Diet of the Lessepsian fishes, *Siganus rivulatus* and *S. luridus* (Siganidae) in the eastern Mediterranean: A bibliographic analysis

by

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ABSTRACT. - The Lessepsian fishes *Siganus rivulatus* and *S. luridus* are common herbivores in the eastern Mediterranean, where they adapted themselves to the algal resources of the new environment. It appears that in the eastern Mediterranean *S. rivulatus* grazes on the majority of available macrophytes, with a preference for certain taxa such as *Sphacelaria* spp., *Polysiphonia* spp., *Ulva* spp., *Jania* spp. and *Halopteris* spp. *Siganus luridus* seems to select some of most common macrophytes found in the eastern Mediterranean (e.g,. *Halopteris* spp., *Padina* spp., *Sphacelaria* spp., *Polysiphonia* spp., *Ulva* spp., *Sargassum* spp.). *Siganus luridus* occasionally ingests the toxic exotic macrophyte *Caulerpa racemosa*. Both Siganidae feed non-selectively during the cold season. Grazing of macrophytes varies in proportion with seasons, reflecting the seasonal variations of macrophyte populations. The proportions also appear to change with fish size, probably in relation to energetic needs as well as changing grazing capabilities with relation to age. In addition, small invertebrates can be ingested accidentally, while the ingestion of sand might have a function in digestion. In the Mediterranean, both Siganidae have considerably modified their diet to adapt themselves to new algal resources, which differ significantly from those found in the Red Sea.

RÉSUMÉ. - Régime alimentaire des poissons lessepsiens, *Siganus rivulatus* et *S. luridus* (Siganidae) en Méditerranée orientale : synthèse bibliographique.

Siganus rivulatus et *S. luridus* sont deux espèces lessepsiennes herbivores communes en Méditerranée orientale où elles ont ajusté leur régime alimentaire aux ressources algales de leur nouvel environnement. Il semble qu'en Méditerranée orientale, *S. rivulatus* broute la majorité des macrophytes disponibles mais avec une préférence pour certains taxa comme *Sphacelaria* spp., *Polysiphonia* spp., *Ulva* spp., *Jania* spp. et *Halopteris* spp. *Siganus luridus* semble choisir davantage certaines macrophytes comme *Halopteris* spp., *Padina* spp., *Sphacelaria* spp., *Polysiphonia* spp., *Ulva* spp. et *Sargassum* spp., qui sont parmi les plus communes en Méditerranée orientale. *Siganus luridus* semble également ingérer occasionnellement l'espèce exotique et toxique *Caulerpa racemosa*. Les deux espèces ont une alimentation non sélective durant la saison froide. La fréquence des macrophytes consommées varie avec la saison en relation avec les fluctuations des ressources algales. Les proportions ingérées changent également avec la taille des poissons, ce qui est probablement dû aux changements des besoins énergétiques et des capacités de broutage avec l'âge. Par ailleurs, divers petits invertébrés peuvent être ingérés accidentellement alors que le sable ingéré pourrait avoir un rôle dans la digestion. En Méditerranée, les deux Siganidae ont modifié considérablement leur régime alimentaire pour s'adapter à des ressources algales très différentes de celles de la mer Rouge.

Key words. - Siganidae - *Siganus rivulatus* - *Siganus luridus* - Rabbitfish - Lessepsian fish - MED - Diet - Herbivory.

Food ingested by carnivores is of a relatively uniform quality and thus more easily digested and assimilated (Stevens and Hume, 1995). Inversely, digestion is more complicated for herbivores and omnivores and specific adaptations of the digestive system are required (Chivers and Langer, 1994). Herbivorous fishes are usually classified as grazers or browsers (Ogden and Lobel, 1978). They generally share, therefore, a particular morphology; specifically characterized by a short blunt snout with closely set teeth as an adaptation to grazing (Ogden and Lobel, 1978; Choat, 1991). Internally, they usually have a much longer digestive tract compared to non-herbivorous species of similar sizes (Horn, 1989), thereby providing them with a larger surface for digestion and assimilation. The majority of herbivorous fishes start their life as carnivores or omnivores before adopting a diet composed of macrophytes (White, 1985). Ultimately, no fish can be an absolute herbivore since it will always ingest small animal material living in close association with macrophytes (Horn, 1989). Herbivores are usually found in shallow water, where macrophytes are abundant and diverse (Sheppard *et al*., 1992).

