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Diversity, structure and function of fish assemblages associated with *Posidonia oceanica* beds in an area of the eastern Mediterranean Sea and the role of non-indigenous species

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Temporal and spatial variation in density, biomass and body size of littoral fish species associated with nearshore *Posidonia oceanica* meadows was studied over an annual cycle in an area of the eastern Mediterranean Sea. A total of 109 350 littoral fishes were collected, belonging to 34 families and 88 species. Density of fishes peaked during the summer due to high numbers of juveniles. Season was a significant factor determining density, although number of species and biomass did not show any obvious seasonal pattern. Throughout the study, schooling planktivorous fish species such as the picarel *Spicara smaris*, the bogue *Boops boops* and the damselfish *Chromis chromis* were dominant, both in terms of density (80%) and biomass (70%). Temporal variation in density and body size of fishes was used to assess the seasonal and ontogenetic habitat use of each species, with their affinity to seagrass assessed by comparing their respective distribution on sand. Four functional guilds were created (juvenile migrants, seagrass residents, seasonal migrants and occasional visitors) to describe the habitat use of *P. oceanica* meadows by each species. Several species associated with *P. oceanica* meadows used this habitat mainly as juveniles during summer, although many others were present concurrently as adults and as juveniles. Among the species encountered, 11 were non-indigenous of Indo-Pacific origin, of which three used seagrasses mainly as juveniles and four as residents. The non-indigenous silverstripe blaasop *Lagocephalus sceleratus* ranked among the 10 most dominant species in terms of biomass (2%) and was classified as a seagrass resident.

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Key words: diversity; Dodecanese archipelago; functional guilds; seagrass.

INTRODUCTION

The ecological importance of *Posidonia oceanica* meadows in the littoral zone of the Mediterranean Sea is well documented, being described as highly productive and with diverse soft-bottom communities (Galil & Zenetos, 2002). Seagrass meadows promote sediment stability (Gacia & Duarte, 2001) and their habitat complexity

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provides food, shelter and a high quality nursery for several fish populations (Francour, 1997; Guidetti, 2000). Such habitats may be crucial for the successful recruitment of juveniles and are thus of major importance for the long-term survival of fish populations (Pihl & Wennhage, 2002). Seagrass ecosystems are under threat; the worldwide loss of seagrass between 1879 and 2006 was estimated to be 3370 km² (*i.e.* 27 km² year⁻¹), representing 29% of the maximum area measured (11 592 km²) (Waycott *et al.*, 2009).

Studies that describe and compare the structure of fish assemblages in different habitats commonly do so through the analysis of several components, *e.g.* species presence or absence, abundance and biomass (Guidetti, 2000). Spatial and temporal measurements of density and biomass are important in order to understand habitat use by fish species. When evaluating fish habitat use, functional groups or guilds are a valuable complement to the use of taxonomic groups. Habitats provide several ecological roles for fish species and can serve as spawning grounds, nursery areas and feeding grounds. Several studies have focused on the fish fauna of *P. oceanica* meadows in the western Mediterranean Sea (Bell & Harmelin-Vivien, 1982; Francour, 1997; Guidetti, 2000; Moranta *et al.*, 2006; Deudero *et al.*, 2008), but information is scarce for the eastern Mediterranean Sea where most work on littoral fishes relates to rocky substrata (Goren & Galil, 2001; Harmelin-Vivien *et al.*, 2005; Golani *et al.*, 2007). Therefore, the diversity, structure and function of fish assemblages in *P. oceanica* meadows of the eastern Mediterranean Sea remain largely unknown.

Approximately 600 indigenous fish species inhabit the whole Mediterranean Sea, with a general decrease in number of species eastwards (Quignard & Tomasini, 2000). The Mediterranean Sea is, from a biodiversity perspective, relatively species-rich and has a high species density for its size (Bianchi & Morri, 2000). In addition, the Mediterranean Sea is considered to be one of the main hotspots for marine bioinvasions (Rilov & Galil, 2009) and is, among European seas, by far the major recipient of non-indigenous species (NIS) including macrophytes, invertebrates and fishes (Streftaris *et al.*, 2005). Shipping and aquaculture are important vectors of NIS, but direct immigration *via* the Suez Canal (Galil, 2006), the so-called Lessepsian or Erythrean immigration (Por, 1978), is extremely significant. The eastern Mediterranean Sea Basin therefore contrasts with the western basin because it is more prone to introductions of subtropical and tropical NIS. These may be aided by several factors such as subtropical physical conditions (*i.e.* aridity), lower numbers of indigenous species (*i.e.* leaving empty niches) and the freshwater barrier of the River Nile inhibiting the westerly expansion of species (Rilov & Galil, 2009).

In recent decades, the rate of introductions into the Mediterranean Sea has increased and this has had both ecological and economic impacts (Zenetos *et al.*, 2005; Streftaris & Zenetos, 2006). Such a trend was also observed in Hellenic waters, where most alien biota records concern species of Indo-Pacific origin and are mainly concentrated in the south-eastern Aegean Sea, particularly in the area around the island of Rhodes (Pancucci-Papadopoulou *et al.*, 2005; Corsini-Foka & Economidis, 2007; Zenetos *et al.*, 2007). Rhodes is the largest island of the Dodecanese archipelago, located between the Levantine and Aegean Seas. Its coastal zone, with a limited continental shelf, has a subtropical open-sea character and is directly influenced by the neighbouring Levantine Basin since the island receives the warm high-salinity Asia Minor Current (AMC) (Pancucci-Papadopoulou *et al.*, 1999). These characteristics

are believed to create suitable conditions for indigenous and non-indigenous thermophilous species. An increase in salt transport from the Levantine to the Aegean Sea (in the upper 200 m) observed from 1987 to 1994 (Theocharis *et al.*, 1999) and changes in water-mass pathways are believed to have enhanced the influx of NIS. During 1991, the source of Eastern Mediterranean Deep Water (EMDW) shifted from the Adriatic to the southern Aegean Sea, with the outflow of EMDW in the eastern Mediterranean Sea through the Cretan Arc Straits compensated for by inflowing Levantine surface water (Rilov & Galil, 2009). Changes in the water-mass characteristics of the southern Aegean Sea influenced the thermohaline circulation of the eastern Mediterranean Sea, leading to the creation of the Eastern Mediterranean Transient (EMT) (Theocharis *et al.*, 2002). These features, combined with the increase in seawater temperature (Bianchi & Morri, 2000, 2003) and other local ecosystem factors, may have enhanced the introduction, establishment and spread of NIS recorded in the area over the last decade. These changes underline the necessity of studying the function of marine ecosystems subject to invasions, in order to reveal possible rearrangements of their composition which could lead to loss of native biodiversity and alteration of ecosystem functioning and fish productivity.

This is the first study to quantitatively assess fish assemblages associated with *P. oceanica* meadows in the eastern Mediterranean Sea. Temporal and spatial dynamics in fish assemblage structure was investigated to develop a system for classifying the fish fauna into functional guilds. In addition, the role of non-indigenous species of Indo-Pacific origin in this habitat was studied.

MATERIALS AND METHODS

STUDY AREA

The study was performed at five shallow (5–35 m) locations around the coast of Rhodes (Fig. 1). The shoreline is characterized by a mixture of rocky and soft sediment areas, with the selected locations representative of the natural variability of *P. oceanica* habitats along the coasts of the island. All five locations selected for this study had sandy sediment with a patchy distribution of *P. oceanica* meadows. Mean surface water temperatures ranged between 16 and 18° C in winter, 21 and 23° C in autumn and spring, respectively, reaching 26–28° C in summer. Surface water was separated from bottom water by a thermocline at 35–45 m in depth, which starts to form in May. Surface salinity varied from 39.3 in winter to 39.7 in summer.

