



Changes in the behavioural complexity of bottlenose dolphins along a gradient of anthropogenically-impacted environments in South Australian coastal waters: Implications for conservation and management strategies



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ABSTRACT

The susceptibility of bottlenose dolphins (*Tursiops* sp.) to disturbance within South Australian coastal waters is of particular importance due to both the ever increasing impact of anthropogenic activities on these waters and their semi-enclosed nature. Currently, little is known about the ecology of dolphins in this region, in particular in relation to anthropogenically-driven disturbances. This study investigates the level of stress experienced by bottlenose dolphins from the complexity of their temporal patterns of dive durations recorded along a gradient of environment types defined as a function of the intensity of anthropogenically-driven pollution and disturbances, including urban development and recreational boating. Dive durations were opportunistically recorded from land-based stations scattered across South Australian coastal waters both in the absence of boat traffic, and the potential for boat-related disturbance was investigated when a motorized vessel was within 100 m from a traveling individual to infer the effect of indirect exposure to boat disturbance. This approach fundamentally differs from more standard assessments of the behavioural effect of direct exposure to boat disturbance, for instance when dolphins chase fishing vessels, flee from motorboats or bow ride. Subsequent analyses were based on nearly 12,000 behavioural observations. No significant differences were found in dive durations measured in the absence of boats and when boats were present. In contrast, fractal analysis consistently identified significant differences in the complexity of dive duration patterns as a function of environment and exposure to disturbance. Specifically, bottlenose dolphins occurring in environments with less anthropogenic pressure exhibit a higher behavioural complexity. This complexity consistently and significantly decreases both within each environment and between environments with increasing anthropogenic pressure. These results further show that the relative changes in bottlenose dolphins' behavioural complexity increase in environments less impacted by anthropogenic activities. These results are discussed in the general context of the adaptive value of fractal behaviour, the susceptibility of bottlenose dolphins occurring in distinct environments to anthropogenic disturbance, and how behavioural properties identified with our fractal methods can be used to establish baseline information that can be used for the design and implementation of conservation and management strategies.

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1. Introduction

The assessment of the nature and intensity of the interactions between anthropogenic activities and cetaceans has been the focus of considerable research effort over the last decade, essentially due to the extensive overlap of human activities with cetaceans in general and dolphins in particular (e.g. Nowacek et al., 2001; Lusseau, 2003a, 2005, 2006; Williams et al., 2006; Baş et al., 2015). Beyond the extreme cases related to propeller strike injuries, blunt trauma caused by vessel collisions and eventual subsequent death (Martinez and Stockin, 2013;

Dwyer et al., 2014) and reports of fast boats disrupting dolphin behaviour and social life (Lusseau, 2005; Lemon et al., 2006), dolphins chasing fishing vessels (Jefferson, 2000), fleeing from motorboats (La Manna et al., 2013), and changing their acoustic behaviour to compensate for the masking noise in the presence of trawlers (La Manna et al., 2013), dolphins are exposed to numerous chronic anthropogenic stressors.

This situation is particularly important in coastal waters where dolphins are increasingly exposed to a variety of potential human disturbances (Kelly et al., 2004), and their consequences in terms of e.g. environmental contamination (Schwacke et al., 2002) and habitat degradation (Adams et al., 2008). These disturbances include commercial (Burdett and McFee, 2004) and recreational (Barco et al., 2010) fisheries, and the drastic increase in the occurrence of recreational motorized

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vessels (Buckstaff, 2006), recreational fishing (Powell and Wells, 2010), dolphin watching (Mustika et al., 2015) and swim-with-dolphin tourism (Peters et al., 2013). The understanding of dolphin responses to anthropogenic disturbance (e.g. the presence and type of boats and their related noise) is, however, not straightforward as a variety of sometimes conflicting responses have been reported. They include dolphins chasing fishing vessels (Jefferson, 2000) and fleeing from motorboats (La Manna et al., 2013), as well as a range of avoidance and anti-predator strategies such as increase in swimming speed, decrease in resting behaviour, directional changes, decreased inter-animal distance, increased breathing synchrony, and longer dive durations (Ribeiro et al., 2005; Lemon et al., 2006; Williams et al., 2006; Christiansen et al., 2013). Note, however, that the observed responses also depend on habitat, social context, physiological conditions and previous encounters with specific stressors (Lemon et al., 2006; Lusseau, 2003b, 2004; Sini et al., 2005). It is hence particularly difficult to disentangle the combined effects of disturbance and habitat on dolphin responses (Balmer et al., 2013; Pirota et al., 2013), especially because it seems likely that dolphins tolerate chronic disturbance rather than flee from exposed areas (Bejder et al., 2009) given the plethora of anthropogenically-impacted coastal waters where dolphins are known residents.

Under chronic exposure to disturbance, dolphins have been shown to develop subtle behavioural responses, such as changes in activity budgets (Gill et al., 2001; Bejder et al., 2009) and the complexity of behavioural patterns (Seuront and Cribb, 2011). Specifically, a recent work conducted in a highly urbanized coastal environment, the Port Adelaide River-Barker Inlet Estuary (South Australia), showed that dive durations of the Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) were not significantly affected by either boat presence or boat type (i.e. kayaks, inflatable motor boats, powerboats and fishing boats). In contrast, the complexity of the temporal dynamics of dive duration – quantified using fractal analysis and used as a proxy of stress, i.e. behavioural complexity decreases under stressful conditions; see MacIntosh (2014) and Seuront (2015) for reviews – was affected by boat presence and type (Seuront and Cribb, 2011). Specifically, the complexity of dive duration patterns did not significantly differ between control behavioural observations conducted in the absence of boat, and behavioural observations conducted in the presence of kayaks. A significant increase in behavioural stress was, however, induced by the presence of fishing boats, motorized inflatable boats and powerboats (Seuront and Cribb, 2011). These results suggest that standard behavioural metrics such as time allocated to different behavioural sequences, and the related statistical comparisons of mean duration or frequency may not be sensitive enough to detect subtle behavioural changes. In addition, the behavioural changes induced by a chronic exposure of dolphins inhabiting anthropogenically-impacted coastal areas to various boat disturbances may be much more difficult to detect than those related to the acute source of stress reported above; see also Seuront (2010, 2015) and MacIntosh (2014) for reviews on the value of fractal analysis to assess behavioural complexity and stress levels in a range of organisms. In addition, due to the semi-enclosed nature of South Australian coastal waters (Fig. 1), any anthropogenic impact to marine life may be considered as a conservation threat (Hoyt, 2005) as subsequent effects on the natural environment are likely to be particularly severe (Notarbartolo di Sciara and Birkun, 2002). In this context, the present work investigates how the fractal properties of dive duration patterns can be used to relate the behavioural complexity of *Tursiops* sp. to the nature of their habitat along a gradient of habitat types defined as a function of the intensity of anthropogenically-driven pollution and disturbances, including urban development and recreational boating.

