Department of Physics, Chemistry and Biology

Master Thesis

The importance of acoustic enrichment for bottlenose dolphins *(Tursiops truncatus)* in human care.

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Nyckelord/Keyword:

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Contents

1. Abstract
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Keywords: acoustic enrichment, bottlenose dolphin, diel patterns, landmark use, passive acoustic monitoring, movement patterns.

2. Introduction
In recent years, animal welfare and environmental enrichment for zoo animals has become of great importance in the western world (Maple & Perdue, 2013). For every accredited zoo, environmental enrichment has become an institutional core value (Maple & Perdue, 2013). Barren captive environments can cause under-stimulation of the animal, which can lead to inactivity (Mason, 2006), and display of a less varied behaviour repertoire. This under-stimulation may also cause animals to behave in an abnormal way, e.g. displayed as stereotypies; this is often caused by a lack of resources or opportunities which enable the animals to behave in their

natural ways (Mendl, 2001). Stereotypies can in severe cases cause serious health issues (Christie, 2008), and are therefore undesirable. Increasing animal welfare is often done by providing environmental enrichment, aiming at keeping the animals physically as well as mentally stimulated and thus to improve their welfare.

It is suggested by Newberry (1995), that environmental enrichment should lead to an improvement in the biological function of the animal, and as a result its health and fitness should be improved. To make sure that an introduced enrichment is actually stimulating the animal in the way that it was intended and if it is thus improving its welfare, behaviour observations and analysis should be done. Economic costs and a lack of time are often the reasons why the effect of enrichments are not properly assessed (Newberry, 1995). Even if there are ways to analyse behaviours in an automated way, this is not always possible, because the test scene and the animals involved are too complex.

Aiming at creating an animal enclosure that is as close as possible to the natural habitat of that species, is not only done to improve welfare, but also has an important educational aspect, which zoological institutions must ensure (Fraser, 2009) (WAZA, 2005). Plants, logs and rocks can be used to create an exciting exhibit which in its turn can stimulate the animal’s senses and encourages natural behaviours (Frediani, 2009). However, to create an exciting captive environment which simulates the natural living conditions for a marine mammal species like the bottlenose dolphin is more challenging than for many of the terrestrial zoo animal species.

Generally dolphin pools are very barren, with almost no objects or structures in the water column. This is, by tradition, due to a strong focus on water quality and on the undisturbed circulation of the pool water, to ensure that faeces and urine produced by the dolphins are effectively brought to the filters (EAAM BD Standards and guidelines). Enrichment that is most often provided consists of mainly floating objects such as buoys and rubber balls. However, these objects leave the water column empty. Echolocation is partially a learnt behaviour (Tyack & Clark, 2000), and is an important and natural part of life for a dolphin, and therefore an empty water column and flat pool floor and walls do not stimulate their use of sonar; for wild dolphins sonar provides the main sensory input on their environment, and is fundamental for navigation, hunting and for exploration of their surroundings (Madsen & Surlykke, 2013).

2.1 The bottlenose dolphin

The most well-know of all small cetaceans is presumably the bottlenose dolphin (*Tursiops truncates)*. It has a wide distribution all over the world and is found in both tropical and temperate waters (Culik, 2010). The bottlenose dolphin is also well-known because of its frequent appearance in media and is the most common cetacean in dolphinaria (Jefferson et al. 2008). Its body length ranges from 2-3.8m and its body weight between 220-500kg (Bloch & Mikkelsen, 2000).

2.1.1 Natural habitat

Due to the wide distribution of this species, bottlenose dolphins exploit a wide variety of habitats. They are found in bays, lagoons, river mouths, seabed areas and occasionally travel up into rivers (Culik, 2010). Their habitat ranges from shallow tropic waters and estuaries to the deepest trenches of the open ocean, with temperatures ranging from less than 0°C to more than 30 °C (Wilson & Mittermeier, 2014). Many populations are found to inhabit coastal waters (Wilson & Mittermeier, 2014). They feed on a wide variety of fish and cephalopods. Certain populations are year round residents of a certain area, whilst other populations undertake large-scale seasonal migrations (Wilson & Mittermeier, 2014).

2.1.2 Communication

The bottlenose dolphin is a very social species, with group sizes of 2-15 animals, but large ‘super-pods’ of hundreds or even thousands of animals are regularly witnessed (Bloch, 1998; Wells and Scott, 2009). Dolphins communicate primarily with whistles, mainly in the audible frequency range (Janik & Slater, 1998). The most studied whistle type is the so called ‘signature whistle’. These whistles are individually distinctive and are believed to be contact calls and convey identity information in order to maintain group cohesion (Janik et al. 2006), which is particularly important when a free-ranging group lives in murky waters, but is also used when dolphins are separated in a pool complex (Wells, 2009).
Pulsed sounds are also used for communication purposes, and can be recognized by their frequency content and inter-click interval (or click repetition rate) patterns that are different from clicks used for echolocation (Blomqvist & Amundin, 2004).

2.1.3 Vision

Vision is important for orientation, foraging and social behaviours. Echolocation may be used to target an object, but in the last approach stage (within a meter), vision is used for close inspection as well (Herman, 1980). Bottlenose dolphins are able to discriminate between still and moving patterns very well, whilst their underwater vision is best on shorter distances (1m). The spectral sensitivity is highest at the blue end of the spectrum, but since bottlenose dolphins have few cones in their eyes, primary colours are not perceived as good (Dawson, Schroeder and Dawson, 1987; Madsen and Herman, 1980, cited by: Herman, 1980). Cetaceans show remarkably large ganglia in the retina; these large ganglia and the interneural connections between them make dolphins able to compensate for low light conditions (Herman, 1980).

2.1.4 Echolocation

Echolocation evolved independently in two mammalian groups, bats and toothed whales, or odontocetes. In both bats and odontocetes, echolocation is mainly used for orientation and foraging (Verfuss et al. 2009).

Odontocetes produce sonar clicks within their nasal passages by pushing air upward across the so called phonic lips, with rod-like dorsal bursae embedded inside (Ridgway et al. 1980, Amundin and Andersen 1983). There are two sets of phonic lips, and the bigger one on the right side is supposed to be the main source of echolocation clicks. These sonar clicks are then transmitted through the fatty melon on the dolphin's forehead, which creates a narrow beam of sound which emerges from the forehead of the dolphin (Cranford & Amundin, 2004; Cranford et al., 2011, Au 1993). The echolocation clicks produced by bottlenose dolphins typically are 50-150µs long and have a power spectrum ranging from a few kHz up to 150kHz (Au, 1993). Two peak frequencies are often seen, at 40-60 kHz and 110-130kHz (Au, 1993; Cranford & Amundin, 2004) and peak amplitudes vary between 190 and 228dB(Au, 1993). The echoes from the transmitted sonar clicks reach the tympano-periotic complex through a thin-walled area in the lower jaw, also called the acoustic window (Norris 1969; Au, 1993; Rigdway, 2000) via a fatty tissue structure called the mandibular fat body (Cranford, et al. 2011) Recent studies also show that sounds may enter the mandibular fat body via a gular pathway (Cranford, et al. 2011)., (Au, 1993; Ridgway, 2000). The hearing of the bottlenose dolphin has its greatest sensitivity between 40 and 100kHz (Au, 1993; Ridgway, 2000). Bottlenose dolphins wait for the echo to return before emitting the next click. Normally there is a lag time between receiving the echo and the emission of the next click, which is called the interclick interval (ICI) and is typically between 20-40ms (Au, 1993). The ICI at a 1m range whilst scanning the object is between 10-25 ms, about 50 ms from a distance of 20m and 175-190 ms from a distance of 120 m (Au, 1993). The ICI is 2-3 ms during prey pursuit or at close range (Au, 1993).

Bottlenose dolphins have excellent hearing, they possess three times more ganglion cells than the human ear and a longer cochlear channel, which enables them to hear and discriminate between high frequency sounds perfectly (Au, 1993; Ridgway, 2000). Even in a noisy environment, they are able to detect and classify weak signals (Au, 1993). The use of echolocation in dolphins triumphs over human-made technology; humans therefore started using this ability in their preference by training dolphins to detect mines and enemy divers during military operations (Au & Martin, 2011).

2.1.5 Click train types and phases

During orientation and prey pursuit tasks, various patterns in the echolocation pulses can be recognized. Two major phases are known, the search and the approach phase (Griffin et al. 1960). The search phase typically has the longest pulse durations and ICI, and is also referred to as 'scanning'. During the approach phase, the pulse duration and ICI decrease, which can be divided into an initial and a terminal part, the latter also referred as a 'buzz' (Surlykke et al. 1993, Kalko and Schnitzler, 1998). A study on harbour porpoises showed a linear decrease in the median ICI with decreasing distance (26-12 m), and revealed that porpoises lock on to a landmark during orientation tasks, and during the search phase (Verfuss et al. 2009). The approach phase starts after the echoes from a suitable prey are detected. The ICI in the initial part is distinctly longer than the ICI in the terminal part, which occurs at distances between 1.9 – 4.4 m from the prey (Verfuss et al. 2009). It is suggested by Verfuss and colleagues (2009) that at distances from 16 to 4 m bottlenose dolphins show a constant ICI and are in the initial part of the approach phase, when they are at distances greater than 16 m dolphins will initially range lock onto the end of the pool and not on the prey item (Verfuss et al. 2009). The terminal part of the approach phase, the buzz, occurs when harbour porpoises are at a distance between 1.9 and 4.4 m from the object, and a sudden drop in ICI can be observed, from around 50 ms to below 10 ms. In the last stage of the buzz phase ICI values of between 1.4 – 16 ms can be seen (Verfuss et al. 2009). In the study of Wisniewska et al. (2014), clicks with ICIs below 16 ms were classified as being part of a buzz.

2.2 Effects of captivity on sound production

A study comparing click-trains between captive and wild bottlenose dolphins reported that most click-trains from wild individuals showed a fluctuating type click-train with irregular ICI change and without increment or decrement, which is suggested to be used when dolphin scan their surroundings but are not locked onto a specific target. However, most click-trains from captive dolphins showed more monotonous ICI decrement, similar to decreasing type click-trains, and were suggested to be correlated to a target range, which is often absent in wild bottlenose dolphins (Akamatsu et al. 1998). Akamatsu and colleagues (1998) also found that captive bottlenose dolphins adapt their echolocation to short-range detection or navigation, which according to Wisniewska and colleagues (2014) is very similar to the stereotyped buzz behaviours displayed by wild toothed whale species. This suggests that buzz behaviour in close-range target perception is a deeply integrated part in toothed whale species, and that it is a critical key to biosonal-based interception of prey (Wisniewska et al. 2014).

2.3 Diel patterns

When it comes to whistle production, a distinct diel pattern was seen in a captive bottlenose dolphin group during the study by Therrien and colleagues (2012). During feeding and training sessions, whistle production increased and peaked in the late afternoon and decreased throughout the night. Similar findings were recorded in three aquaria in Japan, where the overall activity increased when human caretakers were present. Swim speed, respiration rate, production of clicks and whistles peaked in the afternoon between 12.00 and 16.00; these behaviours decreased at night between 24.00 to 03.00 (Fish & Mowbray, 1962 cited by Therrien et al. 2012). However, wild bottlenose dolphins inhabiting the Bermuda Pedestal show an increasing activity, more reported dives, and longer dives at dusk and at night which correlates with the migration patterns of their mesopelagic prey (Klatsky, et al. 2007). Wild Pacific bottlenose dolphins off the coast of San Diego county were found to forage and display social behaviours more at night than during the day, and they also travelled less during the night, which suggest that the night-time periods were utilized for foraging opportunities (Day & Defran, 1995). In other cetacean species, such as in harbour porpoises (*Phocoena phocoena*) in the Scottish waters, recorded echolocation clicks were all found to be significantly higher at night compared to day-time (Carlström, 2005). Also, clicks recorded in Risso's dolphin (*Grampus griseus*) off the coast of Southern California, suggest a higher foraging activity at night (Soldevilla, et al. 2009).

