



Herbivory on the Invasive Alga *Caulerpa cylindracea*: The Role of Omnivorous Fishes

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Herbivory has long been considered an important component of biotic resistance against macroalgae invasions in marine habitats. However, most of the studies on herbivory of invasive algae refer only to consumption by strictly herbivorous organisms, whereas consumption by omnivorous species has been largely ignored and rarely quantified. In this study, we assess whether the commonest omnivorous sparid species in the Mediterranean Sea are consuming the highly invasive alga, *Caulerpa cylindracea*, and determine both, its importance in their diet and their electivity toward it as a source of food. Our results confirm that three of the four fish species studied regularly consume *C. cylindracea*, but in most cases, the importance of *C. cylindracea* in the diet is low. Indeed, the low electivity values indicate that all species avoid feeding on the invasive alga and that it is probably consumed accidentally. However, despite animals and detritus being the main food for these sparid species, several individual specimens were found to have consumed high amounts of *C. cylindracea*. This suggests a potential role that these fish species, being really abundant in shallow rocky bottoms, may play in controlling, to some extent, the abundance of the invader.

Keywords: invasive species, fish-alga interaction, grazing, biotic control, Mediterranean Sea, Sparidae, *Caulerpa cylindracea*

INTRODUCTION

Invasive macroalgae are one of the most successful and conspicuous groups of invaders in marine systems (Schaffelke et al., 2006; Thomsen et al., 2016). These organisms, once established, contribute to the homogenization of marine habitats and affect the structure of native assemblages by reducing both native species biomass and the overall assemblage diversity (Williams and Smith, 2007; Schaffelke and Hewitt, 2008; Thomsen et al., 2009, 2016). In the receiving community, the establishment and persistence of invasive algae can be reduced and affected by biotic and abiotic factors (Dunstan and Johnson, 2007; Catford et al., 2009; Thomsen et al., 2009; Kimbro et al., 2013; Papacostas et al., 2017), thus determining the invasive success of the invader. Among biotic factors, herbivory has long been considered as a potential biotic resistance mechanism and many studies have been conducted worldwide to assess the role of this mechanism on invasive macroalgae success (see references within Kimbro et al., 2013; Papacostas et al., 2017). Until now, assessments on the role of herbivory as a limiting factor for macroalgae invasion have mainly considered strictly herbivorous species (e.g., Lyons and Scheibling, 2008;

Britton-Simmons et al., 2011; Enge et al., 2017; Noè et al., 2017; Caselle et al., 2018), reporting contrasting results depending on the assemblage and the invasive species considered (e.g., Sumi and Scheibling, 2005; Steinarsdóttir et al., 2009; Tomas et al., 2011b; Nejrup et al., 2012; Enge et al., 2017; Caselle et al., 2018). Actually, considering that omnivores have been reported to influence macroalgae and phytobenthos abundance in different ecosystems around the globe (Bellwood et al., 2006; Mendes et al., 2015, 2019; Tebbett et al., 2020), and that they can act as important functional groups, for instance, in the reversal of community phase-shifts in coral reefs (Bellwood et al., 2006; Tebbett et al., 2020), we pose that they could also potentially consume invasive alga species and influence their abundance. Therefore, to improve our understanding on the ecological role of omnivorous fishes and to assess whether they can contribute to the resistance of native habitats against invaders, it is necessary to assess invasive alga consumption by these species.

In the Mediterranean Sea, the most successful and widespread invasive macroalga is *C. cylindracea* (Klein and Verlaque, 2008; Katsanevakis et al., 2016), a green alga native to the Southwestern coast of Australia that was first detected in Mediterranean waters in Libya in 1990 (Nizamuddin, 1991). Since then, it has colonized marine communities throughout the entire Mediterranean basin (Piazzi et al., 2005; Klein and Verlaque, 2008), where it can exert strong detrimental effects on native communities (Piazzi et al., 2001; Klein and Verlaque, 2008; Bulleri et al., 2016, 2017). However, despite its rampant success, several *C. cylindracea* meadows have suffered sudden steep declines in abundance some years after the onset of the invasion (Klein and Verlaque, 2008; García et al., 2016; Santamaría et al., 2021), which may indicate the existence of certain resistance mechanisms against this invasive species. Among these, herbivory on *C. cylindracea* has been described and assessed mainly in relation to the strictly herbivorous species present in the Mediterranean Sea, such as the fishes *Sarpa salpa* and *Siganus luridus* (Azzurro et al., 2004; Ruitton et al., 2006; Tomas et al., 2011b; Santamaría et al., 2021), and the sea urchins *Paracentrotus lividus*, *Sphaerechinus granularis* and *Arbacia lixula* (Ruitton et al., 2006; Bulleri et al., 2009; Cebrian et al., 2011; Tomas et al., 2011a). Nevertheless, there are omnivorous fish species, such as *Diplodus sargus*, *Boops boops*, and *Spondyliosoma cantharus*, that have been occasionally observed feeding on *C. cylindracea* before (Ruitton et al., 2006; Box et al., 2009; Terlizzi et al., 2011). Unfortunately, information is scarce on whether *C. cylindracea* is a common food source for omnivorous fish species, or whether these fish actively elect to feed on it. Since some of these species are the dominant fish in the shallow, infralittoral rocky habitats of the Mediterranean Sea (García-Rubies, 1997; Sala and Ballesteros, 1997; García-Charton et al., 2004), information on their consumption of *C. cylindracea* is needed to assess whether they can potentially contribute to limit the abundance of the invader.

