# **Pilot Whales in the Strait of Gibraltar**



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## Abstract

Long-finned pilot whales *Globicephala melas* are social, pelagic odontocetes whose social structures in the North Atlantic follow environmental gradients like ocean currents and temperature. These gradients are also responsible for the abundance and distribution of the whales' regionally favored squid species. The Strait of Gibraltar is characterized by a complicated but pronounced current regime and is inhabited by a resident population of pilot whales. Statistical analysis of sighting data indicate that the changing currents at high and low tide are associated with a change in location by pilot whales on the east-west axis while remaining over an area of maximum relief south of the middle line of the Strait of Gibraltar.

KEYWORDS: LONG-FINNED PILOT WHALES, ECOLOGY, BEHAVIOR, MOVEMENT, DISTRIBUTION, STRAIT OF GIBRALTAR, CAMARINAL SILL, TIDES, CURRENTS, TOPOGRAPHY,

# Part I: The Long-Finned Pilot Whale (*Globicephala melas*)



Picture 1: A group of Long-Finned Pilot Whales Globicephala melas

## **1. Introduction**

Until some ten years ago, it was hardly known to the public that the Strait of Gibraltar is inhabited by a number of whales and dolphins. Not even the people of the adjacent countries Spain and Morocco took great notice of the populations of the mostly toothed whales right off their coast. It was only some fishermen who knew that these animals were regulars in these waters.

The phenomenon of 'not knowing' what lives in the sea is probably not at all uncommon and holds certainly true for cetaceans in the whole Mediterranean. It has not been that long since the awareness of the public has started to grow. Partly because of cetology becoming somewhat of a popular science branch, with the dolphin being its most prominent ambassador. But also because the effects of human exploitation of the seas have started to show to more than just the well informed scientists. And what was taken for granted for centuries is now being looked at again with a different perspective.

For centuries most of what we learned about our oceans mammals was from the remains of our fishing industries. While these figures can provide very helpful information and could not be obtained otherwise, they say very little about social structure, behavior and often astonishing intelligence of these animals. Only lately, modern scientific approaches like quantitative analyses and hypothesis testing are applied as opposed to qualitative narratives from whalers and scientists (Samuels and Tyack, 2000).



**Picture 2:** Spain and Morocco, separated by the Strait of Gibraltar

This thesis focuses on long-finned pilot whales (*Globicephala melas*), a small toothed whale belonging to the family of dolphins (Delphinidae) (Traill, 1809.) There is a population of an estimated 150-200 animals living in the Strait of Gibraltar between Tarifa (Spain) and Tanger (Morocco), which is resident all year long. Bigger cetaceans like killer whales *Orcinus orca*, sperm whales *Physeter macrocephalus* and

fin whales *Balaenoptera physalus* are only seasonal passers by. The pilot whales have been under constant observation for several years now by the vessels of the whale watching foundation FIRMM (Foundation for Information and Research on Marine Mammals) located in Tarifa (Picture 2). On every cruise, the position of encountered animals is noted as well as several other criteria like direction of swimming and a few basic behaviors. This is not only done with pilot whales but all cetaceans in this area. While other dolphins, which are also resident in this area, are encountered randomly, it soon occurred to the biologists and boat crew of FIRMM that pilot whales were always seen in an area closer to the Moroccan coast, right over the southern of two trenches running through the Strait of Gibraltar, between  $35^{\circ}$  53' - $35^{\circ}$  55' north and  $5^{\circ}$  30' –  $5^{\circ}$ 43' west (Picture 3). The



**Picture 3:** Red dots mark the position of the sightings of pilot whales *G. melas*.

extensive list of pilot whale sighting data by FIRMM comprising 5773 samples was used in this thesis to confirm these observations with the goal to establish a general scheme of use of this habitat by pilot whales.

Unfortunately, many cetacean species are endangered. Intensive exploitation during the 20<sup>th</sup> century, overfished oceans and direct disturbance by human operations have taken their toll on the populations of many species. While pilot whale numbers worldwide seem to remain stable, little is known about the Mediterranean population. There is no reason for immediate concern but the shipping traffic in the strait is constantly increasing, presenting a direct competition over the limited space in this area. This has shown to be problematic in other parts of the world, where ship noise and harmful propellers have shooed away whales and dolphins.

If this happens in breeding and resting areas, it can have very detrimental effects on the fitness of these animals and threaten their survival. On the other hand, if these critical areas are identified, a sometimes very small change in human behavior can make a real difference to the well being of our whales and dolphins. Therefore, it is a necessity to study these animals profoundly in areas where human interference is pronounced, such as the Strait of Gibraltar. Apart from interesting insights in the life of an odontocete, this knowledge, combined with other work on this subject could provide important information when tangible conservation efforts are made. In the first part of this thesis, the knowledge we have today about pilot whales is gathered. Social structures and life history are examined and linked to the special ecology of the Strait of Gibraltar. In the second part, the movements of this species are analyzed and the hypothesis that pilot whales are influenced by tides and currents is tested.

The data in this thesis was also used for the publication of a poster by M. Casanova and the author of this thesis at the 21<sup>st</sup> Conference of the European Cetacean Society in Donostia - San Sebastian. It is printed in the Appendix on the last page of this paper.



## 2. The Long-Finned Pilot Whale Globicephala melas

Picture 4: Long-Finned Pilot Whales Globicephala melas: mother and young

### 2.1 A Brief Description

The long-finned pilot whale *Globicephala melas* is a toothed whale (Suborder *Odontoceti*) belonging to the family of delphinids (*Delphinidae*). The latin name *G. melaena* is found in older literature but the correct nomenclature of today is *G. melas*. Two of its closest relatives are the short-finned pilot whale *Globicephala macrorhynchus*, of the same genus and the well known Orca or killer whale *Orcinus orca* (Amos et al. 1993b). In this paper the use of the shorter term 'pilot whale' will always refer to the long-finned pilot whale unless it is indicated otherwise.

Pilot whales are of very dark charcoal color with a brighter anchor-like figure on the ventral side between the comparatively large, sickle-shaped flippers. They do not have a beak like other dolphins but a very round head that can protrude over the lower jaw on males (Picture 5).

Fully grown males reach an average length of about five and a half meters, although large individuals can grow to more than six meters and three tons in weight, females reach up two five meters (Bloch et al. 1993). Males are sexually mature at 12 years of

age when they reach about 4,6m, females at 8 years and 3,7m (Olson and Reilly in Perrin et al. 2002). Females bear their young up to 14.5-16 months, giving birth mostly in the summer months to a calf of about 1,m, which is nursed for two years or even longer (Reidenberg and Laitman in Perrin et al. 2002).

Pilot whales are social animals, which swim in matrilineal groups



**Picture 5:** Pilot whale head

called pods, ranging from 50 to 200 animals (Bloch et al. 1993). Females play an important social role in these pods. For a long time it's been assumed, that a pod was being guided by a specific 'pilot', hence the name 'pilot whale' (Olson and Reilly in Perrin et al. 2002). Genetic evidence suggests that mature animals of either sex stay with their maternal pod but usually don't mate within (Amos et al. 1993). Females also live longer than males, shifting the sex ratio of the whole population to about 60% females (Bloch et al. 1993). These very important aspects of pilot whale social structure will be discussed in more detail in chapter 2.4.2 'Mating and Reproduction' and 2.4.3 'Social Structure'.

There are two major populations of pilot whales, one in the North Atlantic and one in the cold and temperate waters of the southern hemisphere (Figure 1)(ACS Online



isolated from each and show slight morphological differences. Therefore, they have been accorded subspecies status: *G. melas melas* in the North Atlantic and *G. melas edwardii* in the

2006). The two are totally

**Figure 1:** Worldwide distribution of the Long-Finned Pilot Whales

Southern Hemisphere (Olson and Reilly in Perrin et al. 2002). The majority of scientific work on pilot whales is done in the North Atlantic so we probably know very little about the southern subspecies. The two populations differ in that the

animals on the southern hemisphere often exhibit bright streaks behind the eye and variable grey saddle markings behind the dorsal fin, similar to short-finned pilot whales (Picture 6) (Nelson and Lien, 1996).



**Picture 6:** Short-finned pilot whales *G. macrorhynchus* (top) and long-finned pilot whales *G.* melas (bottom)

Individual pods are generally not known to stay in a certain area, since they travel with their main diet, squid (Hoydal and Lastein, 1993). Although it has to be noted, that the population of the Strait of Gibraltar is resident all year long with the exception of about two weeks every spring, when the animals disappear. Pilot whales have been hunted

traditionally for their meat, blubber and oil in Newfoundland, Cape Cod, Norway, Iceland, the Scottish Islands and the Faroese Islands (Olson and Reilly in Perrin et al. 2002). Today they are only being hunted on the Faroese Islands, where the hunt is thought to have existed for more than 1'100 years (Thorsteinsson, 1986). In a Faroese pilot whale hunt, an entire pod is driven on shore and then slaughtered. What might seem like a brutal massacre, is actually strictly regulated (Bloch et al. 1993) and has very little to do with the very questionable practice of whaling in other places. If the needs of the community are met, the hunt is closed and the meat is shared among all residents (Bloch et al. 1993). Due to this tradition, there exists a continuous written record of Pilot Whales (in Faroese waters), dating back to the year 1584 with a gap only from 1641 to 1709. This makes the pilot whale the animal with the longest recorded history (Bloch et al. 1993). Of course this is a very valuable source of information for scientists. In fact, most of our knowledge today is based on information retrieved from the Newfoundland and Faroese fisheries (Amos et al. 1993).

On the Faroese Islands, an average of about 1'700 animals are caught per year, which isn't thought to threaten the population (Olson and Reilly in Perrin et al. 2002). On the other hand, an estimated number of 54'000 animals caught in Newfoundland between 1947 and 1971 had substantially reduced the local population (Olson and Reilly in Perrin et al. 2002).

Another reference to the long hunting tradition on the Faroese is the other popular name for pilot whale, 'Grind Whale' (pronounced with a short 'i' as in 'spin'.) 'Grind' in Faroese means 'pod' as well as the activity of pilot whaling (Bloch et al. 1993).

#### 2.2 What it Takes to Travel the Ocean - Physiology

Whales are mammals and although they seem cleverly disguised as fish, they are still not so different from us land mammals. They are warm-blooded, breathe air and give birth to living young, which they suckle. In fact, most of their adaptations are extensions or variations of the general mammalian theme (Elsner in Perrin et al. 2002). However, whales lack any apparent limbs, sport flukes and fins instead and with their streamlined appearance, do look strikingly like fish. If we want to understand, how the typical four legged and furry land creature evolved into this highly adapted aquatic animal, we must consider the constraints that the aquatic media imposes on it's inhabitants (Elsner in Perrin et al. 2002).

Whales undertake long travels driven by the seasonality of the oceans. To do this in an energy-efficient manner, their physiology had to adapt to their aquatic environment (Senn, 1997). Therefore, many of the adaptations that whales have undergone during their evolution can be linked to the physical properties of their surrounding medium.

Water is 1000 times denser than air and its viscosity is 60 times greater, which results in greatly enhanced drag forces (Elsner in Perrin et al. 2002). To swim long distances in this medium, having a streamlined body is inevitable. In the open ocean there is also no ground to push off from. Arms and legs are useless and they would create too much additional drag to use them for (long-distance) swimming. The only efficient way to move forward in water is to create a propulsive force by oscillating what are called 'hydrofoils', fins and flukes (Fish in Perrin et al. 2002). And the shape with minimal drag is the spindle or 'fusiform' shape (Fish in Perrin et al. 2002): like an elongate teardrop with a round leading edge extending to a maximum thickness and a tapering tail, which reduces turbulences (Senn, 1997; Fish in Perrin et al. 2002) (Picture 7). All oceanic animals, which travel, exhibit variations of this body shape. Even modern submarines are built around this shape nowadays, using this fusiform design (Fish in Perrin et al. 2002). It is one of the basic 'oceanic themes' and it has been forced upon the 'mammalian theme' of the whales by extreme selection pressure

in an aquatic environment (Buchholtz in Perrin et al. 2002), making them indeed look very similar to the ocean's most typical inhabitants: fish. This shows how a



**Picture 7:** Fusiform shape

common physical regime influences the appearance of an organism over time and it is a beautiful example of evolutionary convergence (Cipriano in Perrin et al. 2002). It is from this point of view that this chapter investigates cetacean physiology in general and odontocete and Pilot Whale physiology in particular.

#### 2.2.1 Locomotion

The fusiform shape of fish and marine mammals minimizes drag forces, enabling them to swim great distances at high speed (Senn, 1997). Interestingly, this shape was first investigated in the dolphin by an English scientist around 1800, looking for a solid of least resistive design (Fish in Perrin et al. 2002).

While a fusiform shape is very important to minimize the pressure drag created by pressure differences around the body, viscous drag is created by the adherence of water particles to the skin surface (Fish in Perrin et al. 2002). Therefore, all hair and glands have been lost in all cetaceans and the skin is kept as clean as possible to avoid the settling of algae, barnacles and other organisms (Marshall in Perrin et al. 2002). It has a very high turnover rate of epidermal cells, so the surface is always smooth (Marshall in Perrin et al. 2002). In Pilot Whales it has been found, that small intercellular lipid droplets move with epidermal cells, corneocytes towards the skin surface (Baum et al. 2003). During this transit, different types of lipid compounds aggregate and form a chemically heterogeneous gel, which coats the skin (Baum et al. 2003). It is assumed that it not only helps to maintain a laminar boundary flow (Fish in Perrin et al. 2002) but also supports the cleaning of the skin from settling organisms during jumping (Baum et al. 2003).

Since epidermal lipid droplets exist in all cetaceans (intra- and inter-cellular) but are hardly expressed in terrestrial mammals (Pfeiffer et al. 1993), it has been speculated that these might also help to insulate and lessen the permeability of the skin (Pfeiffer et al. 1993).

Of course, for cost efficient locomotion in water, minimizing drag can only be a complement to a powerful propulsion system. All fast swimming animals use the aforementioned hydrofoils (Fish in Perrin et al. 2002) in the forms of fins and flukes. These are oscillated to push the animal forward and it allows thrust to be generated during the entire stroke cycle, unlike the drag based swimming style of us humans, for example (Williams in Perrin et al. 2002). The necessary force is produced by body muscles along the vertebra, which functions as a stiffening rod for the attachment of the muscles. This is a basic vertebrate blueprint and the reason why a vertebra was 'invented' during evolution.

While fish can swim fast by oscillating left and right with their vertical tail fin, whales employ their horizontal fluke to achieve the same with powerful up and down strokes, still representing the gallop of early hoofed land mammals, from which whales descend (Senn, during lecture).

The massive epaxial muscles above the vertebra provide force for the upstroke, while hypaxial and abdominal muscles are responsible for the down stroke (Marshall in Perrin et al. 2002). The vertebra itself is stiffened in the thorax region and the cervical (neck) vertebrae are even shortened and partly fused to stiffen the body and contribute to streamlining (Marshall in Perrin et al. 2002). From about a third of the body length



**Picture 8:** Skeleton of a delphinid

towards the tail, vertebrae are elongated to allow for the undulating movement of the body with a maximum amplitude in the tail and fluke (Williams in Perrin et al. 2002). In thoracic and lumbar vertebrae, the spinous and transverse processes are long to provide more surface area for the attachment of the body muscles (Picture 8) (Marshall in Perrin et al. 2002).

Flukes and dorsal fins contain no bony structures in all whales but the two pectoral fins called flipper in whales, are supported by the bones of the forelimb and manus (hand) (Marshall in Perrin et al. 2002). They are attached to the axial skeleton by the scapula but there is no functional clavicle in all whales (Rommel and Reynolds in Perrin et al. 2002).



**Picture 9:** Hyperphalangy in *G. melas*: h: humerus, r: radius, u: ulna, I-V: digits

Radius and ulna are flat and the radius is located on the base of the flipper's leading edge (Marshall in Perrin et al. 2002). In Pilot Whales the flippers are very long and sickle shaped, again a design for minimal drag typical for dolphins (Marshall in Perrin et al. 2002). It is accomplished by 'hyperphalangy': an increase in the number of finger bones (phalanges) per digit, which is unusual among mammals (Marshall in Perrin et al. 2002). (Picture 9) Long-Finned Pilot Whales can have 14-15 phalanges in their second and 8 in their third digits, most other whales have less (Reidenberg and Laitman in Perrin et al. 2002). In delphinids, the bones of the flippers are encased in connective tissue and skin and are relatively immobile, to remain stable while swimming (Marshall in Perrin et al. 2002). In all whales, the pectoral fins are mainly used for steering and don't contribute to propulsion during swimming (Thewissen in Perrin et al. 2002).

The bones of the hind limbs have almost completely been lost. Only a rudiment of the pelvis persists in modern cetaceans, but do not contribute to locomotion in any way. Its main purpose seems to be the attachment of a retractable penis in males (Thewissen in Perrin et al. 2002).

Delphinids are the fastest swimmers among whales. Estimates for short sprints range up to 55 km/h but the speed at which the animal will actually travel, is much lower (Fish in Perrin et al. 2002). Since the Pilot Whale is a very big dolphin and smaller animals generally have a greater muscular power output in relation to body size (Fish in Perrin et al. 2002), it cannot reach a maximum speed as high as the smaller dolphins.

#### 2.2.2 Diving

The ability to swim fast comes at a cost. While for rapid swimming oxygen transportation is important, for diving, increased oxygen storage is also necessary but comes at the expense of oxygen transport capability of the blood (Fish in Perrin et al. 2002). Cetaceans who can stay submerged for a prolonged period of time to reach great depths, possess an increased hematocrit (red blood cell) and hemoglobin concentration, which helps to store oxygen more efficiently (Fish in Perrin et al. 2002). Analyzing cetacean blood can therefore reveal swimming and diving capabilities of a species (Fish in Perrin et al. 2002).

Diving is somewhat critical in cetacean life, as it determines a species' ability to spend time foraging submerged and reach certain food sources in the first place (Fish in Perrin et al. 2002). The possession of lungs and the need to return to the surface will always be a limiting factor to any marine mammal's time it can spend, moving freely in a potentially three dimensional medium. Naturally, there are many modifications in cetaceans, allowing for extended dive time (Marshall in Perrin et al. 2002).

The lungs of cetaceans are not greatly increased. Compared to body size, they are even a little reduced in some deep divers (Marshall in Perrin et al. 2002) but not delphinids (Wartzok in Perrin et al. 2002). A lot of what allows whales to make prolonged dives has in fact to do with adaptations in the cardiovascular system (Marshall in Perrin et al. 2002).

To reduce the use of oxygen during diving, most mammals (even humans) display the so-called 'diving reflex functions': the slowing of the heartbeat and the lowering of the volumes of peripheral blood vessels to maintain overall blood pressure (Marshall in Perrin et al. 2002). Whales can additionally reduce blood supply to internal organs like the liver, pancreas and diaphragm, all tolerant for hypoxic conditions (Marshall in Perrin et al. 2002). Blood supply to the intestine, which normally holds up to 50% of blood volume, can be completely shut off (Marshall in Perrin et al. 2002). This is done by connections between the venous and the arterial system, bypassing the oxygen consuming organs (Marshall in Perrin et al. 2002). Similar structures exist before the capillary beds of the skin, where these functions also provide thermoregulation (Marshall in Perrin et al. 2002). Blood supply to the brain remains untouched and it is regulated by a structure not found in other mammals, the rete

mirabili (Marshall in Perrin et al. 2002). This is a dense net of arteries branching off the thoracic aorta, usually supplying the regions between the ribs in land mammals. In whales, they are the main blood supply to the brain and embedded in muscle tissue, which is thought to be under nervous control to prevent pressure peaks, a function usually attributed to the Circle of Willis in other mammals (Marshall in Perrin et al. 2002).