2.4 Objective

The aim of this study was to enrich the dolphin pool with good acoustically reflective objects that were suspended within the water column, in order to encourage echolocation use. This study evaluated if and in which way these objects were used by the dolphins, e.g. as acoustic landmarks, or play objects. This study also looked at general echolocation click production over a period of 3 months and analysed diel and swimming patterns.

2.4.1 Hypothesis

$H_0$1: the dolphins do not use the click loggers as landmarks

$H_0$2: The dolphins do not use echolocation to a large extent

$H_0$3: The echolocation activity is evenly distributed at night and during day-time

$H_0$4: The echolocation activity is not correlated to light levels

3. Materials and methods

3.1 Location and animals

This study was conducted in the dolphinarium at the Kolmården Wildlife Park, Sweden, from May 2014 till March 2015. In the dolphinarium nine Atlantic bottlenose dolphins (*Tursiops truncatus*) were kept during the time of the study, with ages ranging from 1.5 to 41 years.

The dolphinarium consisted of two public display pools that were connected with a holding pool. The water surface area was approximately 2000m^2 and the pools contained a total of 6400m^3 of water. The main observations were made in the biggest of the two display pools, also referred as "the Laguna". The Laguna had a water volume of 2500m^3, and a surface area of 900m^2. The water depth was 3m in the shallow area and 6m in the deep area. The holding pool was also used during this study, which was ca. 120 m^2 and 3.5m deep. This holding pool had an underwater lifting platform, by which dolphins could be stranded safely in cases of health inspections or medical treatment.

3.2 Experimental setup

Ten C-PODs (Continuous Porpoise Detectors ; Chelonia Ltd., UK; http://www.chelonia.co.uk/) and two PCLs (Porpoise Click Logger or AquaClick 100, Aquatec group Ltd., UK; http://www.aquatecgroup.com) were used to monitor the dolphins' echolocation clicks. Nine CPODs were attached to the bottom of the Laguna pool, and one to the bottom of the holding pool. The two PCLs were introduced in the Laguna later on during the study. The hydrophones of both instruments were suspended 70 – 100 cm above the pool floor. In contrast with the CPODs, the PCLs do not float and needed two floats to keep them suspended from the pool floor.

The CPOD electronics and batteries were contained in a 66cm long plastic tube, 9cm in diameter, and with a hydrophone at the top. Since they were air filled, they provided a strong echo when hit by dolphin sonar clicks. The CPODs automatically logged every click that was transmitted towards it and hence provided a measure of the echolocation activity. The PCL electronics and batteries were also contained in a plastic tube, 8.5 cm in diameter, and 62 cm long, and with a somewhat different design of the hydrophone at the top. Visually it also differed from the CPOD, being black whereas the CPODs are light beige. It was also filled with air, and hence provided a strong sonar target.

The animals were filmed by two CCTV Raspberry Pi cameras, one mounted in the roof and one placed in front of an underwater acrylic panel in the deep section of the Laguna. The roof camera, overviewing the major part of the Laguna, documented the dolphins' movement patterns, while the underwater panel camera documented their close range interactions with a few of the CPODs and one of the PCLs. The cameras were programmed to record continuously every day from 06:00 to 18:00. The recordings were split into 5 minute sequences. Every evening the video files were automatically stored on a local server.

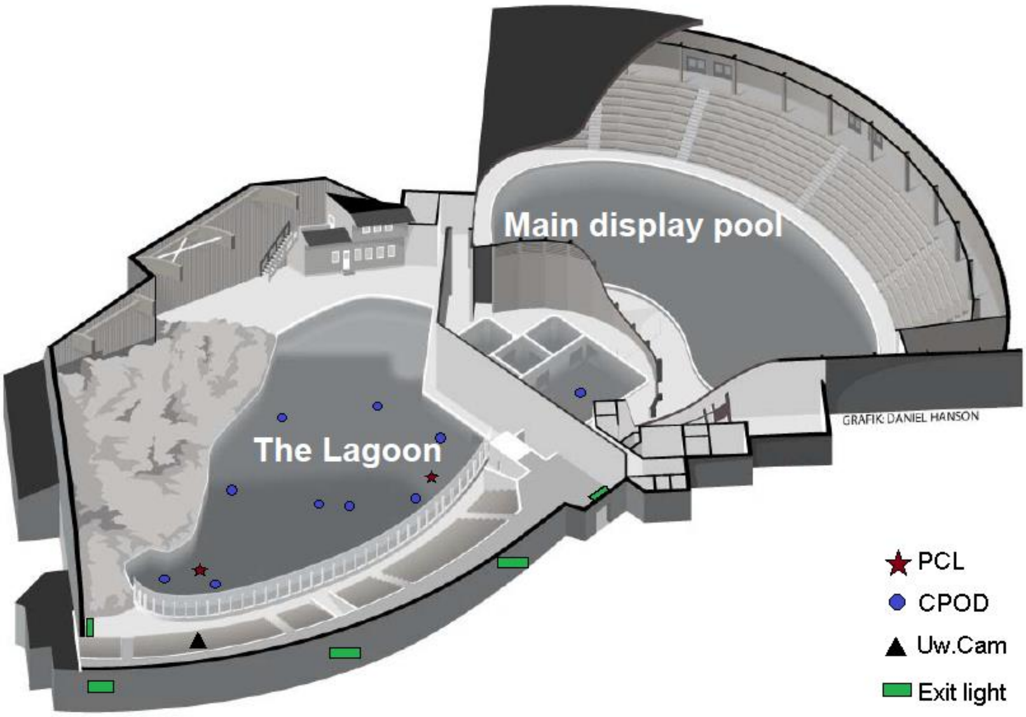

Image 1. Map of the dolphinarium. The roof camera recorded the main area of the Laguna pool. The underwater camera was located in the dolphin centre, underneath the tribune, as displayed in the image by a black triangle. The three

exit lights displayed on the bottom of the image were located over the doors to the Laguna, one at the top of the stands, and two at the bottom level. Exit lights were present in the dolphin centre as well, underneath the tribune, and visible through the underwater windows in the deep area of the laguna.

3.2.1 CPOD and PCL attachment

The CPODs and PCLs were attached to a ring bolt (Image 2) in 11 different positions on the Laguna pool floor and one in the holding pool (Image 1). A rope was attached through a hole in the bottom plug of the CPODs and PCLs, and a rubber hose was covering the rope to prevent entanglement. The rope was attached to the ring bolt in the pool floor with a shackle (image 2).

Approximately once every seven days, the CPODs and PCLs were taken out of the water by a diver. The SD cards were then taken out for analysis, and were replaced by empty SD cards. During this process the battery-packs and functionality of the device were checked as well.

When the devices had be started again, a diver attached the individual CPODs and PCLs in the same location as before, guided by a laminated map of the pool and attachment points, and by one or two people in a rubber boat.

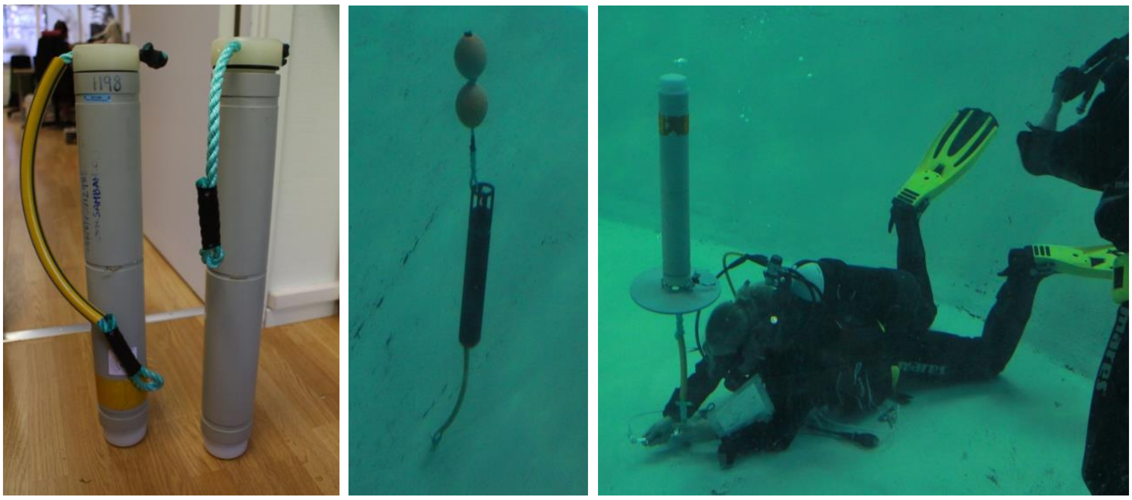

Image 2. The left picture shows two CPODs, upside down, the left one has been used in the deeper area or the pool, with the attached hose being 40cm in length. The right CPOD was used in the shallow area of the pool, with the rope being 20-30cm in length. The middle picture shows a PCL attached to one of the sloped areas in the pool; the two buoys attached are providing extra buoyancy to keep the device suspended from the pool floor. The third picture shows a diver whilst attaching a CPOD to the bottom of the pool. The disk seen at the lower end of the CPOD was later added to prevent the device from being bounced to the pool floor when dolphins played with the device.

3.2.2 Software

The behaviour analysis was done with the professional software Observer XT as well as Pocket Observer (Noldus Information Technology; http://www.noldus.com/). The CPOD data was pre-processed in custom-made software (Chelonia Ltd., UK; http://www.chelonia.co.uk/), after which selected parameters were exported to a computer for further processing. The PCL data was processed by the custom made prototype software Aquaclickview (Aquatec group Ltd., UK; http://www.aquatecgroup.com). The average clicks per hour recorded from both the PCLs and the CPODs were exported for further analysis. All data was analysed with Microsoft Excel and SPSS.

3.3 Observations

3.3.1 Habituation process towards the devices

In order to understand if and how the dolphins would respond to a novel object in their water column, behavioural observations were done one day a week, during the first three weeks after the first introduction of the CPODs in the dolphin pool. Five behaviours (see table 1) were scored continuously for every first five minutes of every hour (from 6.00 to 18.00). A total of 65 minutes for each week was analysed. The program Observer XT 12 was used to score the behaviours and the data was later exported into Microsoft Excel for further analysis.

Table 1. Ethogram used for behaviour analysis in order to examine the habituation process towards the devices.

Functional term	***Descriptive term***
Swimming past	Swimming past the device within approximately 1m distance, no clear interaction with the device.
Quick look	Swimming past the device whilst pointing the rostrum towards the device for a minimum of 1 sec and a maximum of 3 sec.
Approach	Swimming directly at the device, to a distance of at least 0.5m.
Investigation	Pointing the rostrum towards the device for at least 3 sec, swimming either stops or slows down.

Touch	Actively manipulating the device with the head, rostrum, teeth or body.

