# **Marine Mammal Science**



MARINE MAMMAL SCIENCE, \*\*(\*): \*\*\*\_\*\*\* (\*\*\* 2017) © 2017 Society for Marine Mammalogy DOI: 10.1111/mms.12399

# Fractal analysis provides new insights into the complexity of marine mammal behavior: A review, two methods, their application to diving and surfacing patterns, and their relevance to marine mammal welfare assessment

LAURENT SEURONT,<sup>1</sup> Centre National de la Recheche Scientifique, CNRS UMR 8187 LOG, Laboratoire d'Océanologie et de Géosciences, 28 avenue Foch, 62930 Wimereux, France; NARDI CRIBB, School of Biological Sciences, Flinders University, GPO Box 2100, Adelaide, South Australia 5001, Australia.

# Abstract

Fractals have been applied to describe the complexity of behavioral displays in a range of organisms. Recent work suggests that they may represent a promising tool in the quantification of subtle behavioral responses in marine mammals under chronic exposure to disturbance. This paper aims at introducing the still seldom used fractals to the broader community of marine mammal scientists. We first briefly rehearse some of the fundamental principles behind fractal theory and review the previous uses of fractals in marine mammal science. We subsequently introduce two methods that may be used to assess the complexity of marine mammal diving patterns, and we apply them to the temporal dynamics of the diving patterns of killer whales in the presence and absence of sea kayaks, the sequential behavior of harbor and gray seals in environments with distinct levels of anthropogenic influence, and southern right whales with and without calves. We discuss the ecological relevance of identifying fractal properties in marine mammal behavior, and the potential strength of the fractal behavioral parameters in comparison to more standard behavioral metrics. We finally briefly address the relevance fractal methods may have for the design and implementation of management and conservation strategies.

Key words: behavior, stress, disturbance, fractals, conservation and management strategies.

The potential impact anthropogenic activities—including those related to research and whale watching—may have on marine mammals is an area of ever growing interest, (e.g., Stamation et al. 2010, Ellison et al. 2012). These activities are a potential source of both acute and chronic stress, in both offshore and inshore waters (e.g., Balmer et al. 2013, Rossman et al. 2013, Baş et al. 2015, Monnahan et al. 2015). More specifically, coastal ecosystems are impacted by a multitude of anthropogenic disturbances, including commercial shipping and the

<sup>&</sup>lt;sup>1</sup>Corresponding author (e-mail: laurent.seuront@cnrs.fr).

subsequent noise (Hildebrand 2009), pollution (Thompson et al. 2004, 2009), habitat alteration (Waycott et al. 2009), deployment of coastal defense structures (Airoldi et al. 2005), overfishing (Greer et al. 2014), and climate disruption (Firth and Hawkins 2011, Glavovic and Smith 2014). All these disturbances have critical implications in terms of conservation of marine mammals (see Wartzok et al. 2003, Trathan et al. 2014) because even short-term behavioral responses to disturbance could have long-term consequences at both the individual and population levels (Bejder et al. 2006, Lusseau and Bejder 2007). Besides, these disturbances have widely been shown to impact a range of marine mammal species (Lessage et al. 1999; Williams et al. 2002a, b, 2006; Scheidat et al. 2004; Patenaude et al. 2006; Hodgson and Marsh 2007; Brandt et al. 2011; Andersen et al. 2012; Thompson et al. 2013; Isojunno and Miller 2015; Mathews et al. 2016). These issues are particularly relevant for marine mammals inhabiting urbanized coastal areas that have increasingly been exposed to a variety of potential human disturbances (Kelly et al. 2004), including the increase in the occurrence of recreational motorized vessels (Buckstaff 2006), recreational fishing (Powell and Wells 2010), dolphin watching (Mustika et al. 2015) and swimwith-dolphin tourism (Peters et al. 2013) over the last two decades (McCarty 2004, O'Connor et al. 2009).

The increase and diversification of anthropogenic activities have raised concerns about both the effects of anthropogenic noise and the physical presence of boats, as well as their speed and type. For instance, slow-moving or immobile vessels do not cause immediate stress on the dolphin community, while fast moving boats disrupt behavior and social life (Lusseau 2005, Matson et al. 2005, Lemon et al. 2006) and may elicit escape behaviors (La Manna et al. 2013). Dolphins have been reported to chase fishing vessels (Parsons 1998, Jefferson 2000), flee from motorboats (La Manna et al. 2013), and change their acoustic behavior to compensate for the masking noise in the presence of trawlers (La Manna et al. 2013). The responses of dolphins to boats and related noise are, however, not straightforward as it is hard to disentangle the combined effects of noise and the physical presence of boats (Pirotta et al. 2013). For instance, boat noise can mask acoustic cues (Clark et al. 2009), affect the behavior of both the dolphins (Pirotta et al. 2013) and their prey (Popper et al. 2003), and cause stress (Wright et al. 2007). In turn, the physical presence of boats may disrupt activity patterns, particularly when boats seek direct interactions (e.g., dolphin watching and swim-with-dolphin). In such instances, dolphins essentially respond through avoidance and other anti-predatory strategies such as increase in swimming speed, decrease in resting behavior, decreased interanimal distance, increased breathing synchrony, and longer dive durations (e.g., Nowacek et al. 2001; Lusseau 2003a, b; Constantine et al. 2004; Lemon et al. 2006, Williams et al. 2006). Note, however, that the presence of boats and their movement pattern may also affect dolphins, irrespective of the noise that they produce, as suggested by kayaks having significant impacts on both bottlenose dolphin Tursiops truncatus and killer whale Orcinus orca activity (Lusseau 2006, Williams et al. 2011). Besides, the observed responses depend on quality of a foraging patch, social context, condition of an individual and its previous encounters with specific stressors (Lemon et al. 2006; Lusseau 2003b, 2004; Sini et al. 2005). Individuals might hence decide to tolerate disturbance rather than flee from exposed areas (Bejder et al. 2009); this is likely to be the case where dolphins are known residents. Under this type of chronic exposure to disturbance, it has been suggested

that dolphins may exhibit changes in activity budgets (Gill et al. 2001; Bejder et al. 2009). This is consistent with a recent study (Seuront and Cribb 2011) based on the analysis of more than 6,000 dive durations of the Indo-Pacific bottlenose dolphin, Tursiops aduncus, recorded when they were traveling-sensu Constantine et al. (2004), *i.e.*, moving in a persistent, directional way—in a highly urbanized coastal environment, the Port Adelaide River-Barker Inlet Estuary (South Australia). That study showed that dive duration was not significantly affected by either boat presence or boat type. In contrast, the complexity (as estimated using a fractal approach) of the temporal dynamics of dive duration obtained in the absence of boat traffic and under different conditions of boat interferences was affected by boat presence and boat type (Seuront and Cribb 2011). These results-in agreement with behavioral observations conducted on organisms ranging from minute invertebrates to large vertebrates, including humans (Coughlin et al. 1992; Motohashi et al. 1993; Rutherford et al. 2003, 2004; Sturmberg and West 2013; MacIntosh 2014; Seuront 2015)-suggest that standard behavioral metrics (e.g., the mean duration of a given behavior, or the time allocated to different behavioral sequences), and the related statistical inferences of mean duration or frequency may not be sensitive enough to detect subtle behavioral changes, and that the behavioral 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.

