

## MOUTH ALLOMETRY AND FEEDING HABITS OF SOME MEDITERRANEAN FISHES

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**Background.** Mouth characteristics are considered important yet restraining factors for food acquisition in fishes. Nevertheless, their relations with total length (TL) are not thoroughly examined. In the present study mouth characteristics were estimated for 61 fish species from the northern Aegean Sea and their relations with TL were established, and the relation of mouth area with feeding habits was tested.

**Materials and methods.** TL, horizontal mouth opening (HMO), and vertical mouth opening (VMO) were measured in 61 species, and mouth area MA was estimated. Relations between mouth characteristics and TL were established using power regression, and the validity of the power model was tested, using Student's *t*-test. In order to explore whether there is a grouping of species based on their feeding habits, the MA–TL regressions of all species were plotted together and the general regression lines per functional trophic group were compared using analysis of variance. Finally, the relative MA was estimated and related to trophic level.

**Results.** All relations examined were statistically significant ( $P < 0.05$ ), with only one exception (VMO–TL relation in *Dentex dentex*). The allometric model (for HMO–TL, MA–TL, and VMO–TL) was valid for the majority of species (52, 47, and 49 species, respectively), with positive allometry prevailing in the HMO–TL and MA–TL relations, and negative allometry in the VMO–TL relations. The analyses employed revealed that MA, for the same TL, increases faster in carnivores than in omnivores, and that in general carnivorous species tend to have larger mouths than omnivorous ones. Finally, there is a strong positive relation between relative MA and trophic level ( $P < 0.01$ ).

**Conclusion.** There is a strong relation of mouth characteristics to body length and feeding habits. These relations and the way that MA increases in relation to feeding habits could be attributed to structural changes in order for growing fish to meet their increased energetic demands. Establishing such relations is essential for estimating trophic levels of species, which are key parameters for ecosystem-based management models, when data on species' feeding habits are not available.

**Keywords:** mouth dimensions, mouth area relations, ecomorphology, Aegean Sea

### INTRODUCTION

Feeding habits, diet composition, and food consumption in fishes have been related to various morphological characteristics notably the mouth (e.g., Karpouzi and Stergiou 2003), gut length (Kapoor et al. 1975, Kramer and Bryant 1995, Karachle and Stergiou 2010) and tail (Palomares and Pauly 1989, 1998, Pauly 1994, Karachle 2008). In particular, mouth shape and position, dentition, branchial spines (in terms of structure and number) and distance between gill rakers, and pharyngeal bone structure are strongly connected to species' feeding and diet composition (Al-Hussaini 1947, Verigina 1991, Wootton 1998, Boyle and Horn 2006).

Mouth gape is considered as an important, yet restraining, factor for food selection, capture, handling, and consumption (Keast and Webb 1966, Kapoor et al. 1975,

Wainwright and Richard 1995, Karpouzi and Stergiou 2003, Makrakis et al. 2008, Goatley and Bellwood 2009). As fish grow, they tend to prey upon a greater size range of food items, and the mean size of the prey consumed increases, a fact more evident in second order carnivores and apex predators (Scharf et al. 2000, 2009, Stergiou and Karpouzi 2002, Karpouzi and Stergiou 2003, Arim et al. 2010). Such an increase in prey-size consumed is generally attributed to both morphological (e.g., ontogenetic mouth size increase) and physiological factors (e.g., vision acuity, increasing swimming ability), that allow predators to consume larger prey (Keast and Webb 1966, Kaiser and Hughes 1993, Juanes 1994, Juanes and Conover 1994, Hart 1997, Wootton 1998, Fordham and Trippel 1999). Therefore, and especially in carnivorous fishes, mouth shape and size can be used for the explanation of inter-

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and intra-specific feeding diversity (Wainwright and Richard 1995, Karpouzi and Stergiou 2003), whereas mouth opening can be used to explain prey-predator relations (e.g., Keast and Webb 1966, Wainwright and Richard 1995, Karpouzi and Stergiou 2003).

This report expands on that of Karpouzi and Stergiou (2003) who studied the relations between mouth characteristics and body size for 18 fishes from the central Aegean Sea. In this study mouth area was estimated for 61 species from the North Aegean Sea, and mouth characteristics (i.e., horizontal and vertical mouth opening, and mouth area) were related to total length. Additionally, relative mouth area was related to species' trophic level. Finally, patterns of mouth area changes according to species' feeding habits were explored. All the above relations are of great importance, since they contribute to the quantification of prey-size related feeding patterns, which in turn define the ecological role of organisms within the food webs (Karpouzi and Stergiou 2003).

## MATERIALS AND METHODS

Samples were collected in the area of N-NW Aegean Sea, Greece, on a seasonal basis, from June 2001 to January 2006, using commercial fishing vessels (i.e., trawlers, purse-seiners, and gill-netters) and preserved in 10% formalin (for details see Karachle and Stergiou 2008). In the laboratory, total length (TL), horizontal (HMO), and vertical (VMO) mouth opening were measured, and were used for the estimation of mouth area (MA), based on the assumption that MA shape could be that of an ellipse (Erzini et al. 1997):

$$MA = \pi \left( \frac{HMO}{2} \right) \left( \frac{VMO}{2} \right)$$

where  $\pi \approx 3.14$ .

Overall, HMO, VMO, and MA values were estimated for 61 fish species (6796 individuals; Tables 1–2). The number of individuals ( $n$ ) examined ranged from six (for *Lophius piscatorius*, *Pagrus pagrus*, and *Pomatomus saltatrix*) to 744 (for *Engraulis encrasicolus*) (Tables 1–2). The sample size for 49 out of the 61 species was more than 20 individuals (mean = 111.3; median = 55).

For establishing relations between HMO–TL, VMO–TL, and MA–TL power regression ( $Y = aX^b$ ) was used, where  $a$  is the coefficient of shape, and  $b$  is the power fulfilling the dimensional balance (Leonart et al. 2000). The use of the allometric model (i.e.,  $Y = aX^b$ ) was based on the fact that it is the most suitable for the identification changes in shape, which is the objective of morphometrics (Peters 1983, Leonart et al. 2000). Consequently, given the mathematical traits of  $b$  as mentioned above,  $b$  was tested for difference from 2, in the case of MA (since the measurement unit of MA is  $\text{cm}^2$ ),

and for difference from 1, in the cases of HMO and VMO, using Student's  $t$ -test (Zar 1999). The MA–TL regressions of all species were plotted together, so that possible groupings of species and/or trends, according to the functional trophic group of species (as defined by Stergiou and Karpouzi 2002), could be identified. The trophic level ( $\tau$ ) values used for assigning a species into a functional trophic group were taken from Karachle and Stergiou (2006, 2008). Comparisons between the overall regression lines per functional trophic group (i.e., omnivores with preference to animal material (OA); carnivores with preference to decapods and fish (CD); and carnivores with preference to cephalopods and fish (CC); for details see Stergiou and Karpouzi 2002) were compared using analysis of variance (ANOVA; Zar 1999).

