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The littoral fish community of the Lebanese rocky coast (eastern Mediterranean Sea) with emphasis on Red Sea immigrants

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Key words: coastal fishes, community structure, Lessepsian species, Levantine basin, Mediterranean Sea

Abstract

The organisation of the coastal rocky fish community of Lebanon was investigated for the first time, using visual censuses. A total of 62 fish species were recorded between the surface and 32 m depth, 8 species being Red Sea migrants. Species richness and fish abundance were positively correlated first with substrate complexity and second with depth. The trophic structure of the community was dominated by diurnal zooplanktivores (*Chromis chromis*, *Oblada melanura* and *Spicara smaris*) and mesocarnivores 1 (*Coris julis* and *Thalassoma pavo*), and did not vary significantly with depth. The Lessepsian migrants represented 13% of the species richness and 19% of the total abundance of individuals. They dominated among herbivores, nocturnal zooplanktivores and macrocarnivores. The Lessepsian *Siganus luridus* and *S. rivulatus* (Siganidae), *Pempheris vanicolensis* (Pempheridae) and *Sargocentron rubrum* (Holocentridae) were now among the most common fish species on the Lebanese rocky coast. Lessepsian fish species displayed either similar ecological niches in the Red Sea and in the Levantine basin (*P. vanicolensis*, *S. rubrum*) or an enlargement of their depth distribution towards deeper waters in their new environment (*S. luridus*, *S. rivulatus*). This study will serve as a baseline for future studies as eastern Mediterranean communities are subjected to a steady increase in Red Sea migrant species.

Introduction

Modification of local marine biodiversity by introduced species, whatever the access route, is an increasing worldwide phenomenon (Carlton and Geller 1993; Ruiz et al. 1997). When exotic species enter a new environment, they have to face different abiotic and biotic conditions, including new competitors and predators, and may induce drastic changes in native species abundance and niche displacement (Drake et al. 1989; Lodge 1993). Since the opening of the Suez canal in 1869, more than three hundreds Indo-

Pacific marine species have entered the eastern Mediterranean (Por 1978; Boudouresque 1999; Galil 2000). Species immigrating from the Red Sea, named Lessepsian species by Por, have largely modified the qualitative and quantitative composition of marine communities in the Levantine basin (Ben-Tuvia 1985; Fishelson 2000). Among them, 59 fish species have now been recorded (Golani 1998; Golani et al. 2002; Goren and Aronov 2002), and some of these have become important components of local fisheries in Lebanon (George and Athanassiou 1967), Israel (Lundberg and Golani 1995), Turkey

(Gucu et al. 1994) and Greece (Papaconstantinou et al. 1986). However, very few studies on the composition and structure of littoral fish communities in rocky reef habitats of the eastern Mediterranean are available (Diamant et al. 1986; Spanier et al. 1989; Spanier 2000; Goren and Galil 2001), and none on the Lebanese coast. Information on Lebanese littoral fishes is scarce, and related mainly to ichthyoplankton (Lakkis and Zeidane 1988, 1993; Lakkis 1994), siganid fishes (George 1972; Bariche et al. 2003, 2004) and coastal fisheries (Georges and Athanassiou 1967; Mouneimné 1978). The aims of the present study were thus to (1) determine the structure of the littoral fish community along the rocky coast of Lebanon from the surface down to 32 m depth, and (2) quantify the importance of Lessepsian species in this community. This information should serve as a baseline description in a fast changing environment.

Materials and methods

Study sites

Lebanon is located in the eastern part of the Levantine basin of the Mediterranean Sea (33°03' N, 35°22' E–34°35' N, 36°37' E) stretching ~220 km from north to south. Seven sites located from the north (near Tripoli) to the south (Nakoura) were investigated, most of them (Ramkine Islands, Anfeh, El Heri, Hannouch, Selaata and Batroun) being located in the northern part of the country (Figure 1). Dives were conducted from the shore and, according to the underwater topography of the individual sites, encompassed different bathymetric ranges (Table 1).

Visual censuses

Underwater visual census is the most appropriate method for studying littoral rocky reef fish

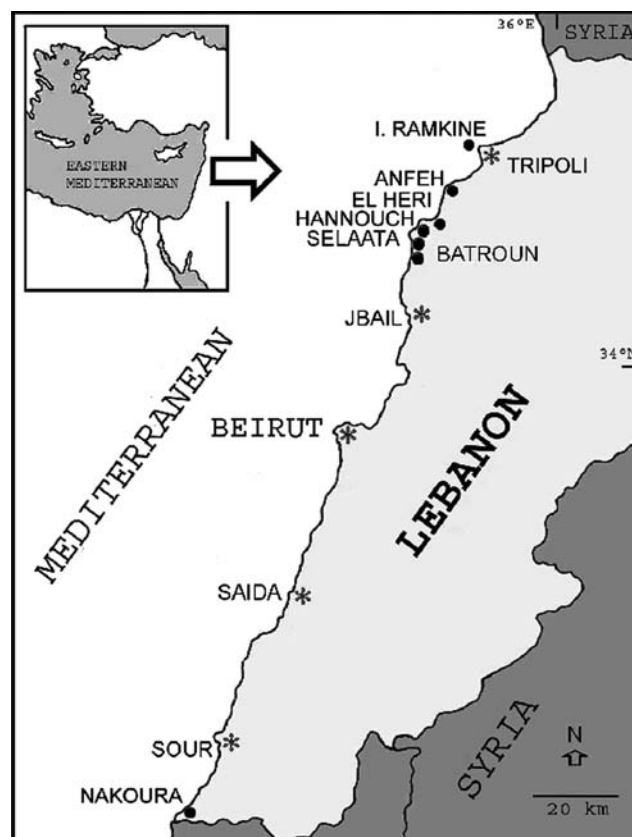


Figure 1. Sites studied along the coast of Lebanon (black dots).

