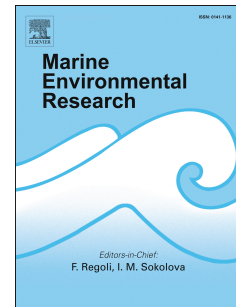


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The effects of fishing on the ontogeny of trophic position and body condition of a small-sized temperate marine fish

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Running page head: Response of *Coris julis* to fishing ban

Authors contribution: **JM:** Conceptualization, Investigation, Formal analysis, Visualization, Writing - Original Draft, **OR:** Conceptualization, Investigation, Data Curation, Formal analysis, Visualization, Writing - Review & Editing; **AG:** Investigation, Writing - Review & Editing; **FS:** Data Curation, Resources; **LC:** Funding acquisition, Project administration, Conceptualization, Investigation, Writing - Review & Editing, Supervision.

Highlights (maximum 85 characters, including spaces, per bullet point):

- Biomass of rainbow wrasse, its predators and competitors increases in No-take areas.
- Trophic position and body condition of rainbow wrasse change in response to fishing.
- An unexpected ontogenetic dietary shift is observed in association to sex change.
- Rainbow wrasses select prey of lower trophic position after sex change.

Abstract (100-150 words in length):

Using rainbow wrasse as a model species, we evaluate the impact of protection on the relationship between body size and: i) trophic position (TP), based on $\delta^{15}\text{N}$; and ii) body condition (BC), based on weight-at-length. We found that the biomass of the rainbow wrasse, their predators and their competitors was higher inside the no-take marine protected area (NTA) than in the area open to fishing. The TP of rainbow wrasse was higher inside the NTA but the BC was lower. A domed relationship between TP and size was observed in both areas: the TP increased with size up to 12.6 cm total length, when all individuals shifted to terminal males, and then decreased. Although other confounding environmental variables may exist, the indirect effects of fishing on competition and predation risk are the most likely explanation for the changes in TP, BC and the ontogenetic dietary shift of the rainbow wrasse.

Key words: isotopes, $\delta^{15}\text{N}$, fish community descriptors, size-dependent mechanisms, body size, dietary shifts, *Coris julis*, Mediterranean rainbow wrasse.

1. INTRODUCTION

Trophic relationships are strongly determined by body size, with the general rule being that predators are bigger than their prey, and so “the bigger the predator, the higher its trophic position” (Jennings et al., 2002; McCann and Rooney, 2009; Ríos et al., 2019). In marine ecosystems, such generalisation should thus be upheld in fish due to their indeterminate growth and lifelong ontogenetic dietary shift (Karpouzi and Stergiou, 2003; Sánchez-Hernández et al., 2019). However, recent reviews revealed that the trophic position of marine fishes does not necessarily increase as they grow in size, providing evidence for size-independent feeding (Ríos et al., 2019; Travers-Trolet et al., 2019).

Ontogenetic dietary shifts in fishes are driven by a combination of intrinsic and extrinsic factors. As fish grow, increase in mouth gape, improved swimming skills and changes in the production of digestive enzymes drive ontogenetic dietary shifts intrinsically, while differences in predation risk, competitive skills and prey availability are extrinsic drivers of change (Sánchez-Hernández et al., 2019). Through the reduction of population density and the interactions between predators and their prey, overfishing, which is currently affecting all of the world’s oceans (Zhou et al., 2015), is a major anthropogenic driver of changes in the strength of the extrinsic drivers (Hinz et al., 2017; McCann and Rooney, 2009). Therefore, areas where no fishing takes place, such as no-take marine protected areas, offer a unique opportunity to study ontogenetic dietary shifts under “natural” conditions and evaluate the strength of the intrinsic and extrinsic factors as the driving mechanisms.

The population density of fish in no-take areas differs compared to adjacent areas open to fishing, due to reduced fishing mortality (Coll et al., 2012; García-Charton et al., 2004; Harmelin-Vivien et al., 2008; Sala et al., 2012). For some species, this may

result in different habitat use patterns due to changes in the availability of space and/or changes in predation risk (Hereu, 2005; Laundré et al., 2001; Skinner et al., 2019). Therefore, fishing activity has the potential to affect the ontogenetic dietary shift of fish species, through direct removal of the individuals from a population and their competitors, as well as through alteration of the number of their predators (via changes in the available food supply and niche space, for example). Currently, scientific research has mainly addressed differences in the mean trophic position of the fish species in open access and no-take areas (e.g. de Lope Arias et al., 2016; Dell et al., 2015; Vizzini and Mazzola, 2009). However, differences in the ontogenetic dietary trajectories experienced by fish species between areas with different fisheries management, specifically mesoconsumer species, have received less attention.

Fishing-induced changes can also affect the fish condition according to the intensity and type of fishing (e.g. Giacalone et al., 2010; Hiddink et al., 2016; Hinz et al., 2019), and the biological traits of the species considered (e.g. Walsh et al., 2012). In coastal areas, higher fishing intensity may indirectly increase fish-body condition of mesoconsumers by reducing predators' abundance and associated predation rates and predation risk (Barley et al., 2017; Hall and Kingsford, 2016; Heithaus et al., 2008; Walsh et al., 2012). Inside the marine protected areas, improved conservation of the benthic communities, resulting in higher habitat complexity, offered through protection from fishing, can result in better fish condition (e.g. Lloret et al., 2005; Lloret and Planes, 2003; Viladrich et al., 2016).