Siganidae are a family of herbivorous fishes living in the Indo-West Pacific (Woodland, 1983). The diet of many Siganidae has been studied extensively (Hiatt and Strasburg, 1960; Tsuda and Bryan, 1973; Westernhagen, 1973a, 1973b, 1974; Bryan, 1975; Tobias, 1976). Siganidae are generally considered as conservative in their diet, which makes their distribution on the tropical reefs more restricted than that of

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Acanthuridae or Scaridae (Choat, 1991). After the opening of the Suez Canal in 1869, many Eritrean species invaded the eastern Mediterranean and are known as Lessepsian migrants (Por, 1978). Two Siganidae are part of this tropical inflow: *Siganus rivulatus* Forsskål, 1775 was first recorded by Steinitz in 1927 (Tortonese, 1970), whereas *Siganus luridus* (Rüppell, 1829) appeared in 1956 (Ben-Tuvia, 1964). Both species have since established large populations in their new environment (Golani *et al*., 2002; Bariche *et al*., 2004), where they feed on algal communities dissimilar from those in their area of origin. Prior to Lessepsian migration, only few native herbivorous fishes existed in the Mediterranean (Verlaque, 1990). For two decades, a significant amount of research focused on the diet of *Siganus rivulatus* and *S. luridus* in the Red Sea (Lundberg and Lipkin, 1979; Lundberg, 1981a), in the eastern Mediterranean (Lundberg, 1980; Karagitson *et al*., 1986; Stergiou, 1988; Dowidar *et al*., 1992; Lundberg and Golani, 1993, 1995; Lundberg and Lipkin, 1993; Lundberg *et al*., 1999a, 1999b, 2004; Hamza *et al*., 2000) as well as studies comparing the diet in the two seas (Lundberg, 1981b, 1989; Lundberg and Golani, 1995). The digestive tract of *S. rivulatus* was studied by Rizkalla *et al*. (1988).

This paper does not provide new data on the diet itself but presents a discussion and a synthesis on the diet of the Lessepsian Siganidae in the eastern Mediterranean in order to draw general conclusions on their diet related to their new environment.

OVERVIEW OF PUBLISHED DATA

Diet in the eastern Mediterranean

Siganus rivulatus

A large majority of macrophytes living on the superficial Vermetid reefs (platforms and walls) and on deeper bottoms were found grazed upon by *Siganus rivulatus* at Mikhmoret (Israel). The selection, however, varied and the frequency of macrophytes in the digestive tract of the fish differed largely (Lundberg, 1980). Some species common among the vegetation were occasionally ingested. *Corallina elongata* J. Ellis & Solander (as *C. mediterranea*) and *Sargassum vulgare* C. Agardh, nom. illeg., represented respectively 12.5% and 3.8% of the algal cover and occurred each by only 0.5% in the digestive tracts of Mediterranean Siganidae (Lundberg, 1980). In contrast, other species were strongly selected, being found in higher proportions in the guts than in the vegetation. *Polysiphonia* spp., *Sphacelaria* spp. and *Ulva lactuca* Linnaeus were found in the digestive tracts (DT) respectively at 13.4%, 12.7% and 12.2% but were represented in the vegetation (VG) only at 3.3%, 1.4% and 7.6%. Other macrophytes were found in similar proportions in the guts and the vegetation. Species of *Cladophora* (DT = 4.4%; VG = 2.1%), *Bryopsis* (DT = 3.6%; VG = 2.4%) and *Enteromorpha* (DT = 3.4%; VG = 2.3%) were among the most frequently represented. Lastly, some rare species of macrophytes present at shallow depths in the vegetation of the eastern Mediterranean (VG ≤ 0,1%) were never found in the digestive tract e.g., *Bangia atropurpurea* (Roth) C. Agardh (as *B. fuscopurpurea*), *Schottera nicaeënsis* (J.V. Lamouroux ex-Duby) Guiry & Hollenberg (as *Petroglossum nicaeënsis*), *Petalonia fascia* (O.F. Müller) Kuntze and *Galaxaura* spp. (Lundberg, 1980).