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. Indeed, the habituation to boat traffic reported for bottlenose dolphins (Sini et al. 2005) did not imply the absence of stress, which may simply be undetectable using standard behavioral metrics, hence may be thought a pernicious threat (Seuront and Cribb 2011, Cribb and Seuront 2016). The assessment of the potential impacts of boat traffic, hence the identification of potential long-term ramifications, requires an objective quantitative assessment of the behavioral complexity as well as the related contextdependent changes in behavioral complexity of dolphins inhabiting anthropogenically impacted coastal areas. However, to our knowledge, behavioral studies in marine mammal ecology still heavily rely on standard behavioral metrics, e.g., the mean duration of a given behavior and the time allocated to different behavioral sequences. This is particularly problematic as those metrics are much less sensitive to changes in behavioral complexity than fractal-based metrics (e.g., Coughlin et al. 1992; Motohashi et al. 1993; Rutherford et al. 2003, 2004; Seuront and Cribb 2011; Seuront 2015: Cribb and Seuront 2016).

In this context, the objectives of this paper are (1) to briefly rehearse some of the fundamental principles behind fractal theory, (2) to review the still seldom uses of fractals in marine mammal science, (3) to introduce two methods that may be conveniently used to assess both the complexity of marine mammal diving patterns and context-dependent changes in behavioral complexity, and (4) illustrate them on original data sets related to a range of marine mammals with distinct behavioral strategies, *i.e.*, the harbor and gray seals (*Phoca vitulina* and *Halichoerus grypus*), the southern right whale, *Eubalaena glacialis*, and the killer whale.

#### FRACTALS IN MARINE MAMMAL SCIENCE

#### What are Fractals?

A fractal is "a rough or fragmented geometric shape that can be split into parts, each of which is (at least approximately) a reduced-size copy of the whole" (Mandelbrot 1977). This property is called *scale invariance*, and means that the observed structure remains unchanged under magnification or contraction. This scale invariance can be observed in two distinct, though conceptually similar, forms referred to as self-similarity and self-affinity.

Self-similarity has originally been illustrated using theoretical objects that were first described in the late 19th and early 20th centuries such as the Cantor set, the Koch snowflake, the Sierpinski carpet and gasket, and the box-fractal (Fig. 1), and sometimes coined "mathematical monsters" (Gordon 2000, Edgar 2004). The fundamental common feature of all these objects-beyond the fact that each smaller portion is a reduced version of the whole—lies in the fact that they are all created using simple iterative processes. Note that these iterative processes also lead to more realistic constructions, such as the fractal tree shown in Figure 2A. There is, however, a fundamental difference between the iterative processes leading to nonfractal and fractal objects. Specifically, nonfractal forms such as points, lines, surfaces, and volumes can be described by Euclidean dimensions of 0, 1, 2, and 3. In practice this means that if one reduces a line, a square, and a cube by a factor k, the number of pieces Nneeded to reproduce the original is linked to the dimension d as  $d = \log N / \log k$ . This relation holds true<sup>2</sup> whatever the value of k. In contrast, the dimension of fractal objects is fundamentally dependent of the reduction factor k applied between two successive steps of the iteration process. For instance, at each step of the construction of the Cantor set (Fig. 1a) and the Koch snowflake described (Fig. 1b), there are respectively two and four elements that are three times smaller than the original one. The fractal dimension D is subsequently defined as  $D = \log 2/\log 3 = 0.631$  and D = $\log 4/\log 3 = 1.2618$ , respectively.

More generally, many natural phenomena have a nested irregularity and may look similarly complex under different resolutions. For instance, the complexity of coastlines will repeatedly become evident if a section of a coastline is studied in finer and finer detail, ultimately until the outlines of individual boulders, rocks, and grains of silt and sand are being traced. A fundamental consequence of this nested structure is that the length of a coastline, or the surface of any two-dimensional fractal structure, does not converge to a fixed value, but keeps increasing, theoretically without any upper limit. As early formalized in the seminal paper titled *How long is the coast of Britain? Statistical self-similarity and fractional dimensions* (Mandelbrot 1967), coastlines do not have a length; instead, they have fractal extents, and common statements such as "the length of coastline of Great Britain plus its principal islands is about 19,491 miles" (Ordnance Survey 2016) are fundamentally flawed (Seuront 2015). The relationship between the length  $L_{\delta}$  of a complex line and the observation scale  $\delta$  can be generally written as

<sup>&</sup>lt;sup>2</sup>Applying reduction factors of 2 and 3 to a cube respectively leads to 8 and 27 cubes 2 and 3 times smaller than the original one, but a constant dimension *d*, that is d = 3; specifically  $d = \log 8/\log 2 = 3$  and  $d = \log 27/\log 3 = 3$  in the former and later cases.



*Figure 1.* Four theoretical fractal objects illustrated the concept of self-similarity. The common feature of all these objects is that they are generated using simple iterative processes. The Cantor set (A) is created by simply removing the middle third of each line recursively; hence from one step of the construction to the next the iterative process leads to two elements three times smaller than the original one, hence the fractal dimension is defined as  $D = \log 2/\log 3 = 0.631$ . The construction of the Koch snowflake (B) necessitates to replace each side of an equilateral triangle by four line segments three times smaller with the middle one forming a baseless equilateral triangle, leading the fractal dimension  $D = \log 4/\log 3 = 1.2618$ . The Sierpinski gasket (C) and carpet (D) may seem more complicated, but are constructed following a similar principle. An equilateral triangle and a square are divided into four equilateral triangles and nine squares that are respectively two- and three-times smaller than the original one. The center triangle and square are subsequently removed, and the iterative procedure can be repeated *ad infinitum*. The related fractal dimensions are  $D = \log 3/\log 2 = 1.585$  and  $D = \log 8/\log 3 = 1.893$  for the Sierpinski gasket and carpet, respectively.

$$L_{\delta} = C \delta^{(1-D)},\tag{1}$$

where *C* is a constant and *D* the fractal dimension. For example, the coastline of the United Kingdom has a fractal dimension of 1.27 (Mandelbrot 1967), and a typical cloud outline has a fractal dimension D = 1.35 (Lesmoir-Gordon *et al.* 2000).



