Allometric growth of swimming-associated elements in Short-finned pilot whales *Globicephala macrorhynchus* Gray 1846 (Cetacea: Delphinidae)

Janitzio Egido-Villarreal*, Juan Pablo Gallo-Reynoso

Abstract - Ongoing research on cetaceans is revealing species-specific traits that reflect adaptations to different environmental conditions. Short-finned pilot whales are no exception to this trend. This species exhibits a specific diving behaviour, characterized by short bursts of acceleration at great depths, which likely necessitates special hydrodynamic adaptations in their body structure. Examining the growth rate of the structures involved in swimming could offer valuable insights. However, research to date has focused only on the allometric growth of these structures in this species from newborns to adults. No studies have yet explored the different growth phases of the species, which are related to its ecological context. This study examined the growth rates of four structural elements associated with swimming in individuals of both sexes, analysed separately across the four main growth phases. This research focused on a group that was stranded in Yucatan, Mexico, in 1986. This group included individuals ranging from newborns to asymptotic adults of both sexes. The findings in this work indicate that there is variation in the growth rate during certain phases. On the other hand, despite this species exhibiting strong social cohesion and often stranding in large groups that include individuals from all age classes, there is a lack of research on its growth. Therefore, a cumulative study of the allometric growth of the swimming structures of this species is proposed. This study will incorporate consecutive stranding data to create a comprehensive body of knowledge. By systematically and cumulatively studying the changes in different strandings of short-finned pilot whales worldwide, researchers around the world, in a joint effort, will identify key factors that will help understand the species' optimal diving behaviour at great depths. With regard to the species' conservation status, global and local information is insufficient at present. It is important that, alongside ecological studies, research is carried out on the species' physiology and biomechanics, which will contribute to effective management and conservation policies.

Key words: allometry, differential growth by age, global knowledge development, incremental knowledge, swimming optimization.

Riassunto - Crescita allometrica degli elementi associati al nuoto nei globicefali di Gray *Globicephala macrorhynchus* Gray 1846 (Cetacea: Delphinidae).

Con il progresso della ricerca sui cetacei, vengono individuate caratteristiche peculiari che consentono a ciascuna specie di adattarsi al proprio ambiente in modi distinti. I globicefali di Gray non rappresentano un'eccezione a questa tendenza. Essi mostrano un comportamento di immersione specifico, caratterizzato da brevi accelerazioni a grandi profondità, che presumibilmente richiede particolari adattamenti idrodinamici nella struttura corporea. L'analisi del tasso di crescita delle strutture coinvolte nel nuoto potrebbe fornire informazioni di grande valore. Tuttavia, fino ad oggi la ricerca si è concentrata esclusivamente sulla crescita allometrica di tali strutture in questa specie, dai neonati agli adulti, senza approfondire le diverse fasi di sviluppo, strettamente collegate al contesto ecologico. Nel presente studio sono stati esaminati i tassi di crescita di quattro elementi strutturali associati al nuoto in individui di entrambi i sessi, considerati separatamente nelle quattro principali fasi di crescita. L'indagine si è basata su un gruppo arenatosi nello Yucatán, in Messico, nel 1986, composto da individui di sesso maschile e femminile, dai neonati fino agli adulti asintotici. I risultati evidenziano variazioni nei tassi di crescita durante alcune fasi dello sviluppo. Tuttavia, nonostante la forte coesione sociale della specie e la frequente presenza di spiaggiamenti di massa che coinvolgono individui di tutte le classi d'età, le conoscenze disponibili sulla sua crescita rimangono limitate. Alla luce di ciò, si propone lo sviluppo di un approccio cumulativo allo studio della crescita allometrica delle strutture natatorie della specie, basato sull'integrazione di dati provenienti da diversi eventi di spiaggiamento. L'analisi sistematica e comparativa dei globicefali spiaggiati in varie regioni del mondo potrà contribuire alla costruzione di un corpus di conoscenze più completo, permettendo di individuare i fattori chiave necessari a comprendere il comportamento di immersione in profondità ottimale di questa specie. Per quanto riguarda lo stato di conservazione della specie, le informazioni disponibili a livello sia globale, sia locale risultano attualmente insufficienti. A questo proposito, è fondamentale che, parallelamente agli studi ecologici, vengano condotte ricerche di carattere fisiologico e biomeccanico, in grado di fornire elementi utili all'elaborazione di strategie efficaci di gestione e conservazione.

Parole chiave: allometria, conoscenza incrementale, crescita differenziale per età, ottimizzazione del nuoto, sviluppo globale della conoscenza.

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INTRODUCTION

Research on the biology of odontocetes reveals that group strandings provide a valuable data source. These events offer a unique opportunity to enhance our understanding of the life history of these organisms. According to Peltier *et al.* (2014), mass strandings are "an important source of information on the status of cetacean populations and biological samples". For morphological research, they serve as a critical

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means for gathering information about the growth and development of individuals within a species, particularly those that are not typically held in captivity, such as the species focus of this study: the short-finned pilot whale *Globicephala macrorhynchus*. According to Martin *et al.* (1987), "Generally, there is no reason to believe that mass strandings do not represent the entire population. Therefore, such events provide a valuable opportunity to study the biology of the species". This genus, comprising two species, has primarily been studied in populations from the Atlantic and North Pacific waters, where their herds are being commercially exploited (Martin *et al.*, 1987; Minton *et al*., 2018a; Minton *et al*., 2018b; Betty, 2019). In contrast, populations from other regions have received limited attention, despite reports of mass strandings of both species, particularly the target species of this study, *G. macrorhynchus*. Such strandings have been documented worldwide, including in Taiwan (Chen *et al.*, 2014), Indonesia (Falahudin *et al.*, 2023), Thailand (Raghunthan *et al.*, 2013), India (Jeyabaskaran *et al.*, 2018), Nicaragua (Huertas & Lagueux, 2016), Puerto Rico (Tellez *et al.*, 2014), both coasts of the United States (Fehring & Wells, 1976; Hall *et al.*, 1971; Mintzer *et al.*, 2008), and both coasts of Mexico (Aguayo *et al.*, 1986; Norris & Prescott, 1961), among others.

It is crucial to take advantage of opportunistic sampling, which Godard (2013) defines as the process where a researcher collects data from individuals or situations that arise spontaneously in their environment, rather than adhering to a predetermined sampling scheme. In other words, this method relies on the availability of participants at the time of data collection.

Pilot whale strandings present a unique opportunity for research due to the species' strong social cohesion. When they strand, they often do so in large groups that comprise individuals from all age classes and developmental stages (Norris & Prescott, 1961; Sergeant, 1982; Betty, *et al.*, 2022). This phenomenon offers valuable insights into the ontogenetic development of the species, insights that would otherwise require tracking an individual from birth to adulthood.

