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An integration of historical records and genetic data to the assessment of global distribution and population structure in *Octopus vulgaris*

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The common octopus (*Octopus vulgaris* Cuvier, 1797) is one of the most widely distributed species belonging to the genus *Octopus* as well as an important commercially harvested species and a model organism for behavioral biology of invertebrates. It has been described for the first time in the Mediterranean Sea but it is considered a cosmopolitan species inhabiting the temperate and tropical seas of the northern and southern hemispheres. In the last few years, several species previously considered as *O. vulgaris* have been recognized as new species, limiting the distributional range of *"vulgaris"* and reinforcing the thesis of a species complex. Where it is an important fishery resource, numerous studies have been conducted in order to define its genetic structure with the purpose of managing different stocks. However, many locations are still poorly investigated from this point of view and others are under taxonomic revision to exclude or confirm its occurrence. Here we provide a summary of the current status of knowledge on distribution and genetic structure in this species in the different oceanic regions.

Keywords: *Octopus vulgaris*, Cephalopoda, genetic structure, species complex, phylogenetics

FROM POPULATIONS TO SPECIES AND SPECIES COMPLEXES

In its simplest form, a population can be defined as "a group of interbreeding individuals that exist together in time and space" (Hedrick, 2000). Several factors, called evolutionary processes, affect the genetic structure of a population leading to phenomena such as genetic divergence, local adaptation or extinction. In presence of high gene flow, populations lack of clear boundaries and form a continuous population, a condition known as panmixy. On the contrary, over a long time, isolated populations tend to diverge genetically up to not being able to interbreed: a new species is raised (Mayr, 1942). When the time of separation between two species is recent or when hybridization occurs among them, they tend to be well differentiated morphologically but not genetically (Shaffer and Thomson, 2007). Conversely, species can be well differentiated genetically, but not morphologically: this is when "cryptic species complexes" can arise (Bickford et al., 2007; Barley et al., 2013).

Within cephalopods, several "cryptic species complexes" are known (Anderson et al., 2011), especially among octopuses (Norman and Finn, 2001; Amor et al., 2014). One of the most investigated is exactly the *O. vulgaris* species complex. To date, more than 10 species were recognized in this complex (Norman, 2000), and only a few have been validated with molecular markers (Söller et al., 2000; Pérez-Losada et al., 2002). However, Voss et al. (1998) highlight that numerous "forms" or subspecies of *O. vulgaris* exist worldwide, although most of them lack of a description or a reference. Despite several authors consider the common octopus as a cosmopolitan species (**Figure 1**), Norman (2000) suggests that several populations, such as the ones from the Caribbean Sea, Japan and South Africa, are likely to be separated species because of the strong isolation and the different environment in which they live. Warnke et al. (2004) rejected this hypothesis and confirmed the presence of *O. vulgaris* in Japan using mitochondrial genes. More recently, Guerra et al. (2010) showed that the Japanese specimens cluster separately from the others. However, these conclusions deriving from mitochondrial data are not ultimate and need to be integrated with nuclear data too because speciation is not a clockwise process and sometimes recent speciation events have not reached monophyly yet. As outlined by Allcock et al. (2014), more analysis including more specimens and multiple genes should be performed.

CURRENT KNOWLEDGE ON DISTRIBUTION AND POPULATION STRUCTURE

MEDITERRANEAN AND BLACK SEA

Together with the Eastern Atlantic Ocean, the Mediterranean region is considered to be one of the areas in the world where more information exist on cephalopods (Mangold, 1998). Here the common octopus is well known by the time of Aristotle, which provided its earliest written observations in the eastern Mediterranean (Mangold, 1983) and it has been intensively studied from the end of the eighteenth century to date. Despite the descriptions of Cuvier (1797) and Lamarck (1798), the holotype is missing and, as far as we know, a neotype has been designated in 1998 from the Catalonian Sea off Banyuls-sur-Mer and the species is being redescribed (Mangold and Hochberg, 1991). It is found in the entire basin, where it finds suitable environmental