*Figure 2.* (A) Illustration of the first five successive steps of the iterative process leading to a self-similar fractal tree. At each step i of the process, each terminal branch of the tree is replaced by a rescaled version of the original tree. Specifically, here the scale ratio between two successive steps is  $\frac{1}{3}$ , *i.e.*, between any two steps of the iterative process, each branch is replaced by a copy of the whole tree three times smaller than the original one. (B) Illustration of the concept of self-affinity based on simulated temporal fluctuations of a given quantity. This kind of fractality is not geometrical, but statistical in nature. The successive magnifications of the original curve (from top to bottom) lead to two statistically identical reproductions magnified by factors 10 and 100.

Self-affinity characterizes an object that may be written as a union of rescaled copies of itself, where the rescaling is anisotropic, that is dependent on the direction. A typical example of self-affinity is given by the temporal fluctuations of a given quantity (Fig. 2B); it looks rough, like the boundary of a fractal object, but with the two axes corresponding to physical quantities that are fundamentally different. This type of fractality is not geometrical, but statistical in nature. Specifically, the fluctuations visible in Figure 2A are fractal as the statistics of the entire time series is repeated in every interval of the time series. Consider the red section of the top curve in Figure 2B and its magnified version in the center curve. These two curves look very similar, and the same can be said from the center curve and the one in the lower panel. When the magnified regions of a time series reproduce the statistics of the original time series, the statistics are fractal. Note that the visual similarity is not representative of the zoomed in portions being exact copies of the original, but in having similar statistical properties. The fractal nature of the distribution manifests itself as a scaling property in the statistical moments and probability density as discussed below.

Generally put, the fractal dimension of any pattern or process measures the degree to which it fills the available space, e.g., see Mandelbrot (1967, 1977, 1983). Fractals dimensions-whether they are considered in a self-similar or self-affine contexthave also more generally been used as a measure of the complexity of natural patterns and processes observed in research fields ranging from landscape ecology to physiology, health, and behavior (e.g., Alados et al. 1996; Alados and Huffman 2000; Commito and Rusignuolo 2000; María et al. 2004; Rutherford et al. 2006; West et al. 2008; Matias et al. 2010; West 2010; Seuront 2010, 2015; Meager et al. 2011; MacIntosh et al. 2011, 2013; Sturmberg and West 2013; MacIntosh 2014). From the aforementioned statements, it implicitly comes that the higher the fractal dimension, the higher the complexity. The geometry of a line (D = 1) is hence the simplest instance of an object embedded in a two-dimensional space, and the complexity of any broken line increases as  $D \rightarrow 2$ . Note that the term "complexity" is here specifically used to describe the level of fractal structure perceptible in a behavioral pattern. It does not provide, however, any information about the complexity of the underlying processes. For instance, the Sierpinski carpet and gasket have different fractal dimensions, hence different fractal complexity, but the generating mechanisms have arguably the same level of complexity.

## Fractals in Marine Mammal Science

The Web of Science (accessed 12 December 2016) returned 25,563 and 60,300 articles, respectively containing the word *fractal* in their title and topic between  $1967^3$  and 2016. Fractals are hence a prolific topic, and have found applications in nearly all scientific areas, including terrestrial and aquatic ecology (Falconer 1985, 1993; Frontier 1987; Feder 1988; Hasting and Sugihara 1993; Kenkel and Walker 1993; Seuront 2010; Barnsley 2014). Fractals have been successfully applied to a wide range of marine biology and ecology topics, including species diversity, the topographic complexity of coral reefs and rocky shores, the morphology of aquatic fauna and flora, the geometric complexity and allometric properties of marine snow, the temporal pattern of dissolved inorganic nutrients, phytoplankton and zooplankton, the spatial distribution of intertidal and pelagic communities, and the behavior of organisms ranging from microbes to large vertebrates (Seuront 2010, 2015; Viswanathan et al. 2011; MacIntosh 2014). In contrast, the concept of fractals and the related tools have still barely been used in marine mammal science. For instance, the Web of Science (accessed 25 April 2016) returned two and seven papers that include the words *fractal* and *whale*, respectively in their title and topic, and one and three papers that include the words *fractal* and *dolphin*, respectively in their title and topic between 1967 and 2016. Fractal approaches have nevertheless been used to assess different aspects of the biology and ecology of a range of marine mammals, including polar bears, Ursus maritimus (Ferguson et al. 1998, Andersen et al. 2008, Wang et al. 2012, Yang and Baleanu 2013), whales (Mouillot and Viale 2001, Havsteen 2002,

<sup>&</sup>lt;sup>3</sup>When Mandelbrot, the father of fractals, defined in his seminal work, entitled *How long is the coast of Britain? Statistical self-similarity and fractional dimensions* (Mandelbrot 1967), what will formally be coined *fractal geometry* a decade later (Mandelbrot 1977, 1983).

Laidre *et al.* 2004, Santhaseelan and Asari 2013), dolphins (Hill *et al.* 2008, Seuront and Cribb 2011) and seals (Austin *et al.* 2004).

Fractals have been used through Equation (1) to assess movement complexity and space use in polar bear (Ferguson et al. 1998, Andersen et al. 2008), fin whale, Balaenoptera physalus (Mouillot and Viale 2001) and narwhal, Monodon monoceros (Laidre et al. 2004). Specifically, Ferguson et al. (1998) and Andersen et al. (2008) found fractal dimensions ranging from 1.20 to 1.96 in movement patterns of polar bears. The movement patterns of polar bears ranging in the Canadian Arctic were characterized by fractal dimensions ranging between 1.29 and 1.96 (Ferguson et al. 1998). These dimensions were significantly correlated with the fractal dimension of sea ice, suggesting a possible mechanism linking geography and population dynamics. Specifically, polar bears ranging within regions consisting mostly of sea ice showed less irregular and less tortuous patterns (low fractal dimension), while bears moving in areas characterized by greater irregularity in the spatial structure of sea ice responded with a greater irregularity in their movement patterns. The fractal dimensions of the movement pathways of two Svalbard polar bears were D = 1.20 and 1.31 (Andersen et al. 2008). The related relatively low tortuosity of movements was explained by the tendency of the movement to be long range and directional as Svalbard polar bears tend to make north-south directed migrations during the year, following the sea ice. Wang et al. (2012) and Yang and Baleanu (2013) also used fractal-based methods to characterize heat conduction in polar bear hairs.

