

Diet of fish populations in *Posidonia oceanica* meadows off the Island of Ischia (Gulf of Naples, Italy): assessment of spatial and seasonal variability

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ABSTRACT

The gut contents of fish in three *Posidonia oceanica* meadows off the island of Ischia (Bay of Naples, Italy) were investigated. A total of 926 individual fish belonging to 28 species was sampled by bottom trawl in the leaf canopy. Labridae, Pomacentridae, Scorpaenidae, and Serranidae were the best represented families (41%, 38%, 8% and 6% of the total number of individuals, respectively). Of the 94 taxa detected in the gut contents, 42 were identified to the species level. The most common food items were decapod crustaceans (15% of the gut contents, on average), copepods (13%), amphipods (14%), brown fragments of *P. oceanica* (6%), and ostracods (6%). The most abundant species of labridae, *Symphodus ocellatus* and *S. rostratus*, showed a broad spectrum of prey. This generalist feeding may positively influence their numerical abundance. Seasonal variations in the diets of fish, also at prey-species level, were demonstrated. The fish taxon plays essentially a macro-carnivore trophic role. In the investigated seagrass meadows the main trophic fluxes start from plant detritus, macrophyta, and microphyta (as primary producers) towards crustacean decapods, copepods, ostracods, and gammarid amphipods (as secondary producers) to fish. A low recycling rate (4%) within the fish community was observed. Larger fish predators (e.g., Sparidae), swimming over the leaf canopy, are the main exporters to adjacent coastal systems.

Keywords: Fish; Food Webs; Spatial Variability; *Posidonia Oceanica*; Seagrass; Seasonality

1. INTRODUCTION

The presence of seagrasses provides effective protection against predation [1-3]; therefore it is accompanied by a great abundance of small invertebrates [4-6]. In fact, the 3-dimensional complex structure provided by seagrasses represents a clear advantage for several invertebrates, as well as for young fish, that find refuge from predation [7]. It has been demonstrated that the capture success of predators is generally higher over bare substrates than in seagrass meadows and this leads settling larvae, juveniles and adults towards coastal meadows [8]. A rich fish population inhabits the seagrass meadows, because it is attracted to the abundant food (*i.e.*, small invertebrates; [9]) and to the shelter from predators typically provided by these structured habitats. In fact, seagrass meadows play the role of nurseries for important fish species [10,11] that, along with decapod crustaceans [12,13], are important consumers of secondary production in these systems [14-16]. According to [7], the relative value of seagrasses as predation defense is correlated to the relative abundance of ambush-, stalk- and chase-attack predators inhabiting seagrass and neighboring substrata.

Several authors have investigated the structure of the food webs in *Posidonia oceanica* meadows (e.g., [5,17-19]). However, there is still a remarkable lack of information on the main pathways of transfer from the plant level to the highest trophic levels [20,21]. In particular, the fate of secondary production in the food webs of *P. oceanica* meadows is partially unknown. Although fish are hypothesized to be the highest level consumers of secondary production in seagrass meadows [22,23] and in other environments [24], the rate and the pathways of transfer are still uncertain.

Another important feature of Mediterranean sea-

grass meadows is their seasonality. Such seagrasses as *P. oceanica* are stable and time-persistent, but their canopy exhibits important seasonal variations due to the characteristic rhythm of growth [17]. These variations are also in accordance with dramatic shifts in the amount of detritus and epiphytes available [25,26]. In addition, seasonal differences in abundance and composition of associated invertebrate populations were observed in the leaf stratum [27]. Similar variations may be observed among differently exposed meadows. In fact, *P. oceanica* beds located in areas influenced by high hydrodynamic pressure exhibit lower abundance of detritus and different epiphyte associations, as compared to meadows exposed to low hydrodynamic forces [2,5]. Due to these spatial and temporal differences in the abundance of potential prey, the general assumption that fish represent important predators for selected invertebrates living in the leaf stratum of seagrasses [1,14,16] should be confirmed by direct data.

The feeding behaviour of fish living within the leaf canopy of three *P. oceanica* meadows has been investigated in the present paper, through the analysis of their gut contents, to assess their role in the consumption of secondary production in two seasons and, therefore, the impact of fish predation [28] on invertebrate populations. Our major questions were: 1) Which is the trophic role played by fish in a range of *P. oceanica* meadows? 2) Are the trophic guilds exhibited by selected species of fish stable in space and time, or are they adapted to spatial and seasonal variations in the structure of the associated algal and animal communities? 3) May fish be considered the highest-level consumers of secondary production in seagrass meadows?

2. MATERIAL AND METHODS

This investigation was carried out on *Posidonia oceanica* meadows off the island of Ischia (Gulf of Naples, Italy; **Figure 1**), extending from 1 to about 30 m depth. Samples were collected at three meadows differently exposed: 1) Lacco Ameno Bay, on the northern sector

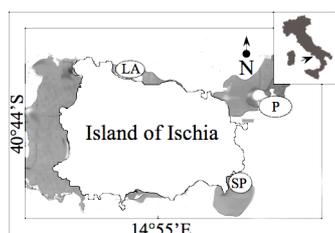


Figure 1. Map of the sampling area and location of the three sampling sites. LA: Lacco Ameno; P: Channel between Ischia and Procida; SP: Cape S. Pancrazio.

of the island; 2) the channel between Ischia and the island of Procida, on the eastern side of the island of Ischia, and 3) off Cape San Pancrazio, on the south-east side. Samples were collected in winter (March) and summer (July) on *P. oceanica* meadows, at depths between 17 and 20 m. This depth was selected as it corresponds to the “intermediate” meadow (as described by [5]), whose animal populations can be regarded as representative of the whole system. It is more stable than the shallow meadow, less exposed to environmental disturbances, and exhibits a higher structural complexity than the deep meadow [5,17]. The two sampling seasons chosen correspond, respectively, to the periods before and after the reproduction of several species of benthic invertebrates. We selected these periods also to point out any difference in the diet of fish due to variations in the availability of their prey.