Table 1. Sites investigated along the Lebanese coast in 2001, with mean and maximum depths of dives (m), total number of visual censuses and fish species per site, and mean density of fish per census (individuals per 25 m²) ± standard deviation (SD) per site. Four small gregarious pelagic species, *Engraulis encrassicolus*, *Atherina boyeri*, *Atherinomorus lacunosus* and Gobiidae sp. were excluded from the calculation of fish density.

Site	Ramkine	Anfeh	El Heri	Hannouch	Selaata	Batroun	Nakoura
Mean depth (max)	14.5 (26)	9.2 (12)	5.5 (11)	11.4 (23)	11.2 (32)	8.5 (9)	5.9 (9)
No. censuses/site	83	34	25	53	67	112	33
No. species/site	32	26	23	30	33	47	26
Mean density (±SD)/census	29.1 (±18.1)	29.7 (±23.8)	38.9 (±30.9)	30.8 (±21.3)	34.3 (±27.9)	28.6 (±22.3)	19.4 (±12.1)

communities, where most sampling gears (trawls, nets, lines) are either useless or too selective (Harmelin-Vivien et al. 1985). For the present study we performed visual censuses at fixed points of a standard surface (25 m²) during day time between 10:00 and 16:00 h. The adaptability and high rate of replication permitted by this method fitted well with the objectives and conditions of the study. At each point, fish species and number of individuals were recorded over a 5 × 5 m² surface in front of the diver. Depth (m) and type of substrate (rock, gravel, sand, macroalgae or *Cymodocea nodosa* seagrass) were also recorded, along with the architectural complexity of the bottom, ranging from 0 (flat) to 4 (highly complex) following Harmelin-Vivien et al. (1994). Each fish species was attributed to a trophic category, following the classification of Bell and Harmelin-Vivien (1983): i.e. herbivore, omnivore, zooplanktivore, mesocarnivore 1 (all labrids, which mainly feed on molluscs and crustaceans), mesocarnivore 2 (other species feeding mainly on small crustaceans and other invertebrates), or macrocarnivore (preying on large crustaceans, cephalopods and fish). A total of 407 such visual censuses were performed from the surface down to 32 m depth along the rocky shores of Lebanon in April 2001 (Table 1).

Statistical analysis

Mean species richness and fish density were calculated for each 25 m² station. As the great abundance or scarcity (i.e. patchiness) of some gregarious pelagic species (*Engraulis encrassicolus*, *Atherina boyeri*, *Atherinomorus lacunosus* and a small unidentified pelagic gobiid) could obscure

any trends in the abundance of demersal species, these were excluded from the analysis. They represented 46% of the total abundance of fish recorded as they formed dense schools, but were each observed only once or twice (Table 2).

Analyses of variance were performed on the numbers of species and on their abundance according to site, level of complexity, depth and type of habitat. A linear model framework was chosen after square root transformation of individual data to symmetrise and normalise the residual distribution. A generalised linear model was discarded because the natural Poisson distribution and log link function did not lead to acceptance of the goodness-of-fit test. Because the factors ‘type of habitat’, ‘level of complexity’ and the covariable ‘depth’ were far from orthogonal, significances of factors were tested using *F*-tests on type III sums of squares.

A principal components analysis (PCA) was applied to the covariance matrix after square root transformation of density values for each fish species, which is equivalent to the use of the Hellinger’s distance between community profiles. Location of the species on the first factorial circle of correlations of the PCA allowed the determination of the most representative species contributing to the pattern observed. Interpretation of the first factorial plane was also performed using projection of stations. To visualise classes related to a factor level, we plotted ellipses whose centres and axes feature mean, variance and covariance of intra-class scores in the first factorial plane. Their sizes were adjusted to cover 80% of points under Gaussian assumption. Analyses were performed using the R software (Ihaka and Gentleman 1996) and the R-package ADE-4 (Thioulouse et al. 1997).

Table 2. Mean density per census (number of fish per 25 m² ± SD) of littoral fish species recorded at the different sites surveyed along the coast of Lebanon in April 2001. Families are placed by alphabetic order. Lessepsian species are indicated by an asterisk (*). TC – trophic category of species; H – herbivore; O – omnivore; Z_D – diurnal zooplanktivore; Z_N – nocturnal zooplanktivore; M₁ – mesocarnivore 1, M₂ – mesocarnivore 2; C – macrocarnivore.