In Hellenic waters, the Danish or boat-seine fishing method, used in this study, is banned from 1 April to 31 September. In addition, fishing at location 1 (Apolakkia) was banned from June 2007 with national legislation preventing the use of trawl nets, dredges, purse-seines, boat-seines, shore-seines or similar nets in *P. oceanica* due to the area being designated a Natura 2000 site according to EC 1967/2006 under Directive 92/43/EEC. Location 2 (Kattavia) is far from Rhodes City and is therefore not a preferred fishing location due to the cost of travelling there. Location 3 (Lardos) was the only site selected on the eastern part of the island and is used sporadically for commercial boat-seining. Location 4 (Trianda) was under high fishing pressure, while fishing is banned at location 5 (Paradisi) due to its proximity to the airport.

SAMPLING

Daylight sampling was undertaken at all locations on four occasions in 2008: February (winter), May (spring), August (summer) and December (autumn), in order to study temporal

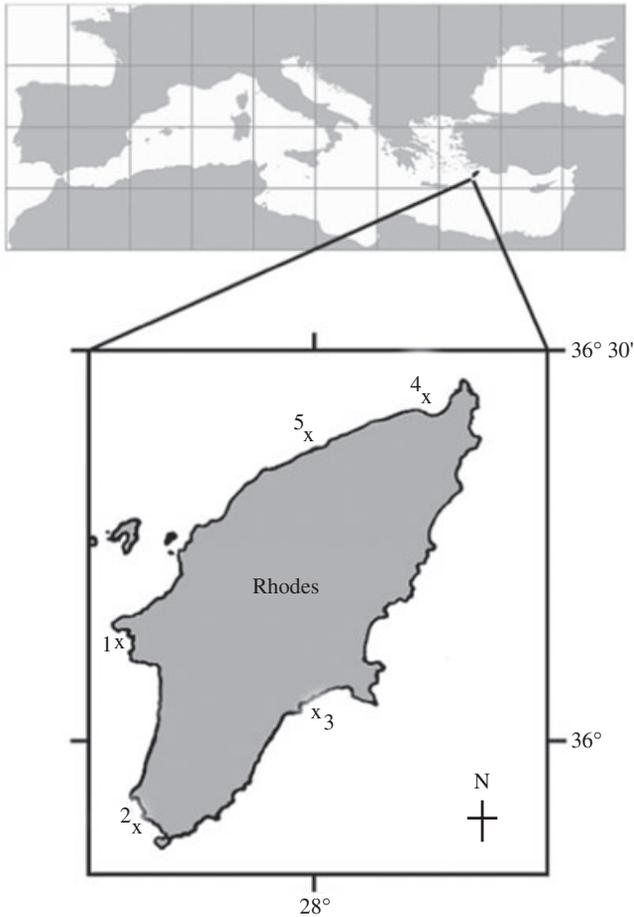


FIG. 1. Map of Rhodes showing sampling locations: 1, Apolakkia; 2, Kattavia; 3, Lardos; 4, Trianda; 5, Paradisi.

and spatial variation in fish assemblages. The Danish seine fishing method was used to sample fishes from the *P. oceanica* habitats with the help of a local fishing boat. The design of the seine used in this study consisted of a set of long warps (400 m), brails (connecting the lines with the wings), a net panel of various mesh-sizes with a codend in the centre. The operating procedure was first to anchor and buoy the end of the start warp, usually 70 m from the shoreline. After the start warp was set out, the boat was headed *c.* 45° from the shoreline. The first wing, followed by the net, the codend and the other wing had a total length of 350 m and were laid parallel to the shoreline before the boat headed back to the buoy with the back warp. The track of the boat thereby formed a triangle. Once both warps were onboard, they were attached to winches and the seine hauled at a constant speed of *c.* 0.3 m s⁻¹. The total time elapsing from deployment of the start line with an anchor to the time the seine was taken onboard was *c.* 35 min. Mesh-size decreased from the outer end of the wing towards the centre in the sequence 500, 180, 32–34, 12 and 11 mm, with a minimum mesh-size of 8 mm in the codend. Three sweeps with the seine were randomly taken at each location and sampling occasion, covering a total area of 0.12 km² (0.04 km² per seining). All fishes were immediately identified to species level (Whitehead *et al.*, 1986; Bauchot, 1987; Golani *et al.*, 2002, 2006; Louisy, 2002), weighed in g and measured (total

length, L_T). Within the Centracanthidae family, the blotched picarel *Spicara maena* (L.) and *Spicara flexuosa* Rafinesque were treated as one species, *S. maena*, following the taxonomy of Arculeo *et al.* (1996) and Froese & Pauly (2009).

DATA ANALYSIS

Temporal variation in density, biomass and number of fish species was investigated with one-way ANOVA (Underwood, 1997). All data were examined for normality and homoscedasticity *via* histograms, Q-Q plots and residuals *v.* fitted plots. Tukey's honest significant difference (HSD) test was used to identify temporal density variation in pair-wise comparisons between seasons. Temporal and spatial variation in assemblage structure based on density was investigated using the Bray–Curtis similarity index (Field *et al.*, 1982). Non-metric multidimensional scaling (MDS) was produced using Primer for Windows (version 6) (Clarke & Gorley, 2006). Dispersion weighting (Clarke *et al.*, 2006) was carried out to reduce the contribution of schooling species in separating samples. Analysis of similarity (ANOSIM) was used to determine if there was a difference in fish assemblage structure between seasons. Two species, the picarel *Spicara smaris* (L.) and *S. maena*, were excluded from measurement of seasonal variation in total density and biomass, since they are strictly planktivorous and are rather more a part of the water column than associated with *P. oceanica* beds. These species were also excluded from ANOSIM when investigating seasonal differences in assemblage structure. Two of the schooling species, the bogue *Boops boops* (L.) and the damselfish *Chromis chromis* (L.), were highly associated with *P. oceanica* beds and were therefore not excluded from the analysis despite their high contribution to the variability among samples.

FUNCTIONAL GUILDS

Fish species density, biomass, average size and maturity stage were analysed seasonally to determine functional guilds. Maturity stage, size at maturity and information regarding sexual dimorphism and hermaphroditism were obtained from Froese & Pauly (2009). These data were combined to construct the functional guilds, which were defined using the approach described by Elliott & Dewailly (1995), although the guilds were modified according to the local ecosystem and ecology of the fish species. Functional guilds for all fish species were defined as: SR, true seagrass residents, species which are stationary and highly dependent on *P. oceanica* meadows where both juveniles and adults can co-occur seasonally; JM, juvenile migrants, species which use seagrass primarily as a nursery ground; SM, seasonal migrants, species which seasonally visit seagrass, usually as adults for spawning or feeding; OV, occasional visitors, species that appear in low abundances or in low association with this habitat. The lowest mean fish size observed during the year in combination with high density indicated a recruitment of juvenile individuals, while a large mean individual size indicated the presence of adult specimens. In addition, for each species and season the percentage contribution of juveniles to the total number of individuals captured throughout the study was calculated to indicate the importance of this habitat as a nursery ground. Maturity status for each species was recorded to determine the importance of *P. oceanica* as a spawning ground. Affinity of fish species to seagrass was evaluated through the construction of a three-rank index based on data from this study and a parallel study on sandy bottoms. This affinity index was used to corroborate the guild classifications and was calculated as the number of individuals in seagrass compared to the total numbers found for each species. The index was only calculated for species with a total number of ≥ 10 individuals. A low affinity (0–30%) indicates a low association with seagrass, intermediate affinity (31–69%) indicates a species with no apparent habitat requirement and high affinity ($\geq 70\%$) indicates a species with a high affinity to seagrass. Species not reaching the threshold of ≥ 10 individuals for at least one season or showing a low affinity to seagrass were classified as occasional visitors.