The movement of living beings encounters biomechanical challenges, not only in propulsion but also in managing the effects generated by the propulsive mechanism and the movement of the body itself. Achieving stabilization is essential, and various strategies are employed to accomplish this.

Swimming presents a unique challenge: the animal must generate propulsive forces by interacting with the surrounding water while simultaneously overcoming the drag generated by its movement through the médium. To navigate this environment effectively, marine mammals have adapted their bodies for optimal movement in water. According to Fish *et al.* (2003), propulsive movements generated at one end of the body induce reactive motions at the opposite end, which are counteracted by stabilizing mechanisms that may be either active or passive.

The pectoral fins serve a dual purpose. First, they have active functions due to their spherical joints, allowing for three degrees of freedom: flexion-extension, abduction-adduction, and rotation (Felts, 1966; Berta *et al.*, 2006). This flexibility provides maneuverability for actions such as turning, surface immersion, and braking (Weber *et al.*, 2009; Weber, 2014). Second, the pectoral fins contribute to passive body stabilization. Their location, which is anterior to the center of mass, along with the dihedral angle they form with the body and their one-plane geometry, helps limit body roll along the longitudinal axis (Fish, 2004). These passive stabilizing systems are particularly noteworthy because, according to Fish (2002), they do not require additional energy to maintain stability and are largely influenced by body morphology, which is the focus of this research.

The cetacean pectoral fin represents one of the most significant modifications from their terrestrial ancestors, retaining the same basic skeletal elements but undergoing major structural changes as a result of exposure to considerable hydrodynamic forces.

On the one hand, long bones that in terrestrial mammals are elongated and hollow – such as the humerus – are shorter in cetaceans, lack cavities, and are denser in their distal and medial regions. These modifications reflect the action of the shoulder complex muscles and the need to support the load of the limb (Felts & Spurrel, 1965). On the other hand, the multiplication of phalanges (hyperphalangy) and their elongation expand the surface area of the fin, shape its structure, and give rise to flattened appendages that reduce drag and are essential for stability and maneuverability (Del Castillo *et al*., 2004).

Displacement in the aquatic environment led to the evolutionary appearance of apomorphic structures such as the dorsal fin and caudal fin in cetaceans (Pavlov *et al*. 2021), the former providing stability when swimming and contributing to greater success in hunting prey and escaping predators (Alves *et al.*, 2018), and the latter generating propulsion. In cetaceans, these two dermal structures evolved *de novo* (Fish, 1998). According to Pavlov *et al.* (2021), their functional role can be unambiguously inferred even from a limited set of morphological features: the dorsal fin provides straight-line swimming stability, whereas the caudal fin is responsible for turn control and propulsion. In this context, several authors (Fish, 1998; Amano & Miyazaki, 1993; Curren *et al.*, 1993) have reported a correlation between total body length and both the span and shape of both fins. Because these correlations vary across developmental stages, Pavlov *et al.* (2021) propose that this variation may be associated with differences in swimming patterns between newborns and adults. This aspect is directly relevant to the objectives of the present study, since fin span and shape depend on the relationships among the morphometric measurements considered here and those discussed in the Discussion section.

The caudal peduncle has received comparatively less attention, despite being an important anatomical structure contributing to stability and maneuverability in cetaceans. According to Fish *et al.* (2003), it plays a significant role in maintaining stability. Its hydrodynamic shape, characterized by lateral compression and dorsoventral elongation, helps reduce the impact of increased mass at the rear. This is crucial because the associated recoil forces, if not managed properly, could hinder the animals' ability to move effectively. In terms of maneuverability,

the caudal peduncle plays a crucial role in turning the body without requiring propulsion, particularly during low-speed turns. This action involves marked lateral flexion of the peduncle, along with bending at the base of the caudal fin, which, as described by Fish (2002), functions as a rudder. Since these large animals are specialized for high-speed movement during diving (Aguilar-Soto *et al.* 2008), it is essential to describe the growth of the various structures involved in swimming control.

In addition, understanding the morphology and function of swimming structures is essential not only to explain the species' locomotor adaptations but also to frame conservation strategies. Despite the ecological importance of short-finned whales, information on their conservation status remains limited and its global conservation status has not yet been accurately determined. Until 2011, the IUCN (Taylor *et al.*, 2011) classified this species as "Data Deficient". Only in 2018, it was classified as "Least Concern" (Minton *et al*., 2018a). However, Minton *et al*. (2018a) remark that there is still little information about the presence and numbers of this species in most of its range. In the Gulf of Mexico, according to a review by Ramirez-León *et al.* (2020) considering the period 1952-2018, this species is widely distributed, ranking fourth in sightings in this region, and it is relatively common for them to strand in herds along the Gulf of Mexico and Caribbean coasts. Despite this, only a few studies about this species are available for the region. It is worth mentioning that this species is protected under Mexican law as a "Subject to Special Protection" species (hunting prohibited), under the Official Mexican Standard: NOM-059-SEMARNAT-2010 (SEMARNAT, 2010).

METHODS

Research was conducted on a group of short-finned pilot whales that stranded offshore of Punta Xpet-Ha (21°23'43.98"N, -88°53'2.01"W), 16 km east of the fishing community of Dzilam de Bravo in the State of Yucatán, Mexico (Fig. 1). The group comprised 28 individuals: 17 females and 11 males, ranging from calves to adults of asymptotic length in both sexes. The growth stages are based on the findings of Kasuya & Matsui (1984), who classified the average growth curves of short-finned pilot whales into four distinct phases (as shown in Tab.1).

The whales were semi-buried in the sand, which hindered the ability to take some measurements such as caudal fin width. Measurements collected from all individuals are presented in Table 2 and illustrated in Fig. 2.

Linear regression analyses were performed using the software STATISTICA© on the raw data obtained for each structure and sex to determine if there was a correlation between the growth of the structure and overall body size. Following this analysis, the allometric behavior of body elements throughout development was examined. This was done by regressing the log-transformed measurements for each structure against log-transformed total body length. Allometric ratios from juvenile stages to asymptotic adults were determined for each sex, and the corresponding graphs were generated.

The analysis included a detailed breakdown of growth behavior in various phases, using the same regression method. The growth regression formula was expressed as $\log y = \alpha \log x + \log \beta$, where α represents the growth coefficient (the slope), which corresponds to the α and β coefficients of the exponential equation used to model the raw data ($y = \beta x^{\alpha}$) Fish (1998), Fish & Rohr (1999), and McLellan *et al.* (2002).

