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Age at maturity of Mediterranean marine fishes

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Abstract

In this review, we collected data on the age at maturity (t_m) and maximum reported age (t_{max}) for 235 stocks of Mediterranean marine fishes, belonging to 82 species, 37 families, 12 orders and 2 classes (Actinopterygii and Elasmobranchii). Among Actinopterygii (mean $t_m \pm SD = 2.20 \pm 1.43$ y, n = 215), t_m ranged from 0.3 y, for the common goby *Pomatoschistus microps*, to 12 y, for the dusky grouper *Epinephelus marginatus*, while among Elasmobranchii (mean $t_m \pm SD = 5.94 \pm 2.47$ y, n = 20), t_m ranged between 2.7 y, for brown ray *Raja miraletus*, and 12 y for the picked dogfish *Squalus acanthias*. Overall, t_{max} ranged between 1 y, for the transparent goby *Aphia minuta*, and 70 y, for the wreckfish *Polyprion americanus*. Mean t_{max} of Actinopterygii ($t_{max} \pm SD = 10.14 \pm 9.42$ y) was lower than that of Elasmobranchii ($t_{max} \pm SD = 14.05 \pm 8.47$ y); t_m exhibited a strong positive linear relation with t_{max} for both Actinopterygii ($\log t_m = 0.58 \times \log t_{max} - 0.25$, $r^2 = 0.51$, $P < 0.001$) and Elasmobranchii ($\log t_m = 0.67 \times \log t_{max} - 0.006$, $r^2 = 0.51$, $P = 0.007$). Mean t_m/t_{max} did not differ significantly with sex within Actinopterygii (ANOVA: $F = 0.27$, $P = 0.60$, n = 90; females: mean ± SD = 0.276 ± 0.143; males: mean ± SD = 0.265 ± 0.138) and Elasmobranchii (ANOVA: $F = 1.44$, $P = 0.25$, n = 10; females: mean ± SD = 0.499 ± 0.166; males: mean ± SD = 0.418 ± 0.133). Finally, the dimensionless ratio t_m/t_{max} was significantly lower (ANOVA: $F = 31.04$, $P < 0.001$) for Actinopterygii (mean ± SD = 0.270 ± 0.135, n = 180) than for Elasmobranchii, (mean ± SD = 0.458 ± 0.152, n = 20), when stocks with combined sexes were excluded from the analysis.

Keywords: Age at maturity, maximum age, empirical equations, life history.

Introduction

The reproductive life history characteristics of stocks, such as spawning period (Tsikliras *et al.*, 2010), length at maturity (Tsikliras & Stergiou, 2014) and fecundity (Despoti & Stergiou, 2013) are important for assessing the effects of fishing on populations and ecosystems (Jennings *et al.*, 1998). Age at maturity (t_m) is a key element of the life history strategies of fishes and has been widely used in modelling and grouping fish species based on their traits (Winemiller & Rose, 1992; Rochet, 2000; King & McFarlane, 2003), as well as a stress indicator for fisheries (Trippel, 1995). Olsen *et al.* (2004) have shown that simultaneous decreases in growth rate and t_m are evidence of fishery-induced evolution in Atlantic cod (*Gadus morhua*) following population decrease that has been attributed to overfishing. The t_m is also essential in demographic analyses (Chen & Yuan, 2006) being the lower limit of generation time (= the mean age of the spawning stock), which is highly correlated with the intrinsic rate of population growth (Ainsley *et al.*, 2011).

The availability of t_m estimates is limited compared to length at maturity data (Tsikliras & Stergiou, 2014) because it requires either ageing of caught individuals or knowledge of the local growth parameters in order for t_m to be estimated from the corresponding length at maturity. Therefore, the literature on the variability of t_m among families and orders of fish is rather scarce. Jennings *et al.* (1998) analyzed the life history traits of 18 fish stocks and report that stocks with high t_m, such as rays and skates, tend to decline more than expected from their rates of fishing mortality. Recently, Drazen & Haedrich (2012) analyzed the life history characteristics of 41 deep-sea demersal fishes and report that t_m increases with depth.

This review article is the third in the series of reviews on the reproductive biology of Mediterranean marine fishes, the first being by Tsikliras *et al.* (2010) on their spawning period, and complements the review on the size at maturity of Mediterranean fishes (Tsikliras & Stergiou, 2014).

The aim of the present work was to collect the available data on the age at maturity (t_m, y) and maximum reported age (t_{max}, y) for Mediterranean marine fish stocks and study: (a) the phylogenetic (between classes), sexual (between sexes) and habitat (among habitats - only for Actinopterygii) variability of t_m, (b) the relationship between t_m and t_{max} per class and (c) the dimensionless ratio

t_m/t_{max} per class and sex, which shows the proportion of lifespan that is covered before and after maturation. The compilation of such a dataset is also important for setting historical baselines against which future estimates of t_m can be compared in order to define trends in t_m with time (i.e. shifting baselines: Pauly, 1995).

Materials and Methods

The available and accessible information on t_m of Mediterranean marine fishes were extracted from journals, conference proceedings, theses, and technical reports for the period up to December 2013. The dataset also includes some stocks from the Marmara Sea, SE Black Sea, Suez Canal, and Bay of Cadiz because of their close proximity to the openings of the Mediterranean Sea (Table 1). Fish were classified in classes (Actinopterygii: actinopterygians or ray-finned fishes; Elasmobranchii: elasmobranchs or sharks, rays and skates), orders and families based on Eschmeyer (2012). Valid species names and authorities were according to FishBase (www.fishbase.org; Froese & Pauly, 2014). All ages were converted to years (y).

In the literature, there are several measures or definitions of sexual maturity (Binohlan, 1998; Tsikliras & Stergiou, 2014). When it comes to age at maturity, the most common definition is the median or mean age at which 50% of the population becomes mature for the first time, i.e. the age of first maturity (Tsikliras *et al.*, 2013a).

We also collected information on t_{max} (also in y) either from the original article or when not available from FishBase (Froese & Pauly, 2014) and consequently we computed the dimensionless ratio t_m/t_{max}. Additional information on the sampling procedure and habitat of each stock was recorded and, for the vast majority of stocks, is given in detail in Tsikliras & Stergiou (2014). Such information included country and specific location of sampling, duration and frequency of sampling, sex of specimens, number of individuals collected and sampling gear (Table 1). The habitat of each species was assigned based on the habitat information provided in FishBase (Froese & Pauly, 2014): demersal (D), pelagic (P), reef-associated (R), benthopelagic (BEP), bathydemersal (BAD) and bathypelagic (BAP). Although there are some inaccuracies regarding habitat allocation in FishBase, we decided to follow the habitat preferences exactly as they appear in FishBase for comparability purposes with previous articles and FishBase itself.

Analysis of variance (ANOVA) and covariance (ANCOVA) were used to compare means and regression lines, respectively. Fisher's Least Significance Difference (LSD) test was used to test for differences in the means between variables in multiple comparisons.

Results

Perciformes were the most represented order (128 stocks; 54.5% of the total) of the dataset, Sparidae the most represented family (38 stocks; 16% of the total) and *Trachurus trachurus* the most represented species (17 stocks) (Table 1).

Overall, we collected data on t_m for 235 stocks, belonging to 82 species, 37 families, 12 orders and 2 classes (Table 1). Among Actinopterygii (n = 215), t_m ranged from 0.3 y, for the common goby *Pomatoschistus microps*, to 12 y for the dusky grouper *Epinephelus marginatus*, while among Elasmobranchii (n = 20), it ranged between 2.7 y, for the brown ray *Raja miraletus*, and 12 y for the picked dogfish *Squalus acanthias*. The mean t_m ± SD was 2.20 ± 1.43 y for Actinopterygii and 5.94 ± 2.47 y for Elasmobranchii (Table 1). The t_{max} ranged between 1 y, for the transparent goby *Aphia minuta,* and 70 y, for the wreckfish *Polyprion americanus*. Mean t_{max} was lower for Actinopterygii (t_{max} ± SD = 10.14 ± 9.42 y) compared to Elasmobranchii (t_{max} ± SD = 14.05 ± 8.47 y). The frequency distribution of t_m was unimodal for both classes, with a peak at 2 y for Actinopterygii and a peak at 5 y for Elasmobranchii (Fig. 1).