RESULTS

FISH ASSEMBLAGE STRUCTURE

A total of 109 350 fishes from 34 families and 88 species were recorded in the study (Table I). The families Centranchthidae, Sparidae, Sphyraenidae, Pomacentridae and Labridae made up 88% of the fish assemblage in terms of both abundance and biomass (Table II). *Spicara smaris* (family Centranchthidae) contributed 36% to total density, while *B. boops* (family Sparidae) and *C. chromis* (family Pomacentridae) contributed 28 and 15%, respectively (Table III). The species diversity of fish families varied between one and 14 species (Table I). Labridae was the most diverse fish family in *P. oceanica* meadows, represented by 14 species. Sparidae was represented by 13 species; Serranidae by six; Gobiidae by five; Mullidae, Scorpaenidae and Syngnathidae by four and Sphyraenidae by three species. The remaining fish families had only one or two species each (Table I).

The mean number of species varied between 20 and 27 in spring and summer and between 15 and 23 in autumn and winter, according to locality (Fig. 2). During winter there was an average of 17 species per location. Numbers of fishes increased from autumn towards summer, with *c.* 2000, 2500, 4000 and 5000 in autumn, winter, spring and summer, respectively (Fig. 2). Fish biomass did not follow the pattern of density or number of species, instead reaching highest mean values per location during spring with *c.* 56 kg and lowest in winter with *c.* 45 kg (Fig. 2).

Density showed significant seasonal differences (ANOVA, d.f. = 3, $P < 0.01$), attributable to significantly higher values during summer compared to December and February (Tukey's HSD, d.f. = 3,40, $P < 0.01$) although not compared to May. Biomass and number of fish species did not show any significant seasonal differences. Non-metric MDS based on fish species density showed that fish assemblages were structured according to season (ANOSIM, permutations = 9999, $P < 0.01$; Fig. 3). Pair-wise comparisons revealed that assemblage structure in August was significantly different from that in both December (ANOSIM, permutations = 9999, $P < 0.01$) and February (ANOSIM, permutations = 9999, $P < 0.01$), although again not from that in May.

FUNCTIONAL GUILDS

The fish assemblage consisted of 23 seagrass residents, 19 juvenile migrants, two seasonal migrants and 44 occasional visitors. Of the 51 species for which seagrass affinity could be evaluated, 49 had intermediate or high affinity to *P. oceanica* and could be assigned to functional groups JM, SR or SM. These species made up >98% of the total number of fish captured. Seagrass resident species were widely represented within the dominant families of the fish assemblage (*e.g.* Centranchthidae, Labridae, Mullidae, Sphyraenidae and Syngnathidae; Table I). Within this functional guild four species of commercial value, *S. smaris*, *S. maena*, the yellow-mouth barracuda *Sphyraena viridensis* Cuvier and the European barracuda *Sphyraena sphyraena* (L.), contributed most to total abundance (Table III). The affinities of *S. smaris* and *S. maena* to *P. oceanica* beds were of an intermediate value, indicating that these species have no strong habitat requirement. All juvenile migrants used seagrass meadows during August, with >80% of the total number of individuals

TABLE I. Fishes recorded in *Posidonia oceanica* meadows along the coast of Rhodes in the eastern Mediterranean Sea. Species were divided into four ecological guilds (SR, seagrass residents; OV, occasional visitors; JM, juvenile migrants; SM, seasonal migrants) according to Elliott & Dewailly (1995). Species were further divided into two groups depending on origin (I, indigenous; NI, non-indigenous) and seagrass affinity (1, low; 2, no apparent habitat requirement; 3, high)

Family	Species	Common name	Origin	Ecological guild	Seagrass affinity
Apogonidae	<i>Apogon imberbis</i>	Cardinal fish	I	OV	
Atherinidae	<i>Atherina hepsetus</i>	Mediterranean sand smelt	I	JM	3
Balistidae	<i>Balistes capriscus</i>	Grey triggerfish	I	OV	
Blenniidae	<i>Blennius ocellaris</i>	Butterfly blenny	I	OV	
Blenniidae	<i>Parablennius tentacularis</i>	Tentacled blenny	I	OV	
Bothidae	<i>Bothus podas</i>	Wide-eyed flounder	I	OV	1
Callionymidae	<i>Callionymus filamentosus</i>	Blotchfin dragonet	NI	OV	
Callionymidae	<i>Callionymus risso</i>		I	OV	
Carangidae	<i>Seriola dumerili</i>	Greater amberjack	I	OV	
Carangidae	<i>Trachurus trachurus</i>	Atlantic horse mackerel	I	OV	
Centracanthidae	<i>Spicara maena</i>	Blotched picarel	I	SR	2
Centracanthidae	<i>Spicara smaris</i>	Picarel	I	SR	2
Clupeidae	<i>Sardina pilchardus</i>	European pilchard	I	JM	3
Clupeidae	<i>Sardinella aurita</i>	Round sardinella	I	JM	3
Dactylopteridae	<i>Dactylopterus volitans</i>	Flying gurnard	I	OV	
Dasyatidae	<i>Dasyatis pastinaca</i>	Common stingray	I	OV	
Fistulariidae	<i>Fistularia commersonii</i>	Bluespotted cornetfish	NI	SR	3
Gobidae	<i>Gobius cobitis</i>	Giant goby	I	OV	
Gobidae	<i>Gobius couchi</i>	Couch's goby	I	OV	
Gobidae	<i>Gobius cruentatus</i>	Red-mouthed goby	I	OV	
Gobidae	<i>Gobius geniporus</i>	Slender goby	I	OV	
Gobidae	<i>Gobius paganellus</i>	Rock goby	I	OV	

TABLE I. Continued

Family	Species	Common name	Origin	Ecological guild	Segrass affinity
Labridae	<i>Coris julis</i>	Mediterranean rainbow wrasse	I	SR	3
Labridae	<i>Labrus merula</i>	Brown wrasse	I	OV	
Labridae	<i>Labrus viridis</i>	Green wrasse	I	OV	
Labridae	<i>Pteragogus pelycus</i>	Sideburn wrasse	NI	SR	3
Labridae	<i>Symphodus cinereus</i>	Grey wrasse	I	SR	3
Labridae	<i>Symphodus doderleini</i>		I	SR	3
Labridae	<i>Symphodus mediterraneus</i>	Axillary wrasse	I	SR	3
Labridae	<i>Symphodus melanocercus</i>	Blacktailed wrasse	I	SR	2
Labridae	<i>Symphodus ocellatus</i>		I	SR	3
Labridae	<i>Symphodus roissali</i>	Five-spotted wrasse	I	OV	
Labridae	<i>Symphodus rostratus</i>		I	SR	3
Labridae	<i>Symphodus tinca</i>	East Atlantic peacock wrasse	I	SR	3
Labridae	<i>Thalassoma pavo</i>	Ornate wrasse	I	SM	3
Labridae	<i>Xyrichthys novacula</i>	Cleaver wrasse	I	OV	
Monacanthidae	<i>Stephanolepis diaspros</i>	Reticulated leatherjacket	NI	SR	2
Mullidae	<i>Mullus barbatus barbatus</i>	Red mullet	I	JM	2
Mullidae	<i>Mullus surmuletus</i>	Striped red mullet	I	JM	2
Mullidae	<i>Upeneus moluccensis</i>	Goldband goatfish	NI	OV	
Mullidae	<i>Upeneus pori</i>	Por's goatfish	NI	OV	1
Muraenidae	<i>Muraena helena</i>	Mediterranean morray	I	OV	
Pomacentridae	<i>Chromis chromis</i>	Damselfish	I	SM	3
Scaridae	<i>Sparisoma cretense</i>	Parrotfish	I	JM	3
Sciaenidae	<i>Sciaena umbra</i>	Brown meagre	I	JM	3