RESULTS

The correlation between body growth and the studied anatomical structures is both direct and very strong (see Figs. 3 and 4). This means that as the body grows, the structures also grow. Notably, the analysis of residuals supports the close relationship observed. This finding allows us to proceed with studying the growth rate of the structures in relation to body growth for both sexes.

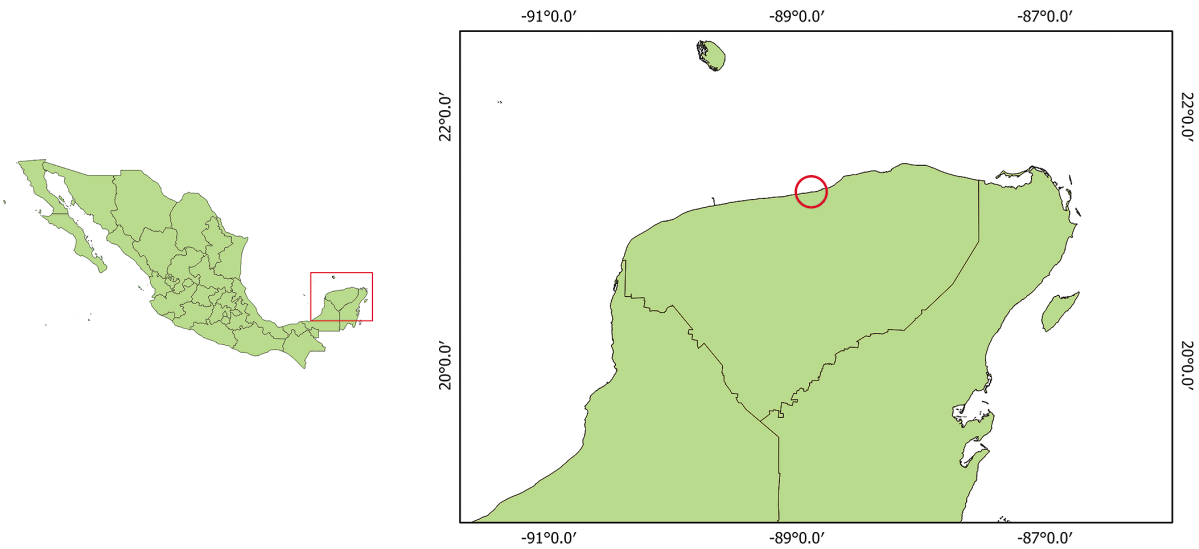


Fig. 1 - Location of the area of Punta Xpet-Ha in Quintana Roo, Mexico. / Posizione dell'area di Punta Xpet-Ha in Quintana Roo, Messico.

Tab. 1 - Growth stages determined by Kasuya & Matsui (1984) for *G. macrorhynchus*. / Stadi di crescita determinati da Kasuya & Matsui (1984) per *G. macrorhynchus*.

Phase	Description	Females (T.L. in cm)	Males (T.L. in cm)
I	Rapid neonatal growth phase	139.5 - 230	139.5 - 254
II	Juvenile phase of less rapid but almost linear growth	248 - 322	254 - 344
III	Phase between puberty and mean asymptotic length	322 - 364	344 - 461
IV	Phase of no increase in body length or asymptotic phase	> 364	> 473.5

Tab. 2 - Structures measured in the field. / Strutture misurate sul campo.

Abbreviation	Measured structure
FTEL	Flipper Trailing Edge Length
DFH	Dorsal Fin Height
CPH	Caudal Peduncle Height
CLLEL	Caudal Lobe Leading Edge Length

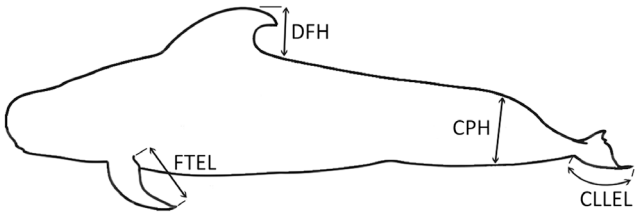


Fig. 2 - Location of measurements taken from each individual. / Posizione delle misurazioni effettuate su ciascun individuo.

However, since there was only one individual representing Phase 1 in females and one representing Phase 4 in males, the individuals and the phases they represent were excluded from the phase analysis. Below are the Growth Coefficient values presented in a bar chart for each phase included for both sexes. Specific graphs detailing the values of the growth formulas, from which the allometric coefficients were calculated, can be found in Supplementary Material A.

It is important to note that values equal to 1 indicate isometric growth, meaning that the structure and body grow at the same rate. Values scoring less than 1 signify negative heterogonic growth, where the structure grows slower than the body. Conversely, values greater than 1 indicate positive heterogonic growth, in which the structure grows faster than the body.