Some taxa such as *Polysiphonia* spp., *Sphacelaria* spp., *Ulva lactuca*, and *Jania rubens* (Linnaeus) J.V. Lamouroux were also well represented in the stomach contents at Mikhmoret (N = 45) (Lundberg, 1981b) while others, such as *Ectocarpus* spp., *Cladophora* spp., *Bryopsis* spp., *Stypocaulon scoparium* (Linnaeus) Kützing (as *Halopteris scoparia*), *Spatoglossum asperum* J. Agardh, *Taonia atomaria* (Woodward) J. Agardh and *Enteromorpha* spp. had a secondary importance in terms of frequency. In Kastellorizo (Greece, off southwestern Anatolia), *Dictyota* spp. (97.6% of individuals, N = 89), *Sphacelaria* spp. (84.7%) and *Cystoseira* spp. (52.9%) were dominant (Karagitson *et al*., 1986). In Alexandria (Egypt) *Ulva* spp., *Cystoseira* spp. and *Corallina* spp. represented the preferred macrophytes of *S. rivulatus* (N = 673) when *Ulva* spp. and *Corallina* spp. were the most abundant taxa (Dowidar *et al*., 1992). At Mikhmoret, among the large variety of macrophytes grazed upon by *S. rivulatus* (N = 307), Lundberg and Lipkin (1993) found a dozen taxa representing 80% of the diet of which *Polysiphonia* spp., *Sphacelaria* spp., *Jania* spp. and *Ulva* spp. represented more than the half. *Sphacelaria* spp., *Polysiphonia* spp., *Ulva* spp., *Jania rubens*, *Hypnea* spp., *Ectocarpus* spp., *Codium* spp., *Gelidiella* spp. and *Spatoglossum asperum* dominated a group of selected taxa and secondarily *Bryopsis* spp., *Cladophora* spp., *Taonia atomaria*, *Stypocaulon scoparium* (as *Halopteris scoparia*) and *Gelidium* spp. as reported by Lundberg and Golani (1995) from the Mediterranean coast of Israel (N = 418). In Cyprus, Lundberg *et al*. (1999b) obtained different results from anywhere else in the Mediterranean with a clear dominance in the digestive tracts of *S. rivulatus* (N = 8), *Cystoseira* spp., *Polysiphonia* spp., *Dictyota mediterranea* (Schiffner) G. Furnari (as *Dilophus mediterraneus*), *Gelidium* spp., *Halopteris filicina* (Grateloup) Kützing and some unidentified "filamentous red algae" and secondarily *Codium* spp., *Ulva* spp., *Padina* spp., *Sargassum* spp., *Jania* spp., *Rytiphlaea tinctoria* (Clemente y Rubio) C. Agardh as well as a small percentage of the seagrass *Posidonia oceanica* (Linnaeus) Delile. Table I shows those macrophytes most frequently reported in the guts of *S. rivulatus* in the eastern Mediterranean.

Non-macrophytic taxa were also found in the digestive tract of *S. rivulatus*. Karagitson *et al*. (1986) reported epiphytic diatoms (100% of individuals, N = 89), hydrozoans

Table I. - Most reported macrophytes in the stomach content of *Siganus rivulatus*. X: occurrence. *[Macrophytes les plus fréquentes dans le contenu stomacal de* Siganus rivulatus. *X : présence.]*

	Siganus rivulatus						
	Lundberg (1981b)	Karagitson *et al*. (1986)	Dowidar *et al*. (1992)	Lundberg and Golani (1993)	Lundberg and Lipkin (1993)	Lundberg and Golani (1995)	Lundberg *et al*. (1999a)
Chlorophyta							
Bryopsis spp.	X				X	X	
Cladophora spp.	X				X	X	
Codium spp.						X	X
Enteromorpha spp.	X				X		
Ulva spp.	X		X	X	X	X	X
Rhodophyta							
Corallina spp.			X				
Gelidiella spp.					X	X	
Gelidium spp.						X	X
Hypnea spp.				X		X	
Jania spp.	X				X	X	X
Laurencia spp.						X	
Peyssonnelia spp.				X			
Polysiphonia spp.	X				X	X	X
Rytiphlaea spp.							X
"Filamentous red algae"							X
Incertae sedis							
(Class Phaeophyceae)							
Cystoseira spp.		X	X				X
Dictyota spp.		X					
Dilophus spp.							X
Ectocarpus spp.	X				X	X	
Halopteris spp.	X				X	X	X
Padina spp.				X			X
Sargassum spp.			X	X			X
Spatoglossum asperum	X				X	X	
Sphacelaria spp.	X	X			X	X	
Taonia atomaria	X				X	X	
Magnioliophyta							
Posidonia oceanica			X				

(27.0%) and some detritus (95.3%). Dowidar *et al*. (1992) reported bryozoans, crustaceans, polychaetes and molluscs representing 28% of the stomach contents whereas Lundberg *et al*. (1999b) reported animal fragments in small quantities. Sand was also reported in considerable quantities (30-70%) from specimens studied in Greece and Egypt (Karagiston *et al*., 1986; Dowidar *et al*., 1992).

