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Sea Lamprey (*Petromyzon marinus*) Attachment to the Common Bottlenose Dolphin (*Tursiops truncatus*)

Jure Miočić-Stošić,[1,2] Grgur Pleslić,[1] and Draško Holcer[1,2]

[1]*Blue World Institute of Marine Research and Conservation, Kaštel 24, 51551 Veli Lošinj, Croatia*
E-mail: jure.miocicstosic@blue-world.org
[2]*Croatian Natural History Museum, Demetrova 1, 10000 Zagreb, Croatia*

Abstract

Limited information is available on cetacean interactions with the parasitic sea lamprey (*Petromyzon marinus*). Direct observations of sea lamprey attachment are rare, and the resulting wounds and scars often provide the only evidence of a parasite–host relationship. In spite of extensive research of natural markings such as nicks and skin scarring patterns, previous studies do not describe sea lamprey attachment marks on the common bottlenose dolphin (*Tursiops truncatus*). Herein, we used opportunistically taken photographs to present direct evidence of sea lamprey attachment on a bottlenose dolphin. Furthermore, we analysed photo-identification data from long-term bottlenose dolphin studies in the Adriatic Sea and found eight skin marks attributable to sea lamprey attachment, providing indirect evidence linking the two species. Size estimation and geographic exclusion were used to corroborate the findings. The presence of scars corresponding to pierced wounds confirms that active feeding took place. Sea lamprey attachment marks on bottlenose dolphins are identifiable but appear to be rare, hard to notice, and short-lived. Therefore, such scars are not suitable for long-term photo-identification. Our findings confirm the bottlenose dolphin is a sea lamprey host and highlight the need to assess possible negative impacts of such interactions.

Key Words: parasite, cetacean, host, Adriatic Sea, photo-identification

Introduction

The common bottlenose dolphin (*Tursiops truncatus*; Montagu, 1821) (hereinafter bottlenose dolphin) is a well-known cetacean species with a global range (Wells & Scott, 2002). Its ecological traits such as variability in foraging strategies allow it to occupy different habitats and respond to a range of environmental stressors (Hoelzel et al., 1998; Allen et al., 2001; Natoli et al., 2005; Gaspari et al., 2013; Leone et al., 2019). Numerous studies on bottlenose dolphins used photo-identification (Defran et al., 1990; Hammond et al., 1990; Würsig & Jefferson, 1990) to analyse population dynamics (Wilson et al., 1999a; Currey et al., 2008; Pleslić et al., 2013; Smith et al., 2013), social structure (Connor et al., 2001; Quintana-Rizzo & Wells, 2001), behaviour (Gero et al., 2005; Lusseau, 2007), health status (Thompson & Hammond, 1992; Wilson et al., 1999b; Van Bressem et al., 2008), and other aspects of its ecology (Defran et al., 1999; Rako-Gospić et al., 2017; Vetters Bichell et al., 2018). Despite the pivotal role of visible marks in photo-identification (Würsig & Würsig, 1977), the origin of lesions and scarring patterns often remains unknown (Flach et al., 2008; Burdett Hart et al., 2012). However, being able to determine the cause of natural markings—for example, predation (Heithaus, 2001), parasitism (Vecchione & Aznar, 2014), intraspecific competition (Scott et al., 2005), or disease (Van Bressem et al., 2007)—is important for monitoring specific populations and describing the ecology of the species.

Some scars observed on cetaceans have been attributed to the parasitic sea lamprey (*Petromyzon marinus*; Linnaeus, 1758) (McAlpine, 2002; Nichols & Hamilton, 2004; Nichols & Tscherter, 2011; Rosso et al., 2011; Samarra et al., 2012; Ólafsdóttir & Shinn, 2013; Silva et al., 2014; Renaud & Cochran, 2019). It is widely distributed across the Atlantic coast of North America and Europe, including the Mediterranean Sea (Holčík et al., 2004; Kottelat & Freyhof, 2007). Juveniles migrate from breeding areas in freshwater systems and attach to an array of marine organisms as adults, feeding on their blood and fluids (Beamish, 1980; Farmer, 1980; Renaud, 2011; Silva et al., 2014). Information regarding its parasitic haematophagous life stage is scarce and based mostly on captures of free-ranging specimens (Nichols & Hamilton, 2004). In the absence of direct observations, a parasite–host relationship is often inferred from resulting wounds and scars (Silva et al., 2014). However, similar markings caused by other parasitic and predatory animals (Dwyer & Visser, 2011) as well as infections and other skin disorders (Harzen & Brunnick, 1997) have given rise to ambiguity in their identification (Pike, 1951; van Utrecht, 1959).

The sea lamprey exploits a wide range of hosts and overlaps geographically with the bottlenose dolphin (Silva et al., 2014), but there is no confirmed relationship between the species. On one occasion only, researchers photographed an unknown species of lamprey attached to a bottlenose dolphin in Shannon Estuary, Ireland (Mulkear LIFE, 2012). Species identification was not possible as it shared morphological characteristics with the sea lamprey and the European river lamprey (*Lampetra fluviatilis*; Linnaeus, 1758), both occurring in the area (Igoe et al., 2004; Kottelat & Freyhof, 2007). Sea lamprey attachment to host animals is transient and may only last for a few days (Kottelat & Freyhof, 2007; Renaud & Cochran, 2019). The occurrence of sea lamprey parasitism may be infrequent and may result in short-lived, indistinctive scarring upon detachment. In addition, studies about the origin of natural markings used in photo-identification of cetaceans are rare (Bruce-Allen & Geraci, 1985; Corkeron et al., 1987; Lockyer & Morris, 1990; Marley et al., 2013; Vetters Bichell et al., 2018), while studies of epidermal disease often disregard wounds and scars attributed to physical injury (Baker, 1992; Harzen & Brunnick, 1997; Wilson et al., 1997, 1999b; Bearzi et al., 2009; Maldini et al., 2010; Burdett Hart et al., 2012; Gonzalvo et al., 2015). Previous studies may have overlooked sea lamprey attachment marks, clustered them with other similar markings, or excluded them from the analysis.

