Active Touch Sensing in Pinnipeds

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Abstract

Active touch sensing in humans is characterised by making purposive movements with their fingertips. These movements are task-specific to maximise the relevant information gathered from an object. In whisker-touch sensing, previous research has suggested that whisker movements are purposive, but no one has ever examined task-specific whisker movements in any animal. Pinnipeds are whisker specialists, with long, mobile, sensitive whiskers and diverse whisker morphologies. The aim of this PhD is to investigate active touch sensing in Pinnipeds (seals, sea lions and walrus), by: i) describing whisker morphology; ii) comparing and quantifying whisker movements; and iii) characterising task-dependency of whisker movements during texture, size and luminance discrimination tasks. Pinnipeds with long, numerous whiskers, such as California sea lions (*Zalophus californianus*) and Stellar sea lions (*Eumetopias jubatus*) have larger infraorbital foramen (IOF) sizes and therefore, more sensitive whiskers. The IOF being a small hole in the skull, allowing the infraorbital nerve (ION) to pass through, which supplies sensation to the whiskers. Comparing whisker movements in Harbor seals *(Phoca vitulina*), California sea lions and Pacific walrus (*Odobenidae rosmarus*), showed these species all protracted their whiskers forwards and oriented their head towards a moving fish stimulus. However, California sea lions moved their whiskers more than the other species, and independently of the head. Due to the movement capabilities and sensitivity of whiskers in California sea lions, this species was used to investigate whether whiskers can be moved in a task-specific way. Results suggested that California sea lions make task-specific movements, by feeling around the edge of different-sized shapes, and focussing and spreading their whiskers on the centre of different-textured shapes.

Therefore, California sea lion whiskers are controlled like a true active touch sensory system, similar to human fingertips. I suggest that active touch sensing is likely to efficiently guide foraging and prey capture in dark, murky waters in these animals. Moreover, the complexity of California sea lion whisker movements and their subsequent behaviours makes them a good candidate from which to further investigate animal decision-making, perception and cognition.

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1 ***Chapter One: Introduction and Overview***

Chapter Summary:

The research presented in this thesis focusses on active touch sensing in Pinniped*s*; specifically looking at the process of acquiring sensory information about the world using whiskers. Whisker movements for many animals are purposive, and used to gather and seek information about the environment. In some cases, these movements are modified to bring whiskers in to contact with the most relevant regions of the environment. This chapter introduces the foundation of the thesis by introducing active touch sensing and emphasising how important whiskers are to Pinniped*s*. It concludes by setting out the aims and objectives of the thesis.

1.1 Why study whiskers?

All mammals possess mystacial vibrissae, more commonly known as sensory hairs or whiskers at some point in their lifetime except for some primates and humans (Hirons et al. 2001; Ling 1977). Whiskers form part of a unique sensory system that has been at the forefront of research across many different fields, including anatomy, neuroscience, behavioural science and even robotics (Dehnhardt et al. 1998; Tuna et al. 2005; Soloman and Hartmann 2006a, 2006b; Pearson et al. 2007, 2010, 2011; Berta 2009; Mitchinson et al. 2011, 2018; Grant et al. 2013a, 2013b, 2016; Milne and Grant 2014; Hanke and Dehnhardt 2016). Taxa that have highly developed whiskers are classified as being whisker specialists and include the Pinnipeds (seals, sea lions, and walruses), rodents and marsupials (Mitchinson et al. 2011; Grant et al. 2013 a, 2016; Milne and Grant 2014). These are adapted to live in the dark (nocturnal, subterranean or aquatic), so rely on their sense of touch to guide them around their environment.

The origin of the word vibrissae comes from watching whiskers and believing that these specialised hairs were in fact *vibrating* (Chernova 2006). However, whiskers do not just vibrate, they are actively moved in response to sensory inputs from the environment (Towal and Hartmann 2006; Mitchinson et al. 2007; Grant et al. 2009; Arkley et al. 2014). This has resulted in the whisker system (the combined neuromuscular anatomy of the region) being proposed as a fruitful model for understanding active sensing, due to whiskers being highly sensitive and moveable (Reep et al. 2001, 2002). Whisker systems across species that have whiskers all include specialist muscles allowing them to move their whiskers independently, with some species having more mobility than others do

(Grant et al. 2013b, 2016). For example, the diurnal terrestrial Guinea pig (*Cavia porcellus*) shows limited whisker movement relative to nocturnal arboreal rodents (Grant et al. 2016). This diurnal terrestrial Guinea pig also possesses few whiskers and they have a disorganized arrangement, although their mystacial musculature is still very similar to that of murid rodents (Grant et al. 2016). In addition, the grey short-tailed opossum, (*Monodelphis domestica)* also has fewer whiskers than rats, but show a similar vibrissal musculature (Grant et al. 2013b). This suggests that even in visual mammals, whiskers still play an important role and are involved in tactile behaviours such as guiding locomotion and prey capture (Grant et al. 2018). However, there are clear differences in vibrissal layout, musculature and movement between species, with well-developed whiskers linked to species that rely more on tactile sensing. Many studies have focused on measuring whisker movements in small mammals (Prescott et al. 2011; Grant et al. 2016, 2018; Arkley et al. 2017), probably due to the ease of studying them in the lab environment. However, Pinniped*s* have been relatively overlooked. Pinniped*s* have long, motile whiskers and a large diversity in whisker morphology, all of which suggests they will help elucidate whisker evolution and function (see section ***2.5 Whisker Anatomy and Morphology***).

1.2 Active touch sensing systems

Active sensing is based on sensory feedback and movements that are controlled, purposive and task-specific (Prescott et al. 2011). Active touch is the control of the movement of touch sensors, such as vibrissae to maximise the amount of relevant information gathered from the environment (Mitchinson et al. 2007; Prescott et al. 2011; Mitchinson and Prescott 2013; Grant et al. 2014). An article by Gibson (1962) makes observations about the relationship between hand movements and the sense of touch stating that:

"…as humans if we explore anything with our hands we actively control our fingers by making each movement purposive in active touch, adjusting them to gather environmental information." (Gibson 1962, page 478).

Human fingertips make purposeful, task-specific movements such as lateral movements to determine object texture and vertical movements for object softness (Gibson 1962). Active touch sensing involves both movement and the ability to control sensory apparatus to detect environmental tactile cues (Gibson 1962; Prescott et al. 2011). Gibson explains that active sensing differs to that of "passive sensing" or "being touched", although both gather tactile information (Gibson 1962; Cullen 2004; Miyashita and Feldman 2013). Indeed, active touch sensing is the difference between whether the animal or person is controlling their sensory apparatus, or whether the tactile sensation is simply being applied (Gibson 1962; Cullen 2004). We therefore, would assume that for vibrissae to engage in active touch sensing, they should make controlled movements that are also task-specific (Prescott et al. 2011). **Although we often assume that whiskers do**

active touch sensing (Prescott et al. 2011; Grant et al. 2014)**, and have documented that whiskers do move** (Wineski 1983; Grant et al. 2012; Milne and Grant 2014) **the task-specificity of movement has never been explored before**.

The study of active touch sensing in animals often takes inspiration from haptic studies in humans (Stansfield 1986; Bajcsy et al. 1987; Roberts 1990; Awter et al. 2002; Iqbal et al. 2005). Many studies of this type have developed discrimination tasks of size, shape or texture, and measure tactile sensation capabilities as well as the movement of the sensors themselves. However, these discrimination tasks are relatively stationary and may not encourage whisker movements. Indeed, previous studies have determined that head positioning mainly determines whisker placement in Pinniped*s*, rather than the whisker movements themselves (Dehnhardt 1994; Grant et al. 2013a). Therefore, it was previously thought that Pinniped*s* did not really control whisker movements and only made simple protractions. However, a more recent study by Milne and Grant (2014) used a novel, dynamic sensorimotor task to promote whisker movements and found, for the first time, that whisker movements were important during a ball-balancing task. Specifically, whiskers responded much quicker than the head to movements of the ball and were employed to help sense and control the ball (Milne and Grant 2014). This PhD thesis will build on the Milne and Grant (2014) study and Milne (2013), by: i) designing a dynamic sensorimotor behavioural task to encourage and measure whisker movements in Pinniped*s*, and ii) developing a series of discrimination tasks to study the task-specificity of whisker movements.

1.2.1 Terrestrial Mammals

Whisker variables such as shape, number and arrangement have been shown to be associated with their environment. The overall shape of vibrissae indicates adaptations for different environments in terrestrial mammal species (Williams and Kramer 2010; Voges et al. 2012). For example, conical vibrissae are more advantageous than cylindrical vibrissae for terrestrial species, as this shape enables vibrissae to skim over different surfaces without getting stuck (Carl et al. 2012; Hires et al. 2013). Hires et al. demonstrated this using rodent whiskers and found that having conical shaped whiskers enabled the whisker tip to be more flexible than the whisker base. This allows whiskers to slip past nearby objects and move freely over rough surfaces without getting stuck, in comparison to cylindrical whiskers, which become stuck behind nearby objects and caught on uneven textures (Hires et al. 2013). Moreover, the sticking of cylindrical whiskers would lead to ‘blind spots’ and therefore not gather all the information available on their environment (Hires et al. 2013). Rodents use a behaviour called “whisking” during spatial exploration (Berg and Kleinfeld 2003). This is a series of active movements, which together with conical whiskers are advantageous gather more information about an environment (Hartmann 2001; Mitchinson et al. 2007).

Blind rodents such as rats change their approach when using vibrissae to explore environments, providing strong evidence for active vibrissal control (Arkley et al. 2014). In addition, small nocturnal and arboreal mammals appear to have longer more densely packed vibrissae than ground-dwelling and burrowing mammals (Pocock 1914; Lyne 1959; Ahl 1986, 1987; Sokolov and Kulikov 1987). Field mice (*Apodemus)* inhabiting a more arboreal habitat had longer vibrissae with a denser vibrissal field in comparison to burrowing field mice (Kratochvil 1968), providing evidence of a correlation between vibrissae and environment. Muchlinski et al. (2013) investigated the presence of vibrissal sensing systems in larger nocturnal, arboreal mammals and discovered that in primates only nocturnal, arboreal prosimians possess the structures necessary to gather information using vibrissae (Birdwell et al. 2007; Muchlinski et al. 2013). In addition, it appeared that primates without vibrissae had increased sensitivity of the hands and vision (Pocock 1914). Overall, animals that live in the dark have longer more numerous and more mobile whiskers.

1.2.2 Marine Mammals

Although it is dark underwater, below about 10m depth, and marine mammals have some of the longest whiskers of any species, research on vibrissae in this group is limited and entirely absent in a number of species. However, what is clear is the great variation of vibrissal specialization across aquatic mammals. Vibrissae are nearly absent in polar bears (Pocock 1914; Huber 1930). Cetaceans (whales, dolphins and porpoises) possess some form of vibrissae but their structure differs between species (Ling 1977). For example, vibrissal structures are found around the lower jaw and lip, chin and blow hole in mysticetes (baleen whales), but odontocetes (toothed whales) have hardly any vibrissae when they are adults and some species lose the vibrissae in embryo (Ling 1977). The exception to this is the *Platanistidae* (river dolphin) who have well-developed vibrissae on their upper and lower jaws (Ling 1977), presumably to aid foraging in murky waters. Sea otters have prominent facial vibrissae, which appear to be arranged densely around the muzzle, but research on their whiskers is absent. Sirenians (manatees and dugongs) have extremely specialized (many, well- innervated) facial vibrissae and are the only aquatic mammals to possess vibrissae covering the surface of the body (Reep et al. 2002; Huber 1930; Wilson et al. 1991).

Pinnipeds have the most highly developed vibrissae of all marine mammals (Ling 1966, 1977). Pinnipeds consist of true seals (Phocidae), eared seals, which include the fur seals and sea lions (Otariidae), and walruses (Odobenidae). Pinnipeds have up to three groups of facial vibrissae: mystacial, supraorbital (eyebrows) and rhinal (nasal), (Ling 1966, 1977). The mystacial vibrissae, located on the muzzle are the most prominent, arranged in parallel rows and columns, varying in number, size and shape between species (Ling 1966, 1977). The supraorbital vibrissae are located above the eyes and, are more developed in Phocidae than in the Odobenidae and Otariidae (Pocock 1914; Ling 1966, 1977). The rhinal vibrissae are only present in Phocidae, usually appearing as a pair of vibrissae on each side of the face above the nose (Ling 1977). The Hawaiian Monk seal (*Monachus schauinslandi*), also has another set of definitive vibrissal-like hairs under the lower jaw which has only ever been observed and not studied due to them being extremely rare (Murphy 2013). This whisker placement is identical to the interramal vibrissae present in terrestrial mammals (Pocock 1914), but further research of the whisker follicle to confirm this would be required (Pocock 1914).

1.3 Why study Pinniped vibrissae?

Pinnipeds retain their whiskers throughout their lifetime, so are a worthy candidate for studying active touch sensing behaviours. They have long, prominent vibrissae, and can move them using a network of voluntary muscles (Berta et al. 2005). They are also very trainable due to their inquisitive nature (Berta et al. 2005). Indeed, vibrissal touch is thought to be more efficient and important in Pinniped*s* than in terrestrial mammals, due to their whiskers being more sensitive (Rice et al. 1986; Hyvärinen 1989) and this sensitivity being unaffected by temperature changes (Dehnhardt et al. 1998; Mauck et al. 2000). Moreover, studies have shown that the sensitivity of Pinniped whiskers is comparable with that of the hands of primates and humans, not only with regard to tactile sensitivity but also with regard to the functional aspects of their sense of touch (Lederman and Klatzky 1987; Dehnhardt 1990, 1994; Dehnhardt and Kaminski 1995; Dehnhardt and Dücker 1996; Dehnhardt et al. 1997).

The function of whiskers in Pinniped*s* has been the subject of a wide body of research confirming that the vibrissal system plays a major role in underwater orientation and foraging (Oliver 1978; Hyvärinen 1989; Dehnhardt and Kaminski 1995). Many studies have discussed how important whiskers are within dark aquatic environments, for hunting and finding food in a similar fashion to nocturnal rats and mice (Mitchinson et al. 2007, 2011). Other aquatic mammals use vision, echolocation (Zimmer 2001) or electrosensing (Iggo et al. 1992; Czech-Damal et al. 2011), but Pinniped*s* mainly rely on their highly sensitive whiskers for foraging.

The employment of the whiskers for tactile discrimination and their sensitivity suggests how important they are for Pinniped*s*. Whisker shape is thought to be associated with function e.g. oval whiskers of sea lions are more sensitive to changes in velocity and undulating whiskers in Harbor seals *(Phoca vitulina*) are more stable for hydrodynamic sensing (detecting the motion of water caused by a moving object such as a fish), (Dehnhardt et al. 2001; Dehnhardt and Mauck 2008; Hanke et al. 2011; Gläser et al. 2011; Muthuramalingam and Brücker 2018). **However, whisker morphology has not been explored systematically in many species of Pinniped, nor linked to whisker positioning or movement capabilities in Pinniped. Whisker movements themselves have also been largely overlooked, with only one study, thus far, measuring the degree of movement of California sea lion (*Zalophus californianus*) whiskers** (Milne and Grant 2014).

1.4 Whisker movements

Whiskers show huge variation across Pinniped*s* in their ability to be moved, which would be a pre-requisite for an ability to actively seek and gather information. Having such a variety of movements indicates these movements could be controlled and altered to gather information that is relevant during a specific task. Walrus (*Odobenidae rosmarus*), are capable of distinguishing between different sized shapes distinguishing a circular disc from an equilateral triangle with the surface area of both shapes being 0.4 cm^2 (Kastelein and Van Gaalen 1988; Kastelein et al. 1990). Otariidae, in particular the California sea lion have the ability to use their whiskers to differentiate between different shapes (Dehnhardt 1990) and different sized objects down to a surface area difference as small as 0.5 cm (Dehnhardt 1994; Dehnhardt and Dücker 1996). Indeed, blindfolded California sea lions can identify differences in diameter between circular discs with the same degree of accuracy as achieved by their vision (Dehnhardt 1990). Considering that number, arrangement, size, stiffness and structure of mystacial vibrissae show considerable interspecific variation in Pinniped*s* (Ling 1977; Watkins and Wartzok 1985), the results of active touch studies in Otariidae (sea lions) and Odobenidae (walrus) may not hold the same for Phocidae (seals). In some species of Phocidae, whiskers have a larger angle of projection from their muzzle than Otariidae. In addition, all whiskers in the Otariidae are smooth and cone-like in shape, whereas most Phocidae whiskers have wavy surfaces. These differences in the structure are likely to have a relationship with tactile stimulation and function.

Out of all Pinniped*s*, the Phocidae, and specifically the Harbor seal are the most well studied. Like the California sea lion, they are able to judge different sizes of objects to the same precision as vision (Dehnhardt et al. 1998). Some studies indicate differences in males and females across some species, with females being able to detect even smaller differences (Dehnhardt and Kaminski 1995). However, more studies are needed to see whether gender plays a significant role. Harbor seals are also found to show hydrodynamic perception, which allow them to detect local water movements and follow hydrodynamic trails (McGovern et al. 2015). Research has shown that both the Harbor seals and California sea lions are able to detect local water movements and follow hydrodynamic trails (Bleckmann et al. 1991; Zimmer 2001; Hanke and Bleckmann 2004). However, there are differences in performance, with California sea lions being more sensitive to local water movements and Harbor seals being superior at following the hydrodynamic trails (Hanke et al. 2013; Gläser et al. 2011). It has been suggested that these differences in performance are due to differences in vibrissal surface structure (Hanke et al. 2013; Gläser et al. 2011). Harbor Seals and California sea lions both have different vibrissal surface structures. Harbor seals containing a combination of peaks and troughs along the length of the whiskers creating a wave effect, while California sea lions have smooth vibrissae. In Harbor seals, the unique surface structure of the vibrissae may explain their higher sensitivity (Miersch et al. 2011). It has also been suggested that the purpose or function of this unique undulating surface structure may be to reduce noise, via vortex-induced vibrations produced by the vibrissae during movement (Hanke et al. 2010; Murphy 2013).

California sea lions possess 38 vibrissal hairs on each side of their face, growing up to 20 cm (Dehnhardt 1994). Their whiskers play a primary role in active touch sensing (Dykes 1975; Hyvärinen 1989; Dehnhardt 1994; Dehnhardt et al. 2001; Mitchinson et al. 2007), hydrodynamic trail following (Gläser et al. 2011; Hanke et al. 2011), and can discriminate between different shapes (Dehnhardt 1990) and sizes (Dehnhardt 1994; Dehnhardt and Dücker 1996). They are also easy to access for study, as they are a popular addition to many captive environments, such as zoos and involved in educational displays. In addition, this species was the first Pinniped species to demonstrate the importance of whisker movement and control (Milne and Grant 2014). **Therefore, California sea lions might be a good candidate Pinniped species, from which to explore active touch sensing further.**

1.5 Conclusions

Despite Pinniped*s* having long, prominent, moveable and sensitive whiskers, there have been few attempts to quantify the movement of vibrissae in Pinniped*s*. Therefore, we do not know whether whiskers are moved purposefully in these animals. In addition, the task-specificity of whisker movements has never been explored in aquatic or terrestrial mammals, despite the number of studies in nocturnal rodents. Therefore, it is not possible to say definitively whether Pinniped*s*, and other mammals, really engage in active touch sensing.

1.6 Content of thesis: aims and objectives

The aim of this PhD is to **investigate active touch sensing in Pinniped*s*** specifically, to investigate the range and task-specificity of whisker movements. There are three main objectives:

1. **To describe whisker morphology in Pinniped*s***
2. **To compare and quantify whisker movements in Pinniped*s***
3. **To characterise task-dependency of whisker movements in California sea lions during texture, size and luminance discrimination tasks.**

This PhD will characterise active touch sensing in Pinniped*s*. As whisker movements are likely to be linked to morphological predictors, with previous studies identifying that whisking mammals had a larger infraorbital foramen (IOF) area (small hole in the skull which allows the infraorbital nerves to pass through), which indicates larger infraorbital nerves (ION) and therefore increased sensory acuity (Grant et al. 2018; Muchlinski et al. 2018), such as skull morphology and whisker length, these will be examined and compared in Pinniped*s* for the first time. To make associations between morphological measurements and whisker movements, comparative tasks promoting whisker movements will be conducted on species of Pinniped, including Harbor seal, California sea lion and Pacific walrus (*Odobenidae rosmarus divergens*). These studies will characterise the movement of whiskers in Pinniped*s*. To examine whether whisker movements are task-specific, a number of discrimination tasks will be designed and participated in by California sea lion including “texture”, “size” and “luminance”. An overview of the structure of the thesis is provided below.

***Chapter Two: Literature Review*,** introduces the background to the research presented in this thesis. Firstly, it will look at the evolution of Pinniped*s*, their diet and distribution. It will discuss various feeding methods and techniques across aquatic mammals before compiling a comprehensive review of sensory systems in Aquatic Mammals, focusing on those with whiskers, primarily Pinniped*s*.

***Chapter Three: Pinniped Whisker and Skull Morphology*,** compares whisker and skull morphology across Pinniped species, and other carnivores. Here, different skull and skin specimens were studied across museums in the United Kingdom. Different whisker variables including whisker numbers, lengths, density and skull morphology (orbit and IOF area) were taken in a range of available Pinniped*s* species to make predictions about sensory abilities, and compared to existing carnivore data. Phylogenetic trees were constructed to observe patterns in evolution and feeding ecology.

Chapter Four: Quantifying Whisker Movements in Pinnipeds compares whisker movements across three Pinniped species. One species from each of the three Pinniped families (California sea lions, Harbor seal and Pacific walrus) was selected. A novel, dynamic behavioural task was designed to encourage whisker movements. Video footage was collected during then task and tracked to extract whisker movement parameters, including amplitudes, frequencies and angles to quantify how their whiskers moved.

Chapter Five: Sea Lion Training Programme provides a detailed account of the design of a series of new behavioural discrimination tasks designed in this thesis, including texture, shape and luminance, as well as describing the animal training that took place. Specifically it gives a detailed overview of the apparatus, animals and training procedures used throughout the experimental work presented in ***Chapter Six: Task-Specific Whisker Movements in California* Sea lions*.*** All experiments were conducted with a breeding group of California sea lions at Blackpool Zoo.

Chapter Six: Task-Specific Whisker Movements in California Sea Lions explores the task-dependency of whisker movements during three discrimination tasks including texture, size and luminance. For each task, California sea lions were trained to select a specific *target fish* amongst two *distractor fish*, which varied in texture, size or colour. Footage was recorded and analysed to track head and whisker movements during the tasks, to examine whether head and whisker movements differed between tasks.

Chapter Seven: Discussion provides a discussion of the findings, and a presentation of evidence that Pinniped*s* **do engage in active touch sensing** using their whiskers.

2 ***Chapter Two: Literature Review***

Chapter Summary:

Presented in this chapter is an overview of the sensory abilities of aquatic mammals, in particular how Pinniped*s* acquire sensory information about the world they live in. Terrestrial and aquatic mammals face different challenges within their environments. Pinniped*s*, belonging to the families Odobenidae (whose only living member is the walrus), Otariidae (the eared seals: sea lions and fur seals), and Phocidae (true seals) from the order Carnivora, are distinct taxonomic families as they are semi-aquatic, and therefore have well-equipped senses adapted for use both in the air and water. This chapter introduces the background behind the current thesis discussing firstly sensory adaptations of aquatic mammals that have vibrissae. It will look deeper into the sensory systems and how they have been adapted in Pinniped*s*. It will finish by looking at Pinniped touch sensing. Using whiskers as an active sensing system Pinniped*s* can gain information regarding their environment.

2.1 Aquatic mammals and the evolution of Pinnipeds

2.1.1 Overview of Aquatic Mammals

Mammals made the transition over sixty-million years ago from land to water (Repenning 1976; Berta et al. 1989). In order to make the transition successful numerous physical, anatomical and physiological changes have been required. Aquatic mammals have evolved from only two terrestrial orders the Carnivora and the Ungulata, despite comprising of over 120 extant species (Rice 1998). At the time, Ungulata included seven orders*,* with two aquatic, including the cetaceans (toothed whales and baleen whales) and sirenians (manatees and dugongs). The three Pinniped families (Odobenidae Otariidae and Phocidae), the sea otters (*Enhydra lutris*) from the Mustelidae family and the polar bear (*Ursus maritimus*) are from the Family Ursidae, all in the order Carnivora. With over 40 years of research on aquatic mammals, still relatively little is understood about how they are adapted to their unique ecology via their behavioural characteristics and sensory systems. Aquatic mammals have specialist physiology, behaviour and ecology depending on the amount of time they spend in the water (Martin and Reeves 2002).

Cetaceans (toothed whales and baleen whales) and sirenians (manatees and dugongs) spend their entire lives in water being fully aquatic. Cetaceans have nostrils located on the dorsal side of their head whereas sirenians have their nostrils located as a pair anteriorly on their head (Martin and Reeves 2002). Sirenians do not echolocate and are primarily herbivorous compared to cetaceans with baleen wales being filter feeders and toothed whales being carnivores using echolocation to find their prey (Martin and

Reeves 2002). Sea otters (*Enhydra lutris*) are well adapted for a mostly aquatic life having adaptations such as large flipper like feet for diving to the seabed and keeping heat loss to a minimum with their specialised hair (Martin and Reeves 2002). Polar bears are not as adapted to the aquatic lifestyle; they have hollow hairs required for thermoregulation (on land and in water, (Dawson et al. 2014) that also gives them buoyancy when swimming, with large long legs providing them with easier locomotion when on land (Martin and Reeves 2002). Pinnipeds have extreme adaptations that separate them from the other marine mammals and their features listed above. Firstly, their limbs are webbed and provide them with locomotion on land and in water. Their nostrils are naturally closed and located at the front of the face surrounded by sensitive vibrissae used to help hunt and guide navigation, along with extremely large eyes to gather information on their environment (Martin and Reeves 2002).

2.1.2 Pinniped Evolution

Pinniped*s*, with a Latin meaning of “fin/wing foot” (Illiger 1811), are one of three major clades of modern aquatic mammals along with cetaceans and sirenians, accounting for approximately 28% of the diversity of marine mammals. Pinnipeds comprise of three extant families: Phocidae, Otariidae, Odobenidae, and two extinct groups, the Desmatophocidae and a basal lineage *Enaliarctos* (Illiger 1811; Bertha 1998). With fossils dating back to the late Oligocene (25-29 million years ago), there has been a complex debate about the evolution of Pinniped*s*. It was believed that Pinniped*s* evolved from two carnivore ancestral lines (Figure 2.1), known as diphyly, with the Otariidae (fur seals and sea lions) and Odobenidae (walrus) linked to the Ursids (bears) and on the other side the Phocidae more related to the Mustelids (weasels, raccoons, skunks and otters) (Lento et al. 1995; Arnason et al. 2006; Sato et al. 2006; Berta 2009). However, today there is an increasingly staggering amount of both molecular and morphological research supporting Pinnipeds as monophyletic (Figure 2.1), descended from just one ancestral line (Berta 2009). There is still a disagreement between scientists today about relationships between Pinnipeds. Most of the debate focusses on whether Odobenidae are more closely related to Phocidae or Otariidae, with current data supporting a strong link with Otariidae (Berta 2009).

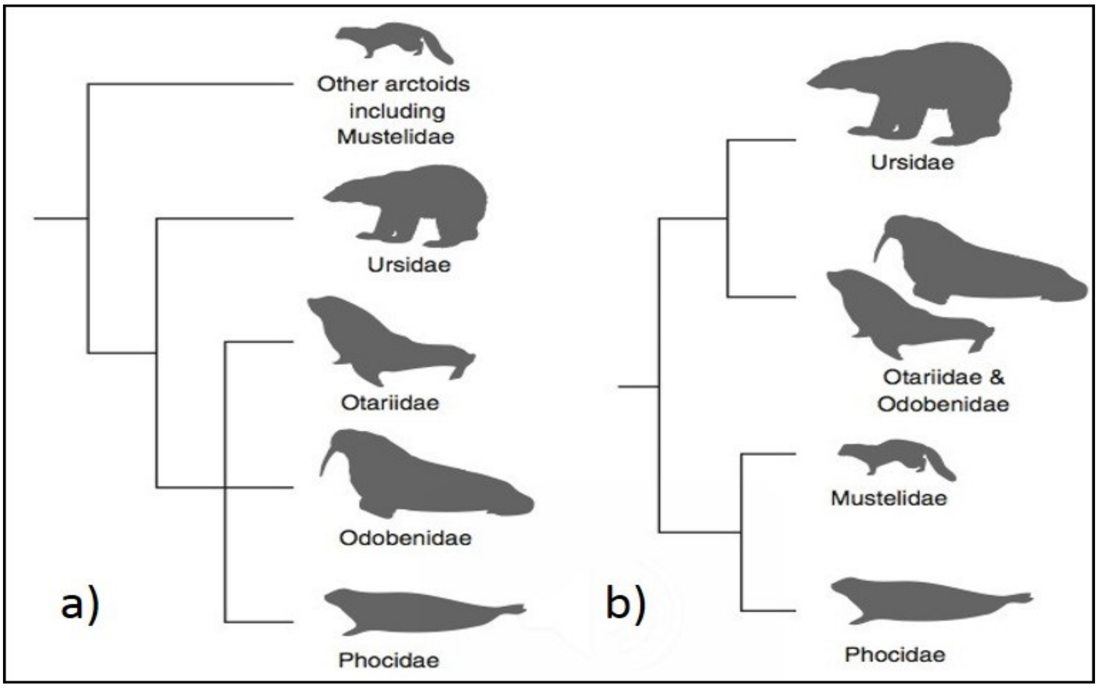


Figure 2.1: Two hypotheses of* Pinnipeds *evolution: *(a) Monophyly (b) Diphyly, taken from Bertha (1998)*

Phocidae, often referred to as the earless seals, are recognised due to the presence of ear holes but no external ear flaps. This, along with their small front flippers, allow them to be easily identified (Berta et al. 2006). Phocidae use their hind flippers to propel themselves through the water known as pelvic oscillation, while their front flippers provide steering and balance, one of three swimming styles seen in Pinnipeds, called hind limb swimming (King 1983). Having these smaller front flippers means movement on land is difficult and Phocidae exhibit an awkward method of terrestrial locomotion, as they lack the ability to turn their hind limbs forward resulting in a wave like motion generated by their entire body (Riedman 1990). The second family Otariidae are known as the eared seals due to the presence of an external ear flap. Their front flippers are much larger and they have a rotating hip joint giving them extra mobility on land. In comparison, they propel themselves through the water using their front flippers, with their back flippers to steer (Riedman 1990). This is the second swimming style known as forelimb swimming where forelimbs and pectoral muscles are used together to generate a thrusting motion by "flapping" as if flying through the water (Riedman 1990). Finally, the Odobenidae whose features are a mix between the previous two families. They lack the external ear flap and use their back flippers to swim, but they possess the rotatable hind flippers giving them greater mobility on land (Riedman 1990). The last swimming style is therefore a mixture of the previous two with the Odobenidae using their hind limbs creating the dominant force when generating power to propel them through the water relying on forelimbs as rudders to steer and change direction (Riedman 1990). Perhaps the most characteristic feature of the modern walrus is their tusks, present in both adult sexes (Repenning and Tedford 1977). Out of the three families, the Otariidae and Phocidae comprise of nearly all of the extant species (Riedman 1990; Rice 1998). To date there is said to be a total of 33 extant species 29 subspecies of Pinniped*s* (five lacking sufficient evidence to be conclusively considered subspecies) along with more than 50 extinct species of Pinniped*s* (Riedman 1990; Rice 1998).

2.2 Pinniped distribution and diet

2.2.1 Pinniped Distribution

Pinnipeds have been able to inhabit most waters, except for lakes and rivers, and are able to survive all year round in water surrounding both poles (Martin and Reeves 2002). The Odobenidae have three main populations: Pacific, Atlantic and Russian Arctic, which occupy the Northern hemisphere, separated by year round sea ice (Martin and Reeves 2002). Otariidae occupy the North Pacific, Southern Ocean and the South Atlantic areas of cool temperature or sub Polar Regions occurring in low latitudes due to colder currents. No Otariidae are found in the North Atlantic but many species tend to overlap in their distribution unlike the Odobenidae, with some species having extensive ranges (Martin and Reeves 2002). However, due to commercial sealing the distribution of Otariidae in particular fur seals has been majorly influenced. Out of the Pinniped families, the Phocidae have the most widespread of distributions spreading across both the Northern and Southern hemispheres (Martin and Reeves 2002). In the North Phocidae tend to occupy temperate Subarctic and Arctic regions while in the South inhabit warmer waters and the Antarctic. While some Phocidae are non-migratory, others need to stay by open water or air holes in the ice while others use their claws to excavate out the ice (Martin and Reeves 2002). This is important when pupping as Phocidae give birth in different areas such as pack ice, fast ice, ice lairs and sea ice.

2.2.2 Pinniped Diet

Phocidae, Otariidae and Odobenidae differ in many aspects including: appearance, ecology, locomotion and behaviour, but they also differ in food preferences, feeding methods and morphology (King 1983). Living around and in water provides a variety of food sources with Pinniped*s* often switching between prey types depending on seasons or geography (King 1983; Gentry and Kooyman 1986). Table 2.1 shows the species of Pinniped*s* studied in this thesis (see ***Chapter Three: Pinniped Whisker Morphology***) and their diet and current distribution. It shows that for most species of Pinniped the major food resource is fish and squid, followed by crustaceans, bivalves, zooplankton and then warm blooded prey (Sergeant 1973; Ling and Bryden 1981). In addition, the type of food eaten may also differ within each species depending on their age (infants, juvenile and adults) and sex (male or female), (Lowry and Fray 1984; Riedman and Estes 1988; Riedman et al. 1988). Research on Pinniped foraging ecology is important as individuals feeding in similar regions may specialise on different food sources or feeding strategies depending on their species, age or sex (Riedman 1990; Berta et al. 2015).

Table 2.1: Summary of species studied, feeding method, brief description of habitat ecology and diet: *Taken from Berta et al. (2015), Riedman (1990), Mammal Tax Review and IUCN Database 2017 (www.iucn.org)*

PINNIPEDS					
FAMILY	***COMMON NAME***	***SOCIAL GROUPING***	***FEEDING METHOD***	***DIET OVERVIEW***	***DISTRIBUTION***
Phocidae	**Harbor seal or Common seal**	SMALL GROUPS	PIERCE	Variety of fish: Menhaden, Anchovy, sea Bass, Herring, Mackerel, members of the Cod family, Whiting, Flatfish) cephalopods (Squid) and crustaceans (shrimp, crabs, molluscs) Their diet is highly varied and occasionally take krill and duck species	Western coast of Europe as far north as the Scandinavian Peninsula, the British Isles, and Iceland. Eastern Canadian Arctic from James and Hudson Bays and southern Greenland, to the coast of New Jersey and Massachusetts. Pribilof and Aleutian Islands south to Baja California. Western Aleutian and Commander Islands to the Kuril Islands and Hokkaido, Japan. Freshwater lakes and rivers of the Ungava Peninsula Quebec
	Ringed seal	SOLITARY	PIERCE	Usually prey is small, schooling fish: Polar Cod, Arctic Cod, Saffron Cod, Redfish, Herring, Capelin in marine waters or Smelt, Perch, Roach, Stickleback, in lakes, Invertebrate prey dominate the diet of young animals, Large Amphipods, Krill, Mysids, Shrimps, and Cephalopods various types of prey are selected across seasons as well as by preference.	Shore-fast and pack ice in all seas of the Arctic Ocean and are found in the southern Bering sea and range as far south as the seas of Okhotsk and Japan. Northern Baltic sea, Lake Ladoga, Russia, sea of Okhotsk, south to northern coast of Hokkaido and Kamatchatka, Saimaa, Haukivesi, Orivesi, Puruvesi, and Pyhäselkä Lakes, Finland
	Grey seal	COLONIAL	PIERCE	Variety of fish: Sandeels, members of the Cod family, Catfish, Saithe, Dover Sole, Flatfish (Dab, Flounder, and Plaice), Gadids, Whiting, Redfish, Pollock, Varies by season, age, location.	Northern Atlantic coastlines of North America and Europe (including the UK, Iceland, Norway, Baltic sea)
	Ribbon seal	SOLITARY	PIERCE	Largely unknown, but prey included Walleye Pollock, members of the Cod family, Capelin, Smooth Lumpsucker, Eelpout, flatfish, Squids, Octopus, and crustaceans. Mostly crustaceans in young fish and nektobenthos in old.	Arctic parts of the Pacific Ocean, from northern Hokkaido Japan to Alaska, northward from Bristol Bay in the Bering sea into the Chukchi, Okhotsk and western Beaufort seas
	Harp seal	SMALL GROUPS	PIERCE	Pups and juveniles: lot of invertebrate prey, especially Euphausiids Amphipods. Adults: Fish (Capelin, Herring, Sandeel, Polar members of the Cod family, Redfish, Sculpin, Snailfish) and crustaceans: amphipods, euphausids (krill), and decapods	Pack ice and coastal arctic Eastern Canada, Russia, Greenland, Iceland, and Norway
	Hooded seal	SOLITARY	PIERCE	Variety of fish and invertebrates: Pelagic Amphipods, Greenland Halibut, members of the Cod family, Red fishes, Sand Eels, Herring, Capelin, Squid, Krill Shrimp sea Stars, and Mussels.	Arctic and North Atlantic regions of eastern Canada, Greenland and Iceland, particularly Gulf of St. Lawrence, coast of Newfoundland Labrador, Davis Strait, and Norwegian sea
	Southern Elephant seal	COLONIAL	PIERCE	Varies between populations and seasons. Variety of myctophid and notothenid fish, molluscs, crustaceans, krill, cephalopods or even algae	Circumpolar sub Antarctic waters, Indian Ocean, Macquarie Island, Heard Island, Kerguelen Islands and Chatham Islands, South Georgia Falkland Islands, Valdez Peninsula.

	Weddell seal	COLONIAL	PIERCE	Notothenoid fish: Antarctic Silverfish, Antarctic Toothfish, Myctophids and Cephalopods.	Circumpolar Antarctic, in areas of fast ice
	Ross seal	SOLITARY	PIERCE	Largely unknown, but limited available data indicates mostly squid, with some fish (Antarctic Silverfish) and some invertebrates including krill.	Circumpolar Antarctic pack ice
	Crabeater seal	SOLITARY	FILTER	Primarily Antarctic Krill (90% of their diet),fish and squid, can compensate when Krill availability decreases by incorporating more fish	Circumpolar Antarctic pack ice
	Leopard seal	SOLITARY	GRIP and TEAR, FILTER FEEDER	Highly varied changes with seasonal and local abundance of prey includes krill, fish, squid, penguins, a variety of other seabirds, and juvenile seals (Crabeater, Southern Elephant and fur seals).	Circumpolar Antarctic waters pack ice, with some dispersal north to southern South America, South Africa, Australia and New Zealand
Otariidae	**South American fur seal**	COLONIAL	PIERCE	Lobster Krill, Pelagic Fish and Demersal Fish Cephalopods, few dominate species	Brazil, Chile, Peru, Argentina, Falkland Islands, Uruguay and **Brazil**.
	Northern fur seal	COLONIAL	PIERCE, SUCTION FEEDER	Schooling and non-schooling fish (Anchovy, Hake, Saury, Salmon, Walleye Pollock, Pacific Herring, Rockfish, Myctophids), and several species of Squid	North Pacific coastal regions in Canada, Japan, Mexico (coasts of Baja California), Russia, USA (Alaska, Washington, Oregon, Southern California, Bering sea, sea of Okhotsk, Pribilof Islands,
	California sea lion	COLONIAL	PIERCE	Variety of fish: Anchovies, Hake, Mackerel, Opaleye, Herring, Salmon, Lamprey, Pacific Cutlassfish, Plainfin Midshipman, Eastern Pacific Flagfin, Deepwater Serrano, some bottom-dwelling fish, as well as Red Octopus, Market and Jumbo Squid, and Clams	Northern Pacific coastal regions of Canada (British Columbia, Alaska), Mexico (Baja California and throughout Gulf of California), USA (Washington, Oregon, California)
	Steller sea lion	COLONIAL	PIERCE, SUCTION FEEDER	Variety of fish: Pollock, Cod, Mackerel, Herring, Flatfish, Capelin, Salmon, Rockfish, Squid and Octopus, Also known to feed on young Northern fur seals, Harbor and Ringed seals.	Northern Pacific coastal regions of America, Canada, China, Japan, Russia, USA (Alaska, Aleutian Islands, Kamchatka Peninsula, Washington, Oregon, California)
Odobenidae	**Walrus**	COLONIAL	SUCTION FEEDER	Bivalve Molluscs, Clams, Worms, Snails, soft shell Crabs, Amphipods, Shrimp, sea Cucumbers, Tunicates, and even slow-moving Fishes. Sometimes birds and other aquatic mammals including seal species	Bering Strait in the Chukchi sea of the Arctic Ocean along the northern coast of eastern Siberia, around Wrangel Island, Beaufort sea along the north shore of Alaska, and in the waters between such as Champlain sea, Canada, Virginia, Alaska-California

Generally, all of the Otariidae studied and the walrus (*Odobenidae rosmarus)* forage between 0-100 meters deep with the exception of the Northern fur seal (*Callorhinus ursinus)* foraging at depths between 100-200 meters (Gentry and Kooyman 1986). The Southern Elephant seal (*Mirounga leonia),* has the deepest foraging range out of all the species diving to depths over 400 m (Leboeuf et al. 1986, 1988). The rest of the Phocidae have a range of foraging depths but all foraged over 100m (Kooyman et al. 1980, 1983). The social grouping of Pinniped*s* varies across species too with all Otariidae living in large colonies, which is the same for the walrus. Weddell seal (*Leptonychotes weddellii),* Southern Elephant seal and the Grey seal (*Halichoerus grypus*), (Riedman 1990). Two Phocidae studied lived in smaller groups the Harbor seals (*Phoca vitulina)* and the Harp seal (*Pagophilus groenlandicus*), with the rest of the species all living solitary only coming together for breeding, (Riedman 1990).

2.3 Feeding strategies and behaviour in Pinnipeds

The diversity in aquatic mammals suggests that there is a variety in feeding methods used to exploit different prey types. Feeding ecology of most aquatic mammals is difficult to research via direct observations due to their extensive habitat and for that reason feeding methods are poorly understood. Most aquatic mammals will feed across vast ranges over remote areas, in deep waters making it hard to understand and assess their feeding techniques. However, with newly developed technology researching the factors influencing feeding methods and diets of aquatic mammals is slowly becoming a possibility.

2.3.1 Feeding Strategies in Pinniped*s*

Feeding methods in Pinniped*s* remains poorly understood due to unique difficulties they present: i) certain species are protected, ii) limited sample sizes, and iii) are scattered globally with some geographic ranges dangerously accessible. There is, therefore, much to be learned about underwater feeding methods of Pinniped*s*. There are two basic foraging strategies employed depending on food source and distribution: *individual foraging* (alone or in a loose group) or *co-operative foraging* (co-ordinated feeding with conspecifics), (Riedman 1990).

Individual foraging strategies are employed by single Pinniped*s* trying to exploit prey that is either non-schooling fish, slow moving invertebrates or warm blooded prey. Pinnipeds that utilise these food resources often live around coastal waters (Riedman 1990). This may be due to the prey often being clumped or distributed in patches so individual foraging may be due to the presence of a few individuals that have found a patch of desired prey, commonly seen in the Odobenidae (Fay 1982; Riedman 1990). These individual foraging strategies are also seen in many Phocidae due to their coastal distribution (Riedman 1990).

Co-operative foraging strategies consist of Pinniped*s* hunting as a group and appears mainly within Pinniped*s* that hunt large schools of fish, possibly improving their chances of finding food. Many Otariidae co-operatively feed in order to herd a large school of fish into a tight ball and pick off loose fish; they can also be seen to sometimes even co-operating with cetaceans and seabirds (Norris and Prescott 1961; Riedman 1990). Sometimes feeding in daytime is done co-operatively but feeding at night is alone, more commonly seen during their breeding season (Fiscus and Baines 1966; Sandegren 1970). This strategy will depend on the type and distribution of prey present and species of Otariidae, including California sea lions (*Zalophus californianus*), South American or Southern sea lion also known as the Patagonian sea lion (*Otaria flavescens*, formerly *Otaria byronia*) and South African fur seal (*Arctocephalus pusillus*), if they hunt together (Riedman 1990). Stellar sea lions (*Eumetopias jubatus*) change feeding strategies depending on the time of year due to food availability; when schools of fish or squid are abundant, they hunt co-operatively but when schooling fish groups are not available they will hunt alone or in small groups (Fiscus and Baines 1966). It has also been shown that female Stellar sea lions, will vocalise and stereotype by the waters' edge before hunting, a behaviour that has been linked to synchronising group foraging (Gisiner 1985) or a pre hunting ritual (Le Boeuf 1978).

2.3.2 Foraging Behaviour in Pinniped*s*

Pinnipeds are important marine predators in many habitats across aquatic ecosystems. Pinnipeds are aquatic carnivores so their teeth differ from that of land carnivores. Land carnivores have more complex teeth in comparison to Pinniped*s*, designed for chewing, grinding and sheering of flesh (Riedman 1990). The majority of Pinniped teeth are sharply pointed, cone like in shape and they also lack carnassial teeth, allowing them to catch and hold slippery fish, generally swallowed whole (Riedman 1990). Several species of Pinniped*s* have teeth specifically designed for their preferred prey type, including the Leopard seal (*Hydrurga leptonyx*), Antarctic fur seal (*Arctocephalus gazella*) and Crabeater seal (*Lobodon carcinophaga*). The Crabeater seal (*L. carcinophaga*) has cheek teeth with three cusps to allow the straining of water when catching krill (King 1961; Bonner 1968, 1982, Repenning et al. 1971). Their teeth are highly modified in comparison to other Pinniped*s*, having five of these specialised cheek teeth, allowing krill to be caught within the mouth and the water drained out by the tongue (King 1961). The smallest post canine teeth belong to the Antarctic fur seal, which are thought to be solely designed for krill straining (Bonner 1968; Repenning et al. 1971). One-third of the Leopard seal diet is made up of krill (Bonner 1982) so it does not possess the same teeth structure as the Crabeater seal, having less cheek teeth designed for straining and larger gaps between the teeth. This is due to Leopard seal having larger canines for catching much larger prey items, including mammals. the Ross seal (*Ommatophoca rossii*) feeds on cephalopods having evolved enlarged throat muscles used for securing and swallowing food along with sharp canines adapted for holding slippery cephalopods (King 1969; Bryden and Felts 1974). Tusks are a common feature of the walrus an extension of their upper canine reaching up to 100 cm in males (Fay 1982). Apart from being used for social interactions, carving out larger breathing holes and hurling themselves out onto ice, it was once suggested that these tusks were used to dig up clams. Research has shown that it is the whiskers of the walrus that are used to search for molluscs, using their powerful tongue accompanied by huge jawbones and solid column teeth for suction feeding to remove the soft-bodied invertebrate from its outer shell (Cobb 1933).

2.3.3 Summary of Feeding and Foraging

Generally, feeding methods include four main types: grip and tear, filter feeding, suction and piercing of prey. Pinniped*s* first discovered would have a feeding style similar to the piercing method (Berta and Sumich 1999), as they were coastal dwellers therefore would have had a diet that consisted of fish and other aquatic prey (Adam and Berta 2002). This suggests that the evolution of the other feeding methods in Pinniped*s* are secondary and independent events with existing studies supporting this idea as Pinniped*s* today are highly specialised feeders (Kastelein et al. 1994).

The first method *grip and tear feeding* is currently only seen in the Leopard seal using incredibly sharp teeth and prominent canines to firstly grab, hold and rip chunks of flesh from larger warm blooded mammals including penguins and other seals (Riedman 1990). Secondly, the *filter feeding* method using specialised teeth with interlocking cusps and enlarged cheek parts to hold and trap krill while draining large amounts of water out their mouth using a muscled tongue, a method that is extensively used by the Crabeater seal, (King 1961; Riedman 1990). *Suction feeding* is the third method and is the second most commonly utilised amongst Pinniped*s*. This feeding method is particularly used by the walrus having an extremely muscular tongue to generate suction and several

Pinniped*s* show adaptations towards this feeding style including Stellar sea lion and Northern fur seal where prey is sucked directly into the mouth, with no use of teeth (Riedman 1990). Finally the fourth and the most common type is *pierce feeding* where Pinniped*s* use their teeth to bite and hold prey before swallowing it whole with no chewing (Riedman 1990). This method is seen in a wide variety of fossils and is likely to be the earliest feeding style documented (Churchill and Clementz 2016).

