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Zhrnutie poznatkov o morských hlaváčoch v Stredozemnom mori

Review of knowledge on the Mediterranean marine gobies

Bakalárska práca

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Prehlásenie:

Prehlasujem, že som záverečnú prácu spracovala samostatne a že som uviedla všetky použité informačné zdroje a literatúru. Táto práca a ani jej podstatná časť nebola predložená k získaniu iného alebo rovnakého akademického titulu.

V Prahe, 15.5.2015

Podpis

Pod'akovanie:

Najviac by som sa chcela pod'akovať mojej školiteľke RNDr. Jasne Vukićovej, Ph.D., za jej trpezlivosť, odborný dohľad a pomoc pri spracovávaní práce. Za pomoc so zháňaním materiálov ďakujem Mgr. Radekovi Šandovi, Ph.D. Ďalej moje pod'akovanie patrí mojej rodine a priateľom za nekonečnú podporu, cenné rady a za to, že akceptovali moju zaneprázdnenosť počas tohto obdobia.

Abstrakt

Hlaváče sú malé nenápadné ryby, ktoré sa vyskytujú v morskom, brakickom a sladkovodnom prostredí. Tvoria veľmi početnú skupinu a v súčasnosti rozpoznávame viac ako 1700 druhov a približne 260 rodov. Sú celosvetovo rozšírené v pobrežných vodách s výnimkou arktických a antarktických oblastí. Viac ako polovica sa vyskytuje v tropických moriach. V Stredozemnom mori je aktuálne známych 60 druhov, ktoré rozpoznávajú štyri typy habitatov: bentický, kryptobentický, hyperbentický a nektonický. Európske hlaváče boli rozdelené do troch odlišných línií. Vo všetkých týchto líniách sú severo-východné atlantické a stredozemné druhy umiestnené spoločne, čo dokazuje spoločný vývoj hlaváčov z týchto dvoch vodných más. V každej tejto európskej línii hlaváča môže byť pozorovaná pestrosť ekologických a biologických vlastností. Nektonický spôsob života sa vyvinul trikrát nezávisle na sebe v priebehu evolúcie. Napriek tomu, že sú druhovo najbohatšia čeľaď rýb v Stredozemnom mori, existuje o nich ešte stále málo informácií. V niektorých prípadoch naše poznatky o geografickom rozšírení sú založené iba na niekoľkých nálezoch. Životnosť a reprodukcia je známa iba u tretiny druhov. Táto práca je zhrnutie zverejnených údajov o hlaváčovitých rybách v Stredozemnom mori. Pre veľkú časť druhov sú v znalostiach mnohých aspektov biológie a ekológie značné medzery. Najviac študované druhy sú tie, ktoré sú ľahko zozbierané bežnými rybárskymi technikami.

Kľúčové slová

hlaváče, Gobiidae, Stredozemné more, ryby, ekológia, biológia, distribúcia, fylogenetika

Abstract

Gobies (Gobiidae, Perciformes) are small, inconspicuous fishes occupying marine, brackish and freshwater environments. They are very abundant group, with more than 1,700 species and around 260 genera currently recognised. Gobies have worldwide geographical distribution in coastal waters with exceptions of Arctic and Antarctic areas. More than half species occur in tropical seas. In the Mediterranean Sea, 61 species are known up to date, which inhabit four main types of habitats: benthic, cryptobenthic, hyperbenthic and nektonic. The European gobies were assigned to three distinct lineages. In all these lineages, north-east Atlantic and Mediterranean species are placed together, which evidences common evolution of the gobies from these two water masses. A variety of ecological and biological traits can be seen within each of the European goby lineage. The nektonic way of life evolved three times independently in the course of evolution. Although Gobiidae are the most specious fish family in the Mediterranean, there is still little information about most of the species. In some cases, the assumption on geographical distribution is based just on several findings. The life-span and reproduction is known for about one third of species. This work is a summarization of the published data about the gobies in the Mediterranean Sea. There are considerable gaps in knowledge of many aspects of biology and ecology for large part of the species. The most studied species are those, which are easily collected by common fisheries techniques.

Key words

gobies, Gobiidae, Mediterranean Sea, fishes, ecology, biology, distribution, phylogeny

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1. Introduction

Gobies are small fishes belonging to the family Gobiidae. They are abundant components of the ichthyofauna of marine and brackish fish communities, while only a small number of goby species are fully adapted to freshwater environments (Tornabene et al. 2013). Due to their generally small size and tendency to morphological reduction of some characters in evolution (e.g., head lateral-line and pore and papillae system, number of scales), our knowledge of their relationships and actual diversity has not been properly explored (Tornabene et al., 2013). They have worldwide geographical distribution with exceptions of Arctic and Antarctic areas (Iwata et al., 2000). Gobies exhibit a spectacular diversity in morphology, ecology and behaviour (Rüber and Agorreta, 2011).

Gobies (family Gobiidae) belong to the suborder Gobioidi of the order Perciformes. In general, we distinguish 270 genera and approximately 2200 species of Gobioidi, which makes it one of the largest suborders of Teleostei (Nelson, 2006). According to Agorreta et al. (2013) the suborder Gobioidi can be divided into seven families: Kurtidae, Apogonidae, Rhyacichthyidae, Odontobutidae, Eleotrididae, Butidae and Gobiidae. There are also other divisions of other authors (Thacker, 2009; Thacker and Hardman, 2005; Tornabene et al., 2013), which differ in higher systematics, but the work of Agorreta et al., (2013) one can be considered the most complex one. In the Mediterranean Sea only representatives of the most numerous family Gobiidae occur (Agorreta et al., 2013). As much as around 260 genera and at least 1700 species belong to this family (Tornabene et al., 2013). The most frequent are small marine benthic species (Thacker, 2003). They represent the most abundant and specious fish family in the Mediterranean Sea, with 61 species currently recognised (Fricke et al., 2007; Kovačić and Patzner, 2011; Miller, 2003). 20 species are strict Mediterranean endemics, whose distribution is restricted to in between the Strait of Gibraltar and the Bosphorus (Franco et al., 2012a; Kovačić and Patzner, 2011; Neilson and Stepien, 2009).

The Mediterranean Sea represents a semi-enclosed basin with complicated circulation (Mejri et al., 2009). It is spatially restricted sea and almost completely enclosed by land as it is surrounded by three continents (Africa, Asia and Europe) (Lasram et al., 2009). The western and eastern parts of the Mediterranean Sea are separated by the Siculo-Tunisian Strait (Lasram et al., 2009). Two peninsulas, Apennine and Balkan, divide the Mediterranean Sea

into distinct marine provinces or sub-basins (Mejri et al., 2011). Mediterranean sub-basins exhibit different hydrographic and ecological features and are variously interconnected (Agostini and Bakun, 2002).

The main characteristic of the Mediterranean which differentiates it from other seas is its high salinity (Emeis et al., 2000). An average salinity is about 38 ppt and it gradually decreases from southeast to northwest. That is given by the fact that there is an inflow of a less saline surface current of cold Atlantic oceanic water (which is counterbalanced by outflow of warm saline Mediterranean deep water) (Gysels et al., 2004; Topper and Meijer, 2015). Moreover, the eastern part of the Mediterranean is characterized by strong evaporation and so sea level tends to decrease (Topper and Meijer, 2015). The surface water temperature varies with season. In winter it ranges from 9°C to 17°C and in summer from 20°C to 30°C (Kovačić and Patzner, 2011; Topper and Meijer, 2015).

According to Kovačić & Patzner (2011), the species richness of gobies divides Mediterranean Sea into six zoogeographic areas. The highest diversity is along the north Mediterranean coast, where 43 (Balearic and Ligurian Seas) and 46 (Adriatic Sea) gobiid species occur, a little less, 29 (Levantine Sea) and 37 (Aegean and Ionian Seas) species, are in two Mediterranean eastern areas. The lowest diversity of gobies is in the south, along the African coast with just 10 (south-western part) and 12 (south-eastern part) gobiid species currently known, see Fig. 1. The species composition differs in various places of the Mediterranean Sea (Kovačić et al., 2013). The highest number (14 (Kovačić and Patzner, 2011)) of endemic species occurs in the northern part of the Mediterranean, e.g. *Speleogobius trigloides*, *Didogobius schlieweni* and *Gobius kolombatovici*. In contrast, the middle part of north African coast, which is the poorest area in terms of number of strict Mediterranean goby endemics hosts only one such species, *Pomatoschistus tortonesei* (Kovačić and Patzner, 2011). New species are still being described from the Mediterranean (Francour, 2008; Kovačić and Golani, 2007a, 2007b; Vanhove et al., 2011).

The fauna of Mediterranean Sea is influenced by several factors. The fact, that some parts of the sea are more species rich than others, may be caused by differences in abiotic factors like temperature, salinity, currents etc. In addition, in case of inconspicuous species, such gobies are, the number of known species is influenced by a research effort at a given place. Ship transport certainly contributes to the dispersal of gobies by gripping bottom of boat or involuntary entry into ballast-water tanks (Ahnelt and Dorda, 2004; Gysels et al.,

2004). One example of a goby species introduced to the Eastern Mediterranean via ballast water in vessels is *Tridentiger trigonocephalus* (Goren, 2009). Moreover, aquariology, trade of living bait and even scientific research contribute to the spread of introduced species in the Mediterranean Sea (Bianchi and Morri, 2000). Composition of the marine Mediterranean fauna is continually changing due to influence of climate (Bianchi and Morri, 2000).