The trajectory of a single B. physalus tracked in the Mediterranean Sea was characterized by a low fractal dimension (D = 1.03); this nearly linear behavior was suggested to be a response to the aggregated distribution of their zooplankton prey (Mouillot and Viale 2001). Laidre et al. (2004) went further through the analysis of the trajectories of 20 narwhals obtained from satellite tracking in the eastern Canadian high Arctic and West Greenland and subsequently divided into three seasons (summer, fall, and winter). These authors found fractal dimension that significantly differ between seasons. Fractal dimensions were the highest during the summer (D = $1.61 \pm 0.04$ ) and winter ( $D = 1.69 \pm 0.06$ ) when narwhals made convoluted movements that suggest searching efforts in localized areas. In contrast, fractal dimensions were the lowest during fall ( $D = 1.34 \pm 0.03$ ) when whales were migrating south ahead of the forming sea ice, suggesting they do not intensively forage on patchy resources until they arrive at summer or winter sites. Noticeably, no significant effects related to size category or sex was found on fractal dimension by season, while significant differences between the fractal dimensions on two separate wintering grounds in Baffin Bay indicate differential movement patterns in response to the dynamics of sea ice. Havsteen (2002) used fractal methods to show that gas transport through sperm whale (*Physeter macrocephalus*) myoglobin significantly diverge from, hence is much more efficient then, simple linear diffusion.

Austin *et al.* (2004) used an alternative approach to assess the movements of 52 gray seals off Sable Island, Canada. These authors investigated if gray seal movements followed a Lévy flight. A Lévy flight is *stricto sensu* a random walk for which each movement direction and step are respectively independently drawn from a uniform distribution and a probability distribution that has a heavy power law tail (ben-Avraham and Havlin 2000); a power law tail meaning that very large steps occur more frequently than in the case of a Normal distribution. The resulting pattern is of clusters of short steps that are connected by rare long steps, in contrast to the classical Brownian motion (Fig. 3). The signature of a Lévy flight is when the probability distribution of move lengths *l* fits a Lévy distribution described as  $P(l) = al^{-\mu}$ , where *a* is a



*Figure 3.* Two-dimensional simulations of a Lévy flight (black line) and a Brownian random walk (gray line) of identical total length of 1,000 units. Note the efficiency of the Lévy flight to explore the available space through rare long steps joining clusters of short steps, when a Brownian walker returns many times to the same location, resulting in a less efficient search strategy.

constant and  $\mu$  ( $1 \le \mu \le 3$ ) is a characteristic exponent; see Reynolds and Rhodes (2009), Viswanathan *et al.* (2011), and Méndez *et al.* (2014) for reviews. Only 8 of the 52 seals had frequency distributions of movement lengths that fit the power law distribution described above; this led the authors to state that food patches used by most seals are not randomly distributed. Note that the results of this study have been recently invalidated on the ground of the inaccuracy and problematic methods used to estimate  $\mu$  (Edwards 2011). The Lévy flight approach has, nevertheless, been increasingly popular (Sims *et al.* 2008, 2012, 2014; Humphries *et al.* 2010, 2012; Viswanathan *et al.* 2011; Reynolds 2015*a, b*)—probably motivated by the Lévy flight foraging hypothesis, which under certain conditions predicts that predators should adopt Lévy search strategies for locating sparsely and randomly distributed prey and Brownian movement where prey is abundant and probably more predictable (Viswanathan *et al.* 1999)—though highly controversial; see *e.g.*, Reynolds and Rhodes (2009), Pyke (2015) and Reynolds (2015*a, b*) for comprehensive reviews and critical assessments.

Fractals have also been used to describe (1) the relationship between size, function, metabolism, and life expectancy for animals that vary in size from mouse to blue whale, *Balaenoptera musculus* (Kuikka 2003), (2) the universal relation for the PR interval (*i.e.*, the time taken by an electrical impulse generated in the sinoatrial node to propagate from atria to ventricles) of the electrocardiogram of mammals (Noujaim *et al.* 2004, Mazgalev 2005), and (3) the relationship between the complexity of hierarchical mammalian society including in the killer whale (Hill *et al.* 2008). More recently, fractals were used as a tool to assess the stress induced in the Indo-Pacific bottlenose dolphin by boat presence and type from the fractal properties of breathing rhythms (Seuront and Cribb 2011) and as a shape analysis tool to detect whale blows from their infrared signature (Santhaseelan *et al.* 2013).

# Fractals as a Stress Assessment Tool

The behavior of a variety of organisms ranging from insects to mammals (including humans) has been shown to be inherently very complex, and there are no simple a priori models to explain spatial patterns and/or temporal structure. This complexity is generally considered as biologically advantageous. For instance, the complex, folded surface area available for absorption in the intestine and the ramification of blood vessels, bile ducts, and bronchiae lead to a higher efficiency in the transport of food and oxygen in humans, the complexity of neuronal connections control the capabilities and synaptic efficiency with which signals are transmitted and processed, and recurvation in bone sutures imparts structural strength (West et al. 2008, West 2010, Sturmberg and West 2013). This complexity is also believed to be biologically adaptive as it avoids restricting the functional response of an organism to highly periodic behavior and it is error tolerant, allowing organisms to cope with both intrinsic and extrinsic stressors (Goldberger et al. 1990, 2000). Specifically, fractal analysis has been introduced in the study of human physiology to distinguish between systems operating in normal vs. pathological states (Goldberger and West 1987, Goldberger et al. 1990); see also Sturmber and West (2013) for a recent review of the applications of fractals in physiology and medicine. The complexity (hence the fractal dimension) of a range of biological systems decreases under stressful conditions. For instance, the time series of heartbeat intervals in healthy subjects have more complex fluctuations than patients with severe cardiac disease (Peng et al. 1995, Ivanov et al. 1999, Mishima 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). In contrast, the complexity of human gait dynamics, though displaying fractal-like patterns in their stride-to-stride intervals (Hausdorff et al. 1995, 1997), has been shown to increase with age and the advancement of neuromuscular disorder to the point of virtually unpredictable fluctuation (Hausdorff et al. 2001).