3.3.2 Movement patterns

The top view camera recordings were used to analyse the movement patterns. For analysis the pool was divided into 12 virtual areas (Image 3). The videos from after the introduction of the PCLs were used (19th of August). From Monday to Thursday, during every first 5 minutes of every recorded hour (from 6.00 to 18.00) the movement pattern of at least one and maximum three dolphins were recorded. As soon as the dolphins' rostrum entered a new area, the number of this area was recorded. The Observer XT 12 software was used to record the areas that the dolphins swam in, by naming the behaviours of the ethogram by the number of the areas. Automatically the time of entrance in a certain area, and time of entrance in the next was recorded within this software. A tranparent plastic sheet with a drawn outline of the pool, and the numbered areas within this pool was attached over the computer screen in order to visualize these areas. The dataset created by The Observer XT 12 was exported to Microsoft Excel for further analysis. In Excel calculations were done concerning the total spend duration and times of visit of each area. A total of 520 minutes of video recordings were used, and a total of 146 dolphin movement patterns were recorded.

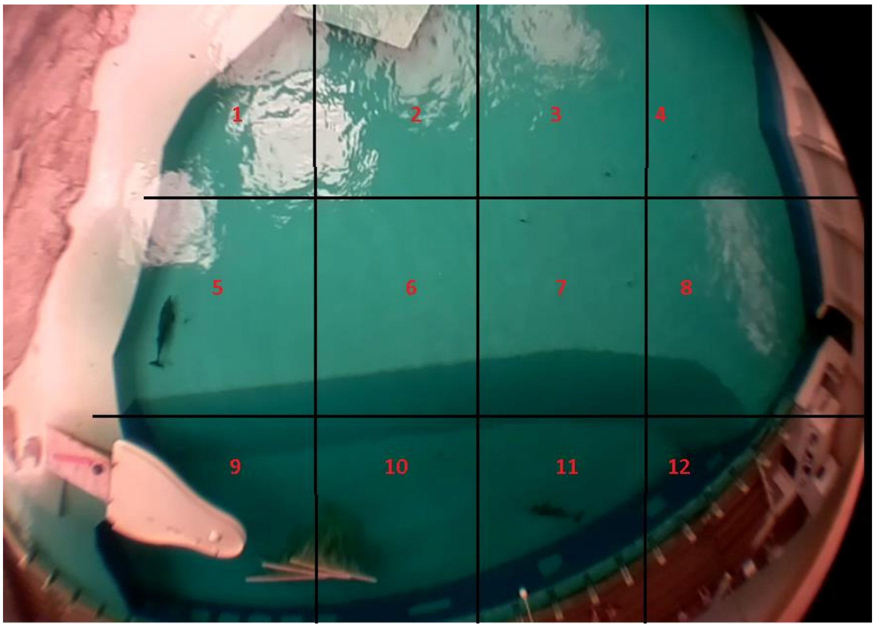

Image 3. Pool area blocks used to record the movement patterns.

3.3.3 Landmark use events

The AquaClickView software was used to find clicks trains directly aimed at the PCL. The inter-click interval (ICI) of these click trains was typically between 100ms and 2ms. Click trains with decreasing, increasing and constant ICIs were classified and used for analysis (image 4). Constant ICIs below 10ms were recognized as a buzz. Underwater video footage or footage from above was used to analyse the behaviour of the dolphin that emitted the click train towards the PCL at that particular moment. The start and end time of the click train, its ICI, the distance and the behaviour of the dolphin were noted in an Excel datasheet.

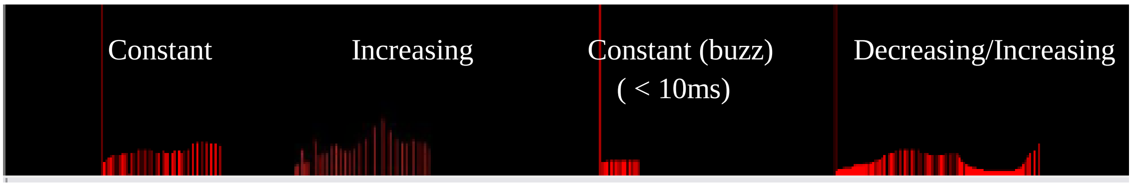

Image 4. Four types of click trains as displayed by the PCL software. The Y-axis represents the inter-click time in seconds.

3.3.4 Landmark use frequency

Several periods during resting were defined, and the data from PCL #002 located under the floating platform was used because this device was covered by the underwater camera. During these periods, the dolphin group was not interacting with trainers, staff, visitors or other enrichment devices such as rubber balls and were seen typically circling the pool clockwise at a slow pace, in groups of between two and six dolphins (Image 6).

During these events, the time that the dolphins were either within a range of 3 meters from the PCL, or pointing towards it whilst being present in the deepest area of the pool was recorded. Correspondingly with the times that the dolphins were present around the PCL, the AquaClickView software was used to find and display the type of click trains, the number of clicks and their ICI to get an idea of the frequency of landmark use during resting periods.

Image 5. Dolphins circling the pool during rest after the staff had left at 17.00. Notice that the dolphins congregate in small groups.

3.3.5. Landmark use during diel phases

To further investigate during which diel phases of the day landmarks where possibly used, the total number of clicks per hour recorded by the PCLs from the 19th of August to the 17th of October were imported into Microsoft Excel. This database was divided in four diel phases: morning (06.00-12.00), afternoon (12.00-18.00), evening (18.00-00.00) and night (00.00-06.00). The possible use of the PCLs as acoustic landmarks were measured as follows: during rest the dolphins were mainly swimming in rather fixed clock-wise loops in the eastern half of the pool, which includes the deep section. The PCLs would be passed at almost every such loop. Assuming that each loop lasted 20 seconds, a dolphin would make 180 loops per hour. One landmark check would require at least ~10 clicks, which would sum up to a minimum of 1800 clicks per hour, if a dolphin checks a PCL once per loop. With ≤1600 clicks/hr the PCLs would have been checked in 89% of the loops, with ≤1400 clx/hr in 78%, ≤1200 clx/hr in 67% and ≤1000 clx/hr 56%, ≤500 clx/hr in 28%, ≤100 clx/hr in 6%, ≤80 clx/hr in 4%, and ≤50 clx/hr in 3% of the loops. Of course it cannot be excluded that a dolphin used more than 10 clicks for a landmark check, so these numbers will only give a very rough picture of possible landmark use. No landmark use was defined at 50 or less clicks per hour.

3.4 Statistics

3.4.1 CPOD analysis

The data gained from the CPODs turned out very noisy due to the devices having too high a sensitivity, and even after reducing the internal gain as much as possible, the CPOD data still turned out very noisy. Therefore it was mainly used to get a general view of echolocation activity over time and to compare this between the different areas of the pool. The export function in the CPOD software was used to export the number of clicks per hour into a text file, which was then imported into an Excel file. The average number of echolocation clicks recorded with the CPODs was used to investigate the echolocation activity in the shallow area vs. the deep area. First an F-test was carried out to calculate if the variance was equal or unequal between these two datasets. This was followed by a two sample T-test, to investigate if there was a significant difference between the echolocation activity in the shallow and the deep areas, respectively.

3.4.2 PCL analysis

The Aquaclickview software allows all data to be exported as a text file, after which it was imported into an Excel file. The total number of clicks per hour was calculated and the synched date and time was listed. These datasets were then exported into SPSS for further statistical analysis.

Week comparisons

The total amount of clicks per week were compared with a one way ANOVA test, to investigate if a significant difference could be found between these weeks. A post-hoc Tukey test was carried out to find where the differences between the different weeks were.

Diel patterns

The PCL database with total clicks per hour was divided into 4 groups; morning (6-12), afternoon (12-18), evening (18-00) and night (00-6). These groups were compared with a one way ANOVA test, to investigate if a significant difference could be found in clicks per hour. A post-hoc Tukey test was carried out to find where the differences were.

4. Results

4.1 Habituation process towards the devices

4.1.1 Behaviour recordings

Presented below is a line graph (Fig 1) showing the behaviours aimed at the CPODs during the first 3 weeks, from the 2nd of July 2014 to the 23rd of

July 2014. A clear decline can be seen in the behaviours ‘touch’ and ‘quick look’ between the first and second week.

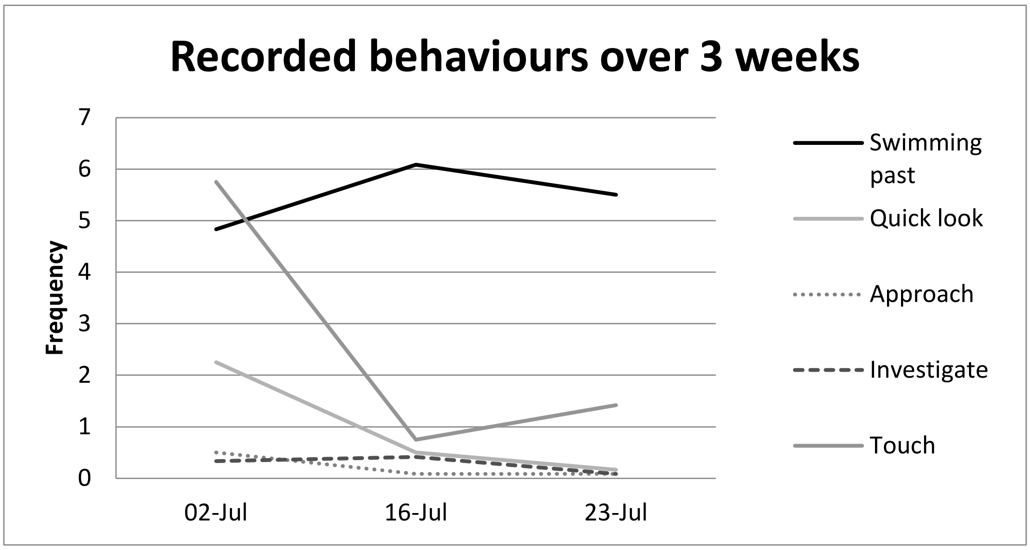

Figure 1. Five behaviours displayed towards the newly introduced CPODs were scored during every first day of the first three weeks. A total of 65 minutes per week were analysed.

On day one (2nd of July), the behaviours displayed towards the CPODs were highest between 6.00 and 9.00, where most incidents involved touching the CPODs, especially with the snout, but also pointing the snout towards the CPOD whilst swimming past it was commonly seen. The overall observed activity in this dolphin group was found to be the highest in the mornings, which coincided with the trainers’ arrival at 7.30, after which the dolphins are fed and the dolphins that are used in the daily dolphin shows are moved to the show pool. Four dolphins were kept in the Laguna during daytime. After most of the dolphins were moved to the other pool, the behaviours displayed towards the CPODs decreased substantially. Between 10.00 and 16.00 almost no behaviours were recorded and when the dolphins swam past the devices it was mostly with no clear interaction displayed towards the CPODs. After 17.00 more behaviours were recorded again, which coincided with the opening of the gate and the ‘show’ dolphins being present in the Laguna pool again.

4.1.2 PCL recordings

Figure 2 shows the PCL recordings as the average number of clicks recorded per hour over the first week after introduction of the device (the

19th of August 2014). The regression line indicates an overall decline in the average number of clicks recorded over time.