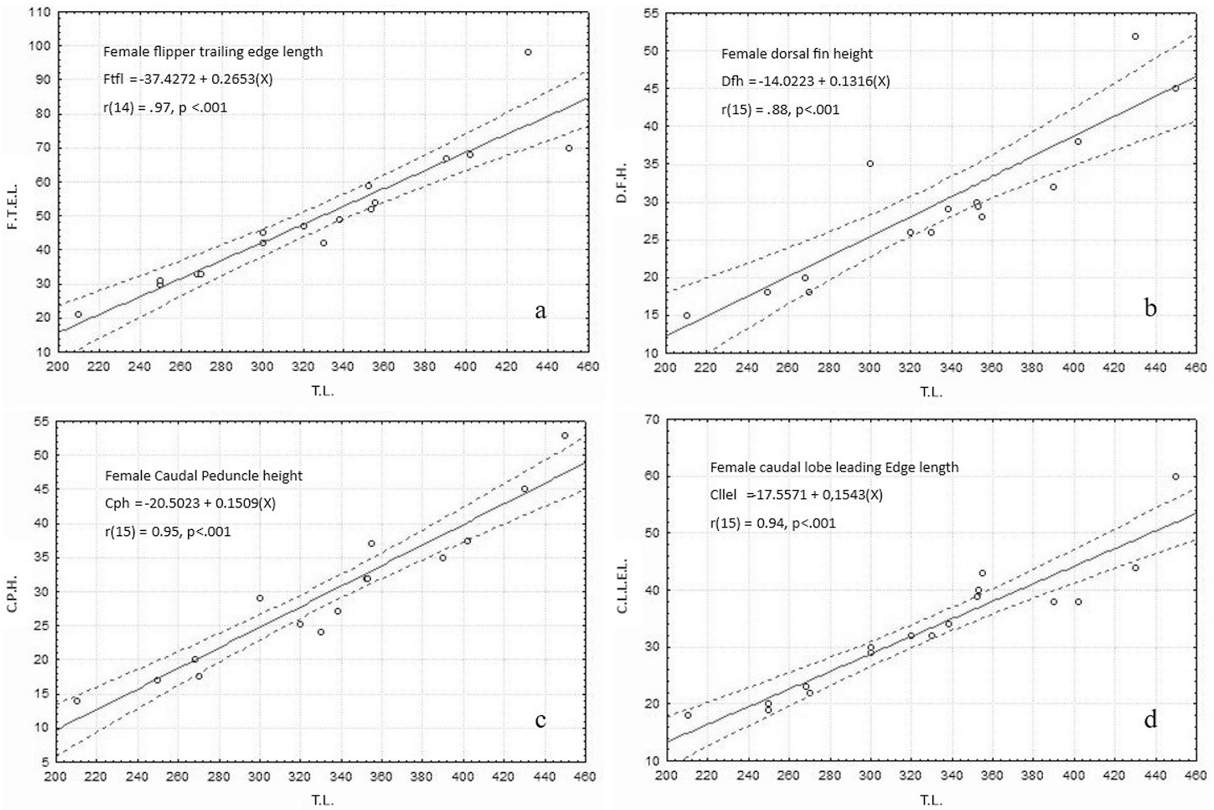


Fig. 3 - Regressions for the structures examined in females. / Regressioni per le strutture studiate nelle femmine.

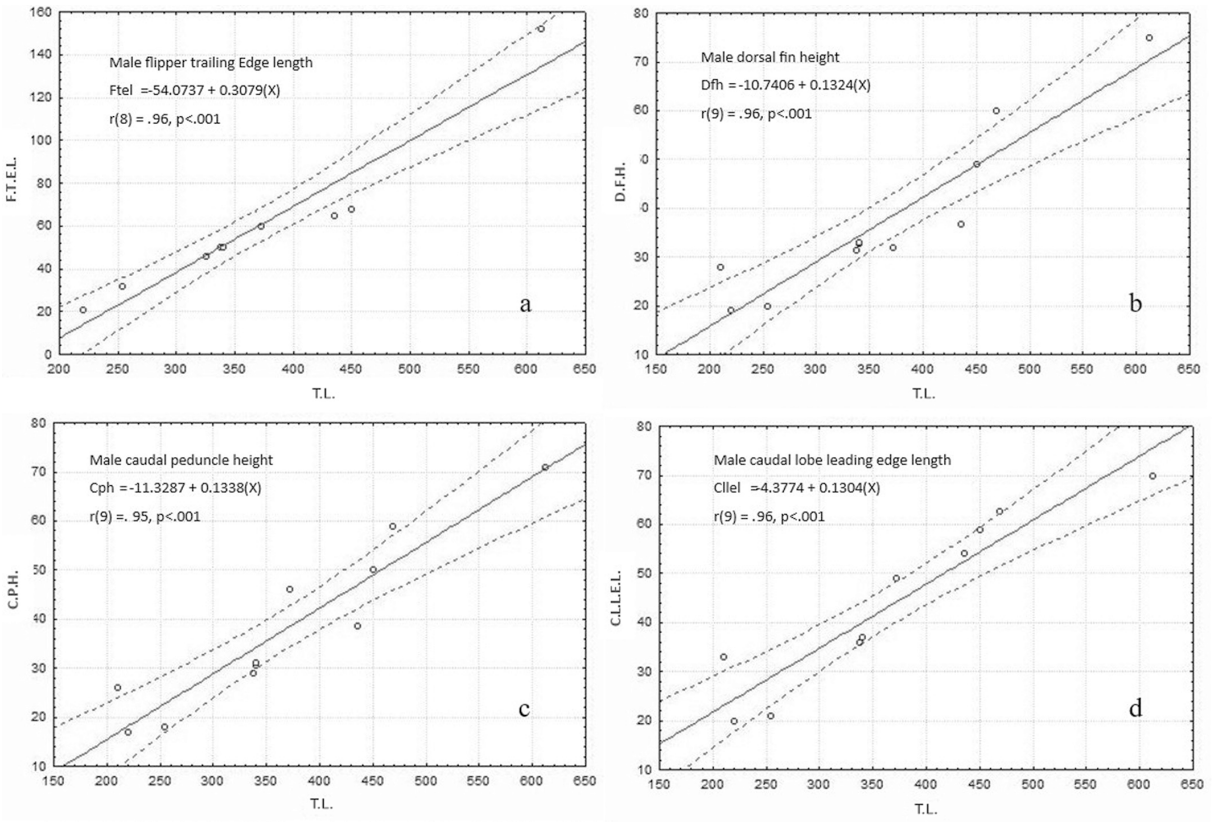


Fig. 4 - Regressions for the structures examined in males. / Regressioni per le strutture studiate nei maschi.

Figures 5 to 8 present bar graphs that illustrate the values obtained from regressions of the log-transformed measurements of the structures against the log-transformed measurements of the total body length (refer to Supplementary Material A for more information).

Flipper Trailing Edge Length

Females

In this sex, the posterior edge of the pectoral fin exhibits clear positive allometric growth during Phase 2, which transitions to a significantly accelerated growth in Phase 3. However, in Phase 4, the growth becomes very slow, showing negative allometry (Fig. 5).

Males

In Phase 1, males display slightly negative allometric growth. In Phase 2, they experience positive allometric growth, with values slightly higher than those of females during the same phase. This growth declines in Phase 3 to negative heterogonic growth (Fig. 5).

Both sexes show identical behaviour during Phase 2, but a sharp contrast is observed in Phase 3: males decrease considerably, while females experience significant growth.

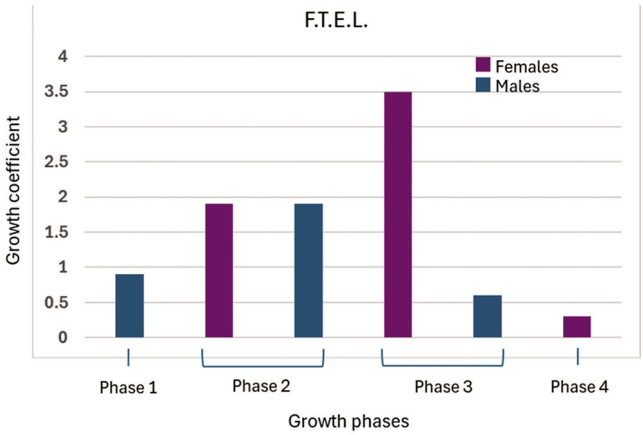


Fig. 5 - Growth coefficients by phase in both sexes, for the flipper trailing edge length. / Coefficienti di crescita per fase in entrambi i sessi, per la lunghezza del bordo d'uscita della pinna pettorale.