The t_m exhibited a strong positive linear relation with t_{max} for both Actinopterygii and Elasmobranchii (Fig. 2). The slopes of the relations did not differ between Actinopterygii and Elasmobranchii (ANCOVA: F = 0.16, P = 0.69) but the intercepts did (ANCOVA: F = 72.45, P < 0.001). The empirical equations on the logarithmic values were (the non-transformed equations are also given for comparability purposes):

Actinopterygii $\log t_m = 0.58 \times \log t_{max} - 0.25$, $r^2 = 0.51$, $P < 0.001$, n = 215

$$(t_m = 0.11 \times t_{max} + 1.10)$$

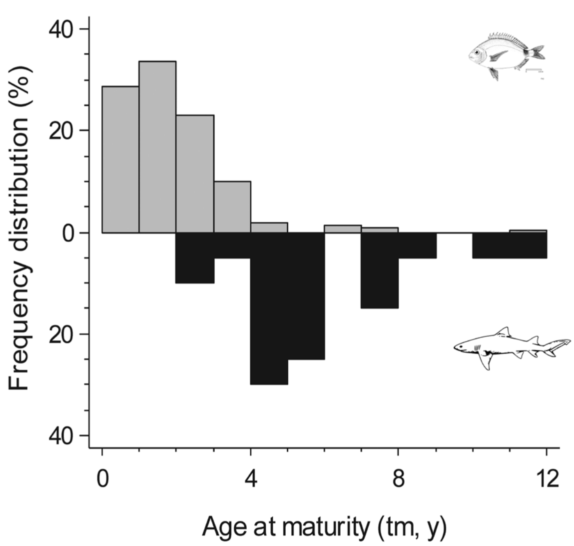

Fig. 1: Percentage frequency distribution of age at maturity (t_m, y) of Mediterranean marine stocks per class. Grey bars refer to Actinopterygii (n=215) and black bars to Elasmobranchii (n=20).

Table 1. Age (t_m) at maturity of Mediterranean marine fish stock and location of study. Habitat (D: demersal, P: pelagic, R: reef-associated, BEP: benthopelagic, BAD: bathydemersal, BAP: bathypelagic), Year: years of sampling, Sex (F: females, M: males, C: combined sexes), N: number of specimens examined; Lmax: maximum length (cm), t_m: age at maturity (y), t_{max}: maximum reported age (y), and the t_m/t_{max} ratio. Nomenclature based on FishBase. Italicized L_{max} and t_{max} values were taken from FishBase (Froese & Pauly, 2014).

No	CLASS/**Order**/Family	Species	Location	Habitat	Year	Sex	N	L_{max}	t_m	t_{max}	t_m/t_{max}	Reference
	ACTINOPTERYGII											
	Aulopiformes											
1	Chlorophthalmidae	*Chlorophthalmus agassizi*	Ionian Sea	BAD	2000	F	3342	19.2	3.0	8	**0.38**	D'Onghia *et al.* (2006)
2	Synodontidae	*Saurida undosquamis*	Levantine Sea	R	1999-2000	F	234	30.0	1.0	8	**0.13**	Ismen (2003a)
3		*Saurida undosquamis*	Levantine Sea	R	1999-2000	M	368	29.0	1.0	7	**0.14**	Ismen (2003a)
	Beloniformes											
4	Belonidae	*Belone belone*	Aegean Sea	P	1997	F	240	57.5	2.0	*8*	**0.25**	Uckun *et al.* (2004)
	Clupeiformes											
5	Clupeidae	*Sardina pilchardus*	Aegean Sea	P	1993-1996	C	1271	15.6	1.0	4	**0.25**	Akyol *et al.* (1996)
6		*Sardina pilchardus*		P		F		19.5	1.0	4	**0.25**	Mouhoub (1986)
7		*Sardina pilchardus*		P		M		17.5	1.0	4	**0.25**	Mouhoub (1986)
8		*Sardina pilchardus*	Aegean Sea	P	2000-2002	F	2849	17.3	1.0	4	**0.25**	Tsikliras & Koutrakis (2013)
9		*Sardina pilchardus*	Aegean Sea	P	2000-2002	M	1993	16.2	0.9	4	**0.22**	Tsikliras & Koutrakis (2013)
10		*Sardinella aurita*	Aegean Sea	P	2000-2002	F	500	24.8	1.0	5	**0.21**	Tsikliras & Antonopoulou (2006)
11		*Sardinella aurita*	Aegean Sea	P	2000-2002	M	500	24.3	1.3	5	**0.27**	Tsikliras & Antonopoulou (2006)
12		*Sardinella aurita*		P	1995-1996	F	5467	25.5	1.5	5	**0.30**	Bouaziz *et al.* (2001)
13	Dussumieriidae	*Etrumeus sadina*	Alexandria coast	P	2008	F	656	25.0	2.0	*3*	**0.67**	Osman *et al.* (2011)
14		*Etrumeus sadina*	Alexandria coast	P	2008	M		25.0	2.0	*3*	**0.67**	Osman *et al.* (2011)
15	Engraulidae	*Engraulis encrasicolus*	Bay of Cadiz	P	1989	F	737	18.0	1.0	4	**0.25**	Millán (1999)
16		*Engraulis encrasicolus*	Bay of Cadiz	P	1990	F	1326	18.0	1.0	4	**0.25**	Millán (1999)
17		*Engraulis encrasicolus*	Bay of Cadiz	P	1991	F	469	18.0	1.0	4	**0.25**	Millán (1999)
18		*Engraulis encrasicolus*	Bay of Cadiz	P	1992	F	505	18.0	1.0	4	**0.25**	Millán (1999)
19		*Engraulis encrasicolus*	Bay of Cadiz	P	1989	M	751	18.0	1.0	4	**0.25**	Millán (1999)
20		*Engraulis encrasicolus*	Bay of Cadiz	P	1990	M	1181	18.0	1.0	4	**0.25**	Millán (1999)
21		*Engraulis encrasicolus*	Bay of Cadiz	P	1991	M	564	18.0	1.0	4	**0.25**	Millán (1999)
22		*Engraulis encrasicolus*	Bay of Cadiz	P	1992	M	612	18.0	1.0	4	**0.25**	Millán (1999)
23		*Engraulis encrasicolus*		P		C		*19.0*	2.0	4	**0.50**	Bouaziz & Bennoui (2004)
	Gadiformes											
24	Gadidae	*Micromesistius poutassou*	Adriatic Sea	BAP		C		32.0	1.0	8	**0.13**	Froglia & Gramitto (1981)
25		*Trisopterus capelanus*	Aegean Sea	BEP	1986-1988	F	1502	25.0	1.2	5	**0.24**	Politou & Papaconstantinou (1991)
26		*Trisopterus capelanus*	Aegean Sea	BEP	1986-1988	M	1011	22.3	1.3	6	**0.22**	Politou & Papaconstantinou (1991)
27		*Trisopterus capelanus*	Adriatic Sea	BEP		C	887	25.0	1.0	5	**0.20**	Froglia (1981)
28	Merluccidae	*Merluccius merluccius*	Mediterranean coast	D	1995-1998	C	423	66.0	4.1	9	**0.46**	Zoubi (2001)

(continued)