Site	TC	Ramkine	Anfeh	El Heri	Hannouche	Selaata	Batroun	Nakoura
Mean depth (m)		14.47 (7.44)	9.19 (2.63)	5.50 (2.74)	11.44 (8.32)	11.17 (7.87)	8.46 (3.57)	5.93 (1.92)
Mean complexity		1.86 (1.32)	1.29 (1.14)	2.40 (1.12)	1.91 (1.15)	2.01 (1.34)	1.68 (0.98)	1.82 (0.77)
Apogonidae								
<i>Apogon imberbis</i>	Z _N	0.15 (0.37)	0.24 (0.54)	0.00	0.29 (0.76)	0.77 (1.28)	0.17 (0.53)	0.00
<i>Apogon nigripinnis</i> *	Z _N	0.14 (0.38)	0.00	0.00	0.00	0.00	0.00	0.00
Atherinidae								
<i>Atherina boyeri</i>	Z _D	0.00	0.00	60.00 (219.85)	0.00	0.00	0.00	0.00
<i>Atherinomorus lacunosus</i> *	Z _D	0.00	0.00	0.00	0.00	0.00	62.50 (176.78)	3.33 (12.91)
Balistidae								
<i>Balistes capriscus</i>	M ₂	0.08 (0.29)	0.00	0.00	0.00	0.00	0.00	0.00
Blenniidae								
<i>Aidablennius sphynx</i>	O	0.00	0.00	0.00	0.00	0.38 (0.74)	0.00	0.00
<i>Blennius nigriceps</i>	O	0.00	0.00	0.00	0.00	0.00	0.22 (0.44)	0.06 (0.24)
<i>Parablennius sanguinolentus</i>	O	0.00	0.00	0.00	0.16 (0.50)	0.29 (0.78)	0.00	0.00
<i>Parablennius svonimiri</i>	O	0.00	0.00	0.00	0.00	0.13 (0.35)	0.00	0.00
Bothidae								
<i>Bothus podas</i>	M ₂	0.00	0.00	0.00	0.00	0.00	0.16 (0.47)	0.00
Carangidae								
<i>Caranx crysos</i>	C	0.00	0.60 (1.85)	0.00	0.00	0.00	0.00	0.00
Centracanthidae								
<i>Spicara smaris</i>	Z _D	0.00	0.00	0.00	0.00	0.00	1.00 (3.16)	1.11 (4.71)
Dasyatidae								
<i>Dasyatis pastinaca</i>	M ₂	0.00	0.00	0.00	0.00	0.00	0.20 (0.45)	0.00
Engraulidae								
<i>Engraulis encrassicolus</i>	Z _D	0.00	0.00	0.00	0.00	0.00	100.00 (316.23)	0.00
Gobiidae								
<i>Gobius bucchichi</i>	M ₂	0.08 (0.29)	0.00	0.00	0.29 (0.47)	0.00	0.11 (0.33)	0.00
<i>Gobius cobitis</i>	M ₂	0.00	0.00	0.00	0.08 (0.29)	0.00	0.44 (1.01)	0.07 (0.26)
Gobiid sp.	Z _D	0.00	0.00	11.11 (33.33)	0.00	0.00	25.05 (111.79)	0.00
Holocentridae								
<i>Sargocentron rubrum</i> *	C	1.14 (2.26)	0.71 (1.74)	0.56 (1.36)	2.09 (4.26)	0.71 (1.55)	0.40 (1.44)	0.17 (0.51)
Labridae								
<i>Coris julis</i>	M ₁	3.24 (4.10)	1.06 (1.54)	1.60 (1.71)	2.49 (2.77)	1.40 (1.73)	3.10 (2.76)	2.85 (3.93)
<i>Pteragogus pelycus</i> *	M ₁	0.00	0.00	0.00	0.00	0.00	0.13 (0.35)	0.00
<i>Symphodus doderleini</i>	M ₁	0.00	0.00	0.00	0.16 (0.50)	0.00	0.13 (0.35)	0.00
<i>Symphodus mediterraneus</i>	M ₁	0.22 (0.51)	0.24 (0.44)	0.00	0.19 (0.47)	0.29 (0.49)	0.21 (0.41)	0.11 (0.32)
<i>Symphodus ocellatus</i>	M ₁	0.17 (0.41)	0.00	0.00	0.00	0.00	0.22 (0.53)	0.00
<i>Symphodus roissali</i>	M ₁	0.00	0.10 (0.32)	0.13 (0.34)	0.10 (0.32)	0.22 (0.51)	0.21 (0.48)	0.12 (0.33)
<i>Symphodus tinca</i>	M ₁	0.26 (0.59)	0.76 (1.18)	0.52 (0.87)	0.45 (0.75)	0.38 (0.63)	0.68 (1.12)	0.24 (0.56)
<i>Thalassoma pavo</i>	M ₁	3.75 (3.12)	9.68 (9.99)	2.96 (1.67)	5.64 (6.26)	6.09 (6.06)	4.55 (6.45)	5.58 (5.36)
<i>Xyrichthys novacula</i>	M ₁	0.21 (0.43)	0.38 (0.65)	0.00	0.00	1.00 (1.30)	0.26 (0.60)	0.00
Monacanthidae								
<i>Stephanolepis diaspros</i> *	O	0.16 (0.42)	0.09 (0.30)	0.36 (0.76)	0.17 (0.60)	0.12 (0.33)	0.22 (0.51)	0.18 (0.46)
Mugilidae sp.								
<i>Mugilidae</i> sp.	O	0.00	0.00	0.00	10.57 (18.54)	0.77 (2.77)	0.67 (1.66)	0.07 (0.26)
<i>Oedalechilus labeo</i>	O	0.00	0.00	0.00	0.00	0.50 (1.41)	4.80 (8.67)	0.00
Mullidae								
<i>Mullus surmuletus</i>	M ₂	0.17 (0.41)	0.00	0.00	0.00	0.22 (0.44)	0.22 (0.58)	0.11 (0.47)

Table 2. Continued.