The Mediterranean rainbow wrasse *Coris julis* (thereafter rainbow wrasse) is a small-sized (maximum length 25 cm) protogynous hermaphrodite, widely spread in the Mediterranean and eastern Atlantic coastal waters, down to 50 m depth (LLoris, 2015). Its reproductive phases are accompanied by striking changes in behaviour and

coloration: from non-territorial yellow-brown initial coloration phase (ICP), exhibited by juveniles, adult females and primary males, to large territorial secondary males with bright body coloration (terminal coloration phase, TCP) (Alonso-Fernández et al., 2014; Bruslé, 1987; Lejeune, 1987, 1985). The species is an opportunistic mesophagous carnivore with a highly plastic feeding strategy (Bell and Harmelin-Vivien, 1983; Jennings et al., 1997). In the Mediterranean its diet is mostly based on gastropods, crustaceans, bivalves and echinoderms (Bell and Harmelin-Vivien, 1983; De Pirro et al., 1999; Hinz et al., 2019; Kabasakal, 2001; Sinopoli et al., 2017). While commercially unexploited, the rainbow wrasse is one of the most frequently captured species by recreational fishing in the Balearic Islands (Cardona et al., 2007; Morales-Nin et al., 2005). Furthermore, the rainbow wrasse is potentially an important prey for some mid-size and large predatory fishes (Linde et al., 2004, personal observations).

In this paper, using rainbow wrasse as the focal species, the impact of protection from fishing on the relationship between body size and i) trophic position (based on stable isotope analyses) and ii) body condition (based on weight-at-length as a proxy of condition) was examined. Firstly, it was hypothesised that, if fisheries' restrictions modify the consumer-prey relationship, both relationships between trophic-position/body-condition with size will also change due to altered intra- and inter-species competition and predatory risk. Specifically, observing a lower trophic position (Drago et al., 2017, 2019; McCann, 2011; Sapority et al., 2016) and a lower body condition (Barley et al., 2017; Hall and Kingsford, 2016b; Walsh et al., 2012) in no-take areas was anticipated due to a higher intra- and interspecific competition and predation risk. Secondly, it is possible that the ontogenetic dietary shift may change depending on the effects of the former hypothesis or due to the effect of other life history traits, such as sex change.

2. MATERIALS & METHODS

2.1. Site description and experimental design

The study was conducted in two areas in the Balearic Islands (western Mediterranean), characterised by similar environmental conditions and different fishing regulations (Fig. 1, Table 1). Sampling, restricted to rocky substrates between 5 and 15 m depth, was carried out at two no-take sites (No-Take Area, NTA hereafter) located within the Cabrera National Park and at two sites open to commercial and recreational fishing (Open Fishing Area, OFA hereafter) located in the western part of Mallorca.

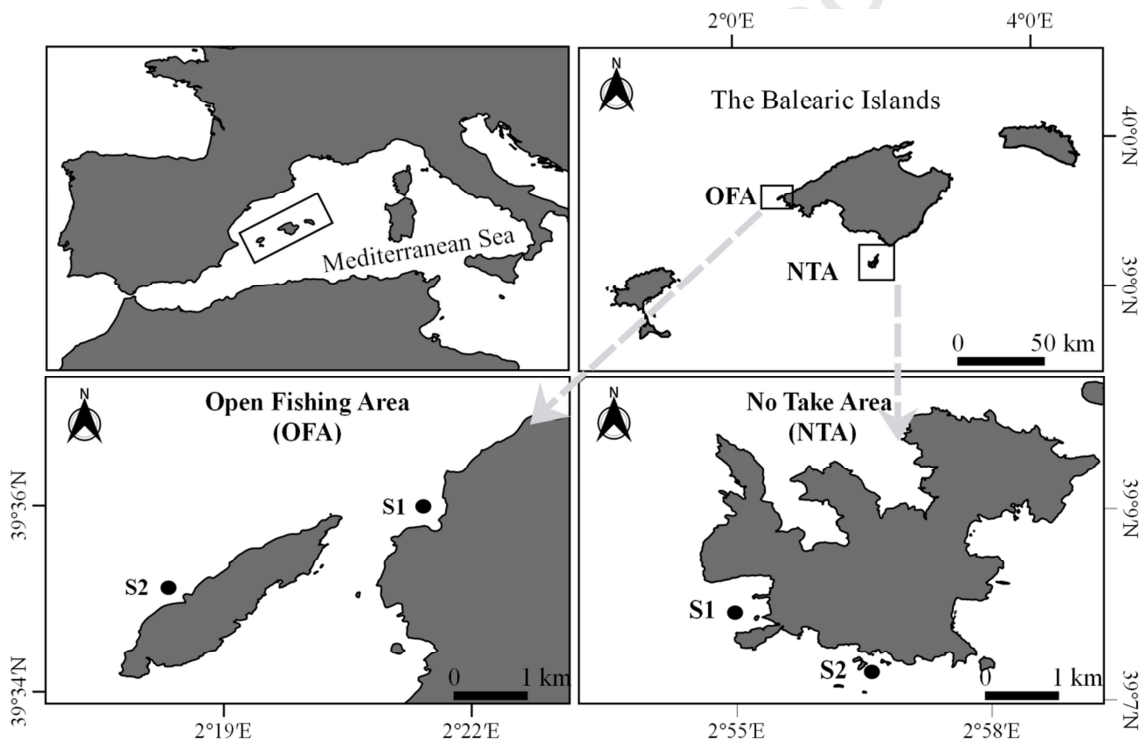


Fig. 1. Map of the study areas showing the location of the four sites sampled: two in the No-Take Area within the *Cabrera* National Park (NTA; S1: *Coll Roig*, S2: *Estels*) and two in the Open Fishing Area located on the west coast of *Mallorca* (OFA; S1: *Cala Embasset*, S2: *Dragonera*).

