Migratory patterns and strategies of Mediterranean marine mammals and relation to intersystem connectivity

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ABSTRACT

This paper reviews and discusses the current knowledge on movement strategies and patterns of Mediterranean marine mammals. Emerging knowledge essential to overcome the existing gaps towards the identification of conservation strategies that systematically and explicitly account for the connectivity between populations, systems and realms is also presented.

INTRODUCTION

The exchange of individuals among populations through connectivity, e.g. dispersal, is an important life-history trait, critical to metapopulation dynamics, demography, persistence and expansion (see Gaylord and Gaines, 2000; Hastings and Botsford, 2006; James *et al.,* 2002; Roughgarden *et al.,* 1988; Simberloff and Wilson, 1969; Wright, 1931). Several factors can mediate the movements of organisms and the probability of their successful dispersal from one location to another (Casabianca *et al.,* 2012). It has been suggested that the knowledge of organisms' dispersal is essential to understand the response of populations and species to climate change, habitat loss and fragmentation, as well as biological invasions (e.g. Tesson and Edelaar, 2013). Understanding the complex dynamics of population connectivity and its relationship to environmental and anthropogenic factors is therefore a prerequisite for successful wildlife conservation and management (e.g. Botsford *et al.,* 2001; Bradbury *et al.,* 2008; Ruzzante *et al.,* 2006; Sale *et al.,* 2005).

While several examples exist for terrestrial species (e.g. Wiens, 2001), it is more difficult in marine systems to directly monitor the exchange of individuals among populations. The resulting limited understanding of the degree of connectivity among populations and systems creates a significant challenge for the management of nearly every marine species. The use of population genetics as a tool for indirectly estimating population and system connectivity (e.g. Bohonak, 1999; Howeth *et al.,* 2008; Lowe and Allendorf, 2010; Palumbi, 2003), despite significant advantages, often results in complex conclusions and possibly misinterpretations regarding connectivity, due to the complex genetic patterns among populations typically observed in marine systems (Bradbury and Bentzen, 2007). In fact, as recently reported, genetic methods provide valuable information on connectivity mostly when combined with alternative approaches, such as capture-mark-recapture methods or data on movement behavior, essential to elucidate the complex role of dispersal in natural populations (Lowe and Allendorf, 2010).

During the last decades, technological advances allowed the tagging and tracking of several marine species (e.g. Block *et al.,* 2011; Calò *et al.,* 2013; Hart and Hyrenbach, 2009; James *et al.,* 2005; Levin, 2006; Pittman *et al.,* 2014; Ropert Coudert *et al.,* 2009; Wood *et al.,* 2000). Concerning marine mammals, animal-borne satellite-linked tags have provided invaluable information on migration routes and patterns, as well as migration timing and distances of several species, contributing vital information to identify and mitigate anthropogenic impacts, and to inform the conservation of migratory species and their critical habitats (Mate, 2015; Rosenbaum, 2014). In particular, these studies, coupled with advanced statistical modelling (Jonsen *et al.,* 2013, 2003; Nielsen *et al.,* 2009; Silva *et al.,* 2014), greatly increase the possibility to integrate movement data to existing knowledge on behavior so as to better understand and quantify the complex processes of individuals' dispersal at multiple spatial and temporal scales, as well as the connectivity between populations and systems.

This paper reviews and discusses the current knowledge on movement strategies and patterns of Mediterranean marine mammals and presents emerging knowledge essential to overcome the existing gaps towards the identification of conservation strategies that systematically and explicitly account for the connectivity between populations, systems and realms.

MEDITERRANEAN SEA MARINE MAMMALS

Conservation status

A number of species of marine mammals have been reported to occur in the Mediterranean Sea over the course of centuries (e.g. Notarbartolo di Sciara and Birkun, 2010), but only few of them are currently considered to regularly inhabit this body of water. Eleven species of cetaceans, including the fin whale (*Balaenoptera physalus*), the sperm whale (*Physeter macrocephalus*), the Cuvier's beaked whale (*Ziphius cavirostris*), the Killer whale (*Orcinus orca*), the long-finned pilot whale (*Globicephala melas*), the Risso's dolphin (*Grampus griseus*), the rough-toothed dolphin (*Steno bredanensis*), the common bottlenose dolphin (*Tursiops truncatus*), the striped dolphin (*Stenella coeruleoalba*), the short-beaked common dolphin (*Delphinus delphis*) and the harbor porpoise (*Phocoena phocoena*) and one species of Pinniped, the Mediterranean monk seal (*Monachus monachus*) regularly occur in the Basin.