Most Pinniped species favour pierce feeding, by grabbing and swallowing their prey whole (Adam and Berta 2002). However, there is a huge diversity when it comes to what feeding methods are used across Pinniped*s* because nearly all species are opportunistic feeders, meaning diets will more than likely vary annually and seasonally, as well as between colonies and individuals (King 1983; Reeves et al. 2002; Sinclair and Zeppelin 2002; Williams et al. 2007). Having a single foraging technique could result in species extinction if they are not able to alter their preferred prey type, and therefore cannot cope with changes in prey availability, due to an environmental or climate change (Springer et al*.* 2003). A decline in a number of Pinniped populations including: Steller sea lion, Northern fur seal and Harbor seal are thought to have been due to having a single feeding method (Springer et al. 2003; Towell et al. 2006). Overall, extant Pinniped*s* are said to be successful predators as they have the ability to hunt a variety of prey including fish, birds, marine mammals, bivalves, crustaceans, decapods, and cephalopods (Siniff and Bengtson 1977; Gentry and Johnson 1981; Fay 1982; King 1983; Riedman 1990; Werth 2000).

2.4 Sensory adaptations of Pinnipeds and aquatic mammals

All animals make decisions within their habitats in order to produce behavioural responses to the environment. Sensory information must be obtained in order to produce the "correct" response to the environment to find food and therefore survive (Kamil 1988; Krebs and Kacelnik 1991). The response produced in the form of a behaviour is not usually defined by one sensory system alone, rather, different sensory systems, which gather information. Different sensory systems have evolved over time and include visual, chemical (gustation and olfaction), mechanical (tactile, hearing and acoustic), and electromagnetic modes (Herman 1980; Reynolds and Rommel 1999). While most terrestrial mammals evolved aspects of each of these sensory channels (Hauser 1997), aquatic mammals have not, primarily because of the challenges of the aquatic environment. Amphibious marine mammals tend to use sensory modes similar to terrestrial mammals, but the strictly marine mammals have different adaptations.

Pinniped*s* are amphibious mammals, foraging exclusively in water, yet resting and giving birth on land or ice; dividing their time between the two; a lifestyle that is challenging for all sensory systems. Just like all aquatic mammals many of the Pinniped*s* sensory systems need to be adapted to suit their lifestyle, designed to be just as useful in air and under water but in particular the challenges they face in an underwater environment (Dudzinski et al. 2009). Pinnipeds, being semi-aquatic, continue to survive in an environment that is constantly changing as they move from land to water - each with its own unique challenges - and therefore, their sensory systems must have the ability to be flexible in order to react and respond to environmental and social variables. The section below will begin to look at the main sensory modalities needed by Pinnipeds. As there is an abundance of marine mammals with huge amounts of literature focused on each, this section will only include a brief overview of ***sirenians*** and ***fissipeds***, as aquatic mammals within these orders also possess functional whiskers. It will briefly describe how the different sensory systems are utilised in order to survive in a complex aquatic environment.

2.4.1 Vision

Vision in aquatic mammals is used in two ways: visual detection and visual acuity. It requires them to have a series of adaptations that maximise visual detection of predators or prey in a challenging environment where light behaves very differently than it does in air, with light becoming absorbed, refracted and scattered when it passes through a water medium (Jerlov 1976). This is dependent on the light wavelength, the chlorophyll concentration and any dissolved organic matter, for example, in coastal waters longer wavelengths are transmitted better, compared to shorter (*bluer*) wavelengths in the open ocean (Jerlov 1976).

Once an animal has detected a predator or its prey, it needs to produce a clear image to determine what behaviour is required. Vision in some aquatic mammals is poorly documented due to sight being used both above and below water, and being hard to gain access to animals in both mediums for research (Reynolds and Rommel 1999). Underwater vision is limited by light levels and therefore can only be used over short range because water movement, plankton blooms, murky water or darkness at depth limits the range and applicability of vision in water (Duntley 1963; Reynolds and Rommel 1999; Mass and Supin 2007). Some aquatic mammals have evolved adaptations for improved vision allowing them to see and communicate via visual displays to gather information. This has been seen in both cetaceans and Pinniped*s* who have the ability to detect and discriminate objects underwater as well as in air. As a result eyes of aquatic mammals are modified in order to efficiently operate in the two mediums and therefore anatomical adaptations vary greatly (Mass and Supin 2007) and will be discussed further below.

Colour vision is a difficult topic to address as there is different evidence supporting various ideas of how colour vision has evolved. Aquatic mammals, in particular Pinniped*s* and sirenians living along the coastal waters or that dive to medium ocean depths show the ability to absorb light across the blue-green part of the colour spectrum absorbing wavelength between 485-505 nm (Munz 1964; Lavigne and Ronald 1975; Kooyman 1989). In the open ocean, deeper diving aquatic mammals are able to see across the blue spectrums. These wavelengths are heavily stimulated in particular across the Odontocetis species with a wavelength absorption between 481-487 nm as seen in the Pinniped deep sea diver, the Southern Elephant seal (*Mirounga leonina*), (Lythgoe and Dartnall 1970; MacFarland 1971). In comparison, polar bears (*Ursus maritimus*) see across the green spectrum with sensitivities of 500-560 nm, (Levenson et al. 2006).

2.4.1.1 Vision in Pinniped*s*

Vision plays a significant role in Pinniped*s*, indicated by their large eyes. Eyes of Pinniped*s* are located on the front of their face and tend to be relatively large for their body size with the exception of the Odobenidae whose eyes are much smaller, located on the side (Riedman 1990; Berta 2002; see section ***2.3 Feeding Methods***). However, the constant shift between water and air is a challenge for the visual system (Jamieson and Fisher 1972; Supin et al. 2001; Griebel and Peichl 2003; Kröger 2008). Underwater Pinniped*s* are usually required to hunt in the dark, due to low light availability, with reduced contrast and short-range visibility, the complete opposite when above water with excessive bright light from intensive solar radiation reflecting off the water surface (Hanke et al. 2009).

Eyes designed for seeing underwater have a greater refractive power so when above water, vision becomes near sighted and the flat corneal will impair vision in air. On the other hand, if Pinniped eyes were designed for vision in air they would display long distance vision in water. The eyes of Pinniped*s* have therefore developed features to make them more suitable to both under and above water: i) the retina has a thick reflective layer of cells, the tapetum cellulosum to reduce above water glare (Johnson 1901; Walls 1942); ii) a large spherical lens and well-developed tapetum lucidum, used for night vision, to increase light sensitivity underwater; and iii) a sensitive retina packed with highly light-sensitive rods to increase light underwater (Landau and Dawson 1970; Jamieson and Fisher 1971; Mass 1992; Peichl et al. 2001) with a peak sensitivity in blue-shift, towards light of shorter wavelengths compared to most terrestrial mammals

(Lythgoe and Dartnall 1970; Lavigne and Ronald 1975; Carlson and LeBoeuf 1998; Fasick and Robinson 2000).

In addition, Pinniped*s* have a muscular iris with a large blood supply, a pear shaped pupil (at bright illumination, it constricts to a small vertical slit, with the exception of the bearded seal, which is more diagonal) and a highly developed dilator muscle giving a great range of pupil dilations, which varies due to illumination and species (Riedman 1990, Mass and Supin 2018). For example, in species that live in deep waters such as the Northern Elephant seal (*Mirounga angustirostris*), dilation variation is much greater reaching almost 470 times (Levenson and Schusterman 1997), in comparison to a shallow diving species, which has a much smaller range of dilation at around 70.5 times in the Harbor seal and only 26 times in the California sea lion (Levenson and Schusterman 1997). The retina is an equal distance from the lens centre and the cornea centre is almost flat, which allows refraction to be possible in water and air (Dawson et al. 1987; Sivak et al. 1989; Riedman). Another adaptation is the highly developed tapetum, a reflective layer within the eye, which reflects visible light back through the retina (Walls 1942; Riedman 1990). This allows for underwater vision by helping Pinniped*s* see in low light luminosity (Walls 1942; Riedman 1990). When on land Pinniped vision in dim light is near-sighted, which is reduced in bright light conditions, due to the retracted pupil reducing both the lens and cornea's ability to bend light (Riedman 1990). Knowledge across Pinniped*s* remains fragmented as research has only been conducted in a handful of species due to the difficulties in gaining access across all species.

It is not known whether Pinniped*s* have colour vision. Several anatomical studies have shown the presence of both rods and cones in Pinniped retina (Jamieson and Fisher 1971; Nagy and Ronald 1975; Peichl and Moutairou 1998; Peichl et al. 2001). However, there is only one type of cone present, indicating an inability to distinguish between colours (Griebel et al. 2006). Pinniped*s* seem to have lost their S-cones (Crognale et al. 1998; Peichl and Moutairou 1998; Levenson et al. 2000; Peichl et al. 2001), which is rather unusual as Pinniped*s* dive in order to catch prey so light underwater is scarce and produced by shorter wavelengths meaning that S-cones would be extremely useful (Jerlov 1976; Loew and McFarland 1990). Within the last decade, many studies have suggested that the loss of S-cones may have been from a very early stage of evolution when aquatic mammal habitats occurred in coastal waters alone (Levenson et al. 2000; Peichl et al. 2001). When Pinniped*s* moved out into the open ocean evolution once again may have shifted their visual spectrum by allowing their rods and L-cones to detect shorter wavelengths (Fasick and Robinson 1998, 2000).

Some studies have found that the rods in the eyes of Pinniped*s* contribute to their sensitivity by having the ability to constrict the pupil into a small slit appearance allowing for both rods and cones to be stimulated by the light and the ability to see in colour possessing a single spectral cone type (Crognale et al. 1999; Griebel and Schmid 2002), a feature also seen in primates (Daw and Enoch 1973; Jacobs et al. 1993). Other behavioural experiments have found Pinniped*s* are able to detect differences in coloured objects, however, these are likely to be void due to a Pinniped*s* high sensitivity for brightness, which may have been used to determine differences in luminance, rather than colour (Wartzok and McCormick 1978; Busch and Duecker 1987; Griebel and Schmid 1992).

The question, if Pinniped*s* see in colour is still very much debated. Several studies including many behavioural experiments show the presence of both rods and cones documented in some species and have shown the presence of some colour vision in the blue–green spectrum. However, Pinniped*s* have a high sensitivity for brightness and potentially brightness may have been used to determine differences in colour instead (Wartzok and McCormick in 1978; Busch and Duecker 1987; Griebel and Schmid 1992). Wartzok and McCormick, studied a Spotted seal (*Phoca largha*) and found it could discriminated between the colours blue and orange; Busch and Duecker also showed species of fur seals (Arctocephalinae), having the ability to identify blue and green from grey but not red and yellow, which was also similar in study done on California sea lions by Griebel and Schmid (Wartzok and McCormick in 1978; Busch and Duecker 1987; Griebel and Schmid 1992). The differences of results from one species to the next could be due to the methods used having differences in advantages and limitations. Research in this area is low, with knowledge only gained across several Pinniped species. What is clear from the research is that the challenge for all Pinniped species is to have a clear image in both air and underwater and possessing some colour vision could be advantageous to allow contrast, helping Pinniped*s* to detect objects underwater (Reynolds and Rommel 1999).

2.4.1.2 Vision in other aquatic mammals

Sirenians: It has been reported that sirenians have poor vision (Walls 1942), which has been seen in both manatees (Chapman 1875) and dugongs (Petit and Rochon-Duvigneaud 1929). Descriptions of eye anatomy in sirenians is extremely limited due to this group only consisting of a few species, but has recently been described in the Amazonian manatee (*Trichechus inunguis*) and in the Florida manatee (*Trichechus manatus latirostris*), (Piggins et al. 1983, Mass et al. 1997). In both species, the eye is spherical in shape but considerably small in diameter (13–19 mm) and is set back within the ocular fascia. The lens itself is set forward, is small and almost spherical, being strong enough for underwater refraction. The anterior chamber is shallow; the cornea is fairly flat and thick towards the edges, similar to the cetaceans (Harper et al. 2005). The sclera is thin, appearing thicker posteriorly (Harper et al. 2005).

Earlier studies suggested poor visual acuity underwater and in air with a retina made up entirely of rods (Mass and Supin 2007). There is one detailed study on the structure of the retina indicating both rod-like and two types of cone-like photoreceptors, indicating the possibility of some colour vision in the West Indian manatee (*Trichechus manatus*), (Cohen et al. 1982; Griebel and Schmid 1996). In addition, a study by Piggins et al. showed little refractive error in the eye underwater (Piggins et al. 1983). In general, the eye morphology resembles that of terrestrial mammals despite a completely aquatic mode of life for manatees. It does however remain unknown whether sirenians are capable of aerial vision.

Fissipeds: The sea otter has the most spectacular visual range being able to see well above and below water level using a unique method by changing the strength of the lens, allowing fluid to flow through, reducing the pressure in the anterior chamber, causing the lens to be pushed forward (Murphy et al. 1990). This is a key adaptation for its lifestyle, living across coastal zones and searching for prey under water.

The eye is extremely similar to terrestrial mammals being spherical in shape (Murphy et al. 1990; Mass and Supin 2000). Compared to the spherical lens of cetaceans and Pinniped*s*, the sea otter's lens resembles the shape of a lentil being lenticular, however, the front surface is crest-like in shape (Berta et al. 2015). A characteristic feature of the eye is the iris is secured to the frontal lens and does not close to a slit or hole like in Dolphins due to the curvature of the lens, relying on the contraction of iris muscles suggesting there is a trade-off between sensitivity in low light and visual acuity, similar to terrestrial mammals (Murphy et al. 1990). Although there are no behavioural studies sea otter acuity and light levels, Schusterman and Barrett (1973) showed that an Asian Short-clawed otter (*Amblonyx cineria cineria)* lost acuity underwater more rapidly than in air when light levels decreased (Schusterman and Barrett 1973).

There is only a hand full of studies available on polar bears due to their extreme solitary nature. One study found they possess both rods and cones in the retina (Ronald and Lee 1981) with another showing the eye structure with little adaptation for underwater vision, with lens strength decreasing massively when underwater (Sivak and Piggins 1975).

2.4.2 Chemoreception: Gustation and Olfaction

The diffusion of chemicals on average is 10,000 times slower in water than air, with water currents approximately 15 times slower than average air currents (Vogel 1994). This means that communication via chemicals in water is less efficient than in air. Tasting dissolved chemicals (gustation) and smelling chemicals (olfactory) in air or water has had little research as these sensory systems have not drawn much attention. Compared to all terrestrial mammals little is known about the chemoreception abilities of aquatic mammals, as they have not been researched widely with the difficulty in being able to control, measure, and present chemical stimuli, but the biggest issue is the number of aquatic mammals for experiments, resulting in slow progress in research.

Across the research done on aquatic mammals' chemoreception in water may be more taste than smell as it is believed smell is poorly developed across all aquatic mammals (Brown 1985; Reynolds and Rommel 1999). As in terrestrial mammals, taste buds of aquatic mammals are found on the tongue however, are modified and reduced in numbers. Their sense of smell has received less research than taste as water is not a good medium for scent particularly over long distances. In comparison to terrestrial mammals the olfactory anatomy and systems of aquatic mammals are to a certain degree reduced in Pinniped*s* and Baleen Whales; in manatees and Dugongs are severely under-developed and almost completely absent in Odontocetes (Lowell and Flannigan 1980; Watkins and Wartzok 1985; Nachtigall 1986). This is because olfaction is not a precise form of communication to gather information in water and this system declines with a more aquatic lifestyle (Reynolds and Rommel 1999). Sirenians, cetaceans, Pinniped*s* and sea otters all keep their nostrils closed under water or at the surface unless breathing preventing smell as a useable sense.

2.4.2.1 Gustation in Pinniped*s*

In comparison to terrestrial mammals, Pinniped*s* have a reduced number of taste buds, which would suggest a low sense of taste (Bradley 1971; Eastman and Coalson 1974; Kastelein et al. 1997). Pinniped tasting abilities have been demonstrated in Steller sea lions (Kuznetsov 1982) and California sea lions (Friedl et al. 1990). Both showing the ability to detect acidic and salty solutions but no response when it comes to sweet sensations (Kuznetsov 1982; Friedl et al. 1990). Some research in Harbor seals suggests they use gustation via salinity levels to help them when migrating having a high sensitivity to small differences of salt that occur in their natural habitat (Sticken and Dehnhardt 2000). In marine habitats, salinity levels vary, if they are able to detect changes Harbor seals could use them for orientation to find breeding beaches after a feeding trip or to find valuable foraging places. Harbor seals are highly sensitive to slight salinity differences that occur in their natural habitat, possessing the basic needs to use gustation to orientate in the marine habitat (Sticken and Dehnhardt 2000).

2.4.2.2 Gustation in other aquatic mammals

Sirenians: Sirenians have the most abundant taste buds (Levin and Pfeiffer 2002). Dugongs have rows laterally located in pits on the dorsal and posterior lateral areas of the tongue whereas manatees have a pair of swellings containing their taste buds in the same place (Yamasaki et al. 1980; Levin and Pfeiffer 2002). These pits and swellings appear larger in the dugongs, which feed mainly on sea grasses, so enzymes may be used in the fluid secreted to breakdown the grasses and stimulate the taste buds (Levin and Pfeiffer 2002). In an early study by Yamasaki et al. in 1980, fungiform papillae were found on the surface of the tongue, which may serve as taste organs, as in humans they have been used to distinguish the five tastes: sweet, sour, bitter, salty, and umami (Yamasaki et al. 1980). Although the number of taste receptors is greater in sirenians than in cetaceans, they are still poorly developed compared to herbivorous land mammals.

Fissipeds: No information is available on taste abilities in sirenians, as no significant work has been conducted. For sea otters and polar bears it is assumed their tasting abilities would be similar to terrestrial counterparts, but due to a lack of research and being able to access these animals the extent of this sense is unknown (Friedl et al. 1990; Perrin et al. 2008).

2.4.2.3 Olfaction in Pinniped*s*

Pinnipeds nostrils are naturally closed in water and on land, except when they breathe. Early research found that Pinniped*s* have both peripheral (Kuzin and Sobolevsky 1976) and central (Harrison and Kooyman 1968) olfactory structures, which appear much more prominent in Otariidae compared to the Phocidae and Odobenidae (Harrison and Kooyman 1968; Reynolds and Rommel 1999). Extensive research into the social behaviour of Pinniped*s* suggests it is important in social groups to use smell to gather information about other colony members (Evans and Bastian 1969; Ross 1972; Miller 1991). In Northern fur seals, males in their rut release a strong odour to mark territories, which is believed to attract females (Ling 1965; Miller 1975; Hardy et al. 1991; Ryg et al. 1992, Reynolds and Rommel 1999). Males also sniff the hindquarters of females to gather information on breeding state (Reynolds and Rommel 1999), which is also seen in South African fur seals (Rand 1955).

Pinnipeds vibrissae are surrounded by the largest gland found in pinnipeds and could play a role in mother–pup recognition. Mothers and pups maintain a great deal of nose-to-nose contact and use odour cues for recognition in air, with very little work done on Pinniped taste (Dudzinski et al. 2009). In Phocidae, more experienced Southern Elephant seals mothers begin smelling a new born pup to form a maternal bond much sooner after birth than first time mothers, resulting in them learning their pups smell much sooner (McCann 1982). Other evidence that olfaction may be a key part for mothers is seen in Northern fur seals who after giving birth forcefully sniff their pup, which in other terrestrial mammals has been related to making a strong bond between mother and baby (Bartholomew 1959; Wyatt 2003).

Pinnipeds may also use olfaction for foraging. Harbor seals have been found to detect dimethyl sulphide (DMS) produced when zooplankton is grazing on phytoplankton (Kowalewsky et al. 2006). Harbor seals have the ability to perceive very low concentrations of DMS, guiding them to places of high marine productivity and good foraging grounds (Kowalewsky et al. 2006). A study by Laska et al. (2008) shows how South African fur seals were trained to discriminate between objects providing different odour cues and showed no sign of forgetting of the task after fifteen weeks (Laska et al. 2008). Since Pinnipeds are considered to have a poor sense of smell this degree of accuracy is remarkable and is similar to some species of Primates that have an impeccable sense of smell and this degree of memory when rewarded for selecting various odours (Laska et al. 1996, Hübener and Laska 1998; Laska et al. 2003). Laska et al. (2008) also tested how Harbor seals sensed the presence and absence of fish oil. They found Harbor seals were able to detect the presence and absence of fish oil supporting the hypothesis that olfaction may play a role in hunting for certain prey (Laska et al. 2008). Studies on the use of olfaction to detect prey are rare because Pinniped*s* nostrils are naturally closed except when exhaling, so being able to detected prey by smell alone is probably not truly possible. Further research and observations may indicate that there may be more information Pinniped*s* receive by using smell and could play a significant role within their life.

2.4.2.4 Olfaction in other aquatic mammals

Sirenians: *sirenians* have a poorly developed olfactory system and no vomeronasal organ, a supporting sense organ made up of sensory cells within the nasal chamber used to detect odour particles (Mackay-Sim et al. 1985). This indicates relying on smell to gather information is highly unlikely (Reynolds and Rommel 1999). However, as aquatic plants have different tastes and smells, manatees and dugongs may use olfaction to a degree when foraging, but no research on taste abilities in sirenians is currently available.

Fissipeds: In sea otters *(E. lutris)*, olfaction has been virtually unstudied and unlike terrestrial otters, they have no scent glands possibly due to an aquatic adaptation where scent marking would lack purpose (Kenyon 1969). Just like other aquatic mammals, sea otters close their nostrils so smell is prevented. There is some evidence that sea otters have a keen sense of smell and social behaviour suggests scent production is important, particularly during pre-copulation. Adult male sea otters are seen surfacing to sniff the air and smell the genital area of females using scent recognition to identify oestrous females suggesting olfactory cues are important over short distances (Kenyon 1975; Riedman and Estes 1990). Sea otters are said to have a musty odour like other mustelids but there is no current evidence to suggest spraints are deposited strategically and they appear to defecate when needed, which in water would usually sink or dilute instantly (Gittleman 2013). On the other hand, research has shown sea otters that enter a group undertake scent recognition through a greeting ritual and individuals that deposited spraints in an others territory were followed by behavioural changes in the resident upon discovery, including the resident otter stopping its current behaviour and resenting over the scent discovered (Mason and Macdonald 1986).

Polar bears are one of the only aquatic mammals to have a very acute sense of smell. Olfaction proves important when hunting and during social interactions. When foraging it is estimated that a polar bear can hunt down their prey from over 20 miles away, locate seals breathing holes or prey hiding under snow or ice using smell alone using their enlarged olfactory turbinals (three small curved bones covered in mucous in the nasal cavity), (Green et al. 2012). On the other hand, olfaction might be used for communication among polar bears with evidence to show that olfaction helps males find females for breeding and mothers find her cubs buried beneath the snow but studies on this are rare (Ovsyanikov 1996; Stirling 1998, 1999). A more recent discovery in 2014 found males were able to smell other individuals' footprints to gather information on if they were a suitable mate in order to follow them (Owen et al. 2014). Collecting scent samples from the feet of 203 wild bears, they gave captive bears the scents to sniff, which included males, females and fertile females. Owen et al. (2014) found that they were more interested in footprint scents from the opposite sex and that the male bears were even more interested in the scents from a fertile female (Owen et al. 2014). These findings suggest that polar bears must be using their sense of smell in order to react to a chemical difference in footprint scents enabling them to gather information about sex and fertility (Owen et al. 2014).

2.4.3 Mechanoreception: Sound, Hearing and Touch

In most aquatic mammals, communication is primarily achieved through acoustic and tactile modes using both vocal and non-vocal acoustic communication. Understanding the context and function of their communication is difficult but studies allow us an insight into their “language” (Dudzinski et al. 2009). Firstly, aquatic mammals have sound systems to enable them to receive or produce sounds under the physical demands of water. Sound travels 4.5 times faster in water with relative ease over a larger area as opposed to in air. Underwater, acoustic sounds appear to be the primary mode of communication for fully aquatic mammals and a predominant mode for semi-aquatic marine mammals (Dudzinski et al. 2009). Research into acoustic behaviour is relatively straightforward when it comes to recording and analysing sounds but difficult when determining the context and function of these sounds.

Fast swimming requires streamlined bodies and therefore external ears are not a common feature found in marine mammals with the exception of the eared seals (Otariidae), polar bears and sea otters. In addition, most marine mammals dive considerable depths so closing mechanisms in the ear canal protect the ear from penetrating water (Dehnhardt 2002). The hearing of large marine mammals has only been measured with trained captive animals in controlled environments as audiometry is difficult to perform and obtaining data on hearing capabilities is challenging (Nachtigall et al. 2000). All marine mammals have evolved unique adaptations of the external ear including closure of ears, wall thickening, wax plugs and alterations of the middle ear such as thickened ear mucosa and broadened tubes, which allow for deep, rapid diving and long-term submersion (Dehnhardt 2002). Despite this, the middle ear does retain the basic configuration of terrestrial species including the air-filled middle (Dehnhardt 2002).

Visual displays are extremely valuable within close-range communication among marine mammals and, in many species; living within close proximity may readily become a form of tactile communication. Tactile communication occurs in both wild and captive animals during all social activities from play and aggression to breeding and maternal behaviours using a variety of social contexts from noses to flippers, fins to flukes, even using the entire body at times. Tactile signals allowed increased information content about an individual or situation: who, where, what and how animals touch, as well as the intensity of that behaviour. More often than not using tactile communication is combined with another form of communication or a signal relating to one another for example being chased, followed by a body slam into a sparring match.

The sense of touch requires touch receptors, which in most mammals are located over the entire body (Dehnhardt 2002). There is huge variation across mammals in the ability of different tactile sensations and receptors. The skin of aquatic mammals, like humans, is said to be able to respond to mechanical stimulation. Sensory hairs such as sinus hairs, vibrissae or whiskers are extremely diverse in their appearance, operation and distribution in aquatic mammals (Ling 1977). Scientifically known as vibrissae, derived from the Latin word "vibrio" meaning vibrate, whiskers are anatomically characterised by their length, large and well-innervated hair follicles and being highly represented in the somatosensory cortex of the brain (Grant et al. 2011).

2.4.3.1 Sound in Pinniped*s*

Underwater, sound can travel over a much larger distance with greater ease in comparison when traveling through air (Dudzinski et al. 2009). However, Pinniped*s* are able to communicate both underwater and on land (Berta 2009). Recording and analysing sounds from Pinniped*s* can be relatively easy, understanding the context and function is much more difficult. Studies of animal communication allows an insight into their language and how animals acquire new terminology from social or environmental experience (Dudzinski et al. 2009).

Communication and sound production across Pinniped species is extremely diverse with how they are produced and the rate of production varying seasonally, by sex and whether or not the individual is in water or air (Watkins and Wartzok 1985, Richardson et al. 1995). Some species of Pinniped*s* have an extensive vocal repertoire compared to others, which are completely silent (Watkins and Wartzok 1985, Richardson et al. 1995). Calls usually involve a mixture of grunts, barks, rasps, rattles, growls, warbles, trills, chirps and chugs (Watkins and Wartzok 1985, Richardson et al. 1995). Phocidae airborne calls are commonly between 100 Hz and 15 kHz but can range as high as 40 kHz (Richardson et al. 1995), Otariidae calls between 1-4 kHz and Odobenidae producing sounds within a much lower range between 500 Hz to 4 kHz (Ray and Watkins 1975; Miller and Bones 1983; Stirling et al. 1987; Verboom and Kastelein 1995; Richardson et al. 1995).

Pinnipeds also produce a variety of sounds under water such as barks, whinnies, moans, thrills, growls and squeals, which range from 0.1-10 kHz (Schusterman 1978). Vocalisations alter slightly in comparison to airborne calls when under water with Otariidae having much louder barks and Odobenidae having a unique bell-like sound produced under water. In addition to these sounds the more conventional whistles, clicks and pulses (Beier and Wartzok 1979; Ralls et al. 1985; Watkins and Wartzok 1985; Miller and Job 1992). Although these pulses and clicks appear to be produced, only in some species there is no clear evidence for echolocation in Pinniped*s* (Renouf et al. 1980; Schusterman 1981; Wartzok et al. 1984).

Generally, sounds that are produced underwater are related to or involved in breeding activities and adult social interactions, whereas sounds which are airborne generally involve mother and pup interactions, threat calls or male-male battles including sounds such as loud barks, grunts or trills being produced with whistles only made by male walrus (Stirling and Thomas 2003). Stirling and Thomas (2003) correlated the number of vocalisations produced by a species of Pinniped*s* within their mating rituals, where some even produced songs or complex noisy repertories. Phocidae are much more vocal when they mate under water, compared to Otariidae, which are more vocal on land, due to larger colonies (Stirling and Thomas 2003). Arctic Pinniped*s* tend to be silent when out on the ice in case of predators, compared to Antarctic Pinniped*s*, which are highly vocal. The adaptation of quitter vocals has evolved in some Northern Phocidae due to the presence of land predators (Ralls et al. 1985). Sometimes Pinniped*s* may vocalise when they are foraging underwater. Leopard seals produce continuous haunting sounds at low frequencies that can be felt as well as heard on the ice when hunting Adelie Penguins (*Pygoscelis adeliae*), (Poulter 1968; Kooyman 1981). All sounds produced underwater will need to be in relation with a Pinniped*s* respiratory abilities for diving, potentially having some adaptations or modifications within their sound pathways to accommodate this (Tyack and Miller 2002; Janik 2014).

Airborne sounds produce by Pinniped*s* have been studied intensely as they are much easier to research than underwater sounds. Again sound can be split into those produced at breeding season, territorial/mating activities and those produced for social interactions. During breeding season, some male Pinniped*s* produce loud receptive sounds that are associated with securing their territory or state their dominance. These calls go on for extremely long periods of time to show how fit a male is, to communicate over a lot of background noise and threaten other males or deter them (Riedman 1990). For example male Northern Elephant seals (*Mirounga angustirostris*) produce "clap threat" calls by rearing up and trumpeting (Le Boeuf 1974), male California sea lions have a distinctive continuous strong bark (Schusterman 1978) and male Southern fur seals (*Arctocephalus gazella*) have a deep bark or whimper followed by a large puff or growl (Bonner 1981).

Mothers and pups also have a unique vocalisation, which varies on an individual basis helping to recognise, locate and contact a pup. Mothers and pups bond by exchanging vocal calls for recognition, especially important when returning from the sea after several days to be reunited in overcrowded beaches (Riedman 1990). The communication between a mother and pup is unique to that pair, it is mainly used on land but can also be used by mothers when coaxing their pups to follow her into the water or out onto land/ice (Riedman 1990).

How sound production is learnt and made is poorly researched (Tyack and Miller 2002). Some research has shown that walrus can alter their breeding songs to adopt new pieces from other males and in a recovered population of elephant seals, neighbouring males in surround areas learned breeding calls by adopting parts from their old populations and new vocals from their current geographic region (Le Boeuf 1969; Sjare et al*.* 2003). More studies are needed to undercover if Pinniped*s* have social learning development when they are pups, which may only be done in isolation so could be deemed unethical unless pups were orphaned. One study by Reichmuth and Schusterman (2009), had the opportunity to document an isolated female Northern Elephant seal (*Mirounga angustirostris*) having a very unusual call not heard in the wild, which she maintained through her lifetime (Reichmuth and Schusterman 2009). Another study by Hughes et al. (2011) also talked about a male walrus raised with females in captivity that developed different components of his song. It never produced an organised breeding song when he reached adult hood (Hughes et al. 2011). The best-known account comes from the captive male adult Harbor seal called Hoover that made human like vocalisations, including tone, accent and attitude (Ralls et al. 1985; Deacon 1997). Hoover inspired other researchers to try to teach other Pinniped*s* to produce speech-like sounds; however, despite being able to train some speech using operant conditioning none of them ever matched the vocabulary of Hoover. Despite only a few studies providing evidence for vocal learning, much remains to be learned about communication in Pinnipeds, with several species not yet investigated. Training Pinnipeds could provide more evidence on vocal sounds and learning in different species, but sound pathways via anatomy, morphology and neurological mechanisms are required to support vocal learning capabilities of seals, sea lions and walruses.

2.4.3.2 Sound in other aquatic mammals

Sirenians: Sirenians have been seen slapping the water surface with their tail fluke as a form of communication, but usually sounds are produced vocally underwater, described as squeaks, whistles, chirps, barks and trills (Sonoda and Takemura 1973; Anderson and Barclay 1995; Richardson et al. 1995). Dugong sounds range from 0.5-18 kHz peaking between 1-8 kHz (Nishiwaki and Marsh 1985; Anderson and Barclay 1995). The West Indian manatee has a sound production range of 0.6-5 kHz (Schevill and Watkins 1965) with the smaller Amazonian manatees having a larger peak spectrum at 10 kHz, with distress calls being produced around the 35 kHz range (Bullock et al. 1980). Sirenians sounds are low in amplitude and probably only travel across short distances. Field observations show that vocalizations between mothers and calves play an important role in keeping them together described as dueting (Reynolds and Odell 1991). Dugongs also have sounds that operate at a low frequency, producing calls ranging from 1 to 18 kHz (Reynolds and Rommel 1999). As dugongs are highly social, vocal communication probably plays an important role in social structures. A study by Reynolds and Odell (1991) suggests that males use low-frequency vocalizations to establish territories and attack females playing a role in mate attraction.

Fissipeds: Little work has been done on sound production in sea otters. No underwater vocal sounds have been reported for sea otters, as they forage on an individual basis they probably do not need to communicate while foraging. Richardson et al. (1995) found sound production in air ranged between 3-5 kHz and were relatively intense, with no data on underwater sound production being available. It is suggested that noises produced are similar to those of terrestrial carnivores comprising of baby cries, hisses, growls, whines, screams, snarls and chuckles with Kenyon (1975) providing a detailed summary of these sounds produced (Kenyon 1975, 1981). Addition to these sounds, a further study by McShane et al. (1995) indicated sea otters used a variety of graded signals, which enhanced the detail of information shared between known individuals, which structured calls allowing for individual recognition (McShane et al. 1995).

As for polar bears vocalisations of Ursidae in general are poorly described (Pruitt and Burghardt 1977; Peters and Wozencraft 1989), with even less known about polar bears. Preliminary investigations of acoustic communication in polar bears indicate they can produce low frequency sounds (Owen 2009). Again, this is mainly due to their inaccessible habitat meaning studies usually have to be done at distance making vocalisation recordings almost impossible (Stirling 1974; Stirling and Latour 1978). Growls serve as a warning sign to others bears, indulging when an individual is protecting or defending a food source. During the breeding season males fight in order to gain breeding rights of a female, thus on occasions sounds such as hissing, growling and even chopping of their teeth would be used to try and intimidate each other, forcing a younger and less experienced male to run instead of fighting. Males are seen to use much gentler tones when communicating with a potential mating female, using a low coughing sound but observation of this is extremely rare as most mating rituals take place in private (Wiig et al. 1993). In captivity, males and females are very vocal during breeding season (Malyov 1991), and it has been documented that females make chuffing vocalisations when communicating with her cubs, so young cubs know her sound (Schneider 1933; Wemmer et al. 1976; Ovsyanikov 1996). Captive polar bears have also been shown to "groan and chuff" when Ringed seals (*Pusa hispida*) their favoured prey, are presented to them underwater (Cushing et al. 1988).

2.4.3.3 Hearing in Pinniped*s*

Pinnipeds are of interest when it comes to hearing because they are faced with two different acoustic environments, above and below water, with sensory information received and processed in different ways (Reichmuth et al. 2013). Firstly, the main difficultly hearing in air is the differences in media from the gaseous air surrounding the head to the cochlear fluids, providing a challenge when transferring the acoustic sound from one media to another (Møhl 1968; Repenning 1972). However, Pinniped*s* spend a lot of their time submerged in water; therefore, the air-filled middle-ear cavity would fill up with water blocking the traditional air-conduction energy-transmission pathway. Due to this Pinniped hearing underwater is thought be acquired by bone conduction, bypassing the air filled cavity, preventing this problem (Møhl 1968; Repenning 1972). In addition the pinnae are different in Pinniped*s*, being completely absent within the Odobenidae and Phocidae and reduced in Otariidae, allowing for voluntary closure during diving, forcing excess air out under pressure (Wartzok and Ketten 1999; Kirkwood and Goldsworthy 2013). Otariidae have middle ear bones, which are more separated from the skull, which might reduce underwater sound amplification but allows for better detection of sound direction (Kirkwood and Goldsworthy 2013). The Odobenidae and Phocidae have relatively enlarged middle ear bones for their body size (Berta 2009). However, both Otariidae and Phocidae possess a valve made from cartilage in the external ear canal, surrounded by muscles, closing the ear canal when underwater (Wartzok and Ketten 1999; Kirkwood and Goldsworthy 2013). In addition to this, tissue surrounding the middle ear space and the external cavity fill with blood to compensate for the external pressure, which in turn reduces the air space as diving depth increases (Kirkwood and Goldsworthy 2013).

Due to these adaptations, there is a lack of understanding when it comes to what frequencies Pinniped*s* hear under water. A lack of research leads to confusion when understanding how Pinniped*s* detect ultrahigh frequencies (Cunningham et al. 2014). It is said that Pinniped*s* can detect signals well above their presumed individual high-frequency hearing limits, due to primary bone conduction, resulting in a sharp decrease in sensitivity and the first step slope of the two slope phenomenon, followed by a second bone conduction, which is more effective at picking up higher frequencies, than the first slope (Kastelein et al. 2009; Møhl 1968b; Mulsow et al. 2012; Reichmuth et al. 2013; Sills et al. 2014). This matches other studies in terrestrial mammals showing bone conduction in this way can be effective in different frequency ranges (Stenfelt 2011).

Some Phocidae lack pinnae in their ears, which is how terrestrial mammals are able to localise sound. This raises the question if Phocidae are able to accurately locate sound around them and if so what features allows this. A study on Harbor seals at the Marine Science Centre, Germany looked at a seals response to a sound played below or above his head. After the signal the seal moves its head to a target signalling, which direction the sound was perceived. This suggests the seal has the ability to localise the direction the sound comes from (Byl and Dehnhardt 2016). Again, it is still unclear how underwater hearing actually occurs and to what extent Pinniped species can actually hear. Earlier studies demonstrate the two slope pattern, which helps to explain how some Pinniped*s* detect sounds that are well above their expected underwater hearing limits but not all Pinniped*s* have currently been researched (Møhl 1968b; Schusterman et al. 1972; Kastelein et al. 2009),

It is suggest that Pinniped*s* have a dual system within their ear, which operates independently within different frequency ranges. The other possibility is that Pinniped*s* are adapted to hearing in only one environment. Phocidae are generally more aquatic, so Renouf (1992) argued that Otariidae and Phocidae could be adapted to different environments, unfortunately research is limited to only a few species so this question remains to be answered. However, looking at recent studies there appears to be a significant difference between Pinniped*s*. Phocidae, including the Harbor seal Harp seal (*Phoca groenlandica)* and Ringed seal (*Phoca hispida)* have underwater frequency limits of 60 kHz, peaking between 10 and 30 kHz, which is also seen in the Hawaiian Monk seal (*Monachus schauinslandi)* with a frequency limit of 30 kHz (Schusterman 1981; Fay 1988; Thomas et al. 1990). In air, peak sensitivities of Phocidae tend to be lower, ranging between 3-10 kHz (Fay 1988; Kastak and Schusterman 1995, 1996), with a larger curve to the audiogram shape, implying that airborne sounds are poorly recognised, which would agree with Phocidae being generally more adapted to aquatic environments (Richardson et al. 1995).

Only two species of Otariidae have been studied, the California sea lion and Northern fur seal. Underwater the high frequency limits are between 35-40 kHz with peak sensitivities from 15-30 kHz (Fay 1988; Richardson et al. 1995). The peak sensitivities in air are also lower, like in the Phocidae, reaching only 10 kHz, only this time there is hardly no difference in the audiogram shape when it comes to air and water. No difference in the shape of the audiogram could indicate that Otariidae may have developed equally powerful hearing strategies for both environments as they spend a similar amount of time on land and in water (Fay 1988; Richardson et al. 1995).

Odobenidae studies on hearing abilities are extremely rare with only one study, with limited data due to it being completed in the field, looking at hearing sensitivity using an aerial free field hearing test on Atlantic walrus (*Odobenidae rosmarus rosmarus*), (Verboom et al. 1993). Another study by Kastelein et al. (1996) looked at the aerial hearing of a male Pacific walrus (*Odobenidae rosmarus divergens*) in captivity using headphones to test the hearing capabilities between 0.125-8 kHz. The results indicated very poor hearing compared to other Pinnipeds, however captive walrus are given many behavioural commands orally during their daily captive life so it was stated that the headphones might have affected sound traveling within the ear canal (Kastelein et al. 1996). A final study by Kastelein et al. (2002) looked at the hearing capabilities of a male Pacific walrus underwater using a "Go" "No-Go" response with frequencies ranging from 0.125-15 kHz. The maximum sensitivity peaked at 12 kHz with the best hearing range sitting between 1-12 kHz. It is clear that more work is needed on Odobenidae hearing capabilities however; studies indicate that they have a lower hearing range compared to other Pinnipeds.

2.4.3.4 Hearing in other aquatic mammals

Sirenians: There are a few studies available for sirenians looking at the West Indian manatee (Patton and Gerstein 1992, Gerstein et al. 1993, Gerstein 1994) and the Amazon manatee (Bullock et al. 1980, Klishin et al. 1990, Popov and Supin 1990). Current behavioural data has found that the hearing range of the West Indian manatee ranges between 0.1-40 kHz, peaking at 16 kHz. They also have an octave (interval between one musical pitch and another with double its frequency) functional hearing range between 7-8 octaves, compared to Odontocetes at 10.5 octaves (Au 1993) and Phocidae at 8-9 octaves (Kastak and Schusterman 1995, 1996).

Fissipeds: For sea otters behavioural measures of hearing was first looked at by Spector (1956) and Gunn (1988). Studying only two North American River otters (*Lutracanadensis*) Gunn (1988) indicated that in air they have a hearing range of 0.45-35 kHz with a peak sensitivity at 16 kHz. There is no audiometric examination on polar bear hearing and no measurements published on the hearing of any Ursidae when researching the literature and looking at an extensive review of animal hearing studies by Fay (1988). The only study was compiled by Nachtigall et al. (2007) looking at three anaesthetised polar bears reaction to various response calls within a similar range to that heard by Ringed seals (*Pusa hispida*). Their results indicated that the best sensitivity in air ranged from 11.2–22.5 kHz using auditory evoked potential (AEP) audiometry (Supin et al. 2001; Yuen et al. 2005; Nachtigall et al. 2005).

2.4.3.5 Tactile: touch in Pinniped*s*

Tactile sensory abilities in Pinniped*s* have been studied anatomically and behaviourally being extremely successful in demonstrating the importance of this tactile sense. Touch is applied across all social activities from play and aggression to breeding activities (including mating and maternal), with different species engaging in different varieties of tactile behaviours, dependant on whether they are solitary (only coming together to breed) or communal (large breeding hareams). To begin with, the most obvious tactile abilities are found within the skin. Pinniped gregarious behaviour varies and therefore the tolerance for tactile stimulation differs. Many species of Pinniped are colonial, grouping together on land for example California sea lions who are often seen over crowding beaches, piling on top of one another, with little thought for an individuals' "personal space." On the other hand, this tolerance for increased body contact could provide a thermoregulatory advantage. In contrast, Leopard seals are solitary predators and are rarely seen with another individual unless breeding. The one exception within al species is of course the relationship between a mother and pup, which is based on touch always remaining in close contact with one another Young Pinniped pups often crawl over their mothers, and sleep touching their mother securing their maternal bond, however grooming is not maternal (Riedman 1990; Wyatt 2003; Dudzinski et al. 2009).

The other tactile system is the highly developed vibrissae network that Pinniped*s* possess. Some species of Phocidae have whiskers over their eyes known as superciliary whiskers and whiskers near their nose known as rhinal whiskers (Riedman 1990). These whiskers are generally used in social events on land allowing Phocidae to convey information to conspecifics by the position of their whiskers, for example being held back or stiffly forward is thought to convey aggression or attentiveness (Riedman 1990). The more sensitive vibrissae are located on the side of the muzzle, the mystacial pad, varying in length, structure, number and position depending on the species of Pinniped (Oliver 1978; Hyvärinen 1989; Dehnhardt and Kaminski 1995). These vibrissae provide Pinniped*s* with an extremely valuable sensory touch system that has very sensitive mechanoreceptors (Yablokov and Klezeval 1962; Ling 1966). Whiskers across the mystacial pad, have ten times more nerve endings that your average land mammal and research by Hyvärinen (1989), shows each individual whisker is supplied by 1000-1600 thick nerve fibres, which have also been shown to play a role in thermoregulation (Mauck et al. 2000).

The first studies found that Pinniped vibrissae were heavily innervated with rapidly adapting nerve fibres providing Pinniped*s* with detailed information about static displacement and vibratory stimuli (Stephens et al. 1973; Dykes 1975; Kastelein and Van Gaalen 1988; Hyvärinen 1989). Miller was the first to describe using whisker for touch to help detect social interactions in 1975. Miller found that in non-social settings, whiskers became erect when grooming, yawning, and olfactory/tactile investigation of objects took place (Miller 1975). In social interactions whiskers were also erect and moved across muzzles during greetings; when whiskers, lips or pads relaxed this indicated being submissive and when being aggressive towards other conspecifics whiskers were lateral with the expansion muzzle, lips and mouth (Miller 1975). Furthermore, walrus also lifted the skin by their tusks and flared their nostrils (Miller 1975). Although not using their whiskers for touch these difference suggest that whiskers may be relying information to others about the individuals' state.

Many studies discuss how important whiskers are to animals in dark environments, such as to rats and mice whom are nocturnal (Mitchinson et al. 2007, 2011). Pinnipeds face this challenge as they forage underwater and cannot rely on vision in dark murky waters dramatically reducing visibility (Dehnhardt et al. 2001). Underwater movements from tides, currents, prey, predators or conspecifics provide Pinniped*s* with a great deal of information if they can decode it (Dehnhardt et al. 1998). Whiskers may be an irreplaceable sensory system in foraging for Pinniped*s* especially as they do not possess features for echolocation like cetaceans (Schusterman 1968). Mystacial vibrissae can be divided into macro-vibrissae usually labelled as the ventral caudal whiskers that extend to the sides of the muzzle and the smaller micro-vibrissae called rostral whiskers below the nostrils that point downwards (Brecht et al. 1997). Most research indicates that macro-vibrissae are larger mobile whiskers that allow Pinniped*s* spatial sensing with the smaller immobile micro-vibrissae used for object identification.

Several studies have looked at prey capture across Pinniped*s*. Research began in 1956 by Lindt observing Southern sea lions (*Otaria byronia*) using their whiskers to search across the seabed. Walruses are renowned for their suction feeding success with an extremely powerful tongue to extract molluscs, but it is their whiskers that are the primary source in finding molluscs buried in the seabed (King 1983; Adam and Berta 2002; Marshall et al. 2008). Whiskers are not only used to find food located within the seabed but also to pick up trails or wakes created by fish, known as hydrodynamic trails. Phocidae and Otariidae use their whiskers to follow trails left by fish in order to catch their prey (Dehnhardt et al. 2001; Schulte-Pelkum et al. 2007; Gläser et al. 2011; Dehnhardt et al. 2014). An early study by Renouf et al. (1980) recorded the time taken for Harbor seals to capture live fish with and without vibrissae. They found that there was no increase in time required to catch fish with or without vibrissae, which could indicate that vibrissae might not play an important role in hunting (Renouf et al. 1980). However, later studies provided more information on how vibrissae may aid prey capture, particular in Southern sea lions who use their vibrissae when swimming by touching the sea bottom to hunt for prey (Lindt 1956), which was also discovered by Kelly and Wartzok (1996) in Ringed seals (*Pusa hispida*) and by Härkönen (1987) in Harbor seals.

In addition there was a study done on blind Pinniped*s* that had no problems finding food being in a “well-nourished” state all year round (Poulter 1963; Newby et al. 1970) suggesting the importance of vibrissae for the detection of prey. Pinnipeds continue to survive in an environment that is constantly changing and vision is impaired. It is important their sensory systems have the ability to be flexible in order to detect prey, react to environmental factors and respond to social variables in order to survive. This portrays their whiskers of great importance for these opportunistic feeders, so much so they have been researched in great depth, which will be discussed below.