There is still little known about the biology, ecology and distribution of most marine goby species in Mediterranean Sea. These data are needed to understand their role in the aquatic food webs (Ahnelt and Dorda, 2004).

The aim of this thesis is to collect available data about biology, ecology, distribution and phylogeny of marine gobies in the Mediterranean Sea, to evaluate which information about the Mediterranean marine gobies is still missing, and which species are still poorly known.

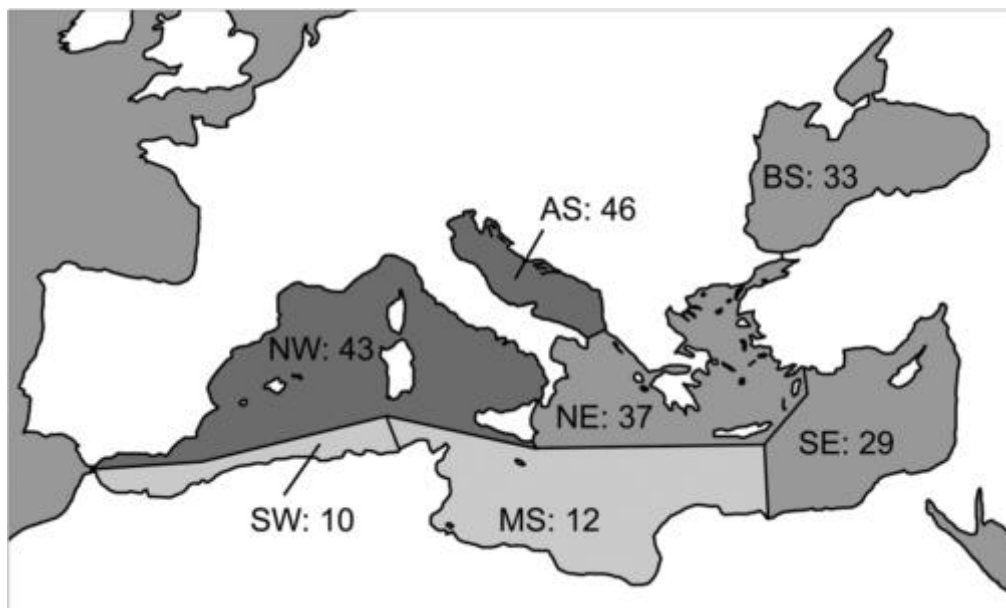


Figure 1 - Diversity representatives of the family Gobiidae in different parts of the Mediterranean and Black Sea (Patzner et al., 2011)

2. Origin, evolution and phylogeography

Suborder Gobioidae belongs to the order Perciformes of the teleost fishes. The age of this suborder is estimated to be nearly 80 million years (Betancur-R et al., 2013). The family Gobiidae evolved approximately 65 million years ago (Betancur-R et al., 2013). The origin of gobies in the Mediterranean Sea is still not resolved. It is, among other factors, closely linked to the geological history of the Mediterranean Sea, which is still not entirely uncovered.

In the late Miocene, the collision of African and Euroasian plates escalated in the desiccation of the Mediterranean known as “Messinian salinity crisis”. It happened about 5.96 million to 5.33 years ago (Hsü et al., 1977) and it was accompanied by a large animal extinction (Bianchi and Morri, 2000). Evaporation caused a drop in a sea level about 1.5 kilometres (Hsü et al., 1973). As a consequence, almost all the former marine fauna disappeared. Later, in “Lago Mare” phase of “salinity crisis”, the Mediterranean and Paratethys seas transformed the structure and created large evaporitic lakes (Bianchi and Morri, 2000; Kovačić and Patzner, 2011). Since the end of the Miocene the Strait of Gibraltar created the connection between the western part of Mediterranean Sea and the Atlantic Ocean (Blanc, 2002). After the opening of the Strait of Gibraltar, a massive invasion of marine biota of Atlantic origin began to occupy the Mediterranean (Goren, 2009) what led to the evolution of gobies in the Mediterranean Sea and their rapid radiation (Huysse et al., 2004). They adapted to wide range of habitats, characterised by different salinities and substratum types (Malavasi et al., 2005). This colonisation probably occurred repeatedly.

According to the hypothesis of Garcia-Castellanos & Villaseñor (2011), the connection of the Mediterranean Sea with the Atlantic Ocean was not completely lost during the Messinian salinity crisis. The sea level drawdown during the early stages of the crisis was only moderate (Garcia-Castellanos and Villaseñor, 2011). If this theory is true, the original gobies may have survived in a newly isolated Mediterranean Sea from the Tethys, and their origin in the Mediterranean can be thus from the common ancestors from the Tethys. These assumptions can be considered partly corroborated by results of Agorreta et al. (2013), which show that sister groups of all European goby clades are clades consisting of goby species currently occurring in Indo-Pacific. On the other hand, as the age of European clades of gobies is not known, immigrations of gobies from the Indo-Pacific to the north-eastern

Atlantic and Mediterranean basins (around the African Cape region) may have repeatedly occurred later (Agorreta et al., 2013).

During Pleistocene glaciation, the alternation of the glacial and warmer interglacial phases resulted in invasion of the Mediterranean which acted like a refuge for warm water Atlantic fauna of boreal or subtropical origin (Almada et al., 2001; Bianchi and Morri, 2000). During this period of alterations of climatic conditions and sea level, the colonisation of the Mediterranean Sea probably occurred repeatedly.

The next important milestone was opening of the Suez Canal in 1869, where organisms from the Red Sea started to migrate into the Mediterranean Sea (Kovačić and Patzner, 2011). They are known as Lessepsian immigrants and to date six species of these nonindigenous gobies (*Papillogobius melanobranchus* (Kovačić and Golani, 2007a), *Oxyurichthys petersii* (Akyol et al., 2006), *Coryogalops ochetica* (Kovačić and Golani, 2007a), *Silhouetta aegyptia* (Golani et al., 2006), *T. trigonocephalus* (Goren, 2009) and *Trypauchen vagina* (Salameh et al., 2010)) (Salameh et al., 2010) were reported from Eastern Mediterranean.

Genetic structure of marine gobies is affected by life history traits, environmental conditions, paleogeographic and paleoclimatic events. Hence the species might be influenced differently by the same habitat conditions and recent history (Giovannotti et al., 2009). Extension and adaptation to new environment might have led to the radiation which is responsible for the composition of actual ichthyofauna (Huyse et al., 2004). In conclusion, the origin of gobiid species in the Mediterranean Sea is still poorly understood, because of lacking data on distribution and thorough phylogenetic studies, which would include all known species of gobies.

2.1 Phylogenetics

There is a trend towards specialization and degeneration of morphological characters of gobies due to wide ecological diversification among them (Iwata et al., 2000). Hence the classification of the genera into families and subfamilies based on morphology might be sometimes very difficult. It is not so easy to identify morphological characters which would show phylogenetic information (Iwata et al., 2000).

In the European goby fauna two different groups were traditionally recognised based on morphological characterization. Those are the “transverse” and “sand gobies”, which were diagnosed mostly by the differences in the head lateral line system. According to Thacker & Roje (2011) European gobies belong to the family Gobiidae with the exception of *Pomatoschistus* and, implicitly, genera closely related to it (*Gobiusculus*, *Knipowitschia*, *Economidichthys*), belonging to sand goby group, which these authors placed in the family Gobionellidae. Later, Thacker (2013) assigned sand gobies to the *Mugilogobius* lineage.

Based on the results of the comprehensive multilocus phylogeny of gobioids, encompassing most major lineages, by (Agorreta et al., 2013), currently, all European goby species are placed to the Gobiidae family. Within this family there are two major subclades recognised, the gobiine-like gobiids and the gobionelline-like gobiids, each of them consisting of several monophyletic groups (Agorreta et al., 2013).

The European gobies were assigned to three distinct, independently evolved lineages, one of them belonging to the gobionelline-like gobiids (designated as *Pomatoschistus*-lineage) and two belonging to the gobiine-like gobiids (*Aphia*-, and *Gobius*-lineages). This fact corroborates the assumption of repeated colonisation of the Mediterranean Sea by gobies. The *Pomatoschistus*-lineage comprises of genera traditionally assigned to the European “sand gobies”, and of six other European Atlantic-Mediterranean genera (*Buenia*, *Deltentosteus*, *Lebetus*, *Speleogobius*, *Crystallogobius* and *Pseudaphya*) (Agorreta et al. 2013). The majority of the native European goby genera are placed in the *Gobius*-lineage, together with all Ponto-Caspian genera included in the study, and several African genera (endemic to the eastern and southern African coast). This lineage contains also all cryptobenthic Mediterranean species (Agorreta et al., 2013). *Aphia*-lineage contains two ecologically distinct groups, pelagic (nectonic) genus *Aphia* and genus *Lesueurigobius*, inhabiting burrows in sand in deeper waters (Agorreta et al., 2013).