The relative MA (RMA) was estimated, as the ratio of MA to squared TL, i.e.,

$$RMA = \frac{MA}{TL^2}$$

in order to eliminate the effect of length on MA. RMA was plotted against species'  $\tau$  (data from Karachle and Stergiou 2006, 2008)

## RESULTS

The HMO–TL, VMO–TL (Table 1) and MA–TL (Table 2) relations were all significant ( $P < 0.05$ ), with the exception of the VMO–TL relation for *Dentex dentex* ( $P > 0.05$ ). The allometric model was statistically significant (i.e.,  $b \neq 1$  for HMO and VMO and  $b \neq 2$  for MA; Student  $t$ -test:  $P < 0.10$ ) for 52 species in the case of HMO–TL relations, 47 species in VMO–TL relations and 49 species in MA–TL relations (Tables 1–4), whereas the linear one was held for 6, 6, and 8 species, in the cases of HMO, VMO, and MA, respectively (Tables 3–4). Positive allometry (i.e.,  $b > 1$  or 2) was predominant in the case of HMO–TL and MA–TL relations and negative allometry (i.e.,  $b < 1$ ) in the case of the VMO–TL relations (Table 1).

There was a statistically significant relation ( $R^2 = 0.32$ ;  $P < 0.01$ ) between RMA and  $\tau$  (Fig. 1). The general model relating MA with TL, which resulted from combining the data from the 61 species, is given in Figs. 2–3. When the regressions between MA and TL (equations given in Table 2) for all species were plotted together (Fig. 2), there was not a clear pattern on MA changes according to feeding habits. Yet, when the regression lines were grouped per functional trophic group based on a species' feeding habits, it was evident that for the same TL, MA increased faster for carnivores than for omnivores (Fig. 2). Additionally, the overall regression lines of functional trophic groups differed significantly (ANOVA: OA–CC,  $F$ -ratio = 2051.20,  $P < 0.001$ ; OA–CD,  $F$ -ratio = 878.62,  $P < 0.001$ ; CC–CD,  $F$ -ratio = 981.42,  $P < 0.001$ ).

Table 1

Relations between horizontal mouth opening (HMO) and total length (TL) and between vertical mouth opening (VMO) and total length of 61 fishes from the North Aegean Sea, Greece, June 2001–January 2006

Species	TL range [cm]	TL <sub>m</sub> [cm]	Horizontal Mouth Opening					Vertical Mouth Opening						
			n	HMO = $aTL^b$	SE <sub>b</sub>	R <sup>2</sup>	b ≠ 1	ToR	n	VMO = $aTL^b$	SE <sub>b</sub>	R <sup>2</sup>	b ≠ 1	ToR
<i>Alosa fallax</i>	15.0–46.8	24.3	27	HMO = 0.0577TL <sup>1.0307</sup>	0.073	0.89	×	Li	27	VMO = 0.4393 TL <sup>0.5865</sup>	0.061	0.79	×	P
<i>Anthias anthias</i>	12.7–16.6	14.6	9	HMO = 0.1574TL <sup>0.7938</sup>	0.183	0.73	×	E	9	VMO = 0.5423 TL <sup>0.5167</sup>	0.088	0.83	×	P
<i>Apogon imberbis</i>	8.6–11.5	10.2	31	HMO = 0.0458TL <sup>1.4769</sup>	0.478	0.25	×	P	31	VMO = 0.0702 TL <sup>1.4823</sup>	0.288	0.48	×	L
<i>Arnoglossus laterna</i>	4.5–16.9	11.7	206	HMO = 0.0077TL <sup>1.8616</sup>	0.032	0.94	×	P	206	VMO = 0.0415 TL <sup>1.4515</sup>	0.022	0.95	×	P
<i>Belone belone</i>	27.2–53.5	33.7	69	HMO = 0.0151TL <sup>1.0898</sup>	0.062	0.82	×	Li	69	VMO = 0.0268 TL <sup>1.0385</sup>	0.090	0.66	×	Li
<i>Blennius ocellaris</i>	7.0–13.2	10.1	20	HMO = 0.0597TL <sup>1.0423</sup>	0.103	0.85	×	Li	20	VMO = 0.1106 TL <sup>0.9283</sup>	0.159	0.66	×	P
<i>Boops boops</i> *	11.2–19.9	15.2	103	HMO = 0.0044TL <sup>1.7734</sup>	0.073	0.86	×	P	103	VMO = 0.0393 TL <sup>1.1838</sup>	0.053	0.83	×	P
<i>Bothus podas</i>	11.3–17.2	13.5	20	HMO = 0.0582TL <sup>0.9267</sup>	0.156	0.66	×	Li	20	VMO = 0.1289 TL <sup>0.8302</sup>	0.146	0.64	×	Li
<i>Cepola macrophthalmia</i>	13.2–54.9	31.3	185	HMO = 0.0924TL <sup>0.6531</sup>	0.038	0.61	×	P	185	VMO = 0.2335 TL <sup>0.5564</sup>	0.017	0.85	×	P