Site	TC	Ramkine	Anfeh	El Heri	Hannouche	Selaata	Batroun	Nakoura
Muraenidae								
<i>Muraena helena</i>	C	0.10 (0.31)	0.00	0.00	0.08 (0.29)	0.00	0.17 (0.39)	0.00
Pempheridae								
<i>Pempheris vanicolensis</i> *	Z _N	2.86 (4.10)	0.00	0.88 (3.50)	1.37 (3.32)	0.00	3.44 (5.64)	0.33 (1.41)
Pomacentridae								
<i>Chromis chromis</i>	Z _D	12.04 (12.04)	15.52 (10.71)	9.28 (15.14)	9.13 (11.54)	16.00 (15.97)	6.15 (8.94)	0.73 (1.91)
Scaridae								
<i>Sparisoma cretense</i>	H	1.39 (3.63)	0.60 (1.90)	4.56 (7.40)	2.05 (5.12)	1.92 (3.71)	2.19 (4.38)	1.21 (3.85)
Sciaenidae								
<i>Sciaena umbra</i>	M ₂	0.13 (0.35)	0.00	0.00	0.00	0.00	0.00	0.00
Scorpaenidae								
<i>Scorpaena maderensis</i>	C	0.17 (0.41)	0.10 (0.32)	0.06 (0.25)	0.15 (0.49)	0.28 (0.60)	0.11 (0.33)	0.00
<i>Scorpaena porcus</i>	C	0.00	0.00	0.00	0.08 (0.29)	0.00	0.00	0.00
Serranidae								
<i>Epinephelus aeneus</i>	C	0.00	0.10 (0.32)	0.00	0.00	0.00	0.00	0.00
<i>Epinephelus costae</i>	C	0.00	0.00	0.00	0.00	0.00	0.17 (0.41)	0.00
<i>Epinephelus marginatus</i>	C	0.32 (0.48)	0.10 (0.32)	0.00	0.14 (0.38)	0.08 (0.28)	0.17 (0.41)	0.07 (0.26)
<i>Mycteroperca rubra</i>	C	0.33 (0.57)	0.95 (1.07)	1.20 (1.55)	0.39 (0.71)	0.24 (0.53)	0.34 (0.56)	0.33 (0.54)
<i>Serranus cabrilla</i>	C	0.53 (0.66)	0.21 (0.41)	0.22 (0.44)	0.40 (0.54)	0.58 (0.50)	0.25 (0.44)	0.00
<i>Serranus scriba</i>	C	0.33 (0.51)	0.19 (0.40)	0.60 (0.76)	0.26 (0.56)	0.16 (0.44)	0.35 (0.61)	0.12 (0.42)
Siganidae								
<i>Siganus luridus</i> *	H	1.04 (1.94)	1.21 (4.31)	3.00 (3.45)	1.96 (2.43)	3.51 (4.94)	2.23 (4.15)	0.21 (0.48)
<i>Siganus rivulatus</i> *	H	1.07 (2.78)	0.50 (1.58)	3.75 (4.81)	0.67 (1.45)	3.82 (6.23)	3.18 (6.19)	0.44 (1.15)
Sparidae								
<i>Boops boops</i>	O	0.00	0.00	0.00	0.00	11.11 (33.33)	20.00 (44.72)	0.00
<i>Dentex dentex</i>	C	0.00	0.33 (1.00)	0.00	0.00	1.78 (1.92)	0.13 (0.35)	0.00
<i>Diplodus annularis</i>	M ₂	0.00	0.00	0.00	0.00	3.00 (3.24)	0.11 (0.32)	0.00
<i>Diplodus cervinus</i>	M ₂	0.00	0.00	0.06 (0.25)	0.00	0.14 (0.38)	0.13 (0.35)	0.09 (0.29)
<i>Diplodus puntazzo</i>	M ₂	0.00	0.00	0.00	0.00	0.00	0.00	0.03 (0.17)
<i>Diplodus sargus</i>	M ₂	0.77 (1.36)	1.48 (1.87)	3.16 (3.36)	1.78 (2.67)	2.45 (3.75)	6.15 (49.43)	1.64 (2.03)
<i>Diplodus vulgaris</i>	M ₂	2.77 (4.80)	4.73 (9.27)	1.40 (2.40)	1.13 (2.51)	0.71 (1.23)	1.10 (2.17)	0.22 (0.43)
<i>Lithognathus mormyrus</i>	M ₂	0.00	0.67 (2.00)	0.10 (0.32)	0.00	1.50 (4.24)	0.00	0.00
<i>Oblada melanura</i>	Z _D	2.25 (5.99)	3.05 (8.85)	4.00 (11.18)	1.26 (4.22)	1.50 (3.31)	2.07 (4.93)	3.03 (6.21)
<i>Pagrus coeruleostictus</i>	M ₂	0.29 (0.76)	0.00	0.00	0.00	0.00	0.00	0.00
<i>Pagrus pagrus</i>	M ₂	0.00	0.00	0.00	0.00	0.00	0.17 (0.41)	0.00
<i>Spondyliosoma cantharus</i>	M ₂	0.79 (1.70)	0.27 (0.69)	0.22 (0.44)	0.08 (0.29)	0.52 (1.88)	0.48 (1.42)	0.00
Sphyraenidae								
<i>Sphyraena</i> sp.	C	0.00	0.00	0.00	0.20 (0.63)	0.00	0.00	0.00
Torpaenidae								
<i>Torpedo marmorata</i>	C	0.00	0.00	0.00	0.00	0.00	0.00	0.07 (0.26)
Tripterygiidae								
<i>Tripterygion tripteronotus</i>	M ₂	0.14 (0.38)	0.00	0.00	0.00	0.00	0.11 (0.33)	0.00
<i>Tripterygion xanthosoma</i>	M ₂	0.14 (0.35)	0.00	0.00	0.00	0.00	0.10 (0.31)	0.00

