Analysis of sperm whale (*Physeter macrocephalus)* vocalisations in the Azores: coda repertoires and their behavioural context

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Abstract

Sperm whales are worldwide distributed cetaceans, demonstrating a highly complex social structure and sophisticated vocalisations. These vocalisations, made up mostly of click sounds, are used for foraging in great depths, but also to perform many other live functions. Short series of 3 to 40 clicks were termed codas, which were related to intraspecific communication, maintenance of social bonds and recognition between groups. Each sperm whale uses different types of codas, representing its coda repertoire, while many coda types and even complete coda repertoires are shared between different individuals and groups. Long term studies incorporating entire ocean basins were able to find differences and similarities between coda repertoires and to define *vocal clans*, that are, at least in some regions, sympatric. In the Azores, sperm whales are found year-round, yet few studies have been dedicated to coda repertoires and sympatric vocal clans had not yet been discovered. This thesis analysed the vocal repertoires of five sperm whales tagged with DTAGs during summer 2020. Via the IDCALL-method, codas were classified and hierarchically clustered into clades and possible vocal clans. The dataset was enlarged by incorporating previously analysed codas from the Azores, recorded between 1988 and 2010, and additionally compared to other regions in the Atlantic. Furthermore, DTAGs allowed to relate the coda production to behavior and movement of individuals. The coda types emitted by the five individuals tagged in 2020 were investigated for relations to dive phase, activity, depth, and diel pattern. Two individuals tagged in 2020 demonstrated a very distinctive coda repertoire that had former not been recorded. Their differences to the remaining repertoires documented in the Azores, which are characterized by the prevalence of regular-click-codas, suggests the existence of two sympatric vocal clans, that have previously not been described. Coda repertoires demonstrated independency from recording year, confirming the stability of coda repertoires in the Azores over time. Further, many repertoires exhibited similarities to the Caribbean EC2-clan. While contextual analysis did not show clear relationships of coda types in certain behavioural situations, it indeed affirmed previously observed individual differences of coda type use, additionally indicated increased frequency and diversity of codas during surface phases, non-foraging, and daytime hours. Future, persistent analysis and increase of datasets are required to confirm the observations about vocal clans and contextual relationships of coda production.

Keywords: Sperm whales – Azores – codas – vocal clans – context

Resumo

Os cachalotes são cetáceos cosmopolitas, demonstrando possuir uma estrutura social altamente complexa e vocalizações sofisticadas. Essas vocalizações, compostas quase inteiramente de sons de cliques, não são usadas apenas para alimantação em grandes profundidades, mas também para executar todas as outras funções da sua vida. As codas foram denominadas as séries curtas de 3 a 40 cliques, relacionadas a comunicação intraespecífica, manutenção de vínculos sociais e reconhecimento entre grupos. Cada cachalote usa diferentes tipos de codas, representando o seu repertório de codas, enquanto muitos tipos de codas e repertórios completos de codas são compartilhados entre diferentes indivíduos e grupos. Estudos de longa duração incorporando bacias oceânicas inteiras encontraram diferenças e semelhanças entre repertórios de codas e definiram *clãs vocais*, que são, pelo menos em algumas regiões, simpátricos. Nos Açores, os cachalotes são encontrados durante todo o ano, no entanto, poucos estudos foram dedicados aos repertórios de codas e clãs vocais simpátricos ainda não tinham sido detectados. Esta tese analisou os repertórios vocais de cinco cachalotes marcados com DTAGs durante o verão de 2020. Através do método IDCALL as codas foram classificadas e hierarquicamente agrupadas em clados e possíveis clãs vocais. O conjunto de dados foi alargado, incorporando codas dos Açores previamente analisadas, registadas entre 1988 e 2010, e adicionalmente comparados com outras regiões do Atlântico. Além disso, as DTAGs permitiram relacionar a produção de codas ao comportamento e movimento dos indivíduos. Os tipos de codas emitidos pelos cinco indivíduos marcados em 2020 foram investigados na tentativa de detetar relações com a fase de mergulho, atividade, profundidade e hora do dia. Dois indivíduos marcados em 2020 demonstraram um repertório de codas muito distinto ao que previamente havia sido registado nos Açores. As suas diferenças relativas aos restantes repertórios gravados nos Açores, que são caracterizados por codas regularmente espaçadas, sugerem a existência de dois clãs vocais simpátricos, que não foram descritos até agora. Os repertórios de codas demonstraram independência do ano de gravação, reforçando a estabilidade dos repertórios de codas nos Açores ao longo do tempo. Além disso, a maioria dos repertórios exibiu semelhanças com o clã EC2 das Caraíbas. Embora a análise contextual não tenha mostrado relações claras dos tipos de coda com os comportamentos, reforçou as diferenças individuais que haviam sido observadas anteriormente no uso do tipo de coda, além de ter indicado um aumento da frequência e diversidade de codas durante fases à superfície, atividades não relacionadas com alimentação, e durante o dia. Análises futuras e persistentes e o aumento do conjunto de dados serão necessários para confirmar a existência de clãs vocais e relações contextuais de produção de codas.

Palavras chaves: Cachalotes – Açores – codas – clãs vocais – contexto

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List of abbreviations

AIC	Akaike Information Criterion
AICc	Akaike Information Criterion corrected (for small sample size)
AoA	Angle of arrival
a.s.l.	above sea level
ATL	Atlantic Mexico
AtlPAN/Pan	Atlantic coast of Panama
AZO	Azores
BAL	Balearic Islands
BIC	Bayesian Information Criterion
C	Clade
CAR/Car	Caribbean
ch	chapter
cd	coda (unspecified if focal or non-focal)
Critfact/CF	factor by which a coda type's production is higher in one clade than in any other clade to be considered an ID coda
dB	decibel
DOP	Department of Oceanography and Fisheries
DTAG	digital acoustic recording tag
EC	Eastern Caribbean
EEZ	Exclusive economic zone
F	Focal coda (produced by the tagged whale)
GOM/GoM	Gulf of Mexico
GPS	Global Positioning System
GrpRep	Group repertoire, all codas recorded during one day/ by a potential social unit
hrs	hours
Hz	hertz
Ice	Iceland
ICI	inter-click interval
ICL	Integrated Completed Likelihood

ID	identification
IPI	inter-pulse interval
kHz	kilohertz
km	kilometre
m	metre
max	maximum
min	minutes
minrep/MR	minimum number of group repertoires to generate a clade
ms	milliseconds
Nfcd/NF	Non-focal coda (produced by another, not tagged sperm whale)
Pa	Pascal
PCA	principal component analysis
photo-ID	photographic identification via capture-mark-recapture analysis
R/REG	regular spacing between coda clicks
RHIB	rigid hull inflatable boats
s	seconds
SaS	Sargasso Sea
SD	standard deviation
Sw/Pm	Sperm whale/ Physeter macrocephalus
TDR	Time-depth-recorder
vs	versus
°	degree
°N/°O/°S/°W	degree of geographic orientation
n°	number
+/++	extended interval between coda clicks

1. Introduction

1.1. The sperm whale

The sperm whale (*Physeter macrocephalus*, former *P. catodon* Linnaeus 1758), the largest species of the toothed whales (*Odontoceti*), is the only living representative of the *Physeteridae* family (Jefferson et al. 2015). This species is known to be extreme in many aspects of its biology and behaviour, showing the largest sexual dimorphism of all cetaceans: while males reach an average length of 16 m, with a maximum of 18 m, females measure on average 11 m, with a maximum of 12.5 m (Clarke 1956; Rice 1989; Whitehead 2018). Sperm whales forage at great depths during extended dives (average 30–45 min and 300–800 m) (Whitehead 2003) and produce the highest levels of sound (max. 239 dB) (Jakobsen et al. 2021). In terms of their appearance, they are also unique and unmistakable: the enormous, quadrangular head makes up one-third of their body length; the very narrow lower jaw holds erupted teeth (Rice 1989); the dorsal fin is rounded and low, followed by various humps leading to the fluke, that they expose over the water surface before deep dives (Whitehead 2003); the body is dark grey, often appearing dark brown in colouration and deeply wrinkled (Rice 1989; Carwardine 2019) and the single blowhole is situated at the front on the left side of the head (Carwardine 2019).

1.2. Distribution, Movements, Population

Often referred to as a cosmopolitan species with worldwide distribution, sperm whales occur from the tropics to the pack ice edge and are even found in relatively enclosed areas as the Gulf of California, the Gulf of Mexico, or the Mediterranean Sea (Whitehead 2003; Engelhaupt et al. 2009; Irvine et al. 2017; Figure 1).

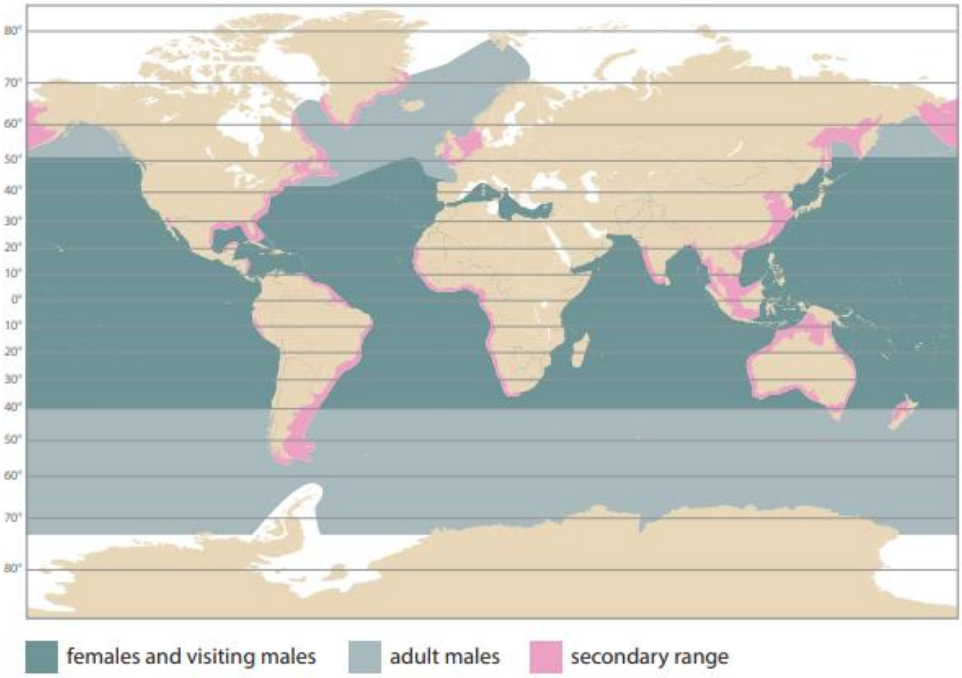

Figure 1: Worldwide distribution of sperm whales, Physeter macrocephalus. From: Carwardine 2019.

Nevertheless, the species does not occur uniformly over the oceans (Whitehead 2003). Unlike baleen whales (*Mysticeti*), sperm whales do not perform predictable, annual migrations between their feeding and breeding grounds, but rather undergo opportunistic, continuous movements (Lockyer & Brown 1981; Whitehead et al. 2008; Engelhaupt et al. 2009), which seem to be orientated mainly by the availability of food (Whitehead 2003; Gero et al. 2007). In constant search for their primary target prey, deep-sea cephalopods, sperm whales mostly use deep, oceanic waters to feed, rarely entering the continental shelf zone (Whitehead 2003). Together with other oceanographic features, highly productive oceanic waters are believed to be determinant to aggregate sperm whales in significant numbers (Jaquet et al. 1996; Whitehead 2003). Those “grounds” were already known and exploited by American whalers (Rice 1989; Whitehead 2003).

Sexual differences in sperm whales are not only found in their morphology, but also in their distribution, movements, and life history (Gero et al. 2007). After reaching maturity, sperm whales present the largest geographically sexual segregation in the animal kingdom (Carwardine 2019): Females form the so-called *social units*, consisting of long-term relationships between adult females, accompanied by calves and immatures of both genders (Whitehead & Kahn 1992). Social units live in tropical to temperate waters (between 40°S–50°N) (Rice 1989; Whitehead 2003; Figure 1). Females’ ranges are about 2,200 km but they are capable of undertaking occasional large-distance movements of over 4,000 km (Kasuya & Miyashita 1988; Jaquet et al. 2003;

Whitehead et al. 2008). Males separate from their social unit as soon as they are subadults and perform much longer journeys to polar regions, where they establish their feeding grounds (Gero et al. 2007; Teloni et al. 2008). After reaching sexual maturity, adult males regularly return to lower latitudes to breed, roaming between several female groups, apparently not including their genetically close relatives (Weilgart & Whitehead 1997; Lyrholm et al. 1999; Whitehead 2003). Home-ranges of adult males have not been quantified but are thought to be much larger than those of females (Whitehead 2003). Given the oceanwide lack of genetic variation, it was suggested that males even alternate between ocean basins for mating (female philopatry and male dispersal) (Lyrholm et al. 1999). However, other studies demonstrated site fidelity in adult males for long periods of time (van der Linde & Eriksson 2020; Girardet et al. 2022). Significantly more data has been collected for females, which evidence a strong grade of philopatry to geographical areas (Whitehead et al. 1991; Engelhaupt et al. 2009; Girardet et al. 2022).

In the Azores, sperm whales are seen year-round; although individual social units do not stay permanently in the area, instead undergo small to large-scale movements between and beyond the archipelago (Matthews et al. 2001; Magalhães et al. 2002, Silva et al. 2014; Steiner et al. 2015). The mean residence time of individual whales has been estimated to be about 3 weeks (Boys et al. 2019). Most sightings of sperm whales are females and their young, while occasionally, large males are also seen, solitary or acompanying females, indicating that the region is not only used as a feeding but also as a breeding ground (Pinela et al. 2009; Silva et al. 2014). Photo-identification-analyses (photo-ID) indicated movements between Macaronesian waters (Steiner et al. 2015), and records between the Azores and Norway (Steiner et al. 2012) and the Azores and Bahamas/Mexico (max. 6,200 km, Mullin et al. 2022). Based on photo-identification records, Boys et al. (2019) modeled a super-population of ~1,470 whales, of which about 300 individuals visit the area around Faial and Pico during summer. A higher population is expected for the whole Azores archipelago (Boys et al. 2019).

Larger-scale population numbers are more difficult to estimate, given the deep-water habitat preferences and extended periods sperm whales spend under water. Rice (1989) reported approximately 190,000 individuals for the North Atlantic and 1,900,000 worldwide (with pre-whaling numbers of about 3,000,000 individuals), while Whitehead (2002) calculated only 360,000 individuals worldwide (pre-whaling estimate of 1,100,000 individuals).

1.3. Feeding strategies

Sperm whales spend 75% of their daily life foraging (Whitehead 2016).

During the whaling period, the analysis of dead specimens enabled the identification of squid marks on sperm whale heads, and studies of stomach contents revealed plenty of information about their diet (e.g., Clarke et al. 1993). Although species of giant (*Architeuthis spec.*), colossal (*Mesonychoteuthis hamiltoni*) and jumbo squid (*Dosidicus gigas*) have been repeatedly found in sperm whale stomachs (e.g., Kawakami 1980), the largest amount of their diet is composed by medium-sized meso- and bathypelagic cephalopods, and to a smaller amount demersal fish and crustaceans (Rice 1989; Jaquet 1996). Diet varies regionally (Kawakami 1980) and depends on the sex and size of the sperm whale, with males generally capturing larger prey than females (Rice 1989). In the Azores, Clarke et al. (1993) revealed *Octopoteuthidae* (39.8%), *Histioteuthidae* (32.7%) and *Architeuthidae* (12.1%) as the three most commonly found families of a total of 52 different cephalopod species in the stomachs of 19 individuals.

Just as their diet, foraging dive time and depth also vary between age, gender, and region with the largest whales generally performing the deepest and longest dives (Whitehead 2003). While dive times of 138 min have been reported (Watkins 1985), the average forage dive time for social units is 40–45 min, exploring depths of 400–1,200 m (Watwood et al. 2006). Capable of much longer dives, males were recorded in high latitudes to explore variable water depths (and probably food layers) of 100–1,900 m in average dives of 30–40 min (Teloni et al. 2008). In some regions, a diel variation in diving behaviour was reported, indicating extended, deeper foraging dives during the day (e.g., Aoki et al. 2007, Miller & Miller 2018; Chambault et al. 2021). This pattern was not confirmed in other regions (Merkens et al. 2019).

Numerous physiological adaptations are necessary to reach such great dive durations and depths (Costa 2007), and to navigate and hunt successfully in the aphotic zone. It was hypothesized that sperm whales may orientate by the light produced by luminous cephalopods (Fristrup & Harbison 2002), but not all prey species produce light (Rice 1989). Other suggestions were random tactile searching and inactive positioning at depth, attracting prey by their bright coloured jaw (Rice 1989; Fristrup & Harbison 2002). The use of hydrophones and studies on stranded specimens revealed that sound production most likely plays an essential role in the species' foraging strategy. During sperm whales foraging dives, continuous click sounds are typically recorded. Those were suggested to be generated by air from the right nasal passage with help of the phonic lips (or *museau du singe*), which are located at the front of the sperm whale's head. From there, the clicks are transmitted through the spermaceti organ, reflected by the frontal air sac until being directed via the junk into the ocean (Norris & Harvey 1972; Figure 2). This theory, referred to as the *bent-horn model*, was later confirmed, and adjusted by several researchers (e.g., Møhl 2001; Madsen et al. 2002a; Møhl et al. 2003; Zimmer et al. 2005). The multiple pulsed clicks are thought to scan the ocean as a way of echolocation (Norris & Harvey 1972). Active prey capture with echolocation is seen in other species of *Odontoceti* and is also comparable to bats (Madsen 2002b). The ingestion of prey is likely made by suction without (much) use of teeth (Rice 1989; Fais et al. 2016). In the Gulf of Alaska, it was possible to film sperm whales depredating black cod (*Anoplopoma fimbria*) from longline fishery. Those observations confirm that echolocation and creak-click production is used during prey capture attempt, even in the photic zone (Mathias et al. 2012). Acoustical tracking showed that sperm whales do not engage in cooperative hunting, instead spread out during the foraging process, only grouping again at the surface (Watkins & Schevill 1977b).

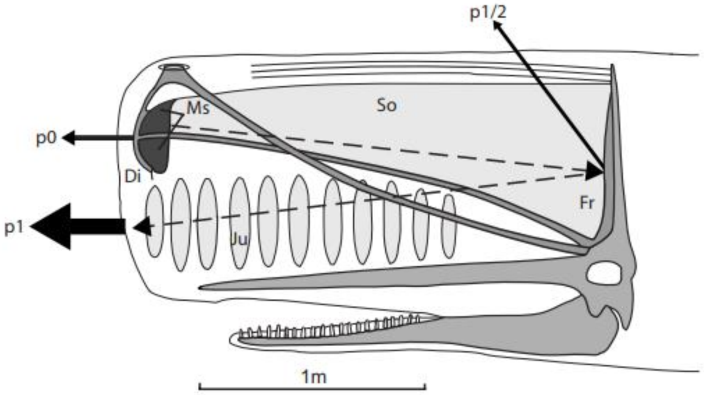

Figure 2: Schematic view of a sperm whale head demonstrating the bent-horn-model of sound production. Ms: museau de singe; So: spermaceti organ; Fr/Di: frontal & distal air sac; px: pulses. From: Schulz et al. 2009.

1.4. Social organization

"In hundreds of days spent with sperms, we have never seen a female without others within a kilometer or two." (Whitehead 2003)

Sperm whale societies are complex and multileveled (Whitehead 2003). As mentioned earlier, female sperm whales live with calves and immatures of both sexes in *social units* (Whitehead & Kahn 1992), with a mean number of 11.3 members (or "constant companions") (Christal et al. 1998). Spending most of their lives together, those matrilineal associations are thought to be stable over time (Rendell & Whitehead 2005). It was hypothesized that some female members of a social group might never leave their family bonds (Whitehead 2003). In contrast, a small degree of flexibility has been observed (Christal et al. 1998; Whitehead 2003). Earlier studies indicated that social units consisted of genetically related females (Whitehead et al. 1991; Stredulinsky et al. 2021). Indeed, genetic analysis demonstrated that, at least in some regions, social units may be composed of several unrelated matrilines, caused by splitting, merging and transfer between social units (Richard et al. 1996; Christal et al. 1998; Schulz et al. 2008). Although sometimes referred as a matriarchal society, it remains uncertain if social units are led by a matriarch, as studies of their movements indicate that groups act in an uncoordinated way, suggesting that a dominant leader is lacking (Whitehead 2016).

Even though the social unit seems to be the most important entity in the sperm whale society, there are other forms of social organization, classified by time and space of the gathering. Ordered from the smallest to biggest in time and space, those associations are called clusters, groups, aggregations, concentrations and (vocal) clans. While clusters and groups act in a coordinated way, aggregations and concentrations do not (Whitehead 2003). Apart from social units and vocal clans, all mentioned associations are short-lived and motivated by prey abundance or caused by orca (*Orcinus orca*) predation attempts (Whitehead 2003; Whitehead et al. 2012). Most of the referred associations are composed of females and their young but subadult males separate from their social units at the age of about six years (Richard et al. 1996), eventually forming short-term “bachelor groups” and getting more and more solitary over the years (Rice 1989). Nevertheless, mass strandings of adult males and recent photo-ID studies suggest long-term bonds between mature males (Kobayashi et al. 2020).

Photo-identification studies in the Azores indicated that social units have a mean number of 12 individuals, associating for at least 19 years (Antunes 2009). Large-group aggregations were hypothesized not to exist in the Azores, because of lower food availability, smaller population numbers, and lower risk of orca predation (Antunes 2009; Whitehead et al. 2012). Although being rare and short-term events, gatherings of up to 50 individuals have been reported by whalers (Clarke 1956) and confirmed by recent surveys (Silva et al. 2014). High genetic diversity and relatedness was confirmed both within and between social units seen in Azorean waters (Pinela et al. 2009). Further, studies suggest that male separation from their social unit may occur at a later age than in other areas (16.6 years) (Pinela et al. 2009).

The reason and benefits for sperm whales' strong and stable social associations has been a continuous research topic and seems to be related to their feeding and breeding strategies. Whilst in other mammals, female unions are partly originated in resource acquisition (Wrangham & Rubenstein 1986), sperm whales do not seem to cooperate while foraging (Whitehead 2003; Oliveira 2014). Sperm whales have a single calf every 3–6 years and lactate as long as 1.6–3.5 years (with the extreme case of 13 years) (Rice 1989). Although being capable of diving deep in their first year of age (Tønnesen et al. 2018), calves spend most of the day close to the surface (Best et al. 1984). Instead, their mothers invest about 75% of their time foraging (Whitehead 2016). Alone at the surface, calves are an easy target to predators (orcas and potentially large sharks) (Arnbom et al. 1987; Whitehead 1996; Pitman et al. 2001). Thus, alloparental care or babysitting by other members of the social unit minimize calves' predation risk, allowing mothers time to feed (Whitehead 1996; Pitman et al. 2001; Gero et al. 2013). Allosuckling (nursing by females other than the calf's mother) is also commonly observed between social units (Best et al. 1984). Predation risk avoidance resulting in alloparental care for calves is seen as the key driver for the evolution of long-lasting social bonds in this species (Pitman et al. 2001; Gero et al. 2013). The fact that adult males, which do not care for calves, live rather solitary lives supports this theory (Lettevall et al. 2002).

In exceptional situations (e.g., in the case of an attack by orcas), sperm whales position themselves into a *marguerite formation,* protecting calves or other fragile members of the social unit in their middle (Rice 1989). Similar proximity and support within social groups have been observed during births (Weilgart & Whitehead 1986; Rice 1989, Whitehead 2003). Further, it was speculated that female sperm whales undergo a menopause and assist the younger members of their social unit during their post-reproductive life phase (McAuliffe & Whitehead 2005). The extent of sperm whales' social, kin-directed, altruistic behaviour remains uncertain, but even epimeletic behaviour towards a dead calf has been documented ('Grief'; Reggente et al. 2016; Bearzi et al. 2017).

A surprisingly high degree of similarities to sperm whales' societies can be found in many matriline and matriarch mammals, including terrestrial representatives (e.g., African elephants, *Loxodonta africana*) (Connor et al. 1998; McComb et al. 2011; Whitehead 2018). Common characteristics are, amongst others, longevity, stability of their group composition (Weilgart & Whitehead 1993), complex social relationships between the group members, including a high degree of cooperation (Gero et al. 2015), social learning and the development of their own culture (Whitehead 1998, 2017).

Differentiated culture can include numerous aspects of a society, such as foraging techniques and diet, movements and habitat use, social structure and behaviour, and the development of their own way of communication and vocalisations (Whitehead 2017).

1.5. Vocal behaviour

In cetaceans, sound is crucial not only for orientation and navigation but for all essential life functions, such as foraging, communication, group cohesion, predator avoidance, and mating (Mooney et al. 2012; Herman 2017; Wei 2021).

Cetaceans produce the widest range of sounds of any mammalian order (Gordon & Tyack 2002) and vocal repertoires differ between species, regions, and possibly individuals. The sounds range from clicks to tonal sounds, as moans, whistles, and even sophisticated songs. As in many other biological features, there is a significant dichotomy between *Mysticeti* and *Odontoceti* according to their hearing capabilities, sound production and use: whilst *Mysticeti* communicate mostly in low frequencies ranges, *Odontoceti* use higher frequencies. Further, all *Odontoceti* use echolocation, with the sperm whale having developed one of the most extreme and advanced echolocation instruments (Mooney et al. 2012; Wei 2021).

Unlike other cetaceans, sperm whale sounds are almost entirely composed of different types of clicks, varying in intensity, frequency, directionality, duration, repetition rate, pattern, and function (Weilgart & Whitehead 1993; Madsen et al. 2002a; Whitehead 2003; Zimmer et al. 2005). As common characteristics, clicks are sharp and broadband, and each single click consists of a series of pulses with decreasing energy amplitude (Norris & Harvey 1972; Whitehead 2003; Zimmer et al. 2005), being the result of the soundwaves travelling twice through the sperm whales' head (Møhl 2001). The distance between those pulses (inter-pulse interval, IPI) can be used to estimate the size of the individual, as their head grows proportionally to the rest of the animal (e.g., Gordon 1991; Rhinelander & Dawson 2004; Bøttcher et al. 2018).