TABLE I. Continued

Family	Species	Common name	Origin	Ecological guild	Seagrass affinity
Scorpaenidae	<i>Scorpaena maderensis</i>	Madeira rockfish	I	OV	
Scorpaenidae	<i>Scorpaena notata</i>	Small red scorpionfish	I	OV	
Scorpaenidae	<i>Scorpaena porcus</i>	Black scorpionfish	I	OV	3
Scorpaenidae	<i>Scorpaena scrofa</i>	Largescaled scorpionfish	I	OV	3
Serranidae	<i>Epinephelus aeneus</i>	White grouper	I	OV	
Serranidae	<i>Epinephelus costae</i>	Goldblotch grouper	I	OV	
Serranidae	<i>Epinephelus marginatus</i>	Dusky grouper	I	OV	
Serranidae	<i>Serranus cabrilla</i>	Comber	I	SR	3
Serranidae	<i>Serranus hepatus</i>	Brown comber	I	OV	
Serranidae	<i>Serranus scriba</i>	Painted comber	I	SR	3
Siganidae	<i>Siganus luridus</i>	Dusky spinefoot	NI	JM	3
Siganidae	<i>Siganus rivulatus</i>	Marbled spinefoot	NI	JM	3
Soleidae	<i>Microchirus variegatus</i>	Thickback sole	I	OV	
Soleidae	<i>Solea solea</i>	Common sole	I	OV	
Sparidae	<i>Boops boops</i>	Bogue	I	SR	3
Sparidae	<i>Dentex dentex</i>	Common dentex	I	JM	3
Sparidae	<i>Diplodus annularis</i>	Annular seabream	I	SR	3
Sparidae	<i>Diplodus puntazzo</i>	Sharpsnout seabream	I	OV	
Sparidae	<i>Diplodus sargus sargus</i>	White seabream	I	JM	3
Sparidae	<i>Diplodus vulgaris</i>	Common two-banded seabream	I	JM	3
Sparidae	<i>Oblada melanura</i>	Saddled seabream	I	JM	3
Sparidae	<i>Pagellus acarne</i>	Axillary seabream	I	JM	3
Sparidae	<i>Pagellus erythrinus</i>	Common Pandora	I	JM	3

TABLE I. Continued

Family	Species	Common name	Origin	Ecological guild	Seagrass affinity
Sparidae	<i>Pagrus pagrus</i>	Common seabream	I	JM	2
Sparidae	<i>Sarpa salpa</i>	Salema	I	OV	
Sparidae	<i>Sparus aurata</i>	Gilthead seabream	I	OV	
Sparidae	<i>Spondyllosoma cantharus</i>	Black seabream	I	JM	3
Sphyraenidae	<i>Sphyraena chrysotaenia</i>	Yellowstripe barracuda	NI	JM	3
Sphyraenidae	<i>Sphyraena sphyraena</i>	European barracuda	I	SR	3
Sphyraenidae	<i>Sphyraena viridensis</i>	Yellowmouth barracuda	I	SR	3
Syngnathidae	<i>Hippocampus guttulatus</i>	Long-snouted seahorse	I	SR	3
Syngnathidae	<i>Nerophis maculatus</i>		I	OV	
Syngnathidae	<i>Syngnathus acus</i>	Greater pipefish	I	SR	3
Syngnathidae	<i>Syngnathus typhle</i>	Broad-nosed pipefish	I	SR	3
Synodontidae	<i>Synodus saurus</i>	Atlantic lizardfish	I	OV	1
Tetraodontidae	<i>Lagocephalus sceleratus</i>	Silverstripe blaasop	NI	SR	2
Tetraodontidae	<i>Lagocephalus suezensis</i>		NI	OV	
Torpedinidae	<i>Torpedo marmorata</i>	Spotted torpedo	I	OV	
Trachinidae	<i>Trachinus araneus</i>	Spotted weever	I	OV	
Trachinidae	<i>Trachinus draco</i>	Greater weever	I	OV	
Triglidae	<i>Trigloporus lastoviza</i>	Streaked gurnard	I	JM	3
Uranoscopidae	<i>Uranoscopus scaber</i>	Atlantic stargazer	I	OV	
Zeidae	<i>Zeus faber</i>	John dory	I	OV	

caught during this season (Fig. 4). The only exception was the streaked gurnard *Trigloporus lastoviza* (Bonnaterre) which had peak densities in February. Several of these juveniles were of commercial importance (Table I and Fig. 4) and most of the species within the diverse and dominant family Sparidae classified as juvenile migrants (Table I and Fig. 4). Spring was the main season spent in seagrass for *C. chromis* and the ornate wrasse *Thalassoma pavo* (L.). Due to their occurrence only as reproductive adults, they were classified as seasonal migrants. Of the 12 most numerous species, seven appeared as juveniles during summer, four as seagrass residents and one as a seasonal migrant (Table I and Fig. 4). Due to their low abundances, 41 species were classified as occasional visitors (Table I). These species

TABLE II. The most abundant fish families caught off Rhodes, Greece, ranked by total density and biomass

Family	Density (%)	Family	Biomass (%)
Centranchthidae	38.60	Sparidae	46.21
Sparidae	31.02	Centranchthidae	23.84
Pomatocentridae	15.22	Pomatocentridae	11.33
Labridae	3.25	Sphyraenidae	4.00
Clupeidae	2.91	Labridae	2.28
Siganidae	2.10	Tetraodontidae	2.10
Mullidae	1.59	Scaridae	1.69
Sphyraenidae	1.48	Clupeidae	1.50
Scaridae	0.98	Mullidae	1.05
Atherinidae	0.97	Serranidae	0.88
Serranidae	0.62	Dasyatidae	0.84
Bothidae	0.29	Siganidae	0.65
Fistularidae	0.28	Fistularidae	0.57
Tetraodontidae	0.14	Bothidae	0.51

were either typical sand (*e.g.* Soleidae, Trachinidae and Dasyatidae) or hard bottom (Gobidae, Scorpaenidae and Serranidae) dwellers (Table I). The three typical sand-dwelling species; wide-eyed flounder *Bothus podas* (Delaroché), Por's goatfish *Upeneus pori* Ben-Tuvia & Golani and Atlantic lizardfish *Synodus saurus* (L.) were classified as occasional visitors due to their low affinity with seagrass (Table I).

THE ROLE OF NON-INDIGENOUS SPECIES (NIS)

Eleven of the 88 species (12.5%) recorded in the study were NIS, all of Indo-Pacific origin (Table I) and accounted for *c.* 4% of the total density and biomass of fish species. In this habitat study, three of the NIS recorded were classified as juvenile migrants, four as seagrass residents, while the remaining four species were occasional visitors. The two early colonizers of the eastern Mediterranean Sea, marbled spinefoot *Siganus rivulatus* Forsskål and dusky spinefoot *Siganus luridus* (Rüppell), together with the recently introduced yellowstripe barracuda *Sphyraena chrysotaenia* Klunzinger, were classified as juvenile migrants. *Sphyraena chrysotaenia* and *S. rivulatus* were also among the 10 most abundant species, contributing 2 and 1.2%, respectively, to overall density (Tables I and III). Among seagrass residents, silverstripe blaasop *Lagocephalus sceleratus* (Gmelin) ranked among the 10 most dominant species, comprising 2% of total biomass (Tables I and III), while bluespotted cornetfish *Fistularia commersonii* Rüppell and reticulated leatherjacket *Stephanolepis diaspros* Fraser-Brunner contributed 0.6 and 0.3%, respectively. Among the labrids, sideburn wrasse *Pteragogus pelycus* Randall ranked second in terms of density after Mediterranean rainbow wrasse *Coris julis* (L.) and was present at a higher density than native labrids such as *Symphodus ocellatus* (Forsskål) and *Symphodus rostratus* (Bloch).