In this study, the diets of four of the most abundant omnivorous sea bream species (Sparidae) were examined in order to determine (i) whether they feed on the invasive alga *C. cylindracea*, (ii) whether *C. cylindracea* is important in their diet, and (iii) whether they actively select or avoid *C. cylindracea* as a source of food.

MATERIALS AND METHODS

Study Area

The samples for this study were collected in the Cabrera Archipelago National Park (North-Western Mediterranean Sea; 39°12'21" N, 2°58'44" E) (**Supplementary Figure 1**) in 2008. This marine-terrestrial protected area was established in 1991 and since then it has maintained an exceptional conservation status for its marine habitats (Sala et al., 2012; Coll et al., 2013; Guidetti et al., 2014). *C. cylindracea* was recorded for the first time in the National Park in 2003 at a depth of 30–35 m and since then its distribution has expanded to cover most of its benthic communities at depths of between 0 and 65 m (Cebrian and Ballesteros, 2009).

Analysis of *Caulerpa cylindracea* Consumption

To determine whether non-strictly herbivorous fish species consume *C. cylindracea*, specimens for this study were captured by artisanal long-lines and gillnets once a month during June and July 2008, at different sites across the Archipelago, at Ses Rates and Foradada Islets (**Supplementary Figure 1**). These two sites were chosen because they are representative areas for the Cabrera Archipelago and have similar benthic community composition and abundances of sparid fishes (Reñones et al., 1997). Fishing campaigns were performed in the summer because it corresponds to the period of the year when the activity of the targeted fishes is higher. The main fishes targeted belong to the family Sparidae: white sea bream (*D. sargus*), annular sea bream (*Diplodus annularis*), two-banded sea bream (*Diplodus vulgaris*) and black sea bream (*S. cantharus*). These species were chosen because they are common representatives of the fish assemblages found in the Western Mediterranean, they are not herbivorous but can feed on macroalgae (Sala and Ballesteros, 1997) and some of them have been observed feeding on *C. cylindracea* before (Box et al., 2009; Terlizzi et al., 2011). These four species have different abundances within the National Park, being *S. cantharus* the least abundant and *D. vulgaris* the most abundant (Reñones et al., 1997; Coll, 2020). Specifically, in a 250 m² area, 1.7 *S. cantharus*, 1.9 *D. annularis*, 5.3 *D. sargus*, and up to 42 *D. vulgaris* individuals, were found.

The long-lines and gillnets, two gears commonly used in artisanal fishing, were deployed in the morning at depths of between 10 and 30 m. Gillnets were 300 m long, had a mesh size of 40 mm, and were left in the water for 4 h; whereas artisanal long-lines were 250 m long, had a total of 150 hooks, and were left in the water for 4 h. In total, two fishing events, one in June and the other in July, were performed at each location and with each gear. Every time a targeted fish species was hauled in, it was gutted and its stomach was stored and preserved in buffered 4% formaldehyde-seawater solution for later analysis of its content. Once in the laboratory, the species composition and abundance of the food items in each fish stomach was determined under a Stemi 2000-C stereomicroscope (Carl Zeiss, Berlin, Germany). The content of each stomach was spread onto a reticulated Petri dish and the food items were classified to the lowest taxonomic

level possible. Both surface area and weight measurements can reflect the dietary contribution of food items (Hyslop, 1980; Macdonald and Green, 1983), but in this case, and to avoid biases that could be derived from the small quantities present in the stomach contents, surface area measurements were preferred over weight measurements to quantify the dietary contribution of each food item. As such, the abundance of a particular food item was estimated as the percentage cover on the reticulated fields of the Petri dish in relation to the cover of the whole stomach content. When a species had a minimal presence and its cover could not be determined, a value of 0.1% of relative coverage was assigned.