This issue is also particularly relevant in welfare assessment, and the design of conservation and management strategies as most behavioral measures, e.g., diving duration, distance traveled, turning rate, are not sensitive enough to detect subtle changes associated with mild or acute stress (Rutherford et al. 2004; Asher et al. 2009; Seuront 2010, 2011; see also Seuront 2015) for a review and a discussion on this topic. Specifically, stressed (e.g., diseased, infested with parasites, under the influence of unnatural conditions such as anthropogenic contamination of their habitats) animals typically reduce the complexity of their behavioral displays (Alados et al. 1996; Alados and Huffman 2000; María et al. 2004; MacIntosh et al. 2011, 2013) though a few exceptions exist, *i.e.*, no change in complexity (Hocking *et al.* 2007) and increase in complexity of behavioral patterns (Rutherford et al. 2003; Kembro et al. 2009a, b). Fractal analysis has hence been extensively used as a noninvasive assessment of the general health of wild and captive animals (Asher et al. 2009), including marine mammals, i.e., the Indo-Pacific bottlenose dolphin (Seuront and Cribb 2011, Cribb and Seuront 2016). Note, however, that caution should be taken when it comes to interpreting a change in the fractal property of the behavioral display of a given organisms as different fractal dimensions could occur simply because of changes in the type of behavior, foraging vs. migration; e.g., see the work of Laidre et al. (2004) on narwhal. The results returned by fractal analysis may then somehow be idiosyncratic, and special care must be taken to avoid this potential source of confounding. For instance, recent studies on the effect of boat presence and boat type on the temporal patterns of diving durations in the Indo-Pacific bottlenose dolphin have specifically been conducted when individual dolphins were only exhibiting one macroscopic behavior that is traveling, *i.e.*, moving in a persistent, directional way (Seuront and Cribb 2011, Cribb and Seuront 2016).

# Two Fractal Methods for Marine Mammals: A Tale of Log-log Plots

We present and briefly illustrate hereafter two methods that can be used to assess the complexity of the typical temporal diving patterns encountered in marine mammals. Specifically, while traveling marine mammals spend most of their time underwater and only briefly surface to empty and refill their lungs, which usually takes no more than 1-2 s. In contrast, when engaged in other activities such as resting, socializing, or a range of foraging activities, their behavioral repertoire gets more complex and their diving patterns may consist of a nontrivial alternation between the time they spent underwater ( $T_D$ ) and the time spent at the surface ( $T_s$ ). In contrast to traditional behavioral metrics such as the mean duration of a given behavior, or the time allocated to different behavioral sequences, fractal methods explicitly take into account the probability of occurrence of one or several behavioral states (hence are independent of any *a priori* hypothesis on the statistical nature of the data) as well as the structure of their temporal fluctuations.

#### A Fractal Method for One Behavioral State

Seuront and Cribb (2011) introduced a method to quantify the complexity perceptible 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:

$$P(t \le T_D) = k_1 t^{-\phi},\tag{2}$$

where  $k_1$  is a constant, and  $\phi$  the scaling exponent describing the distribution; is estimated as the slope of  $P(t \leq T_D)$  *vs. t* in log-log plots, and is expected to decline under stress (Fig. 4A); *e.g.*, see Alados *et al.* 1996; Seuront and Leterme 2007; Seuront 2010, 2011, 2015). The related fractal dimension D, *i.e.*, D = f (Seuront 2010), is hence also expected to decrease under stress. Note that for the sake of simplicity and ease of implementation, Equation (2) can be rewritten in simpler terms following (Seuront and Mitchell 2008):

$$T_D(r) = k_2 r^{-\alpha},\tag{3}$$

where  $k_2$  is a constant, r is the rank of the dive duration  $T_D(r)$ , *i.e.*, in a series of n dives, the longest dive has a rank r = 1 and the shortest a rank r = n, and  $\alpha(\alpha = 1/f)$  is the slope of the log-log plot of  $T_D(r)$  vs. r. The presence of significant differences between two exponents  $\alpha$  and between more than two exponents  $\alpha$  can further be inferred using standard statistical approaches, *i.e.*, a modified *t*-test and an analysis of covariance, respectively (Zar 1999). The exponent  $\alpha$  and the related fractal dimension



Figure 4. Log-log plots of (A) the cumulative probability distribution function  $P(t \leq T_D)$  of dive duration  $T_D$  greater than a determined duration t and the dive durations  $T_D(r)$  vs. their rank their r for Indo-Pacific bottlenose dolphins, *Tursiops aduncus*, observed in the absence of boat traffic (open symbols; B) and when powerboats were present (black symbols; C). The linearity of the log-log plots in (A) and (D) indicates that Equations (2, 3)—i.e.,  $P(t \leq T_D) = k_1 t^{-\phi}$  and  $T_D(r) = k_2 r^{-\alpha}$ , respectively—are verified, hence the presence of an underlying fractal structure in the distribution of dive durations  $T_D$  observed in the absence of boats (B) and where powerboats were present (C). Note the one-to-one correspondence between the fractal exponents  $\phi$  and  $\alpha$  returned by the two methods, *i.e.*,  $\phi = 1/\alpha$ . (A) has been modified from Seuront and Cribb (2011).

D, *i.e.*,  $D = 1/\alpha$  (Seuront 2010), are hence respectively expected to increase and decrease under stress.

The applicability of Equations (2) and (3) to marine mammal behavior as well as the one-to-one correspondence between them are illustrated using a previously published (Seuront and Cribb 2011) data sets assessing the fractal structure of dive durations of the Indo-Pacific bottlenose dolphins travelling (*i.e.*, moving in a persistent, directional way) in the absence of boat traffic (Fig. 4B) and in the presence of powerboats (Fig. 4C). Nonsignificant differences were found in dive duration  $T_D$  between the two conditions, while Equation (3) clearly showed distinct scaling properties in the absence and presence of powerboats with respectively  $\alpha = 0.67$  and 0.98 (Fig. 4D). Note that the one-to-one correspondence between  $\alpha$  and  $\phi$  is verified in both cases (Fig. 4A, D). More fundamentally, both the exponents  $\alpha$  and  $\phi$  derived from Equations (2) and (3) are respectively the slopes of log-log plots of  $P(t \leq T_D) vs.$ t, and  $T_D(r) vs. r$ . As a consequence, their confidence intervals and any comparison needed between individuals, species or environmental conditions can be estimated and run using standard the statistical and inferential tools related to linear regression equations; *e.g.*, see Zar (1999).