The taxonomy of lampreys is based primarily on differences in dentition patterns (Renaud, 2011). Species identification can be difficult, even when examining captured specimens (Kottelat & Freyhof, 2007). Lamprey attachment marks can be identified by matching wound and scar patterns on the host animal to the anatomy and feeding mechanism of lampreys. The existence of a piercing wound and distinctive patterns of tissue damage surrounding it are key identifying features (Ebener et al., 2006; Samarra et al., 2012; Silva et al., 2014). However, species attribution mostly relies on direct observations of attachment in the field (Lantry et al., 2015) or the laboratory (King, 1980). Geographic exclusion of similar species with non-overlapping spatial distribution can aid species identification when using photographs only (Nichols & Hamilton, 2004; Nichols & Tscherter, 2011; Samarra et al., 2012; Lantry et al., 2015).

The sea lamprey is the only extant species of parasitic lamprey present in the Adriatic Sea (Lipej & Dulčić, 2010). It is also the largest European anadromous lamprey (Holčík et al., 2004; Kottelat & Freyhof, 2007). Information on the size of lamprey individuals or their attachment marks can support species identification based on size exclusion (King, 1980; Nichols & Tscherter, 2011; Rosso et al., 2011). A common approach for estimating size from photographs is to use a feature of known size to provide scale such as a calibrated object or laser dots (Rowe & Dawson, 2008; Krause et al., 2017). When photographs of bottlenose dolphins lack a known scale reference, the animal itself can be used as a reference because its morphometric characteristics fall within a finite size range. Therefore, existing morphometric data may be used for calibrating size estimates provided selected characters can be delineated in images (Willisch et al., 2013). Nevertheless, as the true size of features visible in any one image is unavailable, the estimation can only yield size ranges rather than absolute values.

Herein, we investigate the existence and nature of sea lamprey parasitism of bottlenose dolphins. To do so, we focused on images of bottlenose dolphins to obtain both direct (attachment) and indirect (scarring pattern) evidence of interaction as a non-invasive, previously described, and available means of identifying and confirming a relationship between sea lampreys and their respective hosts. Large-scale morphological features such as body shape and colour corroborate the identification of sea lamprey individuals in photographs, whereas distinct lamprey oral disc structures link visible scarring patterns to particular lamprey species. To eliminate ambiguity, we further apply the principle of geographic exclusion and use photogrammetry to obtain size estimates of both lamprey individuals and attachment marks, supporting the identification and eliminating other similar species. In addition to confirming a parasite–host relationship, such an analysis gives an insight into the appearance of sea lamprey attachment marks, their value in photo-identification studies, and conditions for reliable identification of sea lamprey interaction with cetaceans in other regions and study areas.

Methods

Lamprey Attachment Mark Identification

To find occurrences of sea lamprey attachment marks, we examined photographs from long-term boat-based studies on bottlenose dolphins in Vis archipelago and North Dalmatia, Central Adriatic Sea, Croatia. The database contains more than 150,000 images taken between 2007 and 2019, and is hosted by the Blue World Institute (BWI) (Holcer, 2012; Miočić-Stošić et al., 2018; Pleslić et al., 2019). Data collection and handling in both study sites followed procedures described in Pleslić et al. (2019). We used 9,250 best representative photographs from each sighting of 1,491 individuals encountered between 2007 and 2017. Images included in the analysis show the dorsal fin and parts of the back and flank of the animals, which is where sea lamprey marks were observed in other cetaceans (Silva et al., 2014). Two researchers (GP and JMS) with over a decade of experience in photo-identification visually examined all images for the presence of conspicuous scars.

We extracted available scar descriptions (Pike, 1951; Nichols & Hamilton, 2004; Nichols & Tscherter, 2011) and images of dolphins showing wounds and scars believed to have been caused by sea lamprey attachment (Bertulli et al., 2012; Samarra et al., 2012; Ólafsdóttir & Shinn, 2013; Silva et al., 2014; Mariani et al., 2016; Selling et al., 2016). Based on these, we considered the following characteristics to indicate lamprey attachment: (1) circular- or oval-shaped patch of contrasting coloration (lighter or darker than surrounding skin); (2) white, circular coloration surrounding a centrally positioned wound; (3) marks showing a textured abrasion pattern that are not uniform in colour; and (4) parallel "streaks" of white lines alongside the body of the animal originating and/or terminating in an oval or circular scar. When agreed upon by both researchers, we attributed skin marks to sea lamprey attachment and examined the respective individuals in detail. We then examined all available images featuring these animals and obtained the most informative photographs as well as a history of mark presence/absence. We used consecutive observations to assess mark longevity and temporal changes in appearance.

Direct Lamprey Attachment Identification

We checked the BWI photo catalogue for the presence of lamprey individuals attached to bottlenose dolphins. We used the morphological characteristics of sea lampreys described in Kottelat & Freyhof (2007).

In addition, we examined 13 photographs taken opportunistically by a tourist in July 2014 which purport to show sea lamprey attachment on an adult bottlenose dolphin (Figure 1A, B & C). Images were taken in the area between the islands of Mljet and Korčula (Central Adriatic Sea, Croatia; exact location unknown) (M. Knežević, pers. comm., 28 July 2014). According to the tourist, a foreign object attached to the right side of the dolphin was visible by naked eye. The dolphin was behaving erratically, performing high jumps and swimming rapidly. Images of the event were visually cross-referenced with distinguishing features of known lampreys (Kottelat & Freyhof, 2007). We compared the bottlenose dolphin individual against the above-mentioned reference catalogue in an effort to obtain additional information from other potential sightings of the same animal.