Previous authors [29] investigated the methodological bias of sampling instruments applied to the same ecosystem studied in the present paper and they determined that skid trawls can efficiently sample the fish assemblage living close to the canopy. Therefore, a skid trawl with a frame of 1.5 x 0.5 m and a mesh of 8 mm was used, according to the technique described by [30]. Four replicates were collected in each site around noon, both in summer and in winter. Each replicate was obtained by towing the skid for 5 minutes at a constant speed of 1 knot, to cover an area of about 250 m². All fish collected were preserved in 10% buffered formalin.

Individual fish were identified to the species level, measured (total length), weighed (fresh weight), and dissected for the analysis of gut contents. Gut contents were examined under a dissecting microscope and, when necessary, permanent slides were prepared and analysed under a compound microscope. Each prey was identified to the lowest possible taxonomic level and its abundance was evaluated assigning a score from 0 to 4 (*i.e.*, 0%, 25%, 50%, 75%, and 100% of the total gut volume, respectively). Least abundant food items were pooled into larger taxa, to obtain a matrix “species vs. food items” for statistical analyses. The ratio between total gut content of each individual and the gut volume was indicated by a score (from 0 to 4, as above mentioned), to quantify gut “fullness”. This technique was used to obtain a quantitative estimation of the whole gut content, avoiding the experimental error due to the immersion in formalin and to the high fragmentation of some materials [31,32].

Fish populations were statistically analysed to detect variations in their composition, among replicates, sites and seasons. Differences among individual samples were tested by one-way analysis of variance (ANOVA). The significance of differences among individual diets was evaluated by *t*-test. The diets of the most abundant fish

species were analysed for variation in their food sources as a function of the sampling site and season. Gut content data were analysed by the technique described by [18], to classify species in homogeneous trophic groups and obtain an ordination of fish trophic groups according to the site and the season of sampling [27]. The technique involves the calculation, for each species in each sample, of two indices defining a trophic category, based on average prey “type” (plant or animal) and “size” (taking into account the average size in millimetres of each prey item). In particular, the two indices were obtained by the following formulae:

a) Prey type index:

$$Type_i = (\sum V_i - \sum C_i) / \sum M_{ij} \quad (1)$$

b) Prey size index:

$$Size_i = \ln(\sum (PS_j \times M_{ij}) / \sum M_{ij}) \quad (2)$$

with:

- = abundance of plant items;
- = abundance of animal items;
- = abundance of each considered item;
- = mean prey size (measured in mm).

This technique allows for an ordination of species in Cartesian plots showing feeding preferences, to compare the results obtained at different sites or during different seasons, and to simplify the understanding of complex ecosystem food webs. In fact, the positions of species in the 4 quarters of the plot indicate their feeding habits: macro-herbivores are ordered in the 1st sector (upper right), micro-herbivores in the 2nd sector (lower right), micro-carnivores in the 3rd sector (lower left), macro-carnivores in the 4th sector (upper left), omnivores are close to the centre of axes. The information collected was used to draw the main trophic relationships in the considered system.

3. RESULTS

3.1. Fish Populations

No significant differences between the four replicates of each sample were found (ANOVA; $p < 0.01$). Therefore, the specimens collected in each set of four parallel replicates were pooled, prior to be subjected to trophic analyses. A total of 926 individual fish, belonging to 28 species (Table 1), was sampled, identified, and analysed. The most abundant families were Labridae (41% of all individuals), Pomacentridae (39%), Scorpaenidae (8%) and Serranidae (6%). The most abundant species (Figure 2) were *Chromis chromis* (356 ind.; 38%); *Symphodus ocellatus* (187 ind.; 20%) and *S. rostratus* (134 ind.; 14%). The total number of species and individuals in each sample varied according to the site and the season

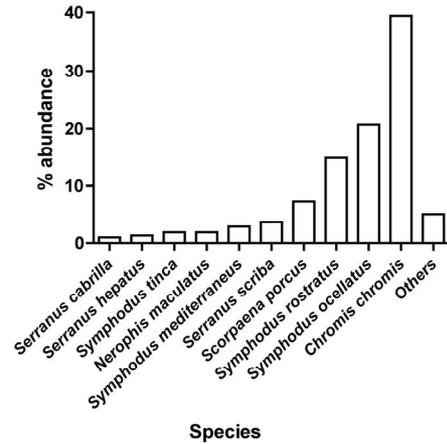


Figure 2. Percent abundance of the most abundant fish species in all samples (pooled).

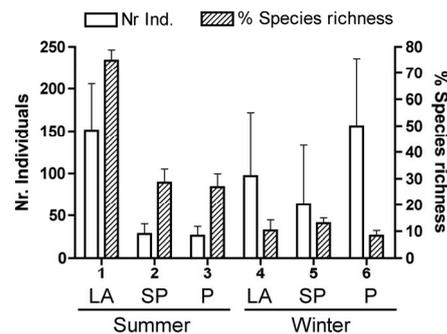


Figure 3. Mean number of individuals collected (left axis) and species richness (right axis) for each sample. LA, Lacco Ameno; SP, S. Pancrazio; P, Channel of Procida. The first three collections were performed in summer, the other three in winter. Standard deviations among the four replicates are indicated by error bars.

and it was highest in Lacco Ameno in summer (Figure 3).