#### A Fractal Method for Sequential Behaviors

In cases where marine mammals are alternating between periods of diving and surfacing, the method described above is not optimal as it cannot take into account the information available in the complexity of both behavioral sequences, though the temporal patterns of both diving and breathing times  $T_D$  and  $T_S$  can be analyzed separately using Equations (2) or (3). The nature of behavioral sequences can be assessed through the construction of a binary sequence z(i) for each behavioral activity *i* taken from continuous observations equally spaced in time. When diving and surfacing is observed, z(i) = 1 and z(i) = -1, respectively. The binary sequences z(i) are subsequently used to construct a behavioral sequence random walk w(t) as:

$$w(t) = \sum_{i=1}^{N} z(i),$$
 (4)

where *N* is the number of behavioral observations equally spaced in time. First, Equation (4) provides a graphical representation of the degree of correlation in the behavioral time series (Fig. 5). Second, the random walk u(t) can be used to quantify those correlations. Specifically, the fluctuations of the random walk u(t) can be characterized by their *q*th order structure functions defined as:

$$\left\langle \left\| \Delta w(t)_{\tau} \right\|^{q} \right\rangle = k_{3} \tau^{\varsigma(q)},\tag{5}$$

where  $\|\Delta w(t)_{\tau}\| = \|w(t+\tau) - w(\tau)\|$  is the norm of the fluctuations observed during a temporal increment  $\tau$ ,  $k_3$  is a constant, the angle brackets " $\langle \rangle$ " indicate



*Figure 5.* Theoretical illustration of a binary behavioral sequence z(i), where z(i) = 1 (black vertical lines) and z(i) = -1 (white vertical lines), and the resulting behavioral sequence random walk  $w(t) = \sum_{i=1}^{N} z(i)$  for H = 0.05 (A, B), H = 0.5 C, D) and H = 0.85 (E, F), where H (0 < H < 1) is the exponent characterizing the fractal structure of the random walk w(t). H = 0.5 and  $H \neq 0.5$  respectively for Brownian motion or a fractional Brownian motion, and H < 0.5 and H > 0.5 for antipersistent (*i.e.*, negatively autocorrelated) and persistent (*i.e.*, positively autocorrelated).

ensemble average, and the moment function  $\zeta(q)$  characterizes the stochastic properties of the random walk u(t) regardless of scale and intensity (Seuront *et al.* 1999). Conveniently, the shape of the function  $\zeta(q)$ —initially introduced in marine sciences to quantify the nature of plankton distribution in turbulent flows (Seuront et al. 1996a, b, 1999) and later used as a diagnostic tool to unambiguously identify the type of motion exhibited by swimming organisms (Seuront and Stanley 2014, Seuront 2015)—is proposed here to characterize the complexity of behavioral random walks without any *a priori* hypothesis on the nature of the data, such as the standard normality and homoscedasticity assumptions. Specifically, when the function  $\zeta(q)$  is linear (*i.e.*,  $\zeta(q) = qH$ , with  $\zeta(1) = H$ ), the behavioral random walk u(t) can either be described as a Brownian motion or a fractional Brownian motion respectively when H= 0.5 and  $H \neq 0.5$ . When H = 0.5 (Fig. 5A), the increments of w(t) are independent of each other; that is an increase in w(t) observed at time t (i.e., z(i) = 1, the observed individual is diving) is as likely to be followed by a decrease (*i.e.*, z(i) = -1, the observed individual is surfacing) than by another increase. In contrast, when H > 0.5and  $H \le 0.5$ , the increments of w(t) are positively and negatively correlated, respectively. More specifically, if H > 0.5 (Fig. 5B), the behavioral random walk w(t) is positively correlated or persistent, in the sense that an increase in w(t) at time t tend to be followed by another increase at time  $t + \tau$ . Hence, an individual observed diving at time t is more likely to still be diving than surfacing at time  $t + \tau$ . Alternatively, if  $H \le 0.5$  (Fig. 5C), the behavior is negatively correlated, or antipersistent; an individual diving at time t is more likely to be at the surface than diving at time  $t + \tau$ . Note that the structure function exponent *H* is related to the fractal dimension *D* as D = 2- H (Seuront 2010); decreasing values of H (hence increasing fractal dimensions) are indicative of greater complexity in the sense that the related random walks present greater fluctuations throughout the sequence (Fig. 5B, D, F). More complex types of variability also exit, such as Lévy walks and multifractal random walks. In the former case, the function  $\zeta(q)$  is (1) bilinear with  $\zeta(q) = q/(\mu - 1)$  for  $q < \mu - 1$  and  $\zeta(q) = 1$ for  $q \ge \mu - 1$ ; the exponent  $\mu (1 \le \mu \le 3)$  characterizes the power-law tail of the probability distribution of the move-step length l as  $P(l) \approx \Gamma^{\mu}$ , where  $1 \le \mu \le 3$ . In the latter case,  $\zeta(q)$  is nonlinear and convex; see Seuront and Stanley (2014) and Seuront (2015) for further examples and discussion. As stressed in the previous section, the moment function  $\zeta(q)$  is fundamentally the slopes of log-log plots, and as such can be compared between individuals, species or environmental conditions using standard inferential tools related to linear regression equations; e.g., Zar (1999).

In the next three sections, we illustrate the generality of the two methods described above to marine mammal sciences through their applications to (1) the temporal dynamics of the diving patterns of killer whales in the presence and absence of sea kayaks, and (2) the sequential behavior of harbor and gray seals in environments with distinct levels of anthropogenic influence in the Dover Strait, and (3) southern right whales with and without calves. We subsequently discuss the ecological relevance of identifying fractal properties in marine mammal behavior, and the potential strength of the fractal behavioral parameters described here in comparison to more standard behavioral metrics. We finally briefly address the implications the use of fractal methods may have in terms of the design and implementation of management and conservation strategies. Note that the three case studies presented here should not be considered as exhaustive studies *per se* due to the relatively low number of individuals considered in our analysis. Instead, they are used as a basis to illustrate the applicability of fractal methods to marine mammals with very distinct biology and ecology.

#### CASE STUDY 1: KILLER WHALE AND SEA KAYAKING

The diving durations of two distinct male killer whales were recorded both in the absence (Fig. 6A) and the presence (Fig. 6B) of sea kayaks while traveling along the West Sound shore of Orcas Island, Washington, in August 2008; observations were consistently conducted from a promontory overlooking West Sound from *ca*. 50 m using binoculars (magnification  $\times$ 20), and dive durations were recorded using a handheld stop-watch and internally stored until analysis. Kayaks were the only vessels present on the water during our observations, and they were consistently travelling along the shoreline without ever moving towards the killer whales, hence no direct interactions were ever observed.