The main, widely accepted classification of click sounds are usual clicks, buzzes, codas, and slow clicks (Figure 3).

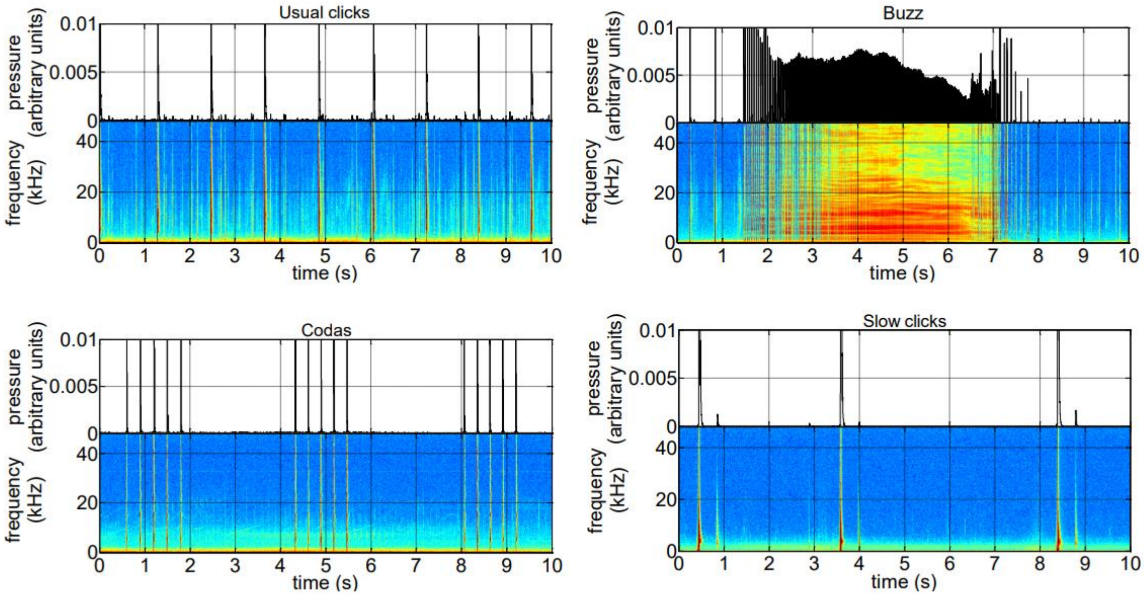

Figure 3: Principal click sound types emitted by sperm whales, illustrated by waveform (top of each block) & spectrogram (bottom of each block). From: Oliveira 2014.

“Usual clicks” (Watkins & Schevill 1977a) also named “regular clicks” (e.g., Goold & Jones 1995; Miller et al. 2004a), “echolocation clicks” (e.g., Bøttcher et al. 2018; Tønnesen et al. 2018) or simply “clicks” (Goold 1999), are almost constantly produced during deep foraging dives. They consist of long series of highly directional clicks with fairly regularly spaced inter-click intervals (ICIs, time between two subsequent clicks) of 0.5–2 s (Whitehead & Weilgart 1991; Zimmer et al. 2005; Whitehead 2003). Usual clicks are not only the most powerful of all click types emitted by sperm whales but are also considered the loudest sound produced in the animal kingdom, reaching source levels of 239 dB (Møhl et al. 2003; Jakobsen et al. 2021). Usual clicks are mostly believed to serve for long-range-echolocation during foraging (Gordon 1987; Whitehead 2003).

“Buzzes” or “creaks” are also highly directional clicks, produced in rapid click trains with ICIs of 0.005–0.1 s (Whitehead 2003), generally getting shorter towards the end of the buzz. Those pulse trains are comparable to echolocation clicks made by bats during prey capture (Madsen et al. 2002b). Being often followed by a silent pause and accompanied by a sudden change in the whales’ orientation (Mathias et al. 2012), buzzes are believed to be produced at the terminal feeding phase (Watwood et al. 2006), when homing and attempting to catch its prey (Whitehead 2003; Miller et al. 2009). Believed to be prey capture attempts, buzzes were used as indicators of local prey availability and sperm whales’ foraging success (Miller et al. 2004a; Watwood et al. 2006; Gannier et al. 2012). Nevertheless, buzzes are also heard during socialization at the surface, referred to as “coda-creaks”, “chirrups”, or “rapid clicks”; (Whitehead 2003[1]).

“Codas” are patterned click sequences mainly produced by social units. Unlike usual clicks and buzzes, they have a low directionality. Codas have source levels of 180 dB, click durations of 35 ms (being the longest of sperm whale click rates), ICIs of 0.1–0.5 s and a hearing range of 2 km (Moore et al. 1993; Whitehead 2003). Codas will be extensively discussed in the following section.

“Slow clicks”, “clangs” (Gordon 1987) or “surface clicks” (Jaquet et al. 2001) have been exclusively recorded from male sperm whales (Whitehead 2003)[2]. As the name reveals, those clicks are produced with a much slower pattern or longer ICIs (5–8 s) (Whitehead 2003). They have a distinguishable sound described as “clanky”, “whamming” or “metallic” (Weilgart & Whitehead 1988). Slow clicks seem generally much louder than buzzes or usual clicks (Weilgart & Whitehead 1988), although having lower source level. This paradox may be explained by their low directionality and frequencies (Whitehead 2003). It was calculated that slow clicks have enough energy to reach their conspecifics up to 60 km distance (Madsen et al. 2002b). In the relatively solitary life of mature males, the wide hearing range seems reasonable, as slow clicks are thought to be used for communication (Madsen et al. 2002b; Oliveira et al. 2013). The low directionality, repetition rate (Madsen et al. 2002b) and the depth range where they are produced (Oliveira et al. 2013) support this theory. Furthermore, they might have an important role in mating activity, being recorded frequently in breeding grounds (Weilgart & Whitehead 1988; Whitehead 2003).

Sperm whales emit several other sounds, including “rapid clicks”[3], “gunshots”[4], “chirrups”, “short trumpets”, “pips”, and “squeals” (Goold, 1999). Especially chirrups, squeals, and trumpet sounds seem to be produced relatively frequently (e.g., Drouot et al. 2004; Weir et al. 2007; Frantzis & Alexiadou 2008). Although the function of these other sounds remains uncertain, chirrups and squeals were suggested to be social sounds (Gordon 1987; Weir et al. 2007), and Pace et al. (2021) recorded trumpet sounds by males in strong correlation with slow clicks, proposing its use for communication in this gender.

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[1] Whitehead & Weilgart (1991) refer to creaks both made in depth and at the surface, latter likely to be chirrups or coda-creaks.

[2] Possibly equal to or variations of “gunshots” reported by Gordon 1987 (Whitehead 2003; Oliveira et al. 2013)

[3] [Usual] clicks with a fast repetition rate of 0.1 s (Goold 1999), according to Whiteheads (2003) characterization at the limit of usual clicks and creaks.

[4] Similar spectrographic structure and repetition rate to slow clicks, possibly used to stun prey (Whitehead 2003)

Codas

First mentioned as “series of sharp clicks” in 1957 (Worthington & Schevill), codas were named by Watkins and Schevill (1977a), describing them as short, repeated sequences of 3–40 clicks[5] with a great diversity of rhythmic click patterns. Codas are identifiable by their particular sound, characterized as “clacking” or castanet-like (Weilgart & Whitehead 1993).

Coda clicks are not produced regularly, instead temporally clustered (Weilgart & Whitehead 1993). They are (almost) never emitted during feeding dives (Watkins & Schevill 1977a), when usual clicks are produced, but during ascents and descents of foraging dives and especially and at much higher rates, while resting and socializing near the surface (Moore et al. 1993; Weilgart & Whitehead 1993; Madsen et al. 2002b). In a few situations, codas have been recorded when no other individual was visually confirmed (Teloni 2005; Schulz et al. 2008) and as a response to unusual sounds (Watkins & Schevill 1977a). While thought to be exclusive to females (Marcoux et al. 2006), mature males have also been documented to produce codas (e.g., Pavan et al. 2000; Frantzis & Alexiadou 2008), but in less extent than females (Pavan et al. 2000).

Codas were first thought to be inherent to each individual and used to identify each other (Watkins and Schevill 1977a; *“identity codas[6]”* Watkins et al. 1988). It was later recognized that some codas are indeed *“shared”* (emitted by different individuals) (Watkins et al. 1988), and that each individual produces more than one type of coda (Weilgart & Whitehead 1993; Rendell & Whitehead 2004). Observations and analysis of coda production and sperm whale behaviour led to the consensus that their primary function is communication (e.g., Watkins & Schevill 1977a; Moore et al. 1993; Weilgart & Whitehead 1993). Apparently, codas help to maintain social bonds and reaffirm social unit cohesion after member separation during foraging dives (Weilgart & Whitehead 1993). Indirect support for this function comes from the clicks’ low directionality (Madsen et al. 2002a), the whales’ cooperative social system (Schulz et al. 2008) and the contexts of coda emission.

Codas are often exchanged as a dialogue or duet-like sequence (Weilgart & Whitehead 1997; Schulz et al. 2008). Weilgart & Whitehead (1993) categorized codas into types, based on their number of clicks and their relative timing pattern of clicks and pauses (ICIs). They found that a specific coda type often started dialogues (“5”, being five evenly spaced clicks). Schulz et al. (2008) noticed frequent matches of overlapping (one coda initiates before the other has finished,

Figure 4) and adjacent codas (separated from each other but within 2 s of finishing of the other whale’s initial coda) by pairs of whales. The high degree of synchrony was

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[5] Most coda analysis include codas with 3–12 clicks only, as they are the most frequently produced.

[6] Not to mistake with “Identity/ID codas” by Hersh et al. 2021, 2022.

suggested not to leave enough time for reflection and answering, instead, matching codas may solely be used to reinforce social bonds. Supporting that theory, matching codas are often the most frequently emitted coda types of a social unit. In case of indeed being a reflected answer, codas may not be a direct response to the coda that they overlap, but to the previously emitted coda (Schulz et al. 2008).

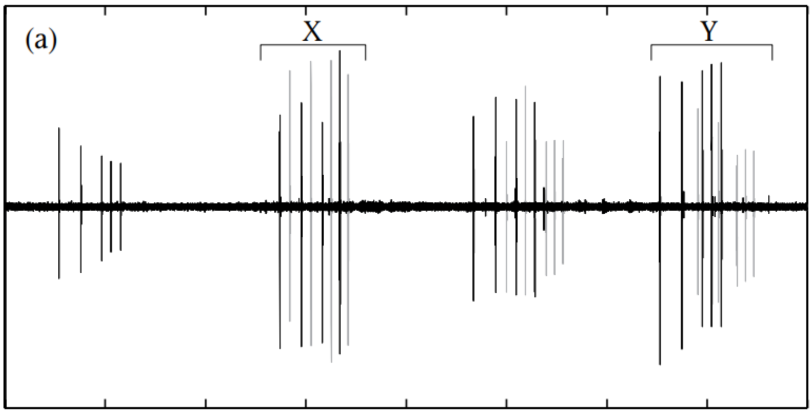

Figure 4: Waveform of a coda dialogue including overlapping and matching (X & Y) codas. From: Schulz et al. 2008.

The classification and nomenclature established by Weilgart & Whitehead (1993) were applied to numerous studies worldwide and are still in use today. However, there was a need for adaptation and expansion because coda patterns vary considerably between distinct regions and groups (Moore et al. 1993; Weilgart & Whitehead 1997). All types used by a group of whales was termed *vocal repertoire* (Weilgart & Whitehead 1997). While some coda types are repeatedly found between vocal repertoires, over time and ocean basins (e.g., “5R” Weilgart & Whitehead 1997; Gero et al. 2016a), other vocal repertoires vary not only between distant geographical areas, but also among different groups of whales sharing similar areas (e.g., Weilgart & Whitehead 1997; Whitehead et al. 1998). It has been shown that vocal repertoires are temporally stable, or at least do not undergo rapid changes (Rendell & Whitehead 2005: 6 years; Gero et al. 2016a: > 30 years). A group of sperm whales sharing the same vocal repertoire was termed a *vocal clan* (Rendell & Whitehead 2003b). The range of one vocal clan can extend over thousands of kilometres and include thousands of whales of many social units, adding another level to the sperm whales’ social structure (Rendell & Whitehead 2003b). At the same time, some clans are sympatric: different stable vocal clans coexist in the same geographic region but rarely associate (Rendell & Whitehead 2003b; Gero et al. 2016b). Clans even show differences in behaviour and movements, foraging and diet and were proposed to represent the limits of altruistic exchanges (Rendell & Whitehead 2005; Bermant et al. 2019).

Seven vocal clans are known in the Pacific (Amano et al. 2014; Hersh et al. 2021, 2022), five were proposed for the Atlantic, including three in the Caribbean (Gero et al. 2016b; Vachon et al. 2022) and two off the Brazilian coast (Amorim et al. 2020), one in the Mediterranean (Hersh et al. 2021) and two in the Indian Ocean (Huijser et al. 2020). These findings suggest that culturally transmitted vocal clan repertoires separate, structure, and define sperm whale populations worldwide, communicating their identity between social units (Rendell & Whitehead 2003b; Gero et al. 2016b). Hersh et al. (2011) define “ID codas”, being “popular” coda types that are frequently used by one group of whales and not by others, to separate vocal clans from each other.

Besides sperm whales, group-specific dialects are only known for a handful of terrestrial mammals and orcas (Weilgart & Whitehead 1997). Both species are known to consist of long-term stable matriline family units, being a possible explanation for the development of specific dialects (Weilgart & Whitehead 1997). The fact that distinct vocal clans show no apparent genetic differences (Weilgart & Whitehead 1997; Rendell et al. 2012) and whales of different ages have different coda repertoires (Watkins et al. 1988; Schulz et al. 2011; Gero et al. 2016a) suggests that coda repertoires emerge from vocal learning (Weilgart & Whitehead 1997). Changing vocal repertoire through imitating or learning is known in birds but has only been observed in a few mammals (Gero et al. 2016b), including cetaceans (e.g., bottlenose dolphins *Tursiops truncatus*, belugas *Delphinapterus leucas*, humpback whales *Megaptera novaeangliae;* Janik 2014).

As an animal with a multileveled social structure, some authors believe there must be some signature encrypted in codas apart from clan recognition (Gero et al. 2016b). Some studies revealed differences in coda repertoire between social units (Gero 2016a) and even individuals (Antunes et al. 2011; Gero 2016a; Oliveira et al. 2016). Individual differences were found in frequently emitted coda types (Antunes et al. 2011; Gero et al. 2016a), ICIs and IPIs (Oliveira et al. 2016), and have been suggested to exist in the spectral structure of coda clicks (Weilgart & Whitehead 1993).

Coda classification and analysis of behavioural context

Owing to variations of coda repertoires and different analytical approaches, comparing coda production between studies is challenging.

The ICIs of a coda were initially standardized by the total coda length as a base for classification (relative ICIs) (e.g., Pavan et al. 2000; Rendell & Whitehead 2003a), based on the believe that coda rhythm is better preserved than tempo (Moore et al. 1993). However, several authors realized that standardizing ICIs lead to a loss of information (Frantzis & Alexiadou 2008; Antunes et al. 2011; Amano et al. 2014), and nowadays the absolute timing of ICIs is used. The classification of coda types itself was at first done by observer classification (e.g., Watkins & Schevill 1977a; Moore et al. 1993), followed by half-automatized k-means clustering (e.g., Weilgart & Whitehead 1997; Amano et al. 2014). Still, as the number of clusters needs to be determined *a-priori*, the technique is not entirely objective (Hersh et al. 2021). Over the years, classification became more and more objective (e.g., PCA-classification, Oliveira et al. 2016; Contaminated Mixture Models, Hersh et al. 2021, 2022; Vachon et al. 2022) until reaching fully automated methodology via Machine Learning (Bermant et al. 2019; Andreas et al. 2021, 2022), reducing the human bias and facilitating the analyses of large datasets (Bermant et al. 2019; Andreas et al. 2022).

Most of earlier coda recordings were obtained from towed-array or less frequently bottom-moored hydrophones (e.g., Weilgart & Whitehead 1997; Newcomb et al. 2002; respectively). With the use of biologging devices, such as digital acoustic recording tags (DTAGs, Johnson & Tyack 2003), codas can be assigned to individual whales, enabling investigation of coda type production in relation to movement and behavioural context (Oliveira et al. 2016). Frantzis & Alexiadou (2008) assorted coda types to coda families and correlated them with dive cycles and behavioural contexts. Oliveira et al. (2016) demonstrated some individual's distinctive use of coda types in particular dive phases (Figure 5).

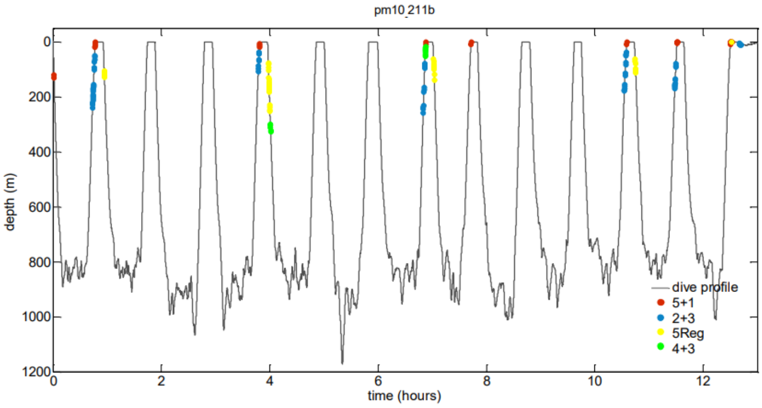

Figure 5: Different coda type use within dive phase context. From: Oliveira 2014.

In the Azores, the only studies conducted on coda repertoires were those by Antunes (2009) and Oliveira et al. (2016). The most common coda types found in both studies were the regularly spaced, prevailing made of 5 clicks (“5R”), although Oliveira’s also mentioned two individuals producing many 3-click-codas (“3R”). Sympatric vocal clans were not described yet. Antunes (2009) compared a dataset recorded in the Azores over 15 years, with codas of different regions of the North Atlantic, including the Gulf of Mexico, Dominica, Panama, Iceland, and the Sargasso Sea (Figure 6). The regularly spaced codas recorded in the Azores showed similarities to those in the Sargasso Sea and to a lesser extent off Dominica and Iceland (Antunes 2009, Figure 6). Antunes (2009) explained the found diversity of coda repertoires with genetic drift (caused by geographic isolation) (cf. Alexander et al. 2016) and cultural drift caused by the imperfect transmission of vocal repertoires between groups, later to be contested by Cantor et al. (2015). The lack of vocal clans in the Atlantic was hypothesized to be related to distinct environmental factors, lesser extent of predation pressure from orcas, whaling effects, and culture (Whitehead et al. 2012). Later studies confirmed indeed the existence of sympatric, vocal clans in the Atlantic (East Caribbean: Gero et al. 2016a; Brazil: Amorim et al. 2020). Still, very little is known about production and function of sperm whale codas, especially in the Atlantic Ocean.

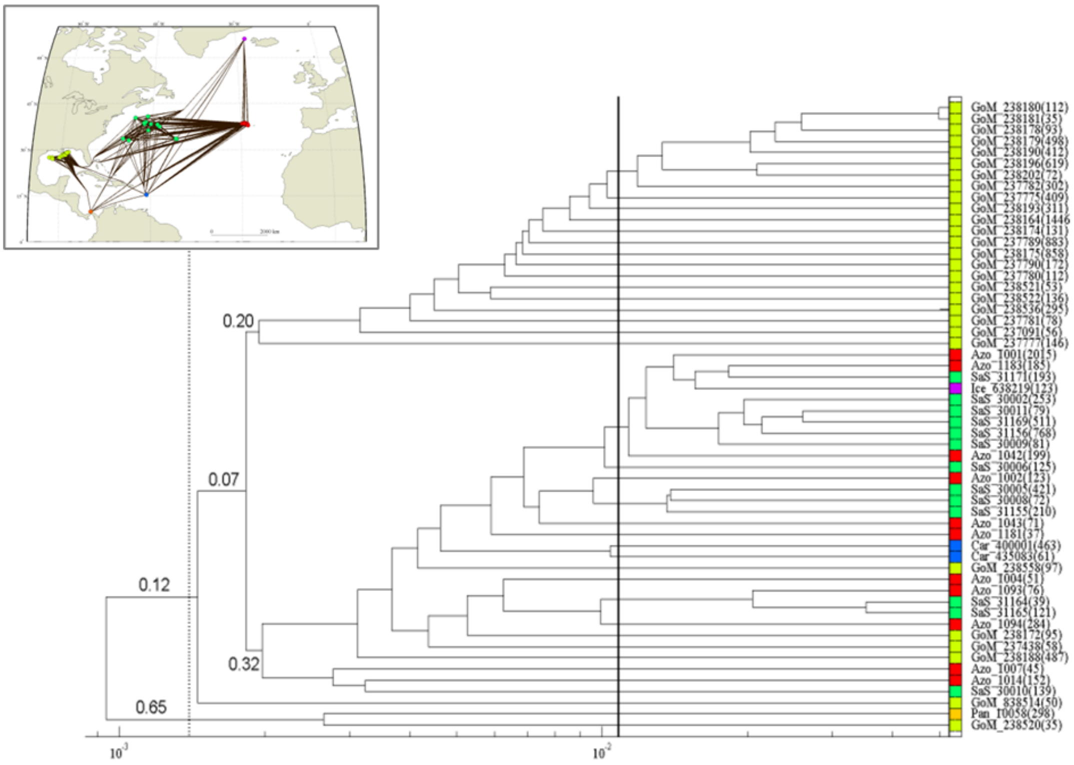

Figure 6: Locations (top right corner) of previously studied coda-repertoires in the Atlantic by R. Antunes, being the Azores (AZO, red), Sargasso Sea (SaS, green), Gulf of Mexico (GoM, light green), Panama (Pan, orange), Dominica (Car, blue) and Iceland (Ice, pink) and their respective similarities calculated by hierarchical clustering (bottom). Adapted from: Antunes 2009.

1.6. The Azores archipelago

Located in the Mid-Atlantic Ridge in the North Atlantic Ocean (between 37°–40°N and 25°–32°W), the Azores archipelago comprehends nine volcanic islands, separated into three main groups (West, Central and East) (Santos et al. 1995).

The ocean currents system around the Azores is highly complex and variable, influenced by the Gulf Stream with multiple branches, meanders, and eddies (Santos et al. 1995; Fernandez et al. 2022). Dynamic ocean currents, complex topography, and the location of the Azores in the middle of the North Atlantic, are thought to influence the high diversity (28 species) but changing composition and abundance of cetaceans throughout the seasons and years (Silva et al. 2014; Tobeña et al. 2016). The ocean around the Azores offers a wide range of habitats and niches (Silva et al. 2014). The lack of continental shelf allows great depths in close vicinity to the islands, presenting ideal habitats for deep divers such as the sperm whale and beaked whales *(Ziphiidae)* (Jaquet 1996; Tobeña et al. 2016). Additionally, hundreds of scattered seamounts in the region (Morato et al. 2008a; Figure 7: The Azores archipelago (white), surrounding large seamounts (green) and small seamount like features (black) inside the EEZ. Water depths from deep (≈5,000 m, dark blue) to shallow (dark red). From: Morato et al. 2008a.) can contribute to aggregate prey (Cascão et al. 2019), attracting a diversity of higher trophic predators including sperm whales (Morato et al. 2008b; Tobeña et al. 2016; Cascão et al. 2020).

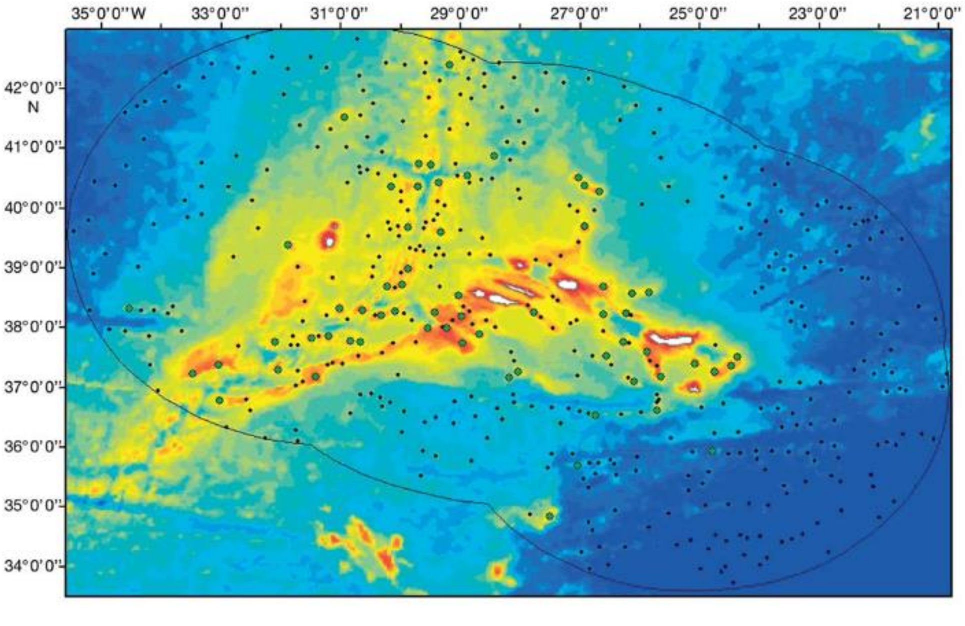

Figure 7: The Azores archipelago (white), surrounding large seamounts (green) and small seamount like features (black) inside the EEZ. Water depths from deep (≈5,000 m, dark blue) to shallow (dark red). From: Morato et al. 2008a.