Recent genetic evidence suggests that some of the cetaceans occurring the Mediterranean Sea constitute distinct sub-populations from the North Atlantic, with little or no gene flow across the Strait of Gibraltar (Bérubé *et al.,* 1998; Drouot *et al.,* 2004a; Engelhaupt *et al.,* 2009; Gaspari *et al.,* 2013, 2007, 2006; Natoli *et al.,* 2008, 2005, 2004; Palsbøll *et al.,* 2004). The conservation status of these Mediterranean sup-populations (*sensu* IUCN) has been assessed according to the International Union for the Conservation of Nature (IUCN), resulting in one species classified as "*Critically Endangered*" (CR), four species classified as "*Endangered*" (EN), four species classified as "*Vulnerable*" (VU), and three species listed as "*Data Deficient*" (Table 1; IUCN, 2012).

Table. 1 Conservation status of the marine mammal species occurring in the Mediterranean and Black Seas

Species-subspecies	Region	IUCN Criterion	Year
Harbour porpoise *Phocoena phocoena ssp. relicta*	Black Sea subspecies	**Endangered** *A1d+4cde*	2008
Common bottlenose dolphin *Tursiops truncatus ssp. ponticus*	Black Sea subspecies	**Endangered** *A2cde*	2008
Short-beaked common dolphin *Delphinus delphis ponticus*	Black Sea subspecies	**Vulnerable** *A2cde*	2008
Sperm whale *Physeter macrocephalus*	Mediterranean subpopulation	**Endangered** *C2a(ii)*	2012
Short-beaked common dolphin *Delphinus delphis*	Mediterranean subpopulation	**Endangered** *A2abc*	2003
Fin whale *Balaenoptera physalus*	Mediterranean subpopulation	**Vulnerable** *C2a(ii)*	2012

Common bottlenose dolphin *Tursiops truncatus*	Mediterranean subpopulation	**Vulnerable** *A2cde*	2012
Striped dolphin *Stenella coeruleoalba*	Mediterranean subpopulation	**Vulnerable** *A2bcde*	2012
Risso's dolphin *Grampus griseus*	Mediterranean subpopulation	**Data Deficient**	2012
Long-finned pilot whale *Globicephala melas*	Mediterranean subpopulation	**Data Deficient**	2012
Cuvier's beaked whale *Ziphius cavirostris*	Mediterranean subpopulation	**Data Deficient**	2012
Mediterranean monk seal *Monachus monachus*	Mediterranean subpopulation	**Critically Endangered** *A2abc; C2a(i)*	2008

Mediterranean marine mammal populations live in precarious condition due to the high volume of pressures coming from human related activities and ever-increasing global changes, making this semi-enclosed sea one of the most degraded ecosystems worldwide (Bianchi and Morri, 2000; Coll *et al.,* 2010; Danovaro *et al.,* 2010; Piroddi *et al.,* 2015). Threats with actual and potential detrimental effects on Mediterranean marine mammals include injuries and mortality from shipping (e.g. Panigada *et al.,* 2006), chemical pollution (e.g. Borrell *et al.,* 2014; Fossi *et al.,* 2013, 2001; Panti *et al.,* 2011), interactions with fisheries (e.g. Lewison *et al.,* 2014; Reeves *et al.,* 2013), direct killings, noise pollution along with severe and widespread habitat loss and degradation.

In this context, the lack of critical information about abundance, trends, occurrence, distribution and movements, among other several ecological and life history traits, hampers the identification of management and conservation priorities.

Reported movements from the literature: examples from the Mediterranean Sea

Long- and mid-distance migrations are well known for several species of large cetaceans (e.g. Calambokidis *et al.,* 2001; Luschi and Luschi, 2013; Mate, 2015; Mizroch and Rice, 2013; Pomilla and Rosenbaum, 2005; Rasmussen, 2007; Stevick *et al.,* 2011; Stone *et al.,* 1990; Torres-Florez *et al.,* 2015) and to a lesser extent for smaller odontocete species. Marine mammals generally exploit resources across the world's oceans, but foraging grounds are often spatially and temporally separated from breeding grounds (Boyd, 2004). As an instance, most of the mysticete cetaceans utilize seasonally rich food supplies in the polar waters during the summer season, but migrate to sub-tropical waters during winter, when mating and birth take place (Block *et al.,* 2011). Migrations tend to follow predictable routes but often species with the largest body size undertake migration over the longest distances.