In all these three lineages, north-east Atlantic and Mediterranean species are placed together (Agorreta et al., 2013), which evidences common evolution of the gobies from these two water masses. A variety of ecological and biological traits can be seen within each of the European goby lineage. The nectonic way of life evolved three times independently in the course of evolution, in two European lineages. Sister lineages to all three European goby lineages are lineages with current distribution of species in Indo-Pacific (Agorreta et al.,

2013). This gives the indication of the origin of the European (and thus Mediterranean) goby species.

Although the study of Agorreta et al. (2013) greatly contributed to the clarification of the relationships between gobies, as the authors concluded by themselves, a detailed study at the species level and the use of relaxed molecular clock analyses is necessary in order to clarify the origin of European gobies.

Table 1 - List of marine gobies occurring in the Mediterranean Sea and their ecological and biological characteristic

species	lineage	life-styles	habitat	distribution	reproduction	eggs	food	max. size (cm)	life-span (year)	depth (m)	references
<i>Aphia minuta</i> (Risso, 1810)	A	Nc	Sd, Gr, Md, Sg	E At, Bt, N Wp Mt (Lg), S Wp Mt, NC Mt (Ad, Tr), N Ep Mt, S Ep Mt, Bl, Az	April-September	900-7000	+	6	1	2.5-100	1, 2, 3, 4, 5
<i>Buenia affinis</i> Iljin, 1930	P	Eb	Sd, Rk	NC Mt (Ad, Tr), N Wp Mt (Lg), N Ep Mt	February-July	457-714	+	3.8	1	3-25	1, 2, 6, 78
<i>Corcyrogobius liechtensteini</i> (Kolombatovic, 1891)	G	Cb	Cv, Hl, Rk	N Wp Mt (Br), NC Mt (Ad, Tr), N Ep Mt (Ag)				3		0.5-90	1, 10, 11, 12, 13, 19, 81
<i>Coryogobius ochetica</i> * (Norman, 1927)	G		Rk, Sd	S Ep Mt							9, 14, 15
<i>Crystalllogobius linearis</i> (Düben, 1845)	P	Nc	Sd, Md	E At, N Wp Mt (Lg), NC Mt (Ad, Tr), N Ep Mt (Ag)	May-September	340	+	4.7	1	1-400	1, 2, 8, 13, 79
<i>Deltentosteus colonianus</i> (Risso, 1820)	P	Eb	Sg, Sd	SE At, NC Mt (Ad), N Ep Mt, S Ep Mt (Lv)				7		5-120	1, 8, 14, 81
<i>Deltentosteus quadrimaculatus</i> (Valenciennes, 1837)	P	Eb	Sd, Md	E At, N Wp Mt (Br), NC Mt (Ad), N Ep Mt, S Ep Mt (Lv), SC Mt	February-May			9.2	5	0-333	8, 13, 16, 17, 30, 70
<i>Didogobius bentuvii</i> Miller, 1966	G	Cb		S Ep Mt				3.65			8, 9, 14
<i>Didogobius schlieveni</i> Miller, 1993	G	Cb	Sg	N Wp Mt, NC Mt (Ad)				5		1.5-14	13, 18
<i>Didogobius splechnai</i> Ahnelt & Patzner, 1995	G	Cb	Sd, Rk, Cv	N Wp Mt (Br, Lg), NC Mt (Ad, Tr), N Ep Mt (Ag), SC Mt				3.8		2-56	12, 18, 19, 20, 30
<i>Gammogobius steinitzi</i> Bath, 1971	G	Cb	Cv, Rk	N Wp Mt (Br), NC Mt (Ad, Tr), Bl				3.8		3-43	8, 10, 12, 20, 21
<i>Gobius ater</i> Bellotti, 1888	G	Cb	Sg	N Wp Mt (Br), NC Mt (Ad), N Ep Mt				7.1		2.5-10	8, 13
<i>Gobius auratus</i> Risso, 1810	G	Eb	Rk, St	N Wp Mt (Lg), NC Mt (Ad), N Ep Mt, S Ep Mt, Bl			+	10		5-35	7, 10, 13, 23, 49
<i>Gobius bucchichi</i> Steindachner, 1870	G	Eb	Sd, Md, Sg	E At, S Wp Mt (Al), N Wp Mt, NC Mt, N Ep Mt, S Ep Mt (Lv), SC Mt, Bl	June-August	1200-10200	+	10	5	0-5	2, 5, 7, 8, 14, 24, 25, 49
<i>Gobius cobitis</i> Pallas, 1814	G	Eb ¹	Rk, Gr	E At, N Wp Mt, S Wp Mt, NC Mt (Ad), N Ep Mt, S Ep Mt (Lv), SC Mt, Bl	March-July	2000-12000	+	30	10	1-10	2, 8, 13, 14, 26, 37

species	lineage	life-styles	habitat	distribution	reproduction	eggs	food	max. size (cm)	life-span (year)	depth (m)	references
<i>Gobius couchi</i> Miller & El-Tawil, 1974	G	Eb	St, Md, Sd, Sg	E At, N Wp Mt, NC Mt (Tr, In, Ad), N Ep Mt (Ag), S Ep Mt			+	9	6	3-22	8, 10, 28, 52, 81
<i>Gobius cruentatus</i> Gmelin, 1789	G	Eb	Rk, Sd, Sg	E At, N Ep Mt, S Ep Mt, NC Mt (Ad, Tr), N Ep Mt, S Ep Mt, SC Mt, Bl				18		1.7-40	2, 5, 8, 29
<i>Gobius fallax</i> Sarato, 1889	G	Eb	Sd, Rk, St	N Wp Mt, NC Mt (Ad), N Ep Mt (Ag), N Sp (Lv)				9		1-32	8, 10, 14, 23, 28, 71
<i>Gobius gasteveni</i> Miller, 1974	G	Eb	Sd, Md, St	E At, N Wp Mt (Br, Al)				12		12-180	8, 30, 31
<i>Gobius geniporus</i> Valenciennes, 1837	G	Eb	Rk, Sd, Md, Sg	N Wp Mt (Br), NC Mt (Ad), N Ep Mt (Ag), S Ep Mt, SC Mt	April- May		+	22			5, 8, 10, 14, 71
<i>Gobius kolombatovici</i> Kovačić & Miller, 2000	G	Eb	Rk, Sd, Gr	N Wp Mt, NC Mt (N Ad)				10		15-60	13, 32, 86
<i>Gobius niger</i> Linnaeus, 1758	G	Eb	Sd, Md, Sg	E At, Bt, N Wp Mt, S Wp Mt, NC Mt (Ad), N Ep Mt, S Ep Mt, SC Mt, Bl	March-October	700-37600	+	16.5	3-5	1-96	1, 2, 8, 30, 33, 35, 36, 49, 71, 77, 80, 85
<i>Gobius paganellus</i> Linnaeus, 1758	G	Eb ¹	St, Rk, Gr	E At, Bt, N Wp Mt, S Wp Mt, NC Mt (Ad), N Ep Mt, S Ep Mt, SC Mt, Bl	January-May	1000-14000	+	16.5	10	1-15	2, 8, 37, 38, 39, 40, 49, 71
<i>Gobius roulei</i> de Buen, 1928	G	Eb	Sd, St	E At, N Wp Mt (Br, Lg), NC Mt (Ad), N Ep Mt (Ag), S Ep Mt	April-August	1200-8000	+	8	7	3-385	5, 8, 30, 41, 71
<i>Gobius vittatus</i> Vinciguerra, 1883	G	Eb	Rk, Sd	N Wp Mt, S Wp Mt (Al), NC Mt (Ad), N Ep Mt (Ag), S Ep Mt (Lv)	April-July	560-3045	+	5.8	4	15-85	1, 10, 42, 43, 44, 71
<i>Gobius xanthocephalus</i> Heymer & Zander, 1992	G	Eb	Cv, St, Rk, Sd	E At, N Wp Mt (Br, Lg), NC Mt (Ad)				9.4		1-36	13, 45
<i>Chromogobius quadrivittatus</i> (Steindachner, 1863)	G	Cb	St, Sg, Rk, Sd	N Wp Mt (Br), NC Mt, N Ep Mt, S Ep Mt (Lv), Bl			+	6.55	2-3	0-2	8, 13, 19, 20, 46
<i>Chromogobius zebratus</i> (Kolombatovic, 1891)	G	Cb	St, Cv, Rk, Sd	SE At, N Wp Mt, NC Mt (Ad, In), N Ep Mt (Ag), S Ep Mt (Lv), Bl				5.3		1-12	8, 10, 12, 20, 46, 87
<i>Knipowitschia caucasica</i> (Berg, 1916)	P	Eb	Sg	N Ep Mt (Ag), Bl, Az	March-July	220-500	+	5.8	2		8, 88, 89, 96