Odontocetes and mysticetes differ considerably in terms of modifications of the venous system. Similar to phocids, odontocetes possess a hepatic sinus and a caval sphincter (Marshall in Perrin et al. 2002). In the beginning of the dive, still oxygenated blood is collected in the hepatic sinus, arriving from the posterior vena cava. It is then continuously fed back to the heart by the caval sphincter, a muscular band forming a circle around the posterior vena cava as it passes through the diaphragm, adding a portion of oxygenated blood with every heartbeat (Marshall in Perrin et al. 2002). Deoxygenated blood from the brain is prevented from entering the vena cava and stored in blood vessels in the lateral abdominal wall, by means of smooth muscles surrounding the veins (Marshall in Perrin et al. 2002). This system is effectively used to store oxygen, in addition to an increased myoglobin concentration in the muscles and the already mentioned hematocrit/hemoglobin increase in the blood (Marshall in Perrin et al. 2002).





Pilot Whales dive for up to 16 minutes and reach a depth of more than 700m (Figure 2) (Stewart in Perrin et al. 2002). To avoid the dangerous loading of the blood with nitrogen at these depths, whales can collapse their lungs, forcing any air out of it, eliminating any gas exchange with the blood (Wartzok in Perrin et al. 2002). A collapsible lung is critical in allowing an animal to withstand the great pressure changes during a dive (Kooyman in Perrin et al. 2002). To further prevent physical stress on nerves, tissues and organs by pressure differences, other air-filled spaces like facial sinuses are absent in whales, except for the middle ear (Kooyman in Perrin et al. 2002). It is protected by a dense net of capillaries which are thought to regulate pressure inside this cavity (Thewissen in Perrin et al. 2002).

In most whales, the lungs are very flexible and allow individual to exhale up to 90%



**Picture 10:** Characteristic blowing by a pilot whale.

of the air in its lungs at once, characteristic resulting in the blowing when the surface at (Wartzok in Perrin et al. 2002). (Picture 10) Since it is necessary to breathe several times to get rid of all the carbon dioxide in the blood and load it again with fresh oxygen, inexhalation optimal and effectively reduces between deep dives (Wartzok in Perrin et al.

2002). In pilot whales, a whole breathing-cycle may last only a second (Olson et al. 1969). To prevent the terminal ends of the airways from collapsing while rapidly exchanging large volumes of gas, they are reinforced by muscles and cartilage

(Wartzok in Perrin et al. 2002). At the end, the blowhole is closed by a thick nasal plug made of fat (adipose) tissue and opened only by the contraction of muscles in the back of the head (Picture 11) (Wartzok in Perrin et al. 2002). There are two blowholes in baleen whales, while in toothed whales, one



Picture 11: Odontocete blowhole

nostril has evolved into a sound producing structure, ending in a vestibular sac just underneath the single blowhole (Frankel in Perrin et al. 2002). It is located on the back of the head in all cetaceans and enables the animals to breathe while swimming at the surface, without having to elevate the head out of the water, assuring smooth and efficient locomotion (Fish in Perrin et al. 2002).

As another modification to facilitate underwater life, odontocetes can completely separate air and food passages by laryngeal cartilage plates, which close the connection between the nasopharyngeal duct and the mouth cavity, avoiding the leakage of water during ingestion of food (Thewissen in Perrin et al. 2002).

During a dive it is important maintain a specific weight close to water in order not to waste energy by overcoming positive or negative lift forces (Marshall in Perrin et al. 2002). The bones of whales are solid and lack a medullar canal (Marshall in Perrin et al. 2002). It is thought that these heavy bones act as a balance weight to the big lipid stores of the blubber (Marshall in Perrin et al. 2002).

#### 2.2.3 Thermoregulation

Blubber is an enlargement of the hypodermis (Marshall in Perrin et al. 2002) and can make up 25-40% of bodyweight (Pfeiffer in Perrin et al. 2002). It is continuous over the whole body and is a dense, vascularized layer of adipose tissue, varying in thickness (Iverson in Perrin et al. 2002). Its lipids are made up of unsaturated fatty acids, which are characteristic for cetaceans (Iverson in Perrin et al. 2002). It is also greatly enriched with collagen and other elastic fibers, making it firm and tough (Iverson in Perrin et al. 2002). Blubber can in many ways be regarded as the ticket to aquatic life for a marine mammal as it serves as a body streamliner helping to achieve the famed fusiform shape and as a spring for hydrodynamic locomotion, providing a counterforce to the muscles (Iverson in Perrin et al. 2002). It also helps to maintain water balance and is an important energy store, holding up metabolism when far away from feeding grounds, so as during long travels, mating season and most importantly, during gestation and lactation (Iverson in Perrin et al. 2002). However, its most important function is to provide insulation (Iverson in Perrin et al. 2002).

Water transmits heat 25 times faster than air (Elsner in Perrin et al. 2002) and the means of thermoregulation in this environment become just as important a theme, for warm blooded mammals, as the inevitable fusiform shape. In general, even the

smallest marine mammals are about one or two orders larger than the smallest terrestrial mammals, because of the lower surface to volume ratio that large bodies possess, minimizing heat loss through the skin (Iverson in Perrin et al. 2002). All marine mammals additionally rely on some form of blubber for insulation, even the furry pinnipeds (seals, sea lions and walruses) and sea otters (Iverson in Perrin et al. 2002) and its other functions become restricted, if insulation capabilities are compromised. While large whales can fast for weeks and months, small whales, with their higher surface to volume ratio, are not capable of this (Iverson in Perrin et al. 2002). Likewise, for the small newborns it is critical to gain weight as fast as possible and the high fat content in whale milk (30-60%) is designed to build up the young's blubber fast (Iverson in Perrin et al. 2002). Migration to warmer breeding grounds can be a means to avoid the stress of the newborn but not for delphinids, as food is often unavailable there and small species cannot lactate without feeding to prevent the loss of their insulation (Iverson in Perrin et al. 2002). Pilot whales always stay in cold to temperate waters and follow their food permanently and do not alter the thickness of their blubber.

In regions of the body where the blubber is thin such as pectoral fins and fluke, arteries are directly surrounded by several veins (Marshal in Perrin et al. 2002). In these circumarterial veins, cooler blood from the periphery is warmed by the blood of the arteries as it flows back towards the core of the body, preventing it from cooling (Marshall in Perrin et al. 2002). These countercurrent heat exchangers can also be switched off by shunting blood away from the central artery towards the skin surface and heat is now actually being dumped to the environment (Marshall in Perrin et al. 2002). Obviously, to regulate temperature not only means to insulate, but also to provide discharge of excess heat. Large whales actually face the challenge of overheating, due to their low surface to volume ratio, but also for smaller species, these thermal windows are very important (Castellini in Perrin et al. 2002).

Reproductive organs are especially sensitive to the build up of body heat. Unlike terrestrial mammals where the testes of males lie outside the body to ensure lowered temperature for sperm production, in whales they lie inside the abdominal slit for streamlining purposes. To keep them at a lowered temperature, even when a lot of heat is generated by the adjacent hypaxial swimming muscles, the arteries leading to the testes are equipped with countercurrent heat exchangers and are supplied directly with cooled blood from the dorsal fin and fluke (Marshall in Perrin et al. 2002). Similar structures are used in pregnant females to cool the abdominal region, as elevated temperatures could harm fetal development (Marshall in Perrin et al. 2002).

#### 2.2.4 Feeding

An animal's capability to swim and dive directly affects its diet, as the ocean provides many food sources that are out of reach of the ones who are bound to stay at the water surface. Even though primary production is highest at the surface, the first trophic stages of life are too small for individual predation and can only be filtered or 'skimmed', the feeding strategy of the great baleen whales.

Odontocetes possess homodont teeth designed to hold on to bigger and prey, like fish and squid, also living deeper in the water column (Hooker in Perrin et al. 2002). Many delphinids posses a large number of cone shaped, teeth. In the spinner dolphin

Stenella longirostris, there are up to 64 teeth on each side of the lower jaw and up to 62 in the upper (Miyazaki in Perrin et al. 2002). In pilot whales they are significantly reduced in number to about 8-13 on each side of the lower jaw and 15-18 on each side of the upper jaw (Miyazaki in Perrin et al. 2002). An adaptation also found in Risso's dolphins



**Picture 12:** Pilot whale skull with homodont, cone shaped teeth.

*Grampus griseus* and sperm whales *Physeter macrocephalus*, all heavy squid consumers like pilot whales themselves (Olson and Reilly in Perrin et al. 2002). To get to their prey, pilot whales are foraging for schools of squid on the continental shelf break and in slope waters of high topographic relief (Olson and Reilly in Perrin et al. 2002). Due to the difficulties of observing an actual dive of an individual whale, the strategy of prey location is not fully known but it is certain that pilot whales like most dolphins make use of their echolocation system, which will be discussed in chapter 2.2.6 'Echolocation and Hearing' (Ballance in Perrin et al. 2002). It is also

assumed that pilot whales track down prey individually (Balance in Perrin et al. 2002) but might forage as a group, exploring an area of suspected prey abundance in a certain formation (Heithaus and Dill in Perrin et al. 2002). How they actually get close to their prey and how they eat it is completely unknown, but existing theories say, that the sounds produced by the echolocation system can be used to stun the prey, making it immobile at least for a few moments (Ballance in Perrin et al. 2002). It then is sucked into the mouth by a piston-like action of the tongue and gular muscles (Ballance in Perrin et al. 2002). However, these theories remain to be tested (Ballance

in Perrin et al. 2002). Pilot whales do not eat squid only, but it has been found that for a Faroese population, the main diet consists of mostly two squid species, *Todarodes sagittatus* and *Gonatus sp.*, but *T. sagittatus* is eaten exclusively



#### Picture 13:

The 'flying squid' *Todarodes sagittatus* is the preferred prey species of pilot whales in the Faroese.

whenever it is available (Picture 13) (Desportes, 1993). In Newfoundland populations, this place is taken by *Illex illecebrosus* (Mercer 1975). The long-finned squid *Loligo pealei* seems to be the favored meal of pilot whales off the coast of the northeastern United States (Gannon et al. 1997).

To reduce the energetic cost of diving, pilot whales, like many other species, largely hunt at night when the squid emerge from the depths to feed in the upper layers of the water column, thus minimizing their own diving depth and synchronizing to the diel life pattern of their prey (Heithaus and Dill in Perrin et al. 2002).

The assumption that odontocetes use a sonar system to locate prey is of course based on the fact that there is little to no light, either at great depth or at night, for the eyes to pick up. It is uncertain whether the bioluminescence of squids plays a role in catching them in the dark and to what extent the eyes are used, even during hunting in light penetrated waters (Silber in Perrin et al. 2002). While young whales are known to eat shrimps and smaller squid species from the onset of weaning at 6-7 months of age and about 2m in length, for immature and for lactating females, as well as males over 5m, fish seem to be an important supplement to the squid diet (Desportes, 1993) and pilot whale pods have been known to follow fishing vessels for opportunistic feeding on fish which escape whatever catch method (Gannon et al. 1997). Still, the importance of squid remains unchallenged, making up close to 80% of the diet and its pursuit forces the broad seasonal migration patterns of squid upon pilot whales (Gannon et al. 1997). This will be further discussed in chapter 2.4.4 'Seasonality and Migration'.

Once food is ingested, it is swallowed into the first of three stomach compartments, the fore stomach (Reynolds in Perrin et al. 2002). It is muscular, very distensible and acts as a receiving chamber, much like a bird crop (Reynolds in Perrin et al. 2002). From there, food enters the second glandular stomach, the primary site of chemical breakdown by enzymes and hydrochloric acid (Reynolds in Perrin et al. 2002). The third stomach compartment, the pyloric stomach is 'U-shaped' and ends in a strong sphincteric muscle, regulating the flow of digestive material into the duodenum (small intestine), which itself is expanded into a sac-like ampulla in all cetaceans (Reynolds in Perrin et al. 2002). There is also a lack of a cecum between the small and large intestines (Reynolds in Perrin et al. 2002).

#### 2.2.5 Osmotic Problems

With the intake of food, inevitably a certain amount of salty seawater is swallowed. The problem with all vertebrate organisms is that the osmolality (electrolyte concentration) of their body fluid is only a third of seawater (Costa in Perrin et al. 2002). Since there is obviously no freshwater available in the ocean to dilute body fluids, marine vertebrates must actively get rid of excess electrolytes in order to maintain homeostasis (the balance of all body functions) and prevent dehydration (Costa in Perrin et al. 2002). Vertebrate food could benefit minimal salt ingestion, but since squids are invertebrate mollusks, they essentially are isotonic to seawater and this diet presents no relieve from osmotic stress (Costa in Perrin et al. 2002).

Whales lack any glands and therefore the possibility to excrete salt via sweat glands or a special gland, like fish or marine birds (Costa in Perrin et al. 2002). To maintain their osmolality, their source of freshwater is metabolic water production from oxidation of fat, carbohydrates and proteins. It can most likely supply the organism of a regularly feeding animal with enough water (Costa in Perrin et al. 2002). The greatest amount yields fat with 1,07g of water produced for every gram oxidized (Ortiz 2001). In this regard, the lipids of the blubber gain a whole new importance in keeping up metabolic functions in addition to their role in insulation and energy storage.

During fasting however, metabolic water production cannot fulfill the body's demands and most marine mammals are suspected to actually drink seawater if necessary, as their kidneys are capable of producing urine of higher concentration than seawater (Costa in Perrin et al. 2002). This is absolutely necessary if the excess of ingested electrolytes is to be excreted without a net water loss. Kidneys of a terrestrial mammal lack this ability and given only seawater to drink, it would die quickly of dehydration (Ortiz, 2001).

Cetacean kidneys differ from ours in being multireniculate, meaning a single kidney is made up of numerous functional units, reniculi, each similar in function to a whole kidney and enclosed in a sheet of connective tissue and peritoneum, the membrane of the abdominal cavity (Beuchat in Perrin et al. 2002). Several of these units can be arranged in a grape-like cluster along the ureter (Beuchat in Perrin et al. 2002). Between the cortex, where filtered blood plasma is converted by numerous nephrons to urine, and the medulla, where they drain through the papilla into the ureter, a structure is found, called sporta perimedullaris, which is also missing in terrestrial mammals (Beuchat in Perrin et al. 2002). It is a layer of connective tissue with smooth muscles and glycogen stores, through which numerous vascular elements from the cortex lead into the medulla (Ortiz, 2001). Most likely, the sporta doesn't contribute to effective urine production, but is an adaptation to ensure renal function during pressure changes while diving (Ortiz, 2001). Analysis of chemical functions has even shown, that cetacean kidneys are not more powerful by the inherent strength of their design and increased urine concentration is achieved by more conventional methods, such as hormonal control and elevated formation rate (Ortiz, 2001).

But water is not only lost during excretion of urine or feces, but also through respiration, lactation and flux through the skin (Costa in Perrin et al. 2002). This 'cutaneous' loss can be quite high, making up 70% of the total water loss in a fasting animal and water conservation becomes vital (Ortiz, 2001).

Respiratory loss is minimized by controlled breathing and the lung's capability to absorb about twice as much oxygen per breath as humans, for example, reducing the number of breaths to be taken for the same amount of oxygen and with it the loss of evaporating water contained in the warm gases exhaled (Costa in Perrin et al. 2002). This way, a whale can save 30-77% of the water which a land animal usually loses by respiration (Ortiz, 2001). The high concentration of fat and proteins in mother's milk in whales is most likely due to the needs of the young and rather a fortunate coincidence than a specialized adaptation for water conservation (Costa in Perrin et al. 2002).

#### 2.2.6 Echolocation and Hearing

While it is the soluble salts of seawater that cause osmotic stress, it is the insoluble compounds that cause turbidity and in the ocean even during brightest daylight visibility can range from several tens of meters to only a few centimeters. Any marine organism will probably spend the most part of its life in an environment with suboptimal visibility. As a result, vision loses much of its usefulness and hearing becomes more important, as it is independent from available light and water conditions (Thewissen in Perrin et al. 2002). This, as well as the difference in sound propagation through water compared to air, has led to great modifications of hearing and sound production in marine mammals (Thewissen in Perrin et al. 2002).

Odontocetes are even more specialized in their ability to echolocate (Hooker in Perrin et al. 2002). They use sounds to actually identify and locate specific targets, i.e. to forage, navigate and avoid predators as opposed to just being able to hear echoes from large obstacles (Au in Perrin et al. 2002). Although the use of this 'biosonar' has only been scientifically tested within a few species of odontocetes, all toothed whales capable of producing short, high frequency click sounds are thought to be able to echolocate, including pilot whales (Hooker in Perrin et al. 2002).

The clicks of most toothed whales are very short and have a broad frequency bandwidth, ranging from 20 to 60kHz (Hooker in Perrin et al. 2002). It can be shifted, at least in bottlenose dolphins *Tursiops truncatus*, Belugas *Delphinapterus leucas* and false killer whales *Pseudorca crassidens* to over 100kHz if background noise exceeds a certain level and usually involves an increase in amplitude, too (Hooker in Perrin et al. 2002). Duration and interval of the clicks can be adjusted to fit distance,

size and properties of the focused object (Hooker in Perrin et al. 2002). The highest amplitude of click signals has yet been measured in bottlenose dolphins and reached a tremendous 225dB re  $1\mu$ Pa (Au in Perrin et al. 2002).

Toothed whales can also produce lower frequency sounds, such as barks and whistles that extend down to human hearing range (Hooker in Perrin et al. 2002). But these are most likely used for communication and identification purposes, as many pods and even individuals are known to have a vocabulary of sounds that differ from others (Hooker in Perrin et al. 2002). This will be discussed in more detail in chapter 2.4.1 'Communication'. These social sounds can be very loud as well, in pilot whales up to 180dB re 1 $\mu$ Pa in order to be heard over several kilometers (Würsig and Richardson in Perrin et al. 2002). The sounds produced by fluking and breaching, though not as far ranging, belong into the same category of social signals and will also be discussed in chapter 2.4.1 (Whitehead in Perrin et al. 2002).

Sound production in toothed whales is not achieved by vocal chords in the larynx as in mysticetes but by two sets of specialized structures called phonic lips or 'monkey-lips' because of their shape (Au in Perrin et al. 2002). They protrude into the upper

nasal passage and are associated with the dorsal bursae, complicated cartilaginous structures of the two nares containing fat and air sacs (Frankel in Perrin et al. 2002). Air is pushed past them into the vestibular sac right underneath the blowhole, where it can be either pushed back or released, causing the



Odontocete sound production by the 'monkey lips' in the dorsal bursae.

phonic lips to slap together (Picture 14) (Frankel in Perrin et al. 2002). The generated vibrations are controlled by muscles and transmitted via the structures of the 'melon' (Au in Perrin et al. 2002). It is a lipid filled sac right above the elongated maxilla and premaxilla on the animals forehead, which is responsible for focusing and directing the beam of sound into the water like an acoustic lens (Frankel in Perrin et al. 2002).

#### 2. The Long-Finned Pilot Whale



#### Figure 4:

Sound propagation by the melon and reception in the lower jaw of delphinids.

Since all odontocetes except the sperm whale *Physeter macrocephalus* possess two of these monkey lips / dorsal bursae complexes, they are thought to be able to produce two different signals simultaneously (Figure 5) (Frankel in Perrin et al. 2002). The signals emitted from the side of the head are slightly distorted from the main beam with the



**Figure 5:** Paired structures in odontocete sound production.

maximum amplitude, which leaves the head straight forward in about a ten degree angle up from the anterior to posterior axis (Au in Perrin et al. 2002). This, as well as the slightly skewed symmetry of an odontocete skull, is thought to support stereophonic imaging by taking advantage of the small phase shifts of the different returning echoes arriving at the ears (Dolphin in Au et al. 2000).