Siganus luridus

Jania rubens and *Corallina elongata* (as *C. mediterranea*) make up almost one third of the vegetation of the Mediterranean coast of Israel. Other abundant species are *Gelidiella pannosa* (Feldmann) Feldmann & G. Hamel, *Polysiphonia* spp., *Sphacelaria* spp., *Sargassum* spp., *Stypocaulon scoparium* (as *Halopteris scoparia*), *Ulva* spp., *Colpomenia sinuosa* (Mertens ex-Roth) Derbès & Solier, *Spatoglossum asperum, Taonia atomaria, Chondracanthus acicularis* (Roth) Fredericq (as *Gigartina acicularis*), *Gelidium* spp., *Amphiroa rigida* J.V. Lamouroux and *Peyssonnelia squamaria* (S.G. Gmelin) Decaisne (Lundberg and Golani, 1995). Specimens from southern Israel (N = 110), *Gelidiella pannosa, Polysiphonia* spp. and *Sphacelaria* spp. composed 49% of the diet whereas *Peyssonnelia squamaria*, *Stypocaulon scoparium* (as *Halopteris scoparia*) and *Ulva* spp. were abundant and *Spatoglossum asperum*, *Colpomenia sinuosa* and *Taonia atomaria* were common as well (Lundberg and Golani, 1995). On the northern coast of Israel, *Padina* spp., *Sargassum* spp., *Dictyota* spp., *Dilophus* spp., *Dictyopteris polypodioides* (A.P. de Candolle) J.V. Lamouroux (as *D. membranacea*), *Taonia atomaria* and *Spatoglossum* spp. composed 60% of the diet. *Polysiphonia* spp., *Sphacelaria* spp., *Ulva* spp., *Gelidiella pannosa* were largely grazed and the consumption of *Laurencia* spp. was common (Lundberg and Golani, 1995). It is impossible to know what taxa were

really avoided. In Kastellorizo, *Dictyota* spp. (95% of individuals), *Cystoseira* spp. (72%), *Sphacelaria* spp. (68%), *Dictyopteris polypodioides* (as *D. membranacea*) (35%), *Rytiphlaea tinctoria* (35%), *Padina pavonica* (Linnaeus) Thivy in W.R. Taylor (30%), *Kallymenia* spp. (23.1%), *Dilophus* spp. (15%) and *Gelidium* spp. (13%) were the most frequent taxa found in the digestive tracts (N = 209) (Stergiou, 1988). Other taxa occurred with lower frequencies and the seagrass *Posidonia oceanica* was present in 4.2% of the individuals (Stergiou, 1988).

Like for *Siganus rivulatus*, *S. luridus* (N = 17) from Cyprus presented different stomach contents from those in other Mediterranean areas. In order of decreasing abundance, the following have been reported: *Polysiphonia* spp., *Dilophus mediterraneus*, *Sphaerococcus* spp., *Halopteris filicina*, *Sphacelaria* spp., *Padina* spp., *Anadyomene stellata* (Wulfen) C. Agardh, *Cladophora* spp., and some "filamentous red algae". *Ulva* spp., *Ectocarpus* spp., *Sargassum* spp. and *Posidonia oceanica* were found in smaller quantities (Lundberg *et al*., 1999b). The presence of the toxic *Caulerpa racemosa* (Forsskål) J. Agardh is noteworthy. Table II shows the most reported macrophytes from the guts of *S. luridus* in the eastern Mediterranean.

As in the case of *Siganus rivulatus*, non-macrophytic taxa were also ingested by *S. luridus*. These included diatoms (100% of individuals, N = 209), hydrozoans (15%) copepods, euphausiids and gastropods. Furthermore, 73% of individuals had ingested sand in Greece (Stergiou, 1988).

Variability with season

Both species of Siganidae show a seasonal difference in the proportions of ingested macrophytes (Tabs III, IV). In *Siganus rivulatus, Ulva lactuca* was dominant in the spring season (Lundberg, 1980; Lundberg and Lipkin, 1993; Lundberg *et al*., 2004). In fact, *Ulva* spp. represented 20-25% of the stomach contents and was followed by *Sphacelaria* spp., *Cladophora* spp., *Taonia atomaria* and *Enteromorpha* spp. (Lundberg and Lipkin, 1993). The presence of *Polysiphonia* spp., although ingested all year round, is minimal in spring (Lundberg and Lipkin, 1993). In Shiqmona, Lundberg *et al*. (1999a) reported also that *Cladophora* spp., *Enteromorpha* spp., *Cladophoropsis membranacea* (Hofman Bang ex-C. Agardh) Børgesen and some "red algae" are largely selected in the spring contrary to *Corallina elongata* and *Jania rubens*. *Spatoglossum asperum* and *Ectocarpus* spp., which were absent from the vegetation in spring (Lundberg and Lipkin, 1993). Chlorophytes, represented mainly by *Ulva* spp., *Enteromorpha* spp. and *Cladophora* spp., represented 66% of the gut contents in 26 fish studied in Shiqmona (Lundberg *et al*., 2004). During the summer, the taxa *Spatoglossum asperum*, *Polysiphonia* spp., *Jania* spp., *Sphacelaria* spp., *Gelidiella* spp. are the most selected macrophytes together with *Caulerpa* spp. (Lundberg, 1980). *Polysiphonia* spp., *Sphacelaria* spp. and *Spatoglossum asperum* were also found in large quantities in