1.7. Motivation and Objectives

The knowledge about sperm whale codas increased significantly over the last decades. Separated, in some cases sympatric vocal clans have been described in all ocean basins, some of them only recently discovered (Amorim et al. 2020; Huijser et al. 2020) in some cases even after long-term research efforts in the same area (Gero et al. 2016b; Vachon et al. 2022). Few studies were undertaken about codas in the Azores but did not describe any vocal clans (Antunes 2009; Oliveira 2014). Thus, the main motivation of the present thesis was to expand the knowledge of the coda repertoires of sperm whales in the Azores.

Specifically, this work aimed to understand the occurrence of vocal clans for Azorean sperm whales, confirming or adding to what was previously presumed (Antunes 2009). After the processing of data obtained with DTAGs in 2020, the dataset was enlarged by adding previously analysed datasets from the Azores, including DTAG data from 2010 (Oliveira 2014) and hydrophone array data from 1988–2006 (provided by J. Gordon, L. Steiner and R. Antunes; Antunes 2009). In this manner, using a larger database, it was possible to analyse and discuss data in a historical perspective.

Few attempts have been done to investigate the particular function of coda types (e.g., Weilgart 1990; Frantzis & Alexiadou 2008; Oliveira et al. 2016). Until today, the meaning of each coda type remains unclear. To improve our understanding of codas, this work attempted further to elucidate the behavioural context of coda production, by relating the different coda types with the whales' behaviour, which was substantially facilitated by the use of DTAGs (Johnson & Tyack 2003; Oliveira et al. 2016). In particular, the DTAGs recorded the individuals' acoustic emissions and three-dimensional movements. From those data, diving depth and the dive cycles were reconstructed. Further, the production of every single coda was related to the time of the day, in order to investigate possible diel patterns.

2. Material and Methods

2.1. Tagging data

The main dataset analysed in this study was collected from eight adult sperm whales (Table 1), tagged in June to August 2020 around Faial and Pico islands of the Azores archipelago (Figure 8). Tag-ID-names were abbreviated original labels (B 1 in annex) composed of the tagging day (year and Julian day) and in case of tagging two whales the same day, the alphabetic order of tagging (e.g., 20_203a means that the sperm whale was tagged in 2020, on the 8th of June, being the first animal to be tagged during that day; Oliveira et al. 2013).

Table 1: Summary of tagging data analysed in this study collected in the Azores in 2020.

Tag-ID	Tagging			Recording duration hrs:min
	Date	Time hrs:min	Location	
20_161	08/06/2020	11:54	38.46769 N 28.61558W	19:31
20_184	02/07/2020	13:48	38.43299 N 28.57684W	12:11
20_189	07/07/2020	9:34	38.44457 N 28.63922W	05:23
20_191	09/07/2020	15:24	38.66036 N 28.59570W	00:17
20_192	10/07/2020	13:06	38.39521 N 28.38805W	14:32
20_203a	21/07/2020	13:06	38.71989 N 28.70243W	01:29
20_203b	21/07/2020	15:43	38.72908 N 28.66537W	02:04
20_225a	12/08/2020	13:21	38.56015 N 28.33303W	17:35

The tags consisted of a digital acoustic recording tag (DTAGs) (Johnson & Tyack 2003). DTAGs recorded acoustic data via two hydrophones at a rate of 120 kHz, and registered depth, temperature, and orientation (via pressure sensor, accelerometer, and magnetometer) (Johnson & Tyack 2003) at a rate of 25 Hz. Whales' three-dimensional movements and acoustic emissions (as also the sounds of their conspecifics, other species, and their environment) were recorded during the deployment periods.

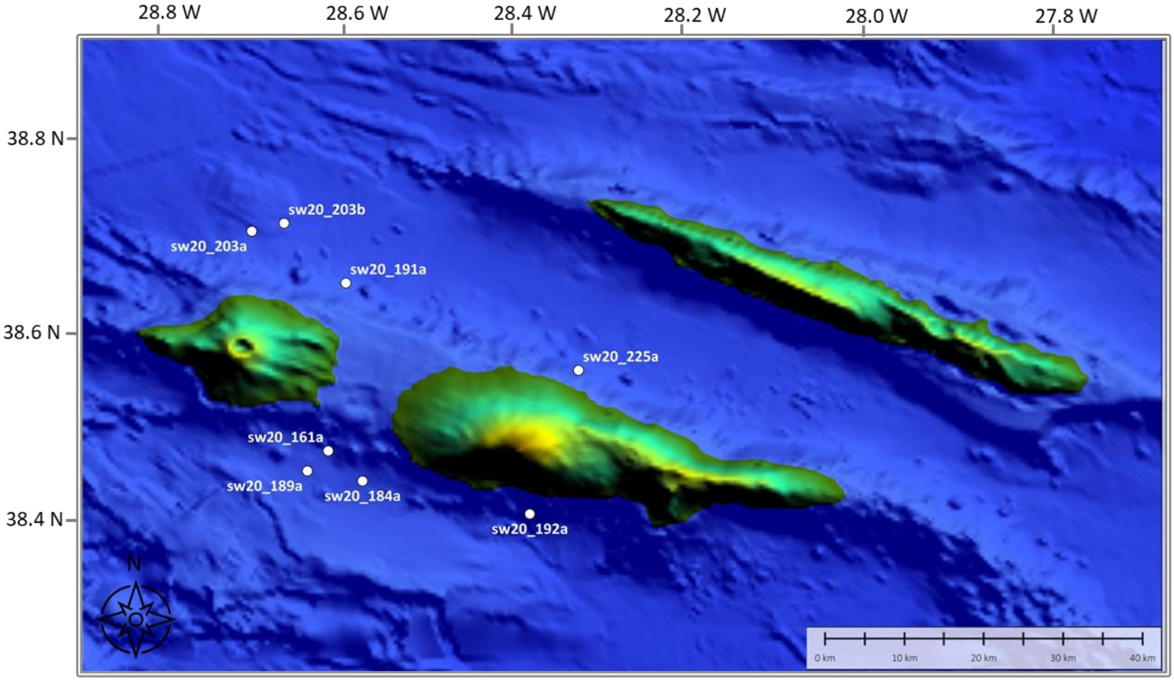

Figure 8: Map of the study area (including islands Faial, Pico, São Jorge and its surrounding ocean) showing the location of sperm whale tagging (white dots) in the Azores in 2020. Island-altitudes from 0 (dark green) to max. 2,351 metres a.s.l (brown) and ocean depths from deep (≈1,500 m, dark blue) to shallow (light blue). Data access: NOAA Ocean Exploration.

Sperm whales were tagged from small rigid hull inflatable boats (RHIB) by slowly approaching the whales from behind and deploying the tag with a 9 m cantilevered or a 6 m hand-held pole. DTAGs were placed on the back or on the dorsal side of the head and attached to the whales' body by suction cups (Figure 9). Whales' responses to tagging were mostly mild to moderate (e.g., shallow dives, changes in speed and direction, defecation). Tags were pre-programmed to release after a maximum of 24 hours after which they floated at the surface, to be recovered by radio tracking.

Before and after tagging, whales were visually accompanied from a distance to document their behaviour, biopsy samples were taken if conditions allowed and photographs taken for individual identification, possible social unit association and to ensure that the same whale was not tagged twice (see A 1 in Appendix). Photo-ID-analysis of animals tagged in 2020 and 2010 was performed by Lisa Steiner, who has established a detailed ID-catalogue of the area (see B 2 in Appendix).

Tagging was conducted under research permits LMAS/2018/3602[7], issued by the Regional Government of the Azores.

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[7] Due to COVID-19, research permits had not been actualized but maintained from pre-COVID year 2018.

Figure 9: DTAG-deployment with a hand pole on a sperm whale (left) and a successfully attached DTAG on a sperm whale back (right). Photo credits: Mónica A. Silva @AzoresWhaleLab.

2.2. Acoustic data processing

The DTAG data were first converted and calibrated using MATLAB (version 2007b and 2016b, Mathworks, Inc.). The accelerometer and magnetometer data were converted into pitch, roll and heading, to obtain the whales' orientation, and the pressure was converted into depth (Johnson & Tyack 2003; Miller et al. 2004a).

The calibrated data were analysed in MATLAB using Audit_Editor (developed by Vicente Fernández Rodilla). The different click types (e.g., usual clicks, buzzes, codas, slow clicks) were identified and annotated by listening to the audio files, while simultaneously inspecting the spectrograms. Only codas were kept for further analysis, although usual clicks were also used to help differentiate focal from non-focal codas (see below).

Codas produced by the tagged individual (focal codas) were used in the analysis of the vocal repertoire of sperm whales in the Azores, as well as to investigate the behavioural context of coda production. Non-focal codas, i.e., codas recorded by the DTAG that were produced by whales other than the tagged individual, were used only in the analysis of coda repertoires. Focal and non-focal codas were distinguished using the angle-of-arrival (AoA), which was calculated from the time-of-arrival difference of sounds in both hydrophones of the DTAG (Johnson et al. 2006). Focal codas were only assigned when the AoA varied < ±20º between the different coda clicks, to subsequent codas, and to usual clicks produced during foraging dives (Oliveira et al. 2016). Coda clicks with higher AoA variability (> ±20º) were excluded from the analysis. Exceptions were made in case of tag movements (which could be acoustically and visually detected in the recordings), resulting in abrupt AoA changes. For non-focal codas, higher AoA variations were allowed. Several other features helped separating focal from non-focal codas. Non-focal codas had higher short-term variability of AoA during subsequent clicks. Coda amplitude, frequency, and the dive depth of the animal were also used to distinguish focal from non-focal codas (Frantzis & Alexiadou 2008; Oliveira 2014). Finally, annotated focal codas were then confirmed by a second experienced observer (C. Oliveira). Whenever the focal animal could not be clearly distinguished, the codas were excluded from further analysis. Only clearly audible and distinguishable non-focal codas were considered, leaving out those with a low frequency (< 30 kHz), whenever the focal animal was at the surface, or when there was too much overlap with other codas, usual clicks, or other noises. As sperm whales observed in the same area and day are assumed to belong to the same social unit and share their coda repertoire (Rendell & Whitehead 2003b; Hersh et al. 2021), focal and non-focal codas recorded on the same day, presumably produced by the same social unit, were combined into a single group repertoire (hereafter GrpRep)[8].

Out of the total of eight individuals, five were analysed further (Figure 10). Two whales (20_203a and 20_203b) did not produce usual clicks, making it impossible to distinguish, with confidence, focal from non-focal codas. Additionally, whale 20_189 only produced six unusually long codas during the recording time, and non-focal codas were not detected. Thus, the data from those three individuals were excluded from all analyses below (see A 2 in Appendix).

The number of clicks and absolute ICIs of all focal and non-focal codas was calculated using the custom-made MATLAB-tool Coda_Editor (developed by V.F. Rodilla). Even though, codas are defined as click sequences with ICIs of 0.1–0.5 s (Whitehead 2003), some of the most frequently emitted codas in our study had five clicks, starting with two very fast clicks with a minimum ICI of 0.02 s (see Figure 11, bottom). Codas with many clicks and short ICIs tend to be very similar to chirrups (Frantzis & Alexiadou 2008), so a minimum ICI of 0.02 s was used to include "short codas" and exclude possible chirrups.

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[8] In the rare cases of joining of several social units, associations are made habitually within whales usinf similar vocal repertoires, as in belonging to the same vocal clan (Rendell & Whitehead 2003; Hersh et al. 2022)

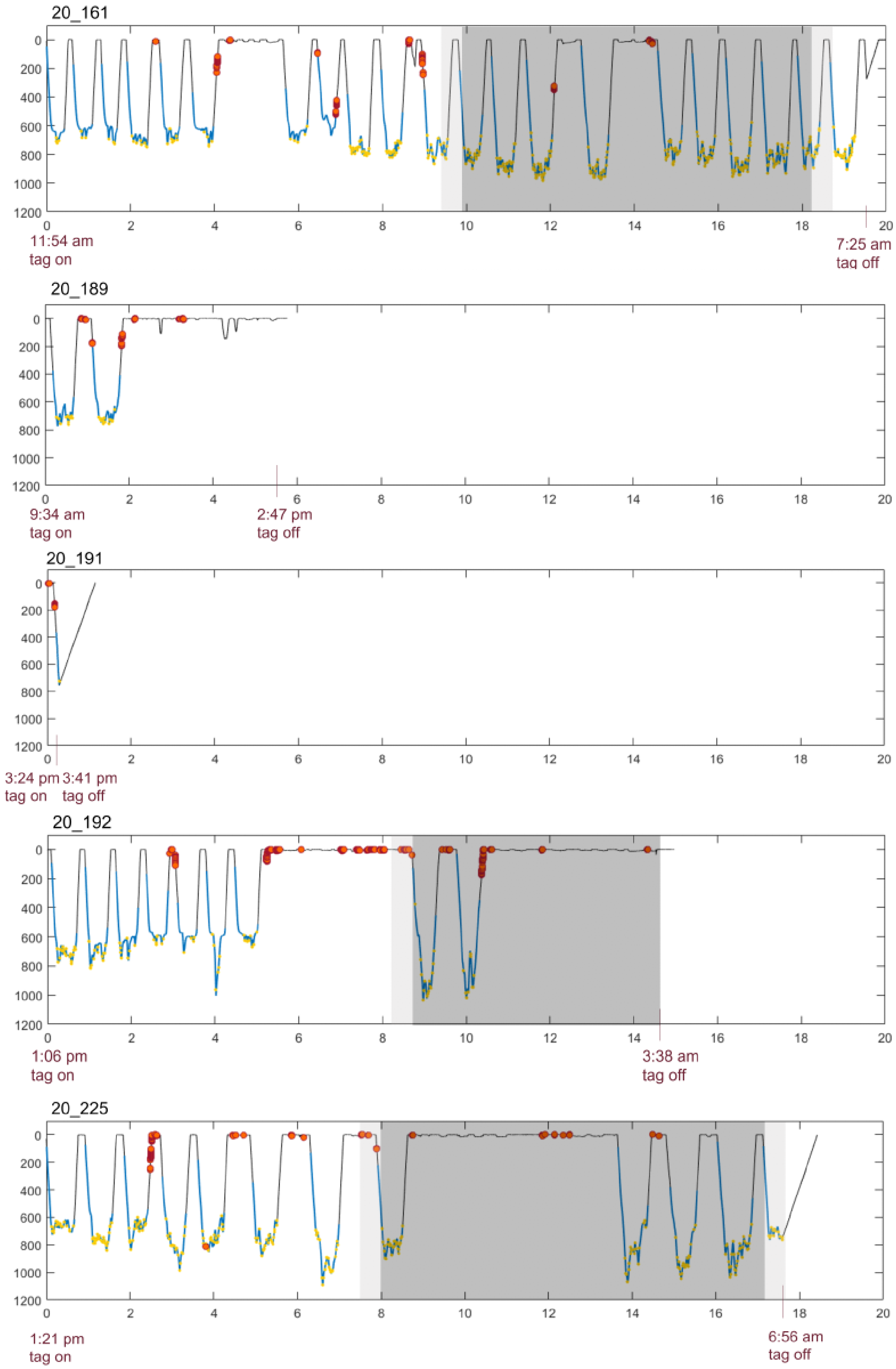


Figure 10: Dive profiles of tagged sperm whales in 2020 included in the analysis, showing the production of clicks. Depth in metres (y-axes), time in hours (x-axes): usual clicks (blue dots), buzzes (yellow dots), focal codas (red dots). The shaded background indicates the daylight hours (white), twilight (light grey) and night period (dark grey). Times of tag-deployment ("tag on") and detachment ("tag off") in magenta.

Existing coda datasets

To increase the number of codas available for the coda repertoire analysis, and the temporal period covered, the sperm whale codas analysed in Oliveira (2014) and Antunes (2009) were added to the data collected in 2020.

The coda dataset from Oliveira (2014) originated from five adult whales equipped with DTAGS in 2010 off Faial and Pico islands (Table 2) and followed the same tagging procedures as explained above. Acoustic data processing was done using the methodology described in the previous section, the only difference being the manual measurement ICIs between coda clicks. Here, only the focal codas identified in the dataset were used in further analysis. As recorded on the same day and area, individuals 10_222a and 10_222b were presumed to belong to the same social unit and were joined into one GrpRep (10_222) for the following repertoire analysis.

Table 2: Summary of tagging data collected in the Azores in 2010. Adapted from: Oliveira 2014.

Tag/GrpRep-ID		Tagging			Recording Duration hrs:min
		Date	Time hrs:min	Location	
10_211		30/07/2010	14:50	38.69038 N 28.68653 W	14:44
10_222a	10_222	10/08/2010	12:20	38.71730 N 28.76214 W	06:14
10_222b			12:36	38.72569 N 28.76872 W	15:08
10_226		14/08/2010	12:06	38.3524 N 28.45743 W	17:03
10_228		16/08/2010	10:16	38.67898 N 28.59582 W	19:53

The coda recordings analysed by Antunes (2009) were collected by Jonathan Gordon off the central and eastern group in 1991, 1993 and 1995, and by Lisa Steiner off the central and eastern group of the Azores archipelago in 2006, using a towed array with two Benthos AQ-4 hydrophones (Table 3; exact GPS coordinates are presented in B 3 in Appendix). Additionally, Ricardo Antunes provided data from several research trips off the Azores in 1988 and 1989, that had not been published by Antunes (2009) but were collected and analysed in the same manner. Those datasets, including six GrpReps, were integrated in the repertoire analysis as well.

With only two hydrophones, it is difficult to assign codas to individual whales, and instead Antunes (2009) assigned each coda to a group of whales i.e., GrpRep. GrpRep-ID was adapted by adding the recording year (see B 1 in Appendix). Using photo-ID-analysis, individuals from different recording days were joined to group repertoires on a few occasions (Antunes 2009; Table 3). Antunes (2009) measured ICIs automatically using Rainbow-Click. In the present study, the dataset from 1988–2006 was only used to investigate the coda repertoires and vocal clans of sperm whales from the Azores.

Table 3: Summary of data collected via hydrophones in the Azores from 1988 – 2006. Adapted from: Antunes 2009.

	Recording			Organization/ project	Recording equipment
GrpRep-ID	Date	Location	Vessel		
88_1042	23/06/1988	N-Faial	Song of the whale (14 m sailing boat)	International Fund for Animal Welfare IFAW, Jonathan Gordon	100 m towed array; 2x Benthos AQ-4-hydrophone elements; Sony TCD-DI DAT recorder at 48kHz
88_1043	27/06/1988	S-Pico			
88_1002	26/06/1988	S-Pico			
	01/07/1988	S-Pico			
	02/07/1988	S-Pico			
89_1051	16/07/1989	N-Pico			
89_1007	07/08/1989	S-Pico			
89_1004	01/09/1989	SW-Faial			
91_1001	13/07/1991	S-Pico			
	14/07/1991	S-Pico			
	18/08/1991	SW-Faial			
93_1014	20/08/1993	W-Faial			
95_1018	24/06/1995	NW-São Miguel			
95_1093	23/08/1995	SE-Pico			
95_1094	03/09/1995	SE-Pico			
06_1181	07/05/2006	SE-Faial	Physeter (12 m catamaran)	Whale Watch Azores, Lisa Steiner	100 m towed array; 2x Benthos AQ-4-hydrophone elements; Minidisc recorder
06_1183	15/06/2006	S-Faial			

2.3. Coda type classification, ID codas & clades

The processed codas were categorized into coda types and their usage amongst GrpReps compared between each other to find potential vocal clans, using the Identity-call (IDCALLS) method, developed, and provided by Hersh et al. (2021) and implemented in R version 4.2.1 (R Core Team, 2022). The method included two main steps, being A) a model-based clustering of the dataset into call types (in this case, the classification into coda types) by parsimonious mixtures of multivariate contaminated normal distributions, using the R package 'ContaminatedMixt' (Punzo et al. 2016) and B) the search for clades and potential vocal clans, by comparing GrpReps pairwise via average linkage hierarchical clustering, based on the usage of IDCALLS (in case of sperm whales, very popular coda types or "ID codas") (Hersh et al. 2021).

To align with recent methodology (Hersh et al. 2021), only 3–9 click codas (representing 91.7%, 93.9% and 93.6% of the codas in the 1988–2006, 2010 and 2020 datasets, respectively) were used for all coda analyses and sorted by GrpRep. Each GrpRep included a different number of codas, varying from 50 to 1877 codas (Table 6).

Following methodology of Hersh et al. (2021, 2022) and Vachon et al. (2022), the classification was performed in different trials, with changing parameters settings to determine the best fit for our dataset (trial 1 – 3; Table 4).

The tested parameters were, during step A) of coda classification, variations of the expectation conditional-maximization algorithm (ECM) initialization strategy, being k-means, random post, and random class (trial 1 – 3). Second, the information criterion was modified between Bayesian Information Criterion (BIC), Integrated Completed Likelihood (ICL), Akaike Information Criterion (AIC) and bias-corrected Akaike Information Criterion (AICc) (trials 1.1 – 1.4). ECM initialization variation led to similar outcomes, comparable to Hersh et al. (2021), while the information criterion variation generated outcomes with higher variances and showing differences to Hersh et al. (2021) (Table 4).

The k-means ECM initialization strategy in combination with AICc Information criterion delivered the best results, being closest to the observer classification (confirming to be the best solution for small datasets, Hersh et al. 2021). The outcome of step A) was a list of coda types with the ICI values of the centre of each cluster (centroid ICIs), a list of each GrpRep with the usage-percentage of each coda type, and a list of each single coda with the probability to be assigned to one of the gained clusters or coda types, which was helpful for the contextual part of the analysis.

Table 4: IDcall-trials of parameter-variation on the 2020 dataset including 1789 codas in five group repertoires, demonstrating the variation of parameter-settings resulting in different outcomes. Selected baseline parameters in bold letters.

Trial N°	Step	Parameter	Setting	Outcome	Table
1	A) Coda classification	ECM initialization strategy	**k-means**	21 types	Table 7
2			Random post	24 types	
3			Random class	27 types	
1.1		Information criterion	**AICc**	21 types	Table 7
1.2			ICL	40 types	
1.3			BIC	43 types	
1.4			AIC	59 types	
1.1.1 – 1.1.3	B) Hierarchical clustering	minrep	1,**2**,3	1 & 3: no delineation into ID-calls	
1.1.2.1 – 1.1.2.4		critfact	1, **14**, 50, 135	The higher CF, the less ID codas CF = 1 → 20_191 = outlier CF ≥ 2 → 2 clades	

When performing the following step B) of hierarchical clustering of GrpReps based on the obtained coda types, the parameters *critfact* (CF) and *minrep* (MR) were manipulated, where CF means the factor by which a certain coda type's production must be higher in one clade than in any other clade to be considered an ID coda (Hersh 2021; Hersh et al. 2021). For example, a CF of 2 significates that a certain coda was produced twice as much by one GrpRep than the other GrpRep, and in case of very similar coda type usage in all the observed GrpReps, no ID codas are assigned. MR is the smallest number of GrpReps that is necessary to form one clade (Hersh et al. 2021). Conform with Hersh et al. (2021), the increase of both parameters leads to a decreasing number of assigned ID codas and clades, but also significates more conservativeness and robustness of the obtained ID codas and clades (Hersh et al. 2021). Starting with the 2020-dataset (trial 1), the best results were obtained with CF 14 and MR 2. A MR of 2 was necessary to generate clades, due to the low number of GrpReps analysed.

If at least one ID coda was found, similar GrpReps were clustered next to each other and assigned to a clade in a dendrogram. Each (ID-)coda type was represented as line and its centroid ICIs was visualized in a click-rhythm plot as well as the percentage of usage in each GrpRep. Vicinity of GrpReps inside the dendrogram indicated similarity of their coda usage. In case of sperm whales, the finding of clades could indicate the existence of different vocal clans, while care must be taken with small datasets not to overinterpret the aligned clades to vocal clans (Hersh et al. 2021). In addition, the proportion of ID coda-use on their whole coda repertoire was calculated for each clade.

Resulting to generate the best outcomes for the 2020 dataset, the baseline parameters k-means, AICc and MR were maintained for the investigation of clades and vocal clans in the Azores to ensure comparability, while CF was varied to test the robustness of the created clades (trial 4.1. – 4.3, Table 5). Last, recordings from other regions in the Atlantic were added to the Azorean datasets in search of similarities of their vocal repertoires (Table 5), including the Balearic (BAL), Caribbean (CAR), Panama (AtlPAN), and the Gulf of Mexico (GOM), provided by Taylor Hersh; Hersh et al. 2021; trial 5) and the Eastern Caribbean (EC, provided by Felicia Vachon; Vachon et al. 2022; trial 6). For both trials, the baseline parameters were modified to BIC information criterion (as being suggested for large datasets, Hersh et al. 2021) and the remaining settings were defined as in the present study (MR 2, CF 14), and also as in the original studies (Hersh et al. 2021: MR 6, CF 14; Vachon et al. 2022: MR 5, CF 8).

Table 5: IDCALL-trials including all datasets from the Azores (AZO) & other regions: Atlantic (ATL) and Eastern Caribbean (EC). Baseline parameters k-means and AICc were maintained for trials 4 and modified to BIC for trials 5 and 6. Critfact (CF) and minrep (MR) parameters were varied in all trials, resulting in different outcomes.