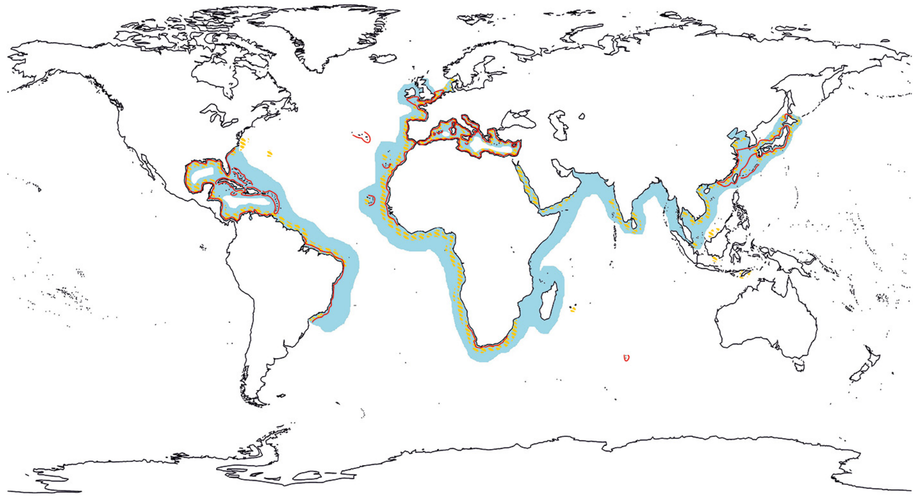

FIGURE 1 | Distribution of *O. vulgaris* after Mangold (1983), Roper et al. (1984) and Norman et al. (2013), in orange, light blue and red respectively.

and ecological conditions, but it is absent in the Marmara and Black Sea, as any other cephalopod species, due to low salinity in the upper waters and reduced gas exchange in the deeper ones (Torchio, 1968; Mangold and Boletzky, 1988).

The first investigation on the genetic structure of *Octopus vulgaris* in the Mediterranean basin has been conducted by Maltagliati et al. (2002) and Casu et al. (2002) using allozymes and a single microsatellite locus respectively (**Table 1**). Both studies focused mainly on the Western and central Mediterranean with just one sample in the Eastern and one in the Atlantic (Casu et al., 2002) and found no isolation-by-distance among populations. Furthermore, the allozyme analysis highlighted a breaking point between western and eastern Mediterranean populations which is not found with microsatellites, probably due to the different resolution of the two markers utilized and to the small representativeness of a single microsatellite locus.

A significant genetic structure has been found in several populations from the central Mediterranean Sea (Strait of Sicily) using mitochondrial markers (Fadhlaoui-Zid et al., 2012; **Table 1**). The authors also mention a significant genetic divergence between western and eastern samples, which could be interpreted as a breaking point between Western and Eastern Mediterranean basin.

The records of *O. vulgaris* in the Levantine Basin (east of 23°E) are less common in the literature compared to the ones from the Western and Central Basin and generally come from Turkish or Israeli waters (Adam, 1967; Ruby and Knudsen, 1972). A recent work by Keskin and Atar (2011) investigated the genetic structure of the common octopus along the Turkish coasts using mitochondrial markers (**Table 1**) and found two clusters compatible with geographical distance, one in the eastern side and the other one in the southern side of the country.

In summary, although it is evident that the use of different molecular markers with different resolution power leads to different scenarios about population structure, the topographic fragmentation of the Mediterranean Basin and the different ecological conditions which occur in the western, central and eastern part should account for a certain degree of population structure (Mona et al., 2014).

NORTHEAST ATLANTIC OCEAN

The Northeast Atlantic region stretches from the coast of Greenland eastward to the North Sea, and from the North Pole southward to the Straits of Gibraltar, including open ocean islands such as the Azores. In this region, *O. vulgaris* reaches its northern distributional limit, being very common (e.g., along the Iberian Peninsula), rare (English Channel) or even absent (North Sea) in different regions. Interestingly, Hoyle (1886) during the "Challenger Expedition" reports this species from the Scandinavian Region and not from the Lusitanian region. On the contrary, Rees (1950) considers it as "a Lusitanian member of our fauna" and reports its occurrence in the English Channel both on British and French coasts up to the German coasts. He also discusses about its abundance during the 1899–1900 years due to a warmer climate in the previous years and hypothesizes that the octopus is probably not able to maintain a breeding population on the English side of the Channel, and so its occurrence is due to an immigrant population from the south. Several records are also reported from Helgoland, in the German part of the North Sea (Hertling, 1936; Rees and Lumby, 1954 both in Jaeckel, 1957) but they are not corroborated by more recent data and might constitute sporadic individuals carried beyond their normal range.

Quite different is, however, the situation in the Iberian Peninsula. Here the occurrence of *O. vulgaris* is unquestioned and information about the population structure is available. Analyzing six populations around the Iberian Peninsula and Canary Islands, Cabranes et al. (2008) found high levels of microsatellite genetic variability and a fine spatial substructure in the Atlantic, which is function of geographical distance (**Table 1**). Furthermore, genetic divergence was also observed between Atlantic and nearby Mediterranean populations, stressing the role of the Gibraltar strait as a genetic break in octopus, as

Table 1 | Resume of the main genetic studies on population structure, phylogeography and phylogenetic relationships in *O. vulgaris* on a global scale.