Cabrera National Park, established in 1991, is an area protected from recreational fishing (both angling and spear fishing) in all the area and from professional fishing in areas shallower than 20 m. Professional fishing in areas deeper than 20 m, is regulated by the effort and gear. Furthermore, within the park, no-take areas, free of all fishing,

professional or otherwise, exist. The sampling inside NTA was conducted in two such no-take areas. By contrast, both commercial and recreational fishing are permitted, and commonly practiced in the two study sites located in the western part of Mallorca. Recreational fishing is highly popular around Mallorca, with one of the main recreational boat harbours located in the proximity of the study area (Morales-Nin et al., 2005, 2015). Previous research characterised OFA sites as fully exploited or overexploited (Coll et. al, 2013) and reported major differences in the structure of the rocky-reef fish communities from Cabrera National Park and the OFA study sites (Coll et al., 2013).

2.2. Underwater visual censuses

Rainbow wrasses, other mesophagous fishes (*Diplodus annularis*, *D. puntazzo*, *D. sargus*, *D. vulgaris*, *Labrus merula*, *Symphodus mediterraneus*, *S. melanocercus*, *S. ocellatus*, *S. roissali*, *S. rostratus*, *S. tinca* and *Thalassoma pavo*) and roving/ambush predatory fishes (*Dentex dentex*, *Epinephelus marginatus*, *Labrus viridis*, *Serranus cabrilla* and *Serranus scriba*) were censused visually along 50 m x 5 m transects between June 24th and July 8th 2016. Four randomly placed transects, parallel to the coast and separated by a minimum of 20 m to prevent spatial autocorrelation of the data (Ordines et al., 2005), were run at each site, between 10:00 a.m. and 12 p.m. All fish on the transects were counted and assigned a 5 cm size class. Prior to field fish size estimation, extensive training using artificial fish was carried out (Bell et al., 1985). The accuracy in the size estimation was 4 cm for total length for fish from 5–40 cm, and 10 cm for larger fish, similar to that obtained previously by Coll et al. (2013).

Table 1. Environmental characteristics (\pm standard error) at the four study sites of the Cabrera National Park (No-Take Area: CR, Coll Roig; ES, Estels) and west of Mallorca (Open Fishing Area: CE, Cala Embasset; DR, Dragonera).

	No-Take Area (NTA)		Open Fishing Area (OFA)	
	CR	ES	CE	DR
Depth (m)	13.46 \pm 0.89	14.44 \pm 1.16	9.80 \pm 0.76	11.34 \pm 0.54
Rugosity	2.38 \pm 0.31	2.63 \pm 0.24	2.13 \pm 0.38	3.00 \pm 0.20
Blocks (%)	58.75 \pm 13.90	77.25 \pm 8.14	55.5 \pm 13.18	80.25 \pm 12.99
Wave Exposure	Low	High	Low	High

2.3. Sampling collection

Following visual censuses, 120 rainbow wrasse (30 per site, Table S1) were captured using hook and line and hand nets. In the laboratory, the colour pattern of each fish, size (total length; TL hereafter) and weight (g) was recorded, and a sample of dorsolateral white muscle was collected. Mouth width was also measured in a subsample of fish from both localities (n=29, Table S2) ranging from 9 cm to the maximum size sampled. Furthermore, we collected specimens of the sea urchin *Paracentrotus lividus*, a species feeding primarily on benthic macroalgae (Agnetta et al., 2013), with the objective of assessing the isotope baseline for calculating the trophic position of each individual. Five sea urchins were collected at each site and their gonads were retained for stable isotope analysis (see below). White muscle and gonads were stored frozen (-20 °C) for the analysis.

2.4. Stable isotope analysis and calculation of trophic position

Samples were thawed at room temperature and dried in a stove at 55 °C for 24 hours. Once dry, fish and sea urchin samples were ground to fine powder with mortar and pestle, dried again for 24 hours at 55 °C and rinsed with a 2:1 chloroform:methanol solution to remove lipids. The chloroform:methanol solution was changed overnight until it was transparent. Samples were dried again for 24 hours at 55 °C. Once

processed, 0.3 mg of the sample were weighed into 3.3 x 5 mm tin cups. All tin cups were combusted at 900 °C and analysed in a continuous flow isotope ratio mass spectrometer (Flash 1112 IRMS Delta C Series EA, Thermo Finnigan; www.thermofisher.com) at Centres Científics i Tecnològics de la Universitat de Barcelona (www.ccit.ub.edu) in Barcelona, Spain.

Although the focus of the current study was on $\delta^{15}\text{N}$, $\delta^{13}\text{C}$ was measured simultaneously. The lipid contents of the sample may strongly bias $\delta^{13}\text{C}$ values (Ingram et al. 2007), hence a chloroform: methanol solution was used to remove lipids from the samples. According to Ingram et al. (2007), this delipidation procedure has a small effect on the $\delta^{15}\text{N}$ values of fish muscle (0.4 ‰) which has a small effect on the estimation of trophic position.

Abundance of stable isotopes is expressed using the δ notation, where the relative variations of stable isotope ratios are expressed as per mil (‰) deviations from predefined reference scales (atmospheric nitrogen for $\delta^{15}\text{N}$). However, due to limited supplies, isotopic reference materials, which included known isotopic compositions relative to international measurement standards, were analysed instead. For nitrogen, isotopic reference materials of known $^{15}\text{N}/^{14}\text{N}$ ratios were used to a precision of 0.2 ‰, and these were namely: $(\text{NH}_4)_2\text{SO}_4$ (IAEA N₁, $\delta^{15}\text{N} = +0.4$ ‰ and IAEA N₂, $\delta^{15}\text{N} = +20.3$ ‰), L-glutamic acid (IAEA USGS₄₀, $\delta^{15}\text{N} = -4.6$ ‰) and KNO_3 (IAEA NO₃, $\delta^{15}\text{N} = +4.7$ ‰). These isotopic reference materials were used to recalibrate the system once every 12 samples and were analysed in order to compensate for any measurement drift over time. The raw data were recalculated taking into account a linear regression previously calculated for isotopic reference materials (Skrzypek, 2013).