<i>Chelidonichthys lucernus</i>	6.0–21.6	11.6	12	HMO = 0.0301TL <sup>1.4299</sup>	0.105	0.95	×	P	12	VMO = 0.1322 TL <sup>1.007</sup>	0.044	0.98	×	L
<i>Chromis chromis</i>	8.6–13.3	10.9	97	HMO = 0.0871TL <sup>0.7421</sup>	0.132	0.25	×	P	97	VMO = 0.2238 TL <sup>0.5872</sup>	0.091	0.30	×	P
<i>Citharus linguatula</i>	3.9–24.3	13.5	166	HMO = 0.0489TL <sup>1.1995</sup>	0.037	0.86	×	P	166	VMO = 0.2013 TL <sup>0.9304</sup>	0.022	0.91	×	P
<i>Coris julis</i>	11.3–18.2	15.9	77	HMO = 0.0133TL <sup>1.4472</sup>	0.148	0.56	×	P	77	VMO = 0.0336 TL <sup>1.3024</sup>	0.143	0.52	×	P
<i>Dentex dentex</i>	11.7–15.3	13.0	9	HMO = 0.0278TL <sup>1.3254</sup>	0.401	0.61	×	Li	9	Non-significant	0.34	0.34	×	P
<i>Diplodus annularis</i> *	6.1–17.5	10.7	406	HMO = 0.0283TL <sup>1.2326</sup>	0.043	0.66	×	P	406	VMO = 0.0666 TL <sup>1.0422</sup>	0.043	0.59	×	P
<i>Diplodus vulgaris</i> *	9.0–16.7	11.6	47	HMO = 0.0345TL <sup>1.1467</sup>	0.096	0.76	×	Li	47	VMO = 0.1054 TL <sup>0.8437</sup>	0.085	0.69	×	P
<i>Engraulis encrasicolus</i>	6.7–16.2	11.4	744	HMO = 0.0821TL <sup>0.888</sup>	0.047	0.33	×	P	744	VMO = 0.2723 TL <sup>0.8852</sup>	0.018	0.77	×	P
<i>Eutrigla gurnardus</i>	12.8–14.8	13.5	9	HMO = 0.0064TL <sup>1.9295</sup>	0.426	0.75	×	P	9	VMO = 0.0069 TL <sup>2.1145</sup>	0.254	0.91	×	P
<i>Gaidropsarus biscayensis</i>	9.0–15.3	12.0	52	HMO = 0.0368TL <sup>1.2281</sup>	0.065	0.88	×	P	52	VMO = 0.0884 TL <sup>1.1388</sup>	0.080	0.80	×	P
<i>Gaidropsarus mediterraneus</i>	8.4–14.5	11.4	14	HMO = 0.1033TL <sup>0.8147</sup>	0.236	0.50	×	P	14	VMO = 0.275 TL <sup>0.6372</sup>	0.344	0.60	×	E
<i>Lesueurigobius suerii</i>	5.8–9.4	8.1	137	HMO = 0.0312TL <sup>1.3572</sup>	0.069	0.74	×	P	137	VMO = 0.0848 TL <sup>1.1364</sup>	0.058	0.74	×	P
<i>Lophius budegassa</i>	5.0–38.4	12.2	45	HMO = 0.5174TL <sup>0.7921</sup>	0.022	0.97	×	P	45	VMO = 0.3902 TL <sup>0.7705</sup>	0.050	0.85	×	P
<i>Lophius piscatorius</i>	7.7–12.7	9.6	6	HMO = 0.7513TL <sup>0.6456</sup>	0.072	0.95	×	P	6	VMO = 0.5704 TL <sup>0.6755</sup>	0.131	0.87	×	P
<i>Merlangius merlangus</i>	14.1–29.1	20.1	44	HMO = 0.0299TL <sup>1.3867</sup>	0.060	0.93	×	P	44	VMO = 0.257 TL <sup>0.8025</sup>	0.039	0.91	×	P
<i>Merluccius merluccius</i> *	11.7–37.0	20.0	22	HMO = 0.0299TL <sup>1.4189</sup>	0.066	0.96	×	P	22	VMO = 0.2142 TL <sup>0.8978</sup>	0.096	0.95	×	L
<i>Micromesistius poutassou</i>	9.2–24.0	12.2	69	HMO = 0.0163TL <sup>1.5378</sup>	0.075	0.86	×	P	69	VMO = 0.1429 TL <sup>0.9839</sup>	0.037	0.91	×	Li
<i>Monochirus hispidus</i>	9.2–12.8	11.2	21	HMO = 0.1127TL <sup>0.5499</sup>	0.245	0.21	×	P	21	VMO = 0.1465 TL <sup>0.6891</sup>	0.121	0.63	×	P
<i>Mullus surmuletus</i> *	9.1–23.1	15.6	55	HMO = 0.003TL <sup>2.1708</sup>	0.112	0.88	×	P	55	VMO = 0.0791 TL <sup>1.0996</sup>	0.040	0.94	×	P
<i>Oblada melanura</i>	12.6–22.7	17.9	56	HMO = 0.0196TL <sup>1.4172</sup>	0.085	0.84	×	P	56	VMO = 0.1146 TL <sup>0.9017</sup>	0.046	0.88	×	P
<i>Pagellus acarne</i> *	11.4–19.2	15.2	55	HMO = 0.0036TL <sup>1.995</sup>	0.133	0.81	×	P	55	VMO = 0.0315 TL <sup>1.4023</sup>	0.078	0.86	×	P
<i>Pagellus bogaraveo</i>	9.3–23.1	15.1	64	HMO = 0.0152TL <sup>1.5147</sup>	0.032	0.97	×	P	64	VMO = 0.0602 TL <sup>1.1492</sup>	0.019	0.98	×	P
<i>Pagellus erythrinus</i> *	8.4–15.8	12.4	53	HMO = 0.058TL <sup>0.984</sup>	0.133	0.51	×	P	53	VMO = 0.1813 TL <sup>0.7728</sup>	0.114	0.47	×	P
<i>Pagrus pagrus</i>	11.1–13.1	11.8	6	HMO = 0.2519TL <sup>0.4235</sup>	0.127	0.74	×	P	6	VMO = 0.0844 TL <sup>1.0926</sup>	0.357	0.70	×	L
<i>Phycis blennoides</i>	8.1–37.4	20.7	28	HMO = 0.0254TL <sup>1.4314</sup>	0.050	0.97	×	P	28	VMO = 0.1048 TL <sup>1.0901</sup>	0.024	0.99	×	P
<i>Pomatomus saltatrix</i>	13.1–18.5	16.1	6	HMO = 0.0043TL <sup>2.0694</sup>	0.204	0.96	×	P	6	VMO = 0.0156 TL <sup>1.7664</sup>	0.186	0.97	×	P