Studies have assessed tactile sensitivity how Pinniped*s* used their vibrissae to detect shape, size and texture. A walrus fitted with an eye mask demonstrated that using vibrissae alone it was possible to detect differences in surface areas down to 0.4 cm as well as the difference between similar shapes including squares and triangles (Kastelein and Van Gaalen 1988). In addition, Dehnhardt (1990) used similar techniques to demonstrate that a California sea lion could also distinguish between different objects when touching them with its vibrissae alone. Furthermore, this same individual could detect diameter differences in disks as small as 0.33 cm (Dehnhardt 1994).

Montagna (1967) suggested that vibrissae may be used to sense speed during swimming, so to test this Renouf and Gaborko (1982) trained Harbor seals to swim at the same speed through a series of hoops. Even without its whiskers the seal was still able to complete the task, however as the seal could see the hoop sequence this was not a good method, as possibly visual cues were used (Renouf and Gaborko 1982). The following year, Sonafrank et al. (1983) used a blindfolded a Spotted seal (*Phoca largha*) with its whiskers intact to swim directly to the centre of a hole within the ice using an acoustic cue. When the seal had its vibrissae restricted, it bumped the underside of the ice around the hole but still managed find the hole. Once at the hole it was also noticed that the seal surfaced more slowly when the whiskers were restricted than when they were free (Sonafrank et al. 1983).

Some forms of communication are non-tactile (and non-vocal) however; this is rarely seen across Pinniped*s*. A few species of seal (Harbor seals and Baikal seals (*Phoca siberica*)) have been known to slap their body with their flippers when disturbed in order to alert intruders and warn others (Dudzinski et al. 2009). Blowing bubbles has also been seen in the Leopard seal to threaten divers, which may have been accompanied by vocalisations unable for the human ear to hear and Harbor seals have also been seen using their flippers to slap the surface of the water although this behaviour is not entirely understood and may be used to help flush out prey (Venables and Venables 1957; Sullivan 1981). Another example is teeth chattering, used as a sign of visual aggression.

It is noted that clicks are said to be within the vocal repertoire of Pinniped*s* however only one study using California sea lions and Harbor seals has tried to re-enact this to see whether they use echolocation. Both studies were unsuccessful however, some researches argue that studying Pinniped*s* in polar regions with complete darkness during winter may give a better indication if echolocation is present as here it would be more likely to occur (Thomas et al. 2004).

2.4.3.6 Tactile: touch in other aquatic mammals

Sirenians: Out of all marine mammals, the Dugongs have the most developed sensory hairs that are present over the entire body (Kamiya and Yamasaki 1981). A study by Marshall et al. (1998) showed that Florida manatees have a similar distribution of hairs, which appear to be modified vibrissae used for tactile exploration (Hartman 1979; Marshall et al. 1998). Across the muzzle, these vibrissae are actively used for grasping during feeding in a prehensile manner, a unique feature seen only in this group (Marshall and Reep 1995; Reep et al. 1998). Manatees investigate objects and play with conspecifics by mouthing and rubbing against one other (Reynolds and Odell 1991). Florida manatees have been seen to “body surf” in a parallel formation, repeatedly on currents generated by partially opened dam floodgates. Often accompanied by gentle nuzzling and vocalizations of other manatee body surfers (Reynolds and Odell 1991).

Fissipeds: Studies on Polar bears are still required to understand tactile communication. As in other Ursids, mother polar bears will have a considerable amount of tactile contact with their young, particular in their den where small cubs are often seen sleeping closely together, probably for safety and to keep warm. During fighting adult male polar bears are seen to use “bear holds,” nose-to-nose or open-mouth threats along with biting.

Sea otters are benthic foragers that use “active touch" to find food via their front paws and whiskers. Tactile senses are important when completing foraging dives and digging for food, which includes bivalves, invertebrates, and cephalopods, even occasionally preying on several species of fish (Kenyon 1975; Kvitek et al. 1988; Riedman and Estes 1990). In otters, feeding behaviour is split into two methods: *mouth-oriented* used mainly for fish and *hand-oriented* predation used when catching invertebrates (Radinsky 1968; Duplaix 1984; Sivasothi and Nor 1994; Jacques et al. 2009; Timm 2013). Sea otters use their forelimbs and vibrissae to explore their environment and when identifying prey, having on average 120 whiskers on their muzzle (Marshall 2014). These whiskers are identical in anatomy to Pinniped*s* as they possess a blood sinus system, elastic tissues and increased number of nerve endings with approximately ~1340 axons per whisker. This is surprisingly high compared to that of the River otters (*Lutra canadensis*), which only have ~500 axons per whisker (Marshall 2014). It is suggested that sea otters whisker sensitivity is almost identical to that of some Pinniped*s*, suggesting that their ability to identify shape, size and texture could be similar (Marshall 2014).

Sea otters do not have extra fat layers beneath the skin so they must keep their underfur dry Grooming is therefore an essential part of their social structure to allow the spreading of waterproofing oil over their fur. Sea otter mothers are the only marine mammal capable of holding their pups for grooming, flowing on their back with their pup held across their stomach. A variety of tactile communication has been documented in sea otters, when it comes to social interactions including rubbing, stroking, pawing and wrestling (Riedman and Estes 1990). Sea otters float on their back when sleeping, which is often synchronised forming a raft of bodies often “holding paws” to maintain the raft as water movement has washed individuals out to sea.

2.4.4 Sensory Adaptations Conclusions

Animals live in environments that are constantly changing, meaning their reactions and responses to environmental and social factors must be flexible to enable them to survive. Environmental and social interactions provide the driving force in the evolution of communication systems (Hauser 1997). In aquatic mammals, those living in or by clear waters are more likely to use visual signals in comparison to those living in deep or murky environments. Communication also differs between species particularly when foraging with social foragers having much more complex signals compared with hunters that are more solitary. Contact with conspecifics also increase communication and in turn increases the rate of information gained for individuals compared for solitary species. Observing sensory adaptations within ones social and ecological environment will help understand evolution and the ability to receive signals to exchange information.

As many Pinnipeds inhabit murky coastal waters, or dark, deeper waters, they are likely to rely less on vision, and, rather, use their whiskers for tactile sensing. Whiskers can be used to sense tactile and hydrodynamic stimuli, and are involved in foraging, navigation and social behaviours.

2.5 Pinniped whisker anatomy and morphology

Pinnipeds are thought to rely heavily on their whiskers for sensing, mainly being tactile specialists (Grant and Arkley 2014). This section of the review will describe Pinniped whisker anatomy and morphology, which leads on to ***Chapter Three: Pinniped Whisker and Skull Morphology.***

Mystacial vibrissae are specialized sensory hairs found on the maxillary region of the face, which have the ability to respond to mechanical stimuli such as tension, pressure, and displacement (Brecht et al. 1997; Marshall et al. 2006). Several studies have now distinguished two types vibrissae: the macro-vibrissae system which are the long, lateral hairs arranged in rows on the muzzle, critical for spatial tasks and the front micro-vibrissae system which appear on the upper lip, appear shorter and un-organized, which are involved in object recognition gathering specific information about an object (Lyne 1959; Brecht et al. 1997; Grant et al. 2012). In addition, it has also been confirmed that both macro-vibrissae and micro-vibrissae systems are required for prey capture (Anjum et al. 2006).

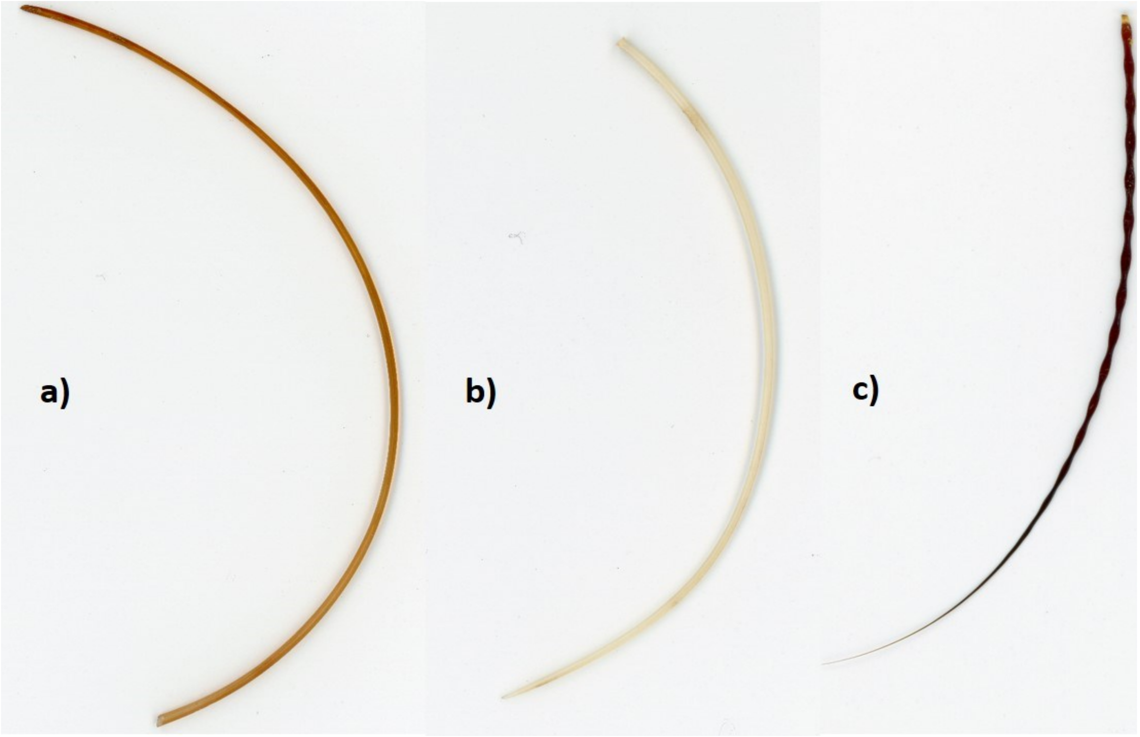


Figure 2.2: Surface Structure of Vibrissae*: (a) Smooth short Pacific walrus (Odobenidae rosmarus divergens) whisker (b) Long smooth California* sea lion *(Zalophus californianus) whisker (c) Undulated Harbor seal (Phoca vitulina) whisker*

Pinnipeds vibrissae differ significantly from each other in size, arrangement, number and structure across different species (Ling 1977; Watkins and Wartzok 1985; Hyvärinen 1989; Dehnhardt and Kaminski 1995). All Pinniped*s* can voluntarily extend forward or relax (lying flat against their muzzle) their whiskers. The size of whiskers ranges from a few millimetres to over 50 cm depending on the species of Pinniped (Riedman 1990). There is also evidence to suggest some whiskers show presence of damage or rubbing, being blunt or trimmed at the ends. Whiskers can also be categorised into two groups, with shorter whiskers being the rostral whiskers and longer whiskers being the caudal whiskers. The arrangement of whiskers is also different between species but the layout is not random and is usually identical on both sides of the muzzle, formed in an ordered grid of columns and rows, with shorter whiskers at the front and longer whiskers at the back (Brecht et al. 1997).

One of the most fascinating features of the vibrissal system is the grid like mapping arrangement of the mystacial pad. Whiskers appear to be arranged into distinct dorsoventral rows and rostrocaudal columns, which differ across Pinniped species. For example, Harbor seal possess seven distinct rows, California sea lion having six rows and the Pacific walrus having the most at fifteen rows. Each whisker is embedded in a follicle enclosed by mechanoreceptors, which translates any stimulation into neuronal signals to the brain (Patrizi and Munger 1966; Dörfl 1985; Rice et al. 1986; Lichtenstein et al. 1990; Dehnhardt et al. 1999; Ebara et al. 2002; Diamond et al. 2008). In addition to these super sensitive receptors, each whisker is surrounded by a solid blood supply and intrinsic muscles, which contract to protract the whiskers, forward (Dehnhardt 1994; Marshall, 2006; Hanke and Dehnhardt 2016).

Numbers of mystacial vibrissae range from as low as 15 (Ross seal) to 350 (Pacific walrus) on each side (Ling 1977). Walrus having the most of any Pinniped, have between 400 to 700 whiskers, distributed within the 15 rows across the muzzle, with the first few rows having less whisker follicles in than the rest (Ling 1977; Marshall et al. 2006). For Otariidae the California sea lion is the species best studied having 38 mystacial vibrissae on each side with 4-6 whiskers in the first two rows, the next three having up to 8 whiskers and the final row having 4 (Dehnhardt 1994). In most Phocidae species there are seven rows of whiskers with the Harbor seal, having the most research compiled about them with approximately 44 whiskers on each side of their muzzle (Dehnhardt and Kaminski 1995) and the Bearded seal (*Erignathus barbatus*) having the highest number of vibrissae among the Phocidae at 244 whiskers. All Otariidae, Odobenidae, along with the Bearded seal and the Monk seal (*Monachus monachus*) from the Phocidae all have smooth vibrissae with the remaining Phocidae all having a wavy corrugated appearance (Figure 2.2).

Shed patterns and whisker growth also differs between Pinniped*s* as moulting cycles vary across individuals due to growing rates (Ling 1966; Hirons et al. 2001; Greaves et al. 2004; Zhao and Schell 2004; Hall-Aspland et al. 2005; Newland et al. 2011). Phocidae have an annual shed pattern, excluding the Leopard seal, (Hall-Aspland et al. 2005) but as whisker length increases growth rate rapidly begins to slow. Otariidae whisker growth is constant and they have multiyear retention of their whiskers (Hirons et al. 2001; Greaves et al. 2004; Cherel et al. 2009; Newland et al. 2011). Even though there are differences between Pinniped*s*, vibrissae growth is determined by length and position of the whisker in the whisker bed (Oliver 1966; Lyne et al. 1974; Greaves et al. 2004). Whisker follicles have a large blood supply, which means whiskers are not affected by temperature allowing Pinniped*s* that face temperatures below 0°C can still utilise their primary sensory system (Stephens et al. 1973; Hyvärinen 1989). Studies have shown that tactile discrimination behaviour does not change even when water temperature does, but a lot of energy must be used to prevent this amount of heat loss from a small area.

There is a wealth of scientific literature that describes the parts of the brain involved in vibrissae sensing and movement (Berg and Kleinfeld 2003; Friedman et al. 2006; Hemelt and Keller 2007; Cramer et al. 2007; Birdwell et al. 2007; Ramamurthy and Krubitzer 2016). Some identify specific parts of the central nervous system, such as the brainstem trigeminal nuclei and ventrobasal thalamus (Waite et al. 1998; Sawyer et al. 2016) and the somatosensory cortex (Catania and Henry 2006; Sawyer et al. 2016). It has been found in California sea lions that each individual whisker on the muzzle has a unique, topographic structural area within the animal's brainstem (Sawyer et al. 2016). These finding are equivalent to areas found within the human brain that relate to individual fingers (Sawyer et al. 2016) and areas of the rodent brain associated with whiskers i.e. barrelettes in rat brainstem, and barrel cortex in rat, mouse and hamster (Woolsey and Van der Loos 1970; Krubitzer et al. 2011).

2.6 Conclusion

Pinnipeds are tactile specialists, occupying a variety of habitats and environments. They use their whiskers to guide navigation, foraging and feeding, and social interactions. Their whiskers are the most sensitive and longest of any mammal. They also have a diverse arrangement of whiskers, with many different shapes. However, a systematic (ordered comparison) description of whisker arrangement and shape has not yet been conducted across many species of Pinnipeds. Understanding more about whisker sensitivity and movement abilities in Pinnipeds will improve our understanding of their tactile sensory ecology and behaviour.

3 ***Chapter Three: Pinniped Whisker and Skull Morphology***

Chapter Summary:

The aim of this chapter is to describe skull and whisker morphology in Pinniped*s*. Skull measurements and whisker measurements were collected from skull, skin and mounted specimens of different Pinniped species from museums around the United Kingdom. Whisker length was significantly correlated to the size of the Pinniped infraorbital foramen (IOF). There were no significant correlations between any of the other variables, including, eye orbit area and whisker numbers. Pinniped whiskers are more variable than other carnivores, both in terms of length and in terms of shape. While many of the Pinniped*s* had fewer whiskers than other carnivores, they had relatively larger IOF areas than other carnivores, indicating that each Pinniped whisker is likely to be more sensitive, compared to other carnivores. Indeed, having larger IOFs indicates increased sensory acuity, due to the infraorbital nerve (ION) running through the IOF supplying whisker sensitivity. Whisker and skull morphology does not map well on to Pinniped phylogeny, therefore, ecological factors, especially feeding ecology, are likely to be a big predictor of skull morphology, whisker length and whisker sensitivity in Pinniped*s*.

3.1 Introduction

Whisker touch sensing allows animals to quickly and accurately identify objects within their environment, including their position, size and texture (Mehta et al. 2007). While studies have suggested that Pinniped whisker are particularly sensitive (Rice et al. 1986; Hyvärinen 1989; Dehnhardt et al. 1998; Mauck et al. 2000), sensitivity is hard to measure and requires challenging anatomical (Rice et al. 1986; Hyvärinen 1989) or behavioural (Dehnhardt et al. 1998; Mauck et al. 2000) procedures. In terrestrial mammals, the infraorbital foramen (IOF), a small hole in the skull (Figure 3.2 a, label 2) is easily measured and thought to reflect the sensitivity of the whiskers. The infraorbital nerve (ION) passes through the IOF, and the IOF area is well-correlated to ION size (Patrizi and Munger 1966; Gasser and Wise 1971; Muchilinski et al. 2010). The ION innervates the mechanoreceptors associated with vibrissae (Brecht et al. 1997; Ebara et al. 2002), and the number, shape and length of these whiskers all influence mechanoreception, and the size of the ION (Ling 1977; Dehnhardt and Kaminski 1995; Reep et al. 2001). The size of the IOF is well correlated with whisker number and movement abilities in terrestrial mammals (Kay and Cartmill 1977; Muchlinski et al. 2010; Grant et al. 2018). However, IOF size in aquatic mammals has not been explored, but is likely to be associated with whisker morphology.

As detailed in ***Chapter One: Introduction and Overview*** and ***Chapter Two: Literature Review***, vibrissae are important in aquatic mammals and they exhibit variation of whisker numbers, lengths, and densities (Kratochvil 1968; Kemble and Lewis 1982; Ahl 986). Currently, however, we know very little about the function of this variation among aquatic mammals and particularly in Pinniped*s*. It is unclear how and if the length or movement abilities of the whiskers affects the size of the IOF in Pinniped*s*. For example, the IOF size of two Pinniped species, with a similar number of vibrissae, may differ if one has longer and motile vibrissae.

The aim of this chapter is to describe whisker morphology in Pinniped*s* and to begin to understand if skull morphological traits correspond to differences within their sensory systems. This study will describe whisker morphology in Pinniped*s*, in terms of whisker length, number, density and IOF area. As whiskers significantly differ in size, shape and number across Pinniped*s* one might expect whisker variables to correlate with some related morphological features in the skull i.e. IOF size and eye orbit size (Renehan and Munger 1986; Munger and Ide 1988; Halata 1993; Dehnhardt et al. 1999; Ebara et al. 2002; Hückstädt et al. 2012). In particular, we can hypothesise that Pinniped*s* with more whiskers will likely have more mechanoreceptors and hence a larger IOF.

3.2 Methods

Pinniped skull and skin collections at three Museums were visited for data collection: Liverpool World Museum (Liverpool, UK), Manchester Museum: The University of Manchester (Manchester, UK) and the National Museums of Scotland (Edinburgh, UK). Within each museum, a number of Pinniped skulls and skins were explored for suitability (Figure 3.1 and 3.2, Table 3.1). Pinniped skins and skulls were all obtained from both wild and captive individuals. When there was an abundance of skulls available for a particular species, three skulls for that species were selected (from that museum collection), so that a larger range of species could be compared (see Table 3.1 for a full list of species). The total number of skulls looked at across the three museums totalled to sixty individual skulls, over sixteen different pinniped species. Skins were much harder to come by, especially with intact whiskers, so in total only sixteen skins were used, across twelve different species. Several criteria had to be met to make sure skulls and skins were suitable (see ***3.2.1 Measurements of Skins*** and ***3.2.2 Measurements of skulls***).

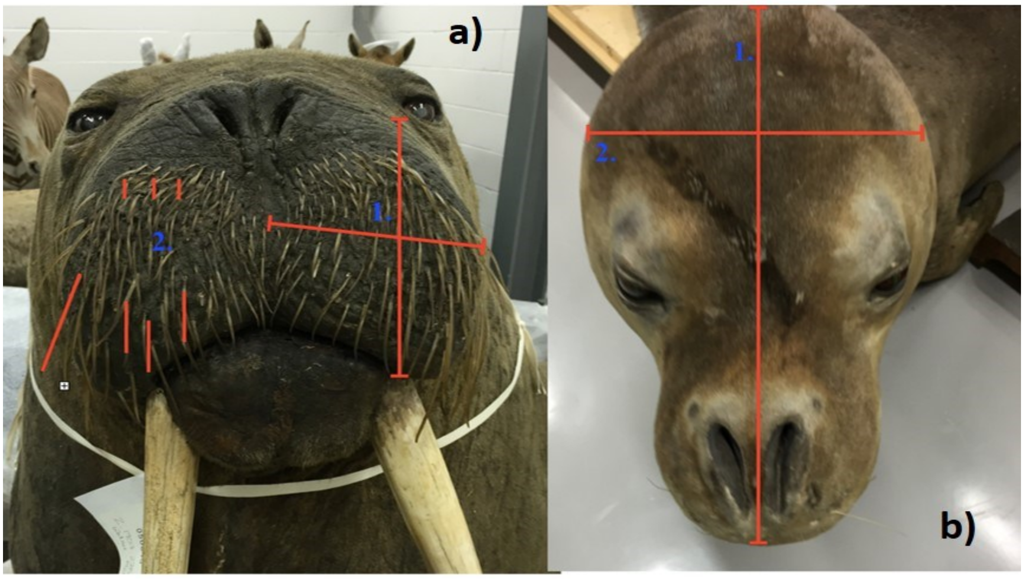


Figure 3.1: **Pinniped*s Skins***: *(a) Pacific walrus (Odobenidae rosmarus divergens) skin indicating measurements taken to calculate 1) muzzle length and width) average length of whiskers on each side of the muzzle and longest whisker, (b) Leopard seal (Hydrurga leptonyx) skin indicating measurements taken to calculate 1) the length and 2) the width of the head*

3.2.1 Measurements of Skins

The requirements for selecting skins were: a) no rips or tears on either side on the face or muzzle, b) whiskers are present on both sides of the muzzle, and finally c) full information available to identify the species. Various measurements and information were recorded for each of the skins, which included the Pinniped museum ID, common name, and scientific name. Whisker shape, texture and size were described, for example if they were flat, wavy, long or short for each of the specimens looked at (Figure 3.1). The head length and width was also measured using the longest points on the skin (Figure 3.1 b), along with the dimensions of the mystacial pad (Figure 3.1 a, measurement 1). We split up the left and right side of the muzzle and approximated whisker number by counting the number of whiskers and visible follicles present on the skin, (Figure 3.1 a). We measured the longest whisker from each side of the muzzle. An average whisker length for the front and back of the muzzle and left and right sides was derived by measuring three whiskers from the front and three from the back (Figure 3.1 a, measurement 2).

For some species' skins, whiskers were not present, in which case whiskers were counted from photographs taken of the Pinniped species. This was true for only four species the Ribbon seal, (*Histriophoca fasciata*), the Harp seal (*Pagophilus groenlandicus)*, the Ross seal (*Ommatophoca rossii*) and the Southern Elephant seal (*Mirounga leonia*). Suitable photos were searched for online through Google Images. Photographs were selected of adult Pinniped*s* with their faces in focus to count whisker number and follicles, with three selected for each species to give an average number for each of the species.

3.2.2 Measurements of Skulls

The requirements for selecting skulls were as follows: a) both top and bottom halves of the skull present and unbroken, b) eye orbits intact on both sides of the skull, and c) full information available on the skull to identify species. This was done by the skulls being photographed, identified through ID, common name, or scientific name, and measured, accordingly. Firstly, the skull length was measured using the front of the upper mandible all the way to the sagittal crest at the back of the skull. For the width of the skull, the linear distance between the most lateral points on the zygomatic arches was measured between the two eye orbits of the skull, (Figure 3.2 c). The eye orbits were also measured using the upper and lower lengths (Figure 3.2 a and b); along with the infraorbital foramen (IOF) measured using the longest and shortest areas due to them being oval, which was done on both the left and right sides of the skull (Figure 3.2 a). Once all the data was collected the mean and standard deviation was calculated, giving an average across all the measurements for each of the individual species. The area of the IOF and eye orbit was also calculated. Initially, to do this the areas were approximated as that of a circle. However, most of the eye orbits and IOF holes were not circular. Therefore, to improve accuracy, the area calculated was that of an ellipse. The formula used was the major radius of the ellipse (a) multiplied by the minor radius of the ellipse (b), multiplied then by pi ($\boldsymbol{a} \times \boldsymbol{b} \times \pi$ = ellipse area), which was used in the final equations (Table 3.1).

It was important to consider variations within skull size relative to body size. Sexual dimorphism affects skull size and shape, and larger Pinniped*s* will have larger eye orbit and IOF measurements. Therefore, in order to compare the IOF areas, the eye orbit areas and vibrissae features across a wide range of body sizes, the variables needed to be sizeadjusted. Therefore, both the eye orbit and IOF measurements were controlled for size, by dividing by the Geometric Mean (GM), which was calculated using the cranial length and width using the following formulas (Muchlinski 2010): $GM = \sqrt{\text{cranial length X cranial width}}$. Controlling for skull size meant both eye orbit and IOF measurements used were relative.

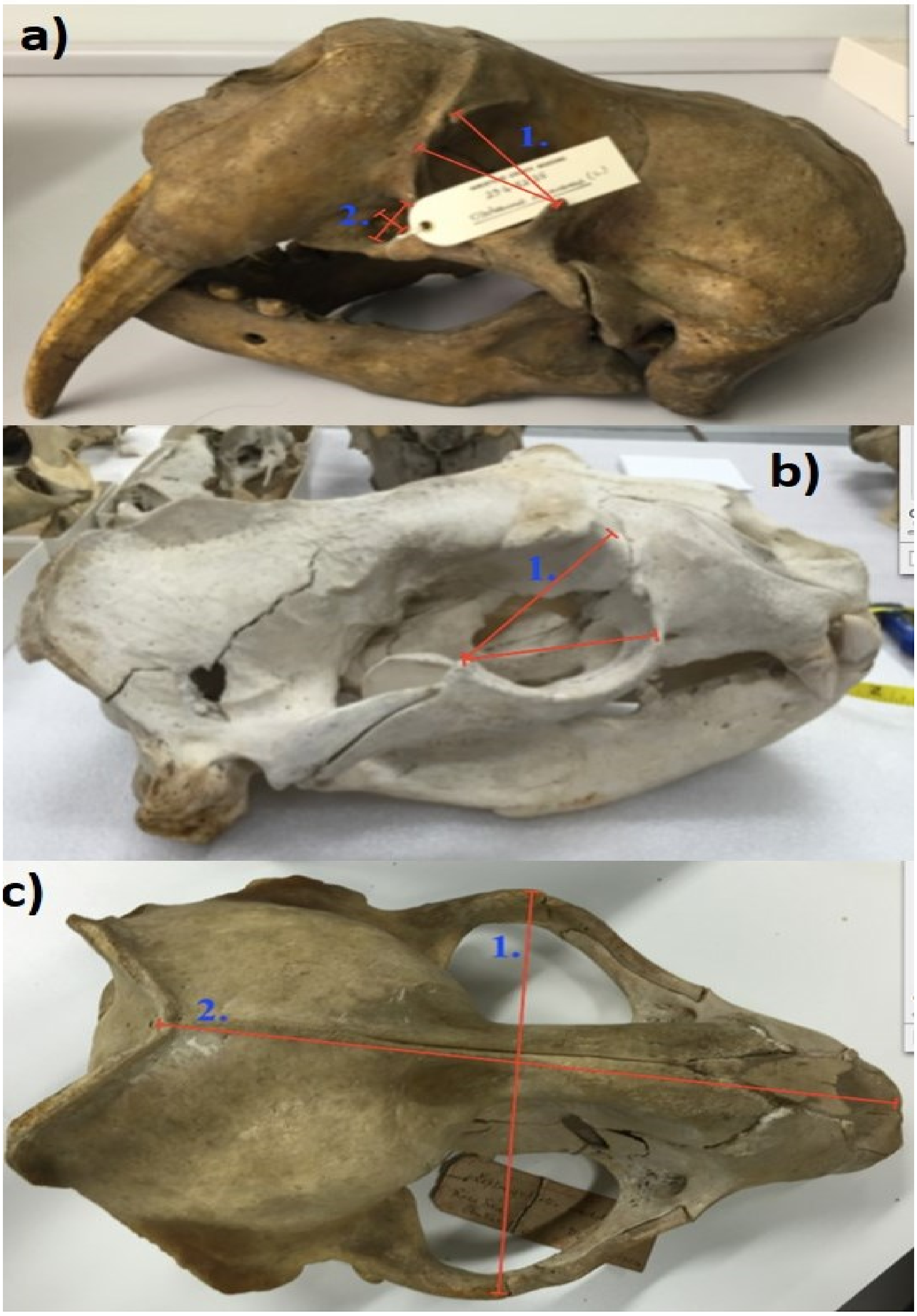


Figure 3.2: Pinnipeds Skulls: *(a) Pacific walrus (Odobenidae rosmarus divergens) and (b) Stellar sea lion (Eumetopias jubatus) skull showing measurements taken to calculate the area of 1) eye orbit and 2) the IOF; (c) Weddell seal (Leptonychotes weddellii) skull with measurements taken for the 1) width and 2) length of each skull*

3.2.3 Statistical Analysis

The measurements of the skull, eye orbits and IOF were correlated using Spearman's Rho with whisker number and whisker length to get a measure of relationships between: (i) IOF and whisker number and whisker length; (ii) eye orbit and whisker number and whisker length; and (iii) eye orbit and IOF (Table 3.1). This was done by pooling the data to see if there was any associations between variables across all Pinniped*s* using a Spearman's Rank correlation, as well as independently on the three different families of Pinniped*s* (seals, sea lions and walrus). A linear regression also investigated which variables predicted IOF area in the seals and sea lions, as there was only one species of walrus.

3.2.4 Pinniped*s* and Other Carnivorous Mammals

In order to compare these relationships between Pinniped*s* and other carnivorous mammals, data from a previous study by Muchlinski (2008, 2010) was used. To do this, the IOF area, geometric mean of the skulls and whisker number data from the Carnivora order was plotted alongside data collected in this chapter to examine how Pinniped whisker and skull measurements compare with other carnivores.

3.2.5 Phylogenetic Trees

Mesquite 3.6 software (to organize and analyze comparative data about organisms) was used to construct a phylogenetic tree using Maximum Likelihood with the following variables: eye orbit, IOF and whisker number (all controlled for size using the GM), to see how these variables were grouped across the 16 species of Pinniped investigated, (Maddison and Maddison 2018). This acts as a cluster analysis for the variables across all the species of Pinniped*s*, no information about species relatedness was included in this analysis. Secondly, using Bayesian inference data of Pinniped phylogeny from “The 10k Trees” (Arnold et al. 2014) an accurate phylogenetic tree were constructed for the 16 species of Pinniped studied. These data were used, as all 16 species of Pinniped were available.

3.2.6 Coding for Feeding Ecology

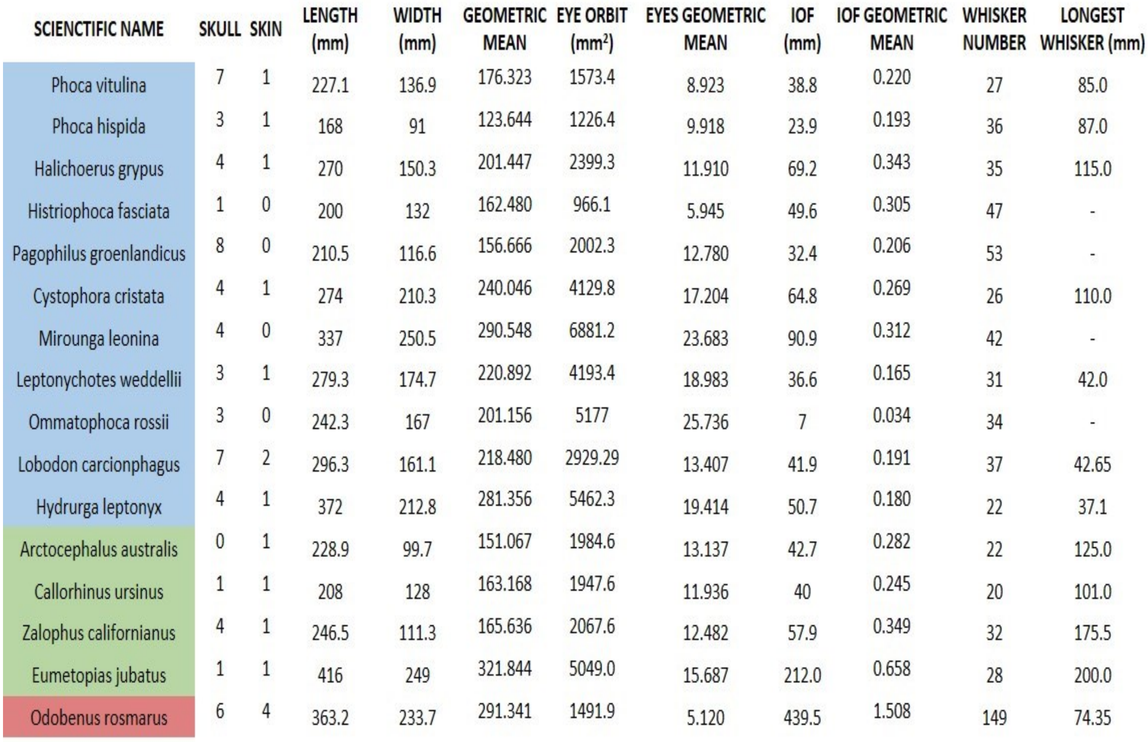
Coding for the ecological variables (diet type, feeding style, social grouping and foraging depth) used data taken from Berta (2015), Riedman (1990) and Mammal Taxa Review on the IUCN Database (2017). This included obtaining information on Pinniped*s*’ primary prey type, feeding type, social grouping and foraging depths (see ***Chapter Two: Literature Review*** and Figure 3.3). Starting with the ecological variables the primary prey type was split into four groups cephalopods and fish, crustaceans, vertebrates and molluscs, along with the primary methods of feeding split into pierce, filter, grip and tear and suction feeding. Average foraging depths for Pinniped*s* were also split up into different groups, 0-100 meters 101-200 m 201-300 m, 301-400 m and over 401 m. As Pinniped*s* can fluctuate between different prey types and feeding types, which in turn will affect what depth they hunt, their primary source was selected for each Pinniped to obtain the groups and gain a definitive selection. Whisker variables (whisker length, whisker number, IOF area and eye orbit) were coded for using the data obtained from the museums (see Table 3.1 and 3.2).

3.3 Results

3.3.1 Describing whisker and skull morphology in Pinnipeds

There are differences present in skull and whisker morphology both within the three Pinniped families and between different individual Pinniped species (Table 3.1). The whisker number (on each side of the muzzle) for the majority of the Otariidae is relative low in comparison to most other Pinnipeds (Phocidae 22-53 whiskers, Otariidae 20-32 whiskers, Odobenidae 149 whiskers).

Table 3.1: Measurements taken across Pinniped Skulls and Skins: *Number of Skulls, Number of Skins, along with Mean Cranial Length, Cranial Width, Geometric Cranial Length for pooled data of Pinniped species, followed by Mean Eye Orbit, Geometric Eye Orbit, Mean Infraorbital Foramen Area (IOF), Geometric Infraorbital Foramen Area (IOF) and finally Whisker Number and the Longest Whisker. (Pinniped families colour coded: Blue - Phocidae (seals), Green - Otariidae (sea lions) and Red - Odobenidae (walrus)*



SCIENCTIFIC NAME	SKULL	SKIN	LENGTH (mm)	WIDTH (mm)	GEOMETRIC MEAN	EYE ORBIT (mm^2)	EYES GEOMETRIC MEAN	IOF (mm)	IOF GEOMETRIC MEAN	WHISKER NUMBER	LONGEST WHISKER (mm)
Phoca vitulina	7	1	227.1	136.9	176.323	1573.4	8.923	38.8	0.220	27	85.0
Phoca hispida	3	1	168	91	123.644	1226.4	9.918	23.9	0.193	36	87.0
Halichoerus grypus	4	1	270	150.3	201.447	2399.3	11.910	69.2	0.343	35	115.0
Histriophoca fasciata	1	0	200	132	162.480	966.1	5.945	49.6	0.305	47	-
Pagophilus groenlandicus	8	0	210.5	116.6	156.666	2002.3	12.780	32.4	0.206	53	-
Cystophora cristata	4	1	274	210.3	240.046	4129.8	17.204	64.8	0.269	26	110.0
Mirounga leonina	4	0	337	250.5	290.548	6881.2	23.683	90.9	0.312	42	-
Leptonychotes weddellii	3	1	279.3	174.7	220.892	4193.4	18.983	36.6	0.165	31	42.0
Ommatophoca rossii	3	0	242.3	167	201.156	5177	25.736	7	0.034	34	-
Lobodon carcionphagus	7	2	296.3	161.1	218.480	2929.29	13.407	41.9	0.191	37	42.65
Hydrurga leptonyx	4	1	372	212.8	281.356	5462.3	19.414	50.7	0.180	22	37.1
Arctocephalus australis	0	1	228.9	99.7	151.067	1984.6	13.137	42.7	0.282	22	125.0
Callorhinus ursinus	1	1	208	128	163.168	1947.6	11.936	40	0.245	20	101.0
Zalophus californianus	4	1	246.5	111.3	165.636	2067.6	12.482	57.9	0.349	32	175.5
Eumetopias jubatus	1	1	416	249	321.844	5049.0	15.687	212.0	0.658	28	200.0
Odobenus rosmarus	6	4	363.2	233.7	291.341	1491.9	5.120	439.5	1.508	149	74.35

The Odobenidae has the largest number of whiskers with 149 individual vibrissae on each side of the muzzle. Phocidae have the widest range of whiskers on each side of their muzzle ranging from less than 20-40 whiskers each side. Their whiskers also vary in size from a few centimetres to much larger whiskers, as seen in the Southern Elephant seal (*Mirounga leonia*) measuring 20 cm. Whisker length between Pinniped*s* also varied across each of the three families here, (Table 3.1). Phocidae had the biggest range of whisker lengths between 3-11 cm. The longest whiskers were found in the Otariidae with all species studied having whiskers longer than 10 cm (10-20 cm). California sea lions (*Zalophus californianus*) had a whisker length of 16-18 cm and the Stellar sea lions (*Eumetopias jubatus)* had whiskers measuring 18-20 cm, which were the longest whiskers observed. The walruses (*Odobenidae rosmarus*) had much smaller whiskers measuring 5-8 cm.

The IOF also varied across Pinniped*s* with the Stellar sea lion and the walrus having the largest IOF recorded at 4.4 cm^2. The Phocidae had a variety of different sized IOF areas ranging from 0.2-0.9 cm^2, while the Otariidae had slightly larger IOF areas in comparison between 0.4 -2.0 cm^2, (Table 3.1). The eye orbit sizes also differed among Pinniped*s*. The walrus having the smallest at 1.4 cm wide, the Otariidae all having very similar large sized eye orbits ranging between 1.9 - 5cm^2. The eye orbits of the Phocidae had a slightly bigger range but generally were larger in size compared to the Otariidae and Odobenidae measuring between 1.5-6.8 cm^2 (Table 3.1).

3.3.2 Do whisker variables correlate to skull morphology?

When all Pinniped*s* studied were included in the analysis (with pooled data for seals, sea lions and walrus) whisker length was significantly and positively related to the size of their IOF, (*Spearman's Rank: r*=0.727, df=12, p= 0.007), (Figure 3.3). As the whisker, length increases so does the IOF Area in Pinniped*s*.

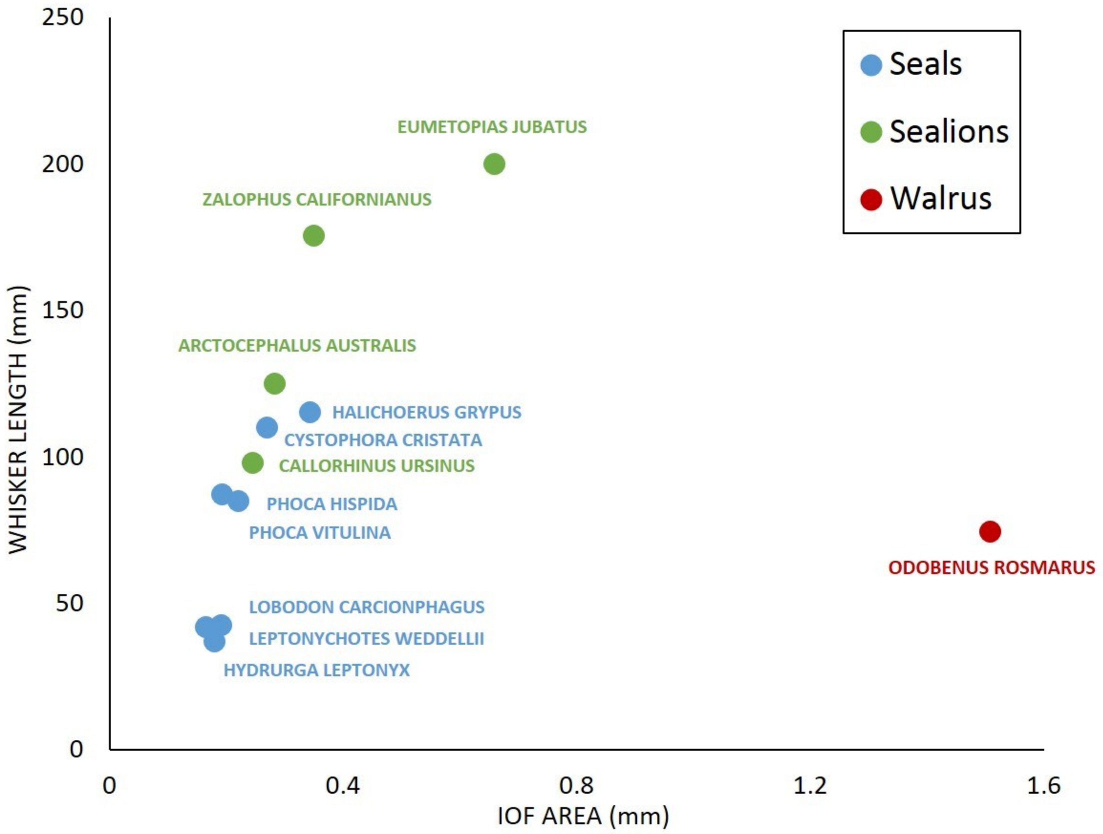


Figure 3.3: Relationship between the whisker length and the inferior orbital foramen (IOF): *Odobenidae (walrus), Otariidae (sea lions), (Linear Regression* r^2 *= 0.6141) and Phocidae (seals), (Linear Regression* r^2 *= 0.223)*

In addition, Figure 3.3 also shows differences between the three families (seals, sea lions and walrus). Unfortunately, the sample sizes for the Odobenidae groups were not large enough for correlations to be conducted across any of the variables individually. However, for the Phocidae there was enough data to show a significant correlation between their whisker length and IOF area (*Spearman's Rank: r*= 0.929, *p* 0.003). There was a stronger positive relationship within the Otariidae (*Linear* Regression: r^2 = 0.614, p=0.037), compared to the Phocidae (*Linear* Regression: r^2 = 0.223, p=0.046), suggesting that an increase in whisker length is associated with a bigger IOF, especially in the Phocidae. (Figure 3.3). It is not possible to see any pattern within the Odobenidae group, as there are only two species of extant walrus, with only one available here. However, the walrus had a much bigger IOF in comparison to all other Pinniped species, being over 50% bigger (Figure 3.3).

There were no significant correlations between any of the other variables that were tested which included, eye orbits and whisker number (*Spearman's Rank: r*= - 0.293, *p* 0.271), eye orbits and whisker length (*Spearman's Rank: r*= - 0.154, *p* 0.633), eye orbits and IOF area (*Spearman's Rank: r*= - 0.444, *p* 0.085), or whisker number and IOF (*Spearman's Rank: r*= 0.205, *p* 0.447), (Figure 3.4). It may be worth mentioning that whisker number and whisker length did not show any correlations with one another across the pooled data in which the Pinnipeds were grouped (*Spearman's Rank: r*= - 0.137, *p* 0.672).

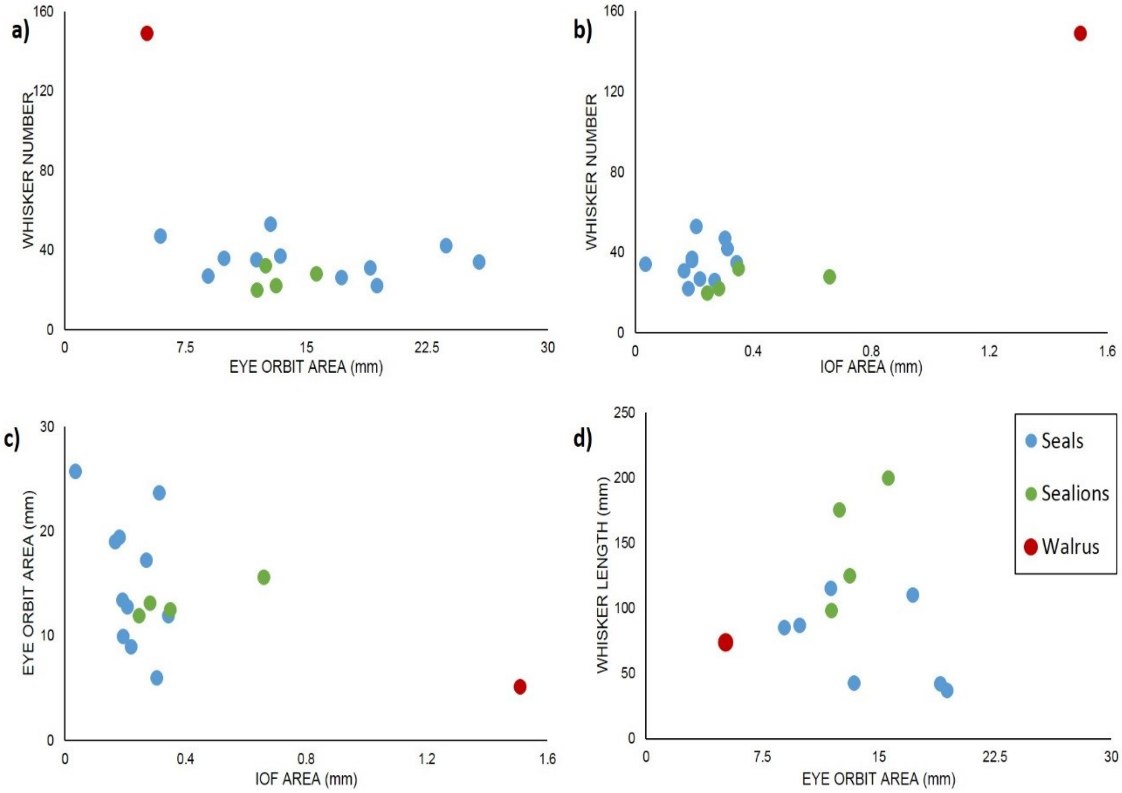


Figure 3.4: Relationship between Pinniped whisker variables and morphological features: *Odobenidae (walrus), Otariidae (sea lions) and Phocidae (seals) - (a)) eye orbit and whisker number (Spearman's Rank: r= - 0.293, p 0.271), (b) whisker number and IOF (Spearman's Rank*: r= *0.205, p 0.447), (c) eye orbit and IOF (Spearman's Rank*: r=*- 0.444, p 0.085), (d) whisker length eye orbit (Spearman's Rank*: r= *- 0.154, p 0.633),*

3.3.3 How do Pinniped*s relate to other carnivorous mammals?*

Figure 3.5 incorporates Carnivora data taken from a study by Muchlinski (2008, 2010) with the Pinniped data collected here. Variation in IOF area and geometric skull means (skull size) among mammals can clearly be observed with a strong positive correlation between the two (Figure 3.5). It is also clear that Pinniped*s* have a larger geometric mean (larger skull) and larger IOF areas compared to most other carnivorous mammals. There are a few exceptions. Firstly, the Ursidae had a smaller IOF area but a larger geometric mean than Pinnipeds. Secondly, from the Felidae family, *Panthera leo* and *Panthera tigris* had a larger geometric mean and IOF area than most pinnipeds, except the walrus and Steller sea lion (Figure 3.5). Indeed, Pinniped IOF areas were similar to some species of Felid (*Felis concolor*) and mustelid (*Enhydra lutris, Lontra canadensis, Melogale moschata and Taxidea taxus*) (Figure 3.5).

