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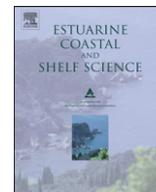
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Non-indigenous species in Mediterranean fish assemblages: Contrasting feeding guilds of *Posidonia oceanica* meadows and sandy habitats

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ABSTRACT

Quantitative sampling in combination with classification of fish species into six major feeding guilds revealed the position and contribution of non-indigenous species (NIS) in the food web of *Posidonia oceanica* and sandy habitats in an area of the eastern Mediterranean. In *P. oceanica* beds and on sandy bottoms 10 and five species, respectively, were non-indigenous fish of Indo-Pacific origin. The proportional contribution of NIS individuals on *P. oceanica* beds was lower than that of sandy bottoms (12.7 vs. 20.4%) a pattern that also followed for biomass (13.6 vs. 23.4%), indicating that low diverse systems may be more liable to introductions than species-rich communities. The two habitats had similar fish feeding guilds, but the biomass contribution from NIS varied within each guild, indicating different degrees of impact on the available resources. This study showed that only few non-indigenous fish species contributed to the differences in biomass between habitats. No support could be found in postulating that taxonomic affiliation could predict invasion success. Size was considered highly important due to habitat shift of species with increased size. Two of the aspects considered in this study, the chance of establishing vs. the chance of being very dominant will depend upon competitive abilities strongly coupled to size and grounds for habitat shift. However, success of establishment will also depend on appropriate food resources in the recipient community as well as competitive abilities and level of competition in the food web within habitats.

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1. Introduction

The Mediterranean Sea is considered to be one of the main hotspots of marine bioinvasions on earth and the rate of introductions appears only to increase (Rilov and Galil, 2009). Zenetos (2010) indicates that nearly 1000 species have already been introduced in the Mediterranean Sea, including species from the Red, the Black and the Atlantic Sea and that the rate of introductions has been elevated to 1 species every 9 days. Since the opening of the Suez Canal, in 1869, the coastal ecosystems of the eastern Mediterranean Sea have been subjected to the establishment of non-indigenous species (NIS) of Indo-Pacific and Red Sea origin (Golani, 2010; Zenetos et al., 2010). Eighty fish species have already been reported in the eastern Mediterranean (Bariche, 2010; EastMed, 2010; Golani, 2010; Zenetos et al., 2011). The fish fauna

of the Mediterranean Sea that developed after the Messinian salinity crisis, 5.3 million years ago, was characterized by a mixture of temperate and sub-tropical species. The number of fish species in the western Mediterranean is considered to be higher than in the eastern Mediterranean (Quignard and Tomasini, 2000), with a general decrease in number of species moving eastwards (Golani et al., 2006). New data for the eastern basin has demonstrated that the introduction of NIS through the Suez Canal has reduced the difference in species richness, increasing the divergence in fauna between the eastern and western Mediterranean, towards an Indo-Pacific and Atlantic fish fauna respectively (Massuti et al., 2010).

Most of the scientific work in the Mediterranean Sea has so far mainly considered large-scale spreading and establishment of NIS. The main vector of fish species introductions is through immigration via the shallow Suez Canal, explaining the dominance of coastal fish species among NIS. The rate of fish immigration has increased in recent decades and has ecological, as well as social and economical impacts. The coastal zone plays an important role for many fish species which may utilize the different shallow habitats during one or several parts of their life cycle (Bell and Harmelin-Vivien, 1982; Francour, 1997; Guidetti, 2000; Pihl and Wennhage,

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2002; Moranta et al., 2006; Deudero et al., 2008). Shallow coastal habitats, such as seagrass meadows, provide food and shelter, and serve as high quality settlement and nursery habitats for many fish species (Francour, 1997; Wennhage and Pihl, 2002; Moranta et al., 2006; Deudero et al., 2008). Such species-rich communities are believed to be resistant to incursions of NIS, according to the biotic resistance hypothesis (Levine and Adler, 2004). Accordingly, the most truly explanation is that less-diverse communities (Leppäkoski and Olenin, 2000) and/or stressed ecosystems (Occhipinti-Ambrogi and Savini, 2003) are believed to be more prone to the introductions of NIS. This is due to the fact that these areas have fewer species and simpler food web interactions, thus providing 'empty niches' for the establishment of NIS. Further, Ricciardi and Mottiar (2006) applies Darwin's "pre-adaption hypothesis" in the context of invasion biology, i.e. to test whether the presence of closely related indigenous species could be used to predict the successful introduction of NIS, as it makes the NIS more likely to possess traits that pre-adapt them to their new environment. While taxonomic affiliation of invaders to the local fish fauna will make species rich communities more prone to introductions, biotic resistance will make these systems less vulnerable.

Several factors have contributed to the increasing rate of reported introductions of NIS during the last decades. Increased scientific interest, gradual deepening of the Suez Canal, increased sea water temperature and gradual equalization of Red Sea salinity with Great Bitter Lakes are among the most important factors mentioned (Por, 2010). Once a NIS is established in a large ecosystem such as the Mediterranean Sea, it is almost impossible to eradicate. The physiological abilities in combination with different life history traits and ecological interactions in the recipient community (e.g. competition for resources, habitat to settle, spawning grounds, grazing or predation, trophic cascading effects, or even, occupying empty niches) will determine the introduced species ability to adapt to the ecosystem in which it arrives. An obvious example of competitive exclusion/displacement of an indigenous species was the introduction of the two herbivorous fish species, *Siganus rivulatus* Forsskal and *Siganus luridus* Rüppell in the coastal zone of Lebanon in the eastern Mediterranean (Harmelin-Vivien et al., 2005). These two species out-competed the native herbivorous species *Sarpa salpa* (L.) and significantly reduced its abundance (Harmelin-Vivien et al., 2005; Azzurro et al., 2007a). Several non-indigenous fish species may have the ability to change the trophic food web by being highly dominant in a habitat or by competing for food resources with indigenous species. The impact of NIS on biodiversity is often referred to as positive simply because more species increase species richness, however Wallentinus and Nyberg (2007) argue that the opposite effect may result from the so-called biological pollution. This is due to the fact that some species become highly abundant or even pests altering the community structure and reducing biodiversity (Boudouresque and Verlaque, 2002).

Given that many of the NIS invade and become highly abundant in shallow coastal areas of the eastern Mediterranean Sea, the study of their impact on the food web is highly important. The established species may already have affected the trophic interactions among species and altered ecosystem functioning. Through temporal quantitative data from both habitats and by classifying species into feeding guilds we studied how non-indigenous fish species may interact and affect native predators, competitors and prey in the food web.

This study investigated the position and contribution of NIS in the food web of two coastal habitats, *Posidonia oceanica* meadows and sandy bottoms, in an area of the eastern Mediterranean. Specifically, we test whether there is a significant higher proportion of non-indigenous fish species on sandy bottoms compared to *P.*

oceanica meadows. Additionally, we investigate temporal trends in the proportion of NIS within and between the two habitats.