Region	Area	Molecular markers	Main results	Degree of differentiation	Investigators
Global	Worldwide	16S, COIII	Attribution of the specimens from Taiwan, Japan and Venezuela to *O. vulgaris*	Sequence divergence 0–3.92%	Warnke et al., 2004
Mediterranean and Black Sea	Mediterranean Sea	20 allozymes	No isolation-by-distance between populations and breaking point between western and eastern Mediterranean populations	$F_{ST} = 0.256$	Maltagliati et al., 2002
	Mediterranean Sea	1 microsatellite	High levels of genetic divergence among the populations of the basin, no isolation-by-distance	$F_{ST} = 0.243$	Casu et al., 2002
	Turkey	COI	Two clusters compatible with the geographical distance	n. a.	Keskin and Atar, 2011
	Central Mediterranean Sea	COIII	Genetic structure in the central Mediterranean Sea	$\Phi_{ST} = 0.046$	Fadhlaoui-Zid et al., 2012
Northeast Atlantic Ocean	Iberian Peninsula	5 microsatellites	Fine spatial substructure in the Atlantic which is function of geographical distance	$F_{ST} = 0.014–0.054^*$	Cabranes et al., 2008
Eastern central and Southeast Atlantic Ocean	Eastern Africa	3 microsatellites	Genetic differences between the two main African banks and significant structuring within populations	$F_{ST} = 0.0003–0.0286^*$	Murphy et al., 2002
	South Africa	COIII	No genetic structure between samples from east and west coasts	n. a.	Oosthuizen et al., 2004
	South Africa	16S, COIII	Two genetically different lineages which reject the findings of Oosthuizen et al. (2004)	Sequence divergence 0.4–1.3%	Teske et al., 2007
Western and Eastern Indian Ocean	Amsterdam and St. Paul Islands	COI, COIII	The specimens from the Southern Indian Ocean belongs to *O. vulgaris*; the Japanese form clusters separately	n. a.	Guerra et al., 2010
Northwest Pacific Ocean	Japan	12S, 16S, COI	Phylogenetic relationships among Japanese coleoid cephalopods	n. a.	Takumiya et al., 2005
	Japan, China	COI, COIII	The Japanese and Mediterranean populations seem to be conspecific due to the low value of sequence divergence between them	Sequence divergence 2%	Kaneko et al., 2011
	China	16S, COI	Phylogenetic relationships among Octopodidae in Chinese waters	n. a.	Lü et al., 2013
Southwest Atlantic and Southeast Pacific Ocean	Brazil	6 microsatellites	Genetic differentiation across the southern coasts of Brazil	$\Phi_{ST} = 0.107$	Moreira et al., 2011
	Brazil	16S, COI	Distinctiveness of *O. vulgaris* from *O. insularis*	Sequence divergence 9.5–11.2%	Sales et al., 2013

*Western central Pacific and Western central Atlantic have been omitted because data are missing or included in the main results of other regions. Degree of differentiation: n.a., not available; F_{ST} and Φ_{ST}, fixation indices; *, only pairwise F_{ST} values were available in the original paper.*

previously showed for many marine taxa (Patarnello et al., 2007). The analysis conducted by Casu et al. (2002) mentioned earlier did not record such a break, probably as a consequence of the use of a single microsatellite locus.

Several reports confirm the presence of the species in the oceanic islands of Azores (Joubin, 1920; Schmidt, 1939), but no genetic studies exist to assess the connectivity between islands and coastal populations.

EASTERN CENTRAL AND SOUTHEAST ATLANTIC OCEAN

Ranging from the Strait of Gibraltar to the South African coasts, this region sustains one of the most productive *O. vulgaris* fishery stock, the Sahara Bank, and studies performed here provided substantial contributions to our knowledge of the biology of the species (Hatanaka, 1979; Mangold, 1983). Its occurrence along the coasts of this region appears in several expeditions' report (Hoyle, 1886; Adam, 1952, 1962; Voss, 1962) and is confirmed in some recent studies which allowed to define the genetic structure in this area. In north-western Africa, two fishery banks occur and they are genetically distinct (Murphy et al., 2002). Furthermore, the authors also hypothesize the existence of a fine spatial structure in this area because samples collected from a research cruise in the same region did not cluster with any of the two banks.