Table 1

continued from previous page

<i>Raja clavata</i>	25.6–46.5	38.7	7	HMO = 0.0476TL <sup>1.2103</sup>	0.075	0.98	×	P	7	VMO = 0.0175 TL <sup>1.3686</sup>	0.169	0.93	×	P
<i>Sardina pilchardus</i>	7.6–16.7	12.7	738	HMO = 0.023TL <sup>1.1319</sup>	0.039	0.54	×	P	738	VMO = 0.1365 TL <sup>0.8583</sup>	0.036	0.43	×	P
<i>Sardinella aurita</i>	8.4–23.9	17.2	217	HMO = 0.0258TL <sup>1.0843</sup>	0.045	0.73	×	P	221	VMO = 0.1146 TL <sup>0.9264</sup>	0.038	0.74	×	P
<i>Sarpa salpa</i>	11.7–19.5	14.9	25	HMO = 0.0102TL <sup>1.4095</sup>	0.122	0.86	×	P	25	VMO = 0.0635 TL <sup>0.9451</sup>	0.097	0.81	×	Li
<i>Sciaena umbra</i>	12.2–16.0	14.2	10	HMO = 0.0326TL <sup>1.2968</sup>	0.355	0.63	×	E	10	VMO = 0.0621 TL <sup>1.225</sup>	0.153	0.89	×	L
<i>Scomber japonicus</i>	8.8–26.8	16.7	360	HMO = 0.0361TL <sup>1.1109</sup>	0.030	0.80	×	P	361	VMO = 0.2111 TL <sup>0.8026</sup>	0.031	0.66	×	P
<i>Scomber scombrus</i>	13.3–27.4	21.4	198	HMO = 0.0052TL <sup>1.9206</sup>	0.074	0.78	×	P	198	VMO = 0.1223 TL <sup>1.0424</sup>	0.028	0.88	×	L
<i>Scorpaena notata</i>	8.3–17.8	14.3	41	HMO = 0.059TL <sup>1.3608</sup>	0.069	0.91	×	P	41	VMO = 0.126 TL <sup>1.1747</sup>	0.048	0.94	×	P
<i>Scorpaena porcus</i> *	8.2–26.4	13.6	90	HMO = 0.0623TL <sup>1.3313</sup>	0.037	0.94	×	P	90	VMO = 0.2151 TL <sup>0.9834</sup>	0.035	0.90	×	Li
<i>Scyliorhinus canicula</i>	24.4–45.1	37.5	34	HMO = 0.0617TL <sup>1.0596</sup>	0.101	0.77	×	P	34	VMO = 0.0992 TL <sup>0.8751</sup>	0.178	0.43	×	P
<i>Serranus cabrilla</i>	9.5–23.1	15.0	41	HMO = 0.0445TL <sup>1.334</sup>	0.088	0.86	×	P	41	VMO = 0.2523 TL <sup>0.839</sup>	0.070	0.79	×	P
<i>Serranus hepatus</i>	5.9–13.1	9.6	120	HMO = 0.0774TL <sup>1.1316</sup>	0.067	0.71	×	P	120	VMO = 0.1743 TL <sup>1.0019</sup>	0.042	0.83	×	Li
<i>Serranus scriba</i> *	10.6–23.6	15.7	84	HMO = 0.0719TL <sup>1.1719</sup>	0.092	0.66	×	P	84	VMO = 0.2579 TL <sup>0.8513</sup>	0.069	0.65	×	P
<i>Sphyaena sphyraena</i>	21.6–45.1	29.7	102	HMO = 0.0389TL <sup>1.0719</sup>	0.153	0.33	×	P	102	VMO = 0.293 TL <sup>0.6746</sup>	0.084	0.39	×	P
<i>Spicara maena</i> *	9.0–20.2	13.5	271	HMO = 0.0506TL <sup>0.9426</sup>	0.053	0.54	×	P	271	VMO = 0.1087 TL <sup>0.896</sup>	0.028	0.80	×	P
<i>Spicara smaris</i>	7.0–18.5	11.8	106	HMO = 0.0128TL <sup>1.4738</sup>	0.129	0.56	×	P	106	VMO = 0.0714 TL <sup>1.0567</sup>	0.054	0.79	×	P
<i>Spondyliosoma cantharus</i> *	9.7–14.0	11.5	82	HMO = 0.1159TL <sup>0.6588</sup>	0.096	0.37	×	P	82	VMO = 0.0936 TL <sup>0.9707</sup>	0.058	0.78	×	P
<i>Symphodus tinca</i> *	11.1–22.0	14.9	217	HMO = 0.0146TL <sup>1.4641</sup>	0.047	0.82	×	P	217	VMO = 0.0293 TL <sup>1.3085</sup>	0.050	0.77	×	P
<i>Symphurus nigrescens</i>	6.4–11.9	9.4	9	HMO = 0.0342TL <sup>0.9354</sup>	0.100	0.93	×	L	9	VMO = 0.1517 TL <sup>0.4435</sup>	0.141	0.59	×	P
<i>Torpedo marmorata</i>	8.8–36.1	16.4	117	HMO = 0.3337TL <sup>0.6798</sup>	0.035	0.77	×	P	117	VMO = 0.3874 TL <sup>0.5079</sup>	0.042	0.56	×	P
<i>Trachinus draco</i>	15.0–30.5	22.6	23	HMO = 0.0256TL <sup>1.3688</sup>	0.331	0.45	×	P	24	VMO = 0.1966 TL <sup>0.8407</sup>	0.136	0.64	×	P
<i>Trachurus mediterraneus</i> *	7.0–25.8	13.4	586	HMO = 0.0379TL <sup>1.124</sup>	0.031	0.69	×	P	585	VMO = 0.1482 TL <sup>0.9067</sup>	0.015	0.85	×	P
<i>Trachurus trachurus</i>	6.3–23.9	12.0	118	HMO = 0.0158TL <sup>1.4868</sup>	0.050	0.88	×	P	118	VMO = 0.0956 TL <sup>1.0915</sup>	0.017	0.97	×	P
<i>Trisopterus minutus</i>	5.7–24.5	12.3	155	HMO = 0.052TL <sup>1.1918</sup>	0.028	0.92	×	P	155	VMO = 0.1738 TL <sup>0.9227</sup>	0.022	0.92	×	P
<i>Uranoscopus scaber</i>	8.7–26.9	14.6	66	HMO = 0.2418TL <sup>0.8216</sup>	0.048	0.82	×	P	67	VMO = 0.3075 TL <sup>0.5114</sup>	0.091	0.33	×	P
<i>Xyrichtys novacula</i>	12.3–17.1	14.0	9	HMO = 0.0018TL <sup>2.1547</sup>	0.296	0.88	×	P	9	VMO = 0.002 TL <sup>2.3359</sup>	0.390	0.84	×	P

\* also included in Karpouzi and Stergiou (2003);  $n$  = number of individuals;  $SE_b$  = standard error of slope  $b$ ;  $R^2$  = coefficient of determination; ToR = type of relation; E = exponential type; L = logarithmic type; Li = linear type; P = power type; × indicates that  $b \neq 1$ .

Table 2

Relations between mouth area (MA) and total length (TL) of 61 fishes from the North Aegean Sea, Greece, June 2001–January 2006