2. Materials and methods

2.1. Study area

As the largest island of the Dodecanese Archipelago, Rhodes is located between the Levantine and the Aegean Sea. The coastal zone of Rhodes Island is categorized as sub-tropical open-sea, since it possesses a limited continental shelf. Rhodes is directly influenced by the neighbouring Levantine Basin, since the island receives the warm-salty Asia Minor Current (AMC) (Pancucci Papadopoulou et al., 1999). Mean surface water temperature ranged between 16 and 18 °C in winter, between 21 and 23 °C in autumn and spring and reaching 28 °C in summer. Surface salinity does not vary and is between 39 and 40 throughout the year. Surface water was separated from bottom water by a thermocline, formed in May and reaching maximum by mid August, at 35–40 m depth. The thermocline breaks up in mid November (Corsini-Foka, 2010).

The investigation was carried out at four locations around Rhodes Island (Fig. 1). The shoreline is characterized by a mixture of rocky- and sediment bottom areas. Two of the selected locations (localities 1, 2; Fig. 1) were considered representative of *Posidonia oceanica* habitats around the coasts of Rhodes Island, while the other two locations (locations 3, 4; Fig. 1) represented unvegetated sandy bottoms. The west side of Rhodes Island is mainly characterized by *P. oceanica* habitats while the eastern part is characterized by sandy and rocky bottoms. We assume no influence linked to

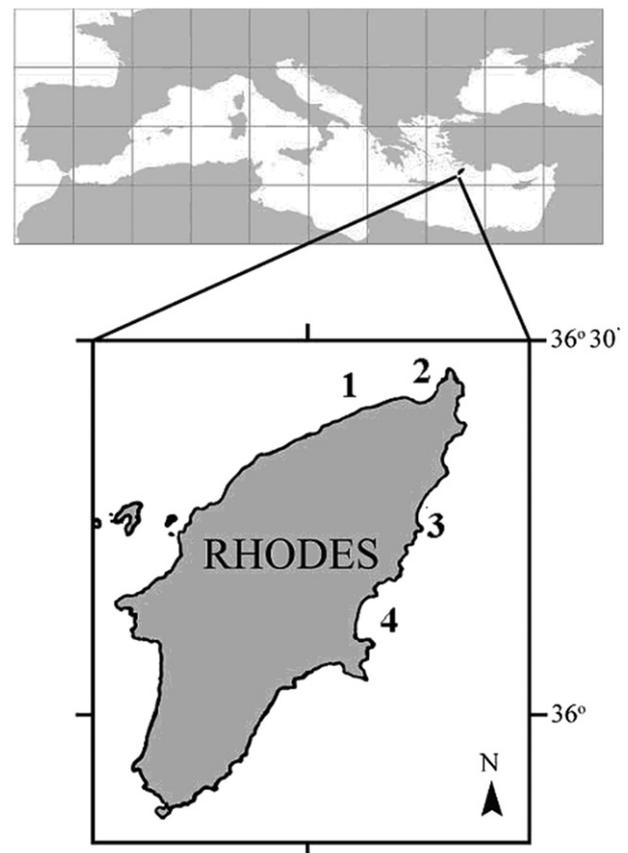


Fig. 1. Map of the investigated area with *Posidonia oceanica* meadows (1, 2) and sandy bottoms (3, 4).

Table 1

Species list of fish recorded in *Posidonia oceanica* beds and on sandy bottom areas on the coasts of Rhodes Island. Fish species are divided into feeding guilds based on Stergiou and Karpouzi (2002) accordingly: Herbivorous, H; zooplanktivorous, ZP; invertebrate feeders, I; piscivorous, P; those feeding on invertebrates and fish, IF and omnivorous, O. Species was further divided into two groups depending on origin (IS: indigenous; NIS: Non-indigenous).