2. Materials and methods

2.1. Study species

Two species of bottlenose dolphins, *Tursiops truncatus* and *T. aduncus*, have been recognised worldwide (Rice, 1998; Wang et al.,

1999). Specifically, *T. truncatus* has a broad distribution and is found both inshore and offshore in cool temperate to tropical waters around the world (Leatherwood et al., 1983). In contrast, *T. aduncus* is only present in coastal and estuarine waters of the Indian and western Pacific Oceans, including south-eastern Australia (Rice, 1998; Wang et al., 1999). Both *T. truncatus* and *T. aduncus* occur in sympatry and parapatry (Wang et al., 1999; Hoelzel et al., 1998) and over a range of different habitats (Bearzi et al., 1997).

In South Australia, *T. aduncus* is found in coastal waters and gulfs (Kemper and Ling, 1991), in particular the Port Adelaide River-Barker Inlet Estuary, which supports a population of resident individuals (Cribb et al., 2008). Note, however, that recent genetic evidence, based on both mtDNA and microsatellite data, suggests that coastal bottlenose dolphins from South Australia, Victoria and Tasmania are evolutionarily distinct from *T. truncatus* and *T. aduncus* (Charlton et al., 2006). The former is likely to represent an undescribed dolphin taxon more closely related to the common bottlenose dolphins *T. truncatus* than to the Indo-Pacific bottlenose dolphin *T. aduncus* (Charlton et al., 2006). As a consequence, we refer to bottlenose dolphins as *Tursiops* sp. throughout this study.

2.2. Study site

The complexity of breathing rhythms in *Tursiops* sp. was investigated from South Australian coastal waters exhibiting a gradient of environments defined as a function of the intensity of anthropogenically-driven pollution and disturbances, including urban development and recreational boating. Specifically, the identification of dolphin stress levels is particularly important in the Port Adelaide River-Barker Inlet Estuary (South Australia), where *Tursiops* sp. is a known resident (Kemper et al., 2008; Steiner and Bossley, 2008). This estuary, located on the north-eastern side of Gulf St. Vincent, is a sheltered, marine dominated estuary (Connolly, 1994) and is considered to have unique conservation significance and commercial value (Tanner et al., 2003). It is, however, in its southern part highly impacted by a number of anthropogenic activities ranging from sewage pollution, horticultural water runoff, recreational and commercial vessel traffic, dredging, urban development, habitat degradation and altered flow regimes (Edyvane, 1991, 1999; Connolly, 1994; Bryars, 2003; Seuront and Cribb, 2011). The recognition of the potential threats in this area therefore led to the declaration of the Adelaide Dolphin Sanctuary (ADS) in 2005, with the intent to protect and conserve both the dolphins and their environment. Although a declared sanctuary, little is still known about the potential links between the nature of their environment and the behaviour of dolphins in this area (Cribb et al., 2008).

To ensure the generality of our approach, our study investigated thirteen sites scattered in three distinct areas across South Australian coastal waters. These include the Adelaide Dolphin Sanctuary, the sandy beaches of the metropolitan coasts of Adelaide in St. Vincent Gulf, and Boston Bay in the Spencer Gulf (Fig. 1). Specifically, four sites were chosen inside the Adelaide Dolphin Sanctuary (ADS) along a gradient of increasing anthropogenic activities (Fig. 1C). These sites include the Angus Inlet at Garden Island, a relatively pristine sheltered water complex, fringed by mangrove forest, and dissected by numerous shallow bare sand channels (Fig. 2A), North Arm in the Barker Inlet which hosts a harbour for fishing, recreational and research vessels (Fig. 2B), Dock 2 (Port Adelaide) a cargo loading facility (Fig. 2C) and the highly urbanized Port Adelaide Inner Port (Fig. 2D). In addition, six sites located along the sandy beaches of the metropolitan coast of Adelaide in the St. Vincent Gulf (i.e. Semaphore, Grange, Henley, Glenelg, Brighton and Port Noarlunga; Fig. 1B,C) and in Boston Bay in the Spencer Gulf (Fig. 1D) were used as controls as they are much less impacted by anthropogenic activities. In contrast to the Adelaide Dolphin Sanctuary, the coastal waters of the Adelaide metropolitan area and Boston Bay are only impacted by both recreational non-motorized and motorized vessels and recreational fishing vessels.