Validation Using Size Estimation

To estimate the size of sea lamprey individual and attachment marks, we used two reference intervals based on reported dorsal fin height (DH) and total body length (TBL) of stranded adult bottlenose dolphins in the Adriatic Sea (Đuras Gomerčić, 2006). Both morphometric characters were treated as normally distributed, and the three sigma rule (Pukelsheim, 1994) was applied to set cut-off values two standard deviations away from the reported mean, encompassing 95% of the size distribution. We accounted for gender differences by overlapping male and female intervals and retaining extreme values: 18.81 and 33.29 cm for the DH, and 265.03 and 324.77 cm for the TBL. We used these values as calibration points and performed subsequent measurements in *Digimizer*, Version 4.6.1 (Digimizer, 2015) by treating each of these values as a single definite scale reference to obtain a minimum and maximum size estimate corresponding to each interval.

Images were imported and rotated in software, so that the base of the dorsal fin (DBL; Figure 2) lies horizontally. This allows for easier identification of DH and TBL endpoints, determined following Đuras Gomerčić (2006) and Rowe & Dawson (2008) (Figure 2). We defined their length to set the scale and subsequently measured the length of the lamprey as a straight line from the tip of the head to the end of the caudal fin (Figure 2). Similarly, we measured the length of the skin marks along the long axis of the scar. Specifically, we measured from the supposed position of anterior-most dentition marks towards the posterior-most dentition marks as determined by the position of the infraoral lamina mark (Figure 2). The same person (JMS) performed the measurements, replicated 20 times for each image (10 replications per calibration point). We subsequently calculated a mean size estimate for each calibration point.

Results

Lamprey Attachment Mark Identification

In 9,250 images, we identified eight sea lamprey attachment marks on five bottlenose dolphin individuals. All marks are composite pale scars contrasting the surrounding darker skin coloration.

Figure 1. (A) Sea lamprey (*Petromyzon marinus*) (white arrow) attached to the right flank of a bottlenose dolphin (*Tursiops truncatus*), (B) enlarged portion of image A showing seven gill openings on the head of the lamprey (white arrow), (C) image showing entire body of the lamprey (white arrow), and (D) sea lamprey appearance (public domain image: E. Edmonson, https://commons.wikimedia.org/wiki/File:Petromyzon_marinus.jpg)

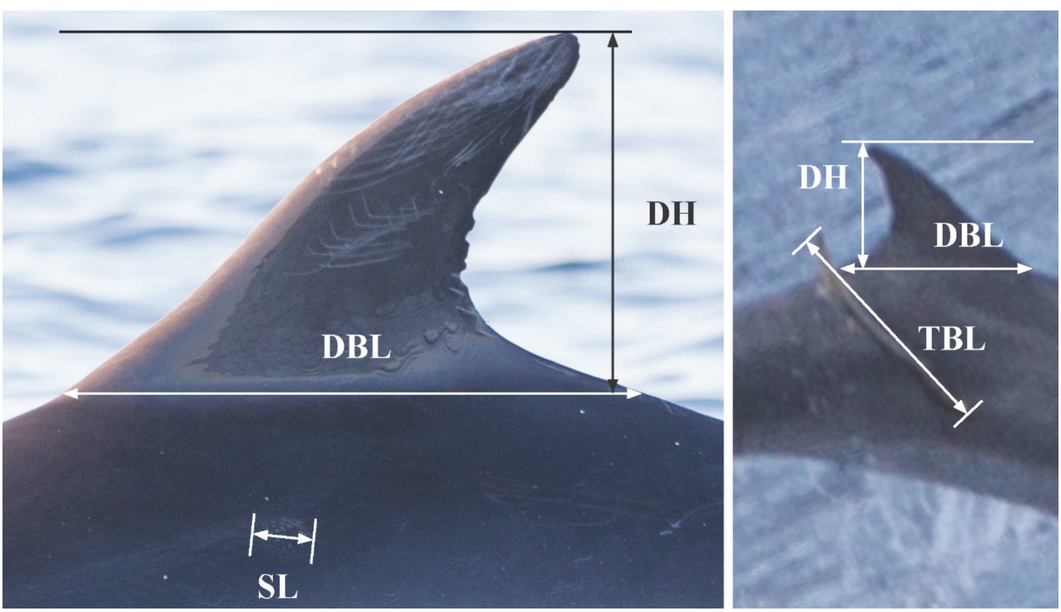

Figure 2. The measurement of scar length (SL) and lamprey total body length (TBL) was calibrated using dorsal fin height (DH) measured from the top of the dorsal fin to the dorsal fin base (DBL). Image brightness adjusted.

They are made up of many individual dots and elongated scratches that form rows which arch from the margin towards the centre of identified scars (Figure 3). Their number and orientation fits particular rows of labial teeth and other associated structures characteristic to sea lamprey oral disc morphology (Renaud, 2011; Figure 4). The count for each row never exceeds known meristic characteristics (Renaud, 2011; Lança et al., 2014). The largest and most prominent scratches appear near the centre of the scars, corresponding to the largest bicuspid teeth and the infraoral lamina. Scarring attributed to posterior rows of teeth, the marginals, and the first anterior row is only faintly visible or not visible at all. There are no visible scratches attributed to soft leathery appendages surrounding the oral disc (oral fimbriae). Two scars show a centrally positioned circular mark corresponding to a piercing wound inflicted by the rasping tongue-like piston of the sea lamprey (Figure 3J). In three cases, parallel streaks of white lines originate from the oval-shaped scar (Figure 3B, G & J).