Dorsal Fin Height

Females

In the three phases described, the growth of the dorsal fin consistently outpaces that of the body. However, this growth rate experiences fluctuations. During Phase 2, the height of the dorsal fin increases significantly faster than the body, but its growth rate then decreases in Phase 3, approaching isometric growth relative to the body. In Phase 4, the dorsal fin's growth rate accelerates again, nearly matching the rate observed in Phase 2 (Fig. 6).

Males

In this group, the height of the dorsal fin shows growth that closely parallels that of the body during Phase 1. In

Phase 2, the dorsal fin's growth accelerates dramatically, before experiencing a slight decrease in Phase 3; however, its growth remains considerably positive. Notably, while the growth patterns for males and females are similar across the overlapping phases, males tend to exhibit higher growth rates (Fig. 6).

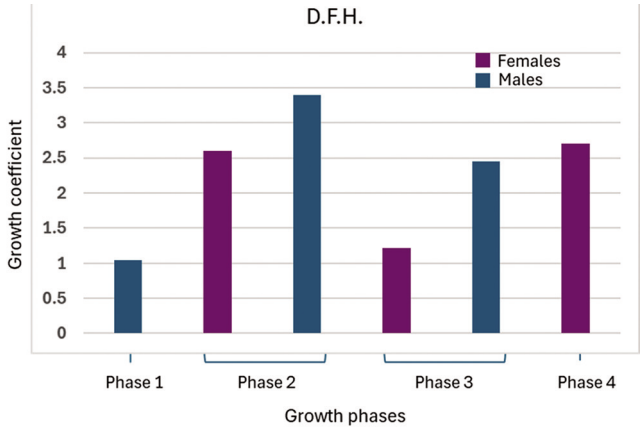


Fig. 6 - Growth coefficients by phase in both sexes, for dorsal fin height. / Coefficienti di crescita per fase in entrambi i sessi, per l'altezza della pinna dorsale.

Caudal Peduncle Height

Females

This structure exhibits positive growth in all phases, albeit at a slower rate in Phase 2. Growth accelerates significantly in Phase 3, reaching its peak for the entire study, and continues to demonstrate fast positive allometric growth, maintaining a high value in Phase 4 (Fig. 7).

Males

In males, this structure shows isometric growth during Phase 1. In Phase 2, growth accelerates dramatically, but then it slows down and eventually becomes negative in Phase 3 (Fig. 7)

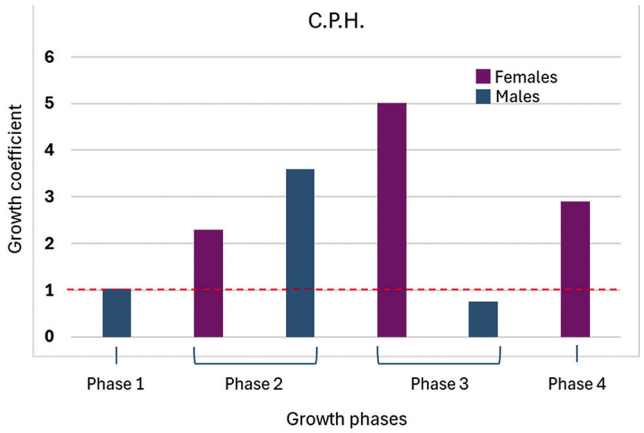


Fig. 7 - Growth coefficients per phase in both sexes, for caudal peduncle height. / Coefficienti di crescita per fase in entrambi i sessi, per l'altezza del peduncolo caudale.

Caudal Lobe Leading Edge Length

Females

In females, the growth velocity of the caudal lobe was greater than that of the body in all the studied phases. In Phase 2, growth was heterogeneously positive for this structure, accelerating significantly in Phase 3. In Phase 4, the growth rate slightly decreased but still maintained a high positive value (Fig. 8).

Males

In males, the caudal lobe growth exhibited isometric characteristics in Phase 1. During Phase 2, the growth velocity increased markedly but then returned to isometry in Phase 3 (Fig. 8).

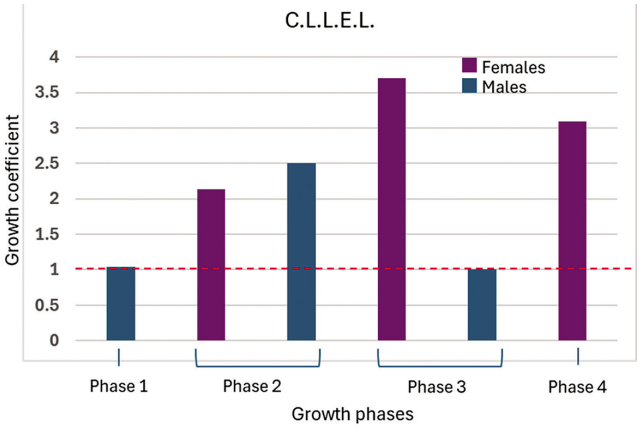


Fig. 8 - Growth coefficients per phase in both sexes, for the caudal lobe leading edge length. / Coefficienti di crescita per fase in entrambi i sessi, per la lunghezza del bordo d'attacco del lobo caudale.

Figure 9 displays the structures organized by phase and grouped by sex. As shown, the only two phases comparable between the sexes are Phase 2 and Phase 3 for the exclusion of Phase 1 for females and Phase 4 for males, with only one individual in each.

In Phase 2, we can compare the sexes, and it is clear that, except for the height of the caudal peduncle, the other three structures exhibit similar growth patterns for both females and males, with males showing consistently higher values. Notably, the length of the rear edge of the pectoral fin demonstrates positive heterogonic growth, with a similar rate (approximately 2) in both sexes. The two completely passive control structures, namely the dorsal fin and caudal peduncle, display significantly higher values in males compared to females. Additionally, the front edge of the caudal lobe exhibits slightly faster growth in males than in females.

In Phase 3, we can again compare the sexes and observe markedly different growth velocity patterns. They appear almost as "opposites". In females, the only structure showing a nearly isogonic value is the height of the dorsal fin, while the other three structures have significantly positive growth. Conversely, in males, only the height of the dorsal fin is positive, while the other three structures are either isogonic or negative. It is also worth noting that the height of the caudal peduncle grows considerably faster than the body in females, reaching an extreme value of 5.