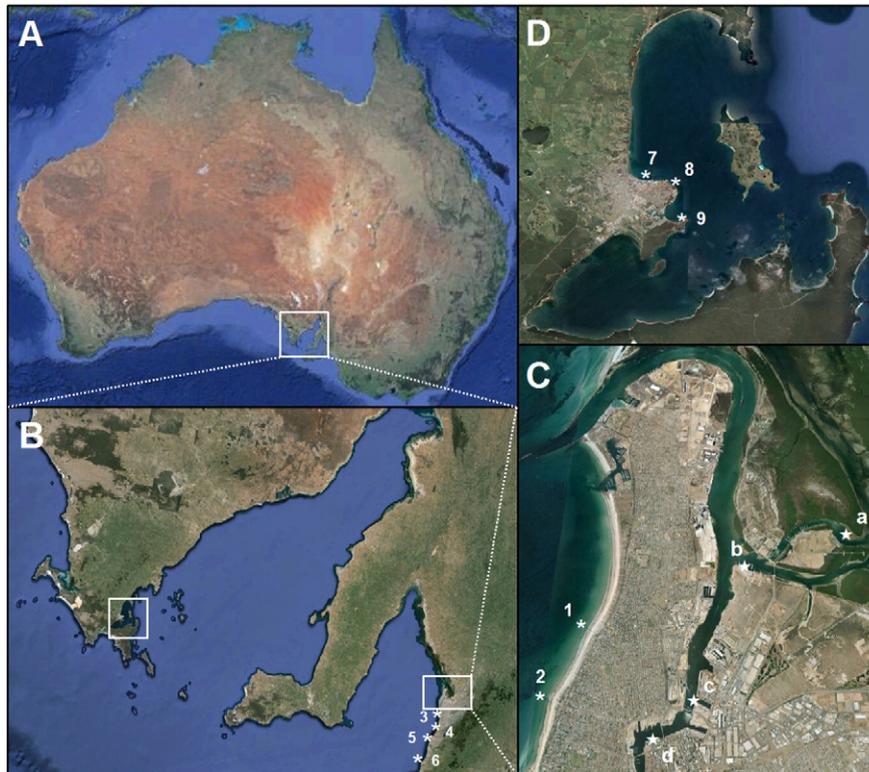


Fig. 1. Locations of the observation sites in South Australia (B), with stars and asterisks respectively indicating the locations impacted by anthropogenic activities within the Port Adelaide River-Barker Inlet Estuary (C) and the control observation sites located both along the metropolitan coast of Adelaide (B,C) and in Boston Bay (D). The numbers indicate the sites investigated along the Adelaide metropolitan coast (1: Semaphore; 2: Grange; 3: Henley; 4: Glenelg; 5: Brighton; 6: Port Noarlunga) and in Boston Bay (7: Port Lincoln Jetty; 8: Lincoln Marine Science Centre (LMSC); 9: Billy Lights Point). The letters indicate the sites investigated within the Port Adelaide River-Barker Inlet Estuary (a: The Angus Inlet at Garden Island; b: North Arms in the Barkers Inlet; c: Dock 2 in Port Adelaide; d: Port Adelaide Inner Port).

2.3. Behavioural observations

Dive duration has previously been shown to increase with increasing boating activity, and it is considered as a typical avoidance behaviour (Nowacek et al., 2001; Janik and Thompson, 1996; Ng and Leung,

2003; Lusseau, 2003b). Here, we specifically investigate the dive durations D_t as the time intervals between two successive surface exhalations, while *Tursiops* sp. individuals were travelling, i.e. moving in a persistent, directional way (Constantine et al., 2003). Dolphin behaviour was observed using binoculars, and dive durations were recorded using

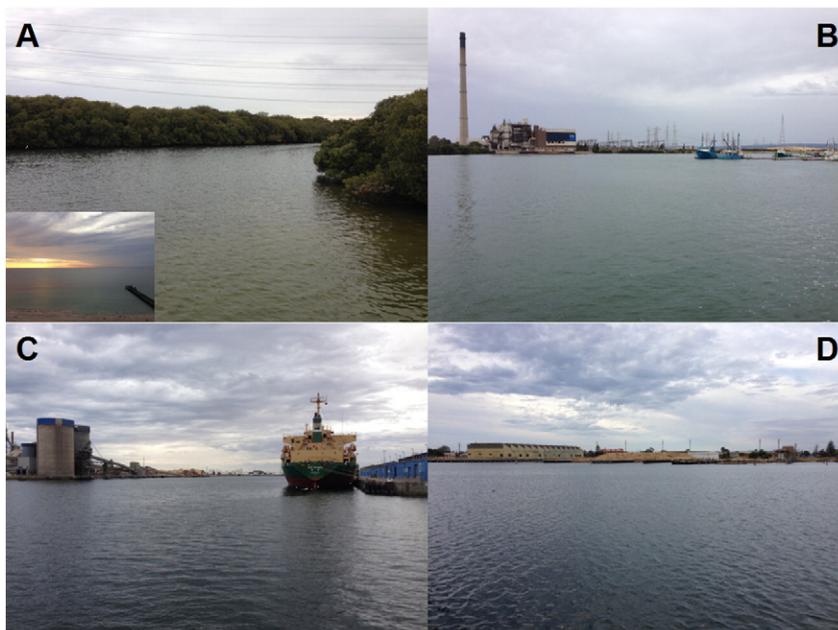


Fig. 2. Details of the study sites within the Port Adelaide River-Barker Inlet Estuary. The Angus Inlet at Garden Island (A), North Arms in the Barkers Inlet (B), Dock 2 in Port Adelaide (C), and the Port Adelaide Inner Port (D). The inset in (A) shows an archetypical example of the environment experienced by dolphins along the metropolitan beaches of Adelaide.

a hand held stopwatch and internally stored until analysis. To avoid any bias related to interactions between individuals, behavioural observations were always limited to solitary individuals. Note that all behavioural observations were conducted in areas with a 4 knot speed restriction to limit the potential bias due to discrepancies in boat speed. Control observations were conducted at each site in the absence of any boat on the water, and the potential for boat interactions was investigated when a motorized vessel was within 100 m from a travelling individual. This distance was specifically chosen as the objective of this work to infer the effect of indirect exposure to boat disturbance on the behavioural complexity of dive duration temporal patterns. Note that this approach fundamentally differs from more standard assessments of the behavioural effect of direct exposure to boat disturbance, for instance when dolphins chase fishing vessels (Jefferson, 2000), flee from motorboats (La Manna et al., 2013) or bow ride (Janik, 2015). Direct signs of boat avoidance or attraction were never observed. All observations were opportunistically conducted from land-based sites from January 2008 to December 2013 in the Port Adelaide River-Barker Inlet Estuary, in December 2002, 2003, 2004, 2005, 2006, 2007, April 2009, 2010 and 2012 in Boston Bay, and from November 2002 to December 2013 along the metropolitan coast of Adelaide (Table 1).