Results

Community composition

A total of 62 fish species, belonging to 27 families, were recorded (Table 2). The most diverse families were the Sparidae (12 spp.), Labridae (9 spp.), Serranidae (6 spp.), Blenniidae (4 spp.) and Gobiidae (3 spp.). Only eight Lessepsian migrant species were recorded, representing 13% of the fish species richness. These were *Atherinomorus*

lacunosus (Atherinidae), *Sargocentron rubrum* (Holocentridae), *Apogon nigripinnis* (Apogonidae), *Pempheris vanicolensis* (Pempheridae), *Pteragogus pelycus* (Labridae), *Siganus luridus* and *S. rivulatus* (Siganidae), and *Stephanolepis diaspros* (Monacanthidae). The total number of fish species recorded at each site was significantly related to the number of visual censuses (linear regression $R = 0.951$, $P < 0.001$), the lowest number of species being observed at El Heri and the highest at Batroun (Table 1). In spite of

specific differences due to numbers of replicates, the fish community at all sites was dominated by similar common species, which represented most of the fish abundance recorded (40–90%). The most abundant families were the Pomacentridae (24% of abundance), comprising the single species *Chromis chromis*, the Labridae (22%), with *Thalassoma pavo* and *Coris julis* being the most abundant species, and the Sparidae (20%), particularly *Diplodus sargus*, *D. vulgaris* and *Oblada melanura*. The families Siganidae represented 9% of the fish abundance, Serranidae 3% and Holocentridae 2%. Lessepsian migrants constituted 19% of the total abundance of fish recorded. In decreasing order of importance, were *Atherinomorus lacunosus* (11.5%), *Siganus luridus* (2.3%), *S. rivulatus* (2.3%), *Pempheris vanicolensis* (1.6%), *Sargocentron rubrum* (1.0%), *Stephanolepis diaspros* (0.2%), *Apogon nigripinnis* (0.02%) and *Pteragogus pelycus* (0.02%). The relative abundance of Lessepsian species in the fish community density differed with sites, ranging from 6% at Anfeh to 22% at El Heri (7% at Nakoura, 13% at Selaata, 14% at Batroun and Hannouche, and 17% at Ramkine islands).

Variation with depth, habitat types and substrate complexity

The analysis of the three quantified environmental factors was made difficult by the non orthog-

onality of factors and their non balanced distribution between sites. If the substrate complexity was weakly linked to depth, it was more strongly related to habitat type. Sandy areas and seagrass beds exhibited a low complexity, whereas rocky areas, while encompassing the whole range of complexity, presented a higher mean complexity. All types of habitats were encountered in shallow waters (0–20 m), out only gravel and rocky areas were present between 20 and 32 m depth. However, the influences of these environmental factors on species richness, abundance and composition of the fish community have been distinguished and quantified.

The ANOVA tables for species richness and total fish density (the four gregarious pelagic species excluded) are given in Tables 3 and 4, respectively. For both analyses, the site factor was highly significant. More detailed comparison between site means showed that most sites were similar, excepted at Nakoura (the most southern site), where both variables were significantly lower. The most important factor controlling the distribution of fish species on the Lebanese coast was the complexity of the substrate. Mean numbers of species and individuals significantly increased with substrate complexity. Types of habitats were also highly significant. Numbers of species and individuals were significantly lower in sandy areas, and always higher on rocky substrates, with macroalgae and seagrass habitats

Table 3. Variability of species richness: ANOVA table of variances for the linear model expressing the root square of the number of species by the factors site (seven sites), complexity (five levels), habitat (five types) and depth (covariable).

Factors	df	Sum of Sq.	Typ. III	RSS	F-value	Pr(F)
Site	6	5.40		76.18	4.9689	6.418e-05***
Complexity	4	30.03		100.82	41.4747	< 2.2e-16***
Habitat	4	13.12		83.91	18.1219	1.147e-13***
Depth	1	0.10		70.89	0.5427	0.4617 (NS)

Residual standard error: 0.4255 on 391 degrees of freedom Adj. R^2 0.611; F-statistic: 43.5 on 15 and 391 DF, P-value: < 2.2e-16.

Table 4. Variability of abundance: ANOVA table of variances for the linear model expressing the root square of fish density by the factors site (seven sites), complexity (five levels), habitat (five types) and depth (covariable).

Factors	df	Sum of Sq.	Typ. III	RSS	F-value	Pr(F)
Sites	6	54.47		1164.96	3.1964	0.0044818**
Complexity	4	243.54		1354.03	21.4377	5.282 e-16***
Habitat	4	64.49		1174.97	5.6764	0.0001891***
Depth	1	9.40		1119.95	3.3111	0.069579(NS)

Residual standard error: 1.685 on 391 degrees of freedom; Adj. R^2 : 0.4052; Global F-statistic: 19.44 on 15 and 391 DF, P-value: < 2.2e-16.

presenting intermediate values. The total number of fish species and the mean number of species per census seemed to decrease slightly with depth, but in both cases coefficients were not significantly related to other factors.

The principal component analysis (Figure 2) performed on the abundance of each species determined a first axis (explaining 30% of the variance) which was naturally linked to the total abundance of fishes, and consequently to factors that significantly explained this abundance. The second axis (explaining 12% of the variance) was linked to depth. This factor, which was not significant for fish density, was conversely influential on species distribution. *Coris julis*, *Serranus cabrilla* and *Chromis chromis* were more characteristic of deeper sites, whereas *Sparisoma cretense*, *Siganus rivulatus*, *S. luridus*, *Diplodus sargus* and *Oblada melanura* were mainly recorded in shallow waters (Figure 2). The numerical importance of Lessepsian species varied with depth (ANOVA, $F_{3,17} = 6.804$, $P < 0.01$) and was significantly higher in shallower (0–4 m) than in deeper (>4 m) waters (Table 5). In shallow waters, *A. lacunosus*, *S. rivulatus*, *S. luridus*, *P. vanicolensis* and *Stephanolepis diaspros* were the most abundant Lessepsian fishes, whereas *Sargocentron rubrum* was more abundant between 12 and 32 m

Table 5. Numbers of species and percentage abundances (mean \pm SD) of Lessepsian species according to depth within the fish community of the Lebanese rocky coast.

Depth (m)	0–4 m	>4–12 m	>12–20 m	>20–32 m
No. species	6	6	4	5
Mean% (\pm SD)	20.4 (\pm 5.3)	11.2 (\pm 4.6)	9.1 (\pm 4.7)	9.1 (\pm 5.4)

depth. *Apogon nigripinnis* was only recorded in deep waters (23 m) at Ramkine Islands. Lessepsian species were observed on all types of substrate and complexity.