When calculating the relative measures of prey quantity (RMPQ), the stomach contents were divided into the following five food categories: *C. cylindracea*, Other algal content, Seagrasses, Animal content and Organic detritus. Subsequently, for each fish species, the percentage frequency of occurrence of each food category (FO) was calculated as:

$$FO_i = (S_i/S_t) \cdot 100$$

where S_i is the number of stomachs containing the food category and S_t is the total number of stomachs analyzed for that particular fish species. The FO_i value is a measure of the consistency with which a species selects a given food category and was used to calculate two dietary indices that allow to compare the diets between species: the Combined Index (Q) and the Geometric Index of Importance (GII).

The combined index, Q, was chosen to assess the relative importance of each food category for each fish species. This index standardizes the abundance of each category and increases the importance of frequent smaller items while reducing the importance of occasional larger items (Nilssen et al., 2019). It was calculated as:

$$Q_i = \frac{V_i \cdot FO_i}{\sum_{i=1}^m (V_i \cdot FO_i)}$$

where V_i refers to the percentage surface of a food category, FO_i refers to the frequency of occurrence of the given food category, and m is the total number of food categories.

On the other hand, the Geometric Index of Importance, GII, represents the degree of feeding specialization on a particular food type (Assis, 1996; Preti et al., 2001) and allows us to classify the food categories as: “Primary prey,” “Secondary prey,” and “Occasional prey” in relation to the larger discontinuities in a decreasing sequence of values (Assis, 1996; Tripp-Valdez et al., 2015). It was calculated as:

$$GII_j = \frac{\sum_{i=1}^n (V_i + FO_i)}{\sqrt{2}}$$

Finally, the degree to which the four fish species tend to elect to feed on *C. cylindracea*, was assessed by Ivlev’s electivity Index (E) (Ivlev, 1961). This Index was determined by:

$$E = \frac{(d_i - a_i)}{(d_i + a_i)}$$

where d_i = % of *C. cylindracea* in the stomach content and a_i = % of *C. cylindracea* available in the environment (see following

section). The values of the Ivlev’s Index (E) can range from -1 (complete avoidance of the food item) to $+1$ (exclusive selection of the item), with positive values indicating that the food item is selected and eaten more than it is encountered by chance in the environment (Ivlev, 1961).

Assessment of the Abundance of *Caulerpa cylindracea* in the Community and Characterization of the Benthic Macroalgae Community

The abundance of *C. cylindracea* at the sampling sites where fish specimens were captured was assessed by means of scuba diving, also in the summer 2008. At each site, a perpendicular transect to shore was done, at depths of 10–30 m, so as to cover the same bathymetric range as that of the fishing gear used to collect fish samples. To estimate *C. cylindracea* abundance, a total of 30 quadrats measuring 25 cm \times 25 cm were randomly positioned within each 10 m-depth range (total of 90 quadrats per sampling site). These quadrats were divided into 25 subquadrats of 5 cm \times 5 cm and the number of subquadrats where *C. cylindracea* appeared was used as the unit of abundance (Sala and Ballesteros, 1997; Cebrian and Ballesteros, 2004; Sant et al., 2017). Subsequently, the average *C. cylindracea* abundance for the study area was calculated and this value was used in the calculation of the Ivlev’s electivity Index.

Additionally, to characterize the benthic macroalgae community, the quadrat methodology was also used. In this case, at each site and at each depth stratum (10, 20, and 30 m depth), six 25 cm \times 25 cm quadrats were randomly positioned and the abundance of each algal species was calculated as a function of the number of subquadrats where each species appeared. Subsequently, as there were no differences in the benthic composition between sites, the average abundance per alga species at the study area was calculated.

Statistical Analyses

To evaluate sampling sufficiency, prey accumulation curves for each of the sampled species were generated using the package *BiodiversityR* (Kindt and Coe, 2005) in the R environment (R Core Team, 2018). Two curves per species were fitted, one to the number of prey taxa and the other to the number of food categories, to assess whether the number of stomachs analyzed was adequate for the diet characterization of each species.