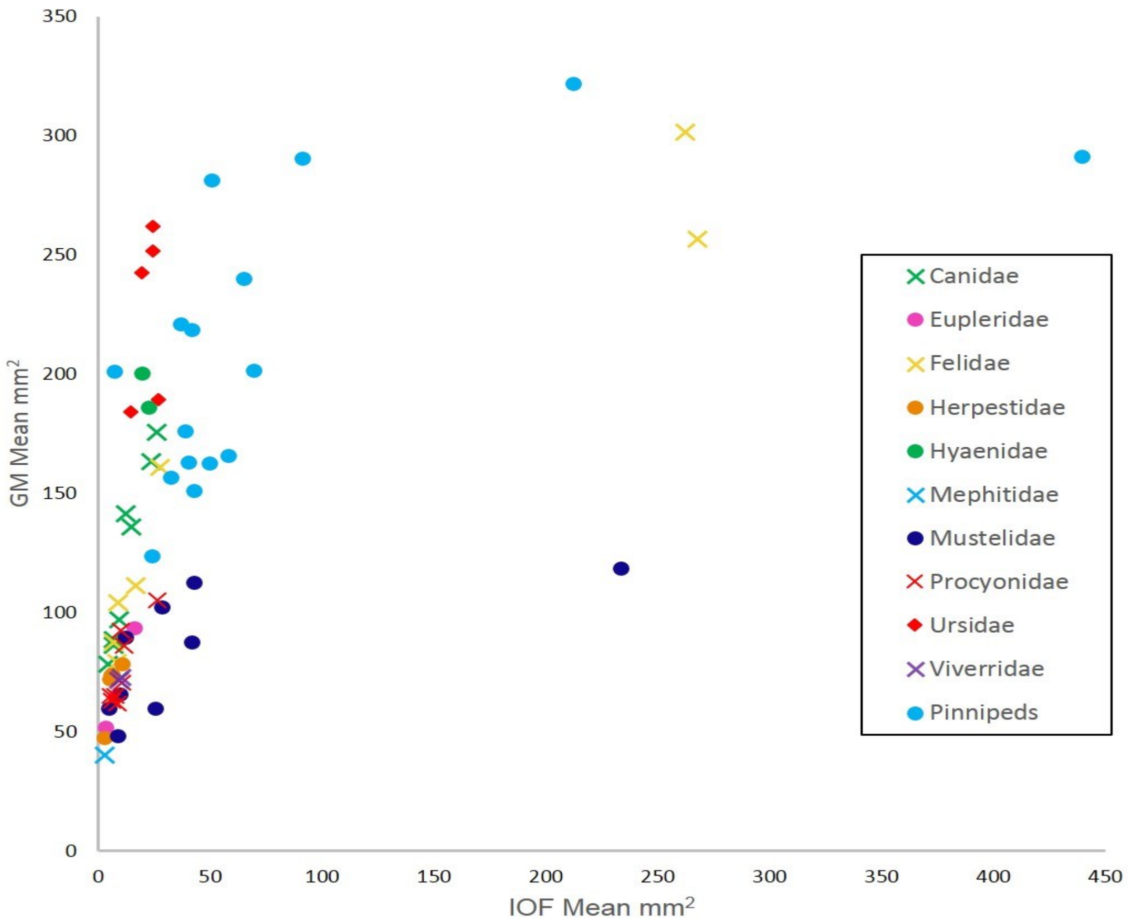


Figure 3.5: Relationship between the geometric mean (GM) of cranial length and width with the inferior orbital foramen (IOF): *Carnivora data taken from Muchlinski (2010) and Pinniped data collected via this study*

In addition, Figure 3.6 shows the relationship between the average number of mystacial vibrissae and IOF area between Pinnipeds and several carnivorous mammals, with data from Muchlinski (2008, 2010). Just like in Figure 3.5, there is a positive correlation between the total vibrissa counts and *IOF area (*Figure 3.6). It is also clear that even though the IOF area varies across carnivorous mammals, most species within a given order share a similar distribution. Phocidae and Otariidae have a lower whisker number compared to an IOF area than other carnivorous mammals (Figure 3.6). However, they have large IOF areas. The Felidae and Odobenidae have the largest IOF area in comparison to other mammals. The Mustelidaes, Felidae and Procyonidae have double the number of whiskers compared to the Otariidae, but the Mustelidaes and Felidae have a much smaller IOF area in comparison. The Odobenidae have an extremely large IOF areas and over double the number of whiskers compared to any of the carnivores seen here (Figure 3.6).

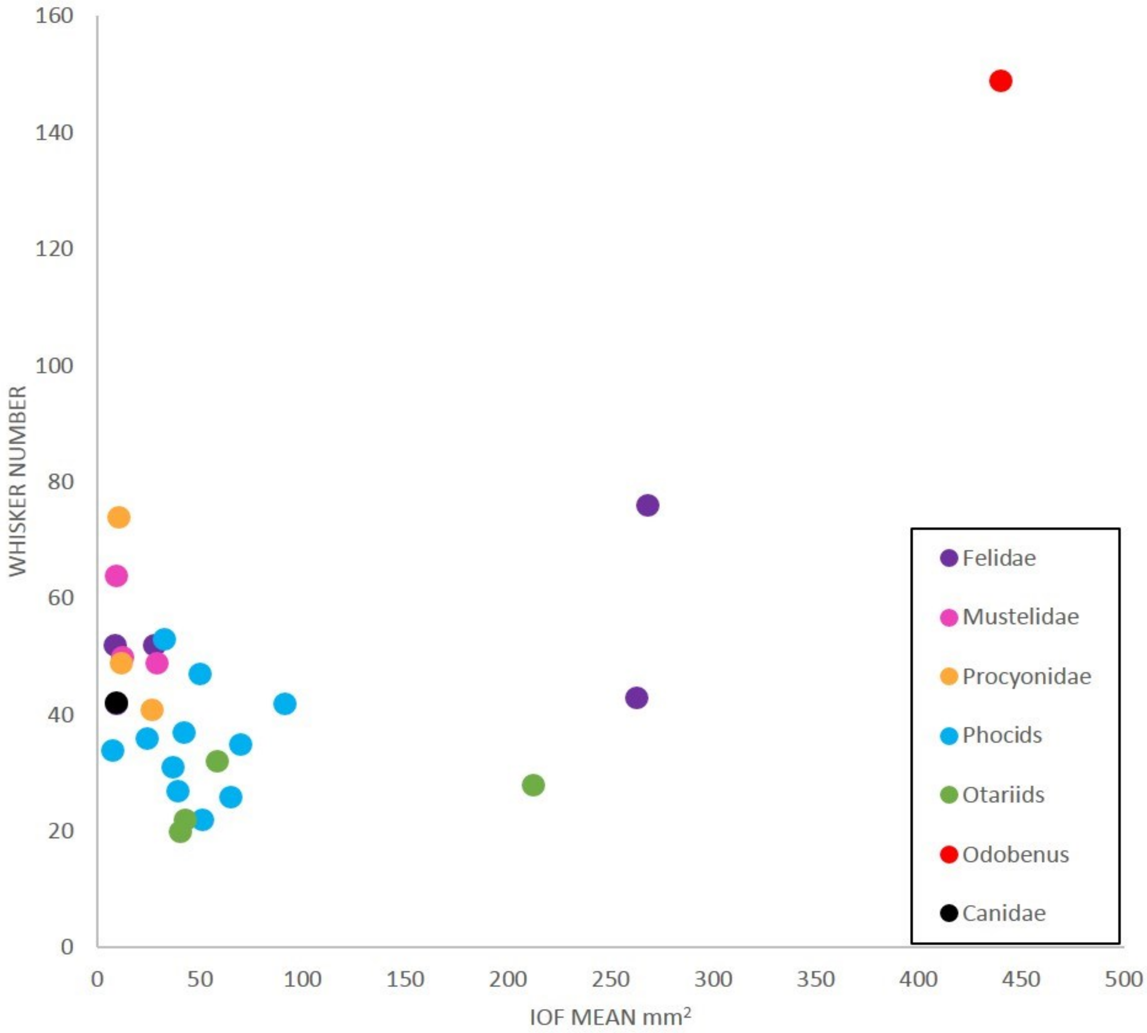


Figure 3.6: Relationship between the whisker number and the inferior orbital foramen (IOF): *Carnivora data taken from Muchlinski (2010) of all animals with whisker numbers present and Pinniped data collected via this study*

3.3.4 Eye orbit, IOF and whisker number are not associated with phylogeny

Figure 3.7 shows a Maximum Likelihood Phylogenetic Tree constructed on the variables for IOF, eye orbit and whisker number. These variables are particularly different in the walrus, compared to the other species. Some of the Phocidae are quite similar, for instance, the Weddell seal, (*Leptonychotes weddellii),* Ross seal *(Ommatophoca rossii)* and Southern Elephant seal *(Mirounga leonine);* however, in many instances the Otariidae and Phocidae data are very similar (for example the South American fur seal (*Arctocephalus australis),* Northern fur seal *(Callorhinus ursinus)* and Harbor seal (*Phoca vitulina)*), even though these are not closely related species (Figure 3.8). This indicates that eye orbit area, IOF area and whisker number are not more similar, in more related species of Pinnipeds (Figure 3.7, Figure 3.8).

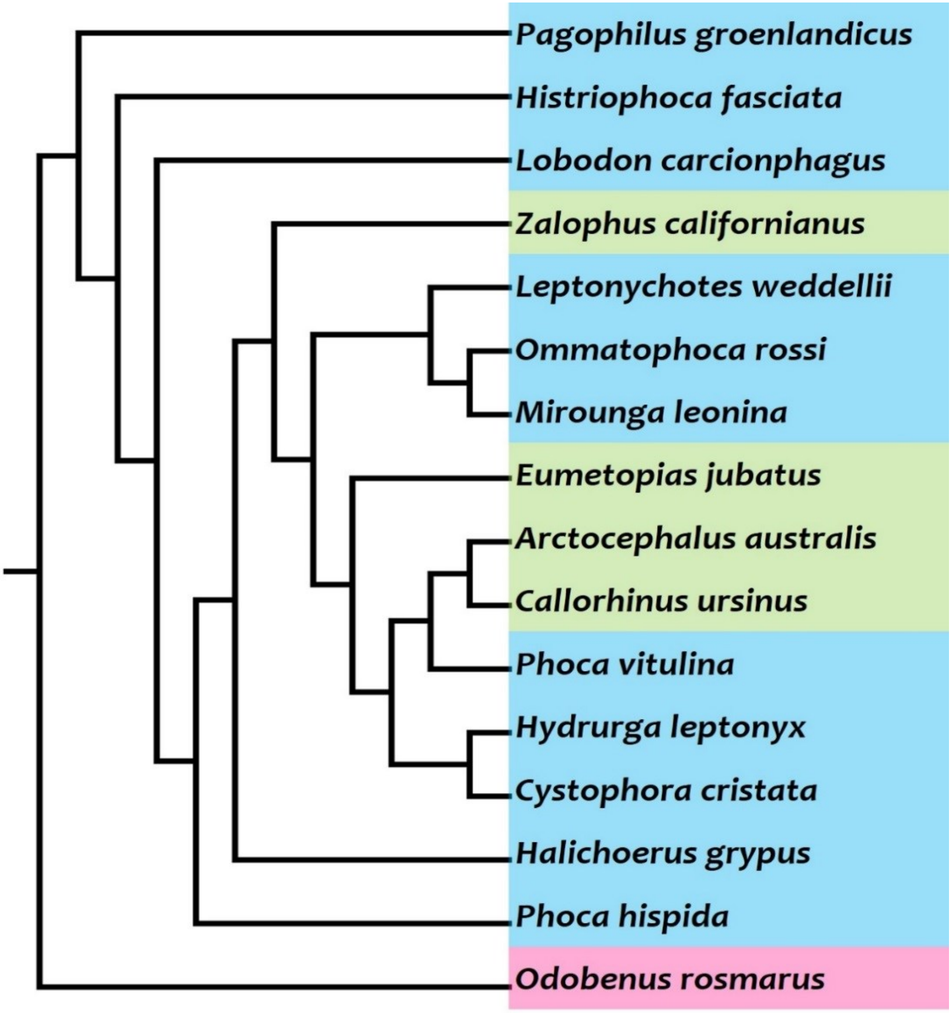
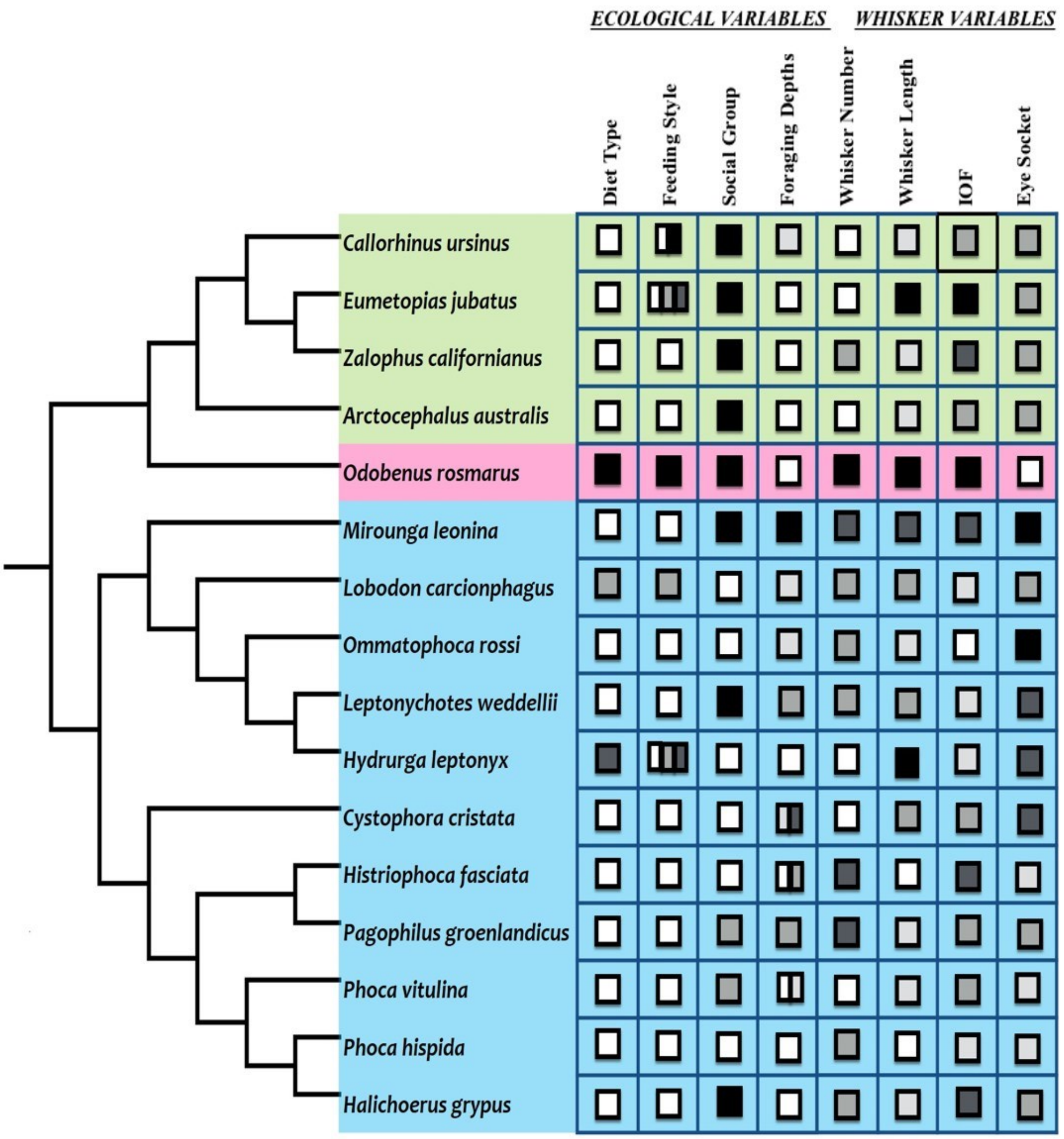


Figure 3.7: Maximum Likelihood Phylogenetic Tree: *Constructed using whisker variables from the museum samples. Colour coded via Pinniped family: Red - Odobenidae (walrus), Green - Otariidae (sea lions) and Blue - Phocidae (seals).*

3.3.5 Feeding ecology and whisker variables

If whisker variables are not similar between related species, perhaps ecological factors are likely to be associated with whisker variables instead. Figure 3.8 shows the relationships between Pinniped species, their ecological variables and whisker variables using a Phylogenetic Tree. Nearly all species of Pinniped predate on fish and cephalopods, with only three species preying on other items, including the Pacific walrus (*Odobenidae rosmarus divergens*), Leopard seal (*Hydrurga leptonyx*), and Crab Eater seal (*Lobodon carcionphagus*)

Figure 3.8 shows longer whiskers and larger IOF appear to be more associated with predating on fish and cephalopods, which can be seen throughout the seals and sea lions. They also seem associated when feeding style is either pierce and grab or rip and tear. Larger eye orbits are more associated with foraging at larger depths especially in the seals but in the sea lions larger IOF and larger eye orbits are more associated with shallow foraging depths (Figure 3.8). More whiskers are slightly better related to deeper foraging depths in the seals. Overall, it appears that the Otariidae possess large eyes, big IOF, long whiskers and forage at depths under 100 m. The walrus having the most whiskers has a larger IOF to compensate for this but has a smaller eye orbit even though they too forage at the same depths as Otariidae. Phocidae have a huge mixed variety between ecological and whisker variables even though nearly all Phocidae feed mainly on fish expect one or two species described (Figure 3.8).



Colour Code	Primary Diet Type	Feeding Style	Social Grouping	Average Foraging Depths (M)	Whisker Number	Whisker Length	IOF Area (MM^2)	Eye Socket Area (MM^2)
□	Cephalopods & Fish	Peirce Feeding	Solitary	0 - 100	<20	< 20	0.00-0.09	0-5
░	–	–	–	101 - 200	–	21 - 25	0.1-0.19	6-10
▒	Crustaceans	Filter Feeding	Small Groups	201 - 300	21 - 30	26 - 30	0.2-0.29	11-15
▓	Vertebrates	Grip & Tear Feeding	–	301 - 400	31 - 40	31 - 35	0.3-0.39	16-20
■	Mollusks	Suction Feeding	Colonial	400 +	50 +	36 +	0.4 +	20+

Figure 3.8: Maximum Likelihood Phylogenetic Tree Analysis: *Whisker variables and ecological variables with a detailed key outlining the differences (Riedman 1990). Colour coded via Pinniped family: Red - Odobenidae (walrus), Green - Otariidae (sea lions) and Blue - Phocidae (seals).*

3.4 Discussion

3.4.1 Pinniped Whisker and Skull Morphology

There is large variation in whisker variables among Pinniped*s*. The walrus had a large IOF with more whiskers than any other Pinniped species, but their whiskers were short, measuring only a few centimetres. They also had the smallest eye orbits out of the Pinniped*s* studied (Table 3.1). In comparison, Otariidae had a low whisker number, yet the longest whiskers compared to the rest of the Pinniped*s* (Table 3.1), with the longest whiskers belonging to the California sea lion and Stellar sea lion. The larger IOF areas were seen within the Otariidae too, with the Stellar sea lion having the largest area, a similar size to that seen in the walrus. Finally, the Phocidae showed the most variability, having a range of whisker numbers and lengths, as well as different sized IOF and eye orbits, with their eye orbits being larger in comparison to Otariidae and walrus.

The area of the IOF was significantly correlated to whisker length in Pinniped*s* (Figure 3.3), but not to whisker number. In a study by Kay and Cartmill (1977), they found that IOF size roughly reflected both the number and length of the mystacial vibrissae in primates. Indeed, longer whiskers are often thicker, with more mechanoreceptors around the base of each vibrissae, which would result in a larger IOF (Kay and Cartmill 1977; Wineski 1983; Ebara et al. 2002). This is reflected here within the Pinniped species, with IOF size increasing with whisker length (Figure 3.5). Previous studies have also noted that whisker number is often correlated with IOF area in primates and other terrestrial mammals (Kay and Cartmill 1977, Muchlinski et al. 2010). The walrus had over a hundred whiskers on each side of the muzzle and the largest IOF area, which indicates the strength of this association. However, overall in Pinniped*s*, whisker number was not correlated to IOF area. Perhaps the variation in whisker length has a larger effect on IOF area in Pinniped*s*.

Certainly, using the IOF area to approximate whisker number has not been encouraged in the literature, as this relationship is not strong (Muchlinki et al. 2010; Grant et al. 2018). Indeed, if IOF area is also associated with whisker length (Figure 3.3) and movement (Grant et al. 2018), perhaps all these factors need to be taken in to account when considering IOF area and ION sensitivity. Moreover, Pinniped vibrissae have considerable variation in arrangement, size, shape and structure (Ling 1977; Dehnhardt and Kaminski 1995), and how these variables affect skull morphology is still unknown. Whisker movement abilities is still not understood in Pinniped*s*, and this will be explored further in ***Chapter Four: Quantifying Whisker Movements in Pinnipeds.***

3.4.2 Pinniped*s* and Other Carnivores

Mammals show a variety of whisker shapes with some having extremely long and mobile vibrissae while others show shorter and immobile vibrissae (Dorfl 1982; Sachdev et al. 2002; Marshall et al. 2006). The most diversity can be observed in the Pinniped*s*. Other mammals such as Canids, Ursids, and primates all have immobile whiskers that are usually thin and very short (Sachdev et al. 2002; Marshall et al. 2006). All terrestrial mammals have smooth and circular whiskers that lack the morphological diversity seen in Pinniped whiskers. Figure 3.6 shows that while many of the Pinniped*s* had fewer whiskers than other carnivores, they had relatively larger IOF areas. Indicating that each Pinniped whisker is likely to be more sensitive, compared to other carnivores. Most of the carnivorous mammals selected from Muchlinski (2008, 2010) have good visual acuity, all being primarily diurnal and terrestrial, compared to the Pinniped*s*. This may indicate that many other carnivores might not rely as heavily on their vibrissae as the Pinniped*s*, and supports further investigation in to Pinniped whisker sensing, as they are likely to be touch specialists. However further investigation into the difference and significance of vibrissae in Pinniped*s* and other carnivores is needed.

Looking at the whisker variables and skull morphology measures in Figure 3.5 and 3.6 in other carnivores, many carnivores of the same order had similar whisker lengths, skull sizes and IOF areas. However, in the Phocidae, there is large variation in these variables, and the IOF area, whisker number and eye orbit size was not similar in related Pinniped species (Figure 3.4). Therefore, whisker and skull morphology might be more associated with ecological factors, rather than with phylogenetic constraints.

3.4.3 Associations with Feeding Ecology

Figure 3.8 shows longer whiskers and larger IOF areas appear to be more associated with species who predate on fish and cephalopods, especially with pierce and grab or rip and tear feeding types. Therefore, perhaps whiskers that are more sensitive are needed for active hunting. Feeding methods of Pinniped*s* are diverse with four major styles pierce, grip and tear, suction and filter feeding (King 1983; Werth 2000; Adam and Berta 2002). Unfortunately, not many studies have looked at how differences within skull shape and size is correlated to feeding methods in Pinniped*s*, and no studies investigated this in terms of whisker variables. Several studies, spanning over the last 50 years, have started to correlate skull shape and jaw structure with feeding methods (King 1983; Adam and

Berta 2002; Marshall and Bloodworth 2005; Marshall and Kane 2009). In addition, perhaps incorporating aspects of whisker number, length, shape and movements, might further compliment this data.

Pinnipeds hunt a variety of prey (Siniff and Bengtson 1977; Gentry and Johnson 1981; Fay 1982; King 1983; Riedman 1990; Werth 2000), so it is not surprising if there is an association between diet, modified skull shapes and whiskers in Pinniped*s* (King 1966, 1983; Adam and Berta 2002). Numerous statements in aquatic mammal literature associate skull shape with feeding mode (e.g., suction, biting, etc.). For example, both "scoop-like" mandibles and wide and blunt mandibles are correlated with suction feeding in Pinniped*s* (Werth 2006). Studying a variety of Pinniped skeletons shows that the skull shape of Pinniped*s* can be used to help us explain differences in feeding strategies. Previous studies have shown a strong correlation between feeding strategies and skull morphology, (Marshall and Bloodworth 2005; Marshall and Kane 2009). Northern fur seals (*Callorhinus ursinus*), South American sea lions (*Otaria flavescens*), Steller sea lions and California sea lions all have very similar skull morphologies, not only related to their similarities in whisker variables but also possibly related to their feeding preference. For example, this study shows that they all possess longer whiskers with a smaller IOF area as well as a similar sized eye orbit. In addition to this, the Steller sea lions alternate their feeding methods from piercing and suction. Evidence of this shown here in their skull morphology having a skull length and width twice the size of the other Otariidae, along with elongated palates and a short rostrum, allowing them the ability to catch prey via biting (Marshall and Kane 2009). The nerve supply to the maxillary region in mammals varies significantly (Loo and Kanagusuntheram 1972, 1973; Montagna et al.

1975, Baron et al. 1990) but is mostly correlated with foraging behaviours and substrate preferences (Loo and Kanagusuntheram 1972, 1973; Montagna et al. 1975). As the IOF area has a direct link to the ION area it may be possible to correlate IOF area to differences in ecology in Pinniped*s*, and could be used to reconstruct ecology and behaviour in fossil mammals.

3.5 Conclusion

This chapter has been the first of its kind to describe whisker morphology in several species of Pinnipeds. It has shown that whisker length is significantly correlated to the area of the infraorbital foramen area, but this relationship is not strong as whisker number and movement are also likely to contribute to IOF area. Results in this chapter indicate that Pinniped whiskers are extremely variable, in terms of length and shape. In addition, as Pinnipeds have a relatively larger IOF area (which is associated with ION size, each Pinniped whisker is likely to be more sensitive than in other carnivores. Whisker and skull morphology does not map well on Pinniped phylogeny, therefore, ecological factors, especially feeding ecology, is likely to be a big predictor of skull morphology, whisker length and whisker sensitivity in Pinnipeds

4 ***Chapter Four: Quantifying Whisker Movements in Pinnipeds***

Chapter Summary:

This study quantifies Pinniped whisker movements. One species out of each of the three Pinniped families was selected: California sea lion (*Zalophus californianus)*, Harbor seal (*Phoca vitulina)* and Pacific walrus (*Odobenidae rosmarus divergens*). Each species participated in a fish-sweeping task, a behavioural task that encouraged whisker movements. All species oriented their head and protracted their whiskers towards the moving fish stimulus. The largest offset values, or most forward-positioned whiskers, were seen in the Pacific walrus. California sea lions moved their whiskers with the largest amplitudes and asymmetry. Harbor seals had the most spread out whiskers. Asymmetry of whisker orientation was related to head orientation in Pacific walrus and Harbor seal; however, the California sea lions could move their whiskers independently of head movements. California sea lions would therefore be a good candidate species in which to investigate active touch sensing further.

4.1 Introduction

Pinniped*s* have whiskers located on their muzzle arranged in regular, densely packed rows and columns. Each whisker follicle is surrounded by a network of intrinsic muscles allowing their whiskers to move independently (Bush et al. 2016). Pinnipeds can lie their vibrissae back against their muzzle or they can be protracted forwards (Dehnhardt et al. 2001; Gläser et al. 2010). They do not “whisk” as rodents do (whiskers repeatedly and rapidly swept back and forth in a cyclic motion) but can protract their whiskers and utilise lateral head movements during object exploration to position their whiskers (Kastelein and Van Gaalen 1988; Dehnhardt 1994; Dehnhardt and Kaminski 1995; Dehnhardt et al. 2001; Miersch et al. 2011). A study by Milne and Grant (2014) showed the importance of whisker movements in California sea lions during a ball-balancing task. This task was thought to specifically encourage whisker movements, as it was a dynamic sensorimotor balancing task. However, not all Pinniped*s* are able to ball-balance; therefore, a behavioural task needs to be designed that promotes whisker movements in many Pinniped species, in order to compare them. Therefore, the aim of this chapter is to compare and quantify whisker movements in Pinniped*s*, using a novel, dynamic, behavioural task to encourage whisker movements in seals, sea lions and walrus. It is hypothesised that each of the three species will move their whiskers differently as they have large differences in whisker number, length, shape and IOF size (see ***Chapter Three: Pinniped Whisker and Skull Morphology***).

4.2 Methods: Pinniped whisker control videos

4.2.1 Animals

One Pinniped species was selected across each of the three families: seals, sea lions and walrus. They included California sea lions at Blackpool Zoo, Harbor seals at Rhyl SeaQuarium and Pacific walrus at Dolfinarium Harderwijk. Five California sea lions were used in this study housed at the Active Oceans in Blackpool Zoo, England. These individuals were Gina (female 16 years old), Anya (female 12 years old), Lo (female 15 years old), Gala (female 16 years old) and Fillipa (female 20 years old). The three Harbor seal housed at Rhyl SeaQuarium, Wales, used in this study were Wanda (female 22 years old), Ina (female 16 years old) and Pamina (female 14 years old). Finally four Pacific walrus, Nikolai (male 22 years old), Olga (female, 35 years old, almost completely blind), Rossita (female 22 years old) and Olivia (female, 9 years old) housed at the Dolphinarium Harderwijk, Netherlands.

All animals were chosen for their current access and availability; these species have also been targeted the most for behavioural and anatomical research on their sensory abilities. As the task was to film the Pinniped*s* catching prey, none of the animals were trained any new behaviours for this study. All animals were trained at their current institutions with the same trainers present. After the animals were trained to stand at specific stations, video sampling could begin. All animals could leave the testing area at any time.

4.2.2 Experimental Procedures

Trial sessions were conducted at varying schedules throughout the day. As the animals take part in public displays, training and feeding sessions, trials were limited to 10 minutes, 3-5 times a day. The fish given in the task comprised a variety of different species and sizes included as part of their daily food amount. Trials were carried out in training areas at each of the institutions so they were familiar to the animals. During the trials, the same trainers were present each time the filming took place. Trainer 1 would feed the animal while conducting the session, with Trainer 2 recording the footage. Once the session was complete, the animals were returned to their pen or to the main pool. To enable the whiskers to be seen clearly, darker areas (shaded, or against a dull background) were selected for filming where possible. Display stations were positioned so the California sea lions could elevate their forelimbs easily during the task. The Harbor seals were placed in a training pool or on the land over a black mat and the Pacific walrus being extremely large, were positioned on the ground standing on their forelimbs with their hind limbs relaxed on the floor. Two behavioural tasks were trialled to encourage whisker movements. Firstly, fish catching, where fish were thrown to the animals. However, during a pilot study, the Pacific walrus were unable to catch the fish, as they prefer suction feeding, and therefore another task had to be designed. Fish sweeping involved a trainer moving fish over the whiskers of the animals, and the animal orienting towards it for feeding. Using fish sweeping, the Pacific walrus were able to use their whiskers to move the fish towards their mouth in a similar way to their preferred method of feeding. There were no problems in readjusting both the Harbor seal and the California sea lion to take their fish in a sweeping action.

For the fish-sweeping task, each animal was taken into a training area with two trainers; this was done in training sessions, only due to the nature of the task and to avoid snatching from the animals. A variety of fish including Atlantic Mackerel (*Scomber scombrus*), Atlantic Herring (*Clupea harengus*), Capelin (*Mallotus villosus*) and European Sprat (*Sprattus sprattus*), were given to the Harbor seal and California sea lions for the Pacific walrus Atlantic Herring (*Clupea harengus*), Sprat (*Sprattus sprattus*) or Squid (*Loligo opalescens*) was given. Trainer 1 would move a fish past the animal's head in a sweeping motion, allowing the animal to take it. Trainer 2 using a waterproof camcorder videoed from above giving a birds' eye view, making sure the video got the full sweep, the animals head and all whiskers. Positive reinforcement was used, which increased the animal's attention and maintained performance. The number of times the sweeping task was completed in a session varied allowing multiple trials to be obtained per video (Milne and Grant 2014). Once the sessions were complete, the animals were returned back to either their own pen or the main pool with the main group.

4.2.3 Video Selection and Analysis

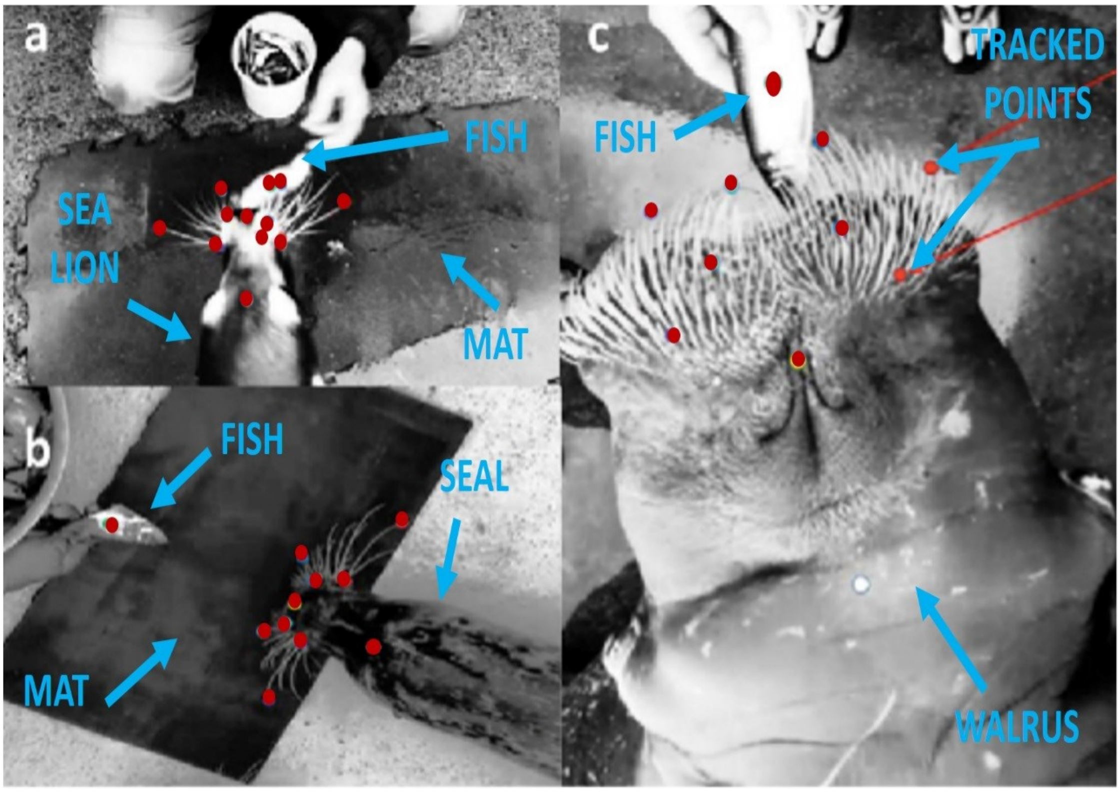


Figure 4.1: Video stills from the footage taken of Pinnipeds fish-sweeping: *Tracking stills showing trackable points in red: (a) California sea lion (Zalophus californianus) (b) Harbor seal (Phoca vitulina) (c) Pacific walrus (Odobenidae rosmarus divergens). Red dots indicate tracked points on the pinnipeds*

Whisker filming for the Harbor seal and the California sea lion was conducted using a waterproof GE DV1 Pocket Digital Camcorder (HD 1080p), and for the Pacific walrus whiskers using a hand held iPhone camera, uploaded and emailed over from the Dolphinarium Harderwijk. Recordings were set at 30 frames per second to eliminate blurring during whisker movements. All video clips were examined to ensure videos selected would show the following: (i) all whiskers were visible by the camera throughout the clip, (ii) the Pinniped was accurately lined up with the camera and (iii) there was enough lighting to see all the whiskers. Each video was tracked manually using an open source ‘Manual Whisker Annotator’ (Hewitt et al. 2016). Two whiskers on each side of the face were tracked along with the nose and head point between the eyes (Figure 4.1).

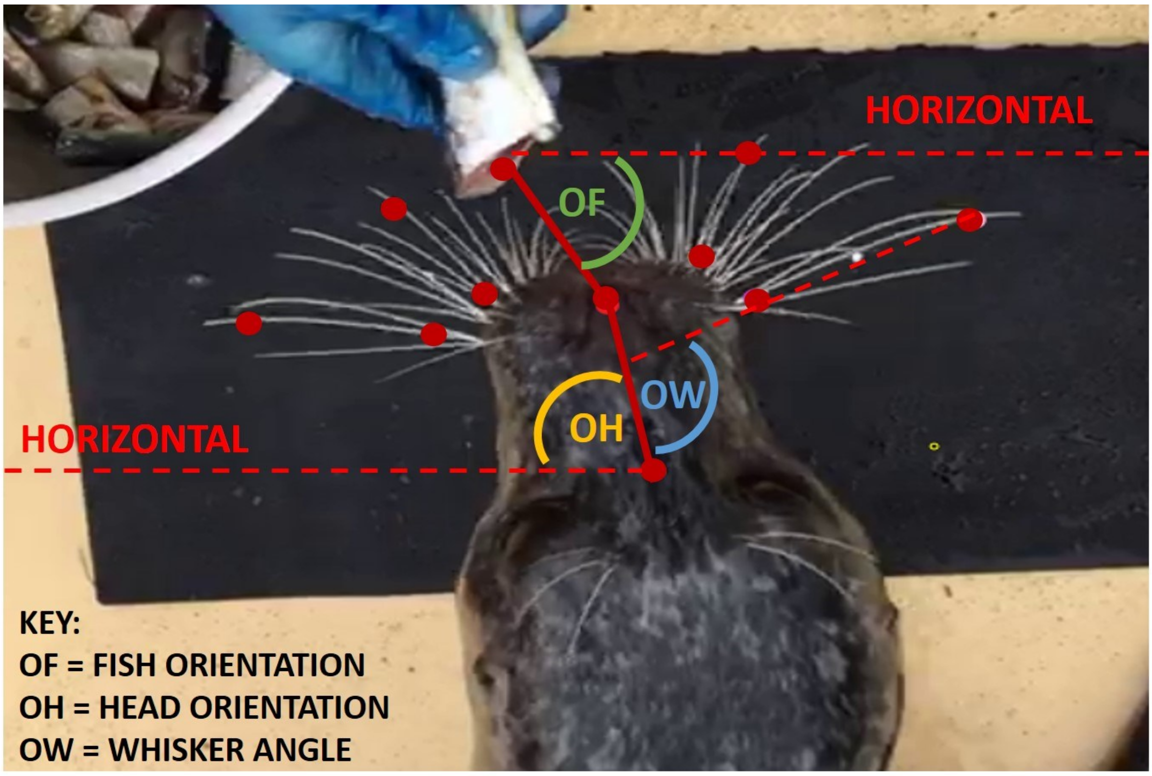


Figure 4. 2 Tracking video still indicating measurements of angles*: Angles showing head orientation, fish orientation and whisker angular position*

The whiskers selected for tracking were from the front and back on each side of the muzzle. Two points were tracked on each whisker: the base and the shaft (a point around two-thirds along the whisker), (Figure 4.1). The tracking was started once the fish had entered the shot from Trainer 1, continued until the animal ate the fish, and stopped on the frame before the whiskers began to return to the relaxed position (flat against the muzzle). After reviewing all videos recorded, the following numbers of clips were used for fish-sweeping tracking: 22 for the Harbor seal 21 for the California sea lion and 5 for the Pacific walrus. From these, fish and head orientation along with whisker angular position were calculated (Figure 4.2) Whisker variables were calculated to allow for differences to be analysed including offset, asymmetry, amplitude and spread (Milne and Grant 2014). All measurements and whisker variable definitions can be found in Table 4.2.

Table 4.1: Measurements and whisker variables: *Whisker variables used with definitions*

MEASUREMENTS AND WHISKER VARIABLES	**DEFINITION**
FISH ORIENTATION	The angle between the fish and nose point, calculated as the angle from each fish point to the nose tip, from the horizontal
HEAD ORIENTATION	The angle between the head and nose point, calculated as the angle from each head point to the nose tip, from the horizontal
WHISKER ANGULAR POSITION	The angle between the whisker and the midline of the head
WHISKER OFFSET	The mean whisker angle calculated by averaging all the whisker angular positions on each side of the muzzle
WHISKER AMPLITUDE	Calculated as the difference between the maximum and minimum whisker angular positions, averaged over whiskers and sides
WHISKER ASYMMETRY	The difference between the left whisker angular positions and the right (left minus right)
WHISKER SPREAD	Calculated as the angular difference between the front and back whiskers.

4.2.4 Statistical Considerations

Differences between each of the three Pinniped species were compared by calculating averages per clip for each of the species whiskers variables and orientations. This data was pooled together for each individual species (seal, sea lion and walrus) and was analysed using Kruskal Wallis H test to examine species differences, and Spearman's rank correlation to analyse the relationships between head and fish orientations and whisker variables. Pairwise comparisons between the three species were analysed using Mann-Whitney U test.

4.3 Results

4.3.1 *Whisker movements and position*

Offset values were significantly different between the Pinniped*s* species (Kruskal-Wallis: χ2=14.001, df=2, p<0.001). Larger offset values were seen in the Pacific walrus (Figure 4.3 a), with their whiskers protracted further forwards than both the Harbor seal (Mann-Whitney U: U=0.000, Z=-3.433, p<0.001) and California sea lion (Mann-Whitney U: U=0.000, Z=-3.416, p<0.001). The Pacific walrus whiskers also moved symmetrically, indicating that whiskers on both sides were positioned equally (Figure 4.3 c). This is visible in the footage recorded via the video stills seen in Figure 4.4 g, h and i, where the Pacific walrus whiskers are protracted forward towards the fish equally from both the left and right side of the muzzle.

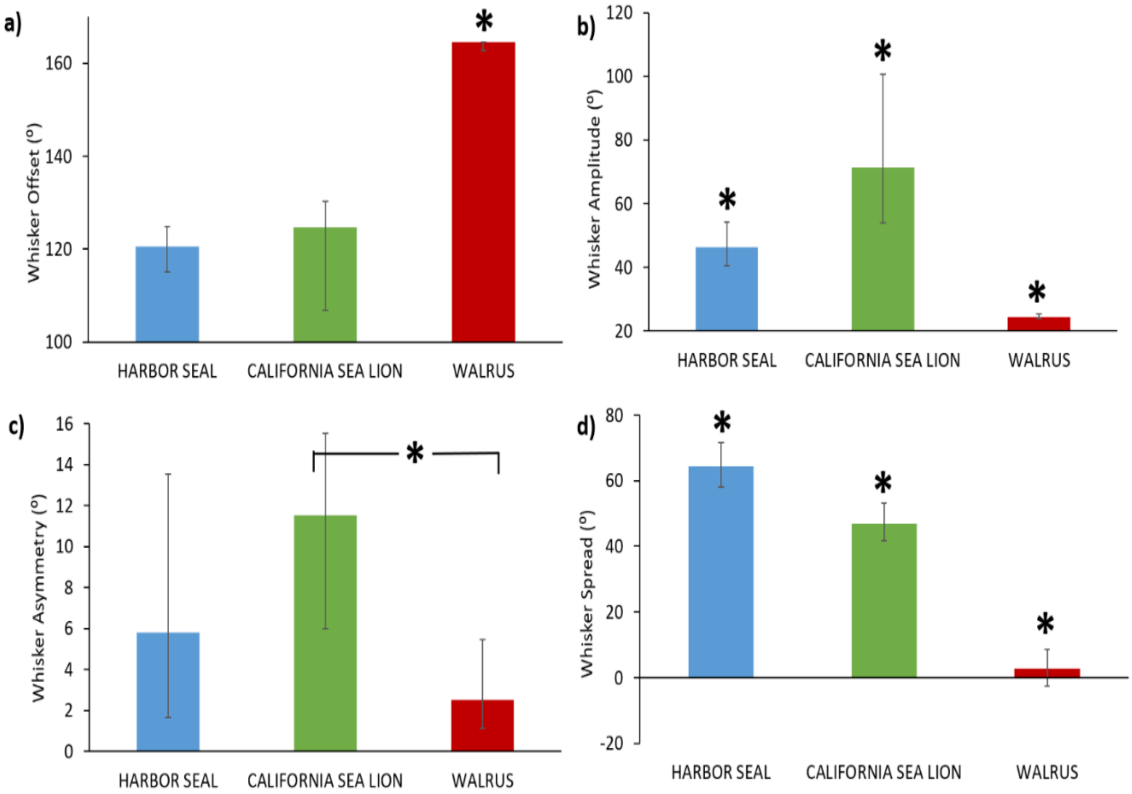


Figure 4.3: Pinniped whisker positions and movements: *(a) Whisker offset values show that Pacific walrus (Odobenidae rosmarus divergens) have higher offset values, (b) Whisker amplitude, which is largest for the California sea lion (Zalophus californianus), (c) Whisker asymmetry, which is lowest in the Pacific walrus (Odobenidae rosmarus divergens), (d) Angular whisker spread, which is smallest for the Pacific walrus (Odobenidae rosmarus divergens) overall. All graphs show median values with interquartile ranges. Asterisks (*) show significant differences Mann Whitney U post hoc (p < 0.05*

During the sweeping task Pinnipeds moved their whiskers at significantly different amplitudes (Kruskal-Wallis: χ2=23.565, df=2, p<0.001). California sea lion whiskers moved with greater amplitudes of 71.220^{o}, than both the Harbor seal at 44.195^{o} (Mann-Whitney U: U=83.000, Z=-3.596, p<0.001) and Pacific walrus, which only moved 24.325^{o} (Mann-Whitney U: U=0.000, Z=-3.416, p<0.001). Harbor seal also moved their whiskers more than the Pacific walrus (Mann-Whitney U: U=0.000, Z=-3.433, p<0.001), (Figure 4.3 b). As the California sea lion oriented towards the sweeping fish, their whiskers moved from the relaxed muzzle positon and protracted forward into a bunched up position in less than one second (Figure 4.4, d, e and f).

There was a significant difference between Pinniped whisker asymmetry when catching the sweeping fish, (Kruskal-Wallis: χ2=8.707, df=2, p=0.013). California sea lions significantly moved their whiskers more asymmetrically during the sweeping task compared to the Pacific walrus (Mann-Whitney U: U=8.000, Z=-2.895, p=0.002). There was no significant difference between the Harbor seal and both the California sea lions (Mann-Whitney U: U=152.000, Z=-1.919, p=0.055) and Pacific walrus (Mann-Whitney U: U=35.500, Z=-1.217, p=0.232) (Figure 4.3 c). Whisker spread significantly differed between Pinniped species (Kruskal-Wallis: χ2=31.644, df=2, p<0.001). The largest spread values were seen in Harbor seal, who had more spread out whiskers than both the Pacific walrus (Mann-Whitney U: U=0.000, Z=-3.433, p<0.001) and California sea lions (Mann-Whitney U: U=30.000, Z=-4.884, p<0.001), (Figure 4.3 d). This can be seen in Figure 4.4 a, b and c, as the Harbor seal rostral whiskers are more forward than the caudal whiskers, causing the spreading out of the whiskers. California sea lions' whiskers were also more spread out that the Pacific walrus whiskers (Mann-Whitney U: U=0.000, Z=-3.416, p=0.001), (Figure 4.4 e and h).