The total number of species per sample varied between 7 (at the Procida channel, summer) and 16 (at Lacco Ameno, summer). The biomass of species sampled in winter was constantly higher than in summer, with the exception of the families Pomacentridae and Congeridae. Labridae reached a winter biomass of about 2 g m^{-2} (fresh weight) in the sampled meadows. The families Labridae, Pomacentridae and Serranidae accounted for 98% of the total fish biomass. Most individuals were small in comparison to the maximum size reached by the species (Table 1). Large intra-specific size variations were observed mainly in the samples collected at Lacco Ameno.

3.2. Analysis of Gut Contents

Ninety-four food items were identified in the guts.

Table 1. Fish species collected, total number of individuals collected in all the samples (pooled), mean length (cm total length) and mean weight (g wet weight) of each species.

Nr.	Species		Total	Mean	Mean
			nr. ind.	length (cm)	weight (g)
1	<i>Chromis chromis</i>	(Linnaeus, 1758)	356	5.43	7.37
2	<i>Symphodus ocellatus</i>	Forsskal, 1775	187	6.04	1.07
3	<i>Symphodus rostratus</i>	(Block, 1797)	134	8.41	13.52
4	<i>Scorpaena porcus</i>	Linnaeus, 1758	69	8.48	4.82
5	<i>Serranus scriba</i>	(Linnaeus, 1758)	42	11.01	3.75
6	<i>Symphodus mediterraneus</i>	(Linnaeus, 1758)	26	5.57	4.65
7	<i>Nerophis maculatus</i>	Rafinesque, 1810	17	20.61	14.75
8	<i>Symphodus tinca</i>	(Linnaeus, 1758)	17	12.48	1.03
9	<i>Gobius cruentatus</i>	Gmelin, 1789	15	4.60	0.93
10	<i>Serranus hepatus</i>	(Linnaeus, 1758)	12	6.22	10.16
11	<i>Syngnathus acus</i>	Linnaeus, 1758	8	20.76	0.76
12	<i>Arnoglossus kessleri</i>	Schmidt, 1915	6	5.00	2.78
13	<i>Symphodus cinereus</i>	(Bonnaterre, 1788)	6	7.73	67.20
14	<i>Scorpaena notata</i>	Rafinesque, 1810	5	8.43	0.99
15	<i>Apogon imberbis</i>	(Linnaeus, 1758)	4	8.08	3.52
16	<i>Gobius geniporus</i>	Valenciennes, 1837	3	4.75	0.96
17	<i>Labrus viridis</i>	Linnaeus, 1758	3	13.65	35.31
18	<i>Mullus surmuletus</i>	Linnaeus, 1758	3	7.40	4.04
19	<i>Conger conger</i>	(Linnaeus, 1758)	2	24.05	12.41
20	<i>Diplodus annularis</i>	(Linnaeus, 1758)	2	12.60	3.59
21	<i>Serranus cabrilla</i>	(Linnaeus, 1758)	2	10.01	18.83
22	<i>Bothus podas</i>	(Delaroche, 1809)	1	4.80	1.27
23	<i>Coris julis</i>	(Linnaeus, 1758)	1	8.80	20.87
24	<i>Deltentosteus quadrimaculatus</i>	(Valenciennes, 1837)	1	6.26	4.87
25	<i>Gobius vittatus</i>	Vinciguerra, 1883	1	5.25	1.12
26	<i>Spicara maena</i>	(Linnaeus, 1758)	1	10.80	14.51
27	<i>Symphodus dodderleni</i>	Jordan, 1891	1	3.90	31.37
28	<i>Symphodus melanocercus</i>	(Risso, 1810)	1	4.80	0.49

Scarcely abundant food items were pooled into larger taxa and a matrix containing 28 species of fish (**Table 1**) and 30 food items (**Table 2**) was obtained. The most abundant species, *Chromis chromis*, fed mainly on plankton items, besides molluscs and decapods. In contrast, the two most abundant species of Labridae, *Symphodus ocellatus* and *S. rostratus*, fed on a wide spectrum of food items shared with the whole fish population. Their diet profiles, however, were different, since *S. ocellatus* fed mainly on copepods and other crustaceans, while *S. rostratus* exhibited a wider spectrum of preferences, including plathelminthes, small crustaceans, natantia decapods, and *Posidonia* tissues. Another important species of Labridae, *Symphodus mediterraneus*, showed a narrower dietary spectrum (21 items) and fed

preferentially on brown *Posidonia* tissues, copepods, reptantia decapods, and other animal items. *Serranus scriba*, *S. cabrilla* and *Scorpaena porcus*, among the other abundant species, fed preferentially on natantia and reptantia decapods, but they exhibited a wide dietary spectrum, including *Posidonia* tissues, amphipods, and other animal items.

The ordination of species according to the "Type" and "Size" indices [18] indicated that the fish community plays essentially a macro-carnivore trophic role (**Figure 4**): species were all ordered in the 4th sector, in a compact cluster. An exception was represented by *Coris julis* and *Spicara maena*, exhibiting a "microphagous" feeding pattern, and *Scorpaena notata* and *Symphodus cinereus*, clustered towards a position indicating herbivorous

Table 2. Food items taken into account in the present investigation and their average abundance (% of gut contents) in all samples.