Table 1. *(continued)*

No	CLASS/**Order**/Family	Species	Location	Habitat	Year	Sex	N	L_{max}	t_m	t_{max}	t_m/t_{max}	Reference
29		*Merluccius merluccius*	Algerian coast	D		F	73	65.5	2.9	9	**0.32**	Bouaziz *et al.* (2001)
30		*Merluccius merluccius*	-	D	1991-1993	F	955	68.0	2.7	9	**0.30**	Garcia-Rodriguez & Esteban (1995)
31		*Merluccius merluccius*	-	D	1991-1993	M	502	52.5	2.2	7	**0.31**	Garcia-Rodriguez & Esteban (1995)
32		*Merluccius merluccius*	Gulf of Lions	D	1989-1991	F	308	50.0	3.5	8	**0.44**	Recasens *et al.* (1998)
33		*Merluccius merluccius*	Gulf of Lions	D	1989-1991	M	619	42.0	3.0	8	**0.38**	Recasens *et al.* (1998)
34		*Merluccius merluccius*	Libyan coast	D	1972	F	81	44.0	4.0	9	**0.44**	Mugahid & Hashem (1982)
35		*Merluccius merluccius*	Libyan coast	D	1972	M	198	41.0	4.0	9	**0.44**	Mugahid & Hashem (1982)
36		*Merluccius merluccius*	Balearic Sea	D	1991-1993	F	955	68.0	2.0	7	**0.29**	Garcia-Rodriguez & Esteban (1995)
37		*Merluccius merluccius*	Balearic Sea	D	1991-1993	M	502	52.5	2.0	7	**0.29**	Garcia-Rodriguez & Esteban (1995)
38		*Merluccius merluccius*	Algerian coast	D		F		60.0	3.0	8	**0.38**	Bouaziz *et al.* (1998)
39		*Merluccius merluccius*	Algerian coast	D		M		60.0	2.0	8	**0.25**	Bouaziz *et al.* (1998)
	Mugiliformes											
40	Mugilidae	*Liza aurata*	Ionian Sea	P	1992-1994	F	393	50.0	1.8	3	**0.61**	Hotos (1999)
41		*Liza aurata*	Ionian Sea	P	1992-1994	M	312	50.0	2.1	3	**0.70**	Hotos (1999)
42		*Liza haematocheila*	Aegean Sea	P	2003-2009	C	32	74.4	5.0	15	**0.33**	Minos *et al.* (2010)
43		*Liza haematocheila*	Black Sea	D	1995	F	87	66.7	3.0	15	**0.20**	Okumuş & Başçinar (1997)
44		*Liza haematocheila*	Black Sea	D	1995	M	79	66.7	2.0	15	**0.13**	Okumuş & Başçinar (1997)
45		*Liza ramada*	Aegean Sea	P	1989-1990	F	39	38.6	3.0	10	**0.30**	Koutrakis (1994)
46		*Liza ramada*	Ionian Sea	P	1990-1995	F	80	54.8	3.0	10	**0.30**	Minos (1996)
47		*Liza ramada*	Ionian Sea	P	1990-1995	M	64	42.0	3.0	10	**0.30**	Minos (1996)
48		*Liza ramada*	Levantine Sea	P	1992-1994	F	114	36.9	3.0	10	**0.30**	Ergene (2000)
49		*Liza ramada*	Levantine Sea	P	1992-1994	M	87	36.9	3.0	10	**0.30**	Ergene (2000)
50		*Liza saliens*	Aegean Sea	D	1989-1990	F	123	30.5	3.0	4	**0.75**	Koutrakis (1994)
51		*Liza saliens*	Aegean Sea	D	1989-1990	M	55	30.5	3.0	4	**0.75**	Koutrakis (1994)
52		*Liza saliens*	Ionian Sea	D	1991-1995	F	217	30.0	2.9	4	**0.73**	Katselis (1996)
53		*Liza saliens*	Ionian Sea	D	1991-1995	M	272	24.0	2.1	4	**0.52**	Katselis (1996)
	Perciformes											
54	Apogonidae	*Apogon imberbis*	NW Mediterranean	R	1998-1999	F	122	12.1	1.0	5	**0.20**	Klein & Raventos (2007)
55		*Apogon imberbis*	NW Mediterranean	R	1998-1999	M	127	12.1	1.0	5	**0.20**	Klein & Raventos (2007)
56	Blennidae	*Parablennius ruber*		D				*14.1*	1.0	*3*	**0.40**	Azevedo & Homem (2002)
57	Carangidae	*Caranx crysos*	Gulf of Gabes	R	2004-2006	F	777	41.4	2.8	11	**0.25**	Sley *et al.* (2012)
58		*Caranx crysos*	Gulf of Gabes	R	2004-2006	M	891	41.6	2.4	11	**0.22**	Sley *et al.* (2012)
59		*Seriola dumerili*	S Mediterranean	R	1990-1992	F	211	150.0	4.0	15	**0.27**	Marino *et al.* (1995)
60		*Seriola dumerili*	S Mediterranean	R	1990-1992	M	205	150.0	3.5	15	**0.23**	Marino *et al.* (1995)
61		*Trachurus mediterraneus*	Aegean Sea	P	1989-1991	F	369	39.3	1.4	10	**0.14**	Karlou-Riga (1995)

(continued)

Table 1. *(continued)*

No	CLASS/**Order**/Family	Species	Location	Habitat	Year	Sex	N	L_{max}	t_m	t_{max}	t_m/t_{max}	Reference
62		*Trachurus trachurus*	Aegean Sea	P	1989-1991	F	595	33.9	2.6	10	**0.26**	Karlou-Riga (1995)
63		*Trachurus trachurus*	Adriatic Sea	P	1986	F	154	*32.0*	2.1	10	**0.21**	Alegria (1990)
64		*Trachurus trachurus*	Adriatic Sea	P	1986	M	150	*32.0*	2.6	10	**0.26**	Alegria (1990)
65		*Trachurus trachurus*	Adriatic Sea	P	1987	F	134	*32.0*	2.7	10	**0.27**	Alegria (1990)
66		*Trachurus trachurus*	Adriatic Sea	P	1987	M	155	*32.0*	2.8	10	**0.28**	Alegria (1990)
67		*Trachurus trachurus*	Adriatic Sea	P	1988	F	201	*32.0*	2.5	10	**0.25**	Alegria (1990)
68		*Trachurus trachurus*	Adriatic Sea	P	1988	M	180	*32.0*	2.7	10	**0.27**	Alegria (1990)
69		*Trachurus trachurus*		P		F		27.5	1.0	10	**0.10**	Korichi (1988)
70		*Trachurus trachurus*		P		M		27.5	1.0	10	**0.10**	Korichi (1988)
71		*Trachurus trachurus*	Balearic Sea	P	2001	F	33	22.0	2.0	10	**0.20**	Abaunza *et al.* (2003)
72		*Trachurus trachurus*	Balearic Sea	P	2001	M	67	22.0	2.0	10	**0.20**	Abaunza *et al.* (2003)
73		*Trachurus trachurus*	Ionian Sea	P	2001	F	43	37.0	1.9	10	**0.19**	Abaunza *et al.* (2003)
74		*Trachurus trachurus*	Ionian Sea	P	2001	M	41	43.0	2.7	10	**0.27**	Abaunza *et al.* (2003)
75		*Trachurus trachurus*	Aegean Sea	P	2001	F	85	34.0	2.6	10	**0.26**	Abaunza *et al.* (2003)
76		*Trachurus trachurus*	Aegean Sea	P	2001	M	67	37.0	0.9	10	**0.09**	Abaunza *et al.* (2003)
77		*Trachurus trachurus*	Alboran Sea	P	2001	F	29	39.0	1.8	10	**0.18**	Abaunza *et al.* (2003)
78		*Trachurus trachurus*	Alboran Sea	P	2001	M	60	37.0	1.8	10	**0.18**	Abaunza *et al.* (2003)
79	Centracanthidae	*Spicara flexuosa*	Ionian Sea	P	1984-1985	F	1870	14.7	1.0	5	**0.20**	Mytilineou (1988)
80		*Spicara flexuosa*	Ionian Sea	P	1984-1985	M	885	16.8	1.0	5	**0.20**	Mytilineou (1988)
81		*Spicara maena*	Aegean Sea	P	2004-2007	F	1766	20.0	2.0	5	**0.40**	Soykan *et al.* (2010)
82		*Spicara maena*	Aegean Sea	P	2004-2007	M	398	20.0	2.0	5	**0.40**	Soykan *et al.* (2010)
83	Cepolidae	*Cepola macrophthalma*	Aegean Sea	D	1986-1988	F	1763	40.0	1.9	5	**0.38**	Stergiou *et al.* (1996)
84		*Cepola macrophthalma*	Aegean Sea	D	1986-1988	M	1588	60.0	2.6	6	**0.43**	Stergiou *et al.* (1996)
85	Gobiidae	*Aphia minuta*	Balearic Sea	P	1985-1993	F	168	4.4	0.7	1	**0.70**	Iglesias & Morales-Nin (2001)
86		*Aphia minuta*	Balearic Sea	P	1985-1993	M	182	4.0	0.6	1	**0.60**	Iglesias & Morales-Nin (2001)
87		*Crystallogobius linearis*	Adriatic Sea	D	1996	F	114	3.3	0.4	1	**0.42**	La Mesa (2001)
88		*Crystallogobius linearis*	Adriatic Sea	D	1996	M	100	4.1	0.4	1	**0.42**	La Mesa (2001)
89		*Deltentosteus quadrimaculatus*	Aegean Sea	D	2004-2007	F	527	9.2	2.0	5	**0.40**	Metin *et al.* (2011b)
90		*Deltentosteus quadrimaculatus*	Aegean Sea	D	2004-2007	M	470	9.2	2.0	5	**0.40**	Metin *et al.* (2011b)
91		*Gobius vittatus*	Adriatic Sea	D	2001-2002	F	402	5.4	*0.8*	*2*	**0.35**	Kovacic (2007)
92		*Gobius vittatus*	Adriatic Sea	D	2001-2002	M	302	5.3	*0.8*	*2*	**0.35**	Kovacic (2007)
93		*Pomatoschistus marmoratus*	Suez Canal	D	1986-1987	F	311	5.6	1.0	2	**0.50**	Fouda *et al.* (1993)
94		*Pomatoschistus marmoratus*	Suez Canal	D	1986-1987	M	115	5.6	1.0	2	**0.50**	Fouda *et al.* (1993)
95		*Pomatoschistus microps*	Mauguio Lagoon	D	1985-1989	C	7363	4.7	0.3	2	**0.15**	Bouchereau *et al.* (1993)
96		*Silhouettea aegyptia*	Suez Canal	D	1986-1987	F	300	5.2	1.0	2	**0.50**	Fouda *et al.* (1993)
97		*Silhouettea aegyptia*	Suez Canal	D	1986-1987	M	178	5.2	1.0	2	**0.50**	Fouda *et al.* (1993)