All marks are consistent with sea lamprey scars observed on Sowersby's beaked whales (*Mesoplodon bidens*; Sowerby, 1804) (Silva et al., 2014) and common minke whales (*Balaenoptera acutorostrata*; Lacépède, 1804) (Ólafsdóttir & Shinn, 2013; Figure 5).

Within our sample, the longest recorded period in which scars remained visible was 36 mo (July 2016 to July 2019 for "Ivano"; Figure 6). Two individuals displayed visible scars for at least 14 mo (May 2016 to July 2017 for "Roquefort" and "Zoran"). Conversely, the scarring on one individual seems to have disappeared within 12 mo (July 2009 to July 2010 for "Fratun"), and another could not be assessed due to poor quality of available images ("Kolumba"). Due to the small sample size and differences in overall quality of available photographs, we could not reliably assess temporal changes in the appearance of attachment marks.

Direct Lamprey Attachment Identification

Photographs from the opportunistic sighting show an elongated, eel-like animal attached centrally on the right flank, below the dorsal fin of the bottlenose dolphin. The individual attached with one end of its body and the rest is hanging freely (Figure 1C). Seven gill openings characteristic to all lamprey species (Renaud, 2011) are visible on the anterior part of the animal (Figure 1B). The proportion of the lamprey relative to frame size is too small to examine species-specific morphological characteristics such as the appearance of the oral disc and the number of trunk myomeres (Kottelat & Freyhof, 2007). In addition, the body of the dolphin is partially obscuring the lamprey in images taken closest to the subject. Mottled body colouration cannot be confirmed (Figure 1D). We found no match between the host dolphin and individuals in the BWI catalogue of bottlenose dolphins of the Eastern Adriatic Sea before or after this encounter. We identified no other sea lamprey individuals attached to bottlenose dolphins in the dataset.

Validation Using Size Estimation

We could consistently delineate and measure six lamprey attachment marks. The resulting estimated minimum mark lengths were between 2.47 cm (SE = 0.03; 95% CI = 2.39 to 2.54 cm) and 3.16 cm (SE = 0.06; 95% CI = 3.02 to 3.29 cm), with a mean minimum length of 2.83 cm (SE = 0.12; 95% CI = 2.52 to 3.13 cm). Conversely, maximum mark lengths measured between 4.22 cm (SE = 0.03; 95% CI = 4.16 to 4.28 cm) and 5.38 cm (SE = 0.07; 95% CI = 5.21 to 5.54 cm), with a mean maximum length of 4.89 cm (SE = 0.21; 95% CI = 4.36 to 5.42 cm).

The size estimates of the observed lamprey using mean DH for scale ranged from 37.22 cm (SE = 0.32; 95% CI = 36.50 to 37.93 cm) to 67.64 cm (SE = 0.83; 95% CI = 65.76 to 69.52 cm). These are underestimates as we applied no correction to account for lamprey body curvature. When using bottlenose dolphin body length for scale, lamprey size estimates ranged from 60.10 cm (SE = 0.28; 95% CI = 59.46 to 60.74 cm) to 73.19 cm (SE = 0.22; 95% CI = 72.67 to 73.70 cm). However, these are overestimates as we applied no correction to account for dolphin body curvature.

Discussion

Lamprey Attachment Mark Identification

The overall appearance of wounds and resulting scars in bottlenose dolphins is affected by the depth and extent of damage to particular dermal and subdermal tissues, with shallow scratches being less prominent and fading away quicker than scars from deeper wounds (Lockyer & Morris, 1990). Sea lampreys secure the attachment by lodging labial teeth of differing size into the skin of the host and create a bleeding wound using repeated rasping action of the lingual lamina (Lennon, 1954). Because damage is simultaneously inflicted by two major physical processes of differing magnitude (Lennon, 1954; Renaud & Cochran, 2019), a non-uniform scar will likely be formed during the healing process. This complex scar consists of many elements reflecting particular oral disc structures (Nichols & Tscherter, 2011; Silva et al., 2014). The stippled appearance and oval shape of the skin marks identified on