	Prey item	% abundance
1)	Copepods	12.93
2)	Gammarid amphipods	10.06
3)	Natantia decapods	9.26
4)	Unidentified animal tissues	8.57
5)	Reptantia decapods	6.45
6)	Brown tissues of <i>Posidonia</i>	6.37
7)	Ostracods	6.23
8)	Unidentified crustaceans	6.01
9)	Isopods	4.29
10)	Caprellid amphipods	3.93
11)	Fish	3.81
12)	Macroalgae	3.19
13)	Unidentified decapods	2.5
14)	Plathelminthes	2.37
15)	Mysidaceans	2.32
16)	Nematodes	2.22
17)	Tanaidacea	1.87
18)	Polychaetes	1.54
19)	Gastropod molluscs	1.12
20)	Unidentified vegetal tissues	0.79
21)	Eggs	0.78
22)	Acarids	0.66
23)	Foraminiferans	0.64
24)	Microalgae	0.59
25)	Sipunculids	0.4
26)	Pantopods	0.4
27)	Cumaceans	0.29
28)	Unidentified molluscs	0.17
29)	Bivalve molluscs	0.16
30)	Echinoderms	0.06

feeding habit. *Chromis chromis* occupied a polar position, also indicating a microcarnivorous diet. The most abundant labridae, *S. ocellatus* and *S. rostratus*, were in a central position in the cluster. Besides the above exceptions, all the Scorpaenidae and Serranidae were grouped in a central compact sub-cluster.

Seasonal variations in the feeding habits of some species were observed (Figure 5). In summer *Labrus viridis* and *S. cinereus* exhibited a more “herbivorous” habit than in winter. In winter *S. ocellatus* preyed almost entirely on animals, while in summer it fed mainly on plant matter. *S. rostratus* did not change its feeding preferences (plant or animal) between the two seasons. No variations in the “Size” index were observed between the two seasons for any species, but the dietary composition changed. The total number of prey items of *S. ocellatus*

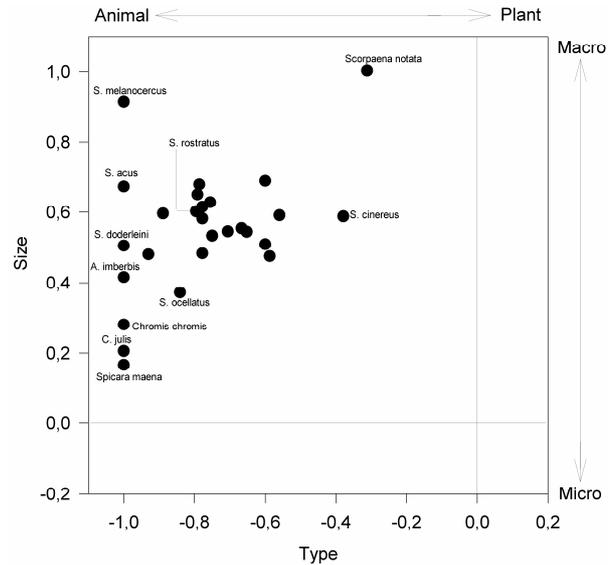


Figure 4. Ordination in the “Type-Size” space of the species collected in all the samples. The horizontal axis discriminates the “type” of diet (based on the abundance of plant or animal prey items); the vertical axis discriminates the “size” of diet (based on small or large prey items). Circles indicate the position of each species of fish (the most abundant are specified).

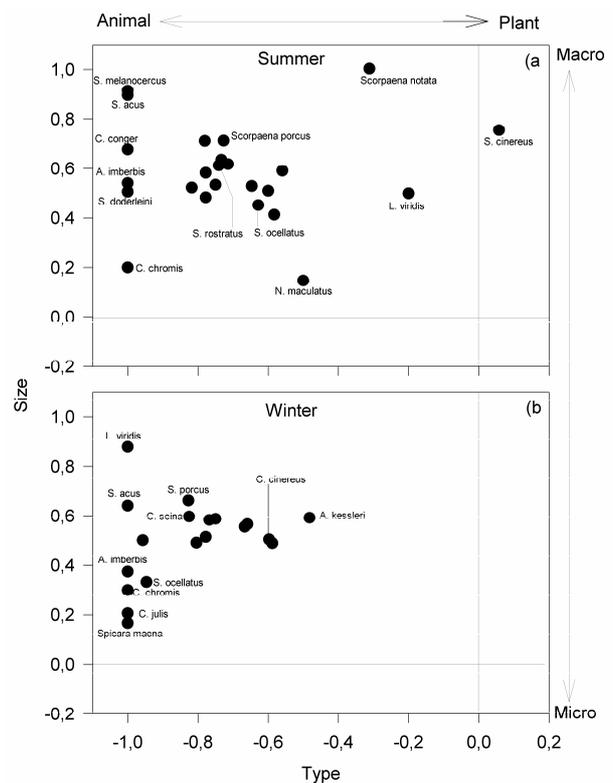


Figure 5. Ordination in the “Type-Size” space of the species according to the season of sampling (a, summer; b, winter). The horizontal axis discriminates the “type” of diet (based on the abundance of plant or animal prey items); the vertical axis discriminates the “size” of diet (based on small or large prey items). Circles indicate the position of each species of fish (the most abundant are specified).

significantly changed according to the season. In fact *S. ocellatus* fed on 24 prey items in summer, and 20 in winter, when its diet was mainly based on copepods (32% of gut contents).

In contrast, the total number of prey items of *S. rostratus* was constant (24) in the two seasons and no significant differences were observed in the food composition.