2.4. Behavioural analysis

In a previous study, Seuront and Cribb (2011) introduced a method to quantify the complexity observable from the temporal patterns of diving durations T_D based on the scaling properties of the cumulative probability distribution function (CDF) of dive duration T_D greater than a determined duration t as:

$$P(t \leq T_D) = k_1 t^{-\phi} \tag{1}$$

where k_1 is a constant, and ϕ the scaling exponent describing the distribution. In the presence of a fractal structure, Eq. (1) will manifest itself as a linear behaviour in a log–log plot of $P(t \leq D_t)$ versus t . The exponent ϕ is then estimated as the slope of $P(t \leq D_t)$ versus t in log–log plots, and is expected to decline under stressful conditions; see e.g. Alados et al., 1996; Seuront and Leterme, 2007; Seuront, 2010, 2011, 2015). Note that for the sake of simplicity and ease of implementation, Eq. (1) can be rewritten in simpler terms following (Seuront and Mitchell, 2008):

$$T_D(r) = k_2 r^{-\alpha} \tag{2}$$

where k_2 is a constant, r is the rank of the dive duration $T_D(r)$ – in a series of n dives, the longest dive has a rank $r = 1$ and the shortest a rank

$r = n -$ and α ($\alpha = 1/\phi$) is the slope of the log–log plot of $T_D(r)$ versus r . The exponent α , hereafter referred to as a stress exponent, is expected to increase under stress, which indicates a decrease in behavioural complexity; see MacIntosh (2014) and Seuront (2015) for more details and reviews on this topic.

2.5. Statistical analyses

Given that dive durations T_D were consistently non-normally distributed, both in the absence and the presence of boats (Kolmogorov–Smirnov test, $p < 0.01$), and the relatively low number of the fractal exponent α estimates (Table 1), non-parametric statistics were used throughout this work. More specifically, all pairwise comparisons between observations conducted in the absence and the presence of boats were conducted using the Wilcoxon–Mann–Whitney U -test (referred to as U -test hereafter). Multiple comparisons between sites were conducted using the Kruskal–Wallis test (referred to as KW test hereafter), and a subsequent multiple comparison procedure based on the Tukey test was used to identify distinct groups of measurements (Zar, 1999).

3. Results

3.1. Dive durations

Besides being non-normally distributed, dive durations T_D (Fig. 3) were consistently positively skewed. This result indicates the presence of long dives interspaced among a background of short dives (Fig. 3). Dive durations typically ranged between 6 and 89 s, and no significant differences were observed within a site (U -test, $p > 0.05$) or among sites (KW test, $p > 0.05$) between observations conducted in the absence and presence of boats. In contrast, the variability in dive duration was significantly higher when boats were present ($p < 0.05$) in all of the 13 sites investigated. Note, however, that no significant differences in dive duration variability were found between the three investigated areas, nor between sites within a given area.

3.2. Fractal analysis of dive duration patterns

Log–log plots of dive durations $T_D(r)$ versus their rank r (see Eq. (2)) were consistently very significantly linear ($p < 0.01$) across sites for observations conducted in the absence and presence of boats (Fig. 4). This observation indicates the existence of a power-law behaviour, the signature of an underlying fractal structure. Note that as stressed elsewhere (Seuront and Cribb, 2011), this result is fundamental as the

Table 1

Locations of the observation sites in the three distinct habitats studied in South Australia coastal waters. n and N are respectively the number of observation sessions and the related number of dive durations recorded. T_D is the range of dive durations observed in the absence of boats (control) and when boats were present (boat). LMSC: Lincoln Marine Science Centre.

Location	Latitude	Longitude	n	N	T_D (sec)	
					Control	Boat
Port Adelaide–Barker Inlet Estuary						
Garden Island	34°48'21 S	138°32'38 E	5	554	6–77	6–81
North Arms	34°48'39 S	138°31'22 E	3	466	7–88	6–82
Dock 2	34°50'12 S	138°30'29 E	6	778	8–89	7–79
Inner Port	34°50'37 S	138°29'57 E	7	1112	6–67	6–70
Adelaide metropolitan beaches						
Semaphore	34°50'13 S	138°28'28 E	5	620	6–78	10–89
Grange	34°54'09 S	138°29'08 E	7	978	7–86	11–88
Henley	34°55'11 S	138°29'27 E	8	888	6–89	8–80
Glenelg	34°58'49 S	138°30'29 E	11	1358	11–88	7–81
Brighton	35°01'02 S	130°30'43 E	7	842	12–80	6–70
Port Noarlunga	35°08'57 S	138°27'52 E	8	1484	10–85	7–84
Boston Bay						
Port Lincoln Jetty	34°42'49 S	135°52'12 E	6	596	10–80	8–83
LMSC	34°43'34 S	135°53'08 E	5	424	8–78	7–81
Billy Lights Point	34°44'40 S	135°53'32 E	12	1554	6–83	6–79

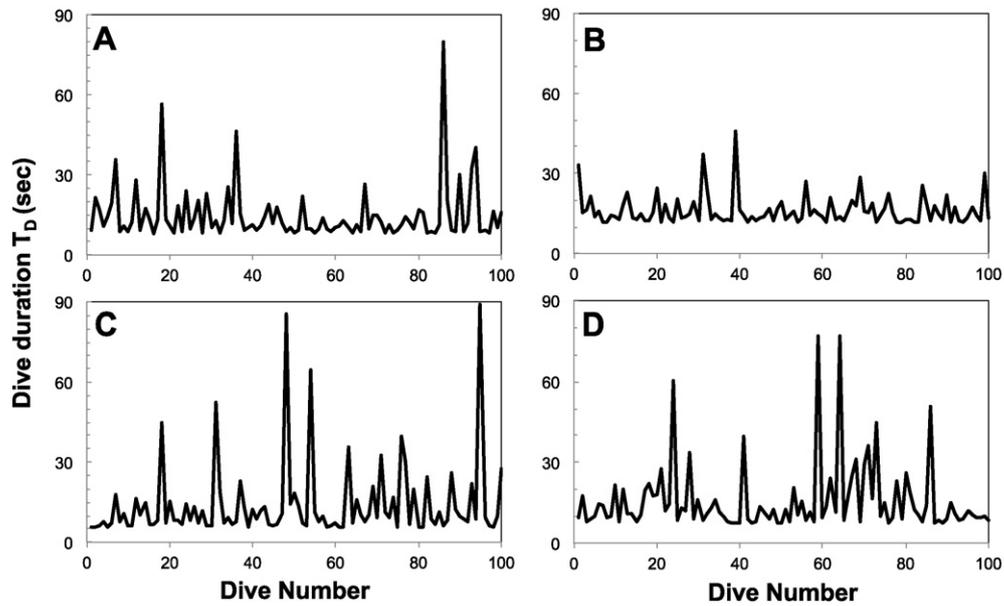


Fig. 3. Examples of dive duration patterns observed in *Tursiops aduncus* in the absence of boats (A,B) and where boats were present (C,D) at Garden Island in the Adelaide Dolphin Sanctuary (A,C) and in Port Noarlunga, the southernmost site investigated along the Adelaide metropolitan coastal waters (B,D).

