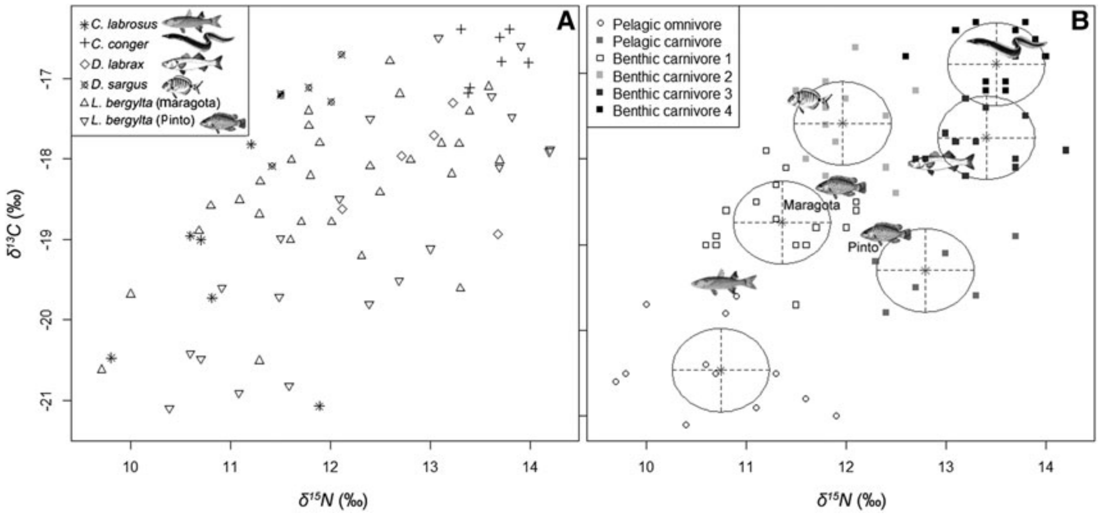

Fig. 2. Diagrams showing: (A) the $\delta^{13}C$ and $\delta^{15}N$ content in muscular tissues of the kelp fish studied species; and (B) groups of $\delta^{13}C$ and $\delta^{15}N$ values (trophic niches) obtained by hierarchical clustering analyses. The symbols of each cluster were categorized into the nominal trophic niches formerly identified in the area by Freire *et al.* (2009). The centroids and confidence interval ellipses of each cluster are also shown, while images of the fish species were plotted in their mean $\delta^{13}C$ and $\delta^{15}N$ values.

main prey for *D. sargus* ($RA_{sp} = 89.98\%$), Maragota ($RA_{sp} = 57.95\%$) and Pinto ($RA_{sp} = 31.94\%$), even though they preyed upon a large range of species (12, 15 and 16 identified prey items, respectively). In this regard, Amphipoda ($RA_{sp} = 8.7\%$) and Isopoda ($RA_{sp} = 19.9\%$) were also important prey for Maragota and Pinto, respectively (Table 1).

Isotopic composition

Muscle tissues of 73 fishes of five different species were sampled: *Chelon labrosus* (Risso, 1827) (N = 6), *C. conger* (N = 7), *D. labrax* (N = 5), *D. sargus* (N = 6) and *L. bergylta* (N = 49; Maragota, N = 29 and Pinto N = 20, were also independently analysed) (Figure 2A).

There were significant differences between fish species in relation with the content in $\delta^{13}C$ (Kruskal–Wallis $\chi^2 = 27.91$, $P < 0.001$) and $\delta^{15}N$ (Kruskal–Wallis $\chi^2 = 23.09$, $P < 0.001$), and only some of the paired comparisons, mainly involving the two morphotypes of *L. bergylta* were non-significant (Table 2). Therefore, except in the case of *L. bergylta*, it was shown that the fish species followed diverse feeding strategies.

Six trophic niches were obtained after hierarchical clustering of $\delta^{13}C$ and $\delta^{15}N$ paired values (the uncertainty in the classification with respect to the optimal BIC values, 0.34 of a maximum on 1, was moderately low for 75% of the data). Following the nominal trophic niches previously identified in the area by Freire *et al.* (2009), four of the identified trophic niches could be associated with benthic predators, while pelagic trophic niches could be divided between predators and omnivores (Figure 2B). Visual inspection of mean isotopic values of the studied fish species (including both morphotypes of *L. bergylta*) showed distributions that in general fitted with the identified trophic niches (Figure 2B).

Moreover, the trophic level (TL) of the fish species showed that *C. labrosus* was the only pelagic omnivore, while all the others showed carnivorous diets (Table 3). Furthermore, *C. conger* and *D. labrax* can be considered between secondary and tertiary consumers of the kelp forest ecosystems, as the length of the food chain estimated here was 3.2 (Table 3).