These apparently lack pinnae and the external auditory meatus is greatly reduced and narrow albeit being still supported by cartilage (Thewissen in Perrin et al. 2002). And the acoustically most sensitive area is not the external opening of the auditory meatus but the skin of the lower jaw, right below the eyes (Au in Perrin et al. 2002). At this mandibular window, sound that enters the skin is propagated through the thin lateral walls of the jaw called pan bones onto a pad of fat, which extends towards the anterior into the hollow mandibular foramen (Thewissen in Perrin et al. 2002). On the

posterior end, this pad touches the extremely thin wall of the ectotympanic bone, housing the middle ear with malleus, incus and stapes, as well as the tympanic membrane (Thewissen in Perrin et al. 2002). In odontocetes, the ectotympanic is fused with the petrosal bones of the inner ear, enclosing the whole hearing and balance apparatus in one capsule, which is connected to the remainder of the skull only by a very small piece of cartilage (Thewissen in Perrin et al. 2002). This whole tympano-periotic complex is suspended by several ligaments and further isolated by a spongy, foam-like tissue (Marshall in Perrin et al. 2002).

To be able to detect small objects more than one hundred meters away and distinguish material properties, such as wall thickness down to 0,3mm, as performed by bottlenose dolphins in a test situation, the response of the auditory nervous system must be very fast, in order to detect and integrate the smallest time intervals and pitch shifts of returning echoes (Au in Perrin et al. 2002). Detection capabilities, calculated from the 0,3mm threshold in wall thickness, result in 0,5-0,6µs for time intervals and 2-3kHz for broadband pitch shifts. And with a measured integration time of 264µs, the auditory response of dolphins is faster than any other mammal (Au in Perrin et al. 2002). Considering the exceptionally large brains and convolute cortex of odontocetes, in absolute and relative measures, this is not too surprising (Oelschläger and Oelschläger in Perrin et al. 2002).

#### 2.2.7 Brain, Size and Navigation

In the echolocating toothed whales the auditory lobes of the brain are well developed and as in higher primates, the olfactory lobes and nerves have disappeared (Oelschläger and Oelschläger in Perrin et al. 2002). Toothed whales are thought to have lost their sense of smell but some dispute is going on about the existence of a vomeronasal organ, a chemoreceptive organ used mainly to detect sexual pheromones (Reidenberg and Laitman in Perrin et al. 2002). Fetal studies show the absence of this organ in both, baleen and toothed whales (Reidenberg and Laitman in Perrin et al. 2002).

In terms of complexity and size, the odontocete brain is comparable to the human and simian (ape) brains (Oelschläger and Oelschläger in Perrin et al. 2002). The brain weight of a pilot whale is about 2670g (Würsig in Perrin et al. 2002). With a body weight of more than three tons, the brain to body weight ratio is about three times

lower than in humans with a brain size of 1500g (Würsig in Perrin et al. 2002). The bottlenose dolphin reaches the highest specs of any animal in this regard (Würsig in Perrin et al. 2002).

However, 50 million years of separate evolution in a totally different environment have most likely left odontocetes with profound modifications in brain morphology (Oelschläger and Oelschläger in Perrin et al. 2002). And at this size, it is very difficult to draw conclusions about the 'smartness' of an animal (Würsig in Perrin et al. 2002). Due to the size of cetaceans, invasive experiments are not possible and we are forced to look at behavioral clues and try to correlate them with anatomical data, as well as compare them with other mammals in order to get some answers on the intelligence of these animals (Oelschläger and Oelschläger in Perrin et al. 2002). This will be done in more detail in chapter 2.4.1 'Intelligence and Communication'.

One hypothetical modification of the odontocete brain is the ability to use the earth's magnetic field for long distance navigation (Walker in Perrin et al. 2002). A feature which has been observed and successfully tested in sea turtles, birds and fish but never actually in any whales (Walker in Perrin et al. 2002). Strandings of whales in places with magnetic anomalies provided first evidence for this theory (Walker in Perrin et al. 2002). Migration patterns of fin whales *Balaenoptera physalus*, occupying areas of low magnetic intensity (Walker in Perrin et al. 2002), as well as sperm whales *Physeter macrocephalus* traveling within 1° of magnetic north, have further raised awareness that many whales might use biomagnetism as a means of navigation (Stern in Perrin et al. 2002). Magnetite crystals have been found in the dura mater, the tissue surrounding the brain, even of the type smaller than 100nm, which is thought to be most useful to detect magnetic fields (Walker in Perrin et al. 2002). Still, serious experimental testing remains to be done on this subject (Walker in Perrin et al. 2002).

Pilot whales are known for mass strandings where whole groups of animals are beached and eventually die, more so than other whales (Olson and Reilly in Perrin et al. 2002). Whether the animals get trapped and confused in shallow water or misguided by magnetic anomalies is not known and mostly, the beached whales show no signs of diseases, injuries or other weaknesses (Olson and Reilly in Perrin et al. 2002). It is true, at least for some dolphins, that very ill individuals beach themselves to die (Olson and Reilly in Perrin et al. 2002). In the case of pilot whales, strong

social bonds between the animals could probably cause a whole pod to strand, whatever the initial reason was (Olson and Reilly in Perrin et al. 2002).

#### 2.2.8 Reproduction and Life History

No matter how intelligent whales may be, their brains have to be well developed at birth, in order breathe and swim with the pod right away, just like their precocial ungulate ancestors (Reidenberg and Laitman in Perrin et al. 2002). The large size of the brain at birth is partly made possible by the almost complete absence of pelvic bones, which usually affect the passage of the fetus (Reidenberg and Laitman in Perrin et al. 2002). Although hind limb buds are present in embryos, they are absorbed in the fetal period and what remains is only a rudiment of the pelvis, which is not connected to the vertebra. In some species a remnant of the femur in the lateral body wall persists (Reidenberg and Laitman in Perrin et al. 2002).

In males, the retractor muscles for the penis are attached to these bones (Atkinson in Perrin et al. 2002). The fibroelastic penis resides in an s-shape caudal to the genital opening when retracted and no inflation occurs when copulating. Odontocete testes are 7 to 25% larger than what would be predicted for average mammals of the same size (Atkinson in Perrin et al. 2002). The testes lie inside the abdominal cavity to provide a streamlined body shape and are cooled by a vascular plexus, receiving colder blood from the dorsal fin and fluke and acting as a counter current heat exchanger (Reidenberg and Laitman in Perrin et al. 2002). Similarly, the uterus of females must be cooled to provide the right temperature for fetal development (Marshall in Perrin et al. 2002).

Cetaceans posses a bicornuate uterus with two horns joined in a Y-shape (Stewart and Stewart in Perrin et al. 2002). Due to the large size of cetacean newborns - about 8-10% of adult body size - only one young is born, as twins would be incompatible with the mother's body size (Stewart and Stewart in Perrin et al. 2002). In pilot whales, the left ovary is usually larger and 70% of the young develop in the left side of the uterus but with increasing size, amniotic sac and allantois extend into the contralateral horn of the uterus (Stewart and Stewart in Perrin et al. 2002). Later in development, the fetus will also grow into the other uterine horn with its tail end, taking on a slant position compared to the mother (Reidenberg and Laitman in Perrin et al. 2002). This is the reason most whales are born with their tail first, as it will find its way to the

cervix easier in this position during the contractions before birth (Reidenberg and Laitman in Perrin et al. 2002).

Whales as most other marina mammals have diffuse placentation, where the entire chorion is covered with villi to provide a large exchange surface (Stewart and Stewart in Perrin et al. 2002). The epitheliochorial placenta can be pulled way from the maternal tissue without hurting the endometrium, so the mother does not bleed when the afterbirth is expelled (Stewart and Stewart in Perrin et al. 2002). Sometimes, the newborn is helped by others to get rid of the umbilical cord in captive dolphins but since it is extremely rare to observe this in nature, we know very little about the process of giving birth in whales (Reidenberg and Laitman in Perrin et al. 2002). It is necessary though for the birth to be rapid and the newborn to get to the surface immediately to prevent it from drowning (Stewart and Stewart in Perrin et al. 2002).

The length of pregnancy in Pilot Whales is 14.5 to 16 months, which, as in most whales, corresponds to terrestrial ungulates with pregnancies lasting over a year (Reidenberg and Laitman in Perrin et al. 2002). This is necessary to ensure sufficient encephalisation and development of all of the newborn's organs, making it able to swim, see, hear and vocalize directly after birth (Reidenberg and Laitman in Perrin et al. 2002). A newborn Pilot Whale is 1,75-1,8m in length and weighs 70-85kg (Reidenberg and Laitman in Perrin et al. 2002).

The rapid fetal growth occurring in late pregnancy continues after birth and is provided for by the high fat and protein content of the mother's milk (Reidenberg and Laitman in Perrin et al. 2002). Two nipples are located in elongated recesses on either side of the congenital slit and become protruded only during nursing, which again contributes to body streamlining (Stewart and Stewart in Perrin et al. 2002). Milk has to be expelled by muscular pressure since the newborn cannot suck, as it has to hold its breath under water (Stewart and Stewart in Perrin et al. 2002). Still, the muscular tongue of toothed whales is thought to support nursing because it enables the young to create suction with tongue movement, a feature which is also important later when capturing prey (Reidenberg and Laitman in Perrin et al. 2002). The mammary glands themselves extend in the connective tissue under the skin on both sides of the ventromedial line, being elongate, narrow and flat organs (Stewart and Stewart in Perrin et al. 2002).

With 10-30%, the milk of odontocetes generally has a lower fat content than milk of mysticetes and lactation is very long with 1-3 years compared to the much shorter 5-7 months of mysticetes (Oftedal, 1997). Prolonged parental care is a means to increase the efficiency of reproduction and the delayed onset of weaning rather serves social than nutritional functions (Olson and Reilly in Perrin et al. 2002). In pilot whales, traces of milk were even found in the stomachs of nearly adult animals (Desportes, 1993). Odontocetes can do this because they do not exhibit the same seasonality as baleen whales, which undergo much longer periods of fasting during migrations from feeding to breeding and mating grounds and back (Reidenberg and Laitman in Perrin et al. 2002). Although pilot whales, as most toothed whales, are in pursuit of their food all year long, mating is broadly seasonal, too. This will be further discussed in chapter 2.4.4 'Seasonality and Migration'.

Pilot whales reach adulthood at about 8 years in females, when they reach an average length of 3,7m, and 12 years and 4,6m in males, respectively (Olson and Reilly in Perrin et al. 2002). Large males grow to more than 6m and three tons of weight, while females reach about half the weight (Bloch et al. 1993). Average lengths of males and females are 5.5m and 5m, respectively (Reidenberg and Laitman in Perrin et al. 2002). Males live up to 46 years and females up to 59 years (Bloch et al. 1993).

With their long lifespan, delayed maturity at different times for males and females, seasonal mating, prolonged birth intervals and the production of a single calf, pilot whales share most life history traits with other odontocetes (Olson and Reilly in Perrin et al. 2002).

#### 2.3 Phylogeny and Evolution

During the previous chapters, it was shown on a number of examples how whales adapted to become fully aquatic. However, the vastly different appearance and lifestyle make it difficult to imagine that they are close relatives of the even-toed ungulates that we humans are so familiar with, as many of them have been domesticated, including pigs, goats, sheep, camels, water buffalos, llamas and alpacas (Price et al. 2005). As early as 1891, British scientist Flower observed similarities between these artiodactyls and cetaceans (Price et al. 2005), namely larynx, stomach and liver, as well as the muscle retracted, fibroelastic penis in males and lumps of tissue along the umbilical cord (called umbilical pearls) in females (Theodor in Perrin et al. 2002).

How cetaceans relate to artiodactyls is still controversial as artiodactyl phylogeny itself is not resolved yet (Price et al. 2005). For a number of years the theory was favored, that cetaceans are a sister taxon to the now extinct mesonychids, four footed land mammals that lived during the Early Tertiary, 65 million years ago (Figure 6)

(O'Leary in Perrin et al. 2002). They were special because they possessed hooves like plant eaters but carnivorous teeth (O'Leary in Perrin et al. 2002) and were thought to descend from the same plant eating condylarth ancestor, like Artiodactyla (Price et al. 2005).



Figure 6: Mesonychid skeleton.

Since the mid 1990's, several molecular studies have pointed in another direction, placing cetaceans in close relation to hippopotamidae, actually including them in the artiodactyl clade, which has therefore been renamed Cetartiodactyla (Price et al. 2005). And since condylarths are no longer seen as a monophyletic group, cetartiodactyl heritage is still somewhat unclear (Price et al. 2005). Nevertheless, it can be assumed that before they left the land, the earliest cetacean ancestors at least resembled the mesonychids (O'Leary in Perrin et al. 2002).

#### 2.3.1 The Ancestors of Whales

The first known direct ancestors of whales are called archaeocetes and represent the first radiation of cetaceans in the Eocene, 55 to 34 million years ago (Thewissen in Perrin et al. 2002). Several families exist within the archaeocetes: Pakicetids are known to have lived from early to middle Eocene in India and Pakistan. They varied in size between a small fox and a larger wolf. Some of their teeth resembled the dentition of hyenas and they had very muscular jaws, a nasal opening near the front of the head and dorsally facing eyes, similar to crocodiles. It was only their ears that

clearly show they were cetaceans /Picture 14, Figure 7) (Thewissen in Perrin et al. 2002).



**Picture 14:** A reconstruction of Pakicetus based upon their skeleton.





Later in the middle Eocene, ambulocetids already show a soft connection between the lower jaw and the inner ear, indicating that hearing adaptation indeed arose early in cetacean phylogeny. Ambulocetidae were about the size of a of a large sea lion, still with a long snout, muscular jaws and short legs with long, paddle-shaped, four-toed feet and five fingers that each terminated in a hoof. They were thought to swim by paddling their hind limbs and creating additional thrust with their tail. Their habitat were near shore marine environments like estuaries or bays. They were better swimmers than the freshwater only pakicetids and ambush hunters like modern crocodiles (Figure 8, Picture 15) (Thewissen in Perrin et al. 2002).



Figure 8: Skeleton of Ambulocetus

Remingtonocetidae also appeared in the middle Eocene and could still support their own bodyweight on land with long hind limbs. Their ears were larger and farther apart and the fatty connection between the lower jaw and the ear was also bigger than in any pakicetid or ambulocetid (Picture 16) (Table 1) (Thewissen in Perrin et al. 2002).

**Picture 15:** Recreation of Ambulocetus head.

In Protocetidae, hind limbs were reduced and the innominate (hip bone) was not connected to the vertebra, suggesting that the hind limbs did not support the full body weight. Instead, the tail was well developed to help with the creation of propulsive force. Their nostrils were located more caudally on the long snout, enabling them to



**Picture 16:** Remingtonocetidae of the species Kutchicetus, about the size of otters.

breathe without lifting the head, a general trend in cetacean evolution that would result in the dorsal blowhole of modern cetaceans. Likewise, in protocetids we observe the trend of reduced occlusal basins in teeth, a feature that was characteristic for the chewing morphology of their ruminant ancestors

(including pakicetids and ambulocetids) but became useless for these predators. Like remingtonocetids, protocetids were thought to live in shallow, near tropical marine
environments but were the first ones to live on all continents (Thewissen in Perrin et al. 2002).

With the occurrence of basilosauridae and dorudontidae in the late middle Eocene, the first major radiation of cetacean species was complete (Fordyce in Perrin et al. 2002) and these animals were the most 'whale-like' of all the archaic archaeocetes. Hind limbs were almost completely missing and there was no sacral vertebra although the caudal peduncle was elongated by homologous vertebrae (Uhen in Perrin et al. 2002). The humerus and radius/ulna of the forelimbs were flattened and the movement of the elbow was restricted to this same plane. While basilosaurids lack the upper third molars and the general structures of masticatory teeth, like basins, they retained heterodonty. They ranged in size from 4 to about 16 meters (Uhen in Perrin et al. 2002).



### Figure 9:

Basilosaurid skeleton: hindlimbs were still present, including toes but tiny in size.\$

Basilosaurids are thought to have given rise to the modern cetaceans, also called Neoceti as opposed to the extinct archaeocetes, in a second major radiation, starting in the early Oligocene, around 30 million years ago (Fordyce in Perrin et al. 2002). Both, baleen and toothed whales share a basilosaurid ancestor, making the modern Cetacea a monophyletic group. Recently, there were arguments that sperm whales *Physeteridae*, were more closely related to mysticetes but the most recent studies confirm an affinity to odontocetes, making each of these two a monophyletic sister taxon to the other (Fordyce



**Picture 17:** An artist's recreation of a dorudont.

in Perrin et al. 2002). A compilation of early archaeocetes is given in Table 1.

The evolution of early archaeocetes. From top: Remingtonocetidae, Protocetidae, Basilosauridae, Dorudontidae



Although ancient Neoceti resembled each other more than today's odontocetes and mysticetes, the divergence in echolocating predators and baleen filter feeders was already established and can be detected by features of the skull. The 'nasal drift', the shifting of the nares towards the dorsal part of the head enabled later archaeocetes to

keep their heads submerged while breathing at the water surface (Figure 10). While in both groups there was a trend towards the elongation of the anterior part of the skull, termed 'telescoping', the filter feeders evolved to have only loosely connected jawbones, which are bent outwards and are mobile to a certain degree, supporting the feeding action of filtering plankton with baleen plates by pressing water out of the mouth cavity (Fordyce in Perrin et al. 2002).



**Figure 10:** Nasal drift with increasingly aquatic lifestyle.

In odontocetes, the jaws are narrow, stiff and connected anteriorly ('symphyseal') and there is the important connection of the mandibular window to the ear by the fatty tissue inside the hollow lower jaw. Also, the maxilla of the upper jaw rises posteriorly over the frontal and builds a concave 'fossa' or trench, which forms the origin of the various facial muscles that control sound production and propagation by controlling the various air sacs in the soft nasal passage, as well as the melon (Fordyce in Perrin et al. 2002). The odontocete skull grew more and more asymmetrical and the inner ear eventually became completely detached from the skull. Again, the most popular distinguishable feature of the two groups is the single blowhole in toothed whales and the paired nostrils of baleen whales (Hooker in Perrin et al. 2002).

## 2.3.2 Toothed Whales and Delphinids

Finally, there was a third major radiation of cetacean species in the Middle Miocene, 12 to 15 million years ago, in which some archaic mysticetes (cetotheres) became extinct and baelenopterid whales, including blue and humpback whales, became the most specious mysticetes. But it was the odontocetes that diversified the most, especially dolphins (Delphinidae), porpoises (Phocoenidae) and Nar- and Beluga Whales (Monodontidae) which all belong to the Delphinoidea superfamily (Fordyce in Perrin et al. 2002). Delphinids themselves became the most specious family of all odontocetes only by the end of the Pliocene, when they were subject to an explosive evolution, probably replacing more ancient delphinoids, which declined at that time (Barnes in Perrin et al. 2002). Today, there are ten extant families in odontocetes with

at least 71 species, half of which, namely 36, are true dolphins (delphinids), including the Long-Finned Pilot Whale (Hooker in Perrin et al. 2002).

Modern odontocetes generally exhibit polydonty, an increased number of teeth, although in



**Picture 18:** Kentriodon, an early delphinid from the Miocene

the pilot whales this has been reduced as a secondary adaptation to their main food source, squid (LeDuc in Perrin et al. 2002). Polydonty is a feature that could have existed before in archaeocets but all modern mysticetes lack teeth, except for teeth buds in juvenile animals (Uhen in Perrin et al. 2002). All odontocetes are monophyodont, meaning there is only one set of teeth growing throughout life, as opposed to the deciduous teeth, which are replaced by adult teeth later, a condition still present in archaeocetes. All delphinids possess homodont cone shaped teeth (Uhen in Perrin et al. 2002). There is however a wide range of tooth counts in different species, ranging from less than 10 in the Risso's dolphin *Grampus griseus* to 250 in the spinner dolphin *Stenella longirostris* (LeDuc in Perrin et al. 2002). Pilot whales can have a total number of 40 to 62 teeth (Miyazaki in Perrin et al. 2002).