Differences in the specific composition of stomach contents between fish species were assessed through multivariate techniques such as non-metric multi-dimensional scaling plots (NMDS plots), analysis of similarities (ANOSIM) and similarity percentage analysis (SIMPER). All of these techniques were performed in R, within the *vegan* package (Oksanen et al., 2018). First, in order to visualize and represent stomach content composition, a NMDS (Clarke and Warwick, 1994; Cox and Cox, 2000) based on the Bray-Curtis dissimilarity matrix of the square root transformed data was plotted and the most important species that determine the least stressful ordination were detected using the *envfit* function within the *vegan* package. Then, the statistical differences in the food items consumed by the fish

species were assessed using ANOSIM (Clarke, 1993), applied to the Bray-Curtis dissimilarity matrix, with fish species as a fixed factor. Additionally, a pairwise ANOSIM was performed by modifying the pairwise.adonis function¹ and the R-values obtained were used as an indication of diet similarity, with values near 1 indicating separation in diet composition and values near 0 indicating diet similarity (Rogers et al., 2012). Finally, a SIMPER analysis based on the Bray-Curtis dissimilarity index was used to assess the relative contribution of each food item to the overall differences between fish species diets.

RESULTS

During the sampling events, a total of 93 fishes were captured, with *D. sargus* being the most abundant ($n = 51$) followed by *S. cantharus* ($n = 22$), *D. vulgaris* ($n = 13$), and *D. annularis* ($n = 7$). All the stomachs examined contained ingested material of some kind, which, as a whole, was composed of a high diversity of taxonomic groups, with 73 different prey items identified, 32 of them to the species level (Supplementary Table 1).

According to the prey accumulation curves (Supplementary Figure 2), sampling sufficiency was a little low to quantitatively characterize the diet of the sampled species using the full resolution of the data (lowest taxonomic level), as all the curves were only beginning to plateau but did not reach the asymptote. However, asymptotes were reached for all the species when prey taxa was combined in food categories, which suggests that our data is adequate to investigate the quantitative contribution of these categories to the diet of the sampled species.

Differences in stomach content were observed between species in terms of the dominant prey categories, although organic detritus and animal content were certainly prominent in all four species (Table 1). In this sense, the Combined Index (Q) and the Geometric Index of Importance (GII), identified the category “Organic detritus” as the primary food item for *S. cantharus*, while the category “Animal content” was the primary prey for the other three fish species (Figures 1, 2). Despite this predominance for “Animal” and “Organic detritus” items, algae and seagrasses were found in all the species, being the stomach contents of both *D. sargus* and *D. annularis* particularly rich in algae, with values of around 18 and 30%, respectively (Table 1).

Regarding the consumption of the invasive alga *C. cylindracea*, 81, 45, and 41% of the *D. annularis*, *D. sargus* and *S. cantharus* specimens contained *C. cylindracea* in their stomachs, respectively; whereas *D. vulgaris* was the only fish species that had not consumed the invader. However, the contribution of *C. cylindracea* to the total stomach content was generally low, except for *D. annularis*, in which 26% of the stomach content corresponded to the invasive species (Table 1). Actually, both dietary indexes, Q and GII, classified *C. cylindracea* as a primary food item for *D. annularis*, being the second most common food category in the stomachs and having values similar to animal content (Figures 1, 2). In contrast to this, *C. cylindracea* was classified as an occasional food item for both *D. sargus* and

TABLE 1 | Summary of the stomach content data for each fish species.

<i>Diplodus annularis</i>	Mean ± S.E. (%)	<i>Diplodus sargus</i>	Mean ± S.E. (%)
Other algal content	4.69 ± 3.10	Other algal content	15.10 ± 3.67
<i>Caulerpa cylindracea</i>	25.73 ± 11.80	<i>Caulerpa cylindracea</i>	3.56 ± 0.96
Seagrasses	0.26 ± 0.21	Seagrasses	9.36 ± 2.84
Animal content	43.28 ± 16.00	Animal content	48.31 ± 5.53
Organic detritus	26.05 ± 15.03	Organic detritus	19.62 ± 4.72
<i>Diplodus vulgaris</i>	Mean ± S.E. (%)	<i>Spondyliosoma cantharus</i>	Mean ± S.E. (%)
Other algal content	8.80 ± 6.91	Other algal content	1.88 ± 0.90
<i>Caulerpa cylindracea</i>	0	<i>Caulerpa cylindracea</i>	5.15 ± 1.94
Seagrasses	0.29 ± 0.25	Seagrasses	0.40 ± 0.26
Animal content	54.75 ± 12.30	Animal content	14.10 ± 4.81
Organic detritus	31.54 ± 11.25	Organic detritus	78.47 ± 5.12

The ingested food items are grouped into categories and the values given are mean percentages ± S.E. for each fish species. Ingested values of *Caulerpa cylindracea* are highlighted in bold.

S. cantharus (Figures 1, 2), but most of the algae content in the stomachs of *S. cantharus* corresponded to the invasive species ($\approx 74\%$; Table 1). However, even with the high proportion of *C. cylindracea* found in some of the studied species, the negative values obtained for the Ivlev's Electivity Index suggest that *C. cylindracea* is generally avoided by all the species (Table 2), despite *C. cylindracea* being the dominant species in the benthic community (Supplementary Table 1).