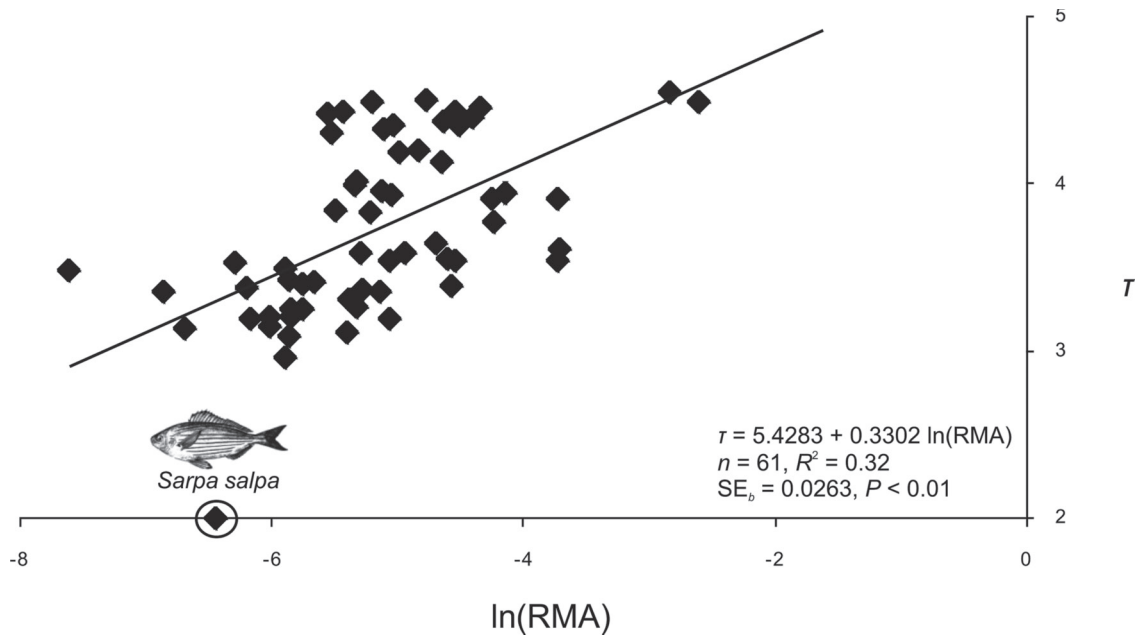
Species	N	MA <sub>m</sub>	MA <sub>min</sub>	MA <sub>max</sub>	SE	MA = aTL <sup>b</sup>	SE <sub>b</sub>	R <sup>2</sup>	b ≠ 2	ToR	τ ± SE
<i>Alosa fallax</i>	27	3.62	1.53	8.27	0.3377	MA = 0.0199TL <sup>1.6172</sup>	0.10479	0.91	×	P	4.32 ± 0.48
<i>Anthias anthias</i>	9	2.25	1.90	2.73	0.0782	MA = 0.0677TL <sup>1.3106</sup>	0.23156	0.82	×	P	3.54 ± 0.52
<i>Apogon imberbis</i>	31	2.52	1.02	3.40	0.0928	MA = 0.0025TL <sup>2.9592</sup>	0.67040	0.40	×	L	3.54 ± 0.56
<i>Arnoglossus laterna</i>	206	1.06	0.04	2.46	0.0467	MA = 0.0003TL <sup>3.3131</sup>	0.04745	0.96	×	P	4.35 ± 0.74
<i>Belone belone</i>	69	0.57	0.37	1.50	0.0244	MA = 0.0003TL <sup>2.1254</sup>	0.09888	0.87	×	Li	3.48 ± 0.45
<i>Blennius ocellaris</i>	20	0.52	0.20	0.89	0.0433	MA = 0.0052TL <sup>1.9706</sup>	0.15986	0.89	×	Li	3.26 ± 0.46
<i>Boops boops</i> *	103	0.32	0.18	0.70	0.0107	MA = 0.0001TL <sup>2.9573</sup>	0.00869	0.87	×	P	3.52 ± 0.52
<i>Bothus podas</i>	20	0.58	0.36	0.88	0.0288	MA = 0.0059TL <sup>1.7569</sup>	0.27250	0.70	×	Li	3.39 ± 0.53
<i>Cepola macrocephala</i>	185	1.13	0.29	2.49	0.0355	MA = 0.0169TL <sup>1.2095</sup>	0.04951	0.77	×	P	3.13 ± 0.31
<i>Chelidonichthys lucernus</i>	12	1.67	0.16	5.28	0.4794	MA = 0.0031TL <sup>2.4369</sup>	0.13074	0.97	×	P	3.64 ± 0.63
<i>Chromis chromis</i>	97	0.37	0.21	0.68	0.0098	MA = 0.0153TL <sup>1.3293</sup>	0.20849	0.30	×	P	3.25 ± 0.37
<i>Citharus linguatula</i>	166	2.06	0.06	6.01	0.0701	MA = 0.0077TL <sup>2.13</sup>	0.05271	0.91	×	P	4.34 ± 0.69
<i>Coris julis</i>	77	0.73	0.23	1.07	0.0196	MA = 0.0004TL <sup>2.7496</sup>	0.23721	0.64	×	P	3.42 ± 0.53
<i>Dentex dentex</i>	9	0.95	0.76	1.40	0.0733	MA = 0.006TL <sup>1.9613</sup>	0.59464	0.61	×	Li	4.49 ± 0.80
<i>Diplodus annularis</i> *	406	0.34	0.10	1.07	0.0058	MA = 0.0015TL <sup>2.2748</sup>	0.07002	0.72	×	P	3.20 ± 0.43
<i>Diplodus vulgaris</i> *	47	0.39	0.18	0.87	0.0201	MA = 0.0029TL <sup>1.9904</sup>	0.14819	0.80	×	Li	3.08 ± 0.28
<i>Engraulis encrasicolus</i>	744	1.35	0.41	3.13	0.0135	MA = 0.0176TL <sup>1.7722</sup>	0.05054	0.62	×	P	3.38 ± 0.44
<i>Euirigla gurnardus</i>	9	1.31	1.03	1.84	0.0893	MA = 0.0003TL <sup>4.044</sup>	0.30579	0.96	×	P	3.58 ± 0.58
<i>Gaidropsarus biscayensis</i>	52	0.94	0.41	1.55	0.0420	MA = 0.0025TL <sup>2.3706</sup>	0.11601	0.89	×	P	3.93 ± 0.67
<i>Gaidropsarus mediterraneus</i>	14	0.78	0.47	1.13	0.0484	MA = 0.0223TL <sup>1.4519</sup>	0.26104	0.72	×	P	3.95 ± 0.61
<i>Lesueurigobius suerii</i>	137	0.39	0.11	0.60	0.0075	MA = 0.0021TL <sup>2.4936</sup>	0.10027	0.82	×	P	3.35 ± 0.43
<i>Lophius budegassa</i>	43	9.32	1.68	58.91	1.9597	MA = 0.1601TL <sup>1.5567</sup>	0.05650	0.95	×	P	4.54 ± 0.60
<i>Lophius piscatorius</i>	6	6.76	5.38	9.99	0.6960	MA = 0.3364TL <sup>1.3211</sup>	0.19627	0.92	×	P	4.48 ± 0.54
<i>Merlangius merlangus</i>	44	4.44	1.58	9.22	0.2610	MA = 0.006TL <sup>2.1892</sup>	0.08135	0.95	×	P	4.38 ± 0.73
<i>Merluccius merluccius</i> *	22	6.62	1.21	18.13	1.3366	MA = 0.005TL <sup>2.3167</sup>	0.24716	0.97	×	Li	4.45 ± 0.74
<i>Micromesistius poutassou</i>	69	0.93	0.47	1.45	0.0259	MA = 0.0018TL <sup>2.5217</sup>	0.00992	0.92	×	P	4.18 ± 0.66
<i>Monoichthys hispidus</i>	20	0.26	0.18	0.34	0.0109	MA = 0.0121TL <sup>1.2634</sup>	0.29700	0.50	×	P	3.19 ± 0.32
<i>Mullus surmuletus</i> *	55	1.72	0.26	3.53	0.1180	MA = 0.0002TL <sup>3.2704</sup>	0.14805	0.90	×	P	3.19 ± 0.37
<i>Oblada melanura</i>	56	1.49	0.51	2.46	0.0683	MA = 0.0018TL <sup>2.3189</sup>	0.11995	0.87	×	P	3.11 ± 0.42
<i>Pagellus acarne</i> *	55	0.99	0.38	2.33	0.0596	MA = 0.0009TL <sup>3.3973</sup>	0.15813	0.90	×	P	3.84 ± 0.55
<i>Pagellus bogaraveo</i>	64	1.19	0.29	2.93	0.1114	MA = 0.0007TL <sup>2.6639</sup>	0.04061	0.99	×	P	4.43 ± 0.76
<i>Pagellus erythrimus</i> *	53	0.70	0.29	1.04	0.0207	MA = 0.0083TL <sup>1.7568</sup>	0.21684	0.56	×	P	3.30 ± 0.39
<i>Pagrus pagrus</i>	6	0.71	0.60	0.81	0.0340	MA = 0.0167TL <sup>1.5161</sup>	0.41100	0.77	×	L	3.36 ± 0.34
<i>Phycis blennoides</i>	28	5.67	0.36	15.59	0.8965	MA = 0.0021TL <sup>2.5215</sup>	0.05853	0.99	×	P	3.55 ± 0.59
<i>Pomatomus saltatrix</i>	5	2.26	0.96	3.38	0.4998	MA = 0.0005TL <sup>3.8246</sup>	0.42269	0.97	×	P	4.50 ± 0.80
<i>Raja clavata</i>	7	8.98	2.63	15.02	1.7595	MA = 0.0007TL <sup>2.5788</sup>	0.22646	0.96	×	P	3.90 ± 0.67