In the Mediterranean Sea, although marine mammals are well studied on their summer foraging grounds (e.g. Azzellino *et al.,* 2008; Druon *et al.,* 2012; Panigada *et al.,* 2011, 2005) and to a lesser extent on their winter grounds (Canese *et al.,* 2006), large knowledge gaps exist concerning their distribution and occurrence for much of the rest of the year. Accidental species have been reported from the Mediterranean Sea following exceptional migrations through the Atlantic and possibly the Northern Pacific Ocean (Bompar, 2000; Capellini, 1877; Gasco, 1878; Pouchet and Beauregard, 1888; Scheinin *et al.,* 2011).

The following paragraphs report on known movement patterns and migrations for five species of cetaceans occurring in the Mediterranean Sea, presenting novel information on the fin whale, recently obtained by means of satellite telemetry studies.

Sperm whale

Mediterranean sperm whales constitute a distinct sub-population from the North Atlantic stock (Drouot *et al.,* 2004a; Engelhaupt *et al.,* 2009). The systematic and extensive use of photo-identification methodology (Arnbom, 1987) across the Region over the last decades revealed how sexually mature male sperm whales undertake mid- to long-distance north–south migrations between the feeding grounds located in the Northern regions and the breeding grounds around the Balearic Islands (Drouot-Dulau and Gannier, 2007; Drouot *et al.,* 2004b; Gannier *et al.,* 2002) (Figure 1). Further extensive evidence have also been provided by Carpinelli *et al.,* (2014) (Figure 2), indicating long-range movements throughout the whole western Mediterranean Sea, with a maximum straight-line distance of about 1600 km. The same authors highlight the absence of photographic recaptures between the Mediterranean Sea and the North Atlantic Ocean, supporting earlier genetic evidence of a distinct Mediterranean sub-population. Finally, Frantzis *et al.* (2011) (Figure 3) provided the first ever conclusive evidence of inter-basin movements of this species following a rare mass stranding (Mazzariol *et al.,* 2011). The authors report that three of the seven stranded whales had been previously photo-identified in different locations of the Ligurian Sea, North Western Mediterranean, and the Hellenic Trench over two decades and have hence undertaken migrations of 1600-2100 km across the Strait of Messina or the Strait of Sicily, Central Mediterranean Sea. Although the authors do not provide exhaustive information on the migration routes, essential to possibly identify critical habitats and trigger protection actions, they provide crucial information on the inter-basin gene flow for the small Mediterranean sperm whale sub-population, that most likely amounts to hundreds (Rendell *et al.,* 2014).

