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The Mediterranean Sea hosts endemic haplotypes and a distinct population of the dolphinfish *Coryphaena hippurus* Linnaeus, 1758 (Perciformes, Coryphaenidae)

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ABSTRACT

The dolphinfish, *Coryphaena hippurus* Linnaeus, 1758, is an important target species for Mediterranean artisanal, recreational and commercial fisheries but to date only scarce genetic data are available for its Mediterranean population(s). The genetic variation of Mediterranean dolphinfishes was thus investigated through the sequencing of fragments of the cytochrome *c* oxidase subunit 1 (COI) gene and the NADH dehydrogenase subunit 1 (ND1) mitochondrial DNA markers with the explicit aims of (i) testing for significant genetic differentiation of the Mediterranean *vs.* non-Mediterranean populations of the species, and (ii) investigating the possible presence of molecular structuring within the Mediterranean basin.

Performed analyses revealed significant genetic differentiation between Mediterranean and Atlantic dolphinfish population, while no significant geographically-based genetic differentiation was detected within the Mediterranean basin. The apparent lack of genetic structuring at the Mediterranean level is likely due to the highly mobile behaviour of the species, which is typical of large pelagic fishes and in agreement with the few tag data currently available.

Based on presented results, the Mediterranean dolphinfishes are thus suggested to be considered a distinct management unit from those outside the Mediterranean. Conversely, in order to test for the presence of a single *vs.* multiple Mediterranean stock units, the fulfillment of further analyses implementing fast-evolving nuclear markers is advisable.

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1. Introduction

With an area of about three million square kilometres, the Mediterranean Sea is the largest enclosed sea on Earth. It is connected with the Atlantic Ocean through the Strait of Gibraltar and, from 1869 onwards, the opening of the Suez Canal connected it with the Red Sea and, thus, with the Indian Ocean. A shallow ridge of about 400 m depth occurring between Sicily and north-eastern Tunisia divides the Mediterranean Sea into "western" and "eastern" sub-basins, characterised by distinct biological and oceanographical features (*e.g.* Coll et al., 2010); in addition, the Adriatic Sea, separated by the Strait of Otranto from the eastern sub-basin, has peculiar ecological and biological features, constituting *de facto* a biologically different sub-basin (*e.g.* Souche et al., 2015; and references therein).

Current Mediterranean biota includes a few pre-Messinian elements which survived *in situ* during the late Miocene Messinian Salinity Crisis (*e.g.* some Cyprinodontidae, see Hrbek and Meyer,

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2003; Meynard et al., 2012), but it largely originates from a post-Messinian colonisation coming from the Atlantic ocean after the opening of the Strait of Gibraltar (Patarnello et al., 2007). Later on, Pliocene and Pleistocene glacial events had a significant impact on Mediterranean physical oceanography, eventually leading to local extinction those species characterised by warm water requirements for spawning; these could return into the Mediterranean Sea at the beginning of the Holocene (*e.g.* the bluefin tuna, see Alvarado-Bremer et al., 2005). Finally, after the opening of the Suez Canal, an ever-increasing number of recent colonisers, known as "Lessepsian migrants", invaded the Mediterranean Sea through the Suez Canal (*e.g.* Coll et al., 2010).

The dolphinfish, *Coryphaena hippurus* Linnaeus, 1758 is an epipelagic fish with a high potential for dispersal at all life stages, which occurs worldwide in tropical and subtropical waters, including the Mediterranean Sea. It is a highly mobile species, whose migratory activity is influenced by the presence of warm ocean currents, which seem to promote its moves (Díaz-Jaimes et al., 2006; Merten et al., 2014a,b, 2015; Furukawa et al., 2014). To date little is known about the migratory pattern of this species inside the Mediterranean basin, whereas the movements of the species were investigated in the Atlantic ocean (*e.g.* Merten et al., 2014a,b, 2015), providing useful data on the migratory circuits and population dynamics of the species.

The dolphinfish is an early maturing and fast-growing predatory species which feeds mostly on clupeid and exocoetid fishes. In the Mediterranean Sea, the dolphinfish is a target species mostly for artisanal and recreational fisheries, whereas in some areas it constitutes one of the most important species for commercial fisheries (*e.g.* Zapata, 1993). In the Mediterranean Sea the species is often caught by commercial fishing along the continental shelf break, and by the recreational fishing vessels above the continental shelf at shallower depths. The species commonly aggregates below floating objects; this well-known behaviour has been exploited by commercial fisheries using artificial fish aggregating devices (FADs), a technique to enhance pelagic fish catches (Díaz-Jaimes et al., 2010; COPEMED II (http://www.faocopemed.org/)).