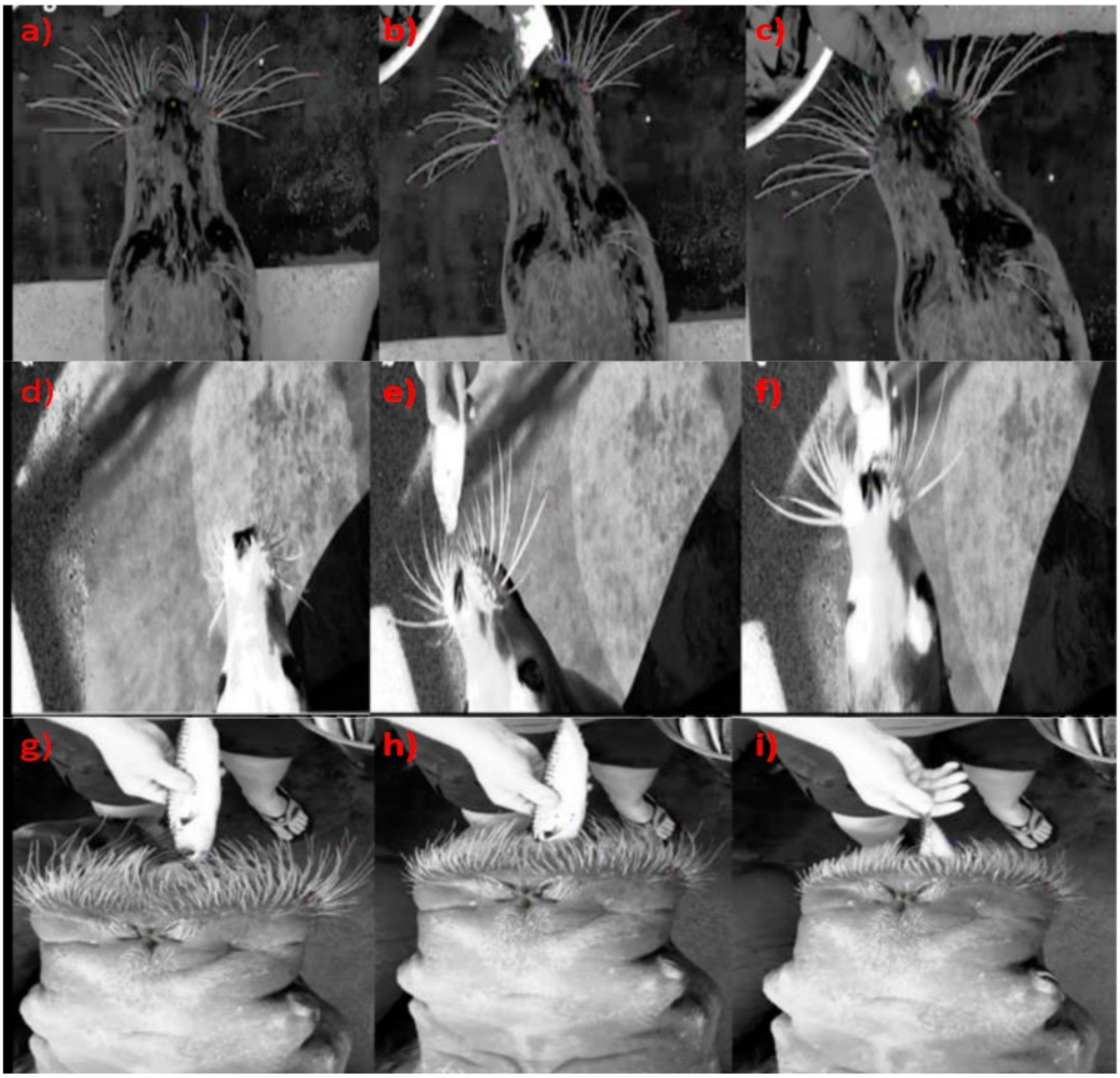


Figure 4.4: Pinniped Tracking Video Stills: *a) b) c) Harbor seal (Phoca vitulina) sweeping showing increased whisker spread of all their whiskers, d) f) e) California sea lion (Zalophus californianus) sweeping with increased whiskers movement from being relaxed on the muzzle to taking the fish, g) h) i) Pacific walrus (Odobenidae rosmarus divergens) sweeping with greater forward protracting whiskers towards the front of the muzzle and the fish. Each video still differs by 500 ms*

4.3.2 *Whisker movements in response to head and fish positions*

Pinnipeds oriented their head towards the sweeping fish. There was a significant negative relationship between head movements in response to fish movement in the Harbor seal (*Spearman's Rank: r=* -0.605, p<0.001), California sea lion (*Spearman's Rank: r=* -0.457, p<0.001) and Pacific walrus (*Spearman's Rank: r=* -0.498, p<0.001). As fish orientation increased head orientation decreased in each Pinniped species (Figure 4.5 a).

This is seen in the video still for each species in Figure 4.4, with the Harbor seal California sea lion and Pacific walrus all positioning their head towards the sweeping fish, presumably in order to take the fish.

California sea lions and Pacific walrus oriented their whisker movements towards the sweeping fish. There was a significant positive relationship between whisker asymmetry and fish movement in the California sea lion (*Spearman's Rank:* r=0.243, p<0.001) and Pacific walrus (r_s=0.280, p<0.001), but not in the Harbor seal (*Spearman's Rank:* r=0.063, p=0.208). Generally, as fish orientation increased, whisker asymmetry increased across the three Pinniped species (Figure 4.4 b, e, h). For example, in Figure 4.4 d, e and f, as the fish approaches from the left, the California sea lion whiskers on the right will move more forward and the left whiskers will be a little further back (Figure 4.4 e), orienting towards the incoming fish.

There were noticeable differences between Pinniped whisker positions and their head movements (Figure 4.5 c). Whisker asymmetry and head orientation was significantly associated between the Harbor seal (*Spearman's Rank:* r= 0.247, p<0.001) and Pacific walrus (*Spearman's Rank:* r= 0.298, p<0.001), with whisker asymmetry increasing with head movements. This pattern can be seen in the series of video stills, as the Pacific walrus and Harbor seal head moves towards and whiskers protract forward to the fish together, creating a decrease in whisker asymmetry and head orientation (Figure 4.4: Harbor seal a, b and c, Pacific walrus g, h and i). Whisker asymmetry and head orientation were not associated in the California sea lion (*Spearman's Rank:* r= -0.004, p=0.935).

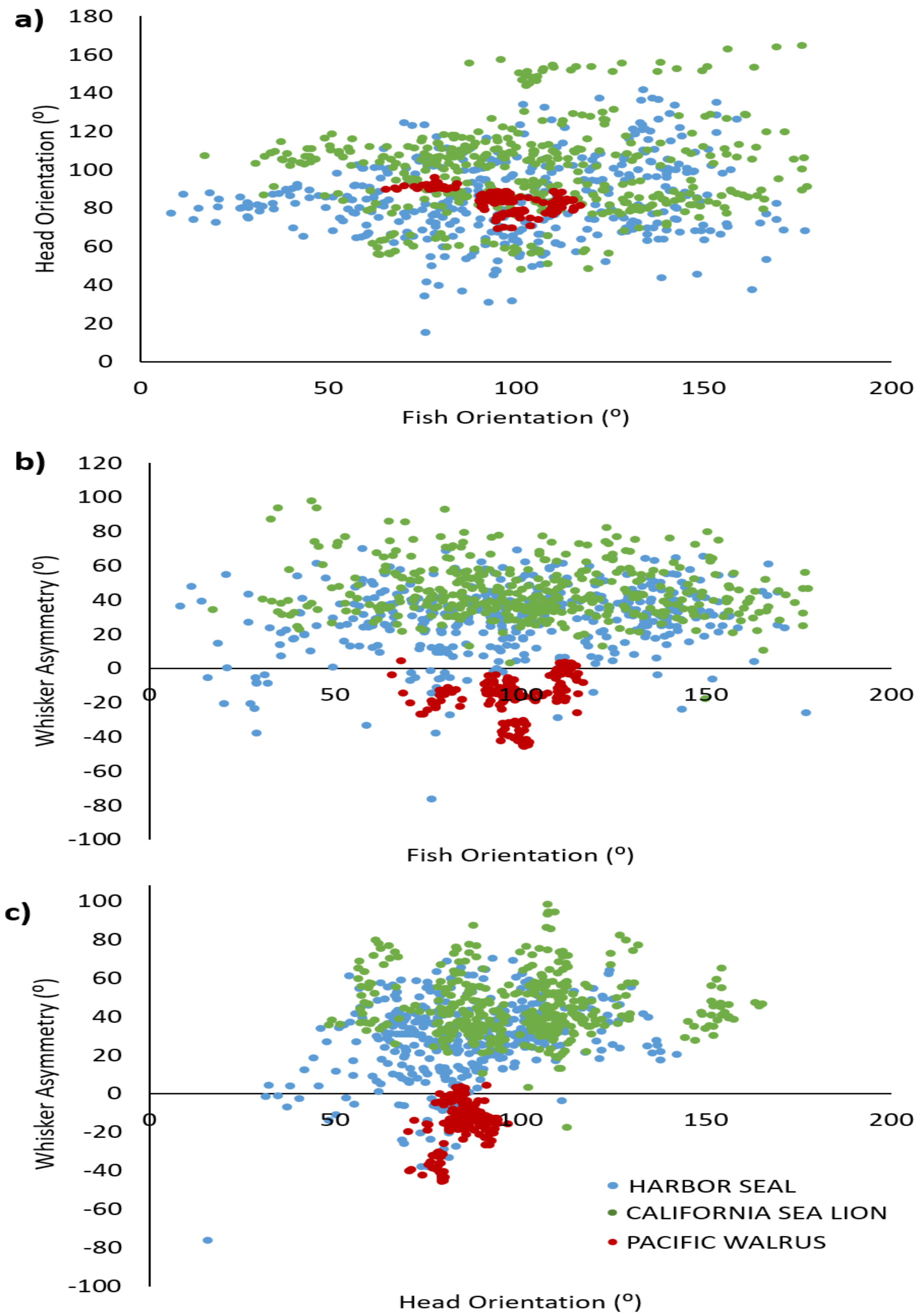


***Figure 4.5: Pinniped head, fish and whisker angles in response to fish sweeping**. Scatter graphs of per-frame angles across all tracked videos for: (a) Fish Orientation vs. Head Orientation, (b) Fish Orientation vs. Whisker Asymmetry, (c) Head Orientation vs. Whisker Asymmetry. Head orientation is correlated to the fish orientation in all species (Spearman's rank Correlation: $p < 0.05$), in panel a. Fish orientation and whisker asymmetry is correlated in California sea lion and Pacific walrus (Spearman's rank Correlation: $p < 0.05$), but not in Harbor seal in panel b. Whisker asymmetry and head orientation is correlated in Harbor seal and walrus in panel c (Spearman's rank Correlation: $p < 0.05$), but not in California sea lion, indicating that California sea lions have the capacity to decouple whisker and head movements.*

4.4 Discussion

4.4.1 Results Summary

The present study supports the hypothesis that Pinniped species move their whiskers differently. All three species oriented their head towards a moving fish stimulus and protracted their whiskers (Figure 4.4; 4.5 a and b); however, they moved and positioned their whiskers differently (Figure 4.3). California sea lions moved their whiskers more than Harbor seals and Pacific walrus and often independently of head movements. The Harbor seals had the largest whisker spread and Pacific walrus had the largest offset values.

4.4.2 Do Whisker Movements Differ Between Pinniped*s*?

Studies in active touch sensing during static exploration and discrimination tasks have been broadly researched (Kastelein et al. 1990; Dehnhardt 1994; Grant et al. 2013a), but few studies show how whiskers move during a dynamic task (Milne and Grant 2014). This study is the first of its kind to design a whisker movement task to truly show that many species of Pinniped significantly move their whiskers. Indeed, all Pinniped species tested here oriented their whiskers towards the fish stimulus, by increasing their whisker offset. California sea lions and Pacific walruses also further oriented their whiskers by positioning them asymmetrically towards the fish, which is likely to increase the number of whisker contacts (Kastelein et al. 1990; Dehnhardt 1994; Grant et al. 2013a; Milne and Grant 2014). This confirms that during this behavioural task, all Pinniped*s* could move their whiskers and control whisker positions towards the fish stimuli.

However, these three species did not move their whiskers in the same way. The Pacific walrus moved its vibrissae with increased forward protraction (offset) angles, the Harbor seal had a much greater whisker spread and the California sea lions moved their whiskers more (at higher amplitudes) with more asymmetry. Milne and Grant (2014) previously demonstrated that California sea lions moved their whiskers quicker than head movements during a ball-balancing sensorimotor task, with whisker movements better matching ball movements than head movements. Results presented here suggest that the Pacific walrus and Harbor seal whiskers closely follow head movements, and only the California sea lions have the capacity to decouple their whisker and head movements. This makes California sea lions an excellent candidate from which to explore active touch sensing further. Therefore, this species will be employed in ***Chapter Five: Sea Lion Training Programme*** and ***Chapter Six: Task-Specific Whisker Movements in California Sea Lions*** to examine the task-specificity of whisker movements.

Differences in whisker movements could be associated with both whisker morphology and feeding ecology in these species see ***Chapter Two: Literature Review, 2.3.2. Foraging Behaviour in Pinnipeds***. The Pacific walrus has more whiskers that are positioned further forwards, with higher offset values, which could enable Pacific walrus to search for stationary prey underwater, using their whiskers much like a brush. Walrus have relatively small eyes positioned on the side of the head (Harington 2008). When they search through a substrate for food, the substrate will become disturbed and water will become murky, making it challenging to use vision to find prey items. When the walrus find food items they use suction feeding (Harington 2008). California sea lions and Harbor seals use the pierce and grab feeding method on mobile prey items; therefore, their whiskers are likely to be more mobile. They have larger whisker amplitudes, spread and asymmetry, so can orient to stimuli, and are likely to be able to sense fast moving prey from many different directions, using both touch and hydrodynamic sensing. Indeed, it has been noted that Harbor seals mainly always have their eyes shut during hunting, and are likely to rely primarily on their whiskers (Marshall et al. 2014).

Whisker asymmetry and head orientation were shown to be positively correlated in the Harbor seal and Pacific walrus. Grant et al. (2013a) reported large asymmetry values of as much as 10 degrees, when Harbor seal were completing a size discrimination task. This value is also similar to what was observed here in Harbor seal (a mean of 9 degrees in Figure 4.2). Whisker asymmetry orients the whiskers towards the fish, and might indicate a reliance on touch sensing when the fish is close and visual cues become impaired. This has been previously documented in rodents and cats (Gottschaldt et al. 1974; Towal and Hartmann 2006; Grant et al. 2012). However, whisker asymmetry has also been found to preceed head rotations in rodents (Towal and Hartmann 2006), marsupials (Mitchinson et al. 2011) and California sea lions (Milne and Grant 2014), and is termed head-turning asymmetry (HTA). HTA is thought to enable whiskers to scan the area that the head is moving in to (Towal and Hartmann 2006). All Pinniped species oriented their head towards the fish, and in Pacific walrus and Harbor seal, the whisker asymmetry was also correlated to head orientations. Therefore, in these species, the orienting of the whiskers by increasing whisker asymmetry, might guide the whiskers towards the fish, or it might just be to guide the orienting of the head towards the fish. Indeed, whiskers can be positioned the most via movements of the head than the whiskers themselves. However, in California sea lions whisker asymmetry was independent of head movements, and not correlated.

Whisker kinematics have been shown to be closely related to facial musculature across a variety of mammals (Grant et al. 2014, 2016, 2018, 2019) with animals that move their whiskers more having thick and regular intrinsic muscles (Grant et al. 2016, 2019). The differences in whisker positions and movements between the three species of Pinniped*s* studied here could also be explained by the anatomical differences that may exist between them. This may include the anatomy of the follicles, mechanoreceptors, nerve fibres and muscle architecture (Kastelein et al. 1990), as well as the variation in whisker shape and length. However, more studies would be required to fully characterize and address these anatomical differences.

4.4.3 Morphology and Whisker Structure Could Link to Whisker Movements

Chapter Three: Pinniped Whisker and Skull Morphology found that Pinniped*s* with longer whiskers and a larger IOF area were more associated with predating on fish and cephalopods in Phocidae and Otariidae. Larger eye orbits were more associated with foraging at deeper depths in the Phocidae, but in Otariidae, larger IOF and larger eye orbits were more associated with shallower foraging depths. Walrus had shorter whiskers, small eye orbits and the largest IOF area. IOF area has previously been linked to whisker movement (Grant et al. 2019), with whisking small mammals having larger

IOFs than animals that did not whisk. Therefore, species with many, long, thick, motile whiskers are likely to have the largest IOF values.

Chapter Three: Pinniped Whisker and Skull Morphology reported that Harbor seals had mean IOF areas of 38.8 mm^2, California sea lions of 57.9 mm^2 and walrus of 439.5 mm^2. It is likely that IOF areas are associated with a complex interplay of whisker length, thickness, movement and number. While walrus whiskers are shorter (74 mm) than both Harbor seal (85 mm) and California sea lion (176 mm) and also move the least (Figure 4.2 b), they have many more whiskers (149 whiskers on each side of their face), compared to both Harbor seal (27) and California sea lion (32). Therefore, this large number of whiskers will require a larger ION and IOF. California sea lions have a similar number of whiskers to Harbor seals, but their whiskers are longer and more mobile, hence they have larger ION and IOF areas. Applying the fish sweeping task to many of the Pinniped species in ***Chapter Three: Pinniped Whisker and Skull Morphology*** will help to quantify whisker movements in many Pinniped species, and further examine the interplay between whisker morphology, whisker movements and IOF area. However, many of these Pinniped species are not in captivity, therefore, access to these animals are limited and probably not possible. Further studies could develop methods for recording whisker movements and exploration in underwater environments during live prey capture in wild animals, and go on to explore the variability in natural whisker movements in Pinnipeds.

4.5 Conclusion

California sea lions, Harbor seals and Pacific walrus all orient their head and protract their whiskers towards moving fish stimuli. However, they show a range of different whisker movements. California sea lions move their whiskers the most, and independently of head movements. Pacific walrus and Harbor seal oriented their whiskers and head together. Harbor seals had the most spread out whiskers, and Pacific walrus whiskers moved less and were positioned the most forward, with the highest offset values. This variety in movements could be explained by their feeding ecology, with more mobile whiskers observed in the Harbor seal and California sea lion who hunt moving prey. Using this novel behaviour task has encouraged whisker movements, but more studies are needed to better record whisker movements during realistic prey capture, and in more species

5 ***Chapter Five: Sea Lion Training Programme***

Chapter Summary:

This chapter describes the experimental apparatus and training procedure for the discrimination tasks. It describes the making of the fish model, the building of the fish rig, the design and alterations of the blindfold along with individual training plans for each of the California sea lions. It discusses in detail, how the various training schedules for the research were implemented, achieved, problems that occurred and how these led to alterations. The procedures for the final research are also listed here along with how incorrect behaviours were dealt with and the roles of the trainers. For each of the discrimination tasks the fish models, fish distractors used and procedures carried out are described in detail.

5.1 Introduction

The aim of this section is to further describe active touch sensing in Pinniped*s* by characterising the task-dependency of whisker movements in California sea lions (*Zalophus californianus*) during texture, size and luminance discrimination tasks. California sea lions were selected due to their large whisker movements that are independent of head movements (see ***Chapter Four: Quantifying Whisker Movements in Pinnipeds***), as well as the ease and availability of testing them at Blackpool Zoo.

No previous study has ever described whisker movements on different tasks, nor trained a series of tasks on the same animals. Therefore, all the discrimination tasks and training had to be developed from scratch and the sea lions had no experience of being trained on these behaviours before. This chapter describes the stages of study design and training that were developed specifically for this thesis, over a period of 18 months. ***Chapter Six: Task-Specific Whisker Movements in California Sea Lions*** will go on to describe the findings from these tasks.

5.2 Making the fish model

The research began by making and designing a fish model for the discrimination tasks. The fish model was first made via three-dimensional print technology at Manchester Metropolitan University using the programme Autodesk Fusion360 (Figure 5.1 a). Once designed, the first model was made measuring 18 x 5 x 3 cm (l/w/d). These sizes has to be re-adjusted to make sure they were safe, so the sea lions could not swallow the fish model, as the first model was too similar to the size of the fish the sea lions were fed. The new fish model was made measuring 32 x 14 x 5 cm (l/w/d), 1 cm tail width, 4 cm fin width, 6.5 cm face width, 4.5 cm head depth and 1.8 cm for the tail depth, made out of SmoothOn Simpact™ 85A Rubber which had a smooth flat surface (Figure 5.1 b). The printed fish was used to make a mould, allowing multiple copies to be made and any differences required (texture, size, colour) added to the mould (Figure 5.1 b). The mould created was made out of Polycraft GP-3481F RTV Silicone Rubber by gluing a silicon straw to the fish model and clamping the printed three-dimensional plastic fish model so it hung over a wooden box measuring 38 x 22 x 12 cm (l/w/d). All fish referred to as ***Standard*** were the same size as the original fish model and used in the ***Texture Discrimination Task*** and ***Luminance Discrimination Task,*** the target fish for the ***Size Discrimination Task*** was the same size as the original fish model, but the distractor fish varied in size (see sections ***5.9 Texture Discrimination Task, 5.10 Luminance Discrimination Task*** and ***5.11 Size Discrimination Task*** below for more dimensions).

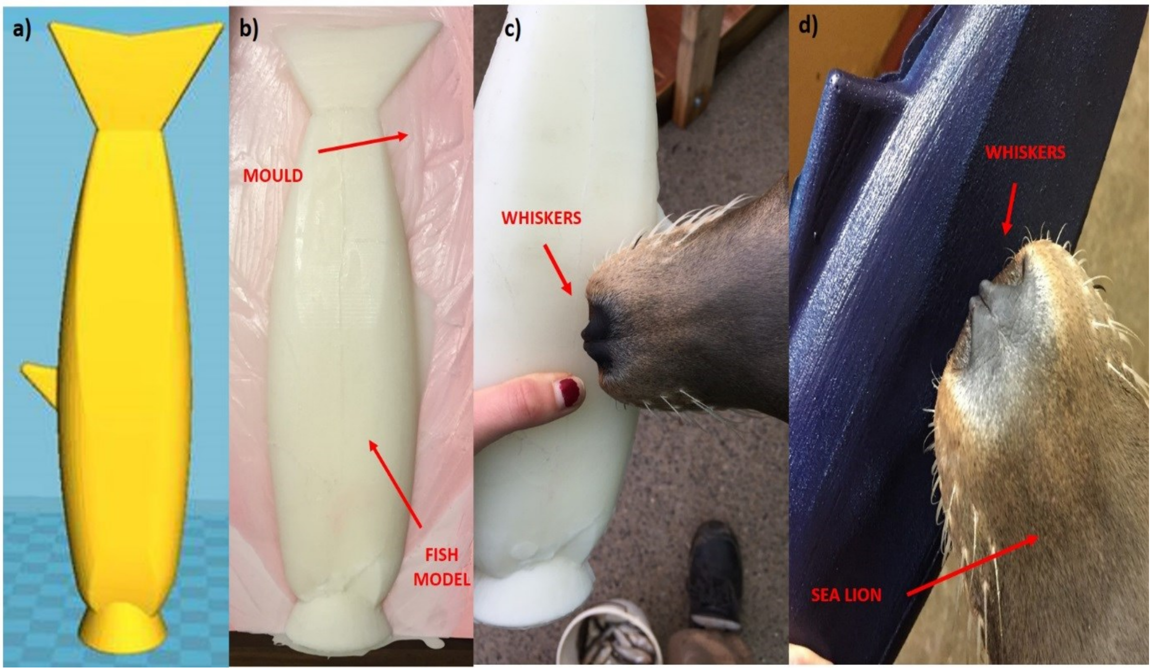


Figure 5.1: Images of the fish prototype, mould and preliminary models: *(a) Digital image of the fish model design (b) First fish model created sitting in the mould, (c) Original colour of fish model matching whisker colour whiskers unable to be detected (d) Coloured fish model against whiskers now visibly clear*

The box was filled with solidified SmoothOn Simpact™ 85A Rubber and left overnight to harden around the fish. This created the mould (Figure 5.1 b). Various textures, sizes and colours were constructed and added to the fish via the same mould. This will be discussed in detail in the relevant sections to follow: ***5.10 Texture Training, 5.11 Size Training*** and ***5.11 Luminance Training***. Fish models will be described as either ***"Distractor"*** fish models, designed to distract or confuse the sea lion and should not be chosen, or ***"Target"*** fish model, which the sea lion should always select and the correct choice. Once all of the fish models were made, each individual fish model was attached using stainless steel screws to a metal 'J' shaped mounting bracket measuring 18.5 cm in length and 6 cm for the hook (Figure 5.2).

In order to be able to see the whiskers against the fish models each had to be painted; because once the silicone had hardened, it was identical in colour to the sea lions whiskers and unable to be detected by eye (Figure 5.1 c). For each task, the fish models were spray-painted accordingly as follows: i) Texture: Navy Blue, ii) Size: Grey and iii) Colour: White, Grey and Black, using Marks Man an animal friendly, environmentally safe and weather resistant spray paint (Figure 5.1 d). Each fish was sprayed with a primer allowed to dry for 48 hours, followed by the chosen paint colour and left to dry for 72 hours before being used. The *target fish* for each task was left white on the top so that the trainers could identify the correct fish model amongst the distractors but was not visible to the sea lion (Figure 5.2 c).

5.3 Building and designing the fish rig

For the discrimination tasks a wooden rig was designed and created called the fish rig, which could be easily moved and used on land or underwater. The rig was built using MDF, consisting of a flat wooden board for the back where the fish models would be attached via the J-hooks (Figure 5.2), and two brackets to enable cameras to be fastened and removed, one on the top and one on the side (Figure 5.2 d). The J-hooks for the fish models rested on the rig but were not fixed so that fish model positions could be switched for various trials (Figure 5.2). Each fish model could be hung onto the fish rig and moved between three various points marked up on the fish rig for each task (Figure 5.2 c). For each discrimination task there were three different fish models used evenly placed across the fish rig and always put in the same position due to identifying markers on the top of the fish rig (Figure 5.2 c). The fish rig also had a metal bar attached to the front to enable extra support for the fish models (Figure 5.2 b). Due to the salt water and presence of cleaning chemicals, the board was checked, tightened and reassessed monthly, as well as before each new discrimination task. Fortunately, nothing was damaged during the research and the rig was the same throughout. One camera bracket was replaced due to a new waterproof camera case.

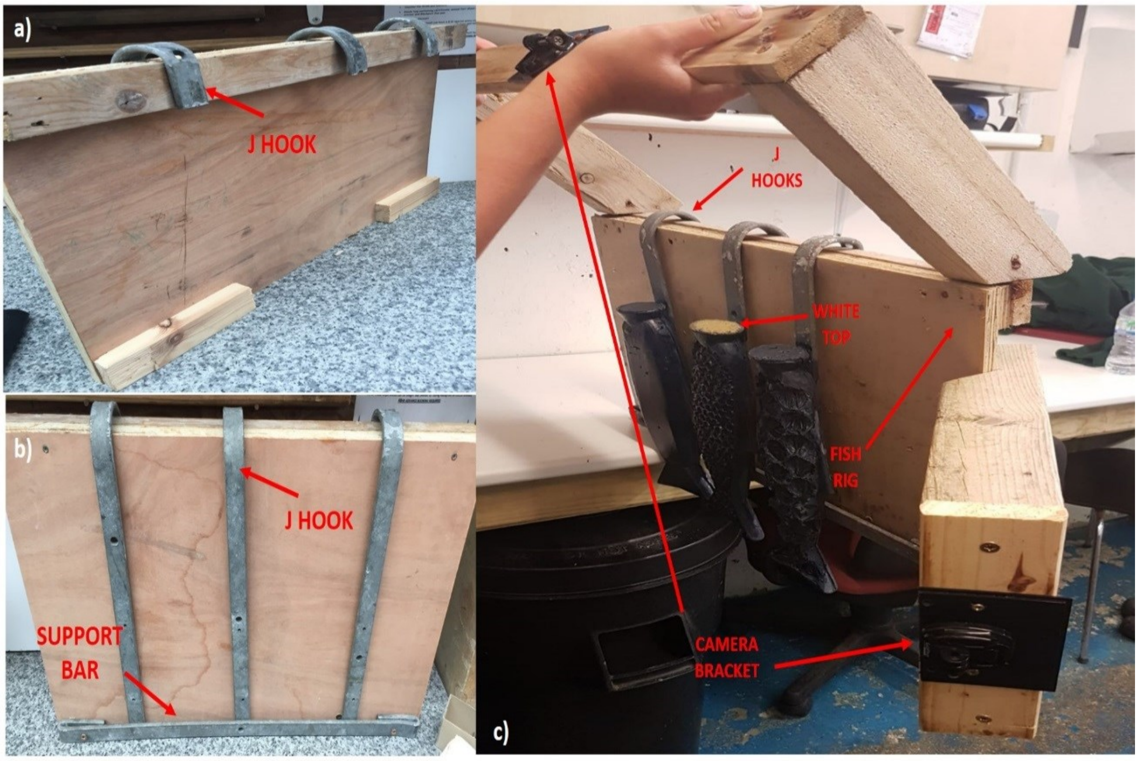


Figure 5.2: Images of the fish rig: *a) Back view of the rig showing fish model hooks; b) Front side of the fish rig showing metal bar where fish model hooks will be slotted into for extra support; c) Fish rig with texture fish models attached to J hooks, camera brackets and target fish with white top for trainer recognition*

5.4 Cameras

To record the training footage and data collection two GoPro HERO4 cameras were used for underwater whisker detection, mounted to top of two wooden brackets attached to the fish rig (Figure 5.2 c). One camera recorded the sea lions whisker movements directly above the fish models in the vertical plane. This was positioned on the top of the fish rig referred to as "***Top***" camera (Figure 5.2 c); while the second was positioned at a 90° angle recording the horizontal plane of the sea lion whiskers approaching (side of the muzzle) referred to as the "***Side***" camera (Figure 5.2 c). This meant that different whisker movements could be viewed, lateral whisker movements in the "***Top***" camera and vertical movements in the as "***Side***" camera. The cameras were attached via a GoPro mount and bracket and could be attached before and removed after each session so footage could be extracted daily. Brackets could be moved forward or backwards, and were positioned and tightened to give the best view during the pilot studies. The GoPro cameras recorded at 30 fps for each of the discrimination tasks. As GoPro cameras have a fish eye effect when recording, the GoPro Studio 2.0 programme (https://gopro-studio.en.softonic.com/) was used to remove this effect prior to video analysis. The whiskers were usually central in the camera view too, so this effect was small.

5.5 Training areas

When training the sea lions for the research two areas within the Active Oceans Arena were used. They were chosen as both were familiar to the sea lions, who had already been trained numerous times in these areas prior to the research and could be utilised at any time in the day. The two areas used were the main display pool where the research took place and the top penning yard where all the basic training began. For each task, one or two trainers would be present, which was always a mixture of the same three people in rotation, keeping it as consistent as possible.

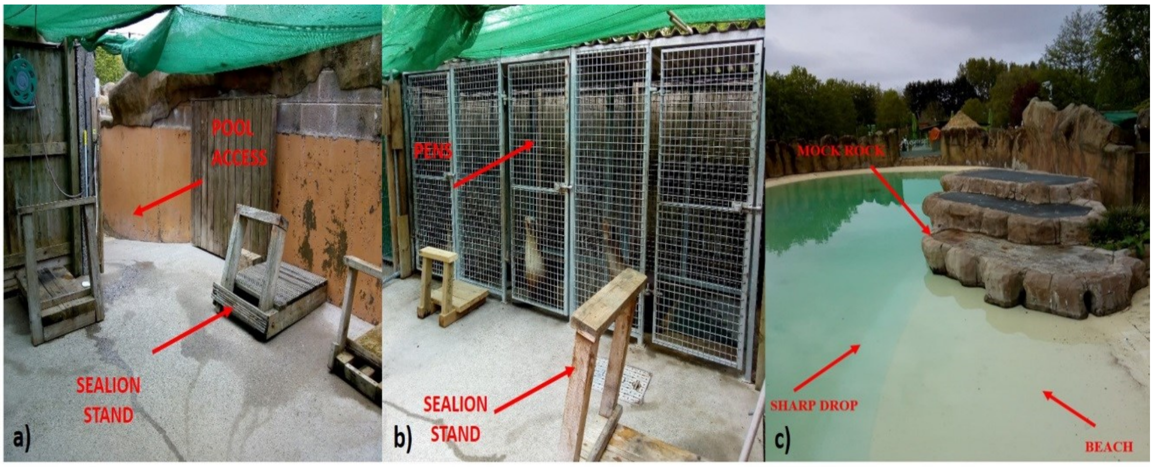


***Figure 5.3: Training Areas: Training Area One** a) Stands of individual sea lions and gate access to the main pool b) Stands and pens where the sea lions would be held prior to training sessions, experiences or displays, **Training Area Two** c) Underwater training and data collection area indicating beach were trainers stood, mock rocks and sharp pool drop where sea lions would complete tasks*

Training Area One was the top penning yard which consisted of a large training space out the back, located in front of three pens where sea lions used for the research were housed prior to training (Figure 5.3 a and b). This area was away from all other sea lions, not visible to the public, easy accessible and could be used while other training, experiences or displays were taking place in the main display area. The area consisted of three sea lion pens and four sea lion stations so multiple sea lions could be worked and trained at one time (Figure 5.3 b). A sea lion station consisted of a wooden stand where the sea lion would sit with its forelimbs on top of a wooden shelf and hind limbs on the bottom of the stand (Figure 5.3 b). Training sea lions in this area occurred on a daily basis along with weekly vet visits and trainer interactions so the sea lions were extremely comfortable there.

Training Area Two was in the main display pool, around the mock rock levels across the back beach (Figure 5.3 c). This area could only be used when all other sea lions were penned up and displays were not happening. This part of the display pool had a gradual slope into the main display pool with a steep drop, ideal for placing the rig underwater and allowing the trainer to stand on the sloped beach (Figure 5.3 c). The sea lion could be in the deeper part of the pool allowing them to swim towards the fish rig, with plenty of space. Again, the sea lions where used to do training, displays and experiences in the main pool so were completely comfortable working here. As the sea lions used all participate in water work with their trainers (trainers working in the water alongside the sea lions), they were used to trainer interactions being done underwater.

5.6 The sea lions

A breeding group of California sea lions from the Active Oceans Arena at Blackpool Zoo were used for the duration of the research. Four adult female sea lions were selected for training. The sea lions were (at the beginning of the study) Gala who was 14 years old, Fillipa mother to Gala at 18 years old, Lo at 15 years old and finally the youngest at only 5 years old was Rubi. Each of these sea lions underwent training outlined below with individual training programmes detailed in section ***5.12 Individual Sea Lion Training Programmes***. All animals were fit, healthy, focused and welfare-assessed in accordance with the Ethics Committees at Blackpool Zoo and Manchester Metropolitan University. All of the sea lions performed each stage voluntarily and could terminate participation at any point. The sea lions that participated in the study were chosen as they were not involved in the daily displays or experiences. Each sea lion received their entire diet through penning, training sessions (including research sessions) and general feeding. Each step within the training was achieved using positive reinforcement with a whistle. This is their usual training method and it could be heard underwater. Sea lions were trained with a variety of different sized pieces and species of fish. The fish used would alter day to day, throughout the year, due to availability, generally being a mixture of Atlantic Mackerel (*Scomber scombrus*), Atlantic Herring (*Clupea harengus*), Capelin (*Mallotus villosus*) and European Sprat (*Sprattus sprattus*). Training occurred at different times and durations depending on their sea lion behaviour, staffing and daily routines. The order of participation of the sea lions was also opportunistic through each of the different training steps, training and research.

5.7 Training processes

Throughout training and data collection of these discrimination tasks, a training log was kept and the number of sessions recorded. Three trainers trained the tasks throughout (Alyx Milne, Gary Jones and Charlie Black) and the training log was used to record any behavioural difficulties, completed training and new training conducted. This ensured the training progressed efficiently and effectively. When two trainers were needed for a task, these positions were rotated daily so the sea lions were not accustomed to a specific trainer and kept the sea lions engaged during sessions.

The training process for the research took various stages of training to complete and will be described in detail below. This training was broken down into a number of different stages including: **(a)** ***Blindfold Training:*** material placement training, material band training, blindfold mask training and blindfold testing; **(b)** ***Texture Training***: texture *target fish* , *target fish* and hand, texture *distractor fish* training, land training, underwater training and texture underwater blindfold training; **(c)** ***Size Training***: size *target fish* , size *distractor fish* training and size underwater blindfold training and **(d)** ***Luminance Training***: luminance *target fish* and luminance *distractor fish* and underwater training. These stages have been added to a flow diagram seen in Figure 5.4 to indicate how training progressed. The blindfold training would run alongside the discrimination task training and come together when the fish models were attached to the fish rig and used underwater.

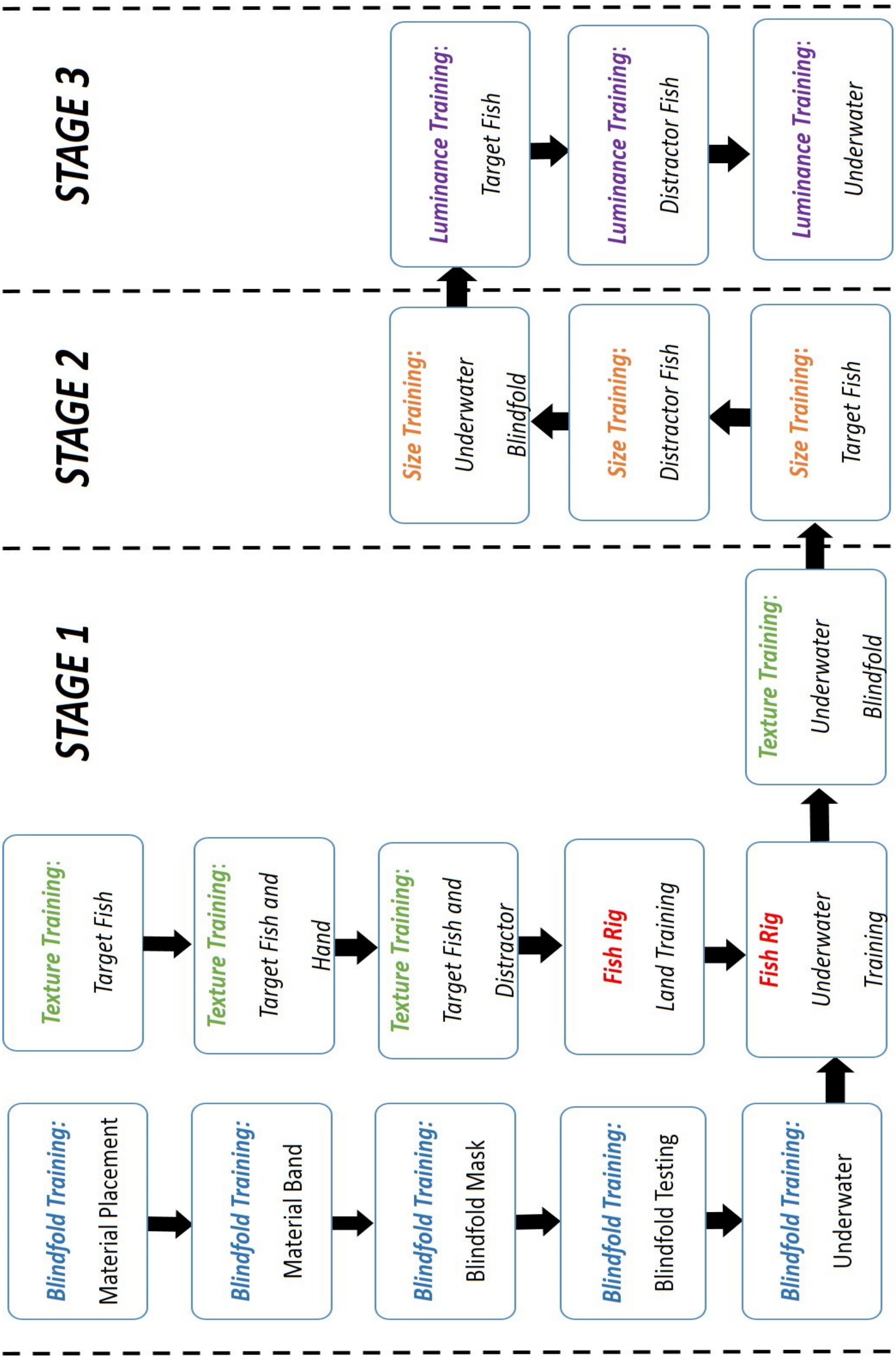


Figure 5.4: Flow diagram indicating the various training stages: *Blindfold Training (indicted in blue), Texture Training (indicted in green), Fish Rig Training (indicted in red), Size Training (indicted in orange) and Luminance Training (indicted in purple).*

5.8 Blindfold training

Blindfold training ran alongside the fish model training with sessions kept entirely separate until both aspects of the training were complete. Training took place in *Training Area One* keeping the sea lions as calm and relaxed a possible, without distractions from other sea lions or the public. Blindfold training was done with all four sea lions. Positive reinforcement was used with jackpot rewards (all of fish weighed out for that session) given when sea lions completed a certain behaviour. If a sea lion gained a jackpot, sessions were ended on this reward with the sea lion being returned to their pen. This is a method used to solidify training and ensure a positive experience from conducting a new required behaviour. Training to introduce the blindfold consisted of several steps, including ***material placement training, material band training, blindfold mask training*** and ***blindfold testing.*** The first blindfold was based on a design developed by the Marine Science Centre, Rostock, Germany (Grant et al. 2013a; Weiskotten 2010a, 2010b; Kruger (personal communication)) and was a latex band. However, the sea lion often could not remove this band themselves and the trainer could not retrieve it, if it was removed in the pool. Therefore, a new blindfold was designed during the training process.

5.8.1 Material Placement Training

Initially, a matt black latex material square measuring 20 x 20 cm was used to desensitise the sea lions to the presence of the material allowing them to look, sniff and investigate using their whiskers. Once sea lions were comfortable with the material being present it was placed on their flippers, neck and head in progressive stages. The piece of material was placed closer and closer to the sea lions' face, achieved by resting the material over the trainer’s arm, who would use the same arm and hand to target the sea lions nose. Using the opposite hand the trainer would pull the material from their arm over the sea lions face for a second, whistling and removing it. The waiting time for how long the material was rested on the sea lions face would increase. The material could then be placed on to the sea lion, left to rest on the face before being peeled back off, and placed back over the trainer’s arm before the whistle was given to the sea lion. That the whistle and fish were given after the blindfold was removed is important, as, with future steps, the blindfold would need to be placed on and off before the animals were rewarded.

5.8.2 Material Band Training

The piece of material was turned into a band, with the sea lion placing their entire face into the piece of material. This meant the band went across the eyes and underneath the chin. The piece of material was big enough to place around the sea lions face leaving a gap under the chin in order for it to rest but not be tight on the sea lions face. Using a larger band meant the Trainer could alter the tightness around the sea lions face, shortening the band underneath the chin using their hands. At each step, the band could be tightened around the sea lion so eventually the band would be secure and the sea lion blindfolded. If at any time the sea lion was uncomfortable they could easily flick the band off with ease and be released, which happened several times when the band was tightened around their face for the first few times. For this stage, the sea lion was not rewarded or whistled if they flicked the band.

To achieve the final behaviour the trainer would place their arm through the band and target the sea lions nose with the same hand. The trainer using their opposite hand would gently pull the band over their arm, hand and onto the sea lions face using the same hand to fix the bands positon so it covered the sea lions eyes. From here, the trainer could alter the tightness of the band under the chin release the material and remove the band back from their face onto their arm before the sea lion got its reward. The trainer would always keep the nose of the sea lion targeting their hand at all times. The amount of time the band was placed onto the sea lion and tightened was lengthened during this process until eventually the trainer could remove the targeting hand and the sea lion would not try to remove the mask.

Progressing forward, each sea lion was measured and fitted with their own individual band made out of black matt latex material. This was due to the band needing to be secure around the sea lion so it did not slip off during the discrimination task. As each sea lion was a different size, shape, weight and age it was required to give them their own band. The bands needed to fit snuggly on the sea lions, which caused some problems (see section ***5.12 Individual Sea Lion Training Programmes***). This caused us to alter the band completely, as eventually the sea lion would be underwater. If the band was too secure and the sea lion swam in the opposite direction, there was no way of retrieving the blindfolded sea lion and could be dangerous for the sea lion.

5.8.3 Blindfold Mask Training

During the development of the blindfold, new features were added making the blindfold safer for both trainer and sea lions. The blindfold was redesigned with a resizable chinstrap, eye mask, quick release and trainer leash (Figure 5.5 a). The measurements for the new design were 22 x 7.5 x 7 cm (l/w/d) with the leash measuring approx. 118 cm. The new design allowed the blindfold to be resized and fitted to all sea lions using heavy-duty stick on velcro (VELCRO product code: 60241) underneath, creating a chinstrap (Figure 5.5). The eye mask its self was made from a scuba diving face piece covered with black matt latex material with a stretched band top to allow it to fit comfortable around the face giving plenty of room around their large eyes. A dog leash was attached to the side of the blindfold allowing trainers to maintain hold of the blindfold at all times (Figure 5.5 b). The leash was placed on the trainers' wrist allowing their hands to remain free for commands, feeding and fitting of the blindfold. The leash clip was attached to a quick release next to the chinstrap (Figure 5.5 c and d). Therefore, if the sea lion got too far away the blindfold would be released under the chin allowing the sea lion to withdraw from the blindfold; but would still be attached via the leash to the trainer (Figure 5.5 c and d). Sometimes several whiskers would be caught underneath the blindfold so the trainer also practiced unhooking any whiskers from the blindfold here too, so all whiskers were free and mobile for the research.

Due to the blindfold being redesigned, trainers took a few steps back to allow the sea lions to be re-accustomed to the new blindfold. This took only one session for the sea lions to allow the new blindfold to be fully fitted and the hand target taken away from their nose. This meant the training could progress by introducing the *target fish* to the sea lion. As the sea lion had stayed still - with the blindfold on and targeting their nose on to the trainer's hand - the sea lion now needed to understand they could move their head in order to 'search' for the *target fish* , required for the discrimination tasks. The trainer would target the sea lion with one hand and use the opposite hand to hold the *target fish* in front of the sea lion. Using the command ***"Find It***", which the sea lion had learnt from previous training (see section ***5.8.4. Texture Land Training***) the sea lion began moving their head in order to find the *target fish.* This was practiced on the sea lions station and then on land with the fish rig, before moving underwater to bring all the training together.

Figure 5.5: Blindfold Training Stages in Sea Lions: *a) Blindfold with clip attachment for leash, b) Blindfolded* sea lion *training on her station, c) Video still showing blindfolded* sea lion *completing the Texture Underwater Training d) Video still of how the quick release removes the blindfold from the* sea lion *after completing the task e) and f) Video still evidence the individuals could not see the fish presented to them while they were blindfolded*

5.8.4 Blindfold Testing: Could the sea lion actually see?

In order to assess whether or not the sea lions could see through the blindfold each sea lion was tested. To do this, the blindfold was placed on the sea lion, while on land. Fish were moved across the sea lions face and past their whiskers (Figure 5.5 e and f). The fish used were whole fish and held still for up to 10 seconds right in front of their face to make sure they could not see (Figure 5.5 e). Sea lions had never been trained to ignore fish in front of them; any fish that was presented to them was theirs to take (Figure 5.5 f). As the sea lions did not try to take the fish at any point or move towards the fish, it was clear that each sea lion could not see through the blindfold and therefore vison was not used during the research.

5.9 Texture training

For the texture discrimination task the fish model material, colour, size and shape were identical, with only the texture of the body being different for each individual fish model (Figure 5.6). Three different fish models were used, each having a different texture: the smooth *distractor fish* (Figure 5.6 a) had a smooth surface, the *target fish* had medium round grooves (0.9 cm diameter), (Figure 5.6 b), and the large *distractor fish* had large round grooves (1.4 cm diameter), termed a large texture (Figure 5.6 c). Each of the fish models for this discrimination task were spray painted in navy blue (Figure 5.6).