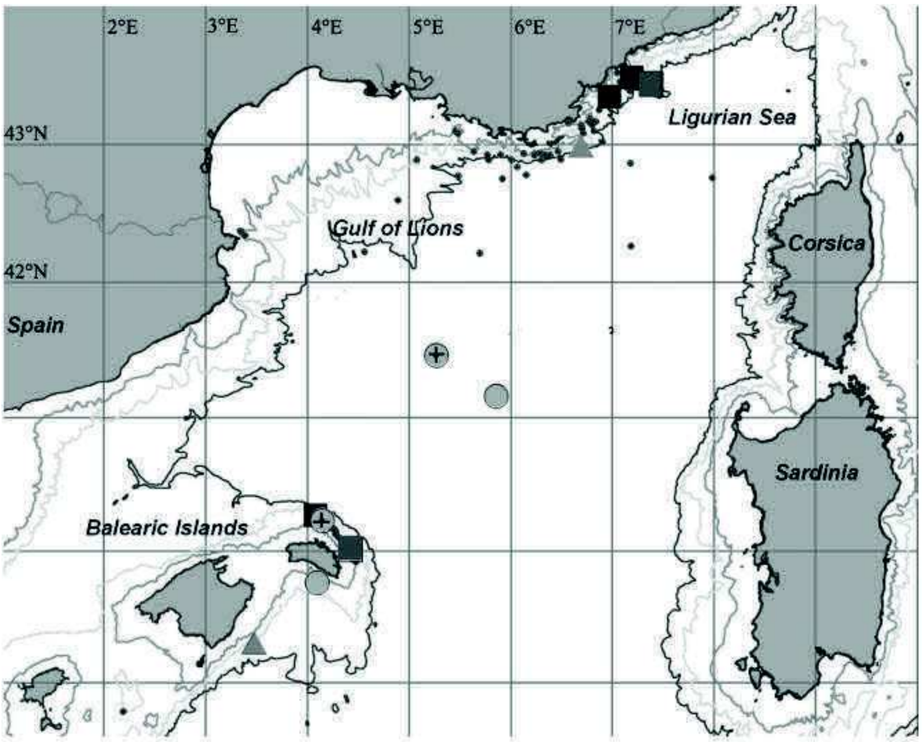

Figure. 1 - Photo-identified whales (dots) and long distance re-captures of sperm whales between the Balearic Islands and the North-Western Mediterranean Sea (from: Drouot-Dulau and Gannier, 2007).

Figure. 2 - Individuals from the Strait of Gibraltar re-sighted in the Mediterranean Sea. Numbers indicate chronological order of observation (from: Carpinelli *et al.,* 2014).

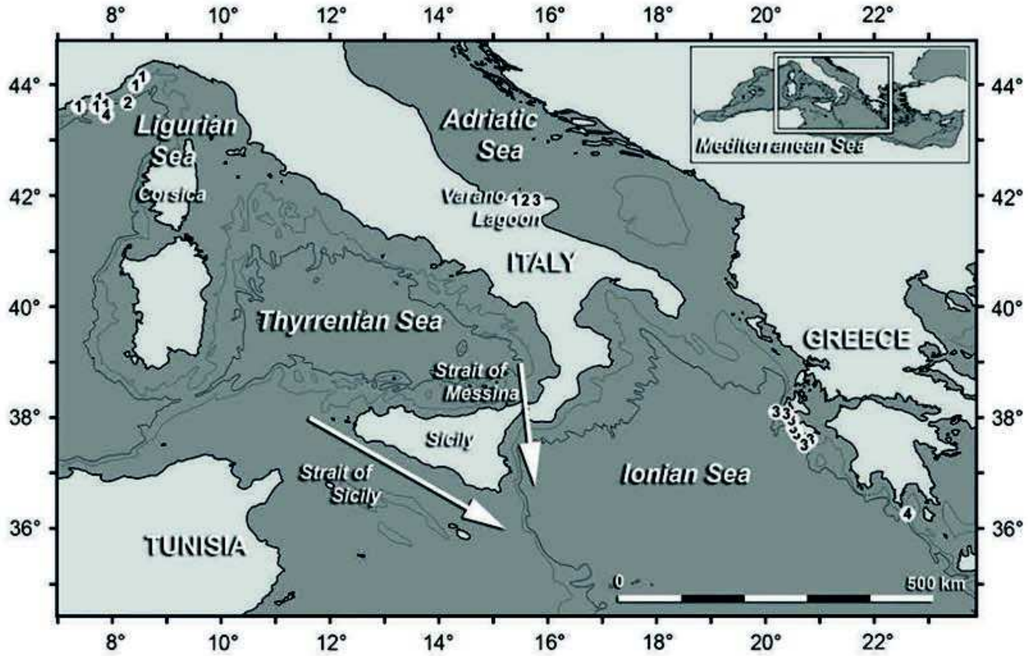

Figure. 3 - Map of the central Mediterranean, west and east of the Straits of Messina and Sicily. The position of the area presented in the map within the limits of the Mediterranean Sea is shown at the top right frame. Depth contours correspond to 1000 m (light grey) and 2000 m (dark grey). All observations of the whales identified in both the Western and Eastern Mediterranean basins and/or identified in the mass stranding are shown by numbered white dots (from: Frantzis *et al.,* 2011).