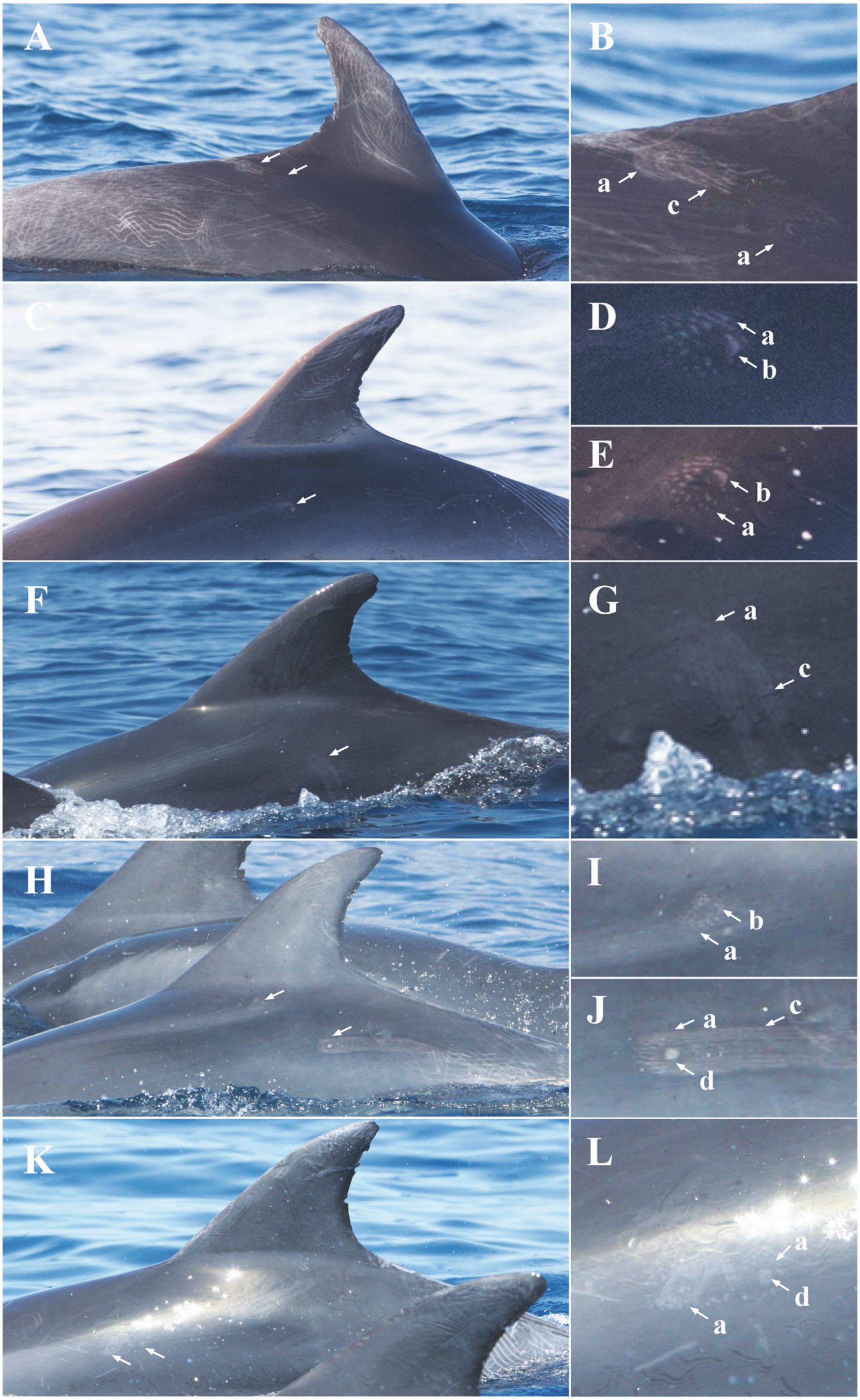

Figure 3. (A, C, F, H & K) Images showing bottlenose dolphin individuals with scars (white arrows) attributed to sea lamprey attachment; and (B, D, E, G, I, J & L) enlarged portions of images showing scars in greater detail (a – dentition marks, b – infraoral lamina mark, c – repositioning scratches, and d – piercing wound scar). Image brightness adjusted (C, D & E)

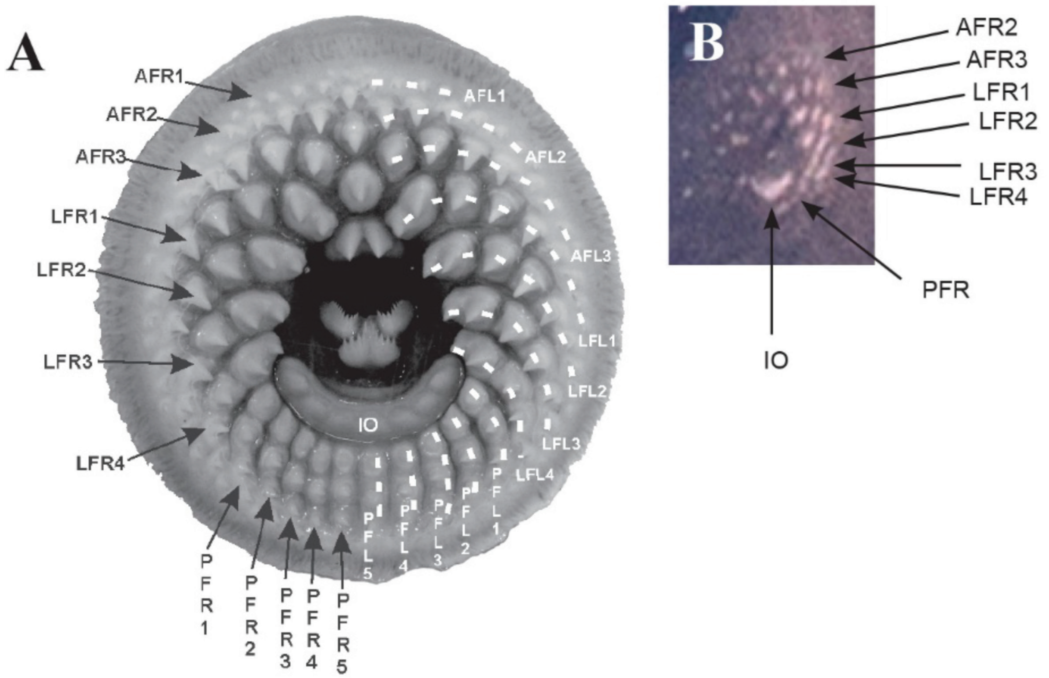

Figure 4. (A) Photograph of the oral disc of an adult sea lamprey showing dentition (Lança et al., 2014); and (B) photograph of a scar on a common bottlenose dolphin with arrows showing marks attributed to different oral structures (AFR = anterior right field, LFR = lateral right field, PFR = posterior right field, and IO = infraoral lamina). Image brightness adjusted (B).