Plots of levels of complexity on the first factorial plane exhibited a strong relationship with the first axis (Figure 3). The species most related to high complexity were *Chromis chromis*, *Siganus luridus*, *Thalassoma pavo*, *Symphodus tinca* and *Sargocentron rubrum*. On the other hand, those species most often associated with flat areas were *Xyrichtys novacula* and *Coris julis*.

Trophic structure

The trophic structure of the Lebanese littoral fish community was numerically dominated by zooplanktivores, more particularly by the diurnal planktivores *Chromis chromis*, *Oblada melanura* and *Spicara smaris* (Table 6). By decreasing order of abundance percentages, the other

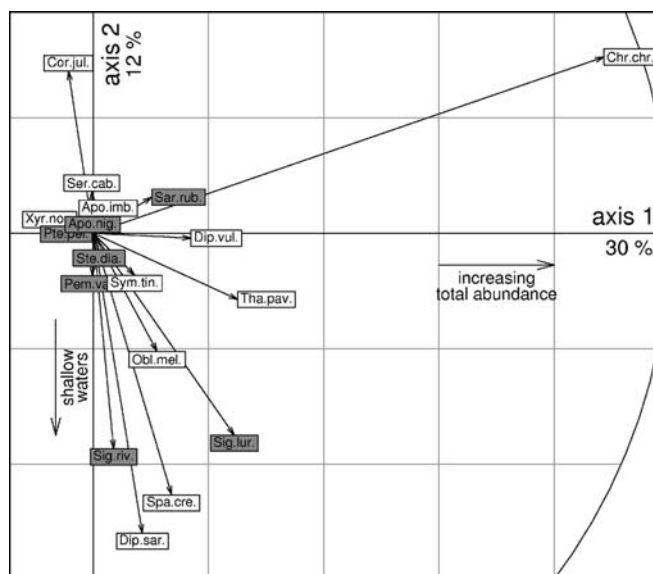


Figure 2. Map of the correlation circle on first factorial plane. Species are plotted in relation to their correlations with the first two components. Labels in grey denote Lessepsian species. The circle has a unit radius (units on the axes being indicated by the background grid of size 0.2 by 0.2).

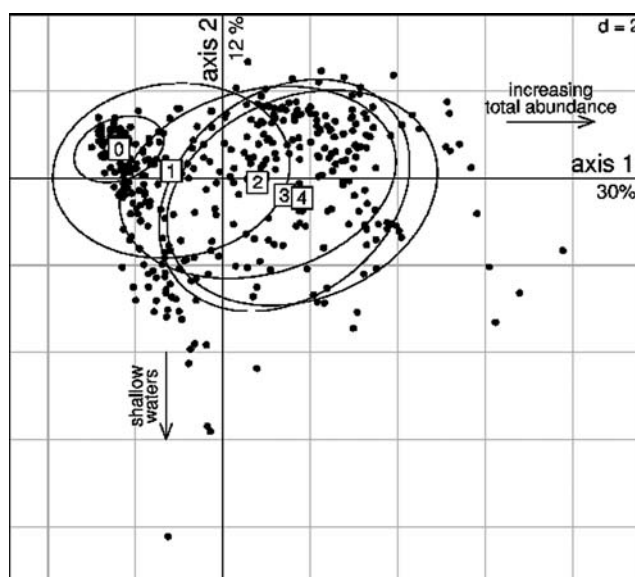


Figure 3. Map of the 402 stations on the first factorial plane. Inertia ellipses are computed for each level of substrate complexity from 0 (flat) to 4 (high complexity) and added (units on the axes are indicated by the background grid of size 2 by 2). Labels of complexity level are placed in the centre of their respective ellipses.

Table 6. Importance of indigenous Mediterranean and immigrant Lessepsian species in the trophic structure of the littoral rocky reef fish community on the coast of Lebanon, expressed as number of species and percentages of abundance in each trophic category (excluded the four gregarious zooplanktivore pelagic species).

	Number of species		% abundance per trophic category	
	Mediterranean	Lessepsian	Mediterranean	Lessepsian
Herbivores	1	2	34.4	65.6
Omnivores	7	1	97.4	2.6
Zooplanktivores	4	2	90.9	9.1
(diurnal)	(3)	(0)	(100)	(0)
(nocturnal)	(1)	(2)	(15.3)	(84.7)
Mesocarnivores 1	8	1	99.8	0.2
Mesocarnivores 2	18	0	100	0
Macro-carnivores	13	1	70.1	29.9

trophic categories were the mesocarnivores 1, the omnivores, the mesocarnivores 2, the herbivores and the macrocarnivores. Among the mesocarnivores 1 (Labridae), the most abundant species were *Coris julis* and *Thalassoma pavo*. Omnivores were represented mainly by the sparid *Boops boops*, the mugilids, the blenniids and the monacanthid *Stephanolepis diaspros*. The mesocarnivores 2 comprised other sparids, sciaenids, mullids, gobiids, balistids and bothids. Only three herbivorous species were recorded, the two siganids and the scarid *Sparisoma cretense*. Macro-carnivores were represented by muraenids, holocentrids, scorpaenids, serranids, carangids

and the sparid *Dentex dentex*. Lessepsian species were not evenly distributed between trophic categories (Table 6). They dominated among herbivores and nocturnal zooplanktivores, and were abundant among macrocarnivores. The two Lessepsian siganids, *Siganus luridus* and *S. rivulatus*, formed on average 66% of the total density of herbivores. They dominated (59–79%) at all sites, except at Nakoura (35%), where the indigenous scarid *Sparisoma cretense* was the most abundant herbivorous species. *Pempheris vanicolensis* was numerically dominant among nocturnal zooplanktivores (85%), and *Sargocentron rubrum* was the most abundant macrocarnivore (30%).