Common bottlenose dolphins

The common bottlenose dolphin (here after 'bottlenose dolphin') is one of the most frequently observed cetaceans in the Mediterranean Sea. The species occurs mostly in coastal waters within the entire basin. The total population size is unknown but may be in the low 10,000s based on observed densities in areas that have been surveyed. Most of the Mediterranean areas inhabited by these dolphins are subject to intensive human presence, and therefore severe detrimental pressures. The Mediterranean sub-population is distinct from those inhabiting the Eastern North Atlantic Ocean and the Scottish Sea (Natoli *et al.,* 2005). For a full review of the existing knowledge on the species ecology and conservation status in the Mediterranean Sea, please refer to Bearzi *et al.* (2009).

In the Mediterranean Sea, based on information obtained through photo-identification methods, bottlenose dolphins are primarily considered resident with some communities showing high levels of long-term site fidelity (Bearzi *et al.,* 1997). The lack of information on long-distance movements has resulted so far on higher emphasis on site fidelity, possibly underestimating the roaming abilities of the species and its potential to use and exploit alternative core habitats.

The longest movements reported in the Region are of 427 and 400 km, described by Gnone *et al.* (2011) in the North-Western Mediterranean, and followed by mid-distance movements of about 250 km presented by Bearzi *et al.* (2010) who present details on the movements of nine individuals photo-identified in different areas in western Greece (Figure 4). Moreover, one individual, photo-identified off Northern Corsica, was re-sighted in South-Eastern continental France, 228 km away from the original location (Dhermain *et al.,*1999). Mid-range movements were also observed among bottlenose dolphins photo-identified off the North-Western coast of Italy, where several individuals were re-sighted 100–130 km apart (Gnone *et al.,* 2006). Genov *et al.,* (2015) presented details on mid-distance re-sightings of a common bottlenose dolphin in the northern Adriatic Sea. One single adult bottlenose dolphin was observed and photographed alive off the Slovenian coast by the end of April 2014 and subsequently found dead on the shores of Goro, Italy, on 5 May 2014, about 130 km from the original sighting location. As reported by the authors, the fresh carcass suggests that the dolphin had died very recently prior to being found, indicating that the reported movement was not an artefact of currents. This further observation shows that bottlenose dolphins inhabiting the Northern Adriatic Sea can undertake substantial movements in relatively short time frames with such movements possibly being more common than documented to date. Very recently, using social network analysis Carnabuci *et al.,* (2016) investigated the association patterns of photo-identified common bottlenose dolphins and the macrostructure of the meta-population inhabiting the Pelagos Sanctuary for Mediterranean Marine Mammals and its connectivity in relation to the landscape characteristics. Their analysis of the network connectivity confirms previous knowledge that animals belonging to this meta-population tend to aggregate primarily with the individuals coming from the same sub-area. However, the same analysis also highlights that some animals tend to roam widely in the area connecting with different subgroups of the same meta-population. In fact, a few long travelling adult erratic males have been found to play an important role in connecting neighbouring clusters.

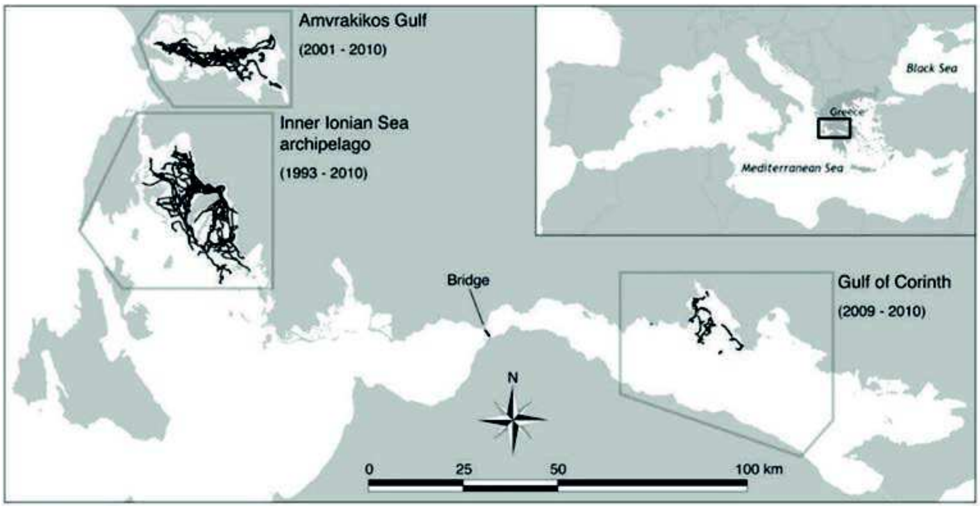

Figure. 4 - Location of the three study areas in Greece (delimited by grey lines). Black lines indicate movements by nine bottlenose dolphins (from: Bearzi *et al.,* 2010).