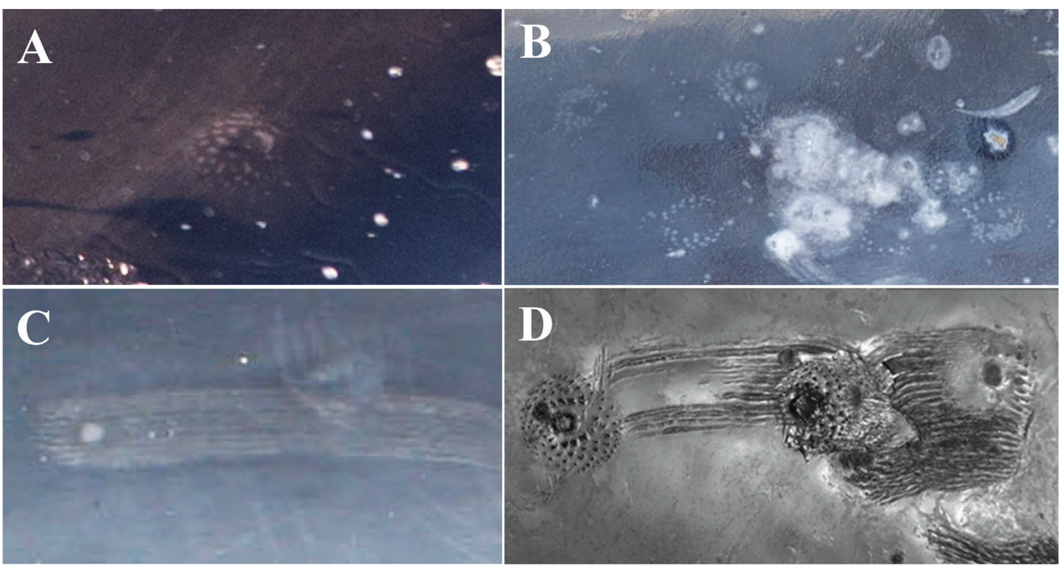

Figure 5. (A & C) Comparison of scars observed on common bottlenose dolphins in this study, and (B) sea lamprey marks on Sowersby's beaked whales (Silva et al., 2014) and (D) common minke whales (Ólafsdóttir & Shinn, 2013). Image brightness adjusted (A). Reference images B & D are cropped.

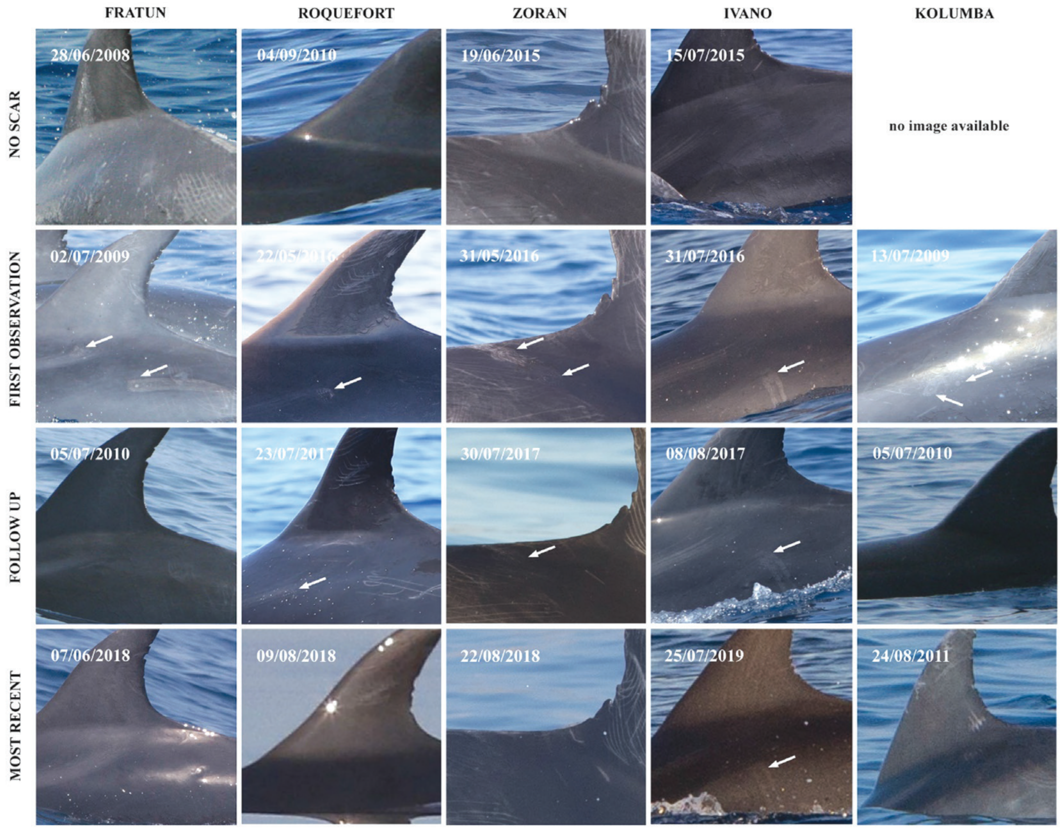

Figure 6. The appearance of scars through time from last sighting prior to sea lamprey attachment to most recent photo. Each column shows best available images of the same individual reflecting variability in quality and level of detail conveyed; date of photo is in top left corner. Image brightness adjusted.

bottlenose dolphins in this study are consistent with the pattern of labial teeth and lingual lamina of the sea lamprey. Furthermore, they are consistent with sea lamprey attachment marks found on fish (King, 1980; Ebener et al., 2006) and other cetaceans (Ólafsdóttir & Shinn, 2013; Silva et al., 2014). The observed scarring is unlikely to be created by other lamprey species due to differing dentition patterns.

The presence of pierced wounds upon sea lamprey detachment is indicative of active feeding and can be used to establish a parasite–host relationship (Silva et al., 2014). In this study, two scars on two individuals show features corresponding to pierced wounds and, thus, provide indirect evidence of active feeding—that is, a parasite–host relationship between sea lampreys and bottlenose dolphins. The remaining six scars indicate attachment only. This is not surprising as not all attachments result in a piercing wound, and sea lampreys may first attach and then seek a more favourable position on the host before feeding occurs (Nichols & Tscherter, 2011). In fact, the low ratio of pierced to non-pierced wounds is also reported for other cetaceans (Silva et al., 2014).