Pilot whales do not have the typical beak that most dolphins possess, a feature, which is also absent in killer whales (*Orcinus*), pygmy- (*Feresa*) and false killer whales (*Pseudorca*) and Melon-headed whales (*Peponocephala*) (LeDuc in Perrin et al. 2002). In all of these species, the forehead is rounded or even bulbous but it is only in the pilot whale that this contributes to a dramatic sexual dimorphism, as the forehead of the larger males is more rounded and can protrude over the lower jaw (LeDuc in Perrin et al. 2002). In most other delphinid species, except for the killer whale with the erect dorsal fin and increased size of the male, there is a much more subtle dimorphism in body size, shape and coloration (LeDuc in Perrin et al. 2002).

Today, most delphinids inhabit tropical to temperate waters on both hemispheres (Forcada in Perrin et al. 2002), making the Pilot-Whale a somewhat unusual dolphin,

as it only exists antitropically, in the waters of the North Atlantic and the cold to temperate oceans on the of the southern hemisphere (Olson and Reilly in Perrin et al. 2002). The two populations never mix and as noted earlier, exhibit slight morphological differences and are therefore divided into two subspecies, *Globicephala melas* in the north and *Globicephala melas* in the south (Olson and Reilly in Perrin et al. 2002).

### 2.3.3 Geographic Events and Major Radiations

Much of the speciation we observe today can be accounted for by the cyclical changes in sea level, associated with global cooling within the last 2.5 million years of the Quaternary period (Pleistocene to recent) (Fordyce in Perrin et al. 2002). Although pilot whales are the only single species with a northern and southern hemisphere population, there are northern / southern species pairs, which are very closely related and must have been separated from each other by changing sea temperatures and currents at earlier times, for example the dusky and Pacific white-sided dolphins (*Lagenorhynchus obscurus / obliquidens*) (LeDuc in Perrin et al. 2002). A recent example is the segregation of short-finned pilot whales off the Pacific coast of Japan, with different schools following different temperature currents and although there is geographical overlap, the schools never mix and morphological differences can be seen (Kasuya et al. 1988). There is also evidence of a division of two North Atlantic subpopulations of pilot whales, also following temperature patterns (Bloch and Lastein 1993)

When investigating the major steps in cetacean evolution it is important to note the climatic, ecological and geographical changes that concurred with the major radiations. Otherwise it would be difficult to understand why and how terrestrial animals could take over the oceans, inhabited by creatures far more adapted (Taylor in Perrin et al. 2002). It is not only ungulates that have made their way back to the sea: this has happened many times in history with birds, reptiles and other mammals (except marsupialians). In fact, the ecological niche modern cetaceans inhabit once belonged to the reptile Ichtyosaurs and their decline in the early Eocene cleared the space for the archaeocetes (Picture 19) (Taylor in Perrin et al. 2002).

These already lived in nearshore and riverine environments, taking the place of ambush hunters, like modern crocodiles (Taylor in Perrin et al. 2002). It can only be

hypothesized what drove them there in the first place, whether it was the local marine productivity of the Tethys seaway between Asia and India that supplied these animals with food inaccessible to others (Fordyce in Perrin et al. 2002), or whether



**Picture 19:** Ichtyosaurus

they were seeking refuge from land predators in shallow waters (Taylor in Perrin et al. 2002). And again the stages of transition from a partially to a fully aquatic lifestyle remain largely unknown (Taylor in Perrin et al. 2002). Fact is, that by the end of the Eocene, the first fully aquatic cetaceans, the basilosaurids had undergone major changes mainly in their locomotory abilities, loosing their hindlimbs and developing sickle shaped, finlike forelimbs (Fordyce in Perrin et al. 2002). (We do not know about the tail fluke and dorsal fin, as they have not been conserved by ossification.) The second major radiation of the Late Eocene gave rise to the Neoceti rather quickly, within about five million years and was triggered by the final breakup of Gondwana land and the resulting cooling of the oceans and increased tropics to polar temperature gradients (Figure 11) (Fordyce in Perrin et al. 2002). For the first time we observe filter feeding mysticetes as well as echolocating odontocetes, clearly distinguishable

by the changes in the inner ear, affecting hearing abilities and resulting in the first dramatic increase of brain size (Marino et al. 2004). This would happen later again with the radiation of Delphinoidea in the Miocene, although this time, the ecological shifts underling this are not as clear (Fordyce in Perrin et al. 2002).



Figure 11: Laurasia and Gondwana, 200 million years ago.

### 2.3.4 The Evolution of Big Brains

It can generally be said that most odontocetes are social animals, living in groups or 'pods', as opposed to the rather solitary lifestyle of mysticetes (Connor in Mann et al. 2000). Due to their size and feeding habits, the large baleen whales cannot benefit from the advantages of group living as the smaller toothed whales and vice versa. And although the initial increase of brain size in odontocetes can clearly be linked to the development of echolocation, the trend to even higher encephalisation among delphinids is harder to understand in just ecological terms (Marino et al. 2004). After all, modern dolphins display a degree of social interaction, communicative and cognitive abilities second only to primates, including the understanding of complex commands and mirror recognition (Oelschläger and Oelschläger in Perrin et al. 2002). Yet, they share the same environment and sensory abilities of all other toothed whales, in which the degree of encephalisation has not changed significantly since their first radiation (Marino et al. 2004).

It can still be assumed, that it is the requirements of a social life in stable groups which has fueled delphinid intelligence (Connor in Mann et al. 2000). And if we look at other highly encephalised mammals, a trend towards raised intelligence becomes apparent for species with strong social bonds, small number of offspring and prolonged parental care (Würsig in Perrin et al. 2002). However, our knowledge about most delphinids and whales in general is yet too limited and the common concepts of measuring intelligence too weak, to enforce this theory with certainty (Würsig in Perrin et al. 2002).

# 2.4 The Ecology of Group Living

Pilot whales live in 'pods' of 50 to 200 animals, in constant pursuit of squid (Hoydal and Lastein, 1993). From genetic analyses we know that the offspring of neither sex leaves the group of their mother and we also observe strong social bonds among the animals (Amos, 1993). Still, it is not clear whether these large schools are actually stable units or aggregations of much smaller 'families' of about 10 or 20 animals which might only form when conditions allow for it (Connor in Mann et al. 2000, Acevedo-Gutiérrez in Perrin et al. 2002). After all, besides the need of well developed social skills and efficient locomotion, there are definite costs to group living and the benefits may be greater or lesser, depending on the situation. And just like in

physiology, the aquatic medium determines many factors of this equation (Connor in Mann et al. 2000).

Predation pressure by killer whales and sharks is regarded to be one of the biggest forces, driving group formation in cetaceans (Norris and Dohl, 1980). This is true even for the biggest baleen whales, as it is the young calves, which are most vulnerable to attacks (Connor in Mann et al. 2000). Forming a group can reduce the risk of an individual being detected by a predator in the first place, assuming that in the water, with its limited range of sight, it does not make that much of a difference to detect an individual or a group (Connor in Mann et al. 2000). In the case of an attack, an individual might be able to locate the predator earlier, as it can be warned by other members of the group and a large, well organized group might even be able to confuse or scare away the attacker. The chances of individuals being attacked are reduced simply by a dilution effect since the predator cannot attack all animals in the group and, given the size of cetaceans, cannot eat the whole group at once (Connor in Mann et al. 2000).

On the other hand, resource competition is one of the factors preventing group formation, as can be seen in the large baleen whales. Their size and feeding habits prevent several fully grown individuals from exploiting the same food sources. Still, aggregations of baleen whales do exist but mostly during their fasting period, for example when seeking shelter in tropical bays to breed and mate. However, these are no stable mutualistic groups and do persist only when conditions allow it (Connor in Mann et al. 2000).

As noted above, it is uncertain whether the largest schools of pilot whales and other odontocetes are true mutualistic groups in that sense, or if the stable units are much smaller. But the fact that these animals hunt relatively big, individual prey, which is abundant in swarms, lets them avoid the dramatic effects of food competition seen in the big mysticetes. In fact, up to a certain group size, greater prey detection and better habitat defense through collaboration are actually beneficial to group stability and the low cost of locomotion for the spindle shaped animals yields further benefit to an individual following a group (Connor in Mann et al. 2000). There are numerous examples of individual animals, pilot whales and other dolphins, which actually have been known to swim together with one or several others for many years (Würsig in Perrin et al. 2002).

With the long parental care from the mother and the time it takes for the offspring to become sexually mature one would expect an extensive set of social skills and behaviors for the young to acquire. In reality, we do observe numerous examples of complicated, even playful interactions between individuals, yet the interpretation of what we see is tricky, due to the difficulties of observing cetaceans in general and analyzing individual behavior in particular (Würsig in Perrin et al. 2002). Still, the fact that certain behaviors differ from one population of the same species to another, like different hunting techniques in killer whales or the ability to herd fish swarms by certain bottlenose dolphins, permits the conclusion that there are skills which are actively learned by the young (Würsig in Perrin et al. 2002).

In matrilineal whales, such as in pilot whales and killer whales, it is of course the mothers who play a major role in transmitting what can ultimately be called 'culture' to the next generation (Whitehead, 1998). This acquired behavioral repertoire represents a great increase in fitness to the individuals who have mastered it over the others. We observe an unusual low diversity of mitochondrial DNA among matrilineal pilot whales and Orcas (killer whales), suggesting that reproductive success is far greater for lineages where these cultural traits and consequently the maternal genes are inherited (Whitehead, 1998). It is also in these two odontocetes that we find a pronounced menopause in females, still living with their group several years after cessation of menstrual cycles. This shows the value of these 'grand mothers' to the group despite their inability to breed and is only known in humans among non cetaceans (Whitehead in Perrin et al. 2002).

### 2.4.1 Intelligence and Communication

In order to orchestrate a group of individuals to behave as one stable unit, sophisticated communication is absolutely necessary along with sufficient processing capabilities of the brain. In a boundary less aquatic medium where sight is often restricted, sound has proven to be far more efficient than sight, as it is transmitted over large distances in the water (Tyack and Clark in Au et al. 2000). Although the short, high pitched sounds of echolocating odontocetes are not transmitted as well as the long, low frequency tones of mysticete songs, animals swimming as a group still hear the returning echoes of their conspecifics (Würsig in Perrin et al. 2002). This way, the group as a whole probably increases its detection ability and it has been

speculated, that the neuronal processing required to distinguish between echoes returning from self emitted sounds and the ones returning from neighbors, is responsible for the actual degree of encephalisation we observe in delphinids (Würsig in Perrin et al. 2002).

However, besides the clicks for echolocation, pilot whales, like many delphinids, can also vocalize sounds of much lower pitch, which are used for direct communication between animals. In long-finned pilot whales, these vocalizations where found to be at an average frequency of about 4500Hz (in the short-finned pilot whale they are at around 7900Hz) and can be heard more often when the group displays increased activity (Olsson and Reilly in Perrin et al. 2002). It has been observed in killer whales and bottlenose dolphins that these sounds can function as a signature whistle, with which the animals recognize their group, as well as individuals, especially mothers and their young (Tyack and Clark in Au et al. 2000). A single whistle sound can change in pitch during its length and it is not surprising, that there are 'dialects' between groups. At least in matrilineal species, this could function as a means to judge the degree of relatedness and possibly avoid inbreeding (Tyack and Clark in Au et al. 2000). Still, these mechanisms have not yet been confirmed for pilot whales, although it is likely they exist in a similar fashion.

Over the years, scientists where tempted to call the diverse vocalizations of dolphins 'language'. And although in experiments individuals have proven to be able to learn to understand a sign language, including interpretations of a simple syntax, it is not sure whether all of the communication happens consciously or if there is simply a certain amount of automatic response mechanisms, which could be triggered by a variety of events (Herman in Perrin et al. 2002). For example, what is interpreted as angry vocal bursts in some dolphins can also be heard in a 'friendly' situation, when an animal is excited over the encounter of another group or the detection of fish (Tyack and Clark in Au et al. 2000).

Of course, as with any animal, one would also expect a repertoire of non verbal forms of communication, especially since there are a number of dolphins that do not produce the whistling sounds for communication (Dudzinski et al. in Perrin et al. 2002). Indeed, we do observe actions such as 'tail slapping' and 'breaching' in many cetaceans and of course in pilot whales. The action of breaching has been described earlier as a means to help remove parasites from the skin. But the fact that we observe

increased breaching activity in more social species (Whitehead in Perrin et al. 2002) and in situations of general excitement or arousal deriving from sexual stimulation, location of food or response to injury and irritation, has led to the assumption that breaching is also a means of communication (Dudzinski et al. in Perrin et al. 2002). It could be an expression of 'honest signaling', an action that accompanies another attribute of the signaler and cannot be faked (Whitehead in Perrin et al. 2002). Honest signaling can be used to add emphasis to a previous vocalization, visual display or any other signal in situations of courtship, extreme annoyance, defiance of an enemy or general display of strength (Whitehead in Perrin et al. 2002). Of course, it could also be a form of play, especially for young animals, although in pilot whales we do not observe the impressive artistic leaps we know by some dolphins. And as it has happened many times that seemingly playful behavior was misinterpreted and later turned out to be important signaling, we should be very careful with our preconception of what looks 'just like play' (Whitehead in Perrin et al. 2002). What is neither understood is the function of the sound produced by the animal reentering the water. It can be heard over a certain distance but not greater than the tones produced in the animal's forehead (Dudzinski et al. in Perrin et al. 2002). It cannot be ruled out that it serves additionally to the aforementioned purposes as a 'sound barrier' during hunting and herding of fish (Whitehead in Perrin et al. 2002).

When tail slapping, the animals slap the water surface with their fluke several times in a row, which also produces underwater sound albeit not a very loud one. This is often observed from boats approaching a group and could be a sign of annoyance or alert to other group members, similar to the clapping noise of jaws (Dudzinski et al. in Perrin et al. 2002).

All these means of communication can still be regarded as an acoustic type, since what goes on above the water surface cannot be seen from below. Visual and tactile communication methods definitely exist as well but are very hard to observe and investigate (Dudzinski et al. in Perrin et al. 2002). Visual displays include for example the 's-shape' posture, often seen in playing or aggressive dolphins. Tactile communication obviously takes place all the time among animals swimming together, and gentle touches with fins, flukes and beaks happen frequently, especially between mothers and the young, of course (Dudzinski et al. in Perrin et al. 2002). It is possible that also loud sonar clicks can be felt by the animals with their sensitive skin, due to

the high energy of the peaks. Scuba divers who were 'scanned' by dolphins from very close, report a distinct feeling on the skin along the line of the sound hitting the body and many animals have been observed to approach the jaw or genital region of another, emitting a burst of clicks and 'buzzing' its conspecific (Dudzinski et al. in Perrin et al. 2002).

Somewhat controversial is the question whether communication in pilot whales and other odontocetes also includes olfactory senses. Most literature states that odontocetes have lost their smelling ability, but pheromones have been found in waters with traces of excrements (Dudzinski et al. in Perrin et al. 2002). And as mentioned before, there is a dispute about the existence of a vomeronasal organ to detect sexual pheromones (Reidenberg and Laitman in Perrin et al. 2002).

### 2.4.2 Mating and Reproduction

The wooing for a partner is certainly an important aspect of life and of course, variations of communication methods and behavior patterns described in the former chapter are also used during courtship. As noted, we see increased breaching when animals meet and there is increased body contact and tactile stimulation between a couple before copulation. But it is important to realize that courtship behavior in cetaceans is not as explicitly specialized for this situation only (Würsig in Perrin et al. 2002). However, the most powerful means of 'sexual communication', in case of the pilot whale, is the dimorphism between males and females, as it is on constant display (Würsig in Perrin et al. 2002). Males are larger, have longer fins and their forehead is more bulbous than their female counterparts'.

In many species, sexual dimorphism and polygyny go hand in hand, as this advertisement of the male is supposed to reach as many females as possible (Würsig in Perrin et al. 2002). In a number of pilot whale pods tested for genetic kinship, all the young came from only one or two males (Amos et al. 1991). This would suggest a certain competition amongst males to gain access to females and we do observe scars on many males, suspected to result from intraspecific fighting. (Amos et al. 1993). Conversely, there are also observations of collaboration among males, forcing themselves onto females (Würsig in Perrin et al. 2002) and there are independent reports from Newfoundland and the Faroese of male mating groups, which were thought to travel between pods (Desportes et al. 1992). It seems very likely that males

segregate temporarily to form independent bachelor schools to mate with a group of non kin females. This would ensure reproductive success, which increases for maximally outbred offspring or, in other words, with genetic dissimilarity of the parents (Amos et al. 2001)

The same test mentioned above also produced results, showing that none of the males in the pods were the fathers of the young (Amos et al. 1991). There is also no evidence for strong male reproductive dominance on a genetic level. This makes sense insofar, as too much competition between related, genetically similar individuals holds no benefit and maybe it is simply not possible, due to short encounters and the difficulties for males to control groups of females in a three dimensional environment (Amos et al.1993). Still, the dilemma between competition and collaboration persists and it could be, that sperm competition is responsible for the contradictory results observed in reality (Ralls and Mesnick in Perrin et al. 2002). Typically for large odontocetes, pregnancy lasts longer than one year and up to 16 months in pilot whales (Reidenberg and Laitman in Perrin et al. 2002). Females can give birth all year long (with a slight increase during summer) since they are not bound to synchronize their reproductive cycles to the seasonal abundance of food and related migrations patterns, as the large baleen whales have to (Trillmich in Perrin et al. 2002). And while mysticetes cows fast during many stages of their reproduction and wean their young already after half a year of lactation at peak feeding season, postnatal care is obviously much longer in pilot whales like in all odontocetes (Trillmich in Perrin et al. 2002). Weaning may also start as early as 6-7 months after birth, but it is not abrupt (Desportes and Mouritsen, 1993). Judging from parasite infections that come from prey, almost all young feed regularly on solid food by the age of two and may feed simultaneously on mother's milk and solid food like small squid and crustaceans for up to five years. There are reports of even older animals (7 and 12 years for a male and a pregnant female individual) with traces of milk in their stomachs (Desportes and Mouritsen, 1993). It is not sure whether these animals just occasionally drink their own mother's milk or if there is some communal nursing that would facilitate an individual to benefit from the readily available resource (Desportes and Mouritsen, 1993). A newborn calf is about 1,6 to 1,7 meters in length and will grow to a little more than two meters before the onset of weaning (Bloch et al. 1993, Desportes and Mouritsen, 1993). Males are sexually mature at 12 years of age when

they reach about 4,6 meters, females at 8 years and 3,7 meters (Olson and Reilly in Perrin et al. 2002).

Although food is available all year round, the cost of intensive postnatal care is considerable and reproductive cycles are longer than the two years generally observed in mysticetes. Still, this strategy yields increased reproductive success and female pilot whales can 'afford' to breed only every 3 to 6 years (Acevedo-Gutiérrez in Perrin et al. 2002) and still ensure a similar proliferation rate as observed in other cetaceans (Olson and Reillyin Perrin et al. 2002). Pilot whale cows may give birth to about 5 or more calves in their life time and may live longer than 20 years past their reproductive senescence (Acevedo-Gutiérrez in Perrin et al. 2002).

## 2.4.3 Social Structure

The importance of old females in the matrilineal society of pilot whales has been pointed out several times and it is not surprising that they live much longer than males, as they are very valuable and probably enjoy more protection and support from the group. The fact that males are not always present in their natal group increases the risks of predation or injury, resulting in a generally higher selection pressure and mortality (Andersen, 1992). Males are thought to live up to 46 years and females up to 59 years. Accordingly, we observe a female sex bias in pilot whale pods of about 60% (Bloch et al. 1993). Genetic evidence stating that males are not always present in their pod corresponds well with male mating behavior, described in the former chapter (Andersen, 1993). But no effect on group composition could be detected by observation, suggesting that the segregation of males is never for too long and not constant (Amos et al. 1993). Sex ratio is also constant for different sized schools, all year long, even during prime mating season in early spring (Bloch et al. 1993). Obviously, males gain benefit by participating in feeding groups with older females but they are probably only tolerated by close relatives, making them follow their own natal pod for life and only the apparent inbreeding taboo within this pod forces the males to leave periodically (Amos et al. 1993).