Trial	Included datasets	N° GrpReps & codas (cd)	Settings	Outcome	Figure
4.1	AZO 2020, 2010, 1988-2006	22 GrpReps, 5607 cd	k-means AICc CF 14, MR 2	56 types, 2 clades	Figure 16
4.2			CF 26, MR 2	1 clade	A 4
4.3			CF 5, MR 2	6 clades	Figure 17
5.1	AZO 2020, 2010, 1988-2006 + ATL T.Hersh	104 GrpRep, 19412 cd	k-means BIC CF 14, MR 2	65 types, 5 clades	Figure 18
5.2			CF 14, MR 6	3 clades	A 5
6.1	AZO 2020, 2010, 1988-2006 + EC F.Vachon	173 GrpReps, 23670 cd	k-means BIC CF 14, MR 2	59 types, 5 clades	Figure 19
6.1			CF 8, MR 5	4 clades	A 6

In every classification trial, a different number of GrpReps and codas entered the analysis, different numbers of coda types were constructed. Labels and colouration of the coda-types are not necessarily comparable from one trial to the other. The 21 different coda types obtained in trial 1 (Table 4) were used for the contextual analysis, as only 2020-data were considered. For the remaining trials, comparisons of coda-types in between trial should be orientated on the rhythm plots.

2.4. Behavioural context of coda production

Only focal codas from 2020 were used to investigate the relationship between coda production and whale's diving and foraging behaviour. Diving and foraging metrics analysed were dive phase, activity, time of day and depth.

Dive Phase

Dives were separated into descent, ascent, and surface to investigate if the total number of codas changed depending on the dive phase and if there was a particular coda type used during a certain dive phase. Chi-square tests were performed for all GrpReps combined and in isolation, and for ID- and non-ID codas.

The surface period was defined as the time the whale spent at or close to the surface, including shallow dives with depths up to 200 m. To define the descent and ascent dive phases, a custom-made MATLAB script was used to calculate the whale's orientation (pitch). The descent was the period since the whale left the surface, changing from a horizontal position (pitch = 0°) to downwards orientation (pitch < 0°) until changing again (pitch > 0°). The ascent corresponded to the period when the whales showed a consistent upwards position (pitch > 0°) until reaching the surface (pitch = 0°) (Miller et al. 2004b). As the duration of tag deployment varied between whales, coda production was divided by the total duration of each dive phase.

Activity

Coda production was investigated for foraging and non-foraging activities, similar to Oliveira et al. (2002), where foraging time included the time spent during dive ascents and descents, the time spent at the bottom of the dive, plus short (≤ 20 min) surface periods between foraging dives. Non-foraging periods (including resting and socializing at the surface) were those when the whale spent more than 20 consecutive minutes at the surface. To standardize coda production in relation to the duration of foraging and non-foraging-periods, the number of codas produced were divided by the time spent in each activity. As before, chi-square tests were performed, for every single GrpRep, all GrpReps together, and separately per clades.

Depth

The depth of the whale during the emission of each coda was plotted to investigate if there were differences in coda type usage as a function of diving depth.

Diel pattern

The times of sunrise and sunset per date and location were calculated using the NOAA ESRL solar calculator (https://gml.noaa.gov/grad/solcalc/). If any codas were produced 30 min after sunset or 30 min before sunrise, defined as twilight time, they were excluded from the analysis. Production of different codas was divided by the deployment hours per day and night, and chi-square tests were used to explore diel patterns in production of coda types, for GrpReps combined and separated.

3. Results

The 3–9 click codas recorded in the three datasets yielded a total of 22 GrpReps (see B1 in Appendix). The 2020 dataset contained five GrpReps, with 668 focal and 1121 non-focal codas, the 2010 dataset (Oliveira, 2014) included four additional GrpReps, containing 753 focal codas, and the 1988–2006 dataset (Antunes, 2009) contributed with another 13 GrpReps to the analysis, with 3,018 codas. The number of codas per GrpRep varied from 50 to 1,877 codas (Table 6). Individual whales produced 0.3 to 91.8 codas per hour (Table 6).

Table 6: Summary of focal and non-focal codas (with 3 – 9 clicks) of the Azorean datasets per GrpRep ordered by recording day and year.

<table>
<tr><th>GrpRep</th><th>N° focal coda</th><th>Focal Coda-rate per hr</th><th>N° non-focal coda</th><th colspan="2">N° of coda per GrpRep</th></tr>
<tr><td>88_1042</td><td></td><td></td><td>194</td><td colspan="2">194</td></tr>
<tr><td>88_1043</td><td></td><td></td><td>68</td><td colspan="2">68</td></tr>
<tr><td>88_1002</td><td></td><td></td><td>112</td><td colspan="2">112</td></tr>
<tr><td>89_1051</td><td></td><td></td><td>29</td><td colspan="2">29</td></tr>
<tr><td>89_1007</td><td></td><td></td><td>29</td><td colspan="2">29</td></tr>
<tr><td>89_1004</td><td></td><td></td><td>48</td><td colspan="2">48</td></tr>
<tr><td>91_1001</td><td></td><td></td><td>1877</td><td colspan="2">1877</td></tr>
<tr><td>93_1014</td><td></td><td></td><td>126</td><td colspan="2">126</td></tr>
<tr><td>95_1018</td><td></td><td></td><td>25</td><td colspan="2">25</td></tr>
<tr><td>95_1093</td><td></td><td></td><td>76</td><td colspan="2">76</td></tr>
<tr><td>95_1094</td><td></td><td></td><td>280</td><td colspan="2">280</td></tr>
<tr><td>06_1181</td><td></td><td></td><td>36</td><td colspan="2">36</td></tr>
<tr><td>06_1183</td><td></td><td></td><td>165</td><td colspan="2">165</td></tr>
<tr><td>10_211b</td><td>155</td><td>10.5</td><td></td><td colspan="2">155</td></tr>
<tr><td>10_222a</td><td>61</td><td>9.8</td><td></td><td>61</td><td rowspan="2">330</td></tr>
<tr><td>10_222b</td><td>269</td><td>17.7</td><td></td><td>269</td></tr>
<tr><td>10_226a</td><td>104</td><td>6.1</td><td></td><td colspan="2">104</td></tr>
<tr><td>10_228a</td><td>164</td><td>8.2</td><td></td><td colspan="2">164</td></tr>
<tr><td>20_161a</td><td>77</td><td>3.9</td><td>241</td><td colspan="2">318</td></tr>
<tr><td>20_189a</td><td>68</td><td>12.6</td><td>89</td><td colspan="2">157</td></tr>
<tr><td>20_191a</td><td>26</td><td>91.8</td><td>24</td><td colspan="2">50</td></tr>
<tr><td>20_192a</td><td>376</td><td>25.9</td><td>340</td><td colspan="2">716</td></tr>
<tr><td>20_225a</td><td>99</td><td>5.6</td><td>427</td><td colspan="2">526</td></tr>
</table>

The most frequently recorded codas amongst the 2020 data contained 5 clicks. The proportions of codas with different clicks were similar between focal and non-focal codas and also between the GrpReps (see B 4 in Appendix). On the contrary, a clear contrast was observed in the coda rhythm: GrpReps 20_161, 20_189 and 20_191 used regularly spaced codas or codas with or slowly increasing ICIs, while 20_192 and 20_225 emitted codas with partially very short ICIs and practically no regular codas (Figure 11).

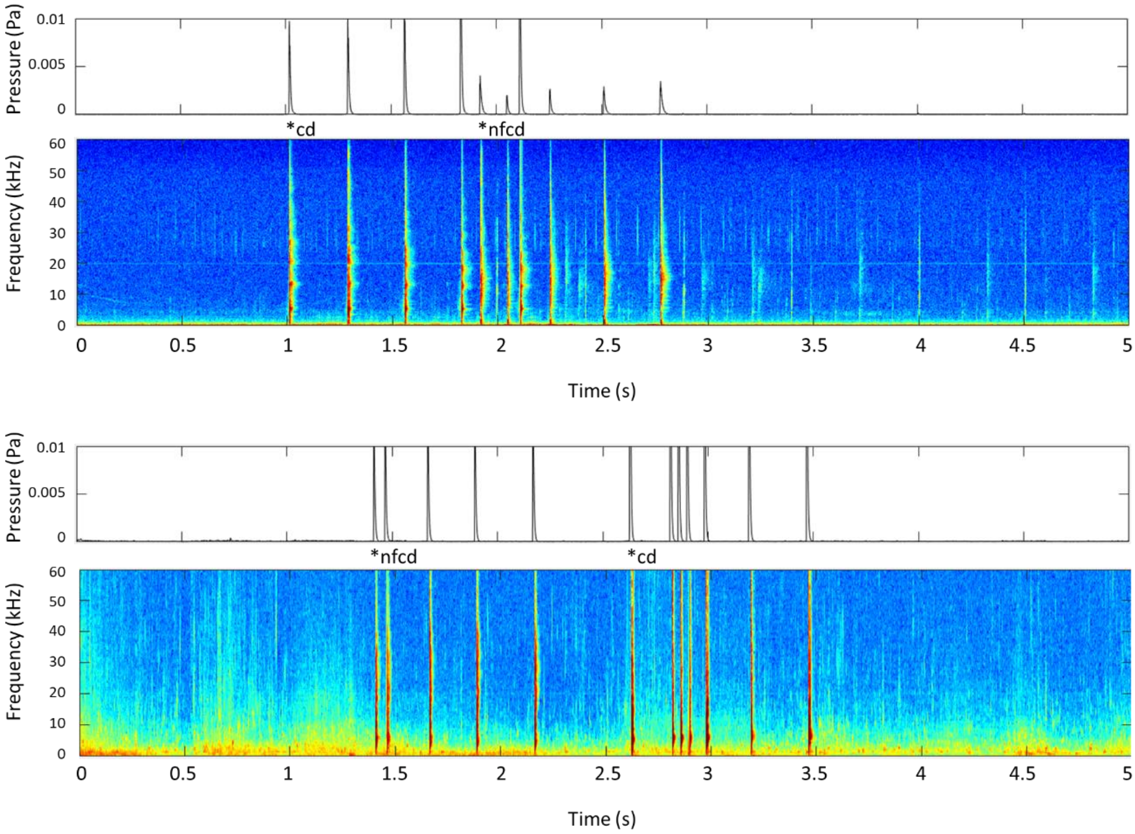


Figure 11: Contrast of frequently recorded codas between GrpReps in the 2020 dataset. Two five-click codas with regularly spaced or slowly increasing ICIs (time between two consequent clicks, each click is represented as one vertical line) (top) and a five-click coda followed by a six-click coda, both with partially very short ICIs (bottom). Each block represents one focal coda (cd) and one non-focal coda (nfcd) in a segment of 5 seconds, illustrating pressure-waveform in Pa (top) and frequency-spectrogram in kHz (bottom).

Although 5-click-codas were also most frequently procuced in the 2010 dataset, it showed a high inter-individual variability in the proportion of codas with different click-number, with two whales producing mostly 5-click-codas, whereas the other two individuals used mainly 3-click-codas.

The data recorded from 1988 to 2006 contained a much higher number of codas and GrpReps. While 5-click-codas were still preeminent, a larger percentage of 4-click-codas and codas with higher number of clicks were observed. Again, a high level of individuality in click-number proportion was noted.

The proportions of codas with different clicks in all three datasets are illustrated in Figure 12.

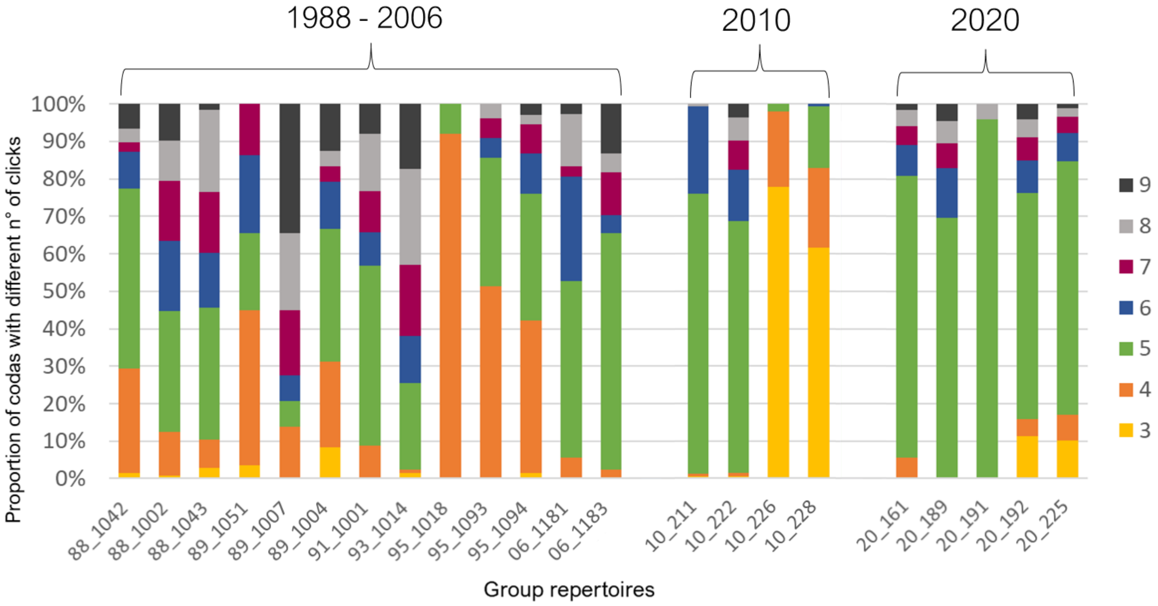


Figure 12: Proportions of codas with different n° of clicks per group repertoire from three datasets per group repertoire, recorded from 1988–2006 in the Azores. Each colour represents a different number of clicks. Assigned colours of coda click length were maintained throughout the study, whilst different rhythms were later illustrated by graduated tonal values of the respective colours.

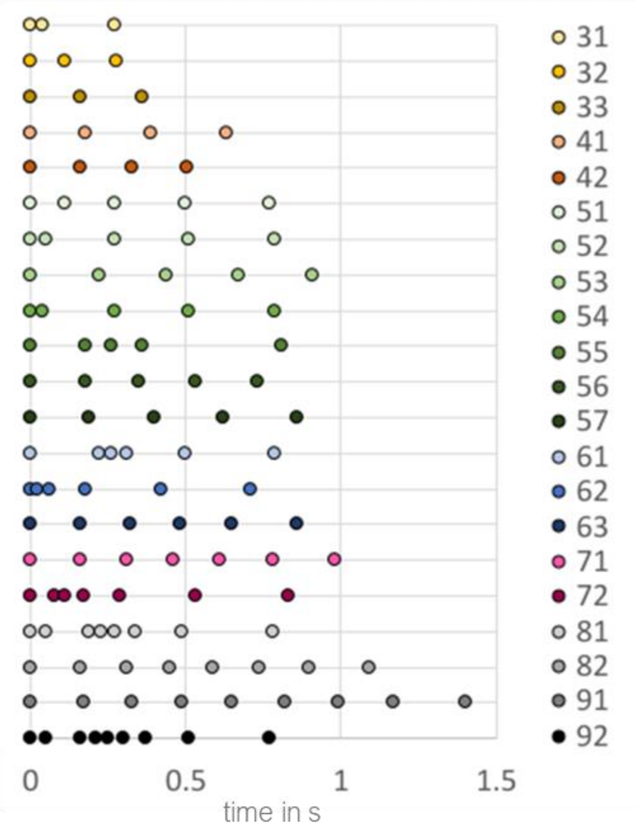
3.1. Coda type classification

Including the 2020-data only (trial 1), the coda type classification generated 21 coda types, their centroid ICIs in seconds are presented in Table 7. As observed before, some coda types have regular ICIs (e.g., 33, 53, 63) whilst others have partly very short ICIs (e.g., 31, 54, 62). Those coda types were used for the analyses of behavioural context of coda production.

The different coda types were not equally emitted per GrpRep nor between the different GrpReps (Figure 13). While most frequently used coda types clearly change between GrpReps 20_161, 20_189, 20_191 and 20_192 and 20_225, the diversity in their coda repertoire also differs, with GrpReps 20_161, 20_189, 20_191 using less coda types than 20_192 and 20_225. Especially 20_191 demonstrated a very limited coda repertoire, using only seven different coda types.

Table 7: Twenty-one coda types of the 2020 dataset with their centroid ICIs (in seconds) created with the IDCALL-method. The created coda type labels are composite numbers, being the first cipher the number of clicks of each coda and the second cipher a subsequent number, separated for every click length. Rhythm plot at the right, with each dot representing one click and each line one coda type. Each coda type was given a different colour per click length as in Figure 12, whilst different rhythms were illustrated by graduated tonal values of the respective colours.

Type	ICI1	ICI2	ICI3	ICI4	ICI5	ICI6	ICI7	ICI8
31	0.04	0.23						
32	0.11	0.17						
33	0.16	0.2						
41	0.18	0.21	0.24					
42	0.16	0.16	0.18					
51	0.11	0.16	0.23	0.27				
52	0.05	0.22	0.24	0.28				
53	0.22	0.22	0.23	0.24				
54	0.04	0.23	0.24	0.28				
55	0.18	0.08	0.1	0.45				
56	0.18	0.17	0.18	0.2				
57	0.19	0.21	0.22	0.24				
61	0.22	0.04	0.05	0.19	0.29			
62	0.02	0.04	0.12	0.24	0.29			
63	0.16	0.16	0.16	0.17	0.21			
71	0.16	0.15	0.15	0.15	0.17	0.2		
72	0.08	0.03	0.06	0.12	0.24	0.3		
81	0.05	0.14	0.04	0.04	0.07	0.15	0.29	
82	0.16	0.15	0.14	0.14	0.15	0.16	0.19	
91	0.17	0.16	0.16	0.16	0.17	0.17	0.18	0.23
92	0.05	0.11	0.05	0.04	0.05	0.07	0.14	0.26



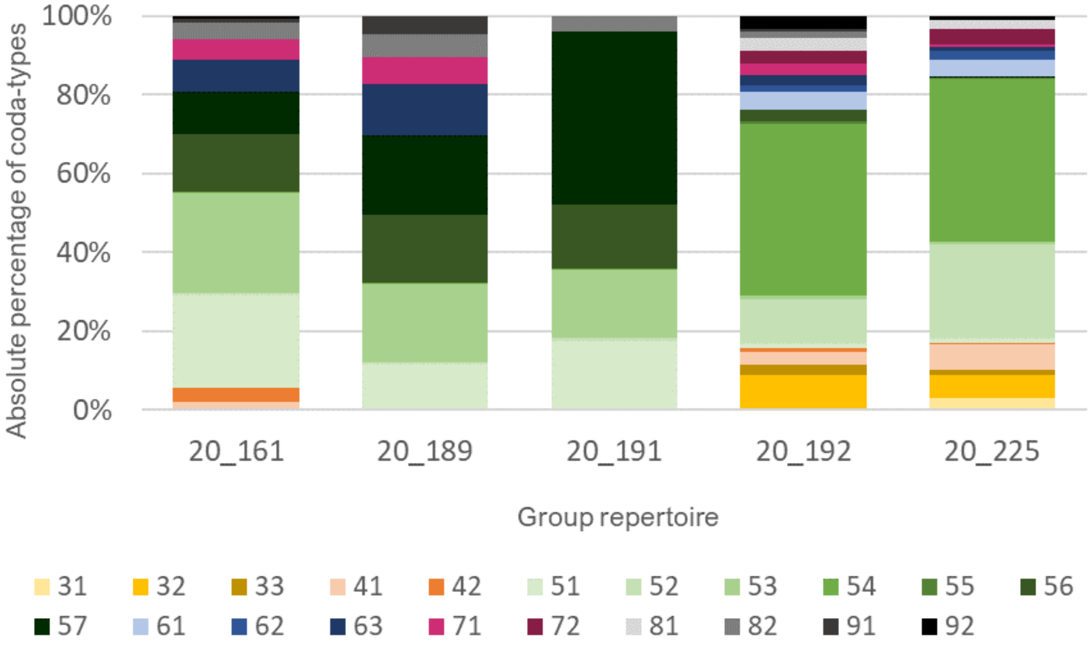


Figure 13: Coda type use proportions per Group repertoire, 2020 dataset. Coda type labels and colours were maintained as in Table 7.

To investigate if the number of coda types produced by individual whales increased with recording time, the cumulative number of coda types was counted in steps of 30 min for all five individuals (Figure 14). The longer the duration of the recording, the more coda types a whale produced. Nevertheless, in whales with longer deployments, coda diversity seems to have reached a plateau. The maximum number of recorded coda types per GrpRep (focal & non-focal codas) exceeded the ones for individual whales.

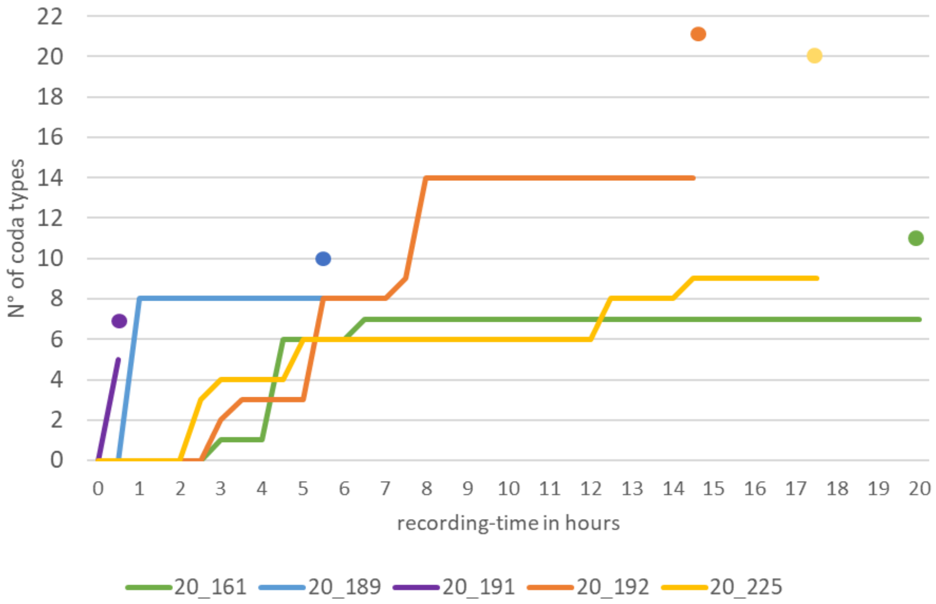


Figure 14: Coda diversity as a function of recording time for 5 sperm whales tagged in 2020, each coloured line representing one individual with its recorded focal codas. The maximum number of coda types recorded per Group repertoire (including non-focal codas) is illustrated with a dot in the respective colour.

The analysis of all three datasets combined (trial 7) generated 56 different coda types, represented in different percentages in each GrpRep (Figure 15). Although the proportion of coda types changed among GrpReps, no clear trend was observed over time. Coda types 51 – 59, with 5 clicks, were dominant in most GrpRep and over time. The three GrpReps recorded in 1995 (95_1018, 95_1093 & 95_1094) and 89_1051 had a large number of 4-click-coda types (coda types 41–48). Two GrpReps recorded in 2010 (10_226 &10_228) differenciated from all other GrpReps by the large amount of 3-click-coda types (coda types 31 – 310). GrpRep 89_1007 and 93_1014 had a relatively large number of 9-click-coda types (coda types 91–97). 20_192 and 20_225 used a different type of 5-click-coda than any other GrpRep (coda type 59).

These generated coda types were used for the further analysis of clades and potential vocal clans amongst the Azorean repertoires.

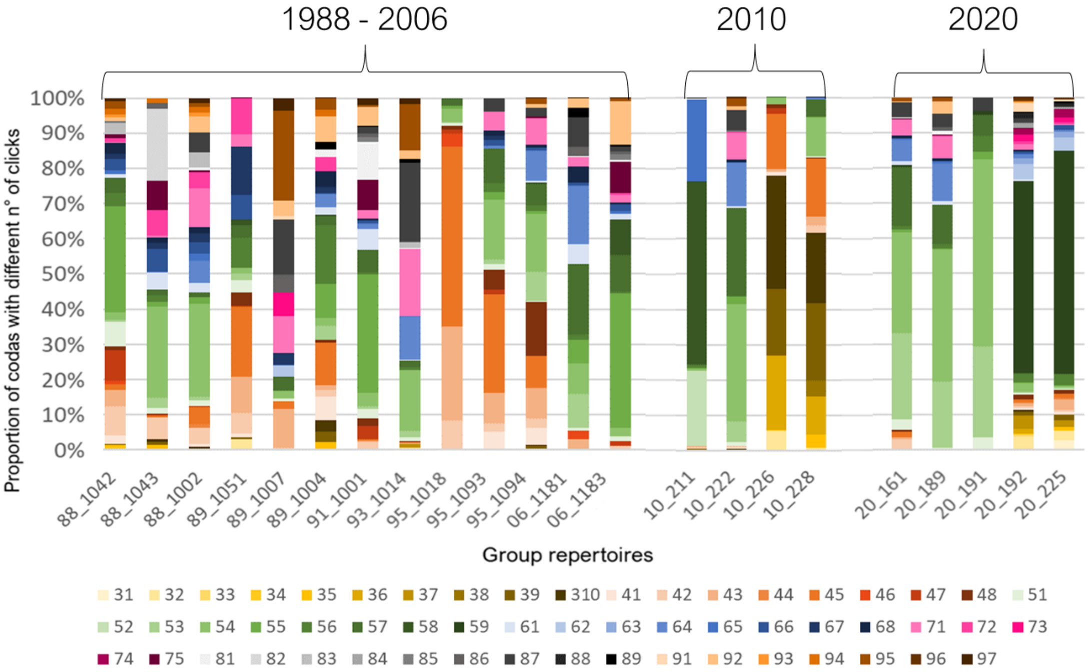


Figure 15: Coda type use proportions per Group repertoire, 1988–2020 dataset, ordered per recording date. Note that, although methodology of labelling and colouration of coda types was maintained, coda-nomenclature changed in each classification trial, thus numbers and colours do not represent the same coda types shown in Figure 13.

3.2. ID codas & clades

Several trials were performed, including datasets of different regions, all of which included different number of GrpReps and codas (Table 5). For this reason, the IDcall-method constructed a different number of coda types in each trial. The labels and colouration of constructed coda types are not necessarily comparable from one trial to the other. Instead, coda-rhythm plots should be used for visualization.