Table 2

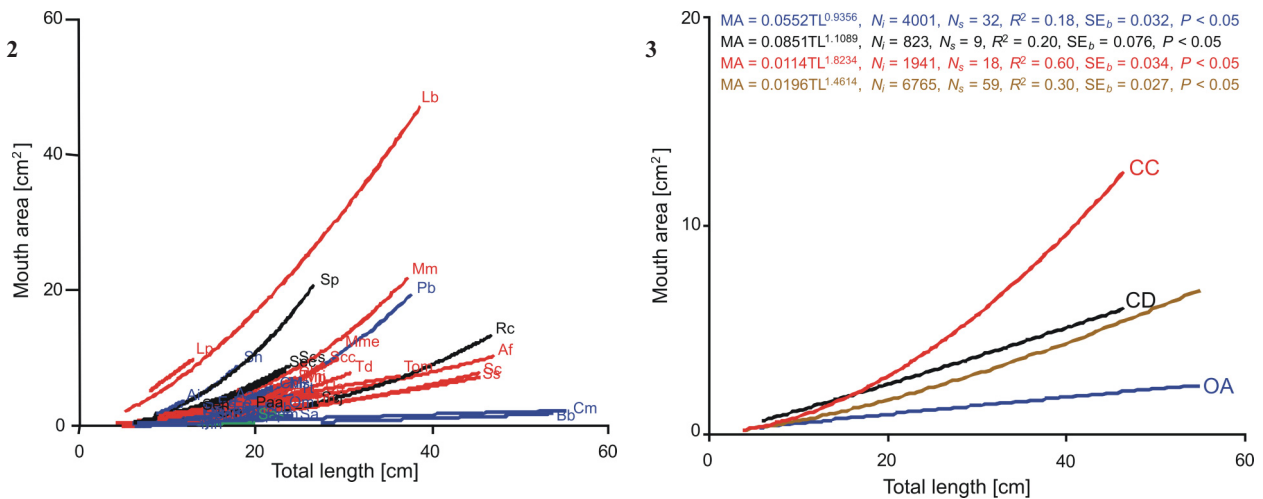
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<i>Sardina pilchardus</i>	738	0.40	0.12	0.91	0.0041	MA = 0.0025 TL <sup>1.9902</sup>	0.05244	0.66	P	3.14 ± 0.29
<i>Sardinella aurita</i>	217	0.75	0.24	1.89	0.0228	MA = 0.0023 TL <sup>2.0078</sup>	0.07269	0.78	E	3.20 ± 0.32
<i>Sarpa salpa</i>	25	0.36	0.19	0.65	0.0227	MA = 0.0005 TL <sup>2.4146</sup>	0.19262	0.87	×	2.00 ± 0.00
<i>Sciaena umbra</i>	9	1.26	0.90	1.75	0.1094	MA = 0.0019 TL <sup>2.4467</sup>	0.47472	0.79	E	3.53 ± 0.54
<i>Scomber japonicus</i>	360	1.37	0.28	3.22	0.0257	MA = 0.006 TL <sup>1.9148</sup>	0.05139	0.80	×	3.99 ± 0.57
<i>Scomber scombrus</i>	198	4.54	0.68	7.21	0.0904	MA = 0.0005 TL <sup>2.963</sup>	0.09519	0.83	×	4.37 ± 0.54
<i>Scorpaena notata</i>	41	5.34	1.36	9.92	0.3802	MA = 0.0058 TL <sup>2.5355</sup>	0.10417	0.94	×	3.60 ± 0.62
<i>Scorpaena porcus</i> *	90	5.10	1.31	19.13	0.4469	MA = 0.0105 TL <sup>2.3147</sup>	0.05784	0.95	×	3.90 ± 0.69
<i>Scyllorhinus canicula</i>	34	5.52	1.75	10.63	0.3072	MA = 0.0048 TL <sup>1.9347</sup>	0.20976	0.73	P	4.41 ± 0.58
<i>Serranus cabrilla</i>	41	3.46	1.19	8.65	0.2947	MA = 0.0088 TL <sup>2.1731</sup>	0.13024	0.88	Li	3.90 ± 0.67
<i>Serranus hepatus</i>	120	1.35	0.55	2.60	0.0403	MA = 0.0106 TL <sup>2.1335</sup>	0.08964	0.83	P	3.77 ± 0.63
<i>Serranus scriba</i> *	84	3.94	1.42	9.69	0.1450	MA = 0.0146 TL <sup>2.0232</sup>	0.13030	0.75	Li	3.94 ± 0.66
<i>Sphyræna sphyraena</i>	102	3.54	1.43	6.55	0.1359	MA = 0.0089 TL <sup>1.7465</sup>	0.21101	0.41	P	4.30 ± 0.46
<i>Spicara maena</i> *	271	0.53	0.16	1.47	0.0098	MA = 0.0043 TL <sup>1.8386</sup>	0.06664	0.73	×	3.24 ± 0.34
<i>Spicara smaris</i>	106	0.40	0.07	1.01	0.0193	MA = 0.0007 TL <sup>2.5305</sup>	0.16864	0.68	×	3.49 ± 0.46
<i>Spondyliosoma cantharus</i> *	82	0.45	0.29	0.70	0.0102	MA = 0.0085 TL <sup>1.6265</sup>	0.11430	0.72	×	3.41 ± 0.46
<i>Symphodus tinca</i> *	217	0.65	0.17	1.69	0.0208	MA = 0.0003 TL <sup>2.7726</sup>	0.08191	0.84	×	2.95 ± 0.25
<i>Symphurus nigrescens</i>	9	0.09	0.05	0.14	0.0083	MA = 0.0041 TL <sup>1.3789</sup>	0.18981	0.88	×	3.35 ± 0.51
<i>Torpedo marmorata</i>	117	2.99	1.04	11.82	0.1761	MA = 0.1015 TL <sup>1.1877</sup>	0.07368	0.69	×	4.39 ± 0.67
<i>Trachinus draco</i>	23	4.15	1.48	8.68	0.3667	MA = 0.0037 TL <sup>2.2331</sup>	0.42614	0.57	P	4.19 ± 0.66
<i>Trachurus mediterraneus</i> *	585	0.92	0.16	4.24	0.0198	MA = 0.0044 TL <sup>2.0313</sup>	0.03960	0.82	P	4.01 ± 0.64
<i>Trachurus trachurus</i>	118	0.98	0.10	5.06	0.0985	MA = 0.0012 TL <sup>2.5783</sup>	0.05867	0.94	×	3.58 ± 0.50
<i>Trisopterus minutus</i>	155	1.57	0.21	7.89	0.0861	MA = 0.0071 TL <sup>2.1146</sup>	0.04172	0.94	×	4.13 ± 0.64
<i>Uranoscopus scaber</i>	66	2.19	0.80	6.48	0.1412	MA = 0.0611 TL <sup>1.3142</sup>	0.13196	0.61	×	4.43 ± 0.75
<i>Xyrichtys novacula</i>	9	0.42	0.21	0.99	0.0801	MA = 0.000003 TL <sup>4.4906</sup>	0.44489	0.94	×	3.37 ± 0.51

\* also included in Karpouzi and Stergiou (2003);  $n$  = number of individuals;  $MA_{\text{yr}}$  = mean MA;  $MA_{\text{min}}$  and  $MA_{\text{max}}$  = minimum and maximum MA values, respectively; SE = standard error;  $SE_b$  = standard error of slope  $b$ ;  $R^2$  = coefficient of determination; ToR = type of relation; E = exponential type; L = logarithmic type; Li = linear type; P = power type;  $\tau$  = trophic level value  $\pm$  standard error (SE), as estimated by Karachle and Stergiou (2006, 2008),  $\times$  indicates that  $b \neq 2$ .