The two NIS of the family Mullidae, *U. pori* and goldband goatfish *Upeneus moluccensis* (Bleeker), together with blotchfin dragonet *Callionymus filamentosus* Valenciennes and *Lagocephalus suezensis* Clark & Gohar, were classified as

TABLE III. Ranking of the 10 most dominant species in *Posidonia oceanica* meadows in terms of total biomass and density. Family, origin (I, indigenous; NI, non-indigenous) and ecological guild (SR, seagrass residents; SM, seasonal migrants; JM, juvenile migrants) are indicated

	Species	Family	Origin	Ecological guild	Biomass (kg)
1	<i>Boops boops</i> *	Sparidae	I	SR	527.69
2	<i>Chromis chromis</i>	Pomacentridae	I	SM	148.48
3	<i>Oblada melanura</i> *	Sparidae	I	JM	33.41
4	<i>Sphyaena viridensis</i> *	Sphyaenidae	I	SR	32.79
5	<i>Lagocephalus sceleratus</i>	Tetraodontidae	NI	SR	27.27
6	<i>Sparisoma cretense</i> *	Scaridae	I	JM	22.08
7	<i>Coris julis</i>	Labridae	I	SR	16.78
8	<i>Sardinella aurita</i> *	Clupeidae	I	JM	13.12
9	<i>Pagrus pagrus</i> *	Sparidae	I	JM	12.17
10	<i>Sphyaena sphyaena</i> *	Sphyaenidae	I	SR	11.85

	Species	Family	Origin	Ecological guild	Density
1	<i>Boops boops</i> *	Sparidae	I	SR	31 202
2	<i>Chromis chromis</i> *	Pomacentridae	I	SM	16 646
3	<i>Sardina pilchardus</i> *	Clupeidae	I	JM	2845
4	<i>Coris julis</i>	Labridae	I	SR	2103
5	<i>Siganus rivulatus</i> *	Siganidae	NI	JM	2055
6	<i>Sphyaena chrysotaenia</i> *	Sphyaenidae	NI	JM	1325
7	<i>Mullus surmuletus</i> *	Mullidae	I	JM	1312
8	<i>Atherina hepsetus</i> *	Atherinidae	I	JM	1156
9	<i>Sparisoma cretense</i> *	Scaridae	I	JM	1077
10	<i>Oblada melanura</i> *	Sparidae	I	SR	750

*Species of commercial value.

occasional visitors due to their irregular occurrence which was in accordance with their low seagrass affinity (Table I). The indigenous striped red mullet *Mullus surmuletus* L. and red mullet *Mullus barbatus barbatus* L. clearly prevailed over the non-indigenous mullids in terms of density, while of the two NIS *U. pori* was caught more frequently than *U. moluccensis*.

DISCUSSION

This study has shown that *P. oceanica* meadows in the eastern Mediterranean Sea sustain a diverse fish community that includes 88 species within 34 families, a number that accounts for 19% of the total number of fish species inhabiting the eastern Mediterranean Sea. Sampling of fish assemblages from seagrass meadows has been carried out in the western Mediterranean Sea using several methods, such as beam trawl (Deudero *et al.*, 2008), visual census and small trawl netting (Bell & Harmelin-Vivien, 1982), with most authors acknowledging potential bias in their sampling methodology. In the present study, repetitive sampling using the boat-seine method at five sites during four seasons ensured that most species utilizing *P. oceanica* meadows were sampled. Boat-seining, a widely used fishing technique in Hellenic

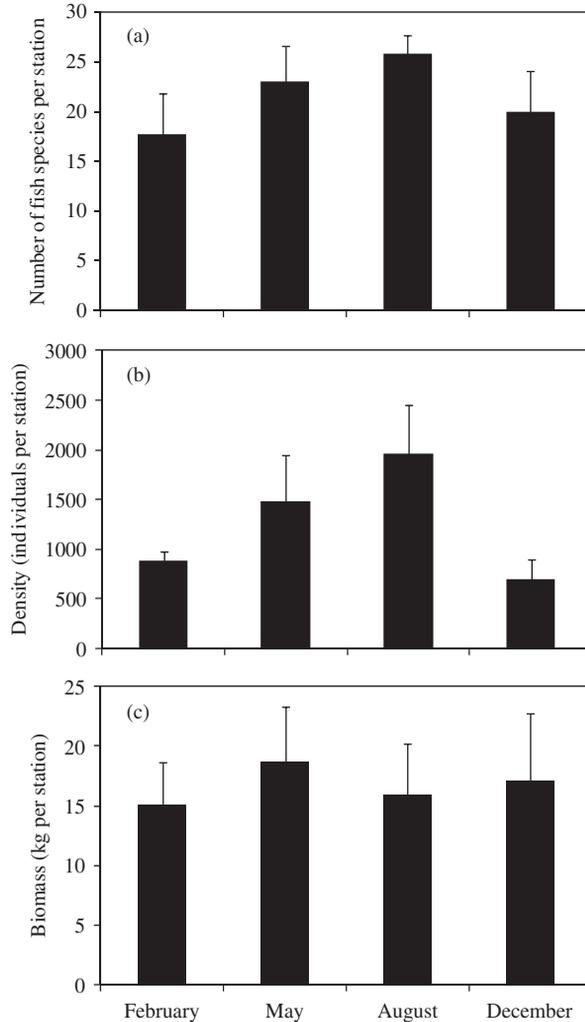


FIG. 2. Mean \pm S.E. (a) number of fish species, (b) density and (c) biomass at each location during sampling in *Posidonia oceanica* meadows during February, May, August and December 2008.

waters, made an effective sampling method because *P. oceanica* meadows occur over a broad depth range (0–35 m) while the seine also covers a relatively large surface area (0.04 ha per seining). In addition, boat-seining captures benthic and suprabenthic as well as pelagic species.

FISH ASSEMBLAGE STRUCTURE

The total number of fish species recorded during this study (88) is much higher than the total number of species recorded in the same habitat in the western Mediterranean Sea (Francour, 1997; Moranta *et al.*, 2006; Deudero *et al.*, 2008). The high mean species richness found in *P. oceanica* meadows during this study, however,

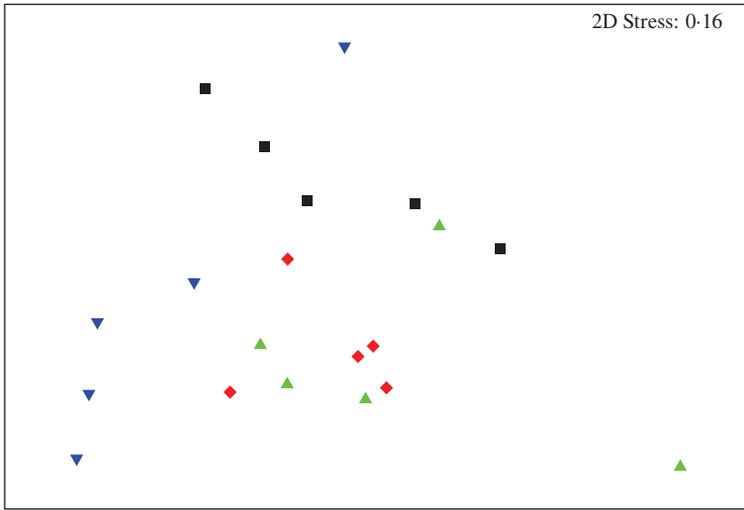


FIG. 3. Multidimensional scaling (MDS) ordination of fish species structure based on a similarity matrix of seasonal abundance (♦, August; ▲, May; ▼, February; ■, December).