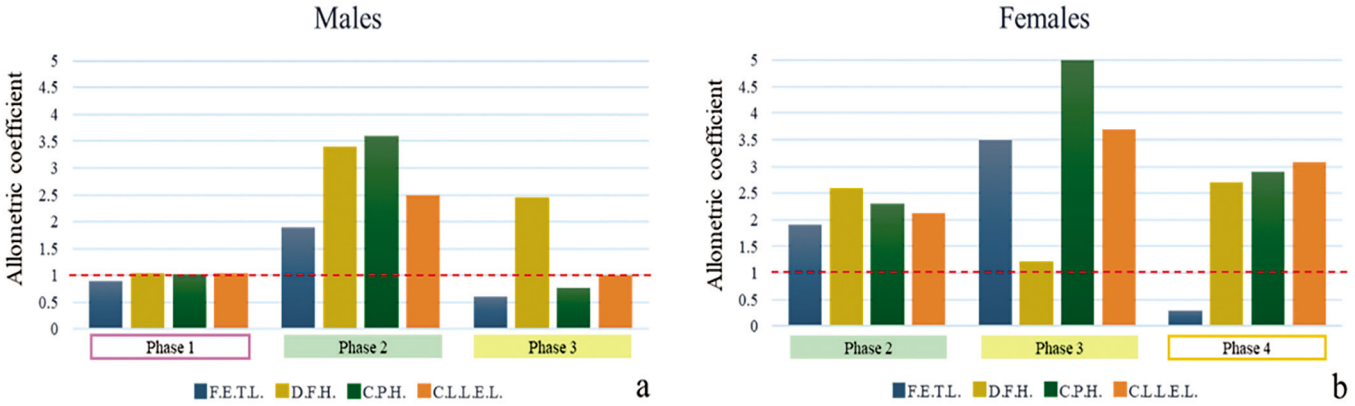


Fig. 9 - Growth Coefficients by phase, grouped by sex. / Tassi di crescita per fase, raggruppati per sesso.

Unfortunately, we only have values for females for Phase 4, which does not detract from the importance of the data. We observe that the growth rate of the posterior edge of the pectoral fin decreases to a significantly negative value, while the other three values show a positive behavior with greater emphasis on the length of the leading edge of the caudal lobe.

DISCUSSION

In general terms, it is evident that in both sexes, swimming-associated elements grow in such a way that they increase their proportional contribution to body length, although periods of negative allometry or differential growth occur at different development stages. Importantly, these structures continue to grow even after asymptotic size is reached.

General

When comparing all structures by phase and sex, we observe that all male structures in Phase 1 exhibited isogonic growth, a pattern noted in several species (Sergeant, 1962; Perrin, 1975). This growth pattern is associated with a concentration of resources to support accelerated overall body growth, which is crucial for actively following the mother and the group. Additionally, there is a simultaneous acceleration in the development of swimming structures during the embryonic stage before birth (Sergeant, 1962; Lee & Ogden, 1982). This ensures that the swimming control structures are appropriately proportioned for nearly passive movement alongside the mother at birth, requiring only control mechanisms rather than propulsion, while the body continues to grow rapidly.

Phase 2 is characterized by a nearly linear and slow growth pattern. As illustrated in Fig. 9, trends in Phase 2 indicate similar growth rates for both sexes, although the absolute values differ. Notably, both sexes exhibit positive growth rates, with males showing particularly enhanced growth in dorsal fin and caudal peduncle heights. In contrast, Phase 3 is characterized by marked sexual divergence, which may account for the differing growth rates observed in the structures studied.

Pectoral fins

The pectoral fins play a crucial role in the overall hydrodynamics of these animals (Felts, 1966). They are important during all life stages, affecting both the passive movement of young and the active movement of both young and adult animals. The pectoral fins function like hydro-wings, helping to maintain stability, reduce drag, and provide control during rotation, pitching (dorsal-ventral roll), and turning.

Notably, Sergeant (1962) found that for *G. melas*, the length measurements of the leading edge of the pectoral fin (F.T.E.L.) and the straight length of the fin showed accelerated growth during the fetal stage, reflecting 20% of the total length (T.L.). This rapid growth prepares for the significant increase in body size that occurs after birth, ensuring that the pectoral fins are optimally sized at birth – with 16% of T.L. in his study – to perform their essential stability functions for newborn calves.

This finding is consistent with Yonekura *et al.* (1980), who reported accelerated growth of the leading edge and the straight length of the pectoral fin in *G. macrorhynchus* before birth, preceding the phase of rapid body growth. This pattern seems to reflect a similar strategy, ensuring that the pectoral fins reach an appropriate size at birth.

In both publications, the growth of pectoral fins shows a positive heterogonic trend from newborns to adults in both sexes.

The findings, although lacking data from pre-birth individuals, align closely with those reported by the authors referenced earlier. Specifically, when comparing various pectoral fin measurements, our particular measurement ranges from 10% relative to T.L. in Phase 1 for both sexes, increasing to a maximum of 17% in females and 24% in males. This male measurement is comparable in size to values found by Sergeant for another species of pilot whale (*G. melas*), which is larger than *G. macrorhynchus*. Please, refer to Supplementary Material B for additional details.

In Figure 9, we can see that, at least in males, the growth of the posterior edge of the pectoral fin is relatively slow during Phase 1 of rapid body growth, which aligns with the earlier observations. In Phase 2, where growth becomes almost linear, both sexes exhibit an accelerated growth rate in this structure, with similar values for each.

However, in Phase 3, a differentiation in growth rates emerges: females show a more pronounced increase in pectoral fin growth compared to the previous phase, while males experience a slower growth rate in their pectoral fins relative to the rest of their body.

In Phase 4, a significant decrease in growth rate is observed in males, eventually leading to negative heterogeneity. It would be beneficial to gather data on the anterior edge of the pectoral fin, as this information could clarify whether there is accelerated growth in this area during the stages when the posterior edge experiences slower growth. Understanding this dynamic could help explain the increasingly pronounced curvature of the pectoral fin over the lifespan of these animals.

Dorsal fin

Yahn *et al.* (2023) found sexual dimorphism in several dimensions of the dorsal fin of short-finned pilot whales, but not in fin height, finding no significant difference between adult females and males. These findings align with those of Yonekura *et al.* (1980) for body lengths up to approximately 500 cm. The current study also supports this conclusion, as both females and males show dorsal fin height proportions ranging from about 8% to 13% of total body length across different growth phases (refer to Supplementary Material B).

Furthermore, in the comparable growth phases examined in this study (Phases 2 and 3), Fig. 9 illustrates that dorsal fin growth follows the same trend in both sexes, although females exhibit lower growth values. By Phase 3, this results in isogonic growth.