Other species, such as *Serranus scriba* and *Scorpaena porcus*, exhibited a comparable reduction of plant items in winter, and different feeding preferences in the two seasons, as revealed by the “Type-Size” ordinations.

The samples obtained at Lacco Ameno (**Figure 6(a)**) and San Pancrazio (**Figure 6(c)**) clustered according to prey size, more tightly in respect to the Channel of Procida (**Figure 6(b)**). In particular, such species as *Mullus sur*

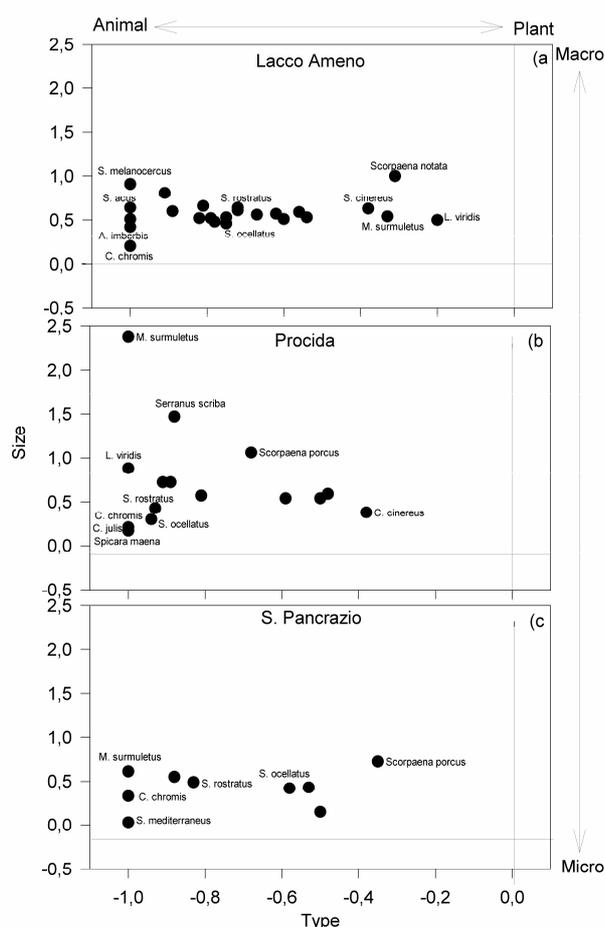


Figure 6. Ordination in the “Type-Size” space of the species according to the site of sampling (a, Lacco Ameno; b, Procida; c, S. Pancrazio). The horizontal axis discriminates the “type” of diet (based on the abundance of plant or animal prey items); the vertical axis discriminates the “size” of diet (based on small or large prey items). Circles indicate the position of each species of fish (the most abundant are specified).

muletus, *Serranus scriba*, and *Scorpaena porcus*, occupied a higher position along the “Size” axis in the samples of the Channel of Procida, indicating a feeding habit with a stronger “macrophagous” character. No significant variations in the diet were detected by ANOVA between Lacco Ameno and the other two sites.

The analysis of diets indicated that the main prey items of fish (**Table 2**), were copepods (12,93% of their gut contents, on average), gammarid amphipods (10,06%), Natantia decapods (about 9%) and, besides unidentified animal tissues (8,57%), *Posidonia* tissues (6,37%) and ostracods (6,23%). Seasonal variations of the diet were observed (**Table 3**) at lower taxonomic levels. The basic structure of the fish food webs was traced based on previous data (**Figure 7**) and the abundances (volumes occupied in the gut contents of fish) of each item in the food webs were organised to permit a comparison of their relative importance. The most abundant items (in terms of volume occupied in the guts) were copepods, amphipods, decapods and other crustaceans.

4. DISCUSSION

The skid trawl, as demonstrated by [29], is a suitable sampling tool to obtain a representative picture of the fish fauna living within the *Posidonia oceanica* meadows, allowing for the study of the upper levels of local food webs [30,31]. Other sampling methods, however, may complete the information on the fish assemblage of meadows, in particular on upper water dwellers, feeding mainly on planktonic micro-crustaceans or other fish [21,29]. The efficiency of the trawl was higher in winter, when the canopy was lower. The investigated meadows were characterised by benthic families of fish (Labridae, Pomacentridae, Scorpaenidae, Sygnathidae, Serranidae) although a few individuals were found that belonged to families with good swimming capabilities (e.g., Sparidae). The number of species collected during this investigation was lower than the number of species found in French meadows of *P. oceanica* meadows using an identical sampling technique (28 as compared to 49 species; [33]). The difference may be due to a higher fishing pressure characterising the meadows investigated in the present paper, in accordance with the results of previous studies [29].

Fresh weight estimates showed the importance of the main three families, *i.e.*, Labridae, Pomacentridae and Scorpaenidae. In fact, they accounted for 99.4 % of the total fish biomass sampled in summer and for 93.7% of the total fish biomass sampled in winter (98% of the total fish biomass throughout the year).

The high fish biomass collected in winter was not correlated with individual fish weight. It was due to a

Table 3. Prey found in the gut contents of the most abundant species of fish collected. A grey square indicates the presence of each prey in summer (S) and/or winter (W) samples.