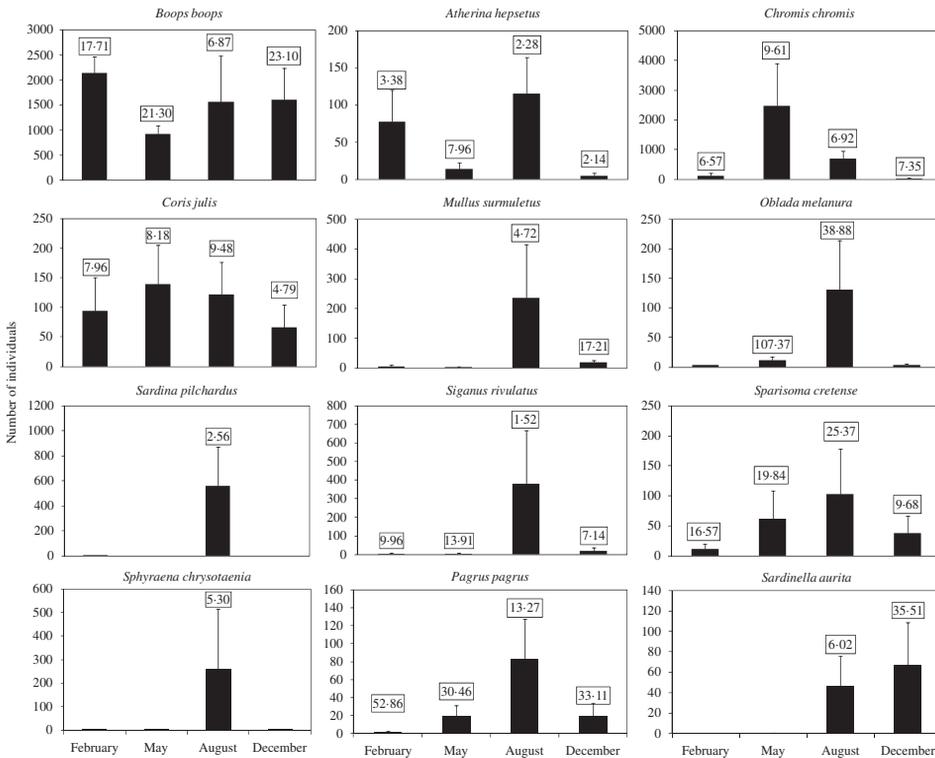


FIG. 4. Mean \pm S.E. density per season for each of the 12 most abundant species. Mean mass (g) per individual and season are indicated in boxes above each bar plot.

is similar to that recorded by several studies in the western Mediterranean Sea (Francour, 1997; Guidetti, 2000), indicating that the physical structure of habitats may be an important factor affecting nearshore fish assemblages (Bell & Harmelin-Vivien, 1982; Guidetti, 2000). During this study, the two-fold higher values of mean fish density in summer could be attributed to an increased number of fish species and to the recruitment of juveniles, a pattern that is also found in *P. oceanica* habitats in the western Mediterranean Sea (Deudero *et al.*, 2008). Several authors from the western Mediterranean Sea have emphasized the important nursery role of seagrass areas for many fish species (Bell & Harmelin-Vivien, 1982; García-Rubies & Macpherson, 1995; Francour, 1997; Moranta *et al.*, 2006; Deudero *et al.*, 2008). Food and shelter are the main factors influencing juvenile and adult fish species, with vegetated habitats thus playing a crucial role in satisfying these requirements (Guidetti, 2000). Both seagrass and algae are well-known sources of primary production in littoral marine areas (Jennings *et al.*, 2007).

Water temperature may trigger migrations of fish species within the shallow coastal zone and offshore waters (Pihl & Wennhage, 2002), but the lack of tides, constant salinity regime and low temperature and depth range of *P. oceanica* may contribute to a more stable community structure (Bell & Harmelin-Vivien, 1982). In addition, the interseasonal similarity in assemblage structure and the consistency of mean fish biomass and numbers of species in the present study indicate a stable community structure with little variation in production over the year. The obvious peak in recruitment of several fish species in summer probably caused the observed seasonal pattern in fish species composition (Fig. 3).

Native zooplanktivorous schooling species (*e.g.* *B. boops*, *S. smaris*, *S. maena* and *C. chromis*) were dominant both in terms of abundance and biomass. Although *S. smaris* and *S. maena* were not considered to be strongly associated with *P. oceanica* beds because they are strictly zooplanktivorous, the omnivorous *B. boops* and *C. chromis* do use this habitat during various stages of their life cycles. As indicated by Bell & Harmelin-Vivien (1983), juveniles of *B. boops* feed on epiphytic algae within the seagrass canopy while *C. chromis* supplements its diet with benthic animals. Another factor that may contribute to the increased abundance of zooplanktivorous species in *P. oceanica* beds may relate to the extensive seagrass coverage in the region (Bell & Harmelin-Vivien, 1982). Labridae and Sparidae were the two most diverse fish families in *P. oceanica* meadows, which is in accordance with previous studies from the western Mediterranean Sea (Bell & Harmelin-Vivien, 1982; Francour, 1997; Moranta *et al.*, 2006; Deudero *et al.*, 2008). Their high abundance may be attributed to a greater availability of their prey items (amphipods and gastropods) which benefit from higher primary production due to increased nutrient levels (Bell & Harmelin-Vivien, 1982).

FUNCTIONAL GUILDS

Functional or ecotrophic guilds have been used widely in European seas (Elliott & Dewailly, 1995) to show how fish species exploit different habitats. The most commonly cited guilds divide the fish assemblage by ecology, vertical distribution, substratum preference, feeding or mode of reproduction. The high proportion of seagrass resident species in *P. oceanica* indicates the important role of this habitat for

both adults and juveniles, as observed by Francour (1997) and Bell & Harmelin-Vivien (1982). The seasonal co-occurrence of juveniles and adults results in higher seasonal biomasses when averaging the seasonal mass of each species. In the case of *C. julis*, a protogynous species that inhabits seagrass meadows throughout the year with no seasonal variation in size, the ratio between females and males (3.5) indicates that most of the specimens collected were mature females. Hence, *C. julis* was classified as a seagrass resident. The majority of species within the seagrass resident guild showed a high affinity to seagrass. Several authors have shown that members of the Labridae recruit to *P. oceanica* meadows (García-Rubies & Macpherson, 1995; Francour, 1997) and that several species use this habitat both as adults and as juveniles. In addition, Bussotti & Guidetti (1999) showed that juveniles of several labrid species occupy the same habitat as the adults, a pattern that is consistent with the results of this study in which most of the Labridae were classified as seagrass residents. Several species of commercial value (e.g. *S. smaris*, *S. maena*, *B. boops*, *S. viridensis* and *S. sphyraena*) were resident in *P. oceanica* meadows (Table III), although these pelagic fishes may also occur over rocky or sandy substrata. The affinity index used in the present study showed that *S. smaris* and *S. maena* had no apparent specific habitat requirement (Table I). Nevertheless, the high densities and various size classes of these species present in *P. oceanica* beds suggest that this may be an important habitat for them.

The high contribution of juvenile migrants indicates the use of seagrass beds as a nursery ground during summer, a pattern consistent with studies of fish assemblages in the western Mediterranean Sea (García-Rubies & Macpherson, 1995; Francour, 1997). As pointed out by authors studying seagrass systems in this area (Bell & Harmelin-Vivien, 1982; García-Rubies & Macpherson, 1995), many species of the families Sparidae and Mullidae have juveniles that migrate to seagrass (Table I and Fig. 4), with several species also returning as adults to feed and reproduce (Deudero *et al.*, 2008). In this study however, although these adults, e.g. white seabream *Diplodus sargus sargus* (L.), common two-banded seabream *Diplodus vulgaris* (Geoffroy Saint-Hilaire), saddled seabream *Oblada melanura* (L.) and parrotfish *Sparisoma cretense* (L.), within the juvenile migrant guild were occasionally observed, they comprised only a small fraction of the total abundance. The main usage of the *P. oceanica* habitat was by early life stages. Among the 10 most numerous species found, five of commercial value [European pilchard *Sardina pilchardus* (Walbaum), *S. rivulatus*, *S. chrysoaenia*, *M. surmuletus* and *S. cretense*] were classified as juvenile migrants indicating the important nursery function of this habitat for the replenishment of exploited fish stocks (Table III). High densities of adult spawners of *T. pavo* and *C. chromis* were present in May, suggesting that this habitat is also important for the reproduction of these species. Although *C. chromis* probably spawns over seagrass meadows, their juveniles move to rocky-algal habitats rich in small crevices (García-Rubies & Macpherson, 1995).