In a large-scale analysis of the Faroese pilot whaling data concerning population structure, there where 26,1% immature males and 13,4% mature males, 20,2% immature females and 40,8% mature females. About 7-10% of a pod's individuals are non pregnant and non lactating females and a total of 46% are immature (Bloch et al.

1993). Again, these numbers demonstrate the higher mortality of males - there are initially more immature males than immature females - as well as the relatively large amount of females which are not in a reproductive state.

Estimation of school sizes based on observational methods range from several tens to 200 to more than 1'000 individuals. And although it is difficult to estimate such big numbers in the field, the 1'200 animals caught in the largest recorded Faroese hunt from 1940 seem to confirm this, even exceeding the expectations (Bloch et al. 1993). But school sizes vary from year to year with smaller but more numerous aggregations in peak periods and larger schools during years when the abundance of pilot whales is low at the Faroese. Interestingly, this trend is not random but follows a 120 year interval, which seems to be somehow related to average surface temperatures (Bloch et al. 1993). It seems likely that pilot whale society shares certain characteristics of the fusion-fission type societies observed in other dolphins, where groups join and split up, depending on the situation (Andersen, 1993). Most likely, it is the abundance of prey (number and kind) dictating the optimal lifestyle of their predators and leading to changes in group size. Stable units are assumed to comprise a minimum of several tens up to 200 individuals (Bloch et al. 1993).

Although the numbers from the Faroese Islands give us a very valuable impression of pilot whale group structure, one should be cautious to expect the exact same numbers for any population of pilot whales, as a population is can be made up of several stocks or subpopulations for which circumstances can differ considerably. Besides suspected local subdivisions (Andersen, 1993), there are at least two major stocks in the North Atlantic (Bloch and Lastein 1993). The one which was subject to increased whaling activity during 1947-72 off the Newfoundland coast suffered greatly and the numbers of animals declined rapidly while no change in abundance could be detected for the moderately hunted population at the Faroese (Mercer 1975). Faroese and Newfoundland populations actually differ significantly in skull and torso lengths and flipper lengths in males (Bloch and Lastein 1993). Differences in parasite composition between populations of the eastern North Atlantic (near France and the Faroese) and Newfoundland show that pilot whales probably do not travel routinely between these areas (Fullard et al. 2000). But the patchiness of the North Atlantic population is difficult to detect on a small scale level because of the low maternal DNA diversity we observe in matrilineal whales and which is used to assess kinship (Thewissen in

Perrin et al. 2002). Still, when examining the data carefully it became clear that isolation occurs between areas of different sea surface temperatures and is not necessarily distance related (Fullard et al. 2000). This fits well into the picture of what we know about certain mechanisms of speciation during odontocete evolution (see chapter 2.3.3 'Geographic Events and Major Radiations') as well as the observed segregation of the short-finned pilot whale *G. macrorhynchus* in Japan, which is also dependent on sea surface temperature (Kasuya et al. 1998). Less is known about the mechanisms of the segregation of the southern population of the long-finned pilot whale (*G. melas edwardii*) except, that it must have occurred during or before one of the last glacial periods, which happen every ten to several tens of thousands of years (Fordyce in Perrin et al. 2002). Differences between these two populations are the white streaks behind the eye and the variable grey saddle markings behind dorsal fins, which rarely seen in the North Atlantic but are quite common on the southern hemisphere (Nelson and Lien, 1996).

There are no estimates on the worldwide abundance of pilot whales. But for the northeastern North Atlantic, a total number 778'000 animals has been calculated from large scale surveys, out of which around 104'000 live around the Faroese (Buckland et al. 1993) and an additional 10'000-12'000 animals are thought to live in the western North Atlantic (Payne and Heinemann 1993). This population might have once contained 60'000 animals, before the whaling in this area grew to an industry (Mercer, 1975). 200'000 Pilot whales *G. melas edwardii* are estimated for the southern population around the Antarctica (Kasamatsu and Joyce, 1995).

### 2.4.4 Seasonality and Migration

Although the movements of odontocetes can be quite far ranging, they cannot be compared to the migration of baleen whales with their timed intervals, traveling from feeding to breeding grounds and back, fasting simultaneously. This is the reason some authors rather call their seasonal movements 'ranging', since it involves a change in 'home range' due to the dependency on a certain resource, squid in the case of pilot whales, which also moves seasonally (Stern in Perrin et al. 2002). There is no predictable pattern like traveling from polar regions to the equator and the movements vary from year to year, according to environmental factors and the routes of the squid schools. There is also no change in life style, i.e. no fasting and no dedicated

migration season. Pilot whales rather pursue their prey constantly and are therefore always moving (Olson and Reilly in Perrin et al. 2002).

It is difficult to say how far an animal might travel over the course of a year but satellite tracking methods have been used to find individuals with a daily travel of up to 234 km and about 70-80 km on average (Nelson and Lien, 1996) (Connor in Mann et al. 2000). The energetic costs of migration are probably not significantly higher than the energy an animal uses to move around in its home range (Stern in Perrin et al. 2002). This also provides for the pods to be able to move as a group, since it is affordable for an individual to participate at a low energetic cost (Acevedo-Gutiérrez in Perrin et al. 2002). And indeed, patchy allele distribution in the North Atlantic population shows that the animals migrate as kin (Andersen, 1993).

Large scale migration patterns of pilot whales in the North Atlantic are still unknown but there is a striking coincidence between several populations and their favored squid species. For example, pilot whales from a population following schools of long-finned squid *Loligo pealei* in Northwestern U.S. waters, have been shown to swim over the shelf edge between the 100-2000 m contours during winter and spring, where the squids themselves hunt for fish, also inhabiting the self edges and slopes (Payne and Heinemann, 1993). In late summer and fall, the squid move onto the shelf, closer to the coast and accordingly, we find pilot whales distributed more widespread but closer to land (Payne and Heinemann, 1993). Similarly, a more northern population off Newfoundland whose main diet is the short-finned squid *Illex illecebrosus* moves in a circular movement inshore in late summer and to the more southern shelf edges during winter (Mercer, 1975). The same goes for a population on the Scotian shelf (Gowan and Whitehead, 1995).

Obviously, shelf edges are important for the squids to hunt for fish, such as blue whiting *Micromesistius poutassou* and juvenile Atlantic mackerel *Scomber scombrus*, which also appear on the pilot whale's menu sometimes (Payne and Heinemann, 1993). The size and number of squids caught in commercial fisheries are always greatest along the shelf edges (Hoydal and Lastein, 1993) and independent findings that pilot whales are consistently associated with areas with the steepest topography illustrate nicely the close association of pilot whales and the locally abundant and favored squid species (Hui, 1985). For the Northeastern U.S. population it could even be shown that not only the yearly movements of pilot whales were dependent on the

squid but their number also varied with the average amount of squid caught, with peaks of pilot whale abundance during peaks of *Illex illecebrosus*. (Although the peaks of pilot whales were declining steadily, indicating depletion of the population in heavy whaling during 1951-61) (Mercer, 1975).

However, it could also be possible that a number of animals simply move to another area in low squid years, as has been suggested for the Faroese population with two suspected stocks, one swimming around the islands all year long, the other moving close to the islands only when conditions allow for it (Hoydal and Lastein, 1993).

Out of all the factors that may influence the abundance of pilot whales, temperature has been shown to have a significant effect. During a period from 1980-1985 with a general low abundance of animals around the Faroese, there was a very notable exception in 1982 when peak catches occurred. During that year, the 5° isobar was reaching much further south, forcing Atlantic water from the south closer to the islands (Hoydal and Lastein, 1993). An increase in the number of schools and total animals around 1920 could be connected to a mean annual increase in the surface water temperature. Even the 120 year cycle already mentioned in the previous chapter follows the mean annual temperatures of the waters south of Greenland (Hoydal and Lastein, 1993). However, this relationship was reversed around 1920 as well, possibly due to the difference in the distribution of squid since that time. General years with high occurrence of pilot whales were 1709-1750, 1800-1880 and 1935 to the present, while already declining (Bloch et al. 1993).

The notion from the previous chapter, that the genetic differences among pilot whales are more related to temperature than to distance (Fullard et al. 2000) seem to emphasize the importance of temperature conditions in the North Atlantic to pilot whales, respectively to their prey. Very likely, the North Atlantic Current and its branches, transporting warm water from the gulf stream further north, are important in determining the conditions in the eastern North Atlantic and the migrations of squid and whales alike (Hoydal and Lastein, 1993).

### 2.4.5 Distribution

Not surprisingly, pilot whales are scarce in the cold northern most waters of the North Atlantic (Buckland et al. 1993). Otherwise they range from Greenland to Iceland to the Barents Sea and possibly the Baltic Sea to cape Hatteras on the U.S. coast in the

west and northwest Africa in the east, including the Mediterranean Sea. On the southern hemisphere they are seen mainly north of the Antarctic Convergence in the cold Humbolt-, Falkland- and Benguela Currents (Nelson and Lien, 1996).

It is not sure whether pilot whales are present in the North Sea and they are not seen often in Dutch and Belgian waters and east of Britain (Nelson and Lien, 1996). No long-finned pilot whales are found in the North Pacific nor in the Bering Sea, only their short-finned relatives *G. macrorhynchus*. Long-finned pilot whales were thought to have inhabited the Sea of Japan only until the  $12^{th}$  century (Nelson and Lien, 1996).

## 2.5 Food Sources

The apparent close relationship of pilot whales and their prey has been described and it becomes very plausible when considering the amount of food a single animal needs. An average whale of 4m in length, weighing 830kg appears to require about 11-14kg of food to fill its stomach. With an estimated digestion time of 8 hours the animal would need to fill its stomach three times a day, resulting in an intake of 4,1-4,9 % of bodyweight a day or 15-18 times its weight in a year (Mercer 1975).

Water is a very good heat conductor and it is very important for the animals to have their isolation and energy store well supplied to keep from cooling and to be able to almost constantly move in a fluid environment (Costa in Perrin et al. 2002). It is also very advantageous to spend as little energy as possible, especially during foraging, which is a more or less constant activity. A close association with prey yields the possible benefit of facilitated hunting by adapting to certain prey behavior (Costa in Perrin et al. 2002). Squid are know to rise in the water column at night, feeding near the surface and returning to greater depths during the day and accordingly, pilot whales are thought to hunt preferably at night when they do not have to dive as deep (Desportes and Mouritsen, 1993). However, there are reports from animals which exhibited the greatest diving activity at dusk and dawn (Nelson and Lien, 1996). And considering that digestion time is less than 8 hours, feeding is likely to occur during the day, too and probably changing according to prey behavior and geographical characteristics (Desportes and Mouritsen, 1993). Pilot whales hunt at depths from 100-500 m although deeper living squid species, such as Gonatus sp. found in the stomachs of some animals, indicate that the whales dive to greater depths at certain times (Desportes and Mouritsen, 1993). Smaller animals tend to consume smaller

prey, which can be younger individuals of the preferred squid species or a different kind. The diel migration effects of moving closer to the surface at night and returning to the bottom during daylight are also more pronounced in immature squid species (Brodziak and Hendrickson, 1998) and younger whales might probably not dive as deep as adults (Desportes and Mouritsen, 1993).

Every population of pilot whales seems to have a favored squid species that can be relied on almost exclusively when sufficiently abundant. This diet can be supplemented with a large range of other food items, including fish and shrimps. In an investigation from the Faroese, it was the younger animals, most notably the ones not exceeding 3 m in length, which appear to have a somewhat more diverse diet with about 24% other species than squid (Desportes and Mouritsen, 1993). Trace food items other than squid seem to be equally important and in eastern and western North Atlantic populations (Gannon et al. 1997).

The most amount of fish and the biggest number of different species are consumed by lactating females (Desportes and Mouritsen, 1993). Obviously, a lot of energy is transferred to the suckling and the available time to forage for the mother becomes restricted due to the intensive parental care. Fish yield greater energy per volume than squid and clearly, lactating females must make up for their energy loss while nursing by eating more potent food. It is not clear why these resources are not exploited more intensively by the majority of the animals. Some fish like cod, herring and mackerel, all reported to be part of a pilot whale diet, where not consumed at all in this study although they were abundant in great numbers (Desportes and Mouritsen, 1993).

### 2.5.1 Prey Species

The fish that are consumed by pilot whales include the aforementioned cod *Gadus morhua*, Greenland turbot *Rheinhardtius hippoglossides*, Atlantic mackerel *Scomber scombrus*, Atlantic herring *Clupea harengus*, hake *Urophycis spp.*, silver hake *Merlucius bilinearis*, Atlantic argentine *Argentina silus*, blue whiting *Micromesistious poutassou* and many others (Olson and Reilly in Perrin et al. 2002). Many of these fish occur on the shelf edges and the number of pilot whales abundant could not only be correlated to the biomass of squid but also to the blue whiting for example, which spawns along west coast of the British Isles from March to April (Hoydal and Lastein, 1993) or the Atlantic mackerel in the Northeastern U.S. (Gannon et al. 1997).

However, squid also feed on these species so it is also possible that the underlying cause is not so much the fish themselves but the squid species sharing the same habitat (Payne and Heinemann, 1993).

Fish make up less than 10% of total food ingestion and the remaining 90% are squid, often dominated by on species (Desportes and Mouritsen 1993). In the Faroese it is the flying squid *Todarodes sagittatus* and occasionally the more northern and deeper living armhook squid *Gonatus sp.* but to a far lesser extent and only when *T. sagittatus* is scarce. This depends particularly on the North Atlantic current as *T. sagittatus* are spawning in an area north of the Azores and migrate to the Norwegian Sea with the current (Shimko, 1989). Different routes are taken every year and not all pass the Faroese. During these absent times, pilot whales are further offshore hunting

for the deeper living species and less abundant around the islands (Desportes and Mouritsen. 1993). There is a general correspondence between good 'squid years' on the Faroese, whales caught and the abundance of squid in Norwegian waters (Hoydal and Lastein, 1993) The diet becomes almost monospecific in August



**Picture 20:** Long-finned squid *Loligo Pealei*.

and September, consisting almost exclusively of *T. sagittatus* when it is abundant on the shelf (Desportes and Mouritsen, 1993).

In Northeastern U.S. waters, the long-finned squid *Loligo pealei* takes the role of *T. sagittatus* in the Faroese, making up 77% of ingested food (Picture 20). Similarly, in years when it is scarce, the preference shifts towards the short-finned species *Illex illecebrosus* (Gannon et al. 1997). *L. pealei* spawns in deep waters in mid winter and moves onto the shelf during late summer, along with the pilot whales (Payne and Heinemann, 1993). It is more neritic, meaning it inhabits the shelf in the neritic zone above 200 m, than the more oceanic *I. illecebrosus* and is more consistently associated with environmental factors such as temperature and depth. It also prefers

warmer waters than *I. illecebrosus* and its diel migrations are more pronounced (Brodziak and Hendrickson, 1998).

# 2.6 Threats and Diseases

In its 1994 edition of the 'Red List of Threatened Species' (also known as the IUCN Red List or Red Data List), the International Union for the Conservation of Nature and Natural Resources (IUCN) ranks the conservation status of the long-finned pilot whale as 'conservation dependent', which means that it might become a threatened species within a short time if no measures are taken (Wikipedia, 2007). But apart from a substantial depletion in Newfoundland waters due to heavy whaling, it is not know how the worldwide population is developing (Mercer, 1975). The Newfoundland population may or may not be recovering and numbers for a worldwide trend are even harder to estimate (Olson and Reilly in Perrin et al. 2002). Yet, as pilot whales are no longer commercially exploited except in the drive hunts of the Faroese where stocks are large enough and the removals are considered to be sustainable (Olson and Reilly in Perrin et al. 2002), it is probably safe to say that pilot whales do not share the same immediate threat to their survival as many of their cetacean relatives. Nevertheless, pollution of the seas and disturbance by human operations present an ever increasing problem which affects all species alike, in addition to the natural threats like predators, parasites and diseases. This increased habitat pressure might very well affect the population on a large scale but of course, it is almost impossible to say to what extent (Evans in Perrin et al. 2002).

# 2.6.1 Natural Threats

Pilot whale are amongst the largest delphinids and due to their size, they do not have many natural enemies. The only real threat in terms of predation comes from sharks and other big delphinid predators, such as the transient killer whales. It is possible that also pigmy and false killer whales (and maybe short-finned pilot whales) could present a certain threat, as they are all predators equipped with harmful teeth (Weller in Perrin et al. 2002). However, the same is true for long-finned pilot whales and given their social organization it seems that only the biggest of predators could pose a serious threat to an individual, which enjoys a certain protection from its group. High speed chases by groups of killer whales do happen but are not as common as in other

smaller dolphins and usually the hunting groups are bigger than average, indicating that a lot more effort is needed to capture a large pilot whale (Weller in Perrin et al. 2002). In many baleen whales predation by killer whales poses the biggest threat to newborn calves and younger animals in general. Even in the biggest odontocetes, sperm whales (*Physeter macrocephalus*), this has led to a more social lifestyle of the females, as the mothers are forced to collectively watch out for their young while they take turns diving for food (Connor in Mann et al. 2000). Whether the predation pressure on pilot whale young is as big is hard to say. Generally, populations in near shore environments exhibit more scars resulting from predation, presumably since the chances to hide and escape after an initial attack are somewhat bigger than in the open ocean, where the animal is more likely to get killed (Weller in Perrin et al. 2002).

But apart from the immediate threat of a predator, there are the dangers of parasites and diseases, which are less obvious to observe but can have a significant effect on populations. Most of these are not specifically limited to just pilot whales and appear in many if not most other marine mammals (Raga et al. in Perrin et al. 2002). Most notably, there is an ancient helminth fauna (parasitic worms) abundant in cetaceans, which has almost disappeared on land and attests to the long isolation of their hosts since the time they moved into the water (Raga and Balbuena, 1993). Some are also found in seabirds and other vertebrates, of which the best studied is *Anisakis simplex*, a parasitic nematode. It uses first crustaceans then fish and squid as intermediate hosts and gets ingested with food. Its eggs are laid in the whale stomach and spread with feces. Pilot whales are thought to be important vectors for these parasites and in

regions where their abundance is low infestation of fish schools is also lower (Raga and Balbuena, 1993).

In total there have been 21 different epizoic or endoparasitic species counted in pilot whales. Most of them inhabit the stomach and inner organs except for three species of crustaceans which live on the skin surface, which is unique among mammals (except for cirripeds in pinnipeds.) The ones detected in pilot



**Picture 21:** Close up view of the hale louse *Isocyamus sp.* 

whales are one cirriped species, one copepod and the whale louse *Isocyamus delphini* of the class *Malacostraca*, which is very common among whales, as its name suggests (Picture 21) (Raga et al. in Perrin et al. 2002). It has a direct life cycle with no intermediate hosts and gets transmitted by body contact. Males appear to be more infested since they fight more and the scars and bruises on their skin present an ideal habitat for the parasites (Raga and Balbuena, 1993). All other parasites are flat whorms (*Plathelminthes*) of the classes *Trematoda* (*Digenea* - 4 species), *Cestoda* (8species), *Acantocephala* (1 species), and round worms *Nematoda* (4 species). The majority of them inhabit the main stomach while a few nematodes live in the air sinuses and the respiratory system as well as the mammary glands (Raga and Balbuena, 1993).

Most of these parasites where not found to have a significant effect on generally healthy individuals, i.e. produce no apparent pathology except for a few. The trematode *P. Gastrophilus* causes cysts in the stomach, mesenteries and blubber. The nematode *A. simplex* is responsible for an increasing amount of ulcers in older animals and *Crassicauda spp.* inhabits reproductive organs in males and females and may affect productivity (Geraci and St.Aubin, 1987). But most harmful is its effect on milk production when infesting the mammary glands, significantly lowering the amount of calories available for the young in a heavily infested population (Raga and Balbuena, 1993). The digenean trematode *Nasitrema sp.*, despite being very inconspicuous, is thought to severely damage the liver and pancreas and is able to enter the brain through the cranial sinuses, supposedly leading to mass mortality in selected populations (Geraci and St.Aubin, 1987).