Family	Species	English name	Sandy	<i>Posidonia</i>	Feeding guild	Origin
Apogonidae	<i>Apogon imberbis</i>	Cardinal fish		X	IF	IS
Atherinidae	<i>Atherina hepsetus</i>	Mediterranean sand smelt		X	I	IS
Balistidae	<i>Balistes caprisicus</i>	Grey triggerfish		X	I	IS
Blenniidae	<i>Blennius ocellaris</i>	Butterfly blenny		X	I	IS
	<i>Parablennius pilicornis</i>	Ringneck blenny		X	I	IS
	<i>Parablennius tentacularis</i>	Tentacled blenny		X	I	IS
Bothidae	<i>Bothus podas</i>	Wide-eyed flounder	X	X	I	IS
Centracanthidae	<i>Spicara maena</i>	Blotched picarel	X	X	ZP	IS
	<i>Spicara smaris</i>	Picarel	X	X	ZP	IS
Carangidae	<i>Caranx crysos</i>	Blue runner	X		IF	IS
	<i>Seriola dumerili</i>	Greater amberjack	X	X	P	IS
	<i>Trachurus mediterraneus</i>	Mediterranean horse mackerel		X	IF	IS
	<i>Trachurus trachurus</i>	Atlantic horse mackerel		X	IF	IS
Clupeidae	<i>Sardina pilchardus</i>	European pilchard		X	O	IS
	<i>Sardinella aurita</i>	Round sardinella		X	O	IS
Dactylopteridae	<i>Dactylopterus volitans</i>	Flying gurnard	X		IF	IS
Dasyatidae	<i>Dasyatis pastinaca</i>	Common stingray		X	IF	IS
Fistulariidae	<i>Fistularia commersonii</i>	Bluespotted cornetfish	X	X	P	NIS
Gobiidae	<i>Gobius cobitis</i>	Giant goby		X	O	IS
	<i>Gobius couchi</i>	Couch's goby		X	I	IS
	<i>Gobius cruentatus</i>	Red-mouthed goby		X	I	IS
	<i>Gobius geniporus</i>	Slender goby		X	I	IS
	<i>Gobius paganellus</i>	Rock goby		X	I	IS
Labridae	<i>Coris julis</i>	Mediterranean rainbow wrasse		X	I	IS
	<i>Labrus merula</i>	Brown wrasse		X	I	IS
	<i>Pteragogus pelycus</i>	Sideburn wrasse		X	I	NIS
	<i>Symphodus cinereus</i>	Grey wrasse		X	I	IS
	<i>Symphodus doderleini</i>			X	I	IS
	<i>Symphodus mediterraneus</i>	Axillary wrasse		X	I	IS
	<i>Symphodus melanocercus</i>	Blacktailed wrasse		X	I	IS
	<i>Symphodus ocellatus</i>			X	I	IS
	<i>Symphodus roissali</i>	Five-spotted wrasse		X	I	IS
	<i>Symphodus rostratus</i>			X	I	IS
	<i>Symphodus tinca</i>	East Atlantic peacock wrasse		X	I	IS
	<i>Thalassoma pavo</i>	Ornate wrasse		X	I	IS
	<i>Xyrichtys novacula</i>	Cleaver wrasse	X		I	IS
Monacanthidae	<i>Stephanolepis diaspros</i>	Reticulated leatherjacket	X	X	I	NIS
Mullidae	<i>Mullus barbatus</i>	Red mullet	X	X	I	IS
	<i>Mullus surmuletus</i>	Striped red mullet	X	X	IF	IS
	<i>Upeneus pori</i>	Por's goatfish	X	X	I	NIS
Muraenidae	<i>Muraena helena</i>	Mediterranean moray		X	IF	IS
Pomacentridae	<i>Chromis chromis</i>	Damselfish		X	I	IS
Scaridae	<i>Sparisoma cretense</i>	Parrotfish		X	O	IS
Sciaenidae	<i>Sciaena umbra</i>	Brown meager		X	IF	IS
Scorpaenidae	<i>Scorpaena maderensis</i>	Madeira rockfish		X	IF	IS
	<i>Scorpaena porcus</i>	Black scorpionfish		X	IF	IS
	<i>Scorpaena scrofa</i>	Largescaled scorpionfish		X	IF	IS
Serranidae	<i>Epinephelus marginatus</i>	Dusky grouper		X	IF	IS
	<i>Serranus cabrilla</i>	Comber		X	IF	IS
	<i>Serranus hepatus</i>	Brown comber		X	IF	IS
	<i>Serranus scriba</i>	Painted comber		X	IF	IS
Siganidae	<i>Siganus rivulatus</i>	Marbled spinefoot		X	H	NIS
	<i>Siganus luridus</i>	Dusky spinefoot		X	H	NIS
Soleidae	<i>Solea solea</i>	Common sole	X	X	I	IS
Sparidae	<i>Boops boops</i>	Bogue	X	X	O	IS
	<i>Dentex dentex</i>	Common dentex		X	IF	IS
	<i>Diplodus annularis</i>	Annular seabream		X	I	IS
	<i>Diplodus puntazzo</i>	Sharpsnout seabream		X	IF	IS
	<i>Diplodus sargus sargus</i>	White seabream		X	IF	IS
	<i>Diplodus vulgaris</i>	Common two-banded seabream		X	IF	IS
	<i>Lithognathus mormyrus</i>	Striped seabream	X		I	IS
	<i>Oblada melanura</i>	Saddled seabream		X	I	IS
	<i>Pagellus acarne</i>	Axillary seabream	X	X	IF	IS
	<i>Pagellus erythrinus</i>	Common Pandora	X	X	IF	IS
	<i>Pagrus pagrus</i>	Common seabream	X	X	IF	IS
	<i>Sarpa salpa</i>	Salema		X	H	IS
	<i>Spondyliosoma cantharus</i>	Black seabream		X	I	IS
Sphyraenidae	<i>Sphyraena chrysotaenia</i>	Yellowstripe barracuda		X	P	NIS
	<i>Sphyraena flavicauda</i>	Yellowtail barracuda		X	P	NIS
	<i>Sphyraena sphyraena</i>	European barracuda		X	P	IS
	<i>Sphyraena viridensis</i>	Yellowmouth barracuda		X	P	IS

(continued on next page)

Table 1 (continued)

Family	Species	English name	Sandy	Posidonia	Feeding guild	Origin
Syngnathidae	<i>Hippocampus guttulatus</i>	Long-snouted seahorse		X	I	IS
	<i>Nerophis maculatus</i>			X	I	IS
	<i>Syngnathus acus</i>	Greater pipefish		X	I	IS
	<i>Syngnathus typhle</i>	Broad-nosed pipefish		X	IF	IS
Synodontidae	<i>Synodus saurus</i>	Atlantic lizardfish	X	X	IF	IS
Tetraodontidae	<i>Lagocephalus sceleratus</i>	Silverstripe blaasop	X	X	IF	NIS
	<i>Lagocephalus suezensis</i>		X	X	IF	NIS
Trachinidae	<i>Trachinus araneus</i>	Spotted weever	X	X	IF	IS
	<i>Trachinus draco</i>	Greater weever	X	X	IF	IS
Trichiuridae	<i>Trichiurus lepturus</i>	Largehead hairtail	X		IF	IS
Triglidae	<i>Chelidonichthys lucerna</i>	Tub gurnard	X		IF	IS
	<i>Trigla lyra</i>	Piper gurnard		X	I	IS
	<i>Trigloporus lastoviza</i>	Streaked gurnard		X	I	IS
Zeidae	<i>Zeus faber</i>	John dory		X	IF	IS

exposition between west and east part of Rhodes Island, as supported from a recent study in the area (Kalogirou et al., 2010).

2.2. Sampling

The Danish-seine method was used to sample the fish, from a local commercial fishing boat. The procedure is to set out the start warp with an anchor near the shore together with a buoy at 5 m depth and while the boat forms a triangle set the net in parallel to the coastline, sampling the habitat from 5 to 35 m depth. The mesh size of the gear decreases from the outer end of the wing towards the centre with the sequence 500, 180, 32–34, 12, and 11 mm, with minimum mesh size of 5–8 mm in the codend. For further details see Kalogirou et al. (2010).

In order to study temporal and spatial variations in fish assemblages, daylight samples were undertaken at all localities on four occasions over the year to represent temporal variations in water temperature. December 2008 represented autumn while March, May and August 2009 represented winter, spring and summer respectively. Three samples with the seine were randomly deployed on each location and sampling occasion, covering a total area of 0.12 km² (0.04 km² per seining). All fishes were identified to species level immediately after capture following available literature (Whitehead et al., 1986; Golani et al., 2002, 2006), weighed (g) and measured for total length, L_T. Two strictly zooplanktivorous species, being the dominants in the coastal pelagic system, *Spicara smaris* (L.) and *Spicara maena* (L.), were excluded from all the analyses since they have been shown to have a patchy distribution and a low association to a specific habitat (Kalogirou et al., 2010). The two *Spicara* species were therefore not considered as relevant in order to describe differences in the fish assemblage structure associated with the habitats of concern.