(continued)

Table 1. *(continued)*

No	CLASS/**Order**/Family	Species	Location	Habitat	Year	Sex	N	L_{max}	t_m	t_{max}	t_m/t_{max}	Reference
98		*Zosterisessor ophiocephalus*	Venice Lagoon	D	2001	F	171	20.0	0.9	5	**0.18**	Franco *et al.* (2012)
99	Moronidae	*Dicentrarchus labrax*	Gulf of Annaba	D	1990-1991	F	300	60.0	3.0	15	**0.20**	Kara (1997)
100		*Dicentrarchus labrax*	Gulf of Annaba	D	1990-1991	M	227	60.0	2.0	15	**0.13**	Kara (1997)
101		*Dicentrarchus labrax*	Tunisian coast	D	1973-1975	F		56.0	4.5	15	**0.30**	Quignard *et al.* (1978)
102		*Dicentrarchus labrax*	Tunisian coast	D	1973-1975	M		56.0	2.5	15	**0.17**	Quignard *et al.* (1978)
103		*Dicentrarchus labrax*	Alexandria coast	D	1981-1982	F	467	67.0	4.0	15	**0.27**	Wassef & El Emary (1989)
104		*Dicentrarchus labrax*	Alexandria coast	D	1981-1982	M	232	44.4	2.0	15	**0.13**	Wassef & El Emary (1989)
105	Mullidae	*Mullus barbatus barbatus*	Mediterranean coast	D	1995-1998	C	104	24.9	1.9	7	**0.29**	Zoubi (2001)
106		*Mullus barbatus barbatus*	Adriatic Sea	D	1972-1975	M		15.4	1.0	6	**0.18**	Jukic & Piccinetti (1981)
107		*Mullus barbatus barbatus*	Adriatic Sea	D	1972-1975	F		18.0	1.0	8	**0.13**	Jukic & Piccinetti (1981)
108		*Mullus surmuletus*	Mediterranean coast	D	2009	F	179	30.0	2.0	6	**0.33**	Lamrini (2010)
109		*Mullus surmuletus*	Mediterranean coast	D	2009	M	113	29.0	2.0	5	**0.40**	Lamrini (2010)
110		*Mullus surmuletus*	Mediterranean coast	D	2007-2008	C	1385	28.0	1.4	6	**0.25**	Mehanna (2009)
111		*Mullus surmuletus*	Aegean Sea	D	1991-1992	F	157	29.9	2.0	6	**0.33**	Vassilopoulou & Papaconstantinou (1995)
112		*Mullus surmuletus*	Aegean Sea	D	1991-1992	M	245	26.4	1.0	5	**0.20**	Vassilopoulou & Papaconstantinou (1995)
113		*Mullus surmuletus*	Balearic Sea	D	1990-1992	F		32.0	1.0	6	**0.17**	Renones *et al.* (1995)
114		*Mullus surmuletus*	Balearic Sea	D	1990-1992	M		32.0	1.0	5	**0.20**	Renones *et al.* (1995)
115		*Upeneus moluccensis*	Levantine Sea	R	2002-2003	F	343	21.1	1.0	5	**0.20**	Ozvarol *et al.* (2010)
116		*Upeneus moluccensis*	Levantine Sea	R	2002-2003	M	121	16.4	1.0	5	**0.20**	Ozvarol *et al.* (2010)
117		*Upeneus pori*	Levantine Sea	D	1999-2000	F	324	17.0	1.0	5	**0.20**	Ismen (2006)
118		*Upeneus pori*	Levantine Sea	D	1999-2000	M	292	15.1	1.0	5	**0.20**	Ismen (2006)
119	Polyprionidae	*Polyprion americanus*	Ionian Sea	D		C	34	131.0	7.5	70	**0.11**	Carbonara *et al.* (2003)
120	Pomatomidae	*Pomatomus saltatrix*	Gulf of Gabès	P	1998-2000	F	288	34.5	1.9	9	**0.21**	Dhieb *et al.* (2006)
121		*Pomatomus saltatrix*	Gulf of Gabès	P	1998-2000	M		34.5	2.4	9	**0.27**	Dhieb *et al.* (2006)
122	Scaridae	*Sparisoma cretense*	Aegean Sea	R	1985-1986	F	157	32.5	1.0	8	**0.13**	Papaconstantinou *et al.* (1988)
123		*Sparisoma cretense*	Aegean Sea	R	1985-1986	M	163	32.5	2.0	8	**0.25**	Papaconstantinou *et al.* (1988)
124	Sciaenidae	*Argyrosomus regius*	Balearic Islands	BEP	2007-2011	F	116		3.5	*42*	**0.08**	Gil *et al.* (2013)
125		*Argyrosomus regius*	Balearic Islands	BEP	2007-2011	M	115		2.7	*42*	**0.06**	Gil *et al.* (2013)
126		*Sciaena umbra*	Gulf of Tunis	D	1995-1996	F	127	59.2	2.6	21	**0.12**	Chakroun-Marzouk & Ktari (2003)
127		*Sciaena umbra*	Gulf of Tunis	D	1995-1996	M	110	53.0	2.6	21	**0.13**	Chakroun-Marzouk & Ktari (2003)
128	Scombridae	*Sarda sarda*	Sea of Marmara	P	2003-2005	C	694	71.0	1.0	4	**0.25**	Ates *et al.* (2008)
129		*Thunnus thynnus*	entire	P	1998-2004		501	290.3	3.0	15	**0.20**	Corriero et al (2005)
130	Serranidae	*Epinephelus marginatus*	Algerian coast	R	1993-1994	F	44	72.0	7.0	50	**0.14**	Kara & Derbal (1999)
131		*Epinephelus marginatus*	Balearic Sea	R	1998-2004	F	196	100.3	6.3	50	**0.13**	Renones *et al.* (2010)
132		*Epinephelus marginatus*	S Mediterranean	R	1994-1996	F	219	119.0	5.0	50	**0.10**	Marino *et al.* (2001)
133		*Epinephelus marginatus*	S Mediterranean	R	1994-1996	M	59	129.0	12.0	50	**0.24**	Marino *et al.* (2001)