**Fig. 1.** Regression between relative mouth area (RMA) and trophic level as estimated by Karachle and Stergiou (2006, 2008) ( $\tau$ ) for 61 fish species from the N-NW Aegean Sea, Greece, June 2001–January 2006; *Sarpa salpa* deviated from the trend, due to its low  $\tau$



**Figs. 2–3.** Regressions between total length (TL, in cm) and mouth area (MA, in  $\text{cm}^2$ ) for 61 fish species from the N-NW Aegean Sea, Greece, June 2001–January 2006 (Equations are given in Table 2); **Fig. 2.** All regressions of species separately; and **Fig 3.** regressions of groups of species, according to functional trophic groups (by Stergiou and Karpouzi 2002); **Green:** herbivores (trophic level ( $\tau$ ) = 2.0–2.1); **blue:** omnivores with preference to animal material (OA;  $2.9 < \tau < 3.7$ ); **black:** carnivores with preference to decapods and fish (CD;  $3.7 < \tau < 4.0$ ); **red:** carnivores with preference to fish and cephalopods (CC;  $4.0 < \tau < 4.5$ ); and **brown:** all species combined; Af = *Alosa fallax*, Aa = *Anthias anthias*, Ai = *Apogon imberbis*, Al = *Arnoglossus laterna*, Bb = *Belone belone*, Bo = *Blennius ocellaris*, Bob = *Boops boops*, Bp = *Bothus podas*, Cm = *Cepola macrophthalmalma*, Chl = *Chelidonichthys lucernus*, Cch = *Chromis chromis*, Cl = *Citharus linguatula*, Cj = *Coris julis*, De = *Dentex dentex*, Da = *Diplodus annularis*, Dv = *Diplodus vulgaris*, Ee = *Engraulis encrasicolus*, Eg = *Eutrigla gurnardus*, Gb = *Gaidropsarus biscayensis*, Gm = *Gaidropsarus mediterraneus*, Ls = *Lesueurigobius suerii*, Lb = *Lophius budegassa*, Lp = *Lophius piscatorius*, Mme = *Merlangius merlangus*, Mm = *Merluccius merluccius*, Mp = *Micromesistius poutassou*, Mh = *Monochirus hispidus*, Ms = *Mullus surmuletus*, Om = *Oblada melanura*, Paa = *Pagellus acarne*, Pab = *Pagellus bogaraveo*, Pae = *Pagellus erythrinus*, Pp = *Pagrus pagrus*, Pb = *Phycis blennoides*, Ps = *Pomatomus saltatrix*, Rc = *Raja clavata*, Sap = *Sardina pilchardus*, Sa = *Sardinella aurita*, Sas = *Sarpa salpa*, Su = *Sciaena umbra*, Scj = *Scomber japonicus*, Scs = *Scomber scombrus*, Sn = *Scorpaena notata*, Sp = *Scorpaena porcus*, Sc = *Scyliorhinus canicula*, Sec = *Serranus cabrilla*, Seh = *Serranus hepatus*, Ses = *Serranus scriba*, Ss = *Sphyraena sphyraena*, Spm = *Spicara maena*, Sps = *Spicara smaris*, Spc = *Spondylisoma cantharus*, St = *Symphodus tinca*, Syn = *Symphurus nigrescens*, Tom = *Torpedo marmorata*, Td = *Trachinus draco*, Tm = *Trachurus mediterraneus*, Tt = *Trachurus trachurus*, Tmi = *Trisopterus minutus*, Us = *Uranoscopus scaber*, Xn = *Xyrichtys novacula*.

Table 3

Horizontal mouth opening (HMO), vertical mouth opening (VMO), and mouth area (MA) expressed as the function of total length (TL) for 31 fishes from the North Aegean Sea, Greece, June 2001–January 2006, for which power type of the relation was statistically non-significant

Species	n	Horizontal Mouth Opening		Vertical Mouth Opening		Mouth area	
		HMO-TL	R <sup>2</sup>	VMO-TL	R <sup>2</sup>	MA-TL	R <sup>2</sup>
<i>Alosa fallax</i>	27	HMO = -0.0381 + 0.0656TL	0.92				
<i>Anthias anthias</i>	9	HMO = 0.5933e <sup>0.0548TL</sup>	0.74				
<i>Apogon imberbis</i>	31	HMO = 0.0458TL <sup>1.4769</sup>	0.25	VMO = -4.9542 + 3.0844Ln(TL)	0.48	MA = -11.379 + 5.977Ln(TL)	0.41
<i>Belone belone</i>	69	HMO = -0.0756 + 0.023TL	0.85	VMO = -0.0711 + 0.0326TL	0.73	MA = -0.8637 + 0.0427TL	0.89
<i>Blennius ocellaris</i>	20	HMO = -0.023 + 0.0684TL	0.85	VMO = 0.1106TL <sup>0.9283</sup>	0.66	MA = -0.4463 + 0.095TL	0.90
<i>Botilus podas</i>	20	HMO = 0.0338 + 0.0457TL	0.69	VMO = 0.1987 + 0.0682TL	0.65	MA = -0.4819 + 0.0785TL	0.73
<i>Chelidonichthys lucernus</i>	12			VMO = -2.0672 + 1.5434Ln(TL)	0.99		
<i>Dentex dentex</i>	9	HMO = -0.3161 + 0.0887TL	0.65			MA = -1.0807 + 0.1552TL	0.65
<i>Diplodus annularis</i>	406			VMO = 0.0666TL <sup>1.0422</sup>	0.59		
<i>Diplodus vulgaris</i>	47	HMO = -0.114 + 0.0596TL	0.81			MA = -0.4568 + 0.0728TL	0.84
<i>Gaidropsarus mediterraneus</i>	14	HMO = 0.1033TL <sup>0.8147</sup>	0.50	VMO = 0.6682e <sup>0.0576TL</sup>	0.61		
<i>Merluccius merluccius</i>	22			VMO = -5.5437 + 2.9759Ln(TL)	0.98	MA = -7.7644 + 0.7186TL	0.99
<i>Micromesistius putassou</i>	69			VMO = 0.0821 + 0.1306TL	0.93		
<i>Pagellus erythrinus</i>	53	HMO = 0.058TL <sup>0.984</sup>	0.51			MA = 0.0083TL <sup>1.7568</sup>	0.56
<i>Pagrus pagrus</i>	6			VMO = -2.1632 + 1.3853Ln(TL)	0.72	MA = -1.9984 + 1.0966Ln(TL)	0.81
<i>Sardina pilchardus</i>	738					MA = 0.0025TL <sup>1.9902</sup>	0.66
<i>Sardinella aurita</i>	217					MA = 0.0842e <sup>0.1214TL</sup>	0.80
<i>Sarpa salpa</i>	25						
<i>Sciaena umbra</i>	10	HMO = 0.2753e <sup>0.0917TL</sup>	0.63	VMO = 0.0403 + 0.0521TL	0.82	MA = 0.1078e <sup>0.1726TL</sup>	0.79
<i>Scorpaena scorpius</i>	198			VMO = -3.54 + 1.9411Ln(TL)	0.89		
<i>Scorpaena porcus</i>	90			VMO = -5.2893 + 2.7087Ln(TL)	0.89		
<i>Scyliorhinus canicula</i>	34	HMO = 0.0617TL <sup>1.0596</sup>	0.77	VMO = 0.0153 + 0.2055TL	0.92	MA = 0.0048TL <sup>1.9347</sup>	0.73
<i>Serranus cabrilla</i>	41			VMO = 0.0992TL <sup>0.8751</sup>	0.43	MA = -4.3732 + 0.5209TL	0.90
<i>Serranus hepatus</i>	120			VMO = -0.0006 + 0.1754TL	0.84	MA = 0.0106TL <sup>2.1335</sup>	0.83
<i>Serranus scriba</i>	84					MA = -4.3143 + 0.5265TL	0.75
<i>Sphyræna sphyraena</i>	102	HMO = 0.0389TL <sup>1.0719</sup>	0.33			MA = 0.0089TL <sup>1.7465</sup>	0.41
<i>Spicara maena</i>	271	HMO = 0.0506TL <sup>0.9426</sup>	0.54				
<i>Spicara smaris</i>	106			VMO = 0.0714TL <sup>1.0567</sup>	0.79		
<i>Symphurus nigrescens</i>	9	HMO = -0.2551 + 0.2398Ln(TL)	0.95				
<i>Trachinus draco</i>	23	HMO = 0.0256 TL <sup>1.3688</sup>	0.45	VMO = 0.1966TL <sup>0.8407</sup>	0.64	MA = 0.0037TL <sup>2.2331</sup>	0.57
<i>Trachurus mediterraneus</i>	585			VMO = 0.1966TL <sup>0.8407</sup>	0.64	MA = 0.0044TL <sup>2.0313</sup>	0.82