The trophic position of each rainbow wrasse was calculated as follows:

$$\text{TP}_{\text{Rw}} = 2 + ((\delta^{15}\text{N}_{\text{Rw}} - \delta^{15}\text{N}_{\text{su}})/3.4)$$

where TP_{Rw} was the trophic position of the rainbow wrasse, 2 was the trophic position of sea urchins, $\delta^{15}N_{Rw}$ was the ratio of stable N isotopes in rainbow wrasse, $\delta^{15}N_{su}$ was the average ratio of N stable isotopes in local sea urchins and 3.4 was the average trophic discrimination factor suggested by Post (2002).

2.5. Statistical analysis

Nested univariate analyses of variance (ANOVA) were carried out to determine differences between NTA and OFA for number of fish species, density (individuals*250m⁻²) and the estimated biomass (g*250m⁻²) of rainbow wrasse and their competitors and predators. Fish density was transformed to biomass using the length-weight equation reported by Morey et al. (2003). The terms included in the ANOVA model were area (NTA vs OFA) and site (nested within area), as fixed factors, and visual censuses (transects) were the replicates. All data were checked for normality and variance homogeneity and log-transformed when necessary.

Analysis of coloration transition size, trophic position and condition of the rainbow wrasse were made at the area level to increase power analysis. The estimation of size at which 50% of the sampled population made the transition from the ICP to TCP was carried out using a generalized linear model (GLM, with a binomial family and logit link function). Differences between two areas, Cabrera National Park and western Mallorca, were also evaluated. The relationship between mouth gape (mouth width) and body size was estimated by means of General Lineal Models (GLM).

Generalised Additive Models (GAM) were used to determine how trophic position of rainbow wrasse varied with size in the two areas studied (NTA vs OFA). The interaction term between both predictor variables (size and area) was included in the model to analyse differences in the shape of the relationship. GAM (with gaussian distribution and identity link function) was carried out in the common size-range at the

two areas (5.7 – 15.6 cm TL), excluding from the analysis the largest individuals captured only in the NTA (see Results). A simple model including only size of the fish as a predictor variable was run to evaluate the strength of the intrinsic factors. Model fit was evaluated by the likelihood ratio test and by inspecting the residuals graphs for potential violation of the model assumptions, particularly normality, constant variance and independence (Zuur et al., 2009).

The condition of individual fish was estimated as the weight-at-length of the fish (Hiddink et al., 2016). Hereafter, we will use ‘body condition’ as a synonym of ‘weight-at-length’. The GAM model described above, with the same size range, was applied to find out how the body condition of rainbow wrasse varied with size.

Statistical analyses were performed using the R version 3.2.2 (*R Core team, 2015*). GAM models were implemented using the *mgcv* library (Wood, 2006).

3. RESULTS

The abundance and biomass of the rainbow wrasse, as well as the species richness, abundance and biomass of predators and competitors are presented in Table 2.

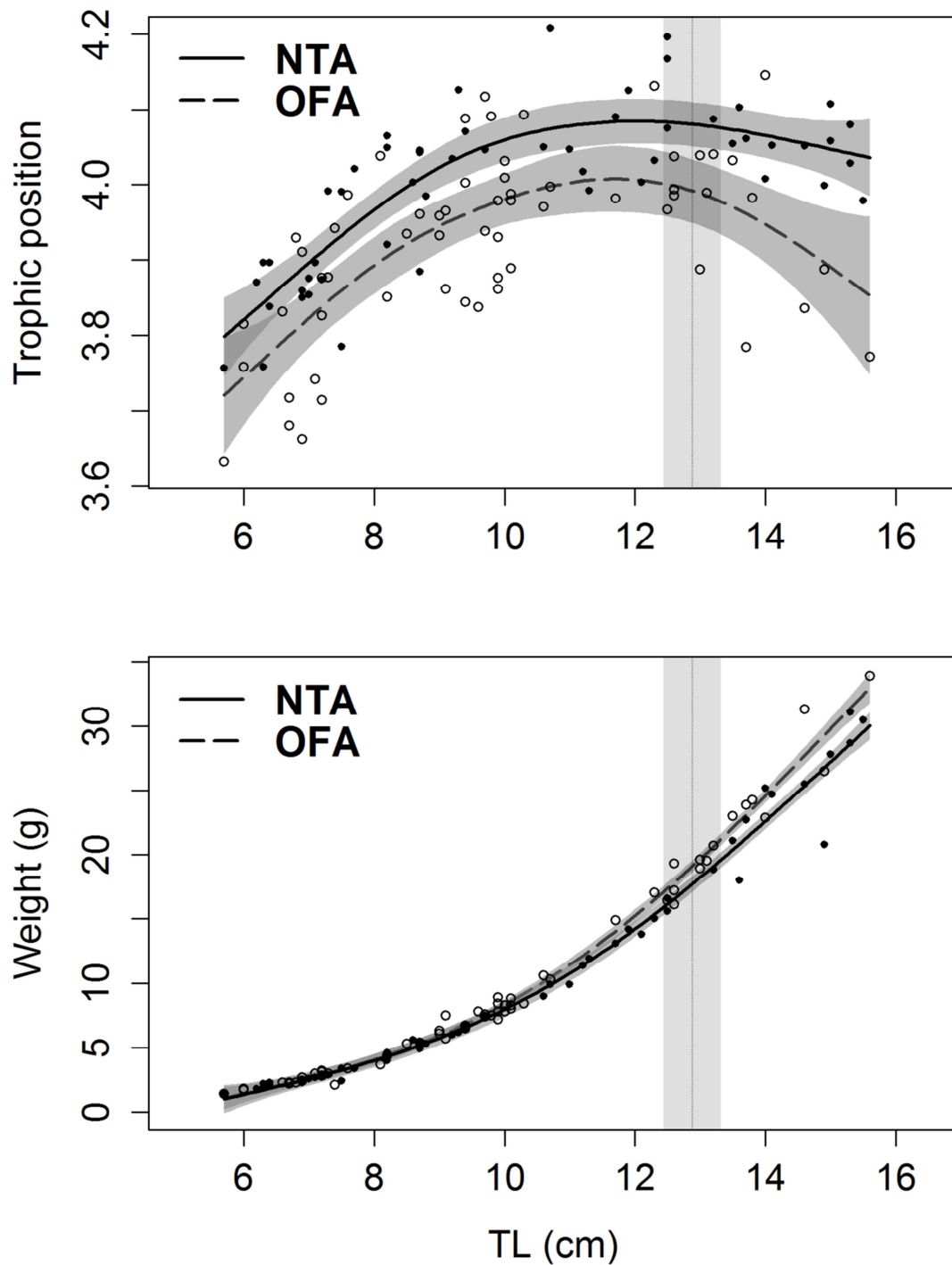
Marginal non-statistically significant differences in the abundance of the rainbow wrasse were observed between the two areas ($F_{1,12} = 3.91$, $p = 0.07$), while significant differences were found between both OFA sites ($F_{2,12} = 4.12$, $p = 0.04$). Biomass was significantly higher in NTA than in OFA ($F_{1,12} = 9.12$, $p = 0.01$). Similarly, the rainbow wrasse biomass was site-scale variable, with marginal non-significant differences found only between OFA sites ($F_{2,12} = 3.66$, $p = 0.06$).