The observed variability in the appearance of scars has been previously described and can be attributed to differences in the behaviour of sea lamprey individuals during attachment (Adams, 2006). Depending on whether feeding occurred or not, skin marks can be distinguished as pierced or non-pierced. They may also feature a characteristic series of elongated scratches resulting from repositioning (Ebener et al., 2003; Nichols & Tscherter, 2011; Silva et al., 2014). In spite of the small sample size, our results feature all three possible examples noted on other marine organisms (Silva et al., 2014).

All marks were situated on the back and flank of bottlenose dolphins which is consistent with previously reported data for other cetaceans (Silva et al., 2014). It has been suggested that dorsolateral positioning is beneficial due to reduced water flow and epidermal thickness in comparison with fin regions (Nichols & Tscherter, 2011). However, we could not infer the prevalence of attachment to different body parts from our dataset due to an insufficient number of photographs showing the entire body of host dolphins.

The variability in the appearance of skin marks can also be attributed to temporal changes during the healing process (Ebener et al., 2006). However, additional data is required to describe the healing process and to reliably assess the longevity of sea lamprey attachment marks on bottlenose dolphins. Adding to the small number of consecutive observations available for analysis, there were notable differences in the appearance of particular scars among observations due to overall image quality (Figure 6). Variability in lighting conditions, image sharpness, and distance to the subject significantly affects the level of detail exhibited by each photograph. Consequently, scars can be difficult to identify, even with prior knowledge of their existence. Identified sea lamprey scars are relatively small and exhibit low contrast in relation to other natural markings. Tooth rakes and other more prevalent scars resulting from physical injury are likely to mask them. We could confirm that only one observed scar remained visible for 36 mo, suggesting attachment mark longevity is comparable to sea lamprey scars observed on other cetaceans (Rosso et al., 2011; Samarra et al., 2012). Despite the small sample size, these results indicate that sea lamprey scars become indistinguishable over time and are not useful as primary markings in long-term photo-identification studies. However, based on the assumed impact of oral disc structures to bottlenose dolphin tissues, it is likely that their longevity is comparable to scars from other shallow and minor wounds such as tooth rakes (Lockyer & Morris, 1990; Wilson et al., 1999a). Researchers routinely use similar scrapes and scratches as ancillary information in photo-identification (Würsig & Jefferson, 1990; Scott et al., 2005). Therefore, the usefulness of discernible sea lamprey marks for identifying individuals in photographs obtained within a short time period (< 1 y) should not be disregarded (Samarra et al., 2012).

Sea lamprey attachment marks identified on bottlenose dolphins are sufficiently distinct not to be confused with scars of similar size, colour, and shape resulting from other underlying causes. These include a wide range of epidermal conditions that affect bottlenose dolphins (Baker, 1992; Harzen & Brunnick, 1997; Wilson et al., 1997, 1999b; Bearzi et al., 2009; Maldini et al., 2010; Burdett Hart et al., 2012; Gonzalvo et al., 2015). In any population, these can have moderate (Gonzalvo et al., 2015) to very high prevalence as noted in the Adriatic Sea (Wilson et al., 1999b). For instance, tattoo skin disease can often produce oval marks with stippled appearance, comparable in size to sea lamprey attachment marks (Van Bressem et al., 2018). In addition, a number of parasitic or predatory species are known to interact with cetaceans such as the copepod (*Pennella balaenopterae*; Koren & Danielssen, 1877) (Vecchione & Aznar, 2014), cookiecutter shark (*Isistius brasiliensis*; Quoy & Gaimard, 1824) (Dwyer & Visser, 2011), and hagfish (*Myxine glutinosa*; Linnaeus, 1758) (Pace et al., 2016). However, it is unlikely that wounds inflicted by these animals can cause a complex scar pattern reflecting rows of sea lamprey labial teeth. Their morphology and feeding kinematics (Abaunza et al., 2001; Clark & Summers, 2007, 2012; Best & Photopoulou, 2016) is notably different from that of the sea lamprey. However, to minimise the probability of false attribution, researchers should use only high-quality images (well lit, in focus, orthogonal to the photographer, and large size in frame) to identify sea lamprey marks.

Direct Lamprey Attachment Identification

Photographs showing the only lamprey identified in our dataset featured morphological characteristics common to all lampreys. Due to the low quality of the photographs, we could not confirm species-specific large-scale features, including mottled colouration (Kottelat & Freyhof, 2007). However, the sea lamprey is the only marine parasitic lamprey present in the Adriatic Sea (Lipej & Dulčić, 2010), and the principle of geographic exclusion can be applied to validate species identification (Nichols & Hamilton, 2004; Nichols & Tscherter, 2011; Samarra et al., 2012). It is common on the west coast of the basin (Zanandrea, 1961) and rare along the eastern coast (Holčík et al., 2004; Mrakovčić et al., 2006; Jardas et al., 2008; Joksimović et al., 2009; Shumka et al., 2009). The majority of other lamprey species within the broader Adriatic region are non-parasitic, and all are exclusively freshwater residents (Mrakovčić et al., 2006; Kottelat & Freyhof, 2007). The only other parasitic anadromous lamprey with a historical distribution in this area is the European river lamprey, but it is considered regionally extinct (Freyhof, 2011). Therefore, it is improbable that the photographed bottlenose dolphin would have encountered any other lamprey species.