(continued)

Table 1. *(continued)*

No	CLASS/**Order**/Family	Species	Location	Habitat	Year	Sex	N	L_{max}	t_m	t_{max}	t_m/t_{max}	Reference
134		*Serranus hepatus*	Adriatic Sea	D	2002-2003	C	1218	9.0	2.0	7	**0.29**	Dulcic *et al.* (2007)
135	Sparidae	*Boops boops*	Mediterranean coast	D	1995-1998	C	110	25.6	1.4	5	**0.29**	Zoubi (2001)
136		*Boops boops*	Adriatic Sea	D	1957-1958	F	335	23.0	2.0	5	**0.40**	Alegria-Hernández (1990)
137		*Boops boops*	Adriatic Sea	D	1957-1958	M	440	20.0	1.5	5	**0.30**	Alegria-Hernández (1990)
138		*Boops boops*	Algerian coast	D		F		23.5	2.0	5	**0.40**	Chali-Chabane (1988)
139		*Boops boops*	Cretan Sea	D	1988-1990	F	778	18.0	1.0	5	**0.20**	Kallianiotis (1992)
140		*Boops boops*	Cretan Sea	D	1988-1990	M	597	18.0	1.0	5	**0.20**	Kallianiotis (1992)
141		*Boops boops*	Cretan Sea	D	1988-1990	F	695	18.0	1.0	5	**0.20**	Kallianiotis (1992)
142		*Boops boops*	Cretan Sea	D	1988-1990	M	456	18.0	1.0	5	**0.20**	Kallianiotis (1992)
143		*Dentex dentex*	Balearic Sea	BEP	1993-1995	F	210	80.0	2.2	*28*	**0.08**	Morales-Nin & Moranta (1997)
144		*Dentex dentex*	Balearic Sea	BEP	1993-1995	M		75.0	6.7	*28*	**0.24**	Morales-Nin & Moranta (1997)
145		*Diplodus annularis*	Adriatic Sea	BEP	2000-2002	F	745	23.0	2.6	13	**0.20**	Matić-Skoko *et al.* (2007)
146		*Diplodus annularis*	Adriatic Sea	BEP	2000-2002	M	780	20.0	2.1	13	**0.16**	Matić-Skoko *et al.* (2007)
147		*Diplodus sargus sargus*	Gulf of Tunis	D	2002-2004	F	108	37.2	4.0	10	**0.40**	Mouine *et al.* (2007)
148		*Diplodus sargus sargus*	Gulf of Tunis	D	2002-2004	M	37	30.0	4.0	10	**0.40**	Mouine *et al.* (2007)
149		*Diplodus sargus sargus*	Algerian coast	D		F	98	34.6	4.0	10	**0.40**	Benchalel & Kara (2010)
150		*Diplodus sargus sargus*	Algerian coast	D		M	143	34.6	4.0	10	**0.40**	Benchalel & Kara (2010)
151		*Diplodus sargus sargus*	Algerian coast	D	2005-2006	F	98	34.6	4.0	10	**0.40**	Benchalel & Kara (2013)
152		*Diplodus sargus sargus*	Algerian coast	D	2005-2006	M	143	24.0	4.0	10	**0.40**	Benchalel & Kara (2013)
153		*Diplodus vulgaris*	Sicilian Channel	BEP	1997-1999	F	235	30.0	1.5	7	**0.21**	Beltrano *et al.* (2003)
154		*Diplodus vulgaris*	Sicilian Channel	BEP	1997-1999	M	209	30.0	2.0	7	**0.29**	Beltrano *et al.* (2003)
155		*Diplodus vulgaris*	Syrian coast	BEP	1999-2001	F		*30.0*	2.0	7	**0.29**	Hammoud & Saad (2007)
156		*Diplodus vulgaris*	Syrian coast	BEP	1999-2001	M		*30.0*	2.0	7	**0.29**	Hammoud & Saad (2007)
157		*Lithognathus mormyrus*	Levantine Sea	D	1998-1999	F	1612	27.7	2.0	12	**0.16**	Türkmen & Akyurt (2003)
158		*Lithognathus mormyrus*	Levantine Sea	D	1998-1999	M	1626	22.8	1.7	12	**0.14**	Türkmen & Akyurt (2003)
159		*Lithognathus mormyrus*	Sicilian Channel	D	1997-1998	F	221	34.0	1.7	12	**0.14**	Vitale *et al.* (2003, 2011)
160		*Lithognathus mormyrus*	Sicilian Channel	D	1997-1998	M	230	34.0	1.7	12	**0.14**	Vitale *et al.* (2003, 2011)
161		*Lithognathus mormyrus*	Sicilian Channel	D	1997-1998	F	142	35.0	1.6	12	**0.13**	Vitale *et al.* (2003, 2011)
162		*Lithognathus mormyrus*	Sicilian Channel	D	1997-1998	M	188	35.0	1.6	12	**0.13**	Vitale *et al.* (2003, 2011)
163		*Lithognathus mormyrus*	Aegean Sea	D	1997-1999	F	821	34.1	3.6	12	**0.30**	Kallianiotis *et al.* (2005)
164		*Lithognathus mormyrus*	Aegean Sea	D	1997-1999	M	477	28.8	2.5	12	**0.21**	Kallianiotis *et al.* (2005)
165		*Pagellus acarne*	Mediterranean coast	BEP	1995-1998	C	101	25.5	1.9	8	**0.23**	Zoubi (2001)
166		*Pagellus erythrinus*	Cretan Sea	BEP	1988-1991	F	1190	27.1	1.8	6	**0.30**	Somarakis & Machias (2002)
167		*Pagellus erythrinus*	Cretan Sea	BEP	1988-1991	M		27.1	2.0	7	**0.29**	Somarakis & Machias (2002)
168		*Pagellus erythrinus*	Gulf of Alger	BEP		F		36.5	1.0	6	**0.17**	Cherabi (1987)
169		*Pagellus erythrinus*	Aegean Sea	BEP	2002-2007	F	1717	24.9	2.0	7	**0.29**	Metin *et al.* (2011a)

(continued)