Humpback whale

The occurrence of the humpback whale (*Megaptera novaeangliae*), considered to be an occasional species in the Mediterranean basin, has been increasingly reported in the last decade with 14 sightings, 3 strandings and 2 by-caught individuals from different locations across the Region since, along with the first re-sighting of a lone individual in three different locations in the Mediterranean Sea between 2012 and 2013. A whale, approximately 8-9-meters long, was first observed in the Ligurian Sea, NW Mediterranean, in June 2012. The same animal was then re-sighted off Lampedusa Island, Sicily Channel, in March 2013 over 1000 km away in a straight line from the previous location and again in August 2013 in the Ligurian Sea (Figure 5).

The increased occurrence of this species in the Mediterranean Sea might be the result of the recent recovery of the North Atlantic humpback whale population, leading to increased migrations of individuals in the Mediterranean through the Gibraltar Strait. This range expansion, possibly leading to a (re)colonization of the Mediterranean in the future, could expose the species to severe anthropic pressures and urges appropriate mitigation measures to be considered and implemented also for this species.

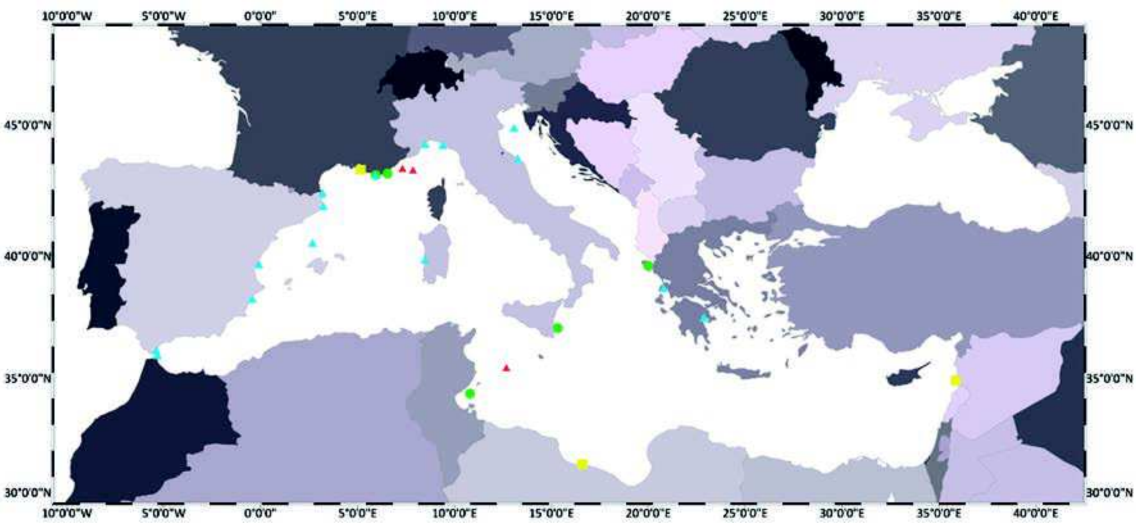

Figure. 5 Map showing the locations of sightings and strandings of humpback whales in the Mediterranean. The red triangles correspond to the re-sighted whale (from: Panigada *et al.,* 2014).

Short-beaked common dolphin

Once one of the most abundant cetacean species in the Mediterranean Sea, the short-beaked common dolphin (hereafter 'common dolphin'), constitutes a distinct sub-population from the North Atlantic (Natoli *et al.,* 2008). The species has declined throughout the region since the 1960s, likely due to overfishing and incidental mortality in fishing gear (Bearzi *et al.,* 2003). In the Mediterranean Sea, long-range movements have been reported only in one single occasion (Figure 6). Genov *et al.* (2012) describe a long-distance migration of one lone individual, encompassing a minimum of 1000 km across the Ionian and the Adriatic Seas, obtained through non-invasive photo-identification. This represents the longest documented movement for any individual of this species worldwide (Figure 6). While the authors could not reconstruct the possible migration route and stopovers, these data provide useful information in an area, the Northern Adriatic Sea, where common dolphins were historically abundant but had virtually vanished since the 1970s (Bearzi *et al.,* 2004; 2003).