Table 2. Descriptors of fish populations and communities at the four study sites of the *Cabrera* National Park (No-Take Area: CR, Coll Roig; ES, Estels) and west of *Mallorca* (Open Fishing Area: CE, Cala Embasset; DR, Dragonera). Abundance is reported as number of individuals*250 m⁻², biomass as kilograms*250m⁻², body size (minimum and maximum size censused by UVC) of the rainbow wrasse *Coris julis* in cm and species richness as a number of species*250m⁻². Data are presented as mean \pm standard error, except for body size.

		No-Take Area (NTA)		Open Fishing Area (OFA)	
		CR	ES	CE	DR
Rainbow wrasse	Abundance	25.00 \pm 4.12	19.25 \pm 1.31	8.75 \pm 2.75	21.75 \pm 4.70
	Biomass	0.46 \pm 0.14	0.34 \pm 0.02	0.10 \pm 0.02	0.30 \pm 0.09
	Body size	7-17	5-17	7-17	7-17
Predators	Species richness	2.25 \pm 0.25	3.00 \pm 0.00	1.25 \pm 0.00	1.00 \pm 0.00
	Abundance	8.75 \pm 1.55	7.50 \pm 1.32	4.50 \pm 1.44	7.00 \pm 1.47
	Biomass	1.87 \pm 0.64	2.19 \pm 0.51	0.24 \pm 0.08	0.38 \pm 0.13
Competitors	Species Richness	7.25 \pm 0.85	6.75 \pm 1.03	5.50 \pm 0.50	6.75 \pm 0.25
	Abundance	37.00 \pm 4.36	34.50 \pm 7.01	35.50 \pm 10.02	29.25 \pm 2.36
	Biomass	6.70 \pm 1.42	5.89 \pm 1.58	1.42 \pm 0.44	2.07 \pm 0.49

The species richness of predatory fishes was significantly greater in the NTA than in the OFA ($F_{1,12} = 72$, $p < 0.001$), with no significant differences between sites. The abundance of predators did not show differences between areas nor sites. However, the biomass of predatory fishes was significantly greater in the NTA than in OFA ($F_{1,12} = 21.32$, $p < 0.001$), with no differences at the sites scales.

No differences in species richness and abundance of competitors were observed between areas nor between sites. However, the biomass was significantly greater in NTA than in OFA ($F_{1,12} = 26.89$, $p < 0.001$), with no significant differences between sampled sites within each area.



275

276 Fig. 2. Relationship between trophic position (top panel) and weight with size (Total Length) of
 277 the rainbow wrasse *Coris julis*, resulting from de General Additive Model analysis. The size
 278 (12.9 cm) at which 50% of all individuals are secondary males is indicated with a dotted line.
 279 NTA (black points): no-take area inside the *Cabrera* National Park; OFA (white points): open
 280 fishing area located on the west coast of *Mallorca*. Grey bands show 95% CI.

Table 3. Values (range and mean \pm standard error) of rainbow wrasse *Coris julis* trophic position obtained in each area and number of individuals and size range of the samples used for the analysis. NTA: no-take area inside the Cabrera National Park; OFA: open fishing area located on the west coast of Mallorca. ICP: initial coloration phase (yellow-brown, associated with females and primary males); TCP: terminal coloration phase (brightly coloured, found only in secondary males). Only individuals ranging 5.7-15.6 cm total length were considered for this analysis. Figures in brackets show the total number of individuals captured and the total size range sampled.