Considering the whole diet of the four sampled sea bream species, the graphical ordination suggested that there might be some overlap between diets (Supplementary Figure 3), yet the ANOSIM detected significant differences in the stomach content composition between all fish species (ANOSIM; $p < 0.05$; Supplementary Table 2), with two exceptions: *D. sargus*—*D. vulgaris* and *D. sargus*—*D. annularis* ($p > 0.05$; Supplementary Table 2). In this sense, the greatest dissimilarities in diet were found between *S. cantharus* and two of the *Diplodus* species, *D. annularis* and *D. vulgaris* ($R = 0.63$ and $R = 0.47$ respectively, Supplementary Table 2), since the diet of *S. cantharus* was more homogeneous (Supplementary Figure 2) and it was dominated by organic detritus rather than by animal content (Table 1 and Figures 1, 2). Actually, the SIMPER analysis identified “organic detritus” as the biggest contributor to the diet dissimilarities between the four fish species, with values ranging from 19 to 40% (Supplementary Table 3). Remarkably, *C. cylindracea* was one of the species most strongly influencing the graphical ordination (Supplementary Figure 3) and the SIMPER analysis identified the invasive alga as the second most important food item in terms of explaining the diet dissimilarities between *D. annularis* and the other fish species (Supplementary Table 3).

DISCUSSION

Stomach content analysis of some of the commonest species in the shallow rocky infralittoral communities in the western

¹<https://github.com/pmartinezarbizu/pairwiseAdonis>

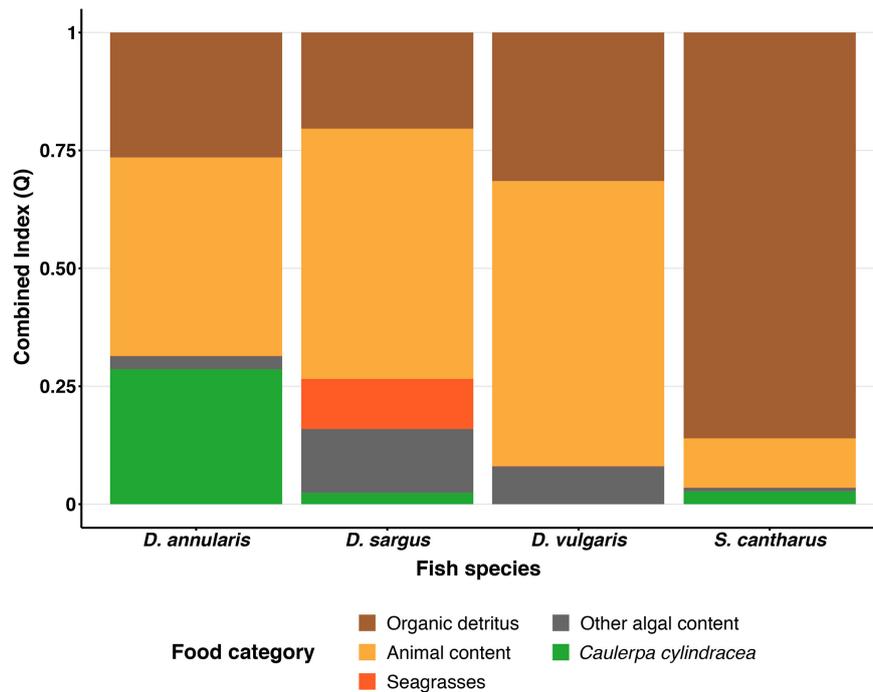


FIGURE 1 | Combined Index (Q) for each fish species. Each color represents one of five food categories (Organic detritus, Animals, Seagrasses, Other algae and *Caulerpa*).

Mediterranean Sea, revealed that three of the four studied fish species have consumed the invasive alga *C. cylindracea*. Actually, the invader was identified as the most prominent algae for two of the fish species, *D. annularis* and *S. cantharus*, and was a primary food item for *D. annularis*. On the contrary, it was only an occasional food item for both *S. cantharus* and *D. sargus*. Complementary, despite these species having a diet predominately based on animal and detritus content (Sala and Ballesteros, 1997; Gonçalves and Erzini, 1998; Pita et al., 2002; Box et al., 2009; Terlizzi et al., 2011; Fellingine et al., 2012, 2017), our results show that they can also feed on considerable amounts of algae, with values exceeding those previously reported for non-strictly herbivorous sea bream species (Sala and Ballesteros, 1997; Sánchez-Jerez et al., 2002; Leitão et al., 2007; Box et al., 2009).