species	lineage	life-styles	habitat	distribution	reproduction	eggs	food	max. size (cm)	life-span (year)	depth (m)	references
<i><u>Knipowitschia panizzae</u></i> (Verga, 1841)	P	Eb	Md	NC Mt (Ad, In)	March-June		+	4			47, 48, 49, 96
<i>Lebetus guilleti</i> (Le Danois, 1913)	P	Eb	Sd	E At, NC Mt (N Ad)				2.5		6-30	1, 8, 13, 51, 81
<i>Lesueurigobius friesii</i> (Malm, 1874)	A	Eb	Sd, Md	E At, S Wp Mt (Al), NC Mt				11		47-117	1, 8, 51
<i>Lesueurigobius sanzoi</i> (de Buen, 1918)	A	Eb	Sd, Md	E At, S Wp Mt (Al), NC Mt				11		47-117	1, 8, 51
<i>Lesueurigobius suerii</i> (Risso, 1810)	A	Eb	Sd, Md	E At, N Wp Mt, NC Mt (Ad, In), N Ep Mt, S Ep Mt (Lv)				5		5-445	2, 8, 30, 51
<i><u>Millerigobius macrocephalus</u></i> (Kolombatovic, 1891)	G	Cb	Cv, Sd, St	N Wp Mt, NC Mt (Ad), N Ep Mt (Ag), S Ep Mt (Lv)				4.35		4-13	1, 8, 10, 12, 52, 55
<i>Neogobius melanostomus</i> (Pallas, 1814) ?	G	Eb	Gr, Sd, Md, Rk, St	Bt, N Ep Mt, Bl, Az	May-September	328-5221	+	25	3-4	20-60	8, 9, 53, 54, 95
<i><u>Odondebuena balearica</u></i> (Pellegrin & Fage, 1907)	G	Cb	Md, Cv	N Wp Mt (Br), NC Mt (Ad, In, Tr), N Ep Mt (Ag), S Ep Mt				3.6		11-70	1, 8, 13, 28, 30, 56
<i>Oxyurichthys petersii</i> * (Valenciennes, 1837)			Md, Sd	N Ep Mt (Ag), S Ep Mt			+	12.2		35-50	8, 15, 57, 72
<i>Papillogobius melanobranchus</i> * (Fowler, 1934)		Eb		S Ep Mt (Lv)							14, 15, 58
<i>Pomatoschistus bathi</i> Miller, 1982	P	Eb	Sd, Gr	N Wp Mt (Lg), NC Mt (Ad), N Ep Mt (Ag), Bl				3.5		1-14	8, 13, 59
<i><u>Pomatoschistus canestrini</u></i> (Ninni, 1883)	P	Eb	Md	NC Mt (N Ad)	March-June		+	6.4			47, 48, 49
<i><u>Pomatoschistus knerii</u></i> (Steindachner, 1861)	P	Hb	St, Rk	N Wp Mt, NC Mt (Ad), N Ep Mt				4		0-30	2, 5, 8, 13, 81
<i>Pomatoschistus marmoratus</i> (Risso, 1810)	P	Eb	Sd, Md	E At, N Wp Mt, S Wp Mt, NC Mt (Ad), N Ep Mt, S Ep Mt (Sc), Bl, Az	March-September	307-1226	+	8	2	20-70	1, 6, 8, 13, 64, 65
<i>Pomatoschistus microps</i> (Krøyer, 1838)	P	Eb	Sd, Md	E At, Bt, N Wp Mt, S Wp Mt, SC Mt	March to June	460-2030	+	6.4	2	1-11	6, 8, 13, 33, 60, 61, 62
<i>Pomatoschistus minutus</i> (Pallas, 1770)	P	Eb	Sd, Md, Sg	E At, Bt, N Wp Mt, S Wp Mt (Al), NC Mt (Ad, Tr), N Ep Mt (Ag), Bl, Az	February-July	998-5100	+	11	2,7	2-200	2, 8, 13, 30, 33, 63, 66, 81

species	lineage	life-styles	habitat	distribution	reproduction	eggs	food	max. size (cm)	life-span (year)	depth (m)	references
<i>Pomatoschistus norvegicus</i> (Collett, 1902)	P	Eb	Md, Sd	E At, N Wp Mt, NC Mt (Ad,Tr), N Ep Mt (Ag), S Ep Mt	March-July	1200-3800	+	8		6-325	8, 13, 30, 67, 81, 94
<i>Pomatoschistus pictus</i> (Malm, 1865)	P	Eb	Sd, Md, Gr	E At, N Wp Mt, NC Mt (Ad), N Ep Mt, S Ep Mt	February-July	669-4690	+	6	2	1-55	6, 8, 51, 68
<i>Pomatoschistus quagga</i> (Heckel, 1837)	P	Hb	Sd, Rk	N Wp Mt, S Wp Mt (Al), NC Mt (Ad), N Ep Mt (Ag)				6	3-20		5, 49, 69
<i>Proterorhinus marmoratus</i> (Pallas, 1814) ?	G	Eb	St, Sg	N Ep Mt, N Sp Mt (Lv), Bl, Az			+	11			1, 8, 9, 93, 95
<i>Pseudaphya ferreri</i> (de Buen & Fage, 1908)	P	Nc ²	Rk, Md, Sd	N Wp Mt (Br), NC (Ad), N Ep Mt, S Ep Mt (Lv)	June		+	3.5	1	2-15	1, 2, 4, 5, 8, 14, 81
<i>Silhouettea aegyptia</i> * (Chabanaud, 1933)			Sd	S Ep Mt		305-408	+	4.35	2		8, 9, 15
<i>Spelegobius trigloides</i> Zander & Jelinek, 1976	P	Cb	Rk, Cv	NC Mt (Ad)				2.4		8-50	1, 8, 13, 52, 70
<i>Thorogobius ephippiatus</i> (Lowe, 1839)	G	Cb	HI, Cv, Rk	E At, N Wp Mt, NC Mt, N Ep Mt (Ag)	May-July	2532-12056	+	13	9	6-40	1, 8, 10, 12, 81
<i>Thorogobius macrolepis</i> (Kolombatovic, 1891)	G	Eb	HI, Cv, Rk	N Wp Mt (Br), NC Mt (Ad, In), N Ep Mt (Ag)				6.8		6-45	10, 12, 71
<i>Tridentiger trigonocephalus</i> * (Gill, 1859)			Sd, St	E Mt	June-July	3400-9700		7.2			72, 83
<i>Trypauchen vagina</i> * (Bloch & Schneider, 1801)			Md	NE Mt			+	21		20-90	15, 84
<i>Vanneaugobius dollfusi</i> (Briwnell, 1978)	G	Eb	Sd, Md	E At, N Wp Mt (Br), NC Mt (Ad), N Ep Mt (Ag)				4.5		30-160	13, 30, 74
<i>Vanneaugobius pruvoti</i> (Fage, 1907)	G	Eb	Rk	SE At, N Wp Mt (Br), N Ep Mt				3.7		60-270	9, 8, 51, 75
<i>Zebrus zebrus</i> (Risso, 1827)	G	Cb	St, Sg, Rk	SE At, N Wp Mt, NC Mt (Ad, In), N Ep Mt (Ag), S Ep Mt (Lv), SC Mt, Bl	July			6.5		0-10	1, 11, 12, 49, 52, 76, 81
<i>Zosterisessor ophiocephalus</i> (Pallas, 1814)	G	Eb	Sd, Md, Sg	N Wp Mt, NC Mt (Ad), N Ep Mt (Ag), SC Mt, Bl, Az	March-May	5000-45000	+	25	5	0-10	1, 2, 8, 22, 49, 77, 90, 91, 92

Key to abbreviations:

underlined species are endemics

? reported but not clear

* Lessepsian immigrant

¹ this species sometimes considered cryptobenthic

² this species sometimes considered hyperbenthic

lineage: A- *Aphia*, G- *Gobius*, P- *Pomatoschistus*; **life-style:** Cb- cryptobenthic, Eb- epibenthic, Hb- hyperbenthic, Nc- nektonic; Cv- caves, Gr- gravel, Hl- holes, Md- mud, Rk- rock, Sd- sand, Sg- sea-grass, St- stones; **direction:** E- east, N- north, S- south, W- west, C- central, p- part; **distribution:** Ad- Adriatic Sea, Ag- Aegean Sea, Al- Alboran Sea, At- Atlantic Ocean, Az- Azov Sea, Br- Balearic Sea, Bt- Baltic Sea, Bl- Black Sea, In- Ionian Sea, Lv- Levant Sea, Lg- Ligurian Sea, Mt- Mediterranean Sea, Sc- Suez canal, Tr- Tyrrhenian Sea