DISCUSSION

Analyses of fish stomach contents have been traditionally used to study the feeding habits of fish (Hyslop, 1980), but the use of stable isotope ratios in organic tissues is increasingly popular (Peterson & Fry, 1987; Brodeur *et al.*, 2017). Therefore, $\delta^{13}C$ and $\delta^{15}N$ have been used extensively to study ecological relationships of different marine animals (e.g. Bucci *et al.*, 2007; Freire *et al.*, 2009), including coastal fishes (e.g. Hansson *et al.*, 1997; Melville & Connolly, 2003; Correia *et al.*, 2011). Furthermore, stable isotope content in fish tissues has been already used as valuable inputs in fisheries management (e.g. Weidman & Millner, 2000; Jennings *et al.*, 2002; Pinnegar *et al.*, 2002).

The average enrichment in $\delta^{15}N$ per trophic level in any given ecosystem (and used in this study) is 3.4‰, but it may be quite variable (Minagawa & Wada, 1984; Post, 2002). On the other hand, standard values used in trophic level estimations typically include $\delta^{15}N$ of local organisms as baseline references. As an example, Fredriksen (2003) used $\delta^{15}N = 4.4‰$ as a reference in kelp forests ecosystems

Table 2. Paired Mann–Whitney tests used to evaluate differences in $\delta^{13}C$ and $\delta^{15}N$ content in muscular tissues of kelp fish species.

	Conger conger				*Dicentrarchus labrax*				*Diplodus sargus*				*Labrus bergylta* (Maragota)				*Labrus bergylta* (Pinto)			
	$\delta^{13}C$		$\delta^{15}N$		$\delta^{13}C$		$\delta^{15}N$		$\delta^{13}C$		$\delta^{15}N$		$\delta^{13}C$		$\delta^{15}N$		$\delta^{13}C$		$\delta^{15}N$	
Species	*W*	*P*	*W*	*P*	*W*	*P*	*W*	*P*	*W*	*P*	*W*	*P*	*W*	*P*	*W*	*P*	*W*	*P*	*W*	*Pp*
Chelon labrosus	42	**0.0098**	42	**0.0131**	3	0.0707	0	**0.0130**	1	**0.0240**	4	**0.0323**	140	0.0681	146	**0.0442**	45	0.3766	20	**0.0323**
Conger conger					35	**0.0112**	31	0.0664	36	**0.0434**	42	**0.0131**	198	**0.0006**	193	**0.0014**	131	**0.0032**	108	0.0664
Dicentrarchus labrax									4	**0.0436**	30	**0.0102**	61	0.5755	35	0.2039	33	0.2621	38	0.5446
Diplodus sargus													22	**0.0188**	106	0.8350	20	**0.0296**	79	0.5446
Labrus bergylta (maragota)																	354	0.3996	252	0.8350

The value of the statistic *W* is shown. The tests were considered significant when the adjusted *P*-values for multiple comparisons, estimated following a Holm procedure, were <0.05 (significant comparisons are highlighted in bold type).

Table 3. $\delta^{13}C$ and $\delta^{15}N$ content in muscular tissues and estimated trophic level (TL) of kelp fish species.

Species	Weight (g)	Length (mm)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	TL
Chelon labrosus	1225.0 ± 387.39	478.53 ± 31.14	−19.53 ± 1.13	10.83 ± 0.69	2.34 ± 0.20
Conger conger	8252.57 ± 2909.98	1459.29 ± 163.69	−16.74 ± 0.33	13.61 ± 0.25	3.17 ± 0.07
Dicentrarchus labrax	1670.0 ± 471.62	537.2 ± 53.56	−18.10 ± 0.65	12.94 ± 0.59	2.97 ± 0.17
Diplodus sargus	1391.67 ± 477.51	410.33 ± 34.32	−17.27 ± 0.46	11.71 ± 0.29	2.61 ± 0.09
Labrus bergylta (Maragota)	1284.48 ± 262.18	384.42 ± 22.78	−18.38 ± 0.93	12.04 ± 1.05	2.70 ± 0.31
Labrus bergylta (Pinto)	1592.50 ± 387.39	430.71 ± 39.78	−18.91 ± 1.46	12.37 ± 1.28	2.80 ± 0.38

Mean weight and total length of analysed fishes is also provided for informative purposes.

of Norway, while the reference obtained by Carabel *et al.* (2006) in similar kelp ecosystems and used in this paper was 6.3‰. Isotopic data estimated for the same species in different studies should be compared with care, for example, the trophic levels shown in this paper are lower than those that would be obtained by using 4.4‰ as a reference.