In general, being *C. cylindracea* a widespread and regionally abundant alga (Klein and Verlaque, 2008; Katsanevakis et al., 2016), our findings clearly suggest that it can potentially become a recurrent food item for omnivorous fish species, similarly to what has happened with the herbivorous fish *S. salpa*, which has adopted the invader as a preferred food item (Tomas et al., 2011b). Actually, several studies involving lower sample sizes, had previously reported the ability of *D. sargus*, *S. cantharus*, and *D. vulgaris* to occasionally feed on *C. cylindracea* on other locations in the Mediterranean Sea (Box et al., 2009; Terlizzi et al., 2011; Fellingine et al., 2012, 2017; Gorbi et al., 2014). In our assessment, however, *C. cylindracea* consumption seems frequent, as a high proportion of the sampled individuals (41%) was found with the invader in the stomach. Interestingly, our findings are, to our knowledge, the first evidence of *D. annularis*

feeding on *C. cylindracea* in the Mediterranean Sea, but given that almost all the fished individuals (86%) had consumed the invader and that they had high amounts of *C. cylindracea* in their stomachs, this fish species should be included in subsequent assessments to further elucidate whether this feeding behavior is common across the Mediterranean region. Unfortunately, it should be taken into account that sample sizes, mainly for *D. vulgaris* and *D. annularis*, were low (**Supplementary Figure 2**), so the findings reported here should be interpreted as a first exploration. Therefore, to fully characterize the contribution of *C. cylindracea* to the diet of the different seabream species and to thoroughly quantify *C. cylindracea* consumption, the analysis of more stomach contents is definitively needed. Despite this, however, our data clearly shows that the invader has become a recurrent food source for at least three of the four assessed species, according to *C. cylindracea* being found consistently in the stomach contents of these species.

Concurrently, despite previous studies reporting the consumption of *C. cylindracea* by omnivorous fishes, none of them reports the availability of *C. cylindracea* in the environment, making it impossible to assess whether the omnivorous fishes are actually targeting the invader. In this sense, in our study area, *C. cylindracea* was found to be the dominant species in the benthic communities where the fish species were fished, with mean coverage values close to 55% (**Supplementary Table 1**). However, electivity of the fish species for *C. cylindracea* suggests that all the species were avoiding feeding on the invader, although laboratory experiments should be considered to have a more detailed interpretation on the avoidance/preference