1 (Agorreta et al., 2013); 2 (Giovannotti et al., 2007); 3 (Iglesias and Morales-Nin, 2001) 4 (La Mesa et al., 2005a); 5 (Kovačić, 2003); 6 (Kovačić and La Mesa, 2010); 7 (Kramer et al., 2012); 8 (Miller, 1986); 9 (Kovačić and Patzner, 2011); 10 (Kovačić et al., 2011); 11 (Kovačić et al. 2012); 12 (Patzner, 1999); 13 (Kovačić pers. comm.); 14 (Kovačić and Golani, 2007a); 15 (Salameh et al., 2010); 16 (Metin et al., 2011); 17 (Mytilineou et al., 2005); 18 (Francour, 2008); 19 (Herler et al., 1999); 20 (Colombo and Langeneck, 2013); 21 (Kovtun and Manilo, 2013); 22 (Malavasi et al., 2004); 23 (Herler et al., 2005); 24 (La Mesa et al., 2006); 25 (Sasal et al. 1996); 26 (Gibson 1970); 27 (Giovannotti et al., 2009); 28 (Kovačić and Golani, 2007b); 29 (Engin et al., 2007); 30 (Ahnelt and Dorda, 2004); 31 (Miller 1984); 32 (Kovačić and Miller, 2000); 33 (Bouchereau and Guelorget, 1998); 34 (Kovačić, 2007a); 35 (Filiz and Toğulga, 2009); 36 (Mazzoldi and Rasotto, 2002); 37 (Malavasi et al., 2008); 38 (Parmentier et al., 2013); 39 (Hajji, 2012); 40 (Miller, 1961); 41 (Kovačić, 2001); 42 (Kovačić, 2007b); 43 (Kovačić, 2007a); 44 (Kovačić, 2006); 45 (Villegas-ríos and Bañón, 2010); 46 (Van Tassell, 2001); 47 (Franco et al., 2012a); 48 (Malavasi et al., 2005); 49 (Penzo et al., 1998); 50 (Gibson & Ezzi, 1978); 51 (Miller, 1990); 52 (Kovačić et al., 2013); 53 (Hempel and Thiel, 2013); 54 (Sapota, 2012); 55 (Vanhove et al., 2011); 56 (Ahnelt et al., 1994); 57 (Akyol et al., 2006); 58 (Thacker and Roje, 2011); 59 (Patzner et al., 2011); 60 (Pampoulie, 2000); 61 (Pampoulie, 2001); 62 (Bouchereau et al., 1989); 63 (Bouchereau et al., 1990); 64 (Mejri et al., 2011); 65 (Verdiell-Cubedo et al., 2007); 66 (Stefanni et al., 2003); 67 (Gibson & Ezzi, 1978); 68 (Bouchereau et al., 2003); 69 (Huyse et al., 2004); 70 (McKay and Miller, 1997); 71 (Ahnelt and Kovačić, 1997); 72 (Goren, 2009); 73 (Kovačić, 2008); 74 (Pallaoro and Kovačić, 2000); 75 (Van Tassell, 1988); 76 (Kovačić et al., 2005); 77 (Fiorin et al., 2007); 78 (Kovačić and Patzner, 2009); 79 (La Mesa, 2001); 80 (Hajji et al., 2013); 81 (Kovačić et al. 2012b) ; 82 (Mejri et al., 2009); 83 (Hwang and Baek, 2013); 84 (Akamca et al., 2011); 85 (Boban et al., 2013); 86 (Francour and Mangialajo, 2007); 87 (Engin and Dalgic, 2008); 88 (Stoyanov et al., 2015); 89 (Kovačić and Pallaoro, 2003); 90 (Franco et al., 2012b); 91 (Mazzoldi et al., 2000); 92 (Malavasi et al., 2003); 93 (Naseka et al., 2005); 94 (Stefanni, 2000); 95 (Fricke et al., 2007); 96 (Miller, 2003)

3. Morphology

There are some typical characters which characterise the family Gobiidae. The body form is moderately elongate and on the depressed head dorsolateral eyes dominate with narrow inter-orbit and prominent rounded cheeks (Miller, 1986). The head and body bear neuromast organs like sensory papillae, ciathiform organs and genipores. Pelvic fins protrude from the body and form a disc on ventral side. In some species (e.g., *Odondebuenia balearica*) pelvic fins are almost completely separated, having only a piece of membrane (Miller, 1986). A typical character of the gobies is that the spinous and rayed dorsal fins are in the most species separated. The colouration varies in bright patterns (Thacker and Roje, 2011). Diagnostic features is a presence of fused pelvic fins and a single, median anterior interorbital pore (Thacker, 2009).

The shape of scales varies from ctenoid to cycloid. The body covered with cycloid scales, usually absent on the head and predorsal area, was described for instance in *Aphia minuta* (La Mesa et al., 2005) and *Zebrus zebrus* (Kovačić et al., 2013). Some species like *Pseudaphya ferreri* (Kovačić and Golani, 2007a) and *D. schlieweni* (Francour, 2008) have both types of scales, a few rows of cycloid and the remaining ctenoid ones. *Deltentosteus colonianus*, *Gobius geniporus*, *Gobius fallax* and *Gobius cobitis* have ctenoid scales (Kovačić and Golani, 2007a). For *Crystallogobius linearis* a total absence of scales is typical (La Mesa, 2001).

The main characters used for species determination are a presence or absence of head lateral system papillae and pores, squamation and types of scales and numbers and structure of fin rays (Kovačić, 2008).

3.1. Sexual dimorphism

Sexual dimorphism is very often documented on a shape of urogenital papillae of adult gobies (Miller, 1961). Among common dimorphism features belong larger size of males, known in *Gobius roulei*, *Gobius bucchichi* (Kovačić, 2001), *Pomatoschistus minutus* and *Pomatoschistus microps* (Bouchereau and Guelorget, 1998). Longer rays of the first dorsal fin of males were observed in several species (*O. balearica*, *G. roulei*, *Gobius niger*). Moreover,

in males of *G. roulei* larger and stronger pectoral and caudal fins have been observed (Kovačić, 2001). The trunk, head and throat of a male can be more robust, like in *A. minuta*, with better developed fins and teeth in males (Jaime et al. 2000; La Mesa et al. 2005). The pelvic disc in female of *C. linearis* is reduced or completely missing, the same as the first dorsal fin with only two spinous rays (Miller, 1986). Males of *Pomatoschistus pictus* have brighter nuptial colouring than females (Bouchereau et al., 2003). In both sexes of *Thorogobius macrolepsis* a difference in coloration is evident during spawning period, with dark males and lighter females (Ahnelt and Kovačić, 1997).

3.2. Size

The gobies are inconspicuous fishes of small sizes (Thacker, 2003) and usually do not exceed the length of 10 cm (Kovačić et al., 2013). Males often have larger length than females in the same age-group (Filiz and Toğulga, 2009). In the Mediterranean Sea, 27% of goby species are smaller than 5 cm (e.g., *Buenia affinis* 3.8 cm; (Kovačić & La Mesa 2010)), 39% are between 5-10 cm of total length (e.g., *G. roulei*; (Kovačić 2001)) and 34% are longer than 10 cm (e.g., *Zosterisessor ophiocephalus* 25 cm; (Fiorin et al. 2007)) (Kovačić and Patzner, 2011). The smallest known fish in the Mediterranean Sea is the goby *Speleogobius trigloides* which attain size only to 2.4 cm (Kovačić et al., 2013). Other very small gobies in the Mediterranean are *Lebetus guilleti* (2.5 cm long; (Kovačić & Patzner 2011)), *C. liechtensteini* (2.5 cm long; (Herler et al., 1999)) and *O. balearica* with the length of 3.2 cm (Miller 1986)). *Millerigobius macrocephalus* stands out with the smallest known juveniles (Kovačić et al., 2013).

It is believed that life-history theory predicts that small species will exhibit short life-spans and fast growth rates (Hernaman and Munday, 2005). Naturally, there are a lot of differences depending on season or gender. Growth rate of gobies is higher in the summer than in winter (Hernaman and Munday, 2005). In some cases there is an evidence of sex-specific differences in growth, where males are growing faster and attaining a larger maximum size than females. This may be related to interspecific differences in intensity of sexual selection, mating system, and reproductive behaviour (Hernaman and Munday, 2005).

3.3. Coloration

The most Mediterranean goby species have a discreet coloration with beige and brown colour prevailing (Thacker and Roje, 2011). However, several species have very intensive colours (e.g., *S. trigloides*; (Miller 1986)), orange spots (e.g., *T. macrolepis*, (Ahnelt & Kovačić 1997); *G. kolombatovici*, (Kovačić & Miller 2000)), dark spots (*Thorogobius epphippiatus*; (Kovačić et al. 2012)), or have a prominent longitudinal stripe (*Gobius vittatus*; (Kovačić 2008)), Several goby species are transparent (*C. linearis*, *A. minuta*, *P. ferreri*; (Giovannotti et al. 2007)) and some of them are dark (*Gobius paganellus*; (Miller 1961)).

4. Biology and ecology

4.1. Life-span

It is known that gobies are characterised by short life-spans and all or most of their life they invest in growth. Selection pressures, which caused high mortality rates and short adult life-spans, influence the timing of maturation and reproductive ability (Herler et al., 2007). Most goby species live only around one or two years (Hwang and Baek, 2013). Some tiny and mainly nektonic species, as *A. minuta*, do not even reach age of one year (Caputo, 2002). On the contrary, bigger ones, mostly belonging to genus *Gobius* (*G. roulei*, *G. couchi*), live more than five years and some of them can even reach ten years (*G. paganellus*, *Lesueurigobius friesii*) (Miller, 1961, 1986; Kovačić, 2001). The goby species with longer life-spans are usually larger and grow at slow rates (Kovačić, 2001). Kovačić (2006) observed shorter lifespan in female of *G. vittatus* than in male on the basis of average ages in both sexes of studied specimens.