However, it can be concluded that the trophic attributes of the kelp fish species shown in this study by analysing $\delta^{15}N$ and $\delta^{13}C$ contents are consistent with those attributed to these species in other European regions (a comparison can be found in Table 4). Moreover, although the low number of fish stomachs analysed in this study may be considered insufficient to characterize diet, results have proven to be useful to support the analysis of isotopes and obtain a global interpretation.

Previous studies on the food webs of the study area (Carabel *et al.*, 2006; Freire *et al.*, 2009), showed $\delta^{13}C$ values that indicate that *Conger conger* and *Diplodus sargus* fed mainly on benthic organisms of the area. By contrast, *Chelon labrosus* consumes organisms and/or organic matter related to pelagic environments, while *Dicentrarchus labrax* and the two morphotypes of *Labrus bergylta* showed intermediate values. Therefore, these last species use less selective feeding strategies (Table 3).

The relatively high values of $\delta^{15}N$ in tissues of *C. conger* and of *D. labrax* and the associated trophic levels (Table 3), as well as the high frequency of fishes in their stomachs (despite the large amount of unidentified prey in the latter) (Table 1), indicate that these species are important predators of the European coastal ecosystems, from the Mediterranean (Pinnegar & Polunin, 2000) to the Atlantic (Pinnegar *et al.*, 2002; Spitz *et al.*, 2013). However, both predators differed in relation to the origin of the organic matter; the sedentary and benthic lifestyle of *C. conger* (Pita & Freire, 2011) is consistent with the $\delta^{13}C$ content showed in this study (Tables 3 and 4) and in the Mediterranean (Pinnegar & Polunin, 2000) (Table 4). Furthermore, it is also consistent with a specialist diet (Bauchot & Saldanha, 1986). Conversely, *D. labrax* was less dependent on benthic sources of C than *C. conger*, as shown by their relative $\delta^{13}C$ content (Table 3), which may indicate that it can also feed on pelagic prey in the water column, as stated by Spitz *et al.* (2013). Furthermore, this is also consistent with an active and complex spatial behaviour on a large geographic scale (Fritsch *et al.*, 2007; Pita & Freire, 2011) and suggests more generalist feeding habits (Kelley, 2009). Moreover, Franco-Nava *et al.* (2004) found similar results to that shown in this paper, while lipid extraction could explain the relatively lower values shown by Spitz *et al.* (2013) (Table 4).

Isotopic signatures of *D. sargus* shown in this study were also similar to those obtained in the Mediterranean Sea by Jennings

Table 4. $\delta^{13}C$ and $\delta^{15}N$ values and trophic level (TL) of fish species in different studies.

Study	Area	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	TL
Franco-Nava *et al.* (2004)				
Dicentrarchus labrax	Captivity	−18.60	15.40	–
Fredriksen (2003)				
Labrus bergylta	Norway	−18.03	12.67	3.20
Jennings *et al.* (1997)				
Diplodus sargus	Spain (Mediterranean)	−16.30	13.60	–
Diplodus sargus		−17.80	11.20	–
Diplodus sargus		−18.50	11.60	–
Pinnegar & Polunin (2000)				
Conger conger	Spain (Mediterranean)	−17.25	9.49	3.30
Diplodus sargus		−18.95	9.13	–
Pinnegar *et al.* (2002)				
Dicentrarchus labrax	Celtic Sea (Atlantic)	–	15.80	4.53
Spitz *et al.* (2013)				
Dicentrarchus labrax	Bay of Biscay (Atlantic)	−17.00	13.80	
This study				
Chelon labrosus	Spain (Atlantic)	−19.53	10.83	2.34
Conger conger		−16.74	13.61	3.17
Dicentrarchus labrax		−18.10	12.94	2.97
Diplodus sargus		−17.27	11.71	2.61
Labrus bergylta (Maragota)		−18.38	12.04	2.70
Labrus bergylta (Pinto)		−18.91	12.37	2.80

The values obtained in this paper are shown for comparison purposes.

et al. (1997) (Table 4). Furthermore, molluscs and fishes (Pinnegar & Polunin, 2000) and molluscs and algae (Sala & Ballesteros, 1997) were the main prey for *D. sargus* in the Mediterranean, while algae and echinoderms (Figueiredo *et al.*, 2005) and crustaceans and molluscs (Leitão *et al.*, 2007) were the main preys in the Azores and southern Portugal, respectively. In this paper, molluscs were by far the main prey of *D. sargus*, followed to a substantially lesser extent by algae, crustaceans and fish, which could explain the different isotopic signatures shown by Pinnegar & Polunin (2000) (Table 4), while echinoderms were almost absent from the diet (Table 1). This variety of prey in different geographic areas suggests a rather opportunistic predator behaviour.