In South Africa the situation is more complex. A first study by Oosthuizen et al. (2004) showed no distinction between the samples collected on the eastern and western coasts using the COIII region. On the other hand, reanalyzing these samples with different molecular markers (16S and COI), Teske et al. (2007) found two different lineages: one containing all the analyzed populations from South Africa and another one characterized by samples from Durban (see **Table 1**). This divergent lineage is interpreted by the authors either as a recent introduction by ships' ballast water or as a long-established lineage disappearing in most of its southern African distribution, but only a larger sampling plan can resolve this controversy.

WESTERN AND EASTERN INDIAN OCEAN

Our knowledge about the occurrence of *O. vulgaris* in this region is limited to the Red Sea and the St. Paul and Amsterdam Islands, because the specimens from the Andaman's and Sri Lanka analyzed by Goodrich (1896) actually belongs to *O. cyanea* according to Adam (1939). Anyway, also in the Red Sea the situation is not controversy free. Despite numerous expeditions and reports, *O. vulgaris* is specifically reported in the area only by Hoyle (1886); other authors such as Wülker (1920) and Adam (1942) just list it based on previous reports, and it was not found in following expeditions (Adam, 1955, 1960). Torchio (1968) considers the species absent in the Red Sea and questions about its occurrence in the Indo-Pacific region. The most recent record from the Red Sea refers to the comparative study between specimens from the Mediterranean (Alexandria) and the Red Sea (Suez) based on the assessment of morphological characters (Riad and Gabr, 2007). In general, due to the scarcity of records, it is possible to assume that the species is rare in the Red Sea, where it could have migrated from the Mediterranean Sea (i.e., anti-Lessepsian migrant).

Different is the situation for the specimens from the St. Paul and Amsterdam Islands in the southern Indian Ocean (Guerra et al., 2010; **Table 1**). According to morphological and genetic analysis, these animals match *O. vulgaris sensu stricto* (from the Mediterranean), even if molecular data rely only on two mitochondrial genes. Anyway, up to now and to new findings, it can be considered the only effective evidence for this region.

WESTERN CENTRAL PACIFIC OCEAN

In this region, which extends from the south of Vietnam up to the northern coasts of Australia including the Malay Archipelago, just historical data of the "Challenger Expedition" exist (Hoyle, 1886). The author reports *O. vulgaris* specimens from what he calls "the Indo-Malayan region" but since such region was intended to extend from the Red Sea eastward up to the Malay Archipelago, it is possible that the specimens where collected in the present western and eastern Indian Ocean region (see paragraph above). If so, the occurrence of the species in this Western central Pacific Ocean region is questioned.

NORTHWEST PACIFIC OCEAN

In this area, the common octopus is reported from the Chinese waters northwards up to Tsugaru Strait, even if it is more common in central and southern Japan (Nesis, 1987). In respect to the populations from China and Korea, only the Japanese ones have been studied for a long time under several aspects of their biology (Sasaki, 1929; Tanaka, 1958), probably because of their commercial value. Despite Norman (2000) argues about this Japanese form as the most likely to be a valid species due to its geographical isolation with the Atlantic and South African ones, Kaneko et al. (2011) consider it conspecific with the Mediterranean populations on the basis of the low value of sequence divergence of mitochondrial markers. Other studies in this area focus on the phylogenetic relationships between coleoid cephalopods (Takumiya et al., 2005) or within the Octopodidae (Lü et al., 2013) but just at a local scale, providing no information about the degree of connectivity between different populations (**Table 1**). The development of a new set of microsatellite loci by Zuo et al. (2012) from samples in Chinese waters might be a starting point for this kind of investigations.