4.2. Life-style

The majority of Mediterranean gobies are epibenthic. The examples are species of the genus *Gobius* (e.g., *G. buccichi*, *G. roulei* (Kovačić, 2003)), *P. pictus* or *B. affinis* (Kovačić and La Mesa, 2010). They live close to the substratum on top of the bottom surface (Kovačić et al. 2012). They have characteristic motion defined by intermittent swimming, which is accompanied by short darting movements when disturbed (Miller, 1986).

Cryptobenthic species, such as *Chromogobius zebratus*, *C. liechtensteini* and *Didogobius splechnai* (Patzner 1999; Kovačić et al. 2012), inhabit various burrows, like caves, cavities, crevices or are hidden under stones, boulders and mollusc shells and therefore cannot be seen from the above (Miller, 1996). Their microhabitats are spatially restricted and are situated underneath the bottom surface of the substrate or biocover (Kovačić et al. 2012; Depczynski & Bellwood 2003). There are 13 strictly cryptobenthic species of gobies in the Mediterranean Sea, see Table 1.

Only two goby species in the Mediterranean are hyperbenthic (*Pomatoschistus knerii*, *Pomatoschistus quagga* (Kovačić, 2003)). They are characterized by hovering or swimming above the bottom surface not more than one meter above the bottom (Kovačić et al. 2012). These species occur in flocks.

Three goby species in the Mediterranean Sea, *A. minuta*, *C. linearis*, *P. ferreri*, are nektonic dwellers living freely in the water column and gathering in flocks. They are paedomorphic, i.e., adapted to pelagic lifestyle by persistence of larval anatomical features in adulthood, such as presence of swimbladder during whole life (Giovannotti et al., 2007). They show short life-spans and early achievement of sexual maturity (Giovannotti et al., 2007). *A. minuta* and *P. ferreri* are sometimes treated as hyperbenthic species, as they were also found in flocks no more than one meter above the substratum Kovačić (2003). In this work, I consider them nektonic. Interestingly, the adaptation to life in pelagial in European marine gobies evolved three times independently in the course of evolution; the three Mediterranean nektonic species are not genetically related (Agorreta et al., 2013).

4.3. Habitat

Marine gobies occupy a range of habitats, from coastal lagoons and intertidal pools through various inshore ecosystems to offshore regions. They occur in marine shelf or in brackish waters or estuarine ecosystems at least seasonally in large numbers (Demestre and Abello, 2000).

The Mediterranean gobies favour mostly soft bottom dwellings or live between pebbles on rocky substrates or in rock crevices (Ahnelt and Kovačić, 1997; Herler et al., 1999; Iwata et al., 2000). Typical habitat for Mediterranean gobies is considered to be coralligenous bottom. More than 60% of the epibenthic gobies prefer soft bottoms (e.g., *B.*

affinis (Kovačić and La Mesa, 2010), *Gobius gasteveni* (Ahnelt and Dorda, 2004) or *G. roulei* (Kovačić, 2001)), while about 40 % of them live on hard bottoms (e.g. *Gobius cruentatus* or *Gobius auratus* (Miller, 1986)), and in caves (e.g., *D. splechnai* (Herler et al., 1999), *Gammogobius steinitzi* (Kovtun and Manilo, 2013) or *T. ehippiatus* (Patzner 1999)). Cave dwellers have life closely connected to cavities or crevices because it provides them shelter and protection against the predators (Munday and Jones, 1998).

Kovačić et al. (2012) recognised three types of habitats preferred by cryptobenthic species including inclined bedrock, infralittoral algae and deeper infralittoral mixed bottom. Sea-grasses contribute high protection and represent a refuge for small fishes (Hindell et al., 2000). It has been observed that larger species, such as *G. niger* and *Zosterisessor ophiocephalus* occur more in sea-grass habitats than in the unvegetated habitats, whereas smaller species belonging to the genera *Knipowitschia* and *Pomatoschistus* prefer mud flats and salt marsh creeks (Malavasi et al., 2005).

Some species are not strictly bounded to one type of habitat and they can be found in several habitats with different abundance in each season. On the other hand, some species permanently occupy the same place or are present only on selected types of habitats. Among specialists, which occur only in one type of habitat belong *D. splechnai*, *G. steinitzi*, *C. liechtensteini* and *T. ehippiatus*. All of them inhabit caves and last species is bound to caves with a sandy bottom (Malavasi et al., 2005; Patzner, 1999). Nevertheless, according to the recent findings of *C. liechtensteini* and *T. ehippiatus* by (Arko-Pijevac et al., 2001), these species are also known from outside of caves. In contrast, *G. steinitzi* strictly occurs in deep dark parts of the caves. *C. liechtensteini*, *G. steinitzi* and *Z. zebrus* were even found in holes of endolithic bivalves (Patzner, 1999).

About 27 % of Mediterranean goby species have preferred living range between the surface and a depth of 2 meters, 31 % between 2 and 10 m. 29 % of gobies live mostly in depths between 10 and 50 m, while only 13 % prefer deeper waters (Kovačić and Patzner, 2011).

4.4. Migrations and diurnal activity

In sand gobies *P. microps* and *P. minutus* is known a thermal migration during spawning period. They migrate to the superficial waters in order to ensure warmer conditions

(Boissin et al., 2011; Pampoulie, 2001). A nectonic species *A. minuta* is characterised by an offshore migration in spring. Adults inhabit predominantly cold waters and for that reason they migrate in spring to the deeper waters. In summer they migrate to the areas of a high zooplankton production, as in that period they have high energy requirements (for growth) (Iglesias and Morales-Nin, 2001). A passive migration of planktonic larvae via currents contributes to the distribution of gobies, but there is no information about this phenomena. It is not known whether adult gobies perform migrations, not how long they can be.

A nocturnal activity in *D. schlieweni* was observed. During the day it is hidden among the pebbles or rocks, while at night it leaves its shelter and swims among sea-grass *Posidonia oceanica* or *Caulerpa racemosa* (Francour, 2008). It is probable that most other cryptobenthic species exhibit nocturnal activity, too.

4.5. Adaptations

Morfological adaptations follow wide range of microhabitats which marine gobies occupy. This is reflected mostly by different body shape (Herler, 2007). It is comprehensible that larger gobies residing bottom have fusiform body shape, other gobies hovering above bottom have elongated body and the species that live inside caves and crevices tend to be laterally flattened (Herler et al., 2007). A notable adaptation for species living in shoreline is the development of a sucker formed by uniting the pelvic fins to cling to a substratum (so-called pelvic disc). Goby species in deeper areas or inhabiting non-turbulent waters (e.g. *T. macrolepis*, *G. vittatus*, *C. lichtensteini*, *G. steinitzi*), have the tendency towards a separation of the pelvic fins and show less developed ventral disc (Ahnelt and Kovačić, 1997). The adaptation to water movements might be also reduction of head lateral-line system notable in the genus *Lesueurigobius* (Ahnelt and Kovačić, 1997). The adaptation to epibenthic way of life includes camouflage colours and shapes.

In cryptobenthic gobies there are the evolutionary trends leading to small body size and cryptic life habits (Miller, 1996). Along with a cryptic way of life a perfect adaptation to environment and close association with benthos gradually evolved (Depczynski and Bellwood, 2003). For cryptobenthic species living under stones inside a layer of pebbles (e.g., *Ch. zebratus*) a lateral flattening of body and small sizes are typical (Kovačić et al. 2012).

Obligatory cryptobenthic species are influenced mostly by the epilithic fauna compositions covering interiors of their dwellings (Kovačić et al. 2012).

For the species exhibiting pelagic lifestyle (*A. minuta*, *C. linearis*, *P. ferreri*) features such as body transparency, lack of melanophores, lateral compression of the body, lateral positioning of the eyes, persistence of the swimbladder and short and straight alimentary canal are typical (Giovannotti et al., 2007). Transparency of body is very beneficial because these species are preyed by other fishes and cephalopods (La Mesa et al. 2005). This feature has an important meaning for nektonic species as protection against predators by being less visible in water column.

An adaptation to life between anemone tentacles was described for one Mediterranean goby (i.e., only for some of his populations) (La Mesa et al., 2006). This relationship between a goby species *G. buccichi* and anemone species *Anemonia viridis* is not a true symbiosis. Anemone gains no benefit from the presence of goby, while the goby gains protection. The goby is allowed to move among the tentacles of anemone bearing the nettle cells and thus obtain complete protection from predators. Other populations of the same goby species do not have a direct contact with anemone tentacles but also live close to it (Kovačić and Patzner, 2011; La Mesa et al., 2006).