This is difficult to observe when happening far from land in the open ocean and several of these events might have been overlooked. It is more easily detectable when a population near shore is affected since ill or weak animals will beach themselves deliberately in order to be able to stay at the water surface and keep breathing (Perrin and Geraci in Perrin et al. 2002). During the late 1980's, there was an unusual increase of such strandings and despite the difficulties of figuring out the reasons (see also chapter 2.6.3 'Mass Strandings') they were related to an outbreak of a Morbillivirus among marine mammals, decimating some populations by more than 50% (Di Guardo et al. 2005).

Morbilliviruses are known from terrestrial mammals and are causing canine distemper, the measles as well as the cattle-plague (rinderpest-virus) and during the last 20 years, at least 8 epidemics where recognized (Di Guardo et al. 2005). Two strands of this type of virus (the Porpoise and Dolphin Morbilli Virus) are known from many other cetacean species while one strand has been isolated in pilot whales only, dubbed 'Pilot Whale Morbilli Virus' (PWMV) accordingly (Taubenberger et al. 2000).

The origin of this virus remains largely unknown, although it is likely to have been transferred from land mammals. After a mass die off of seals in Lake Baikal and the northern European coasts in 1988, killing several ten thousand animals, a novel virus was found named 'Phocid Distemper Virus' due to the symptoms. Further investigations showed that it was a Morbillivirus and in the case of the Baikal seals, similar to one which is found in most dogs of this area (Di Guardo et al. 2005). Still, the Siberian and European epidemics did not seem to be caused by the same agent and the relationships between the different strands and epidemics are not clear. By the beginning of the 1990's first cases of ill dolphins occurred in the western Mediterranean and by now there are reports from all over the world. Again, pilot whales are suspected to be an efficient vector for these pathogens, importing them from the North Atlantic (Di Guardo et al. 2005). There are some recent reports of pilot whale populations becoming resistant to the virus (Olson and Reilly in Perrin et al. 2002) but this must be taken with caution since most likely, marine mammals had never been affected by this kind of virus before, otherwise the effects would not have been so devastating (Di Guardo et al. 2005).

The degree of infestation by a parasite and the general well being of a population is highly influenced by water temperature and chemistry. Especially the whale louse and other epizoic parasites are more prevalent in warmer waters. A population of intermediate hosts can also account for the spread of a disease but since the major parasites of pilot whales are either directly transmitted or swallowed with their favored prey with which they are consistently associated, this has a limited over all effect. Probably all pilot whales become infested with several parasites when starting to eat solid food and normally, they do not seem to be greatly affected in their doings (Raga and Balbuena, 1993). Yet, when an animal's immune system is already impaired, relatively innocuous organisms can suddenly become a big threat to the

weakened animal. To an individual this can be relevant when injured or exhausted or ill but it is hardly of great concern regarding the well being of the whole population. Bad water quality and chemical pollution however can seriously lower the average fitness of a population to the extent, where the accumulative 'losses' of the individuals present the parasites and pathogens with a great advantage (Raga and Balbuena, 1993). The outbreak of the Morbillivirus in the 1980's was linked to an increasing pollution by organochlorine compounds (Perrin and Geraci in Perrin et al. 2002), mainly to PCB, in northern U.S. waters, the Baltic seas and the Mediterranean (Jiménez et al. 2001).

### 2.6.2 Pollution, Disturbance and Fishing

The fact, that human caused changes of the ecosystem pose a more and more serious threat to whales and dolphins, cannot be ignored. The world of many of our marine species is invaded on several levels and cetaceans are particularly sensitive to this habitat pressure with their peculiar lifestyle and specific requirements (Evans in Perrin et al. 2002). In addition, many species still suffer from the raging whaling industry of the last century, bringing many to the brink of extinction. But yet, whenever conservation efforts are undertaken, biologists are faced with the difficult task to find direct evidence for the observed demographic changes, which do not always follow direct interferences with humans (Evans in Perrin et al. 2002).

Pollution, for example, is a major factor whose effects cannot be easily recognized in animals. Organic substances like PCB and DDT accumulate in living tissue, getting concentrated in every step of the food chain and putting the top predators, to which pilot whales belong, at the highest risk (Evans in Perrin et al. 2002). Meanwhile, concentration in the water where the end consumers live might not even be significantly elevated. These compounds, which had been used in plastic production and as pesticide affect the reproductive and immune system of marine mammals and increase susceptibility to disease to a point where many populations and species are drastically reduced in numbers, as has happened with the morbillivirus described in the previous chapter (Olson and Reilly in Perrin et al. 2002). Increasing levels of heavy metals like cadmium and mercury on the other hand are better tolerated with little signs of toxicity in pilot whales (Olson and Reilly in Perrin et al. 2002).

In the 20<sup>th</sup> century, fishing industry intensified to an extent, where the large-scale removal of biomass has begun to change species abundance and composition (Evans in Perrin et al. 2002). Whether cetaceans themselves are being caught or their prev species, the very efficient exploitation of marine net productivity can cause a dramatic habitat change. Even so when not directly consumed by pilot whales or other predators, when certain elements of the food web are missing or their numbers drop below a critical level, the whole system can become compromised. In heavily exploited areas, fishing can account for as much as 35% of the locally produced biomass and worldwide for an estimated 8%, or over 90 million tons (with a suspected bycatch of an additional 20-30 million tons which is thrown overboard) (Northridge in Perrin et al. 2002). Of course, most species will change their diet when forced and their distribution will change but again, it is difficult to affiliate demographic trends to changes in food abundance with certainty. It is seldom clear whether the animals are just temporarily absent or if they abandon an area for good, as it seems to be the case in population of short-finned pilot whales, which left southern Californian waters after an extraordinarily hot 'el niño' event drove away their favored squid species (Evans in Perrin et al. 2002).

Whenever fish stocks are in decline and competition for the remaining resources becomes tighter, more direct conflicts between humans and cetaceans arise (Fertl in Perrin et al. 2002). Fishing activities can open up niches and concentrate potential prey species. Many whales and dolphins will take advantage of decreased energy expenditure by feeding opportunistically on fish and squid which are trapped in nets and long lines. In some areas, 'blackfish' – both kinds of pilot whales, killer whales and false killer whales – are notorious fish stealers. Pilot whales even frequent traps, which are used to catch squid off of Newfoundland (Fertl in Perrin et al. 2002). Unfortunately, during these attempts many animals get hurt or killed either when they become trapped or entangled in the nets and suffocate or when they get hit by a ship's propeller. Not surprisingly, pilot whales are a quite frequent bycatch in squid fishing vessels in the western North Atlantic (Gannon et al. 1997).

Nevertheless, most animals avoid ships whenever they can (Evans in Perrin et al. 2002). For one, because they are aware of the physical threat a fast moving vessel poses but also because ships introduce a lot of under water noise, which can be a big annoyance to these animals with their sensitive hearing. The low frequency noise of

motors and other human activities like oil and gas mining, dredging and construction seem to affect mysticetes more strongly, as their biggest hearing sensitivity lies under 5kHz and can range down to 5Hz. While odontocetes with the best hearing ability above 10kHz are most vulnerable to side scan and military sonars as well as speedboats but in turn have been observed to tolerate high levels of low frequency sound (Evans in Perrin et al. 2002). Still, animals can get frightened and confused and exhibit stress reactions when exposed to constant noise and even shock after very loud incidents (Würsig and Richardson in Perrin et al. 2002). This can vary with the type of sound since many animals learn to distinguish sound sources and associate them with potential dangers. Many dolphins react fiercely when they hear the sound of contracting nets to catch tuna below them, resulting in a stampede like attempt to escape. Killer whales and possibly other big odontocetes on the other hand respond to the hauling of nets like to a dinner bell (Würsig and Richardson in Perrin et al. 2002). However, most of the time whales avoid loud sound sources, sometimes by several tens of kilometers. After all, human introduced noise is not only an annoyance or sign of danger but can also impair communication and orientation. When background noise exceeds a certain level it masks other sounds. Pilot whales are know to fall silent during periods of loud noise levels and other dolphins are thought to alter the sonic frequency of their calls to avoid overlap with noise frequencies (Würsig and Richardson in Perrin et al. 2002). And of course, extremely loud events can seriously alter or damage an individual's hearing, which in odontocetes has the potential side effect of completely robbing an animal of its orientation and communication capabilities, reducing its chances of survival to a minimum (Evans in Perrin et al. 2002). There are even reports of physical injury from explosions and the loudest of sonars, used for ocean tomography and submarine detection (Würsig and Richardson in Perrin et al. 2002).

The amount of traffic and activity in and on our oceans has steadily increased and shipping routes have proliferated over the past decades and at least on the northern hemisphere, noise disturbance becomes increasingly difficult to avoid, even for populations on the open ocean. Therefore it should be of great concern to establish areas with minimum ship traffic where the animals are not constantly being distracted and irritated or even molested by overly anxious whale watchers and fishermen, fearing for their catch. This is especially critical in waters where important activities such as mating, giving birth or nursing of the young take place and a lot of research should be concentrated on finding these places (Würsig and Richardson in Perrin et al. 2002).

## 2.6.3 Mass Strandings

Pilot whales, as has been mentioned a few times before, are often subject to mass stranding events where whole groups can die. Several mechanisms have been discussed to contribute to the severity of these events, such as behavioral traits and group dynamics. The initial reasons are less clear but from what is known today all of the mentioned threats and diseases could account for a mass stranding event. Animals which strand in groups may be victims of poisoning, infectious disease, intensive local fisheries operations or unusual environmental events (Perrin and Geraci in Perrin et al. 2002). What makes it difficult to determine is the fact that the initial cause may no longer be evident by the time of investigation (pathology) and in the case of a panic reactions or loss of orientation may not even be detectable at the stranding site (Perrin and Geraci in Perrin et al. 2002).

While an illness could affect orientation and there is pathological evidence that widespread disease or parasitism can be causal or contributory, there are just as many examples of stranded groups where all the individuals are in seemingly good health (Perrin and Geraci in Perrin et al. 2002). Reports of whole groups deliberately following an individual which might have stranded itself due to old age, illness or injury, are not uncommon. False killer whales have been observed to follow a large moribund male to a beach and didn't return to sea for three day until the male was dead (Perrin and Geraci in Perrin et al. 2002). In such an event, if there is no human intervention, it is very likely that the whole group perishes and there are even reports of rescued animals deliberately returning to ill or injured individuals on the beach. This type of social cohesion must be highly adaptive in other situations but can obviously have devastating effects. Other whales and dolphins which are know to strand with an above average frequency include short-finned pilot whales G. macrorhynchus, sperm whales Physeter macrocephalus, false killer whales Pseudorca crassidens and Fraser's dolphins Lagenodelphis hosei (Perrin and Geraci in Perrin et al. 2002).

Ultimately, the possibility of an accident can neither be ruled out. Either because of navigation errors and impaired echolocation in too shallow water, or strong and unusual currents and extreme tidal volume. Pilot whales pursue squid into shallow waters during late summer and strand more



**Picture 22:** The sad view of a group of stranded pilot whales in New Zealand

often in these times. Not necessarily as whole groups but the same reasons that make an individual strand could also affect an entire pod (Perrin and Geraci in Perrin et al. 2002).

# 2.7 Whale Watching

Observing whales is a difficult and time consuming task. The animals are submerged most of the time and can only be detected when surfacing, individuals are hard to identify and even harder to follow. But there are several places where cetaceans pass by regularly or stay for a certain part of their journey. It is in these places where the interest and fascination by researchers has spilled over to a well informed public. The first whale watching enterprises started out in southern California and the east coast of the U.S. in the 1950's, usually from land based lookouts. Scientists soon found out that a paying public could provide an excellent opportunity to fund their research and whale watching has become a commercial enterprise early on. In the seventies, it was the humpback whale *Megaptera novaeangliae* who drew a greater crowd to places like New England, Baja California and Hawaii. Over the years whale watching has grown to an estimated business volume of over a billion dollars worldwide and today it is a common tourist attraction in many places from Japan to Australia, Norway, Canada, northern and southern U.S. waters, the Mediterranean and the Caribbean.

Humpback whales breach more often than other baleen whales and are generally more active. They also show friendly behavior and like bottlenose dolphins, orcas and certain mink whales even approach boats sometimes, making them ideal subjects for wildlife photographers. Pilot whales are seldom the stars amongst cetaceans. They are not as big as the baleen whales and not as acrobatic and playful as some other dolphins. (Although dolphins in the wild rarely exhibit the stunts they perform in orchestrated shows in zoos.) Even their uniform dark color does not draw too much attention and most people probably are not very familiar with them. But they are just as fascinating to encounter in the wild, albeit appealing a little less to the ones who have their mind set on 'cute' dolphins.

Already, Aritstotle learned from fishermen to recognize individual dolphins by scars and markings on their fins and flukes and today's photo-identification methods rely on the same principle. There are data bases resulting from joint archives of different observers with photo collections of several thousands individual whales and dolphins. By being able to get as many 'snapshots' of an individual animal, it is slowly becoming possible to assess a life history pattern, especially when this animal can be identified by different researchers in different areas.

The alliance between commercial and scientific enterprises has proven very valuable for this, as it permits the scientists to get close to the whales on boats way more often and in turn, they can share their knowledge to a much greater public and raise awareness of conservation and environmental issues. On a quality whale watching trip, explanations about other marina fauna and the special ecological features of the area should be included in the standard lecture by a well educated guide.

However, this is not always provided and given the amount of money which can be made in this business, many whale watching companies have abandoned their scientific programs and started carrying tourists for mere entertainment on increasingly bigger boats. In turn, there are many self styled whale and dolphin 'enthusiasts' who already have seen a lot and demand to see something more spectacular every day. This has led to a concurrence situation among the enterprises and it is increasingly common to approach the animals too fast and too close with the potential danger of disturbing them and disrupting their important resting and dive cycles. Especially big baleen whales have to breathe on the surface for a certain amount of time to exhale all the  $CO_2$  in their system and replenish their oxygen reserves. This is often ignored and many would rather return with a trophy snapshot of a tail fluke of a whale forced to dive by an approaching boat than admiring it from an adequate distance.

It is not known whether this presents only an annoyance to the animals or whether the additional stress affects their fitness and survival more seriously. But in any case, people who truly love whales would certainly be concerned about the well being of the animals over the quality of their own amusement. Spectators planning to watch cetaceans can do them a big favor by choosing whale watch companies with an established scientific program and a firm policy of being as unobtrusive to the animals as possible (Hoyt in Perrin et al. 2002).

# 3. The Strait of Gibraltar



Picture 23: The Strait of Gibraltar from Space

# **3.1** The Door to the Mediterranean

When standing on the southern most tip of Spain in Tarifa, one can see the mountains of northern Morocco and the lights of Tanger at night. To the west there is the open Atlantic Ocean and to the east the entrance to the Mediterranean Sea at Gibraltar. As impressive the site is, a look on the map reveals the comparably tiny dimensions of this connection between two oceans.

When the African continent started to drift towards the Eurasian plate, it forced the Tethys sea covering large parts of Europe to retreat towards the east and eventually shut the Mediterranean off from the Indian Ocean, 20 million years ago (Tichy et al. in Hofrichter, 2002). Ever since, the Strait of Gibraltar has been the only connection to the Atlantic and the most important supply of water. It has been closed several times in history, the last time 5.6million years ago in the Messinian era of the Miocene. The Mediterranean almost dried out but the strait reopened 5.3 million years ago and remained so ever since. The large amounts of evaporite sediments found in the seafloor suggest several of these events (Wikipedia, 2007)

Increasing evaporation in the eastern and southern Mediterranean pushes the total annual evaporation to 156cm, which is more than double the total annual input by rain and freshwater supply from rivers and the black sea together. And so, an annual mass of 1200 billion  $m^3$  of water ( $10^6 m^3$  per second / 95.6 cm per year) has to flow through this 'pin hole', which is 14 km wide and on its most shallow sill, only between 286 and 320m deep. (Klein and Roether in Hofrichter, 2002).

No wonder, there is an intricate regime of water currents in the strait with its tides and strong winds. At ancients times it was only the Phoenicians who were capable of leaving the known world past the 'columns of Herakles', the Rock of Gibraltar and the Mount Musa in Morroco, about 700 B.C. (Hofrichter in Hofrichter, 2002). They were the first ones to know about deep water currents, which flow east, out of the Mediterranean, into the Atlantic and they used 'under water sails' to carry them against the winds and surface currents (Hofrichter in Hofrichter, 2002).

Today, the Strait of Gibraltar is one of the most heavily used sea lanes and there is a constant line of huge tankers and cargo ships passing by. And amidst these winds, currents and traffic, there is a surprising abundance of marine life, including many cetaceans and a population of about 180 long-finned pilot whales *G. melas*. It is a resident population, which is present all year long but there are many other species, which only visit the Mediterranean seasonally. Along with their predators, they too have to pass the strait, making the door to the Mediterranean a very crowded place.

# 3.2 Geography and Climate

The Sierra Nevada on the Spanish coast and the adjacent branch of the North African Atlas Mountains are remainders of the tectonic movements of the African plate towards the Eurasian plate. While the eastern Mediterranean is characterized by subductions of Eurasia, the west around Gibraltar and the northern Moroccan coast form a compression boundary and the same forces responsible for lifting the Alps created these two mountain ranges. Despite being relatively young formations, most continental edges around the Mediterranean are passive today, except for the Hellenic ridge below southern Italy. The edges around Gibraltar are steep and rocky and fall quickly to great depths in the Alboran Sea off the northern Moroccan coast and the shelf edge is only a few kilometers wide (Tichy et al. in Hofrichter, 2002).

#### 3. The Strait of Gibraltar

Two winds are predominant in the region, the 'Levante' coming from the east the 'Poniente' and from the west. Except middle for the of summer, these steady winds blow almost constantly with 150 days of Levante and



**Picture 24:** Inflated 3D-relief of the Spanish highlands on the left and the Moroccan Atlas branch on the right.

180 days of Poniente every year, the latter being associated with more humid and stormy weather from Atlantic low pressure zones during winter. The Spanish highlands and the Moroccan Atlas Mountains funnel the strong winds and can accelerate them by 3-4 knots with considerable benefits for a myriad of kite-surfers on the nearby Atlantic coast (Picture 21) (Hofrichter et al. in Hofrichter, 2002).

The climate is very mild with average temperatures dropping seldom under 13°C in winter and reaching up to 30° in summer but the winds and the cool water of the Atlantic ocean can make it quite chilly at night (Gibraltar.gov.gi). Despite the winds, occasional fogs and a relatively moderate annual average temperature of about 16-17°C, it is very dry around the strait with an annual precipitation of less than 200mm. The abundant woods are mostly every every every with thick sclerophyll leaves, like olive trees Olea europaea, Laurel bushes Laurus nobilis, stone oaks Quercus ilex, cork oaks Quercus suber, kermes oaks Quercus coccifera and fan palms Chamaerops humilis. But the south Spanish and north African grasslands are distinguished from the typical Mediterranean 'Macchia' vegetation in that they are dominated by grasses (Graminaceans) like the Halfah grass Stipa tenacissima (used for paper making) and Esparto grass Lygeum spartum, as well as Mauritian grass Ampelodesmos mauretanica, which all prosper on dry, sandy or clayey and often gypsaceous soils (Hofrichter et al. in Hofrichter, 2002). To the enjoyment of the author, the also abundant Ericaceans, Myrtaceans and Apiaceans give flavor to the excellent local Pacharán liquor.