Similarly, *L. bergylta* showed in this study a similar isotopic signature (Table 4) to fishes from Northern Europe (Fredriksen, 2003). However, as shown by Figueiredo *et al.* (2005) in the Azores Islands, by Dipper *et al.* (1977) in the Isle of Man and by Norderhaug *et al.* (2005) in Norway, crustaceans are the main prey through the distribution area of the species, while in this paper molluscs, *Mytilus galloprovincialis* in particular, were more relevant in its diet (Table 1).

Regarding stable isotopes analysis for the study of the trophic niches of the kelp fish assemblage, $\delta^{13}C$ and $\delta^{15}N$ values were extremely useful. In fact, all the studied fish species could be associated with a trophic niche (Figure 2B). However, it is remarkable that the high degree of variation in the isotopic signatures shown by both morphotypes of *L. bergylta* led to some degree of niche overlap with one or another species of the assemblage (Table 2; Figure 2). This niche overlap was even shown with respect to *D. sargus*, a species with a differentiated diet behaviour in nearby areas of the Atlantic (Figueiredo *et al.*, 2005).

Furthermore, there was some degree of diet overlap between the two morphotypes of *L. bergylta* (Table 2). Although benthic prey seem to be more important for Maragota than for Pinto (Table 1), these differences could be due to the larger size of Pintos in general (Villegas-Ríos *et al.*, 2013), and also in this paper (Table 3), that might allow them to hunt other fish in the water column (Table 1). However, as stated by Almada *et al.* (2016), these results provide insufficient support to the view that the two morphotypes should be treated separately in fisheries management (Villegas-Ríos *et al.*, 2013; Quintela *et al.*, 2016).

Predatory fishes are good indicators of ecosystem health (e.g. Christensen *et al.*, 2003; Myers & Worm, 2003; Myers *et al.*, 2007). Subsequently, they can be used to infer general trends for the whole community (Molloy *et al.*, 2010), even when dealing with complex fish-kelp interactions (Peterson *et al.*, 2000; Efird & Konar, 2014). In this sense, the fishes studied in this work are important species in terms of abundance (Pita *et al.*, 2014; Pita & Freire, 2016) and trophic role of the kelp forest ecosystems (Arim *et al.*, 2010; Rooney & McCann, 2012). Furthermore, the length of the food chain estimated here (3.2) is consistent with full lengths estimated by Hall & Raffaelli (1993) for all types of ecosystems. Consequently, the ecological role of the fish species studied here is very relevant for the ecosystem functioning of the kelp forests of the NE Atlantic and for their fisheries management.

Taking this into account, and since *D. labrax* is the only species with seasonal and access restrictions, along with limitations of their fishing opportunities in a European context (Council of the European Union, 2015), a combination of initiatives to increase the effectiveness of traditional top-down regional management (e.g. Macho *et al.*, 2013; Pita *et al.*, 2016) and the creation of MPAs (European Parliament & Council of the European Union, 2008) are the main management measures expected to improve the sustainability of the kelp fish assemblages in the future. The relevance of *M. galloprovincialis* in the diet of *D. sargus* and *L. bergylta* (Table 1) is an important finding. Coastal managers must ensure that this mollusc is available, for example when developing plans to create new coastal MPAs to protect kelp ecosystems. Furthermore, a very relevant mussel culture is developed in Galicia, mainly based in the growing of small mussels extracted from rocks (Pérez-Camacho *et al.*, 1991). Since small mussels are also the main prey for *D. sargus* and *L. bergylta*, the exploitation of the wild mussels by aquaculture farmers must be controlled, evaluated and regulated.

Herbivores are also important elements to consider in marine ecosystems (Madin *et al.*, 2010). If their abundances are increased, for example after a reduction of their predators, the kelp forests could be severely altered (Steneck *et al.*, 2002; Byrnes *et al.*, 2006; Harley *et al.*, 2012). In this regard, antagonistic ecological relationships between sea urchins and kelp forests have been well established in the literature (Harley *et al.*, 2012). Therefore, the presence of sea urchins in the diet of the kelp fishes, relevant in the case of *L. bergylta* (Table 1), has potential implications for ecosystem management since the reduction of the abundances of this fish could hamper the resilience of kelp forests to grazing by sea urchins. Consequently, the trophic role of *L. bergylta* shown in this study is relevant for the management of the European kelp forest ecosystems. For instance, this species could be considered a keystone species (Simberloff, 1998) and, therefore, monitoring programmes on this species can be useful, e.g. for setting minimum requirements for the conservation of kelp forests and for the planning of MPAs (Roberge & Angelstam, 2004). Further research would be desirable to identify potential benefits and tradeoffs of the use of *L. bergylta* as a keystone species, but in the meantime, it is urgent to reverse human impacts that have severely reduced the abundances of this fish in the last decades (Pita & Freire, 2014, 2016).

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