nested structure of fractal patterns – see e.g. Seuront (2010) for further details – and implies that comparing experiments with different durations using mean values of behavioural metrics (here dive duration) are unlikely to be meaningful, because those mean values intrinsically depend on the duration of the experiment.

The stress exponents α ranged from 0.27 to 0.69 in the absence of boats, and from 0.57 to 0.78 when boats were present. More specifically, dive durations recorded in the absence of boats were characterized by exponents α that were consistently significantly smaller than those obtained when boats were present ($p < 0.01$), except at the two innermost sites (Dock 2 and Inner Port) of the Port Adelaide-Barker Inlet Estuary where no significant differences could be detected ($p > 0.05$; Fig. 5A,B).

This observation indicates a decrease in behavioural complexity in the presence of boats, irrespective of the overall level of anthropogenic activities in *Tursiops* sp. environment.

In the absence of boats, significant differences were found in the stress exponent α between sites within each of the three areas considered ($p < 0.05$). Specifically, in the Adelaide Dolphin Sanctuary, α significantly differed between all sites ($p < 0.05$), with $\alpha_{\text{Garden Island}} < \alpha_{\text{North Arms}} < \alpha_{\text{Dock 2}} < \alpha_{\text{Inner Port}}$ (Fig. 5A). This result suggests a significant decrease in behavioural complexity along a gradient of increasing anthropogenic activities. In the Adelaide metropolitan area, no significant differences were found between the exponents α estimated from Semaphore to Brighton ($p > 0.05$). In Port Noarlunga, α was, however,

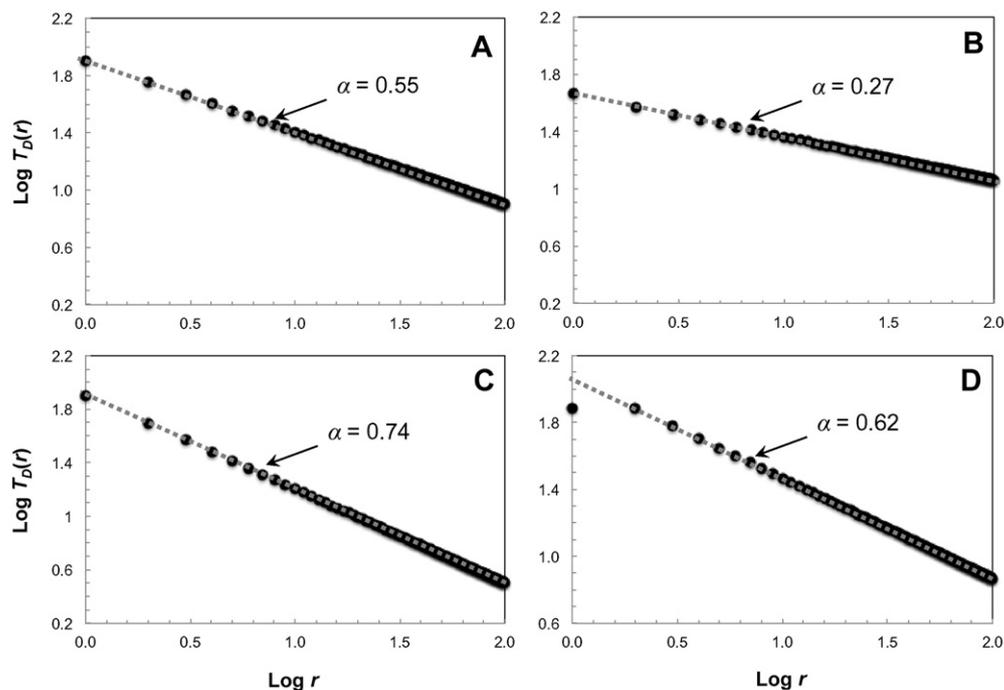


Fig. 4. Log–log plots of dive durations $T_D(r)$ versus their rank r observed in *Tursiops aduncus* in the absence of boats (A,B) and where boats were present (C,D) at Garden Island in the Adelaide Dolphin Sanctuary (A,C) and in Port Noarlunga, the southernmost site investigated along the Adelaide metropolitan coastal waters (B,D). The dashed line is the best linear regression fit of the empirical function $T_D(r) = k_2 r^{-\alpha}$.