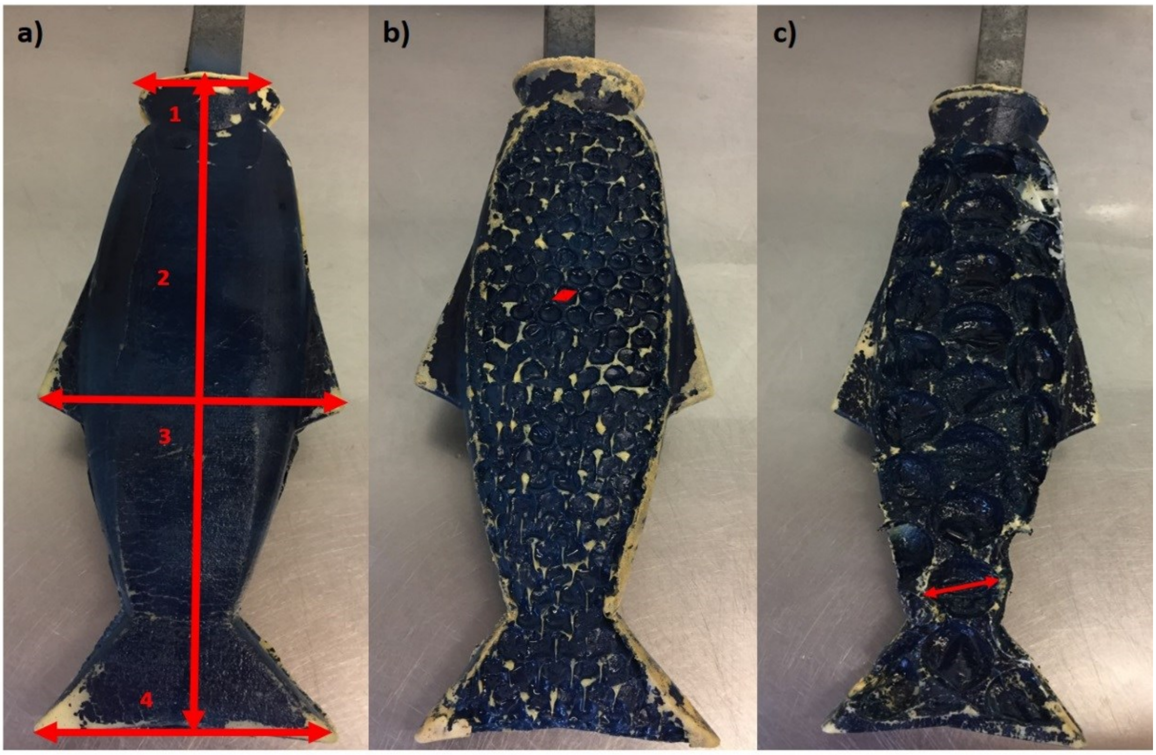


Figure 5.6: Textured Fish Models: *a) Smooth Distractor fish indicting 1) face width (6.5 cm) 2) standard length (32 cm), 3) fin width (14 cm) and 4) tail width (11 cm), b) Target Fish indicating texture size (0.9 cm), c) Large Distractor fish indicating texture size (1.4 cm)*

5.9.1 Texture *Target Fish*

This first part of training was to get the sea lions accustomed to the *target fish;* the fish that the sea lion would need to find and choose in the texture and shape discrimination task. The *target fish* was the textured fish, seen in Figure 5.6 b. *Training Area One* was used with the sea lion being asked to station on their individual stands by trainer 1. Each sea lion was presented with the *target fish* and asked to "*Target*" onto the surface. The sea lion would move forward with whiskers erect, find the *target fish* and place their nose onto the *target fish* relaxing their whiskers once comfortable known as "***Targeting or Target"*** (Figure 5.7 a). Once this had been achieved, trainer 1 would blow the whistle giving the sea lion the signal to release off the *target fish* and receive their reward. The trainer would continue to present and remove the fish, asking the sea lion to complete this behaviour until the sea lion began to hold their nose onto the *target fish* surface (Figure 5.7 a). At this stage, all training was new to the sea lions; therefore, they were given many chances to target on the *target fish*. Once complete, the sea lion would be returned to their pen then back into the main pool.

5.9.2 *Target Fish* and Hand

Once the first stage was complete, training began to determine if the *target fish* was being recognised by the sea lion as their new target, by introducing a *distractor* (the trainers' hand). This was done in *Training Area One* on their station. Trainer 1 would not only present the *target fish* but also a blank, flat hand (Figure 5.7 b). Once presented with both the *target fish* and a flat hand, the sea lions had to select the *target fish* in order to get their reward by *targeting* onto the fish model. To begin with, if the sea lion chose the flat hand trainer 1 would say the words "*Target*" and wiggle the *t target fish* to gain the attention of the sea lion. This was repeated serval times in order to help the sea lion recognize which selection was the correct choice (Figure 5.7 b). For the next step, a "*No*" command was added to help with later training. This meant if the sea lion chose the flat hand then trainer 1 would use the "*No*" command and the sea lion would change their selection. The flat hand and *target fish* were mixed between the left and right hands of trainer 1 so decisions and selections were random (Figure 5.7 b).

5.9.3 Texture *Distractor Fish* Training

The sea lions now understood that in order to gain a reward they must touch and target, staying on the *target fish.* Following on from the flat hand, the first *distractor fish* was added in place of the hand so the trainers now held two different fish models. The first *distractor fish* to be added was the smooth fish, as this would represent a similar texture as a flat hand and should make it easier for the sea lion to discriminate between that and the *target fish*. Both fish models visually looked very similar to the sea lions. Both fish were presented to the sea lion at the same time and the hand they were presented in (left or right) was randomly selected. Once the sea lion was presented with both the *target fish* and the smooth *distractor fish* the sea lions were given the "*Target*" command had to select the *target fish* to get their reward, by *targeting* their nose onto a fish and relaxing their whiskers to make their choice. To begin with, if the sea lion chose the smooth *distractor fish* trainer 1 would say the "*No*" command and allow the sea lion time to alter their decision. This section of training took the longest time. The sea lions were allowed time and several chances to use their whiskers to feel over the fish repeatedly in order to make their selection.

5.9.4 Land Training

When the sea lion choose the *target fish* from the *distractor fish* 100% of the time, the fish models were then added to the fish rig. For this, sea lions would no longer be on their individual stands but now situated on the floor and positioned in front of the fish rig (Figure 5.7 c). The fish rig was fitted out with the entire equipment going to be used for the final research, including the camera brackets and cameras attached in order to desensitise the sea lions to the complete fish rig prior to the research (Figure 5.7 c). Although the sea lions would eventually be blindfolded, this training was all carried out without the blindfold.

This section of training was done in *Training Area One*. When ready, trainer 1 would ask the sea lion to come off their stand and line them up directly in front of the fish rig. The signals given were now changed from "*Target*" to "*Find It*" another phrase the sea lions were familiar with, over a few sessions. The sea lion would be presented with both the smooth *distractor fish* and the *target fish* on the fish rig. Once the command was given, they were expected to find the *target fish* (Figure 5.7 c). Again, the sea lions had to target on their chosen fish before the signal (whistle) was given for them to release and obtain their reward. For the first, few sessions if the sea lion chose the smooth *distractor fish* trainer 1 would use the "*No*" command and follow the incorrect behaviour procedure (see section ***5.13 Incorrect Behaviour Procedures)***.

Initially, the sea lion only had to choose between the smooth *distractor fish* and the *target fish.* When the sea lion became fully competent in selecting the *target fish,* the large textured *distractor fish* was added straight onto the fish rig amongst the other two fish models. Competency was indicated as achieving more than 80% correct choices in three consecutive sessions. This meant the sea lions now had three different textures to choose from located on the fish rig.

5.9.5 Underwater Training

Underwater training was conducted in the main display pool, *Training Area Two*. As the sea lion group were a breeding group of sea lions, all other sea lions were penned during these sessions with the exception of any pups. Pups were untrained as they were at the time still feeding from their mother's milk, and did not cause too many distractions for the sea lions when training (Figure 5.7 d). The fish rig was submerged until both cameras were underwater (Figure 5.7 d). In between each trial, the fish models were swapped when needed and the board re-submerged. This section of training required two trainers: trainer 1 would target the sea lion, give commands, whistle and reward the sea lion; trainer 2 would swap the fish models around and submerge the fish rig. During the training sessions, the sea lions did not usually approach the fish rig head on and often came in from the right side, causing only half the muzzle to be in shot of the camera. The sea lion needed to approach the board head-on in order for the camera to pick up all whiskers from both sides of the muzzle, and for accurate whisker angle tracking. To achieve this, a long two-metre target stick was used to target the sea lion a short distance in front of the board, so the sea lion would approach directly from the front of the fish rig, before searching for the *target fish.* This meant all whiskers were visible on the cameras and trackable. This also enabled sessions to be completed with only one trainer. Once the sea lion had selected their chosen fish model by targeting, trainer 1 would whistle and the sea lion would release and be rewarded. If the sea lions did not detect the fish underwater correctly, they would be given the "*No*" signal and allowed time to move making another choice and follow the incorrect behaviour procedure (see section ***5.13 Incorrect Behaviour Procedures)***.

5.9.6 Texture Underwater Blindfold Training

Adding in the blindfold to the underwater texture discrimination task was the final stage of the training for this task (Figure 5.10 a). The sea lion was taken into *Training Area Two* and blindfolded on the edge of the water. Firstly, this was done several times above the water and then underwater with the guidance of the trainers' hand. This allowed the sea lions to get familiar with being blindfolded in and round the pool, as all blind fold training prior to this point had taken place in *Training Area One*. As the sea lion was now blindfolded, they could not see the long target stick which had been used to allow the sea lion to be positioned in front of the fish rig. To make sure the sea lion was swimming straight towards the fish rig, trainer 2 would place the fish rig into the pool angled towards the sea lion so once released the sea lion would swim forward, directly to the fish rig. Both trainers were required for this training see section ***5.12 Trainer Roles.*** This procedure would be repeated 10 times in each trial, with the number of trials varying for each session, keeping it random for the sea lions see section ***5.13.3 Targeting on the Target Fish.*** Data collection could then take place, once this task was trained, working efficiently and correctly (see ***Chapter Six: Task-Specific Whisker Movements in California Sea Lions***).

Figure 5.7: Sea lion Discrimination Training: *a) Image showing target fish being presented to the* sea lion *and targeted, b)* Sea lion *making a correct decision choosing the target fish instead of trainers hand, c)* Sea lion *choosing target fish against smooth texture distractor fish on the fish rig on land, d)* Sea lion *choosing target fish against both the smooth and large texture distractor fish on the fish rig underwater, with the company of a* sea lion *pup*

5.10 Size training

For the size discrimination tasks the fish model material, colour, texture and shape was identical with only the size (width) of the fish model being different (Figure 5.8). All fish models now had the same texture as the *target fish* from the texture discrimination task (small hemisphere shaped grooves measuring 0.9 cm in diameter). Three different fish models were used each having a different sized fish body: small *distractor fish* being half the size of the target fish (Figure 5.8 c); *target fish* (Figure 5.8 b) and *distractor fish* which was double the width of the *target fish* (Figure 5.8 a). The measurement details for each sized fish model were as follows: Small Size *Distractor fish* : 4 cm anterior width, 6 cm fin width, 4 cm posterior width, all other measurements ***Standard*****,** with small hemisphere shaped grooves measuring 0.9 cm in diameter; Middle Size *Target fish* : ***Standard*** with small hemisphere shaped grooves measuring 0.9 cm in diameter; and Large Size *Distractor fish* : 16 cm anterior width 0 cm fin width 4 cm posterior width 0 cm tail width, 2.5 cm fish body diameter, all other measurements ***Standard*** (Figure 5.8). Each of the fish models for this discrimination task were spray painted in grey (Figure 5.8).

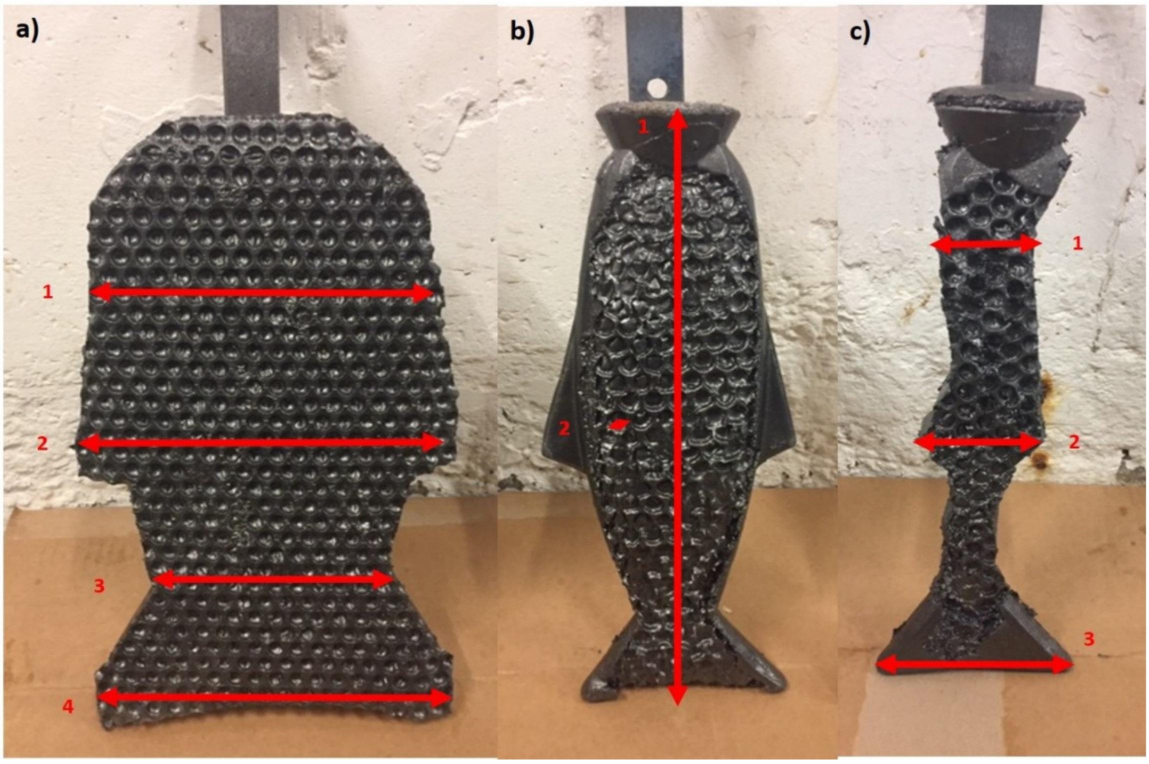


Figure 5.8: Size Fish Models: *a) Big Distractor Fish indicating 1) anterior width (16 cm) 2) fin width (20 cm), 3) posterior width (14 cm), 4) tail width (16 cm), (b) Target Fish indicating 1) standard fish length (32 cm)) texture size (0.9 cm), c) Small Distractor Fish indicating 1) anterior width (4 cm)) fin width (6 cm), 3) posterior width (4 cm)*

5.10.1 Size *Target Fish*

The second task was a size discrimination task. The *target fish* remained the same as that used in the previous texture discrimination task. No extra training was therefore required to identify the *target fish,* as this had already been done previously. As the sea lions were blindfolded it did not make any difference to the sea lion, but colours were chosen to enable whisker visibility for the trainers and cameras. The sea lions would start their training without the blindfold so they could adjust to the new distractor fish. The sea lions had previously been desensitised to the fish rig and all attachments, so the fish rig was directly submerged underwater. As the *target fish* was now painted grey, the first session was done with only the *target fish* on the rig. Trainer 1 would take the sea lion to *Training Area Two* and place the fish rig underwater. On the command "*Find It*", the sea lion would target on to the *target fish,* before the signal (whistle) was given for them to release and obtain their reward. As the *target fish* was the same fish as the previous texture discrimination task, the sea lion never missed the target fish.

5.10.2 Size *Distractor Fish* Training

As the sea lion had previously experienced the training procedures necessary, (see section ***5.11 Target Training),*** the two *distractor fish* were both directly added to the fish rig at the same time. The underwater training also began instantly with all three fish models. Underwater training was done in *Training Area Two*, once all other trained sea lions had been penned with the exception of the pups. The procedure used is the same as in section ***5.9.3. Texture Distractor Fish Training*** and is outlined in detail above.

5.10.3 *Size Underwater Blindfold Training*

Adding the blindfold in underwater was the final stage of training (Figure 5.10 b). This followed the procedures described above in sections ***5.9.6 Texture Underwater Blindfold Training, 5.11 Trainer Roles*** and ***5.13.3 Targeting on the Target Fish.*** Data collection could then take place, (see ***Chapter Six: Task-Specific Whisker Movements in California Sea Lions)***.

5.11 Luminance training

For the luminance discrimination task the fish model material, size, texture and shape were all identical, with only the colour of the fish model being different (Figure 5.9). All fish models (*target fish* and *distractor fish*) now had the same smooth texture described in section ***5.9 Texture Training***. Three different fish models were used, each having a different shade (or luminance), black (Figure 5.9 a), grey (Figure 5.9 b) and white (Figure 5.9 c). The *target fish* was now the grey smooth fish, with the smooth black fish and the smooth white fish being the *distractor fish*. The measurement details for each sized fish model now were all ***standard.***

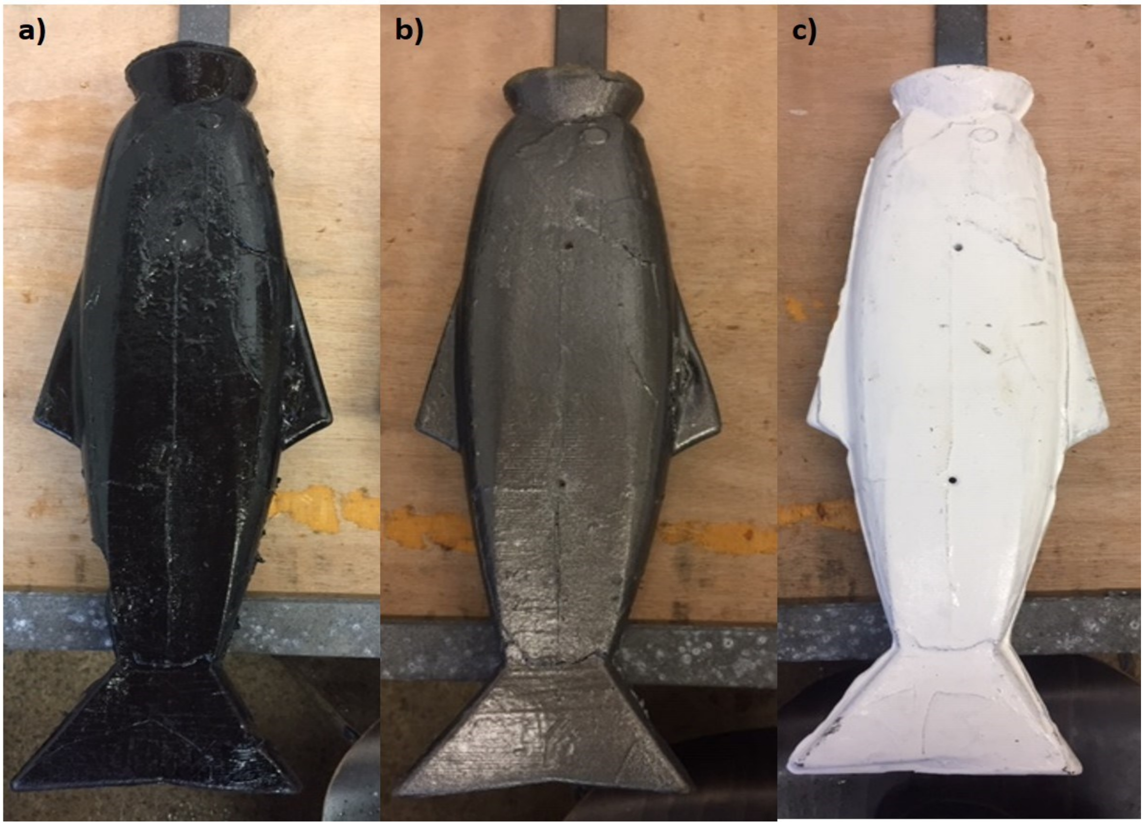


Figure 5.9: Colour Fish Models: *a) Black Distractor Fish, b) Grey Target Fish, c) White Distractor Fish, all of which are the standard fish model size*

5.11.1 Luminance *Target Fish*

The final discrimination task was a visual task, to distinguish between different shades of fish models. As the sea lion had been previously looking for a small grooved textured fish, extra training was required for this discrimination task for the smooth, grey *target fish.* The sea lions would not need to be blindfolded for this discrimination task, as vision was required to determine the correct colour and therefore correct choice. As the sea lions were now desensitised to all aspects of training and apparatus, training for the luminance discrimination task started straight with the fish rig underwater with the *target fish* (see section ***5.10 Size Discrimination Task***). To begin with, only the *target fish* was placed on the rig. Trainer 1 would take the sea lion to *Training Area Two* with the *target fish* already on the fish rig, and place the fish rig on the sloping beach so the sea lion and rig were half submerged. They would use the command "*Find It*" to ask the sea lion to target on the *target fish* following ***Targeting Procedures*** in section ***5.13.3 "Targeting" on the Target fish.*** To begin with, for the first few sessions, the rig was kept half submerged before being fully submerged once the sea lion understood their new *target fish.* Once submerged, the long two-metre target stick was added back into the training, so the sea lions approached the fish rig head on capturing all whiskers. Trainer 1 would use the "*Find It*" command so the sea lion would swim forwards towards the fish rig and selected a fish model. If the sea lion failed to choose the *target fish* the ***New Behaviour Procedure*** would be followed, see section ***5.13.1 New Behaviour Procedure.***

5.11.2 Luminance *Distractor Fish* and Underwater Training

Once the sea lion was selecting the correct *target fish* with no hesitation, the other *distractor fish* were added to the fish rig. To start with, the white *distractor fish* was added. Trainer 1 would take the sea lion to *Training Area Two* submerged the fish rig and using the target stick target the sea lion. Giving the command "*Find It*" the sea lion would be asked to find a fish model, hold target on the fish before the signal (whistle) was given to release, and obtain their reward. If the sea lion chose the white *distractor fish* trainer 1 would follow the ***Incorrect Behaviour Procedure,*** see section ***5.13 Incorrect Behaviour Procedure***. Once the sea lion had selected the *target fish* 80% correct choices in three consecutive sessions, the black *distractor fish* was added to the fish rig (black fish). The training began again allowing the "*No*" command to be used if either *distractor fish* was selected and ***Incorrect Behaviour Procedure*** followed see section ***5.13 Incorrect Behaviour Procedure***. To finalise the training both *distractor fish* were added onto the fish rig together with the *target fish* (Figure 5.10 c). Once complete the data collection could then take place following the procedures in sections ***5.13 Trainer Roles: Final Training Stages and Data Collection Procedure*** (see ***Chapter Six: Task-Specific Whisker Movements in California Sea Lions***).

5.12 Trainer Roles: Final training stages and data collection

Both trainers were required for the final stages of training and the data collection stage. Each time a new session began the following procedure was followed which outlines the roles for both trainer 1 and trainer 2. Trainer 1 would always be in control of the sea lion, put on the blindfold, give commands, whistle and reward the sea lion. Trainer 2 would record the footage, swap the fish models around and submerge the fish rig underwater in between trials.

Specifically, trainer 1 would collect the sea lion from their pen in *Training Area One* and bring them poolside to *Training Area Two* (Figure 5.3). This would be after all the sea lions had been penned up and removed from *Training Area Two*. Standing on the edge of the sloping beach before the drop (Figure 5.3 c), trainer 1 would target the sea lion and put on the blindfold, unhooking any whiskers caught underneath. Using the verbal command "*Find It*", they would direct the sea lion towards the fish rig and await the sea lion's decision. Once made, trainer 1 would whistle if the sea lion's choice were correct, while the sea lion released itself from the blindfold underwater and surfaced for their reward. If the sea lion did not make the right the decision trainer 1 would give the "*No*" command up to three times (see section ***5.8.2 Incorrect Complete Behaviours)*** before pulling tight on the blindfold to release the sea lion, giving the indication to surface and restart. Trainer 2 would switch the fish models once the blindfold was fitted so the sea lion could not see beforehand where the fish models were placed, and making sure both cameras were submerged, place the fish rig underwater before trainer 1 released the sea lion. Trainer 2 would hold the rig in place until the sea lion had resurfaced after the whistle from trainer 1. If the sea lion has three consecutive "*No*" commands by trainer 1, trainer 2 would remove the fish rig at the same time as trainer 1 was removing the blindfold to restart the trial. Between each trial trainer 2 would swap, the fish models following a pseudorandom table (Gellermann 1933) and re-submerge the board. This would be repeated around 10 times per trial, with the number of trials per session varying daily depending on pool availability, training sessions and subject cooperation. The duration and number of trials were varied and random, so the sea lion could not predict the end of session (*variable duration reinforcemen*t), which the trainers found to increase attention and maintain performance in multiple consecutive trails in the sea lions (Milne and Grant 2014). Once finished, trainer 1 would pen the sea lion while trainer 2 removed the fish rig.

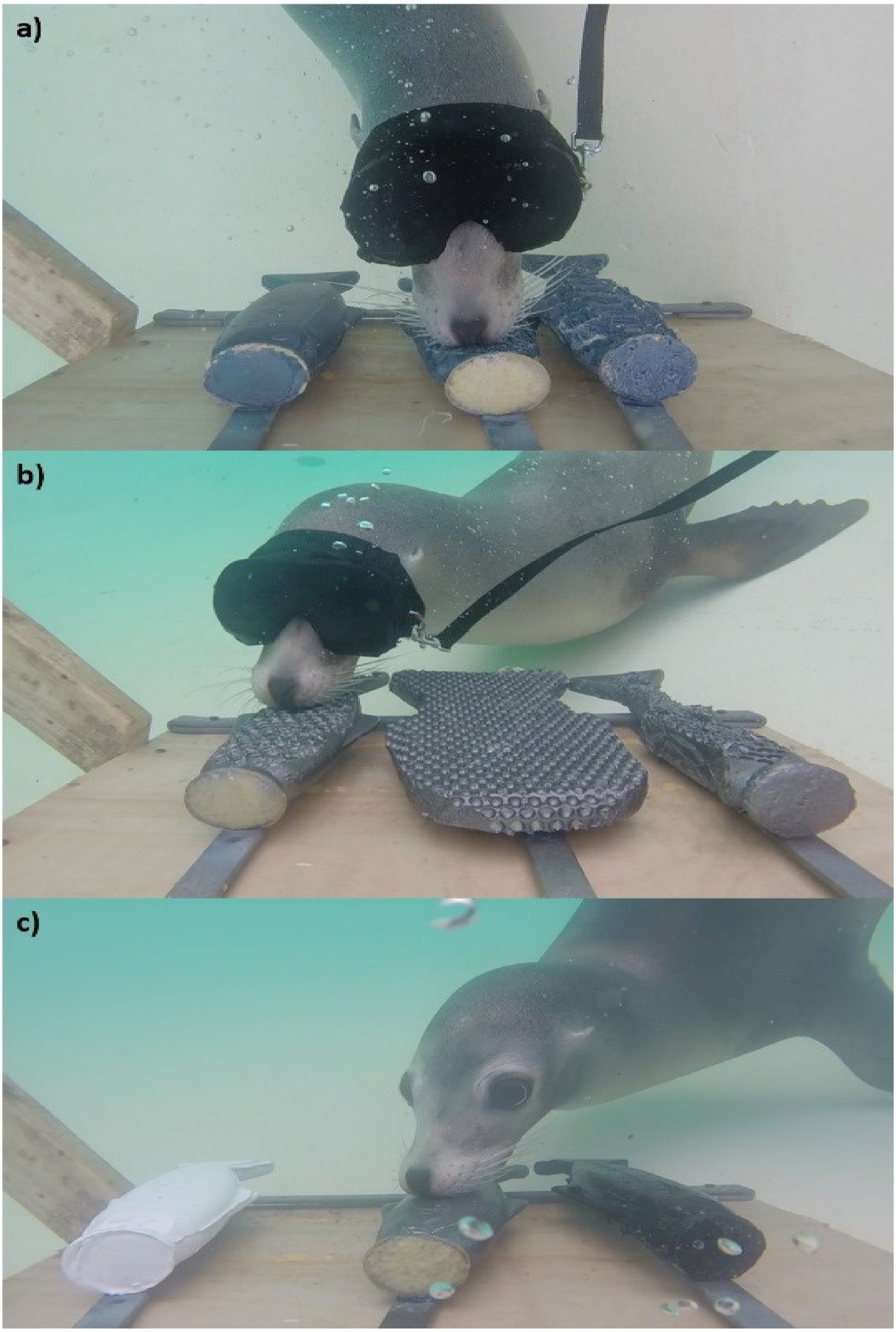


Figure 5.10: Video stills of **sea lion** ***choosing correct target fish for each discrimination task underwater:*** *a)* Sea lion *choosing the correct target fish amongst distractor fish while blindfolded for the texture discrimination task, b)* Sea lion *choosing the correct target fish amongst distractor fish while blindfolded for the size discrimination task, c)* Sea lion *choosing the correct target fish amongst distractor fish for the colour discrimination task*

5.13 Incorrect behaviour procedures

5.13.1 Training New Behaviours

Training new behaviours means that there will be times the sea lions will make a wrong decision until they understand the correct behaviour. During this time, allowances are made to help the sea lions establish the correct behaviour. However once the sea lions begin to learn the behaviour required boundaries were set in order to allow the sea lions to distinguish from the wrong behaviour. When training the sea lions, two phrases were used: the "*Target*" and "*Find It*" command, which were consistent throughout the three discrimination tasks and training stages. Once the sea lions began to learn, the behaviour these phrases were used a maximum of three times. If the sea lion did not find the correct *target fish* after three consecutive times then the trial would be reset. If, after being reset, the sea lion continued to get the trial wrong over three consecutive times, the session would be stopped and the animal asked to do some different behaviours (any from their display behaviour repertoire not related to the research), before returning to their pen so each session ended on a positive note for the sea lions. Over time, the "*No*" command was also used by the trainers. Sea lions understood the "*No*" command from previous training sessions. As the sea lions were learning behaviours the "*No*" command was simply there to help aid the sea lion learn the new behaviour and make the correct choice. Once the sea lion understood the training, the "*No*" signal was dropped, allowing the sea lion to work out the correct behaviour themselves to acquire the reward.

5.13.2 Complete Behaviours

Once behaviours were complete and the sea lions were getting correct choices over 80% of the time, the "*No*" command could be used again indefinitely. During the final stages of training if the trainers had to use the "*No*" command three consecutive times, then the trial would be reset. To do this, the sea lion would be given instructions to perform several other behaviours from their display routine in any order to try to regain their attention. If after being reset the sea lion continued to get the trial wrong three consecutive times, the session would be stopped and the animal asked to do some stationary behaviours before returning to their pen. Again, the training session was always finished on a positive note for the sea lions and not a "*No*" signal. During the pilot study and data collection period if the sea lions selected a *distractor fish* instead of the *target fish* they were allowed up to three seconds to change their decision to the *target fish.* If they did not change, trainer 1 would give the "*No*" command while pulling tight on the blindfold to release the sea lion, while trainer 2 removed the fish rig. That same trial would then be reset and if the sea lion chose incorrectly in three trials, the session was terminated as above.

5.13.3 *"Targeting"* on the *Target Fish*

For a sea lion to indicate their decision, they had to target their nose on the *target fish* (correct choice). When the sea lion selected the *target fish* (*targeting)* this was the indication to the trainer that the sea lion had made their choice. The sea lion had to hold target for several seconds (between 3-10 seconds) by relaxing their whiskers against their muzzle. This meant the sea lions would not predict the timing of the whistle (the signal to release due to a correct behaviour) and subsequently the reward. This made the sea lion always wait for the command to release from the *target fish.* This method is called *variable duration reinforcemen*t, which maintains the sea lions attention and eliminates potential premature or rushed stimulus-choice (Milne and Grant 2014).

5.14 Individual sea lion training programmes

5.14.1 Training Alterations

For the duration of the discrimination tasks, the trainers recorded sea lion training progress. During the training, it became clear that not all individuals would be suitable for the research. Rather early on, it was noted that Fillipa had a bias for her right hand side. This was observed in the training footage collected during the "***Distractor Texture Training***" with Fillipa choosing the fish model on the right hand of the trainer 88% of the time, regardless of the texture. Therefore, unfortunately due to Fillipa not hitting the levels required, she was dropped from the remaining training sessions, leaving us with three individuals. The blindfold caused problems for the youngest sea lion Rubi, especially when changing from the material to the band. The individual bands had to be tight and for whatever reason, towards the end of training, Rubi did not seem to like the band being secured onto her face. Each time the trainers hand was taken away from her nose she would try to flick off the blindfold from around her face. As a result, the decision was made to remove Rubi from further training, leaving us with two individuals.

Gala and Lo both completed all parts of the training, and both began data collection for the texture discrimination task. At the beginning of data collection both sea lions, Lo and Gala, gave birth to two healthy pups, so were given time to readjust and be a mother until they were ready to come back to training. Both sea lions were first time mums. Lo returned to penning and training within a month. However, Gala became aggressive and over-protective of her new pup, so her part in the research was halted until further notice. Lo completed most (90%) of the texture discrimination trials.

Towards the end of the year, it was decided that some of the sea lions would be moved for breeding purposes, this included both Fillipa and Gala. This meant that even though Gala was fully trained for the remainder of the research, unfortunately she could no longer be used due to her move to another zoological park. With this move in mind, Rubi was taken back on board with the new blindfold to see if after having time away from the training improved her performance on the task. Rubi was trained with the new blindfold following the stages outlined above, and began finding the texture fish models on the fish rig, when blindfolded. However, Rubi and Lo both pupped the following year, with Rubi being a young sea lion and a first time mum. Due to the issues previously seen with Gala the year before, Rubi was removed from the rest of the study. As Lo was now the only sea lion to do both the texture and size discrimination tasks, for consistency, she was the only sea lion used for the final colour discrimination. Using just one animal to complete all discrimination tasks has been done across many previous studies (Dehnhardt and Dücker 1996; Schulte-Pelkum et al. 2007; Wieskotten et al. 2010a, 2010b, 2011; Gläser et al. 2011, Hanke et al. 2010, 2011; Grant et al. 2013a).

5.14.2 <u>The Training of Lo</u>

Lo, the 15-year-old female sea lion completed all the training and tasks over the course of the research. During each training stage, the task was always to select the *target fish* from two *distractor fish*. Figure 5.11 shows the learning curves of Lo being trained to complete each of the tasks. The learning criterion was 80 % correct choices in three consecutive sessions; this had to be achieved before moving on to the next training stage. Pre-training occurred on land and underwater including a number of steps, such as: ***texture target fish recognition, target fish*** **and hand*****,*** **texture *distractor fish* training*,***

land training, underwater training, texture underwater blindfold training, size *target fish* , size *distractor fish* training, size underwater blindfold training, luminance *target fish* , luminance *distractor fish* and **underwater training.** The data presented here shows each of the training stages for the discrimination tasks: texture (Figure 5.11 a), size (Figure 5.11 b) and luminance (Figure 5.11 c).

Looking at Figure 5.11, we can see that throughout the different stages Lo takes different amounts of time to correctly pass each different training stage. Starting with the texture training (Figure 5.11 a), Lo was presented with the *target fish* for the first time, and this was also the first time she had ever been trained a discrimination task. Therefore, this task had noticeably more steps than the other two discrimination tasks. Once Lo was desensitized to the *target fish* (Figure 5.11 a) she took a while to understand that her role was to target onto the *target fish* in order to make her selection (Figure 5.11 a 1 and 2). Once established the addition of the blindfold caused the most problems and this is where most of the training time was spent with around 40 sessions taken to finally reach the criteria needed (80%) in order for Lo to be deemed successful (Figure 5.11 a 6).

During the size discrimination task, adding in the distractors (Figure 5.11 b 4) and the blindfold (Figure 5.11 b 6) took the most time for Lo to hit the 80% success level. When adding in the size distractor fish Lo dropped in her number of correct choices, but quickly adapted, and after approximately 20 sessions hit the 80% criteria. The blindfold training underwater again took the longest amount of time for the size discrimination task; in fact, it needed double the amount of training sessions than in the texture task, to make sure the training was solidified before data collection began (Figure 5.11 b 6).

Finally, for the luminance discrimination task the early stages were re-visited due to the absence of the blindfold for this task (Figure 5.11 c). Lo took an extremely long time when it came to distinguishing the grey *target fish* from the two distractor fish (black and white). This may have been due to the texture of the fish also being smooth as for the previous two task the *target fish* texture had been textured (0.9 small grooves). Lo dropped her correct choices down to 20% for this task, the lowest across all three of the discrimination tasks. It took Lo approximately 120 sessions before she was able to move on to the final part of the training for the luminance task (Figure 5.11 c 4). Once Lo had mastered the behaviour required for the luminance discrimination task, she was most successful for the *fish rig* training under water for this discrimination task, compared to the same stage in the other two discrimination tasks (Figure 5.11 c 5).

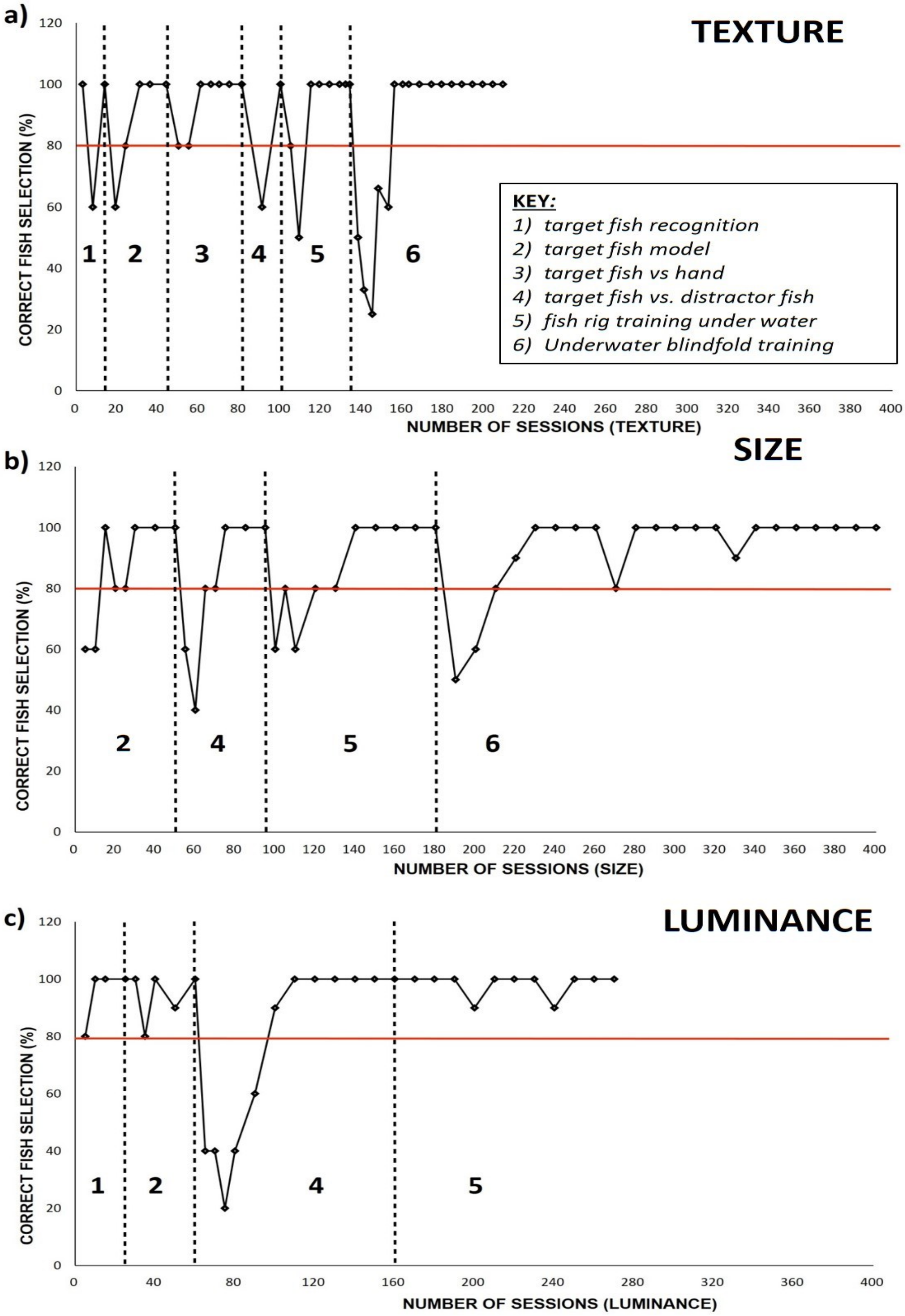


Figure 5.11: Learning during the experiment with learning criterion set as >80 % correct, for three consecutive sessions: *a) The pre training learning curve (percentage correct) of Lo during the texture discrimination task b) The pre training learning curve (percentage correct) of Lo during the size discrimination task, c) The pre training learning curve (percentage correct) of Lo during the illuminance discrimination task. The learning data presented here is in size stages:* 1*) target fish recognition;* 2) *target fish;* 3) target fish vs. hand; 4) *target fish* vs. *distractor fish* training rig 5) fish rig *training under water; 6) underwater blindfold training (pre testing)*

5.15 Conclusions

This chapter has outlined all the training procedures that took place to enable the data collection in ***Chapter Six: Task-Specific Whisker Movements in California Sea Lions***. The training began using a *target fish,* which was adapted and changed for three different discrimination tasks. These discrimination tasks were texture, size and luminance. Training took place for each discrimination task prior to data collection. Once training was underway, sea lions needed an 80% success rate on three consecutive session in order to move onto to the next stage. Behavioural issues and training problems made it difficult for all sea lions selected for the tasks to be used in the final data collection. Lo, a female sea lion was finally picked as the best candidate, to examine whether sea lions make task-specific movements with their whiskers in a texture, size and luminance discrimination task.

6 Chapter Six: Task-Specific Whisker Movements in California Sea Lions

Chapter Summary

This experimental chapter explores whether California sea lions (*Zalophus californianus*) make task-specific movements with their whiskers during a texture, size and luminance discrimination task. In each discrimination task, a California sea lion was trained to find a *target fish* amongst various *distractor fish.* Results suggest that sea lions make task-specific movements. In particular, they move their whiskers and head around the fish models over a greater area during a size discrimination task, and they spread their whiskers out and focussed on the centre of the fish model, during the texture discrimination task. Whiskers moved less over the fish models and over a reduced area during a visual luminance task, compared to both the texture and size task. The findings that whiskers move purposively, making task-specific movements, suggest that California sea lions use their whiskers for active touch sensing. These task-specific whisker movement strategies are likely used to extract the most relevant information from an object, in order to efficiently complete the task.

6.1 Introduction

While whiskers have been found to move in Pinnipeds (Kastelein and Van Gaalen 1988; Dehnhardt 1994; Dehnhardt and Kaminski 1995; Dehnhardt et al. 2001; Miersch et al. 2011; Milne and Grant 2014 and see ***Chapter Four: Quantifying Whisker Movements in Pinnipeds***), there has been no evidence to say whether whiskers are used to make task-specific movements in Pinnipeds, or indeed, in any animal. During active touch sensing tasks in humans, fingertips both move and make purposive, task-specific movements. For whiskers to be wholly recognized as an active touch system, they also need to both move and make task-specific movements.

Findings from ***Chapter Three: Pinniped Whisker and Skull Morphology*** reported that California sea lions had longer, thicker whiskers and larger IOF areas (of 57.9 mm^2); compared to most other Pinnipeds (see Table 3.1 and Figure 3.3). Therefore, each whisker is likely to be very sensitive, as the size of their ION is likely to be large. Results presented in ***Chapter Four: Quantifying Whisker Movements in Pinnipeds*** demonstrate California sea lion move their whiskers more than Harbor seal (*Phoca vitulina)* and Pacific walrus (*Odobenidae rosmarus divergens)*, and was the only species that decoupled their whisker and head movements. The whiskers of California sea lions have also previously been shown to be quick and reliable at haptic discrimination behaviours between different sizes and shapes, using small-scale head movements while the vibrissae are in contact with an object (Miersch et al. 2011). As well as head movements, whisker movements are important during sensorimotor tasks. Milne and Grant (2014) demonstrated that California sea lions moved their whiskers to track the movement of a ball during a ball-balancing task, and that whiskers quickly and accurately followed the ball movements, more so than movements of the head. California sea lions are, therefore, the chosen species to further explore active touch sensing in this chapter. Particularly, the aim of this chapter is to examine whether California sea lions can make task-specific movements with their whiskers during a texture, size and visual luminance discrimination task.

6.2 Methods

This section provides a brief summary about the methodology used for each of the three discrimination tasks. Further information on training, set up and experimental procedures can be found in detail in ***Chapter Five: Sea Lion Training Programme*.**

6.2.1 Animals

Lo, a female California sea lion was used throughout this study, and was 15 years old at the beginning of the study (Figure 6.1). Lo was chosen after successfully completing all aspects of the training programme outlined in sections ***5.6 The Sea Lions*** and ***5.14 Individual Sea Lion Programmes*** and achieving a success rate of over 80**%** when attempting to select the *target fish* across each of the discrimination tasks (see section ***5.14.2 The Training of Lo)***. Lo was selected prior to the research, as she was not involved in any of the other daily displays or experiences at the zoo. During the research period, Lo received all parts of her diet through penning, training, research data collection and general feeding sessions. Lo was also checked daily via routine health checks by her trainers, and quarterly throughout the year by a vet unless any issues arose. Lo also possessed long thick whiskers, of which none appeared blunt at the ends due to damage via rock rubbing (Figure 6.1). The distribution of her vibrissae was also identical on both sides of the face and her mystacial pad was arranged in six rows with a total of 38 vibrissae, (Row 1: five vibrissae, Row 2: seven vibrissae, Row 3: seven vibrissae, Row 4: seven vibrissae, Row 5: eight vibrissae and Row 6: four vibrissae). Even though 38 whiskers is marginally higher than the 32 whiskers noted in Figure 3.1 for California sea lions, it matches the total number of whiskers for several California sea lions used in previous studies (Dehnhardt 1994; Sawyer 2016).

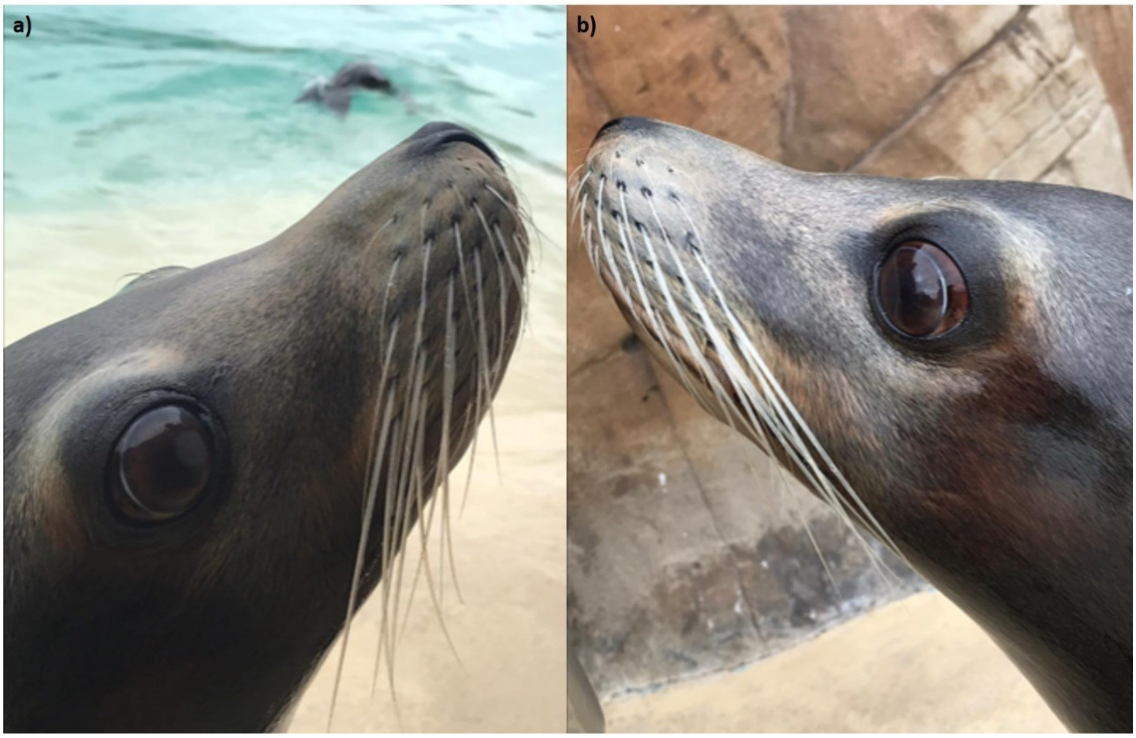


Figure 6 1: Profiles of Lo the experimental California sea lion (Zalophus californianus): *a) Right profile of Lo, b) Left profile of Lo*

6.2.2 Apparatus

For the discrimination tasks, a fish rig was designed and created to attach the fish models (Figure 6.2). Two brackets were attached to enable cameras to be fastened and removed, one on the top and one on the side, to give top-down and side-on filming (Figure 6.3). Two GoPro HERO4 cameras were used for underwater filming at 30 f/s (see section ***5.4 Cameras****)*; inspection of the high-resolution video showed that this was sufficient for filming the whiskers underwater, without any blurring to the whiskers (i.e. see Figures 6.2, 6.4 and 6.9). As GoPro cameras have a fish eye effect when recording, the GoPro Studio 2.0 programme (https://gopro-studio.en.softonic.com/) was used to remove this effect prior to video analysis. The whiskers were usually central in the camera view too, so this effect was small.