Table 1. *(continued)*

No	CLASS/**Order**/Family	Species	Location	Habitat	Year	Sex	N	L_{max}	t_m	t_{max}	t_m/t_{max}	Reference
170		*Pagellus erythrinus*	Aegean Sea	BEP	2002-2007	M	136	27.8	3.0	7	**0.43**	Metin *et al.* (2011a)
171		*Sarpa salpa*	Adriatic Sea	BEP	2004	M	601	36.8	2.0	15	**0.13**	Pallaoro *et al.* (2008)
172		*Spondyliosoma cantharus*	Gulf of Tunis	BEP	2005-2006	F	330	31.6	4.0	*13*	**0.31**	Mouine *et al.* (2011)
173	Sphyraenidae	*Sphyraena chrysotaenia*	Mediterranean coast	P		F		27.0	1.0	8	**0.13**	Wadie *et al.* (1988)
174		*Sphyraena chrysotaenia*	Mediterranean coast	P		M		27.0	1.0	8	**0.13**	Wadie *et al.* (1988)
175		*Sphyraena chrysotaenia*	Gulf of Gabès	P	2003-2005	F	432	28.3	2.0	8	**0.25**	Zouari-Ktari *et al.* (2009)
176		*Sphyraena chrysotaenia*	Gulf of Gabès	P	2003-2005	M	516	24.9	2.0	8	**0.25**	Zouari-Ktari *et al.* (2009)
177		*Sphyraena sphyraena*	Mediterranean coast	P		F		42.0	1.0	8	**0.13**	Wadie *et al.* (1988)
178		*Sphyraena sphyraena*	Mediterranean coast	P		M		42.0	1.0	8	**0.13**	Wadie *et al.* (1988)
179		*Uranoscopus scaber*	Tunisian coast	D		F	537	33.0	2.0	*5*	**0.40**	Kartas & Bondka (1986)
180		*Uranoscopus scaber*	Tunisian coast	D		M	347	26.0	1.0	*5*	**0.20**	Kartas & Bondka (1986)
181	Xiphiidae	*Xiphias gladius*	Ligurian Sea	P	1990-2001	F	1847	334.5	4.0	10	**0.40**	Orsi Relini *et al.* (2003)
	Pleuronectiformes											
182	Scophthalmidae	*Lepidorhombus boscii*	Aegean Sea	D	1990-1992	F	1422	29.5	2.0	13	**0.15**	Vassilopoulou *et al.* (1997)
183		*Lepidorhombus boscii*	Aegean Sea	D	1990-1992	M	1009	23.5	1.0	11	**0.09**	Vassilopoulou *et al.* (1997)
184	Soleidae	*Bathysolea profundicola*	Sardinia	BAP		F		16.5	2.9	*12*	**0.24**	Cau & Deiana (1983)
185		*Bathysolea profundicola*	Sardinia	BAP		M		14.7	2.0	*10*	**0.20**	Cau & Deiana (1983)
186		*Buglossidium luteum*	Aegean Sea	D	2004-2007	F	563	11.6	2.0	13	**0.15**	Ilkyaz *et al.* (2010)
187		*Buglossidium luteum*	Aegean Sea	D	2004-2007	M	395	10.1	2.0	13	**0.15**	Ilkyaz *et al.* (2010)
188		*Buglossidium luteum*	Adriatic Sea	D		C	3400	14.5	1.0	13	**0.08**	Giovanardi & Piccinetti (1981)
189		*Microchirus azevia*	Algarve Coast	D	1998-1999	F	623	37.6	2.9	*8*	**0.36**	Afonso-Dias *et al.* (2005)
190		*Monochirus hispidus*	Sardinia	D		F		*14.1*	2.2	13	**0.17**	Cau & Deiana (1983)
191		*Monochirus hispidus*	Sardinia	D		M		*10.7*	0.8	13	**0.06**	Cau & Deiana (1983)
192		*Synapturichthys kleinii*	Sardinia	D		F		*39.5*	3.6	*9*	**0.40**	Cau & Deiana (1983)
193		*Synapturichthys kleinii*	Sardinia	D		M		*38.9*	1.9	*8*	**0.24**	Cau & Deiana (1983)
	Scorpaeniformes											
194	Sebastidae	*Helicolenus dactylopterus*	Algerian coast	BAD		F		32.0	4.0	40	**0.10**	Nouar (2003)
195		*Helicolenus dactylopterus*	Algerian coast	BAD		M		28.0	4.0	40	**0.10**	Nouar (2003)
196	Scorpaenidae	*Scorpaena elongata*	Sicilian channel	D	1985-1998	F	664	57.0	8.0	*30*	**0.27**	Ragonese *et al.* (2003)
197		*Scorpaena porcus*	Gulf of Gabès	D		F	540	22.9	3.0	10	**0.30**	Bradai & Bouain (1991)
198		*Scorpaena porcus*	Gulf of Gabes	D		M	684	20.8	3.0	10	**0.30**	Bradai & Bouain (1991)
199		*Scorpaena loppei*	Balearic Islands	D	2005-2010	F	85	12.8	1.0	5	**0.20**	Ordines *et al.* (2012)
200		*Scorpaena loppei*	Balearic Islands	D	2005-2010	M	90	12.8	1.0	5	**0.20**	Ordines *et al.* (2012)
201	Triglidae	*Chelidonichthys cuculus*	Tyrrhenian Sea	D	1994-1997	F		27.0	2.0	21	**0.10**	Colloca *et al.* (2003)
202		*Chelidonichthys cuculus*	Tyrrhenian Sea	D	1994-1997	M		27.0	2.0	13	**0.15**	Colloca *et al.* (2003)
203		*Chelidonichthys lucerna*	Gulf of Gabes	D	2003-2004	F	195	36.0	3.0	15	**0.20**	Boudaya *et al.* (2008)

(continued)

Table 1. *(continued)*

No	CLASS/**Order**/Family	Species	Location	Habitat	Year	Sex	N	L_{max}	t_m	t_{max}	t_m/t_{max}	Reference
204		*Chelidonichthys lucerna*	Gulf of Gabes	D	2003-2004	M	91	26.0	1.5	14	**0.11**	Boudaya *et al.* (2008)
205		*Chelidonichthys lucerna*	Iskenderun Bay	D	1999-2000	F	199	30.3	2.0	15	**0.13**	Ismen *et al.* (2004)
206		*Chelidonichthys lucerna*	Iskenderun Bay	D	1999-2000	M	143	21.2	2.0	14	**0.14**	Ismen *et al.* (2004)
207		*Chelidonichthys lucerna*	Marmara Sea	D	1996-1997	F	98	41.5	3.0	15	**0.20**	Eryilmaz & Meric (2005)
208		*Chelidonichthys lucerna*	Marmara Sea	D	1996-1997	M	45	37.0	3.0	14	**0.21**	Eryilmaz & Meric (2005)
209		*Lepidotrigla cavillone*	Aegean Sea	D	1976-1978	F	1429	16.0	1.5	5	**0.30**	Papaconstantinou (1982)
210		*Lepidotrigla cavillone*	Tyrrhenian Sea	D	1985-1995	F	308	14.0	2.0	5	**0.40**	Colloca *et al.* (1997)
211		*Lepidotrigla cavillone*	Tyrrhenian Sea	D	1985-1995	M	2196	14.0	2.0	5	**0.40**	Colloca *et al.* (1997)
212		*Lepidotrigla cavillone*	Aegean Sea	D	2004-2007	F	824	14.0	2.0	5	**0.40**	Ilkyaz *et al.* (2010)
213		*Lepidotrigla cavillone*	Aegean Sea	D	2004-2007	M	603	15.0	2.0	5	**0.40**	Ilkyaz *et al.* (2010)
	Zeiformes											
214	Zeidae	*Zeus faber*	Aegean Sea	BEP	2006-2008	F	97	52.8	4.0	17	**0.24**	Ismen *et al.* (2013)
215		*Zeus faber*	Aegean Sea	BEP	2006-2008	M	60	42.9	4.0	18	**0.22**	Ismen *et al.* (2013)
	ELASMOBRANCHII											
	Rajiformes											
216	Dasyatidae	*Dasyatis pastinaca*	Levantine Sea	D	1999-2000	F	110	88.0	4.5	*10*	**0.45**	Ismen (2003b)
217		*Dasyatis pastinaca*	Levantine Sea	D	1999-2000	M	146	73.0	4.5	*10*	**0.45**	Ismen (2003b)
218	Rajidae	*Dipturus oxyrinchus*	Aegean Sea	BAD	2005-2007	F	89	100.0	8.0	9	**0.89**	Yigin & Ismen (2010)
219		*Dipturus oxyrinchus*	Aegean Sea	BAD	2005-2007	M	90	86.5	6.0	9	**0.67**	Yigin & Ismen (2010)
220		*Raja radula*	Gulf of Gabes	D	2007	F	550	80.0	5.9	*12*	**0.49**	Kadri *et al.* (2013)
221		*Raja radula*	Gulf of Gabes	D	2007	M	400	65.0	4.5	*9*	**0.50**	Kadri *et al.* (2013)
222		*Raja miraletus*	Gulf of Gabes	D	2007	F	95	56.0	4.4	*9*	**0.49**	Kadri *et al.* (2012)
223		*Raja miraletus*	Gulf of Gabes	D	2007	M	85	58.0	2.7	*7*	**0.39**	Kadri *et al.* (2012)
224		*Raja undulata*	Algarve Coast	D	1999-2000	F	93	88.2	9.0	*14*	**0.64**	Coehlo & Erzini (2006)
225		*Raja undulata*	Algarve Coast	D	1999-2000	M	94	83.2	8.0	*14*	**0.57**	Coehlo & Erzini (2006)
226	Rhinobatidae	*Rhinobatos cemiculus*	Gulf of Gabes	D		F		198.0	5.1	14	**0.36**	Enajjar *et al.* (2012)
227		*Rhinobatos cemiculus*	Gulf of Gabes	D		M		198.0	2.9	10	**0.29**	Enajjar *et al.* (2012)
	Squaliformes											
228	Squalidae	*Squalus acanthias*	Black Sea	BEP		F		150.0	12.0	38	**0.32**	Demirhan & Seyhan (2007)
229		*Squalus acanthias*	Black Sea	BEP		M		150.0	10.5	38	**0.28**	Demirhan & Seyhan (2007)
230		*Squalus blainville*	Sicilian Channel	D	1985-1991	F	812	92.0	5.1	*14*	**0.36**	Cannizzaro *et al.* (1995)
231		*Squalus blainville*	Sicilian Channel	D	1985-1991	M	1038	73.5	3.3	*13*	**0.25**	Cannizzaro *et al.* (1995)
232		*Squalus blainville*	Gulf of Gabès	D	2004-2005	F	81	100.0	7.4	*14*	**0.53**	Marouani *et al.* (2007, 2010)
233		*Squalus blainville*	Gulf of Gabès	D	2004-2005	M	71	100.0	4.8	*13*	**0.37**	Marouani *et al.* (2007, 2010)
	Carcharhiniformes											
234	Carcharhinidae	*Prionace glauca*	E Mediterranean	P	1998-2003	F	178	349	5.5	12	**0.46**	Megalofonou *et al.* (2009)
235		*Prionace glauca*	E Mediterranean	P	1998-2003	M	323	330	4.9	12	**0.41**	Megalofonou *et al.* (2009)