	Number of individuals		Range Size (cm)		Trophic position (range)		Mean trophic position	
	NTA	OFA	NTA	OFA	NTA	OFA	NTA	OFA
ICP	42(43)	48	5.7(5.3) – 13.6	5.7 – 13.1	3.76 – 4.21	3.63 – 4.11	3.98 \pm 0.02	3.91 \pm 0.12
TCP	12(17)	12	12.5 – 15.5(17.1)	11.7 – 15.6	3.98 – 4.20	3.77 – 4.15	4.06 \pm 0.02	3.97 \pm 0.04
Total	54(60)	60						

The values of rainbow wrasse trophic position obtained in each area and the number and size range of captured individuals are shown in Table 3 (see Table S1 for the raw data). The sizes ranged from 5.3 to 13.6 cm TL ($n = 91$) for the initial phase specimens and from 11.7 to 17.1 cm TL ($n = 29$) for the terminal phase specimens. The size at which 50 % of the individuals exhibited the TCP were estimated at 12.9 cm TL (95% confidence interval = 12.4 – 13.3 cm TL) with no significant differences between areas or significant interaction between size and area (Table 4, Fig. 2). The mouth gape increased linearly with body length ($R^2_{adj.} = 0.96$, $p < 0.001$) (Fig. 3): mouth width was 1 mm for specimens 9 cm TL and 6 mm for specimens 15 cm TL.

Table 4. Results of the generalized linear model estimating the size at which 50% of the rainbow wrasse population sampled made the transition from the initial coloration phase (ICP) to the terminal coloration phase (TCP) (see introduction for coloration description). SE: standard error; z: statistic; p: probability.

Parameter	Estimate	SE	z	p
Intercept	-34.92	14.18	-2.46	0.01
Size	2.64	1.07	2.47	0.01
Area	12.94	16.23	0.80	0.42
Area * Size	-0.90	1.24	-0.72	0.47

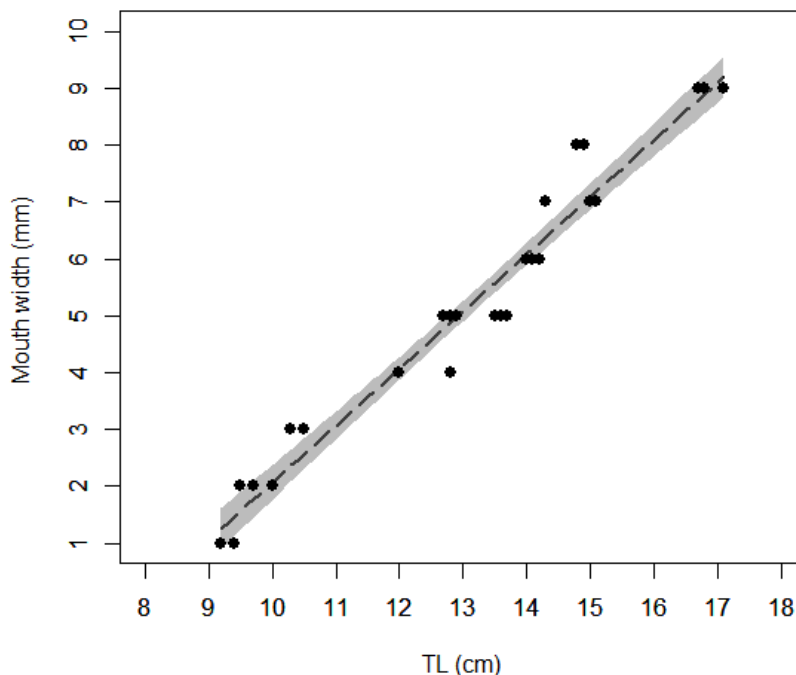


Fig. 3. Relationship between Total length and Mouth width for the Mediterranean rainbow wrasse *Coris julis* resulting from the General Lineal Model ($y = 0.10 * x - 7.99$; y and x in mm). Individuals from both areas (NTA, OFA) are included.

Table 5 and 6 summarise the results of the GAMs used to evaluate differences in the trophic position/body condition size relationships between both areas. The simplest model analysing the relationship of trophic position with size explained 47% of the variability in individual trophic position at size. This result indicated that size is the primary predictor of trophic position. All the variables and the interaction terms included in the most complex model are significant (Table 5).

Table 5. Results of the generalized additive models estimating the relationship between the trophic position (TP) and size (total length cm) in the two areas (No-Take Area and Open Fishing Area). Edf: Effective degrees of freedom; F: statistic; p: probability; Dev: explained deviance; AIC: Akaike information criterion, d-AIC: % improvement of the model respect to the simplest model.

Model Equation	Parameter	Edf	F	p	Dev	AIC (d-AIC)
$TP = \beta + f_1(size_i) + \varepsilon_i$	Size	3.01	25	< 0.001	47.1%	-226.6
$TP = \beta + f_1(size_i) * f_2(Area_i) + \varepsilon_i$	Area		29253	< 0.001	61.3%	-258.0 (13.9)
	Size	3.09	24	< 0.001		
	Area * Size	1.67	13125	< 0.001		

Table 6. Results of the generalized additive model estimating the relationship between the body weight (W, gr) and size (total length, cm) in the two areas (No-Take Area and Open Fishing Area). Edf: Effective degrees of freedom; F: statistic; p: probability; Dev: explained deviance; AIC: Akaike information criterion.