n = number of individuals, R<sup>2</sup> = coefficient of determination.



Table 4

Type of relations between horizontal mouth opening (HMO), vertical mouth opening (VMO), and mouth area (MA) with total length (TL) for 61 fishes from the North Aegean Sea, Greece, June 2001–January 2006

Type of relation		HMO*	VMO*	MA*
Power ( $b \neq 1$ or 2 statistically significant)	$Y = aX^b$	45 (73.8)	42 (70.0)	42 (68.9)
( $b \neq 1$ or 2 statistically non-significant)		7 (11.5)	5 (8.3)	7 (11.5)
Linear	$Y = a + bX$	6 (9.8)	6 (10.0)	8 (13.1)
Exponential	$Y = ae^{bX}$	2 (3.3)	1 (1.67)	2 (3.3)
Logarithmic	$Y = a + b \ln X$	1 (1.6)	6 (10.0)	2 (3.3)
Positive allometry	$b > 1$ or 2	45 (73.8)	25 (41.7)	37 (60.7)
Negative allometry	$b < 1$ or 2	16 (26.2)	35 (58.3)	24 (39.3)

\* Number of species (percentages are given in parentheses).

## DISCUSSION

In the presently reported study all relations between mouth characteristics (HMO, VMO, and MA) and TL were significant. The allometric model was the dominant model describing the above-mentioned relations, since it accounted for more than 2/3 of the species examined. The same has been reported for other species (Honda 1984, Eggold and Motta 1992, Karpouzi 2001, Lukoschek and McCormick 2001, Karpouzi and Stergiou 2003, Chalkia and Bobori 2006), although other types of models have also been reported (e.g., Erzini et al. 1997, Scharf et al. 2000, Ward-Campbell et al. 2005). The prevalence of the allometric relation could be attributed to the fact that, as fish grow in size the amount of energy required is gradually increasing. In order for the organism to meet the new energetic demands, it is essential to modify its structural capacity (Galis et al. 1994), in order for larger amounts of food and/or bigger size food items to be consumed. An allometric growth of the mouth would ensure that these increased energetic demands will be met, while at the same time the energy required for the acquisition of food will be significantly reduced (i.e., higher amounts of food consumed in fewer feeding attempts). This is consistent with the optimal foraging theory (Gerking 1994). In the majority of cases, MA–TL and HMO–TL relations were positive allometric, while in the case of VMO–TL negative allometry prevailed. The latter can mainly be attributed to the fact that VMO is largely dependent on the bone structure of the skull, whereas HMO is more affected by the muscles and the structure of lips. Additionally, the slower increase of VMO in relation to TL, might be balanced by the way the four-bar-linkage system of the buccal cavity (Gerking 1994, Muller 1996) operates, an hypothesis that need further investigation.

Relations between HMO, VMO, and MA, and TL from the Greek seas are also available for 18 species in the Cyclades (Karpouzi and Stergiou 2003), of which 13 are also included in this study (Tables 1 and 2). In six cases (i.e., *Boops boops*, *Diplodus annularis*, *Diplodus vulgaris*, *Mullus surmuletus*, *Scorpaena porcus*, and *Symphodus tinca*), the type of the relation presented here agreed with those reported by Karpouzi and Stergiou (2003). In the remaining seven cases (i.e., *Merluccius*

*merluccius*, *Pagellus acarne*, *Pagellus erythrinus*, *Serranus scriba*, *Spicara maena*, *Spondyllosoma cantharus* and *Trachurus mediterraneus*) the type of model was different in the two studies. Such differences could be attributed to the following:

1. Different number of specimens [higher in Karpouzi and Stergiou (2003) for: *M. merluccius*, *P. acarne*, *P. erythrinus*, *S. maena*; and lower for the remaining three] and/or their length range (where it differed noticeably for *M. merluccius*, *P. erythrinus*, *S. cantharus*, *T. mediterraneus*);
2. Different fishing gears used for sampling [in Karpouzi and Stergiou (2003), specimens were caught using only longlines and gillnets]; and
3. Differences in the quality and/or quantity of available food sources in the different habitats.

Additionally, the validity of the power model was not evaluated statistically by Karpouzi and Stergiou (2003). Nevertheless, usage of such relations should be restricted to the observed length ranges, since many morphologic characteristics are being affected by body size (Piet 1998).

Our results showed that there is a strong positive relation between MA and  $\tau$ , regardless of TL, indicating that the more carnivorous is a species, the larger is the mouth area, a fact agreeing with the findings of Karpouzi and Stergiou (2003). This also includes small pelagic filter feeders (e.g., anchovies, sardinellas, and sardines) that in general have a relatively low trophic level but relatively large mouth size for their body size. Indeed, when the effect of body size is removed (i.e., estimation of RMA), these species do not deviate from the general trend line. There is only one species that deviated, *Sarpa salpa*, which has a herbivorous diet (Karachle and Stergiou 2008, Froese and Pauly 2011) and thus a  $\tau = 2$ . This was also clearly revealed when all MA–TL regressions were plotted together. Indeed, MA increased faster with length for carnivorous species than for omnivorous ones, a fact that coincides with the findings of Karpouzi and Stergiou (2003). In general, species with greater mouth gape tend to consume larger prey (Piet 1998). Thus, as proposed by Hugueny and Pouilly (1999) mouth gape could be a good indicator of piscivory in fishes, as well as an indicator of ontogenetic shift in the feeding habits of a given species.

Establishing general relations between mouth characteristics and trophic levels (and body length) for a large number of species differing in size, shape and habitat will allow us to estimate trophic level of species for which no information on their diet is available. Such estimates are essential for developing of ecosystem-based models for fisheries management, where trophic level values are key parameters.

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