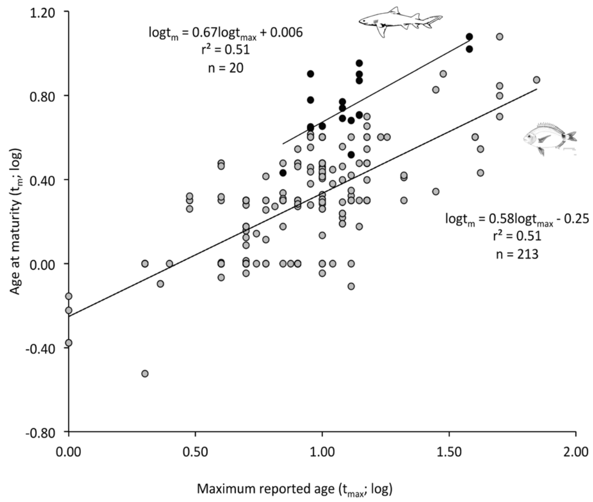

Fig. 2: The relationship of age at maturity (t_m, y) with maximum reported age (t_{max}, y) of Mediterranean marine fish stocks per class. Grey dots and dashed trend line refer to Actinopterygii (n=215) and black dots and continuous trend line to Elasmobranchii (n=20). All values have been logarithmically transformed.

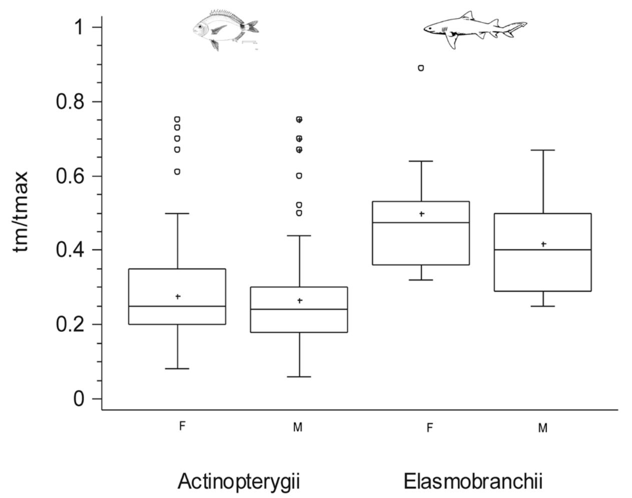

Fig. 3: Variability of age at maturity (t_m, y) to maximum age (t_{max}, y) ratio per sex (F: females, M: males) within each class (Actinopterygii and Elasmobranchii). The rectangular part of the plot extends from the lower quartile to the upper quartile. The horizontal line within each box shows the location of the median and the cross the location of the mean. The whiskers extend from the box to the minimum and maximum values and circles indicate outliers.

Elasmobranchii $logt_m = 0.67 \times logt_{max} + 0.006$, $r^2 = 0.51$, P = 0.007, n = 20

$$(t_m = 0.23x\ t_{max} + 2.72)$$

Mean t_m/t_{max} was not significantly different (ANOVA: F = 0.27, P = 0.60) between female (mean ± SD = 0.276 ± 0.143, n = 90) and male (mean ± SD = 0.265 ± 0.138, n = 90) Actinopterygii (Fig. 3). Similarly, mean t_m/t_{max} was not significantly different (ANOVA: F = 1.44, P = 0.25) between female (mean ± SD = 0.499 ± 0.166, n = 10) and male (mean ± SD = 0.418 ± 0.133, n = 10) Elasmobranchii (Fig. 3). Consequently, sexes were combined per class and mean t_m/t_{max} was then compared between classes. Mean t_m/t_{max} was significantly higher (ANOVA: F = 31.04, P < 0.001) in Elasmobranchii (mean ± SD = 0.458 ± 0.152, n = 20) compared to Actinopterygii (mean ± SD = 0.270 ± 0.135, n = 180) (Fig. 4).

With respect to habitat, the mean t_m/t_{max} of Actinopterygii ranged between 0.06 and 0.43 for benthopelagic (BEP: mean ± SD = 0.22 ± 0.086, n = 23), between 0.06 and 0.75 for demersal (D: mean ± SD = 0.29 ± 0.142, n = 107), between 0.09 and 0.70 for pelagic (P: mean ± SD = 0.28 ± 0.143, n = 63), and between 0.10 and 0.27 for reef-associated stocks (R: mean ± SD = 0.19 ± 0.053, n = 16) (Fig. 5). Elasmobranchii (n = 20) as well as bathydemersal (BAD: n = 3) and bathypelagic (BAP: n = 3) actinopterygian stocks were excluded from this comparison because of their small sample size. Overall, mean t_m/t_{max} values were significantly different among the four habitat categories of Actinopterygii (ANOVA: F = 3.67, P = 0.013). Based on Fisher's LSD test, there were no differences in the means between benthopelagic and reef-associated (BEP and R), between benthopelagic and pelagic (BEP and P) and between demersal and pelagic (D and P) stocks, whereas reef-associated stocks, which had the lowest mean t_m/t_{max}, differed significantly from demersal and pelagic ones (Fig. 5).