Azorean datasets

Two clades (C1, containing codas with partly short ICIs, and C2, containing more regularly spaced codas) were created while maintaining the baseline settings (CF 14, MR 2), in which 20_211 was considered an outlier (trial 4.1, ID codas Figure 16, all coda-types see A 3 in Appendix). The proportion of ID codas on the whole coda-repertoire is much higher in C1 (0.754) than in C2 (0.0965). With varying CF, those two clades were maintained up to a CF 25, whilst from CF 26 onwards, only C1 was maintained (trial 4.2, see A 4 Appendix). When CF was lowered, the diversity of the previous C2-clade could be demonstrated, creating a maximum of six clades at CF 5 (trial 4.3, C3 – C7, Figure 17). We can observe in Figure 16 and Figure 17 that similarity of GrpRep was independent from recording year. When augmenting the baseline parameter MR, C1 was considered an outlier.

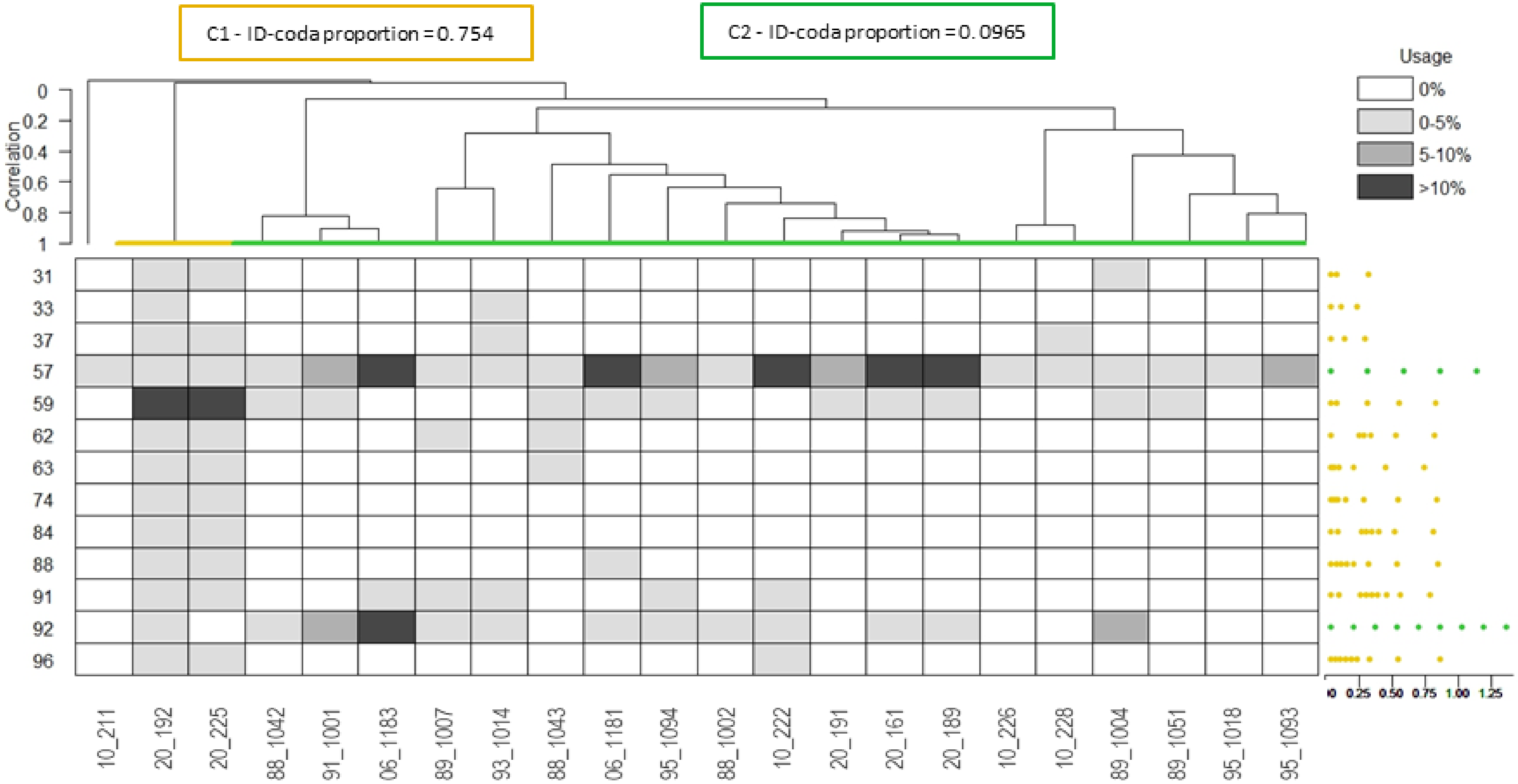


Figure 16: Trial 4.1: Dendrogram with two created clades and ID coda types for the Azorean 1988–2020 dataset, demonstrating similarity of sperm whale group repertoires (GrpReps)(columns). Generated clades are coloured in yellow (C1) and green (C2) and were named with the letter "C" and a running number. Nomenclature and colour of clades were maintained from one trial to the other in case the same GrpReps were included in the clade. Heat map (bottom) demonstrates the percentage of ID coda type (rows) production per group repertoire in shades of grey, with ID coda type labels (left) and their rhythm plot in seconds, each dot representing one click (right). ID coda proportion per clade (above). Coda type labels are equal to Figure 15. Created with baseline settings critfact 14, minrep 2.

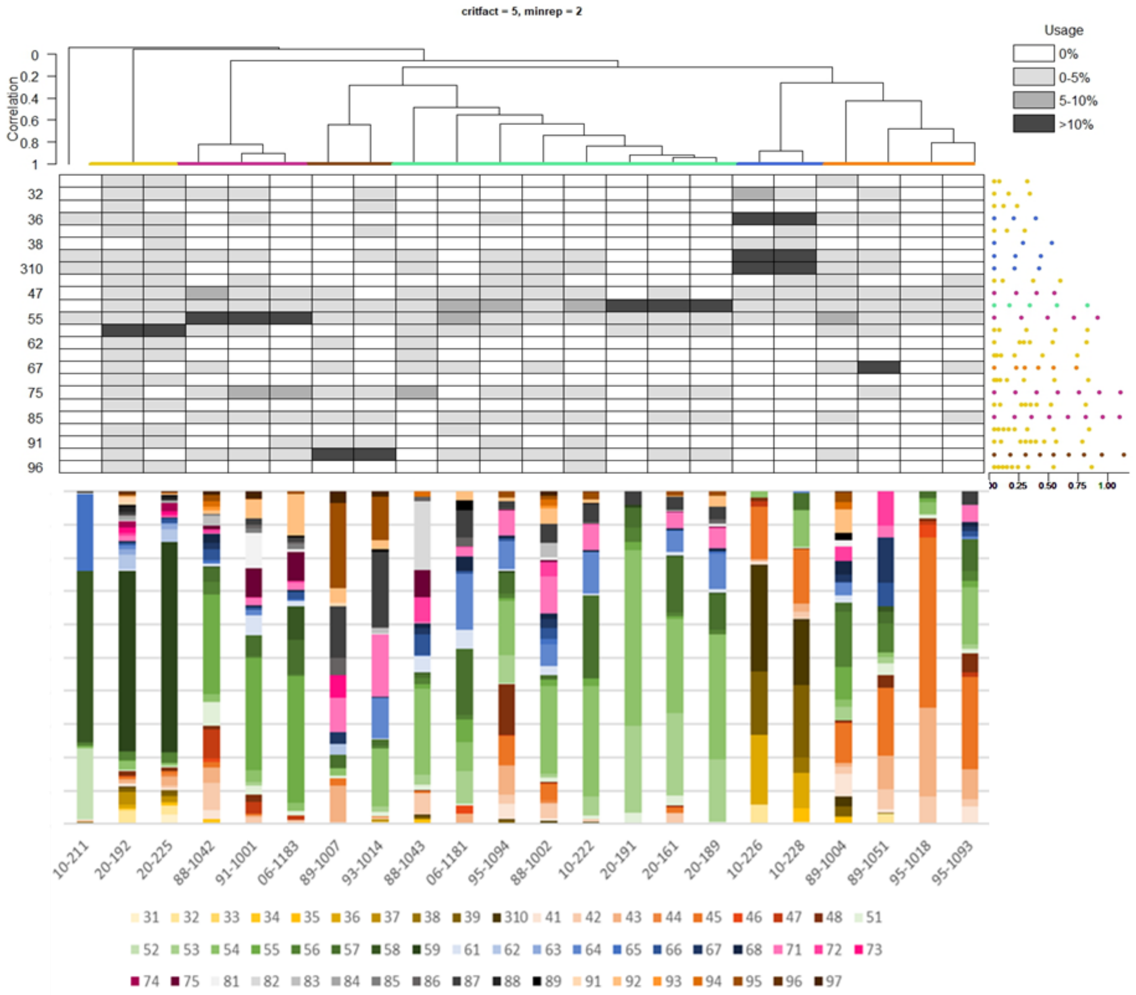


Figure 17: Trial 4.3: Dendrogram with six created clades and ID coda types for the Azorean 1988–2020 dataset, demonstrating similarity of sperm whale group repertoires (GrpReps)(columns). Generated clades are coloured in yellow (C1), magenta (C3), brown (C4), aquamarine (C5), blue (C6) and orange (C7) and were named with the letter "C" and a running number. C1 represents the same clade as in Figure 17. Heat map (middle) demonstrates the percentage of ID coda-type (rows) production per group repertoire in shades of grey, with ID coda type labels (left) and their rhythm plot in seconds, each dot representing one click (right). Bar graphs (bottom) show the percentage of all coda types per GrpRep. Coda type labels are equal to Figure 15. Created with settings critfact 5, minrep 2.

Integrating other regions of the Atlantic

The IDcall-Method was applied with the parameters CF 14 and MR 2 as in the previous trials, to the Azorean dataset amplified by datasets from other regions in the Atlantic (trial 5.1, Figure 18) and the EC (trial 6.1, Figure 19). In both trials, all the Azorean GrpReps were grouped in a single clade with the EC2 clan (C10), with the exception of 20_192 & 20_225 (C1). Also, in trial 6.1, GrpRep 10_211 was joined with two GrpRep that were considered outliers in Vachon et al. (2022), sharing the ID coda 67 ("5+1"; C13). Using the settings applied in Hersh et al. (2021) and Vachon et al. (2022), less clades were created, where C1 was an outlier (see A 5 and A 6 in Appendix).

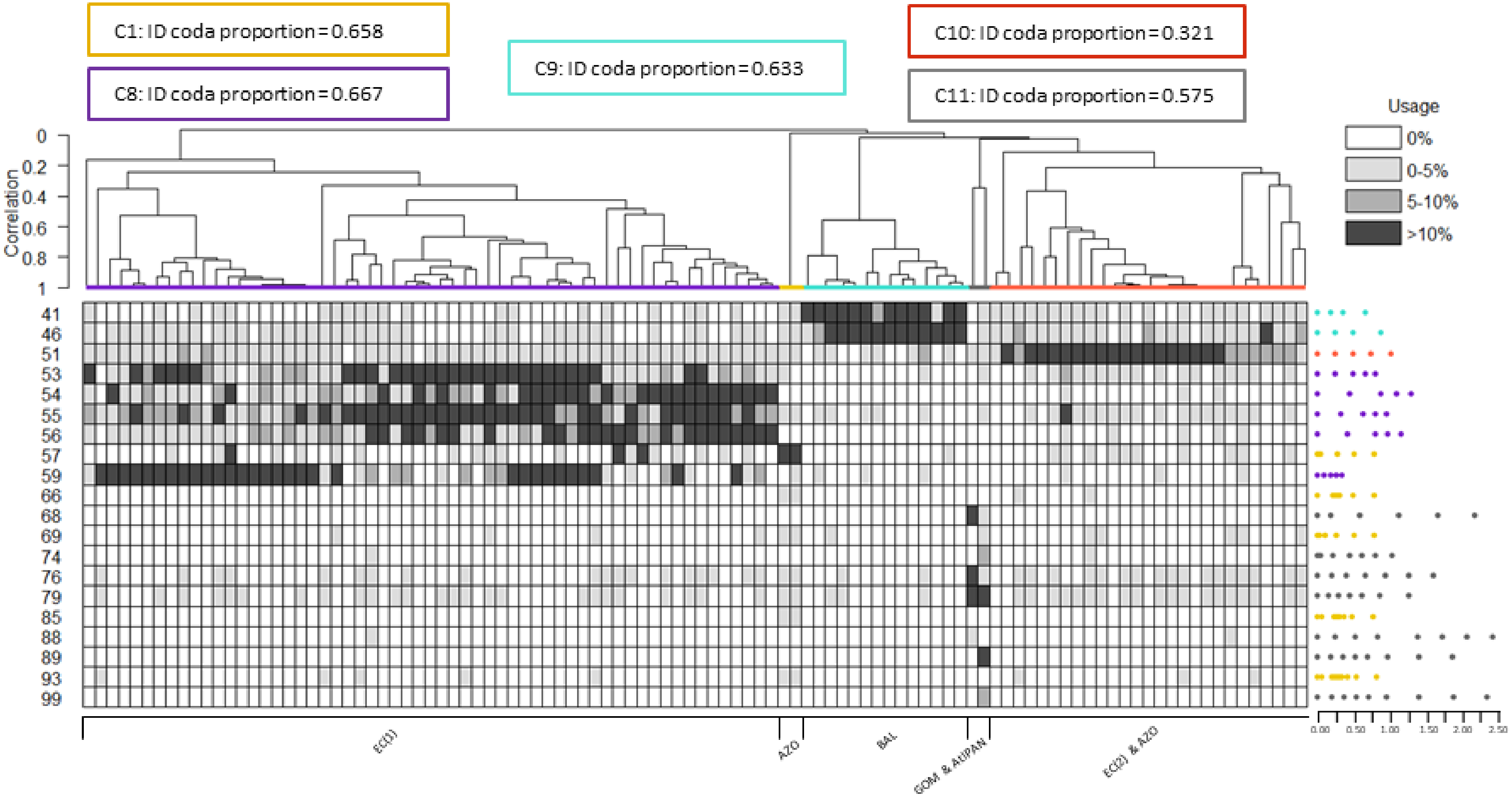


Figure 18: Trial 5.1: Dendrogram with five created clades and ID coda types for the Azorean 1988–2020 dataset and the Atlantic dataset from Hersh et al. 2021, demonstrating similarity of sperm whale group repertoires (GrpRep)(columns). Generated clades are coloured in yellow (C1), violet (C8), turquoise (C9), red (C10) and grey (C11) and were named with the letter "C" and a running number. C1 represents the same clade as in previous figures. Heat map (bottom) demonstrates the percentage of ID coda type (rows) production per group repertoire in shades of grey, with ID coda type labels (left) and their rhythm plot in seconds, each dot representing one click (right). ID coda proportion is added per clade (above) and recording location (bottom), being the Azores (AZO), EC (Eastern Caribbean, in parenthesis the respective vocal clan), Balearic (BAL), Gulf of Mexico (GOM) and Panama (AtlPAN). Note that coda type nomenclature changed in each classification trial, thus numbers and colours do not represent the same coda types shown in previous figures. Created with baseline settings critfact 14, minrep 2.

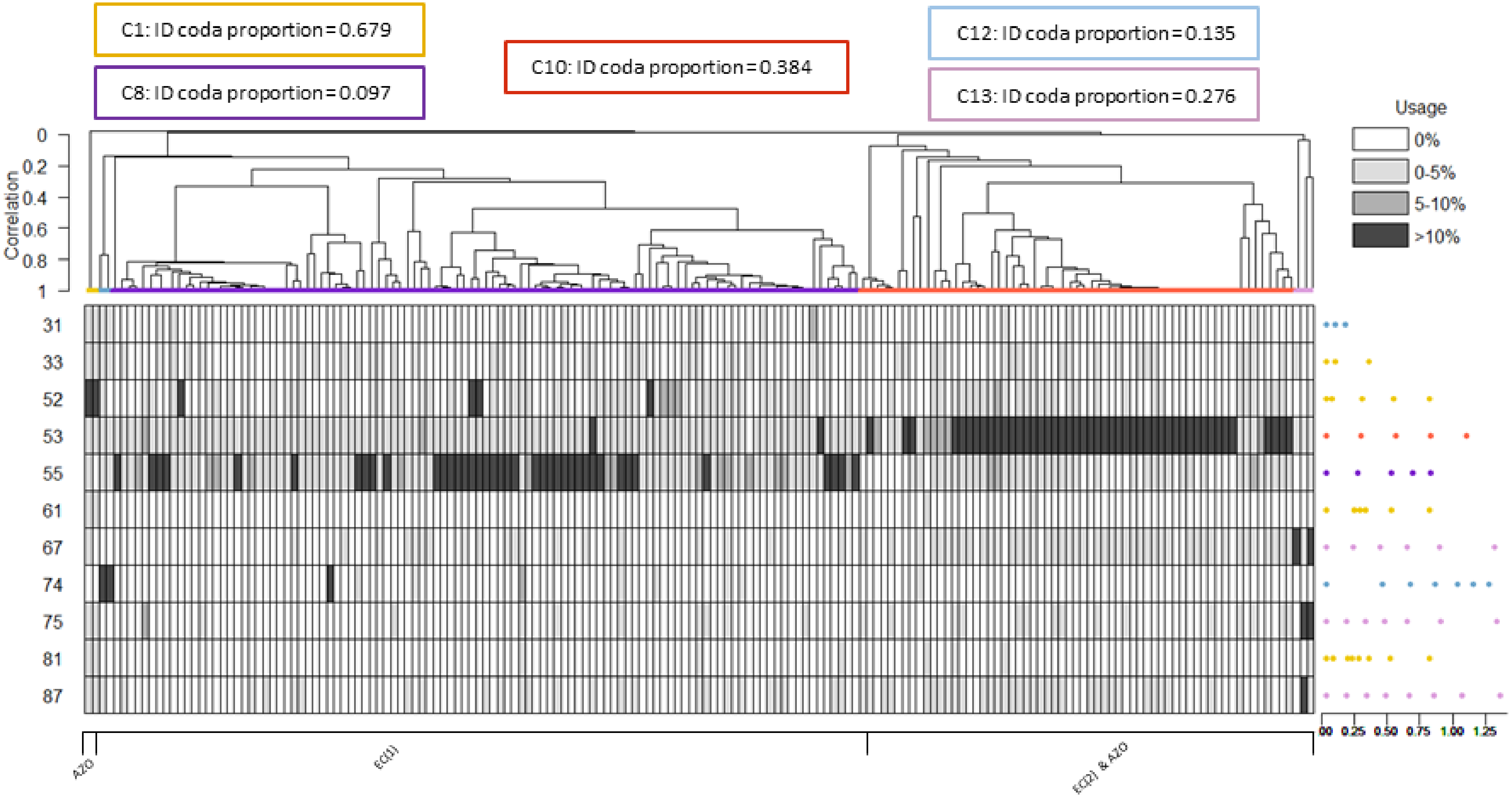


Figure 19: Trial 6.1: Dendrogram with five created clades and ID coda types for the Azorean 1988–2020 dataset and the EC dataset from Vachon et al. 2022, demonstrating similarity of sperm whale group repertoires (GrpRep)(columns). Generated clades are coloured in yellow (C1), violet (C8), red (C10), light blue (C12) and rose (C13) and were named with the letter "C" and a running number. C1, C8 and C10 represent the same clades as in the previous figure. Heat map (bottom) demonstrates the percentage of ID coda type (rows) production per group repertoire in shades of grey, with ID coda type labels (left) and their rhythm plot in seconds, each dot representing one click (right). ID coda proportion is added per clade (above) and recording location (bottom), being the Azores (AZO) and EC (Eastern Caribbean, in parenthesis the respective vocal clan). Note that coda-nomenclature changed in each classification trial, thus numbers and colours do not represent the same coda types shown in previous figures. Created with baseline settings critfact 14, minrep 2.

3.3. Photo-Identification

The photo-Identification-analysis was able to match the five sperm whales tagged in 2010 and four out of six tagged whales from 2020 (see B2 in Appendix), most of them were confirmed sightings in the Azores over several years, and some individuals belong to well-known social units of the area. As assumed, 10_222a and 10_222b were former sighted together, likely belonging to the same social unit. None of the other individuals are thought to belong to the same social unit. Whales 20_192 and 20_225, which were noted to use a very distinctive, similar vocal repertoire (C1), belong to two well-known but different social units.

3.4. Behavioural context of coda production

Contextual analysis calculations are presented in B5 in the Appendix. The mean forage dive time for all 5 individuals was 44.6 min, the mean surface time between foraging dives (not including prolonged surface periods >20 min) was 9.8 min. Summing prolonged surface periods, the whales spent on average 44% at the surface contrasting to 56% foraging (deep foraging dives plus short surface times between foraging dives).

Dive Phase

Production of different coda types by individual whales varied significantly between dive phases (see B 6 in Appendix).

Some coda types (31, 41, 61, 62, 81, 92) were only produced at the surface (Figure 20). However, these coda types were generally produced very rarely (5% of all codas). The diversity of coda types was also higher at the surface (19) than during ascents (13) and descents (5). Coda production rate showed the same pattern, with fewer codas per hour during descents (3.7 cd/hr) than during ascents (15.4 cd/hr) and at the surface (20.4 cd/hr), although coda types and rates varied between the individuals (Figure 21).

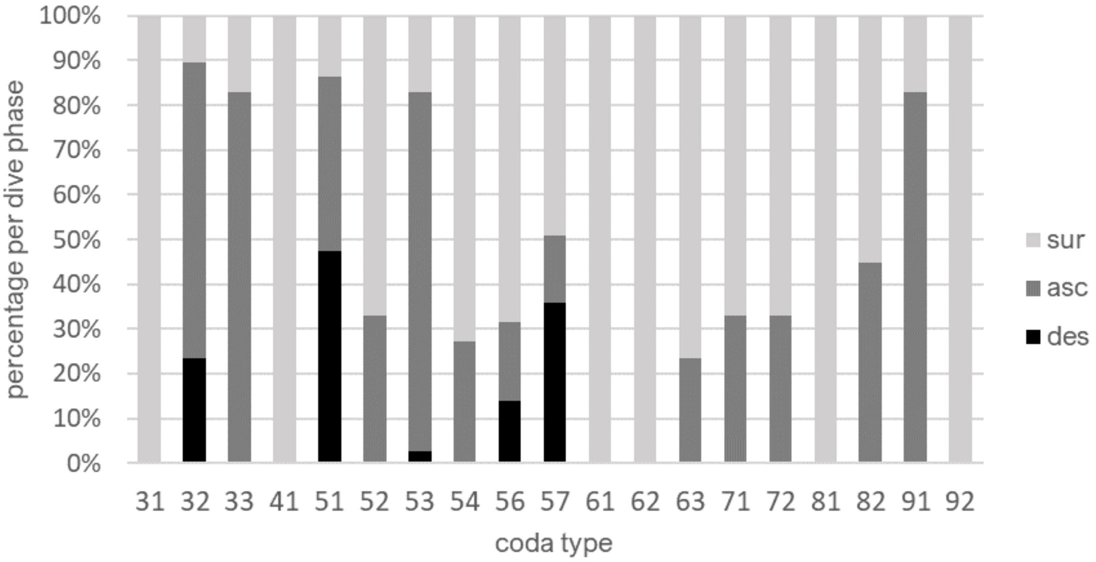


Figure 20: Coda type use in dependency of dive phase, joined for 5 sperm whales tagged in 2020. Relative proportion of descent (des), ascent (asc) and surface (sur) periods per coda type.

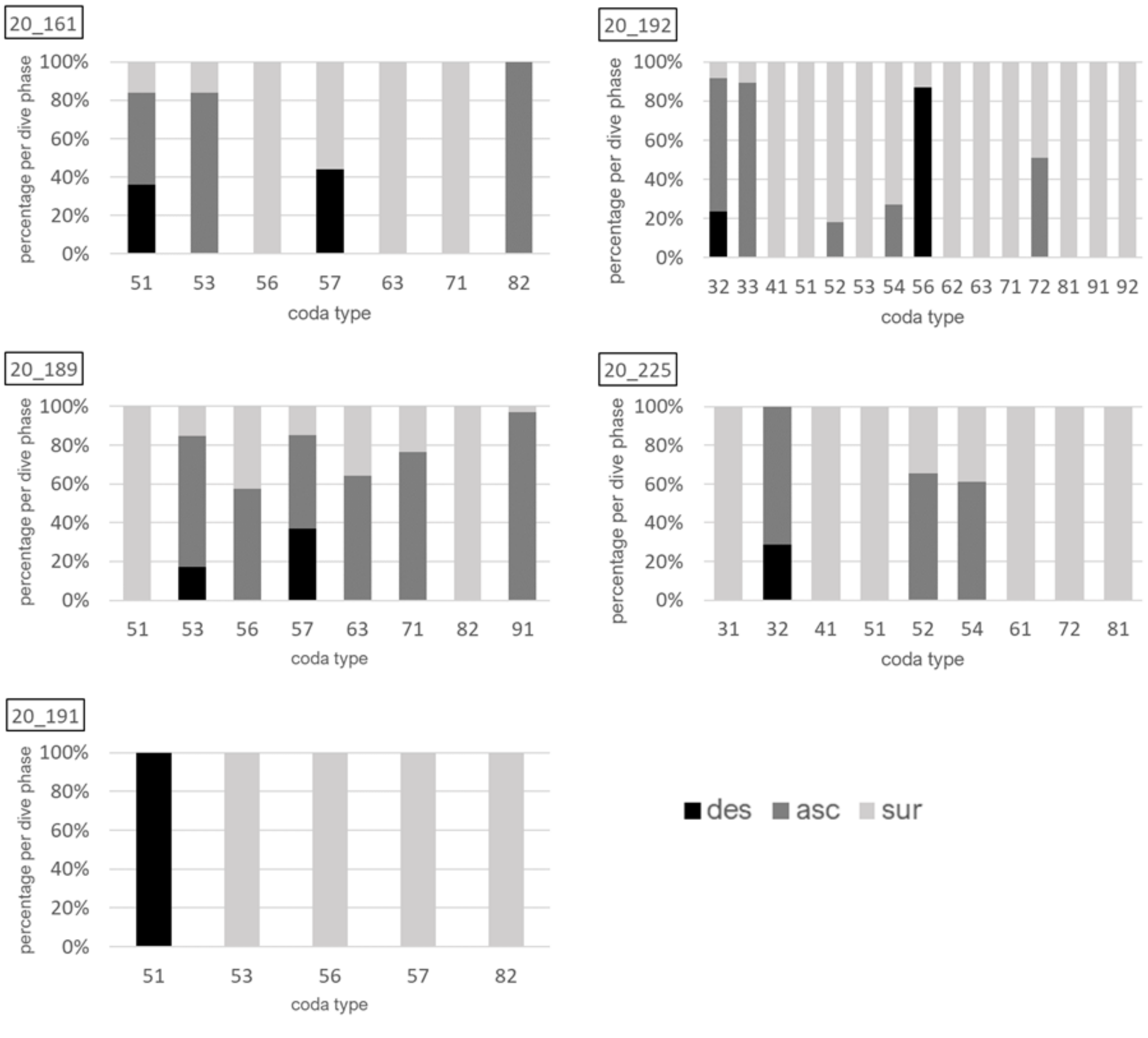


Figure 21: Coda type use in dependency of dive phase, separated for 5 individual sperm whales tagged in 2020. Relative proportion of descent (des), ascent (asc) and surface (sur) periods per coda type.