Table II. - Most reported macrophytes in the stomach content of *Siganus luridus*. X: occurrence. *[Macrophytes les plus fréquentes dans le contenu stomacal de* Siganus luridus. *X : présence.]*

	Siganus luridus			
	Stergiou (1988)	Lundberg and Golani (1993)	Lundberg and Golani (1995)	Lundberg *et al*. (1999a)
Chlorophyta				
Anadyomene spp.				X
Caulerpa racemosa				X
Chaetomorpha spp.	X			
Cladophora spp.	X			X
Ulva spp.		X	X	X
Rhodophyta				
Gelidiella spp.		X	X	
Gelidium spp.	X			
Kallymenia spp.	X			
Laurencia spp.			X	
Peyssonnelia spp.		X	X	
Polysiphonia spp.	X	X	X	X
Rytiphlaea spp.	X			
Sphaerococcus spp.				X
"Filamentous red algae"				X
Incertae sedis				
(Class Phaeophyceae)				
Colpomenia spp.			X	
Cystoseira spp.	X			
Dictyopteris polypodioides	X		X	
Dictyota spp.	X		X	
Dilophus spp.	X		X	X
Ectocarpus spp.				X
Halopteris spp.	X	X	X	X
Padina spp.	X	X	X	X
Sargassum spp.		X	X	X
Spatoglossum asperum			X	
Sphacelaria spp.	X	X	X	X
Taonia atomaria			X	
Magnioliophyta				
Posidonia oceanica	X			X

Table III. - Seasonal variation in the most common macrophytes grazed by *Siganus rivulatus* in the eastern Mediterranean. *[Variation saisonnière des macrophytes les plus communes broutées par* Siganus rivulatus *en Méditerranée orientale.]*

	Siganus rivulatus		
	N	307	74
	Location	Israel (Mikhmoret)	Israel (Shiqmona)
	Reference	Lundberg and Lipkin (1993)	Lundberg *et al*. (1999b)
Winter	Chlorophyta	-	-
	Rhodophyta	*Jania* spp.	-
		Polysiphonia spp.	
	Phaeophyceae	*Sphacelaria* spp.	-
Spring	Chlorophyta	*Ulva* spp.	*Ulva* spp.
			Enteromorpha spp.
			Cladophora spp.
			Cladophoropsis membranacea
	Rhodophyta	-	-
	Phaeophyceae	-	-
Summer	Chlorophyta	-	-
	Rhodophyta	*Jania* spp.	-
	Phaeophyceae	-	-
Autumn	Chlorophyta	-	-
	Rhodophyta	*Polysiphonia* spp.	-
	Phaeophyceae	*Sphacelaria* spp.	*Sphacelaria* spp.
			Sargassum spp.
			Padina spp.

Table IV. - Seasonal variation in the most common macrophytes grazed by *Siganus luridus* in the eastern Mediterranean. *[Variation saisonnière des macrophytes les plus communes broutées par* Siganus luridus *en Méditerranée orientale.]*

	Siganus luridus		
	N	209	61
	Location	Greece (Kastellorhizo)	Israel (Shiqmona)
	Reference	Stergiou (1988)	Lundberg *et al*. (1999a)
Winter	Chlorophyta	-	-
	Rhodophyta	-	-
	Phaeophyceae	*Dictyota* spp.	-
		Cystoseira spp.	
		Dictyopteris polypodioides	
Spring	Chlorophyta	-	*Ulva* spp.
	Rhodophyta	-	-
	Phaeophyceae	*Dictyota* spp.	*Sargassum* spp.
		Sphacelaria spp.	*Padina* spp.
Summer	Chlorophyta	-	-
	Rhodophyta	-	-
	Phaeophyceae	*Dictyota* spp.	-
		Sphacelaria spp.	-
		Cystoseira spp.	-
Autumn	Chlorophyta	-	-
	Rhodophyta	*Gelidium* spp.	-
	Phaeophyceae	*Cystoseira* spp.	*Sargassum* spp.
		Padina spp.	*Padina* spp.
		Dictyota spp.	*Sphacelaria* spp.