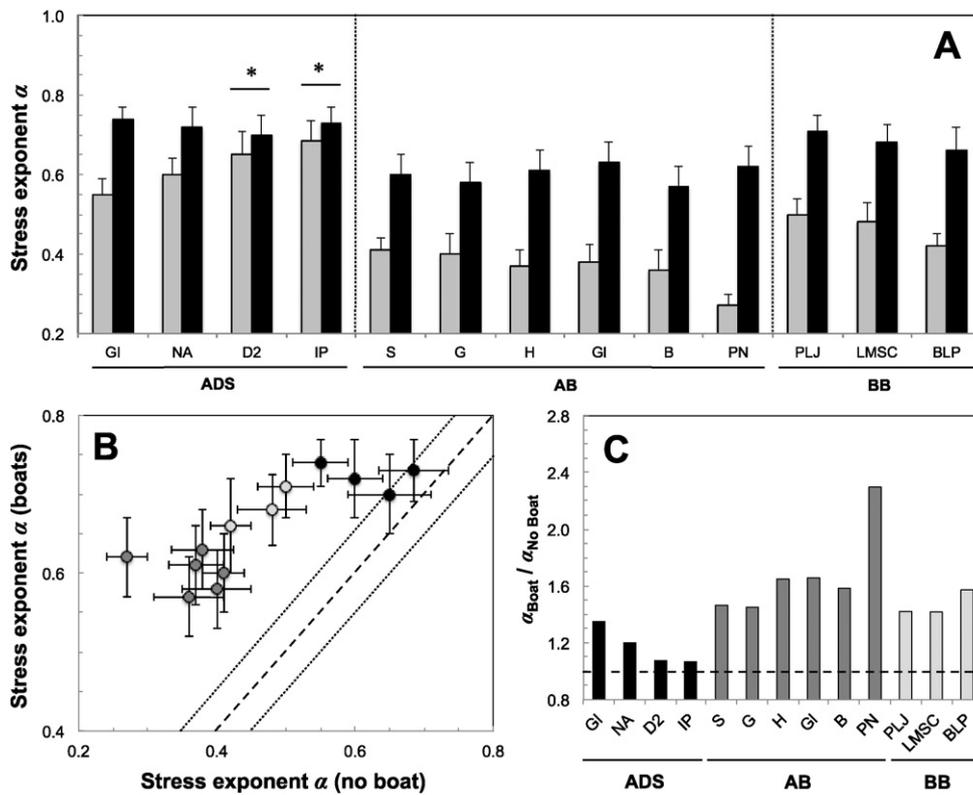


Fig. 5. (A) The stress exponent α estimated in the absence (grey bars) and presence (black bars) of boats at 13 sites scattered over 3 distinct areas (ADS: Adelaide Dolphin Sanctuary, Gulf St. Vincent; AB: Adelaide beaches, Gulf St. Vincent; BB: Boston Bay, Spencer Gulf) across South Australian coastal waters. (B) The stress exponent α estimated in the absence of boat ($\alpha_{No boat}$) and when boats were present (α_{Boat}) in the Adelaide Dolphin Sanctuary (black dots), Boston Bay (light grey dots) and along the metropolitan coast of Adelaide (dark grey dots). (C) The relative difference in behavioural complexity induced by boat presence, estimated as the ratio between the stress exponents estimated in the absence and presence of boats, i.e. $\alpha_{Boat}/\alpha_{No boat}$. The dashed line in (B) is the first bissectric, i.e. $\alpha_{No boat} = \alpha_{Boat}$, and the dotted lines its 95% confidence limits. The dashed line in (C) indicates the case where $\alpha_{Boat}/\alpha_{No boat} = 1$, i.e. $\alpha_{No boat} = \alpha_{Boat}$. The error bars in (B) and (C) are the 95% confidence intervals. GI: Garden Islands; NA: North Arms; D2: Dock 2; IP: Inner Port; S: Semaphore; G: Grange; H: Henley; B: Brighton; PN: Port Noarlunga; PLJ: Port Lincoln Jetty; LMSC: Lincoln Marine Science Centre; BLP: Billy Lights Point.

significantly smaller than anywhere else ($p < 0.05$), suggesting a higher level of complexity in dive duration patterns (Fig. 5A). Finally, in Boston Bay, no significant differences were found in α between Port Lincoln Jetty and Lincoln Marine Science Centre ($p > 0.05$), while $\alpha_{Billy Lights Point}$ was significantly smaller, hence *Tursiops* sp. behaviour was less complex, than at the other two sites (Fig. 5A). Overall, the exponents α significantly differ between all study areas ($p < 0.05$), with $\alpha_{ADS} < \alpha_{Boston Bay} < \alpha_{Adelaide}$ (Fig. 5B).

When boats were present, no significant differences were found in the stress exponent α between sites within each of the three study areas ($p > 0.05$; Fig. 5A). The exponents α significantly differed, however, between study areas ($p < 0.05$), with $\alpha_{Adelaide} < \alpha_{ADS} = \alpha_{Boston Bay}$ (Fig. 5B). Finally, highly significant differences were found between the stress exponents α estimated in the absence and presence of boats at all sites, but Dock 2 and Inner Port in the Adelaide Dolphin Sanctuary (Fig. 5A). These differences result in relative differences between the stress exponents estimated in the absence and presence of boats, i.e. the ratio $\alpha_{Boat}/\alpha_{No boat}$, ranging from 1.07 to 1.35 in the Adelaide Dolphin Sanctuary, from 1.45 to 2.3 in the Adelaide metropolitan area, and from 1.42 to 1.57 in Boston Bay (Fig. 5C).

4. Discussion

4.1. Standard behavioural metrics are not sensitive enough to assess the behavioural effect of exposure to anthropogenic disturbance

The dive durations of *Tursiops* sp. did not significantly differ between our three study areas, nor between sites within each area. This is consistent with previous work that assessed the effect of boat presence and type (kayaks, motorized inflatable boats, powerboats and fishing

boats) on *Tursiops* sp. dive durations in the Adelaide Dolphin Sanctuary (Seuront and Cribb, 2011). Specifically, in this preliminary work no significant differences were found in *Tursiops* sp. dive durations between control observations conducted in the absence of boat and observations conducted when boats were present. As stressed earlier (Seuront and Cribb, 2011), the non-significant differences induced by boat presence and type in the dive durations of *Tursiops* sp. would erroneously indicate the absence of behavioural impact of boat traffic. The related stress induced by boats was hence referred to as pernicious (Seuront and Cribb, 2011) as standard metrics (here dive duration) did not seem sensitive enough to detect any behavioural changes.

In contrast, the present work consistently showed a greater variability in dive durations irrespective of areas and sites, when boats were present. This result is consistent with the increase in dive duration variability observed from control observations to observations conducted in the presence of boats, with a clear increase in variability from kayaks, motorized inflatable boats and powerboats, with fishing boats having a milder effect (Seuront and Cribb, 2011). As suggested earlier (Seuront and Cribb, 2011), this observation is consistent with an increase in inter-individual variability under the punctual acute stress caused by the presence of boats. The lack of differences in variability estimates between sites and areas reported in the present work suggests, however, that dive duration variability is not sensitive enough to infer differences in the behavioural properties of dolphins inhabiting environments that essentially differ in their level of chronic exposure to anthropogenic disturbances.