4.6. Reproductive biology

The process of reproduction of most gobiid fishes involves several breeding strategies starting with male nest building and competition for nesting sites, male courtship, female mate choice and finally paternal egg care (including fanning, cleaning and defence of eggs) (Robinson et al., 2007). Males build nests in the well-hidden places to protect offspring from adverse environmental conditions, such as extreme temperatures, wind or water and certainly from predators (Svensson, 2004). The nest is often built from a stone or bivalve shell covered with sand. After completion of the dwelling, male goby courts female into his nest (Kvarnemo, 1998; Mazzoldi and Rasotto, 2002) and then the mating and releasing eggs occurs (Myrberg and Lugli, 2006; Malavasi et al., 2008). Female lays a single layer of eggs (Bouchereau et al., 2003) which are supported by adhesive structures to stick to hard substrates as stones, shells and other objects (Iglesias and Morales-Nin, 2001). Males fertilize eggs by sperms and stay close to them until hatching (Malavasi et al., 2008; Myrberg and Lugli, 2006). In some species (e.g. *Z. ophiocephalus*) it has been observed that males release

sperms onto the nest surface in the form of a trail which consists of a band of mucin produced by sperm duct glands. Releasing sperm trails occurs twice: before and during deposition of eggs by female. Eggs may be released freely in the nest, do not have to be laid over trails, because sperms are able to reach them via the surrounding water. Oocytes can be fertilized during several hours whereas sperm motility lasts on average about 80 minutes. Males do not need to stay close to the female to secure fertilization, they can invest energy and time to defending nest from intruders (Scaggiante et al., 1999). Badly-hidden eggs are easily eaten by predators and thus eggs depend on males' protection that increases their survival (Vasconcelos et al., 2011). Before the spawning season, males probably accumulate nutrients and store energy for the reproduction and paternal care (Hwang and Baek, 2013). In *Pomatoschistus marmoratus* males are specially preparing for eggs' guarding by cleaning the inside of empty bivalve shells and covering the top surface with sand (Mazzoldi and Rasotto, 2001). Among nectonic goby species, egg care has been confirmed in *C. linearis* (La Mesa, 2011). The tube of a Polychaeta species was used as a nest. In cryptobenthic and hyperbenthic species the parental egg care has not been observed so far, but it probably occurs.

In the Mediterranean Sea breeding season includes spring and summer, with a repeated spawning (iteroparity) (Miller, 1986; Mazzoldi and Rasotto, 2001). Females can lay eggs more than once during the life cycle. This was confirmed for e.g., *G. paganellus* (Miller, 1961), *P. marmoratus* (Fouda, 1993) or *A. minuta* (Caputo, 2002). In this period, females can be found with ovaries in different conditions of maturation (Franco et al., 2012b).

The type of reproduction with a long reproductive season and several spawning events is called abbreviate iteroparity (Kovačić and La Mesa, 2010). This reproductive strategy occurs in stable environments with high resource availability (Giovannotti et al., 2009). As an example, a nectonic species *A. minuta* has two spawning events during a short life and high reproductive effort in a long breeding season followed by death of all breeders (Caputo, 2002). For other annual gobies, such as *B. affinis*, *C. linearis*, *P. microps* and *Knipowitschia caucasica*, a death after spawning is known, probably caused by apoptosis of intestinal epithelium (Pampoulie 2000; Mesa et al. 2005; Kovačić & La Mesa 2010). Second, more frequent reproductive strategy, is protracted iteroparity also with more spawning events but with life-span longer than one year. A typical protracted iteroparous spawner is for example *G. niger* (Giovannotti et al., 2009).

Both monogamous (e.g. *P. pictus*; (Bouchereau et al. 2003)) and polygynous mating system (*P. microps*, (Manica 2002)), has been observed, what is documented by the presence of eggs at different stages of development inside the nest (Mazzoldi and Rasotto, 2002). In this case, the males (two or several) and their sperms compete over the fertilization of the eggs. This duel between sperm of different males is called sperm competition (Svensson, 2004).

All Mediterranean nectonic species are paedomorphic, i.e., they retain larval morphology in adulthood. The paedomorphosis is achieved by heterochrony. This process is defined as a developmental change in the timing of events, leading to changes in the ontogenetic formation of morphological characters (Caputo, 2002; La Mesa et al., 2005; Giovannotti et al., 2007; La Mesa, 2011).

The eggs of gobies are demersal, differently shaped and in size of 0.4-5 mm (Miller, 1986). There is a wide range in number of eggs oviposited, from 220 (*K. caucasica*) to 45,000 (*Z. ophiocephalus*) per one batch (Miller, 1986). Duration of egg development may vary. In Mediterranean gobies so far known it is about six days in *G. bucchichi*, 15 days in *Z. ophiocephalus* and 20 days in *G. paganellus* (Miller, 1986; Malavasi et al., 2004). The young hatches out as a planktonic larva with size of 8 mm to a maximum of about 50 mm (Giovannotti et al., 2007). Planktonic life stages have variable duration of larval period (Iwata et al., 2000), but usually they last one month (Planes, 1998). The planktonic larval duration in the Mediterranean goby species so far known is between 13 days in *Zosterisessor ophiocephalus* and 35 days in *Gobius cobitis*. At metamorphosis, larvae start to settle to the bottom.

Reproductive biology of *Aphia minuta* quite differs from other species and is divided in three phases. A „pelagic phase” of planktonic larval stages hatched from demersal eggs occupying inshore in close proximity of the shoreline; an „aggregated phase” of juveniles grouping in schools in shallow waters during winter; and the last „demersal phase” consisting of adults in spring migrating offshore with scattered distribution close to the bottom (La Mesa et al., 2005). This species has an abbreviate iteroparity. It has a short reproductive season, during which it can spawn more times which ends by the death of all breeders (La Mesa, 2011).

Generally, gobies attain sexual maturity on average at the age of one year (the case of e.g., *Z. ophiocephalus* (Mazzoldi et al., 2000)), but for a nectonic *A. minuta* a rapid achievement of sexual maturity in several months is known (La Mesa et al., 2005).

The reproductive cycle and spawning season are influenced by periodical changes of water temperature and photoperiod in habitats. Warmer temperature and longer day length is obviously connected with a longer spawning period and an activation of gonadal development, whereas high temperatures in summer cause gonadal degeneration (Hwang and Baek, 2013; Silva and Gordo, 1997).

Female fecundity, in terms of number of eggs per clutch, strongly depends on body size (Healey, 1971). Differential maturity and reproductive readiness is probably responsible for the differences in the sex ratio (Kvarnemo, 1996).

4.6.1. Mating choice

It was experimentally proved that females tend to prefer larger males with a “higher quality”, relative to body length, whereas males seem to be unselective (Kvarnemo and Forsgren, 2000). Larger specimens are more successful nest competitors and nest protectors (Magnhagen and Kvarnemo, 1989) and often have better parental qualities than smaller individuals. Exactly these aspects are considered by females as good parenting abilities. On the other hand, there is a contradictory observation of Forsgren (1997). According to this author, it is not proved that dominant individuals are better in parental care and thus are not preferred by females.

Females also select males on the basis of the material resources, i.e. they select males which may offer nuptial feeding, parental care and territory quality (Andersson, 1994). If there are males which hazard during mating and female is thus in higher predation risk or harassed by other males, then she selects safe mating (Svensson, 2004) and large males exhibiting better protection abilities (Andersson, 1994). Moreover, when there is a risk of transmission of diseases and parasites, a female chooses a healthy male (Svensson, 2004).

4.6.2. Filial cannibalism

Filial cannibalism is the act of eating own progeny and possibility for parents to reduce the parental costs (Manica, 2002). This method of increasing fitness in males, has been observed in *P. minutus* (Forsgren et al., 1996). If filial cannibalism is present, female should be careful and rather choose a male that already has eggs in his nest to prevent a risk of cannibalism. Two different types are recognised: whole clutch cannibalism and partial clutch cannibalism. Total filial cannibalism means that whole brood is eaten whereas in the partial cannibalism are eaten only some of the eggs in the nest (Manica, 2002). Whole clutch cannibalism usually occurs when the costs of parental care are bigger than the reproductive value of the clutch, for instance when the clutch is too small. It leads to a termination of care (Svensson, 2004). Rohwer (1978) have suggested that males that cope with several brood cycles in the course of a breeding season have possibility to increase their chances of re-nesting by eating parts of their clutches. The general conditions which need to be fulfilled and which favour the evolution of filial cannibalism are that 1) the male takes care of more clutches, 2) his food resources are restricted by the demands of egg guarding, and 3) there are more benefits from egg eating than losses.

4.6.3. Sound vocalisation

Like in other teleost fishes, sound production of gobies occurs especially during breeding season and is associated with territorial defence and mating activities (Myrberg and Lugli, 2006). Acoustic signalling has been described in several species, such as *P. pictus* (Amorim and Neves, 2007), *Pomatoschistus canestrinii*, *G. niger*, *G. paganellus*, *G. cobitis* (Malavasi et al., 2008), *G. cruentatus* (Sebastianutto et al., 2008) and *Z. ophiocephalus* (Malavasi et al., 2003). It makes an important form of social communication which is needed for successful mating (Amorim and Neves, 2007). Males build nests and attract females using vibrant vocalization (Malavasi et al., 2008; Myrberg and Lugli, 2006). Male's vocalization occurs during courtship, spawning and prespawning, while females are choosing newly built homes (Myrberg and Lugli, 2006). It is known that sound production influences reproductive success of goby males. In addition, it seems that females and other competing males are informed about the size and quality of males through vocalisation (Vasconcelos et al., 2011).