Occasional visitors were a major group in terms of number of species, but represented only a small fraction of density and biomass. This could be attributed to either the sandy or rocky habitat affinity of many of the species, or simply reflect that some of the species occur only rarely in this region. At a time of an alarmingly high introduction rate of non-indigenous species, information regarding the invasion process is highly important. Tracking invasion from temporary to permanent establishment is crucial to understanding how the process works. At the same time, the

integration of indigenous species with newcomers results in new ecological links, hence the need to continuously monitor the changing structure of fish assemblages.

THE ROLE OF NON-INDIGENOUS SPECIES

The results of this study illustrate successful invasion and habitat use by several recently arrived and longer established non-indigenous species in the eastern Mediterranean Sea. The majority of NIS use *P. oceanica* meadows during their early life stages indicating the importance of this habitat during their arrival, as well as during the temporary and permanent establishment stages of their invasion process. Classification of NIS fish species into functional guilds revealed that three were juvenile migrants and four were seagrass residents. Only four NIS recorded during this study (*S. diaspros*, *U. moluccensis*, *S. luridus* and *S. rivulatus*) are early colonizers (Galil, 2006), while the remaining seven have recently become established in the area (Corsini-Foka & Economidis, 2007). The number of fish species inhabiting the eastern Mediterranean Sea has increased to c. 470, due to the influx of >60 NIS of Indo-Pacific origin which now comprise 14% of the total ichthyofauna (Golani *et al.*, 2006).

The recently introduced labrid species *P. pelycus* was one NIS found to be a seagrass resident, ranking second in terms of density among labrids after *C. julis* and ahead of *S. ocellatus* and *S. rostratus*, which suggests that a restructuring of fish assemblages has taken place in seagrass areas. Whether the range of *P. pelycus* will further expand towards the western Mediterranean Sea is yet to be confirmed, but it is likely since the assemblage structure of labrids is similar in eastern and western Mediterranean seagrass habitats (Moranta *et al.*, 2006; Deudero *et al.*, 2008). High densities of juveniles of a further two NIS species, *F. commersonii* and the toxin-containing *L. sceleratus*, were caught during August. Significant numbers of adults were also occasionally found, leading to their classification as seagrass residents. Several studies have shown that *F. commersonii* ontogenetically shift towards more generalist feeding and habitat selection (Bilecenoglu *et al.*, 2002; Takeuchi *et al.*, 2002; Kalogirou *et al.*, 2007; Bariche *et al.*, 2009; Takeuchi, 2009). *Lagocephalus sceleratus* ranked among the 10 most dominant fish species in terms of biomass, a pattern resulting from the capture of a few large specimens during winter. The socio-economic impact of *L. sceleratus* on local fisheries relates to its toxicity and has led to the development of new methods for cleaning fishing gear (Streftaris & Zenetos, 2006).

Juvenile migration was a common feature of three non-indigenous species where functional classification was possible, while *P. oceanica* was an important habitat for the recently introduced *S. chrysotaenia* and the two earliest-arrived non-indigenous species, *S. rivulatus* and *S. luridus*. Their classification as juvenile migrants was due to the presence of high densities of juveniles during summer. *Siganus luridus* and *S. rivulatus* are well established in the area and are of high commercial value for local fishermen (Papaconstantinou, 1990; Corsini-Foka & Economidis, 2007). As herbivores, *S. rivulatus* and *S. luridus* ranked lower in biomass than many native herbivorous species such as *S. cretense*, although higher than the native salema *Sarpa salpa* (L.). In the present study, the two NIS siganids made up 56% of the total abundance of herbivorous fishes occurring in *P. oceanica* beds, a number slightly lower than that of a previous study in Lebanon (Bariche *et al.*, 2004). The present

study, however, also recorded a nine times higher abundance of *S. rivulatus* compared to *S. luridus*, in accordance with the previous Lebanese investigation (Bariche *et al.*, 2004). Another two NIS, *U. pori* and *U. moluccensis*, were less associated with *P. oceanica* meadows than the two native mullid species.

Further research is required to reveal more details about the habitats essential for the establishment of non-indigenous species in the area, while also providing insights into the integration of indigenous and non-indigenous populations. The lack of adequate habitat maps was a limiting factor in explaining spatial differences within the fish assemblages. Furthermore, a paucity of historical studies on fish assemblage structure in *P. oceanica* beds precluded an evaluation of how ecosystem functioning may have changed following the establishment of NIS. More extensive investigation into the role of NIS should be a priority at both local and regional scales.

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References

- Arculeo, M., Mauro, A. G., Scelsa, S., Brutto, M. & Cammarata Parrinello, N. (1996). Protein differences among the Mediterranean species of the genus *Spicara*. *Journal of Fish Biology* **49**, 1317–1372.
- Bariche, M., Alwan, N., El-Assi, H. & Zurayk, R. (2009). Diet composition of the Lessepsian bluespotted cornetfish *Fistularia commersonii* in the eastern Mediterranean. *Journal of Applied Ichthyology* **24**, 460–465.
- Bariche, M., Letourneur, Y. & Harmelin-Vivien, M. (2004). Temporal fluctuations and settlement patterns of native and Lessepsian herbivorous fishes on the Lebanese coast (Eastern Mediterranean). *Environmental Biology of Fishes* **70**, 81–90.
- Bauchot, M.-L. (1987). Poissons Osseux. In *Fiches FAO d'identification des especes pour les besoins de la pêche (Revision 1). Méditerranée et mer Noire. Zone de pêche 37* (Fischer, W., Bauchot, M.-L. & Schneider, M., eds), pp. 891–1421. Rome: FAO.
- Bell, J. D. & Harmelin-Vivien, M. I. (1982). Fish fauna of French Mediterranean *Posidonia oceanica* seagrass meadows. 1. Community structure. *Tethys* **10**, 337–347.
- Bell, J. D. & Harmelin-Vivien, M. L. (1983). Fish fauna of french Mediterranean *Posidonia oceanica* seagrass meadows. 2. Feeding habits. *Tethys* **11**, 1–14.
- Bianchi, C. N. & Morri, C. (2000). Marine biodiversity of the Mediterranean Sea: situation, problems and prospects for future research. *Marine Pollution Bulletin* **40**, 367–376.
- Bianchi, C. N. & Morri, C. (2003). Global sea warming and “tropicalization” of the Mediterranean Sea: biogeographic and ecological aspects. *Biogeographia* **24**, 319–328.
- Bilecenoglu, M., Taskavak, E. & Kunt, B. K. (2002). Range extension of three lessepsian migrant fish (*Fistularia commersonii*, *Sphyræna flavicauda*, *Lagocephalus suezensis*) in the Mediterranean Sea. *Journal of the Marine Biological Association of the United Kingdom* **82**, 525–526.
- Bussotti, S. & Guidetti, P. (1999). Fish communities associated with different seagrass systems in the Mediterranean Sea. *Naturalista Siciliano* **23**, 245–259.
- Clarke, K. R. & Gorley, R. N. (2006). *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation*. Plymouth: PRIMER-E Ltd.