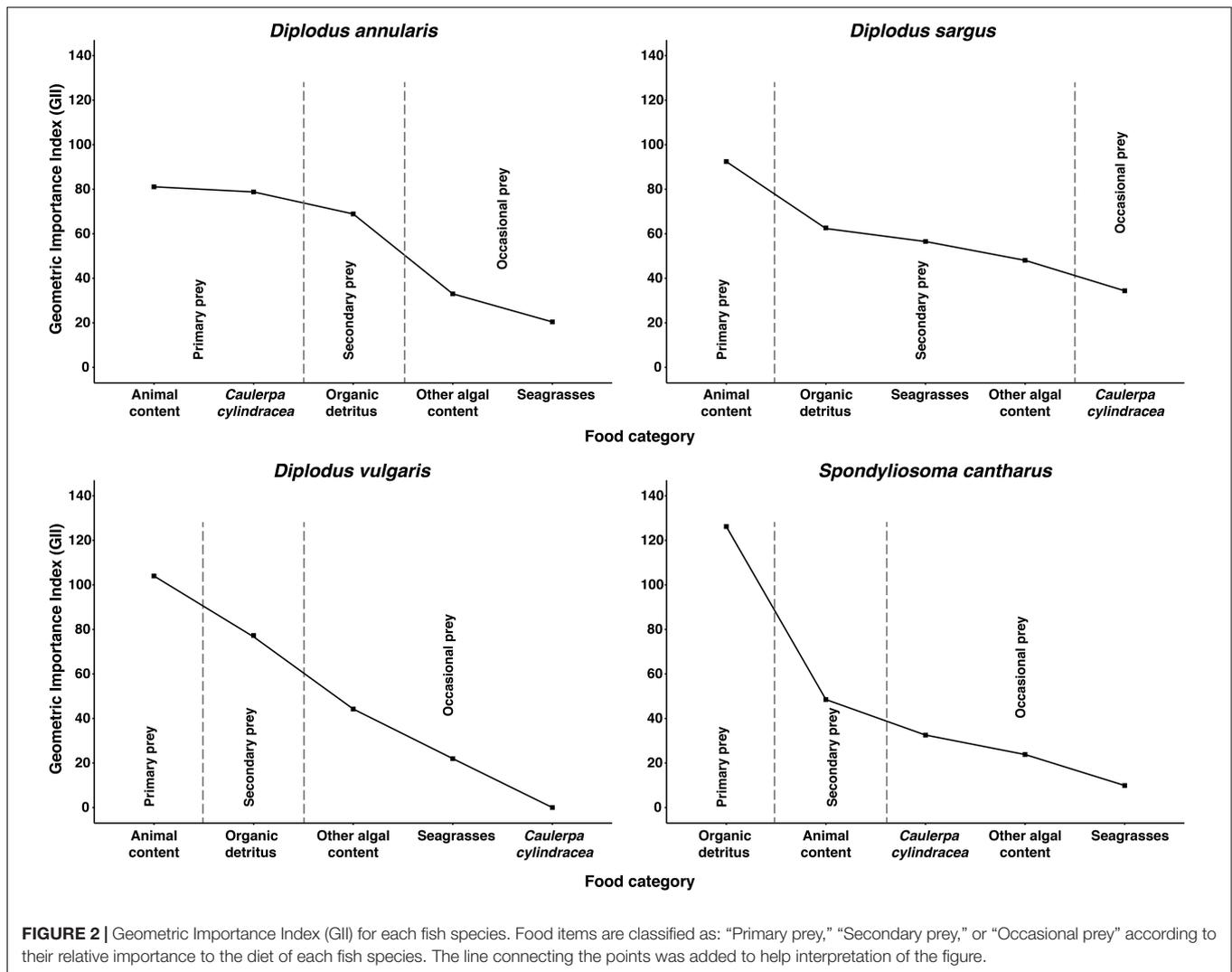


FIGURE 2 | Geometric Importance Index (GII) for each fish species. Food items are classified as: “Primary prey,” “Secondary prey,” or “Occasional prey” according to their relative importance to the diet of each fish species. The line connecting the points was added to help interpretation of the figure.

for the invader. Therefore, the low electivity suggests that the consumption by the omnivorous fishes was more occasional than that of the strictly herbivorous fishes, which show a positive electivity for the invader (Tomas et al., 2011b). Surprisingly, despite this general avoidance of *C. cylindracea*, high amounts of the invader were found in the stomach contents of some individuals, with values reaching over 35%. This suggests that

the invasive alga is probably consumed accidentally when the fish are trying to feed on other prey living within the dense meadows of *C. cylindracea*. In fact, polychaetes, mollusks, and decapods—which are the preferential prey for most of the sea breams studied (Bauchot and Hureau, 1986; Sala and Ballesteros, 1997; Gonçalves and Erzini, 1998; Pita et al., 2002; Leitão et al., 2007)—have been found to be very abundant under the stolons of *C. cylindracea* (Carriglio et al., 2003; Galil, 2007; Box, 2008; Klein and Verlaque, 2008). Furthermore, the suggestion that consumption of the alga is accidental is also supported by the low assimilation of *C. cylindracea* in the stomach contents, as in most cases it was found intact and undigested (Supplementary Figure 4). However, taking into account that some of the sea breams considered here have small home ranges and show strong site fidelity (D’Anna et al., 2011; March et al., 2011; Alós et al., 2012; Di Lorenzo et al., 2014), it cannot be ruled out that they might also be forced to feed on *C. cylindracea* in heavily colonized areas, and this might have a negative impact on the physiology of the fish species. In fact, previous evidence relates *C. cylindracea* consumption to a decrease in certain essential

TABLE 2 | Mean \pm S.E. values for Ilev’s electivity Index (E), as a measure of the electivity of the four sparid fish species studied towards the invasive alga *C. cylindracea*.

<i>E</i> _{Caulerpa}	
<i>D. annularis</i>	-0.52 ± 0.18
<i>D. sargus</i>	-0.90 ± 0.02
<i>D. vulgaris</i>	-1
<i>S. cantharus</i>	-0.86 ± 0.05

An *E* value approaching -1 indicates that the food item is avoided; whereas an *E* value approaching 1 indicates the species only feeds on that item.