Caudal Peduncle

As previously mentioned, this structure is crucial for stability due to its shape and orientation in the dorsoventral plane, which prevent the animal's body from recoiling with each flap (Fish *et al.*, 2003). It was observed that total growth in both sexes exhibits positive heterogony with very similar values (see Supplementary Material A). However, variations in behavior were noted during the growth phases (Fig. 9). For females, the growth of the caudal peduncle is positive in all represented phases, but it is during Phase 3 that a significantly accelerated growth compared to the rest of the body was observed. This is also the phase when females reach sexual maturity (Kasuya & Matsui, 1984) and begin to reproduce. Thus, they may require greater optimization in body stability management, as gestation leads to an increase in weight and changes in body mass distribution. The rapid growth of the caudal peduncle in females compared with the significant slowdown in the growth of the dorsal fin during the same phase (Fig. 9) suggests that the allocation of energy and metabolic resources may be preferentially allocated to the development of the caudal peduncle, potentially at the expense of the dorsal fin growth. The caudal peduncle not only helps counterbalance changes in body mass distribution, but also serves a function similar to that of the dorsal fin. Therefore, this shift in resource allocation might be a strategy to conserve energy.

In Phase 4, females remain positive but at a lower level, as this phase includes both reproductively active and menopausal females.

The analysis in males is somewhat more complex due to the absence of values from Phase 4. However, it is evident that, based on the available data, Phase 2 shows a faster growth rate compared to Phases 1 and 3. In contrast, Phase 3 displays significantly lower values than those observed in females, even reaching negative heterogony.

Caudal lobe

As previously mentioned, it was only possible to measure the curvilinear length of one caudal lobe per-animal because they were partially buried in the sand. Therefore, the discussion of fin growth behaviour will be addressed in a general manner, referencing the findings of other authors regarding different dimensions of the caudal fin. This is intended to highlight potential trends that may elucidate the ecological significance of the measurements.

In the first phase, the growth observed in males was isogonic, similar to the other structures we considered. This finding aligns with the research conducted by Sergeant (1962) on caudal fin expansion in *G. melas*, as well as studies by Perrin (1975) and Amano & Miyazaki (1993) on *Phocoenoides dalli*. Additionally, Lang (1966 in Fish, 1998) noted that young animals in these circumstances may experience disadvantages when swimming. This situation may lead them to adopt free-riding behaviours to keep up with their mothers, a point we elaborate on at the beginning of the conclusions. In Phase 2, both sexes exhibit positive heterogonic growth, which aligns with the onset of autonomous swimming in juveniles. Males show a higher caudal lobe growth rate during this phase. However, in Phase 3 the differences between the sexes become very pronounced. Females experience an increase in the growth rate of structures related to manoeuvrability, which corresponds to the earlier discussion regarding gestation and the caudal peduncle. In contrast, males experience a significant decrease, resulting in a negative heterogonic growth rate.

Sergeant (1962) noted that more research is needed on the body measurements of *G. macrorhynchus*, among other aspects. Insights into the allometric growth of four swimming-related structures are provided in this work, emphasizing their contribution to the animals' stability and propulsion. This research was based on an opportunistic sampling of a stranded group. While this approach is basic and inconclusive due to the limited number of animals and the few aspects measured, it serves as a foundational idea for studying the body development of this species, especially considering the mass strandings that occur around the world. Recognizing the limited dataset, it would be beneficial to incorporate additional and more diverse measurements. For instance, rather than focusing solely on one dimension of the pectoral fin, such as axillary length, a greater range of measurements should be incorporated. This is the case for changes in the anterior margin, which confer the characteristic falcate shape to the pectoral fins of this species. This feature is noteworthy, as this morphology was described by Weber *et al.* (2009) as

typical of fast-swimming species. This approach would help provide insights into the development of swimming structures in relation to the ecological needs of the species throughout its life. To achieve this, field data from various strandings may be gathered, and methodology standardized to allow synthesis of the data from each new stranding with previously published data from other strandings. This should be regarded as a preliminary exercise aimed at highlighting mass strandings of this species as a useful source of data for investigating the development of swimming control surfaces, their potential cumulative function, and appropriate measurements for their morphological study.

CONCLUSIONS

According to our observations, all the swimming-associated structures studied exhibit slow growth during Phase 1, which could impact swimming performance (Amano & Miyazaki, 1993; Curren *et al.*, 1993). In newborns, this stage matches with a significant dependence on the mother, suggesting a need for mother-assisted swimming. This aligns with the findings of Shoele & Zhu (2015), which indicate that newborn calves are positioned in the front third of their mother's body, utilizing the suction forces generated by the laminar flow of water. In the following weeks, they shift to a staggered position, eventually moving to the rear third of the mother's body to take advantage of the vortex thrust created by the mother's caudal fin (Fig. 10).

In all instances of drafting – defined in cetaceans as the transfer of forces between individuals without actual physical contact – stability is crucial to prevent rolling along the longitudinal axis. This stability is achieved through relatively long pectoral fins in proportion to the body. The pectoral fins develop quickly during the embryonic stage. For this reason, they do not need to rapidly grow immediately after birth, which leaves resources to be channelled to the overall growth of the body.

All the structures studied demonstrate a general positive heterogonic growth, which is significant for the short-finned pilot whale, a species known for being a fast swimmer.

While low-speed turns are important, stability at high speeds is crucial for these animals. They have a unique hunting method that involves chasing prey at great depths and high speeds, which is uncommon for organisms that need to surface to breathe. Aguilar-Soto *et al.* (2008) noted that short-finned pilot whales can reach accelerations of 9 m/s for an average of 26 seconds while diving at depths between 540 and 1,019 meters, with dives lasting approximately 15 minutes. This behaviour supports the earlier findings of positive heterogonic growth throughout the entire development of both females and males.

In general, it is evident that growth tends to follow the changes in the maturation stages of individuals. Growth may "fall" from one stage to another and then either recover its growth rate or adapt to the new physiological conditions or biological demands of each stage. This



Fig. 10 - Short-finned pilot whale mother-calf joint swim. Photograph by Sergio Hanquet (used with the author's permission). / Nuoto congiunto mamma-piccolo di globicefalo di Gray. Fotografia di Sergio Hanquet (utilizzata con il permesso dell'autore).

assumption is based on the limited opportunistic data currently available, highlighting the need for more comprehensive data collection. Ideally, this data should come from different stranding events, preferably within the same geographic area, to accurately characterize the growth patterns of specific populations.

In the long term, this approach could facilitate a global study of the species. Cumulatively building on the data from each new stranding event and comparing it with previously published data from other group strandings would strengthen our understanding. This strategy would help create a substantial dataset for a more robust and reliable analysis of the growth behaviour of the different body structures in this species.

Sergeant (1982) noted that, due to population dynamics, mass strandings of cetaceans may occur more frequently during certain periods and be less common at other times. As a result, individual strandings – which are more evenly distributed – can be combined with mass strandings to provide an index of natural mortality and, consequently, of abundance. Furthermore, these findings could enhance studies on the morphology of the species and contribute to the cumulative research on allometric growth that we propose in this work.