Fish	S	W	Prey
<i>Apogon imberbis</i>	■	■	<i>Eualus occultus</i> (Lebour, 1936)
	■	■	<i>Processa acutirostris</i> Nouvel & Holthuis, 1957
<i>Chromis chromis</i>	■	■	<i>Hippolyte</i> sp. Leach, 1814
	■	■	<i>Jujubinus</i> sp. Monterosato, 1884
	■	■	<i>Liljeborgia dellavallei</i> Stebbing, 1906
	■	■	<i>Siriella clausii</i> G.O.Sars, 1876
	■	■	<i>Synisoma appendiculatum</i> (Risso, 1816)
<i>Scorpaena notata</i>	■	■	<i>Cymodoce hanseni</i> Dumay, 1972
	■	■	<i>Galathea intermedia</i> Lilljeborg, 1851
	■	■	<i>Hippolyte</i> sp. Leach, 1814
<i>Scorpaena porcus</i>	■	■	<i>Apherusa vexatrix</i> Krapp-Schickel, 1979
	■	■	<i>Cheirocratus sundevallii</i> (Rathke, 1843)
	■	■	<i>Cymodoce hanseni</i> Dumay, 1972
	■	■	<i>Cymodoce hanseni</i> juv. Dumay, 1972
	■	■	<i>Eualus occultus</i> (Lebour, 1936)
	■	■	<i>Eualus pusiolus</i> (Kroyer, 1841)
	■	■	<i>Eualus</i> sp. Thallwitz, 1891
	■	■	<i>Galathea bolivari</i> Zariquiey A., 1950
	■	■	<i>Hippolyte inermis</i> Leach, 1815
	■	■	<i>Hyale carinata</i> (Bate, 1862)
	■	■	<i>Inachus thoracicus</i> (Roux, 1830)
	■	■	<i>Liocarcinus arcuatus</i> (Leach, 1814)
	■	■	<i>Liocarcinus pusillus</i> (Leach, 1815)
	■	■	<i>Lysmata seticaudata</i> (Risso, 1816)
	■	■	<i>Macropodia</i> sp. Leach, 1814
	■	■	<i>Munida intermedia</i> A. Milne-Edwards & Bouvier, 1899
	■	■	<i>Palaemon</i> sp. Weber, 1795
	■	■	<i>Platynereis dumerilii</i> (Audouin & Milne-Edwards, 1833)
■	■	<i>Processa acutirostris</i> Nouvel & Holthuis, 1957	
■	■	<i>Synisoma appendiculatum</i> (Risso, 1816)	
■	■	<i>Thoralus cranchii</i> (Leach, 1817)	
<i>Serranus hepatus</i>	■	■	<i>Amphiura chiajei</i> Forbes, 1843
	■	■	<i>Clibanarius erythropus</i> (Latreille, 1818)
	■	■	<i>Liocarcinus arcuatus</i> (Leach, 1814)
	■	■	<i>Phthisica marina</i> Slabber, 1769
	■	■	<i>Processa</i> sp. Leach, 1815
<i>Serranus scriba</i>	■	■	<i>Clibanarius erythropus</i> (Latreille, 1818)
	■	■	<i>Galathea bolivari</i> Zariquiey A., 1950
	■	■	<i>Leptomysis mediterranea</i> G.O.Sars, 1877
	■	■	<i>Liljeborgia dellavallei</i> Stebbing, 1906
	■	■	<i>Liocarcinus arcuatus</i> (Leach, 1814)
	■	■	<i>Parasiphaea sivado</i> Risso, 1816
	■	■	<i>Processa acutirostris</i> Nouvel & Holthuis, 1957

Table 3. (Continued)

	<i>Processa canaliculata</i> Leach, 1815 <i>Thoralus cranchii</i> (Leach, 1817) <i>Vargula mediterranea</i> Costa, 1845
<i>Symphodus mediterraneus</i>	<i>Achelia echinata</i> Hodge, 1864 <i>Galathea</i> sp. Fabricius, 1793 <i>Platynereis dumerilii</i> (Aud.&M.Edwards, 1833)
<i>Symphodus ocellatus</i>	<i>Callipallene brevisrostris</i> (Johnston, 1837) <i>Gnathia</i> sp. Leach, 1814 <i>Nymphon</i> sp. Fabricius, 1794 <i>Parategastes sphaericus</i> Claus, 1863 Praniza of <i>Gnathia</i> sp. Leach, 1814 <i>Synisoma appendiculatum</i> (Risso, 1816)
<i>Symphodus rostratus</i>	<i>Alpheus dentipes</i> Guérin, 1832 <i>Athanas</i> sp. Leach, 1814 <i>Cymodoce</i> sp. Leach, 1814 <i>Galathea bolivari</i> Zariquiey A., 1950 <i>Galathea</i> sp. Fabricius, 1793 <i>Gnathia</i> sp. Leach, 1814 <i>Hippolyte</i> sp. Leach, 1814 <i>Inachus thoracicus</i> (Roux, 1830) <i>Munida intermedia</i> A. Milne-Edwards & Bouvier, 1899 Praniza of <i>Gnathia</i> sp. <i>Processa macrophthalma</i> Nouvel & Holthuis, 1957 <i>Siriella clausii</i> G.O.Sars, 1876 <i>Synisoma appendiculatum</i> (Risso, 1816)
<i>Symphodus tinca</i>	<i>Cymodoce</i> sp. Leach, 1814 <i>Galathea</i> sp. Fabricius, 1793 <i>Harmothoe</i> sp. Kinberg, 1855 <i>Hippolyte inermis</i> Leach, 1815 <i>Laetmonice hystrix</i> (Savigny, 1820) <i>Lepadogaster candollei</i> Risso, 1810 <i>Paranthura nigropunctata</i> (Lucas, 1849) <i>Pontogenia chrysocoma</i> (Baird, 1865) <i>Synisoma appendiculatum</i> (Risso, 1816)
<i>Syngnathus acus</i>	<i>Ampelisca rubella</i> A.Costa, 1864 <i>Anapagurus laevis</i> (Bell, 1846) <i>Athanas nitescens</i> (Leach, 1814)

high numerical abundance; more individuals were caught in winter, probably due to the greater winter efficiency of the trawl in the lower canopy or to lower trophic resources of surrounding benthic systems [34]. Differences in the abundance of species at the three sites were demonstrated to be not significant, and several species were present with a low number of individuals and low biomass. Therefore we focused our investigation

upon the most abundant species, *i.e.*, the foremost 14 reported in **Table 1**. Most of the sampled fish species are carnivorous and should represent the top consumers within the meadow [7,33]. However, seasonal variations in the diet (plant or animal) of some species were detected in the present investigation.