Coda type relation with dive phases was further investigated, by separating ID codas and non-ID codas (Figure 22). Both groups were produced during descents, ascents and on the surface. During descents, only one non-ID coda was produced, which corresponded to an unusual movement from individual 20_192 (see A 7 in Appendix).

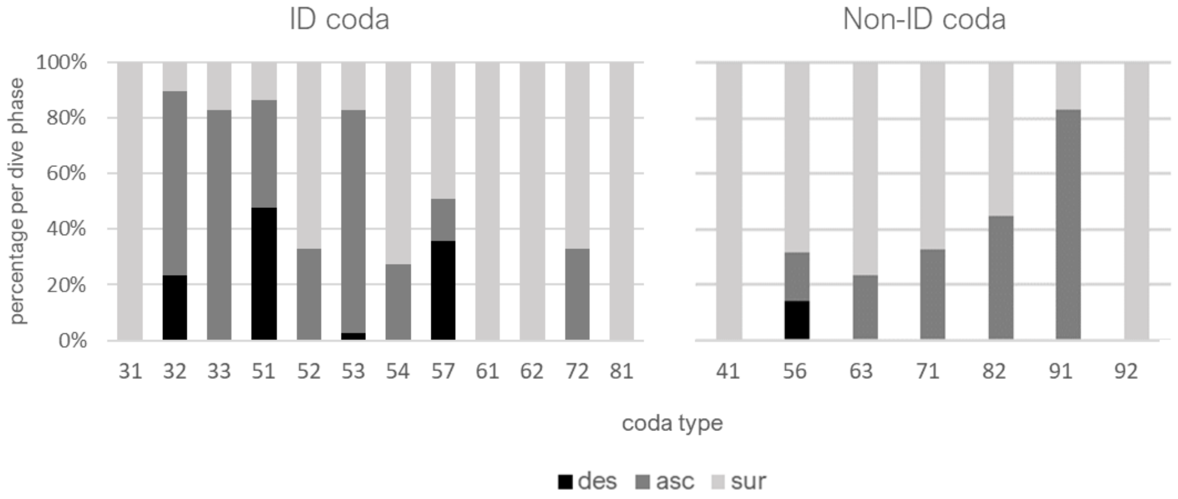


Figure 22: Coda type use in dependency of dive phase, joined for 5 sperm whales tagged in 2020, separated for ID codas (left) and non-ID codas (right). Relative proportion of descent (des), ascent (asc) and surface (sur) periods per coda type.

Activity

In whales 20_189 and 20_225, coda type production was not independent from the whale's activity (see B 6 in Appendix), whereas for the other two individuals the results were not significant.

Coda diversity and production rate were higher during non-foraging phases (22.1 cd/hr and 18 types) than during foraging phases (3.8 cd/hr and 15 types, Figure 23). One coda type (31) was only used during foraging while others were produced solely during non-foraging (41, 61, 81 and 92; Figure 23). Those codas were very rarely produced (together accounted for <5% of all codas) and differed from individual to individual (Figure 24).

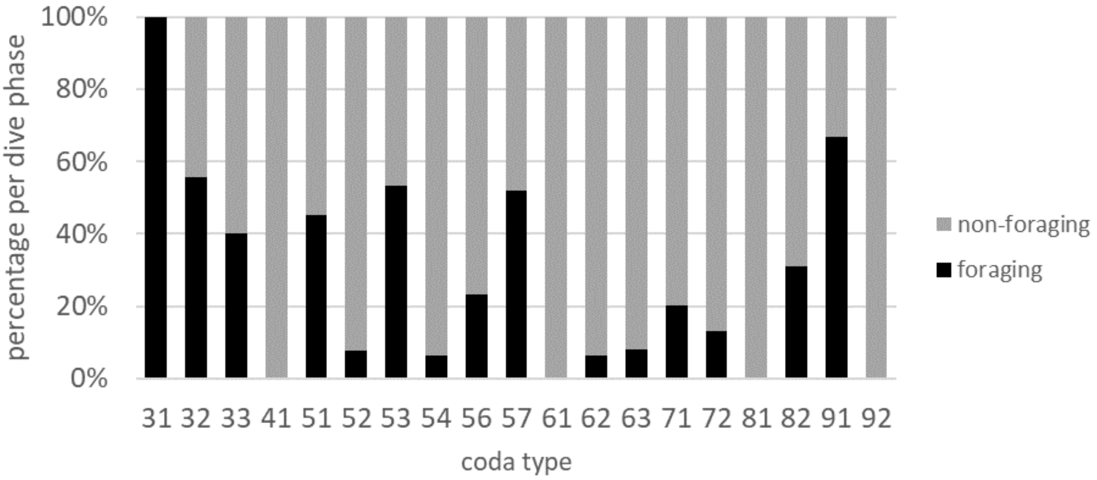


Figure 23: Coda type use in dependency of activity, joined for 4 sperm whales tagged in 2020. Relative proportion of foraging and non-foraging periods per coda type.

In C1 (individuals 20_192 & 20_225), coda type 31 was only produced during foraging dives, while 41, 51, 53, 56, 61, 63, 71, 81, 91 and 92 were only produced during non-foraging dives. The remaining codas were produced both during foraging and non-foraging dives. But the absolute coda rate per foraging and non-foraging demonstrates that some codas were very rarely produced. In C1, during foraging dives, only ID codas were produced (Figure 25). For the individuals in C2 (20_161 & 20_189), both ID codas and non-ID codas were produced during foraging and non-foraging dives. In C2, there was only one coda type (91) used solely during foraging dives, but this coda was only emitted three times in total by the two individuals.

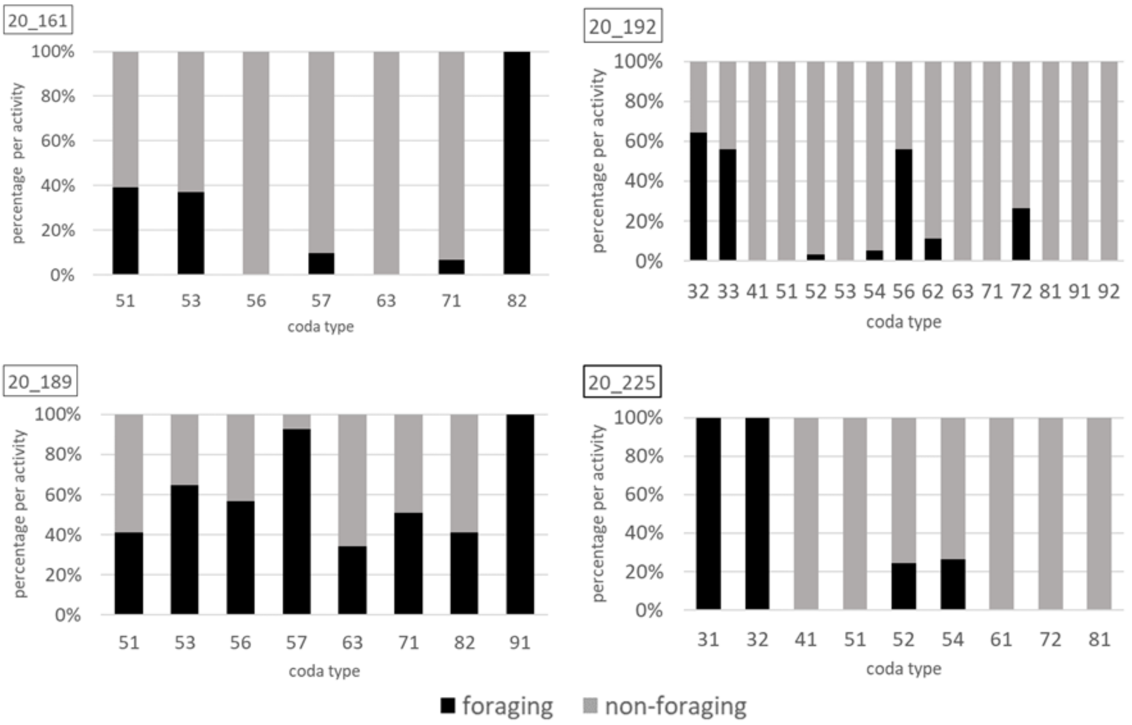


Figure 24: Coda type use in dependency of activity, separated for 4 individual sperm whales tagged in 2020. Relative proportion of foraging and non-foraging periods per coda type.

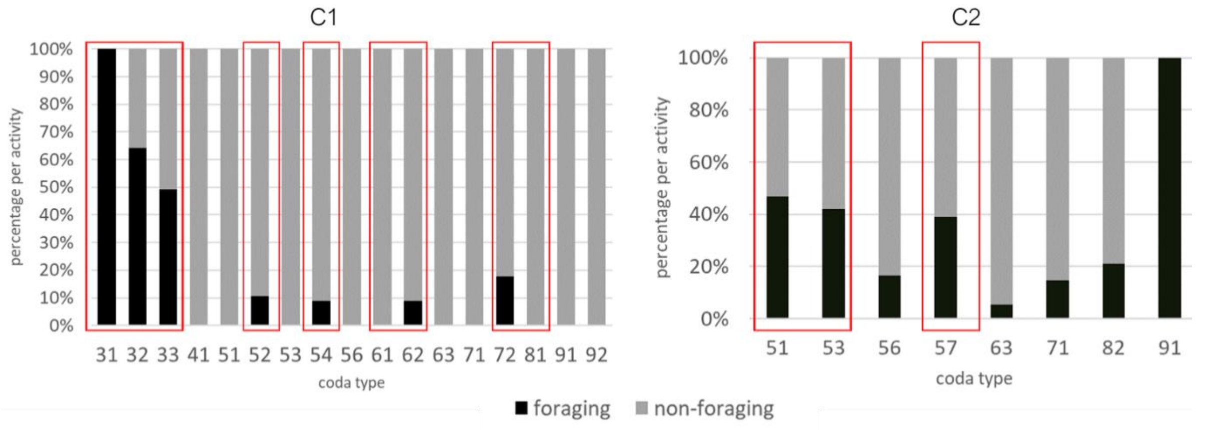


Figure 25: Coda type use in dependency of activity phase, for 4 individuals tagged in 2020, separated per clades. ID codas are framed in red. Relative proportion of foraging and non-foraging periods per coda type.

Diel pattern

Diel period had no significant influence on coda type production (see B 6 in Appendix). Although a few codas were recorded only at night or during the day, these codas represented 3.5% of all codas (Figure 26).

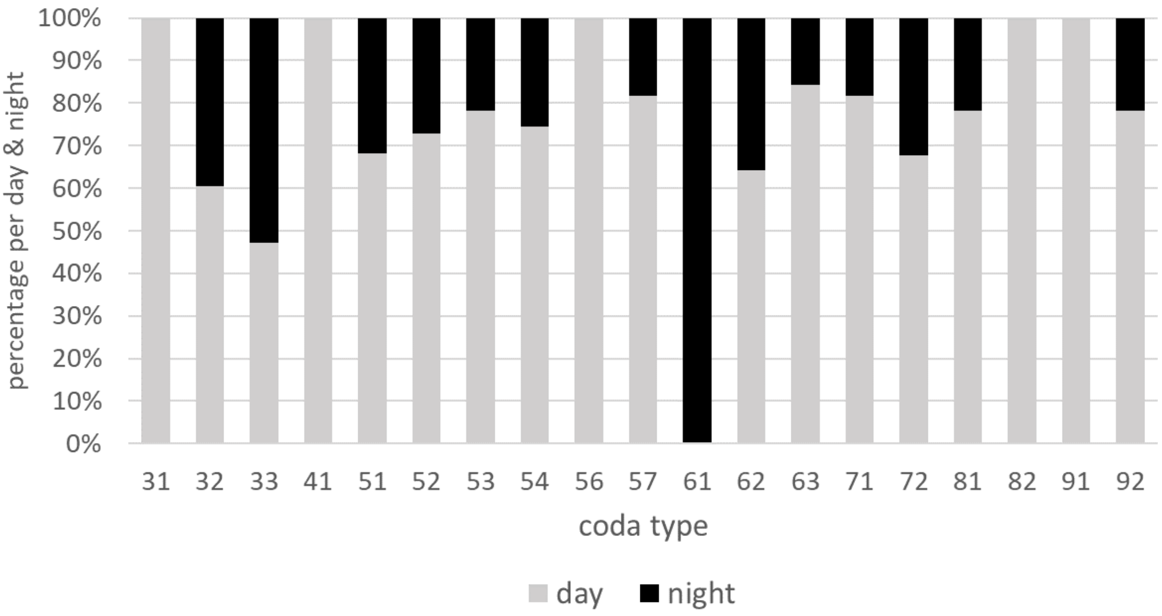


Figure 26: Coda type use in dependency of day and night, joined for 3 sperm whales tagged in 2020. Relative proportion of day and night periods per coda type.

In contrast, a higher coda production rate was observed during daytime (15 cd/hr) than at night (6 cd/hr) and this pattern was similar across all individuals (Figure 27).

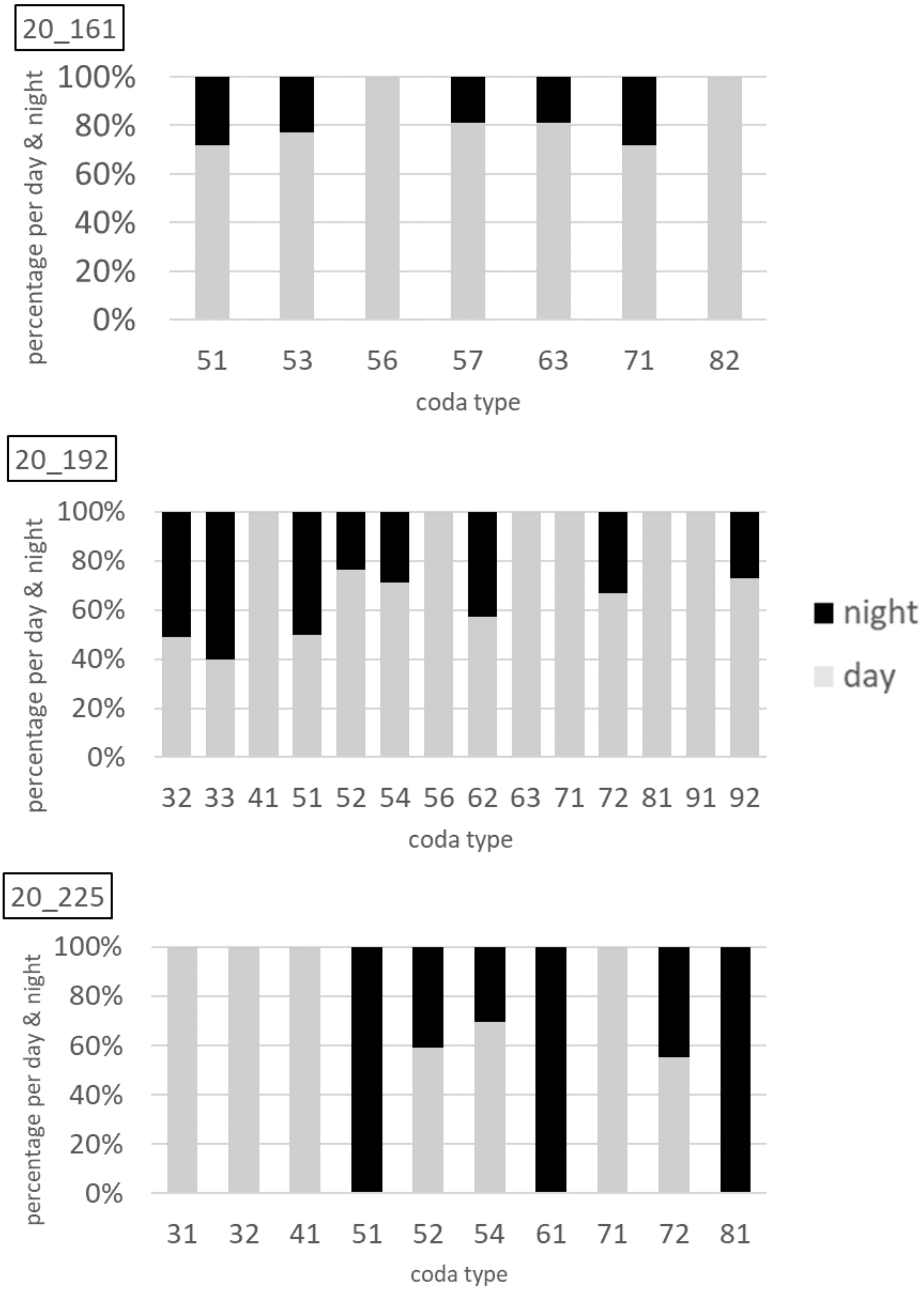


Figure 27: Coda type use in dependency of day and night, separated for 3 individual sperm whales tagged in 2020. Relative proportion of day and night periods per coda type.

Depth

Codas were produced between 0 and 520 m depth (Figure 28). Many coda types were used both close to the surface and in deeper waters. Individually, some coda types were solely produced in a particular depth but there was no clear pattern across whales or clades.

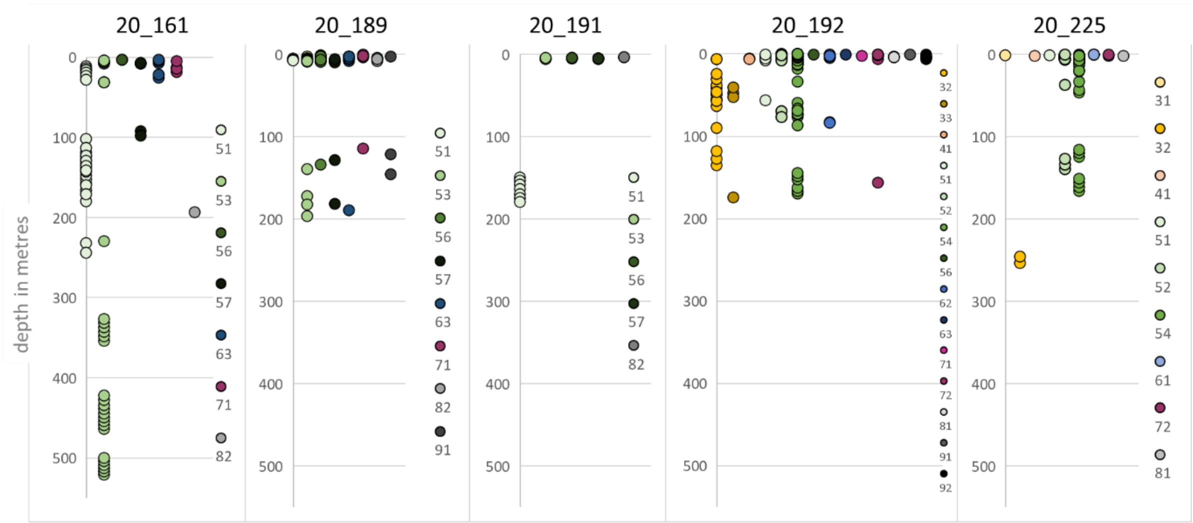


Figure 28: Coda type use in dependence of depth in the water column, separated for 5 individual sperm whales of 2020. Each dot represents one coda, each coda type is illustrated in a different colour equal to Table 7. The y-axis in each graph represents the depth (in metres) of coda production.

4. Discussion

Coda type classification

Coda type classification via the IDcall-method is based on contaminated mixture modelling. The “contamination”, i.e., the outliers of the generated coda-types, can be controlled, and evaluated throughout the modelling (Punzo & McNicholas 2016), favourizing this methodology over others that are more sensitive to outliers as e.g., k-means-clustering (Hersh 2021). Being one of the previously most often utilized methods (e.g., Weilgart & Whitehead 1997; Rendell & Whitehead 2003a; Amano et al. 2014), k-means-clustering requires the determination of numbers of clusters, i.e., the resulting coda types, *a-priori*, making it more subjective (Oliveira et al. 2016; Hersh 2021). This parameter setting is not necessary for contaminated mixture modelling (Hersh et al. 2021). While k-means-clustering fits clusters into Voronoi cells of equal, but unnatural shape and size (Oliveira et al. 2016), contaminated mixture modelling permits the clusters to differ in volume, shape, and orientation, further allowing the dataset to vary in dimension (Punzo & McNicholas 2016, Hersh et al. 2021). Last, k-means-clustering standardized ICIs, potentially losing important features when distinguishing coda types (Frantzis & Alexiadou 2008; Antunes et al. 2011; Amano et al. 2014), while absolute ICIs were used in the present study.

Thus, the automated method delivered 21 coda types for the classification of the 2020 dataset, resulting to be similar to the manual classification but returned a higher diversity of coda types. Manual classification could not differentiate coda types 52 and 54, or 53 and 57 (Table 7). If only rhythm would have been considered, even less coda types would have been identified (e.g., 53, 56 and 57 joined as “5R”). Classification of all Azorean datasets generated 56 different coda types, demonstrating that the diversity of coda repertoires increases with augmenting datasets. Such a positve correlation of sampling effort and number of repertoires has been observed by Hersh et al. (2022).

Earlier studies based on standardized ICIs also impeded comparisons between coda repertoires reported by different studies. Uniformity of classification strategies and inclusion of more data and regions in the analysis, seem the only options to overcome slight differences in classification outcomes. Especially the subjective nomenclature, which diverges across regions and studies, causes confusion and incomparability. In our study, the coda types with very short ICIs did not fit adequately into any existing nomenclature. However, it seems redundant to create a way of naming the classified coda-types, as the IDCALL-script (Hersh et al. 2021) creates a table with centroid values of each coda type, which enables quantitative comparisons among coda types.

A few parameters of the IDCALL-method are indeed to be defined by the user, meaning the results always need to be confirmed by the analyst or by a second classification approach. During the classification of coda types, those parameters are the ECM initialization strategy and the information criterion. Whilst variation of ECM initialization strategy did not lead to big differences in the resulting coda type, the choice of information criterion did. Nevertheless, slight differences in coda type classification are not critical for clade and clan assignment, nor impede the comparison among regions, as long as all data are combined in a single analysis. In terms of the behavioural context analysis, much more care must be taken not to overinterpret coda type classification in relation to a particular behaviour or movement.

In the present study, a large number of coda types contained unusually short ICIs between some of the clicks, and, per definition, would not even be classified as codas (ICIs of 0.1–0.5 s, Whitehead 2003). Their prevalence amongst two GrpReps and the successful separation from chirrups gives great confidence that they are in fact coda-clicks (e.g., ID codas 52 & 54). Similar codas have been mentioned in a few other studies but with slight differences. The “short codas” (Pavan et al. 1997; Drouot et al. 2004) recorded in the Mediterranean have a distinct rhythm and click length, being almost entirely composed of “3+1”-codas. Huijiser et al. (2020) mentioned many codas with “fast middle clicks” in Mauritius, the majority of which were 8-click-codas. Indeed, some codas from Mauritius are similar to the short ID codas in our study (Figure 29, bottom left). The geographic distance between Mauritius and the Azores makes it unlikely that similarity in these coda types indicates a shared vocal repertoire or common vocal clan. Within regions in closer proximity, such short 5-click-codas where parenthetically mentioned in the Caribbean (Gero et al. 2016a & b; Figure 29, right) but they were considered infrequent coda types.

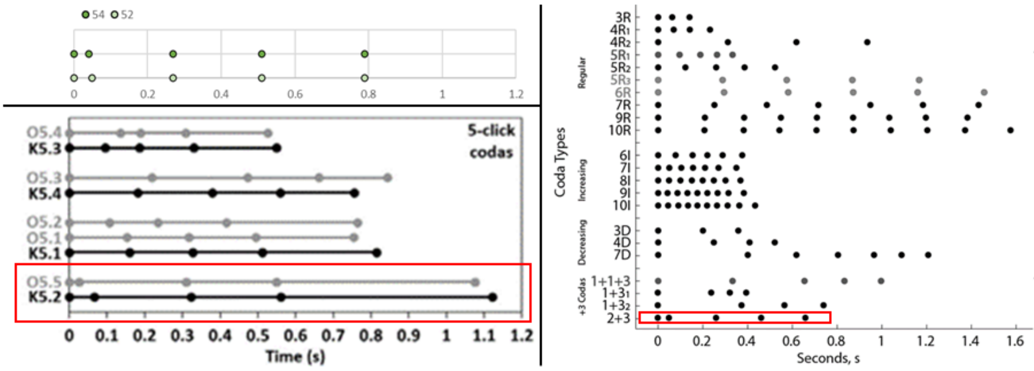


Figure 29: „Short” codas emitted by C1 in the Azores (left, top), also reported in Mauritius (bottom left), adapted from: Huijser 2020 and the Eastern Caribbean (right), adapted from: Gero 2016a.