In this framework, we suggest employing the set of measurements presented in Fig. 11 and described in Table 3, which follow the works of Yonekura *et al.* (1980), Fish (1998), Weber *et al.* (2009), and Yahn *et al.* (2023). These measurements, whether considered individually or in combination, enhance our understanding of the hydrodynamics of both control and propulsion structures. The goal is to characterize the changes in these swim control structures and their relationship to behavior and ecology in this fast-diving species. Efficient body hydrodynamics are crucial for optimizing swimming performance and energy expenditure.

Advances in this understanding will contribute to the conservation of this species, which is listed in the Least Concern category, although knowledge about it is "data deficient" in many respects. In addition to the limited information highlighted in the introduction, there is a general lack of biological data, particularly concerning the morphological and biomechanical changes that occur in pilot whales during development. It is important to understand the biomechanical aspects and development of a species not only from a functional point of view, but also from an ecological one. According to Castro-Santos & Haro (2005), muscle kinetics, body and fin morphology, and sensory control characterize the interactions of animals with their habitat, which in turn defines the organism's ability to exploit its environment, reproductive success, energetics, and trophic interactions. This can influence the development of management policies, such as guidelines for orderly cetacean observation, which take into account the biomechanical needs of calves, avoiding separating them from their mothers in an effort to observe them for long periods of time.

Domenici & Seebacher (2020) highlight the link between climate change and biomechanics, stressing that climate-driven alterations in tissue properties and biomechanics can affect performance and, in some cases, population persistence. Therefore, they point out that the integration of biomechanical research with ecology is essential for predicting the future responses of natural systems to climate change and emphasize that much work remains to be done in this regard.

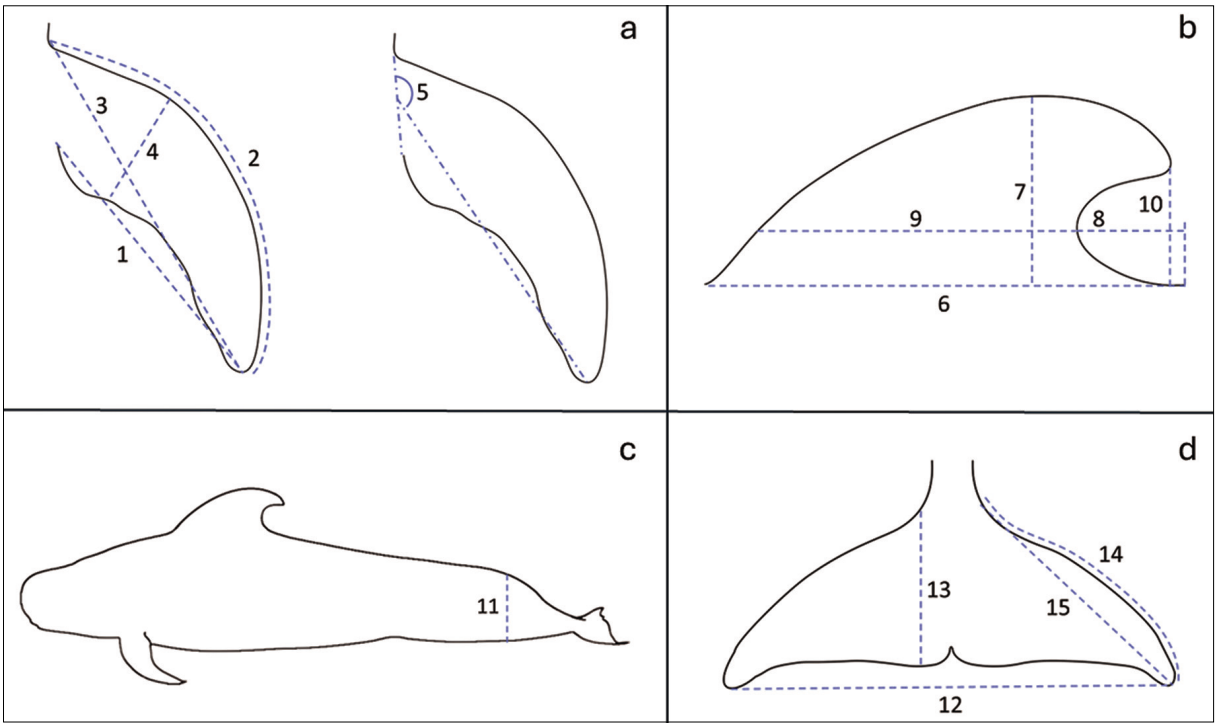


Fig. 11 - Proposed measurements for the study of allometric growth of swimming and control structures. / Misure proposte per lo studio della crescita allometrica delle strutture natatorie e di controllo.

Tab. 3 - Proposed measurements for the study of allometric growth of swimming and control structures. / Misure proposte per lo studio della crescita allometrica delle strutture natatorie e di controllo.

Structure	No.	Abbreviation	Measured structure	Description
Flipper	1	FSTEL	Flipper Straight Trailing Edge Length	Axilla to tip (Measured in a straight line)
	2	FLEL	Flipper Leading Edge Length	Anterior insertion to tip curvilinear. (Measured in a curviliear line following the anterior edge)
	3	FL	Flipper Length	Anterior insertion to tip. (Measured in a straight line)
	4	FMW	Flipper Maximal Width	Measured perpendicular to flipper axis
	5	FSA	Flipper Sweep Angle	Angle formed by the base of the Flipper and it´s tip, taked from the center of the base
Dorsal Fin	6	DFB	Dorsal Fin Base	From anterior insertion to posterior insertion parallel to body suface
	7	DFH	Dorsal Fin Height	Perpendicular to body surface
	8	DFDFA	Dorsal Fin Depth at Falcation Apex	From the caudal insertion of dorsal fin to deepest point on caudal side, parallel to the body surface
	9	DFWFA	Dorsal Fin Width at Falcation Apex	From deepest ápex, to frontal edge, perpendicular to body surface
	10	DFHPP	Dorsal Fin Height at Posterior Point	From body Surface to posterior point of fin, perpendicular to body surface
Caudal Peduncle	11	CPH	Caudal Peduncle Height	Maximum height of caudal peduncle perpendicular to body axis
Fluke	12	FTS	Fluke, total spread	From ápex to apex
	13	CLRC	Root Chord	From base to trailing edge
	14	CLLEL	Caudal Lobe Leading Edge Length	Caudal base to tip curvilinear. (Measured in a curviliear line following the anterior edge)
	15	CLL	Caudal Lobe Length	Caudal base to tip. (Measured in a straight line)

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