The individual with the attached lamprey was behaving erratically, exhibiting high jumps and swimming fast. It has been hypothesized that aerial manoeuvres of spinner dolphins (*Stenella longirostris*; Gray, 1828) (Weihs et al., 2007) and even blacktip sharks (*Carcharinus limbatus*;

Müller & Henle, 1839) (Ritter & Brunnschweiler, 2003) are used for removal of remoras. Remoras and sea lampreys are similar in size, shape, and attachment methods to large marine vertebrates (Fertl & Landry, 1999, 2002). It is therefore reasonable to interpret the described behaviour as a response to sea lamprey attachment and an attempt to dispose of the parasite. The skin along the back of the bottlenose dolphin is sensitive to external stimuli and changes in pressure (Ridgway, 1990; Ridgway & Carder, 1990). The resistant pressure of dislodgement for sea lampreys measured in the laboratory can exceed -61.65 kPa (Adams, 2006), and it has been observed that mechanical disturbances entice frequent changes in residual negativity in the sucker, reinforcing the attachment (Gradwell, 1972). In this case, we could not confirm the presence of a piercing wound as we identified no subsequent sightings of the same bottlenose dolphin individual. However, the bottlenose dolphin would have likely been able to sense the presence of the lamprey due to suction pressure alone.

Validation Using Size Estimation

Researchers commonly describe sea lamprey–cetacean interactions using photographic evidence (Nichols & Hamilton, 2004; Samarra et al., 2012). Species identification relies on large-scale morphological features, including size. However, it is often unclear which features were used to identify attachment marks (McAlpine et al., 1997) and lamprey individuals (Samarra et al., 2012) or in what way their size was determined. Nichols & Hamilton (2004) and Nichols & Tscherter (2011) report using body length > 50 cm as a distinguishing feature of sea lampreys without further reference to size estimation. Rosso et al. (2011) provided images of Cuvier's beaked whales with sea lamprey attachment marks estimated to be > 4 cm using approximate dorsal fin width as a size reference but give no other details on the methodology used. However, providing exact measurements from captured specimens or a relevant quantitative estimate is required to use size as a distinguishing feature.

Ideally, to obtain accurate measurements, all characters of interest should be on the same two-dimensional plane lying exactly perpendicular to the photographer. There should be no variation in identifying measured morphometric characters and no three-dimensional distortion due to body curvature. We could not minimise sources of bias and measurement error by altering fieldwork procedures as we used existing data in the analysis. However, morphometric characters can be applied as a measure of scale in photogrammetry (Willisch et al., 2013). Error arising from repeated identification of dorsal fin height in photographs is acceptable, and such measurements are considered replicable (Rowe & Dawson, 2008). In addition, fieldwork procedures within both study sites require photographs to be taken orthogonally (Pleslić et al., 2013), and all included images were taken approximately perpendicular to the photographer. No physical measurements were available to estimate the accuracy of our estimation method.

The size estimates of the observed lamprey and attachment marks in our dataset are broad and give an indication of size with a high degree of uncertainty. However, the resulting intervals are constrained enough to support species identification based on size exclusion. Based on the results, it is likely the true length of identified attachment marks falls within the 2.4- to 5.4-cm size range. Both Holčík et al. (2004) and Renaud (2011) report similar oral disc lengths of sea lampreys expressed as a percentage of TBL, with 4.5 to 9.2% (TBL range: 192.0 to 827.5 mm; mean: 6.8%; n = 46) and 4.5 to 9.3% (TBL range: 135 to 835 mm; n = 58), respectively. Holčík et al. also provide original measurements ranging from 13.6 to 60.0 mm, with a mean oral disc length of 38.0 mm (SE = 1.5). However, these measurements were done with the oral disc in closed position and the lateral margins touching each other (i.e., with distorted oral disc shape). Conversely, Lennon (1954) measured the oral disc by pressing it firmly against a glass plate, emulating more closely the shape of the disc during attachment. The resulting mean oral disc size for different TBL size categories was 124 to 561 mm (7.8 to 10.0% ratio to TBL; TBL range: 12.2 to 56.1 cm; n = 487). In spite of inherent bias in reflecting the true size of attachment marks arising from oral disc distortion and assumption of uniform impact (morphometry) as well as spatial distortion and observed low impact along scar edges (photogrammetry), both can be used to approximate their size and are comparable. The estimated size of identified attachment marks on bottlenose dolphins likely overlaps with the reported oral disc measurements and supports the attribution of such marks to sea lamprey attachment.

Similarly, the resulting estimates indicate that the true TBL of the observed individual likely falls within the reported size range of adult sea lampreys (TBL range: 11.4 to 120.0 cm; Kottelat & Freyhof, 2007; Renaud, 2011). Moreover, both size intervals overlap with the size range of specimens captured in the Adriatic Sea (TBL range: 192.0 to 653.0 mm; n = 32) (Holčík et al., 2004). However, the resulting estimates cannot entirely exclude the European river lamprey in species identification as the more conservative size estimate (37.22 to 67.64 cm) overlaps with its reported size range (max. TBL: 45 cm; Kottelat & Freyhof, 2007). Even so, both methods of providing scale used to obtain the size intervals are biased due to the low quality of opportunistically acquired photographs. Considering their range of overlap (60.10 to 67.64 cm), it is likely that the true length of the lamprey exceeds the maximum reported length of the European river lamprey.

Conclusions

Our study demonstrates that sea lampreys interact with bottlenose dolphins, possibly inducing specific behavioural responses and resulting in temporary skin marks upon detachment. The resulting attachment marks are reliably identifiable in photographs due to their complex structure. Disease, predation, or interaction with other parasitic species are unlikely to cause the same pattern. However, because of their apparent rarity, small size, and low contrast in relation to other natural markings as well as temporal changes in appearance, these scars are difficult to spot and track through time. Attachment marks appear to be short-lived, with longevity on par with similar superficial scratches and minor wounds. Therefore, sea lamprey attachment marks are not suitable for use as primary markings in photo-identification. The apparent low prevalence of such interactions and low distinctiveness probably account for the absence of previous references to sea lamprey parasitism on bottlenose dolphins. However, the existence of scars corresponding to pierced wounds indicates active feeding takes place and confirms the bottlenose dolphin is a true sea lamprey host.

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