The early detachment of DTAGs in some of the whales implied a low number of codas and coda types recorded, unlikely to represent the individuals' full repertoire. Generally, the longer the recording, the more coda types were detected, but the coda repertoire still differed between individuals, GrpReps and clades. The variation in the number of ID codas between vocal clans has previously been observed (Hersh et al. 2022). This could be caused by differences in the duration of recordings during surface phases, when coda production increases, as observed in this and other studies (Weilgart & Whitehead 1993; Madsen et al. 2002b). When separating focal and non-focal codas, it was also noticed that none of the tagged individuals reached the full repertoire of its corresponding GrpRep. This suggests that either the individual vocal repertoire has not been recorded to its full extent, or that, within a social unit, individuals only share a limited number of codas (including the ID codas also shared within their vocal clan). Individual differences in coda type use inside a social unit have previously been reported (Antunes et al., 2011; Gero et al. 2016a). Documenting the full vocal repertoire of an individual would require long term recordings of the same whale, possibly over several seasons and years, a task difficult to achieve.

Clades and vocal clans

The hierarchical clustering of the coda types identified into clades and possible vocal clans required setting the parameters *critfact* (CF) and *minrep* (MR). Different values of these parameters generated very different outcomes. A more objective classification could be achieved by applying machine learning techniques (Andreas et al. 2022). Nonetheless, the IDcall-method is becoming widely used (Hersh et al. 2021, 2022; Vachon et al. 2022). Compared to these studies, the Azorean dataset based on all data recorded between 1988 and 2020 contained fewer GrpReps, resulting in a substantial decrease of MR to a value of 2 (i.e., two GrpReps with ID codas) to generate separation into clades, but no clades were formed by increasing this parameter, indicating the necessity of augmenting sampling effort to confirm the observations. On the other hand, CF could be set to 25 while still separating two clades. This value means that the ID codas considered were produced 25 more times by one clade than by the other. When only regarding the 2020 data (trial 1, Table 4: IDcall-trials of parameter-variation on the 2020 dataset including 1789 codas in five group repertoires), CF could be set to 135 while still separating two clades. This demonstrates that there were strong differences in the vocal repertoires of the two clades and provides robustness of their classification as "true" ID clades and, likely, as vocal clans.

When CF was decreased, a maximum of six clades (C1, C3–C7) was formed. Clades 3–7 were less robust, varying substantially with different CF values. Except for C1, the other clades were composed mostly of regular-click-codas. The separation of these 5 clades was based on the number of clicks and the total coda length. When CF was increased, these clades gradually grouped into a single clade (C2). It is not impossible that the differences between these clades indeed imply true separate vocal clans, but a larger dataset would be necessary to separate them with confidence. Results show that similarity in vocal repertoire between GrpReps was not associated with the year or period of recording. For example, the vocal repertoire of 88_1042, 91_1001 and 06_1183, recorded in the years 1988, 1991 and 2006, respectively, was very similar (correlation ≈ 0.8) although the recordings spanned 18 years. These results indicate that coda repertoires of sperm whales in the Azores are stable over time, as found in other areas (e.g., Rendell & Whitehead 2005).

Hersh et al. (2022) mention the typical rhythmic “motifs” of ID codas inherent to many vocal clans. These differences are clearly visible between the two formed clades in the Azorean dataset, where C1 consists almost entirely of codas with partly very short ICIs, and C2, containing more regularly spaced codas. While C2 represents the vocal repertoire described for the Azores previously (Antunes 2009; Oliveira 2014), C1 is new to the Azores and could demonstrate a potential separated, sympatric clan, undiscovered for the region so far. The fact that this particular clade only contains recordings from two tagged individuals, gives reason to be cautious. In any way, these two individuals belong to two well-known social units that visited the Azores over a number of years (Lisa Steiner, *pers. Commn,* see B 2 in Appendix). New coda repertoires and possible vocal clans have kept undiscovered for many years in other areas, despite of intense research. Only after more than 30 years of research effort, a second vocal clan was detected in the Eastern Caribbean besides the well-known “1+1+3”-clan (Gero et al. 2016b). In 2022, a potential third clan sharing the same area was described (Vachon et al. 2022). This third clan was proposed based on the recordings of a single social unit. In another case, a new vocal clan was proposed based on four animals (and 94 codas, Amorim et al. 2020). Considering the few studies undertaken in the Azores so far, it seems likely that new coda types and even new clans emerge with increasing research effort. As individuals 20_192 and 20_225, belonging to the potential new vocal clan C1, were identified, and confirmed to be repeatedly sighted in past years in the Azores, sampling effort could focus on those social units, associating their individuals via photo-identification in order to augment the data for the C1 clade, as successfully performed in other regions (e.g., Rendell & Whitehead 2003b; Gero et al. 2016b; Vachon et al. 2022).

Comparison of the coda repertoires from the Azores with those from other areas in the Atlantic revealed that ID codas from C1 were not found to a similar extent in other vocal clans. Conversely, the ID codas of the remaining clades showed similarities to two types of ID codas of the EC2 clan of the Eastern Caribbean, being regularly spaced ("5R") and slowly increasing 5-click-codas ("2+1+1+1") (Vachon et al. 2022).

Antunes (2009) compared the coda repertoires from the Azores with those from the Gulf of Mexico, Dominica, Panama, Iceland, and the Sargasso Sea. The results of the average linkage clustering demonstrated similarities in the regularly spaced codas between the Azores and the Sargasso Sea, and to a lesser extent, with Dominica and Iceland (Antunes 2009). It is not impossible that vocal clans range over such large areas; for example, the "short-clan" spanned over 10,000 km, covering the whole Pacific Ocean basin. Other clans were geographically more restricted ("Plus-one"-clan, 1,000 km; Hersh et al. 2022). When codas from the Azores were analysed with those off the Balearic Islands (BAL), the Caribbean (CAR), the Atlantic side of Panama (AtlPAN) and the Gulf of Mexico (GOM) (Hersh et al. 2021) and from the Eastern Caribbean (EC) (Vachon et al., 2022) the Azorean regular-click codas GrpReps grouped again in the same clade as the EC2 clan (C10), while the C1 clade formed a separate clan. With the settings as in Hersh et al. (2021), the Azorean C1 clade was considered an outlier.

The regular home range of female sperm whales has been estimated at ~2,200 km (Whitehead et al. 2008). Sperm whales from the Azores would be expected to show strong similarity in coda repertoires with those from Macaronesian waters such as the Canary Islands, given documented movements between the areas (Steiner et al. 2015) and Macaronesia being proposed a regional "core habitat" for the species (Boys et al. 2019). Instead, recordings from this area show that 3-click-codas with decreasing ICIs ("L+S") were the most frequent coda type (Schaar & André 2006). This type of coda was not documented amongst the analysed datasets from the Azores. On the other hand, the shared vocal repertoires between the Azores and the Caribbean demonstrate the species high mobility (Gero et al. 2007; Engelhaupt et al. 2009), which had been formerly proven by photo-identification recaptures of the Azores and the Caribbean (with a max. distance of 6,200 km, Mullin et al. 2022).

Differences between sympatric vocal clans have shown to be accompanied by differences in several other biological and behavioural characteristics, such as diving patterns (Amano et al. 2014), horizontal movements, defecation rates, and stable isotope composition, likely associated to differences in foraging strategies (Whitehead 2003; Rendell & Whitehead 2005; Marcoux et al. 2007). No obvious differences in diving pattern were detected between C1 and C2 clades in the Azores, but as skin samples have been collected from several tagged individuals analysed in this work, future studies could investigate other behavioural differences between the two clades.

Behavioural context of coda production

There was no obvious nor consistent relationship between usage of specific coda types and particular whale movements or behaviours. Instead, strong individual differences were observed in all analyses, which can be explained by high individual differences in the use of coda types.

Mean values of dive metrics used in behavioural analyses were within the range of values reported for sperm whales in the Azores (Gordon & Steiner 1992; Oliveira 2014) and are therefore representative of sperm whale behaviour in the area. Mean foraging time exceeded the reported average (Whitehead 2016), but results might be insignificant as no tagging deployments lasted 24 hours.

Coda type production varied during descents, surface, and ascents. Codas were produced more frequently at the surface (20.4 cd/hr) than during ascents (15.4 cd/hr) or descents (3.7 cd/hr). These results agree with those from other studies (Frantzis & Alexiadou 2008). Coda type diversity was also higher during surface periods, summing up to 19 different types compared to 13 types during ascents and 5 types during descents. The use of codas during each dive phase differed between individuals, even between whales belonging to the same clade. While for example individual 20_161 only produced coda type 82 during ascents, the other two individuals from C2 sharing a similar vocal repertoire (20_189 & 20_191) produced the same coda type only at the surface. However, these results were solely based in a total of 8 times that coda type 82 was produced by all 5 individuals. 20_191 also produced only one coda type during descent (51) but recording period and the number of produced codas were too small to take any strong conclusions. There was no specific coda type that was produced just during descents or ascents by all individuals, but some coda types (31, 41, 61, 62, 81, 92) were only produced at the surface. In addition, only one non-ID coda was produced during descents. These results were likely influenced by the fact that few codas (n=26) were produced during descents. Considering 53, 56 and 57 as “5R” codas according to their rhythm, individual 20_189 only produced 5R-codas during descents. The same finding was made already by Oliveira (2014), reporting specific coda types linked to certain dive phases.

Coda type production as function of the whales' activity showed less clear results, only being significant for half of the observed individuals. Coda rates were much higher in non-foraging (22.1 cd/hr) than foraging (3.8 cd/hr) periods. Those results are concordant to Frantzis & Alexiadou (2008), noticing a much higher coda production in "altered dive cycles" than in normal feeding activity. One coda type (31) was only emitted during foraging and several coda types only during non-foraging (41, 61, 81, 92), but as all of them were generally very rarely produced, these results remain inconclusive. In C1, during foraging dives, only ID-codas were produced, a pattern that was not observed in the individuals of the other clade. Frantzis & Alexiadou (2008) similarly noticed that the most frequent coda was emitted more frequently during foraging activity and unusual coda types were solely produced during non-foraging activity. Thus, although some sperm whale coda types varied with whales' activity, no vocalisation could be specifically linked to foraging or non-foraging, as seems to be the case with several baleen whale species (Cerchio & Dahlheim 2001; Casey et al. 2022).

The diel pattern could only be explored for three of the five animals, as the early DTAG-detachment in the other two individuals resulted in recordings during daytime only. Coda type was independent from the day/night cycle, yet a higher production rate was noticed during the day (15 cd/hr day vs. 6 cd/hr night). Although Oliveira (2014) detected a higher number of non-foraging periods during the night, this does not necessarily imply a higher coda production during those periods, and a proper diel analysis is still needed to confirm the occurrence of such a trend.

Coda production occurred between 0 and 520 m depth, but the majority of codas were produced close to the surface. Oliveira et al. (2016) noted a maximum coda depth of 650 m. Similar to the other metrics investigated, there was no clear pattern in coda type with depth, and the results instead point towards significant individual variability.

The findings about the relationship of coda production with depth, dive and activity phase are obviously connected. The production and diversity of codas increases when whales are at the surface, resting or socializing. Some coda types were also restricted to surface activities, being the rather unusual, rarely produced codas, while the most frequent (ID) codas seem to be more connected to foraging behaviour.

5. Conclusions

The present work contributes new information to sperm whale coda production in the Azores. The acoustic repertoires that had been found in previous studies (Antunes 2009; Oliveira 2014) were confirmed and expanded. Furthermore, two individuals tagged in 2020 demonstrated such a distinct coda repertoire that they are suggested to belong to a separate vocal clan, being the first time that sympatric vocal clans have been shown in the Azores. Analysis of a large coda dataset including previously documented codas (Antunes 2009; Oliveira 2014), that spanned from 1998 to 2020, showed that the coda repertoire consists mainly of regularly spaced codas, while showing slight differences in the number of clicks and total lengths. Those latter differences resulted in a maximum of six clades, of which not all were suggested to be true vocal clans. More data is necessary to confirm these clades and whether they represent true vocal clans. Sperm whale coda repertoire showed no obvious pattern with recording year, confirming the stability of sperm whale vocalisations over time (Rendell & Whitehead 2005). Comparisons to other regions in the Atlantic demonstrated similarities between one of the clades identified in the Azores and the EC2 vocal clan in the Caribbean (Gero et al. 2016b; Hersh et al. 2021; Vachon et al. 2022).

The analysis of the behavioural context of coda production did not show a clear relationship of any coda type or coda rates with specific behaviours but affirmed individual differences in coda type use. Nonetheless, results confirm an increased frequency and diversity of codas during surface activities, non-foraging, apparently during the day.

Even with a few contextual patterns emerging from this work, the function of codas remains unknown. Sperm whale vocalisations are very complex and include a number of other sounds in addition to codas that had to be disregarded in this work. If frequently used "ID codas" may be used for group cohesion and cultural identity, differing from one vocal clan to the other (Hersh et al. 2022), it might be necessary to focus more on the unusual codas and sounds, neglected in most studies, to unveil coda function. Although the IDCALL-method appears an excellent tool to detect differences in general worldwide coda repertoires (Hersh et al. 2021, 2022; Vachon et al. 2022), machine learning could enable detection of finer nuances in sperm whale vocalisations, going beyond the coda click number, total coda length and rhythm, which are the basis of coda research until today. Once clearer patterns are found, playbacks of codas, while observing the whales' reactions, might be the only way to unveil the function of these sounds.

Having such strong social bonds, sperm whales probably need to coordinate movements, babysitting and allocare, reproduction, as well as responses to potential threats. Even if sperm whales do not hunt cooperatively (Watkins & Schevill 1977b), it is possible that they communicate about feeding success or failures in a certain area, making decisions about further movements depending on their former foraging experience. It further should not be forgotten that much of sperm whale communication might also be made over aerial behaviour (Whitehead 1985; Würsing and Whitehead 2018) and touch (Tyack 2019). Behavioural observations of wide-ranging, deep-diving sperm whales are extremely challenging (Janik et al. 2000). Long-term and/or repeated recordings of codas would be needed, together with observation of the animals while vocalising. Advances in video technology in combination with DTAGs and drones might enable overcoming some of these difficulties.

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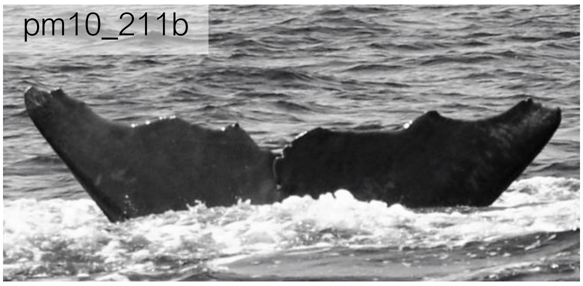
Appendix

pm10_211b

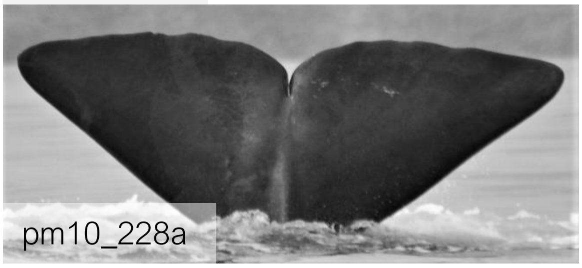


pm10_222a

pm10_222b

pm10_226a

pm10_228a



pm10_228a

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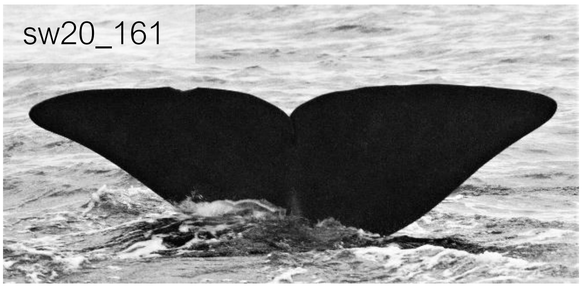
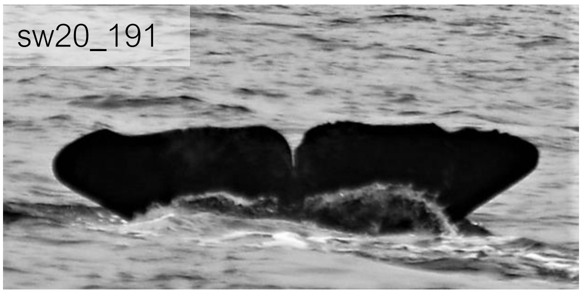
sw20_161



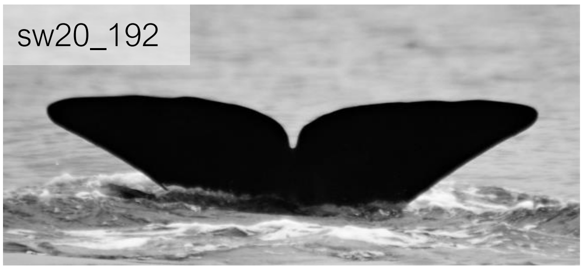
sw20_184a

sw20_189a

sw20_191

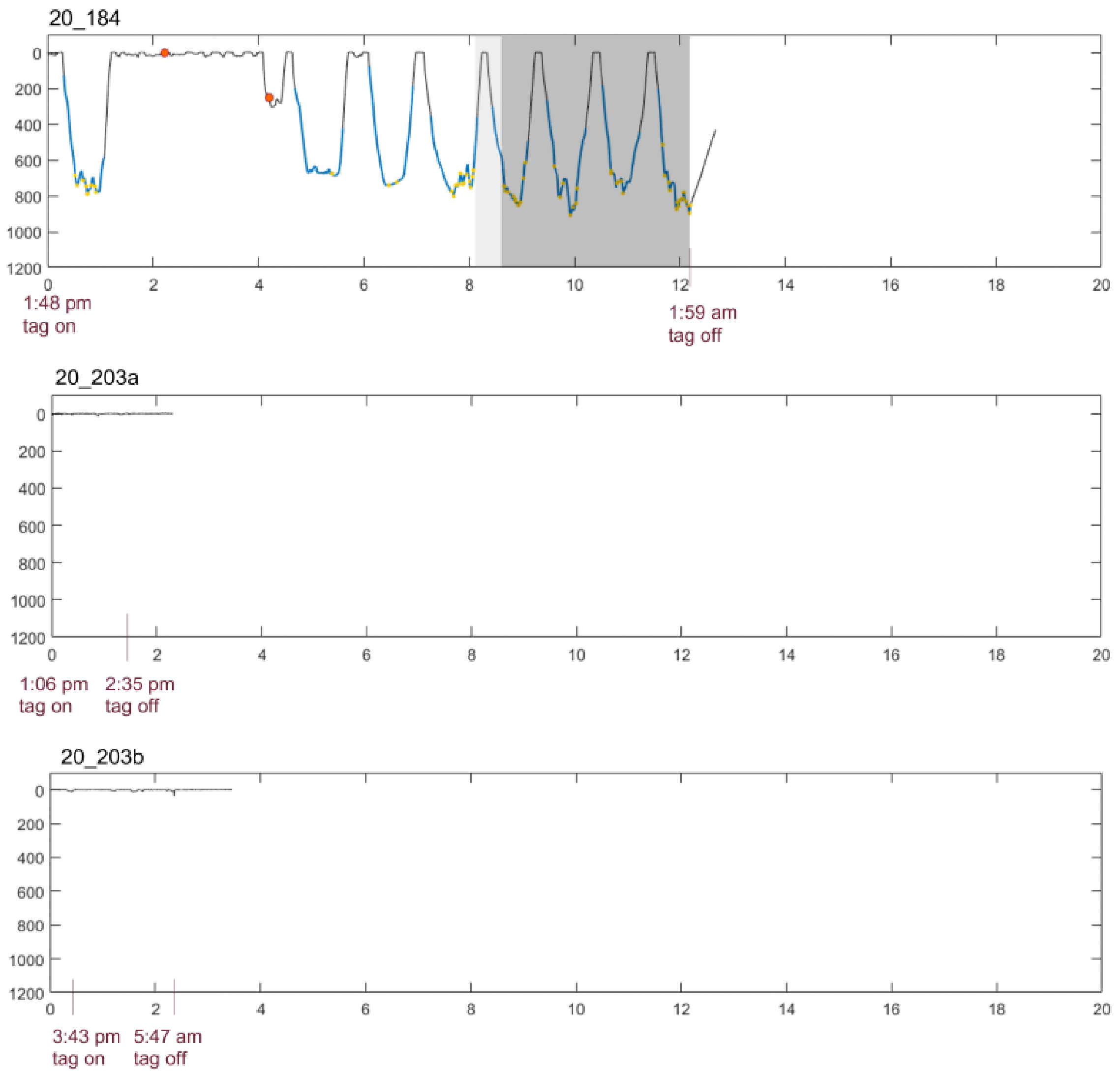


sw20_192

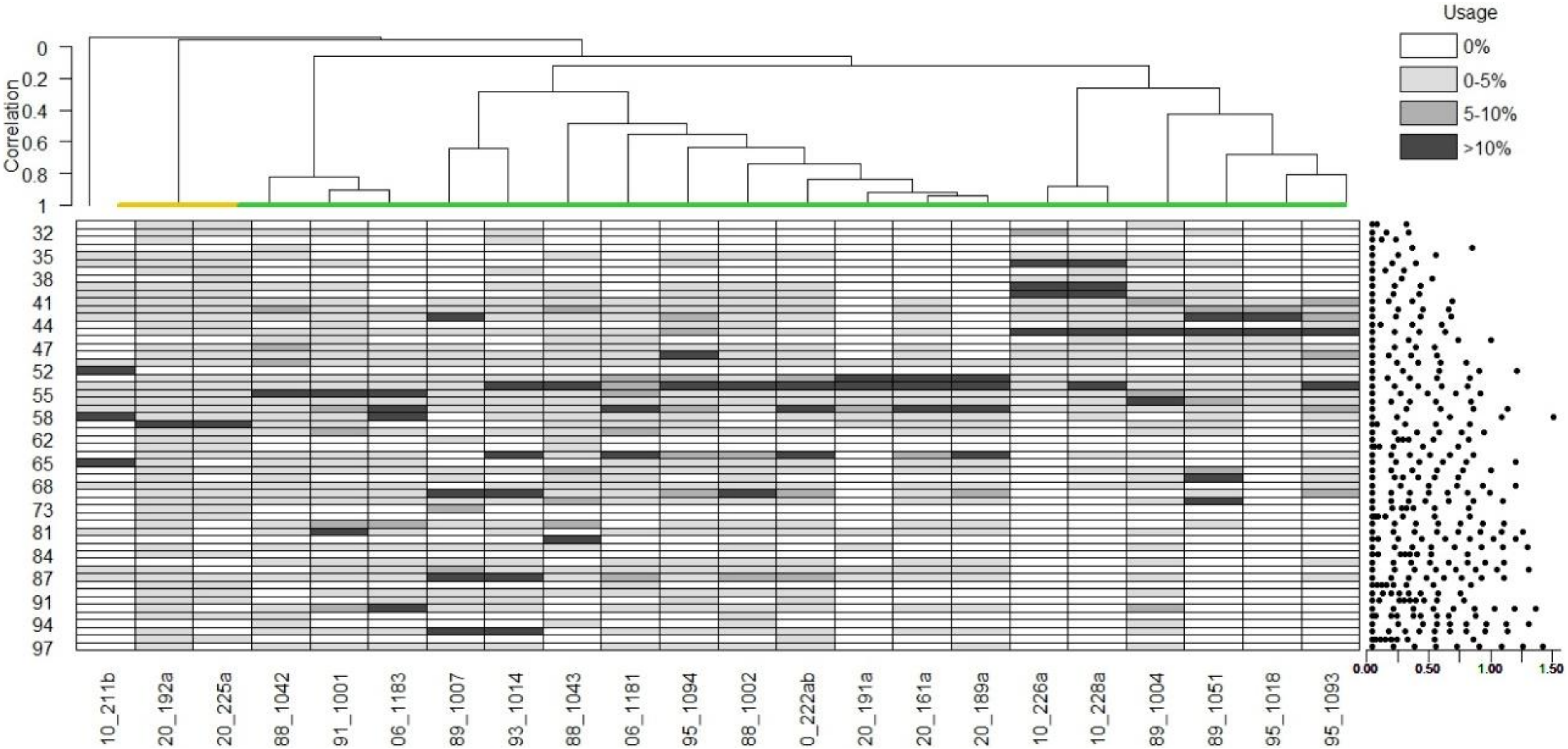


sw20_225

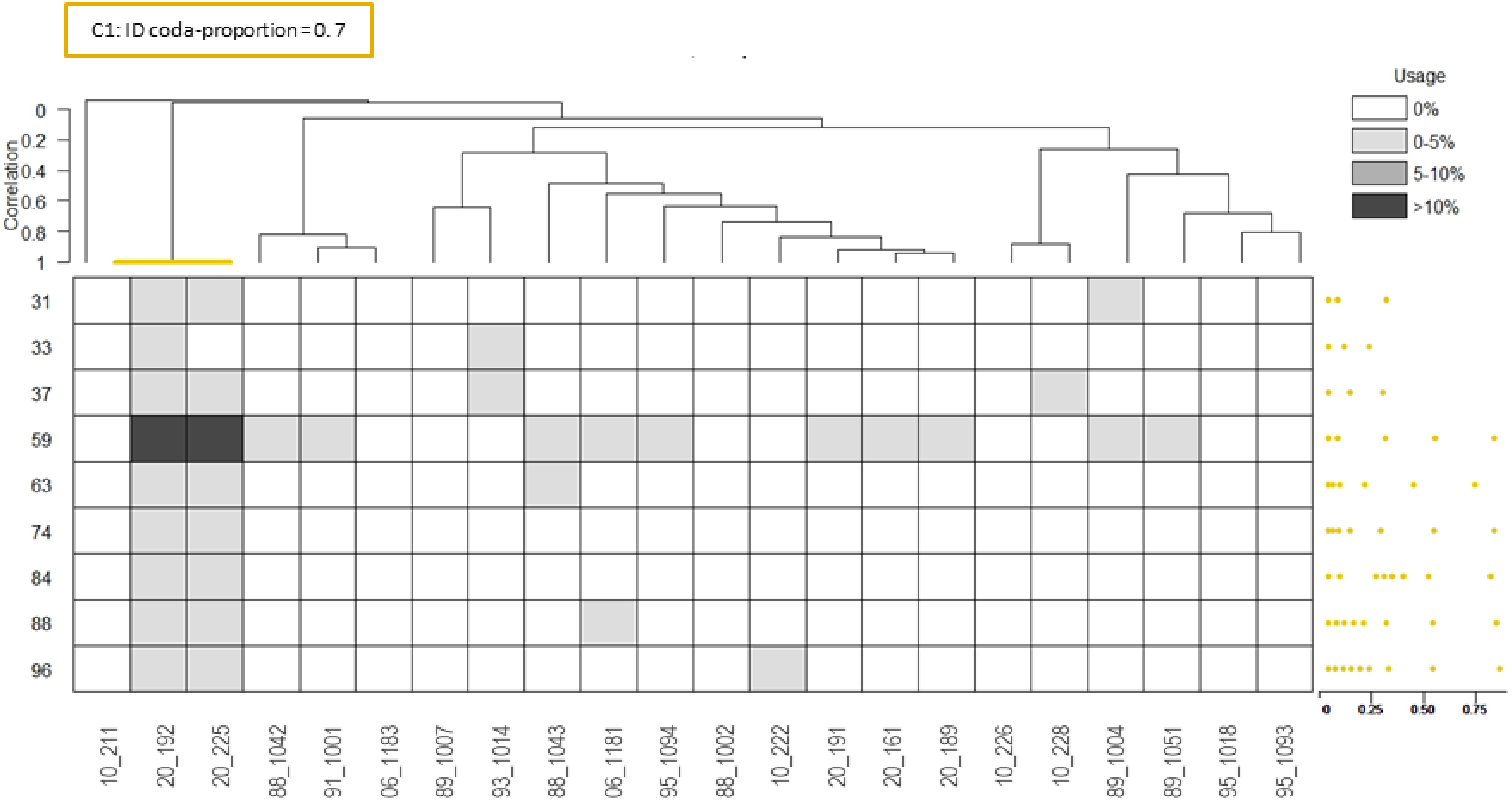
A 1: ID-photos of individuals tagged in 2010 (top) & 2020 (bottom). Credits: @AzoresWhaleLab.