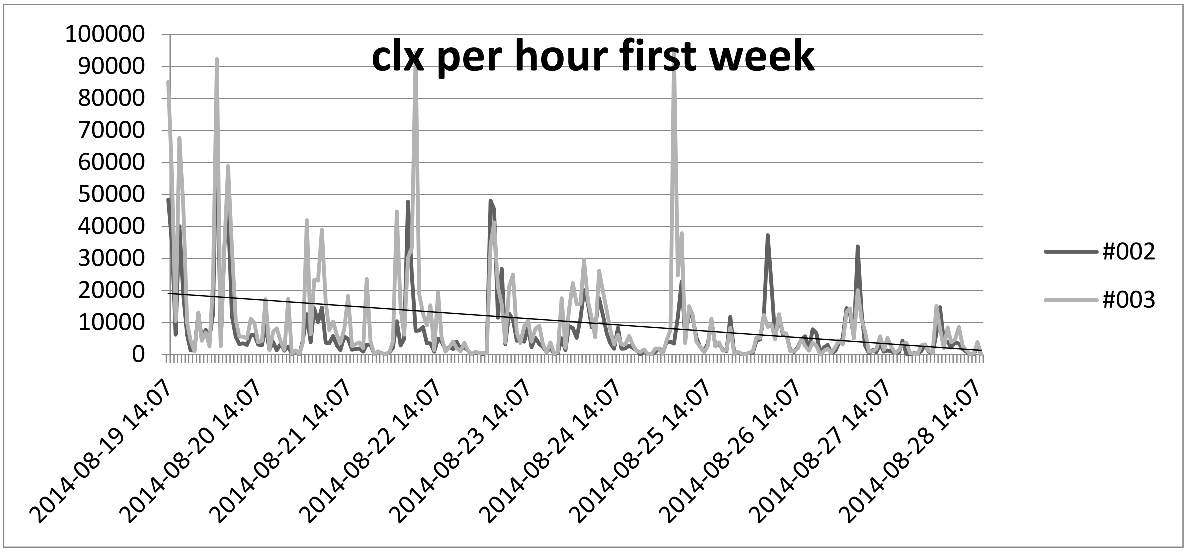

Figure 2. A line graph visualizing the average number of echolocation clicks emitted per hour during the first week after introduction of both PCL devices (PCL #002 and #003).The decreasing trend line indicates the average clicks per hour as recorded by PCL #003. There was a clear diel pattern in the click activity.

4.2 Week comparisons

Between week one and three a significant decrease was found in recorded average number of clicks per hour (0.01 < P<0.05), and between week one and seven (0.01 < P = 0.05) with a One-way ANOVA and post-hoc Tukey test. The average number of click per hour recorded in week one was significantly higher than those recorded in week three and seven.

Presented below are two boxplots showing the average number of clicks per hour in the seven weeks, recorded by PCL #002 and #003.

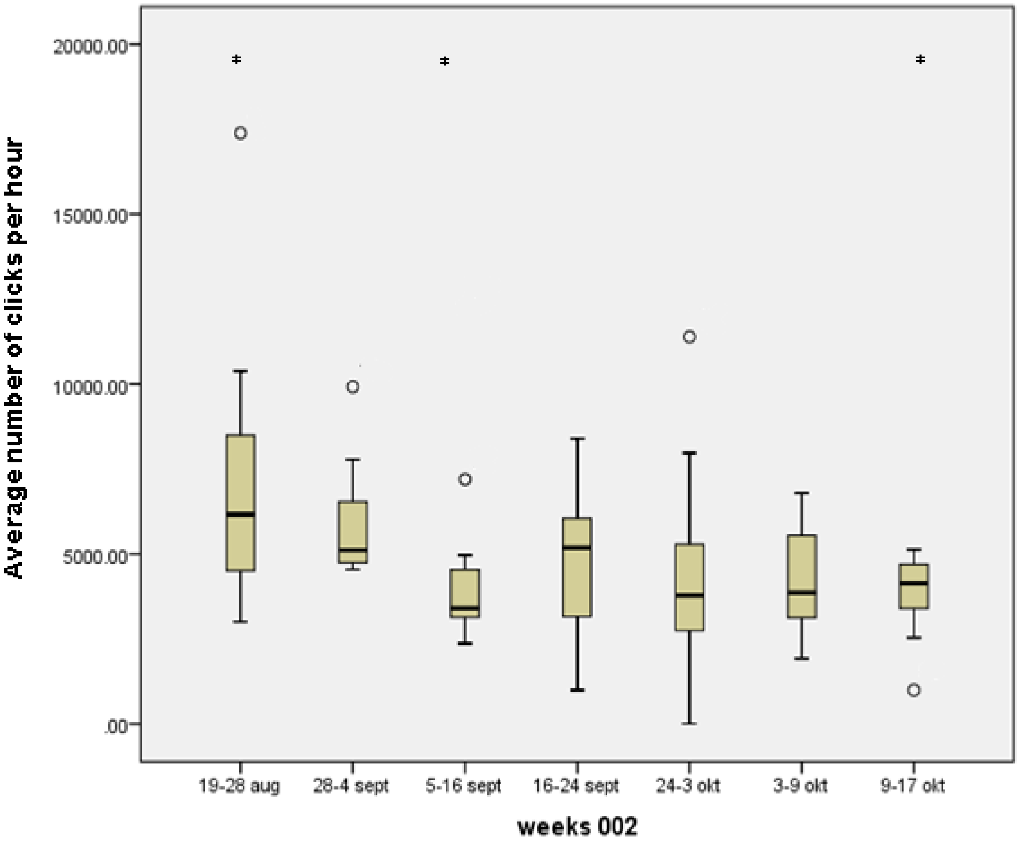

Figure 3. Boxplot presenting the average number of clicks per hour recorded every day for seven weeks, as recorded by PCL #002. The high outlier in the first week represents the average clicks per hour recorded during the first day after attaching the PCLs. A significant difference was found between the first week and week three and seven (represented by asterisks at the top of the plot). On the 28th of August, plastic disks were attached to the CPOD;, this change did not seem to influence the recorded clicks per hour.

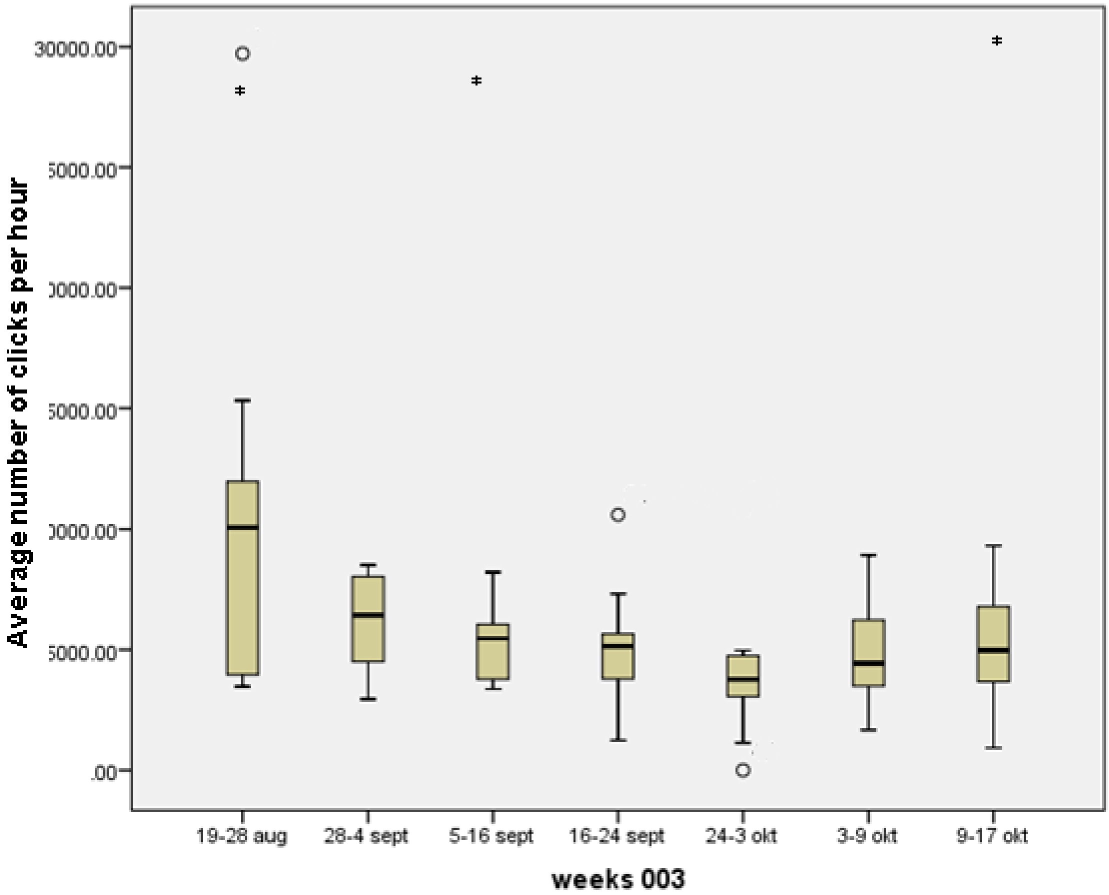

Figure 4. Boxplot presenting the average number of clicks per hour averaged over each of the seven weeks by PCL #003. The high outlier in the first week represents the average clicks per hour recorded during the first day after attaching the PCLs. A significant difference was found between the first week and week three and week seven (represented by asterisks at the top of the plot). On the 28th of August, plastic disks were attached to the CPODs; this change did not seem to influence the recorded clicks per day.

4.3 Diel patterns

4.3.1 PCL recordings

The results from the Two Tukey test of the comparison between morning, afternoon, evening and night are presented in Table 2. The average number of clicks per hour recorded by the PCLs from the 19th of August to the 17th of October was used for these calculations.

Table 2. The average number of clicks per hour recorded by PCL #002 were analysed by a Two Tukey test. The mean values are displayed in the subset groups, and are placed in a separate column if they differ from the other mean values. A significant difference is found between evening and the other times of day (the mean value of evening is placed in a column separated from the other mean values), and between night and afternoon.

clicks per hour #002

Tukey HSD

morning, afternoon, evening, night	N	Subset for alpha = 0.05		
		1	2	3
evening 18-00	400	1295.4900		
afternoon12-18	397		5306.9446	
morning 6-12	401		7553.7756	7553.7756
night 00-6	402			8728.2065
Sig.		1.000	.278	.785

Table 3. The hourly averages are used and presented in the table below. The mean values are displayed in the subset groups, and are placed in a separate column if they differ from the other mean values. All times of day are found to be significantly different from each other as recorded by PCL #003 as they are all placed in separate columns.

clicks per hour #003

Tukey HSD

morning, afternoon, evening, night	N	Subset for alpha = 0.05			
		1	2	3	4
evening 18-00	400	1978.4275			
afternoon 12-18	398		4822.5402		
morning 6-12	396			7201.1263	
night 00-6	400				9767.7050
Sig.		1.000	1.000	1.000	1.000

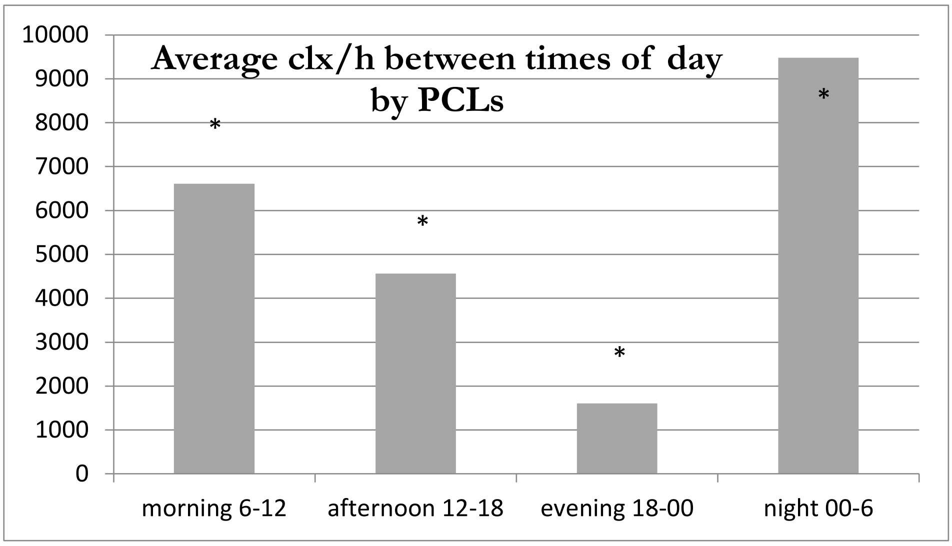

Figure 5. Average number of clicks recorded per hour during four diel phases, over a period of seven weeks. All four groups were found to be significantly different (represented by asterisks).