The genus *Symphodus* was the most abundant, accounting for more than 40% of the total fish population.

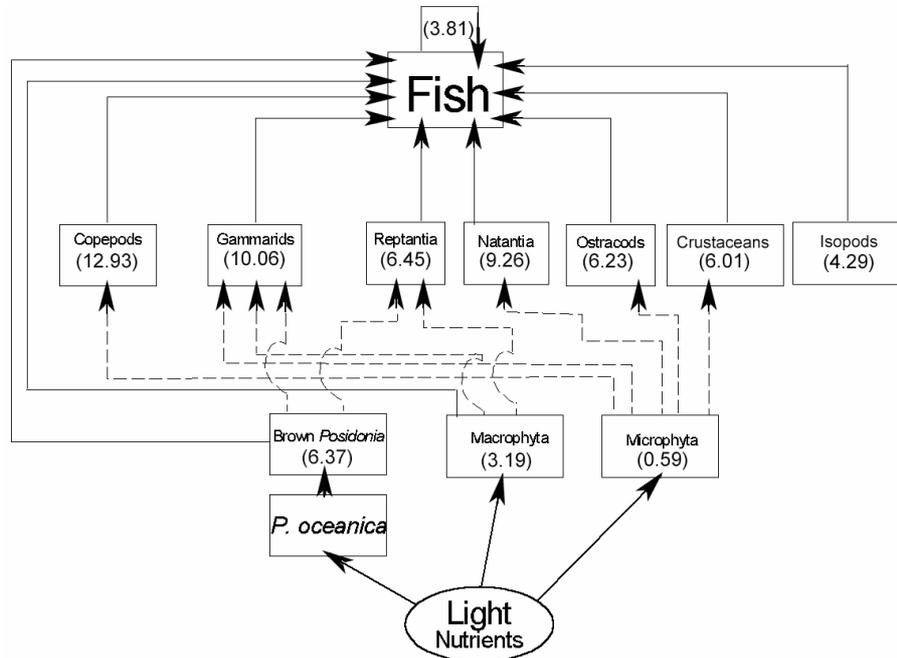


Figure 7. Pathways of matter transfer (volumes of gut contents) in the fish food webs, based on the data of the present paper (solid links between secondary producers and fish) and literature data (dotted links between primary producers and secondary producers; see text). Only vertical links were taken into account, to highlight the role of fish predation. The fish compartment is mainly represented by Labridae, Pomacentridae, Scorpaenidae and Serranidae. Numbers in parenthesis indicate the average volumes occupied by each item in the guts.

The diet of species in this genus was based on vagile organisms of the leaf stratum, grazers of the epiphyte layer. Therefore the genus *Symphodus* represents one of the pathways from secondary producers within the leaf-stratum to the export chain. The large spectrum of prey items found in the guts of the most abundant species, *Symphodus ocellatus* and *S. rostratus*, indicates high trophic adaptability, and this may be responsible for their success within the studied meadows, as documented by their abundance. In contrast, the diet of the most abundant species, *Chromis chromis*, was based on a few items, scarcely present in the guts of other fish. Therefore, this species has the advantage to use a rich, unexploited microphagous trophic niche. Other abundant species, such as *Scorpaena porcus* and *Serranus scriba*, fed almost exclusively on abundant [5] items in the meadow (e.g., decapod crustaceans and gammarid amphipods). *Symphodus rostratus*, *S. porcus* and *S. scriba* were efficient predators of decapod crustaceans, since decapods accounted for more than 30% of their gut volume. The abundance of these three species of fish may explain the high predation pressure observed on various decapod populations [35,36].

The diet of *S. ocellatus* and *S. mediterraneus*, in contrast, was based on smaller crustaceans (copepods and amphipods) accounting for more than 30% of their gut

volume. The abundance of brown tissues of *Posidonia* in the guts of these species indicates that it is not an occasional item, although the actual trophic role of leaf detritus is unclear [37]. It could be used per se, or ingested to digest bacteria and small prey present on its surface [25,38,39].

The ordination of species in the “Type-Size” plots confirmed that fish play essentially a macro-carnivore role in the meadow food webs. Given the low rate of recycling (fish represented less than 4% of prey in the gut contents), it may be assumed that most of the biomass produced within the system is exported to other coastal systems through predation by fish swimming over the canopy, or lost through fishing activities [6]. The main variations were observed in the “Type” index, indicating that some species, such as *Symphodus cinereus* and *Labrus viridis*, can adapt their diets according to the availability of animal or plant items, while the average size of their prey did not vary. However, the diets of the most abundant species exhibited slight seasonal variations. The prey taxa consumed by most fish were abundant throughout the year [5], although variations of prey at a lower taxonomic level (*i.e.*, species) were detected (Table 3).