Based on the analysis of allozymes, Pla and Pujolar (1999) stressed the presence of a single panmictic dolphinfish population in the Mediterranean Sea and eastern Atlantic Ocean. Conversely, Díaz-Jaimes et al. (2010), based on the study of the mitochondrial DNA NADH dehydrogenase subunit 1 (mtDNA ND1) sequences throughout the known distribution range of the species, highlighted the isolation of Mediterranean dolphinfish from those inhabiting the world oceans, including the Atlantic. However, due to the presence of a single Mediterranean sample in their study, Díaz-Jaimes et al. (2010) could provide only a limited insight on the pattern of molecular diversity of *C. hippurus* within the Mediterranean Sea, so that detailed data on the mtDNA diversity of Mediterranean dolphinfish populations are to date lacking, and their extent of differentiation from Atlantic populations needs to be measured rigorously.

In the frame of the present study, two fragments of the mitochondrial genes cytochrome *c* oxidase subunit 1 (COI) and NADH dehydrogenase subunit 1 were amplified and sequenced in dolphinfish specimens collected throughout the Mediterranean basin in order to get a clearer frame of actual mtDNA diversity of Mediterranean dolphinfish and to investigate the pattern of genetic diversity of *C. hippurus* at two geographical scales: (i) between Atlantic Ocean and Mediterranean Sea, and (ii) within the Mediterranean Sea. The explicit aims of present work are (i) to test for the actual differentiation of Mediterranean *vs.* Atlantic populations of the species, and (ii) to investigate the possible presence of molecular structuring within the Mediterranean basin. Based on the high dispersal potential of the species, the presence of a single, genetically homogeneous population within the Mediterranean Sea is expected; however, the increasing evidences for substructure within the Mediterranean basin in other pelagic species (*e.g.* see Souche et al., 2015; and references therein) stress the need to describe population structure of dolphinfish in the Mediterranean Sea.

2. Methods

2.1. Sample collection

Tissue samples were collected from a total of 190 dolphinfish specimens obtained from commercial fishing vessels from 11 different landing localities of the Mediterranean Sea (Table 1), *i.e.* from the localities where the species is more regularly harvested (Fig. 1). The origin of the samples (*i.e.* the fishing area) is reported according to what was declared by the owners of the fishing vessels themselves. Further *C. hippurus* ND1 sequences from the Atlantic Ocean were downloaded from GenBank (www.ncbi.nlm.nih.gov/genbank) (Table S1). Unfortunately, no mtDNA sequences of dolphinfishes inhabiting the eastern Atlantic Ocean are to date available.

2.2. DNA extraction, PCRs, and sequencing

Genomic DNA was isolated with the Real Genomics kit of the RBC Bioscience following the manufacturer's protocol. The analysis of the distribution pattern of molecular diversity in the Mediterranean dolphinfish populations was based on the sequencing of fragments of the cytochrome *c* oxidase subunit 1 gene and the NADH dehydrogenase subunit 1 gene, which are documented to be sensitive markers in the detection of genetic diversity and population genetic structures of marine fish.

A 751 bp fragment of the mitochondrial ND1 was amplified using the primer pair NADH163 (5′- TAA TCC TGC CGC AAT TAT CC -3′) and NADH1128 (5′- AGG CCT TCC AGG TTA GGT GT -3′), described by Díaz-Jaimes et al. (2006, 2010); a 551 bp fragment of mitochondrial COI was amplified using the "universal" primer pair LCO1490 (5′- GGT CAA CAA ATC ATA AAG ATA TTG G -3′) and HCO2198 (5′- TAA ACT TCA GGG TGA CCA AAA AAT CA -3′) described by Folmer et al. (1994). For both primer pairs, the following PCR thermal cycle was implemented: a hot start at 95 °C for 4 min was followed by 30 cycles at 95 °C for 50 s, 58 °C (ND1) or 48 °C (COI) for 50 s, 72 °C for 1 min, and then followed by a final elongation step at 72 °C for 10 min.

For both mitochondrial fragments, the PCR mix consisted of 19.05 μl of double-distilled water, 2.5 μl Buffer 10 × including $MgCl_2$ (25 mM), 0.25 μl dNTPs (10 mM of each), 1 μl of each primer (10 μM), 0.2 μl of Roche Taq Polymerase 5 u/μl and 1 μl of DNA template, for a total volume of 25 μl.

After PCR, 5 μl of each PCR product were separated by electrophoresis on a 2% agarose gel at 80 V for 30 min and visualised with a UV Transilluminator. When PCR products showed a clear and single band of the correct expected length, they were purified using the Exo-SAP-IT kit and sequenced in an ABI 3700 (Applied Biosystem) sequencer. The forward primers were used for direct sequencing of the PCR products. When the sequences were not of sufficient quality, the complement/reverse sequences were obtained additionally.

Obtained ND1 and COI sequences were deposited in GenBank (Accession Numbers: KX109227–KX109416 for ND1; KX109417–KX109606 for COI; see Table S2).

2.3. Data analyses

Sequences were edited, aligned, and trimmed to a common length using the ClustalW alignment facility implemented in soft-

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