4.3.2 CPOD recordings

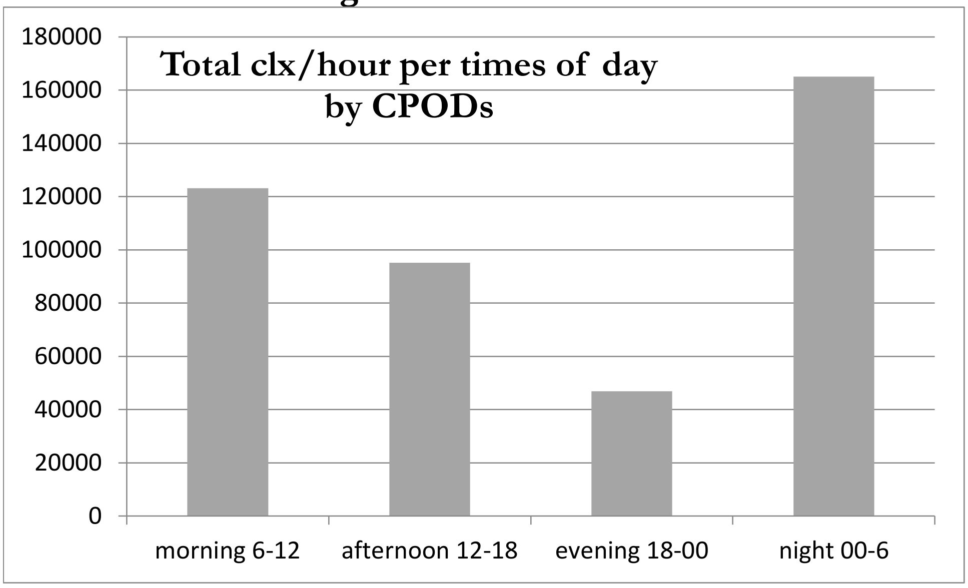

Figure 6. The average number of clicks per hour recorded during 4 six-hour diel phases, over a period of seven weeks by the ten CPODs. Note that the number of clicks in these recordings are much higher than in the PCL recordings, caused by the noise recorded by the CPODs.

4.3.3 Diel patterns September compared to October

Figure 7 shows the average number of clicks per hour in a week in August / September and a week in October. Between the 29th of August and 4th of September, the time of sunrise was between 05.36 – 05.50 and the time of sunset was between 20.01- 19.42. Between the 10th of October and the 17th of October, the time of sunrise was between 07.14-07.31, and the time of sunset was between 17.54-17.34 (www.timeanddate.com). Staff arrived around 7.30 and left at 17.00 daily.

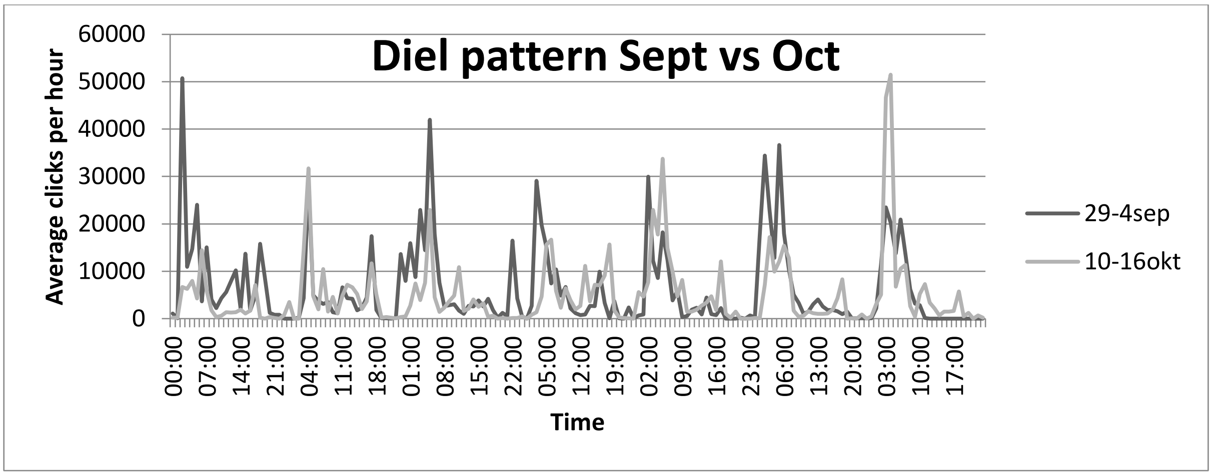

Figure 7. Average number of clicks per hour in a week in August / September and a week in October. Time of sunset and sunrise differs around two hours between the two compared weeks.; note that the diel pattern did not seem affected by this.

4.4 Movement patterns

Figure 8 shows the total duration spent in each of the 12 pool areas, and figure 9 shows the total duration divided by the number of visits in each area. In each of the cases, three areas in the deeper part of the pool (9, 10 and 11) show the highest duration. Also area 8, located at the gate towards the holding pool has a high duration.

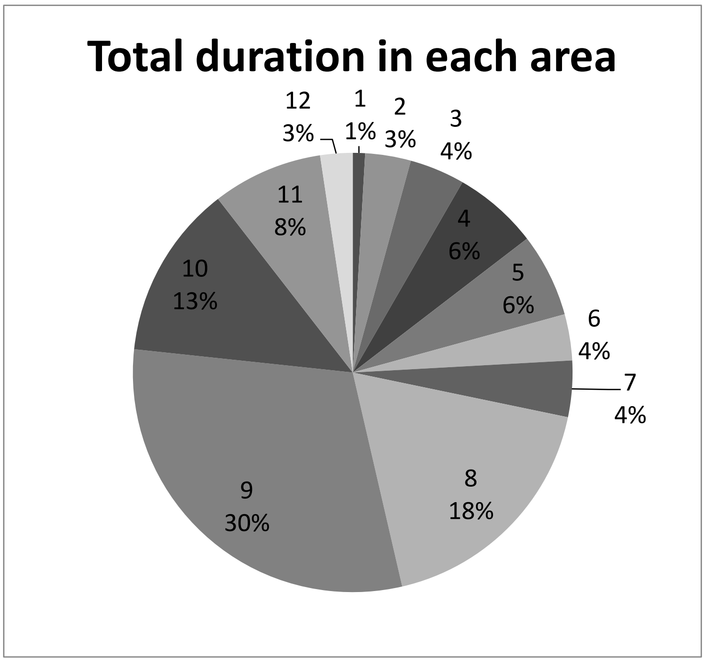

Figure 8. The total duration spent in each of the 12 areas.

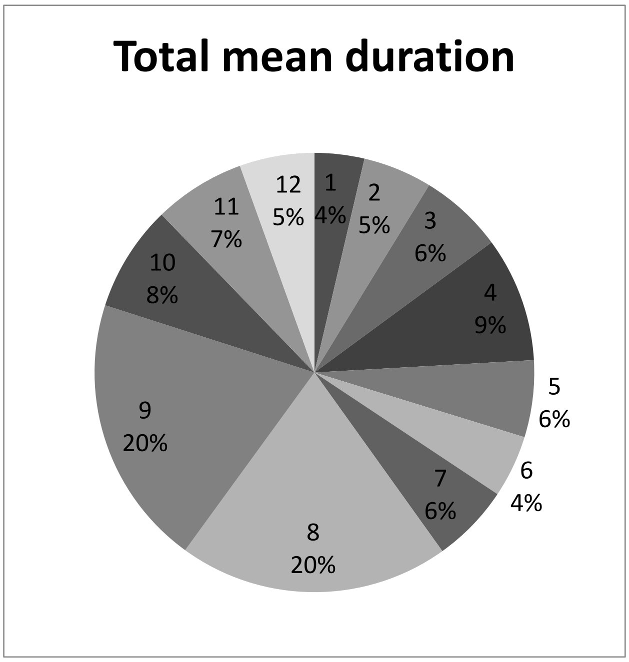

Figure 9. The total mean duration, relative to the amount of times visited in each of the twelve areas.

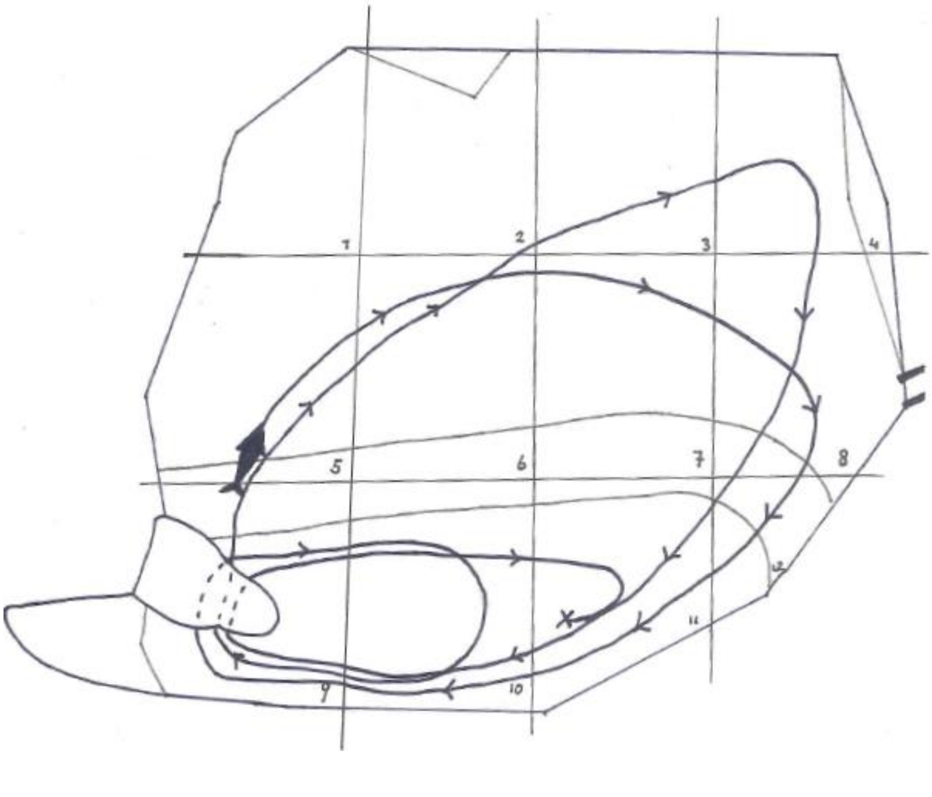

Image 6. Drawing of typical swimming tracks seen during rest, in this case of a group of three to four resting dolphins. The dolphins were often observed circling the whole pool or circling the deeper part of the pool. This swimming pattern was recorded on the 3th or October 2014 at 17.42 - 17.44.