Table 7. Modification of the fish community trophic structure with depth, expressed as percentage of fish abundance in the different trophic categories.

Depth (m)	0–4 m	>4–12 m	>12–20 m	>20–32 m
Herbivores	30.7	14.6	7.4	8.5
Omnivores	3.4	4.0	0.3	6.7
Zooplanktivores	21.6	35.3	45.6	38.1
Mesocarnivores 1	26.5	24.9	25.1	28.9
Mesocarnivores 2	14.0	16.4	14.0	9.8
Macrocarivores	3.8	4.8	7.6	8.0

The trophic structure did not vary significantly with depth ($\chi^2 = 1.373$, $P = 0.712$), except in very shallow waters (0–4 m) where herbivores dominated (Table 7). The three herbivorous species were all abundant in shallow waters, but *Siganus luridus* was the only herbivore also commonly found deeper than 20 m. Zooplanktivores dominated numerically in all depth ranges, except in surface waters, but the most abundant planktivorous species differed with depth. *Pempheris vanicolensis* (along with the four gregarious pelagic species not included in the abundance percentages) were most abundant in shallow waters, whereas the importance of *Chromis chromis* and *Apogon imberbis* increased in waters deeper than 12 m. The importance of the mesocarnivores 1 category did not change with depth, but *Thalassoma pavo* was more abundant in shallow waters and *Coris julis* in deep waters. The relative abundance of the mesocarnivores 2 category remained stable from the surface down to 20 m, and decreased for all species below this depth. Conversely, the percentage of macrocarivores increased with depth, a trend related to the increased abundances of *Sargocentron rubrum* and *Serranus cabrilla*.

Discussion

Community composition

Fish species observed on Lebanese littoral rocky shores display different biogeographic distributions (Quignard and Tomasini 2000). Most species (71%) are distributed throughout the whole Mediterranean Sea, while others (16%) live preferentially in the warmest areas of the Mediterranean (in the southern parts of the occidental basin and in the oriental basin), like *Scorpaena mader-*

ensis, *Mycteroperca rubra*, *Epinephelus aeneus*, *Caranx crysos*, *Diplodus cervinus*, *Pagrus coeruleostictus*, *Thalassoma pavo*, *Sparisoma cretense* and *Balistes caprisacus*. Most fish species observed in Lebanon (61–69%) have been also recorded on the rocky coast of Israel (Diamant et al. 1986; Spanier et al. 1989; Goren and Galil 2001). Only eight Lessepsian species were recorded in the littoral fish community of Lebanese rocky coast, which together represented 13% of the total fish species richness observed. This percentage is in accordance with the values previously obtained for the rocky coast of Israel (11–12%) (Spanier et al. 1989; Goren and Galil 2001) and the whole Levantine basin (13.4%) (Golani 1996; Quignard and Tomasini 2000). Lessepsian species formed only 19% of the numerical abundance of fish recorded in Lebanon, while they represented from 37 to 46% of fish abundance in Israel (Diamant et al. 1986; Spanier et al. 1989; Goren and Galil 2001). The high percentages of Red Sea migrants observed in these last studies, compared to the lower value obtained in Lebanon, could originate in the particular habitats investigated, vermetid platforms in shallow waters (Diamant et al. 1986; Goren and Galil 2001) and an artificial reef made of car tyres (Spanier et al. 1989, Spanier 2000). Seasonal changes were not taken into account in this study performed in April 2001. Goren and Galil (2001) observed a minimum in fish species richness and abundance during this month in a study of fish community done over 1 year on a shallow vermetid reef. A seasonal study of the littoral fish community of Lebanon remains to be done to see if such a spring decrease is also observed in deeper waters or if there are bathymetric migrations of species with season.

Influence of environmental factors

The littoral fish community in Lebanon varied according to various environmental parameters, including substrate complexity, habitat type and depth, the first parameter being the most important. Fish species richness and abundance of individuals both increased with substrate complexity, a pattern well evidenced on coral reefs (Luckhurst and Luckhurst 1978; Friedlander and Parrish 1998), tropical rocky reefs (Ferreira et al. 2001) and on Mediterranean rocky shores (Harmelin-Vivien et al. 1994; Garcia-Charton and

Perez Ruzafa 1998, 2001). The effect of habitat complexity on fish species richness and abundance reflected an increase and diversification in food and shelter resources that resulted in a greater carrying capacity of these habitats (Garcia-Charton and Perez Ruzafa 2001). The type of habitat also highly influenced the specific composition and abundance of the fish community. On the rocky coast of Lebanon, diversity and density of fishes were higher on rocky substrates, lower in macroalgal and *Cymodocea nodosa* beds, and lowest on sandy areas. In the Adriatic Sea, Guidetti (2000) also found the lowest fish species richness and abundance on unvegetated sands, but recorded higher values in *Posidonia oceanica* seagrass beds than on rocky-algal reefs. Such a difference was due to the higher structural complexity of *P. oceanica* seagrass beds compared to the *C. nodosa* beds (Buia et al. 2000). In Lebanon, Lessepsian species were recorded in all types of substrate and complexity, indicating no preferential habitat for colonisation as observed by Por (1978) and Golani (1996).