Temporal and spatial variations in total density, biomass and number of fish species were investigated with a three-way nested ANOVA. The same nested design was also applied for total NIS and proportions of NIS. Habitat (*Posidonia* beds or sandy bottoms) and time (T1 = winter, T2 = spring, T3 = summer and T4 = autumn) were fixed factors with localities (1–4) nested in habitats. No transformation was applied for total density, biomass and number of fish species since homogeneity of variances and normality assumptions were met. Transformation was neither applied for total density, biomass and number of NIS since assumptions of normality and homogeneity of variances was met. Arcsine transformation was applied only for proportions of NIS (Sokal and Rohlf, 1995; Underwood, 1997; Quinn and Keough, 2002). Tukey's HSD (Honest Significant Difference) test was used to discriminate temporal variations within each habitat. In addition, fish assemblage structure was compared among times and between habitats

using non-parametric multivariate analysis. A Bray–Curtis similarity matrix based on fish biomass was used to produce a non-metric Multi Dimensional Scaling ordination (MDS) (Clarke and Gorley, 2006) in order to 2-D visualize differences in the fish assemblages between habitats and times. The biomass data had been log-transformed prior to analysis. A bubble-plot was superimposed on the MDS to show patterns in the proportions of non-indigenous species that could be attributed to habitat and time. ANOSIM was used to discriminate temporal and habitat differences in the fish assemblages (Anderson, 2001a, b; McArdle and Anderson, 2001). In addition, a SIMPER analysis (Clarke and Gorley, 2006) was performed to identify the species mainly responsible for similarities and differences in fish assemblage structure between habitats.

2.3. Feeding guilds

The fish assemblage was divided into feeding guilds based on a review of the feeding habits of Mediterranean fish by Stergiou and Karpouzi (2002). For fish species not included in this review additional information was obtained from Bell and Harmelin-Vivien (1983); Whitehead et al. (1986); Cardinale et al. (1997) as well as local diet analyses (Kalogirou, unpublished). Primary information on the diet of each species was used to construct the following feeding guilds: herbivorous (H), zooplanktivorous (Z), invertebrate feeders (I), piscivorous (P), invertebrate and fish feeders (IF) and omnivorous (O). To be classified to the feeding guild H, Z, I and P, 90% of the diet had to belong to the respective food category. Further, to be classified as IF, invertebrates and fish together had to add up to 90% of the total diet while when vegetation together with invertebrates and/or fish were among the food categories and contributed to 90% of the total diet it was classified as O. This classification aimed to reveal new interactions in the food web and give insights on the impact on food resources and potential competitors, following the introduction of non-indigenous fish species.

3. Results

3.1. Fish species

Altogether, 85 species within 32 families were identified during this study. The two strictly zooplanktivorous species, *Spicara smaris* (L.) and *Spicara maena* (L.), excluded from the analysis together contributed with 164087 individuals and 556 kg. *S. smaris* contributed with 76097 individuals weighing 221.51 kg on *Posidonia oceanica* and with 80170 individuals weighing 132.23 kg on sandy bottoms. *S. maena* contributed with 2235 individuals

Table 2a

Nested ANOVA on fish density, biomass and number of fish species per habitat (*Posidonia* beds and sandy bottoms), locality (two *Posidonia* and two sandy) and time (T1 = winter, T2 = spring, T3 = summer and T4 = autumn).

Source	d.f.	Density F	Biomass F	Species number F	Density P	Biomass P	Species number P	Error term
Habitat	1	24,27	22,33	409,17	***	***	***	Locality (Habitat)
Time	3	5,50	1,39	2,33	**	NS	NS	Time*Locality(Habitat)
Locality (Habitat)	2	0,49	2,18	0,90	NS	NS	NS	Residual
Time*Habitat	3	4,3	2,63	0,29	*	NS	NS	Time*Locality(Habitat)
Time*Locality (Habitat)	6	0,08	0,49	0,51	***	NS	NS	Residual
Residual	32							

NS, not significant.

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

weighing 29.44 kg on *P. oceanica* and with 5585 individuals weighing 172.82 kg on sandy bottoms. Seventy-nine species occurred in *P. oceanica* beds and 25 were found on sandy bottoms, of which 19 species were common to both habitats (Table 1). The number of fish species recorded was significantly higher (Tukeys

HSD; $p < 0.001$) in *P. oceanica* beds compared to sandy bottoms (Table 2a; Fig. 2a). In *P. oceanica* beds and on sandy bottoms 10 and five species, respectively, were non-indigenous fish. All NIS found on sandy bottoms were also found in *P. oceanica* beds. Non-indigenous species contributed 13% of the species numbers in *P. oceanica* beds, and to 20% of the species on sandy bottoms. All non-indigenous fish species observed during this study were of Indo-Pacific origin (Table 1).

3.2. Density and biomass

Density and biomass of fish were higher (Tukey's HSD, $p < 0.001$, Table 2a) in *Posidonia oceanica* beds compared to sandy bottoms (Fig. 2b and c). Additionally, density showed significant temporal differences (Nested ANOVA; $p < 0.01$, Table 2a) with higher densities during summer (Tukey's HSD; $p < 0.01$). Significant interactions between time and habitat (Nested ANOVA; $p < 0.05$) and time and locality (Nested ANOVA; $p < 0.001$) were also found (Table 2a).

Non-indigenous species density and biomass differed significantly between habitats and times (Nested ANOVA; $p < 0.01$) with *Posidonia oceanica* habitat possessing significantly higher numbers of NIS during summer (Tukey's HSD; $p < 0.01$, Fig. 3).

The proportion of non-indigenous fish in terms of both density and biomass were significantly different (Nested ANOVA; $p < 0.01$) between sandy and *Posidonia oceanica* habitats (Table 2b). Additionally, the interactions between time and habitat showed significant differences (Nested ANOVA; $p < 0.01$, Table 2b, Fig. 3). The overall proportional contribution of NIS individuals on *P. oceanica* beds was lower than that of sandy bottoms (12.74 vs. 20.32%), even though there was a 12-fold difference in the actual number of individuals (6133 vs. 416). In terms of biomass of non-indigenous fish species, catches in *P. oceanica* beds amounted to 97.2 kg and catches on sandy bottoms to 27.1 kg. The proportional contribution of non-indigenous fish species in terms of biomass was approximately two times higher over sandy bottoms (23.3%) compared to *P. oceanica* beds (13.6%). The proportions of NIS showed similar temporal variation, both in terms of density and biomass (Table 2b, Figs. 3 and 4). The highest contribution of NIS to the fish assemblage in *P. oceanica* occurred during the summer, whereas during this time the contribution of NIS on sand was at the lowest (Fig. 3). The NIS contribution during summer was significantly higher than all other times on *P. oceanica*, while on sandy bottoms spring and autumn had significantly higher contributions of NIS compared to the other two times (Tukey's HSD, $p < 0.01$; Figs. 3 and 4).