summer along with *Ectocarpus* spp., *Jania* spp., *Ulva* spp. and *Halopteris* spp. (Lundberg and Lipkin, 1993). In autumn, Lundberg and Lipkin (1993) found that *Polysiphonia* spp. and *Sphacelaria* spp. were grazed in large quantities at Mikhmoret. Lundberg (1980) noticed a preference for *Polysiphonia* spp., *Sphacelaria* spp. and *Jania* spp. although *Sargassum* spp., *Padina* spp. and *Sphacelaria* spp. were selected more often in September (Lundberg *et al*., 1999a). Brown algae (*Sargassum* spp., *Padina* spp., *Sphacelaria* spp.) were found in the guts of most collected fish (N = 17) in Shiqmona (Lundberg *et al*., 2004). In winter, *Polysiphonia* spp. and *Sphacelaria* spp. were consistently found in large quantities together with *Jania* spp., *Bryopsis* spp., *Ulva* spp. but no *Spatoglossum asperum* and *Ectocarpus* spp. (Lundberg and Lipkin, 1993) while *Gelidiella* spp., *Jania* spp. and *Bryopsis* spp. were found in the same proportions at all seasons (Lundberg and Lipkin, 1993). Some macrophytes are selected when they are abundant in the vegetation and, conversely, ignored when scarce. The consumption of *Ulva* spp. decreased only in the summer and autumn when this species was rare in the vegetation at Mikhmoret. On the contrary, *Spatoglossum asperum*, which was abundant during the same period, was heavily selected (Lundberg, 1980). This switching in the diet may be due to better reward rates in grazing different sub-habitats (Murdoch and Oaten, 1975). *Ulva* spp. occurred more on the Vermetid reefs platforms while *Spatoglossum asperum* was more common on the reef walls and on bottoms (Lundberg, 1980). Finally, it has been suggested that vision and also schooling behaviour may influence this diet switching (Ayala and Campbell, 1974; Murdoch and Oaten, 1975); *S. rivulatus* is a schooling fish and both macrophytes are large in size.

In *Siganus luridus*, "green algae" were not found at Kastellorizo in the spring when *Dictyota* spp., *Cystoseira* spp. and *Sphacelaria* spp. dominated in frequency and in biomass in spring and summer (Stergiou, 1988). In Shiqmona, *S. luridus* selected *Sargassum* spp., *Padina* spp., *Ulva* spp. and some "red algae" but avoided *Corallina elongata* and *Jania rubens* (Lundberg *et al*., 1999a). *Sargassum* spp., *Dictyota* spp. and *Ulva* spp. were found in important

quantities in specimens (N = 5) sampled from Shiqmona (Lundberg et al., 2004). In autumn, stomach contents changed significantly since *Gelidium* spp., *Kuckuckia spinosa* (Kützing) Kornmann in Kuckuck and *Padina pavonica* became higher in biomass (Stergiou, 1988) while in Shiqmona, *Sargassum* spp., *Padina* spp. and *Sphacelaria* spp. were the most selected (Lundberg *et al*., 1999a, 2004).

Variability with size

Like with many fishes, the diet of Siganidae changes with size (Lundberg, 1980; Dowidar *et al*., 1992; Lundberg and Lipkin, 1993).

Siganus rivulatus (N = 258) of small sizes (< 130 mm TL) seem to prefer large and coarse macrophytes such as *Spatoglossum asperum* (about 28% of the stomach contents) and *Sargassum* spp. (about 8%). This can be compared to individuals of intermediate size (130-220 mm TL), which consume these same algae at about 16% and 1%, or even larger ones (> 220 mm TL) (5% and 0%) respectively (Lundberg and Lipkin, 1993). In contrast, small and tender, *Polysiphonia* spp. were less selected by the smallest fishes (about 8%) than by those fishes of intermediate and big sizes (about 16%). The smallest fishes also ingested less *Jania* spp. (6%) than the intermediate (16%) and the largest ones (25%) (Lundberg and Lipkin, 1993). The intermediate size individuals seem to have their own preferences since the selected macrophytes are not intermediate in size, the fish having ingested *Cladophora* spp. at about 7% and which was found in the smallest size class at about 3% or in the largest size-class at about 8%. These individuals of intermediate size had stomach contents comprising less *Ulva* spp. (1%) than small (3%) or large sizes (9%). The largest had a higher preference for *Jania* spp. than for *Sargassum* spp. At Alexandria, Dowidar *et al*. (1992) found that the composition of stomach contents was different where the macrophytes portion decreased and the animal material portion increased with the increase of fish size (Tab. V).

No information on the diet of *Siganus luridus* with regard to size is found in the literature.

Variability with sex

No significant difference was found between the diet of males and females of *Siganus rivulatus* (N = 673) studied along the coast of Alexandria (Egypt) (Dowidar *et al*., 1992) and no information regarding *Siganus luridus* was found in the literature.

DISCUSSION

In the eastern Mediterranean

The diet of an animal depends usually on the availability of the resources in different habitats. Herbivores and corals are very abundant in the Red Sea, which make the algal resources scarce and restricted to some unreachable refuges. Contrarily, the Mediterranean Sea is poor in herbivores and corals, which make it conversely rich in algal resources. Both species of Siganidae have modified their diet in the new environment compared to the populations of the Red Sea (Lundberg, 1981b, 1989; Lundberg and Golani, 1995). The two species are selective when macrophytes are diverse and present in large quantities and will eat what is available during the "bad" season (October-November), such as *Sargassum* spp., *Padina* spp. or *Sphacelaria* spp. (Lundberg *et al*., 1999a).