## **3.3 Oceanic Conditions and Currents**

The Mediterranean Sea is a 'concentration basin' where annual evaporation exceeds the replenishment of freshwater by rivers and rain, which is determinant for its ecology. Its salt content is well above that of the Atlantic and ranges up to 40psu in the eastern most Levantine basin. And while the average sea surface temperature (SST) oscillates around 17°C by about  $\pm 2.6^{\circ}$  at the Spanish and North African Atlantic coast, temperature differences increase to  $\pm 4^{\circ}$  in the western Mediterranean and more, further in the east, although restricted to a thin upper most layer. During the winter cooling, the concentrated surface water in the Levantine basin becomes heavier than the underlying layers and starts to sink, creating a circulation through the whole Mediterranean. This mass of water passes the Strait of Sicily and propagates in a depth of 400-600m through the western Mediterranean. Parts of it eventually pass the Strait of Gibraltar underneath the inflowing water masses. There, it sinks rapidly to depths of 1000-1500m. Sometimes, the flow branches and a part of it flows on the shelf towards Portugal and can be traced to as far as the Irish coast.

This outflow is essentially more concentrated than the inflow and big enough to deplete the Mediterranean of an important part of its nutrients, making it oligotrophic. The Strait of Gibraltar is also very shallow and this barrier prevents nutrient rich deep Atlantic water to enter the Mediterranean. Therefore, plankton production cannot thrive like in other places and the water is exceptionally clear in many places. The euphotic zone generally extends deeper than in other oceans but overall there is less productivity. Of course the whole ecosystem has evolved around these conditions and it is one of the reasons why big baleen whales are rare visitors in the Mediterranean: there is simply not enough food. (See also the next chapter.)

The Atlantic water which streams into the western basin of the Mediterranea with a rate of about 1 Sv (1 Sverdrup =  $10^6 \text{ m}^3 \text{ s}^{-1}$ ) balances the water loss by evaporation to the biggest part. The average input remains the same in all seasons but is temporarily affected by tides and air pressure. Salt content is at 36psu at the strait and as the water remains on top of denser, saltier layers, it forms a coherent unit propagating eastwards, which can be traced until the Levantine basin. Of course, on its way it gets modified as it evaporates and mixes with other water and by the time it passes the Strait of Sicily, salt content has increased to 38psu and its layer thickness has greatly reduced.
Despite the pronounced temperature stratification of the upper water layers, below 600m the water column becomes very uniform in the western basin and from 1000m on downwards there is hardly a change in temperature. With more than 12°C it is exceptionally warm compared to typically 1-4°C in the worlds oceans and with a high amount of oxygen, it is evidence of an effective deep mixing process in the Gulf of Lyon. The western Mediterranean is dominated by cyclonal (counter-clockwise turning) currents, which concentrate dense water at the surface. In the winter when cold Mistral winds hit the sea from the north, temperature loss can happen very quickly, making the surface water sink similar to the Levantine water but by a magnitude faster. Bodies of water sink in 'plumes' with a very high speed of up to 10cm/s to the depths where they dissipate and mix with the surrounding water (Klein and Roether in Hofrichter, 2002).

#### 3.3.1 Underwater Topography and Water Regime in the Strait

Given the relatively small size of the Mediterranean, it is unusually turbulent due to the factors described in the former chapter. And it seems inevitable that the strong forces at work would also be felt in the narrow Strait of Gibraltar. Even the tides, which are not very distinct throughout most of the Mediterranean get amplified in the 'bottleneck' of the strait and contribute significantly to the temporary hydrographic conditions, working with or against surface currents and influencing the deeper out flowing currents.

When the water rises at Gibraltar, the inflow stops and reverses its direction and outflow occurs at all depths (Wesson and Gregg, 1994). The top speeds range up to 120cm/s in the strongest semidiurnal tides at the surface but decrease fast with depth (Tsimplis, 2000). The reason for this is the sharp seafloor rise from about 800-1000m before Gibraltar to only 284-320m at the Camarinal Sill west of Tarifa at about the height of Tanger (Klein and Roether in Hofrichter, 2002). It pushes the water masses flowing out within 10-50m of the surface before they sink to the Atlantic sea floor, causing permanent turbulences right above the sill. Usually, the denser water separates from the overlying water at a transition zone, which lies at about 150-200 m. At the sill, these masses are forced upwards to 'compete' against each other for space, resulting in a complex mixing process (Wesson and Gregg, 1994). Roughness patterns at the surface are visible from 1h to 6h after low tide (Brandt and Alpers, 1994).

When the sea level falls after high tide, Atlantic water flows again into the strait and as always when the directions

shears near the

strong

change,



#### Figure 12:

The Camarinal Sill at the western end of the Strait of Gibraltar and under water topography in the strait.

land are created. Although during low tide the outflow at depth is not reversed but only stopped (Wesson and Gregg, 1994).

A consequence of the movement of this oscillating 'stop and go' of the deep currents are 'bores', waves of denser water which bounce off the slope of the Camarinal sill and propagate along the transition zone between the heavier deep water and the lighter surface water currents. These internal waves move back east into the strait with



#### Picture 25:

An internal wave between surface and deeper water layers propagating into the Alboran Sea to the east of the Strait of Gibraltar.

a speed of 2ms<sup>-1</sup>. They bounce off its walls and become visible more than 20km east of the sill in the Alboran Sea, when their wavelength has grown from about 1.1 to 10km (Picture 22) (Brandt and Alpers, 1994). Sometimes similar waves are also seen west of the sill moving into the Atlantic (Izquierdo et al. 2003).

As if this was not enough turmoil, the winds also come into play when the Levante causes an upwelling of cold water along the African coast of the strait in summer. After strong west wind events, surface water temperature has been found to drop from about 22° to 15°C which would correspond to temperatures at 80-120m depths. The upwelling gets channeled between the African shelf and the underwater ridge in the middle of the strait, separating it into two parallel trenches. Plumes of cold water move out to the Atlantic but can be carried back east, depending on the currents (Stanichny et al. 2005).

It is no wonder sailors have struggled for a long time to ship through the strait. The flows can change in an instant and the forces of winds and currents are intensified by the peculiar topography on land and under water. Much of this is very unpredictable and hydrographic conditions can differ vastly during seemingly similar weather and tides. Local differences are big and seasonal changes additionally affect the general flow schemes.

#### 3.4 Life in the Strait of Gibraltar

Maybe due to the notoriously difficult conditions at the strait it has long been overlooked that there is a very diverse abundance of marine life between the Spanish and the Moroccan coast. Many migration routes of species traveling in and out of the Mediterranean meet at the strait and since many of theses species are swarm fish like tunas, mackerels and sardines, they in turn attract many predators. Swarms of big tunas *Thunnus thynnus* migrate into the Mediterranean to spawn in May, June and July. They can grow to more than 500kg and are the favored prey of not only humans but many top predators (Maack and Rademaker-Wolff in Hofrichter, 2002). Killer whales (*Orcinus orca*) are particularly fond of tunas and usually appear at the strait around mid summer. They cannot swim as fast as individual tunas and are hated by fishermen for eating the tuna caught in their longlines before they have the chance to haul them aboard. Sperm whales *Physeter macrocephalus* are also seen mainly during summer but sightings have also occurred in other seasons.

The only baleen whale which is seen regularly but scarcely is the big fin whale *Balaenoptera physalus*. There is a suspected population of a few thousand animals in the Mediterranean and while it was thought for a long time that the Mediterranean was too oligotrophic to support the big baleen whales with sufficient food of a low trophic level. But fin whales are not limited in their diet to krill only and also eat small swarm fish, which might account for their ability to exist in the Mediterranean. Smaller delphinids are present year round including common dolphins *Delphinus delphis*, striped dolphins *Stenella coeruleoalba*, bottlenose dolphins *Tursiops truncatus* and of course long-finned pilot whales *Globicephala melas* (FIRMM, 2007) Other marine mammals are not abundant except for the Mediterranean Monk seal *Monachus monachus*. But its numbers have declined substantially and it is extremely rare in the Mediterranean and hardly ever seen anymore. Only a colony of about 500 animals manage to survive at Cabo Blanco, further south on the Mauritanian coast of Africa (Smith, 2006). Big sharks are also scarce in the Mediterranean and the occasional sightings near the strait are exceptions to the rule.

It can generally be said that the fauna near the strait resembles the North Atlantic fauna to a great extent and the sill at the strait is more of a hydrographical barrier than a biological one. Further east we find more and more endemic species, which are only found in the Mediterranean. And although its surface area is only 0,82% and its volume 0,32% of the worlds oceans, we find 6,2% of all marine species in the Mediterranean. The low nutrient content providing only small but numerous biological niches as well as the isolation have led to the diversity of species we observe today (Glaubrecht and Golani in Hofrichter, 2002).

# 4. The Food Web



Picture 26: Microscopic view of Diatom primary producers.

To finally complete the picture about pilot whales and their ecology, a quick excursion into the dynamics of the food web is appropriate at this point. During chapter 2.4 'The Ecology of Group Living' the close association between pilot whales and their prey, squid was described. The squids in turn depend on other animals as their food source and so on. But like in any ecosystem, the primary productivity by autotrophic plants is the fuel upon which any other living creature relies, whether directly as in herbivores or indirectly as in carnivores. (There are exceptions to this but to address them here would exceed the limits of this thesis.) However, the ocean water establishes certain laws for the cycling of nutrients, which are unique to an aquatic environment and worth a quick investigation.

# 4.1 Temperature, Radiation and Productivity

Our oceans are the biggest coherent ecosystem of the earth. They cover almost 70% of the earths surface and connect polar regions to tropical to opposite polar regions

without presenting barriers to the animals who are able to travel the high seas. Most importantly, it is in the sunlit upper layer of the seas where the biggest amount of  $O_2$  is produced and  $CO_2$  is fixated by the photosynthesis of microscopic unicellular algae, phytoplankton. It is the site of the biggest primary production, fixing 50 giga tons  $(5*10^{10}t)$  of carbon every year (Petz in Hofrichter, 2002). This productivity is limited in several ways and does not reach near many terrestrial systems but it is made up for by the vast size and continuity of its turnover of nutrients (Thurman, 1991).

In the polar regions, the biggest limiting factor for primary production is light. Since the water is very cold from the surface throughout the deep, there is no temperature based stratification and mixing processes always provide the upper layers with nutrient rich water from the deep. In Antarctica, the continental shelf is thought to cause upwelling of deep ocean currents, forcing them to surface after having spent several hundred years traveling form north to south and indeed, the maximum rate of productivity is higher in southern polar waters than around the north pole (Thurman, 1991). Of course, during the dark winters this comes to a halt and the polar regions become void of life only to bloom again in the next spring. This distinct seasonality is responsible for the numerous north to south migrations we observe in so many species (Thurman, 1991).

In the rest of the world's oceans, where light is abundant all year long, the upper layers become depleted of nutrients. Since photosynthesis is limited to a very thin layer reaching from the surface down to about 100m (with big local differences), the

increasing temperature stratification over the course of the warmer season prevents deeper water from mixing with the surface. After an initial spring bloom the organisms start to use up the nutrients abundant in the euphotic zone, limiting their growth. In tropical regions these conditions remain constant and are the reason for the oligotrophy of warm waters.



**Picture 27:** Thriving coccolithophorids 'bloom' in British waters

Effectively, large parts of our oceans are limited by nutrient abundance in their productivity, the most critical being Nitrogen and to a lesser extent Phosphorus in the forms of Nitrate and Phosphate. One can easily spot the areas where nutrient supply is above average by the turbidity of the water caused by thriving algae. The infamous 'red seas' are caused by dinoflagellate algae, which can reach a concentration of over 2 million individuals in 1Liter of sea water (Thurman, 1991).

#### 4.1.1 Phytoplankton and the Role of Bacteria

The most important primary producers are the silicate Diatoms (Picture 26), the calciferous Coccolithophorids and Dinoflagellates (Picture 28). The latter are made of cellulose and are decomposed quickly as opposed to the former two, whose microscopic shells have been produced in such quantities over million of years that they contributed significantly to the formation of sediment rocks (Thurman, 1991).

Cyanobacteria are also among the top producers but there is an even larger percentage of heterotroph bacteria in the which unable water, are to photosynthesize, yet they are still indispensable for primary production. Since the micro algae cannot incorporate Nitrogen in the form of N<sub>2</sub>, they rely on bacteria, which provide them with the Nitrogen in the appropriate form of



**Picture 28:** Dinoflagellate algae

Nitrate (NO<sub>3</sub>). Similarly, they depend on the breakdown of phosphate by the bacteria to be able to take it up. Nutrient limitation would not be a problem if the algae were not dependent on the bacterial processes, as the ratio by which the chemical elements are taken up are the exact same ratios in which they are present in sea water (Thurman, 1991).

The bacteria themselves rely on photosynthesis byproducts in the form of dissolved organic matter (DOM), which is actually the biggest portion of organic matter in the oceans (Petz in Hofrichter, 2002). The reuse and mineralization of DOM and particulate organic matter (POM) by heterotroph bacteria has an important channeling effect, as they are consumed themselves by flagellates which in turn provide food for

other ciliates. Nutrients that would otherwise be lost are recycled and made accessible to higher trophic consumers.

However, in warmer waters, viruses are more virulent and the destruction and turnover rate of bacteria is bigger with the effect of more DOM and essentially more Nutrients locked in this 'Microbial Loop'. In the western Mediterranean this is an estimated 55% but increases to 85% in the Levantine Sea, where this notably affects the productivity on higher trophic levels (Petz in Hofrichter, 2002).

Once the carbon and nutrient elements are fixated on the level of micro algae, the first trophic levels of primary consumer start to feed on them, including protozoans and juvenile as well as small enough adult stages of all animal phyla present in the sea: zooplankton. Small crustacean Copepods are the most abundant though and can make up 92% of the zooplankton in the Mediterranean (Zander in Hofrichter, 2002).

From all the net primary productivity, 10% sink below the euphotic zone. 2% reach the deep seas in 4000m and only about 0,2% is lost in the sediment (Petz in Hofrichter, 2002).

#### 4.1.2 The Shelf

On place where these mechanisms are partly overcome is the continental shelf, also called neritic zone. Only 8-10% of the oceans are shelf area, ranging from 0 to about 200m depth on average yet, they account for 25% of the sea's productivity (Tichy et al. in Hofrichter, 2002). Rain and Rivers wash nutrients from land into coastal waters, macroscopic algae and plants can use the substrate close enough to the sunlit surface to anchor themselves and present numerous habitats and niches for all kinds of life. Primary production, measured as the fixation rate of Carbon, can reach to a maximum of about 100g/m in a year in shelf areas (Tichy et al. in Hofrichter, 2002).

But there is additional energy input into this system from the open ocean. The niches provided by a solid substrate enable many sessile filter feeders to catch POM delivered by ocean currents. Coral reefs are a prime example of this, pushing (secondary) productivity to extreme rates in the otherwise unproductive tropical waters. Many organisms spending an early stage of their life as eggs or larvae in the plankton move to shelf areas in later juvenile and adult stages. Especially sea grass meadows are important for giving shelter and food to many juvenile fish species (Zander in Hofrichter, 2002). This of course enables higher predators to find food and

so the diversity and abundance of life in the neritic province is many times greater than in the uniform open ocean. Even pronounced oceanic species visit the shelf on special occasion, the reproduce or hunt for example, and its edges are the place where many biological cycles in the sea are connected (Zander in Hofrichter, 2002).

## 4.2 Transfer Energy and Top Predators

When an animal is killed and eaten by its predator, only 10 to 20% of the energy used to compose its structure can be passed on to the next level of biomass production. The rest is either indigestible, or transformed to heat by muscle movement, respiration and to generally maintain body functions of the predator. In the first step from phytoplankton to zooplankton it is even less and only 1% of the chemically fixed energy can be passed on to next consumer (Petz in Hofrichter, 2002).

This has the consequence that only a small percentage of the net primary production can be passed on to the highest trophic levels on top of the food 'pyramid'. The biggest terrestrial and aquatic animals therefore have taken the 'shortcut' of feeding on the lowest possible trophic level such as elephants and other big plant eaters on land. In the oceans it is the baleen whales as well as the biggest fish, a prime example being the whale shark *Rhincodon typus*, who skim the oceans for krill, small crusraceans which feed directly on algae (Zander in Hofrichter, 2002).

Large predators do not have this advantage and are faced with increasingly scarce prey of the right size. Especially the big, warm blooded odontocetes had to specialize their diet and hunting techniques in order to meet their energy demands. Compared to equal sized but cold-blooded sharks, which are the generalists of the seas, their diet is very restricted.

#### 4.2.1 The Importance of Squid

Pilot whales are not the only species whose diet is based on squid although they might be more specialized than others with 80% of their diet consisting of these cephalopods. Many large predators rely on this energy supply for various reasons. Squid grow very fast and to sufficient size to make a substantial meal and become worth the energy expenditure by a big animal to hunt them. They are abundant in big swarms capable of supplying a whole group of predators all year round and their mobility is important for transferring huge amounts of biomass to different parts of the ocean, like the shelf, where they are available as prey. Extrapolations of abundance and consuming rates of squid predators predict a significant amount of the ocean's biomass to be fixed in squid swarms and their function as the predominant energy 'currency' in the ecosystem of our oceans can hardly be overestimated (Senn, during lecture).

Yet, we still know very little about them. Giant squids of several meters length have been speculated to exist for years without further proof (besides the occasional seaman's tale). Injuries and scars by squid tentacles son sperm whales have suggested the existence of very large quid specimens. But apart from this, the sheer size of

sperm whales indicate that their squid prey must reach enormous sizes, otherwise it could not cover the energy expenditure during a dive of such a huge animal.

Only recently, the catch of two entire giant squids has confirmed their existence. The one caught off the Antarctic coast by a New Zealand fishing vessel in February 2007 weighed 495kg and was more than 10m long (Wikipedia, 2007)

Squid ecology dominates the life of many species, like pilot whales, drawing them to the places where they spend their life.



**Picture 29:** A giant squid caught by fishermen.

# Part II: Long-Finned Pilot Whales (*Globicephala melas*) in the Strait of Gibraltar and their Local Abundance in Relation to Tides, Currents and Underwater Relief

# 5. Introduction



Picture 30: A group of pilot whales with their characteristic dorsal fluke.

A population of about 150-200 long-finned pilot whales *Globicephala melas* is present throughout the year in the Strait of Gibraltar. This is unusual since this species is known to be constantly on the move to follow the migrations of squid, their favorite prey, in the temperate areas of the North Atlantic and the circumpolar oceans on the southern hemisphere (Nelson and Lien, 1996). Pilot whales are so closely associated

with a particular squid species that the environmental factors, which determine the squid's ecology are also the boundaries along which social structures form in the whole population (Fullard, 2000; Amos, 1993). The specialization of pilot whales in their diet is a necessity to overcome the energy constraints for a warm blooded top predator in an aquatic environment. Pilot whales are very social and live in pods ranging from several tens to 200 animals. This also is determinant for their foraging behavior, energy balance and general life strategy.

The fact that pilot whales are able to survive in the Strait of Gibraltar raises the question of the peculiarities of this spot and what the factors are, which allow the pilot whales to give up their nomadic lifestyle. The strait is characterized by strong currents, resulting from the Mediterranean's negative net water household. Atlantic water flows through the Strait at a rate of 1 Sverdrup at the surface (Klein and Roether in Hofrichter, 2002) and there is an outflowing current at 400 m depth which is forced to the surface at the Camarinal Sill at the western end of the strait (Wesson and Gregg, 1994). Strong 'Levante' winds from the east drive upwelling events along the northern African coast (Stanichny et al. 2005).

Apart from pilot whales, there are other delphinids who are resident to the strait, like common dolphins (*Delphinus delphis*), bottlenose dolphins (*Tursiops truncatus*), striped dolphins (*Stenella coeruleoalba*). Other cetaceans can be seen seasonally, including fin whales *Balaenoptera physalus*, sperm whales *Physeter macrocephalus* and killer whales *Orcinus orca*.