The evolution of acoustic signals may be influenced by more aspects. One of them are selective forces which are responsible for shaping adaptations and the other one are

constraints related to phylogeny and morphology (Ryan, 1986). It has been revealed that sounds are produced by the forcible ejection of water through the gill cover, small apertures in the opercles (hydrodynamic mechanism) (Parmentier et al., 2013). On the basis of signal similarity we can distinguish three groups of species, each producing different kind of sound. The first concerns larger-sized species producing tonal sounds, exhibiting high values of pulse rate and short values of duration (*G. paganellus*), the second are larger-sized species producing grunt sounds with low pulse rate and short duration (genera *Gobius* and *Zosterisessor*) and the third are small-sized species producing grunt sounds, showing low pulse rate and long duration (genera *Pomatoschistus* and *Knipowitschia*). It seems that sound duration is the most important acoustic factor and it inversely correlates with body size of the species. According to the analysis of sound production fish is able to modulate the production of sounds from the grunt-like to the tonal-like sound (Malavasi et al., 2008), probably due to the contraction frequency of the sonic muscles which establishes the fundamental frequency of vocalizations (Bass and McKibben, 2003).

4.6.4. Territoriality

A territorial behaviour is known in several species of Mediterranean. This behaviour is connected with reproduction. These species are *Z. ophiocephalus* (Mazzoldi et al., 2000), *P. marmoratus* (Mazzoldi and Rasotto, 2001) and *G. niger* (Mazzoldi and Rasotto, 2002). This territorial behaviour concerns the sperm release which is accompanied by several upside-down movements during courtship and egg-spawning whereas female is in front or inside of the cavity (nest) (Ota et al., 1996). These movements have been described in all stages of the reproductive behaviour - before, during and after the egg-laying phase of the breeding cycle (Malavasi et al., 2007).

Another alternative reproductive tactic includes sneaking by rival males and was observed in the grass goby (*Z. ophiocephalus*) and the black goby (*G. niger*). In this case, the reproductive success depends on the result of an aggression and duel between males. Large territorial males spend more time by defending their territory and providing egg parental care in the presence of rival sneakers. Sneakers are smaller and younger males which are not such a good female attractors and nest defenders as the territorial males and thus exhibit parasitic reproductive behaviour. They sneak inside the nests of a territory of another male and release sperm to fertilize eggs during pair-spawns (Scaggiante et al., 1999; Mazzoldi et al., 2000;

Rasotto and Mazzoldi, 2002; Mazzoldi and Rasotto, 2002). Field observations showed that sneakers stay firstly in front of the nest and then, only after entering the nest, territorial male exits to patrol its dwelling. Afterwards he attacks the intruder to protect his territory and spawning partner (Mazzoldi and Rasotto, 2002; Rasotto and Mazzoldi, 2002; Scaggiante et al., 2005). An intrasexual variability in alternative male tactics of *G. niger* was observed. The first dorsal fin was elongated and body surface was visibly darker in larger males who were taking care of offspring. On the contrary, young sneakers exhibited opposite features: lighter body colouration and shorter dorsal fin (Mazzoldi and Rasotto, 2002).

Sound vocalisation, nest building and egg parental care are considered expressions of territorial behaviour, and were discussed in previous chapters.

4.7. Food biology and ecology

Most of the gobies exhibit carnivorous food strategy (Miller, 1986). A typical predator is *G. roulei*. It prefers mobile food against sessile (Kovačić, 2001). The most common way how it obtains food is that it hunts for prey close to the substratum. Some individuals search for their prey in the water column but always close to some shelter or burrow (Herler et al., 2007).

Sand dwelling species feed on small invertebrates by sifting sand through gill rakers (Hernaman et al., 2009). Dietary specialisation depends on the size, way of life and feeding habits of the fish and certainly the availability of the prey.

Large gobies like *Z. ophiocephalus* and *G. cobitis* feed predominantly on macrofauna consisting of fishes, polychaets, gastropods and pagurids (Kovačić, 2001; Zander, 2011). The smaller ones, not only schooling gobies but also benthic gobies (e.g. *P. tortonesei*, *B. affinis*), feed mostly on meiofauna consisting of small invertebrates, primarily crustaceans (Miller, 1986; Saeki et al., 2005; Kramer et al., 2012). Tiny structure of their body enables them to gain food resources which are not easy to get for larger fishes (Herler et al., 2007). Also *P. pictus* was observed to move from bottom into swarms of mysids, in order to hunt some crustaceans (Zander, 2011).

Food composition depends on layer of foraging in the benthal, suprabenthal or pelagial (Zander, 2011). Nectonic species *A. minuta*, *C. linearis*, *P. ferreri* represent planktotrophic

feeders with pelagic lifestyle, favouring especially copepods, cirripede and mysid larvae (La Mesa et al., 2005). In these nektonic species evolved loss of functionality of the digestive system (La Mesa, 2001).

Seasonal changes in food content were recorded in *G. vittatus*, which is a generalist with wide range of hunted food (Kovačić 2007). Intensity of feeding and number of hunted prey was significantly higher in summer than in autumn. Amount of food correlated with the size of the individual. Food composition differed depending on the season. In winter and spring Copepoda, Gastropoda and Bivalvia dominated, whereas during summer dominant preys were Ostracoda and Isopoda.

A change in the composition of food in *G. roulei* depending on age was documented. The young prefer gastropods, bivalves and polychaets whereas fishes and pagurids dominate in diet of older individuals (Kovačić, 2001). Green algae form a significant part in diet of *G. buccichi* (Kramer et al., 2012).

5. Geographical distribution

A geographical distribution of the Mediterranean gobies greatly varies, but the exact distribution is still not known at all for the majority of species. Table 1. summarises the geographical distribution (i.e., so far known occurrences) of the Mediterranean goby species. The highest species diversity and abundance of gobies is in north-western part of the Mediterranean and in the Adriatic Sea. In these regions host the highest number of strict Mediterranean endemic goby species (e.g., *S. trigloides*, *D. schlieweni* or *G. kolombatovici*). In contrast, the smallest number of goby species is known from African part of the Mediterranean Sea.

The number of findings and diversity on different parts of Mediterranean correlates with the number of studies in various locations of the given part of the sea. In some cases the known localities of species occurrence rather indicate which areas are better explored than real distribution of the species. Most records of goby occurrences are from the northern part of the Mediterranean. The best researched sea in a view of the number of records of the occurrences of gobies is the Adriatic Sea. It represents the region with the highest number of gobiid species in the Mediterranean Sea (Kovačić and Patzner, 2011).

6. Role of gobies in ecosystem

As an important component of marine ecosystems, Mediterranean gobies form a significant link between invertebrates and fish, cuttlefish or piscivorous birds (Kovačić, 2001). They represent important secondary consumers (Ahnelt and Dorda, 2004) but also preys.

Due to their small size Mediterranean gobies have only a small local economic exploitation (Kovačić, 2001). Some species like *P. ferreri* (Miller, 1986), *C. linearis* (La Mesa, 2001), *A. minuta* (La Mesa et al., 2005) *G. niger* (Filiz and Toğulga, 2009), and *Z. ophiocephalus* (Franco et al., 2012b) are exploited by small local fisheries. They are caught by both semi-pelagic and small bottom trawls and brought to the market (La Mesa et al., 2005). *C. linearis*, *P. ferreri* and *D. quadrimaculatus* are sometimes caught like a by-catch in the *A. minuta* fishery (La Mesa, 2001; La Mesa et al., 2005).

In research, gobies are increasingly used as model organisms in many comparative studies aimed at understanding the evolutionary processes (Gracey, 2008; Nakatsuji et al., 1997; Sayer, 2005).

7. Conclusion

Despite the fact that gobies are the most specious fish family in the Mediterranean Sea, there is still a lack of actual information about many aspects of their life. Our knowledge is still being updated but there are many obsolete data which need to be replaced with newer ones. In the Mediterranean Sea, 61 species of gobies are known up to date, of which 20 are Mediterranean endemics.

Mediterranean gobies exhibit four main types of life-styles: epibenthic, cryptobenthic, hyperbenthic and nektonic. The epibenthic life-style of gobies is the prevailing one in the Mediterranean Sea.

The origin and age of Mediterranean gobies remain still unclear. The European gobies were assigned to three distinct lineages. In all these lineages, north-east Atlantic and Mediterranean species are placed together (Agorreta et al., 2013), which evidences common evolution of the gobies from these two seas. A variety of ecological and biological traits can be seen within each of the European goby lineage. The nektonic way of life evolved three times independently in the course of evolution.

The knowledge on geographical distribution of Mediterranean gobies is far from being complete. In some cases the known localities of species occurrence rather indicate which areas are better explored than real distribution of the species. The highest species diversity and abundance is in north-western part of the Mediterranean and in the Adriatic Sea. Generally, European coastline is much more researched than poorly investigated area along the North African coast.

Reproduction has been studied in about 30 % of Mediterranean goby species; however the knowledge on e.g., larval development is scarce and based on a small number of species. In most of the species larval stages are not known at all. The information on feeding preferences is available for 50 % of Mediterranean gobies, but the feeding strategy was studied in detail only in a few species.

Epibenthic species are the most researched ones among the Mediterranean gobies, while the information about the cryptobenthic species is scarce. These species are well hidden in caves, crevices, under stones, among pebbles or under the gravel and it is difficult to see or to collect them.

There are still many gaps in our knowledge on the Mediterranean gobies.

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