Model Equation	Parameter	Edf	F	p	Dev	AIC
$W = \beta + f_1(size_i) * f_2(Area_i) + \varepsilon_i$	Area		1431	< 0.001	98.7%	336.9
	Size	3.70	837	< 0.001		
	Area * Size	1.67	330	< 0.001		

The inclusion of area and the interaction term, in addition to fish size, resulted in an improvement of model performance (lower AIC and residual pattern). Both in NTA and OFA areas, a domed relationship between trophic position and size was observed (Fig. 2). While, for the individuals up to 11 cm TL the trophic position increased with size, a decrease in the trophic position was observed for the individuals of 12.6 cm TL

or larger. Thus, the positive relationship was only composed of ICP individuals, whereas the decreasing relationship was observed from the size at which 50 % of the individuals shifted to TCP. The trophic position of rainbow wrasse was slightly higher in NTA than OFA throughout the size range sampled but with different curve trends (interaction term statistically significant), due to the more pronounced decreasing tendency in the largest size range observed in the OFA than in the NTA (Fig. 2).

The results of the GAM analysis also indicated a significant progressive increase of body condition with increasing size (Fig. 2). Nevertheless, individuals from OFA had a slightly higher body condition than individuals of the same size from NTA. The interaction term was also significant indicating that the differences between both areas increased differently at larger sizes.

4. DISCUSSION

The results revealed an unexpected ontogenetic dietary shift in the rainbow wrasse. The trophic position increased with fish size up to 12 cm TL and then decreased, both in NTA and in OFA. Furthermore, the results demonstrated a higher trophic position and lower body condition of rainbow wrasse in NTA, while the size at sex shift remained unaffected. The most pronounced differences in trophic position of the rainbow wrasse between NTA and OFA were observed for the largest fish, thus revealing differences in the trajectories of the ontogenetic dietary shift. It is likely that the effects of fishing on trophic position, body condition and the ontogenetic dietary shift of rainbow wrasse are related to changes in the biomass of conspecifics, predators and competitors in AOF.

It is unlikely that the results were affected by sample processing and the trophic discrimination factor used. All samples were processed using the same technique, while delipidation has a very small effect on the $\delta^{15}\text{N}$ value in fishes (Ingram et al. 2007). On

the other hand, due to absence of experimentally derived trophic discrimination factor for the rainbow wrasse, a general discrimination factor (Post, 2002), previously used in the western Mediterranean, was deployed (Deudero et al., 2004; Valls et al., 2014).

Protection from fishing has allowed an effective recovery of the biomass of vulnerable species, as well as higher biomass of the rainbow wrasse population. Similarly, in the study area, the level of protection has previously been identified as the most important factor for the recovery of fish biomass (Guidetti et al., 2014; Sala et al., 2012). Nevertheless, fishing is not the only factor influencing the structure of Mediterranean fish assemblages with other environmental variables having an important role in driving spatial variations of Mediterranean reef fish assemblages (Coll et al. 2013; Gacía-Charton et al. 2004). Thus, the observed differences could also, in part, be related to other environmental influences. As a result, while fishing was likely the most important, other environmental factors, not considered in the current study, could have also influenced the findings.

Previous research in the study areas demonstrated differences in fish communities biomass following the establishment of Cabrera National Park, with biomass around 4 times greater in NTA than OFA (Coll et al. 2013). Similar differences were observed at the time of the study; the NTA harboured nearly 4- and 7-fold greater biomass of mesocarnivorous and piscivorous species than the OFA. Fish community recovery patterns alike were reported in other areas of the Mediterranean following the prohibition of fishing (Coll et al., 2012; Guidetti et al., 2014; Harmelin-Vivien et al., 2008; Sala et al., 2012), suggesting that protection from fishing could indeed be a major determinant of fish community structure at the study sites.

The differences in the biomass of rainbow wrasse between OFA and NTA are due to the lower abundance of larger specimens in OFA. These results are in accordance

with the size-selective impact of recreational angling for this species, mainly because the catches are dominated by terminal phase males (Cardona et al., 2007; Harmelin et al., 1995; Morales-Nin et al., 2005; Seytre et al., 2013).

The similar pattern of ontogenetic dietary shift expressed by the rainbow wrasse in areas with different levels of competition and predation risk suggests that body size, and the morphological and behavioural changes associated, are the most important drivers determining prey selectivity and diet composition. The observed size-related changes in the trophic position indicated an increase in prey of higher trophic position for the specimens of up to 12 cm TL. Subsequently, a progressive change in selectivity towards prey of lower trophic position was likely. This size-associated dietary pattern is in agreement with those previously informed by the studies using stomach contents analysis (Bell and Harmelin-Vivien, 1983; De Pirro et al., 1999; Hinz et al., 2019; Kabasakal, 2001; Sinopoli et al., 2017). Small-sized rainbow wrasse mainly prey on gammarid amphipods and other small crustacean and gastropod species, with specific selection for larger, soft-bodied, elongated prey (Hinz et al., 2019), whereas large-sized individuals consume higher amounts of bivalves (Veneridae), gastropods (Rissoidae and Turritellidae) and sea urchins (Echinoidea), as it has also been observed for other labrids (Gillanders, 1995; Hamilton et al., 2011; Jones, 1984; Lek et al., 2018; Platell et al., 2010). Thus, the increased consumption of these hard-body taxa and sea urchins, generally characterised by lower nitrogen isotope values than crustaceans (Agnetta et al., 2013; Allmon, 1988; Pinnegar and Polunin, 2000), likely results in the lower trophic position observed in larger rainbow wrasse and other temperate labridae species (Hamilton et al., 2011). Statistical analysis of most studies analysing size-based feeding ecology of coastal fishes using stable isotopes are mainly based on linear regression techniques (see Galván et al. 2010 for a detailed revision), showing negative, positive or

no trends in the relationships. However, the use of non-linear statistical models, such as those used in the present study, may reveal other, previously unreported, patterns of these relationships.