No significant differences in diving durations  $T_D$  were found between individuals in the absence and presence of kayaks (Wilcoxon-Mann-Whitney *U*-test, p > 0.05). Similarly, no significant differences were found between observations conducted in the absence ( $T_D = 37.9 \pm 3.5$  s;  $\bar{x} \pm SE$ ) and presence ( $T_D = 36.5 \pm 5.0$  s) of kayaks (Wilcoxon-Mann-Whitney *U*-test, p > 0.05). In both the absence and presence of kayaks, Equation (3) fits very well the dynamics of dive duration  $T_D$  (Fig. 6C, D). This indicates the presence of an underlying fractal structure in dive duration dynamics whether sea kayaks were present or not. The exponent  $\alpha$  (*i.e.*, the slope of the loglog plot of dive duration  $T_D$  versus their rank r) did not significantly differ (modified t test, p > 0.05) between the two killer whales in the absence of kayaks with  $\alpha = 0.60$ 



*Figure 6.* Dive duration  $T_D$  of a male killer whale *Orcinus orca* in the absence (A) and the presence (B) of whale watching sea kayaks, shown with their corresponding rank analyses C, D). The linearity of the log-log plot of dive duration  $T_D$  vs. rank r C, D) is indicative of the presence of an underlying fractal structure in dive duration dynamics whether sea kayaks were present or not. Note, however, that the exponent  $\alpha$  (*i.e.*, the slope of the log-log plot of dive duration  $T_D$  vs. rank) significantly increased from 0.6 in the absence of kayaks, to 0.74 in the presence of kayaks, indicating an overall decrease in the complexity of dive durations.

(Fig. 6C) and  $\alpha = 0.64$ . Similarly, no significant differences were found between the two killer whales when kayaks were present with  $\alpha = 0.74$  (Fig. 6D) and  $\alpha = 0.76$ . These results suggest a lack of interindividual variability in the fractal structure in killer whale duration dynamics, though this conclusion needs to be considered with caution given our limited sample size. In contrast, these exponents significantly increased (modified *t*-test,  $p \le 0.01$ ) from 0.62 in the absence of kayaks to 0.75 in the presence of kayaks, indicating an overall decrease in the complexity of dive durations. Note that the different sample size of the two data sets used in the analysis of the dive duration pattern of the first killer whale male were very different with n = 98 and n =50 in the absence and presence of kayaks, respectively (Fig. 6A, B; Table 1). This difference, however, did not impact the results of the subsequent rank frequency analysis as a repeated (n = 50) bootstrap resampling procedure without replacement of 50 points from the original n = 98 points data set followed by a subsequent rank-frequency analysis led to a distribution of the exponent  $\alpha$  ( $\alpha = 0.61 \pm 0.02$ ) that cannot be statistically distinguished (modified *t*-test, p > 0.05) from the exponent estimated from the original data set ( $\alpha = 0.60$ ).

# CASE STUDY 2: HARBOR AND GRAY SEALS AND HUMAN DISTURBANCE

The temporal patterns of the diving and surfacing times of the harbor and gray seals, were investigated from two sites, Fort de Croy (50°45.766'N, 1°35.962'E) and Phare de Walde (50°59'36.64"N, 1°54'52.98"E), respectively located along the French coast of the eastern English Channel and the North Sea. Fort de Croy is located near a sailing club, along a shoreline essentially made of concrete seawalls and coastal defense structures, and is punctually visited at high tide by harbor and gray seals that were only very rarely observed hauling out on anthropogenic structures (LS, personal observations). In contrast, at Phare de Walde both species are regularly observed hauling out at low tide on a remote sand bar void of anthropogenic disturbance, and located 700 m away from the lowest limit of the intertidal zone, parallel to the coast, 6 km long and 1 km wide at low tide. Opportunistic observations were conducted noninvasively at both sites, consistently at high tide in spring and summer 2012, 2013, and 2014 at Fort de Croy, and at low tide in spring and summer 2002, 2003, 2004, and 2005 at Fort de Walde (Table 1). Both sites share a flat bottom, essentially made of soft sandy sediment. The times spent underwater and at the surface were recorded (1) using a digital camera (DV Sony DCR-PC120E) mounted on a second floor window of the "Marine Station of Wimereux" that overlooks Fort de Croy, and later classified as diving and surfacing durations  $T_D$  and  $T_S$  upon review of the footages, and directly using a hand held chronometer from the beach using binoculars (magnification  $\times 60$ ) at Phare de Walde.

Significant interindividual differences were found for diving and surfacing durations at both sites for harbor seals and at Phare de Walde for gray seals (Wilcoxon-Mann-Whitney *U*-test, p < 0.05). This result is consistent with the widely reported individual variability in behavior reported for those species, *e.g.*, Van Parijs *et al.* (2000), Wilson *et al.* (2014), and Russell and McConnell (2014). In contrast, diving and surfacing durations did not significantly (Wilcoxon-Mann-Whitney *U*-test, p >0.05) differ between sites for both harbor and gray seals (Table 1). No significant differences were found for diving duration between species (Wilcoxon-Mann-Whitney *U*-test, p > 0.05), though significant interspecific differences exit for surfacing durations, which were significantly shorter (Wilcoxon-Mann-Whitney *U*-test, p < 0.05) in the harbor seal than in the gray seal (Table 1). Note, however, that both maximum