The three dominant species of fish showed seasonal variations of prey at species level and some prey-species,

abundant in the gut contents in summer (such as *Hippolyte inermis*) were absent in winter (**Table 3**), according to their known [35] seasonal patterns of abundance in the meadows.

They were replaced in the diet by prey-species with a similar shape and size, such as *Eualus sp.* and *Processa acutirostris*. The seasonality in the prey availability was also demonstrated by the fact that such fish as *S. ocellatus*, *S. rostratus*, and *S. porcus*, showed a larger diet spectrum in summer than in winter.

The ordination of species in the “Type-Size” space according to sites indicated that fish sampled off the island of Procida used prey characterised by a broader spectrum of sizes, as compared to the other two meadows. In fact, the maximum “Size” index reached by fish sampled at Lacco Ameno and San Pancrazio was about 1, while some species sampled at Procida, such as *Mullus surmuletus*, *S. scriba* and *S. porcus*, reached higher Size index scores. The comparable size of these fish species at the three sites suggests that differences shown in the Size index are dependent on prey availability.

A diagram of the main pathways of transfer, from primary producers to the top-level predators, can be drawn for the investigated *P. oceanica* meadows, based on the data of the present work and literature information on the feeding habits of the most abundant grazers. The guts contained mainly small invertebrates, typical of the leaf stratum, feeding on microphyta, macrophyta, and *Posidonia* detritus [12,40-44]. Taking into account the abundance (% of gut volume) of each food item in the two seasons, 12.9% of prey (in terms of gut volume) was represented by copepods, feeding, in their turn, mainly on diatoms and bacteria [34,41,45,46]. Gammarid amphipods accounted for 10.0% of fish prey and they feed mainly on micro-algae [47-51]. Reptantia decapods accounted for 6.4% of the fish prey and they feed mainly on *Posidonia* detritus and macrophyta [18], although horizontal links should be taken into account [52]. In fact, reptantia decapods also feed on other secondary producers, such as natantia decapods, amphipods, copepods, molluscs, tanaidacea, isopods, sipunculids, polychaetes [19,43,53,54]. Natantia decapods accounted for 9.2% of the fish prey and they feed mainly on micro-algae and small organisms of the leaf stratum (amphipods, copepods, acarids; [5,35]), although horizontal links should be taken into account and also for this taxon [43,52,55,56]. Ostracods accounted for 6.2% of fish prey and they feed mainly on micro-algae [26,34]. Other small crustaceans accounted for 6.1% of the fish prey and they feed mainly on nematodes, copepods, and ciliates [57]. Isopods accounted for 4.3% of the fish prey and they mainly feed on micro-algae and detritus [58]. A low recycling rate in the fish compartment must be taken into account, since it was calculated that 3.8% of fish

prey is represented by teleosts. Scorpaenidae, Serranidae, Pomacentridae and Congridae were the main fish feeders.

Our data indicated a pathway of transfer from *Posidonia* detritus, macrophyta and microphyta (as primary producers) to crustacean decapods, copepods, ostracods, and gammarid amphipods (as secondary producers) to fish (as consumers), mainly represented by Labridae, Pomacentridae, Scorpaenidae, and Serranidae. The rate of recycling through these families is low (about 4%). Crustacean decapods represent another important loop of biomass recycling, since they can feed also on the other secondary producers described above [14,18]. Therefore, besides natural mortality, the biomass stocked in the fish compartment (in terms of volumes) may be exported to other systems by means of predation by other fish [33], non resident in the meadows and characterised by higher swimming capabilities, such as Sparidae, larger Serranidae, and Congridae.

A comparison with studies in other seagrasses [10,13,20,59,60,61] and different sites of the Mediterranean [33] allows for detecting a general trend of fish assemblages, with respect to the feeding behaviour of dominant species. They generally show a clear preference for epibenthic fauna and extensively feed on crustaceans. Only few herbivorous and herbivorous-detritivorous species were detected in *P. oceanica* meadows, despite the large abundance of plant material available. In contrast, herbivorous and omnivorous fish are common in other seagrass communities [28,60,61,62], characterised by a larger variety of trophic levels. Most species were carnivorous, both macrophagic and microphagic, in accordance with the results obtained in French *P. oceanica* meadows [33]. The only herbivorous fish, well known in Mediterranean seagrass meadows, is *Sarpa salpa* (L.) [33]; however this species is generally restricted to shallow meadows (less than 10 m depth), characterised by a higher abundance of plant epiphytes. Therefore, it did not occur in the depth range investigated in the present paper and its feeding impact scarcely influences the food webs of deeper meadows, exhibiting a higher stability and complexity.

Labride are consistently dominant in Mediterranean *P. oceanica* meadows [22] and they feed on a broad spectrum of prey items, with a preference for crustaceans (mainly amphipods and decapods). However, they can adapt their diet according to the site and the time of sampling. In fact, our analyses indicated seasonal changes in the diet of some species and a lower abundance of molluscs in their gut contents, as compared to the results of [33]. Gastropod molluscs were mainly consumed by *Chromis chromis*, the most abundant species. In contrast, Labridae may be considered as mesophagic carnivores [33] feeding on copepods, gam-

marid amphipods, decapods, ostracods and other crustaceans, as well as molluscs. Decapods and other small crustaceans of the leaf stratum were demonstrated to be keystone items in the fish food webs [36], transferring biomass from the primary producers to the top predators. This trend appears to be a general feature of seagrass meadows [60,63], since it is in accordance with the results obtained in other seagrass ecosystems, both temperate and tropical.

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