Discussion

The ranges of t_m values reported in the present work for Mediterranean marine fishes fall within the previously reported range of t_m values for actinopterygian and elasmobranch fishes. Actinopterygii generally mature earlier in life compared to Elasmobranchii (Goldman *et al.*,

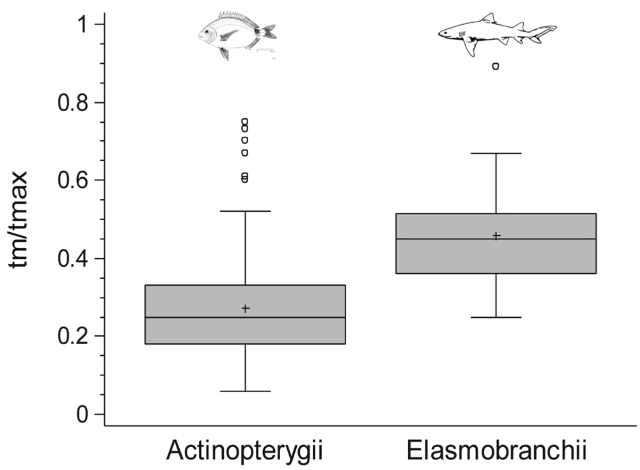

Fig. 4: Variability of age at maturity (t_m, y) to maximum age (t_{max}, y) ratio per class (Actinopterygii and Elasmobranchii), sexes combined. The rectangular part of the plot extends from the lower quartile to the upper quartile. The horizontal line within each box shows the location of the median and the cross the location of the mean. The whiskers extend from the box to the minimum and maximum values and circles indicate outliers.

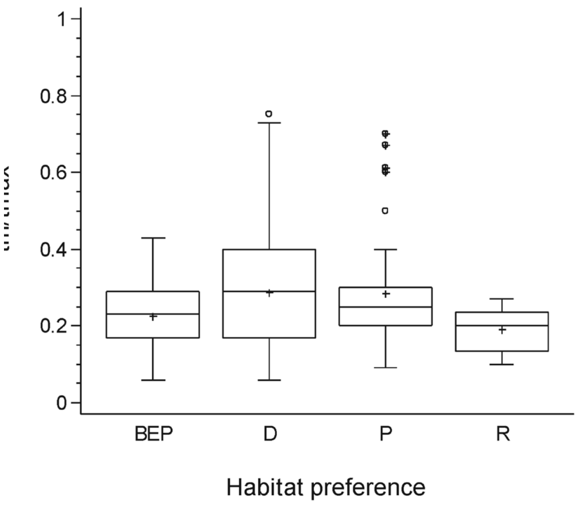

Fig. 5: Variability of age at maturity (t_m, y) to maximum age (t_{max}, y) ratio of Actinopterygii per habitat category (BEP: benthopelagic, D: demersal, P: pelagic, R: reef-associated). Elasmobranchii and the categories bathydemersal (BAD) and bathypelagic (BAP) were excluded because of their small sample size. The rectangular part of the plot extends from the lower quartile to the upper quartile. The horizontal line within each box shows the location of the median and the cross the location of the mean. The whiskers extend from the box to the minimum and maximum values and circles indicate outliers.

2012). For the latter, t_m is variable, and has been reported to range from 2 to 26 y in 18 populations of 15 species (Chen & Yuan, 2006). The same range has been reported by Cailliet & Goldman (2004), with a bimodal distribution with one peak at 5–6 y and a second one at 15–25 y. Higher t_m values have been reported for long-lived elasmobranchs, such as the whale shark *Rhincodon typus* (> 22 y) and the picked dogfish *Squalus acanthias* (25-26 y) (Chen & Yuan, 2006; Dulvy *et al.*, 2008). Similarly, for long-lived actinopterygians, such as the bluemouth rockfish *Helicolenus dactylopterus*, ages at maturity higher than 15 y are known (Kelly *et al.*, 1999). In their work, that reviewed the life history traits of 41 actinopterygian species, Drazen & Haedrich (2012) report that t_m ranges between 2 and 36 y, with six species having t_m that exceeds 20 y and five species having t_{max} that exceeds 100 y. A similar range of ages at maturity (0.5 to 35.5 y) has been reported by He & Stewart (2001) in their review of 235 fish stocks, including marine and freshwater finfishes, as well as a few elasmobranchs. It seems that, at least regarding elasmobranchs, and considering their small sample size in the present work, long-living, late-maturing sharks are rare in the Mediterranean Sea. Given that the larger elasmobranchs are more susceptible to overfishing (Dulvy *et al.*, 2014), this under-representation may be due to their overexploitation that is known to occur in the Mediterranean (Stergiou & Tsikliras, 2011; Tsikliras *et al.*, 2013b).

The positive relation between t_m and t_{max} (Fig. 2) confirms the general pattern that longer-lived species mature later and grow slower compared to their shorter-lived counterparts (Frisk, 2010). Indeed, elasmobranchs are located at the upper end of that spectrum (Fig. 2). A significant positive relation between longevity (t_{max}) and t_m has been reported previously for female and male batoids (females: $t_m = 0.57 \cdot t_{max} + 1.02$; males: $t_m = 0.57 \cdot t_{max} + 0.47$) (Frisk, 2010). The empirical relation between t_m and t_{max} can be used for estimating t_m for species for which only t_{max} is known.

The dimensionless t_m/t_{max} ratio shows that actinopterygians mature very early, at around 1/3 of $t_{max,}$ within their lifespans. In contrast, elasmobranchs mature later, close to 1/2 of their t_{max}. Similar results have been reported for several shark and skate stocks with this ratio being generally higher for skates than for other elasmobranch groups and teleosts generally (Frisk, 2010). In general, the onset of maturity may depend mainly on age for short-lived species that mature early, and mainly on size for their longer-lived, late-maturing counterparts, with developmental or genetic constraints more evident in longer lived species (Archibald *et al.*, 1983; Roff, 1983). There are benefits and costs associated with reproducing early or late in life. Benefits associated with early maturity include increased probability of surviving to reproduce and reduced generation time, while the costs of early maturity include reduced survival and fecundity later in life (Roff, 1992). High adult mortality, as a result of fishing, may favour earlier maturation (Rochet, 1998). Such a cost of reproduction, i.e. a trade-off between present reproductive effort and future age-specific reproductive success, is evident across animals (Williams, 1966; Bell, 1980).

Although t_m might differ between sexes, the fact that, in the present work, we found no difference in the t_m/t_{max} ratio between males and females within both classes, may simply be attributed to the fact that t_m and t_{max} vary simultaneously and, within species, are determined by the corresponding growth and mortality patterns (e.g. Tsikliras *et al.*, 2007; Gislason *et al.*, 2010). For instance, a male that matures earlier will experience higher future mortalities and will have a shorter lifespan compared to a female that will mature later (e.g. Tsikliras & Koutrakis, 2013), i.e. age at maturity may co-vary with maximum age and, in the same way, size at maturity co-varies with asymptotic length (Beverton, 1992). Thus, the t_m/t_{max} ratio will remain the same and bi-maturism will be absent, as has been reported to occur for the length at maturity to maximum reported length (L_m/L_{max}) ratio (Tsikliras & Stergiou, 2014).

With the exception of reef-associated species, which exhibited the lowest t_m/t_{max} values, the t_m/t_{max} ratio of actinopterygians remained rather constant among the remaining habitat categories (Fig. 5) and had similar values with the overall t_m/t_{max} ratio for actinopterygians. A similar constancy among habitat categories has been reported for the L_m/L_{max} ratio of Mediterranean marine fishes (Tsikliras & Stergiou, 2014). Although there are several large-sized, long-lived, and late-maturing reef-associated species (e.g. groupers) in the Mediterranean Sea, in the present dataset these species were rare in favour of small- and medium-sized reef inhabitants (Table 1). This might explain the lower t_m/t_{max} ratio for reef-associated species. Drazen & Haedrich (2012) report that t_m increases with depth but in our dataset there are no real deep-water species given that most of the species are commercial living on the continental shelf. Thus, we could not test this hypothesis. Besides deep-water species, special or complex cases of reproductive strategies, such as hermaphrodism and strategies involving spawning migrations were also rare in the dataset. Such strategies could also result in deviations from the general pattern that is presented here.

Finally, it should be noted that length at maturity and t_m should be independently estimated in reproductive biology, instead of t_m being indirectly estimated from the von Bertalanffy growth equation. This is because the growth trajectory may differ as a result of quicker or slower rates of approaching asymptotic lengths among individuals (He & Stewart, 2001). Hence, maturity can be reached at same length and different age and *vice versa* (Kozlowski, 1996).

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