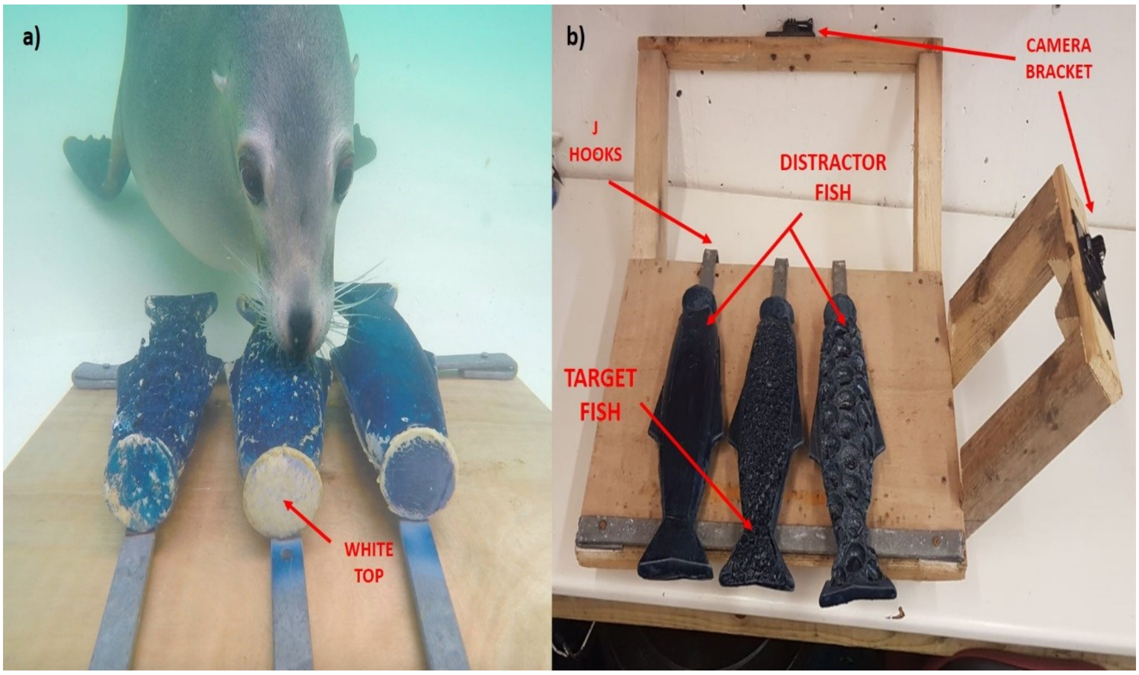


Figure 6.2: The fish rig: *a) Lo training on the fish rig with target fish white top recognition for trainer; b) Fish rig with texture fish models attached to J hooks, camera brackets and fish models*

Fish models were attached to hooks that rested on the rig but were not fixed, so they could be placed and rotated on to a fish rig, following a pseudo-random table (Gellermann 1933) between three different positions on the rig (Figure 6.2). For each of the three discrimination tasks fish models were made using SmoothOn Simpact™ 85A Rubber (Figure 6.2). Each of the discrimination tasks had various *target fish* and *distractor fish*. The *target fish* was the standard fish model and was always sized measuring 32 x 14 x 5 cm (l/w/d), with widths of 11 cm at the tail , 14 cm at the fin, and 6.5 cm at the head, as were all the other fish models, apart from those in the size discrimination task. For the texture discrimination task, the fish models were smooth, medium textured (diameter texture of 0.9 cm) and large textured (diameter texture of 1.4 cm), with the *target fish* being the medium textured fish (Figure 6.3 a, b and c). For the size discrimination task, the fish models were small-sized (with widths of 4 cm head, 6 cm fin, and 4 cm tail), medium-sized (standard fish model sizes) and large-sized (with widths of 16 cm head, 20 cm fin, and 20 cm tail), with the *target fish* being the medium-sized fish (Figure 6.3 d, e and f). For the luminance discrimination task, the fish models were white, grey and black, with the *target fish* being the grey fish model (Figure 6.3 g, h and i), (see section ***5.9 Texture Training, 5.10 Size Training*** and ***5.11 Luminance Training***).

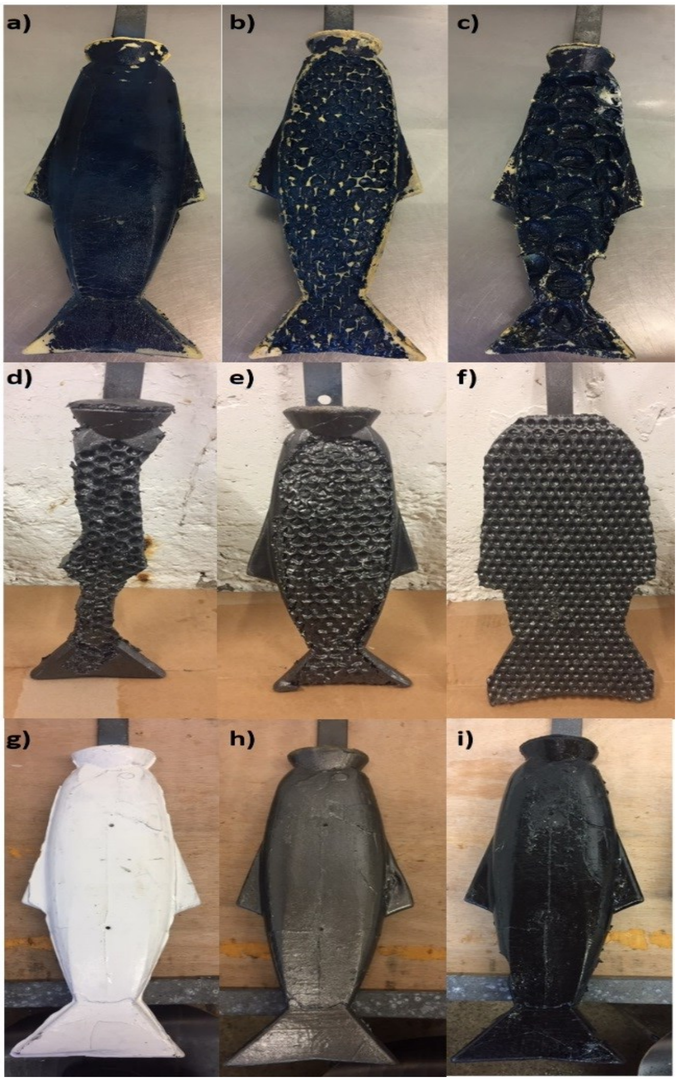


Figure 6.3: Fish models used for the three discrimination tasks: *for the Texture Discrimination Task all fish were painted navy blue with the material, size, luminance and shape being identical, only the texture being different a) Smooth distractor fish , b) Target fish (texture of small hemisphere grooves measuring 0.9 cm) c) Large distractor fish (texture of large hemisphere grooves measuring 1.4 cm); for the Size Discrimination Task all fish were painted grey with the material, texture, and luminance being identical, all three with a texture consisting of small hemisphere shaped grooves measuring 0.9 cm, with only the size being different d) Small distractor fish , e) Target fish and f) Large distractor fish ; and finally for the Luminance Discrimination Tasks all fish were the same size, shape, texture (smooth) and material with only the luminance being different g) White distractor fish , h) Grey target fish and i) Black distractor fish*

6.2.3 Experimental Procedures

All procedures took place at Blackpool Zoo's Active Oceans Arena. Experiments were carried out in the main show pool, called *Training Area Two* (see ***5.5 Training Areas****)*. Sessions occurred at 8:30, 11:30, 14:30, 16:30 or 17:30, depending on daily display times, pre-booked experiences or staffing. Pilot studies of each of the full discrimination tasks took place over three days prior to data collection to make sure the sea lion was fully desensitised to the experimental procedure, the apparatus and to check the positioning of the camera for whisker detection. For each of the three tasks, sampling took place over the following time frame: for the *Texture Discrimination Task* three months throughout May, June and July 2017; for the *Size Discrimination Task* three months during November, December and January 2017-2018; and finally for the *Luminance Discrimination Task* sampling took place over two months in February and March 2019. Sampling included the pilot study without data collection. During the task, the same trainers were present on each occasion. The sea lion was taken poolside to *Training Area Two* alone (see ***5.5 Training Areas****)*. The sea lion was blindfolded for both the *Texture* and *Size* discrimination task, but not for the *Luminance* discrimination task. For each task, the sea lion had to find the *target fish* from two *distractor fish*. During a session, each sea lion received approximately 20% of their daily food amount. This was freshly thawed cut Atlantic Mackerel (*Scomber scombrus*), Atlantic Herring (*Clupea harengus*), or whole Capelin (*Mallotus villosus*) and European Sprat (*Sprattus sprattus*). Each task involved the sea lion exploring the three fish models with their whiskers to find the *target fish*. Fish model positions were changed after each trial, and the position was determined using a pseudorandom table (Gellermann 1933). The sea lion could undertake up to 100 trials per day. This depended on sea lion co-operation, display times and staff. Once the session was complete, the sea lion was returned to its pen, or to the rest of the group in the main pool. A total of 30 days of footage was collected for the texture and size tasks and 20 days of footage for the visual discrimination task (luminance). This gave 7200 trials (2700 for texture, 2700 for size and 1800 luminance trials). The sea lion was trained using positive reinforcement and if the sea lion performed an incorrect behaviour, the procedure outlined in section ***5.13 Incorrect Behaviour Procedures*** would be followed.

6.2.4 Data Selection and Video Analysis

All video clips were examined to see if they met the following criteria: (i) all whiskers on both sides were visible for the *Top Camera,* and all whiskers on one side were visible for the *Side Camera,* from approach to contact with the fish models, (ii) the head was lined up with the camera, with no extreme rolling or pitch, (iii) the sea lion did not pre-emptively choose the target before the rig was placed in the water, (iv) the sea lion gave the correct answer. In total, after viewing all the video footage, the flowing clips outlined in Table 6.1 met the above criteria and were selected for each of the discrimination tasks.

Table 6.1: Number of clips selected for analysis for each of the three discrimination tasks: *Texture, Size and Luminance*

DISCRIMINATION TASKS	FISH MODEL	FISH MODEL CODE	TOP CAMERA	SIDE CAMERA
TEXTURE CLIPS	Smooth	T1	59	48
	Target	T2	84	66
	Large	T3	60	55
	Total Clips	-	203	169
SIZE CLIPS	Small	S1	56	42
	Target	S2	72	55
	Large	S3	65	46
	Total Clips	-	193	143
LUMINANCE CLIPS	White	C1	2	3
	Target	C2	66	58
	Black	C3	7	6
	Total Clips	-	75	67

Each video was then tracked manually using the open source 'Manual Whisker Annotator' (Hewitt et al. 2016). Tracking started from the frame the sea lion whiskers came into contact with any fish model and ended on the frame prior to the sea lion either turning its head away and releasing their whiskers off the fish model to search for another, or the frame before the sea lion began to relax their whiskers once they had made a decision, which was the first frame that the whiskers begin to move backwards, identified by eye by a trained observer.

For the *Top Camera* view two whiskers on each side of the face were tracked along with the mid-point of the head (between the eyes identified by a dip on the blindfold), and the tip of the nose. The whiskers selected for tracking were the second from the front and second from the back on each side of the muzzle (Figure 6.4). Two points were tracked on each whisker: the base of the whisker and a point around two-thirds along the whisker shaft. This made ten tracked points in total. For the *Side Camera* view two whiskers on the right side of the face were tracked along with the mid-point of the head (between the eyes identified by a dip on the blindfold), and the tip of the nose. The whiskers selected for tracking were the second from the top and second from the bottom (Figure 6.4). Two points were also tracked on these whiskers: the base and a point around two-thirds along the whisker shaft. This made six tracked points in total. The tracking was conducted every three frames, which was sufficient for following the whiskers as they did not move very far or fast.

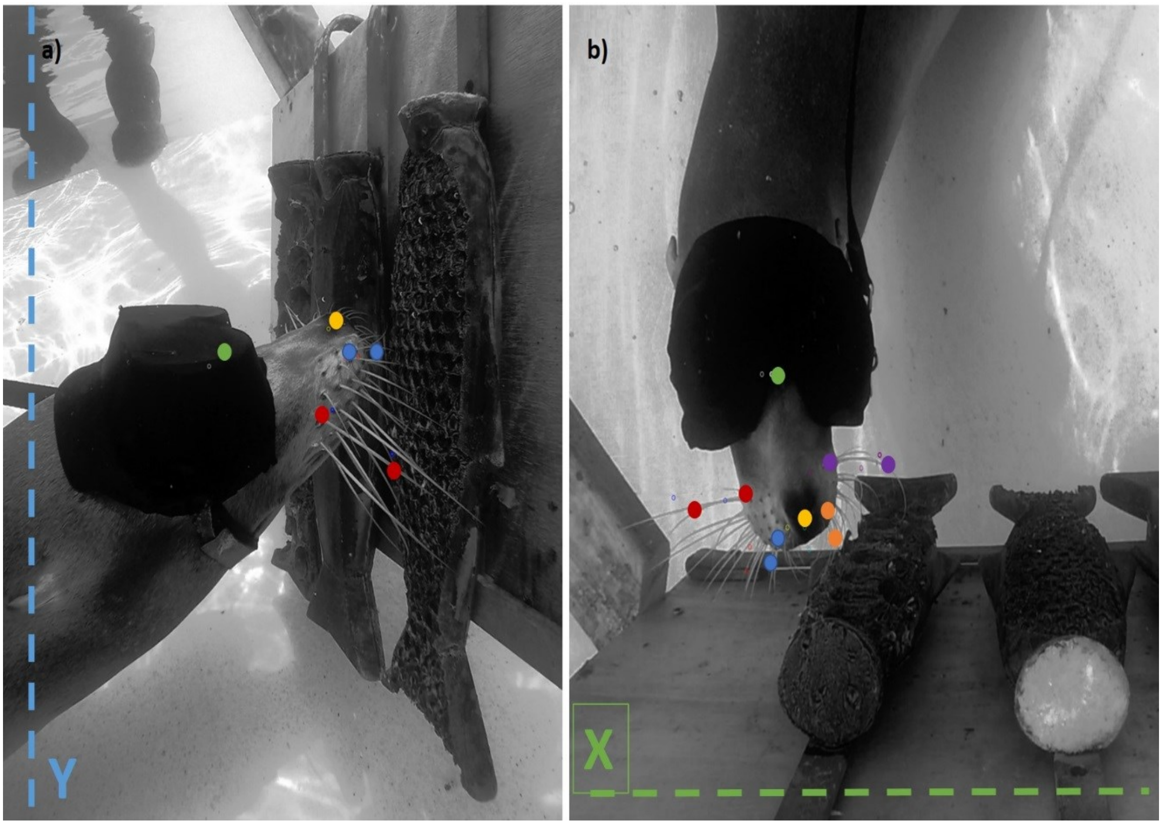


Figure 6.4: Video stills indicating tracked points: *a) Side video still indicating tracked points, red dots back whiskers, blue dots front whisker, yellow dot nose orientation and green dot head orientation, blue dashed line indicating movements up and down for y pixels; b) Top video still indicating traced points red dots right back whiskers, blue dots right front whisker purple dots left back whisker, orange dots left front whisker, yellow dot nose orientation and green dot head orientation, green dashed line indicating movements left and right for x pixels*

From the tracked points nose and whisker variables could then be calculated. Nose amplitude in the x (maximum amount of sideways movement) and y (maximum amount of up and down movement) were measured separately to enable the amount of head movements to be calculated and allow clarification of any observed differences in behaviour ad movements depending on the discrimination task in hand. These were calculated by finding the difference between the minimum and maximum nose tip coordinates, and calibrating to give a measure in mm. Nose amplitude in x was calculated from the x pixels in the top camera (Figure 6.10 b, d and f) and nose amplitude in y was calculated from the y pixels in the side camera (Figure 6.10 a, c and e). The nose distance from the centre of the fish model was also calculated as the average distance of the nose tip coordinates from the middle of the fish model, by using the x pixels from the top camera (Figure 6.5). Whisker angular position was calculated as the angle between the whisker and the midline of the head, such that forward moving whisker positions (protractions) gave larger whisker angular positions (see Figure 4.2). Whisker offset was calculated by averaging all the whisker angular positions per side. Whisker amplitude was the difference between the maximum and minimum whisker angular positions (averaged over whiskers and sides). Whisker spread was the difference between the rostral and caudal whisker angular positions (averaged over sides). Whisker asymmetry was calculated as the difference between the left whisker angular positions and the right. Time taken to explore the fish models was calculated by taking the number of frames for each individual tracked trail and dividing it by the number of frames per second (30 f/s).

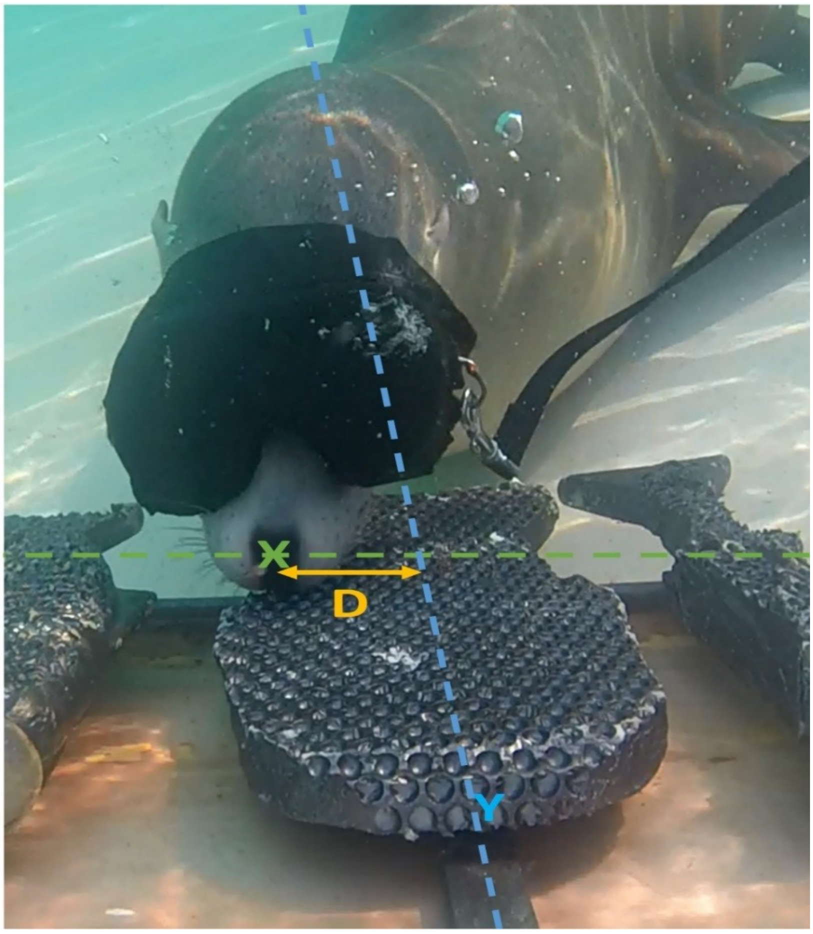


Figure 6.5: Video still indicating measurements for nose distance*: D= Distance of sea lion nose from fish model centre, Y= Centre of fish, X= Nose tracking point, green horizontal dashed line x amplitude, blue vertical dashed line y amplitude*

6.2.5 Statistical considerations

As some of the data was not normally distributed, all reported statistics were calculated using nonparametric tests. To compare differences in whisker and nose variables between the discrimination tasks, per clip measures were compared, using a Kruskal-Wallis Test. Further analysis was also conducted for grouped and individual tasks to examine the differences in whisker and nose variables between the fish models, and the position of the fish models, using a Kruskal-Wallis test. Any significant results were further analysed for pair-wise comparisons using a Mann-Whitney *U* test (between either the three tasks or the three stimuli). Main statistical findings will be reported in the text in the results section, below, and all statistical tests (along with median and 95% confidence intervals) can be found in Table 6.2.

6.3 Results

6.3.1 *Whisker movements and positions differed between the tasks*

Comparing whisker movements and positions between tasks in the top-down view

California sea lions made different whisker movements depending on the task. Overall, when doing a tactile discrimination task (texture and shape), compared to visual (luminance), whiskers were protracted further forward, with higher offset values (Kruskal-Wallis: χ2=19.957, df=2, p<0.001), and were moved greater distances, with higher amplitudes (Kruskal-Wallis: χ2=201.139, df=2, p<0.001) in the top-down view (Figure 6.6). In addition, whiskers moved significantly more in the size discrimination task compared to both the texture and luminance discrimination tasks (amplitude: Kruskal-Wallis: χ2=19.957, df=2, p<0.001), (Figure 6.6 e). Whisker spread between size and texture tasks also significantly differed, with texture having the most splayed out whiskers (Kruskal-Wallis: χ2=12.099, df=2, p<0.001), (Figure 6.6 g). There was no significant difference in whisker asymmetry between any of the three discrimination tasks (Kruskal-Wallis: χ2=1.182, df=2, p=0.5538), and therefore this was not explored further.

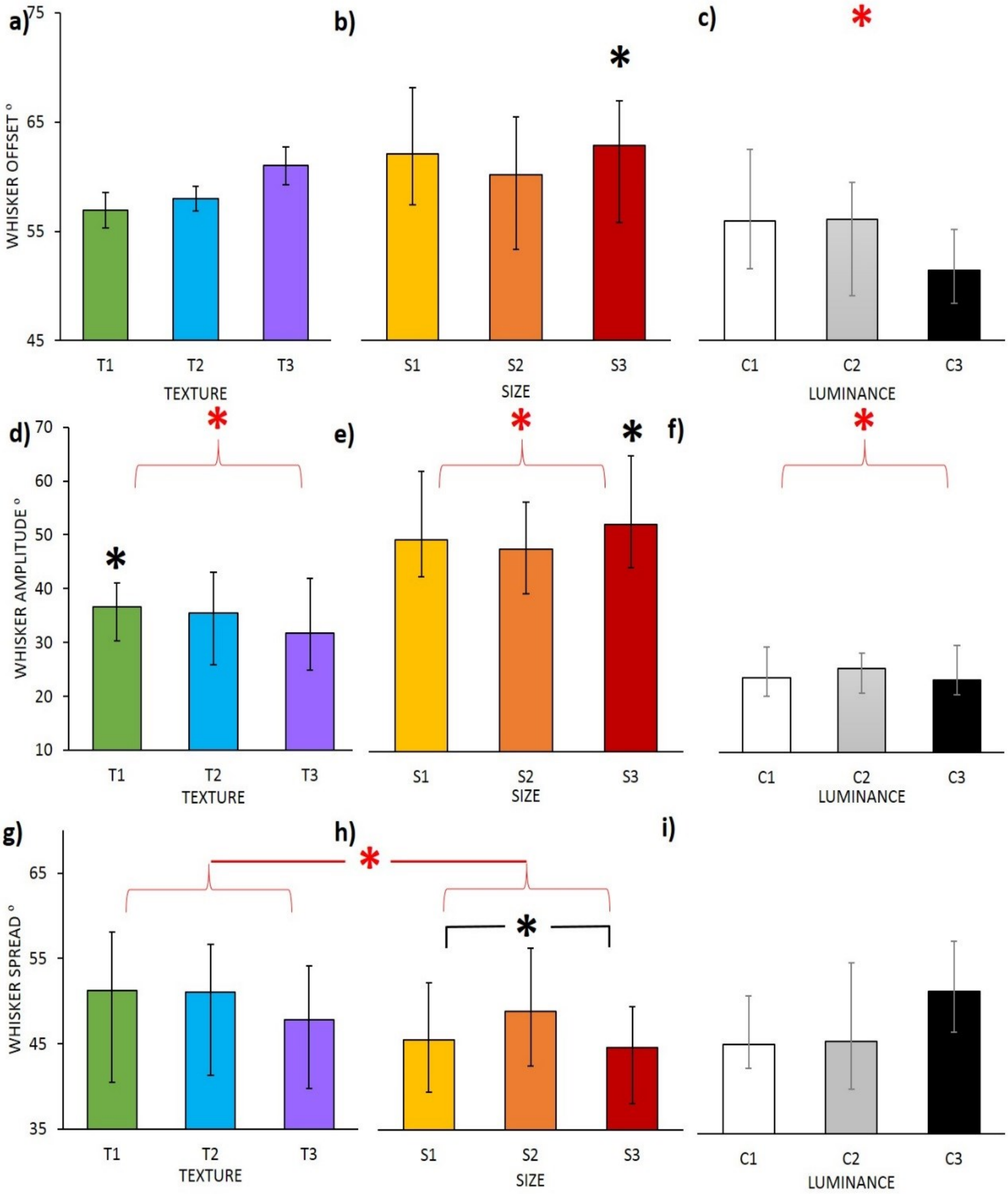


Figure 6.6: Sea lion whisker positions and movements from the top camera: *(a) Whisker offset values for the texture discrimination task, largest for the large distractor fish (T3), (b) Whisker offset values for the size discrimination task, which is smallest for the target fish, with the large distractor fish (S3) having significantly more spread out whiskers than both the small distractor fish and the target fish , c) Whisker offset values for the luminance discrimination task, are significantly less compared to both other discrimination tasks; d) Whisker amplitude for the texture discrimination task is significantly larger for the smooth distractor fish (T1), e) Whisker amplitude for the size discrimination task, is significantly larger for the large distractor fish (S3), f) Whisker amplitude for the luminance discrimination task; g) Angular whisker spread, for the texture discrimination task, which is smallest for the large distractor fish (T3), h) Angular whisker spread for the size discrimination task, which is significantly different between all fish models and significantly larger for the target fish (S2), i) Angular whisker spread for the luminance discrimination task, which is largest for the black distractor fish (C3). All graphs show median values with interquartile ranges. Black asterisks (*) show significant differences Mann Whitney U post hoc between fish models within discrimination tasks ($p < 0.05$). Red asterisks (*) show significant differences Kruskal-Wallis between the three discrimination tasks ($p < 0.05$).*

Describing whisker movement and positions in individual tasks in the top-down view

As well as differences in whisker movements and position between tasks, there were also differences within the discrimination tasks, between the fish models. Specifically, whiskers were positioned and moved differently between fish models in the texture and size task, but not the luminance task. In the texture discrimination task there was a significant difference in amplitude (Kruskal-Wallis: χ2=8.034, df=2, p=0.018). Whiskers moved more on the smooth textured *distractor fish* compared to both the *target fish* (Mann Whitney U: U= 1889.000, *Z*= -2.415, p=0.016) and large texture *distractor fish* (Mann Whitney U: U= 1283.000, *Z*= -2.588, p=0.010), (Figure 6.6 d). The position of the fish models on the fish rig also had a significant effect on whisker offset in the texture discrimination task (Kruskal-Wallis: χ2=8.100, df=2, p=0.017).

In the size discrimination task, offset was significantly different (Kruskal-Wallis: χ2=12.031, df=2, p=0.002). The large sized *distractor fish* had higher offset values than the target sized fish model (Mann Whitney U: U= 1170.000, *Z*= -3.379, p<0.001) and the small sized *distractor fish* (Mann Whitney U: U= 1835.000, *Z*= -2.177, p=0.029), (Figure 6.6 c). There was a significant difference in amplitude (Kruskal-Wallis: χ2=52.235, df=2, p<0.001). Whiskers moved more over the larger sized *distractor fish,* compared to both the *target fish* (Mann Whitney U: U= 722.000, *Z*= -6.974, p<0.001) and small sized *distractor fish* (Mann Whitney U: U= 859.000, *Z*= -4.996, p<0.001). Spread was also significantly different between the fish models for the size discrimination task (Kruskal-Wallis: χ2=5.848, df=2, p=0.050). The spread of whiskers was significantly bigger on the target sized fish model, compared to the large and small sized *distractor fish* (Mann Whitney U: U= 1397.000, *Z*= -2.199, p=0.028), (Figure 6.6 h). The position of the fish models on the fish rig, significantly affected the spread of the whiskers during the size discrimination task (Kruskal-Wallis: $\chi2=8.224$, df=2, p=0.016).

<u>Comparing whisker movements and positions between tasks in the side-on view</u>

Looking at the footage from the side camera in the vertical plane, significant differences between whisker positions and movements (whiskers moved up and down) were also clearly visible between the three discrimination tasks (offset: Kruskal-Wallis: $\chi2=88.997$, df=2, p<0.001, amplitude: Kruskal-Wallis: $\chi2=119.677$, df=2, p<0.001 and spread: Kruskal-Wallis: $\chi2=57.670$, df=2, p<0.001). Whiskers were protracted further forwards (offset), moved more (amplitude) and were more spaced-out (spread) during the size discrimination task compared to both the texture and luminance discrimination tasks (Figure 6.7).

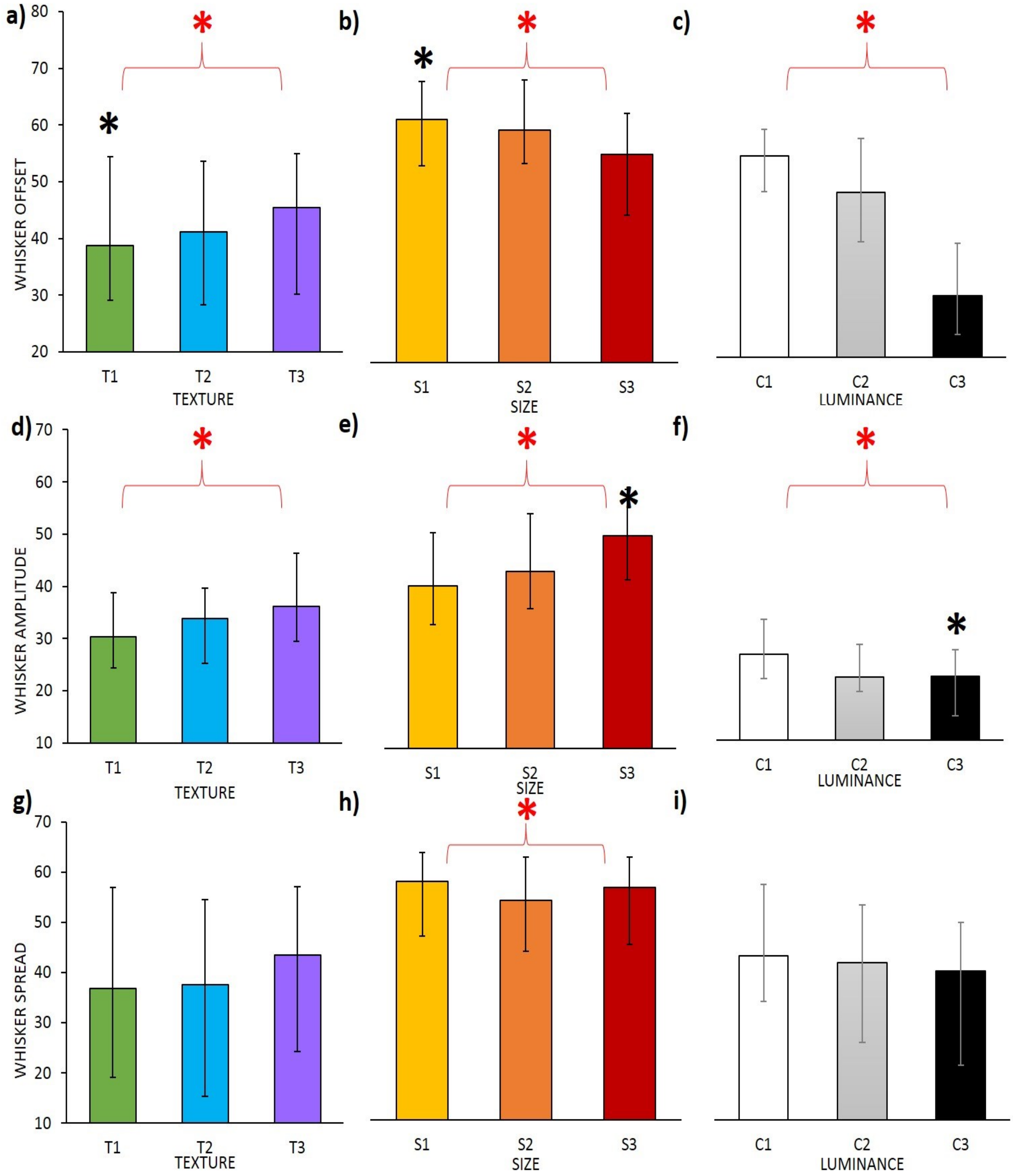


__Figure 6.7: Sea lion whisker positions and movements from the side camera:__ (a) Whisker offset values for the texture discrimination task was significantly smallest for the smooth distractor fish (T1) compared to the target fish and large distractor fish, (b) Whisker offset values for the size discrimination task, which is significantly largest for the small distractor fish (S1) compared to the target fish and large distractor fish,, c) Whisker offset values for the luminance discrimination task; d) Whisker amplitude for the texture discrimination task which is largest for the large distractor fish (T3), e) Whisker amplitude for the size discrimination task, which is significantly largest for the larger distractor fish (S3) compared to the target fish and small distractor fish, f) Whisker amplitude for the luminance discrimination task is significantly smallest for the black distractor fish (C3) compared to the grey target fish and white distractor fish,, g) Angular whisker spread, for the texture discrimination task, h) Angular whisker spread for the size discrimination task, which significantly larger than the other two discrimination tasks, i) Angular whisker spread for the luminance discrimination task. All graphs show median values with interquartile ranges. Black asterisks (*) show significant differences Mann Whitney U post hoc within discrimination tasks (p < 0.05). Red asterisks (*) show significant differences Kruskal-Wallis between discrimination tasks (p < 0.05).

Describing whisker positions and movements in individual tasks in the side-on view

As in the top-down view, there were also differences in whisker movements and positions in all tasks (Figure 6.7). Offset was significantly different in the texture discrimination task (Kruskal-Wallis: χ2=13.381, df=2, p=0.001). Whiskers were positioned further back on the smooth textured *distractor fish,* compared to both the *target fish* (Mann Whitney U: U= 946.000, *Z*= -3.663, p<0.001) and the large textured *distractor fish* (Mann Whitney U: U= 1005.000, *Z*= -2.082, p=0.037), (Figure 6.7 a).

Offset was also significantly different in the size discrimination task (Kruskal-Wallis: χ2=9.336, df=2, p=0.009). Whiskers were positioned further forward on the small sized *distractor fish* when compared to the *target fish* (Mann Whitney U: U= 764.000, *Z*= -2.847, p=0.004) and the large sized *distractor fish* (Mann Whitney U: U= 668.000, *Z*= -2.489, p=0.013). Whisker amplitude significantly differed in the size discrimination task (Kruskal-Wallis: χ2=10.450, df=2, p=0.005). The large sized *distractor fish* had the most whisker movements with whiskers moving more compared to both the small sized *distractor fish* (Mann Whitney U: U= 634.000, *Z*= -2.774, p=0.006) and the *target fish* (Mann Whitney U: U= 849.000, *Z*= -2.837, p=0.005), (Figure 6.7). There was also significant difference in fish model positions on the fish rig, for whisker amplitude in the size discrimination task (Kruskal-Wallis: χ2=7.514, df=2, p=0.023).

There was a significant difference in whisker amplitude within the luminance discrimination task (Kruskal-Wallis: χ2=6.179, df=2, p=0.046). Whiskers moved slightly less over the black *distractor fish* compared to the white *distractor fish* (Mann Whitney

U: U= 1.000, *Z*= -2.066, *p*=0.048) and grey *target fish* (Mann Whitney U: U= 79.000, *Z*= -2.188, *p*=0.027).

6.3.2 *Nose movements differed across the discrimination tasks*

<u>Comparing nose movements between tasks</u>

Nose amplitude (in x), significantly differed between all of the different discrimination tasks (Kruskal-Wallis: χ2=165.926, df=2, p<0.001 (Figure 6.8)). More side-to-side nose movements were seen in the size discrimination task compared to the texture discrimination task (Mann Whitney U: U= 10575.500, *Z*= -7.918, p<0.001) and luminance discrimination task (Mann Whitney U: U= 899.000, *Z*= -11.128, p<0.001). There was also more side-to-side nose movements in the texture discrimination task compared to the luminance discrimination task (Mann Whitney U: U= 2391.000, *Z*= -8.776, p<0.001), with the least nose movements seen within the luminance discrimination task (Figure 6.8).

Nose amplitude (in y) significantly differed between all the different discrimination tasks (Kruskal-Wallis: χ2=155.232, df=2, p<0.001). There was increased up and down movements of the sea lion nose in the size discrimination task, compared to the texture discrimination task (Mann Whitney U: U= 5831.500, *Z*= -7.875, p<0.001) and the luminance discrimination task (Mann Whitney U: U= 295.000, *Z*= -10.953, p<0.001). There was also more up and down nose movements in the texture discrimination task compared to the luminance discrimination task (Mann Whitney U: U= 1896.000, *Z*= -7.963, p<0.001), with the least nose movements being seen within the luminance discrimination task (Figure 6.8).

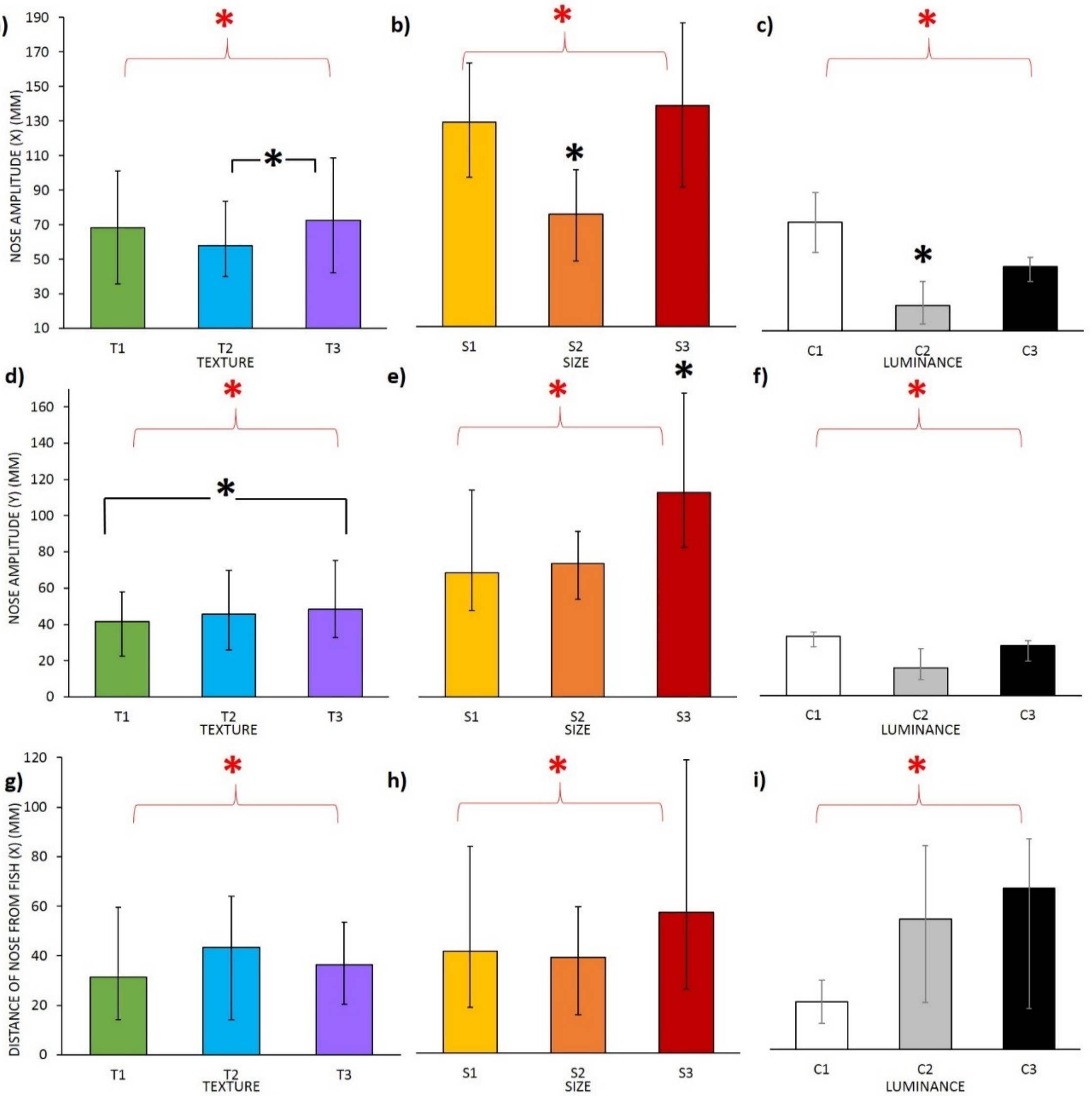


Figure 6.8: Sea lion nose positions and movements: *(a) Nose amplitude from the top camera for the texture discrimination task, highest for the large distractor fish (T3), significantly higher than the target fish (b) Nose amplitude from the top camera for the size discrimination task, which is significantly smallest for the target fish (S2) compared to the target fish and large distractor fish, c) Nose amplitude from the top camera for the luminance discrimination task, which is significantly smallest for the target fish (C2) compared to the black and white distractor fish; d) Nose amplitude from the side camera for the texture discrimination task which is significantly different between all fish models, significantly largest for the large distractor fish (T3), e) Nose amplitude from the side camera for the size discrimination task, which is significantly largest for the larger distractor fish (S3), f) Nose amplitude from the side camera for the luminance discrimination task smallest for the target fish (C2); g) Distance of nose from fish centre for the texture discrimination task which is larger in the target fish (T2); h) Distance of nose from fish centre for the size discrimination task, larger in the large distractor fish (S3), i) Distance of nose from fish centre for the luminance discrimination task. All graphs show median values with interquartile ranges. Black asterisks (*) show significant differences Mann Whitney U post hoc within discrimination tasks ($p < 0.05$). Red asterisks (*) show significant differences Kruskal-Wallis between discrimination tasks ($p < 0.05$).*

<u>Comparing nose movements within tasks</u>

On the texture task, nose amplitude in x was larger on the large textured *distractor fish,* compared to the *target fish* (Mann Whitney U: U= 2063.000, Z= -2.058, p=0.042). Nose amplitudes in y was larger on the large texture *distractor fish* compared to the smooth textured *distractor fish* (Mann Whitney U: U= 998.500, *Z*= -1.995, *p*=0.046). Both the smooth textured *distractor fish* and the target textured fish model had similar movements in x and y (Figure 6.8).

In the size discrimination nose amplitude in x differed between the fish models (Kruskal-Wallis: χ2=39.734, df=2, p<0.001) (Figure 6.8). Nose amplitude in x was smallest on the *target fish* compared to the small sized *distractor fish* (Mann Whitney U: U= 886.500, *Z*= -5.425, p<0.001) and the large sized *distractor fish* (Mann Whitney U: U= 967.500, *Z*= -5.916, *p*<0.001). Nose amplitude in y differed between the fish models (Kruskal-Wallis: χ2=13.550, df=2, p=0.001); they were much greater on the large sized *distractor fish* compared to the small sized *distractor fish* (Mann Whitney U: U= 510.000, *Z*= -3.81, p<0.001) and the *target fish* (Mann Whitney U: U= 579.000, Z= -4.678, p<0.001). Both the target fish and small sized *distractor fish* having similar vertical nose movements (Figure 6.8).

In the luminance discrimination task there was a significant difference in nose amplitude in x between the fish models (Kruskal-Wallis: χ2=9.639, df=2, p=0.008). The grey *target fish* received smaller side-to-side nose movements compared to both the white *distractor fish* (Mann Whitney U: U= 3.500, *Z*= -2.269, p=0.005) and the black *distractor fish* (Mann Whitney U: U= 66.000, *Z*= -3.092, p=0.002). There was no significant difference in the nose amplitude in y in the luminance discrimination task (Kruskal-Wallis: χ2=2.622, df=2, p=0.269) (Figure 6.8).

Comparing nose position in relation to the fish model in top-down view

The distance of the nose from the center of the fish models differed between each of the discrimination tasks (Kruskal-Wallis: $\chi 2=7.140$, df=2, p=0.028), (Figure 6.8). There was a significant difference between the texture discrimination task and both the size discrimination task (Mann Whitney U: U= 17059.000, Z= -2.223, p=0.026) and the luminance discrimination task (Mann Whitney U: U= 6192.000, Z= -2.236, p=0.025). With nose positioning being more central on the textured fish models in comparison to the size and luminance fish models. Nose positions did not significantly differ between the size discrimination task and the luminance discrimination task (Mann Whitney U: U= 6978.000, Z= -0.289, p=0.773). Within each of the discrimination tasks there was no significant differences observed on each individual stimulus (Figure 6.8).

6.3.3 *Time taken to make decision*

Comparing time taken to make a decision between tasks

Using the footage from the top camera, the time taken to make a decision significantly differed between the three discrimination tasks (Kruskal-Wallis: $\chi 2=284.166$, df=2, p<0.001). Significant differences were seen between the texture and size discrimination tasks (Mann Whitney U: U= 224.500, Z= -15.323, p<0.001) and the size and luminance discrimination tasks (Mann Whitney U: U= 349.500, Z= -12.119, p<0.001), (Figure 6.9). There was no significant difference seen between the texture and luminance discrimination tasks (Mann Whitney U: U= 6701.500, Z= -1.574, p=0.116). The longest time was being spent in the size task, then the texture and luminance task (Figure 6.9).

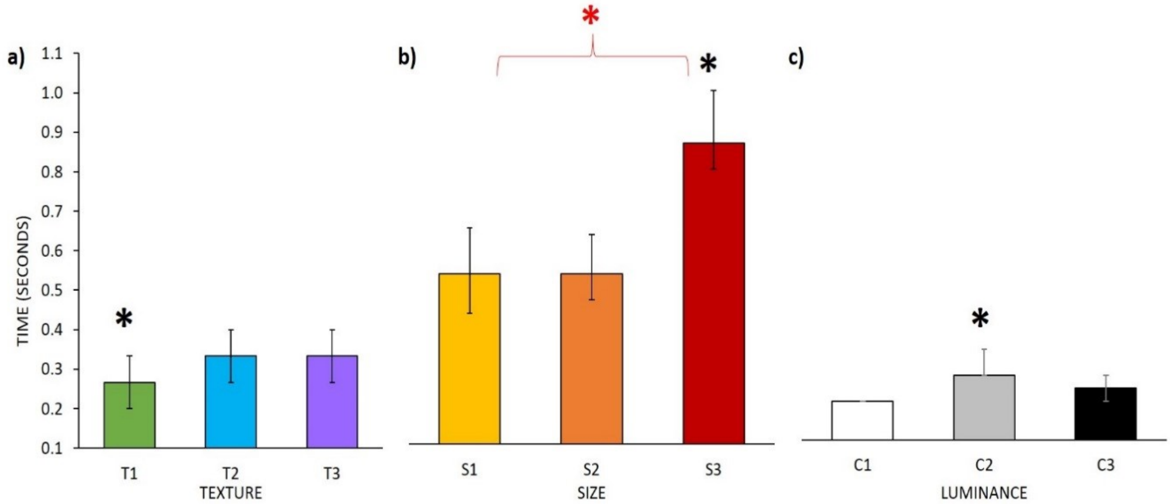


Figure 6.9: Time spent on each fish model by the sea lion from the top camera: *(a) Time spent for the texture discrimination task, was significantly lowest for the small distractor fish (T1), (b) Time spent for the size discrimination task, which is significantly higher for the large distractor fish (S3), c) Time spent for the luminance discrimination task, which is significantly largest for the target fish (C2). All graphs show median values with interquartile ranges. Black asterisks (*) show significant differences Mann Whitney U post hoc within discrimination tasks (p < 0.05). Red asterisks (*) show significant differences Kruskal-Wallis between discrimination tasks (p < 0.05).*

Comparing time taken to make a decision in individual tasks

Significant differences were seen within the individual discrimination tasks (Figure 6.9). In the texture discrimination task, there was a significant difference in the decision time on the fish models (Kruskal-Wallis: χ2=15.197, df=2, p=0.001). The sea lion spent less time (approx. 0.2 seconds) investigating the smooth textured *distractor fish* compared to the large texture *distractor fish* (approx. 0.35 seconds, Mann Whitney *U*=1089.000, *Z*= -3.823, p<0.001) and the target dish model (approx. 0.3 seconds, Mann Whitney *U*= 1730.000, *Z*= -2.916, *p*=0.004), (Figure 6.9). There was a significant difference between the decision time in the size discrimination task (Kruskal-Wallis: χ2=80.045, df=2, p<0.001). Almost twice as much time was taken (approx. 0.85 seconds) to investigate the large sized *distractor fish* over the *target fish* (Mann Whitney U: U= 498.500, *Z*= -7.949, p<0.001), and the small sized *distractor fish* (Mann Whitney U: U= 386.500, *Z*= -7.463, p<0.001), (Figure 6.9). There was also a significant difference between the time spent on the different luminance fish models (Kruskal-Wallis: χ2=8.488, df=2, p=0.014). Increased amount of time (approx. 0.2 seconds) was spent on the grey *target fish,* compared to both the white *distractor fish* (Mann Whitney U: U= 12.000, *Z*= -2.047, p=0.043) and the black *distractor fish* (Mann Whitney U: U= 120.000, *Z*= -2.173, p=0.030), (Figure 6.9).