Depth was recognised as an important factor determining fish community structure on western Mediterranean rocky shores (Bell 1983; Garcia-Rubies and Zabala 1990; Fasola et al. 1997; Reñones et al. 1997; Garcia-Charton and Perez Ruzafa 1998; Letourneur et al. 2003). Depth gradient affected the specific composition of the fish community more than it did for total species richness or abundance. Some fish species were recorded preferentially in distinct depth ranges. In Lebanon, the scarid *Sparisoma cretense*, the siganids *Siganus rivulatus* and *S. luridus*, the sparids *D. sargus* and *O. melanura*, and the labrid *T. pavo* were all recorded at higher abundances in shallow waters (0–12 m). The serranid *S. cabrilla*, the pomacentrid *C. chromis* and the labrid *C. julis* were more numerous in deeper waters, as also observed in north-western Mediterranean (Bell 1983; Garcia-Rubies and Zabala 1990; Francour 1991; La Mesa and Vacchi 1999; Garcia-Charton and Perez Ruzafa 2001). On the rocky coast of Lebanon, Lessepsian species were more numerous and numerically abundant in shallow waters (<12 m) than in deep waters. The higher importance of Lessepsian fishes in shallower waters was reported also in mullid family (Golani 1994). On the continental shelf of north-eastern Levant Sea, Gucu and Bingel (1994)

recorded a higher abundance of Lessepsian fishes in the trawl catches performed on shallower rather than deeper soft bottoms. This distribution pattern was generally attributed to temperature which was considered as the most important factor responsible for the colonisation success of Lessepsian species (Por 1978). However, some Lessepsian species may colonise deeper bottoms than their native Mediterranean counterparts, as observed for the bathymetric distribution of the immigrant *Saurida undosquamis* compared to the indigenous *Synodus saurus* (Golani 1993a). On the Lebanese rocky coast, it did not seem that the depth distributions of native species were modified by the arrival of Lessepsian species, at least when compared to those exhibited in the north-western Mediterranean. However, the lack of data on fish community structure in the eastern Mediterranean did not allow to definitively conclude.

Trophic structure

The trophic structure of the littoral fish community of Lebanon was characterised by a higher percentage of herbivores (13% in fish abundance) and a lower percentage of zooplanktivores (32%) than observed in analogous north-western Mediterranean communities (mean 4% herbivores and 55% zooplanktivores) (Bell 1983; Harmelin 1987; Harmelin et al. 1995; Garcia-Rubies and Zabala 1990; Garcia-Charton and Perez Ruzafa 2001; Guidetti 2000). The numerical importance of herbivores in the Lebanese fish community was essentially due to the two Lessepsian siganids, that are now amongst the most abundant littoral species in the eastern Mediterranean (Georges and Athanassiou 1967; Papaconstantinou et al. 1986; Gucu et al. 1994; Goren and Galil 2001). At the beginning of the 20th century, the native *Sarpa salpa* was the most abundant herbivorous fish in the catches of Lebanese fisheries, whereas siganids were then rare (Gruvel 1931). The drastic decrease in *S. salpa* populations in this region could be the result of a competitive exclusion of this native sparid species by the more competitive and fecund Lessepsian siganids (Bariche et al. 2003). *Sarpa salpa* has been rarely observed during a two year survey of herbivores conducted in this region (Bariche et al. 2004) and Diamant et al. (1986) observed only a few individuals in their

study. The success of Lessepsian herbivores may be due to the existence of underexploited niches, as few large herbivorous fishes occur in the Mediterranean Sea (Verlaque 1990). The lower relative importance of zooplanktivores in Lebanon compared to the north-western Mediterranean could be linked to the lower primary productivity of waters in the eastern Mediterranean, which have always supported a lower fisheries production, and particularly since the construction of the Aswan high dam on the upper Nile River (Turley et al. 2000).

Environmental adaptation of Lessepsian species

Red Sea migrants have to face new environmental conditions in the eastern Mediterranean Sea. Golani (1993b) showed that most display high trophic adaptations and that niche partitioning between them and their native relatives is achieved mainly by bathymetric distribution. Among the Lessepsian species recorded on the Lebanese rocky coast, two types of habitat adaptation to the Mediterranean environmental conditions could be observed. Some species displayed similar depth distributions and benthic habitats in the eastern Mediterranean as those which they occupy in the Red Sea. This was the case for *Pempheris vanicolensis*, which occupied overhangs in shallow waters in both seas, and *Sargocentron rubrum*, which sheltered in cavities during the day from shallow waters down to at least 30 m depth. Conversely, the two siganids exhibited a different spatial distribution in the Mediterranean compared to the Red Sea. On the coral reefs of Aqaba, these siganids were restricted to the reef flat and reef front, and were not observed deeper than 6 m (Bouchon-Navaro and Harmelin-Vivien 1981). In Lebanon, the two Lessepsian siganids were recorded from the surface down to 40 m (JGH pers. obs.), although they exhibited higher densities in shallow waters. The enlargement of their ecological niches to deeper waters might be explained by the lack of competition from autochthonous herbivores that were poorly represented in the Mediterranean waters (Verlaque 1990). In the Red Sea, as in other coral reef areas, the Siganidae were less abundant than the more speciose and competitive herbivorous families Scaridae and Acanthuridae (Choat 1991). Success of Lessepsian migrants

could be the result of both their occupation of an unsaturated niche and an efficient competition with local species on the same resources (food and shelter).

The characteristics of the target community are as important as those of the introduced species in determining invasion success, and it is well recognised that less diverse communities are more prone to biological invasions due to vacant niches (Lawton 1982; Lodge 1993). The eastern Mediterranean is characterised by a low fish diversity (Fredj and Meinardi 1989) which may explain in part the success and steady increase of Lessepsian species. However, the lack of ecological studies on fish community structure in the eastern Mediterranean Sea prior to the opening of the Suez Canal, and the scarcity and limited spatial scale of those carried out since, prevent any comprehensive interpretation of the dynamics of the establishment of Lessepsian species in their new environment. More studies on the organisation in space and time of littoral fish communities in the eastern Mediterranean in general are urgently needed.

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