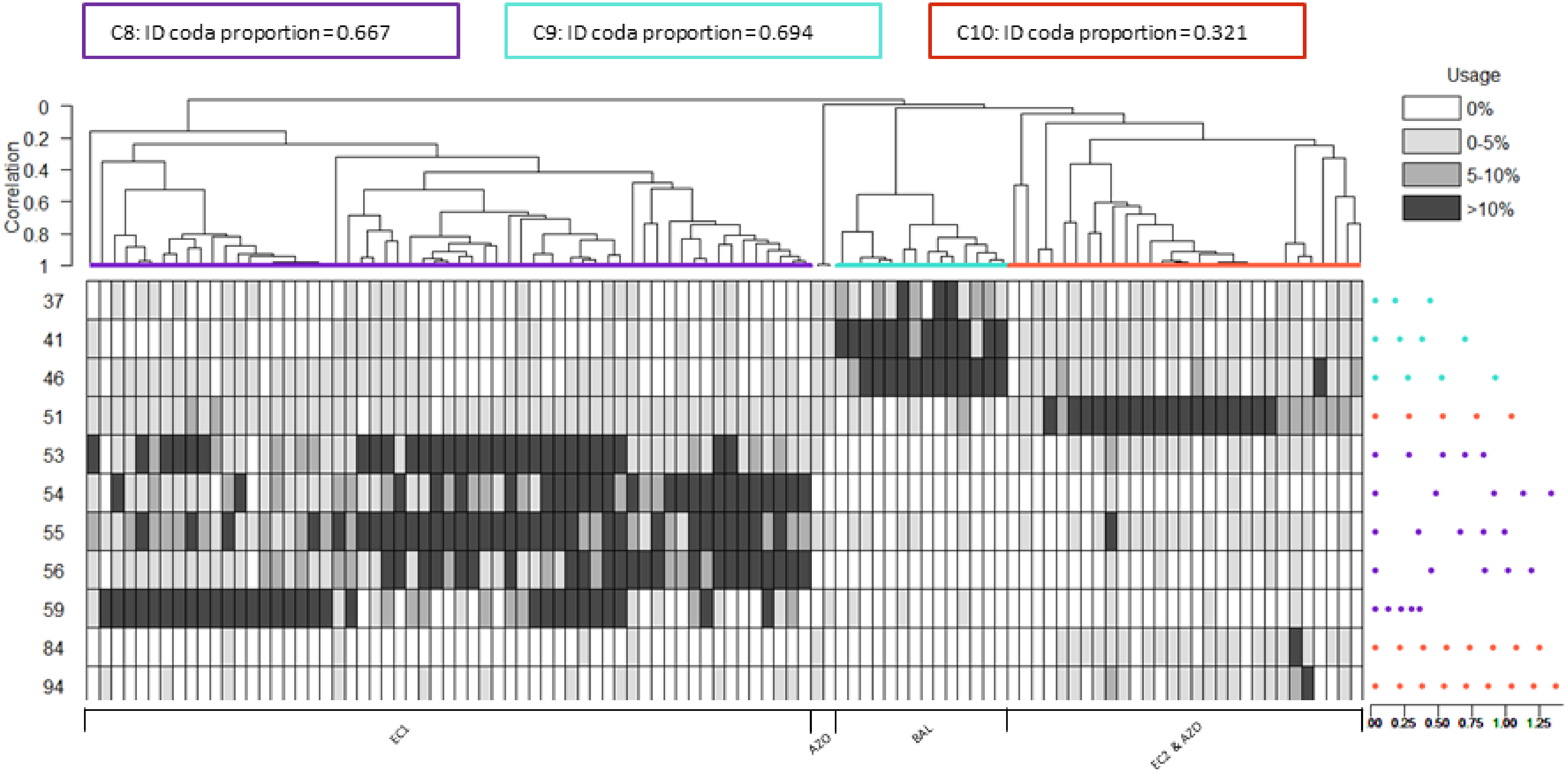
A 2: Dive profiles of tagged sperm whales in 2020 excluded from the analysis showing the production of clicks. Depth in metres (y-axes), time in hours (x-axes): usual clicks (blue dots), buzzes (yellow dots), focal codas (red dots). The shaded background indicates the daylight hours (white), night period (dark grey), and twilight (light grey). Times of tag-deployment ("tag on") and detachment ("tag off") in magenta.



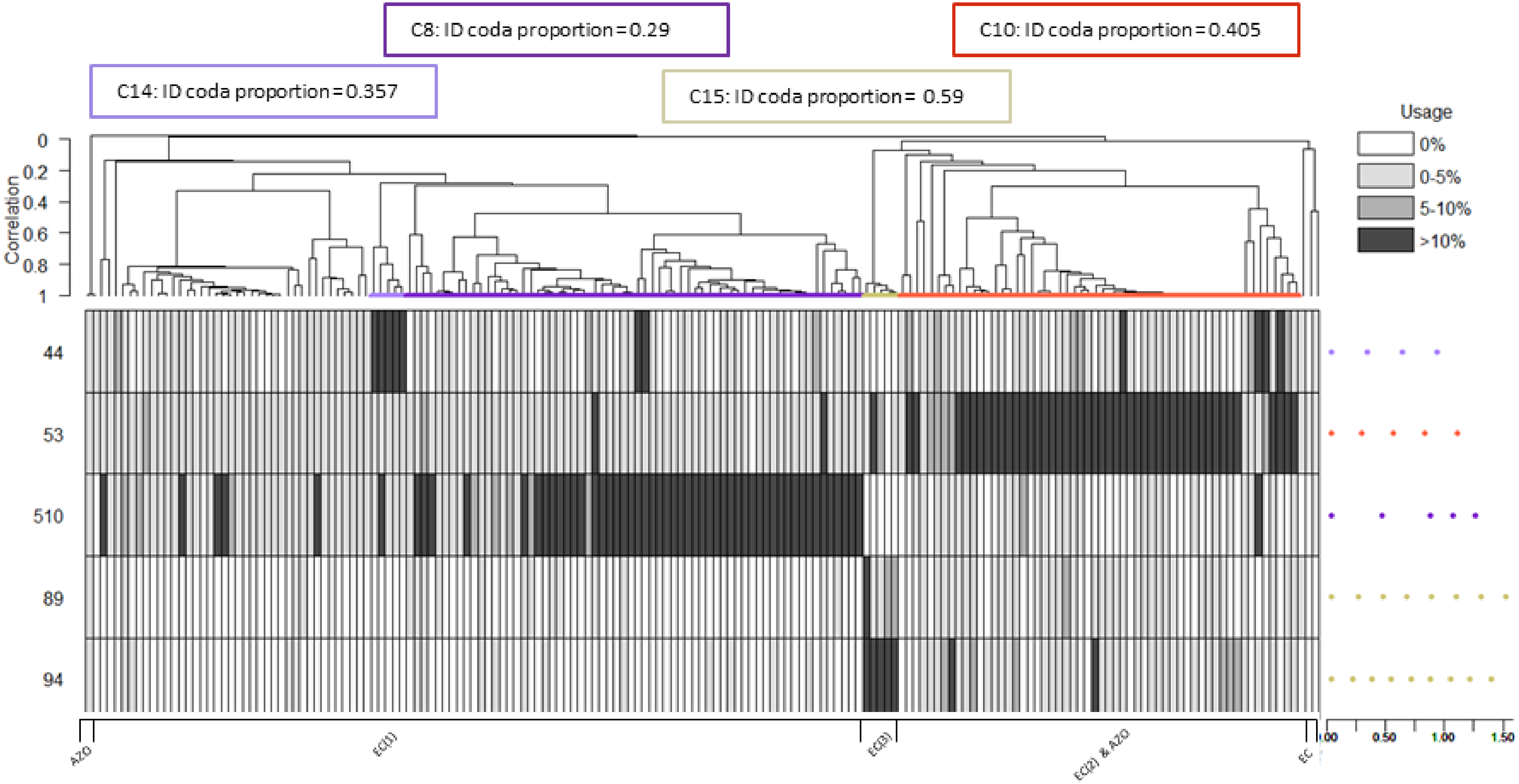
A 3: Trial 4.1: Dendrogram with two created clades and all coda types for the Azorean 1988 – 2020 dataset, demonstrating similarity of sperm whale group repertoires (GrpReps) (columns). Generated clades are coloured in yellow (C1) and green (C2) and were named with the letter "C" and a running number. Nomenclature and colour of clades were maintained from one trial to the other in case the same GrpReps were included in the clade. Heat map (bottom) demonstrates the percentage of coda type (rows) production per group repertoire in shades of grey, with coda type labels (left) and their rhythm plot in seconds, each dot representing one click (right). Coda type labels are equal to Figure 15. Created with baseline settings critfact 14, minrep 2.



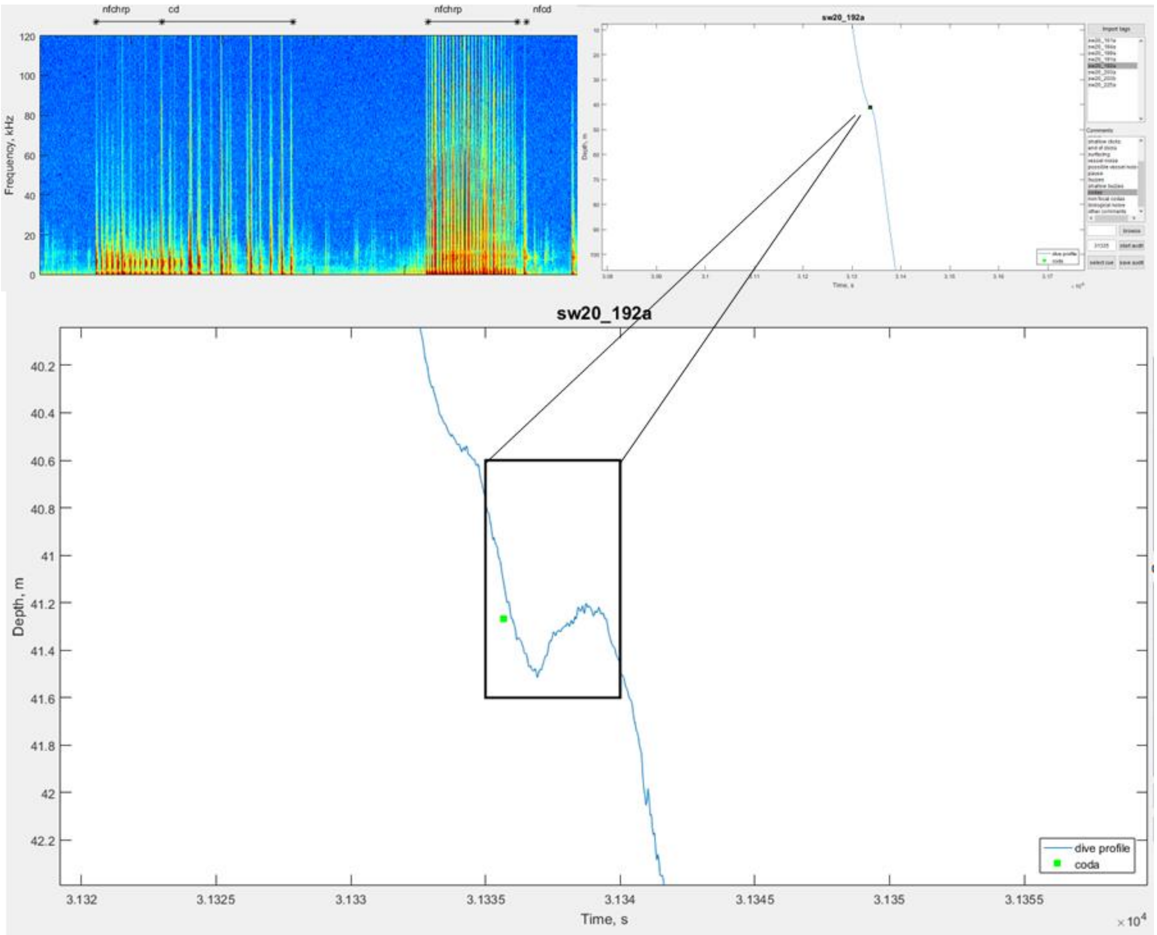
A 4: Trial 4.2: Dendrogram with one created clade and ID coda types for the Azorean 1988 – 2020 dataset, demonstrating similarity of sperm whale group repertoires (GrpReps)(columns). Generated clade is coloured in yellow (C1) and named with the letter "C" and a running number. All other GrpReps were considered outlier. Nomenclature and colour of clades were maintained from one trial to the other in case the same GrpReps were included in the clade. Heat map (bottom) demonstrates the percentage of ID coda type (rows) production per group repertoire in shades of grey, with coda type labels (left) and their rhythm plot in seconds, each dot representing one click (right). Coda type labels are equal to Figure 15. Created with modified settings critfact 26, minrep 2.



A 5: Trial 5.1: Dendrogram with three created clades and ID coda types for the Azorean 1988 – 2020 dataset and the Atlantic dataset from Hersh et al. 2021, demonstrating similarity of sperm whale group repertoires (GrpRep)(columns). Generated clades are coloured in violet (C8), turquoise (C9) and red (C10) and were named with the letter "C" and a running number. Heat map (bottom) demonstrates the percentage of ID coda type (rows) production per GrpRep in shades of grey, with ID coda type labels (left) and their rhythm plot in seconds, each dot representing one click (right). ID coda proportion is added per clade (above) and recording location (bottom), being the Azores (AZO), EC (Eastern Caribbean, in parenthesis the respective vocal clan), Balearic (BAL), Gulf of Mexico (GOM) and Panama (AtlPAN). Coda type labels equal as in figure 18. Created with settings from Hersh et al. (2021) critfact 14, minrep 6.



A 6: Trial 6.1: Dendrogram with four created clades and ID coda types for the Azorean 1988 – 2020 dataset and the East Caribbean (EC) dataset from Vachon et al. 2023, demonstrating similarity of sperm whale group repertoires (GrpRep)(columns). Generated clades are coloured in violet (C8), red (C10), light violet (C14) and beige (C15) and were named with the letter "C" and a running number. Heat map (bottom) demonstrates the percentage of ID coda type (rows) production per GrpRep in shades of grey, with ID coda type labels (left) and their rhythm plot in seconds, each dot representing one click (right). ID coda proportion is added per clade (above) and recording location (bottom), being the Azores (AZO) and EC (in parenthesis the respective vocal clan). Coda type labels equal as in figure 19. Created with settings from Vachon et al. (2021) critfact 8, minrep 5.



A 7: Spectrogram and dive profile during production of an unusual coda during descent, individual 20_192.

B 1: Abbreviated names of tagged sperm whales or Group repertoires (GrpReps) used during this study, containing the most important information, being a combination of the recording year and the original number, and in case of tagging two animals on the same day, the alphabetic order). The 22 GrpReps in bold in the right column were used for investigation of vocal clans in the Azores.

Recording date(s)	Names of individuals/ GrpReps in the original studies	Abbreviated names in this study	
23/06/1988	1042	**88_1042**	
27/06/1988	1043	**88_1043**	
26/06/1988, 01/07/1988, 02/07/1988	1002	**88_1002**	
16/07/1989	1051	**89_1051**	
07/08/1989	1007	**89_1007**	
01/09/1989	1004	**89_1004**	
13/07/1991, 14/07/1991, 18/08/1991	1001	**91_1001**	
20/08/1993	1014	**93_1014**	
24/06/1995	1018	**95_1018**	
23/08/1995	1093	**95_1093**	
03/09/1995	1094	**95_1094**	
07/05/2006	1181	**06_1181**	
15/06/2006	1183	**06_1183**	
30/07/2010	pm10_211b	**10_221**	
10/08/2010	pm10_222a	10_222a	**10_222**[9]
10/08/2010	pm10_222b	10_222b	
14/08/2010	pm10_226a	**10_226**	
16/08/2010	pm10_228a	**10_228**	
08/06/2020	sw20_161a	**20_161**	
02.07.2020	sw20_184a	20_184	
07.07.2020	sw20_189a	**20_189**	
09.07.2020	sw20_191a	**20_191**	
10.07.2020	sw20_192a	**20_192**	
21.07.2020	sw20_203a	20_203a	20_203
21.07.2020	sw20_203b	20_203b	
12.08.2020	sw20_225a	**20_225**	

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[9] sw20_203a & sw20_203b and pm10_222a & pm10_222b were joined into two repertoires (20_203 & 10_222) as individuals of each pair were tagged on the same day

B 2: Photo-ID-analysis matches from tagged sperm whales in 2010 & 2020, performed by Lisa Steiner. Individual 20_189 could not be matched because of low image quality, while 20_184 could not be matched with any of the individuals of the catalogue because of never having been sighted and/or photographed before.

DOP-catalogue	L. Steiner catalogue	Match found	Years of previous sightings	notes
sw20_161a	5587	Yes	2014, 2015, 2017, 2019, 2020	Group goes back to 1995
sw20_184a	NA	No		Possible male
sw20_189a	NA	No		insufficient picture quality
sw20_191a	5807	Yes	2016, 2018, 2019, 2021, 2022	
sw20_192a	6053	Yes	2017,2018,2019,2020,2021	Calf of 2578 from the “Whitehead group”, probably born in 2016
sw20_225a	2941	Yes	2005,2006,2008,2011,2012, 2018, 2020, 2021	“Chrissy/Willie Group”
pm10_211b	3339	Yes	2007	
pm10_222a	3979	Yes	2010, 2011, 2018, 2019, 2021	Previously seen together with 222b
pm10_222b	3957	Yes	2010, 2011, 2013, 2018, 2019, 2022	“Northern Ladies group”
pm10_226a	3644	Yes	2008, 2010, 2015	
pm10_228b	3386	Yes	2007,2009, 2010, 2011, 2012, 2013, 2015	

B 3: Locations of coda-recordings via hydrophone in the Azores from 1988 – 2006. Provided by Ricardo Antunes, recorded by Johnathan Gordon (1988-2005) and Lisa Steiner (2006).

ID	Date	Latitude	Longitude
1042	23/06/1988	38.68333 N	28.50000 W
		38.70500 N	28.55999 W
		38.72166 N	28.57666 W
		38.75667 N	28.63167 W
		38.83666 N	28.70833 W
		38.84167 N	28.73666 W
1043	27/06/1988	38.23833 N	28.42000 W
		38.25667 N	28.30833 W
		38.22000 N	28.36667 W
1002	26/06/1988	38.35667 N	28.38500 W
		38.34333 N	28.36167 W
	01/07/1988	38.33000 N	28.36000 W
	02/07/1988	38.20999 N	28.30500 W
		38.20832 N	28.25000 W
1051	16/07/1989	38.56833 N	28.14833 W
		38.54499 N	28.11666 W
1007	07/08/1989	38.19500 N	28.34333 W
1004	01/09/1989	38.47999 N	29.52166 W
1001	13/07/1991	38.24666 N	28.14666 W
		38.23332 N	28.15332 W
	14/07/1991	38.30667 N	28.28833 W
		38.30500 N	28.29166 W
		38.31000 N	28.24333 W
		38.30332 N	28.25499 W
		38.30667 N	28.28833 W
		38.36666 N	28.51000 W
		38.38333 N	28.51000 W
	18/08/1991	38.26667 N	29.00167 W
1014	20/08/1993	38.58533 N	29.00799 W
		38.65449 N	29.07316 W
1018	24/06/1995	38.33649 N	26.18983 W
1093	23/08/1995	38.35800 N	28.01700 W
		38.36299 N	28.02700 W
		38.36000 N	28.02512 W
1094	03/09/1995	37.97166 N	27.62516 W
		37.90082 N	27.54866 W
		37.81733 N	27.48766 W
		37.93466 N	27.60549 W
1181	07/05/2006	38.46699 N	28.59800 W
1183	15/06/2006	38.48500 N	28.79300 W
		38.49000 N	28.78500 W

B 4: Recorded codas separated per n° of clicks, GrpReps and focal & non-focal (NF) codas. All codas marked in black were included in the subsequent analysis.

N° clicks	161a (NF)	184a	189a (NF)	191a (NF)	192a (NF)	225a (NF)	Total (NF)	Total F&NF
3					21 (64)	4 (49)	25 (113)	138
4	(18)				2 (31)	1 (35)	3 (84)	87
5	66 (173)	1	39 (66)	24 (24)	348 (103)	83 (271)	560 (637)	1197
6	6 (20)	1	10 (10)		12 (54)	4 (35)	32 (119)	151
7	4 (12)		6 (4)		10 (36)	3 (20)	23 (72)	95
8	1 (13)		4 (5)	2	7 (29)	1 (11)	15 (58)	73
9	(5)	1	3 (4)		7 (23)	(6)	10 (38)	48
10	(3)		1		9 (9)	(9)	10 (21)	31
11	(1)	1	1		10 (7)	1 (7)	12 (15)	27
12	(1)	1	3		9 (8)	1 (6)	13 (15)	28
13			1		2 (6)	1 (12)	4 (18)	22
14					(6)	(2)	(8)	8
15						(2)	(2)	2
16						(3)	(3)	3
19						(2)	(2)	2
Total	77 (246)	6	68 (89)	26 (24)	437 (376)	99 (470)	707 (1205)	1912
Total 3-9	77 (241)		62 (89)	26 (24)	407 (340)	96 (427)	668 (1121)	1789

B 5: Calculations for the contextual analysis. All times in hrs:min.

Whale	Total recording	day	Night	mean forage dive time	mean forage surface	mean buzz rate/hr	foraging	Non-foraging
20_161	19:31	10:18	08:13	00:40	00:06	17.6	16:04 (82%)	3:27 (18%)
20_184	12:11	08:04	04:07	00:58	00:07	6.7	08:06 (67%)	4:05 (33%)
20_189	05:23	05:23	NA	00:42	00:19	12.5	01:45 (32%)	03:38 (68%)
20_191	00:17	00:17	NA	NA	NA	NA	NA	NA
20_192	14:32	08:13	05:49	00:37	00:07	9.7	6:25 (44%)	8:07 (56%)
20_225	17:35	07:30	09:14	00:46	00:10	22.5	9:52 (56%)	7:43 (44%)
mean	11:34	6:42	6:50	00:45	00:10	13.8	8:26 (56%)	5:24 (44%)

B 6: Results of all scenarios tested with chi-square test for the analyses of behavioural context of coda production.

scenario	X-squared	df	p-value	significant
Dive phase				
All	= 291.31	36	< 2.2e-16	yes
20_161:	44.859	12	1.089e-05	yes
20_189	13.822	14	0.463	yes
20_191	26	4	3.164e-05	yes
20_192:	161.04	28	< 2.2e-16	yes
20_225	39.246	16	0.001002	yes
ID coda:	458.93	54	< 2.2e-16	yes
Non-ID coda	12.558	12	0.4019	yes
Activity				
All:	172.8	18	< 2.2e-16	yes
20_161:	21.494	6	0.001495	yes
20_189:	12.778	7	0.07772	no
20_192:	89.467	14	4.784e-13	yes
20_225:	13.523	8	0.09507	no
C1	6.471	16	7.149e-10	yes
C2:	23.932	7	0.001171	yes
Diel pattern				
All	20.501	18	0.3053	no
20_161	1.2676	6	0.9734	no
20_192:	10.486	13	0.6538	no
20_225:	13.143	9	0.1562	no