Siganus rivulatus

Siganus rivulatus ingests the majority of macrophytes present in the eastern Mediterranean, but all the species are not consumed in the same proportions; selection depends on the season and fish size. Therefore, *S. rivulatus* is a selective species but its diet is influenced by the seasonal availability of macrophytes (Lundberg and Lipkin, 1993). The most consumed macrophytes are *Sphacelaria* spp., *Polysiphonia* spp., *Ulva* spp., *Jania* spp. and *Halopteris* spp. as well as other taxa found in important quantities such as *Ectocarpus* spp., *Cladophora* spp., *Bryopsis* spp., *Cystoseira* spp., *Spatoglossum asperum* and *Taonia atomaria* (Tab. I). "Calcareous red algae", abundant at Mikhmoret, are avoided by *S. rivulatus*

Table V. - Variation with fish size in the most common macrophytes grazed by *Siganus rivulatus* in the eastern Mediterranean. *[Variation en fonction de la taille des poissons des macrophytes les plus communes broutées par* Siganus rivulatus *en Méditerranée orientale.]*

	Siganus rivulatus					
N	258			673		
Location	Israel (Mikhmoret)			Egypt (Alexandria)		
Reference	Lundberg and Lipkin (1993)			Dowidar *et al*. (1992)		
Fish size	Small (<130 mm TL)	Medium (130-220 mm TL)	Large (>220 mm TL)	Small (<150 mm TL)	Medium (150-240 mm TL)	Large (>250 mm TL)
Chlorophyta	-	*Cladophora* spp.		*Ulva* spp.	-	-
Rhodophyta	-	*Polysiphonia* spp.	*Polysiphonia* spp. *Jania* spp.	*Corallina* spp.	-	-
Phaeophyceae	*Spatoglossum* spp. *Sargassum* spp.	- -	- -	- -	- -	*Cystoseira* spp. *Sargassum* spp. *Colpomenia* spp.

except for *Jania rubens* (Tab. I). Being calcified, these are probably hard to detach from the substrate and poor in energy (Larkum *et al*., 1967; Paine and Vadas, 1969). The large quantities of *Jania rubens* are likely to be explained by accidental ingestion when the Siganidae are searching for filamentous algae (e.g. *Polysiphonia* spp., *Sphacelaria* spp., *Cladophora* spp., *Ceramium* spp.), which grow side by side with *Jania* spp. (Lundberg, 1980). *Siganus rivulatus* grazes on the seagrass *Posidonia oceanica* (Lundberg, 1999a) but not *Cymodocea nodosa* (Ucria) Ascherson or the Lessepsian *Halophila stipulacea* (Forsskål) Ascherson, which in the Red Sea is grazed upon by *Siganus argenteus* (Quoy & Gaimard, 1825) (Lundberg and Lipkin, 1979).

Some taxa seem to be rather inaccessible. This is the case of *Chondrophycus papillosus* (C. Agardh) Garbary & Harper (as *Laurencia papillosa*), whose presence in the stomach contents of *Siganus rivulatus* is scarce (0.2%) but more represented in the environment (3.2%) (Lundberg, 1980). The reason seems to be that it grows more on the Vermetid platform (8.8%) than on deeper bottoms (0.2%). The zone where *C. papillosus* occurs is not grazed by Siganidae but it is certainly not an avoided species as suggested by Lundberg (1980). In the summer season, Lebanese fishermen collect *C. papillosus* in large quantities from the Vermetid platforms and use it in traps as bait to capture specifically Siganidae (Bariche, 2002). Furthermore, the presence of *Laurencia* spp. (probably *C. papillosus*) was common in the individuals studied by Lundberg and Golani (1995) in Israel. Another example is *Bangia atropurpurea* (as *B. fuscopurpurea*), which was never eaten by *S. rivulatus* (Lundberg, 1980). This species is also found in the intertidal zone and thus can also be considered as inaccessible.

Other non-macrophytic taxa can also be found in the digestive tract of Mediterranean Siganidae but in small proportions. Polychaetes, molluscs and crustaceans are probably ingested accidentally since they are part of the fauna living in close association with macrophytes. Epiphytic diatoms, found in all stomach contents (100%), are certainly ingested unintentionally. However, the energetic contribution of these taxa for the grazer is not clear. Possibly the sand found in large quantities in the stomach contents (30-70%) and usually considered as accidental has a role in grinding the ingested seaweeds. According to Lundberg and Lipkin (1993), small-sized *Siganus rivulatus* feed preferably on hard and large macrophytes whereas larger individuals prefer small macrophytes. These authors concluded that the choice of macrophytes is not related to the fish size but to their nutritional values. However, Lundberg (1980) indicated that this was observed only in autumn and not in other seasons. Equally significant, this observation was not reiterated by Lundberg and Lipkin (1993) when they pooled all seasons. One should also note that the reasoning of the authors was based on four dominant taxa in the digestive tract and not on the entire number of ingested taxa (Lundberg and Lipkin, 1993). Schools of *S. rivulatus* of all sizes are frequently observed in Lebanon grazing on low algal turfs. Microhabitat studies on nurseries showed that settlers of *S. rivulatus* were the most represented (44.7%) on this type of vegetation (Bariche *et al*., 2004). Here young individuals graze on many species of different sizes. It is necessary to study their diet in detail before drawing conclusions.