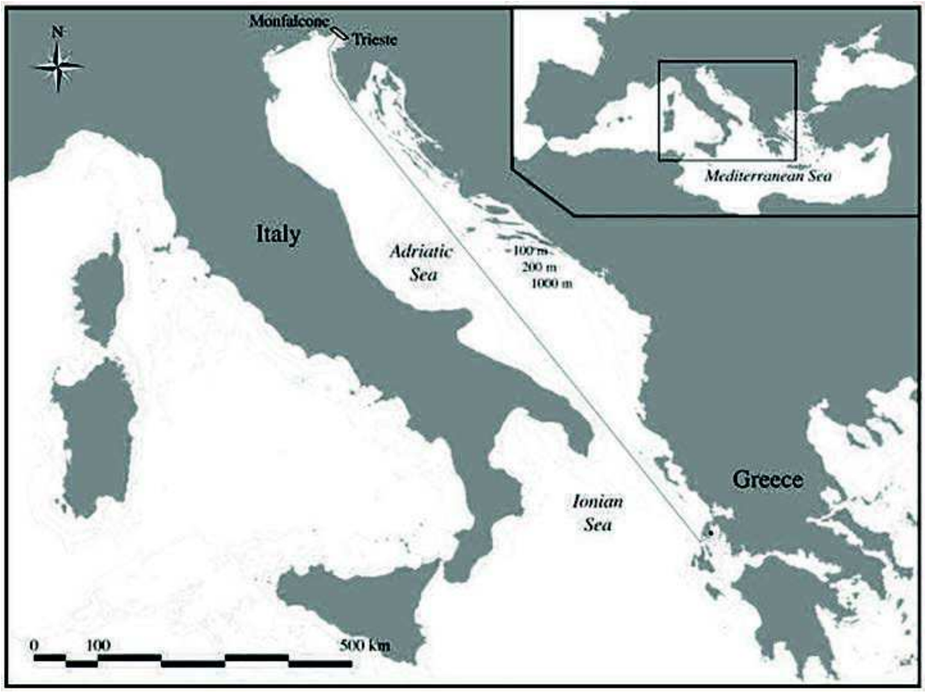

Figure. 6 - Minimum distance travelled by the adult common dolphin, with some of the locations cited in the text (from: Genov *et al.,* 2012).

Fin whale

The fin whale, mostly found in deep pelagic waters (Azzellino *et al.,* 2008; Notarbartolo di Sciara *et al.,* 2003; Panigada *et al.,* 2008), is abundant in the western basin with seasonal concentrations in highly productive areas such as the Ligurian Sea in the North-Western Mediterranean and the waters surrounding the Island of Lampedusa in Sicily Channel (Canese *et al.,* 2006; Notarbartolo di Sciara *et al.,* 2003; Panigada *et al.,* 2006). Genetic studies (Bérubé *et al.,* 1998; Palsbøll *et al.,* 2004) indicate differences between the Mediterranean population, which is thought to be resident, and fin whales in Atlantic coastal waters of Canada, Greenland, Iceland and Spain, with limited but recurrent gene flow between the Mediterranean and the North Atlantic populations. Recent acoustic studies (Castellote *et al.,* 2012) and stable isotope (Giménez *et al.,* 2014, 2013; Roubira *et al.,* 2015) have shed some light on the existence of two separate populations of fin whales utilizing primarily the Western Mediterranean, with one travelling back and forth between southern Spain and the actual Mediterranean sub-population. Ship strikes are reported to be the most detrimental threat and the main cause of direct mortality in the region (Panigada *et al.,* 2006).

In part due to a lack of information, or to often contradictory information, the knowledge and understanding of seasonal movements and migrations of Mediterranean fin whales across and outside the basin is scant and only limited to portions of the potential range of the species in the region. Fin whales are known to congregate in the Ligurian Sea during the summer months (Notarbartolo di Sciara *et al.,* 2003; Panigada *et al.,* 2005) and to possibly remain in the area if favorable conditions would occur, but no extensive and comprehensive information exist on yearly movement patterns. Castellote *et al.* (2012) reported consistent movements of Mediterranean fin whales from the Ligurian Sea towards the Alboran Sea and the northern coast of Algeria, with presence in these areas higher in spring and autumn, suggesting seasonal movements to and from the summer feeding areas located in the Ligurian Sea.

Recent information on large-scale movements describes the first north-south migration of one single animal between the Strait of Sicily and the Ligurian Sea through the Central and Southern Tyrrhenian Basin. The whale, equipped with a satellite transmitter, migrated in about five days between the two areas after spending several days in the only known winter feeding area around the Island of Lampedusa (Canese *et al.,* 2006). While the migration of one single individual might not represent conclusive evidence, and despite the lack of information on the identity of the whales occurring in the waters surrounding the Island of Lampedusa, it certainly shows a direct connection between the two feeding areas and highlights the need to preserve the migration route.

DISCUSSION

While connectivity plays a central role in sustaining marine populations, our understanding of this process and of its complexity is still largely underdeveloped.

From an ecological point of view, the understanding of demographic connectivity among populations is essential to understand the dynamics of populations and how they respond to natural and/or human disturbances (Hannah *et al.,* 2007; Lowe and Allendorf, 2010; Roberts, 1997; Roberts *et al.,* 2003; Saenz-Agudelo *et al.,* 2011; With *et al.,* 1997). Hence, quantifying the magnitude of retention within and connectivity among sub-populations is vital to metapopulation dynamics (e.g. Hixon *et al.,* 2002; Levin, 1974) and to model the effects of human pressures and natural fluctuations on marine ecosystems (Hughes *et al.,* 2005).

A detailed understanding of dispersal pathways and population connectivity in marine populations is necessary to trigger and guide the design of MPAs networks.

In the Mediterranean Sea, a hotspot of biodiversity, as well as one region most impacted by human activity (Coll *et al.,* 2010), natural fluctuation and anthropogenic stressors affect both the structural connectivity – the area and spatial configuration of habitats – and the functional connectivity – the rate of movement of individuals or genes among populations.

For marine mammals, in particular for cetaceans, it has been reported that high connectivity can buffer genetic diversity against demographic decline (Foote *et al.,* 2013). This is mostly relevant for the Mediterranean Sea where all the resident species of cetaceans constitute sub-populations that show distinctive genetic differences from the North Atlantic ones, with reduced gene flow between the two areas. The fragmentation and the general habitat loss and degradation of several Mediterranean ecosystems, primarily in coastal waters (Claudet and Fraschetti, 2010), is resulting into a general large-scale simplification and homogenisation of the marine environment, with potential severe detrimental effects at all levels and components of diversity.

Cetaceans are highly mobile species whose seasonal occurrence, site fidelity, movement patterns and connectivity are greatly determined by foraging and reproductive needs, with intrinsic barriers to movement being mainly represented by finding access to a suitable mate and/or breeding ground, as well as presence and seasonality of food resources (e.g., Foote *et al.,* 2009; Guzman *et al.,* 2015). Mediterranean cetaceans have been reported to perform short- to mid- and long-distance migrations with a high rate of seasonal or inter-annual site fidelity to some areas. For some of these species, a limited gene flow across the Strait of Gibraltar has been described, suggesting minimal genetic connectivity between separate sub-populations.

Further genetic fragmentation within the Region has only been investigated for the most accessible species and the lack of essential baseline data on this aspect is hampering further speculations. In this contest, the very recent gathering of movement data for some species such as the fin whale is therefore essential to integrate existing knowledge based on molecular techniques and to be complemented by the use of other remotely sensed information (e.g. Bauer *et al.,* 2015; Burtenshaw *et al.,* 2004; Druon *et al.,* 2012).

In this contest, modern technology can be essential to identify previously unknown movement corridors (Zeh *et al.,* 2016) which are often unknown (Hyrenbach *et al.,* 2000) or change following natural dynamics and processes (Grüss *et al.,* 2011; Lascelles *et al.,* 2014).

Investigating whales' migrations and movement patterns in conjunction with the presence of feeding grounds and the potential shift of prey occurrence could help identifying factors leading to isolation of populations on a timesòe not detectable by genetic analysis, hence providing critical information to conservation.

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