Table 6.2: Summary of all discrimination task data (medians and 95% confidence intervals), with statistics: *Bold text indicating significant differences Kruskal-Wallis between fish models and all task data is between the three discrimination tasks (p < 0.05).*

CAMERA	**VARIABLE**			**OFFSET °**			**AMPLITUDE °**			**ASYMMETRY °**			**SPREAD °**		
				MEDIAN	**UQ**	**LQ**	**MEDIAN**	**UQ**	**LQ**	**MEDIAN**	**UQ**	**LQ**	**MEDIAN**	**UQ**	**LQ**
TOP	**TEXTURE**	*SMOOTH*	T1	56.936	6.058	7.076	36.557	4.525	6.245	-4.392	12.606	-20.506	51.253	6.884	10.706
		TARGET	T2	58.017	8.553	5.730	35.436	7.651	9.516	-2.394	8.457	-12.351	51.075	5.584	9.760
		LARGE	T3	61.014	11.192	6.129	31.824	10.084	6.989	-4.062	12.203	-14.630	47.802	6.353	8.044
	FISH MODELS	Kruskal-Wallis		χ2=3.180, df=2, p=0.204			**χ2=8.034, df=2, p=0.018**			χ2=2.549, df=2, p=0.280			χ2=0.083, df=2, p=0.960		
	SIZE	*SMALL*	S1	62.777	5.279	5.377	48.432	12.383	6.751	-4.198	9.049	-20.098	45.434	6.551	6.057
		TARGET	S2	60.137	5.233	6.799	46.733	8.472	8.091	-1.332	11.044	-13.241	48.730	7.266	6.370
		LARGE	S3	62.035	4.815	6.253	51.273	12.317	7.939	-0.536	8.138	-10.745	44.499	4.745	6.532
	FISH MODELS	Kruskal-Wallis		**χ2=12.031, df=2, p=0.002**			**χ2=52.235, df=2, p<0.001**			**χ2=10.873, df=2, p=0.004**			**χ2=5.848, df=2, p=0.050**		
	LUMINANCE	*WHITE*	C1	55.671	2.556	1.808	23.598	5.567	3.403	-2.078	8.542	-12.242	45.225	5.447	2.745
		TARGET	C2	55.809	8.682	1.069	25.242	2.796	4.457	-2.569	8.025	-9.967	45.515	8.957	5.398
		BLACK	C3	51.240	4.547	1.718	23.181	6.246	2.724	1.991	6.366	-4.634	51.256	5.686	4.644
	FISH MODELS	Kruskal-Wallis		χ2=2.808, df=2, p=0.246			χ2=0.091, df=2, p=0.956			χ2=0.651, df=2, p=0.722			χ2=5.990, df=2, p=0.051		
	ALL TASKS	Kruskal-Wallis		**χ2=19.957, df=2, p<0.001**			**χ2=201.139, df=2, p<0.001**			χ2=1.182, df=2, p=0.5538			**χ2=12.099, df=2, p<0.001**		
SIDE	**TEXTURE**	*SMOOTH*	T1	38.785	15.678	9.699	30.295	8.409	5.967	-	-	-	36.861	20.093	17.676
		TARGET	T2	41.088	12.453	12.755	33.826	5.874	8.580	-	-	-	37.656	16.869	22.392
		LARGE	T3	45.467	9.512	15.333	36.121	10.257	6.602	-	-	-	43.555	13.562	19.275
	FISH MODELS	Kruskal-Wallis		**χ2=13.381, df=2, p=0.001**			χ2=4.447, df=2, p=0.108			-	-	-	χ2=3.896, df=2, p=0.143		
	SIZE	*SMALL*	S1	61.440	6.423	7.919	40.838	10.040	7.337	-	-	-	57.392	5.847	10.838
		TARGET	S2	59.650	8.540	5.670	43.655	10.942	7.152	-	-	-	53.617	8.744	10.075
		LARGE	S3	55.447	7.074	10.323	50.433	8.676	8.498	-	-	-	56.229	6.061	11.276
	FISH MODELS	Kruskal-Wallis		**χ2=9.336, df=2, p=0.009**			**χ2=10.450, df=2, p=0.005**			-	-	-	χ2=2.763, df=2, p=0.251		
	COLOUR	*WHITE*	C1	48.119	3.923	2.265	26.288	6.602	4.606	-	-	-	41.588	13.848	8.719
		TARGET	C2	46.237	14.559	1.912	21.999	6.150	2.754	-	-	-	40.360	11.016	15.340
		BLACK	C3	53.630	18.222	7.439	22.014	5.023	7.373	-	-	-	38.787	9.289	18.270
	FISH MODELS	Kruskal-Wallis		χ2=1.512, df=2, p=0.470			**χ2=6.179, df=2, p=0.046**			-	-	-	χ2=0.263, df=2, p=0.877		
	SIDE ALL TASKS	Kruskal-Wallis		**χ2=88.997, df=2, p<0.001**			**χ2=119.677, df=2, p<0.001**			-	-	-	**χ2=57.670, df=2, p<0.001**		

6.4 Discussion

6.4.1 Results Summary

Results in this chapter revealed that a California sea lion moved and positioned its whiskers and head differently during three discrimination tasks, suggesting that California sea lions can control their whiskers in a task-specific way, in certain contexts. During the texture task, whiskers were more splayed out, positioned slightly forward (offset) and were always presented to the fish model towards its center (nose distance from fish center), (Figure 6.10 a and b). During the size task whiskers were protracted furthest forward (offset) and both the head (nose amplitude in both x and y) and whiskers (amplitude) moved the most (Figure 6.10 c and d). Finally, in the luminance task there was not much movement in the head or across whiskers (nose and whisker amplitude). Whiskers were not very protracted forward (offset), presumably, due to vision being the primary sense used (Figure 6.10 e and f). This study is the first of its kind to design three different discrimination tasks to show California sea lions move their whiskers in a task dependent manner.

It has been observed that humans make lateral, stroking movements during texture discrimination tasks (Katz 1925) and using the distance between their thumb and forefinger judge object size during a size discrimination task (Stevens and Stone 1959; John et al. 1989; Santello and Soechting 1997). Due to this, we may expect to see lateral whisker movements during a texture task and changing whisker span, or an increase in whisker spread, during a size task. However, while whiskers were moved in a task-specific way, they did not move in agreement with these predictions based on human fingertip movements.

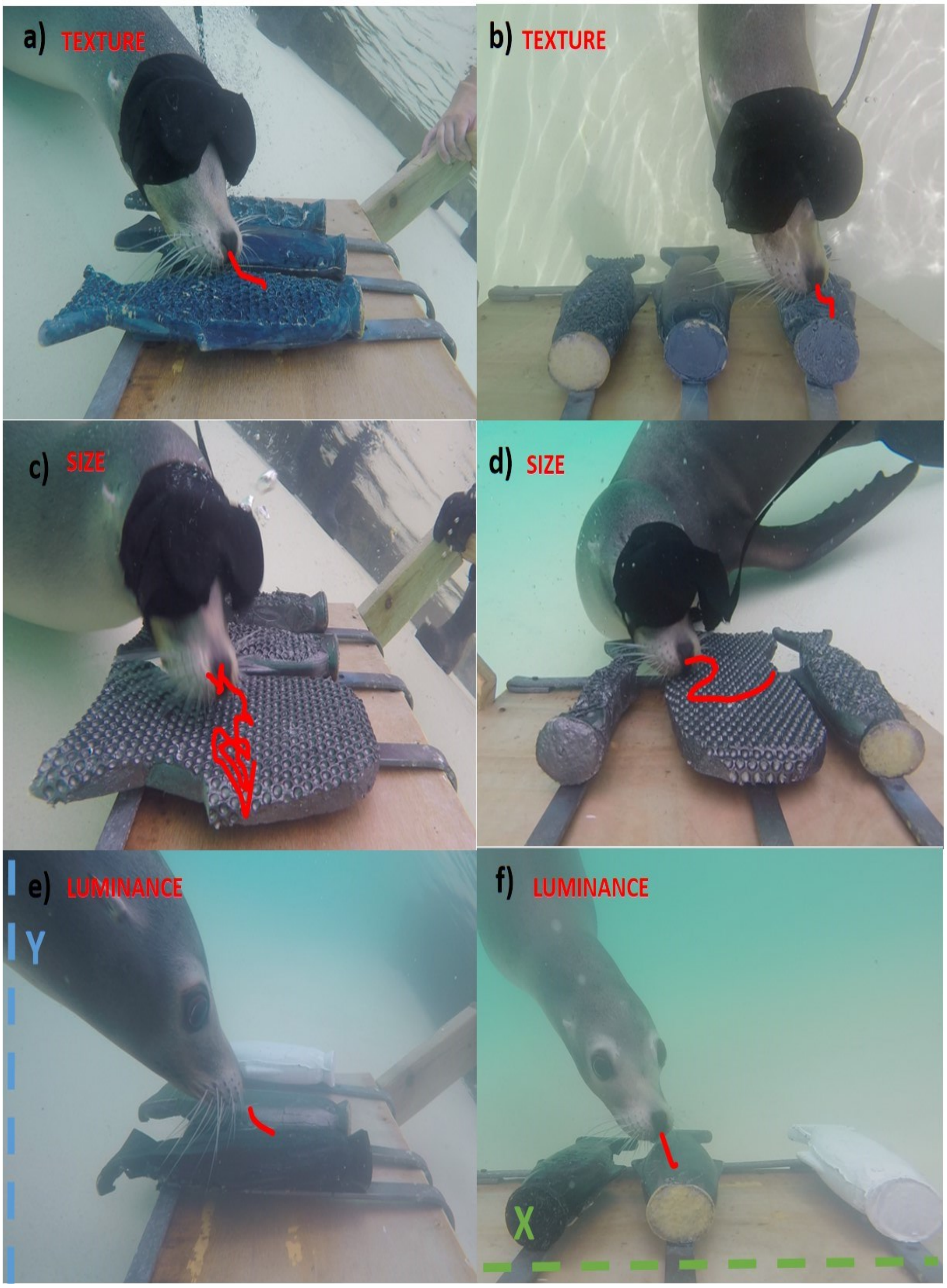


Figure 6.10: Six example video-stills of Lo with nose tracking overlaid: Texture Discrimination Task a) Exploring the textured fish models from the side-on camera blindfolded underwater; b) Exploring the textured fish models from the top-down camera blindfolded underwater; **Size Discrimination Task** c) Exploring the size fish models from the side-on camera blindfolded underwater; d) Exploring the size fish models from the side-on camera blindfolded underwater; **Luminance Discrimination Task** e) Exploring the luminance fish models from the top-down camera underwater; b) Exploring the luminance fish models from the side-on camera underwater. Red line indicates nose movements towards and on various fish models in each of the three discrimination tasks (size, texture and luminance), *green horizontal dashed line x plane (side-to-side view), blue vertical dashed line y plane (up-and-down view)*

6.4.2 Texture

During the texture task, whiskers were more spread out, they moved less than on the size task, and were positioned towards the center of the fish model. Putting the nose on the center of the fish model positions the whisker on to the textured surface. Increasing whisker spread provides a larger searching surface area and enables many whisker tips to be in contact across the surface of the fish model. The centrally positioned nose trace can clearly be seen in Figure 6.10 a and b, as well as the spread out whiskers. Sea lions can judge textures to the same accuracy as human fingertips (Gibson 1962; Grant et al. 2014). Humans use vibrations of their fingertips over a surface to judge textures. California sea lions do move their head and whiskers over the surface (see traces in Figure 6.10 a and b), and their whisker amplitudes are larger on the textured surfaces (Figure 6.7 b, side-on view). However, whisker and head movements are not as large during the texture task as those seen in the size discrimination task. However, the movement of the whiskers do not necessarily have to be large, according to the whisker resonance hypothesis.

Whisker resonance is thought to be important for texture coding (Neimark et al. 2003; Andermann et al. 2004). Each whisker is a slightly different length and width; therefore, it has different physical properties and will vibrate at its own unique intrinsic resonance frequency. When whiskers are swept over a texture, certain whiskers will become excited if the movement across the surface matches its resonance frequency. Whisker frequencies within the “excited range” could decode the texture by judging the amplitudes of the excitation caused across multiple whiskers (Neimark et al. 2003; Andermann et al. 2004). For this to happen the resonance frequency hypothesis has two predictions, firstly the texture-driven vibrations must be filtered by each whiskers resonance and secondly this resonance caused and therefore will excite individual whiskers depends on the spatial properties of the texture. These whisker frequencies depend on whisker length (Neimark et al. 2003) and as whisker lengths increase from front to back (Brecht et al. 1997) there is an increase in resonance frequencies in rostral whiskers compared to caudal whiskers. This technique has never been seen in Pinnipeds but is utilised by rats as they sweep their whiskers across a textured surface, creating whisker vibrations, which is determined by the texture (Hartmann et al. 2003; Wolfe et al. 2008; Rabey et al. 2014). The rostral whiskers respond more strongly to finer textures, while the longer caudal whiskers would respond to coarser textures. Within the texture discrimination task here, the whiskers are pushed forward and spread out over the surface, they are then moved across it, perhaps to pick up vibrations and excite the resonance frequencies texture (Hartmann et al. 2003).

In addition to whisker resonance frequencies, it could be that California sea lions are utilising stick-slip events, as seen in rodent whiskers (Diamond et al. 2008, Wolfe et al. 2008, Zuo et al. 2011; Hires et al., 2013). Slip-stick events are generated during active touch sensing as moving sensors (in this case whiskers) contact different surfaces (Schwarz, 2016). These events are visible within rodent whisker movements when they are in contact with textured surfaces and thought to contribute to the neural coding of texture (Arabzadeh et al. 2005; Wolfe et al. 2008; Jadhav and Feldman 2010; Hires et al. 2013). As whiskers move over objects, stick-slip events are brief spatially-localized accelerations and decelerations of the whisker tip (Arabzadeh et al. 2005; Wolfe et al. 2008; Hires et al. 2013), which induce spikes in the somatosensory cortex (Jadhav et al.

2009). These spikes are precise, yet vary with friction interactions, therefore a higher firing rate is hypothesized to code for rougher surfaces (Jadhav and Feldman 2010; Zuo et al. 2015). Indeed, previous research has documented that whiskers in contact with rougher, irregular surfaces generate large amplitude, high-velocity stick-slip events, while smooth surfaces generated smaller amplitude stick-slip events (Ritt et al. 2008, Wolfe et al. 2008, Lottem and Azouz 2009). Therefore, the sea lion could be moving its whiskers over the surfaces of the fish model during the texture task to produce stick slip events. They would then use these events to code for texture, given that the large textured fish might produce large amplitude whisker movements, compared to the medium textured and smooth fish.

6.4.3 Size

Whisker and head movements were increased during the size discrimination task, particularly on the large sized *distractor fish.* This may indicate that the California sea lion was exploring around the edge of the fish model in order to judge size. The large sized *distractor fish* would, indeed, require bigger whisker and head movements in order to feel around the widely spaced edges. This can be clearly seen in Figure 6.10 c and d, were the nose traces (in red) are much larger than in the other tasks (Figure 6.10 a, b, e and f), and move from edge to edge. A previous study by Grant et al. (2013) conducted a size discrimination task in Harbor seals, and found that whisker spread, amplitude and offset were all not used to judge size. Rather, the seals oriented their small rostral whiskers to the stimuli and probably could calculate the number of whiskers contacted by the stimuli. However, the stimuli used in this chapter are much bigger than those used by Grant et al. (2013), therefore, differences between the stimuli are also larger, and it is clear to see that the larger stimuli causes larger whisker and head movements.

6.4.4 Luminance and Vision

Vision, rather than touch, was used in the luminance task, so whiskers were not recruited in the same way as during the texture and size tasks. There was not much head or whisker movements during the luminance discrimination task, and the whiskers were not protracted forward as much. The head was not very central to the fish model, and often oriented to the side, so the eyes could get a good look at the fish model stimuli (see Figure 6.10 e and f). However, the California sea lions usually used their whiskers in the task too; therefore, this task involved both visual and tactile processing, in order to i) recognise the visual stimulus, and ii) guide the nose to the fish model. It did take a longer time for the California sea lion to learn to choose the *target fish* from the *distractor fish* s in this task, compared to the other tactile discrimination tasks (texture and size), (Figure 5.12 c, Training stage 4). Therefore, it might be that the multi-sensory integration involved in this task, is slightly more challenging that solely a tactile task. Alternatively, the switching between learning two tactile tasks, and then a visual task was just the challenge.

6.4.5 Tactile Exploration

Comparing the visual (luminance) to the tactile (texture and size) tasks, it is clear that protracting the whiskers forward and moving the head and whiskers is common to tactile tasks. From video footage is it clear that the rostral whiskers are often oriented towards the fish models and contact them first; rostral whiskers are positioned both by moving the head and the whiskers themselves. Protracting the whiskers and moving the rostral whiskers to a stimulus using the head has also been observed in Harbor seals (Dehnhardt 1994; Grant et al. 2013) and a Pacific walrus (Kastelein et al. 1990), (and in ***Chapter Four: Quantifying Whisker Movements in Pinnipeds*** within this thesis). It is suggested that these whiskers have a higher resolving power than the caudal vibrissae, so perhaps rostral whiskers are used for contact detection, which would be useful when decoding differences in both texture and size. In addition, behavioural studies using California sea lions to detect hydrodynamics indicate that their whiskers are also protracted in to an erect position while detecting and following trials (Dehnhardt et al. 2001). However, while whisker protractions and head movements have been discussed in the literature before (Dehnhardt 1994; Grant et al. 2013), no study has really emphasised the importance of whisker movements in Pinnipeds. This study shows that California sea lions make purposive and focused whisker movements that are task-specific, indicating that California sea lions use their whiskers for active touch sensing.

6.4.6 Decision Times

Not only can California sea lions move their whiskers with purposive control, they also do so quickly, with decision and initiation of movement times of less than a second. The longest time spent investigating the fish models was seen in the size discrimination task, especially on the large sized *distractor fish* , as the California sea lion took time to explore around the edges, which were quite far apart on the large sized *distractor fish.* This would be expected due to the large sized *distractor fish* taking up more space on the fish rig. Indeed, this took almost twice as much time (median approx. 0.85 seconds) as the *target* *fish* (approx. 0.5 seconds) and small sized *distractor fish* (approx. 0.5 seconds). The California sea lion also spent more time in the texture task, investigating the large textured *distractor fish* and *target fish* (approx. 0.35 seconds), compared to the smooth textured *distractor fish* (approx. 0.2 seconds). This may indicate that it was more difficult to identify between the two different textures, than the smooth *distractor fish.* Increased time was also spent on the grey *target fish* compared to both *distractor fish* s in the luminance discrimination task; this may be the California sea lion just checking it is the correct fish before choosing and in addition the California sea lion consistently choosing the grey *target fish* over 92% of the trials and therefore would logically spend more time on this fish model. All decision times in the luminance task were very small, so this difference is minimal. Decision times were similar, but a bit larger, than those of Harbor seals in a size discrimination task (Grant et al. 2013) who always took less than 0.4 seconds to make a decision, which is equivalent to the decision time values in the texture and luminance discrimination tasks here. It is likely that quick decision times are important for tactile tasks, to enable efficient and effective foraging and prey capture.

Indeed, making strategic, task-specific whisker movements allows the animal to efficiently extract relevant information from an object, in order to quickly complete a task. This is likely to be especially important during foraging, especially when informing decisions about prey capture, which have to be both quick and directed in order to be successful (Hoyle 1958; Camhi et al. 1978). This will be discussed more in the next chapter, along with the limitations of this work (see ***Chapter 7 Discussion***).

6.5 Conclusion

This is the first study to show that any animal can make task-specific movements with their whiskers. Results in this chapter show that a California sea lion moved and positioned their whiskers and head purposively during different discrimination tasks, texture, size and luminance. Specifically, during a size discrimination task, the whiskers were protracted far forward, and the head and whiskers were moved a lot, especially round the edge of a shape. During a texture discrimination task, whiskers were spread out, positioned towards the center of the fish model, and moved over the surface. During a visual luminance task, whiskers were not protracted far forward, and there were not many head and whisker movements. That California sea lions move their whiskers in a task-specific way indicates that they are able to actively touch sense objects of interest, perhaps much like human fingertips.

7 ***Chapter Seven: Discussion***

Chapter Summary:

The final chapter of this thesis consolidates the key findings, implications and limitations of this work. The importance of active touch sensing in Pinniped*s* is highlighted, especially for foraging and prey capture. Finally, this chapter introduces the potential applications of the research, including for welfare, biomechanics, neuroscience, technology and in studies of animal cognition.

7.1 Summary of findings in this thesis

The thesis introduction in ***Chapter One: Introduction and Overview*** revealed that while animals studies of touch sensing have demonstrated that whiskers move, especially in rodent studies (Vincent 1912; Mitchinson et al. 2007, 2011; Grant et al. 2009, 2012, 2013b; Arkley et al. 2014), and that these whisker movements are purposive (Arkley et al. 2014; Grant et al. 2009; Mitchinson et al. 2007), no one has ever investigated whether animals make task-specific movements. Human fingertips are thought to be an active touch sensing system because they both move and make task-specific movements (Gibson 1962). Therefore, this thesis investigated whether Pinniped whiskers are a true active touch sensing system.

Pinnipeds were chosen as the group of animals to explore this further, as their whiskers are diverse and sensitive. In addition, Milnes' (2013) MSc thesis showed that whisker movements are important in California sea lions (*Zalophus californianus*) during dynamic sensorimotor tasks (Milne 2013; Milne and Grant 2014). Therefore, this thesis has built upon this previous knowledge and has produced the following novel findings: i) description of the morphology of Pinniped whiskers and their infraorbital foramen size (IOF) as an approximation of sensitivity; ii) quantified whisker movements in Harbor seals (*Phoca vitulina*), California sea lions and Pacific Walruses (*Odobenidae rosmarus divergens*); and iii) identified that California sea lions can make task-specific movements with their whiskers.

The first task of the thesis was to describe whisker morphology in Pinnipeds. Findings in ***Chapter Three: Pinniped Whisker and Skull Morphology*** discovered differences in Pinniped whisker and skull morphology. Just as the whisker shape varies between the Pinniped*s* (round, oval and undulating), skull shape and whisker length also varies greatly. The area of the IOF tended to be larger in the Pinniped*s* that had more whiskers, such as the Odobenidae, as more whiskers would naturally require a larger IOF, although whisker number and IOF area was not correlated in Pinnipeds. IOF area and whisker number are correlated in primates and other terrestrial mammals (Muchlinski et al. 2013, 2018). Results in ***Chapter Three: Pinniped Whisker and Skull Morphology*** indicated that whisker length was correlated with the size of the IOF in Pinnipeds. Indeed, Otariidae that had the longest whiskers also had the largest IOFs, larger than many Phocidae. Therefore, their whiskers are likely to be more sensitive. Comparing the Pinniped*s* to other carnivores showed that Pinnipeds had fewer whiskers, but larger IOF areas, indicating that each whisker is likely to be more innervated in Pinniped*s*. Animals that move their whiskers also have larger IOF areas (Muchlinski et al. 2018), as an active sense is likely to be associated with higher sensory acuity. Therefore, movement is also likely to be involved with sensitivity, which leads on to ***Chapter Four: Quantifying Whisker Movements in Pinnipeds.***

Chapter Four: Quantifying Whisker Movements in Pinnipeds compared and quantified whisker movements in Pinniped*s*. Out of the three Pinniped families, one species was selected from each, including the Harbor seal, California sea lion and the Pacific walrus to undertake a novel sensorimotor “fish sweeping” task. All the species oriented their head towards the moving fish and protracted their whiskers. However, the California sea lion moved their whiskers the most and these movements were independent of the head movements. This meant that the California sea lions were actively controlling and moving their whiskers, and made them a great candidate species from which to explore active whisker sensing further.

Finally, three discrimination tasks were designed and employed in ***Chapter Five: Sea Lion Training Programme*** to investigate whether California sea lions made task-specific whisker movements. ***Chapter Six: Task-Specific Whisker Movements in California Sea Lions*** investigated these three discrimination tasks including texture, size and luminance. Findings provided evidence for task-specific movements occurring in Pinniped*s*. Specifically, during size discrimination, whiskers were protracted far forward and the head and whiskers were moved round the edge of a shape. In a texture discrimination task, whiskers were more spread out and positioned towards the center of the fish. In a visual luminance task, whiskers were not protracted forward and did not move much at all. The findings that whiskers move purposively, making task-specific movements, suggest that California sea lions are able to do active touch sensing with their whiskers.

7.2 Thesis limitations

The methods for measuring the IOF area differed between the Pinniped*s* in ***Chapter Three: Pinniped Whisker and Skull Morphology*** and the other carnivore species data from Muchlinski et al. (2010). Muchlinski et al. (2010) used moulds to determine the area of irregularly shaped IOFs, which are especially common in rodentia. However, the Pinniped IOF areas were relatively uniform (see Table 3.1 in ***Chapter Three: Pinniped Whisker and Skull Morphology***), therefore, approximating area from diameter estimates should be sufficient. Oval and circular estimations both gave the same result patterns in the data in ***Chapter Three: Pinniped Whisker and Skull Morphology***. A recent paper (Muchlinski et al. 2018), also used the Muchlinski (2010) data and compared their data from measuring IOF area from light microscope image analysis, and the two methods were found to not differ significantly. Most museums will not allow wax moulds to be made of their specimens; therefore, my measurement method was entirely non-invasive, involving minimal handling of the specimen and enabled the specimen to remain on site. Extreme care was also taken across all measurements samples to make sure measurements taken were from the same positions on the skull for consistency. More skull and skin specimens could be sourced to increase the sample number. The numbers of skin specimens were limited, due to population numbers and access to species.

Chapter Four: Quantifying Whisker Movements in Pinnipeds used three different facilities to obtain the video footage for each of the three Pinniped species used. This meant that each of the Pinniped*s* were exposed to different trainers and procedures.

Even though the animals were all given the same task, the trainers will naturally differ in their approach. Indeed, the Pacific walrus trainer did not move the fish as much as trainers of the other species did (see Figure: 4.5), although this did not appear to significantly affect the results. Observed differences between individual Pinniped*s* in Milne and Grant (2014) also flagged up difficulties with conducting experiments using only a limited number of animals (Dehnhardt and Dücker 1996; Wieskotten et al. 2010a, 2010b; Grant et al. 2013). Milne and Grant (2014) used three California sea lions and found differences between them: one had slower head movements, another higher amplitude whisker movements and the third reduced whisker asymmetry. However, it is extremely common in studies of this type to use individual Pinnipeds as it is difficult to access large numbers of trained marine mammals (Dehnhardt and Dücker 1996; Wieskotten et al. 2010a, b; Grant et al. 2013).

Although using captive animals for research has huge advantages, such as being accessible, trainable and enable experimental repeats, animals in captivity are generally under controlled feeding conditions. Their diet in captivity could affect vibrissae growth (Rosas-Hernández et al. 2018), causing limitations for ***Chapter Three: Pinniped Whisker and Skull Morphology*** and ***Chapter Six: Task-Specific Whisker Movements in California Sea Lions***. Indeed, diet is likely to affect the quality of proteins available for vibrissal growth. Vibrissal growth rates in California sea lions are affected by environmental and isotopic oscillations (peaks in various isotope values within their whiskers), (Rosas-Hernández et al. 2018). Captive Pinniped vibrissae differ from their wild counterparts, who experience seasonal variation in prey abundance and availability (Kernaléguen et al. 2012; Beltran et al. 2016). Therefore, whisker lengths and shapes might be different between captive and wild Pinnipeds. Vibrissal length in captive Pinniped*s* can also be underestimated due to rock-rubbing resulting in whisker abrasion; a factor, which is not typically taken into account when measuring vibrissae (McHuron et al. 2016). Rock rubbing is likely to both wear the surface of the whisker and make it shorter, thus impacting its mechanical interactions against surfaces. However, whiskers are constantly wearing, growing and being replaced, so whether this would affect the sensory capabilities of the animals is unknown.

Whisker number and distribution can also vary between individuals. A study by Sawyer (2016) used a California sea lion that had six rows of vibrissae consisting of four, six, eight, eight, eight, and four whiskers, per row totalling 38. Contrary to this, a study by Dehnhardt (1994), the California sea lion used had five, seven, seven, seven, eight, and four, in each row. This could create differences between animals, especially in terms of movement and sensitivity (Dehnhardt et al. 2001; Glaser et al. 2011; Murphy, 2013). Other factors may also effect sensory abilities and movement, such as the size, age or weight of the animals, as well as their skull shapes. All these limitations were considered when choosing the sea lions for the data collection in ***Chapter Six: Task-Specific Whisker Movements in California Sea Lions.*** Lo, the California sea lion, who completed all three of the discrimination tasks, had no blunt whiskers, no evidence of rock rubbing and an identical number of whiskers on each side of the muzzle. In addition, Lo's whisker number matched those of other California sea lions that have been used in behavioural research (Dehnhardt 1994; Sawyer 2016).

Although Lo the California sea lion in ***Chapter Six: Task-Specific Whisker Movements in California Sea Lions*** was blindfolded, she did not have earphones. These are often employed to prevent picking up on auditory cues during experiments (Grant et al. 2016; Kruger et al. 2018). While some auditory cues might have been perceived during stimulus changeover, this appeared unlikely. Indeed the California sea lion did not go straight to the *target fish* in the texture and size discrimination tasks (as they did during the visual task), but felt many of the fish models with their whiskers in order to make a choice based on tactile information.

Some studies have also suggested that over-training of tasks might affect whisker movements (Grant et al. 2013; Dehnhardt and Kaminski 1995), where the animal might choose the most efficient way to undertake a task, rather than making natural whisker movements. However, in these studies, there was a small number of stimuli and only one task undertaken. In ***Chapter Six: Task-Specific Whisker Movements in California Sea Lions***, there were nine stimuli and obvious changes were observed in whisker movement or strategy throughout exposure to each task and stimuli. However, this is still a relatively small sample and constrained task. Developing tests in a more natural setting, such as looking at tactile exploration during a food preference study would not require training, and would further address this point. The ideal scenario would be to film wild animals making decisions about live prey items based on tactile information, but this would be extremely challenging, both experimentally and ethically.

Finally, since the number, arrangement, size, stiffness and structure of the hair shafts of mystacial vibrissae of Pinniped*s* show considerable variation (Ling 1977; Watkins and

Wartzok 1985), the results obtained here indicate that California sea lions can make task-specific movements of their whiskers, may not be true for other Pinnipeds. For example, the Harbor seal have undulating, oval vibrissae which, when not protracted forwards, have a larger angle of protrusion from the snout compared to sea lions. This difference in whisker structure would affect whisker sensing, and may impact whisker movement, positioning or sensitivity. Harbor seals also orient their whiskers asymmetrically towards the fish stimulus during the fish sweeping task in ***Chapter Four: Quantifying Whisker Movements in Pinnipeds***, therefore, they might be the least likely species to make task-specific movements. The Pacific walrus might be the next most likely species to make task-specific whisker movements, and I would recommend examining these next, due to them having extremely large IOF's and therefore more sensitive whiskers.

7.3 Active Touch Sensing, Foraging and Ecology

Chapter Three: Pinniped Whisker and Skull Morphology showed that aspects of Pinniped skull and whisker morphology do not map well to Pinniped phylogeny, therefore, ecological factors are likely to be associated with skull and whisker morphology in Pinniped*s*. It is challenging to investigate associations between phylogeny and ecology, especially as my sample sizes in ***Chapter Three: Pinniped Whisker and Skull Morphology*** are too small to conduct phylogenetic statistical analyses. Szalay (1981) recorded variation in vibrissae in primates and found that IOF area was more associated with phylogeny than function. However, Kratochvil (1968) correlated vibrissae number with activity patterns in small, terrestrial mammals such as true mice and rats, finding that nocturnal species have more vibrissae than diurnal species, concluding that as nocturnal animals rely less on vision, vibrissae are of greater importance to them for foraging and navigation (Kratochvil 1968). The association of whisker morphology and IOF area with function has been further supported by more recent literature in terrestrial mammals (Muchlinski et al. 2008, 2010, 2018; Grant et al. 2014, 2018), with nocturnal, arboreal mammals having larger IOF areas (Muchlinski et al. 2018) and more numerous, longer whiskers (Muchlinski et al. 2008, 2010, 2018; Grant et al. 2014, 2018).

This might suggest that animals in darker environments, such as Pinniped*s* in deeper waters, are likely to have more numerous, longer and more sensitive whiskers. Here, I found that larger eye sockets were more associated with foraging at deeper depths in the Phocidae. In Otariidae, larger IOF and larger eye sockets were more associated with shallower foraging depths. Therefore, the link between whisker-use and light availability was not clear across the Pinnipeds, and I suggest that feeding ecology and prey capture is likely to be more associated with whisker morphology and movement in Pinnipeds.

Vibrissae morphology has previously been linked with diet, as vibrissae have been seen to aid prey location and capture (Kemble and Lewis 1982). Numerous studies have also associated skull shape with feeding styles, diet and whiskers in Pinnipeds (King 1966; 1983; Adam and Berta 2002; Marshall and Bloodworth 2005; Marshall and Kane 2009). Indeed, I suggest that longer whiskers and larger IOF areas are more likely to be associated with Phocidae and Otariidae who predate on moving prey items, such as fish and cephalopods, especially in species who use pierce and grab or rip and tear feeding strategies (Figure 3.8). Therefore, perhaps whiskers that are more sensitive are needed for active hunting. Indeed, the whiskers sensory system of Pinnipeds is not only important for locating prey, but also for prey capture. We show in ***Chapter Four: Quantifying Whisker Movements in Pinnipeds*** that Harbor seals, California sea lions and Pacific walrus will all move their whiskers forward when presented with a fish and orient their heads towards it. These behaviours are likely to also be observed in the wild when catching fish. Indeed, Figure 6 in Milne and Grant (2014) shows California sea lions orienting their whiskers towards thrown fish, and they suggest that this is likely to be how the sea lions orient their head and whiskers towards swimming fish prey.

Whiskers are also associated with aiding prey capture in terrestrial mammals, such as shrews (Anjum et al. 2006; Munz et al. 2010) and rats (Favaro et al. 2010). Furthermore, small mammals with longer whiskers tend to be insectivorous (Muchlinski et al. 2018; Grant et al. 2018). The interaction between predator and prey requires both the whisker movements and resultant orienting movement to be fast. This has previously been described in shrews (Hoyle 1958; Camhi et al. 1978). Results in ***Chapter Six: Task-Specific Whisker Movements in California Sea Lions*** also show that California sea lions respond to whisker touches to make decisions very quickly, with all choices being made in under 0.35 seconds (except when investigating the large size fish model, which took 0.85 seconds). Grant et al. (2014) have also found this in Harbor seals, who also all made decisions based on whisker touches in less than half a second. These similarities seen here could suggest that the active use of whiskers allows sea lions to hunt and catch prey in a comparable manner to other whisker specialists, such as rats and shrews. The sensitivity and speed of their whisker movements and resulting head movements could also be essential for guiding the prey towards the sea lions mouth, similar to that seen in rodents (Brecht et al. 1997; Favaro et al. 2010).

Here in this study we see that California sea lions move their whiskers the most, and independently of head movements. Whereas Pacific walrus and Harbor seals, orient their whiskers and head together. California sea lions use their whiskers for navigating through complex environments (Kemble and Lewis 1982) and hunt fast moving prey (Lowry et al. 1990, 1991). This might be why California sea lions have such long, moveable, sensitive whiskers. Indeed, I suggest that feeding ecology is likely to be a key predictor of whisker sensitivity and control. However, it may also be worth mentioning that sea lions and seals are, themselves, also prey to larger marine mammals. Rats have been shown to detect predator movement initially in the upper visual field (Dean et al. 1988), with prey being detected in the lower visual field and by the whiskers (Dean et al. 1988; Comoli and Canteras 2000; Furigo et al. 2010). Sea lions could adopt a similar strategy, whereby the whiskers could gather the information necessary for prey capture, while vision scans for predators' threats.

As well as feeding and prey capture, whiskers are also used for social interactions such as snout-to-snout contact with conspecifics, breeding and mother-pup recognition (Peterson and Bartholomew 1967). Having increased sensitivity and the ability to actively sense by controlling whiskers movements could provide a major advantage to successful social behaviours; including making it easier for pups to find their mother in order to suckle or males selecting a potential mate for breeding. This may be more important in California sea lions and other Otariidae, due to them living in large colonial social groups in comparison to Phocidae, who tend to live in solitary or small social groupings (Riedman 1990).

7.4 Future directions and applications of active touch sensing research

The research described and completed in this thesis provides a strong body of knowledge from which to design future research questions on active touch sensing in Pinnipeds. As whisker length, shape, sensitivity and movement varies across the three Pinniped families, it would be interesting to examine task-specific movement capabilities in both the Phocidae and Odobenidae, as well as in other marine and terrestrial carnivores. As well as carrying on my research in active touch sensing in Pinnipeds, findings from my PhD research also has important implications for animal welfare, whisker mechanics and neuroscience, technology and robotics, and animal cognition.

Welfare and Enrichment

Many animals are held in captivity, but for marine mammals in particular, their welfare has recently come under heavy scrutiny. California sea lions are used in educational displays and receive many types of training. Therefore, it is paramount that their trainers and keepers continue to provide exceptional welfare and additional enrichment. Zoos are progressively involved in participating in research (Stoinski et al. 1998; Loh et al. 2018), with research in cognitive behaviour and animal welfare being increasingly popular (Makecha and Highfill 2018). In order to maintain high standards of animal welfare, environmental enrichment is a key element of animal husbandry. Across the literature, there is a staggering number of environmental enrichment definitions (Newberry 1995; Shepherdson 1998; Swaisgood and Shepherdson 2005). For the purpose of this section the definition widely cited by Shepherdson (1998) will be used which states that "*Enrichment is using animal husbandry to enhance the quality of care by providing environmental stimuli via psychological and physiological means, providing choices and stimulating species typical behaviours to enhance welfare in ones' environment*".

Different types of enrichment work better for particular species or for certain individuals, depending on their personalities or behavioural traits (Vazire and Gosling 2004; Swaisgood and Shepherdson 2005). There are five main types of enrichment structural (adding toys or new apparatus), food (hiding, variety), sensory (scents), social (different counterparts or mixed exhibits) or cognitive (puzzles or games) (Grindrod and Cleaver 2001; Hunter et al. 2002; Azevedo et al. 2007; Yeater et al. 2013; Samuelson et al. 2017). Different techniques, therefore, need to be designed and employed to try to stimulate individuals. Not all types of enrichment are deemed successful when it comes to marine mammals with cognitive enrichment being the most successful when compared to the other four types (Mackay 1981; Kastelein and Wiepkema 1998; de Azevedo et al. 2007; Clark et al. 2013).

Studies show that providing enrichment can reduce stress (Wood-Gush and Vestergaard 1989; Wemelsfelder 1991; Goldblatt 1993; Newberry 1995; Carlstead and Shepherdson 2000; Swaisgood and Shepherdson 2005), and giving animals choices of enrichment can reduce stereotypical behaviours and wanted behaviours, such as social interactions (Ross 2006). This thesis has demonstrated how whiskers movements are important to California sea lions as they use their whiskers to perform task-specific movements when presented with different sensory and tactile tasks. As cognitive enrichment is deemed as the most successful, using the findings here can help us design and implement new enrichment devices to stimulate more natural behaviours providing enhanced welfare. Understanding species' behaviour and cognitive abilities is extremely important for developing appropriate enrichment. No study has ever emphasized the importance of purposive and focused active touch sensing in animal whiskers, nor approached this from an enrichment point of view.

Sensory enrichment is used to stimulate an animal's senses encouraging them to access all areas of their environment and promoting natural behaviours. Scents are often used as a form of sensory enrichment, but tactile enrichment - using objects or devices that animals have to manipulate and interact with - is often not a common type of enrichment used in zoos. Introducing how keepers present the sea lions' food (sweeping, catching, or scatter feeding) and introducing different textured toys for sensory and structural enrichment could help promote more natural whisker movements, which in turn provides better welfare for Pinnipeds. Specifically, we might imagine that: i) introducing varieties of textures to Pinniped enclosures could be a useful form of sensory enrichment; ii) encouraging natural whisker movements, such as with fish-sweeping, could encourage natural sensorimotor behaviours; and iii) developing choice in a cognitive discrimination task, could be a form of cognitive enrichment. Further developing these ideas will help to inform zoos how to increase sensory and cognitive enrichment in their Pinniped enclosures, which would promote healthy brain development and reduce unwanted behaviours (such as stereotyping and aggression).

Whisker Mechanics and Neuroscience

Whisker resonance is thought to be important for texture coding with whiskers being swept over various objects causing unique whisker vibrations, creating intrinsic resonance frequencies (Neimark et al. 2003; Hartmann et al. 2003; Andermann et al. 2004; Wolfe et al. 2008; Rabey et al. 2014). Here we see the California sea lions push forward their whiskers and spread them out over the surface, during the texture discrimination task texture, possibly trying to pick up vibrations and exploit resonance frequencies texture (Hartmann et al. 2003). In addition whisker “sticks and slips” (spatially localised accelerations and decelerations of whisker tips) have also shown to be important when coding textured surfaces (Arabzadeh et al. 2005; Wolfe et al. 2008; Hires et al. 2013). California sea lion whiskers would likely generate large amplitude, high-velocity stick-slip events on the larger textured fish (irregular rough surfaces), and smaller amplitude stick-slip events on the smooth fish (regular smooth surfaces).

California sea lions could be using resonance or stick-slip events during the texture discrimination task to identify different textures. This had never before been suggested in Pinniped*s*, but they too like rodents, have a grid-like layout of whiskers which get longer rostro-caudally. Ways to investigate this might include i) mechanical testing of dissected whiskers by investigating their resonance frequencies, and ii) designing a texture study for use in the new Pinniped MRI (Magnetic Resonance Imaging) facility, opening in the next few years at the Marine Science Center, University of Rostock, Germany.

Indeed, sea lions might code tactile stimuli much like rodents. A recent study by Sawyer et al. (2016) identified that California sea lion brains have specific areas (somatosensory brainstem, thalamus, and cortex) used to process touch information. Furthermore, each individual whiskers on the muzzle has a unique, corresponding area within the animal's brainstem especially dedicated to it. These finding are equivalent to areas found within the human brain that relate to individual fingers (Sawyer et al. 2016) and areas of the rodent brain associated with whiskers (i.e. barrelettes in rat brainstem, barreloids in thalamus, and barrel cortex in rat, mouse and hamster) (Woolsey and Van der Loos 1970; Krubitzer et al. 2011). Findings in this thesis confirm that California sea lion whiskers play an important role in active sensation and further work should address sensory coding in these animals.

Technology and Robotics

Whisker number, shape, length and function are all likely to affect whisker sensitivity (Ling 1977; Dehnhardt and Kaminski 1995; Reep et al. 2001), and active control behaviours are likely to strongly affect sensory signals (Prescott et al. 2011; Miyashita and Feldman 2013). Whisker morphology, sensitivity and control are all important aspects of designing bio-inspired tactile sensors. Robotics has been used to demonstrate the power of active touch sensing (Stansfield 1986; Bajcsy et al. 1987; Roberts 1990). Bajcsy (1988) mentioned the importance of feedback to determine a change, based on where and how the sensory apparatus move next to maximise information from touch. This is observed here in the California sea lion, making alterations in their whisker movements, depending on the task type (texture, size or luminance) and stimulus position (i.e. during fish sweeping). Robotics could utilise the same strategies that we have observed in Pinnipeds; i.e. spacing sensors out and focussing them on to the surface in a texture task, and edge-following in a size or shape identification task (Fox et al. 2009; Sullivan et al. 2012). Using a biomimetic whisker system in robotics helps us to further understand how whiskers contribute towards an animal's spatial orientation and how animal brains gather information to produce behaviours based on tactile sensations (Pearson et al. 2007, 2010, 2011). Robots with whisker-like features could detect underwater currents, movements and pressure points (Soloman and Hartmann 2006a, 2006b, 2010; Schroeder and Hartmann 2012), and also be used to identify objects and textures (Fend 2005; Soloman and Hartmann 2006a, 2006b, 2010; Pearson et al. 2010; Sullivan et al. 2012). These types of tactile sensors could then be utilised in submarine robots, space rovers or search and rescue drones (Soloman and Hartmann 2006a, 2006b; Pearson et al. 2010, 2011).

Animal Cognition

Shettleworth et al. (2001) define cognition as being all the ways that "*animals take in information through the senses, process, retain and decide to act on it*." The studies in this thesis highlight the sensitivity and morphology of the sensors (see ***Chapter Three: Pinniped Whisker and Skull Morphology***), the movement abilities of the sensors (see ***Chapter Four: Quantifying Whisker Movements in*** **Pinniped**) and how California sea lions move their sensors to make efficient decisions (see ***Chapter Six: Task-Specific Whisker Movements in California Sea Lions***). To continue from this whiskers are likely to be involved in informing decisions, especially about foraging and prey capture; however, they may also play a role in social behaviours too (section ***7.3 Active Touch Sensing, Foraging and Ecology***). Cognitive processes, such as perception, learning and memory all inform decisions about mate-choice, foraging and focussing of attention (Shettelworth 2001). Whisker-touch in Pinniped is involved, to some extent, in guiding all of these behaviours; therefore, as well as being a specialised sensory system, the Pinniped whisker system also plays an important role in cognition.

Primates and humans are often used as models of cognition, especially looking at haptic sensing during discrimination and grasping tasks (Ling 1977; Stansfield 1986; Bajcsy et al. 1987; Roberts 1990; Hirons et al. 2001; Awter et al. 2002; Iqbal et al. 2005), due to their extremely sensitive and moveable fingertips, as well as their advanced cognitive abilities and large brains (Baron et al. 1990). Human fingertips make task-specific movements (Gibson 1962), with active touch sensing involving both movement and the ability to control the sensory apparatus being utilised to detect environmental tactile cues (Gibson 1962; Prescott et al. 2011). This thesis shows that California sea lions are also able to do active touch sensing. Moreover, the sensitivity and movement abilities of Pinniped whiskers is likely to be comparable with primate and human fingertips (Guic-Robles et al. 1989, 1992; Carvell and Simons 1990; Prigg et al. 2002; Arabzadeh et al. 2005; Kleinfeld et al. 2006; Wolfe et al. 2008). Therefore, Pinnipeds, especially California sea lions, are likely to be ideal candidates to use as a new model for haptic and cognitive research. Furthermore, the Pinniped whisker system should be involved in future cognitive experiments to precisely examine its role in perception, attention, mate-choice and foraging.

7.5 Final Conclusion

This thesis demonstrates that California sea lion whiskers engage in active touch sensing behaviours that are likely to maximise the relevant information gathered during object exploration. The work in this thesis demonstrates that Pinniped whiskers are prominent, sensitive and make purposive movements, and that California sea lion whiskers are also controlled independently of the head and can make task-specific movements. I suggest that active touch sensing is likely to efficiently guide foraging and prey capture in dark, murky waters in these animals, and potentially plays a role in social behaviours too. The complexity of whisker movements and their guidance of subsequent behaviours make me suggest that the California sea lion whisker system be used in future studies of animal perception, decision making and cognition.

8 Chapter Eight: References

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