WESTERN CENTRAL ATLANTIC OCEAN

The western-central Atlantic Ocean region embraces the Atlantic Ocean section from Cape Hatteras to the regions of South America within the Northern Hemisphere, including the Caribbean Sea and the oceanic islands. Despite the numerous contributions of some of the major cephalopod workers such as d'Orbigny and Verrill in the nineteenth century and Adam, Pickford and Voss in the twentieth century systematic problems remain. Here this species (or similar species) is distributed along the coasts of United States (Vecchione et al., 1989; Whitaker et al., 1991) and Bermuda (Voss, 1960), in the Gulf of Mexico and Caribbean Sea (Pickford, 1945; Voss, 1955; Judkins, 2009), in Central America (Hochberg and Camacho-García, 2009) and in Venezuelan waters (Arocha and Urosa, 1982). In some regions of Central and northern South America it is known just from few specimens (Pickford, 1945). One of the most evident problems in this geographic region is the abundance of synonymous and uncertain species due to the resemblance of many specimens collected there with the Atlantic-Mediterranean "form" or to the lack of a holotype to be used as reference. Consequently, the western Atlantic "form" of *O. vulgaris* is referred to as *O. americanus* despite no holotype exists for this entity, as *Octopus* cf. *vulgaris*, or just as *O. vulgaris*. Pickford (1945) raised the issue if the American octopus is conspecific with *O. vulgaris* "Lam." and, after a morphological examination, she concluded that "even in respect to the hectocotylus, the American *vulgaris* is identical with its European counterpart." She also reported geographical variations in specimens from Bermuda and coastal waters of United States and little concrete differences with museum specimens labeled as *Octopus rugosus*.

Up to date, no genetic studies have been conducted in this area to clarify the relationships among the different forms of *O. vulgaris*. Moreover no genetic structure studies exist. The development of microsatellite loci in *O. maya* (Juárez et al., 2013), one of the most harvested octopus species in the Gulf of Mexico, and the following analysis of population structure could stimulate similar analysis also in the common octopus.

SOUTHWEST ATLANTIC AND SOUTHEAST PACIFIC OCEAN

The knowledge of *O. vulgaris* in the southwest Atlantic is limited to Brazil, where it constitutes the most important fishery resource. After the description of a new species (*O. insularis*) from the northeastern coasts of Brazil by morphological and genetic characters (Leite et al., 2008), new genetic data limit the distributional range of *O. vulgaris* to southern Brazil (downstream of Rio de Janeiro) and several localities in the northern and western part (Sales et al., 2013). In southern Brazil, Moreira et al. (2011), using microsatellite loci, highlighted the occurrence of four genetic populations with no significant evidence for isolation by distance, although several bordering populations were the less divergent (**Table 1**).

No records exist about the occurrence of *O. vulgaris* in Argentina and the southeast Pacific Ocean, where it is probably replaced by *O. mimus*, but a deeper investigation in countries such as Peru, Ecuador and Colombia is still needed.

THE PROBLEM OF *O. RUGOSUS*

An important step for the definition of the distributional range in *O. vulgaris* is the assessment of the taxonomic status of *O. rugosus* Bosc (1792). Robson (1929) considers it as a distinct species based on the rough, finely granular skin and shorter arms and hectocotylus compared with *O. vulgaris* but Pickford (1945) and Adam (1952) refer to it as synonymous of *O. vulgaris*. Anyway, its occurrence is recorded from the Red Sea (Adam, 1942), the western and eastern Indian region (Goodrich, 1896; Adam, 1939, 1942), the Caribbean island of Bonaire (Adam, 1937) and along the African, Japanese, Australian and Atlantic coasts (Adam, 1942). If subsequent analysis will prove that this species is actually a synonymous of *O. vulgaris*, all the localities in which it has been reported might be included in the distributional range of the common octopus.

CONCLUSIONS

This review aimed to provide a general picture of the distribution and genetic structure in *Octopus vulgaris* on a global scale, highlighting pitfalls and clues, which could represent the basis for following investigations. The amount of data available in literature is huge and often incomplete, so here we just selected the main and most useful information. In general, few data support the occurrence of *O. vulgaris* in several regions and they are quite doubtful and controversial, making the range hypothesized by Mangold closer to the reality in respect to the one by Roper et al. (**Figure 1**). Regarding the genetic structure, some regions have been investigated more than others, but almost all analysis are concordant in finding genetic structure among populations (**Table 1**), which could derive from low dispersal and enhanced homing of adults, although the potential dispersal of larvae remains to be addressed. Hence, several questions are at the moment unsolved: (i) is *O. vulgaris* a real cosmopolitan species or the hypothesis of species complex is correct? (ii) is there a fine population structure as consequence of the limited adult dispersal or do paralarval meso-scale migrations connect nearby populations? (iii) are these migrations affected by water mass circulation? The answers to all of these questions will contribute to a major comprehension of the ecology of this species and of its biogeographical patterns, with strong impact in fishery and biodiversity management. The FAO statistics reveal that there are real problems in the identification of the cephalopod species caught by the fisheries, with *O. vulgaris* being the only octopus identified to species level (Boyle and Rodhouse, 2005). We know that this can be not always correct. In this context, genetic approaches will constitute a useful tool to investigate biodiversity, assign the catches to the species level and define the stocks in order to prevent their overexploitation.

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