3.3. Assemblage structure

The results showed that the fish assemblages (in terms of biomass) were mainly structured according to habitat, although a separation according to time was also obvious (ANOSIM;

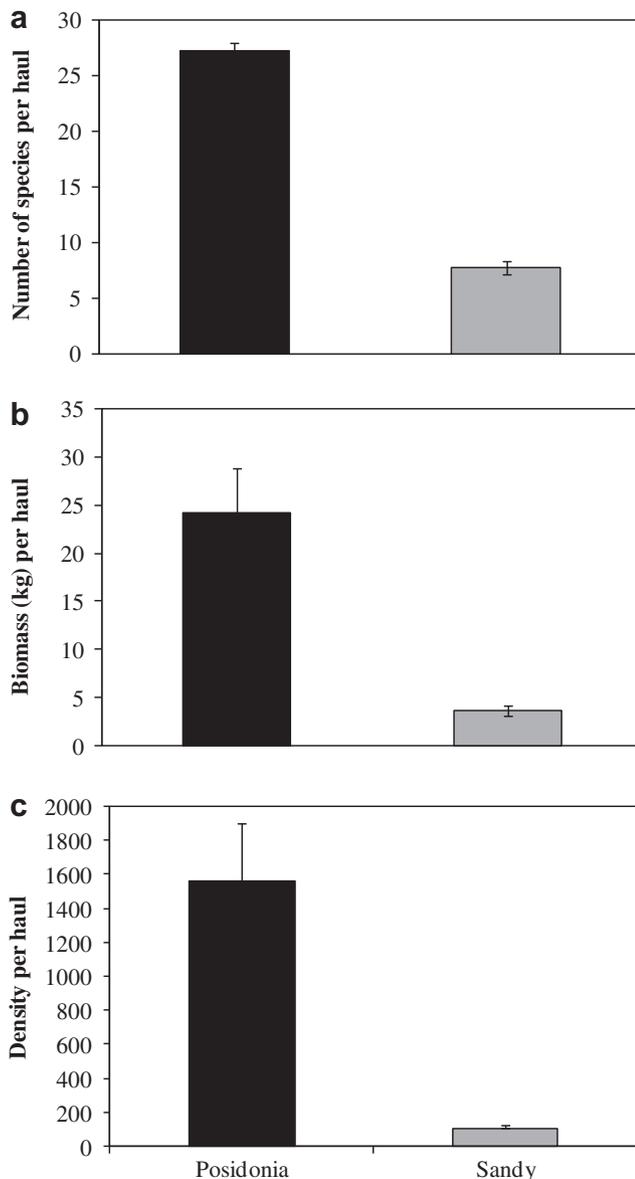


Fig. 2. Mean ± SE number of species (a), biomass (b) and density (c) per haul in *Posidonia oceanica* beds (■) and sandy bottoms (□).

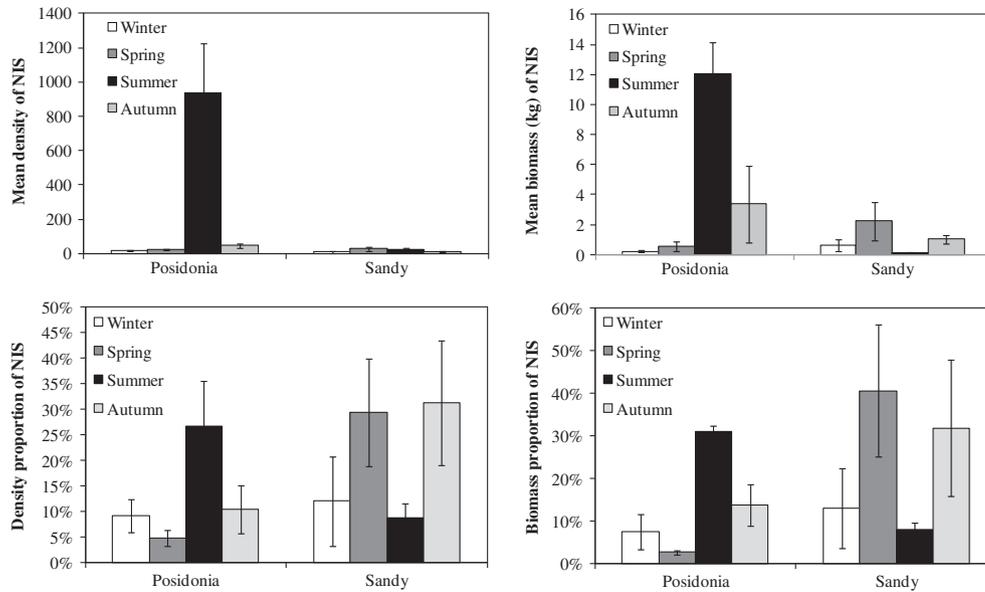


Fig. 3. Mean and proportion \pm SE of non-indigenous fish species in terms of density and biomass per habitat (*Posidonia oceanica* beds and sandy bottoms) and time (□: winter; ■: spring; ■: summer; ■: autumn).

$p < 0.001$, Fig. 4). August was clearly separated from all the other times, a pattern that was consistent for both habitats (ANOSIM, $p < 0.01$, Fig. 5). The proportion of non-indigenous species clearly dominated in spring and autumn on sandy bottoms and in summer on *Posidonia* beds (Figs. 3 and 4).

Twenty fish species explained 90% of the difference in fish assemblage structure, based on biomass, between habitats (Table 3). Among these, four species *Lagocephalus sceleratus* (Gmelin), *Siganus rivulatus*, *Siganus luridus* and *Fistularia commersonii* were non-indigenous. In *Posidonia oceanica*, *Lagocephalus sceleratus* ranked third in terms of biomass being the only NIS that was among the 10 most dominant species (Fig. 5). In terms of density, the NIS *S. rivulatus* and *S. luridus* ranked second and third in *P. oceanica* habitats (Fig. 5). On sandy habitats, the NIS *L. sceleratus* and *Upeneus pori* ranked second and tenth in terms of biomass respectively (Fig. 5). In terms of density, *L. sceleratus* and *Fistularia commersonii* ranked fifth and tenth on sandy habitats respectively (Fig. 5).

3.4. Feeding guilds

The fish assemblage in *Posidonia oceanica* beds consisted of three herbivorous species (two NIS), one zooplanktivore (0 NIS), 35 invertebrate feeders (three NIS), six piscivores (three NIS), 28 invertebrate and fish feeders (two NIS) and four omnivores (0 NIS) (Table 1). The two non-indigenous species *Siganus rivulatus* and

Siganus luridus made up more than 99% of the herbivorous species both in terms of density and biomass (Fig. 6a), and the indigenous herbivorous species *Sarpa salpa* represented only a fraction (<0.3%) over *P. oceanica* beds. In terms of density, *S. rivulatus* and *S. luridus* represented 62.3 and 37.6% of the individuals, respectively. Non-indigenous species were also dominating within the IF guild in *P. oceanica* beds (Fig. 6a). Among the 28 species in the IF feeding guild the NIS *Lagocephalus sceleratus* made up 62% of the total biomass (Fig. 6a). Within the piscivorous feeding guild the three NIS, *Fistularia commersonii* Rüppell, *Sphyræna chrysotaenia* Klunzinger and *Sphyræna flavicauda*, contributed with 22% in terms of biomass (Fig. 6a). Among the 35 invertebrate feeders found in *P. oceanica* meadows the three NIS *Pteragogus pelycus* Randall, *Stephanolepis diaspros* Fraser Brunner and *Upeneus pori* together made up 1 and 2% in terms of biomass and density, respectively (Fig. 6a).