4.5 CPOD locations

Represented below is a plot showing the number of clicks per hour, averaged over a period of seven weeks as recorded by the 10 CPODs in the Laguna. The recordings have been grouped between CPODs located in the shallow area, the slope and the deep area. The recordings from the shallow and the deep area have been compared with a two sample T-test, which indicated that the deep area had a significantly higher number of recorded clicks compared to recordings from the shallow area ($0.02 < P < 0.05$).

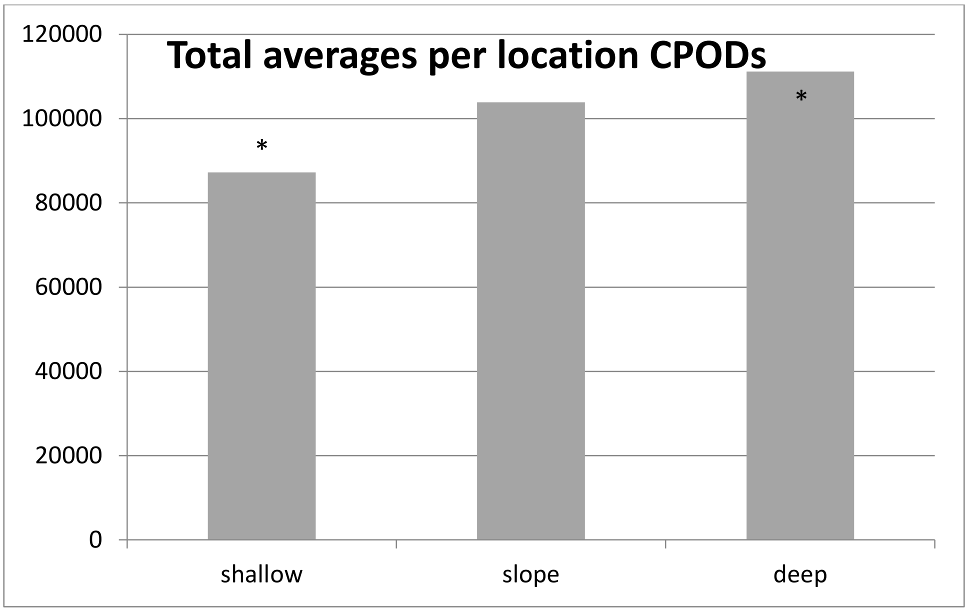

Figure 10. The total number of clicks per hour, averaged from three CPODs in the shallow, slope and deep areas, respectively. The number of clicks per hour was was significantly lower in the shallow areas than in the deep area (indicated by asterisks).

4.6 Landmark use events

A total of 33 click trains were recognized on the 19th of August (at 15.00), the 3rd of October (between 11.36 and 16.03), the 9th of October (between 10.51 and 14.27) and the 12th of October (between 9.16 and 9.18). A total of 101 seconds of click trains were investigated, and 87 seconds of video were used to investigate behaviours during these recordings.

In 17 events the click trains were recognized as decreasing ICI type, having an average ICI of 40 – 10ms, of which 12 of these click-trains ended with a buzz (ICI below 10ms). In three events the click trains were recognized as increasing ICI type, having an average ICI of 14 – 60ms. At 13 events the click trains were recognized as constant ICI type, with an average ICI of

29ms. Two constant ICI type click-trains were recognized as a buzz, having an ICI of below 10ms.

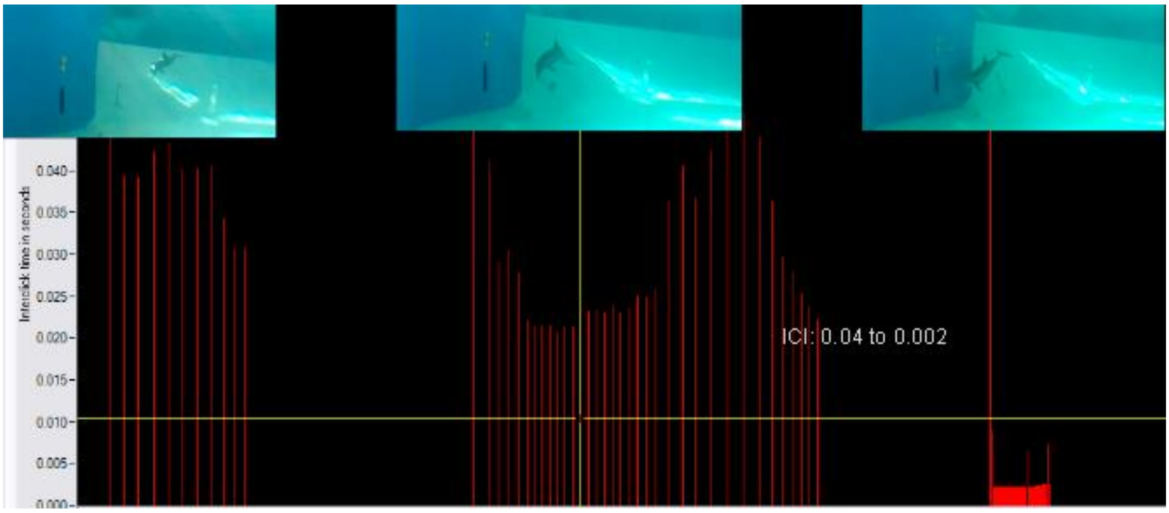

Image 7. Decreasing ICI type click train and separate buzz at the end, during approach and investigation of the PCL.

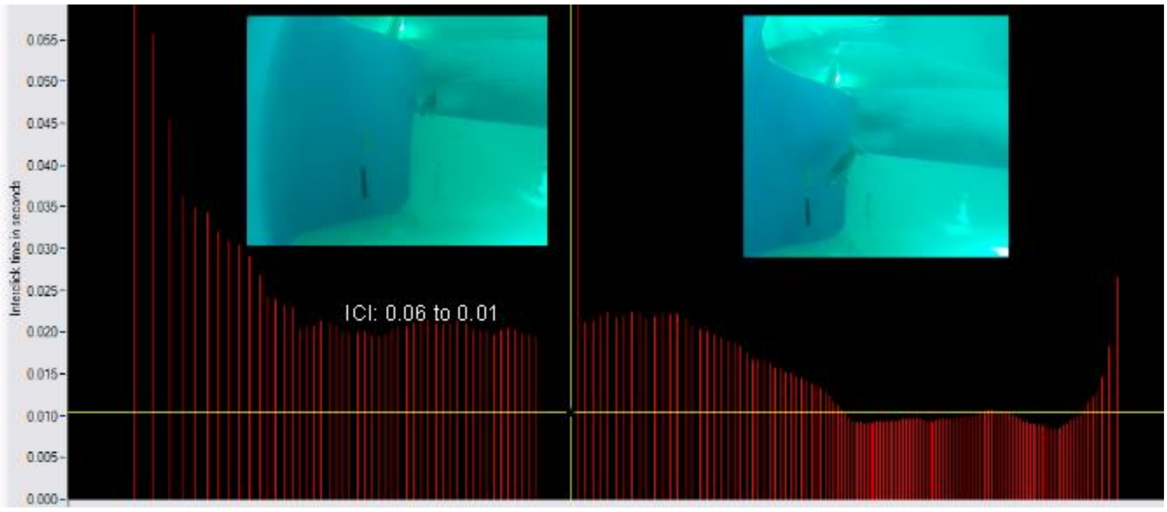

Image 8. Decreasing ICI type click train during approach, quick investigation and swimming past the PCL.

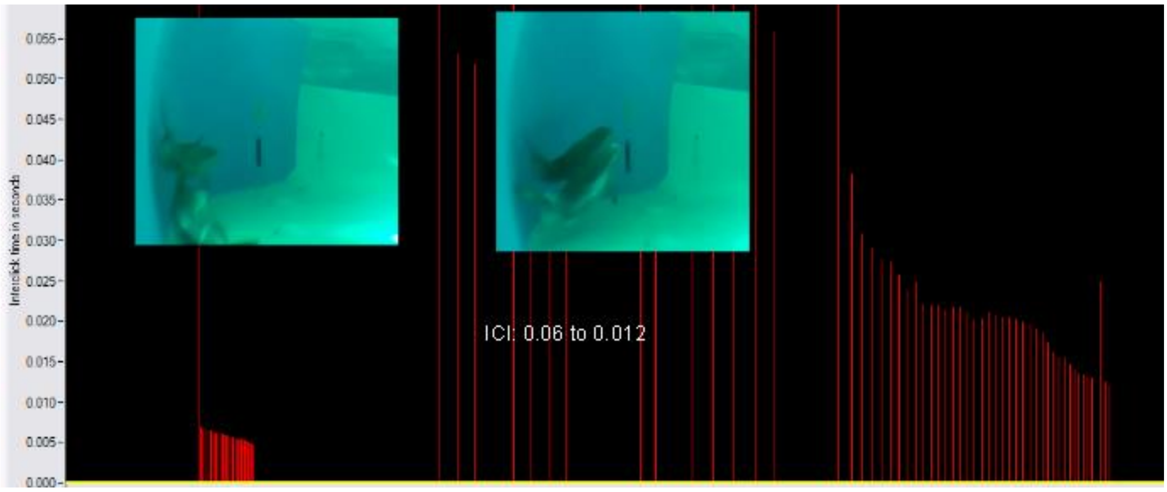

Image 9. Short buzz locked on target, followed by a decreasing ICI click train recorded whilst two dolphins swam past the PCL.

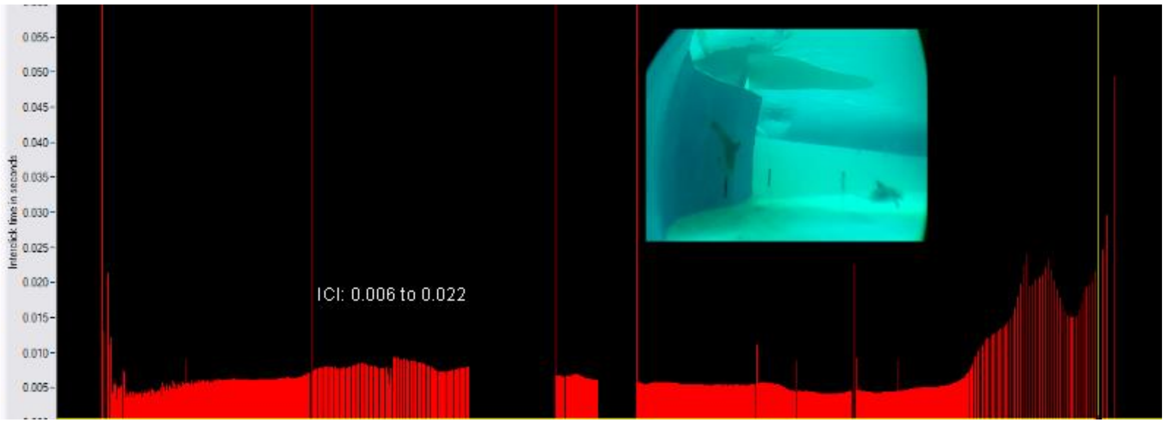

Image 10. Long buzzes recorded during a play session with the PCL.