4.2. On the fractal nature of bottlenose dolphin dive duration patterns

Our results show that the dive duration patterns of *Tursiops* sp. consistently followed a power-law behaviour in the absence of boats and

when boats were present in the three distinct environments investigated here (Fig. 4). This indicates the presence of an underlying fractal structure, which is independent on both the nature of the environment and the level of stress exposure. The presence of fractal fluctuations in biological systems is adaptive because it serves as an organizing principle for highly complex, nonlinear processes and it avoids restricting the functional response of an organism to highly periodic behaviour (Golberger et al., 2000). Fractal fluctuations are also error tolerant, as they allow organisms to cope with stress and unpredictable environments (Goldberger et al., 1990). Over the last two decades, fractal fluctuations have hence been reported in a range of biological systems. These systems include human physiology – e.g. neuronal discharges during sleep (Yamamoto et al., 1986), heart rate (Meesmann et al., 1993), the stride interval of human gait (Hausdorff et al., 1995, 1997), human eye-movement (Yokoyama et al., 1996; Billock et al., 2001), displacement of centre-of-pressure during upright stance (Delignières et al., 2003), lung function (Thamrin and Stern, 2010), welding behaviours underlying haptic perception (Stephen et al., 2010) – but also tree growth (Zeide and Gresham, 1991), respiratory intervals in cats (Kawahara et al., 1989), cat vascular structure (Herman et al., 2001), mammalian social hierarchies (Hill et al., 2008) and the foraging behaviour of a range of aquatic and terrestrial organisms including both invertebrates and vertebrates (see Seuront (2010) for a review) including marine mammals (Laidre et al., 2004). Note, however, that fractal fluctuations are not unique to biological systems, but can virtually be found everywhere (Barnsley, 2014). In particular, fractal properties have been identified in abiotic and biotic systems related to dolphin behaviour such as the topographic complexity of coral and rocky reefs (Bradbury et al., 1984; Le Tourneux and Bourget, 1988), coastline (Simon and Simon, 1995; Chattopadhyay and Kumar, 2007) and sea-floor (Ashalatha, 2007), the spatial patterns of seagrass meadows (Manzanera and Romero, 2000), the architecture of sessile flora and fauna (Burlando et al., 1991; Abraham, 2001), sound attenuation in sediment (Qian, 1996), wave propagation (Dimri and Srivastava, 2007), oil spills (Redondo and Platonov, 2009), marine traffic (Hu et al., 2009; Chen et al., 2009) and the foraging behaviour of fish and fish schools (Tatsuro et al., 2001, Tikhonov et al., 2001, Medvinsky et al., 2002). As a consequence, the distribution of information needed to fulfil basic activities such as foraging and navigation fundamentally spans from relatively short temporal scales (changes in the trajectory of fish and fish schools, or in wave field) and small spatial scales (sound propagation in sediment when scanning for prey) to much longer temporal scales (migratory patterns of prey species) and larger spatial scales (coastline topography). Because behaviour is the product of continuous interactions between the internal state of an organism and the nature of its environment, the fractal properties identified in the present work in the dive duration pattern of *Tursiops* sp. are consistent with the fractally-coloured environment in which they are embedded. In particular, the adoption of fractal strategies is highly adaptive as it allows an organism to efficiently scan a wide range of scales (Sagan, 1994), and optimize key processes such as searching patterns (Sims et al., 2012; Humphries et al., 2012) and predator–prey encounter rates (Seuront and Stanley, 2014).

4.3. Environment-dependent dive duration patterns in bottlenose dolphin

Our results show that in the absence of boats the complexity of *Tursiops* sp. dive duration patterns significantly differs between the three study areas (Fig. 5). Specifically, the stress exponents α were the highest, hence the related behavioural complexity the lowest, in the Adelaide Dolphin Sanctuary (ADS). This is consistent with the overall high level of anthropogenic activities impacting this area, especially compared to the Adelaide metropolitan coast and Boston Bay, and to previous work consistently showing a reduction in behavioural complexity under stressful conditions (Alados and Huffman, 2000, María et al., 2004, Seuront and Cribb, 2011; MacIntosh et al., 2011, 2013). The

observed differences in behavioural complexity may hence be related to an adaptive response to different levels of chronic stress that decrease from the ADS, where the background anthropogenic activities are the highest, to the Adelaide metropolitan coast. Note, however, that the four sites investigated in the ADS also differ from the other ones as their waters are typically embedded in relatively shallow channels or harbour basins with bare sand bottoms. These waters sharply contrast with the deeper open coastal waters characterizing Boston Bay and the metropolitan coast of Adelaide (Fig. 1). It is hence likely that the lower levels of behavioural complexity observed in the Adelaide Dolphin Sanctuary in the absence of boats may also be related to differences in the nature of the environment, as dolphin behaviour has widely been shown to be influenced by environmental features such as water depth, bottom topography and coastal features (Cribb et al., 2015). This hypothesis is consistent with the observed increase in behavioural complexity observed from the ADS to the metropolitan coast of Adelaide (Fig. 5A,B). This increase in behavioural complexity hence matches the increase in foraging space, the variety of available environments (typically a patchwork of bare sand and seagrass meadows) and the related resources occurring in Boston Bay and along the metropolitan coast of Adelaide, and suggests a potential environment-dependence of the complexity of *Tursiops* sp. dive duration patterns.

4.4. Environment-dependent behavioural response of bottlenose dolphin to pernicious anthropogenic stress

Fractal analysis has early been introduced in the study of human physiology to distinguish between systems operating in normal or pathological states (Ivanov et al., 1999; Mishima et al., 1999). The complexity of a range of biological systems has hence been shown to decrease under stressful conditions. For instance, beat intervals in healthy subjects have more complex fluctuations than patients with severe cardiac disease (Ivanov et al., 1999). Similarly, the geometry of the lung terminal airspace branching architecture is more complex in normal subjects than in patients with chronic obstructive pulmonary disease (Mishima et al., 1999). Fractal analysis is also increasingly acknowledged as a novel analytical tool in the field of behavioural ecology (Asher et al., 2009), especially because fractal analysis has the desirable properties to be independent of measurement scale and to be very sensitive to even subtle behavioural changes that may be undetectable to other behavioural variables (Coughlin et al., 1992; Rutherford et al., 2004). Besides, because stressed (i.e. diseased and parasited) animals typically reduce the complexity of their behavioural display (Alados et al., 1996), fractal analysis has been extensively used as a non-invasive assessment of the general health of wild and captive animals (Rutherford et al., 2004; MacIntosh, 2014; Seuront, 2015).