The fish assemblage on sandy bottoms consisted of seven invertebrate feeders (two NIS), two piscivorous (one NIS), 13 invertebrate and fish feeders (two NIS) and one omnivorous species (0 NIS) (Table 1). On sandy bottoms, NIS were highly represented within the invertebrate and fish feeding guild, contributing with 59% in terms of biomass (Fig. 6b). *Lagocephalus sceleratus* made up 56% and *Lagocephalus suezensis* made up 3% of the total biomass within the same feeding guild (Fig. 4). Non-indigenous species were also highly represented within the piscivorous and invertebrates feeding guild, contributing with 26 and 19% in terms of biomass, respectively (Fig. 6b). Out of the seven invertebrate

Table 2b

Nested ANOVA based on the proportion of NIS density, biomass and number of fish species per habitat (*Posidonia* beds and sandy bottoms), locality (two *Posidonia* and two sandy) and time (T1 = winter, T2 = spring, T3 = summer and T4 = autumn).

Source	Density F	Biomass F	Species number F	Density P	Biomass P	Species number P	Error term
Habitat	1 8,13	7,22	11,50	**	*	**	Time*Locality (Habitat)
Time	3 3,90	3,10	3,94	*	*	*	Locality (Habitat)
Locality (Habitat)	2 1,37	0,25	2,12	NS	NS	NS	Residual
Time*Habitat	3 8,00	6,62	0,32	**	**	NS	Time*Locality(Habitat)
Time*Locality (Habitat)	6 0,61	0,38	0,94	NS	NS	NS	Residual
Residual	32						

NS, not significant.

* $P < 0.05$.

** $P < 0.01$.



Fig. 4. Multidimensional scaling ordination of the fish assemblage structure in terms of biomass per habitat (*Posidonia oceanica* beds, ■; sandy bottoms, □), and time (spring, ●; summer, ×; autumn, ■ and winter, ◆). Superimposed bubbleplots (i.e. radius of each circle) corresponds to the proportion of non-indigenous species per replicate.

feeders found over sandy bottoms, the two NIS *Stephanolepis diaspros* and *Upeneus pori* made up 8 and 19% in terms of density and biomass, respectively.

4. Discussion

This investigation was designed to study the fish assemblages associated with seagrass and sandy substratum, two dominating coastal habitats in the eastern Mediterranean. To our knowledge this is the first study in the eastern Mediterranean to quantitatively compare the density and biomass of fish species in the two habitats under the influence of NIS (Guidetti, 2000). In order to investigate the contribution and position of non-indigenous species in the food web, contrasting the two habitats, each fish species was assigned

a feeding guild. Absolute contra proportional values of NIS density and biomass give different results but since the objective of this study was to investigate the potential impact on the food web, proportional biomass values were considered most relevant. Absolute values of NIS give an estimate on the abundance and biomass of the species found within habitats. On the other hand, proportional values give an estimate on the degree of food utilization within assemblages. When investigating the ‘impact’ of NIS within each assemblage, the proportion in terms of biomass is translated as total amount of biomass utilized within an assemblage (i.e. the higher the proportion in biomass the higher the impact). In other perspectives of investigating essential fish habitats for NIS or potential impacts of NIS on fisheries or recruitment contrasting different habitats, absolute density and biomass values can be more important. Identification of essential fish habitats for NIS or investigation of NIS impact on the recruitment of native species would rather require absolute values of the population structure within habitats.

The proportion of non-indigenous fish species was 13% in *Posidonia oceanica* meadows and 20% on sandy substrata. Non-indigenous species made up a significantly higher proportion of fish biomass on sandy bottoms (23%) compared to *P. oceanica* meadows (13%). Both in terms of density and biomass, the highest contribution of NIS to the fish assemblage in *P. oceanica* occurred during the summer, whereas during this time the contribution of NIS on sand was at the lowest. Instead, the highest contribution of NIS on sandy bottoms was encountered during spring and autumn.

The sampling method used in this study was an active gear, found to be highly effective in catching a large variety of fish species, a large size range of fish, and sampling *Posidonia oceanica* meadows and sandy bottoms similarly efficiency (Kalogirou et al., 2010). The standard sampling area covered (0.04 km² per replica) was assumed to give reliable estimates of fish density, biomass and number of fish species. While records of NIS provides valuable information upon arrival of a species e.g. Papaconstantinou (1990),

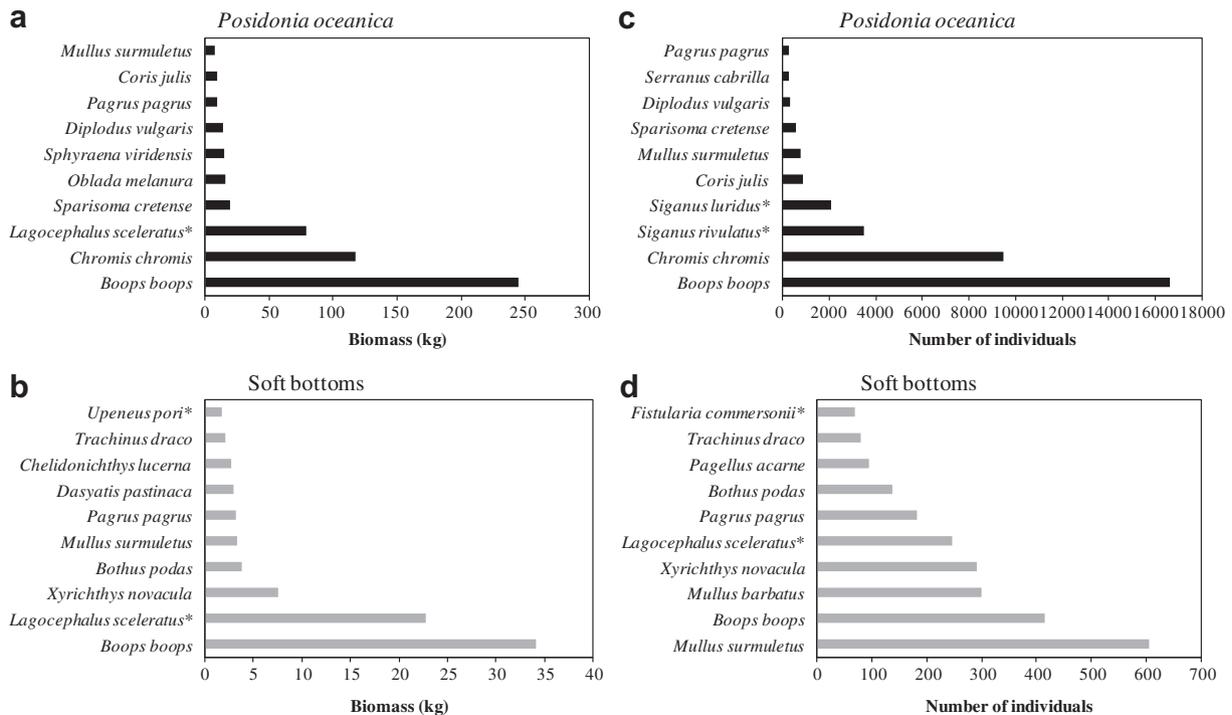


Fig. 5. Ranking order of the 10 dominant fish species (given as total biomass in kg, and number of individuals) in *Posidonia oceanica* beds and on soft bottom localities. Non-indigenous species are indicated with an asterisk (*).

Table 3
Results of similarity percentage (SIMPER) analysis in biomass (g.) of fish species for *Posidonia oceanica* beds and sandy bottoms. Fish species with a cumulative contribution <90% are presented. Origin (IS: indigenous; NIS: Non-indigenous) is indicated.

Species	Origin	Contribution to difference in %	Cumulative %	Average biomass in <i>Posidonia</i> beds	Average biomass on sandy bottoms
<i>Boops boops</i>	IS	39.60	39.92	10203.53	1419.52
<i>Lagocephalus sceleratus</i>	NIS	12.84	52.44	3279.13	948.37
<i>Chromis chromis</i>	IS	9.87	62.31	4905.65	0.00
<i>Oblada melanura</i>	IS	3.26	65.57	661.23	0.00
<i>Sparisoma cretense</i>	IS	3.02	68.60	789.01	0.00
<i>Pagrus pagrus</i>	IS	2.40	71.00	386.29	128.34
<i>Xyrichtys novacula</i>	IS	2.36	73.36	0.00	311.25
<i>Diplodus vulgaris</i>	IS	2.26	75.62	559.52	0.00
<i>Coris julis</i>	IS	2.19	77.81	379.21	0.00
<i>Mullus surmuletus</i>	IS	1.78	79.59	287.29	138.35
<i>Sphyaena viridensis</i>	IS	1.68	81.27	598.28	0.00
<i>Mullus barbatus</i>	IS	1.24	82.51	155.66	43.62
<i>Bothus podas</i>	IS	1.24	83.74	6.32	155.79
<i>Siganus rivulatus</i>	NIS	1.22	84.97	240.79	0.00
<i>Siganus luridus</i>	NIS	1.21	86.17	266.19	0.00
<i>Fistularia commersonii</i>	NIS	1.19	87.36	164.51	17.43
<i>Serranus scriba</i>	IS	0.97	88.33	122.93	0.00
<i>Chelidichthys lucerna</i>	IS	0.81	89.13	0.00	108.79
<i>Dasyatis pastinaca</i>	IS	0.80	89.94	0.00	118.74
<i>Trachinus draco</i>	IS	0.78	90.72	18.32	85.66

Corsini-Foka (2010), Corsini-Foka and Economidis (2007), temporal quantitative measurements and classification of fish species into feedings guilds allowed us to compare the abundance and biomass contribution of non-indigenous fish species in the fish assemblage between habitats. Density of fish species can temporally vary due to migration of fish species between habitats, a common pattern found when studying fish assemblage structure of seagrass meadows. Several studies report that juveniles of many fish species are highly abundant over seagrass meadows during spring and summer, a pattern attributed to the nursery and refuge function provided by the canopies of the seagrass (Bell and Harmelin-Vivien, 1982; Francour, 1997; Guidetti, 2000; Moranta et al., 2006; Deudero et al., 2008). Since a main objective of this study was to investigate the position and contribution of non-indigenous species in the food web of the two habitats under study, we mainly based our analyses on biomass of fish to better estimate the impact of non-indigenous species in the food web. Assessing possible rearrangements in the food web, attributed to the introduction of non-indigenous fish species will be an important step for future research on the impact of NIS. We hereby provide a good quantitative study in order to reveal possible rearrangements attributed to the introduction of NIS in future studies.

The two dominating habitats investigated (*Posidonia oceanica* and sandy bottoms) within the coastal zone of Rhodes Island were found to harbour a highly diverse indigenous and non-indigenous fish fauna including at least 85 species, belonging to 32 families. Not surprisingly, all NIS recorded during this study were of Indo-Pacific origin, the result of the presence of the man-made Suez Canal in the eastern Mediterranean. The fish fauna of the Mediterranean Sea, which developed after the Messinian salinity crisis, is characterized by a mixture of temperate and sub-tropical species. A species immigrating from the Red Sea to the Mediterranean must pass through substantial physical and ecological difficulties such as the shallowness and narrowness of the Suez Canal, its high salinity and its lack of rocky substratum (Golani, 1998, 2010). When succeeded, species physiological demands must fall into similar abiotic conditions (temperature, salinity) to the source area. However, the high number of NIS in the eastern Mediterranean indicates that species which have succeeded to overcome the Suez Canal's barriers have a good chance of becoming established and to spread to other areas (Golani, 2010). Success to establish will also depend on appropriate food resources in

the recipient community, predation as well as competitive abilities and level of competition in the food web within habitats.

Four out of six feeding guilds found within *Posidonia oceanica* meadows were matched by similar feeding guilds on sandy bottoms, although both the relative and absolute contribution in biomass differed between habitats. The *P. oceanica* fish assemblage had all feeding guilds previously described, while sandy substrata lacked herbivores and true zooplanktivores. The sandy bottom

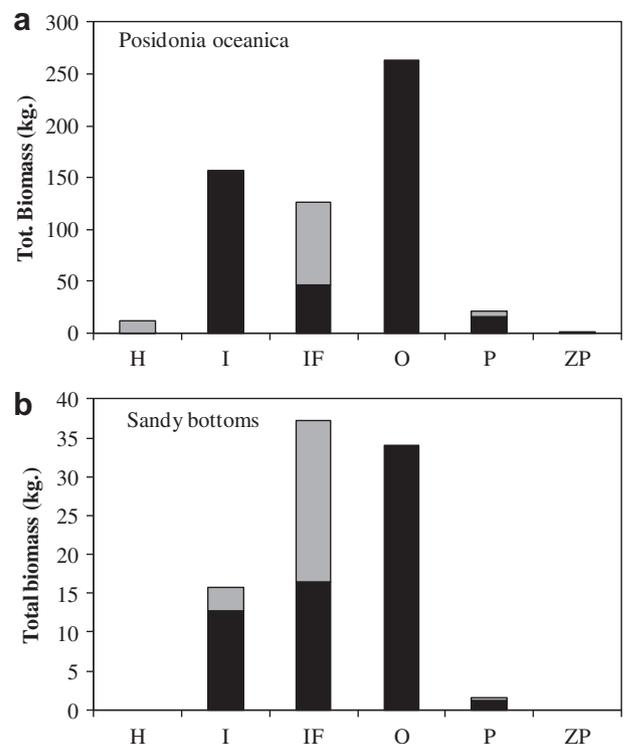


Fig. 6. Biomass per feeding guild (H: Herbivorous; I: invertebrate feeders; IF: invertebrate and fish feeders; O: omnivorous; P: piscivorous; ZP: zooplanktivorous) and origin (■: indigenous and □: Non-indigenous species) among the fish assemblage in *Posidonia oceanica* beds (a) and on sandy bottoms (b).

habitat was characterized mainly by infauna feeding fish, utilizing the various invertebrates found in this substratum. Macro-vegetation is the main difference between the two habitats and the habitat forming *P. oceanica* meadows can be hypothesized to support a higher number of species and guilds than the sand habitat. Since the investigation included the contribution of ten cf. five NIS in *P. oceanica* and sandy habitats respectively, individual species will be conclusive. The contribution of true non-indigenous invertebrate feeders in *P. oceanica* meadows (1%) was lower than that in sandy habitats (19%). *Pteragogus pelycus* made up 0.7% of true invertebrate feeders in *P. oceanica* indicating its ability in finding a suitable niche. On sandy habitats, *Upeneus pori* represented 10% of true invertebrate feeders and it is suggested that lack of competition over the available resources might be the driving force. The contribution of NIS in the IF feeding guild was similar in the *P. oceanica* habitat (2 species; 63%) and on sandy bottoms (2 species; 59%). *Lagocephalus sceleratus* represented 62% of IF on *P. oceanica* and 56% on sand. When comparing size structure of *L. sceleratus* between habitats, this species was found to inhabit *P. oceanica* as an adult while spending its earlier life stages on sandy bottoms (Kalogirou, unpublished). This indicates that *L. sceleratus* success during early life stages on sandy bottoms might be attributed to low level of competition over the available resources while its presence only as an adult on *P. oceanica* during summer and autumn is attributed to improved feeding and competitive capabilities with increased size (Kalogirou, unpublished). *L. suezensis* usually does not exceed 15 cm and since it was classified as an occasional visitor in *P. oceanica* habitats of the studied area we extend the knowledge of the preferred habitats of *L. suezensis* by showing that its greater contribution on sand indicates that size is a crucial component of invasion success and spread for these two species. The zooplanktivorous species, excluded from the analysis, mainly rely on pelagic food items brought in with water currents to both habitats, explaining the lack of difference in affinity between the habitats. The only ZP species included in the analysis was *Sardinia pilchardus* found to spend its juvenile stages in the *P. oceanica* beds. The contributions of non-indigenous piscivorous species were similar in both habitats (22% in seagrass; 26% on sand) and consisted primarily of *Fistularia commersonii* and *Sphyræna chrysootaenia*. Native piscivores mainly rely on small-sized coastal zooplanktivorous species and species using the coastal habitats as a nursery ground, while also to a lesser extent on the juveniles of resident species (Golani, 1993). This pattern holds for the non-indigenous piscivorous species *F. commersonii* (Kalogirou et al., 2007). The high prevalence of the blue-spotted cornetfish, *F. commersonii*, among the piscivores within both habitats studied clearly suggests that this invasive species now has become established in the area. Several studies have emphasized the impact of the non-indigenous rabbitfish among herbivorous species in different coastal areas of the eastern Mediterranean and report the competitive exclusion of the indigenous *S. salpa*. (Bariche et al., 2004; Harmelin-Vivien et al., 2005; Azzurro et al., 2007b). Accordingly, in the present study, the two non-indigenous rabbitfish made up more than 99% among the herbivores in the *P. oceanica* habitat while *S. salpa* contributed only a very small fraction to this guild.

The spread and establishment of NIS is a major concern from a conservation perspective (Galil, 2007). Given the ecological, social and economical costs of species introductions, understanding the environmental driving forces has become a major goal for ecologists and managers. In marine systems the introduction of NIS can have major effects on the structure and function of ecosystems (Groscholz, 2002). The relationship between indigenous species richness and non-indigenous species ability to colonize new habitats, i.e. the community “invasibility” (Stachowicz and Byrnes,

2006) is of main interest (Francour et al., 2010). This concept implies that highly diverse systems are difficult to invade while species-poor communities, or stressed ecosystems are more prone to introductions, attributed to a lack of biotic resistance (Occhipinti-Ambrogi and Savini, 2003). The underlying theory is that high diverse assemblage of plants or animals utilizes its resources more efficient than less-diverse communities. Through this mechanism, increased competition intensity makes it more difficult for new species to establish (Francour et al., 2010). Even though it was impossible to directly test the biotic resistance hypothesis there is a good indication that this hypothesis might hold true. In another context, taxonomic affiliation of invaders to the local fish fauna will make species rich communities more liable to introductions. Our data do not support this hypothesis since several families in the *Posidonia oceanica* habitat include both indigenous and NIS. Even if NIS do not constitute a high proportion of the *P. oceanica* fish assemblage, shelter is found more easily in this habitat but the risk of becoming a pest might be controlled by other factors.

The significant higher proportion and invasion success of NIS over sandy bottoms might be attributed to lower level of competition for benthic food resources within this habitat. Size was found highly important and thus growth rate is considered as highly important when predicting potential invaders. The opposite might hold true during summer due to ontogenetic habitat shift of species since feeding and competitive abilities increase with increased size. Many species uses *Posidonia oceanica* meadows as a habitat to reproduce or feed, explaining the high proportions of NIS during summer. Additionally, non-indigenous species were represented in different amounts within the various feeding guilds and their feeding preferences could be represented in more than one feeding guild. For that reason, the impact on the local invertebrate and fish resources is higher than that described for each guild simply because invertebrates and fish are represented in more than one feeding guild.

In conclusion, since NIS made up a larger proportion of the fish assemblage biomass on sandy bottoms compared to *Posidonia* meadows, there is a potential support to the hypothesis that more diverse systems are less prone to invasions. No support could be found in postulating that taxonomic affiliation could predict invasion success. In addition, size was considered highly important due to habitat change of species with increased size. Two of the aspects considered in this study, the chance of establishing vs. the chance of being very dominant will depend upon competitive abilities strongly coupled to size and grounds for habitat shift. The function of *Posidonia oceanica* meadows as a habitat for reproduction and feeding for many fish species explain the high proportions of NIS in this habitat. However, success of establishment will also depend on appropriate food resources in the recipient community as well as competitive abilities and level of competition in the food web within habitats.

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