Image 11. Variable ICI click trains recorded during a state of arousal, most likely not locked on the PCL. Trainers just appeared.

4.7 Landmark use

Moments of rest were used for this analysis, on the 3rd of October (between 17.15 – 17.40), the 9th of October (between 17.30 – 17.35) and the 12th of October (between 6.36 – 6.40 and 17.00 – 17.55). A total of 50 minutes of video was analysed, during which one or more dolphins were present in the deep area of the pool, whilst pointing towards the device for a total of 34.19 min. A total of 15 click trains were recorded during this period of time, having ICIs between 4 and 30ms; typically a constant, buzz or decreasing/increasing (not locked on target) type click trains were seen. Between 17.14 and 18.18 on the 9th of October, no clicks were recorded at all even though the dolphins were swimming past the device repeatedly.

4.8 Landmark use during diel phases

Presented below is a figure with the percentages of hours when no landmarks were used (<50 clicks per hour), when landmark use was a possibility (>100 – 1000 clicks per hour) and when landmarks were most likely used (>1800 clicks per hour) during morning (06.00-12.00), afternoon (12.00-18.00), evening (18.00-00.00) and night (00.00-06.00). The average number of clicks per hour recorded by the two PCLs from the 19th of August to the 17th of October was used for these calculations.

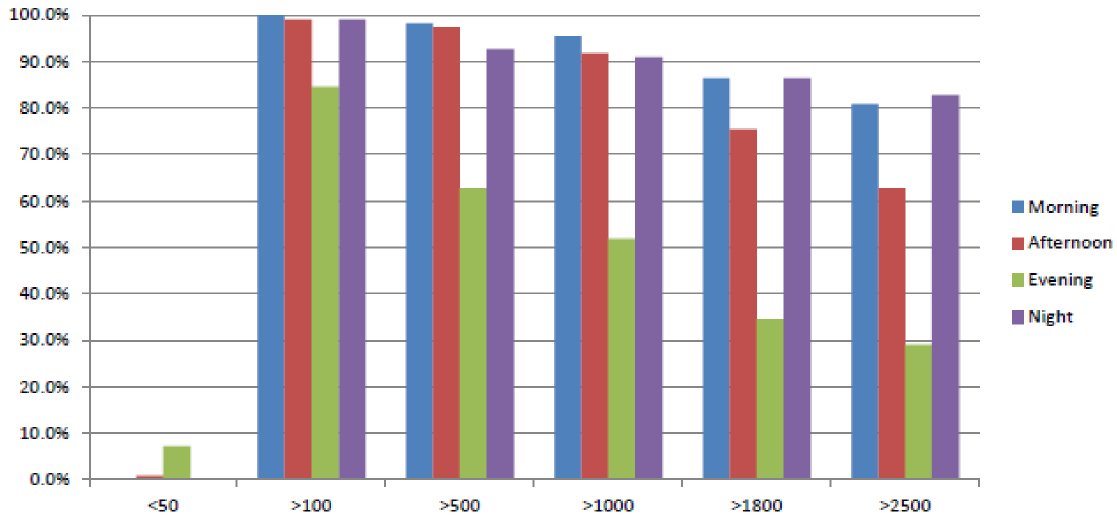

Figure 11. Percentage of hours with no landmark use (<50 clicks per hour) and possible landmark use during morning, afternoon, evening and night. Notice that the highest possibility of landmark use (>1800 clicks per hour) is highest in the night and morning and lowest in the evening, during rest.

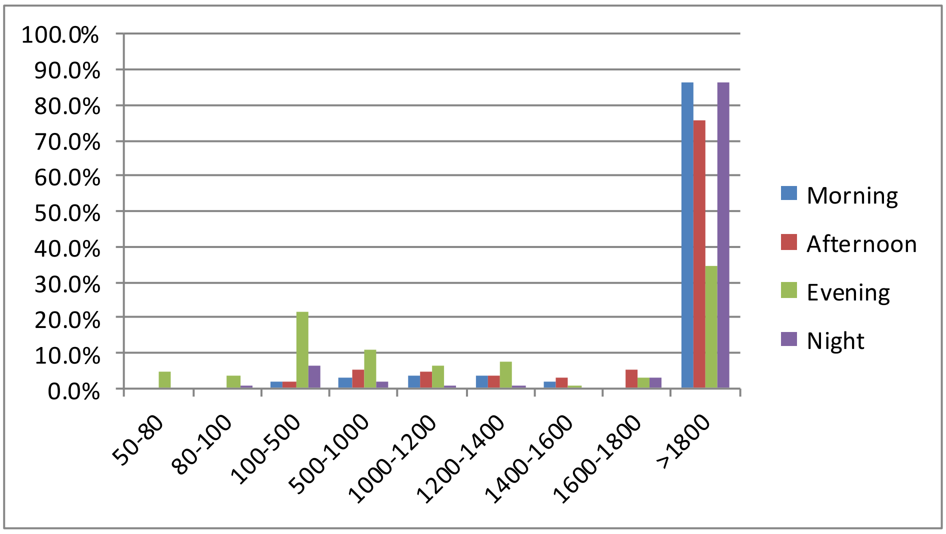

Figure 12. Percentage of hours with varying degree of the dolphins using the PCLs as acoustic landmarks. Provided that the dolphin is swimming in regular loops during resting in the evening and passing the PCLs once per loop, aiming 1800 clx/hr at them would indicate an echolocation check at each loop (according to the definition of a loop duration and clicks per passage), 1600-1800 clicks/hr in 89-100% of the loops, 1400-1600 clx/hr in 78-89% of the loops, 1200-1400 clx/hr in 67-78%, 1000-1200 clx/hr in 56-67%,500-1000 clx/hr in 28-56%, 100-500 clx/hr in 6-28%, 80-100 clx/hr in 4-6%, and 50-80 clx/hr in 3-4% of the loops. The graph shows that in e.g. the 22% of the evening hours (18.00 to 00.00), the dolphins aimed 100-500 clicks per hour at the PCLs, i.e. in 6-28% of the loops, and in 11% of the hours, they aimed 500-1000 clicks/hr at them, i.e. in 28-56% of the loops. In 34% of the evening hours the dolphins aimed >1800 clicks/hr at the PCLs, thus checked them in every loop. For the rest of the diel phases, the dolphins aimed >1800 clicks/hr at the PCLs in a majority of the hours; this includes, however, all other echolocation activities, which will mask possible landmark checks.

5. Discussion

5.1 Habituation process towards the devices

Results from the behaviour recordings showed a decreasing amount of behaviours performed towards the CPODs during the first three weeks after first introduction, indicating that the novelty of the CPODs decreased. The results showed that there was a high interest in the CPODs after they were first introduced on day one. During recordings on day one, most behaviours displayed towards the CPODs were recorded in the morning and decreased throughout the day. This low frequency of interactions may be due to the

fact that the dolphins were resting, during which they are typically seen swimming in a clockwise direction at a slow pace around the pool. At some periods of time none of the selected behaviours were displayed at all, which may be due to the fact that the dolphins were present and occupied in another part of the pool during interactions with the trainers or visitors. At 17.00 the gates between the different pools were opened, which was observed as a moment of high activity in the dolphin group. At 17.00 more behaviours were recorded once again. This higher activity at the end of the day coincided with the general high activity in the dolphin group, and the fact that more dolphins were once again present in the pool. It is possible that the dolphins that stayed in the performance pool showed more interest in the CPODs after having been separated from these novel objects for several hours during the day, making them exciting once again.
After this first week, a considerable decline in the behaviours ‘touch’ and ‘quick look’ was seen in the second and third week after the introduction of the CPODs. This decline was probably due to the fact that the dolphins habituated to the CPODs, i.e. that the novelty of the devices decreased because the dolphins had explored and played with them and over time, lost their interest. This habituation to novel objects is well known and documented in many species, and is one of the biggest challenges when it comes to improving the animals’ welfare over a longer period of time by the introduction of enrichments (Vick, et al. 2000). It is known that habituation occurs very quickly after repeated presentation of a novel object (Celli, et al. 2003). In this case the CPODs and PCLs were placed in the pool continuously from mid-July till mid-October, and only taken out of the pool for a short period on a weekly basis to extract the data. Even though the dolphins were observed to still show occasional interest in the CPODs, the behaviours, the frequency and patterns of these behaviours recorded during the first day were not observed again. A similar pattern is also described by Powell (1997) who studied the effect of environmental enrichment in captive ocelots (*Leopardus partialis)*. The process of habituation can be reduced by lowering the frequency and the duration of the presentation of the object (Celli, et al. 2003; Tarou & Bashaw, 2006), and novelty responses can be regained after removal or replacement of the object (Renner, et al. 2000). When looking at the other scored behaviours, not much change was seen in the behaviour ‘swimming past’. The behaviours ‘approach’ and ‘investigate’ were not often documented during any of the weeks, and not much change were seen in the performance of these behaviours during the weeks; this is most likely due to the fact that the dolphins often approached an object to touch or play with it, in which case only ‘touch’ was recorded, and not ‘approach’ or ‘investigate’.

Unfortunately no CPOD recordings could be used during these first 3 weeks, due to technical problems.

Several weeks later we were able to analyse the echolocation activity recorded by the two PCLs. In figure 3 the echolocation activity during the first week after the PCLs were first introduced is visualized. Several high peaks in the recorded clicks can be seen in this graph. The first peak originated from the moment the PCLs were first deployed in the pool by divers. The dolphins were observed to investigate the divers and the new objects intensely with their sonar. The other high peaks were normally recorded during night and early mornings, whereas the afternoons showed less echolocation activity. In this graph the trend line shows a decline in overall echolocation activity throughout this week, starting at the start of the week with an average of around 20000 clicks per hour, and ending the week with an average of around 5000 clicks per hour. This again indicates a process of habituation. These recorded echolocation click results match the findings of the behaviours displayed towards the newly introduced CPODs, which also showed a significant decline in investigative behaviours, and where echolocation was most likely used during the display of these behaviours as well. The dolphins were already habituated to the CPODs for several weeks, before the introduction of the PCLs. The latter have a distinctly different colour, and had two small buoys attached to the top, which probably had enough novelty to regain their interest. This finding suggests that changing the look and acoustic target profile of an enrichment will recover habituated behaviours. This agrees with the findings of Renner and colleagues (2000), which were mentioned previously. A week after the PCLs were introduced, the CPODs were provided with round plastic disks at the lower end of the devices. But this did not seem to encourage the dolphins to investigate the CPODs significantly more than they already did (figure 3-4). However, since the disks were at the lower end of the CPODs and the hydrophone at the upper end, the sonar inspection of the disks may not have been recorded. Also the sonar target strength of these disks was very low, which may be another explanation to the low interest. The decrease in novelty of the devices is also very clear in the week comparisons as recorded by the two PCLs. A significant decline in average recorded clicks per hour for each day was recorded between the first week and the third week after introducing them to the dolphins.