The presence of boats consistently significantly decreases the behavioural complexity of *Tursiops* sp. across areas and sites, except at Dock 2 and Inner Port in the Adelaide Dolphin Sanctuary (Fig. 5A). This observation is consistent with the generally expected decrease in behavioural complexity under stressful conditions. This observation also suggests that there may exist a threshold of chronic anthropogenic disturbance above which the occurrence of more acute stress (here boat presence) may not induce further decrease in behavioural complexity. This hypothesis is consistent with the high level of anthropogenic pressure occurring at Dock 2 and Inner Port, where water bodies are entirely contained by concrete walls, crossed by a series of bridges constantly holding heavy traffic, and in direct proximity of a range of anthropogenic disturbances related to urban development (both residential and industrial estates have been constantly growing in this area over the last 10 years), recreational activities such as dolphin-watch tours, yachting and fishing. Finally, even in the absence of significant differences in the stress exponents α observed along the metropolitan coast of Adelaide and in Boston Bay (Fig. 5A,B), the clear increase in the relative difference in behavioural complexity induced by boat presence, i.e. the ratio $\alpha_{\text{Boat}}/\alpha_{\text{No boat}}$ (Fig. 5C), suggests that *Tursiops* sp. is much more

sensitive to boat disturbance along the metropolitan coast of Adelaide (especially in Port Noarlunga) and Boston Bay than in the Adelaide Dolphin Sanctuary.

4.5. Fractal analysis of diving patterns as a tool to identify distinct bottlenose dolphin populations?

The clear differences in behavioural complexity exhibited by bottlenose dolphins may also be related to different dolphin populations or species. If *Tursiops* sp. is a known resident in the Adelaide Dolphin Sanctuary (Cribb et al., 2008; Kemper et al., 2008, Steiner and Bossley, 2008), there is still no information on the biogeography of this species in South Australian coastal waters and on potential connectivity patterns between the Spencer Gulf and the Gulf St. Vincent. A recent photo-identification survey conducted over the last 10 years in both the Adelaide Dolphin Sanctuary and at the southernmost part of Gulf St. Vincent showed no evidence of latitudinal connectivity in Gulf St. Vincent (Cribb, 2016). Under the hypothesis that there is similarly no longitudinal connectivity between bottlenose dolphins populating Gulf St. Vincent (hence occurring along the metropolitan coast of Adelaide) and the Spencer Gulf, we suggest that distinct populations evolving in different environments may indeed be characterized by distinct dive duration patterns. Note that this hypothesis is supported by a study using data from mitochondrial DNA control region sequences and 6 microsatellite loci showing marked genetic differentiation and low migration between dolphins of Spencer Gulf and dolphins inhabiting coastal areas west of the gulf in the Great Australian Bight (Bilgmann et al., 2007). Further work is still needed, however, to unambiguously assess the level of relatedness and connectivity patterns of *Tursiops* sp. in South Australian waters – in particular because the taxonomy of the species in South Australian waters is still debatable, with genetic evidence that coastal bottlenose dolphins from South Australia, Victoria and Tasmania are evolutionarily distinct from the 2 other recognised bottlenose dolphin species (Charlton et al., 2006) – and the resolution of this issue goes far beyond the scope of the present work.

4.6. On the importance of assessing pernicious stress for dolphin conservation

Chronic exposure to even low levels of stress has implications for energy balance, physiological conditions and vital rates (New et al., 2013), and is likely to induce long-term consequences at the population level (Lusseau, 2004; Bejder et al., 2006). This is a critical issue for dolphin welfare as well as the related development and implementation of effective mitigation and management strategies because the habituation to boat traffic reported for bottlenose dolphins (Sini et al., 2005) did not imply the absence of stress, hence may be thought as a pernicious threat as suggested in a preliminary study (Seuront and Cribb, 2011). As such, it is stressed that the assessment of the potential impacts of boat traffic, hence the identification of potential long-term ramifications, may require more efficient ways to infer the behavioural stress of dolphins inhabiting anthropogenically-impacted coastal areas.

Specifically, bottlenose dolphins occurring in environments with less anthropogenic pressure exhibited a higher behavioural complexity. This complexity consistently decreased both within and between environments with increasing anthropogenic pressure. Our results further showed that the behaviour of *Tursiops* sp. occurring along the metropolitan coast of Adelaide and in Boston Bay was more affected to the boat presence than those living in the Adelaide Dolphin Sanctuary (ADS). This observation may indicate that bottlenose dolphins are more susceptible to be affected by the development of human activities than in Boston Bay and the ADS. In turn, this also suggests that their baseline behavioural repertoire is richer, hence allow them more behavioural flexibility to respond to disturbances, than in dolphins living in less pristine habitats. Similarly, the relatively moderate differences in behavioural complexity observed in the ADS in the absence of boat and when

boats were present does not necessarily imply a habituation to boats as observed elsewhere (Sini et al., 2005). This may indicate instead that these dolphins have a limited ability to modify their behaviour in response to boat traffic in particular and to anthropogenic disturbance in general.

5. Conclusion

This work illustrates how standard behavioural metrics failed to identify changes in the patterns of dive durations of bottlenose dolphins occurring in distinct environments under different levels of exposure to anthropogenic chronic and acute disturbances. In contrast, the fractal methods used here, beyond being very easy to implement, provides an objective, quantitative and non-intrusive way to quantify subtle behavioural changes. This method is then suggested as a potential powerful tool to assess both absolute and relative behavioural changes in bottlenose dolphins. It may hence provide baseline information on the actual level of stress and related behavioural flexibility bottlenose dolphins – and ultimately any marine mammal – might have to respond to anthropogenic disturbance, an absolute prerequisite to the development of conservation and management strategies.

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