Siganus luridus

In the eastern Mediterranean, *Siganus luridus* seems to select certain taxa such as *Dictyota* spp. or *Padina* spp. but generally ingests the most frequent macrophytes. The diet of this species changes seasonally and probably also with size. Among the most ingested taxa are *Halopteris* spp., *Padina* spp., *Sphacelaria* spp., *Polysiphonia* spp., *Ulva* spp. and *Sargassum* spp. whereas *Cladophora* spp., *Dictyopteris polypodioides* (as *D. membranacea*), *Dictyota* spp., *Gelidiella* spp., *Peyssonnelia* spp. and the seagrass *Posidonia oceanica* come in second (Tab. II).

The toxic *Caulerpa racemosa* is ingested by *S. rivulatus* in the Red Sea but this species has never been reported from stomach contents of the two other Siganidae (i.e., *Siganus luridus* and *S. argenteus*) (Lundberg, 1989; Lundberg and Lipkin, 1979; Lundberg and Golani, 1995). *Caulerpa racemosa* was introduced into the Mediterranean but is not a Lessepsian species (Verlaque *et al*., 2003). *Caulerpa racemosa* has never been found in the guts of Siganidae from Israel or Greece, but only in *S. luridus* from Cyprus where this macrophyte is abundant (Hadjichristophorou *et al*., 1997; Lundberg *et al*., 1999b). In Lebanon, it is common knowledge among fishermen that consumption of *S. luridus* may cause dizziness (pers. obs.). Ciguatera poisoning in Israel has been attributed to *S. luridus* and *Sarpa salpa* (Linnaeus, 1758) (Herzberg, 1973; Spanier *et al*., 1989), but it has also been suggested that the poisoning was more probably due to *Caulerpa* ingestion by these fishes (Chevaldonné, 1990).

The population density of Siganidae in Cyprus has decreased considerably in comparison with that elsewhere in the Mediterranean Sea, following a peak in the 1980s (Lundberg *et al*., 1999b). The authors' results differ from those obtained in other areas. Since the sample size (*S. rivulatus*, N = 8; *S. luridus*, N = 17) in their study is very small, these results should be interpreted with caution.

It seems that in the Mediterranean, *Siganus rivulatus* has become more selective than in the Red Sea. In the new area, it avoids ingestion of certain macrophytes (e.g. *Corallina elongata* (as *C. mediterranea*) and searches for less frequent species such as *Sphacelaria* spp. or *Taonia atomaria* (Lundberg, 1980; Lundberg and Lipkin, 1993). In the Red Sea (Gulf of Aqaba), *Laurencia* spp. and *Caulerpa racemosa* were abundant both in the stomach contents and in the vege-

tation (Lundberg and Lipkin, 1993). Red algae such as *Laurencia* spp. and *Hypnea* spp. were heavily grazed by *S. rivulatus* while brown algae such as *Sargassum* spp., *Lobophora variegata* and *Cystoseira myrica* were the most selected (Lundberg and Golani, 1995). According to Golani (1993), selectivity being more important in the Mediterranean is probably due to a larger choice in resources. *Siganus luridus* has also modified its diet considerably (Stergiou, 1988; Lundberg and Golani, 1995). This change is characterized by a large trophic flexibility in the new environment but with marked preferences for certain taxa also ingested in the Red Sea such as *Sargassum* spp. or *Sphacelaria* spp. (Lundberg and Golani, 1995).

Obvious differences exist between stomach contents of both species collected in the same locations as well as between same species but collected in different seasons (Lundberg and Golani, 1995). Future studies should compare the diet of the two Siganidae species simultaneously in different areas of the Levantine basin, as well as on the Mediterranean coasts of Africa, where *S. luridus* was present before *S. rivulatus* (Por, 1978). These studies should also take into consideration the seasonal variations, age and sex of the fishes. The diet of the planktonic larvae in the wild remains completely unknown as well as the diet of Siganidae settlers in the nurseries. Studying the diet of settlers would help to determine if a nursery is linked to a mosaic of benthic organisms or if it is simply any shallow calm zone as already suggested for *S. rivulatus* (Bariche *et al*., 2004).

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