5.2 Diel patterns

Clear diel patterns have been recorded in many other dolphin species, both in the wild and under human care. Most documented diel patterns are based on recordings of the physical or acoustic activity of the dolphin, such as diving depth and frequency, or whistle and click production. The diel patterns recorded in wild dolphin species often correlate with the behaviour of their prey. Risso’s dolphins and harbour porpoises are found to forage mainly at night, and in these species more clicks are recorded during dusk and night time (Soldevilla, et al. 2009, Carlström, 2005§). But also wild bottlenose dolphins in the Bermuda Pedestal and off the coast of San Diego county show more diving, foraging and social activity during dusk and night time, indicating that also this species is more active at night, and utilizes the night-time for foraging opportunities (Klatsky, et al. 2007; Day & Defran, 1995). However, two studies recording the activity of bottlenose dolphins under human care found contrasting results. These studies both found that activity was highest during the afternoon. Whistle and click production, as well as swim speed and respiration rate peaked around the time the trainers were present during working day hours (Therrien, et al. 2012; Fish & Mowbray, 1962 cited by Therrien et al. 2012). These contrasting results suggest that management routines may influence the natural diel pattern of the bottlenose dolphin. Contrasting, during the present study, echolocation clicks were recorded continuously throughout the day for a duration of three months, and found a clear diel pattern pointing towards a significantly higher click production during night time and early morning (00.00 to 6.00). Average recorded clicks per hour decreased throughout the day, with lowest click activity recorded during evening hours (18.00 to 00.00). The dolphin group seemed to go into a resting mode after the trainers leave (>18.00), and rested until 00.00 – 03.00AM (6 to 8 hours). This resting pattern matches with the study of Ridgway (1990) who concluded that bottlenose dolphins rest approximately 33.4% of their day. The diel pattern of this dolphin group relates more to the diel pattern seen in wild dolphin species than those recorded in other captive bottlenose dolphins, which is interesting since this nocturnal activity is not related to foraging, as it is in their wild counterparts. The reason that higher click activity was recorded during night time might be due to a combination of the dolphins becoming active after having rested for 6 to 8 hours and the reduced visibility at night in an otherwise clear and light pool. Possibly some of the click trains were part of social communication and part of navigating in the pool whilst avoiding collision with the walls or the click loggers. Apart from several illuminated exit signs surrounding the pool area, the dolphinarium is dark. It is however very likely that these exit lights provide the dolphins with enough light to be able to navigate visually. Furthermore, the high night time click train activity seen in the present study does not seem to have been influenced by the time of sunset and sunrise, as can be seen in figure 7. In this figure a weekly pattern of average clicks per hour in a week in August/September is compared to a week in October, and the diel patterns in both months show a lot of similarities, and no obvious correlation with the day light cycle.

5.3 Movement patterns

It was observed that when the dolphins rested they often were in close contact with one or more individuals and typically swam in a circular pattern around the whole pool or deeper part of the pool. Outside of resting periods the dolphins were seen to swim faster, more scattered and show exploratory behaviours directed at the gate between the Laguna and the holding pool. Similar behaviours were also observed during the study of Ugaz and colleagues (2012), where in particular one dolphin was observed to swim in circular patterns around the area where trainers were present during the majority of the time. These findings match the results of previous studies on the movement patterns in captive bottlenose dolphins, reporting that dolphins spend the majority of their time swimming in a continuous circular pattern (Gygax, 1993, Ugaz et al. 2012). Ugaz and colleagues (2012) also found that dolphins in roofed/indoor facilities spend more time swimming in circular patterns and floating than dolphins in open facilities (outdoor). Dolphins in indoor facilities are also less active than those in open facilities, and the author of this study suggested that the shape and size of the pool might influence the type and intensity of the movement patterns (Sobel et al., 1994). When consulting fig. 9, it is shown that the dolphins in the Laguna spent most time (69% of 520 min.) in the deep part (areas 9, 10 and 11). They spent 18% of their time in area 8, which is where the gate is located. This result comes mainly from times when the gate was closed, due to ongoing performances in the show pool, or the separation of individuals in the adjacent holding pool due to health or mating issues. The dolphins have acoustic contact with the dolphins on the other side of the gate, and communicate directly with dolphins in the adjacent holding pool. They can also maintain visual contact through the gate with the individuals on the other side, but most importantly, they can keep an eye on the trainers and their activities in the fish kitchen, located close to the holding pool. As presented in fig. 10, the mean duration of time spent in each area can be seen. The dolphins spent 40% of the time in the four deep areas , 36% in the sloped/ shallow areas, and 24% in the shallow areas . Again the deep areas seemed the most popular, especially area 9 which is located in the left corner under a floating platform. One reason for this may be that three CPODs and a PCL were suspended in that corner, and the dolphins spent time investigating the devices. Another reason may be that during the circular patterns, both taking the longer and shorter route, the dolphins swim around the whole side in the deeper area, swimming around the full curve in area 9 and take a longer time to swim on to the next area. Still so, the deep areas, 9, 10 and 11 were the most visited by the dolphins, and a longer time was spent in these areas, suggesting a preference for the deeper part in the pool whilst swimming undisturbed or resting.

5.4 CPOD locations

Significantly more clicks were recorded with the CPODs located in the deep area. This relates to the findings of the movement patterns, showing that the dolphins visited and spent most time in the deeper part of the pool, especially in area 9, where three CPODs were located. There may be several reasons for this finding; first of all, more echolocation clicks were recorded in the deep area simply because the dolphins spent more time in these areas. A second reason might be that echolocation clicks were easier detected by CPODs lower down in the pool, because the hydrophone was located at the top of the CPOD, and the hydrophones of the CPODs in the shallow area might just be too high up in the water column. A third reason might be that the CPODs in the deeper areas were more interesting during play. When the dolphins played with the CPODs, they were often seen positioning themselves above the CPODs whilst pushing the CPOD down to the floor with the snout, which would then bounce up again. The CPODs in the shallow area might have been too close to the surface for this interaction. Also the CPODs in the shallow area had a shorter anchoring rope, which leaves less space for the CPOD to be manipulated by the playing dolphins.

5.5 Landmark use

Of the several types of click-trains analysed, 12 decreasing type click-trains were recognized to have a terminal phase below 10ms, which is classified as a buzz. These type click-trains relate to the findings of Verfuss and colleagues (2005; 2009) where range locking click trains, with decreasing ICIs from approach to terminal phase, were recorded in harbour porpoises during navigational tasks, indicating the use of acoustic landmarks. Also in bottlenose dolphins similar type of range locking click trains have been recorded (Verfuss et al. 2009). The click-trains recorded during this study were emitted whilst the dolphin was swimming past or approaching the device from a minimum distance of 5m. But, as seen from image 7 to 10, the behaviours displayed by the dolphins were mainly exploratory, where the dolphin approached the click logger, and quickly investigated it (pointing snout towards it, and often emitting a constant or decreasing like click-train). A total of 13 constant like click trains were observed where two were classified as a buzz. These constant like click-trains were mainly recorded during play behaviour, but also when dolphins swam closely past the click logger, which might suggest that they did not scan the environment for a target to lock onto, but that the target was already detected visually and inspected acoustically whilst swimming past it.

During rest a total period of 50 min. was analysed where the dolphins were in target range of the PCL for approximately 34 min. During these 34 minutes, 15 click trains were recorded. For a period of 62 min. the dolphins repeatedly swam past the devices, but no clicks were recorded, which indicates that for long periods of time the dolphins did not use the PCL as a landmark but manage to navigate past them, most likely by using visual cues. They were often seen to swim in close groups and might have also relied on each other instead. This found result in low echolocation activity relates to the diel pattern found in this dolphin group, with a low number of recorded clicks after the trainers left at 17.00, and until 00.00 – 03.00. The dolphins would have been able to use visual cues very well until sunset, but this does not seem to have an influence on the use of echolocation during rest, as discussed earlier in the paragraph ‘diel patterns’. This finding suggests that during rest, the dolphins are fairly quiet, and only on some occasions use echolocation for orientation. It could very well be possible that they are able to orientate with visual cues, even at night time when most of the lights in the dolphinarium are turned off, but the exit signs are still on as mentioned previously. A total of two illuminating exit signs surround the visitor’s tribune at the deep part of the Laguna, and can be seen from within the water through the high glass wall on this side. In the dolphin centre, located underneath the tribune, are also three exit lights which can be seen through the glass at a depth of six meters (Image 1.). Both will provide illumination of the pool. The eyes of cetaceans have large ganglia which makes them able to compensate for low light conditions, and the spectral sensitivity of dolphins is highest on the blue-green end of the spectrum (Herman, 1980), which makes it plausible that they might have had enough light to orient visually.

Coinciding with the found diel patterns and the frequency of landmark use during resting patterns is the possible landmark use during the different diel phases. As seen in figure 11 and 12, a similar pattern to that of the diel echolocation patterns is seen, where during the evening the possibility that landmarks are used is the lowest, but note that there is still a possibility since in around 35% of the evening hours more than 1800 clicks were recorded. In 52% of the evening hours, the dolphins aimed >1000 clicks at the PCLs, which would be a sonar check in 56-100% of the loops. Hence in many loops they passed quietly, and most likely relied on visual cues instead. Landmarks were possibly used most often during the night and morning hours, where between 80 to 90% of the hours contained more than 1800 clicks. However not all these clicks were used for orientation purposes, but were very likely part of communication (Blomqvist and Amundin, 2004), investigation and play with the devices, also during these more active times of the day the dolphins did not swim in stable loops.

5.6 Societal and ethical considerations

The dolphins at Kolmården are kept under more than sufficiently good conditions, under the permit from the Board of Agriculture and the Östergötland County Administration. The study was conducted under a permit from the Boards for research and ethics. Mats Amundin, who supervised the study, is the approved head of experiments.
The welfare of captive species is of great importance in modern society, and to improve the welfare of a species, the behaviour of the animal must first be studied in every way possible. This study has provided information for a better understanding of the echolocation behaviour of the bottlenose dolphin in a captive environment, and how this natural behaviour might be encouraged in order to improve the general welfare of the species in this unnatural environment. This study provides information on echolocation behaviour and daily activity patterns of bottlenose dolphins, which can be used and implemented by other dolphinaria.

6. Conclusion

When first applying the CPODs as enrichment devices in the water column, the dolphins displayed a range of behaviour patterns when investigating the devices, but soon habituated to the devices fairly quickly, probably because they soon became a static part of the environment. This also became clear in the echolocation recordings from the later introduced PCLs, where the number of clicks recorded were found to decline weekly, and the number of clicks recorded during the 3rd week proved to be significantly lower than those recorded during the first week. After this 3rd week the number of clicks recorded per hour levelled at around a mean of 5000 per PCL. Changing the look and acoustic properties of the devices resulted in regained exploratory and play behaviours apparently because of the novelty properties. The echolocation patterns seen throughout the day showed a clear diel pattern, with a lot of echolocation activity recorded from midnight to early morning, decreasing throughout the day, and reaching the lowest level after the trainers leave at the end of the day until midnight. This pattern is verified in both the PCL and CPOD recordings. Based on this low echolocation activity, it is suggested that the dolphins were mainly resting from 17.00 and until 00.00. During day-time resting they were often seen swimming in small groups in a clockwise circular pattern. They spent on average most of their time in the deep part of the Laguna, which correlated with more clicks being recorded there. During rest the dolphins were found to be fairly quiet, and did not emit much echolocation clicks, although they occasionally emitted a few clicks or a short constant or buzz-like click train when passing one of the devices. For long periods of time the dolphins did not use the devices as landmarks at all, but after calculating click-train use during overall evening hours, half of the time the dolphins may have used the devices as landmarks. The number of clicks recorded during rest did not seem to be influenced by the time of sun rise, sun set or season. Most click trains recorded during non-resting throughout the day appeared to be locked on target (i.e. the PCLs) with an average ICI of 20ms and emitted within a range of 5m. The dolphins generally emitted echolocation clicks when they approached and investigated the device, played with the device or swam closely past the device.

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