- Clarke, K. R., Chapman, M. G., Somerfield, P. J. & Needham, H. R. (2006). Dispersion-based weighting of species counts in assemblage analyses. *Marine Ecology Progress Series* **320**, 11–27.
- Corsini-Foka, M. & Economidis, P. S. (2007). Allochthonous and vagrant ichthyofauna in Hellenic marine and estuarine waters. *Mediterranean Marine Science* **8**, 79–101.
- Deudero, S., Morey, G., Frau, A., Moranta, J. & Moreno, I. (2008). Temporal trends of littoral fishes at deep *Posidonia oceanica* seagrass meadows in a temperate coastal zone. *Journal of Marine Systems* **70**, 182–195.
- Elliott, M. & Dewailly, F. (1995). The structure and components of European estuarine fish assemblages. *Netherlands Journal of Aquatic Ecology* **29**, 397–417.
- Field, J. G., Clarke, K. R. & Warwick, R. M. (1982). A practical strategy for analysing multispecies distribution patterns. *Marine Ecology Progress Series* **8**, 37–52.
- Francour, P. (1997). Fish assemblages of *Posidonia oceanica* beds at Port-Cros (France, NW Mediterranean): assessment of composition and long-term fluctuations by visual census. *Marine Ecology* **18**, 157–173.
- Gacia, E. & Duarte, C. M. (2001). Sediment retention by a Mediterranean *Posidonia oceanica* meadow: the balance between deposition and resuspension. *Estuarine, Coastal and Shelf Science* **52**, 505–514.
- Galil, B. S. (2006). The marine caravan – the Suez Canal and the Erythrean invasion. In *Bridging Divides* (Gollasch, S., Galil, B. S. & Cohen, A., eds), pp. 207–300. Dordrecht: Springer.
- Galil, B. S. & Zenetos, A. (2002). A sea change – exotics in the eastern Mediterranean. In *Invasive Aquatic Species of Europe: Distribution, Impacts and Management* (Lepakoski, E., Olenin, S. & Gollasch, S., eds), pp. 325–336. Dordrecht: Kluwer Academic Publishers.
- García-Rubies, A. & Macpherson, E. (1995). Substrate use and temporal pattern of recruitment in juvenile fishes of the Mediterranean littoral. *Marine Biology* **124**, 35–42.
- Golani, D., Orsi-Relini, L., Massuti, E. & Quignard, J. P. (2002). *CIESM Atlas of Exotic Species in the Mediterranean*. Monaco: CIESM Publishers.
- Golani, D., Öztürk, B. & Başusta, N. (2006). *The Fishes of Eastern Mediterranean*. Istanbul: Turkish Marine Research Foundation.
- Golani, D., Reef-Motro, R., Ekshtein, S., Baranes, A. & Diamant, A. (2007). Ichthyofauna of the rocky coastal littoral of the Israeli Mediterranean, with reference to the paucity of Red Sea (Lessepsian) migrants in this habitat. *Marine Biology Research* **3**, 333–341.
- Goren, M. & Galil, B. S. (2001). Fish biodiversity in the Vermetid Reef of Shiqmona (Israel). *Marine Ecology* **22**, 369–378.
- Guidetti, P. (2000). Differences among fish assemblages associated with nearshore *Posidonia oceanica* seagrass beds, rocky-algal reefs and unvegetated sand habitats in the Adriatic Sea. *Estuarine, Coastal and Shelf Science* **50**, 515–529.
- Harmelin-Vivien, M. L., Bitar, G., Harmelin, J.-G. & Monestiez, P. (2005). The littoral fish community of the Lebanese rocky coast (eastern Mediterranean Sea) with emphasis on Red Sea immigrants. *Biological Invasions* **7**, 625–637.
- Jennings, S., Kaiser, M. J. & Reynolds, J. D. (2007). *Marine Fisheries Ecology*. Oxford: Blackwell Publishing.
- Kalogirou, S., Corsini, M., Kondilatos, G. & Wennhage, H. (2007). Diet of the invasive piscivorous fish *Fistularia commersonii* in a recently colonized area of eastern Mediterranean. *Biological Invasions* **9**, 887–896.
- Louisy, P. (2002). *Guide d'identification des Poissons Marins: Europe et Méditerranée*. Paris: Ulmer.
- Moranta, J., Palmer, M., Morey, G., Ruiz, A. & Morales-Nin, B. (2006). Multi-scale spatial variability in fish assemblages associated with *Posidonia oceanica* meadows in the Western Mediterranean Sea. *Estuarine, Coastal and Shelf Science* **68**, 579–592.
- Pancucci-Papadopoulou, M. A., Simboura, N., Zenetos, A., Thessalou-Legaki, M. & Nicolaidou, A. (1999). Benthic invertebrate communities of NW Rodos island (SE Aegean Sea) as related to hydrological and geographical location. *Israel Journal of Zoology* **45**, 371–393.

- Pancucci-Papadopoulou, M. A., Kevrekidis, K., Corsini-Foka, M. & Simboura, N. (2005). Changes in species: invasion of exotic species. In *State of the Hellenic Marine Environment* (Papathanassiou, E. & Zenetos, A., eds), p. 336–342. Athens: Hellenic Centre of Marine Research.
- Papaconstantinou, C. (1990). The spreading of Lessepsian fish migrant into the Aegean Sea (Greece). *Scientia Marina* **54**, 313–316.
- Pihl, L. & Wennhage, H. (2002). Structure and diversity of fish assemblages on rocky and soft bottom shores on the Swedish west coast. *Journal of Fish Biology* **61**, 148–166.
- Por, F. D. (1978). *Lessepsian Migration: The Influx of Red Sea Biota Into the Mediterranean by Way of the Suez Canal*. Berlin-Heidelberg: Springer.
- Quignard, J. P. & Tomasini, J. A. (2000). Mediterranean fish biodiversity. *Biologia Marina Mediterranea* **7**, 1–66.
- Rilov, G. & Galil, B. (2009). Marine bioinvasions in the Mediterranean Sea – history, distribution and ecology. In *Biological Invasions in Marine Ecosystems* (Rilov, G. & Crooks, J. A., eds), pp. 549–575. Heidelberg: Springer-Verlag.
- Streftaris, N. & Zenetos, A. (2006). Alien marine species in the Mediterranean – the 100 ‘worst invasives’ and their impact. *Mediterranean Marine Science* **7**, 87–118.
- Streftaris, N., Zenetos, A. & Papathanassiou, E. (2005). Globalisation in marine ecosystems – the story of non indigenous marine species across European Seas. *Reviews in Oceanography and Marine Biology* **43**, 419–454.
- Takeuchi, N. (2009). Ontogenetic changes in foraging tactics of the piscivorous cornetfish *Fistularia commersonii*. *Ichthyological Research* **56**, 18–27.
- Takeuchi, N., Hashimoto, H. & Gushima, K. (2002). Short-term foraging patterns of individual cornetfish, *Fistularia commersonii*, based on stomach content analysis. *Ichthyological Research* **49**, 76–80.
- Theocharis, A., Nittis, K., Kontoyiannis, H., Papageorgiou, E. & Balopoulos, E. (1999). Climatic changes in the Aegean Sea influence the thermohaline circulation of the Eastern Mediterranean (1986–1997). *Geophysical Research Letters* **26**, 1617–1620.
- Theocharis, A., Klein, B., Nittis, K. & Roether, W. (2002). Evolution and status of the Eastern Mediterranean Transient (1997–1999). *Journal of Marine Systems* **33–34**, 91–116.
- Underwood, A. J. (1997). *Experiments in Ecology: Their Logical Design and Interpretation Using Analysis of Variance*. Cambridge: Cambridge University Press.
- Waycott, M., Duarte, C. M., Carruthers, T., Orth, R. J., Dennison, W. C., Olyarnik, S., Calladine, A., Fourqurean, J. W., Heck, K. L., Hughes, R. A., Kendrick, G. A., Kenworthy, W. J., Short, F. T. & Williams, S. L. (2009). Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *PNAS* **106**, 12377–12381.
- Whitehead, P. J. P., Bauchot, M. L., Hureau, J.-C., Nielsen, J. & Tortonese, E. (Eds) (1986). *Fishes of the North-eastern Atlantic and the Mediterranean*. Paris: UNESCO.
- Zenetos, A., Çinar, M. E., Pancucci-Papadopoulou, M. A., Harmelin, J.-G., Furnari, G., Andaloro, F., Bellou, N., Streftaris, N. & Zibrowius, H. (2005). Annotated list of marine alien species in the Mediterranean with records of the worst invasive species. *Mediterranean Marine Science* **6**, 63–118.
- Zenetos, A., Vassilopoulou, V., Salomidi, M. & Poursanidis, D. (2007). Additions to the marine alien fauna of Greek waters (2007 update). *JMBA2 – Biodiversity Records* **1**, 1–8.

Electronic Reference

- Froese, R. & Pauly, D. (2009). *Fishbase*. Available at <http://www.fishbase.org/>