Size-related changes in morphological traits are important factors in ontogenetic dietary shifts (Clifton and Motta, 1998; Sánchez-Hernández et al., 2019). In labridae, as fish increase in body size, their mouth size, crushing power of pharyngeal teeth and handling ability also increases, extending the range of prey which can be integrated in the diet (Gill, 2003; Grutter, 2000; Lek et al., 2018; Wainwright, 1988). In addition, some species of this family have the ability to hold and smash large prey against the substrate before ingesting it, thus extending the prey size that can be ingested (Gill, 2003; Helfman, 1990; Jones et al., 2011; Sala, 1997). As a result of this behaviour, these species are not as constrained by the mouth gape as other benthic carnivorous fish, which, lacking this ability, have to eat their prey whole. The rainbow wrasse has a very small mouth gape that increases linearly with body size allowing for positive size selection and diversification of the trophic niche. However, if these morphological traits were the only drivers, it would be expected that the ontogenetic dietary shift would show null, negative or more steady change along the size range sampled (Ríos et al., 2019). By contrast, in both areas, the change in the slope of the trophic position occurred in the restricted and common size range (11.7 – 13.6), in which the fish became terminal males and dropped when all individuals were secondary males. Sala (1997) and Guidetti (2004) described predation by rainbow wrasse on sea urchins, observing that terminal males exhibited a higher capture efficiency, reduced handling time and carried out a greater proportion of attacks on juvenile sea urchins ($< 1\text{cm}$) than initial phase individuals. Hence, secondary males are considered as dominant consumers within populations –independently of their higher ability to prey on sea urchins due to their

large size (Guidetti, 2004; Sala, 1997). The social dominance and greater aggressiveness acquired by the secondary males can be considered as the main behaviour influencing the different steps of the predation sequence.

The decrease in trophic position was more pronounced in the OFA than in the NTA, indicating to a diet with higher contribution of prey of lower trophic position in the OFA. Differences between areas according to relative prey abundance, shelter availability for mobile prey species, as well as behaviour of prey and predators induced for differences in predation risk, are all important extrinsic factors that may contribute to the observed differences (Gillanders, 1995; Guidetti, 2004; Lek et al., 2018; Sinopoli et al., 2017). Among the different prey species consumed by rainbow wrasse, predation has been identified as a key process in determining sea urchin population and dynamics (e.g. Sala & Zabala 1996; Sala et al. 1998; Hereu et al. 2005; Guidetti & Sala 2007; Hamilton et al. 2011). In addition to rainbow wrasse, the main sea urchins' predatory fish are *Diplodus vulgaris* and *Diplodus sargus*, which prey on sea urchins smaller than 4 cm, and *Thalassoma pavo* which prey only upon juvenile sea urchins (Sala, 1997). This group of species showed a 4.8 –fold greater biomass in the NTA than in the OFA. In addition, predation risk could also have an effect on the selectivity of prey (Barley et al., 2017; Heithaus et al., 2008; Houtman and Dill, 1998; Sánchez-Hernández et al., 2019), mainly because of the trade-off between the risk of being predated upon and the value of the prey, determined by its respective energetic benefit and handling time (Gill, 2003). Thus, in order to reduce predation risk, rainbow wrasse may change their diet to less profitable prey that require less handling time and/or are more abundant. The time required to ingest a sea urchin < 1 cm is about 45 s (Sala, 1997), while the time required to feed on small invertebrate from the algae fronds is on average 7 s (Gouraguine, unpublished data). Consequently, in the NTA, rainbow wrasse likely switch to

alternative prey that require a reduced handling time in order to minimize competition and predation risk.

At high population densities, predators may increase the consumption of suboptimal prey of smaller size and lower trophic position (Jennings et al., 1997; McCann, 2011), which results in a decrease of their trophic position (Drago et al., 2017, 2009; Saporiti et al., 2016). In contrast, our results revealed that the rainbow wrasse feed at a relatively high trophic position throughout the size range sampled in the NTA area characterised by higher biomass of potential competitors and predators.

Finally, the results also indicated that the body condition of rainbow wrasse differed between areas with distinct structure of fish assemblages, with the body condition lower in the NTA than in the OFA. This finding is in agreement with those reported for other mesocarnivorous species and has been mainly attributed to differences in competition and predation risk (Barley et al., 2017; Hall and Kingsford, 2016b; Walsh et al., 2012). As indicated, the differences in fish assemblage could not only lead to changes in diet composition but also to alteration of behavioral and physiological traits, which may have important indirect effects on energy allocation of prey species (Heithaus et al., 2008; McPeck et al., 2001; Werner and Peacor, 2003). In areas with high predator biomass, prey need to allocate more energy to predator avoidance, which can in turn reduce the foraging time and ultimately the individuals' fitness (Lima, 1998; Ryer et al., 2004) and body condition (Lloret et al., 2013). The differences in body condition of rainbow wrasse between OFA and NTA were only observed in individuals larger than 11 cm TL, which can also be explained by increased per capita food availability due to decreased inter- and intra-specific competition for food in the OFA (Hinz et al., 2017). This result supports the idea of a diet change to a less profitable prey in order to reduce competition or predation risk.

In conclusion, the results reported here indicate that the indirect effects of fishing likely cause changes in the trophic position, body condition and ontogenetic dietary shift of a small-sized marine fish. It was observed that fishing induced changes in the biomass of fish populations and altered their intra- and inter-specific relationships, which ultimately affected their preferences for some prey and the behaviour of fish. Future research is needed, to evaluate differences in prey availability between OFA and NTA and how it may affect the behaviour of predators, thus also taking into account the bottom-up effects.

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Declaration of interests

X The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐ The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: