

## DEPARTMENT OF ENVIRONMENTAL BIOLOGY "CHARLES DARWIN" SAPIENZA UNIVERSITY OF ROME

#### PHD IN ENVIRONMENTAL AND EVOLUTIONARY BIOLOGY Animal Biology Curriculum XXVIII Cycle

On the sperm whale (*Physeter macrocephalus*) ecology, sociality and behavior off Ischia Island (Italy): patterns of sound production and acoustically measured growth

by

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# Goals and thesis outline

The main goal of this research is to contribute to the overall knowledge of the sperm whales' (*Physeter macrocephalus*) ecology, sociality, and behavior in the Mediterranean Sea. The combined use of visual and acoustic methods allows me to:

- 1) give a detailed outline of the encounters around Ischia Island (Tyrrhenian Sea, Italy) over 2002-2015 period;
- provide insights into the acoustic repertoire in encounters with social units (females with immatures), clusters of presumed/confirmed males and solitary individuals; this information was then used to:
  - a. model habitat suitability (Pace *et al.*, submitted) and use via analysis of different vocalization types,
  - b. analyze a type of social sound (*i.e.* coda),
  - c. investigate an unusual tonal sound (*i.e.* trumpet),
- 3) present acoustically derived estimates of individual whale growth.

This involved the application of acoustic methods to groups or individual sperm whales located in the area. Using passive acoustics to study animal behaviour is a developing field. As such, many of the recent publications describe methods, models and algorithms that can be used to investigate cetaceans in the wild.

In this thesis I attempt to apply these tools to a larger sample size than previous studies in the Mediterranean Sea, taking advantage of the long-term data set of audio recordings made around Ischia Island between 2004 and 2015.

The thesis is organized in 6 chapters.

- Chapter 1 and 2 describe sperm whale general biology and acoustics;
- Goal 1 is addressed in Chapter 3; it provides fundamental background information on:
  - ✓ the study area;
  - ✓ the distribution of sperm whale encounters around Ischia Island (published in Pace *et al.*, 2014; Mussi *et al.*, 2014 and updated to 2015);
  - ✓ the individual photoidentification and group composition (published in Pace *et al.*, 2014; Carpinelli et al., 2014 and updated to 2015);

and new insights on:

- the habitat suitability (Pace *et al.*, submitted);
- ✓ diving/resting at surface cycle.
- Goal 2 is addressed in Chapter 4;
- Goal 3 is addressed in Chapter 5 (partially presented in Pace *et al.*, 2013);
- The final Chapter (#6) provides conclusions and outlines directions for future research.



# Chapter 1 Sperm whale biology

The sperm whale, *Physeter macrocephalus* Linnaeus, 1758, is the only species in the monophyletic family Physeteridae and is the most sexually dimorphic member of the toothed whales of the suborder Odontoceti (Rice, 1989). This whale is an ecologically important oceanic predator (mainly of mesopelagic cephalopods), that occurs in all of the world's oceans (Clarke *et al.*, 1976; Rice, 1989; Rendell *et al.*, 2004).

While there is scientific consensus that only one species of sperm whale exists, debate has been ongoing as to which of the two Linnaean names for the sperm whale, *P. catodon* or *P.* macrocephalus, is the correct name and should be used. The sperm whale was categorized first by Linnaeus in 1758, recognizing four species in the genus Physeter. Until 1911 the species was generally known as *P. macrocephalus*, however in that year Thomas (1911) concluded that *P.* catodon was the correct name. Later, Husson and Holthuis (1974) showed that the correct name should be *P. macrocephalus*, the second name in the genus *Physeter* published by Linnaeus concurrently with *P. catodon*. Grounds for this proposal were that the names were synonyms published simultaneously and therefore the International Code of Zoological Nomenclature (ICZN) principle of "First Reviser" should apply, in this instance leading to the choice of P. macrocephalus over P. catodon, a view re-stated by Holthuis (1987) and Rice (1989). This has been adopted by most subsequent authors. Schevill (1986, 1987) argued against this and upheld the name *catodon*, stating that *macrocephalus* lacked accuracy when it was described, therefore rendering the principle of "First Reviser" inapplicable. However Linnaeus described macrocephalus as attaining a length of 60 feet, and having spermaceti in the head – a description that can apply to no other species of whale. Currently, most authors have accepted P. *macrocephalus* as the correct name.

#### **1.1 General anatomy**

The sperm whale is the largest species in the suborder Odontoceti and has the largest brain of any animal (on average 7.8 kg in mature males); however, compared to their large body size, the brain is not exceptional in size. Males reach maximum lengths of 18–21 m and weights of 60 t, and females' up to 12 m and 30 t (Berzin, 1971). Adult sperm whales have a mean weight of approximately 40 t. At birth, both male and female calves average 4 m in length and weigh approximately 1 t (Gosho *et al.*, 1984). Sperm whales are mostly dark grey to brownish–grey. The interior of the mouth is often bright white. Some individuals also have white patches on the belly. The flippers are paddle–shaped and small compared to the size of the body, and their flukes are triangular with a nearly straight trailing edge, rounded tips, and a deep notch. Sperm whales have a small dorsal fin that is low, thick, and usually rounded, while a series of bumps, or crenulations, on the dorsal ridge of the tail stock tend to be more prominent in females (Jefferson *et al.*, 1993). The body has a corrugated, or shrivelled, appearance posterior to the head (Leatherwood and Reeves, 1983). Sperm whale is the only living cetacean that has a single blowhole asymmetrically situated on the left side of the head near the tip. The lower jaw is

narrow and underslung (Jefferson *et al.*, 1993). There are between 17–29 large conical teeth, up to 27 cm (Berzin, 1971), in each side of the lower jaw of the sperm whale. The teeth in the upper jaw rarely erupt in juvenile whales and are deeply curved, and absent or atrophied in adults (Gibbs and Kirk, 2001). It appears that teeth may not be necessary for feeding, since they do not break through the gums until puberty.

The genus name *Physeter*, means 'blower', and the species name *macrocephalus* means 'big head'. The immense forehead of sperm whales is possibly the largest, and one of the strangest, anatomical structures in the animal kingdom. The distinctive head of the sperm whale, which takes up 25–35% of its total body length (Leatherwood and Reeves, 1983) and can be up one fourth of the body mass, contains the spermaceti organ and the junk (Berzin, 1971; Clarke, 1978a,b). The spermaceti organ provides the highly valued spermaceti oil for which this species was extensively hunted during the 18<sup>th</sup> to 20<sup>th</sup> Centuries. The junk, which lies under the spermaceti organ and is derived from the odontocete melon, is filled with denser, less-valued oil (Berzin, 1971; Carrier et al., 2002). Although the unique structure of the junk certainly serves multiple functions, results from Panagiotopoulou and colleagues (2016) are consistent with the hypothesis that the structure also evolved to function as a massive battering ram during malemale competition. The spermaceti organ and nasal passages of the sperm whale have been The spermaceti organ and nasal passages of the sperm whale have been extensively described and studied; several theories have been proposed about the possible functions and evolution of the system (Raven and Gregory, 1933; Berzin, 1971; Carrier et al., 2002). It has been suggested that these structures function as a biosonar to locate prey, for acoustic sexual selection, and for buoyancy control (Clarke, 1978a). Although the functions of the huge nasal complex have not been definitely proven, it is evident that the sperm whale uses it to produce and direct a wide variety of sounds (Madsen et al., 2002). The production of sound by sperm whales may serve in male-male agonistic competition, as evidenced by head-butting during aggressive behaviour (Carrier et al., 2002); it could be used for acoustic debilitation of prey (Norris and Møhl, 1983; Møhl et al., 2000; Miller et al., 2004), and it could also indicate the size of males to females (Norris and Harvey, 1972; Cranford, 1999; Møhl, 2001; Møhl et al., 2003). The spermaceti organ and the anatomical dimorphism of male and female sperm whales may have significant implications on the feeding biology and ecology of both genders. Males are known to dive deeper and for longer periods than females, migrating to higher latitudes in their search for food (Gosho et al, 1984; Rice, 1989). This will affect the prey species that males and females encounter and will be reflected in the composition of the diet of both genders.

#### 1.2 Abundance, distribution and movements

At present, estimates for the worldwide population of sperm whales is fragmented and incomplete. The most accepted global population estimate of 300,000 – 450,000 whales is proposed by Whitehead (2002) and considered to be imprecise (NOAA Northeast Fisheries Science Center, 2015). Inaccurate and underreported modern catch data, the wide-ranging distribution of the whales, and minimal time spent at the surface complicates efforts to attain accurate global abundance numbers (NOAA Northeast Fisheries Science Center, 2015). In the Mediterranean Sea sperm whales quantitative abundance estimate is currently not available (Reeves and Notarbartolo di Sciara, 2006; Notarbartolo di Sciara *et al.*, 2012). The

species numbers 'more likely in the hundreds rather than the thousands' (Reeves and Notarbartolo di Sciara, 2006) and very likely 'fewer than 2,500 animals' (Notarbartolo di Sciara *et al.*, 2012). A recent study in the Western Mediterranean (Rendell *et al.*, 2014) showed that photo-identification data collected in the period 1990-2008 is inconsistent with population sizes of greater than 1000 animals or lower than 200, with the best estimates suggesting that the population using the study area numbers around 400. Although there is no overall abundance estimate for the Mediterranean population, records from various research groups in different areas seem to indicate that the species has declined over the past 20 years (Cañadas *et al.*, 2005; Aguilar and Barroell, 2007; Lewis et al., 2007; Pirotta et al., 2011; Carpinelli et al., 2014). Sperm whales are found throughout the world's deep oceans, from the tropical waters of the equator to the polar regions (Berzin, 1971; Best, 1979), inhabiting all oceans and most semienclosed areas (Whitehead, 2003). The distribution of this species is not uniform: it is determined by gender and age group, and is closely related to prey availability and various factors like bathymetry and primary/secondary productivity (Jaquet et al., 1996; Davis et al., 2002), continental shelf breaks, cyclonic eddies, oceanic fronts, warm core rings, submarine canyons, and other oceanographic features (Jaquet and Whitehead, 1996; Waring et al., 1993; André, 1997; Griffin, 1999; Gregr and Trites, 2001; Waring et al., 2001; Whitehead, 2003; Biggs et al., 2005; Watwood et al., 2006; Pace et al., 2012).

Based mostly on sighting surveys or land station whaling data, it is thought that they are often concentrated around oceanic islands in areas of upwelling, and along the outer continental shelf, continental slope, and mid–ocean waters (Hain *et al.*, 1985; Kenney and Winn, 1987; Waring *et al.*, 1993; Gannier, 2000; Gregr and Trites, 2001; Waring *et al.*, 2001). However, based on pelagic whaling data, sperm whales were found in large numbers in a broad band around 40°N in the northeastern North Pacific and a broad band around 30°N in the northwestern North Pacific (Mizroch and Rice, 2006). Sperm whales show a strong preference for deep waters (Rice, 1989), especially in areas with high sea floor relief. They also converge around areas with temperature gradients, which provide ideal conditions for the schooling of their main prey, the cephalopods (Clarke, 1996; Jarre–Teichmann, 1998).

- Mature males and females exhibit different distributional (Figure 1) and diving behaviours, and spend most of their adult lives segregated (Berzin, 1971; Best, 1979; Clarke *et al.*, 1993). Mature females, calves and juveniles form social groups that inhabit tropical and temperate waters year-round (from the equator to around 45°N, rarely found at latitudes higher than 50°N and 50°S), and have ranges of approximately 1,000 km over time spans of ten years (Rice, 1989; Richard *et al.*, 1996; Reeves and Whitehead, 1997; Weilgart and Whitehead, 1997; Whitehead and Weilgart, 2000). It has been suggested that groups of females and juveniles may be restricted to lower latitudes because of: a) the energetic requirements imposed on females by deep diving, reproduction and lactation (Best *et al.*, 1984); b) the thermoregulatory constraints of calves in colder waters (Lyrholm *et al.*, 1999); and c) because prey at higher latitudes occurs too deep and outside the diving capabilities of females and juveniles (Best, 1979). Male sperm whales progressively move to higher latitudes with age (Best, 1979). Adult males are mainly solitary, and have a broader distribution, reaching the drift ice in both polar oceans
  - are mainly solitary, and have a broader distribution, reaching the drift ice in both polar oceans during the austral and boreal summers (Berzin, 1971; Best, 1979; Rice, 1989).



*Figure 1. Global distribution of the sperm whale. The red dashed lines indicate the range of females and immature males.* 

In the Northern Hemisphere boreal groups of sperm whales of both sexes range between 0° and 25°N from October to March, travelling north to 25–40° N between April and September (Bolau, 1895; Townsend, 1931). In the Southern Hemisphere, groups of males and females move southward from the Equator during the austral winter, between April and September, then return north between October and March, during the austral summer (Berzin, 1971). Rice (1989) suggested that it was reasonable to expect some inter-basin movement around the Cape of Good Hope (Atlantic Ocean-Indian Ocean) and through the passages between the Lesser Sunda Islands or round the south coast of Tasmania (Indian Ocean-Pacific Ocean), but the author considered exchange via Cape Horn (Pacific Ocean-Atlantic Ocean) to be "almost entirely restricted, except possibly for a few males". Mostly adult males move into high latitudes, while all age classes and both sexes range throughout tropical and temperate seas. Discovery mark data from the days of commercial whaling (260 recoveries with location data) show extensive movements of both males and females from U.S. and Canadian coastal waters in to the Aleutian Islands and Gulf of Alaska, and for males into and within the Bering Sea (Omura and Ohsumi, 1964; Ivashin and Rovnin, 1967; Ohsumi and Masaki, 1975; Wada, 1980; Kasuya and Miyashita, 1988) although, of nearly 60,000 sperm whales killed in the North Pacific above 50° N, approximately 57,000 were males (Mizroch and Rice, 2006). Sperm whales are widely distributed within the Mediterranean from the Alboran Sea to the Levantine basin, with the exception of the Black Sea (Azzellino *et al.*, 2008; Boisseau *et al.*, 2010; Cañadas et al., 2002; Frantzis et al., 2003; Gannier et al., 2002; Lewis et al., 2007; Pace et al., 2012). Different authors have investigated relationships between sperm whale distributions, bottom topographies and environmental parameters in the Mediterranean (David, 2000; Drouot et al., 2004b; Gannier and Praca, 2007; Azzellino et al., 2008; Praca and Gannier, 2008; Moulins et al., 2008; Aïssi et al., 2012; David and Di-Meglio, 2012). It has been shown that the species seems to prefer deep continental slope waters (Azzellino et al., 2008) thought to be areas where mesopelagic cephalopods – the species' preferred prey (Clarke, 1996; Whitehead, 2003) – are most abundant (Azzellino et al., 2008; Praca and Gannier, 2008). Sperm whales, however, can

also be found in deep offshore waters (Praca and Gannier, 2008; Praca *et al.*, 2009), in coastal areas where there is deep water and in proximity to features like sea mountains and submarine canyons (Drouot *et al.*, 2004; Mussi *et al.*, 2014) and those habitats associated with oceanographic frontal systems with marked temperature discontinuities (Gannier and Praca, 2007). In the North–Western Mediterranean, for example, the occurrence of the species seems to be positively related with such topographical configurations (David, 2000; Gannier and Praca, 2007; Moulins *et al.*, 2008; Aissi *et al.*, 2012, 2014; David and Di–Meglio, 2012), highlighting the need to improve the understanding of the importance of deep sea features such as submarine canyons for top predators like sperm whales.

The Mediterranean is an enclosed sea consisting of two main basins, the Eastern and the Western, separated by the Straits of Sicily and Messina, and connected to the Atlantic Ocean by the narrow shelf of the Strait of Gibraltar. Several observations suggest a high degree of isolation in the sperm whale population in the Mediterranean. There is no evidence of crossing through the Strait of Gibraltar into the Atlantic Ocean, and genetic evidence supports the view that there is no connection between populations in the Mediterranean and the adjacent waters of the North Atlantic (Drouot et al., 2004a; Engelhaupt et al., 2009; Carpinelli et al., 2014). Within the Mediterranean, the degree to which sperm whale groups in the two basins are connected is largely unknown. From east to west the Mediterranean measures about 3,800 km and the widest distance north to south is around 900 km, distances over which sperm whales from other populations are known to regularly move (Whitehead, 2001; Whitehead et al., 2008). Surveys report an absence or very low density of sperm whales in the Strait of Sicily and Ionian Sea which link the two areas (Lewis et al., 2007), and these transition areas are much shallower than the typical sperm whale habitat. These areas are not absolute barriers, however, a recent study has provided conclusive evidence that at least three sperm whales have made the transition from the western to the eastern basin in the last 20 years (Frantzis et al, 2011). Nonetheless, as these individuals represented about 1% of the identified animals examined in that study, and there is no evidence of east to west movements, it seems reasonable to consider movements between the basins as relatively rare events.

All age and sex classes appear to be present year round (Frantzis et al., 2014; NOAA Northeast Fisheries Science Center, 2015) in both the east and west basins of the Mediterranean (Frantzis et al., 2003; Drouot et al., 2004b; Drouot-Dulau and Gannier, 2007). In the western basin, larger groups as well as calves are more common in the southern part (Drouot *et al.*, 2004b), and males appear to travel to and from the more northern areas of the basin in an apparently restricted version of the movements made by males in larger ocean basins (Drouot-Dulau and Gannier, 2007; Whitehead, 2003). Surveys have reported that, similar to sperm whales in other areas, during summer months the Mediterranean population displays a degree of segregation of mature male sperm whales in the northern region from females, calves, and immature males in the southern one. It appears that mature males travel between feeding and breeding grounds while females, calves, and immature males display a more sedentary lifestyle (Drouot et al., 2004a; Frantzis *et al.*, 2011; Carpinelli *et al.*, 2014; Pace *et al.*, 2014). However, due to a variety of factors, movements of Mediterranean sperm whales remain poorly understood (Carpinelli et al., 2014; Rendell et al., 2014), although they seem to aggregate in certain areas that provide unique feeding grounds or nurseries, making these regions of critical importance for species conservation (Cañadas et al., 2002; Gannier et al., 2002; Drouot, 2003; Drouot et al., 2004a; Gannier and Praca, 2007; Mussi et al., 2014; Pace et al., 2014; Pace et al., 2015).

#### 1.3 Reproduction and social structure

Information on the reproduction of sperm whales, obtained mainly from whaling specimens and observations made aboard catcher boats, has been reviewed by several authors (Best and Butterworth, 1980; Best *et al.*, 1984; Clarke *et al.*, 1980; Whitehead, 2003). Sexual maturation in female sperm whales typically occurs between 7–13 years of age. Maturation in males usually begins in this same age interval, but most individuals do not become fully mature until about 20 years of age and older (Clarke *et al.*, 2011). Since females within a group often come into estrus synchronously, the male need not remain with them for an entire season to achieve maximal breeding success (Best and Butterworth, 1980).

In the northern hemisphere, the peak breeding season for sperm whales occurs between March/April and June, and in the southern hemisphere, the peak breeding season occurs between October and December (Best et al., 1984). In both cases, some mating activity takes place earlier or later. The average calving interval in South Africa ranges from 5.2 (west coast) to 6.0–6.5 years (east coast) (Best *et al.*, 1984). Clarke *et al.* (1980) proposed a 3-year reproductive cycle for the southeast Pacific. These inter-birth intervals are related to primeaged females and, apparently, they are much longer for females over 40 years of age. Female sperm whales rarely become pregnant after the age of 40 (Best et al., 1984; Whitehead, 2003). Gestation lasts well over a year, with credible estimates of the normal duration ranging from 15 months to more than a year and a half. Lactation lasts at least two years, although there have been cases of sperm whales with milk in their stomachs at up to 13 years of age (Best et al., 1984). Nursing females have been reported to separate from their breeding groups while caring for their offspring (Gero et al., 2014). However, it has also been well documented that sperm whales participate in alloparental care and allonursing, with females from the entire clan being involved in the care, and even nursing, of offspring (Gero *et al.*, 2009). Young sperm whales will begin to wean and ingest solid food at about 1 year of age.

Sperm whales are organized in breeding groups (or social units) in which sexually matured females (some related and some not related to each other) form long-term associations with their immature offspring of both sexes (Whitehead, 2003). The evolution of highly structured social units that persist over long periods of time in schools of female sperm whales appears to be driven by benefits brought about by communal living (Whitehead, 1996a; Christal and Whitehead, 2001). Benefits include: shared knowledge about the presence of ephemeral food resources, over the sperm whale's vast spatial ranges; utilising the echolocation of other sperm whales nearby; increasing foraging efficiency while diving in groups (Whitehead, 1989, 1996b); and communal nursing and care of calves, and cooperative protection against predators (Best *et al.*, 1984; Arnbom *et al.*, 1987; Whitehead, 1996a).

Maturing and adult males are mainly solitary but can form small temporary associations called "bachelor groups" that become progressively smaller as males increase in size and age (Best, 1979; Lettevall *et al.*, 2002). The cohesion among males within a bachelor school declines as the animals age, although bonding is evident by the fact that males mass strand (Bond, 1999; Mazzariol *et al.*, 2011) and by the relative stability of associations in groups (Pace *et al.*, 2014). The stability of these associations appears to depend on food availability, as they persist over shorter periods of time; they also seem to be more stable geographically than the aggregation of females and juveniles (Lettevall *et al.*, 2002).

Males disperse from these social groups at approximately six years of age and gradually move to the cold–water feeding grounds at higher latitudes, reaching 70°N in the Atlantic and 70°S in the

Southern Ocean (Richard *et al.,* 1996; Santos *et al.,* 1999; Rendell and Whitehead, 2003). Males exploit highly productive feeding grounds at higher latitudes, and in doing so may reduce competition for resources with females and juveniles, increasing males' growth rates to maturation (Lyrholm *et al.,* 1999). When males reach sexual maturity in their late twenties, they leave their feeding grounds in colder waters and return to lower latitudes, travelling between family groups during the breeding season (Whitehead, 1993). It is during these migration periods that most of the strandings occur (Santos *et al.,* 2002).

#### 1.4 Feeding and main prey

A full description of the digestive system of the sperm whale can be found in Berzin (1971). The mouth, tongue, oesophagus and first stomach are covered with a tough cuticular lining that is though to protect the whale from the hooks and beaks of struggling squids (Clarke, 1980). How sperm whales catch their prey can only be inferred from dietary examination (stomach content analysis), functional analyses of the whales' anatomy, and examination of the distribution, abundance and nature of scars in their skin. It is thought that after capturing the prey, the sperm whale swallows it by moving forward with little or no aid of the tongue, as nearly undamaged flesh of cephalopods and fish was often found in the first stomach of commercially caught whales (Berzin, 1971; Clarke, 1976, 1980; Martin and Clarke, 1986). Digestive juices are secreted in the second stomach, acting on the flesh and digesting it. The hard parts of the prey, such as fish bones and otoliths, and the chitinous beaks of cephalopods, all withstand chemical digestion to a certain extent and tend to accumulate in the second stomach for several days or even weeks (Clarke, 1980). Ambergris, a non-volatile alcohol of high molecular weight, forms in the large intestine and can be found in lumps of up to 10 kg, often with cephalopod beaks embedded in it, in 1–5% of sperm whales (Rice, 1989).

From bioacoustical and dietary studies, it is known that sperm whales are slow animals that feed at great depths, where there is no light except for bioluminescence (Heezen, 1957; Nemoto and Nasu, 1963; Clarke, 1976; Watkins, 1980; Watkins *et al.*, 1993). Bioluminescent cephalopods can comprise 0–97% of the diet of sperm whales in different areas, and slow swimming, neutrally buoyant cephalopod species comprise 82% of the diet of sperm whales in the central Atlantic (Clarke, 1980; Clarke *et al.*, 1993). Light emitted by prey could be used by the sperm whale to locate it but the way that they capture fast swimming cephalopods is still debated (Miller *et al.*, 2004).

Sperm whales appear to be opportunistic and voracious predators (Clarke, 1980). Their primary prey in most areas of the world seems to be mesopelagic and bathypelagic cephalopods weighing less than 1,000 g (Clarke, 1980; Rice, 1989; Whitehead, 2003; Gannier and Praca, 2007); however, the larger species of cephalopods (over 13 m long and weighing more than 500 kg) may be an important source of energy (Clarke, 1996b), and constitute an important part of the diet of sperm whales where they are consumed. In some areas, fishes may comprise a substantial part of sperm whale diets (Kawakami, 1980; Whitehead, 2003).

It has been calculated that the sperm whale needs to consume between 2.0–3.5% of its own body mass per day (Lockyer, 1981). For a sperm whale that weighs 40 t, this means it has to consume from 800–1,400 kg of food a day, a rather large and significant impact on deep ocean food webs and nutrient cycling in the ocean. It has been estimated that the world sperm whale population consumes about 100 Mt/yr (Clarke, 1976; Kanwisher and Ridgeway, 1983; Whitehead, 2003; Watwood *et al.*, 2006). To meet its high energetic demands, the sperm whale apparently targets aggregations of squid, preying on slow and sluggish ammoniacal squid, but also consumes some of the largest species of cephalopods (Santos *et al.*, 1999; Bjørke, 2001). Even though muscular species have a higher nutritional value, they are faster and possibly harder to capture than the slower ammoniacal squid (Clarke *et al.*, 1985). By using all these strategies, the sperm whale may be able to acquire energy from a relatively poor environment such as the deep sea.

In addition to differences in diet based on area of the world, sperm whale foraging can differ based on sex (Whitehead, 2003). In general, male sperm whales are found in the higher latitudes and closer to shore, thus in shallower waters; female sperm whales are rarely found in shallow waters above continental shelves (Caldwell *et al.*, 1966; Best, 1999; Gregr *et al.*, 2000; Whitehead, 2003). This variation in distribution also affects the whales' method of hunting. Due to their presence in shallower waters, male sperm whales are more likely to dive to the bottom, their diet consists of more bottom–dwelling animals and a larger amount of cephalopods. In contrast, fish make up a significant part of the female sperm whale diet along with cephalopods (Whitehead, 2003). Off Durban, male sperm whales eat squid weighing approximately 1 kg, while females and juveniles eat smaller squid of approximately 500 g (Clarke, 1980). This could be a reflection of the vertical migration of squid as they grow, as well as differential diving provess for different sexes and ages (*e.g.* Clarke, 1980).

Cephalopod behavior has also been suspected to influence sperm whale distribution by aggregating pods to certain areas (Jaquet and Whitehead, 1996; Connor, 2000; Whitehead, 2003). During spawning, cephalopods tend to aggregate in groups that could yield relatively easier prey sources for sperm whales (Clarke, 1980). Different species of cephalopod exhibit different spawning times and modes, which could be a contributing factor to the sperm whale wide dietary range (Whitehead, 2003).

A number of studies have tried to distinguish any type of diurnal variation in sperm whale foraging; however, most have failed to find any diurnal pattern in feeding success and have found clear evidence that sperm whales forage at all times of day (Okutani and Nemoto, 1964; Clarke, 1980; Whitehead, 1996b; Best, 1999; Whitehead, 2003). There also seems to be no evidence of patterns in sperm whale foraging related to lunar cycles or seasonal variations (Clarke *et al.*, 1988; Clarke, 1980; Whitehead, 1996b; Best, 1999; Whitehead, 2003).

#### 1.5 Diving behaviour

Sperm whales spend most of their time underwater (Jaquet *et al.*, 2000). Their diving behaviour has been studied using hydrophones (*e.g.* Madsen *et al.*, 2002), sonar (Papastavrou *et al.*, 1989; Watkins *et al.*, 1993), acoustic recorders (*e.g.* Watkins, 1980), time–depth recorders (Watkins *et al.*, 2002), video cameras (Marshall, 1997), and tags (*e.g.* Zimmer *et al.*, 2003; Oliveiera, 2014). The diving behaviour of sperm whales is influenced by body size, sex, oceanographic conditions, prey availability, and social conditions (Perry *et al.*, 1999). Mature female and male sperm whales exhibit different diving behaviours and appear to reduce competition by vertically partitioning the habitat they feed in, with larger whales being able to exploit deeper resources (Gordon, 1987b). Adult males can dive for more than 90 minutes at depths between 300 and 2,000 m (Clarke *et al.*, 1993; Watkins *et al.*, 1993; Papastavrou *et al.*, 1989; Whitehead, 2003; Watwood *et al.*, 2006). Females however, dive for shorter periods at depths between 200 and

1,200 m, normally staying in the top 500–800 m of the water column (Papastavrou *et al.*, 1989; Gordon and Steiner, 1992; Watkins *et al.*, 1993). The social condition of sperm whale groups also affects the duration of dives (Gordon, 1987a); groups of females with calves have average dive times of eight minutes, whereas groups of females without calves have average dive times of 25 minutes at shallower depths (Gordon and Steiner, 1992). Although large male sperm whales are capable of prolonged dives of up to 138 minutes to depths exceeding 2,000 m, most dives by both sexes are shallower than 1,000 m and usually last about 30 to 45 minutes (Clarke, 1976; Lockyer 1981, Watkins *et al.*, 1985; Oliveira, 2014).

While sperm whales perform short dives, typically only to move away from a disturbance at the surface, most of their dives are deep, preceded by a 'fluke up' and commonly associated with foraging (Whitehead, 2003). These deep foraging dives make up a significant part of sperm whale behavior, comprising approximately 62–72% of the whale's life (Whitehead, 2003; Watwood *et al.*, 2006). The composition of a sperm whale foraging dive can be broken up into three stages: descent, foraging at depth, and ascent. Spending approximately 15 minutes descending, 15–30 minutes foraging, and 15 minutes ascending; the sperm whale dive profile often, but not always, has a U–shape (Gordon, 1987a; Whitehead, 2003). The dives are normally separated by periods of rest at the surface, which can last between 7–15 minutes (Oliveira, 2014).

#### 1.6 Threats and conservation

With low reproductive rates and long life spans averaging 60-80 years, sperm whales are considered a 'K-selected' species, and populations are controlled strongly by member competition for resources (Whitehead, 2003). Natural mortality in sperm whales also includes disease and predation (Rice, 1989). The killer whale (Orcinus orca) is a natural enemy of the sperm whale and has a number of documented attacks on the species, particularly on social units comprised of females and immature whales (Best et al., 1984; Brennan and Rodriguez, 1994; Visser, 1999; Pitman et al., 2001; Whitehead, 2003). It should be noted, however, that killer whale attacks on sperm whales are rare and far less numerous than observations of the two species in non-predatory interactions (Jefferson *et al.*, 1991; Whitehead, 2003). The most significant threat to sperm whales are humans. Although the direct harvest of sperm whales has been banned since the IWC Whaling moratorium of 1986, the effects from years of heavy, targeted whaling may continue to have disproportionately negative effects on a population that has been slow to recover (Best et al., 1984; Whitehead et al., 1997; Mizroch and Rice, 2013; Ivashchenko and Clapham, 2014; NOAA Northeast Fisheries Science Center, 2015). Furthermore, vessel strikes, interaction with fisheries, anthropogenic noise, oils spills and contaminants and climate change are all current potential threats whose degree of negative impact on the recovery of populations remains uncertain (Notarbartolo di Sciara et al., 2012; NOAA Northeast Fisheries Science Center, 2015).

The species is currently listed as 'vulnerable' in the Red List by the IUCN, International Union for the Conservation of Nature and Natural Resources (Taylor *et al.*, 2008). Sperm whales are classified in the Red List because the species is in danger from a long time (has been in danger for a long time). The cause of the population reduction in this species (commercial whaling) is reversible, understood, and is not currently in operation. However, commercial whaling at a

large scale for this species in the North Pacific and Antarctic within the last three generations (82 years) certainly resulted in a global decline during this period.

Mediterranean sperm whale is a genetically distinct population, listed as 'endangered' on the basis of the IUCN Red List criteria since 2012 (Notarbartolo di Sciara *et al.*, 2012). The species is subjected to a number of threats that can result in direct mortality, such as bycatch in illegal driftnets (Pace et al., 2008) and collisions with ships (Pesante et al., 2002; Abdulla and Linden, 2008), as well as the noxious effects of noise, pollution, ingestion of solid debris, disturbance from irresponsible whale watching operations, and possibly prey depletion and climate change. These threats affect the survival of the Mediterranean sperm whale population and are the cause of an inferred continuing decline (Notarbartolo di Sciara, 2014). Recommendations to sustain the presence of sperm whales in the Mediterranean in the future include respecting existing fishery, pollution and whale watching regulations, and introducing precautionary noise and maritime traffic regulations in areas characterized by high sperm whale densities, some of which could be considered for MPA designation (Notarbartolo di Sciara, 2014; Pace et al., 2015). Finally, the regular monitoring of sperm whale population ecology, behaviour and mortality at the regional scale, to detect trends and help to understand links between the observed phenomena and their possible cause(s), could help to address other potential threats, such as prey depletion and climate change (Notarbartolo di Sciara, 2014).

Most of the strandings in Italy and Mediterranean Spain were caused by entanglement in driftnets (Notarbartolo di Sciara, 2008), as evident from the reported presence of net fragments or characteristic marks on the whales' bodies (Podestà and Magnaghi, 1989; Lazaro and Martin, 1999). Mass strandings (*i.e.*  $\geq$ 2 individuals) of sperm whales are known in the Italian waters, but infrequent. In the Adriatic Sea, for example, sperm whale mass strandings have occurred five times since historical times, with the oldest known instance dating back to 1584. In addition, in December 2009, a pod of 7 males sperm whales stranded along the coastline of the Gargano Promontory, in the Southern Adriatic Sea (Mazzariol *et al.*, 2011) and in September 2014, a group of 7 (a pregnant female and 6 immatures) stranded at Punta Penna, near Vasto. There is also a theory based on the social factor as when an animal is sick he decides to head (voluntary or not) toward a low bathymetric and becomes snared (Drouot, 2003). More generally, solar cycles and related changes in the geomagnetic field, variations in water temperature and weather conditions, coast geographical features and human activities have been proposed as possible causes for sperm whale strandings (Mazzariol *et al.*, 2011).



# Chapter 2 Sperm whale acoustics

Acoustics is a powerful tool to explore the ocean, to obtain useful information on various marine organism as well as on the underwater environment. The acoustic waves propagate easily and for long distance into the seawater, with far better transmission capabilities than into the air. In the last decades, several scientists have confirmed that sound is indispensable for the life of many marine mammals, who have exceptional acoustic abilities used for the intra-species communication and the exploration of the environment (echolocation). Underwater acoustics is a crucial instrument to collect meaningful information about sperm whales, who spend most of their time underwater. They are highly vocal animals and although not all the functions of the huge nasal complex have been definitely proven, it is evident that they use it to produce and direct a wide variety of sounds (Madsen *et al.*, 2002), mainly clicks. Sperm whales are massive click producers and due to their size are considered the world's largest biological sound generators. Clicks are impulsive vocalizations lasting between 100µs - 20ms, with energy mainly between 5 and 25 kHz. They can be very powerful – up to 223 dB re 1 micron Pa @1m, the highest biologically produced source levels that have ever been recorded, and also are strongly directional (Møhl *et al.*, 2000; Zimmer *et al.*, 2005a,b).

The study of sperm whale vocalizations has evolved to include a number of different methods and tools including new tagging techniques, depth-meters, hydrophones, accelerometers and magnetometers (Johnson and Tyack, 2003; Zimmer *et al.*, 2003; Miller *et al.*, 2004; Zimmer *et al.*, 2005a, 2005b; Laplanche *et al.*, 2005). Some forms of acoustic data collection run the risk of disrupting or altering the natural behavior of the animals, such as tagging. Underwater acoustic is therefore considered an indispensable instrument to collect information about sperm whales' daily life (distribution, movements, feeding and socializing behaviors) and can be used to identify their presence in the environment for scientific research, mitigation activities and conservation efforts (Mellinger and Barlow, 2003; Cato *et al.*, 2005; Barlow and Gisiner, 2006; Zimmer *et al.*, 2008; McCauley and Jenner, 2010; Gavrilov *et al.*, 2011). The use of hydrophones and passive acoustics monitoring/tracking have proven to be efficient techniques that permit scientists to attain meaningful results (Jaquet and Whitehead, 1996; Pavan *et al.*, 1997; Gordon *et al.*, 2000; Barlow and Taylor, 2005; Lewis *et al.*, 2007; Pirotta *et al.*, 2011) while maintaining high levels of discreetness and allowing for more natural behavior from the whales (Leaper *et al.*, 1992; Gannier *et al.*, 2002; Madsen *et al.*, 2002; Laplanche *et al.*, 2005).

Furthermore, the combination of acoustic recordings through hydrophones and behavioral surface studies gives us a better understanding of the daily lives of these animals (Whitehead, 2003). While the information attained through these two channels is far from a complete view of sperm whale behavior, it does allow us to compile baseline behavioral data as we work to reveal new approaches in the study of sperm whale behavior.

### 2.1 The spermaceti organ

The body of a sperm whale is not unlike that of other cetaceans (Berta and Sumich, 1999). Nonetheless, sperm whales possess a feature not found in other species, the spermaceti organ, an oil-filled structure that dominates the sperm whale head and comprises about 25-33% of the animal's body length (Cranford, 1999; Whitehead, 2003). The spermaceti organ is somewhat barrel-shaped and is situated anterior and dorsal to the sperm whale's skull [Figure 2(1); Huggenberger *et al.* 2014]. The spermaceti organ is encased in a muscular sheath and surrounds a mass of spongy tissue saturated in a lipid substance called spermaceti oil. The skull forms a concave structure and it is situated at the posterior of the spermaceti organ. An air-filled structure (the frontal air sac) separates the skull from the spermaceti organ. The frontal air sac is connected to the right nasal passage, which runs beneath the spermaceti organ and above a second mass of oil-soaked tissue. The whalers called this mass of tissue thought to function as an acoustic lens, the "junk".



Figure 2(1). (A), Left lateral view (dorsal pointing up) of the reconstructed sperm whale head; dense connective tissue (case, rein of case) and maxillonasolabialis muscle semi-transparent. (B), Sagittal view of the reconstructed sperm whale head (dorsal pointing up, tip of nose facing left). The green line represents the proposed acute-angled main acoustic pathway throughout the bent acoustic horn (Møhl, 2001) and their (preceding) reverberation within the spermaceti organ (theory of Norris and Harvey, 1972). On its presumed path, the sound waves travel through the connecting acoustic window (CAW) into the junk and are released via the terminal acoustic window (TAW) into the water (bent acoustic horn hypothesis (Møhl, 2001).

*Figure 2(2). Position and structure of the monkey lips in the sperm whale nasal complex (both figures from Huggenberger et al., 2014).* 

The right nasal passage is connected at the anterior of the spermaceti organ to the distal air sac. This air-filled sac is also connected to the blowhole and is the location for a valve-like (or lip-like) structure called the *museau du singe* (or "monkey lips"), which allows air to enter the sac [Figure 2(2)]. The whale breathes through the left nasal passage that runs directly from the blowhole to the main airway passage (Cranford, 1999; Madsen, 2002).

According to most recognized theories, the functional significance of the massive size and structural specialization of the spermaceti organ has focused on sound production; however, roles in acoustic sexual selection (Cranford, 1999), acoustic prey debilitation (Norris and Møhl, 1983), buoyancy control (Clarke, 1978a) and male—male aggression/competition (Panagiotopoulou et al., 2016) cannot be excluded.

The spermaceti organ has had a particular evolutionary path. Species possessing characteristic sperm whale features – the family Physeteridae – are found from about 25 Ma onward (Berta *et* al., 2006) and soon evolved some highly specialized features. The sperm whales had radiated into a number of different species by about 15 Ma (Rice, 1998), but only three survive today: the sperm whale itself, the pygmy sperm whale (*Kogia breviceps*) and the dwarf sperm whale (Kogia simus). The kogiids are closely related to the sperm whale, all being characterized by the presence of a spermaceti organ. However, this organ is much reduced in kogiids and may have become functionally different (Velez-Juarbe *et al.*, 2015). The results of phylogenetic analysis indicated that an enlarged spermaceti organ is most likely the plesiomorphic condition for crown physeteroids. This suggested that reduction of the organ has been evolved iteratively within kogiids: once in Thalassocetus antwerpiensis, and secondly in Kogia spp. (Figure 3). In P. macrocephalus the spermaceti organ is related mainly to sound generation, while in Kogia it seemed that reduction of the organ has been resulted in changes in its functionality relative to *Physeter*, and it has been become part of a complex sound-generating system. It has been hypothesized that strong sexual selection has influenced the hypertrophy of the spermaceti organ and nose of Physeter (Cranford et al., 1996), so the smaller organ of Kogia may be the result of less intense sexual selection.



Figure 3. Evolutionary tree of sperm whales, showing the relationships of extinct and living species, and when reduction of the spermaceti organ took place (Source: Natural History Museum of Los Angeles County).

#### 2.2 Click structure

Backus and Schevill (1966) first defined the fine structure of the sperm whale clicks. They described the acoustic waveform of the clicks as a series of pulses with decreasing amplitude spaced regularly over several milliseconds. After few years, Norris and Harvey (1972) proposed the theory that acoustic reflections within the head of a sperm whale could explain the occurrence of these multiple decreasing pulses. Their hypothesis linked the time between pulses, called inter-pulse interval (IPI), to the distance between the *museau de singe* and the frontal air sac, as well as the speed of sound through the spermaceti acoustic fat. In this model, sperm whales produce sound pneumatically, by forcing air through the museau du singe at the anterior end of the spermaceti. The sound pulse propagates inside of the spermaceti being reflected from the frontal air sac at its posterior end where it is reflected off the frontal air sac and directed forward along the longitudinal axis of the whale exiting the whale's head just below the distal air sac [Figure 3(1)]. About thirty years later, other researchers further developed the Norris and Harvey theory, suggesting an acoustic pathway of the pulse from the frontal air sac through the junk (Møhl et al., 2003). This refined concept, called the bent-horn model of sound production, better explained various properties of sperm whale clicks such as high directionality. The bent-horn model was then improved by Zimmer et al. (2005a). These authors analyzed multi-hydrophone recordings of 13,000 clicks collected from a sperm whale together with concurrent data on orientation (to estimate the 3D radiation pattern), confirming that clicks were highly directional, with most of the sound energy focused in a beam within  $\pm 20^{\circ}$  of the acoustic axis (on-axis), and explaining the waveform of a click by dividing it into a minimum of 3 components which they labelled the *p0*, *p1*, and *Lf*. Off-axis clicks contained an additional pulse which they call p1/2, which merged with either the p0 or p1 pulses when recording onaxis (Figure 4). As Zimmer *et al.* (2005a) describe:

- the <u>pOpulse</u> is a backwards propagating pulse that is loudest along the longitudinal axis behind the whale. Possibly, the pO pulse is the initial pulse from the *museau de singe* and is not reflected off of any structure within the whale's head. The source levels from the pO pulse are 10 dB greater than the p1 pulse when recording from directly behind the whale.
- 2) the <u>*p1* pulse</u> originates at the *museau de singe* and is the forward propagating pulse, which is reflected from the frontal air sac and passes through junk. This pulse is the loudest sound produced by sperm whales and is likely the pulse used by the whale for echolocation because of its favourable qualities as a sonar signal (Møhl *et al.*, 2003). Along the acoustic axis, the *p1* pulse can be as much as 39 dB louder than the *p0* pulse. For an on-axis click recorded ahead of the whale the *p1* pulse arrives later than *p0* at time delay  $\tau_1$ . This time delay is believed to be dependent on the distances and speed of sound between the *museau de singe*, frontal air sac, and the anterior surface of the junk, as well as the pitch and roll of whale with respect to the hydrophone. The equation for this time delay can be expressed as:

$$\tau_1 = \left\|\mathbf{F}\right\| + \left\|\mathbf{J} - \mathbf{F}\right\| / v_s + \mathbf{J} \circ \hat{\mathbf{Q}} / v_w$$

where the origin (0,0,0) is the *museau de singe*, **F** is the location of frontal air sac (0, f, 0), J is the location of anterior surface of junk (0, 0, j),  $\hat{Q}$  is the unit vector in the direction of the hydrophone, and vs and vw are the speed of sound in spermaceti and in the water respectively (Zimmer *et al.*, 2005a).

3) The p1/2 pulse explains the structure of clicks that were recorded off of the acoustic axis of the whale. The p1/2 pulse is believed to occur when sound reflects off the frontal air sac and passes through whale tissue other than the junk. This pulse, which is observed at time delay  $\tau_{1/2}$ , is a strongly aspect dependent pulse that sometimes occurs in between p0 and p1. The p1/2 pulse merges with p0 when the hydrophone is directly behind whale, and it merges with p1 when recording from in front of whale. Thus it is only distinct when recording from off the acoustic axis. This pulse is typically lower in amplitude than p1, and the time delay of this pulse can be computed as:

$$\tau_{1/2} = \|\mathbf{F}\| + \mathbf{F} \circ \hat{\mathbf{Q}} / v_s$$

where F,  $\hat{Q}$  and  $v_s$  are the same as those defined above. The *p0*, *p1*, and *p1/2* pulses are broadband pulses with frequency content between 3-20KHz.

4) the <u>LF pulse</u> is an omni-directional, low-frequency pulse spanning frequencies between 0.5-3KHz. This pulse, like *p0* is not reflected off of any anatomical structures within the whale. Zimmer *et al.* (2005a) report that the start of this pulse occurs at same time as *p0*, but the duration of this pulse is much longer than the *p0* pulse. They suggest that this pulse could be a by-product of sperm whale sound production.



*Figure 4. On-axis and off-axis clicks according to the bent-horn model of sound production (from Zimmer et al., 2005a, 2005b; Teloni et al., 2007).* 

Several studies have taken advantage of the fact that the waveform of sperm whale clicks can provide information about the size of the sound production organs. Clarke (1978b), Møhl and colleagues (1981), Gordon (1991), Growcott *et al.* (2011) proposed equations for computing the length of a sperm whale by measuring the IPI of that whale's clicks. Using allometric relationships and photographic length estimates, they were able to compute equations relating the IPI of sperm whales to the size of the whale. Similarly, Rhinelander and Dawson (2004) in Kaikoura (New Zealand) and Pierantonio *et al.* (2016) in the Mediterranean found a relationship relating IPI and the photogrametrically measured size of male sperm whales.

# 2.3 Types of sounds

Sperm whales' clicks have been categorized into several types based on spectral cues, decay rate and inter-click interval (ICI, *i.e.* the amount of time between consecutive clicks), which is the inverse of repetition rate; however, the principal four main categories include 'usual click', 'creak', 'coda', and 'slow clicks' (Whitehead and Weilgart, 1991; Weilgart and Whitehead, 1997; Zimmer *et al.*, 2005a). These four principal types of clicks can be separated by a number of characteristics, including their inferred primary functions (Table 1) (Whitehead, 2003).

Click Type	Apparent Source Level (dB re 1µPa [Rms])	Directionality	Centroid Frequency (kHz)	Inter-click Interval (s)	Duration of Click (ms)	Duration of Pulse (ms)	Range Audible to Sperm Whale (km)	Inferred Primary Function
Usual	230	High	15	0.5-1.0	15-30	0.1	16	Searching echolocation
Creak	205	High	15	0.005-0+1	0.1-5	0.1	6	Homing echolocation
Coda	180	Low	5	0.1-0.5	35	0.5	-2*	Social communication
Slow	190	Low	0.5	5-8	30	5	60	Communication by males

This value is inferred from values for other click types and subjective relative audibility of click types at sea.

Usual clicks are associated with searching echolocation, and creaks with homing echolocation; both are used during foraging activities (scanning the habitat, searching for food and targeting a prey). Codas are thought to function in social communication, and slow clicks are believed to be a type of communication by males (Madsen, 2002; Whitehead, 2003). Some types of creaks emitted at surface may also have socializing function.

Clicks comprise the overwhelming majority of sperm whales sounds but these animals also emit tonal sounds, or non-click vocalizations, including 'squeals' and 'trumpets' (Gordon, 1987a; Goold, 1999; Whitehead, 2003; Teloni, 2005; Oliveira *et al.*, 2013).

#### 2.3.1 Usual clicks

Usual clicks are the most commonly heard sound from sperm whales. They are long trains of highly directional regularly spaced clicks (Figure 5), typically lasting for several minutes and usually made during deep dives (Whitehead, 2003). Usual click ICI's range between 0.5-2.0 seconds and they can be heard at ranges of up to 16km (Goold and Jones, 1995; Jaquet *et al.*, 2001).

Previous studies support the idea that sperm whale usual clicks are associated with long and mid-range echolocation to scan for potential prey (Backus and Schevill, 1966; Norris and Harvey, 1972; Gordon, 1987; Weilgart, 1990; Goold and Jones, 1995; Møhl *et al.*, 2000; Jacquet *et al.*, 2001; Madsen *et al.*, 2002; Whitehead, 2003), also providing orientation cues to the whale (Møhl *et al.*, 2003; Zimmer *et al.*, 2005b). Maximum source levels of 236dB re 1µPa @1m have been recorded, making these clicks the loudest biologically produced sounds (Møhl *et al.*, 2003). Several independent approaches have also revealed that usual clicks have a highly directional radiation pattern focused ahead of the longitudinal axis of the whale (Møhl *et al.*, 2000; Zimmer *et al.*, 2007).



*Figure 5. Spectrogram and waveform of a usual click sequence produced at depth in the Mediterranean Sea (© Oceanomare Delphis Onlus).* 

#### 2.3.2 Creaks

Creaks, which are clicks with high repetition rates, sometimes referred to as *buzzes* (analogous to the buzzes produced by bats as they close in on prey; Gordon, 1987b; Miller *et al.*, 2004), have an ICI below 0.5s (generally between 0.005-0.1s) (Figure 6).

They are also highly directional but less powerful and much shorter than usual clicks, which can make detecting creaks difficult when whales are far away or the environment is noisy (Madsen *et al.*, 2002; Wahlberg, 2002; Kandia and Stylianou, 2006); however, they can be heard at ranges of up to 6 km (Whitehead, 2003). Creaks produced during dives and at depth are believed to be close range echolocation signals that occur just before prey are captured during the final approach phases of foraging (the click rate typically accelerates over the course of the creak and can be interpreted as the sperm whale homing in on prey (Jacquet *et al.*, 2001; Whitehead, 2003; Miller *et al.*, 2004; Oliveira *et al.*, 2013; NOAA Northeast Fisheries Science Center, 2015). High repetition rate buzzes at low output levels provide high temporal and spatial resolution tracking to inform motor patterns in the last few meters before capture. While some prey targeted by sperm whales appear to be easy to subdue, others, often at shallower depths, require lengthy chases, leading to prolonged buzzes and higher than average swimming speeds (Fais et al., 2016). Studies have shown that in certain areas, creak rates during various times of the day could be related to prey availability (Gannier *et al.*, 2012).

Surface creaks tend to be shorter than creaks emitted during dives and to have more constant ICI (possibly to scan nearby social partners, or the boat, or other objects; Whitehead, 2003), and are sometimes designated differently from the creaks made at depth. They may be subdivided into 'coda-creaks' (Weilgart, 1990; Figure 7), 'rapid clicks' or 'chirrups' (Gordon, 1987b; Goold, 1999; Figure 8).



*Figure 6. Spectrogram and waveform of a creak sequence produced at depth in the Mediterranean Sea (© Oceanomare Delphis Onlus).* 



*Figure 7. Spectrogram and waveform of a coda-creak sequence produced at surface in the Mediterranean Sea (© Oceanomare Delphis Onlus).* 



*Figure 8. Spectrogram and waveform of a fast click (or chirrup) sequence produced at surface in the Mediterranean Sea (© Oceanomare Delphis Onlus).* 

#### 2.3.3 Codas

The most interesting click pattern of the sperm whale is the coda (Figure 9), stereotyped repetitive patterns of clicks (short rhythmic series of three to about twenty clicks lasting about 0.2-5 s) having a different structural make-up than any other type of click; they display less directionality, longer click duration, more pronounced secondary clicks, and reduced power (Madsen *et al.*, 2002a). These mean that they are produced to communicate than for echolocation (Madsen *et al.*, 2002a). It happens by changing the shape of the distal air sac to allow for more reflections within the spermaceti organ (Madsen *et al.*, 2002a). Codas' ICI is between 0.1-0.5 seconds.

Coda sequences can vary in their click-pause patterns and in the circumstances during which they are emitted. They can sometimes be heard at the end of a usual click train (Pavan *et al.*, 2000) or occasionally at the end of long dives (Teloni, 2005), just before the whale surfaces (Pavan *et al.*, 2000), but most frequently are heard in groups socialising at the surface (Weilgart and Whitehead, 1993) as exchanges with other whales (Watkins and Schevill, 1977; Whitehead, 2003). Codas can also be heard by themselves, with no apparent exchange involved, as well as in very complicated, multiply overlapping sequences in which several animals seem to be vocalizing at once. In the duet like "echo-coda" two whales make almost exactly the same coda nearly simultaneously (Weilgart, 1990). Possibly, this aids social coesion.

Codas containing a particular number of clicks can be subdivided into quite well defined and distinct "types" depending on their relative inter-click intervals (Weilgart and Whitehead, 1993), with evidence of coda type sharing among individuals (Schultz *et al.*, 2011). Some types are very common while others, especially those with very irregular inter-click intervals, may have been rarely heard. Studies from different locations have reported 23 (Weilgart and Whitehead 1993), 25 (Nuuttila, 2004; Frantzis and Alexiadou, 2008), 26 (Drouot *et al.*, 2004b), 28 (Moore *et al.*, 1993), 33 (Rendell and Whitehead, 2003b) and 47 (Weir, 2003) coda types, although the

number of coda types identified may depend on the methods used. The analysis of a large set of codas in two oceans revealed 70 coda types (Whitehead, 2003), while in the Mediterranean Sea one single type seems to dominate the sperm whale repertoire (Pavan *et al.*, 2000).



*Figure 9. Spectrogram and waveform of a coda sequence produced at surface in the Mediterranean Sea (© Oceanomare Delphis Onlus).* 

It has been noted that there are acoustic differences in coda types among sperm whale populations (Rendell and Whitehead, 2003a,b), and it has been suggested that coda types may have distinct functions (Antunes *et al.*, 2011; Ferguson *et al.*, 2013; Amano *et al.*, 2014). It has also been proposed that coda types could be genetically inherited based on mitochondrial DNA similarities in whales with similar coda repertoires (Whitehead, 1998; Antunes, 2009). At the level of the ocean basin, sperm whale social units can be assigned to vocal clans with their own coda repertoires (Rendell and Whitehead, 2003a). Vocal clans may share common coda types; however, the frequency of occurrence of each coda type differs among vocal clans. Based on the presumed matrilineal transmission of coda repertoires by one generation to the next within sperm whale social units, Rendell and Whitehead (2001) concluded that these "dialects" constitute nonhuman culture.

Despite the progress made, whether the distinctive coda types are used and served different communication needs or functions in various kind of social assemblages of males and females remains not fully known. Some coda types (or group of coda types) have been associated with particular male sperm whale behavior (Frantzis and Alexiadou, 2008) and with the recognition of individuals within a social unit (Antunes *et al.*, 2011). Patterns of variation between coda types suggest divergent functions, perhaps representing selection for identity signals at several levels of social structure (Gero *et al.*, 2016).

#### 2.3.4 Slow clicks and gunshots

Slow clicks (sometimes called 'clangs') are loud clicks that are repeated every 5-8 s (Gordon, 1987b; Weilgart and Whitehead, 1988; Jaquet *et al.*, 2001; Whitehead, 2003). These clicks can be distinguished from other click types, not only by their structural make-up - which includes much lower repetition rates, longer duration, and very low frequency and directionality - but also by their general sound. Slow clicks include emphasized "ringing" frequencies and seem much louder than any other type of click. These clicks can be heard by counter-specifics at ranges of up to 60km (Gordon, 1987b; Weilgart and Whitehead, 1988; Goold, 1999; Whitehead, 2003). The ICI of a slow click is generally between 3-8 seconds (Figure 10). Source levels of slow clicks have been measured at 175-190 dB re  $1\mu$ Pa @1m.

Slow clicks have only been heard sporadically in the presence of mature or maturing males; however, it is possible that females emit slow clicks on rare occasions (Weilgart and Whitehead, 1988; Whitehead, 2003). Because of this uncommonness, there are few published studies on their properties, and their function(s) remain somewhat mysterious.



*Figure 10. Spectrogram and waveform of a slow click sequence produced at depth in the Mediterranean Sea (© Oceanomare Delphis Onlus).* 

While several authors have suggested that slow clicks may have a communication function (*i.e.* they provide conspecifics information about the presence, location, identity and perhaps size of the vocalizer; Gordon, 1987b; Weilgart and Whitehead, 1988; Mullins *et al.*, 1988; Whitehead, 1993; Tyack and Clark, 2000; Madsen *et al.*, 2002; Barlow and Taylor, 2005; Oliveira *et al.*, 2013), it remains to be seen whether slow clicks are used for long distance echolocation (Gordon, 1987b; Mullins *et al.*, 1988; Goold, 1999; Tyack and Clark, 2000; Jaquet *et al.*, 2001; Oliveira *et al.*, 2013), some combination of these, or for other purposes entirely. It is thought that, from the recent collection of diving and acoustic data, it is more likely that slow clicks are related to long-range acoustic communication more so than for foraging and orientation (Oliveira *et al.*, 2013), with a function in the mating system as acoustic displays during male-

female and male-male interactions (Gordon, 1987b; Weilgart and Whitehead, 1988), perhaps attracting females and/or repelling other males (Bradbury and Vehrencamp, 1998), and as a courtship display (Mullins *et al.*, 1988; Whitehead, 2003) (frase molto lunga e complessa) Other forms of sperm whale clicks include 'gunshots'. These are extremely rare, loud and impulsive sounds with long duration (Whitehead, 2003). They have been reported in two separate instances, off Sri Lanka (Gordon, 1987b) and in Scapa Flow from a pod of entrapped males (Goold, 1999). There is similarity in structure to slow clicks and it has been discussed that gunshots might be a variation of slow clicks (Goold, 1999). Another proposed function of gunshots is for the debilitation or stunning of prey through intense low frequency (Norris and Møhl, 1983; Gordon, 1987b; Cranford, 1999; Whitehead, 2003; Oliveira *et al.*, 2013). An exact function for gunshots is still unresolved.

#### 2.3.5 Tonal sounds and other unusual vocalizations

Clicks comprise the overwhelming majority of sperm whales sounds but sperm whales also emit tonal sounds, or non-click vocalizations, including 'squeals' and 'trumpets' (Goold, 1999; Whitehead, 2003; Teloni, 2005; Oliveira *et al.*, 2013).

Squeals (Figure 11) have been described as narrowband sounds with a frequency-modulated structure perceived as tonal to the human ear (Goold, 1999; Druout, 2003). However, the possibility exists that sperm whales may produce modulated click trains (Backus and Schevill, 1966) and it is currently unclear whether squeals represent a non-click tonal sound or are in fact burst-pulse sounds comprising clicks at very high repetition rates. These vocalizations have been reported from a group of immature male sperm whales off Scotland (Goold, 1999) and from social units of sperm whales in both the Tyrrhenian and Ionian Seas (Priano *et al.*, 2001; Drouot, 2003).



*Figure 11. Spectrogram and waveform of a squeal produced at surface in the Mediterranean Sea (© Oceanomare Delphis Onlus).* 

Trumpets are low intensity, narrowband vocalizations arranged in short sequences lasting between 0.6s to 3.5s, with harmonics (Figure 12). These sounds are made of a series of repeated units, around 0.2s long; each of these units comprises an amplitude modulated tonal waveform with a complex harmonic structure, and a spectrum composed of a low frequency component at 500 Hz and a mid-frequency component at 3 kHz. The apparent source level was estimated to be 172 dB re: 1µPa at lm with energy flux density of 147 dB re: 1µ Pa @1m.

They have been described as tonal signals (Teloni *et al.* 2005) and are said to sound like the "*muffled trumpeting call of an elephant*" (Gordon, 1987b; Whitehead, 2003). The true functions of tonal sounds remain largely unknown. Some of the literature has attributed these sounds to socialization while others have considered them to be a form of "clearing the throat" or readying the vocal apparatus for use (Gordon, 1987b; Whitehead, 2003; Teloni *et al.*, 2005).



*Figure 12. Spectrogram and waveform of a trumpet produced close to surface in the Mediterranean Sea (© Oceanomare Delphis Onlus). The armonic structure and the modulation frequency of the sub-units are well represented.* 

Vocalizations variously described as 'yelps', 'squarks' and 'chirps' have been reported from Brazilian sperm whales (Perkins *et al.*, 1966), which Gordon (1987b) considers to be a likely result of rapid sequences of clicks. Similar may be true of the 'short trumpets' and 'series of pips' described by Goold (1999) from entrapped sperm whales in Scotland. Low intensity tonal components have been occasionally heard in the vocalizations from sperm whale calves (Watkins *et al.*, 1988).

#### 2.4 Clicks development

Watkins *et al.* (1988) offered a preliminary investigation of the development of click sounds in sperm whales. They made recordings of four stranded calves and compared the recordings to those made of larger calves free-swimming in natural settings. Though, animals of all sizes in the Watkins *et al.* (1988) study made 'typical' sperm whale sounds, the smaller calves appeared to produce sounds with noisy, tonal components resulting in improperly formed clicks. Furthermore, the appearance of patterns in the click sequences appeared to increase as a function of calf size (and, accordingly, with calf age). The results of this study must be interpreted with caution. The signals of the four stranded animals were obtained under extraordinarily stressful conditions (*i.e.* strandings). Animals that strand usually are injured or ill and can experience disorientation as a result of their injury or illness; thus, these signals may not serve as a valid comparison against the free-swimming, non-stressed sample animals. This investigation of sperm whales again faces the off-axis recording problems inherent in the analysis of 18 free-swimming animals, calling into question the conclusions of improperly formed clicks.

Madsen et al. (2003) also discuss neonate sound production in two sperm whale calves. One male calf stranded in Texas in 1989 and the second female whale stranded in Hawaii in 2001. The female subsequently died while undergoing rehabilitation and no disposition was given for the male calf. Again, differences from general adult norms were observed. The clicks of the neonates were low in directionality, of long duration (2-12 ms), and of low frequency (centroid frequency 300-1700 Hz). Directionality was determined when sound pressure levels registered 4-8 dB higher directly in front of the animal then when placed laterally to the eye for both calves. Calves echolocated in short trains but did not show the stereotyped, repetitive click patterns reported for adult codas. The authors further hypothesize that although the low frequency and long duration of the clicks make them poor candidates for echolocation, these features would be more suited to interspecific communication and may serve to convey information between calf and mother or calf and an allomaternal female. Madsen et al. (2003) drew parallels to the Watkins et al. (1988) study by finding similar click properties in the recordings from the calves in both studies; they correctly note, however, that these results should be taken cautiously, given that the animals were recorded in less than ideal acoustic surroundings and likely were in poor health.

#### 2.5 Ears and hearing

The sperm whale ear consists of the same parts as in the quadruped (animals, credo serva un sostantivo), an external opening, with membrane tympani, an Eustachian tube, a tympanum with its processes, and the small bones. There is no external projection forming a funnel; we can easily assign a reason why there should be no projecting ear, as it would interfere with progressive motion, but the reason why it is not formed as in birds is not so evident. The external opening begins by a small hole scarcely perceptible, situated on the side of the head a little behind the eye; it is much longer than in other animals, as a consequence of the size of the head being so much increased beyond the cavity that contains the brain. The Eustachian tube opens on the outside of the upper part of the fauces. The bony part of the organ is very hard and brittle, rendering it difficult to be cut with a saw without its chipping into pieces, and there is on the whole area a more solid bone than in the corresponding parts in quadrupeds, it being thick

and massy (Beale, 1839). The eardrum separates the outer ear from the average and is linked to the three tiny bones: the hammer, anvil, and bracket, which have the function of amplifying the sound waves and transmit them to the oval window. The middle ear of the sperm whale is surrounded by a complex system of breasts: the bags connected with the nasal passages filled with foam formed by an emulsion of oil and mucus (Romero, 2009). The middle ear cavity is connected to the pharynx through the Eustachian tube. The inner ear consists of a tubular structure wound in a spiral (cochlea), very rich in nerve endings, which are stimulated by the pressure waves caused by the sound transmitted by the bracket to the oval window. The anatomy of the sperm whale ear indicates that it appears tailored for ultrasonic (>20 kHz) reception. The sperm whale may also possess better low frequency hearing than some of the other odontocetes, although not as low as many baleen whales. Southall et al. (2007) placed sperm whales in the same hearing group (mid-frequency cetaceans), as 'dolphins', toothed whales, beaked whales, and bottlenose whales (estimated hearing range 150 Hz to 160 kHz). The only existing data on the hearing range of sperm whales is obtained by auditory brainstem response (ABR) experiments from a stranded neonate male (Ridgway and Carder, 2001), which suggest that neonatal sperm whales respond to sounds from 2.5 to 60 kHz, with best hearing sensitivity results at 5, 10, and 20 kHz, and a better sensitivity at 40 kHz than at 2.5 kHz. This frequency range matches the spectral content (-10 dB) of an on-axis click from an adult male sperm whale (Madsen and Møhl, 2000). Assuming that sperm whales possess the U-shaped hearing curve characteristic of all mammals investigated, it seems reasonable to believe that sperm whales have a lower best hearing range than most other odontocete species, but not as low as baleen whales.

It is believed that the animal uses a directional sound beam. Approximately once a second the whale emits a powerful directional click from its huge nose. The clicks propagate away from the whale and bounce back as echoes from the bottom of the sea and from the intended (or targeted) prey. Thanks to these echoes, the whale creates an acoustic picture of the surroundings, allowing the animal to navigate, locate, avoid obstacles as well as locate and catch prey: this process is the echolocation (Whitehead, 2009). As other Odontocetes species, sperm whales receive the acoustic waves through the vibration of the skull, especially from the jaw, and teeth probably have a specific meaning of '*beam forming*' to better discriminate the sound. The jaw is connected to the tympanic bulla and the whole system becomes an acoustic window.



# **Chapter 3** Setting the scene: what do we know about sperm whales off **Ischia Island?**



Guest Editors: Daniela Silvia Pace, Barbara Mussi, Jonathan Gordon, Maurizio Würtz.

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#### Sociality of sperm whale off Ischia Island (Tyrrhenian Sea, Italy)

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Occurrence and spatio-temporal distribution of sperm whale (Physeter macrocephalus) in the submarine canyon of Cuma (Tyrrhenian Sea, Italy)

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Assessing sperm whale (Physeter macrocephalus) movements within the western Mediterranean Sea through photo-identification

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#### 3.1 Study area

The study area (Figure 13) is located in the central Tyrrhenian Sea (Mediterranean Sea, Italy), a region featuring one of the most complex structures in the seas around the Italian peninsula due to its morphological and geophysical characteristics and water mass dynamics. The area includes the Pontine Archipelago (Lazio region, Gulf of Gaeta) and the Campanian Archipelago (Campania region, Gulf of Naples), both situated on the eastern Tyrrhenian continental margin. The Pontine Archipelago, about 35 km offshore the Italian peninsula, is generally divided into two main domains: the western group (Ponza, Palmarola and Zannone islands) and the eastern group (Ventotene and Santo Stefano islands). The western group is located on a structural high, while the eastern islands represent the summit of a large, and only partially known, volcanic complex developed within the Ventotene basin (Ingrassia et al, 2015). The Campanian Archipelago, found in the Gulf of Naples, comprises the Phlegraean islands (Ischia and Procida, with the two small islands of Viavara and Nisida), a volcanic district surrounding the western part of the Gulf, and Capri, a geologically distinct island placed in the eastern part of the Gulf. The core part of the study area is located in the waters surrounding Ischia (40° 43' 52.68" N, 13° 53′ 44.52″ E) and Ventotene (40° 47′ 51″ N, 13° 25′ 48″ E) islands. This marine region is characterized by the presence of complex and varied geological structures, with some submarine canyons (D'Argenio *et al.*, 2004; Pace *et al.*, 2012). The continental shelf (up to 200 m) extends from the shores of Campania and Lazio regions; its extension tends to decrease from NW to SE in the Gulf of Gaeta, narrowing from around 20 km near the mouth of the Garigliano to less than 10 km south of the river Volturno, where the platform is furrowed by the Cuma canyon, a topographical system including the NW part of Ischia island as far as the large submarine valley between the islands of Ischia and Ventotene (Figure 14). This system represents a great sedimentary basin for detritus and materials transported along the coast by the Volturno and Garigliano rivers (Gulf of Gaeta) (Figure 14; red lines represent the axes of the canyons and broken red lines mark out the same axes submerged by the sand; see Pennetta *et al.*, 1998; de Alteriis and Toscano, 2003). Several small canyons (called Cuma, Punta Cornacchia and Punta Imperatore) and erosional channels (Forio) along the island's edge from north to west, to south, were indentified (Figure 14; red boxes delimitate the canyons' and channels' heads).



Figure 13. The study area is located in the central Tyrrhenian Sea (Mediterranean Sea, Italy) and includes the Pontine Arcipelago in the Gulf of Gaeta (white circle) and the Campanian Archipelago in Gulf of Naples (red cirlce).


*Figure 14. The submarine canyon of Cuma (modified from Pennetta et al., 1998; de Alteriis and Toscano, 2003).* 

In the Gulf of Naples, the shelf is interrupted at a certain distance offshore, between the islands of Ischia and Capri, by two large canyons – the Magnaghi and the Dohrn – which form the Magnaghi-Dohrn canyon system (Figure 15).



Figure 15. The marine region around Ischia and Capri Islands (source: D'Argenio et al., 2004).

These complex canyon systems, and their variations in bottom topography and bathymetry, influence oceanographic processes that concentrate nutrients and structure prey availability vertically in the water column (e.g. upwelling phenomena), consequently attracting key species in the pelagic trophic web such as the euphasiacean *Meganyctiphanes norvegica* and large, apex predators such as sperm whales (Mussi et al., 1999, 2014; Pace et al., 2014). The entire area also provides an important and thriving economic and recreational resource, supporting a large amount of commercial and leisure activities that may detrimentally influence its ecosystems. Among these, tourism and fisheries are the most evident factors during the summer season, when the frequency of both maritime (mostly ferries and fast ferries) and recreational boat traffic, as well as the intensity of the fishing effort, usually increase. Together with the islands of Procida and Vivara, Ischia was designated as a Marine Protected Area (MPA) called "Regno di Nettuno" in 2007. The MPA was meant to mitigate some of the effects that the large amount of human activity could have on marine species. The MPA includes the coastal regions between the above-mentioned islands and the mainland (thus presenting the challenge of balancing the conservation of aquatic biota with the continuation of a variety of human activities), and a more pelagic area located north of Ischia specifically intended as an important site for cetaceans' diversity and a critical habitat for the endangered Mediterranean short-beaked common dolphin Delphinus delphis (Reeves et al., 2003; Pace et al., 2012; Mussi et al., 2014) (Figure 16). However, the comparison of short-beaked common dolphin habitat to sperm whale habitat in the waters surrounding Ischia (Pace et al., 2012) shows a vast, unprotected stretch of water that could be a critical area for the currently endangered sperm whale Mediterranean population.



*Figure 16. Map of Regno di Nettuno MPA. Zones A-D fall under the protection of the MPA with varying levels of restrictions.* 

## 3.2 Surveys and data collection

Here I used visual and acoustic data collected in the field from 2002-2015 during a long-term research project started in 1999 (named *Ischia Dolphin Project*) off Ischia Island, conducted by the NGO Oceanomare Delphis Onlus. No specific permissions or ethical committee approval (location, species, activities) were required for this purely observational, *i.e.* non-invasive and non-interactive study. The program follows both ASM research guidelines on live animals (Sikes *et al.*, 2016) and "Guidelines for the purpose on non-lethal *in situ* research" provided by ACCOBAMS (2010) (MOP4/2010/Res4.18).

Survey trips were taken daily (regularly five days a week from June to October each year, few additional outgoings were completed in winter and spring) when conditions were at a sea state of 0 to 4 on the Beaufort scale, during good light conditions, and at a steady speed of 2-4 knots. Surveys were conducted from a 1930 oceanic oak cutter (R/V *Jean Gab*), a sailing vessel that is 17.70 m in length with a 4.45 m beam, 2.50 m draft, and a 145 hp diesel engine (Figure 17). Each survey trip covered an area of approximately 60x74 km, limited by the distances that could be travelled by the research vessel within a single day.

Searches for sperm whales were made by 1) continuously scanning water surface with the naked eye or with 8-16x50 power binoculars from a 3 m height of eye, and 2) acoustic detections using a towed stereo hydrophone array incorporating two hydrophones (100Hz – 22 kHz bandwidth, ENEA UT-APRAD Radiation Sources Laboratory), with ASD Schaller pre-amps, spaced 3 meters apart and towed on a 100 m cable. The system was connected to the PC through RME Fifeface 400 audio interface (sample rates up to 192 KHz; sample rates selected for recording on the computer: 44, 44.1 and 48 kHz with 16 bit resolution). The output signal was also connected to headphones and to a pair of stereo speakers located in the pilothouse. While the vessel was underway, a continuous listening of sounds from the array was conducted. During all surveys, the data logging software 'Logger 2000' developed by the International Fund for Animal Welfare, IFAW; http://www.ifaw.org (which collects data in Microsoft Access 2000 format) was used on a PC connected to the GPS receiver to record the position of the research vessel every 180 seconds. Automatically detected acoustic contacts with sperm whale were also entered in Logger 2000, after visual/acoustic inspection by an operator.

Survey routes were chosen to optimize encounters with the sperm whales and were determined on a daily basis through the analysis of previous sightings, reports of sightings during the present day, bottom topography and depth, weather and sea state. Data recorded included start and end time of the survey trips, weather and sea state, location, species, start and end times of each observation, best estimate of group size and composition, behavioral categories, and acoustics.

When at the surface, whales were approached carefully. Once within 300 m visual range, the boat would slow and stop behind the whales. A 'focal or a group follow' (Mann, 1999) was then initiated to collect behavioural data, and continued for as long as possible or until the weather conditions deteriorated (*e.g.* poor visibility, sea state > 3) or until all animals at sight had been photographically identified. A digital camera (Canon Eos 10D) SLR equipped with a high quality, image stabilised telephoto zoom lens (100–400mm F4.5–5.6) was used to take photo-identification images. Images were stored in JPEG format (12 bit, 2.4 MB, 3072x2048 pixel). The number of whales comprising a group was first estimated visually, and then acoustically; group composition (*i.e.* the 'encounter type') was assessed in the field considering direct

observation of the whales' genital area and size estimates, and confirmed afterwards through the analysis of photo-identification images and underwater videos. Sperm whale encounters were classified into three types (Table 2). Encounters with sperm whales were considered as distinct sightings if they had been made on different days or were of distinct social units or groups encountered on the same day separated by more than 45 minutes (group identify was determined afterwards through examination of photo-identification images). The number of whales comprising a group was estimated visually, and then acoustically; group composition was confirmed afterwards using photo-identification images.



Figure 17. The research vessel Jean Gab (© Oceanomare Delphis Onlus).

Table	2.	Types	of sperm	whale	encounters.
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Encounter type	Definition
Social unit (SU)	All whale groups that included calves (whales having a visually estimated total length of about 4-5 m, less than half the length of an accompanying animal) or juveniles (whales having a visually estimated length of about 7 m, more than half the length of an accompanying animal, but less than full size).
Cluster (CL)	A set of whales (in the study area, generally 2-8 of presumed or confirmed males) staying or moving together in a coordinated fashion over periods of at least hours (Whitehaead, 2003). These clusters included also 'bachelor groups', <i>i.e.</i> aggregations of similar sized/aged whales comprising immature males (individuals of an estimated lenght of 9-11 m).
Solitary individuals (SI)	A single large-size individual (estimated at $\geq 12$ m) with no other sperm whales visually or acoustically detectable around.

# 3.3 Distribution and encounter rate

Analysis of occurrence and distribution patterns is essential to understanding the role of an animal in its environment, and can provide information on spatial use, territoriality, reproduction and residency (White and Garrott, 1990). It is likely to reflect patterns of both resource and predatory distribution (Brown and Orians, 1970; Whitehead, 1996b; Jaquet and Whitehead, 1999). In the marine realm, cetaceans range widely over the course of a year or a lifetime, but may also focus their activities in smaller localized regions and within particular habitat parameters. Such different distributions are usually interpreted as resulting from a wide diversity of behavioural and life-history traits, such as feeding strategies (Baumgartner, 1997; Davis *et al.*, 1998; Forcada, 2002; Hastie *et al.*, 2004) and reproductive-related decisions (Forcada, 2002; Elwen and Best, 2004); however, habitat-related factors (temperature, depth, bottom topography), distribution and behaviour of predators and anthropogenic influences (pollutants, human induced sounds, incidental and direct kills) may also have a significant role (Hooker *et al.*, 1999).

Together with the waters off Crete (Frantzis *et al.*, 2003), the Balearic Islands (Pirotta *et al.*, 2011), and, recently, the Ligurian Sea (Notarbartolo di Sciara and Birkun, 2010), the Tyrrhenian Sea (Drouot *et al.*, 2004a; Mussi *et al.*, 2014; Pace *et al.*, 2014) is one of the few regions in the Mediterranean Sea in which both social units and male assemblages are observed consistently, suggesting a possibly important role as breeding ground. Here, I report updated data on the sperm whale distribution in the study area (considering both social units and different male assemblages, as well as solitary individuals) and discuss possible relationships with topographical peculiarities of the zone.

## 3.3.1. Methods

Raw data collected in the field through Logger software were stored into a database (Postgresql 9.1) and Postgis 2.0 geographical extension and the PL/R library with R 2.14 were used to implement spatial and statistical analysis. Data were assigned to a grid of 8,800 1 km cells and covariates (depth, slope, distance from the nearest coast, aspect, gradient) were calculated for each cell using inverse distance weighting interpolation (IDW) using a 50 m resolution bathymetric layer. Monitoring and sighting effort, size and composition of groups and all other distribution values were computed at grid level. Relevant descriptive statistics were calculated. To assure better performances, database has been organized to generate shapes on fly choosing periods for grid, routes and sighting points.

A Cell Sighting Rate (CSR) was calculated as [Sighting effort (km)/Survey effort (km)], where the Sighting effort is the number of kilometres spent following the sperm whales and the Survey effort is the number of kilometres spent searching for the animals.

A group's location was taken as being its position when initially encountered, however long it might be followed for. Depth, slope and distance from coast for an encounter were calculated as the values detected at the beginning of each sighting.

Relative abundance of sperm whales was scaled by a yearly encounter rate (ER). ERs were calculated for each year by the ratio n/L, where n is the total number of sightings and L is the total number of km spent on effort. This is equivalent to computing the weighted mean of the

encounter rates  $(n_i/l_i)$  recorded within each cell, where  $n_i$  and  $l_i$  are the number of sightings and the number of km spent on effort in each cell, respectively, and the weights are given by the ratio  $l_i/L$  (Bearzi *et al.*, 2005). The sampling variance of the encounter rate was then calculated using the formula (Buckland *et al.*, 1993):

$$\operatorname{Var}(n/L) = rac{\sum\limits_{i=1}^k rac{l_i}{L} \left(rac{n_i}{l_i} - rac{n}{L}
ight)^2}{k-1}$$
,

where k is the number of cells surveyed (n=1731). Cells with a total survey effort lower than a cell's diagonal (1415 m) in any year were excluded from the analysis of encounter rates for all years, resulting in a single set of representative cells used for all analyses.

The correlations between ERs and km surveyed, and between ERs and number of sightings were tested to check if encounter rates for these cells were effort-biased. Neither correlation was significant.

#### 3.3.2. Results

A total of 1085 daily surveys were conducted in 2002-2015, during which about 47,050 km of track line were completed in 8,342 hours of effort (Figure 18). There were 138 encounters with 396 sperm whales; animals were tracked for a total of about 1,554 km and followed for about 365 hours (Table 3).



Figure 18. Routes effort (2002-2015).

		Search effort	:	Tracking e	ncounters	N. of encounters
Year	n	km	h	km	h	тот
2002	58	2374,00	466	14,05	02:05:00	2
2003	70	1798,32	427	18,99	06:23:24	3
2004	64	2215,11	406	59,95	15:24:53	5
2005	68	2794,13	545	86,98	21:57:01	9
2006	75	3608,96	607	123,45	29:19:57	7
2007	85	3758,72	609	101,85	26:48:57	10
2008	90	4243,38	702	223,07	53:20:21	15
2009	95	4567,75	788	255,21	56:03:29	19
2010	91	4248,73	721	136,07	30:16:47	18
2011	72	2992,47	545	59,51	14:38:21	4
2012	72	2907,69	553	99,81	21:03:44	7
2013	85	3858,27	723	108,80	26:50:36	11
2014	74	3638,12	588	107,76	23:13:42	6
2015	86	4044,20	662	158,68	37:17:12	22
Overall	1085	47049,85	8342	1554,17	364:43:24	138
	2.2.2.2		(2757) (A)	and the second second		

*Table 3. Summary of effort and encounters over the study period (2002-2015).* 

Encounter rates of sperm whale show an overall value of 0.72 groups/100 km, with a slightly increasing trend over the study period (Figure 19). No significant differences were found between years by regression analysis.



Figure 19. Sperm whale encounter rate in the study area (2002-2015).

Encounters and movements were principally located northwest of Ischia Island (about 60% of the total encounters), with different patterns observed over the years (Figure 20). The region corresponds to the deepest parts of the Cuma and Punta Cornacchia canyons, between 300 and 900 m deep (see Figure 15). Within this area, sperm whales seem to prefer the 600-800 m bathymetric range. The average depth for all encounters was 663.84 m (SD=140.42; range=278-1000; median=647.04), with a non significant trend through years or encounter type (Two-way ANOVA:  $F_{(13, 138)}$ =1.624, p=0.0872). Notwithstanding, SI and CL seem to be spread over the entire area, extending from relatively shallow waters (where the bottom depth is about 300m) to deepest ones (900-1000m), while SU appear to be more isolated (four occasions over a total of eight) and far from regions where higher number of other types of encounters were recorded.

The mean value for bathymetric slope (%) for all sperm whale encounters was 3.95 (SD=2.76; range=0-12.35; median=2.87), with significant differences between years (Two-way ANOVA:  $F_{(13, 138)}$ =4.231, p<0.0001); the mean distance from the nearest coast for all encounters was 12.21 km (SD=4.09, range=3.16-26.21; median=11.91), again with significant differences between years (Two-way ANOVA:  $F_{(13, 138)}$ =3.201, p<0.0005) (Table 4; Figure 21).

Table 4. Descriptive statistics of bottom depth (m), slope (%), and distance from coast (km) (2002-2015).

		Depth	(m)		Slope (	%)	Distance form the coast (km)			
Year	min depth	max depth	average ±SD	min slope	max slope	average ±SD	min coast distance	max coast distance	average ±SD	
2002	463.95	789.90	626.93 ±230.48	5.08	12.35	8.72 ±5.14	3.16	11.49	7.33 ±5.89	
2003	498.46	1000	751.70 ±250.80	0.70	7.55	3.89±3.41	9.40	16.61	12.33 ±3.79	
2004	595.14	741.81	668.21 ±68.85	1.78	4.25	2.74±0.92	9.60	15.26	12.47 ±2.66	
2005	428.30	796.52	602.83 ±112.04	1.88	10.87	$5.80 \pm 2.78$	4.68	12.14	9.49 ±2.59	
2006	491.39	847.02	627.33 ±108.06	1.76	5.53	$3.49 \pm 1.48$	7.55	14.65	11.34 ±2.34	
2007	278.27	799.87	592.95 ±186.84	1.63	11.11	4.47±3.35	5.99	13.56	10.41 ±2.48	
2008	562.82	805.23	678.43 ±90.67	0.00	4.85	2.20±1.33	8.87	19.32	13.43 ±2.81	
2009	456.82	973.99	694.90 ±127.60	1.63	6.46	3.40±1.66	7.25	18.36	12.94 ±3.22	
2010	395.39	860.32	691.32 ±116.31	0.36	6.47	3.03±1.67	5.84	17.00	13.41 ±3.27	
2011	643.02	971.40	768.58 ±151.35	1.81	9.33	$5.35 \pm 3.54$	6.82	19.21	13.47 ±5.28	
2012	336.31	719.51	506.03±127.30	1.37	9.45	4.13±3.21	6.65	20.66	10.98±4.83	
2013	345.20	999.98	583.23±173.04	0.00	12.18	6.97±3.83	3.68	17.56	8.49±4.38	
2014	407.30	800.99	653.15±134.48	2.16	7.99	$5.39 \pm 2.04$	6.15	14.33	9.68±3.08	
2015	472.73	1007.64	712.49±148.24	0.00	5.36	2.39±1.44	6.89	26.21	15.04±5.02	



2006

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Figure 20. Overall and yearly encounters and tracking lines during 2004-2015 period. Different encounter types (see section 3.5) are represented as following: ¥ indicates social units (SU) of females and immatures; ◆ indicates clusters (CL) of whales comprising immature males ('bachelor groups') or individuals of unknown sex/age class (possibly males); ○ indicates solitary whales.



*Figure 21. Mean values of depth (m), slope (%) and distance from coast (km) of the encounters over the study period (2002-2015).* 

#### 3.3.3 Discussion

The occurrence of animals and the distribution of their populations vary in space and time, often predictably with the availability of the key components that are necessary for life (Litvaitis *et al.*, 1994). It is well-known that environmental, oceanographic, social and anthropogenic factors can influence the occurrence and distribution of cetacean species in some interrelated ways (Davis *et al.*, 1998; Cañadas *et al.*, 2002), particularly insofar as they determine the distribution, local abundance, and availability of prey.

The results presented here suggest that sperm whales do not use the region uniformly. Similarly to other studies where the research effort was likewise focused on the continental slope and adjacent waters (e.g. Cañadas et al., 2002; Pirotta et al., 2011), topography seems to be the key, driving factor affecting and shaping sperm whale distribution in the study area. The continental shelf in the region is characterized by a complex bathymetry, including submarine canyons systems, a deep basin between Ischia and Ventotene, submarine mountains and some shallow banks. Within the morphological variables, submarine canyons can strongly modify flow, shelfslope exchanges of water and material (Hickey, 1995; Perenne *et al.*, 2001) and this coupling can both aid the transport of particulate organic matter that influences productivity and generate upwelling events. Mixing rates inside canyons could be as much as 1,000 times greater than rates measured in the open ocean and upwelling associated with canyons enhances local primary productivity and the effects extend up the food chain to include top-level marine predators such as fish, marine birds and cetaceans that occur within them (Moors-Murphy, 2014). This enrichment may attract prey like squids in deep water (Smith and Whitehead, 1993; Gregr and Trites, 2001; Hamazaki, 2002; Whitehead, 2003) and, as a consequence, teutophagic cetaceans such as sperm whales. This is what was observed in the Gully, a prominent submarine canyon on the edge on the Scotian Shelf (eastern Canada; Hooker et al., 1999), in Bleikdjupet, a submarine canyon that cuts into the continental shelf northwest of Andenes (Norway; Letteval, 2001, 2002), and in Kaikoura, a submarine canyon located just south the Kaikoura Peninsula (New Zealand; Childerhouse et al., 1995).

In this study, sperm whales seem to prefer waters of about 600 m depth (corresponding to the deepest parts of the Cuma and Punta Cornacchia canyons; see Figures 14 and 21), but they are also present over the 300 to 1000 m contour. These results appear in contrast with other studies both within the Mediterranean (e.g. Cañadas et al., 2002 in the Alboran Sea; Pirotta et al., 2011, in the Balearic Archipelago; Fiori *et al.*, 2014 in the Pelagos Sanctuary, Ligurian Sea) and outside the basin (e.g. Davis et al., 2002 in the Gulf of Mexico; Embling, 2008 off the west coast of Scotland), where sperm whales seem to prefer waters deeper than 1000 to 2500 m. However, a spatially bimodal distribution for the sperm whale in the western Mediterranean basin as a result of its opportunistic feeding strategy was proposed by Gannier et al. (2002) and Gannier and Praca (2007), an idea that was subsequently supported by Azzellino and colleagues (2008) in the Pelagos Sanctuary. Even though the prey targets might change, sperm whales would be able to exploit profitable food resources in different habitats (Gannier et al., 2002). Considering the extreme, general oligotrophy of the Mediterranean basin (Walle et al., 1993; Notarbartolo di Sciara *et al*, 2008), and the influence of oceanographic parameters, such as currents and bathymetry (Bakun and Csirke, 1998; O'Dor, 1992) on resource distribution and abundance (depth might be associated with the bathymetric zonation of cephalopod assemblages; Quetglas *et al.*, 2000), the study area may represent a significant feeding hotspot for the sperm whale in the Tyrrhenian Sea (Mussi *et al.*, 2014).

The peak of encounters in our study area in the months of July and August (n=64, about 50% of the total), is a matter of concern. A number of expanding arrays of human activities at sea present the potential to have an impact on sperm whales, the most significant possibly being habitat disturbance/degradation (including noise pollution). Vessel traffic (ferries, fast ferries and hydrofoils) in the Gulf of Naples and in the nearby Phlegrean Islands exceeds 200,000 trips/year, and up to 2,000 recreational boats may be moored during the summer in Ischia harbours (Strada, 2000). In a recent report on the Mediterranean noise spots (Maglio et al, 2016), the Gulf of Naples was listed as one of the areas showing highest noise values in the Mediterranean Sea, accumulating all considered types of noise-producing activities: commercial and recreational marine traffic, harbor activities, commercial and scientific seismic surveys, oil and gas drilling activities, and military exercises. This may have had temporary effects on local sperm whale groups such as stress or displacement (for a review, see Pace et al., 2015), changes in behavioural (*i.e.* deviation from normal activity, avoidance of an area) and acoustic (*i.e.* changes in the type and timing of vocalizations) responses (Nowacek et al., 2007), as well as chronic consequences (e.g. changes in distribution) that may affect populations over the longer term (Arcangeli et al., 2014). Furthermore, marks of propeller were noted on the whales back and ship collisions in the area have been documented for four cetacean species, including sperm whale (Mussi and Miragliuolo, 2003; Pace et al., 2006). The risk of collision is particularly heavy in the study area, considering its overlapping with Naples harbor business, as it is the threat of boat based harassment like that occurred to Grampus griseus (Miragliuolo et al., 2004), a kind of interaction involving also surfacing sperm whales that is becoming an every day routine in the busy summer months.

# 3.4 Habitat suitability

Efficacious management decisions and current mitigation measures depend on information on the population status of a species, which implies knowledge on its distribution and movements, habitat and feeding preferences, trend in abundance, and threats (Sveegaard *et al.*, 2015). Such evidence is often difficult to obtain for cetacean populations, particularly for deep-diving species such as sperm whale, where standard visual survey methods are not sufficient to detect and study the species. Underwater acoustics is considered an indispensable instrument to collect information about sperm whales' daily life (distribution, movements, feeding and socializing behaviors) and can be used to identify their presence in the environment. The integration of passive acoustic monitoring and visual observation ('presence-only' data) may offer the most effective approach to identify suitable/critical habitats for the species in a particular region. A combination of visual/acoustic presence data in different sperm whale encounters (2007-2015 period) testing predictive species' distribution using Maximum entropy modeling (Maxent) is here reported. Maxent is a 'presence-only' technique that has been applied to a number of ecological studies (Phillips et al., 2006; Phillips and Dudik, 2008; Elith et al., 2011), and can be used for conservation and policy planning. Maxent is specifically benefical in areas that have not yet been surveyed or with poor survey effort because it may be able to predict where a species is likely to occur based on environmental and physical variables (Thorne *et al.*, 2012). Due to its positive performance compared to other well-established techniques (Elith et al. 2006; Gastón and García-Viñas, 2011), Maxent is seeing a rapidly growing number of

applications in cetacean studies (Edrén *et al.,* 2010; Thorne *et al.,* 2012; Bombosch *et al.,* 2014; Gomez and Cassini, 2015; La Manna *et al.,* 2016; Linsday, 2016).

Among other factors influencing species habitat usage, life stage and group composition could play an important role. Various sperm whale group types are encountered surrounding the island of Ischia, including social units, solitary individuals, and clusters that include immature males (Pace *et al.*, 2014). The ultimate goal of this parte of the study is to use the Maxent modeling technique to investigate habitat usage by the various sperm whale group types surrounding Ischia and Ventotene Islands for the purpose of detecting possible differences between groups of varying composition and life stages.

## 3.4.1. Methods

A total Encounter Rate (ER) was calculated as n/D\*100, where n is the total number of distinct encounters on effort and D is the distance sampled on-effort in nautical miles (nm). Raw data collected in the field with Logger 2000 were stored in a database (Postgresql 9.1) and PostGIS 2.0 geographical extension and the PL/R library with R 2.14 were used to implement spatial and statistical analysis. Data were assigned to a grid of 8,800 0.0125x0.0125 deg cells and covariates (depth, slope, distance from the shoreline, aspect, etc) were calculated for each cell. Three environmental variables were used to generate the potential distribution models: depth, slope, and Euclidean distance from the shoreline. These variables were chosen as proxies of environmental characteristics that could affect the distribution of sperm whales and/or their prey. In addition, these variables have been commonly used in other works involving the cetacean habitat modelling, suggesting that they might be good predictors of their distribution (*e.g.* Edrén *et al.*, 2010; Thorne *et al.*, 2012; Bombosch *et al.*, 2014; Correia *et al.*, 2015; Gomez and Cassini, 2015; La Manna *et al.*, 2016). The environmental variables were obtained from GIS raster layers at the same resolution of the grid used for the analyses. Maximum entropy modeling using the software Maxent (version 3.3.3k http://www.cs.princeton.edu/~schapire/maxent/) was used to provide predictions of sperm whale occurrence. Maxent is founded "on the bedrock of probability theory" (Brierley et al., 2003) and a complete description of the mechanics underlying the algorithm is given by Elith and colleagues (2011) and Baldwin (2009). The general approach of Maxent is to estimate a target probability distribution for a species by contrasting occurrence data with background data (pseudo-absences) rather than true absence data (Smith *et al.*, 2012). Maxent employs a maximum likelihood method that models distributions of species by generating a probability distribution over the pixels in a grid of the study area subject to a set of constraints derived from measurements of assumed suitable habitat values at species occurrence locations (Thorne *et al.*, 2012). The output of Maxent is a probability distribution of environmental suitability for a species, where higher values correspond to a prediction of better conditions and a higher probability of occurrence (Phillips et al., 2006; Phillips and Dudík, 2008; Elith et al., 2011).

The species distribution model was created using sperm whale visual/acoustic 'presence' location over the years in all encounters pooled together and stratifying data per different encounter types (see Table 1). In Maxent, almost 20% of the data were randomly drawn from the dataset for model training over a maximum of 5,000 iterations. Several models were priory tested in Maxent, with and without bias files, as this is known to influence model output (Phillips *et al.,* 2009). In this study, the circumscribed geographical extent of the region prevented a latitudinal bias correction (*i.e.* the area occupied by a square of sea did not vary with latitude;

Brown, 2014), however we created an explicit bias file reflecting the surveyed section within the study area and applied it as a template for the extraction of background ('pseudo-absence') points in zones of search effort (Elith *et al.*, 2010; Bombosch *et al.*, 2014; Fourcade *et al.*, 2014). Maxent provided both threshold-dependent and threshold-independent measures of model outputs using the area under the curve (AUC) of the receiver operator characteristic (ROC), which assess the performance of the model predictions discriminating between locations where observations are present and random background data (pseudo-absence points) (Thorne *et al.*, 2012). The ROC curve plots sensitivity (true positives) against 1-specificity (false positives), representing how well the data predicts presence and how correctly absences are predicted, respectively (Thorne et al., 2012). The AUC is one of the most widely used threshold-independent evaluators of model discriminatory power (Fielding and Bell, 1997), and can range from 0 to 1. Values close to 1 indicate that there is a good fit of the model, suggesting perfect discrimination between suitable and non-suitable habitat; values near 0.5 indicate that model performance is equal to that of a random prediction (Phillips et al., 2006; Smith *et al.*, 2012). Based on other studies with cetaceans (*e.g.* Thorne *et al.*, 2012; Lindsay, 2014) AUC values of ROC were evaluated as follow: <0.5 indicates no discrimination; 0.5–0.7 indicates poor discrimination; 0.7–0.8 indicates an acceptable discrimination; 0.8–0.9 indicates excellent discrimination and finally, >0.9 indicates outstanding discrimination. A jackknife test was used for define variable importance and select the variable(s) having the most useful information (Baldwin, 2009). Relative contributions of the environmental variables to the Maxent model were estimated as 'percent contribution' and 'permutation importance'. To determine the first estimate, in each iteration of the training algorithm, the increase in regularized gain is added to the contribution of the corresponding variable, or subtracted from it if the change to the absolute value of lambda is negative. To define the second estimate, for each environmental variable in turn, the values of that variable on training presence and background data are randomly permuted; the model is re-evaluated on the permuted data, and the resulting drop in training AUC is shown, normalized to percentages.

### 3.4.2. Results

A number of 30,501.61 km was surveyed (5,282 hours) between 2007 and 2015 in the study area (Figure 22), with 103 visual encounters with sperm whales (CL=63, SI=34, SU=6) and 208.5 hours of acoustic tracking. The total ER was 0.62.

Mexent models obtained AUC values of 0.844 for all sperm whale encounters (excellent discrimination), 0.739 for SI (acceptable discrimination), 0.831 for CL (excellent discrimination) and 0.906 for SU (outstanding discrimination) (Figure 23a, b, c, and d respectively). Table 5 reports the estimates of relative contributions of the environmental variables to the Maxent model (see methods for detail). Overall, for the variables used in these analyses, 'depth' had the greatest explanatory (predictive) power in all encounter types and clusters (CL) throughout the study period (Table 5; Figure 24a and 24c, respectively). The highest logistic probability for finding sperm whales was between 500 and 800m, with a peak around 600m for social encounters (CL and SU) and around 1000m for solitary individuals (SI). 'Distance from coast' (Figure 24b) and 'slope' (Figure 24d) appeared to have the most useful information by themself in encounters with SI and SU, respectively (see also Table 5), with a higher probability of finding solitary individuals at a distance >5km from the nearest coast, and for localizing social units at slope steepness >15%.



Figure 22. Survey effort during 2007-2015 period.



Figure 23. Mean AUC (red line) for assessing the predictive accuracy of suitable habitat on a scale of 0 to 1 in (a) all sperm whale encounters, (b) solitary individuals (SI), (c) clusters (CL), and (d) social units (SU).

		Percent contri	bution			Permutation imp	ortance	
Variable	All encounters	Solitary Individuals (SI)	Clusters (CL)	Social Units (SU)	All encounters	Solitary Individuals (SI)	Clusters (CL)	Social Units (SU)
Depth (m)	87.7	37.8	78.5	32.3	73.1	98.1	73.7	25.2
Distance to coast (km)	11.1	52.6	15.6	24	24.3	1.9	18.9	39
Slope (%)	1.2	9.7	6	43.7	2.7	0	7.4	35.8

Table 5. Estimates of relative contributions of the environmental variables to the Maxent model.





The predictive map of habitat suitability for all sperm whale encounters pooled showed that the highest suitability areas ranged from zones located on the southeast and southwest coast of Ponza Island, along the Magnaghi-Dohrn canyon system margin and south Capri Island (Figure 25a). However, when stratifying data per different encounter type (SI, CL and SU; see Table 2), the specific maps revealed diverse patterns of suitability. The maps showed that suitability areas are wide ranging in sperm whale solitary individuals (Figure 25b), while for clusters (Figure 25c) they are considerably less extended, ranging from zones surrounding Ventotene Island to the Cuma's canyon system in the northwest of Ischia (including the valley between Ischia and Ventotene), to the southern part of Ischia Island. The most suitable areas (depicted in orange and red in Figure 25) resulted in the uninvestigated zone around Capri Island (SE Ischia), particularly the south coast and south-eastern waters along the Magnaghi-Dohrn submarine canyon heads, a small marine portion between Ponza and Ventotene Islands, and some regions north Ventotene. For sperm whale social units (Figure 25d) the suitability area was more highly concentrated than for the other encounter types, with an important extension through an almost uninvestigated area in the southern part of the island of Ponza (in orange and red). The zone south Capri was also predicted as a suitable area for SU (analogously to CL encounters), as well as the deepest part of the Magnaghi-Dohrn canyon system. Additionally, the inshore, southern part of Ischia showed high suitability.



*Figure 25. Suitability habitat map for (a) all sperm whale encounters, (b) solitary individuals (SI), (c) clusters (CL) and (d) social units (SU).* 

#### 3.4.3. Discussion

The vocalizations produced by sperm whales make them a suitable species to use passive acoustic techniques for estimating their distribution, monitoring their habitat use and inferring their behaviour. This study provides detailed visual/acoustic 'presence' data of sperm whales in a specific geographic area of the Mediterranean Sea. Such information was used to produce suitability habitat maps using Maxent, a 'presence-only' modeling technique able to predict the location that species are likely to occur based on environmental and physical variables. The main strengths of the Maxent method lie in its ability to efficiently handle complex relationships (Phillips and Dudìk, 2008), its robustness at small sample sizes (Hernandez et al., 2006; Wisz et *al.*, 2008; Williams *et al.*, 2009) and its adaptability to a range of data types and sources. However, a number of consideration regarding its application must be taken in order to minimize the bias and validate the models obtained (Bombosch et al., 2014). Furthermore, Maxent's central assumptions and known limitations must be considered when results gained through Maxent are proposed or adopted as possible conservation instruments (Hastie and Fithian, 2013; Yackulic *et al.*, 2013; Monk, 2014). For example, Maxent is not immune to the obstacles posed by imperfect detectability (Dorazio, 2012) and it does not provide measures of occupancy; Maxent merely yields relative maps of suitability (Phillips et al., 2006). In the presence of detection heterogeneity, however, Maxent has been suggested as an adequate avenue for analysis of cryptic species at small sample sizes (Rota et al., 2011; Tsai-Yu et al., 2012), resulting in a reliable option for this sperm whale study.

The AUC values obtained for all models in this study were high, similar to results found in other cetacean papers using Maxent (e.g. Moura et al., 2012; Thorne et al., 2012; Gómez and Cassini, 2015). These results could reveal an effective method for predicting sperm whale distribution in the study area. It was indicated that AUC values tend to increase when the absences are selected from a large area. (Wisz et al., 2008). However, in this study, the absences include a specific region restricted to the sea portion effectively surveyed and therefore, they cannot generate high AUC values. This evidence supports the reliability of the results, suggesting that they may have few biases. Furthermore, considering that Maxent is a generative approach as opposed to GLM/GAM models which are discriminative, it enables users to attain better prediction with a small quantity/amount of training data. Variables retained by the complex model are sensitive to other predictors included in the model. In order to reduce potential biases in the study, three environmental characteristics were selected to test the simple model and allow for strong distinction of the relevant variable for species' (as suggested by Merow et al., 2013). However, the exclusion of some environmental variables from this study, which have previously been shown as important predictors in other studies of sperm whales' distribution (*e.g.* sea surface temperature SST or chlorophyll), could lead to less accurate prediction maps. Nevertheless, the models generated in this study show some degree of concordance, as well as differences, with published scientific knowledge of sperm whale distributions in Italian waters and in the Mediterranean Sea, adding novel and functional information on regions potentially useful for the species.

Results of environmental variables showed that 'depth' was the overall most important predictor of habitat suitability for sperm whales in the study area. The species tended to be sighted at water depths of 500-800m but are also present over the 300 to 1000 m contour. These results appear different from other studies within the Mediterranean (*e.g.* Cañadas *et al.*, 2002 in the Alboran Sea; Pirotta *et al.*, 2011, in the Balearic Archipelago; Fiori *et al.*, 2014 in the

Pelagos Sanctuary, Ligurian Sea) and outside the basin (e.g. Davis et al., 2002 in the Gulf of Mexico; Embling, 2008 off the west coast of Scotland; Correia et al., 2015 in the Northeast of the Canary Basin), where sperm whales seem to prefer waters deeper than 1000 to 2500 m. However, a spatially bimodal distribution for the sperm whale in the western Mediterranean, as a result of its opportunistic feeding strategy, was proposed by Gannier *et al.* (2002) and Gannier and Praca (2007), a hypothesis that was reinforced by Azzellino and colleagues (2008) in the Pelagos Sanctuary. The species was sighted over the continental slope, where topographies such as canyons are considered main drivers for habitat selection, and in the offshore waters, where the presence of the animals appears to be linked to the position of downwelling/ upwelling water movements associated with frontal zones (Gannier and Praca, 2007). In this way, sperm whales would be able to capitalize on the food resources available in both habitats by shifting to different prey targets (Gannier et al, 2002). The interaction between complex seafloor characteristics and water circulation appears to be relevant to the species' distribution in the Mediterranean Sea, as well as in other regions (e.g. Jaquet 1996; Davis et al., 2002; Tynan et al., 2005; Skov et al., 2008). As shown, particular topographical features characterize the continental slope of the study area, incised by large scars and a network of canyons and tributary channels (strong erosion along canyons and channels occurs; Marsella *et al.*, 2001) which likely enhance primary productivity and thus sustain a richer biomass along the entire trophic web. In this study, bottom depth significantly influences sperm whale distribution; additionally depth might be associated with the bathymetric zonation of sperm whale prey, *i.e.* cephalopod assemblages (Quetglas et al., 2000). In particular, the pelagic cephalopods fauna in the southern Tyrrhenian Sea seems to be dominated by Sepiolidae (in terms of abundance in epipelagic and mesopelagic zones, most commonly in depths between 200 and 300 m; Jereb and Roper, 2005; Romeo et al., 2012), Ommastrephidae and Onychoteuthidae (in terms of biomass, at depth >500 m; Romeo *et al.*, 2012). These factors highlight the importance of these widely distributed families as key-species in the Mediterranean pelagic food web and in the ecosystem of the area. Moreover, it is well known that Ommastrephidae and Onychoteuthidae, muscular fast-swimming squids, are high-speed, growing, active predators that efficiently convert their prey into biomass (Clarke, 1996). These squid species therefore represent a primary source of food and energy for large marine predators (Romeo *et al.*, 2012). Sperm whales in the study area may benefit from the occurrence of these cephalopod assemblages, as also suggested by the concomitant presence of pelagic top-predators considered efficient 'cephalopods collectors' (Romeo et al., 2012) such as swordfish, Xiphias gladius, bluefin tuna (Thunnus thynnus), albacore (*Thunnus alalunga*), and Mediterranean spearfish (*Tetrapturus belone*) (Mussi and Pace, unpublished). However, direct information on the availability and movements of sperm whale prey would be beneficial for a better understanding of the relationship of this species with its environment (Jaquet and Gendron, 2002; Friedlaender *et al.*, 2006). The habitat occupied by sperm whale groups versus single animals seemed to diverge. Although

depth showed a high level of reliability for the prediction of habitat suitability for sperm whale in the study area, particularly for clusters (CL), we also found a relevant relationship with the slope steepness >15% (which has been deemed crucial in aggregating prey; *e.g.* Praca *et al.*, 2009) and the distribution of social units (SU). Furthermore, in contrast to groups (CL and SU), we observed an increased probability in the presence of singletons (SI) with distances >5km from the nearest coast. A potential explanation of these dissimilarities between encounter types may be associated with individuals' different ecological requirements and habitat preferences

related to different behaviors, such as searching/feeding activities and socializing. Although sperm whales spend a considerable amount of time foraging at depth, they are highly social mammals (Whitehead, 2003). Sociality was found to be an important component for animals encountered in the study area (Pace *et al.*, 2014), for females with immatures (SU), as well as for clusters/bachelor groups (CL) of males (or presumed ones). While singletons can focus the choice of their habitat on prey availability (Pirotta et al., 2011), significantly moving within the study area to find suitable food patches far from anthropogenic disturbance near the coasts, individuals in CL and SU might be required to trade-off foraging efficiency and the cost/benefit ratio that emerges from social interactions. It is believed that sociality reaches its pinnacle in species where groups are composed of closely related members with overlapping generations and that cooperatively care for young (Lutermann *et al.*, 2013). Some of the benefits of sociality, such as increased predator detection and offspring survival, are intimately linked to an individual's energy budget and could lead individuals in sperm whale groups to target other prey species with different spatial distributions (Whitehead, 2003) than singletons. Furthermore, Whitehead (2003) suggested that female sperm whale occurrence and movements are better explained by the model of a nomadic animal moving in response to changes in food availability, also considering that the presence of immature individuals is known to heavily affect the behavior of adults (Whitehead, 1996). The output of the Maxent model for social units seems to underlay these evidences by mostly showing suitable areas where upwelling phenomena are more likely to occur (near canyon heads and steep slope zones). The distinction seen in this study between single individuals and groups, also stigmatized by Pirotta and colleagues (2011) in the Western Mediterranean, should be taken into account when an evaluation of the area used by sperm whales is predicted and proposed for conservation purposes. This study showed that high habitat suitability and related sperm whale CL and SU potential distribution are expected in "new" regions comprising the south of Ponza Island in the northwest (Pontine Archipelago), the area of the Magnaghi-Dorhn canyon system in the southeast, and the southern part of Capri Island (Campanian Archipelago). It is advisable to increase the research effort for the collection of additional "presence" data of the different encounter types in order to test the reliability of the model and to ascertain that the new areas defined by the model as being suitable, fit with the prediction.

Based on published data regarding animals utilizing the study area (Mussi *et al.*, 2014; Pace *et al.*, 2014), the entire region seems to be vital for foraging, breeding, social cohesion, mixing and possibly mating, therefore containing critical habitat for sperm whales. Critical habitat is defined as scientifically important and critical to the survival of listed threatened species or listed threatened ecological communities. Cetaceans, such as sperm whales, occupy an extensive range and there is a strong potential that by protecting their critical habitat, a wide variety of other species that regularly occur within the area and ecosystem processes will be protected (Hoyt, 2011). Marine protected areas designed for cetaceans can provide safeguard; however, resources for conservation are limited (Halpern *et al.*, 2008). In order to ensure that these limited resources are effectively directed, it is important to identify clear conservation objectives and to pinpoint priority areas that can meet these objectives most successfully. This study contributed to the development of a modelling framework for sperm whales in a delimitated area of the Tyrrhenian Sea. The identification of sperm whale key areas is the first step in developing specific conservation measures for the Pontine and the Campanian Archipelagos as a whole,

which would likely have positive effects on the 'endangered' stock of Mediterranean sperm whales (Reeves and Notarbartolo di Sciara, 2006; Notarbartolo di Sciara and Birkun, 2010). Despite its 'endangered' status in the IUCN Red List, this species is not present inside the annex I of the Habitat Directive (Council Directive 92/43/EEC on the Conservation of natural habitats and of wild fauna and flora), which has created the network of SACs known as "Natura 2000", including areas with particular habitat types or hosting particular species (respectively listed in Annex I and II) as identified by each Member State. This exploratory study shows that Maxent effectively models sperm whale habitat suitability. The predictive maps developed in the study may be used (and updated with new data) as planning tools to help manage dedicated marine reserves, in addition to defining what activities can occur in specific locations in order to regulate anthropogenic activities and mitigate their impact.

Moreover, results of this study show that consideration should be taken regarding type of social aggregation (cluster of whales and social units), group composition, and life stage when using modeling techniques for generating suitable habitat maps for conservation purposes.

## 3.5 Photoidentification and group composition

Photo-identification is based on recognition of individuals through natural markings, which are recorded photographically (Arnbom, 1987). Whitehead and Gordon (1986) developed photo-identification techniques as a non-invasive tool for the study of sperm whales based largely on markings in the trailing edge of the animals' flukes. These marks accumulate with age but remain stable (Dufault and Whitehead, 1995), and can be readily photographed at the beginning of dives. This has allowed the application of mark–recapture analysis techniques to investigate population size and life history parameters (Hammond, 1987; Whitehead, 2003) and the study of many aspects of sperm whale sociality, behaviour, ecology and life history (Lettevall *et al.,* 2002; Whitehead, 2003).

The sperm whale is sexually dimorphic, with males and females reaching maximum lengths of about 18 and 12 m, respectively, and fully-grown males approximately three times as heavy as mature females (Best, 1979; Rice, 1989). Sexually mature females (approximately 8.3–9.2m long) and their dependent offspring (immature individual of both sexes) form stable social units, which in some cases are based around matrilines (Whitehead *et al.*, 1991; Richard *et al.*, 1996; Mesnick *et al.*, 2003). Female sperm whales are believed to remain in the same group throughout their life, but males leave to form 'bachelor groups', loose aggregations of similar sized and aged individuals. Bachelor groups typically contain either pubescent males (approximately 8.7–10.3m long) or sexually, but not socially, mature males (11–12m long) (Rice, 1989). "Socially mature" males, able to compete for access to females, are typically found in the cold waters of higher latitude in very small groups; largest males (>16m long) are often observed as solitary individuals (Rice, 1989).

Here I report data on photo-identification and group composition during the 2003-2015 period, discussing the peculiarity of the region as important habitat for male assemblages and social units, also suggesting its possibly important role as breeding ground for the sperm whale in the Mediterranean Sea.

### 3.5.1. Methods

Individual whales were photographed on the right and left side of the dorsal fin area, the trailing edge and both the dorsal/ventral side of the flukes. Patches, nicks, notches, scars or other irregularities were used to identify individuals (Whitehead and Gordon, 1986).

The pictures taken during the study period were analyzed using multiple photographs of each individual. We analyzed separately (1) the total exposed flank, from blowhole to caudal peduncle, including the dorsal fin; (2) the dorsal fin (similar to Rosso *et al.*, 2011); and (3) the fluke when it was raised in the air, from both the ventral and dorsal side. Photographs were compared in order to identify recaptured individuals, considering separately photographs from fluke, left side flanks and right side flanks.

We assigned a quality value to each photograph ranging from 1 to 5 following the method used in previous studies (Ottensmeyer and Whitehead, 2003; Auger Methè and Whitehead, 2007). Photographs with value 1 represent the lowest quality. Q-value was independent from the marking degree of the individual. This depends on focus, exposure, angle of the individual to the sensor plane, and the distance of the individual from the camera (similar to Dufault and Whitehead, 1993). Photographs with quality equal to or greater than three were generally used for photoidentification; however, in few cases, lower quality photographs were also considered. Encounters were classified into three types (see Table 2 for details). Whenever possible, individual whales were assigned to a sex/age class (Table 6), considering visual observation of the genital area and size estimates (modified from Pace *et al.*, 2014).

Sex/Age class	Definition
Newborn/Calves (C)	All whales having a total length of about 4-5 m (visually estimated); calves bearing foetal folds were considered as newborns
Juveniles (J)	All whales having a length of about 7 m (visually estimated)
Adult female (FA)	All whales having a length of 9 to approximately 11 m (visually estimated), associated with a J or a C within a social unit
Immature males (MI)	All whales having a length of approximately 8 to approximately 11 m (visually estimated), certainly sexed with direct observations
Possible immature males (MIK)	All whales having a length of approximately 8 to approximately 11 m (visually estimated), always seen within a MI cluster
Adult males (MA)	All whales assumed to be mature having a length of 12 to approximately 15 m (visually estimated)
Unknown sex/age (UK)	All whales other than C, J, FA, MI, MIK, MA, ML (possibly mature females and immatures of both sexes are included)

Table 6. Definitions used to define/classify sperm whale individuals into sex/age class.

#### 3.5.2. Results

A total number of 396 sperm whales were observed during 138 encounters made in the course of 1085 days at sea between 2003-2015. Approximately 158,000 photographs were collected over the study period. Useful photo identification images were taken during 120 of 138 encounters. This dataset contained 249 identifications of 80 individuals obtained between 20 August 2003 and 11 November 2015 (mean identification per sampling period=2.26; mean individuals identified per sampling period: 2.24; proportion of individuals identified per sampling period: 0.02795). For a number of 147 observed whales no good photographs suitable for photoidentification was obtained.

The discovery curve plotted in Figure 26 shows that the rate of identifying new individuals did not decrease significantly over the course of the study, indicating that the local population was not close to being fully sampled. Twenty-five (31%) of identified individuals were resighted between years, and of these, 13 (52%) were encountered over 3 to 6 years.



Figure 26. Discovery curve by cumulative number of identifications.

Table 7. Capture-recapture matrix (2003-2015).

Year	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015
2003	1												
2004	0	5											
2005	0	2	9										
2006	0	2	4	3									
2007	0	1	2	1	9								
2008	0	1	0	2	0	8							
2009	0	1	1	2	5	3	10						
2010	0	1	1	2	0	1	3	6					
2011	0	0	0	1	5	1	7	1	7				
2012	0	1	0	1	0	0	0	0	0	3			
2013	0	1	0	0	5	0	0	0	0	0	5		
2014	0	1	0	0	0	0	1	0	1	0	0	6	
2015	0	0	0	0	0	0	2	2	1	1	0	0	10

Capture–recapture patterns are plotted in Table 7 and Table 8. Thirthy-three whales (41%) were captured once, 18 (22%) twice, and 29 (37%) from 3 to 20 times.

*Table 8. Capture-recapture histories by individuals over the study period (2003-2015). Black cells indicate the presence of each individual in different encounters; light grey rows indicate members of the social unit sighted in 2007, 2009, 2011 and 2013.* 



About 33% of the encounters (n=43) were with solitary individuals (SI) (Table 9). Social units (SU), mainly seen in autumn on alternate years (2007-2009-2011-2013 and 2015), were quite rare (n=8, ~ 6% of the encounters) and mixing of more than one social unit in large aggregations was never observed in the study area. Clusters of whales (including bachelor groups) occurred every year and were the most prevalent encounter type in the study area (n=87, about 61% of the encounters). Group size ranged from singletons to a maximum of eight whales.

							Ye	ear							
Encounter type	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	Total
Social unit (SU)	1	1	0	0	0	1	0	2	0	1	0	1	0	1	8
Cluster (CL)	0	0	4	6	5	4	14	9	7	3	3	7	5	20	87
Solitary individuals (SI)	1	2	1	3	2	5	1	8	11	0	4	3	1	1	43
Total	2	3	5	9	7	10	15	19	18	4	7	11	6	22	138

*Table 9. Number of encounters by type and year* 

Over a total of 80 whales photographically indentified, a number of 11 (13.7%) was catalogued as male after visual inspection of the genital area, while a number of 7 (8.7%) was classified as female because of the presence of associated newborn/calf individuals over the years and the

stability of association. A number of 62 whales remained of unknown sex/age class (UK). As for the composition of the social units, two were sighted over two consecutive years (2002-2003); however, no good quality photographic/acoustical data is available from these encounters, therefore preventing any inference on membership. Members of a social unit (named SU1) were identified on five occasions over four different years (2007, 2009, 2011 and 2013; see Table 10). The composition of SU appears to be changed slightly over time. In 2007, this unit included 8 individuals, one female (NARSIL) with an associated juvenile (DIDI), another female (MILA) and 5 animals of unknown sex/age class (EIWAZ, SIRIO, GIANCA, AURO and HAGALAZ). In 2009, the unit counted only 5 whales, DIDI associated with a calf (MENKAR) and MILA with a newborn (CHRIS), plus EIWAZ and SIRIO. In 2011, the unit had the same core membership as in 2009 (NARSIL, DIDI, MILA, EIWAZ, SIRIO and MENKAR), with one additional individual of unknown sex/age class (NIHAL). The newborn individual (CHRIS) observed in 2009 was no longer present in 2011. In 2013 the unit comprised again the stable group of five individuals NARSIL, MILA, DIDI, SIRIO and EIWAZ, with one additional animal of unknown sex (DEDALO) and one possible male (ICARO); MENKAR was no longer present and possibly he left the unit at the age of 4-6. Finally, a likely new social unit was seen in 2015 (named SU2; Table 10), including three possible adult females –ASPASIA, ILDEGARDA and IPAZIA – and two juveniles (named DIOGENE and ZENONE).

			24						
Photoidentified	Sov	A go class	Social			Encount	ers (date)		
individual	Sex	Age class	Unit #	28/10/2007	20/11/2009	21/11/2009	26/08/2011	08/12/2013	08/11/2015
Mila	Female	Adult	1	Х	Х	Х	Х	Х	
Narsil	Female	Adult	1	Х	Х	Х	Х	Х	
Didi*	Female	Immature in 2007 Adult in 2009	1	Х	Х	Х	Х	х	
Sirio	Possible female	Adult	1	Х	Х	Х	Х	Х	
Eiwaz	Possible female	Adult	1	Х	Х	Х	х	х	
Menkar**	Unknown	Immature (calf) in 2009	1		Х	Х	Х		
Chris***	Unknown	Immature (calf) in 2009	1		Х	Х			
Hagalaz	Unknown	Adult	1	Х					
Gianca	Unknown	Adult	1	Х					
Auro	Unknown	Adult	1	Х					
Nihal	Unknown	Adult	1				х		
Icaro	Possible male	Adult	1					х	
Dedalo	Unknown	Adult	1					Х	
Aspasia	Possible female	Adult	2						Х
Ipazia	Possible female	Adult	2						Х
Ildegarda	Possible female	Adult	2						Х
Diogene	Unknown	Immature	2						Х
Zenone	Unknown	Immature	2						Х

*Table 10. Social units' composition (2007-2015). Blue box marks individuals in SU1, red box marks individuals (possibly males) associated with the stable members of the SU1 on different occasions, green box marks individuals in SU2.* 

\*this animal was associated with Narsil in 2007

\*\*this animal was associated with Didi in 2009

\*\*\*this animal was associated with Mila in 2009 and never encountered later

Long term associations were found between members of male assemblages as well. Three whales - NETTUNO, MARK and CRESCENZO - were identified tightly clustered together in bachelor groups on 3 occasions in 2008; MARK and NETTUNO were also seen together on 7 occasions on different days within the same year and in different years (2006, 2008 and 2009). Other two whales, ALETES and BRUNONE, were sighted together 8 times in 2009 and 2010, and an additional pair, LOLITA and MANWE (both possible males), was located and photoidentified 3 times together in 2008 and 2009. The gender of NETTUNO, MARK, CRESCENZO, ALETES and BRUNONE was confirmed by direct observation of the genital area or/and viewing underwater video (see methods and Figure 27).



*Figure 27. Genital area of a male sperm whale from underwater video (from Pace et al., 2014; © Oceanomare Delphis Onlus).* 

### 3.5.3 Discussion

Globally, sperm whale populations present strong separations among age/sex classes, with tropical and subtropical social units of females plus immatures and juveniles segregating from mid-latitude groups of maturing males ('bachelor' groups), and large high-latitude solitary mature males (Whitehead, 2003; Whitehead and Weilgart, 2000). At least in the western Mediterranean Basin, sperm whale seems to still maintain a scaled down version of the above social division (Drouot *et al.*, 2004b); however, the restricted latitudinal range available in the Mediterranean seems to not allow for such segregation, and it appears to be the norm there for these age/sex classes to inhabit the same waters, even if they do not closely associate (Pirotta *et al.*, 2011; Frantzis *et al.*, 2014; Pace *et al.*, 2014; Rendell and Frantzis, 2016). In the study area, solitary males (SI), loose possible male aggregations and small bachelor groups (CL), and social units (SU) have been observed to coexist (Pace *et al.*, 2014). The photo-id discovery curves showed no signs of reaching an asymptote indicating that the number of individuals visiting or using the area is probably larger than the total identified. At least some (35%) of the identified individuals returned the area and were resighted on occasions over a

year apart. Since no quantitative information is available in other parts of the Tyrrhenian Sea, between Corsica/Sardinia and mainland Italy, we can only speculate about the possibility that the area could be a relevant site for the species, known and exploited by certain animals. Good foraging conditions may explain the regular occurrence of sperm whales in this area. Our acoustic recordings indicate that creaks were produced during sperm whale encounters, suggesting that feeding activities (Miller *et al.*, 2004) take place in the area. Considering the general oligotrophy of the Mediterranean basin (Walle *et al.*, 1993; Notarbartolo di Sciara *et al.*, 2008) and the influence of oceanographic parameters - such as currents and bathymetry (Bakun and Csirke, 1998; O'Dor, 1992) - on resource (squid) distribution and abundance, this area may represent a significant feeding hotspot for the sperm whale.

The majority of sperm whale encounters in the study area was with assemblages of individuals belonging to different sex/age class, ranging from clusters to bachelor groups (CL), to rare social units (SU). Despite the low number of social units seen during the study period (Pace *et al.*, 2014), their presence in the area was mainly concentrated in autumn (October, November, and December), with a couple of newborns observed. Assuming 15 to16-month gestation period (Best *et al.*, 1984), the presence of very small calves in October-November suggests a calving season around August-September, and a mating season in May-June, with a shifting of about two months than the results reported by Drouot and colleagues (2004). The scarcity of encounters with social units (and calves too) may be due to a non-homogeneous sampling effort. In fact, SU were generally observed in autumn, when a reduced effort was applied due to weather conditions; furthermore, the area around Ventotene island – where 4 out of 8 encounters occurred – received a lower searching effort (see Figure 18), therefore limiting our detection probability. Some novel regions to investigate for SU presence were identified applying Maxent habitat suitability model (see 3.4 paragraph and figure 25d), suggesting the potential for adding new knowledge on sperm whale distribution within the study area.

The small number of SU encounters also affected the opportunity of comparisons for the size of these groups. Values of 5-6 individuals found in this study were similar to the Gulf of Mexico (Jaquet and Gendron, 2009), showing much lower values than other well-known geographical areas in the Atlantic and Pacific oceans (Jaquet and Gendron, 2009; Whitehead *et al.*, 2012). By contrast, the average group size for bachelor groups was higher than those reported in other areas (Letteval *et al.*, 2002). If the local high productivity associated with the presence of canyon systems would seem to indicate better feeding, with the possibility to sustain groups of males larger than in other parts of the Mediterranean Sea (Pace *et al.*, 2014), the association of topographical factors and warm waters in the study area (we are south of 41° latitude, where the water temperature remained above 14° C down to 15m depth all year round), could provide not only suitable feeding conditions, but also breeding ones for females and their offspring (see also Drouot *et al.*, 2004).

Our observations showed long-term relationships between some immature males. These 'bachelor' individuals formed tight surface clusters and exhibited all the surface behaviours seen within social units. Bachelor groups in sperm whale had previously been described as 'loose, apparently unstructured, relationships among non-breeding males' (Letteval *et al.*, 2002) and socialising behaviour at surface was considered 'exceptionally rare among these males' (Whitehead *et al.*, 1992; Jaquet *et al.*, 2000) and 'when it happened, it was usually in cluster of two animals and for no more than few hours' (Whitehead, 2006). Our observations, in contrast, suggest that sexually immature individuals in bachelor groups form long term associations. We

don't know if these males are related to each other, or share group-specific feeding specializations (Whitehead and Lusseau, 2012). Young males may benefit in several ways from belonging to stable all-male groups after they leave their SU. They may feed cooperatively, sharing information on the location of prey patches for example; group living may also allow individuals to establish breeding alliances and to practice fighting skills (Chiyo et al., 2011). Large bulls were never seen in the study area; this is similar to Drouot *et al.* (2004) observations in the Tyrrhenian Sea. Large specimens were known to inhabit the Mediterranean Sea until the early 1990s, however the heavy impact of driftnetting activities possibly changed the population composition with a possible depletion of large, physically mature males (Northridge, 1991). The high re-sighting rate deduced from photo-identification results (59%, n=47 individuals, with a number of 29 re-sighted with at least 1 year between the first and last sighting; Mussi et al., 2014; Pace et al., 2014) suggests a degree of site-fidelity and remarks the importance of the area through years. This site-fidelity regarded both social units and assemblages of males (the re-sighting rate was 20% for females and their relatives, 40% for immature males, 35% for individuals of unknown sex, and 5% for adult males). Individuals in CL (including bachelor groups) showed the largest re-sighting range, with repeated identification of the same individuals over the course of years, indicating their tendency to return to or remain in the same area over time (rather than just passing through) (Pace et al., 2014). Patterns of residency and site fidelity are often indicative of the ecology of a population; evidence of repeated sightings in the same area can be used to establish core ranges of individuals and reveal the importance of a particular habitat. In the Western basin, males appear to travel to and from the more northern areas of the basin, in an apparently restricted version of the movements made by males in larger ocean basins (Drouot and Gannier, 2007; Whitehead, 2003). However, although male immigration from the Western basin to Eastern one (Hellenic Trench) has been recently demonstrated (Frantzis et al., 2011), so far it does not seem to represent a common event and no emigration in the opposite direction has been recorded. Therefore, many of the sperm whales inhabiting the eastern Mediterranean and the Hellenic Trench, and especially the females, may spend most of, if not all, their life in this basin (Frantzis et al., 2014).

Matching analysis of our photo-identification catalogue with the Ligurian Sea and Gulf of Lyon (CIBRA-University of Pavia, Tethys Research Institute, DISTAV-University of Genoa, CIMA Foundation, GREC and Menkar Association), N-E Sardinia (DIPNET-University of Sassari) and Gibraltar Strait (CIRCE Research Institute) revealed several correspondences between individuals (17 photo-identified animals over a total of 80, all confirmed or presumed males), indicating that movements between the Tyrrhenian Sea, the Ligurian Sea and the Strait of Gibraltar exist. This is analogous to other findings (Frantzis *et al.*, 2011; Carpinelli *et al.*, 2014), with matching correspondences regarding only male individuals, thus suggesting that Mediterranean sperm whales behave in a similar way to those in other places, where males move between feeding and breeding grounds whereas females with their calves are more sedentary. Comparison between photo-identification databases is still quite rare in the Mediterranean Sea, but the few recent attempts (Carpinelli *et al.*, 2014; Rendell *et al.*, 2014) demonstrated that it could help to reveal new information.

In this study, a first effort to delineate sperm whale social distribution and organization in the Tyrrhenian Sea - around Ischia and Ventotene islands - was attempted. We found evidence that females and young live in stable social units, as has been observed in other areas. One unexpected finding was that groups of maturing bachelor males were stable between years and

individuals within groups showed similar behaviour to those in social units. The spatial scale of the observations is very small and the number of unknown sex/age class of most of the individuals frequenting the study area is high, thus limiting the possibility of a more robust analysis. Despite these caveats, this study represents a significant contribution to improve our limited knowledge of the species in the basin and a first assessment to support conservation efforts to reduce activities that might disrupt both the behaviour and social organisation of a species in which this aspect of their biology is so significant.

# 3.6 Diving and resting at surface

Sperm whales spend their time either searching/foraging at depth or resting at or near the sea surface (Miller *et al.*, 2008). Sperm whale social units usually forage for about 30-45 min between 400 and 1200 m depth in lower latitudes (Amano and Yoshioka, 2003; Watwood *et al.*, 2006). Males perform approximately hour-long dives (which may take them to over 1000m) in search of deep-sea squid and fish to feed on, interspersed with periods spent breathing at the surface in preparation for the next dive. Typically, they move only slowly during these surface bouts. They seem intent on recovering from their last dive and preparing for the next one as quickly as possible, and exhibit a limited repertoire of behaviours. Usually they end their period at the surface by raising their tail-flukes above the surface of the water (fluking up) to initiate their nearvertical dives.

The resting behaviour of sperm whales has frequently been associated and interspersed with socializing periods (Whitehead and Weilgart, 1991; Watkins *et al.*, 1999). The whales are usually observed quiet at the surface and sometimes take a vertical position while passively drifting (Gordon, 1991b; Miller *et al.*, 2008). At present, very little is known about the diving and resting activities of sperm whales around Ischia Island and how individuals balance dive cycles and periods at surface.

## 3.6.1 Methods

Sperm whale surface behaviour was logged both manually (by the means of a chronometer) and directly into a tablet running a specially written event-recording application (since 2012; courtesy of Fernando Liebana). A separate data file was made for each encounter. Data recorded from whales on surface included the time of occurrence of such activities as blows, side-flukes, head-outs, dives without fluking, shallow dives and fluking up. Here I report data analysis on blows and fluking up, as well as social behavior at surface classified as reported in Table 11. When a sperm whale was sighted, the time and position of the beginning and ending of the dives were recorded, and the number of blows during the surface period was counted. The beginning of the dive was recorded when the whale fluked-up (*i.e.*, the moment when the fluke disappeared from the surface). The end of the dive (*i.e.*, the start of the surfacing period) was recorded by the time the whale was first sighted at the surface. The approximate position of a whale surfacing was typically calculated by taking an optical range and bearing measurement (since the boat and a surfacing whale would not be co-located) and computing its position relative to the GPS position.

A dive cycle was defined as the period between two successive fluke-ups from a given whale (Drouot *et al.*, 2004b). The following dive cycle parameters were calculated: (1) the dive duration – time from fluke-up until the whale was re-sighted at the surface, (2) the surface duration – time from the surface re-sighting of the whale until the time it fluked-up, (3) the blow rate – number of blows divided by the surface duration. Dive cycle parameters were only included in the data set for analysis when it could be ascertained with high confidence that the same individual whale was being photoidentified and/or acoustically tracked (*i.e.* in cases where continuous acoustical contact of the whale was kept over the dive and no other whale was acoustically detected in the area). This stringent approach significantly reduced the sample size [I was able to incorporate in the analysis only 38% of the complete dives measured in the 2009-2015 period (n=158) as only in these cases all dive cycle parameters were precisely measured).

Sidefluke	A portion of one fluke seen oriented vertically, but moving horizontally, above the water surface (indicating that the whale is turning sharply) (Whitehaead, 2003).
Surface roll	A whale rolling (> 90°) at the surface of the water along its principal axes.
Lobtail	Flukes lifted above the water and then thrashed onto the water surface (Whitehaead, 2003).
Spyhop	A slow raising of part of the whale's head above the water surface (indicating that the whale is oriented nearly vertically in the water (Whitehaead, 2003).
Breach	A leap from the water, showing at least half of the whale's body (Whitehead, 2003).
Rubbing	A whale actively rubbing a body part on another individual.
Synchronously blowing	Two or more whales blow simultaneously.
Synchronously diving	Two or more whales dive simultaneously.
Floating	Hanging or lying flat on the water surface.

Table 11. Different behaviours at surface observed in social contexts.

**Behaviour** 

Definition

Each day was considered as a single sampling period. When consecutive dive measurements were performed from the same individual in the same day, the mean of each measured variable was computed for that animal so that the sample size represents the number of individuals sampled (and not the number of dives recorded, to avoid pseudo-replication). ANOVA and Kruskal Wallis tests were used to investigate if the entire dive cycle, diving and surface phases' duration, as well as blow rate, were distinctive features of encounter types. The relationships among variables were assessed by calculating the Pearson's correlation coefficient (r) and its probability (p).

#### 3.6.2 Results

A total of 61 complete dive cycles (diving and surface periods) of 36 different animals was measured in the 2009-2015 period [n=16 for solitary individuals (SI); n=34 for cluster of whales (CL); n=11 for social units (SU); Table 12]. On average, the complete dive cycle lasted for 62.5 min for SI (males and/or possibly males), 58.2 min for CL (males and/or possibly males) and 47.8 min for SU (females only; calves/juveniles were not included in the analysis as well associated whales not members of the social unit) (Figure 28).

The duration of the dive cycles in different encounter types fitted a normal distribution (Jarque-Bera test for SI: JB=1.723, p=0.422; CL: JB=2.753, p=0.252; SU: JB=2.013, p=0.182). ANOVA showed that there were significant differences in the dive cycle duration between encounter types ( $F_{2,60}$ =11.365, p<0.0001), being SU values significantly lower than both SI and CL. The length of dives was 52.0 min in SI, 48.5 in CL and 39.2 in SU (Table 12; Figure 29). The duration of dives in different encounter types fitted a normal distribution (Jarque-Bera test SI: JB=0.764, p=0.683; CL: JB=1.066, p=0.587; SU: JB=2.765, p=0.212). ANOVA revealed that there were significant differences in diving duration between encounter types ( $F_{2,60}$ =12.001, p<0.0001), being SU values lower than both SI and CL.

Encounter type Dive cycle paramethers	N. of Whales	N	average±SD	min	max	cv
Solitary Individuals (SI)	16					
Dive duration (min)		16	52.044±5.516	43.9	60.117	0.103
Surfacing time (min)		16	10.777±2.052	6.367	13.517	0.184
Cycle duration (min)		16	62.522±6.395	49.183	70.417	0.099
Blow rate (/min)		16	3.919±0.324	3.247	4.554	0.080
Clusters (CL)	62					
Dive duration (min)		34	48.511±7.446	35.617	64.567	0.151
Surfacing time (min)		62	9.628±2.616	4.701	18.983	0.269
Cycle duration (min)		34	58.201±8.728	43.383	80.383	0.148
Blow rate (/min)		62	3.931±0.313	3.392	5.009	0.079
Social Unit (SU)	14					
Dive duration (min)		11	39.188±6.505	33.833	57.252	0.158
Surfacing time (min)		14	9.281±2.989	6.967	18.751	0.310
Cycle duration (min)		11	47.888±7.338	42	66.833	0.146
Blow rate (/min)		4	3.861±0.246	3.498	4.040	0.055

*Table 12. Descriptive statistics of sperm whale dive cycles during 2009-2015 surveys.* 



Figure 28. Boxplots of the dive cycle duration in different encounter types during 2009-2015 surveys.



Figure 29. Boxplots of the diving phase duration in different encounter types during 2009-2015 surveys.



Figure 30. Boxplots of the surfacing phase duration in different encounter types in 2009-2015 surveys.

On average, the whales spent 10.7 min in SI, 9.6 in CL and 9.3 in SU recovering at the surface (Figure 30), with a blow rate of about 3.9/min in all encounter types (Table 12; Figure 31). Surfacing time in different encounter types not fitted a normal distribution (Jarque-Bera test for SI: JB=27.958, p<0.05; CL: JB=52.524, p<0.0001; SU: JB=30.923, p<0.0001) and significant differences emerged in surfacing time between encounter types (Kruskal-Wallis test: K<sub>(2, 92)</sub>=7.643, p=0.022), being SI values higher than both CL and SU. Blow rates fitted a normal distribution (Jarque-Bera test for SI: JB=0.045, p=0.978; CL: JB=1.009, p=0.432; SU: JB=0.798, p=0.671) and no significant differences were emphasized by ANOVA test between encounter types ( $F_{2,81}$ =0.100, p=0.905).



*Figure 31. Boxplots of <u>blow rate</u> in different encounter types during 2009-2015 surveys.* 

Surface time and dive duration paramethers were found to be significantly related in 'social' encounters CL and SU (with a growing surface time as the dive duration increased; Figure 32). Such positive correlation was not observed in solitary individuals (SI). Surface time was also significantly related to blow rate in CL encounters (with a negative correlation; Table 13 and Figure 32), while no relevant correlation was identified in SI.

	Dive duration (min)	Surfacing time (min)	Blow rate (/min)
Solitary Individuals (SI)			
Dive duration (min)	-	-	-
	-	-	-
Surfacing time (min)	0.0990	-	-
	p=0.596	-	-
Blow rate (/min)	0.0843	-0.0841	-
	p=0.652	p=0.653	-
Clusters (CL)			
Dive duration (min)	-	-	-
	-	-	-
Surfacing time (min)	0.2603	-	-
	p=0.0272*	-	-
Blow rate (/min)	-0,2123	-0.3423	-
	p=0.073	p=0.0032*	-
Social Unit (SU)			
Dive duration (min)	-	-	-
	-	-	-
Surfacing time (min)	0.5394	-	-
	p=0.0002*	-	-
Blow rate (/min)	-	-	-

Table 13. Values of Pearson's correlation coefficient (r) and associated probability (p) between themeasured variables. \*Indicates a significant correlation.

SU members generally displayed all of the behaviours listed in Table 11 during social sessions at surface. Typical behaviours included synchronously diving and blowing, rubbing and breaching. Tail slap and float were rare, being recorded only once. Side fluke and breach were quite common within CL social sessions, with tail slapping events mainly recorded during interactions between male members of bachelor groups. Mean duration of social sessions at surface of different encounter types of sperm whales varied significantly (Kruskal-Wallis: H = 6.403, p = 0.040), with an average ( $\pm$ SE) value of 24.75 $\pm$ 5.45 min for SU and 16.27 $\pm$ 5.99 for CL.



*Figure 32. Scatterplots of the relationship between dive cycle variables in different encounter types during* 2009-2015 surveys.

#### 3.6.3 Discussion

Sperm whales are well-known for the deep dives they perform to reach foraging depths (Papastavrou *et al.*, 1989; Watkins *et al.*, 1993). In different regions it has been shown that sperm whales commonly dive for 40–50 min, performing U-shaped dives and moving principally horizontally during the bottom phase (Amano and Yoshioka, 2003; Zimmer *et al.*, 2003; Watwood *et al.*, 2006). The majority of dive times measured by Gordon (1987) in Sri Lanka ranged between 25 and 50 min. Off the Galapagos Island, Papastavrou *et al.* (1989) measured dives of about 40 min, followed by 10 min at the surface. Watkins *et al.* (1985) described sperm whale dives of over 2 h duration in the southeast Caribbean. Sperm whale diving behaviour studied in the Azores suggested that most dives were 40-55 min long and the maximum time spent at the surface for foraging sperm whales (*i.e.* between foraging dives) was 25% (Gordon and Steiner, 1992; Oliveira, 2013). In the Mediterranean Sea, sperm whales exhibite dive cycle parameters reliable with those measured in other parts of the world: approximately 43-45 min dive duration (with a range of 31-53 min), 9-10 min surface period (*i.e.* inter-dive interval), with 5 blows/min (Drouot *et al.*, 2004b; Teloni, 2005; Gannier *et al.*, 2012).

It is likely that sperm whales lengthen their dive duration to extend the distance covered at foraging depth in order to maximize food intake, adapting the duration of their foraging dive and horizontal movement at depth according to prey availability in a given region (Gannier *et al.*, 2012). This is coherent with the biological needs of different sized animals and seems particularly true for larger whales, which were observed to extend their dive duration to possibly catch bigger preys than smaller ones (Gannier *et al.*, 2012).

In this study, mean dive duration and surface time of sperm whales studied are comparable with values reported from Mediterranean Sea, but a smaller number of blows per minute was always measured. In particular, the average dive and surface periods are: 1) higher in encounetrs with single animals (SI) ( $52.04\pm5.51$  and  $10.77\pm2.05$  min, respectively), 2) slightly higher or consistent with other studies in animal clusters (CL) ( $48.51\pm7.44$  and  $9.62\pm2.61$  min, respectively), 3) consistent or lower in social units (SU) ( $39.18\pm6.50$  and  $9.28\pm2.98$  min,

- respectively). Furthermore, results indicate that there is a relationship between the length of the dive and the length of the recovery time at the surface in 'social' encounters CL and SU, with a growing surface time as the dive duration increased. Such positive correlation was not observed in SI. Gordon (1987) also measured no significant correlation between these variables, while Lockyer (1977) reported that surface times increased with dive time. These contrasting results in different locations suggest flexibility in the relationship between dive phase duration and surface phase duration in different sites (Watwood *et al.*, 2006).
  - Furthermore, other variables could influence the time required to recover at the surface, such as the depth of dives, which could not be measured here, and the type of the sperm whale encounter (singletons vs clusters and social units). As a number of different social behaviors was recorded during CL and SU surface periods, with a considerable amount of time spent in these activities, the competing demands between time spent feeding (to maintain survival) and time spent socialising (to ensure the benefits of sociality, including cooperation, and to care calves) have to be examined. One of the major foraging theories used to explain animals' foraging behaviours is the optimal foraging theory (Emlen, 1966; MacArthur and Pianka, 1966). The basis of this theory is that in order to increase their fitness, animals have to maximize their net rate of energy gain while foraging by making decisions on where and what to eat (Stephens and Krebs, 1986).
When a sperm whale is feeding during a dive, it needs to decide when to break off from foraging and return to the surface. If returning to the surface represents leaving a patch, optimal foragin theory suggests that divers should remain in the patch at depth longer when prey density is high (Stevens and Krebs, 1986), balancing the cost of remaining at depth (aerobic dive limit). Thus, the sperm whales need to have an efficient locomotion behavior during transit to and from foraging depth: in the Ligurian Sea, for example, sperm whales increase their vertical velocities by increasing their ascendant pitch angle during longer duration dives (Watwood *et al.*, 2006). However, moving to surface to breath obviously reduces the ability of sperm whales to relocate the same patch (Ydenberg and Clark, 1989; Kooyman and Ponganis, 1998; Miller et al., 2004). Alternative theories to the optimal foraging theory have also been proposed, such as the idea that instead of maximising energy gain, foragers should only forage long enough to acquire sufficient energy gain to survive and reproduce (Ward, 1992). This idea has been developed as the concept of "energy maximization" and "time-minimization", which differentiates the foraging strategies of animals that maximise their food intake to increase their fitness (energy maximizers) from those who forage long enough to meet their energy needs while saving time for highly-relevant, non-foraging activities (such as social interactions) to increase their fitness (time minimizers) (Hixon, 1982; Bergman et al., 2001). Moreover, the evolutionary trade-offs between foraging and social interaction was recently used to develop a simulation model to explore the conditions under which complex social systems evolve, underlying that species living in predator-risky, open habitats (like the ocean) may be able to reduce their dependency on foraging time, thereby favouring an increased social time budget and hence higher levels of social interaction (Sutcliffe et al., 2016).

The significant differences in the dive duration found in this study between larger singletones (individuals with an eximated length of more than 12m, a size generally attained by males; Rice, 1989) and smaller clustered animals (both 'bachelor groups'/clusters of males or presumen ones, and social unit) seem to support evidences that:

(a) large, solitary male individuals at lower predation risk may act to maximize their food intake, increasing the lenght of the dive duration;

(b) groups of pubescent males as well as females with immatures within social units may need to balance foraging time at depth and social interactions at surface, positevely correlating the duration of the dives with the time spent socializing at surface.

Since calves are apparently unable to make prolonged foraging dives for the first few years of their lives, they remain dependent upon their mother's milk during that time. Mothers however need to forage continuously to sustain lactation and so have no choice but to leave their calves at the surface, during which time they are exposed to predation risk in the refuge-less pelagic surface waters (Rendell and Frantzis, 2016). Calves left at the surface are regularly escorted by other adults in their natal social unit, and the suggestion is that sociality in female sperm whales are largely driven by these interactions (Gero *et al.*, 2013; Whitehead, 2003; Whitehead and Weilgart, 2000). The presence of conspecifics and the 'maternal' social context may therefore have consequences for individuals' behavioural decisions, and these have to be considered as drivers of the trade-off between foraging and socializing. Furthermore, different individuals from a single population can exhibit:

(1) different behaviours that are consistent within individuals across time and contexts (referred as different personalities), and

(2) different behavioural adjustments to environmental gradients/conditions, thus

showing different patterns of behavioural plasticity (Dingemanse *et al.*, 2010). Under an "ecological hypothesis", individuals who experience similar ecological or social conditions (*e.g.* food patch, predation risk, or group size) and have similar traits (*e.g.* age-sex class, body size, or reproductive state) should experience the same ecological constraints and behave in the same way. However, the "behavioural hypothesis" under which individuals should exhibit different personalities even when experiencing similar conditions and having similar characteristics, and may also show different patterns of plasticity (Dingemanse *et al.*, 2010), cannot be ignored when observing the results here presented [well-known individuals repetitively sighted over the years, forming stable (SU) or recurrent associations (CL) in the study area].





# Chapter 4 Patterns of sound production



# 4.1 Data collection

Searches for sperm whales were made by continuously scanning water surface with the naked eye and by continuously listening underwater for whales' clicks. Acoustic recordings were collected by a towed stereo hydrophone array incorporating two hydrophones (100Hz – 22 kHz bandwidth, ENEA UT-APRAD Radiation Sources Laboratory), with ASD Schaller pre-amps, spaced 3 meters apart and towed on a 100 m cable.

The system was connected to the PC through RME Fifeface 400 audio interface (sample rates up to 192 KHz; sample rates selected for recording on the computer: 44, 44.1 and 48 kHz with 16 bit resolution). The output signal was also connected to headphones and to a pair of stereo speakers located in the pilothouse. While the vessel was underway, a continuous listening of sounds from the array was conducted. During all surveys, the data logging software 'Logger 2000' developed by the International Fund for Animal Welfare, IFAW; http://www.ifaw.org (which collects data in Microsoft Access 2000 format) was used on a PC connected to the GPS receiver to record the position of the research vessel every 180 seconds. Automatically detected acoustic contacts with sperm whale were also entered in Logger 2000, after visual/acoustic inspection by an operator. The software used for audio recording and acoustic data collection included Rainbow Click, a program designed to locate and analyze sperm whale clicks and other odontocete acoustics (Marine Conservation Research, 2010). Once sperm whales were detected, the vessel route was maneuvered to estimate the relative bearing of vocalising animal(s), to track and approach it or them until their emersion and sighting at surface. Rainbow Click analysed the stereo signal using time of arrival differences between the same clicks on the two channels to estimate a bearing to each click source (Clark et al., 2012; De Vos et al., 2012). Only clear/very loud acoustic detections were considered for the analysis.

## 4.2 Acoustic repertoire and habitat use

### 4.2.1 Methods

Acoustic recordings, taken over a period of seven years [2009-2015, plus one encounter with the social unit (SU1) in 2007] were analyzed to identify acoustic categories. Much of the literature categorizes sperm whale clicks into four basic click types: Usual Clicks, Creaks, Codas, and Slow Clicks (Gordon, 1987b; Whitehead and Weilgart, 1991; Weilgart and Whitehead, 1997; Madsen *et al.*, 2002a; Whitehead, 2003; Zimmer *et al.*, 2005a). For analysis purposes in this project, the basic click types, along with other acoustic categories, were broken down further into different acoustic types in order to describe the acoustic behaviour in more detail and with greater accuracy. Seven patterns of clicks were identified as well as two categories of tonal sounds and two categories for Silence (Table 14).

*Table 14. Acoustic single codes used to describe the sperm whale sound patterns off Ischia Island.* 

#### Acoustic codes and function

Search (SEA) Usual Click (UC)

**Feed (FEE)** Transition (TR) Creak (CR)

Socialize (SOC) Coda (CO) Rapid click and chirrups (RC) Coda Creak (CC) Slow Click (SC)

**Tonal sounds (TONAL)** Trumpet (TM) Squeal (SQ)

Silence (SIL or SUR) Clicking pause (SL) Surfacing (SR)



Usual Clicks (UC) hold an ICI of greater than 0.5 seconds, are emitted during a dive, and are considered to be used for orientation/searching echolocation; they have been mainly attributed to orientation/searching/foraging behaviors, even a possible communication function cannot be excluded (Pavan, *personal communication*).

A click sequence with an ICI between 0.2-0.5 seconds, generally emitted during dives and seemingly utilized as a targeting form of echolocation during foraging activities, was identified during analysis and named as 'Transition Clicks' (TC). TCs maintain an ICI in between the Usual Click (ICI  $\geq$  0.5 seconds) and the much faster 'true' Creak (ICI  $\leq$  0.2 seconds), and seem to be a transition phase between UC and CR (Figure 33). In the majority of the cases, however, a UC sequence continues with TC and then again UC (Figure 34), without a defined creak sequence. In other circumstances, UC sequences are combined with pauses in click emission (silence; Figure 35).



*Figure 33. Spectrogram of a sperm whale usual click (UC) sequence, followed by a phase of transition clicks (TR) continunuing in a creak (CR) sequence.* 



Figure 34. Spectrogram of a sperm whale usual click (UC)-transition click (TC) sequence.



Figure 35. Spectrogram of a sperm whale usual click (UC) sequence followed by a pause (SL, silence).

Creaks (CR) have an ICI of less than 0.2 seconds, are emitted during dives, and are thought to function as a homing type of echolocation and are considered to be specific to foraging behavior. However, click sequences with an ICI of less than 0.2 seconds may also be emitted at the surface, where they are referred to as Rapid Clicks and/or Chirrups (RC). Rapid Clicks/Chirrups are thought to be related to socialization behavior. Codas (CO), which are generally emitted at the surface but can also be detected during a dive (Pavan et al, 2000), have an ICI between 0.1-0.5 seconds and are in association with socialization. Coda-creaks (CC), which are a rapid click sequence combined with a Coda at the end, are also recognized as a socialization type of acoustic. Slow Clicks (SC) have an ICI between 3-8 seconds, are emitted during dives or at the surface and are considered to be used for socialization among males. Trumpets (TP) are tonal sounds generally emitted just after the beginning of a dive and their true functions are generally unknown. Squeals (SQ) are also tonal sounds that can be emitted at the surface or during dives, although, it is currently unclear whether Squeals are truly a non-click tonal sound or a burstpulse sound comprised of clicks at very high repetition rates (Weir et al., 2007). Finally, pauses in click emission during dives (SL, clicking pause), lasting 3 or more seconds, together with surfacing time without click emission (SR, surfacing), comprise their own basic category of Silence.

Acoustic codes and related function (behaviour) were assigned to events according to the guidelines listed in Table 14 and descriptions of acoustic types/click arrangements from the body of literature (Gordon, 1987b; Whitehead and Weilgart, 1991; Weilgart and Whitehead, 1997; Madsen, 2002; Madsen et al., 2002a; Whitehead, 2003; Zimmer et al., 2005a). The ICIs of clicks were measured using Audacity, Version 2.1.0, in order to assign acoustic types. For Usual Click (UC), Transition Click (TR), and Slow Click (SC) types, code was assigned after the occurrence of 3 or more consecutive clicks. For Creaks (CR), Rapid Clicks (RC), Codas (CO), Coda-creaks (CC), Trumpets (TP), and Squeals (SQ), code was assigned at first occurrence. This was justified in that these acoustic type events are short in duration and can be identified on first occurrence. For clicking pause during dives (SL), code was given after a time interval of silence of at least six times previous ICIs, while surfacing time (SR) without clicks was assigned when the animal(s) first appeared at surface and a silence period followed. The data collected was used to represent the time spent per acoustic code in Single Code events and Combination Events. For Single Code events, the acoustic code was the only code heard from one or multiple whales. For Combination Code events (Table 15), the acoustic code was heard simultaneously with one or two other acoustic codes from multiple whales.

The rate of clicking pause during dives (SL) and the creak rate (CR+TR) was measured for complete dives only. The main limitation of creak counting was the risk of confusion in the case of multiple audible whales in the case of encounters with social units and clusters. Only data obtained from clear recordings, with a maximum number of three different audible diving whales, was used to determine the creak rate.

To estimate the habitat usage via acoustics, the GPS coordinates of the position of the boat were assigned to click types and their related functions every 3-min. This information was then plotted onto the study area map using Heat map plugin in QGIS 2.0. A heat map (or density map) is a graphical representation of point data which is used to visualize geographic data in order to show areas where a higher density or cluster of activity occurs. Heat map plugin is considered one of the best tool to find out the cluster where there is a high concentration and it is also used to map hotspot analysis. While they look similar and the terms are often used

interchangeably, heat maps and hot spot maps are not identical processes. The Heatmap plugin uses Kernel Density Estimation (KDE) to create a density (heatmap) raster of an input point vector layer. Kernel density is a non-parametric method used to identify one or more areas of disproportionately heavy use (i.e. core areas) within a home-range boundary (Worton, 1989), with appropriate weighting of outlying observations. The density is calculated based on the number of points in a location, with larger numbers of clustered points resulting in larger values. The resulting density surface is visualized using a gradient that allows the areas of highest density to be easily identified. Hotspot analysis uses vectors to identify locations of statistically significant hot spots and cold spots (areas of high occurrence versus areas of low occurrence) in the data by aggregating points of occurrence into polygons or converging points that are in proximity to one another based on a calculated distance. The analysis groups features when similar high (hot) or low (cold) values are found in a cluster. To test for the presence of clustering in the data, two available methods involving spatial autocorrelation Moran's I and Getis-Ord General G were applied in QGIS. They work by looking at each feature in the dataset within the context of neighbouring features in the same dataset. There may be a feature with a high value but it may not be a statistically significant hotspot. In order to be a significant hotspot a feature with a high value is surrounded by other features with high values. The local sum for a feature and its neighbors is compared proportionally to the sum of all features; when the local sum is very different from the expected local sum, and that difference is too large to be the result of random choice. The designation of an area as being a hot spot is therefore expressed in terms of statistical confidence. A z-score and a p-value are returned for each feature in the dataset. A high z-score and a low p-value for a feature indicates a significant hotspot. A low negative z-score and a small p-value indicates a significant cold spot. The higher (or lower) the z-score, the more intense the clustering. A z-score near 0 means no spatial clustering. Since hot spot areas are related to a statistical approach, the end visualization is less subjective than the heat map.

Search/Feed (SEA/FEE)	
Usual Click/Transition	UC/TR
Usual Click/Creak	UC/CR
Usual Click/Transition/Creak	UC/TR/CR
Socialize (SUC)	
Coda/Coda Creak	CO/CC
Coda/Slow Click	CO/SC
Coda/Rapid Click (chirrup)	CO/RC
Coda/Coda Creak/Slow Click	CO/CC/SC
Coda/Coda Creak/Rapid Click (chirrup)	CO/CC/RC
Slow Click/Coda Click	SC/CC
Slow Click/Rapid Click	SC/RC
Search /Socialize (SEA /SOC)	
	110/00
Usual Click/Coda	00/00
Usual Click/Coda Creak	UC/CC
Usual Click/Rapid Click (chirrup)	UC/RC
Usual Click/Slow Click	UC/SC
Usual Click/Coda/Coda Creak	UC/CO/CC
Usual Click/Coda/Rapid Click	UC/CO/RC
Usual Click/Coda/Slow Click	UC/CO/SC

Table 15. Acoustic combination codes used to describe the sperm wh	hale sound patterns off Ischia Island.
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Acoustic Code

**Vocalization Type and function** 

#### 4.2.2 Results

A total of 557 .wav file, corresponding to 251 hours of audio recordings, was analysed to represent the time spent per acoustic code in Single Code events and Combination Events (see methods). A number of about 49 recording hours were excluded from the analysis (20% of the total) as the noise level did not allow a correct click classification and accurate estimates of duration, therefore only the remaining time, corresponding to 198 hours (712,674 seconds), was examined. Overall, sperm whales off Ischia Island spent the majority of the recording time (both entire and partial dive cycles, see paragraph 3.6.1) in searching activities (72.51%; Table 16). This behaviour included the usage of usual clicks (UC) with pauses (SL) between UC sequences. UCs were produced while whales descended to the depth, after about 15-120 sec from the starting of the dive, and ended in the ascent phase about 60-240 sec before first blowing at surface. The mean number of pauses within a dive was  $19\pm8$  and they lasted  $12.54 \pm 10.12$  seconds. Feeding comprised 5.75% of the time (acoustic codes: TR and CR), as well as a mix of searching-feeding activities (5.23%, combined acoustic codes). To measure creak rate and CR/TR mean duration, only a subsample of the recording time was used (see methods), correponding to 455,642 seconds in 158 complete dives. Sperm whales off Ischia produced an overall number of 14.49±4 TR/CR per dive, ranging from 0 to 33. TR and CR had a mean duration of  $10.81 \pm 12.47$  seconds and  $4.68 \pm 7.82$  seconds, respectively. Socializing behaviour was recorded for a total of 2.22% of the total recording time (acoustic codes: CO, CC, RC, SC) and a mix of searching-socializing activities were observed for the 1.78% of the analysed time. About 12.5% of the time was used in surfacing periods. The G-test of goodness-of-fit (likelihood ratio test) and Chi-square test (with Monte Carlo simulation) were applied to test independences of behaviour duration within encounter types. Both tests revealed significant differences between SI, CL and SU (G<sup>2</sup> Wilks=124,003, DoF=75, p<0.0001; Chi-square=170.40, DoF=15, p<0.0001) (Figure 36). A focus on social clicks duration revealed a different usage of these sounds between encounters, with a prevalence of rapid clicks/chirrups (RC) at surface in SU and slow clicks (SC) in CL encounters (Figure 37). As expected, social sound in SI resulted very rare, so they were excluded from this analysis.

	En	counter T	Total	Time		
Behaviour	SU	SU CL SI		time (sec)	spent (%)	
SURFACE	3974	57774	27325	89073	12,498	
SEARCH	62267	386498	68001	516766	72,511	
FEED	227	40756	0	40983	5,7506	
SEARCH/FEED	0	30440	6850	37290	5,2324	
SOCIALIZE	9419	5905	525	15849	2,2239	
SEARCH/SOCIALIZE	9801	2912	0	12713	1,7838	
Total time (sec)	85688	524285	102701	712674	100%	

*Table 16. Time spent (sec) in each acoustically assessed behavioural activity in different encounter types.* 



Figure 36. Time spent (%) in each acoustically assessed behavioural activity in different encounter types.



Figure 37. Time spent (%) in social activities (pattern of social clicks) in different encounter types.

The distribution of the acoustic behaviour was investigated using kernel density estimation (KDE) and hotspot analysis to identify areas of core habitat use. Figures 38 (searching), 39 (feeding), 40 (socializing), 41 (click pauses) and 42 (surfacing) plots the results, highlighting that specific 'core' areas for behaviour like searching, feeding, socializing and surfacing existed, and that behaviour like click pauses are spread in a larger area than the others.



*Figure 38. Heatmap (Kernel Density Estimator, KDE) and hotspot (spatial autocorrelation Moran's I and Getis-Ord General G methods) plots of sperm whale <u>searching behaviour</u> in the study area.* 



*Figure 39. Heatmap (Kernel Density Estimator, KDE) and hotspot (spatial autocorrelation Moran's I and Getis-Ord General G methods) plots of sperm whale <u>feeding behaviour</u> in the study area.* 



*Figure 40. Heatmap (Kernel Density Estimator, KDE) and hotspot (spatial autocorrelation Moran's I and Getis-Ord General G methods) plots of sperm whale <u>social behaviour</u> in the study area.* 



*Figure 41. Heatmap (Kernel Density Estimator, KDE) and hotspot (spatial autocorrelation Moran's I and Getis-Ord General G methods) plots of sperm whale <u>click pauses</u> in the study area.* 



*Figure 42. Heatmap (Kernel Density Estimator, KDE) and hotspot (spatial autocorrelation Moran's I and Getis-Ord General G methods) of sperm whale <u>surfacing behaviour</u> in the study area.* 

#### 4.2.3 Discussion

Results on sperm whales' sound production here presented are consistent with other studies, with some peculiarities and differences. The acoustic repertoire is dominated by usual clicks, produced in sequences interrupted by short pauses. Sperm whale usual clicks have properties suited for searching and detection (at a maximum range of more than 500 m) of cephalopod prey patches (Madsen et al., 2002b; Møhl et al., 2003; Zimmer et al., 2005a), such as high directionality, high source levels and frequencies around 15 kHz suitable for long-range sonar (Møhl et al., 2003). Regular clicks are generally heard during the descendent and the bottom phases of the dives, as part of search behavior (Thode et al., 2002; Zimmer et al., 2003), but also during the ascent phase (Teloni et al., 2008). In this study, the context and the amount of usual click (UC) production seems to be consistent with the use of echolocation for spotting prey during all phases of the dive, reaching an overall value of more than 72% of the the total dive time. UCs were produced while whales descended to the depth, after about 15-120 sec from the starting of the dive, and ended in the ascent phase about 60-240 sec before first blowing at surface. This means that sperm whales around Ischia island possibly begin the searching activity using usual clicks at an estimated depth of about 19-156 m (considering a descendent swimming speed of 1.3 m s<sup>-1</sup> as reported by Watwood *et al.*, 2006 in the Ligurian Sea), which is a detection range well within the theoretical one (500 m) over which sperm whales should be able to perceive their prey based on the acoustic properties of regular clicks (Møhl et al., 2003). These results seem to be similar to Teloni and colleagues (2008), who reported that male sperm whales in Norway, in dives less than about 500 m, started usual clicking within the first 15 m, while in dives deeper than 500 m at about 150 m, connecting this behavior with a bimodal foraging pattern. In our study, sperm whales stopped the detection at a probable depth of 90-360 m (estimating a return to the surface at a rate of 1.5 m s<sup>-1</sup> as reported by Watwood *et al.*, 2006 in the Ligurian Sea). It seems, therefore, that sperm whales' searching activity in the study area occurred over a wide range of depths and at any stage of the dive (meaning that sperm whales in the study area may encounter prey items throughout a large part of the water column), with a possible whale's deliberate decision of whether to forage shallow or deep prior to dive (Teloni *et al.*, 2008).

As already described (see paragraph 3.4.3), the pelagic cephalopods fauna in the southern Tyrrhenian Sea seems to be mainly dominated by Sepiolidae (in terms of abundance in epipelagic and mesopelagic zones, most commonly in depths around 200 m; Jereb and Roper, 2005; Romeo *et al.*, 2012), Ommastrephidae and Onychoteuthidae (in terms of biomass, at depth over 500 m; Romeo *et al.*, 2012). Garibaldi and Podestà (2014) reported that the stomach contents of a single whale stranded in the Ligurian Sea was dominated by histioteuthid beaks, confirming the findings of previous studies in the Mediterranean Sea showing that *H. bonnellii* represents the main prey species for sperm whales (Roberts, 2003; Mazzariol *et al.*, 2011; Praca *et al.*, 2011). In the southern Tyrrhenian Sea both species of the Histioteuthidae family, *H. reversa* and *H. bonnellii*, are found in the depth range of 530-645 meter (Giordano *et al.*, 2001), hinting possible exploitation by sperm whales.

The use of regular clicks during the ascent phase here observed - a fact in contrast with other studies in lower latitudes showing that sperm whales do not echolocate for food on the way back up to the surface (Medsen *et al.*, 2002b; Watwood *et al.*, 2006), but in accordance with Teloni and colleagues (2008) at higher latitudes – suggests the search for the presence of shallow water prey, indicating that animals may come across preys not only during the descendent and bottom phases, but in those portions of the dive as well. This means that sperm whales in this habitat may adapt searching behavior according to the mobility of target species (Teloni *et al.*, 2008), exploiting all available resources in the water column (for example, *H. bonnellii* undergoes significant vertical migrations). However, not knowing details on sperm whale prey items in the study area, we cannot undoubtedly link the whales' use of regular clicks to specific prey types.

Together with type, distribution and abundance of prey, features that are believed to influence the production of usual clicks and creaks are dive location, bottom topography, productivity, time of the day, whales' body mass, individual traits that may determine foraging efficiency, sociality (Gannier et al., 2012). Periods of time where creaks are detected have been described as prey capture attempts (Miller et al., 2004; Watwood et al., 2006). In this study, creaks (CR) and transitional clicks (TR; see methods) were heard only after the onset of regular clicking. Watwood and colleagues (2006) compared click emissions in the western Mediterranean Sea, in the Gulf of Mexico and in the western Atlantic Ocean, finding an average of 18.5 creaks per dive emitted by 12 sperm whales tagged in the Ligurian Sea (a count significantly different from values obtained in the two other regions). In the nort-western Mediterranean Sea, Teloni (2005) got creak counts ranging from 5 to 21 creaks per dive, while Gannier and colleagues (2012) using surface hydrophones rather than on-animal tags, measured an average of 25 creaks per dive. It is not clear whether the difference between Mediterranean studies on creaks is simply sampling noise or some systematic difference between the remote and on-animal recording methods, but in either case the broader point still stands—sperm whale foraging behaviour in the Mediterranean appears to be very typical of the species as a whole, suggesting, along with the stomach contents analyses, that this population occupies a very similar ecological niche to those in other oceans (Rendell and Frantzis, 2016).

In this study, the mean number of CR+TR per dive  $(14.49\pm4)$  was lower than the values found in other studies, and about 30% of the dives were not associated with any creaks, which is higher than what Teloni and colleagues (2008) reported in Norway (15%) and lower than what Mathias and Thode (2012) reported in the Gulf of Alaska (50%). These findings may be the result of both: a) the stringent criteria applied to select useful recordings (see methods); as creak pulses have a lower source level than usual clicks (Madsen *et al.*, 2002a), they might not be audible in sound sequences recorded from whales clicking at distance from hydrophones, therefore limiting their counting;

b) a possible lower efficiency in sperm whales' foraging around Ischia than in other areas. Creaks are mostly produced as soon as the whale has reached its preferred depth range, where most of active feeding takes place (Gannier et al., 2012). In this study, it was not possible to assess the position of the clicking whale in the water column; however, searching and feeding hotspot maps obtained with the acoustic tracking indicate higher activity at depths deeper than 500 m, near the main canyon heads. These results may be interpreted as a combination of external factors (*e.g.* prey type and distribution, and bottom topography) and to a unique set of individual features related with individual auditory and phonating capabilities. The influence of each of these factors remains a matter of speculation but the lower number of creaks produced by sperm whales off Ischia may plausibly indicate that they consume fewer but more nutritious, rewarding prey item than in other sites, targeting prey layers of larger-sized squids. Deep dive species like Ommastrephidae and Onychoteuthidae muscular fastswimming squids are highspeed growing active predators, which efficiently convert their prey into own biomass (Clarke, 1996a), therefore representing a primary source of food and energy for large marine predators (Romeo et al., 2012). Sperm whales in the study area may benefit the occurrence of these cephalopod assemblages, together with Histioteuthid ammoniacal, slow moving squids known to represent the main prey species for sperm whales in the Mediterranean Sea. According to all the evidence we are aware of, the sperm whale dependence on deep-sea squid is a key factor in the persistence of such a large predator in the oligotrophic Mediterranean Sea, since it confers a degree of independence from the main food chain that passes from phytoplankton to zooplankton to fish in the surface waters, although just how independent they can be remains to be seen (Rendell and Frantzis, 2016).

As shown, this study highlighted an uncommon sympatry of solitary male individuals, social units of females with immatures and clusters of possibly juvenile males off Ischia island (Pace et al., 2014), with differences in searching and feeding acoustic behaviour between singletons and social encounters. Such overlapping may imply a modification of the ecological niches splitting between different age/sex classes, resulting in an increased competition for resources (Rendell and Frantzis, 2016). Comparisons based on the modelling work presented in this study (see paragraph 3.4.2) and in the data offered by Pirotta and colleagues (2011) seem to suggest that, within a given region, there might be fine-scale partitioning evident in the differing habitat preferences of singletons and groups (see also Jones *et al.*, 2016). Differences between sexes in habitat utilization and feeding behavior are consistent with both studies on single males in Norway (Teloni et al., 2008) and females with immatures at lower latitudes (Watwood et al., 2006), and with findings from stomach contents, which have shown differences in the composition of the diet of males and females (Evans and Hindell, 2004). Additionally, it has to take into account that Watkins and Schevill (1977) and Oliveira (2014) mentioned the underwater dispersion behaviour of sperm whales at higher depths (>550 m) to forage singly, adding the notion of increased foraging success by not interfering with each other while at depth, even when exhibiting synchrony with other individuals close or at the surface and at shallow depths. Finally, individual differences either associated with the emission, reception and interpretation of acoustic signals, the swimming and manoeuvrability to capture prey, and the

physical features of each individual, cannot be excluded in this context (Oliveira, 2014). Although such hints (*i.e.* fine-scale partitioning/suitable habitat, dispersion behavior at depth and individual peculiarities) are far to be conclusive, they could be of help to understand whether there are likely to be competition effects as a result of this age/sex class sympatry. Further studies on sperm whale diving, searching and foraging behaviour are needed to try to elucidate possible competition mechanisms that could lead to constraints in population growth rate that are not predicted by studies outside the Mediterranean Sea (Rendell and Frantzis, 2016).

To summarize, sperm whale diving, searching and foraging behaviour off Ischia island seems to be highly patterned, as described in other locations (Watwood *et al.*, 2006; Miller *et al.*, 2008; Oliveria, 2014). However, differences in the usage of usual clicks and creaks between Ischia island and other sites in the Mediterranean Sea may be related to the type, movements and distribution of prey that sperm whales are consuming in this area and to the peculiar bottom topograpy. Analysis of stable isotopes or identification of prey collected in whales' faeces may help elucidating this hypothesis.

Searching and foraging behaviours in social encounters are usually interspersed by periods of interactions through social sounds (codas, rapid clicks/chirrups, coda creaks and slow clicks). These vocalizations are varied and representative of the intimate interactions among members of the group (Whitehead, 2003). In social unit encounters (SU), animals spent the majority of the socializing time in rapid clicks/chirrups click sequences. These sounds are usually shorter than the foraging creaks and may intentionally communicate information (Gordon, 1987a; Weilgard, 1990), as has been suggested for the click series of other odontocetes (Whitehead, 2003; Watkins and Wartzok, 1985). Gordon (1987a) reported chirrups, together with codas, as social sounds heard when in the presence of many animals apparently socializing at surface. Codas are the most representative click type in both CL and SU encounters, so in the following section (4.3), features in coda clicks are reported in detail. In encounters with clusters of possibly subadult males (CL), slow clicks are significantly represented within the social repertoire. Slow clicks have only been heard sporadically in the presence of mature or maturing males. Because of this uncommonness, there are few published studies on their properties, and their function(s) remain somewhat mysterious. It is thought that, from the recent collection of diving and acoustic data, it is more likely that slow clicks are related to communication more so than for foraging and orientation and that may vary depending on the behavioural context in which they are produced (Oliveira et al., 2013). The click interval and conceivably waveform of slow clicks could carry individual information, making these sounds a possible long-range acoustic communication signal where both sender and receiver are at depths at which such propagation is supported (Oliveira et al., 2013). In this study, slow clicks were frequent in groups of presumably maturing males, so the function of providing conspecifics with information about the presence, location, identity and perhaps size of the vocalizer (Gordon, 1987b; Weilgart and Whitehead, 1988; Mullins et al., 1988; Whitehead, 1993; Tyack and Clark, 2000; Madsen et al., 2002b; Barlow and Taylor, 2005; Oliveira et al., 2013) cannot be excluded. Trumpets and other tonal sounds are not often reported in the literature (Gordon, 1987a; Doruot, 2003; Teloni et al., 2005). In particular, being trumpets lower in amplitude than clicks,

they might not be recognizable at distances where clicks are still heard; however, since in this study it was possible to detect a significant number of these vocalizations, a dedicated analysis was perfomed (see section 4.4).

## 4.3 Social vocalizations: codas

Codas have been studied mostly from groups of female and immature whales socializing at surface or close to it (Watkins and Schevill, 1977; Whitehead and Weilgart, 1991; Moore *et al.*, 1993; Weilgart and Whitehead, 1993, 1997; Rendell and Whitehead 2003a, 2003b; Drouot et al., 2004c; Marcoux et al., 2006), but have been also heard during dives (Pavan et al., 2000; Madsen et al. 2002a; Oliveira et al., 2016). They can be exchanged among whales (Schulz et al., 2008) and are believed to serve a communication function (Watkins and Schevill, 1977; Weilgart, 1990; Whitehead and Weilgart, 1991; Weilgart and Whitehead, 1993; Schulz et al., 2008, 2011). Codas were initially thought to be unique for each sperm whale (Watkins and Schevill, 1977) but evidence of sharing of coda types by several individuals, did not support the hypothesis of individual specific coda types (Moore et al., 1993; Weilgart and Whitehead, 1993). Codas are thought to function in reinforcing group cohesion via a shared vocal repertoire (Weilgart and Whitehead, 1993; Whitehead, 2003). Some coda types are geographically distinct (Moore et al., 1993; Weilgart and Whitehead, 1997; Pavan et al., 2000; Rendell and Whitehead, 2005; Antunes, 2009), and there are prominent unit-specific coda repertoire dialects among groups that share coda types (Weilgart and Whitehead, 1997). Besides geographical and unit-specific variations, the pattern of coda exchanges has a sequential structure (Weilgart and Whitehead, 1993) and some coda "families" (groups of coda types, e.g., root, regular and progressive coda groupings) seem to be related to different behavioral contexts such as foraging and socializing (Frantzis and Alexiadou, 2008). Mature male sperm whales are solitary and perform little if any social interactions (Weilgart and Whitehead, 1988). Their acoustic repertoire in both the Atlantic and Pacific oceans differs from that of socializing groups of whales in tropical waters by the lack of coda exchanges (Weilgart and Whitehead, 1988; Madsen and Møhl, 2000). In the Mediterranean Sea, the acoustic behavior of male sperm whales is diverse from male conspecifics in the ocean and codas seem to play a particular role at least during their deep feeding dives (Frantzis and Alexiadou, 2008).

### 4.3.1 Methods

Codas were distinguished from other click types by listening and visual inspection of waveform on Audacity 2.0.5 software. Then, Rainbow Click software was used to individually mark each distinguishable coda, and to measure inter-click intervals (ICIs). Codas were categorized based on the number of clicks in the coda and the structure (*i.e.* temporal pattern or rhythm) of the clicks. Each coda was then represented by its ICIs, using absolute time intervals (Absolute ICI), and its total duration. The time at the positive peak of each coda click waveform was measured to determine the start time and ICIs of the coda (ICI1 is the time interval between the first and the second click, ICI2 is the time interval between the second and third click, and so on). Since codas have a degree of variation that makes it difficult to draw distinct boundaries between patterns, automated sorting methodologies were tested to classify coda into types. kmeans cluster analysis on the Euclidean distances between ICI vectors of codas with the same number of clicks was run (for details, see Rendell and Whitehead, 2004). The Calinski Harabasz index (Calinski and Harabasz, 1974), Duda and Hart's (Duda and Hart, 1973) ratio criterion and average silhouette width were applied to help determining the number of clusters to be used in cluster analysis. These automated methodologies, however, resulted to be inappropriate to sort our data, with outputs containing no consistent clustering. This is analogous to Drouot et al.

(2004c) outcome on 751 codas recorded in the Mediterranean Sea, possibly highlighting less differences between ICIs of codas with the same number of click than expected. It was therefore decided to base the coda classification on pre-defined pattern categories, as described below. Initially, codas were visually and aurally classified by two observers. Repeatability coefficient (r) between observers, calculated as  $r = S^2A/(S^2 + S^2A)$  where S<sup>2</sup>A is the between group variance and  $S^2$  is the within group variance, was good (r=0.892). Later, codas with the same number of clicks were compared using principal component analysis (PCA) of ICIs and were then classified into different coda types with the PCA score for each coda (as Oliveira et al, 2016). The observer classification was confirmed by the PCA classification, except for rare codas, where the PCA was not able to recognize their distinct ICIs. Therefore, a combination of the PCA classification with observer classification for the rare codas was used for the subsequent analysis. Coda types were given names based on the patterning of the clicks following previous nomenclature [Weilgart and Whitehead, 1997; Rendell and Whitehead, 2003b; Schultz et al., 2011; see also Apple, 2002 for *variable* codas). Codas with similar ICIs were designated by the number of clicks followed by a "R", those having a long interval used a "+" to indicate the gap (e.g. 2+1 indicates a longer gap before the 3<sup>rd</sup> click than that between the first 2 clicks), and codas with variable ICIs containing unevenly-spaced but 'rhythmic' clicks were labelled as "V". Because of the frequency of codas with progressively increasing ICIs, a fourth category based on this structure was added in this study and designated by the number of clicks followed by a "P" (see also Frantzis and Alexiadou, 2008). Rare long coda types (>8 clicks; <0.05% of all codas recorded) were excluded from the analysis. The number of clicks in each coda and overall repertoire (proportion of each coda type relative to the total), as well as coda rate, were analyzed in different sperm whale encounter type (CL=cluster, SI=solitary individual; SU=social unit). Kruskal-Wallis tests and multiple analysis of variance (MANOVA) in multivariate generalized linear model (GLM) were applied to examine differences in ICIs and total duration of codas with the same number of clicks between encounter types, with Hotelling's Trace test, Wilk's Lambda test, and Pillai's Trace test involved as significant tests. Of the three, Pillai's Trace is considered the most robust (i.e., least sensitive to departures from the assumptions; Anderson, 2003); thus, here we report results from this test only. All statistical analyses were performed with R 2.14.

#### 4.3.2 Results

We collected about 271 hours of acoustic recordings during 52 encounters with different sperm whale clusters (n=35), social units (n=6), as well as solitary individuals (n=11), in the water off Ischia Island over 2004-2015 period. Codas were most often produced when whales were socializing at the surface (about 75% of the recording time) and to a lesser extent during dives. A total of 3,598 codas (14,102 clicks) ranging from 3 to 8 clicks were identified. The majority of the recorded codas was class 4-click (75%; n=2,695), followed by 3-click (18%; n=640) and 5-click classes (5%; n=183). Considering that 3- and 4-click codas resulted the most frequent ones, comprising about 93% of the recorded codas, further investigations were conducted on this restricted dataset only (Table 17).

MANOVA in multivariate GLM indicated significant differences between Social Unit (SU) and other types of encounters, being all ICI values significantly lower in both 3-click (Pillai Trace value=0.229; F=13.7; df=3;639; p<0.0001; Figure 43) and 4-click codas (Pillai Trace value=0.414; F=415.2; df=4;2694; p<0.0001; Figure 44).

Table 17. General statistics of codas in 3- and 4-click classes in different encounter types.
ICIs' values are in seconds.

Coda Class 3-click		CLUSTER (CL	)	SOLITARY INDIVIDUALS (SI)			SOCIAL UNIT (SU)				
Statistics	ICI1	ICI2		ICI1	ICI2		ICI1	ICI2			
No. of observations	314	314		24	24		302	302			
Median	0,199	0,263		0,209	0,259		0,164	0,233			
Average	0,188	0,271		0,209	0,259		0,163	0,223			
Standard Deviation	0,064	0,067		0,024	0,021		0,075	0,101			
Coda Class 4-click	Coda Class 4-click										
Statistics	ICI1	ICI2	ICI3	ICI1	ICI2	ICI3	ICI1	ICI2	ICI3		
No. of observations	1467	1467	1467	105	105	105	1123	1123	1123		
Median	0,224	0,237	0,472	0,235	0,246	0,470	0,156	0,160	0,295		
Average	0,220	0,231	0,455	0,219	0,228	0,452	0,156	0,160	0,283		
Standard Deviation	0,038	0,043	0,082	0,063	0,063	0,120	0,059	0,060	0,091		



Figure 43. Absolute ICIs boxplot of 3-click codas in different encounter types.



Figure 44. Absolute ICIs boxplot of 4-click codas in different encounter types.

Since codas in SI encounters were rare (n=141, less than 4% of the total), the following analysis are mainly related to encounters with cluster of whales (CL) and social units (SU). To group patterns, ICI values of codas in CL and SU encounters within class 3-clicks and class 4-clicks were analyzed using principal component analysis (PCA). Figure 45 shows the scree plots related to class 3-clicks in CL and SU. The variability between first two PCA components has been estimated, with first component explaining about 61.5% and 87% of the variability in CL and SU, respectively.

Figure 46 shows the biplot of the coda types in class 3-click in CL and SU encountes. Two main clusters of coda types emerged (2+1 and 3R, with their fast and slow variants), confirming the manual classification.



*Figure 45. Scree plots explaining the variability of the first two PCA components of codas within class 3-clicks in CL and SU encounters.* 



*Figure 46. Biplots showing two main clusters of coda types within class 3-clicks (2+1 and 3R, with fast and slow variants) in both CL (on the left) and SU (on the right) encounters.* 

Figure 47 shows the scree plots related to class 4-clicks in CL and SU. The variability between first two PCA components has been estimated, with the first explaining 70.77% and the second 21.18% of the variability in CL encounters, and the first explaining 82.52% and the second 12.72% of the variability in SU encounters. Figure 48 illustrates the biplot of the coda types in class 4. Two main clusters of coda types emerged in CL (3+1 slow and fast variants), while 3 clusters appeared in SU encounters (3+1 fast and slow variants, and 4R), again confirming the manual classification.



*Figure 47. Scree plots explaining the variability of the first two PCA components of codas within class 4clicks in CL and SU encounters.* 



*Figure 48. Biplots showing two clusters of coda types within class 4-clicks in CL (3+1 slow and fast variants; panel a) and three clusters in SU (3+1 slow and fast variants, and 4R; panel b) encounters.* 

The complete coda repertoire (found with PCA and observer classification) comprised a number of 17 distinct patterns of "+", "R" and "P" coda types, and 25 different arrangements of "V" coda types (see Table 18).

One single type '3+1' and its 'slow' (*i.e.* codas with an average of about  $0.24\pm0.028$  sec for ICI1 and ICI2, and  $0.49\pm0.067$  for ICI3; see Figure 49) and 'fast' (*i.e.* codas with an average of about  $0.15\pm0.042$  sec for ICI1 and ICI2, and  $0.28\pm0.068$  for ICI3; see Figure 49) variants made up about 68% of the codas recorded (n=2446).

The next most common type, '2+1' and its variants (n=427), encapsulated about 12% of all codas. Regular pattern of clicks ("R") were observed in 7.2% of the recorded codas (n=261) in 3-4-5-click categories only, while progressive ones ("P") in 2.3% (n=82) in 4-5-6-7-click categories. Variable ("V") patterns included a number of 48 codas (1.3%) in all -click categories.

Table 18. Type of codas produced by sperm whales in different encounter types off Ischia Island.

Coda typ cla	e in -click sses	Cluster (CL) encounters (n=35)	Social Unit (SU) encounters (n=6)	Solitary Individual (SI) encounters (n=11)	Total
	2+1s	60	57	16	133
	2+1f	144	149	1	294
3-click	3R	109	91	7	207
	3V	1	5	0	6
	total	314	302	24	640
	3+1s	1304	145	88	1537
	3+1f	141	753	15	909
	1+2+1	10	9	0	19
	2+1+1	4	14	0	18
4-click	2+2	2	16	0	18
	4R	2	33	1	36
	4P	1	33	0	34
	4V	3	3	1	7
	total	1467	1123	105	2695
	4+1	23	65	7	95
	2+2+1	2	13	0	15
	3+1+1	3	8	0	11
r aliala	3+2	2	5	0	7
5-CHCK	5R	2	14	2	18
	5P	0	28	1	29
	5V	0	8	0	8
	total	32	141	10	183
	5+1	1	32	2	35
6 aliale	6P	0	13	0	13
0-CIICK	6V	2	4	0	6
	total	3	50	2	55
7-click	6+1	1	2	0	3
	7 <b>P</b>	0	6	0	6
	7V	0	5	0	5
	total	1	15	0	16
8-click	8V	1	8	0	9
Тс	otal	1818	1624	141	3598
Coda	a rate	0,22	1,32	0,05	



*Figure 49. Spectrogram and absolute ICIs boxplot of '3+1' coda 'slow' (a) and 'fast' (b) variants (all encounters).* 

Table 18 also shows the coda rate (n. of codas per minute) and the occurrence of codas within encounter types categorized in number of clicks. The coda rate was 1.32 for Social Units (SU), 0.22 for Clusters (CL), and 0.05 for Solitary Individuals (SI). Codas repertoire in SU encounters included all categorized patterns, while codas in CL and SI were less differentiated. About 45.5% (n=1,624) of the codas were recorded during 6 encounters with two different SU (1 in 2007, 2 in 2009, 1 in 2011, 1 in 2013 and 1 in 2015; see Table 10 in paragraph 3.5.2 for details), while 50.6 % (n=1,818 codas in 35 encounters) and 3.9% (n=141 in 11 encounters) were listed in encounters with CL and SI respectively. The SU1 sighting in 2007 (group size=8) was characterized by the presence of three individuals (possibly males associated to the SU1) other than the stable group of five whales belonging to the SU1. The coda rate in this encounter was quite low (0.40 codas per minute) but all coda types were recorded. Some important changes in the structure of the SU1 occurred in 2009 (group size=7, both sightings), when one calf and one neonate were observed within the group of five (no other whales were detected associated to the unit). The codas rate was rather high in both encounters, with a value of about 2 codas per minute. The repertoire was highly differentiated and dominated by the 3+1 'fast' variant. In the encounter with SU1 in 2011 (group size=8), the unit was composed by the stable group of five and only one of the two calves observed in 2009, plus other two individuals (possibly males associated to the SU1). The codas rate was higher than the other encounters (about 2.3 codas per minute), again with a well differentiated repertoire dominated by the 3+1 'fast' variant. In the last encounter with SU1 in 2013 (group size=7) the unit comprised again the stable group of five individuals, with one additional animal of unknown sex and one possible male; the immature observed in 2009 and 2011 was no longer present and possibly he left the unit at the age of 4-6. The coda rate was 0.27 codas per minute. Finally, a likely new social unit was seen in 2015 (named SU2; Table 8), including three possible adult females and two immatures. The coda rate in this unique encounter was 0.13 codas per minute.

Coda rate was found not related to group size in CL encounters [average group size:  $3.4\pm0.23$  (range 2-7) respectively; Spearman rank correlation test r=-0.4698 in CL].

A similarity between encounters emerged in the proportion of coda types within 3-click category, with '2+1' variant recorded over 62% in all encounter types and '3R' one reached over 30% in SU and CL, and 18% in SI. Within 4-click category, '3+1' fast variant represented about 75% in SU, while '3+1' slow one was the most frequent coda type in CL (92%) and SI (84% for both encounter types). Overall, codas with many clicks were less common than those with a few clicks in all encounters.

#### 4.3.3 Discussion

The variation in vocal dialects of codas is a nongenetic aspect of population structure in sperm whales (Whitehead *et al.*, 1998; Rendell *et al.*, 2012). These dialects can divide populations in sympatry (Rendell and Whitehead, 2003a), and there are some types of codas that appear to mark or delineate discrete populations (Gero *et al.*, 2016). Every study published to date agrees that vocal dialects in the Mediterranean are distinctive. These studies give the impression that the coda repertoire of Mediterranean sperm whales is almost completely dominated by a single type (*e.g.* Pavan *et al.*, 2000; Drouot *et al.* 2004c). This is very unusual compared to every other study published from recordings made in other regions that report a much higher diversity (Weilgart and Whitehead, 1993; Rendell and Whitehead, 2003a; Gero *et al.*, 2016).

#### Comparison with previous studies in the Mediterranean Sea and other regions

It has been suggested that the coda repertoire can present geographical variation and be regionally specific (Watkins *et al.*, 1985; Gordon, 1987a; Weilgart and Whitehead, 1997; Rendell and Whitehead, 2003a; Rendell and Whitehead, 2005). It has also been shown that genetically related individuals share similar group-specific coda dialects (Whitehead *et al.*, 1998), with little relationship with geography (Rendell *et al.*, 2012). Therefore, the identification of the coda repertoire from sperm whales in a given area can provide information about group vocal behavior, group affiliation and group structure (Whitehead, 2003).

In this study, different encounters types showed distinct vocal repertoires, but all were substantially dominated by the '3+1' and its 'slow' and 'fast' variants (just over 70% of all codas) and, to a lesser extent, by 2+1 coda types. This allowed us to assign animals in social units, bachelor groups, clusters and solitary individuals to '3+1 Mediterranean vocal group' based on the production frequency of this coda type, also highlighting a possible regional variation in coda repertoire in the Tyrrhenian basin of the Mediterranean Sea. Previous studies suggest that the single 3+1 coda pattern predominate in the Mediterranean Sea, with a mean duration of 1.051 ms (SD=42.6; n=44; see Borsani and Pavan, 1994) and some variations in length [i.e. 'short codas' of 486 ms (SD=15.6); see Pavan et al., 1996]. Drouot and Gannier (1999) identified 86 codas, all contained either three, four, five or seven clicks with variable spacing, of six distinct types (three in the Ionian Sea, three in the Tyrrhenian Sea). In the Ionian Sea, the '3+1' type was 76.1% of the dataset, while in the Tyrrhenian Sea it represented a lower percentage (33.3%). Pavan and colleagues (2000) measured 138 codas from different locations in the Mediterranean Sea (Ligurian, Tyrrhenian and western Ionian Seas) over a 12-year period. Almost all codas (97.1%) matched a well defined '3+1' click pattern (as evidenced by the normalized analysis of the ICI intervals) such as the one described in this study and two 'miscellaneous' codas matched a 5-click pattern. In a later study, Drouot and colleagues (2004c) reported a larger study in both Tyrrhenian, Ionian and South Western (Balearic Islands) regions in which 751 codas were identified. The codas ranged in length from three to eleven clicks with 4-click codas being the most common (mainly 3+1, predominant in coda repertoires of the Tyrrhenian Sea but poorly represented in the recordings from the Ionian Sea). These authors recognized that most recording sequences (from 200 ms to 600 ms duration) were similar to the 'short coda' previously recorded by Pavan and colleagues (1996), although a great deal of variation was observed. All these studies, however, reported a very low number of codas in the Tyrrhenian Sea (ranging from 9 in Pavan et al., 2000 to 45 in Drouot et al., 2004c) and few or no information was provided on the composition of the encountered groups. This makes very difficult a sound comparison with this study, where data on the acoustic repertoire (consisting of 3,598 codas) in diverse aggregations of both sexes was analyzed.

A comparison between coda repertoires identified in various parts of the world (Gulf of Mexico, Caribbean, South Pacific, and the Mediterranean) reveals more differences than similarities between the Mediterranean and the other locations and depicts the obvious differences in the most commonly occurring coda type between the Mediterranean and the other study locations. Studies from other regions have reported coda repertoires that have one or two major types [for example, Gero *et al.* (2016) showed that a single 1+1+3 type accounted for 39% of the codas recorded off Dominica] but they do not dominate the repertoires in the same way as the 3+1 does in the Mediterranean. Furthermore, while social unit and other group types in this study can be statistically distinguished based on 3-click and 4-click coda repertoire (and their ICIs),

the preponderance of 3+1 pattern suggests that all of the groups studied off Ischia Island are from the same vocal clan, in the sense that the term is used for the Pacific. Although some coda patterns are common to those of sperm whales in other oceans, it was proposed that the species in the Mediterranean has a coda repertoire, in terms of frequency, that is fairly distinct from other regions. Several authors have suggested that geographical variations might exist in coda repertoire (Gordon 1987a; Borsani and Pavan 1994), whereas genetic studies supported that similarities in coda repertoire might result from maternal transmission of the coda repertoire through generations (Whitehead *et al.*, 1998). Since coda repertoires are almost certainly acquired by cultural transmission (Rendell *et al.*, 2012), this suggests that cultural evolutionary processes may have affected coda dialects differently in the Mediterranean compared to other regions. Differentiation in the Mediterranean dialect might reveal a restricted exchange between groups of females and their offspring living in the Mediterranean Sea and those of the adjacent ocean. Genetic studies tend to confirm this hypothesis, as sperm whales living in the Mediterranean Sea appear to constitute a distinct maternal entity from those of the adjacent North Atlantic Ocean.

#### Coda repertoire in different SU encounters

Sociality is vital to the way sperm whales live. There is a wealth of studies to support the idea that complexity in the type of social interactions drives communicative complexity (Wilkinson *et al.*, 2013), in particular vocal communication, among a wide variety of species (Whitehead, 1996a; Tyack, 1999; McComb and Semple, 2005; Gero *et al.*, 2009). The 'social complexity hypothesis' posits that groups with complex social systems, like sperm whale, require more complex communicative signals to regulate both flexible patterns of interaction and relations among group members (individuals frequently interact in many different contexts with different individuals, and often repeatedly interact with many of the same individuals in networks over time; Wilkinson *et al.*, 2013).

In this study, the codas repertoire in SU context – dominated by 3+1 'fast' variant – was complex and highly differentiated, comprising all coda types. These results seem to support findings by Drouot and colleagues (2004c), highlighting that SU may articulate a wider coda repertoire than previously assumed in the Mediterranean Sea. Some authors (Whitehead and Weilgart, 1991; Marcoux *et al.*, 2006) have shown that an extensive coda repertoire is associated with the presence of tight groups at the surface, or close to it, and occurred particularly as exchanges or 'conversations' between whales that are close together and often maneuvering about one another (Watkins and Schevill, 1977; Weilgart and Whitehead, 1993). Furthermore, given that dependent calves in social units do not make deep dives with their mothers, unit members provide alloparental care in the form of babysitting (which acts as anti-predator vigilance) and, in some units, allonursing (Whiteheaed, 1996a; Gero et al., 2009). Pressures that can have implications for fitness, like predation, may therefore explain specific memberships and bonds between sperm whale individuals - even based on coda vocalizations used for individual recognition - that allow for alloparenting while mothers dive deeply in search of food. Our data collected in different contexts on a single SU seem to support the idea that codas have an important communication function amongst adult females, perhaps most plausibly in order to establish and/or maintain social bonds (Shultz *et al.*, 2011), and may be used to signal identity either to their age-class (*i.e.* mother or calf; females can and do switch repertoires depending on their reproductive status; Shultz et al., 2011) or individually (Watkins and Schevill, 1977; Watkins et al., 1985; Tyack 1999). Living in cooperative, stable social units in

which individuals have preferred associates creates a selective environment which favors individual recognition (Crowley et al., 1996; Tibbetts and Dale, 2007). The variability in coda repertoire observed here would suggest that the whales are likely able to distinguish among individuals, but this has not been explicitly tested in this study. Individual recognition is thought to be a crucial ability facilitating the evolution of animal societies (Townsend *et al.*, 2012) and this explains why individually distinctive vocal features have been found in many social mammals. In the same sperm whale social unit studied by Schulz and colleagues (2011), Antunes and colleagues (2011) found individually-specific characteristics in the '5R' coda type which were robust across recording days, but not in the other most common types in the unit's repertoire, suggesting that sperm whales have specific cues to identify not only themselves as individuals using a specific coda type, but also their social roles by varying their coda repertoire when rearing a dependent calf. We were not able to assess if mothers and their dependent calves may have distinctive coda repertoires compared with the other adult and subadult unit members as a result of a need for individual recognition; however, given the complexity of social interactions between individuals within units, and the possibility that sperm whales may also use codas to mark for higher levels of social structure, variation in coda usage and production at the level of the individual demands closer examination to understand how the variation at higher levels arises.

#### *Coda repertoire in CL and SI encounters*

The repertoire in CL encounters – dominated by 3+1 'slow' variant – comprised 17 distinct patterns of coda types over a total of 20, and a number of 18 over a total of 25 irregular, 'variable' coda types emitted both at surface or during dive cycles. Although Pavan and colleagues (2000) speculated that males may have smaller repertoires than females, possibly reflecting their less social life once they leave their maternal groups, the repertoire here reported for CL is as rich as those recorded from males in the Hellenic trench (Frantzis and Alexiadou, 2008), and socializing social units in both the eastern (Drouot, 2003; Frantzis and Alexiadou, unpublished data) and the western (Drouot, 2003; Nuuttila, 2004) Mediterranean basins (24 and 25 coda types, respectively), or the oceans (for a review see Weir, 2003). In our study, the diversity observed between SU and CL might be associated not only to the gender /maturation status of the emitting whales and the possible lack of relationship with the SU (immature males use a similar coda repertoire to that of their natal unit; Schultz *et al.*, 2011) but also to the different function of codas in different context (socializing/foraging) and place (at surface and/or in the water column). As discussed, codas in SU at surface are thought to be signals primarily directed to other unit members (to indicate affiliation and maintain social bonds; Shultz *et al.*, 2008), also functioning to signal unit membership (Shultz *et al.*, 2011), and associated with cooperation for both alloparenting (Whitehead, 1996a; Gero et al., 2009) and communal defense (Pitman et al., 2001). We speculate that codas in CL at surface may be similar in function to those of SU, allowing possible maturing males to affiliate and maintain social bonds. This hypothesis seems to be supported by the observation of long-term relationships between some immature males in bachelor school around Ischia Island (Pace et al., 2014). Bachelor groups in sperm whale had previously been described as 'loose, apparently unstructured, relationships among non-breeding males' (Letteval et al., 2002) and socialising behaviour at surface was considered 'exceptionally rare among these males' (Whitehead et al, 1992; Jaquet et al., 2000) and 'when it happened, it was usually in cluster of two animals and for no more than few hours' (Whitehead, 2006). Our observations, in contrast, suggest that

immature individuals in bachelor groups can form long-term associations (Pace *et al.*, 2014) and that this relationship may be maintained at least for 2-3 years by codas exchange, possibly carrying different or more complete information than just presence. We do not know if these males are related to each other, or share group-specific feeding specializations (Whitehead and Lusseau, 2012). Young males may benefit in several ways from belonging to stable all-male groups after they leave their maternal SU before reaching a length of 9-10 m. They may feed cooperatively, sharing information on the location of prey patches for example; group living may also allow individuals to establish breeding alliances and to practice fighting skills (Chiyo et al., 2011). In this frame, coda patterns of Mediterranean male sperm whales – apparently different from male conspecifics in both the Atlantic and Pacific oceans – seem to play a particular role at least during their deep feeding dives (Frantzis and Alexiadou, 2008), even if the exact message that is communicated through the dive cycle codas remains unknown. Through the specific characteristics of their clicks (Madsen et al., 2002a,b), dive cycle codas may help males identify one another and remain in close contact, or display their size, assess one another, and define the limits of their moving feeding territory acoustically (Pavan *et al.*, 2000). Therefore, they may serve competition, coordination, or both depending on the conspecific to whom they are addressed (Frantzis and Alexiadou, 2008). In our study, visual contact with one another and physical interaction between whales in CL encounter were less probably to occur due to the physical distance between individuals. Codas may therefore serve all functions previously listed for SU and the diversity in patterns may be associated to the need of individual recognition within the CL. The requirement for the whales in CL to localize, reunite with, and transfer information to surrounding animals necessitates an obvious means of individual identification, or at least distinctive features in the communication repertoire. What is more unusual is the possibility that flexibility in the coda repertoires of sperm whales permits individuals to switch between repertoires depending on the context and need to broadcast individual and/or group identity (Shultz et al., 2011).

We recorded 141 codas – again dominated by 3+1 'slow' variant – from solitary sperm whales individuals on 11 occasions. Basing on the prevalence of this coda type, we speculate that all recorded animals were males. Single male (but also female) sperm whales when alone are usually silent while resting at the surface between dives (Pavan *et al.*, 2000; Madsen *et al.*, 2002b; Whitehead, 2003; Teloni, 2005). As already reported by Frantzis and Alexiadou (2008), this results may be related to the presence of the research platform as a response to possible disturbing actions. Codas in this context may be an alarm produced by single whales at surface when they are distressed, to contribute to controlling and mitigating the disturbance induced by human activities. However, we cannot exclude that other whales were present in the area although the lack of acoustic and/or visual detections.

#### Differences between male and female social aggregations

Results here reported show that: a) sperm whale individuals in diverse social aggregations regularly emit codas off Ischia Island; b) codas are mainly produced in SU, with complex and well-differentiated patterns, high repetition rate and shorter duration than in other encounter types (2+1 and 3+1 coda types); c) coda-type repertoire of possible male groups (CL) is ample and diversified too, with lower repetition rate and longer duration than in SU; d) codas may serve diverse functions within different encounter types.

Effective communication between conspecifics is essential to fitness at both the individual and species level. Sex differences in auditory communication are prevalent in the animal kingdom

(Kelley and Bass, 2010) and to date they have been largely identified in the context of attracting conspecific mating partners and/or defending territories, as well as of connecting dams and dependents within parent/offspring unit. The existence of gender differences is often reported also in the human speech articulation and language processing, ranging from the acoustic parameters of frequency and pitch to the speed of vocal production (Simpson, 2009). Bowers and colleagues (2013) postulated that different levels of Foxp2 - a member of the forkhead family of transcription factors with a highly conserved amino acid and DNA sequence as well as conserved distribution in the brain across a wide range of species that have some component of vocal communication (Fisher and Scharff, 2009) - in males and females are one avenue by which quantitative and qualitative sex differences in communication are initiated and/or maintained in the mammals' developing brain. To date, the origins and significance of said differences are highly controversial (for a review see Wallentin, 2009). While the findings revealed herein may expand the knowledge base regarding coda repertoires, sex differences and general acoustic behavior of sperm whale groups in the Mediterranean Sea, further research is called for to supplement the existing data.

### 4.4 Unusual vacalizations: trumpets

Sperm whales are able to produce non-impulsive vocalizations apart from clicks. So-called trumpets are low-frequency tonal sounds consisting of units arranged in short sequences. Each unit, lasting around 0.2 s, has an amplitude modulated wave-form with decaying amplitude composed of two frequency components (at 500 Hz and 3 kHz), and harmonics with upsweeps (Teloni *et al.*, 2005). The number of units ranges from 2 to 15, and the entire sequence in a trumpet takes between 0.6 s to 3.5 s (Teloni et al., 2005). Gordon (1987) made the earliest reference of these vocalizations: "This sound, like a muffled trumpeting call of an elephant, was recorded very clearly on three occasions after the fluking-up of one particular whale and before it started clicking". Then, few research groups (Goold, 1999; Priano et al., 2001; Drouot, 2003; Teloni *et al.*, 2005) have recorded trumpet sounds occasionally. Results by Teloni *et al.* (2005) showed that trumpets were produced by the same individual animal at the start of the descendent phase of a dive (at shallow depth) before the onset of usual clicks, and that the time interval from the trumpet to the first usual click averaged 28 s. Teloni (2005) also reported that in some instances the trumpet was preceeded by codas, explaining this as a preparation for the following click emissions. Trumpets are thought to be by-products of the click generation mechanism when the sperm whale nasal complex is adjusted to switch from a configuration appropriate to respiration and codas' production to one suitable for echolocation clicks (Teloni et al., 2005), but the function of these tonal signals remains uncertain. The low source level and the apparent lack of directionality seem to exclude echolocation, and the possible trumpets' communicative role was not clearly inferred from available data. This part of the study aimed at defining a) structural characteristics of trumpets in Mediterranean sperm whales on a larger sample and b) behavioural context in which they are produced. To date, only few information is available on trumpets and behaviors associated to these sounds.

#### 4.4.1 Methods

The recordings have been analyzed with SeaPro 2.0j software (Sound Emission Analyser Professional; Pavan *et al.*, 1997) by using an FFT of 1024 points with hanning windows sized 256 or 512 samples depending on the quality of the recordings. The scan step was set to allow an overlap of 75% or more.

Since trumpets appear to be tonal sounds composed of a series of units in short sequences, the following paramethers were measured per each trumpet: total duration, number of units, duration per unit, min and max fundamental frequency per unit, difference of final frequency between the first and the last unit. A PCA analysis was performed to assess the parameters that contribute more to trumpets discrimination.

Some recordings had a high pass filter that attenuated or canceled the lower harmonics. Whenever possible, the fundamental frequency was measured directly, otherwise it was estimated by measuring the harmonic interval. Measures in the frequency-time plane have been made with a cursor moved on the spectrogram image.

The identity and the size of the emitting whale were assessed whenever possible through photoidentification and IPI (inter-pulse interval) estimates. Both Gordon (1991) (1) and Growcott and colleagues' (2011) (2) formulas from the IPI values were applied to acoustically estimate the Total Length (TL) of the whales (see Chapter 5 for details):

> (1) TL=4.833+1.453\*IPI-0.001\*IPI<sup>2</sup> (2) TL=1.258\*IPI+5.736

Details on the contex of the trumpets' production were also measured and provided as: DT interval (the time in seconds from the fluke-up to the onset of the trumpet), TFC interval (the distance in seconds from the end of the trumpet to the first usual click of the dive), the vocalization sequence (the onset order of different vocalizations, including trumpets, after the fluke-up), the estimated group size (the number of whales visually or acoustically assessed during the encounter).

The Ordinary Least Squres (OLS) regression procedure was used to evaluate the relationship between the total duration and the number of units in a trumpet, as well as the relationship between the size of the emitting whales and 1) the trumpets' total duration, 2) the number of units in a trumpet, 3) the unit's duration and 4) the time interval between units.

#### 4.4.2 Results

A total number of 29 trumpet sounds was recorded and analysed in this study (Table 19). All trumpets were recorded during visual/acoustic encounters with more than one whale. Trumpets appear to be tonal sounds composed of a series of units in short sequences. The total duration of the series of units in a trumpet had an average of 2.33 s (SE=0.17; CV=0.41), lasting between 1.12 and 4.35 s, per a mean number of units of 10, ranging from 5 to 18. The OLS regression procedure showed that trumpets' total duration was strongly related to the number of units ( $R^2$ =0.943; t=22.33; p<0.0001; Figure 50). Table 19. List of the sperm whale trumpets used in the analysis. The total duration is the lenght in seconds of each trumpet; the number of sound units is the sum of the pulses in each trumpet; DT interval represents the time in seconds from the fluke-up to the onset of the trumpet; TFC interval is the distance in seconds from the end of the trumpet to the first usual click of the dive; the vocalization sequence indicate the onset order of different vocalizations (including trumpets) after the dive; the PHID individual indicate the name of the whale producing each trumpet; the IPI is the Inter Pulse Interval measured in the clicks emitted after the trumpet (or in other clicks of the same identified animal), used to estimate the size of the emitting whale; the estimated group size is the number of whales visually or acoustically assessed.

Trumpet			Total	Number	DT	TFC		PHID			Estimated
number	Date	Time	duration (s)	of sound units	interval (s)	interval (s)	Vocalization sequence after fluke-up		Sex	IPI (ms)	group size
ODO_001	19/09/2006	10:31:19	3.97	17	78	4	Dive (fluke-up)→First Clicks→Trumpet→First clicks	Brunone	Male	4,4178	2
ODO_002	20/11/2007	17:44:13	1.30	6	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	4
ODO_003	21/06/2008	19:01:07	1.60	7	133	11	Dive (fluke-up)→Trumpet→First clicks	Leonidas	n.d.	n.d.	3
ODO_004	25/06/2008	19:43:51	1.70	6	11	6	Dive (fluke-up)→Trumpet→First clicks	n.d.	n.d.	n.d.	4
ODO_005	01/07/2008	15:02:42	1.16	5	47	22	Dive (fluke-up)→Trumpet→Codas→First clicks	Crescenzo	Male	4,8937	2
ODO_006	02/08/2008	14:06:05	2.28	9	23	13	Dive (fluke-up)→Trumpet→First clicks	Nettuno	Male	5,2405	4
ODO_007	02/08/2008	14:49:42	1.67	7	10	5	Dive (fluke-up)→Trumpet→First clicks	Mark	Male	5,008	4
ODO_008	02/08/2008	16:35:11	1.68	7	n.d.	16	Dive (fluke-up)→Trumpet→First clicks	n.d.	n.d.	n.d.	4
ODO_009	12/08/2008	15:18:38	1.60	7	44	16	Dive (fluke-up)→Trumpet→1 Isolated Click→First clicks	Crescenzo	Male	4,8937	2
ODO_010	14/08/2008	11:13:15	2.55	11	20	9	Dive (fluke-up)→Trumpet→4 Isolated Clicks→First clicks	Mark	Male	5,008	4
ODO_011	14/08/2008	13:52:28	1.12	5	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	4
ODO_012	14/08/2008	17:47:14	1.70	7	51	51	Dive (fluke-up) $\rightarrow$ Trumpet $\rightarrow$ Codas $\rightarrow$ Fast clicks/Chirrup $\rightarrow$ 2 Isolated Clicks $\rightarrow$ First clicks	Crescenzo	Male	4,8937	4
ODO_013	08/10/2008	12:10:02	2.32	9	52	8	Dive (fluke-up)→Trumpet→First clicks	Nettuno	Male	5,2405	5
ODO_014	12/05/2009	12:57:25	1.75	8	28	10	Dive (fluke-up)→Trumpet→First clicks	Giasone	Male	5,6032	2
ODO_015	12/05/2009	13:56:57	1.97	9	4	14	Dive (fluke-up)→Trumpet→1 Isolated Click→First clicks	Giasone	Male	5,6032	2
ODO_016	23/06/2009	15:38:27	1.86	8	93	7	Dive (fluke-up)→First Clicks→Trumpet→First clicks	Brunone	Male	4,7652	2
ODO_017	05/08/2009	11:07:55	3.26	14	50	12	Dive (fluke-up)→Trumpet→1 Isolated Click→First clicks	Brunone	Male	4,7652	4
ODO_018	11/08/2009	15:57:21	3.99	16	57	42	Dive (fluke-up)→Trumpet→Codas→Fast clicks/Chirrup→First clicks	Brunone	Male	4,7652	2
ODO_019	17/04/2010	13:19:54	2.59	11	190	3	Dive (fluke-up)→First Clicks→Trumpet→5 Isolated Clicks→First clicks	Aletes	Male	4,8591	2
ODO_020	10/07/2010	17:45:22	1.68	7	70	n.a.	Dive (fluke-up)→Trumpet→Silence	Aletes	Male	4,8591	3
ODO_021	10/07/2010	18:06:53	2.48	10	14	13	Dive (fluke-up)→Trumpet→Codas→Fast clicks/Chirrup→First clicks	Aletes	Male	4,8591	3
ODO_022	10/07/2010	18:16:36	2.74	13	69	n.a.	Dive (fluke-up)→Coda→Trumpet→Fast clicks/Chirrup	Aletes	Male	4,8591	3
ODO_023	20/07/2012	17:47:03	2.36	10	36	14	Dive (fluke-up)→Trumpet→First clicks	Nettuno	Male	5,5842	3
ODO_024	28/08/2014	12:22:32	4.02	17	3	10	Dive (fluke-up)→Trumpet→2 Isolated Clicks→First clicks	Andromeda	n.d.	4,0899	2
ODO_025	28/08/2014	13:08:59	4.35	18	5	11	Dive (fluke-up)→Trumpet→4 Isolated Clicks→First clicks	Andromeda	n.d.	4,0899	2
ODO_026	09/07/2015	14:08:42	1.15	5	33	7	Dive (fluke-up)→Trumpet→First clicks	Talete	n.d.	4,6353	3+
ODO_027	11/07/2015	13:46:51	2.04	10	58	29	Dive (fluke-up)→Trumpet→Codas→3 Isolated Clicks→First clicks	Talete	n.d.	4,6353	3+
ODO_028	24/06/2016	12:12:34	3.27	14	6	183	$Dive (fluke-up) \rightarrow Trumpet \rightarrow Fast clicks/Chirrup \rightarrow Codas \rightarrow 5 \ Isolated \ Clicks \rightarrow Fast clicks/Chirrup \rightarrow First clicks/Chirrup \rightarrow Fast clic$	Talete	n.d.	4,7084	3+
ODO_029	24/06/2016	13:55:09	3.52	18	4	19	Dive (fluke-up)→Trumpet→2 Isolated Clicks→First clicks	Talete	n.d.	4,7084	3+



Figure 50. Linear regression of the trumpets' total duration vs. number of units.

The initial fundamental frequency of each trumpet averaged 438.52 Hz (SE=31.21; CV=0.32), ranging from 260 to 859 Hz, whereas the final one averaged 690.54 (SE=31.97; CV=0.31) and ranged between 510 and 1001 Hz, regularly decreasing at the end of each trumpet. Each unit lasted an average of 0.12 s (SE=0.00; CV=0.01; min=0.04; max=0.24), with a quite stable mean time interval between the onset of each unit of 0.25 s (SE=0.00; CV=0.00; min=0.09; max=0.34). The initial fundamental frequency of each unit averaged 352 Hz (SE=14.84;

CV=0.19), ranging from 247 to 494 Hz, whereas the final one averaged 578.6 (SE=23.620; CV=0.18) and ranged between 420 and 892 Hz, regularly increasing at the end of each unit. All trumpets were recorded at the beginning of a new dive after the fluke-up, following a period at surface. However, one individual (Aletes) showed an unusual behavior in 2010, remaining in a shallow dive condition and producing three trumpets (ODO\_020-021-022) in about 30 minutes. The time interval from the beginning of a dive and the trumpet (DT interval; Table 19) had an average of 45.73 s (SE = 8.50; CV = 0.94), ranging from 3 s to 190 s. The time interval from the trumpet to the onset of first usual clicks (TFC interval; Table 19) averaged 21.40 s (SE=7.10; CV=1.65), ranging from 3 to 183 s.

In 25 out of 29 trumpets, the identity of 9 different emitting whales was assessed through photoidentification, with a number of 6 positively sexed as males. The total length (TL) of these individuals, acoustically estimated through IPIs using Gordons' (1991) formula, ranged from 10.75 m to 12.94 m, and from 10.88 m to 12.78 m using Growcott et al. (2011) formula, suggesting that perhaps all animals were maturing/matures males. The OLS regression procedure showed that no significant relationships between the size of the emitting whales and the trumpets' total duration ( $R^2=0.395$ ; t =-0.808; p=0.130), number of units in a trumpet  $(R^2=0.292; t=-0.140; p=0.209)$ , unit's duration  $(R^2=0.029; t=0.387; p=0.714)$  and time interval between units (R<sup>2</sup>=0.027; t=0.376; p=0.722) were found. Two of the photo-identified male individuals generating trumpets in 2006 (Brunone) and 2008 (Nettuno) respectively were 'recaptured' after 3 (Brunone in 2009) or 4 (Nettuno in 2012) years apart from the first recording, again producing trumpet sounds. Trumpets emission by the same whale over two consecutive years (2015-2016) was also documented for another identified individual (Talete). The total duration of the trumpets in 9 photo-identified whales is plotted in Figure 51. Three individuals showed very similar values, between 1 and 2 s, per a variable number of units (5-9) in each trumpet (Giasone, Crescenzo and Leonidas); four individuals (Mark, Nettuno, Aletes and Talete) presented trumpets with total duration between 2 and 3 s per 5-18 units, one (Brunone) between 3 and 4 s per 8-17 units, and one (Andromeda) over 4 s per 17-18 units (see also Table 19). The trumpets' total duration mainly depends on number of units (see Figure 50) and it seems the parameter that mainly contribute to the trumpet discrimination (Figure 52).



Figure 51. Boxplot of the averaged total duration of trumpets in photo-identified whales.

For 27 trumpets, out of a total of 29, it was possible to assess the vocalisation sequence after the fluke-up dive. The time interval from the trumpet to the onset of first usual clicks (TFC interval; see Table 19) averaged 14 s, ranging from 3 to 51 s. The time interval from the beginning of a dive and the trumpet (DT interval) had an average of 52 s, ranging from 3 s to 190 s.



*Figure 52. PCA analysis to show which parameters contributes more to trumpets discrimination. Duration strongly depends on the number of units.* 

In 9 cases, the emission of trumpet followed the dive (fluke-up), and first usual clicks (with an inter-click interval, ICI, of 0.5-2 s) followed the trumpet (Table 19). In 3 cases (ODO\_001-016-019), after the animal dove, first usual clicks were recorded, then a trumpet, followed again by usual clicks. On seven occasions (ODO\_005-012-018-021-022-027-028), the trumpet was preceded (n=1) or followed (n=6) by social vocalizations such as codas, and in one event (ODO\_020) the trumpet was followed by a complete silence period of about 15 minutes. In 11 cases (ODO\_009-010-012-015-017-019-024-025-027-028-029), the vocalization arrangement after the trumpet emission included click sequences made by 1-5 clicks with an inter-click interval (ICI) of 3-7 s (*i.e.* slow clicks; see Figure 53); after these sequences, the series of first usual clicks started.



Figure 53. A trumpet followed by 2 'isolated clicks' with long ICI, and the sequence of first usual clicks.

A pilot comparison of recorded whales to possibly associate trumpets from unknown individuals to photo-identified whales is shown in Figure 54. It plots the units' duration, the time interval between units, the minimum and final frequency. The combination of the tested paramethers seems to support the discrimination of the different emitting whales, with individual, recognizable peculiarities. However, this analysis is very preliminar and is worthy of further investigations as well as in-depth elaborations.



*Figure 54. Comparison of recorded whales to possibly associate trumpets from unknown individuals to photo-identified whales. a) unit duration; b) time interval between units; c) minimum and d) final frequency* 

#### 4.4.3 Discussion

This part of the thesis reported both the acoustic structure and the context in which sperm whale trumpets are emitted in the Mediterranean Sea, off Ischia Island. Trumpets seems to be relatively infrequent when compared to other vocalizations of the sperm whale in the Mediterranean Sea and reports of these vocalizations are rare in literature (Gordon, 1987; Goold, 1999; Drouot, 2003; Teloni, 2005). A possible reason is that trumpets are lower in amplitude than clicks, and therefore they are less detectable at distances where clicks are still audible (Teloni, 2005). These tonal sounds are produced at the beginning of a dive (just after the fluke-up), below the surface, with a well recognizable and stereotyped acoustic structure. Out of 80 whales tracked for more than two complete dives in the Tyrrhenian Sea off Ischia Island, only a number of 9 (11%) emitted trumpets, with only 5% of their dives effectively began with such a sound. This is a lower value than in Teloni (2005), which reported trumpets occurring in the 16% of the analysed dives. Teloni et al. (2005) also reported that trumpets are not generated by all whales, nor are they emitted in all dives by the same animal. In this study, photoidentification records made it possible to assign recordings of trumpets made in different years to the same whale in three cases. The trumpeting photo-identified individuals were Brunone (recorded in 2006 and 2009), Nettuno (recorded in 2009 and 2012) and Talete (recorded in 2015 and 2016). To our knowledge, this is the first time that trumpets produced by the same individuals have been documented across a wide time period, suggesting that this sounds may be a long-lasting component of the individual repertoire.

According to published literature (Gordon, 1987; Teloni *et al.*, 2005), trumpets are always emitted at the beginning of a dive, prior to the usual clicks. This was true for the majority of the trumpets analyzed in this study although, on three occasions, the sequence of usual clicks began

before the trumpet's emission. In our knowledge to date, this is the first time that an observation of this kind has been reported. Teloni (2005) illustrated that in some instances the trumpet was preceded by codas, as also observed in this study in one case. No mention in the literature was found of codas or other social vocalizations, such as fast and slow clicks, following the emission of the trumpet, as was reported here in seven circumstances.

It is known that sperm whale can change the acoustic characteristics of the sound generated in the nasal complex when switching between codas and echolocation clicks, two highly different click patterns in terms of directionality and acoustic output (Madesen et al., 2002a). Teloni and colleagues (2005) suggested that trumpets might be a by-product of airflow in the vocal tract of the sperm whale as it modifies the sound production apparatus from a configuration appropriate for respiration and codas, to one appropriate for sonar clicks. Our observations seem to add evidences of a more flexible scheme than this previously described, with trumpets that can be emitted both before and after the onset of either codas (and other social sounds) or usual clicks. Interestingly, one third of the trumpets analyzed were followed by short sequences of 1-5 slow clicks (sounds with a metallic and reverberant timbre; Gordon, 1987; Weilgart & Whitehead, 1988; Oliveira et al., 2013), a click type – only recorded in males – that has a possible long-range communicative function due to both the long inter-click interval and the waveform (Oliveira *et al.*, 2013), and may vary depending on the behavioural context they are produced (in presence of females or other males). In addition, the estimated length of the trumpeting whales, both in this study and in previously published papers (see Goold, 1999; Teloni et al., 2005), suggests that all the sampled animals were maturing/mature males. The type of aggregations observed during trumpets recordings in this study (bachelor groups and male clusters; Pace et al., 2014) seems to indicate that trumpet may be a type of sound of maturing/mature males, possibly having a social role in male-male context. To date, in literature as well as in our dataset, there are no records of trumpets in social units of female groups with calves/immature members, suggesting a potential sex asymmetry in the acoustic repertoire between males and females. Some acoustic signals can be sexually selected if they generate information about the signaller that enables the signaller or receivers to increase their success in the context of possible competition (Andersson, 1994; Espmark et al., 2000). The "frequency code" theory suggests that frequency characteristics of different vocal signals can simultaneously encode for static signaler attributes (size or sex) and dynamic information, such as motivation or emotional state (for a review, see Taylor and Reby, 2010; see also Dunlop, 2016, for humpback whale Megaptera novaeangliae). We are not aware if this hypothesis may find applications to sperm whale trumpets in combination with these isolated clicks, however, these results provide a basis to carry out more targeted research on the function of these sounds in sperm whales. While the new findings on trumpets presented here and the hypotheses suggested in this discussion are intriguing, the meaning and the function of these sounds, as well as the reasons behind the observed differences in some acoustical parameters between individuals, remain largely unknown and matter of speculations.

# **Chapter 5**

# Acoustically derived growth rates of sperm whales off Ischia Island



## **5.1 Introduction**

Body size, growth and age of individuals are key biological and ecological traits, and are intimately related to the physiology and genetics of an organism. Size can indicate age and physical maturity (Gaskin and Cawthorn, 1973), and different lengths, as well as their distributions and changes within a population, can be used to estimate its parameters (Waters and Whitehead, 1990) and to indicate the degree of depletion of a stock (highly exploited populations are likely to have older and thus fewer larger animals; Cooke and de la Mare, 1983). Furthermore, patterns of growth possibly provide a tool to understand ecological variances among populations, habitats and, in the case of sexually dimorphic species, between the sexes (Miller et al., 2013). The growth strategy of a species influences many fundamental aspects of its life-history, including survival, development, and reproduction (Vinicius and Mumby, 2013; Mumby et al., 2015). Animals can either grow indeterminately (throughout life), or grow determinately, ceasing at maturity. Mammalian growth has long been thought to be determinate (Charnov et al., 2001; Sebens, 1987), though some candidate species for indeterminate growth have been suggested in the literature (e.g. apes: Leight and Shea, 1995; elephant seals: Deutsch et al, 1994). Mammals range in size from minute shrews to gigantic whales (Evans et al, 2012) but by the time of adulthood, growth has generally reduced dramatically or ceased. This cessation or near cessation of growth does not occur abruptly, but rather is progressive: body growth is rapid in early life but then gradually slows, determining a decline in growth rate and thus imposing a limit on adult size (Lui and Baron 2011).

To answer to many of the most interesting questions related to the biology, ecology and sociality of species, individuals have to be measured repeatedly throughout their life-span lives, but this is not an easy task for cetacean species (Palomares et al., 2008). Given their adaptation to aquatic living, large size, elusivity, remoteness, and quite simply the logistics of measuring, sperm whales are among the most difficult animals to measure alive and have made obtaining accurate size measurements difficult. Moreover, how intraspecific variation in the body sizes of these animals relates to sex, population structure, the environment, and interactions with humans remains underappreciated (McClain et al., 2015). The largest known sperm whale individual was captured off the Kuril Islands in 1950 and measured 20.7 m in length (Carwardine, 1995). However, the jaw of the specimen in the Natural History Museum in London is supposed to belong to a 25.6 m long individual (Carwardine, 1995). Size data obtained for *P. macrocephalus* from the International Whaling Commission (IWC) whaling records (extending as far back as the 1880s) shows that the overall distribution of total lengths for sperm whale was right-skewed (Figure 55a), with some geographic differences (McClain et al., 2015). Individuals in the seas of the Southern Ocean and North Atlantic obtain larger mean lengths relative to individuals in other regions (Figure 55b). In the North Atlantic and Southern Hemisphere pelagic whaling, the differences in sizes only occur in males, while at South Georgia and South Shetlands both males and females are larger (McClain et al., 2015). In general, the total length differs between sexes, with males being larger than females [females stop growing at approximately 30 years of age and 10.9 m in length, while males continue growing until they are 50 years old and approximately 16 (Lockyer, 1981) - 18 m long (Berzin, 1971)]. McClain and colleagues (2015) also found a significant temporal decline in the sizes of both males and females for almost all investigated regions (Figure 55c). Declines may be due to heavy whaling on larger individuals, but may be also due to a shift from targeting only large lone males to more indiscriminate targeting of immature males and females, especially during the later period of Soviet whaling (about 1958-1973) when misreporting was common (Ivashchenko and Clapham, 2014). Nevertheless, whaling data have been useful in quantifying basic growth parameters of species (Kasuya, 1991). Whaling-derived information on length is not available for the Mediterranean Sea, where organised whaling targeting sperm whales never occurred (Notarbartolo di Sciara, 2014), with the only exception of the Strait of Gibraltar - largely on the Atlantic side - during the early to mid-20<sup>th</sup> century (Sanpera and Aguilar, 1992). Various photogrammetric approaches have been applied to the task of measuring free-ranging sperm whales (e.g. Gordon, 1991a; Dawson et al., 1995; Jaquet, 2006). More recently, new empirical relationships between the click Inter-Pulse Interval (IPI) and the sperm whale total body length was obtained combining a photogrammetric method and acoustic analysis (Growcott et al., 2011; Pierantonio et al., 2016). The measurement of individual whales via acoustics is conceivable because sperm whale clicks have a multiple pulse structure (Backus and Schevill, 1966). As reported in Chapter 2, Norris and Harvey (1972) postulated that this structure derives from a single impulsive sound produced by the *museau de singe* and reflected within the head of the whale. The time interval between these pulses represents the time taken for sound to travel the length of the spermaceti organ. Hence, the hypothesis predicts that due to allometric relationships between head size and whale length, IPI can be used to make measure estimates of whale length. By recording the same individuals over many years, it is possible to quantify their growth.



*Figure 55. Distribution of total length (a), boxplots of total length by region and sex (b), total length vs year by region for Physeter macrocephalus (source: McClain et al., 2015).* 

Clarke (1978b) measured the total length and spermaceti length in five whales and Gordon (1991a), using this information, found the following polynomial equation to fit its data on 11 individuals:

(1) TL=9.75-0.521\*SL+0.068\*SL<sup>2</sup>+0.057\*SL<sup>3</sup> (Gordon 1991a; modified from Clarke 1978b)

TL is the sperm whale total length (m) and SL is the sperm whale' spermaceti length. In the same paper, Gordon (1991a) calculated a new empirically derived relationship between IPI and body length to obtain a more accurate and reliable equation. In this approach, Gordon (1991a) - and later Rhinelander and Dawson (2004), Growcott and colleagues (2011), and Pierantonio and colleagues (2016) - used photogrammetric techniques to measure whale length and quantified the relationship between photogrammetrically measured length and IPI. Gordon (1991a) derived this relationship from mostly juvenile and female whales, Rhinelander and Dawson (2004), and Pierantonio and colleagues (2016), measured maturing and mature male sperm whales. Derived allometric equations were:

- (2) TL=4.833+1.453\*IPI-0.001\*IPI<sup>2</sup> (Gordon, 1991a)
- (3) TL=1.257\*IPI+5.736 (Growcott *et al.*, 2011)
- (4) TL=1.417\*IPI+4.632 (Pierantonio *et al.*, 2016)

TL is the sperm whale total length (m), IPI is the interpulse interval in msec, SL is the sperm whale' spermaceti length (calculated as IPI\*SO/2, where SO is 1430 m/s, *i.e.* sound speed in the spermaceti organ; Goold, 1996). Gordon's formula seems to be highly reliable for measurement of sperm whales with a length  $\leq 11$  m (Madsen *et al.*, 2002a,b; Growcott *et al.*, 2011; Mathias *et al.*, 2009), while Growcott and colleagues (2011) formula is proposed to estimate the size of sperm whales over 11 m.

Signal processing techniques and classification criteria have been used for computing IPI from selected, small number of sperm whale clicks, discarding the others (Gordon, 1991a; Goold, 1996; Pavan et al., 1997; Rendell and Whitehead, 2004; Rhinelander and Dawson, 2004). For example, Gordon (1991a) measured the IPI only using usual clicks recorded 2-8 minutes after the whale fluked and discarded all others; Goold (1996) applied the signal processing techniques of cepstral analysis as well as autocorrelation analysis; Pavan and colleagues (1997) developed a software to simultaneously visualize the real-time spectrogram and the cepstrogram (cepstrum vs time) of the acquired signal, showing the pulse delays for every wellstructured click; Rendell and Whitehead (2004) applied cepstral analysis to compute the IPI of codas; Rhinelander and Dawson (2004) used autocorrelation analysis for clicks recorded 2-8 minutes after the whale dived (like Gordon, 1991a). Few years later, Teloni et al. (2007) suggested that the stable IPI (*i.e.* the Inter Pulse Interval between p1–p2, p2–p3, etc., is stable for all clicks emitted by the same sperm whale; see Chapter 2) can be consistently estimated by processing a few number of clicks and averaging their power cepstra. Cepstral techniques have long been used to identify reflections of broadband signals (Bogert et al., 1963) and ensemble averaging is a long-standing technique in signal processing. This method can be applied for sperm whales recorded in an unknown orientation (see on and off-axis clicks reported in Chapter 2; Zimmer *et al.*, 2005b). As pointed out by Miller and colleagues (2013), the advance offered by the Teloni and colleagues (2007) method is considerable; it is not only objective, which facilitates automation, but also requires fewer assumptions than previous criteria for
computing IPI, and hence allows for analysis of additional recordings not previously considered suitable for IPI measurement, thus increasing sample size. Antunes and colleagues (2010) compared various stable IPI estimation methods (manual measurement, waveform averaging, autocorrelation averaging, cepstrum averaging) on a known dataset. Among all the automatic techniques tested, the best performance in the analysis was obtained by averaging the autocorrelation, but under some conditions, the cepstrum analysis found the stable IPI where the autocorrelation did not.

In the Mediterranean Sea, the size of sperm whales was reported in a limited number of papers and, in some cases, the length data was a corollary information (e.g. Gannier et al., 2012). Drouot et al. (2004b) estimated the sizes of 31 animals sampled across the entire Mediterranean, with a maximum size estimate of 13.5 m. Teloni et al. (2008) measured two whales in the Ligurian Sea, finding IPIs consistent with lengths of about 12.5-13.5m, depending on the used equation. Along the Hellenic Trench, a range of 8.9–14.6 m for 19 males (mean length=11.4 m), and a range of 8.6–9.5 m for 9 females (mean=9.1 m) were reported (Frantzis and Alexiadou, 2008; Frantzis et al., 2014). A dedicated study was recently published by Caruso et al. (2015) in the Ionian Sea. The authors analyzed 156 different sperm whale acoustic encounters, resulting in 183 IPI estimates from an unknown number of individuals. The results revealed that recorded whales were distributed in length from about 7.5 to 14 m, and no estimates greater than 14 m were found. This seems consistent with other measurements in the Mediterranean Sea (Pavan et al., 1997, 1999, 2000; Drouot et al., 2004b), but in contrast with length estimates from other regions, where male sperm whales consistently grow longer than 15 m and regularly attain lengths in excess of 17 m, although the sizes of females do not appear quite so anomalous (Whitehead, 2003; Rendell and Frantzis, 2016).

Acoustically derived growth-rates in sperm whale are quite rare for the Mediterranean Sea as well. Pavan *et al.* (1999) first and then Fossati *et al.* (2003) described that during a 15-months period, one individual in the Ligurian Sea had a variation of about 30 cm, depending on the applied allometric equation using IPI estimates. A preliminary IPI analysis by Pace *et al.* (2013) on two known whales in the Tyrrhenian Sea showed an estimated growth-rate of 10-21 cm/year per total lengths between 10 and 11.13 m. Pierantonio and Airoldi (2014) presented the growth of 16 individuals repeatedly recorded and photoidentified in the Ligurian Sea by IPI analysis, reporting lengths between 11.4 and 13.12 m, and growth-rates of 0-28 cm/year. Briola (2015), analyzing data on two whales in the Ligurian Sea, showed that one individual grew 68 cm in sixteen years and the other one 79 cm in twenty years. The resulting growth rates were 4.25 and 3.95 cm/year respectively. Basing on the length results, all growth-rates were estimated in presumably male whales.

This chapter reports individual growth estimates and average growth rates of photographically identified sperm whales off Ischia Island by IPI analysis. This acoustic method was used to measure whales that have been recorded repeatedly between 2004 and 2015.

#### **5.2 Methods**

Acoustic data was gathered as part of a long-term research program on sperm whale off Ischia Island, Italy. The data set contains a number of individuals that have been recorded many times, and over many years (max 12 yr), and audio recordings in this data set come from photographically identified whales. Data collection involved making acoustic recordings of all encountered whales, principally made directly behind whales after they fluked up to ensure that the first minutes of recordings contained primarily clicks emitted along the body axis as the whale descended. However, the technique implemented by Teloni and colleagues (2007) permitted the analysis of additional recordings from outside that time period as well as recordings made from aspects other than directly behind the whale, so all available recordings of photographically identified whales were used.

Acoustic recordings were collected by a towed stereo hydrophone array incorporating two hydrophones (100Hz - 22 kHz bandwidth, ENEA UT-APRAD Radiation Sources Laboratory), with ASD Schaller pre-amps, spaced 3 meters apart and towed on a 100 m cable. The system was connected to the PC through RME Fifeface 400 audio interface (sample rates up to 192 KHz; sample rates selected for recording on the computer: 44, 44.1 and 48 kHz with 16 bit resolution). The output signal was also connected to headphones and to a pair of stereo speakers located in the pilothouse. While the vessel was underway, a continuous listening of sounds from the array was conducted. During all surveys, the data logging software 'Logger 2000' developed by the International Fund for Animal Welfare, IFAW; http://www.ifaw.org (which collects data in Microsoft Access 2000 format) was used on a PC connected to the GPS receiver to record the position of the research vessel every 180 seconds. Automatically detected acoustic contacts with sperm whale were also entered in Logger 2000, after visual/acoustic inspection by an operator. The software used for audio recording and acoustic data collection included Rainbow Click, a program designed to locate and analyze sperm whale clicks and other odontocete acoustics. Once sperm whales were detected, the vessel route was maneuvered to estimate the relative bearing of vocalising animal(s), to track and approach it or them until their emersion and sighting at surface. Rainbow Click analysed the stereo signal using time of arrival differences between the same clicks on the two channels to estimate a bearing to each click source (Clark et al., 2012; De Vos et al., 2012).

The softwares used for the analysis were SeaPro 2.0j (Sound Emission Analyser Professional; Pavan *et al.*, 1997) and Adobe Audition. SeaPro is a software developed by CIBRA and AEST to make easy the real-time analysis and recording of bioacoustics signals in a wide range of frequencies and in different applications. By using the software SeaPro it was possible to display graphically in real time the click recorded, to distinguish the direct click, its reflection on the sea surface (Figure 56) and the cepstrogram with the cepstral peak that shows the IPI interval (Pavan *et al.*, 1997). The IPI analysis was carried out by using the spectrogram and cepstrogram tools available SeaPro software, where the cepstrum is computed as:

$$C_t = FFT [log (|FFT (x_t)|)]$$

where xt is the digital representation of the time domain waveform and FFT is the fast Fourier transform. The time delay at the peak of the cepstrum was stored as the IPI of that click. AdobeAudition software was used for a detailed waveform visualization.



Figure 56. Waveform of the click (direct click and then the surface reflected click) and its cepstrogram produced by SeaPro. Notice the delay stability (5.39 ms) in both the direct click and its echo from the sea surface. In many cases is possible to see the inversion of phase in the direct and in the echo; we can see the direct click up to the guideline, while the echo is upside-down (© CIBRA).

For each click sequence were considered the time position, the intensity and the category of each click (regular click, coda, etc). For each recording related to a specific individual gathered in the same year (no more than 7 months apart), the best series of at least 30 clicks have been selected and analyzed. IPI measures were carried out only on clicks in a sequence which displayed a stability; the average, standard deviation and the variation coefficient of the ensemble IPI as described by Teloni et al. (2007) were calculated for each animal (the ensemble IPI computation allows analysis of recordings that were made from arbitrary locations with respect to the whale). This method was used in order to estimate the size and growth of 25 whales that have been recorded repeatedly between 2004 and 2015. However, the dataset was reduced to 18 whales since low quality recordings or difficulties in assigning clicks to a known whale didn't allow reliable individual IPI measures (out of a total of 372 analysed recordings, corresponding to more than 133 hours, 104 were excluded due to high uncertainty). If other individuals other than the analized whale were present in the same recording, then the time of the fluke-up at the beginning of the dive (and relative photoidentification images) as well as the time of the first click sequence after the dive were considered to target the studied animal. For the computation of acoustically derived growth rates, all recordings of each individual whale were considered for analysis if the total time between first and last recordings spanned seven months or more. Then they were averaged to yield an average measure of IPI for each individual during the years that they were recorded. Average growth rates, g(t), were then computed for each consecutive pair of average IPIs as in Miller and colleagues (2013):

$$g(t) = \frac{L(t_{n+1}) - L(t_n)}{t_{n+1}^{-t_n}}$$

where t<sub>n</sub> is the time of the average measurement and L is the length derived from the average IPIs using equations 1, 2, 3 and 4 (see paragraph 5.1). Comparisons among individual growth off Ischia Island and growth curves published by Nishiwaki *et al.* (1963), Gaskin and Cawthorn (1973), and Lockyer (1981) were made through fitting our data with the above growth curves. This was possible thanks to the courtesy of Brian S. Miller, who provided me with digitized curves (all growth curves were hand-drawn, without the raw data) (Figure 56).



*Figure 56. Growth curves published by Nishiwaki et al. (1963), Gaskin and Cawthorn (1973) and Lockyer (1981) (courtesy B.S. Miller).* 

#### **5.3 Results**

Twenty-five over a total of 80 photoidentified whales were recorded over multiple field seasons (Table 20). A number of eighteen was retained for IPIs analysis (see methods), including one immature (neonate/calf sperm whales emit clicks unsuited for biosonar, but can potentially convey homing information between calves and submerged conspecifics in open waters; Madsen *et al.*, 2003).

All whales showed an increasing IPI and total length over time (Table 21; Figure 57 for 15 males or presumed ones, Figure 58 for 2 females and 1 immature). Seven photoidentified whales were recorded on at least three occasions over 9 years time spans and all of these whales showed an increase in IPI values between sampled years. Average estimated lengths ranged between 9.4 and 13.1 for males (or presumed ones) and 8.2 and 10.9 for females. An overall, individual variation between whales was observed in the estimated growth rate ( $\Delta$ ETL/ $\Delta$ t), ranging from 6 to 24 cm/year, with the most evident differences found in one of two females (DIDI) and in her possible male calf (MENKAR).

#	Whale	Sex	Years		Notes
1	ALETES ANDROMEDA	M N.D.	2009 2010 2009 <mark>2010</mark>	2015 2014 2015	
3	BRAHMA	N.D.	2012 2015	2011 2010	
4	BRUNONE	M	<b>2004</b> 2005	2006 2009 2010 2014	
5	COREY	N.D.	2005 2006		
6	CRESCENZO	М	2008 2009		
7	DIDI	F	2007 2009	2011 2013	Member of the social unit SU1; the possible mother is NARSIL (she was associated with NARSIL in 2007 and she was associated with MENKAR IN 2009, possibly being her mother)
8	<del>EIWAZ</del>	F	<del>2007</del> <del>2009</del>	<del>2011</del> 2013	Member of the social unit SU1
9	ENEA	N.D.	2005 2007		
10	EROS	N.D.	2011 2015		
11	GIASONE	М	2009 2011		
12	IDRA	<del>N.D.</del>	2010 2015		
13	ILIO-MILA	F	2007 2009	<del>2011</del> <del>2013</del>	Member of the social unit SU1
14	KATIA	N.D.	2005 2006		
15	LEONIDAS	<del>N.D.</del>	2004 2008		
16	MANWE	N.D.	2008 2009	2010 2011	
17	MARK	M	<del>2006</del> 2008	2010 2011	
18	MENKAR	M?	2009 2011		Member of the social unit SU1 since 2009 (possibly he was born late 2007 or in 2008); the mother is DIDI; he was not encountered anymore with SU1 in 2013 (an immature male leaving the social unit of origin?)
19	NARSIL	F	<del>2007</del> 2009	<del>2011</del> 2013	Member of the social unit SU1
20	NETTUNO	М	2006 2008	2009 <mark>2011</mark> 2012	
<del>21</del>	NIHAL	<del>N.D.</del>	2011 2014		
22	NORMA	N.D.	<b>2004</b> 2005	2006 2007	
<del>23</del>	PERSEO	<del>N.D.</del>	<del>2010</del> <del>2015</del>		
<del>2</del> 4	<del>SIRIO</del>	F	<del>2007</del> <del>2009</del>	<del>2011</del> 2013	Member of the social unit SU1
25	ZORA	ND	2004 2010	2012 <del>2013</del>	

Table 20. Dataset used for IPIs and growth estimates.

Table 21. IPI measurement summary showing the number of years covered (t), initial IPI<sub>0</sub>, last IPI<sub>n</sub>, initial size (ETL<sub>0</sub>), last size (ETL<sub>n</sub>), change in size  $\Delta$ ETL, and average growth over years ( $\Delta$ ETL/ $\Delta$ t for each whale). IPIs are measured in milliseconds (msec), while lengths are measured in meters (m).

Whale	Sex	t (year	rs) IPI <sub>0</sub> (msec)	IPI <sub>n</sub> (msec)	ETL <sub>0</sub> (m)	ETL <sub>n</sub> (m)	ΔETL (m)	$\Delta \text{ET}L/\Delta t$	Notes
				5 646657	10,99046	12,50613	1,51567	0,24212	
ALETES	Male	6.26	4,744607		11,70440	13,00571	1,30131	0,20788	Similar to individual MTR100
		0,20	.,	-,	11,70472	12,83949	1,13478	0,18127	(Miller et al., 2013)
					11,35511	12,63331	1,27821	0,20419	
	N.D.	5,9		4,259635	9,71981	10,40430	0,68449	0,11602	Similar to individuals HP210
ANDROMEDA			3,426304		9,79968	11,00411	1,20443	0,20414	MTR100 (Miller et al. 2013)
					9.48707	10.66790	1,18083	0.20014	
	N.D.	3,05	5,399451	5,601476	12,03187	12,41597	0,38409	0,12593	
BRAHMA					12,64925	12,94057	0,29132	0,09551	HL160, LSR100, NN40 (Miller et al., 2013)
Divinium					12,52851	12,78266	0,25415	0,08333	
					12,28302	12,56929	0,28627	0,09386	
			4,274603	5,443750	10,42020	12,11340	1,69326	0,18149	Similar to individuals I SI 20
BRUNONE	Male	9,33			11,02373	12,71313	1,47079	0,15764	HR210 (Miller et al., 2013)
					10,68911	12,34579	1,65668	0,17756	
				4,250363	10,31423	10,39451	0,08028	0,09445	
COREY	N.D.	0,85	4,172336		10,87800	10,99071	0,11272	0,13261	See Miller at al., 2013
					10,98480	11,08296	0,09816	0,11548	
					11 20130	11 33908	0,11056	0,13008	
		1,98	4,893690	4,985779	11,91958	12.05248	0.13290	0.06712	Similar to individuals LNL100
CRESCENZO	Male				11,89226	12,00811	0,11585	0,05851	NN20 (Miller et al., 2013)
					11,56636	11,69685	0,13049	0,06590	
				4,607710	10,57594	10,80983	0,23388	0,11299	
ENEA	N.D.	2,07	4,414966		11,22845	11,50677	0,27832	0,13445	See Miller at al., 2013
					10,00001	11,53250	0,24247	0,11714	
					9.88350	10 17625	0,27312	0,13194	
			0.0=(0.00	4,020833	10.15706	10.67114	0.51409	0.13284	
EROS	N.D.	3,87	3,356009		10,35722	10,80469	0,44747	0,11562	See Miller at al., 2013
					9,83731	10,34133	0,50402	0,13024	
					12,41933	12,69109	0,27176	0,11276	
GIASONE	Male	2,41	5,603175	5,736961	12,94302	13,13589	0,19288	0,08003	See Miller at al., 2013
					12,76479	12,95510	0,10050	0.07866	
-		0,79	4,349206	4,435374	10.50147	10.59960	0.09812	0.12421	See Miller at al., 2013
KATIA	ND				11,13348	11,25793	0,12444	0,15753	
KATIA	N.D.				11,20730	11,31570	0,10840	0,13721	
					10,79483	10,91693	0,12210	0,15456	
				4,578231	10,68172	10,77252	0,09081	0,09559	See Miller at al., 2013
MANWE	N.D.	0,95	4,504545		11,33781	11,40421	0.09270	0.09758	
					11,01494	11,11935	0,10441	0,10991	
		2,91	5,007955	5,309001	11,37313	11,86982	0,49668	0,17068	Similar to individuals HL40,
MARK	Male				12,08448	12,51879	0,43431	0,14925	LNL160, LNL240, LSL20,
					12,03601	12,41472	0,37872	0,13014	LSR60, MLS70, MTR140 (Miller
					11,72827	12,15485	0,42658	0,14659	et al., 2013)
			5 9 4 9 5 9 9	5 50 44 45	12.42004	12,91561	0.49557	0.12483	Similar to individuals HL140,
NETTUNO	Male	3,97	5,240539	5,584167	12,32860	12,76088	0,43228	0,10889	MTL40, NN80 (Miller et al.,
					12,05784	12,54476	0,48692	0,12265	2013)
		1,97	4,553288	4,852608	10,76221	11,10930	0,34709	0,17619	
NORMA	N.D.				11,45233	11,82756	0,37524	0,19048	See Miller at al., 2013
					11,48506	11,81205	0,32699	0,16599	
		8,15		5,006250	10.17027	11.37050	1.20023	0.14727	
7004	ND		4,022676		10,66177	12,08202	1,42025	0,17426	See Miller et al. 2012
ZUKA	N.D.				10,79653	12,03386	1,23734	0,15182	See Miller at al., 2013
					10,33213	11,72586	1,39372	0,17101	
		4,05	3,961231	4,147917	10,11491	10,28985	0,17495	0,04320	
NARSIL	Female				10,57298	10,84272	0,26974	0,06660	
					10,71725	10,50960	0.26454	0.06532	
			2,659864	3,243750	<del>9,37425</del>	<del>9,6185</del> 4	0,24429	0,03979	
DIDI*	Female	6.14			8,54954	9,53565	0,98611	0,16060	
	i cinaic	0,1 7			8,95945	9,81664	0,85719	0,13961	
					8,26286	9,22839	0,96553	0,15725	
		1,76	1,070068	1,669823	7.00532	8,22091	1.21559	0,69068	
MENKAR**	Male				7,61872	8,67395	1,05523	0,59956	
					6,75268	7,94129	1,18861	0,67534	-

\* this whale was a juvenile in 2007 and then a mother in 2009 \*\* this whale was a calf in 2009 and a juvenile in 2011 Clarke equation (1978) modified in Gordon (1991) Gordon equation (1991) Growcott et al. equation (2011) Pierantonio et al. equation (2016)





Figure 57. Individual growth of male (or presumed ones) sperm whale individuals off Ischia Island.



Figure 58. Individual growth of two female sperm whale individuals and one immature off Ischia Island.

Results of fitting our length data with the three digitized age-lengths curves by whaling (see Figure 56) are shown in Figure 59. Age-length keys from Nishiwaki and colleagues (1963) give age estimates of approximately 8.8-19.6 years, Gaskin and Cawthorn (1973) 5.5-17.8 years, while Lockyer (1981) estimates 13.9-25.3 years for individuals of these sizes. Sperm whale average growth ( $my^{-1}$ ) vs mean length between measurements for all male individuals (n=15) in relation with data by whaling is plotted in Figure 60. Growth rate estimates obtained in this study via equations (1)-(4) were all lower than the average growth rates measured during industrial whaling in other oceans than Mediterranean Sea.



*Figure 59. Sperm whale length data estimated by IPI analysis off Ischia Island fitted with curves published by Nishiwaki et al. (1963), Gaskin and Cawthorn (1973) and Lockyer (1981).* 



Figure 60. Sperm whale average growth (my<sup>-1</sup>) plotted with mean length between measurements for all male individuals (n=15). Mean lengths are derived from IPIs using the equations by Clarke (1978 b, modified in Gordon, 1991a; dots), Gordon (1991a; squares), Growcott et al. (2011; triangle), and
Pierantonio et al. (2016; crosses). The dashed, dotted and solid lines show growth of male sperm whales derived from Nishiwaki et al. (1963), Gaskin and Cawthorn (1973) and Lockyer (1981), respectively.

#### **5.3 Discussion**

Size is the result of the interaction of multiple sources of variation in growth. Many processes are known to contribute to the realized growth of organisms, such as individual intrinsic variation (*i.e.* genetic), size-selective mortality, environmental cues (temperature, food), intraand inter-specific competition (social) (Peters, 1983; Vincenzi, 2014). The role of each of these factors, and their reciprocal influence, is crucial to improve our understanding of individual population dynamics, help conservation and management of endangered species, and increase our ability to predict future growth trajectories of individuals and populations (Vincenzi *et al.*, 2014). However, teasing apart the contribution of individual and environmental factors necessitates biological insights and the use of longitudinal data in powerful statistical methods; unfortunately, most of these requirements are only partially available for sperm whale in the Mediterranean Sea, where studying these animals has always been a challenge because of their low accessability and limited resources to research.

This is one of the few times that acoustic estimates of sperm whale size have been used to derive measurements of the growth in lenght of individual whales non-lethally and non-invasively. Most of the lengths and/or growth rates measurements were made during whaling (Nishiwaki 1963; Gaskin and Cawthorn 1973; Lockyer 1981; Best *et al.*, 2016) or from stranded animals (e.g. Evans and Hindell, 2004; Mazzariol *et al.*, 2011). This study showed that by applying the SeaPro cepstral analysis to a long term dataset an increase in IPI over time for 18 whales photoidentified off Ischia Island was observed, undoubtedly as a result of individual growth. No individuals presented evident or dramatic oscillations in IPI over time (apart the calf/juvenile

individual), most likely providing further support of the IPI computation method indicated by Teloni et al. (2007), and incidentally reinforce for the bent horn model of sound production (see Miller *et al.*, 2013). The use of equations (1)-(4) to these IPI estimates allowed to calculate consecutive whale lengths with acoustic recordings collected greater than seven months apart, estimating growth through time. Continuous growth in male sperm whales until they reached physical maturity at an average length of 15.85 m was reported by Lockyer (1981). Recent evidences suggest that the growth deceleration with age in mammals is caused by potent suppression of cell proliferation in multiple tissues and is driven primarily by local, rather than systemic, mechanisms (Lui and Baron, 2011). This program does not appear to be driven simply by time, but rather depends on growth itself, suggesting that the limit on adult body size is imposed by a negative feedback loop (Lui and Baron, 2011). Most of the male whales (or presumed ones) recorded repeatedly in Ischia were found to be between 9.4-13.1m and were still growing, which according to Lockyer (1981), suggests that these whales are socially mature, but not yet physically mature. These results are also consistent with other findings in the Mediterranean Sea, which estimated sizes from IPIs ranging from 8.9 m (unknown sex) to 14.6 m for male sperm whales (Pavan et al., 1997; Pavan et al., 1999; Pavan et al., 2000; Drouot et al., 2004b; Teloni et al., 2008; Frantzis and Alexiadou, 2008; Gannier et al., 2012; Frantzis et al., 2014), but in contrast with lenghts from other regions, where male sperm whales consistently grow longer than 15 m and regularly attain lengths in excess of 17 m (Berzin, 1971; Rendell and Frantzis, 2016). For example, Gaskin and Cawthorn (1973) reported a range of 10.7-16.8 (mean: 14.09 m) during whaling. Both Kasuya (1991) and Kahn and colleagues (1993) found density dependent effects on the growth of sperm whales resulting from the removal of large numbers of whales during commercial whaling. Kasuya (1991) found an increase in the length distribution of males, and attributed this change to an increase in available food (or decrease in competition for food). Similarly, Kahn and colleagues (1993) found differences in length distribution of females off the West coast of South America. Both of these studies observed changes five to ten years after the end of the intensive whaling effort. The sizes of the two females (8.2-10.9 m) in this study appear quite similar to the range of of 8.6–9.5 m reported by Frantzis and colleagues (2014) in the Mediterranean and coherent with other studies worldwide. For example, in the northern Indian Ocean, photogrammetric measurements of 49 sperm whales (females+immature males) off Sri Lanka in 1983-1984 produced lengths ranging from 7 to 11 m (Gordon, 1991a), a size distribution also observed in 79 females and immature sperm whales measured photogrammetrically off the Seychelles in 1990 (8-11 m) (Kahn et al., 1993) and in at least 200 different sperm whales (females+small males) off the Galapagos Islands in 1985-1987 (Waters and Whitehead, 1990). Lockyer (1981) reported that the length of a sperm whale at birth is about 4.05 m, with an estimate of 6.7 m in the second year, when weaning is possible to occur. Our acoustic estimates in 2009 on one calf possibly born in 2008 seem to be coherent with the size and growth described by Lockyer (1981). The consistency of the sperm whale acoustically derived length distributions reported in this study seem to be aslo supported by length data from 147 strandings in Italy between 1714 and 2016 (Table 22; see the Italian Stranding Data Bank at <u>http://mammiferimarini.unipv.it/</u>). The average length for stranded whales >6 m is 12.2 (range: 11.2-19 m) m and 9.24 m (range: 6.1-12.6 m) for males and females, respectively, while the average length of individuals >11 m (presumably males) of unknown sex is 14.1 m (range: 11.5-19 m). Although this data is indicative, possible inaccuracies in measures and estimates in the older stranding reports also

including animals fond death at sea may have been occurred during time (Pavan G., *personal communication*), therefore dropping the reliability of the information shown in Table 22. However, detailed length data coming from a mass stranding of a pod of seven male sperm whales along the Adriatic coast of Southern Italy in 2009 seems to confirm body lengths between 10.5 and 12.1 m for males of an estimated age of 20-25 years.

Time period	1714-September 2016
N. of strandings	183
N. of stranded whales	279
N. of strandings with lenght estimates/measurements	147
N. of strandings of females with lenght estimates/measurements	28
N. of strandings of females with lenght estimates/measurements <6m	5
N. of strandings of females with lenght estimates/measurements >6m	23
Average lenght of females >6m	9.24 m
N. of strandings of males with lenght estimates/measurements	55
N. of strandings of males with lenght estimates/measurements <6m	11
N. of strandings of males with lenght estimates/measurements >6m	44
Average lenght of males >6m	12.2 m
N. of strandings of whales without sexing	64
N. of strandings of whales without sexing <11m	40
N. of strandings of whales without sexing >11m (possibly males)	24 (23 are >12m)
Average lenght of whales without sexing >11m (possibly males)	14.1 m

Table 22. Sperm whale stranding data in Italy between 1714 and 2016.

Most prior knowledge of length and growth in male sperm whales has come from fitting growth curves to size data gained from whaling. Using our derived relationships between IPI and total length, we find that age-length keys from Nishiwaki and colleagues (1963) give age estimates of approximately 12-20 years, Gaskin and Cawthorn (1973) 6-19 years, while Lockyer (1981) estimates 15-26 years for individuals of these sizes. Growth rates in this study resulted below those derived from whaling (see Figure 60). Our acoustically measured growth rates match most closely with those derived from whaling in Cook Strait in 1963-1964 (Gaskin and Cawthorn 1973) for whales >11 m in length, and appear to be lower than values both in the Southeast Pacific (Lockyer, 1981) and North Pacific (Nishiwaki et al., 1963) for individuals <11 m. As discussed by Miller and colleagues (2013) for 26 sperm whales in Kaikoura (New Zealand), this could indicate either that the whales that repeatedly return to Ischia are not growing as fast as the whales caught during whaling, or that these individuals do not grow to the same average size as those taken during whaling. In the Mediterranean Sea acoustically derived growth-rates in sperm whales are quite rare. However, results from Fossati and colleagues (2003) showing a variation in leght of about 30 cm in 15 months in one whale, and from Pierantonio and Airoldi (2014) presenting values of 0-28 cm/year in 16 whales, are comparable to our study, supporting evidences of similarities between individual growth rates in Mediterranean male sperm whales. It is impossible to say whether size difference between Mediterranean and other regions is due to an evolved reduction in growth in this population or a phenotypic response resulting from a lack of access to the highly productive high-latitude waters in which male sperm whales outside

the Mediterranean Sea grow to their mature lengths (Whitehead and Weilgart, 2000), but it does suggest that Mediterranean sperm whales may be subject to different ecological and evolutionary forces than those experienced by their open ocean counterparts (Rendell and Frantzis, 2016). Temporal and geographical variation in body size of animals is a common phenomenon, and has been related to many factors (reviewed by Yom-Tov and Geffen, 2011 for terrestrial mammals). Quite recently, McNab (2010) argued that the tendency of mammals to vary in size depends on the abundance, availability and size of resources, and termed this pattern the "resource rule". Food availability, especially during the growth period, is a key predictor in determining final body size in mammals as quantity and quality of nutrition during this period affects growth rates and final body size (Yom-Tov and Geffen, 2011). Food availability is influenced by both biotic and abiotic factors and fluctuates accordingly in time and space, in turn affecting body size. Only one study to date (Best *et al.*, 2016) has revealed significant geographical variation in morphometrics or other phenotypical characters in the sperm whale, which is otherwise regarded as a monotypic species (Rice, 1989; Mizroch and Rice, 2013). These authors found that the body size of mature (pregnant) female sperm whales taken in Soviet pelagic whaling expeditions in the Southern Hemisphere, en route to and from the Antarctic, varied with latitude. The length of mature females tends to decline from south to north, with individuals taken in tropical waters being significantly smaller than those in temperate regions, suggesting that the observed trends are consistent with the "resource rule" of McNab (2010).

In conclusion, the cepstral analysis of sperm whale growth via IPIs using SeaPro presented here seems to be robust, as suggested by Miller and colleagues (2013) in the analogous study conducted in New Zealand. While growth of individuals could be measured using photogrammetric techniques only (*eg.* Webster *et al.*, 2010), there are several advantages to the acoustic methods such as a higher precision (Growcott *et al.*, 2011) and a lower disturbance on animals (stereo-photography requires manoeuvring alongside of the whale at surface which can cause the whale to turn away or dive early; Dawson *et al.*, 1995). Coupling SeaPro analysis techniques with long-term monitoring efforts (in the form of photographic identification and audio recordings) has provided a unique opportunity to measure the acoustic growth of sperm whales off Ischia Island, and continued data collection and analysis may yield insights into how growth affects the immigration/emigration of bachelor males in the study area, as well as social units.



# **Chapter 6**

# **Conclusions and future directions**

Sperm whales are massive click producers that spend the majority of their lives underwater in deep environments, which we have a limited ability to survey and describe. The vocalizations produced by sperm whales make them a suitable species with which to use passive acoustic techniques for assessing their presence and movements, monitoring their habitat use, inferring their behaviour and, under precise circumstances, estimating their size.

This thesis has addressed the original aims, presenting an extensive body of work on the distribution, sociality, pattern of sounds production and acoustically derived growth in sperm whales off Ischia Island.

Why do sperm whales have fidelity to waters near the island of Ischia? Sperm whales are generally thought to occur in areas with high cephalopod abundance, where foraging success tends to be greater. Therefore, the key to understanding how sperm whales interact with their environment will ultimately be resolving the dynamics between this predator and their elusive cephalopod prey.

I have shown that there are zones in the study area where whales clearly prefer to occupy, feed or socialize in. The bathymetric variability in the study area seems to drive sperm whale occurrence and the prediction of suitable zones within the study area that may act as proxies for prey distribution and abundance at the scale of the analysis. In theory, bathymetric features may provide a means of predicting and important foraging habitats for upper trophic-level marine predators like sperm whales. This study and many others have demonstrated that submarine canyons, and complex and steep topographies, are important to this specie, possibly as centres of trophic transfer. These habitats are likely to be associated with elevated marine productivity and prey retention, thereby making dense prey patches available to predators. The composition of the sperm whale acoustic repertoire off Ischia Island seems to support this hypothesis, with the majority of the recording time spent for echolocation that is emitting clicks, receiving and interpreting the echoes from prey items and other structures. However, at a fine spatial and temporal scale, seems that individuals (singletons, members of a cluster aggregation or a social unit) may use different cues to search for patches of prey. Generally, the structure of prey patches changes more rapidly at fine than broad spatial scales. It is feasible that sperm whale movements are more closely associated with the aggregation behaviour of prey at fine-scales than overall prey abundance. The diet of sperm whales in the study area is not known, however prey aggregation behaviour would be an important proponent of feeding success. Since predator behaviour can also affect prey distribution, the dynamics between predator abundance and prey availability are potentially highly complex.

Furthermore, since an increasing number of recent studies have recognized that both fixed spatial but also variable oceanographic features, and their functional relationships with cetaceans, can be of great importance for conservation and management, a description on how and why animals use specific habitats and the prediction of the most suitable ones can help to identify the nature and location of critical hotspots. The predictive maps developed in the study

may be used (and updated with new data) as planning tools to help manage dedicated marine reserves, in addition to defining what activities can occur in specific locations in order to regulate anthropogenic activities and mitigate their impact.

It is evident that a key limitation in this work was the lack of measurement of prey availability within the study area. Measuring prey availability would improve our understanding of sperm whale distribution and habitat selection. Jaquet and Gendron (2002) related sperm whale distribution with the abundance of squid. They did not find a relationship between distribution of squid and sperm whales but they found that sperm whales change their distribution in response to a decline in squid. Such studies within the submarine canyon systems in the study area will help our understanding of sperm whales off Ischia and the possible impact of the shift of their main prey. Furthermore, analysis of stable isotopes or the identification of prey items (cephalopods beaks) collected in whales' feces may be a quali-quantitive source of information on targeted prey species in the study area as well. Coupling this information with photoidentification data, a better understanding of the differences observed between singletons and individuals in groups may be achieved. Feces collection and analysis may be also important to assess fecal metabolites of reproductive hormones such as estrogens, progestins, and androgens, and their natural variations according to life-history state. Additionally, the characterization of the baseline variations in stress-related fecal hormones according to sex, age, and reproductive state may be applied as a method to ultimately determine whether exposure to anthropogenic disturbance may cause measurable physiological changes that can potentially lead to biologically significant effects on individuals or populations.

In this study, a first effort to delineate sperm whale social distribution and organization in the Tyrrhenian Sea - around Ischia and Ventotene islands - was attempted. I found evidence that females and young live in stable social units, as has been observed in other areas. One unexpected finding was that groups of maturing bachelor males were stable between years and individuals within groups showed similar behaviour to those in social units. The spatial scale of the observations is very small and the number of unknown sex/age class of most of the individuals frequenting the study area is high, thus limiting the possibility of a more robust analysis. However, complex social organization in this study emerged as a key factor influencing sperm whale distribution patterns as well as composition of the acoustic repertoire. Individuals that associate regularly are more likely to possess shared behaviours, since close interactions between group members can enhance social learning and conformism in behaviour. This study demonstrates that single, possible male individuals, cluster of males (ore presumed ones) and social units vary in the time spent in the study area searching for prey, the space occupied, and the type/amount of communication clicks (codas), indicating that social organization is an important source of variability in distribution and vocal behaviour within sperm whale populations. Besides differences in coda types (Chapter 4), I also found variances in the underwater dive behaviour (Chapter 3), in the general acoustic behaviour and in some patterns of clicks production (Chapter 4), and in the acoustically derived growth rates (Chapter 5). These differences may be strongly linked with individual peculiarities. Under an "ecological hypothesis", individuals who experience similar ecological or social conditions (*e.g.* food patch, predation risk, or group size) and have similar traits (*e.g.* age-sex class, body size, or reproductive state) should experience the same ecological constraints and behave in the same way. However, the "behavioural hypothesis" under which individuals should exhibit different personalities even when experiencing similar conditions and having similar characteristics, and

may also show different patterns of plasticity, cannot be ignored when observing the results here presented.

To answer to many of the most interesting questions related to the biology, ecology and sociality of species, individuals have to be measured repeatedly throughout their life-span lives, but this is not an easy task for sperm whales. While growth of individuals could be measured using photogrammetric techniques only, there are several advantages to the acoustic methods, such as a higher precision and a lower disturbance on animals (stereo-photography requires manoeuvring alongside of the whale at surface which can cause the whale to turn away or dive early). Chapter 5 in this thesis offered one of the few cases in which acoustic estimates of sperm whale size have been used to derive measurements of the growth in lenght of known, repeatedly visually/acoustically 'captured' individuals non-lethally and non-invasively. The cepstral analysis of sperm whale growth via IPIs using SeaPro seems to be robust and derived results coherent with the scarce information available in the Mediterranean basin. However, greater effort is needed to increase sample size, improve acoustic acquisition technology, and compare different tools of analysis.

Despite the fact that the present dissertation produced original information about several aspects of the behavioural ecology of sperm whales off Ischia Island, several gaps remain that I would like to address in upcoming activities:

- future surveys need to be conducted over extended areas than this here investigated, in order to examine the distribution and behaviour of sperm whales further offshore. Multiplatform data collection such as aerial-surveys and passive acoustic techniques will increase the efficiency in finding and locating sperm whales at a larger spatial scale around the Ischia area. This will also allow us to determine if 'resident' sperm whales leave the study area or only move further offshore.
- 2) future research to investigate if (a) sperm whale foraging behaviour is similarly related with bottom depths (due to location of their prey layer) in the study area and in more offshore locations, and (b) if contexts in which different click types are produced are just individual or also group-dependent are strongly needed. The use of D-tags or satellite tags can provide substantial information on the animal movements and acoustics with a higher level of detail than in this study.
- 3) future feces collection and stable isotope analysis are required to initiate the process of understanding feeding habits and the diet of sperm whale in the area. If possible, the fecal material will also be used to measure multiple hormones to monitor physiological status and assess relative levels of stress-related hormones in this species. These analyses can provide information on how acoustic (noise) and other stressors affect these species, which will be critically important for evaluating operational and management options in different habitats.
- 4) considering that acoustic analysis techniques coupled with long-term monitoring efforts (in the form of photographic identification and audio recordings) has provided the unique opportunity to measure the acoustic growth of sperm whales off Ischia Island, a future effort to obtain new insights into how growth affects the immigration/emigration of bachelor males in the study area, as well as social units, will be completed.

The contribution of the results gathered through this kind of future research may range far beyond Ischia waters, as baseline data can be extrapolated and/or compared to sperm whale populations.

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