fatty acids in fish tissues and liver (Felline et al., 2014), to an increase in the levels of antioxidants and in pro-oxidant effects (Box et al., 2009; Terlizzi et al., 2011; Felline et al., 2012), to a decrease in the condition factor (Terlizzi et al., 2011) and to a decrease in the gonadosomatic index (Felline et al., 2012), all of which may negatively affect the fish fitness. It is not yet clear what causes these physiological responses, although they could be caused by the accumulation of some of the compounds produced by *C. cylindracea*, such as caulerpenyne, a toxic, secondary metabolite that has herbivore-deterrent properties (Paul et al., 2007). However, considering that *Caulerpa prolifera*, a native species in the Mediterranean Sea, has much higher caulerpenyne concentrations than *C. cylindracea* (Box et al., 2010) and that sea breams can often consume the native *Caulerpa* species (Supplementary Table 1; Chaouch et al., 2013, 2014; Marco-Méndez et al., 2017), it is likely that the fish might have developed a certain tolerance and effective detoxification pathways for the toxic metabolites, as other herbivores do (Cornell and Hawkins, 2003; Sotka and Whalen, 2008; Sotka et al., 2018). In any case, more studies are needed to understand the possible long-term consequences of *C. cylindracea* consumption on the health of fish assemblages and whether these consequences could propagate throughout the food web, potentially affecting the functioning of the ecosystem through cascading effects.

Overall, our findings confirm that the invasion of *C. cylindracea* in the Mediterranean Sea has the potential to influence the feeding habits of the omnivorous fish species as it has already done with some of the strictly herbivorous organisms (Azzurro et al., 2004; Ruitton et al., 2006; Cebrian et al., 2011; Tomas et al., 2011a,b). In this sense, the assessment of *C. cylindracea* consumption by omnivorous (i.e., non-strict herbivores) fish presented here is noteworthy since most of the previous research into the effects of herbivory on invasive algae has focused only on the strict herbivores, disregarding the effect that omnivorous organisms might have (e.g., Davis et al., 2005; Sumi and Scheibling, 2005; Ruitton et al., 2006; Wikström et al., 2006; Lyons and Scheibling, 2008; Vermeij et al., 2009; Britton-Simmons et al., 2011; Cebrian et al., 2011; Tomas et al., 2011a,b; Nejrup et al., 2012; Hammann et al., 2013; Enge et al., 2017; Caselle et al., 2018). Furthermore, while some of the previous studies have highlighted the contribution of some of these herbivores to limit the abundance of invasive algae, our findings suggest that non-strict herbivores could also potentially have a similar, albeit less important contribution. Therefore, these findings provide another example on the important role that omnivorous fish species might have on marine ecosystems, where they have been reported to play a key role on the coral-algae equilibrium in coral reefs from several regions (Bellwood et al., 2006; Tebbett et al., 2020), and to become an important link between primary producers and higher trophic levels in rocky reefs (Mendes et al., 2015, 2019). In our case, given the high amounts of *C. cylindracea* found in some specimens and considering that omnivorous sparid fishes dominate the shallow rocky infralittoral habitats in the Mediterranean Sea (García-Rubies, 1997; Sala and Ballesteros, 1997; García-Charton et al., 2004; Coll et al., 2013) with abundances of up to 60 individuals per 250 m² and biomasses of more than 40 g/m²

(García-Rubies and Zabala, 1990; Sala and Ballesteros, 1997; Di Franco et al., 2009; Guidetti et al., 2014; Coll, 2020), it seems that they could potentially have some impact on the abundance of *C. cylindracea*. Therefore, we suggest that the lower impact exerted by omnivorous fish could complement the higher impact exerted by strictly herbivorous organisms (Santamaría et al., 2021) and that, taken together, they might significantly reduce the abundance of *C. cylindracea* in shallow habitats. Still, considering our limited sample sizes, we pose that more in depth assessments are needed to better quantify the impact that omnivorous fish might have on the success of *C. cylindracea*. Finally, considering that sea breams are highly targeted by fisheries and have already suffered important declines in the Mediterranean basin (Sala et al., 1998; Coll et al., 2004; Sala, 2004; Morales-Nin et al., 2005; Guidetti, 2006; Lloret et al., 2008), places that promote their recovery, such as well-enforced marine protected areas (MPAs) (Mosquera et al., 2000; Micheli et al., 2005; Claudet et al., 2006; Guidetti, 2006; Guidetti and Sala, 2007; Guidetti et al., 2008, 2014; Sala et al., 2012; Coll et al., 2013), might also foster the strength of this complementary control mechanism on the abundance of *C. cylindracea*.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

Ethical review and approval was not required for the animal study because the sampling was performed during 2008 in the framework of a big project carried out by the National Park and the Autonomic Government. The sampled species are commercial species usually fished in the area. For our study we received only the stomach of the fishes already sampled and we did not take part on the manipulation of the species.

AUTHOR CONTRIBUTIONS

FT and EC conceived the ideas and the experimental design. FT, EB, and EC collected the data. JS, FT, EB, and EC analyzed the data. JS and EC drafted the manuscript. All authors contributed substantially to revisions and accepted the final version before submission.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2021.702492/full#supplementary-material>

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