During the last ten years, a small whale watching industry has formed in Tarifa, at the western end of the Straight on the Spanish coast. A number of companies sell their services to tourists, including the Foundation for Information and Research on Marine Mammals (FIRMM), which was founded 1998. During early cruises FIRMM scientists and marineros soon noticed the abundance of pilot whales, which are seen on almost every cruise and seem to always reside in the same area south of the middle line of the strait, close to Moroccan waters, between  $35^{\circ}$  53' -  $35^{\circ}$  55' north and  $5^{\circ}$   $30' - 5^{\circ}$  43' west. Initially, the boats where crossing the strait randomly in a more or less perpendicular line from the harbor in Tarifa towards Morocco but it occurred to boat personnel that the animals were found more to the west during high tide and more eastern during low tide.

On all cruises sightings of animals are noted, including time, position and basic types of behavior. After a few years of observation, a considerable amount of data has gathered on all cetaceans of the strait. But since pilot whales are more consistently abundant in the same area than others, it became practice at FIRMM around 2002 to cruise directly towards the suspected location of these animals and so the majority of sighting data is on pilot whales.

With the availability of precise tide schedules for the strait starting in 2001, it became possible to link the positions of the animals more closely to the environmental factors of the strait. The charts indicate the times of maximum high and low tides as well as their strength characterized by the 'coefficient'. The opportunity was given to find out more about pilot whales and their ecology with the advantage of a resident population, which can continuously be observed over a long period of time.

Ocean currents influence where the animals are located in many parts of the North Atlantic by distributing squid along temperature gradients. In this thesis, it was tested whether the changing currents at the Strait of Gibraltar are responsible for the perceived different locations pilot whales are found at during high and low tides and whether the strength of the flood affected this. Unfortunately, no SST charts of sufficient resolution were available to test the possible effects of water temperature in the upwelling areas along the North African coast in conjunction with west wind events.

# 6. Materials & Methods

# 6.1 Data Collection

Sighting data were collected using whale watching boats crossing the Strait of Gibraltar. Starting from the port of Tarifa perpendicular to the strait, these two hour cruises lead close to Moroccan waters and back with no exact course. They have been taking place several times every day during the whale watching season from April to October, starting in 1998.

Whenever pilot whales where sighted, the time of the encounter and the direction in which the animals swim was noted as well as the coordinates, using the boats GPS (Global Positioning System). Categories for the directions were 'west', 'north-west', 'north', etc. Other data was also collected including the number of animals in a group, basic behavior, recognition of a few known individuals and percentage of juvenile animals but is not included in this study. The survey started in 1998 and continues today as the data list of FIRMM is updated with every cruise.

Since precise times and coefficients for the tides at the strait are only available



Figure 13:

Official depth chart of the Strait of Gibraltar. Whale watching boats leave the port of Tarifa, crossing the strait southwards until close to Moroccan waters.

starting from 2001, sighting data from the years 1998 until 2000 were excluded from the test. At the time of this study. the FIRMM data list was updated up to the year 2004 so the sighting data included in this study comprise the years 2001-2004. Analysis of the direction in which

the animals swim, revealed a general predominance of east-west movements along the strait, with very few samples indicating that the animals also move north and south. Only unambiguous samples were used and western movements exceeded eastern movements by 2130 to 392 samples. Therefore, a general western movement of the animals was assumed and for further analysis of time and position data, the directional information was excluded from testing procedures.

Underwater topography was given in an official depth chart of the Strait of Gibraltar (Figure 13).

## 6.2 Data Filtering and Correction

Until the year 2001, the routes of the boats leaving the Tarifa harbor were more or less random, crossing the strait perpendicularly but from 2002 on, it was established among FIRMM personnel that the pilot whales were found more eastern or western, depending on the tides. This led to the possibility that the data could be biased due to human preconception. If the pilot whales were distributed evenly across the southern strait area, they could be observed in the east and the west and an observer who decides to only look for them in the west during high tide and in the east during low tide might create the observed effect himself. To account for this possible bias, the data from 2001 alone was processed parallel to all data from 2001-2004.

When conditions are too rough for the tourist boats in Tarifa, the cruises start from the nearby port of Algeciras, close to Gibraltar. Observations made during these cruises and the boat transfers form Tarifa to Algeciras could easily be distinguished from observations on the regular route using a visual plot of the coordinates. These data were excluded from the test. Offshoot coordinates resulting from estimations over greater distances than the immediate surroundings of the observation boat were also identified. Knowing the usual course of the boats, it was possible to eliminate coordinates out of the range in which exact positioning is possible. In the end, only data located within  $35^{\circ}50$ " to 62" north and  $5^{\circ}42$ " to 20" west were used.

Assuming that the influence of the currents is greatest at maximum tide, a time window of 6h was selected around the time of the high and low tide maxima as stated by the official tides bulletin and only data within this time frame was used. A second series of tests was performed using only a 1h time frame to see whether the influence of the currents was greater at the tide maxima. This second series was additionally

tested for the influence of high coefficients, indicating the strength of the tide for the years 2001-2004. In total there were 5 data series:

Series 1	2001-2004,	6h timeframe
Series 2	2001-2004,	1h timeframe
Series 3	2001-2004,	1h timeframe, high coefficient $> 0.75$
Series 4	2001 only,	6h timeframe
Series 5	2001 only,	1h timeframe

The number of samples for the different categories ranged from 2067 samples for Series 1 to 64 for Series 5. One sample consists of the sighting time and coordinates.

Series 1	2067 samples
Series 2	607 samples
Series 3	222 samples
Series 4	209 samples
Series 5	64 samples

## **6.3 Statistical Methods**

Each data series was first divided into high tide (HT) and low tide (LT) categories and then the paired coordinates were split into north and west constituents. All sample series met the criteria for a normal distribution and could be further processed without transformation. NCSS 2007, SPSS and JMP statistical analysis programs were used for the analysis. A paired sample t-test was applied separately to the west and north coordinates of all categories to test for significance.

There were an uneven number of samples between HT and LT categories in all series. To be able to perform a paired samples test of repeated measures, exceeding samples of the bigger group were excluded randomly and several tests showed no significant differences. The mean differences for pairs of HT and LT categories in each series were calculated as well as the standard deviations. Effect size was calculated using the mean difference divided by standard deviation.

# 7. Results

### 7.1 Direction of Movements

When initially visualizing the data on a scatter plot, it was evident that the pilot whales in the strait moved predominantly in eastern or western directions as the spread out distribution of the dots indicate in figure Z. However, only 15% of the total recorded movements were in eastern direction compared to 82% in western direction as shown in figure X.



Figure 14: Prevailing western movements of pilot whales during 2001-2004



Figure 15: Percentage of directional movements comprising all sighting data.

When including all the sightings, where no directed movements of the animals could be noticed, the ratio shifted to 58% western movements, 11% eastern and 31% with no direction (Figure Y). Other data were left out since their percentage was negligible.

# 7.2 Topography

A comparison with the underwater topography of the strait revealed that north-south distribution of the whales was centered around the deepest areas of the southern of the two trenches with the underwater ridge in the middle of the strait coinciding with the northern limit of the whales' distribution. The southern limit was shown to be at the shelf edge along the Moroccan coast. The topography of the strait seems to be determinant for the location of the whales and east-west movements are 'channeled' over the southern trench (Figure Z)

Initial tests showed a significant difference for the north-south distribution but since the effect size was very small, further analysis was only done with the west coordinates relating to the east-west movements of the animals.



#### Figure 16:

Distribution of pilot whales coincides with the steep topographic relief on both sides of the deeper, southern trench running along the Strait of Gibraltar, with the middle ridge approximating the northern distribution limits.

# 7.3 Location at High Tides and Low Tides

All data series showed a highly significant difference between west locations during HT and LT with a p-value < 0,01. Effect sizes were very strong with values close to 0.5 and higher. The 2001 series were no different in this regard than the 2001-2004 series, except that effect sizes were even greater. Effect size was also greater within the smaller 1h timeframe in the 2001 and 2001-2004 series whereas the high coefficient series did not differ much from the 2001-2004 1h series. The individual calculations for each series are given in table 2 and 3. Graphic plots for each series are given in table 4.

Table	2:
-------	----

Taneu Samples Statistics				
	Mean	Ν	Std. Deviation	
01 - 04 6h LT w	34.4468	977	2.6245081	
01 - 04t 6h HT w	35.9452	977	2.2946465	
01 - 04 1h LT w	33.8611	283	2.8541156	
01 - 04 1h HT w	36.7446	283	2.3680118	
01 - 04 1h hi coeff LT w	33.9451	89	3.3158127	
01 - 04 1h hi coeff HT w	36.9752	89	2.5540724	
2001 6h LT w	33.1394	93	2.2998997	
2001 6h HT w	36.2302	93	2.2752359	
2001 1h LT w	32.0744	27	2.1621205	
2001 1h HT w	37.6066	27	1.7043351	
	01 - 04 6h LT w 01 - 04t 6h HT w 01 - 04t h LT w 01 - 04 1h LT w 01 - 04 1h HT w 01 - 04 1h hi coeff LT w 01 - 04 1h hi coeff HT w 2001 6h LT w 2001 6h HT w 2001 1h LT w 2001 1h HT w	Mean           01 - 04 6h LT w         34.4468           01 - 04t 6h HT w         35.9452           01 - 04 1h LT w         33.8611           01 - 04 1h LT w         33.8611           01 - 04 1h HT w         36.7446           01 - 04 1h hi coeff LT w         33.9451           01 - 04 1h hi coeff HT w         36.9752           2001 6h LT w         33.1394           2001 6h HT w         36.2302           2001 1h LT w         32.0744           2001 1h HT w         37.6066	Mean         N           01 - 04 6h LT w         34.4468         977           01 - 04t 6h HT w         35.9452         977           01 - 04 1h LT w         33.8611         283           01 - 04 1h LT w         33.8611         283           01 - 04 1h HT w         36.7446         283           01 - 04 1h hi coeff LT w         33.9451         89           01 - 04 1h hi coeff HT w         36.9752         89           2001 6h LT w         33.1394         93           2001 6h HT w         36.2302         93           2001 1h LT w         32.0744         27           2001 1h HT w         37.6066         27	

## **Paired Samples Statistics**

# Table 3:

## **Paired Differences**

		Mean Difference	Std. Deviation	Std. Error Mean
Series 1	01 - 04 6h	-1.49837	3.5575201	0.11382
Series 2	01 - 04 1h	-2.88347	3.9485274	0.23472
Series 3	01 - 04 1h hi coeff.	-3.03018	4.3751736	0.46377
Series 4	2001 6h	-3.09078	2.9127788	0.30204
Series 5	2001 1h	-5.53226	2.8941903	0.55699

95% Confidence Interval of the Difference:	lower	upper
Series 1	-1.72172	-1.27502
Series 2	-3.34549	-2.42145
Series 3	-3.95182	-2.10854
Series 4	-3.69066	-2.49091
Series 5	-6.67716	-4.38736

	t	DF	Sig. (2-tailed)	Effect Size
Series 1	-13.16495	976	0.000	0.42
Series 2	-12.28495	282	0.000	0.73
Series 3	-6.533834	88	0.000	0.69
Series 4	-10.23299	92	0.000	1.1
Series 5	-9.932472	26	0.000	1.9

Locations at HT are marked red and LT are marked green in all diagrams. The left plot of each series shows the actual location of the animals at the Strait of Gibraltar. In the right plot means of the western distribution are shown by vertical lines for HT and LT categories. With increasing effect sizes (ES) from series 1-5, means are spaced further apart. Regression lines and confidence borders are also shown. Note that the west-axis is reversed in the right plots. Data labels on X-axes show 35° north plus x minutes, Y-axes show 5° west plus x minutes.

Series 1: 2001-2004, 6h time frame, ES=0,42



Series 2: 2001-2004, 1h time frame, ES=0,73



#### 7. Results



Series 3: 2001-2004, 1h time frame, high coefficient (>0,75), ES=0,69

**Series 4:** 2001, 6h time frame, ES=1,1



**Series 5:** 2001, 1h time frame, ES=1,9



## 8. Discussion

#### 8.1 Effect Size and Directions of Movements

The series with the most samples (Series1: 977 samples) showed the smallest Effect size (ES). Series 5 with the least samples (27 samples) showed the biggest effect sizes. This was surprising as it was expected for all the 2001 series (Series 4 and 5) to show the weakest effects since the boat cruises where thought to be more random than during the following years and sighting data less biased. Therefore, it can be assumed for all the data to be sufficiently unbiased to validate the observations.

Increasing ES with increasing resolution of the test setup, meaning smaller time frames and sample sizes, indicate that temporary conditions have even more influence than those shown in this long term observation. It is also possible that these effects change with the seasons, which was not accounted for in the initial test setup as available information on tides and currents was too general to justify an increase of the testing resolution of this study. Nevertheless, the locations of the animals differ significantly in all series.

However, mean difference values range from 1.5" in Series 1 to 5.5" in Series 5 and when calculated into actual measures result in differences of only 1,7 to 6,3 km. This is less than the water in the strait of Gibraltar would travel over the intermittent period between two tide maxima, assuming a flow top speed of 4,3 km/h (which of course is not held up during the whole period) (Tsimplis, 2000).

Pilot whales must obviously travel actively to remain in their position. In this regard the prevalence of western over eastern movements coincides with the large net inflow in eastern direction at the surface. There are times when the inflowing current comes to a halt and even reverses while the flood is rising in the western Mediterranean (Wesson and Gregg, 1994). The 31% of animals moving in no direction and the small percentage of eastern moving pilot whales also fit well into this picture. Yet, the ratio of this reversed current to the 'normal' inflowing conditions is not known.

#### 8.1.1 Effects of High Coefficients

High coefficients did not seem to influence the distribution. ES in series 3 was even smaller than series 2 with the same time frame. Only series 1 had a smaller ES. Mean

differences between HT and LT groups were intermediate. Again, this is evidence for an active movement. Otherwise ES and mean difference would be expected to be larger in the high coefficient series 3 than the control series 2, as the animals would be swept east or west much further than during weak tides with low coefficients.

## 8.2 Topography

The underwater topography in the Strait of Gibraltar has a big influence on the distribution of pilot whales. They seem to be located predominantly south of the underwater ridge in the strait and north of the shallow shelf waters close to the African coast. Only few sightings were made in waters less deep than 100m closer to Morocco. Well in accordance with Hui (1985), the steep relief of this area seems to suit the needs of pilot whales. (See figure Z)

The relief of the Spanish side of the strait is just as steep but whales are scarcely seen there. There is probably more boat traffic in the northern half of the strait since the area is a well known tourist spot and many small boats travel from Tarifa to nearby Algeciras and back. Nevertheless, it is unlikely that this had such a pronounced effect. After all, there are many other dolphins which can be seen regularly in this area, even in close proximity to the Gibraltar and Algeciras harbors. More likely, pilot whales prefer the waters over the southern trench for some reason.

This could be related to the abundance of food in this area. Many species of squid not only spend their life on shelf edges, but are also sensitive to water temperature gradients (Brodziak and Hendrickson, 1999). Upwellings occur in this area together with heavy west winds (Stanichny et al. 2005) and cooler eastward outflowing currents are forced to the surface at the Camarinal Sill (Wesson and Gregg, 1994). In all temperate or tropical regions of the world, upwelling of deep water is associated with a marked increase of productivity. It could be that the hydrographic conditions in this part of the strait in conjunction with its special topography are responsible for the persistence of these resident pilot whales.

#### 8.3 Conclusions

The fact that pilot whales actively move in order to keep their preferred positions seems somewhat contradictory to their notion to vary the use of their habitat with respect to tidal conditions. They are certainly capable of swimming against the strongest currents without greater effort, as their usual traveling speed exceeds the maximum current velocities (Nelson and Lien, 1996). And they could definitely navigate as freely in the strait as most of their worldwide relatives do on the open ocean and shelf edges. According to the statistical analyses, the effects of the tides are very distinct, yet their magnitude is comparably small. One possible explanation is that the whales might not be influenced by the water movements directly but by one or several other factors, which depend on the currents instead and pass its effects on to the pilot whale population.

The close association of pilot whales and their favored squid prey serves well as a hypothetical model and relationships between social structures of pilot whales, environmental gradients and squid species have been discussed before (Amos, 1993; Fullard et al. 2000.) But the little which is known about most squid species suggests that they undergo considerable migrations in many parts of the world to meet their energy needs, even in the productive regions of the North Atlantic (Brodziak and Hendrickson, 1999). Therefore, the conditions at the strait would have to be exceptional to constantly produce enough biomass to support the whole local food pyramid, not only compared to the rest of the Mediterranean but also to most parts of our oceans.

This is not entirely impossible as the in- and outflowing water masses constantly transport nutrients in the form of dissolved and particulate organic matter (DOM and POM) through the strait. Additional biomass is funneled in this narrow passage, as big swarms of pelagic fish visiting the Mediterranean seasonally are passing the strait. But the dimension and complexity of the biomass cycles in our oceans and the Strait of Gibraltar in particular are too big to assert a fully integrated theory of energy flows and ecology of this region.

However, the consistency with which pilot whales exhibit their movements in relation to tides and currents corroborates a determining role of the water regime for their ecology in the strait. In this regard, the small scale but distinct differences of pilot whale locations at high and low tides probably represent an important adaptation to presently unknown underlying causes. Accordingly, the steep relief in the middle of the strait and the shelf edges would be expected to partition this habitat along the corresponding small scale boundaries. In other words, pilot whales are to a great degree dependent on the conditions they find only in certain locations of their habitat. The persistence of their population in the strait indicates a complex nutrient cycling and underlines the importance of this place for many other cetacean and marine species.

#### 8.3.1 Future Research Recommendations

The shipping traffic in the Strait of Gibraltar has been constantly increasing in the past and is this trend is not likely to stop anytime soon. On the contrary, there are new speedboat lines planned, crossing the strait between Spain and Morocco and there is a big military harbor under construction on the Moroccan coast. To ensure the future well being of the pilot whales as well as other cetacean populations, we need a more complete picture of their ecology.

Analysis of the hydrographic conditions in the strait with a bigger resolution than what is available today could allow for a more precise matching of sighting data and water regime. Transect temperature measures could be a viable method to gain a more complete picture of the influence of major currents caused by tides and winds and could be performed easily by the whale watching boats crossing the strait several times a day. The specific pilot whale diet in this area and the abundance of important food species could provide a link to these conditions as well as the nutrient ecology of the strait. The identification of the predominant squid species consumed by the whales and its characteristic lifestyle in the slope waters would certainly help to decipher the intricate relationship between the whales and their surroundings. Further sighting data is mandatory and it should be the goal of the research in this area to assess a precise scheme of habitat use by cetaceans.

Major shipping traffic in the Strait of Gibraltar cannot be restricted on the whole, as this passage is of great economical importance to the region. A sanctuary like the one established in the Ligurian Sea, where speedboats and big ships are banned entirely from certain areas and only allowed on narrow routes is out of the question for the strait. But if the critical areas for the whales and dolphins can be identified, a simple restriction or small scale change of the shipping routes could probably ensure the future coexistence of cetaceans and humans in the strait.



**Picture 31:** Pilot whale pod in the Strait of Gibraltar

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# 9. Acknowledgements

I would like to thank my good friend Michael Casanova for arranging for me to be able to do this thesis under the premises of FIRMM in Tarifa, Spain. Thanks for friendship and support (and letting me live in his flat for my time in Tarifa.)

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Special thanks to Marion Huber for enduring hellfire in her support in the statistical analysis of the wickedest set of numbers since the great revision of the string theory. Hope the single malt is not too peaty.

# **10. Pictures**

# **Pictures:**

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0 0	http://atlas.cms.udel.edu/main.html
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# 12. Appendix

This poster by M. Casanova and M. Tobler was published at the 21<sup>st</sup> Conference of the European Cetacean Society, Donostia - San Sebastian, Spain. April 22-25, 2007.



Statistical analysis shows highly significant differences between the distribution of the pilot whale population during high tide compared to low tide. It is obvious that the animals are locally influenced by and moving with the tides. These results may help to define adapted traffic rules in the Strait of Gibraltar.

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