| Killer whate,<br>Drinus ora         West Sound,<br>Occas Island $48^{\circ}36'12^{\circ}N$ $122^{\circ}57'12^{\circ}W$ Made         1         98 $36.5(5,0)$ -           Drinus ora         Occas Island $48^{\circ}36'12^{\circ}N$ $122^{\circ}57'12^{\circ}W$ Male         1 $101$ $31.92,237'$ -           Abox $48^{\circ}36'12^{\circ}N$ $122^{\circ}57'12^{\circ}W$ Male         1 $101$ $34.8(4,39)$ -           Abox $48^{\circ}36'12^{\circ}N$ $122^{\circ}57'12^{\circ}W$ $Male$ 1 $101$ $34.8(4,2)^{\circ}$ -           Abox $50^{\circ}36'4^{\circ}4^{\circ}N$ $1^{\circ}36'07^{\circ}E$ $2$ $2$ $2$ $2$ $3$ $3$ $2$ $3$  | Species                          | Location                    | Latitude   | Longitude   | Sex    | и             | N     | $T_D$   | $T_S$                  |
|---|----------------------------------|-----------------------------|------------|-------------|--------|---------------|-------|---|------------------------|
| $ \begin{array}{llllllllllllllllllllllllllllllllllll$   | Killer whale,<br>Orcinus orca    | West Sound,<br>Orcas Island | 48°36'12"N | 122°57′12″W | Male   |               | 98    | 36.5 (5.0)  |                        |
| $ \begin{array}{c ccccccccccccccccccccccccccccccccccc$  |                                  |                             |            |             |        |               | 55    | [13-255]<br>37.9 (3.5) <sup>a</sup>                                 |                        |
| Harbor seal,       Forr de Croy $50^{\circ}45'49^{\circ}N$ $1^{\circ}36'07''E$ $2$ $38.6(4.2)^{\circ}$ $-$ Phota vitulina       Forr de Croy $50^{\circ}45'49''N$ $1^{\circ}36'07''E$ $2$ $244$ $8.6(1.3)$ $7.0(1.3)$ Phota vitulina       Phare de Walde $50^{\circ}35'36''N$ $1^{\circ}54'53''E$ $2$ $11$ $1,211$ $95(4.2)^{\circ}$ $-$ Gray scal,       Fort de Croy $50^{\circ}35'36''N$ $1^{\circ}54'53''E$ $2$ $11$ $1,211$ $95(4.3)$ $7.0(1.3)$ Gray scal,       Fort de Croy $50^{\circ}45'49''N$ $1^{\circ}36'07''E$ $2$ $11$ $1,211$ $95(4.3)$ $21.4(5.7)$ Haliovers grapus       Fort de Croy $50^{\circ}45'49''N$ $1^{\circ}36'07''E$ $2$ $1$ $12.211$ $11-401$ $11-601$ Gray scal,       Eot de Croy $50^{\circ}45'53''E$ $2$ $1$ $87$ $20.5(6.8)$ $21.1(45)$ Haliovers graphus       Encounter Bay       Encounter Bay $1^{\circ}54''53''E$ $2$ $7$ $878$ $25.3(6.9)$ $92.1(4.5)''10^{\circ}$ Southenr right whale,       Encounter Bay $35^{\circ}52''15''S$ |                                  |                             | 48°36'12"N | 122°57′12″W | Male   | 1             | 101   | $[11-222]^a$<br>34.8 (4.8)  |                        |
| $ \begin{array}{c ccccccccccccccccccccccccccccccccccc$  |                                  |                             |            |             |        |               | 98    | $\{10-205\}$<br>38.6 $(4.2)^{a}$                                    |                        |
| $ \begin{array}{c ccccccccccccccccccccccccccccccccccc$  | Harbor seal,<br>Ploca vitulina   | Fort de Croy                | 50°45′49″N | 1°36'07"E   | ς.     | $\mathcal{C}$ | 244   | {10-233f<br>8.6 (1.3)   | 7.0(1.3)               |
| $ \begin{array}{cccccccccccccccccccccccccccccccccccc$   |                                  | Phare de Walde              | 50°59′36″N | 1°54′53″E   | ο.     | 11            | 1,211 | [1-51]<br>9.5 (1.4)   | [1-48]<br>5.8 (1.1)    |
| $ \begin{array}{cccccccccccccccccccccccccccccccccccc$   | Gray seal,<br>Halicoreus orvitus | Fort de Croy                | 50°45'49"N | 1°36'07"E   | ς.     | 1             | 87    | $10^{-40}$<br>20.3 (8.7)  | 11–00<br>23.4 (5.7)    |
| Southern right whale, Encounter Bay [2 <sup>-152</sup> ] [1 <sup>-7</sup> ]<br><i>Eubalaema glacialis</i> Freeman's Knob 35°32′15″S 138°41′52″E Adult 1 188 32.5 (6.9) 9.2 (2.1) [1-34]<br>Freeman's Knob 35°32′15″S 138°41′52″E Female 1 138 35.4 (8.7) 8.1 (1.6) [1-59]<br>(11-58] [1-59]<br>Calf 1 30 15.5 (3.1) 13 (3.2) [3-57]   | card ( Q car car and c           | Phare de Walde              | 20°59′36″N | 1°54′53″E   | ς.     |               | 878   | $\begin{array}{c} [4-151] \\ 25.3 (6.8) \\ 125.3 (5.3) \end{array}$ | [2–88]<br>21.1 (4.5)   |
| Eubataena glactatis<br>Freeman's Knob 35°32′15″S 138°41′52″E Adult 1 188 32.5 (6.9) 9.2 (2.1)<br>Freeman's Knob 35°32′15″S 138°41′52″E Female 1 138 35.4 (8.7) 8.1 (1.6)<br>(1-568] [1-59]<br>Calf 1 30 15.5 (3.1) 13 (3.2)<br>[3-56] [2-71]  | Southern right whale,            | Encounter Bay               |            |             |        |               |       | [2-152]   | 14/-11                 |
| Freeman's Knob         35°32'15"S         138°41'52"E         Female         1         138         35.4 (8.7)         8.1 (1.6)           Remain         Remain         Remain         1         36         1         1         35.4 (8.7)         8.1 (1.6)           Remain         Remain         Remain         1         1         35.4 (8.7)         8.1 (1.6)           Remain         Remain         Remain         1         36.1 (1.6)         8.1 (1.6)           Remain         Remain         Remain         1         30         15.5 (3.1)         13 (3.2)           Remain         Remain         Remain         1         30         15.5 (3.1)         13 (3.2)  | Eubataena glacialis              | Freeman's Knob              | 35°32′15″S | 138°41'52"E | Adult  | 1             | 188   | 32.5 (6.9)  | 9.2 (2.1)              |
| Calf     1     30 $11-5061$ $11-5061$ $13-561$ $13-561$ $13-621$ $13-561$ $12-711$  |                                  | Freeman's Knob              | 35°32′15″S | 138°41'52"E | Female | 1             | 138   | 11-5451<br>35.4 (8.7)   | 8.1 (1.6)<br>8.1 (1.6) |
|   |                                  |                             |            |             | Calf   | 1             | 30    | 11-5081<br>15.5 (3.1)<br>[3-56]                                     | [2-71]<br>[2-71]       |

SEURONT AND CRIBB: FRACTALITY IN MARINE MAMMAL BEHAVIOR

17

diving durations and maximum surfacing durations were consistently longer in *H.* grypus than in *P. vitulina* (Table 1). In contrast, both the temporal patterns of the binary behavioral sequence of diving and surfacing durations z(i) and the exponents  $\zeta(q)$  estimated from the behavioral random walk w(t) vary depending on species and sites. Specifically, the alternation of diving and surfacing durations was clearly less random in *P. vitulina* at Phare de Walde (Fig. 7A, C) than at Fort de Croy (Fig. 7B, D). In contrast, no clear differences were visible between the binary behavioral sequences of *H. grypus* observed at both sites (Fig. 8). This qualitative information is specified by the shape of the function  $\zeta(q)$  that has been estimated for each individual seal through Equation (5). From a methodological perspective, it should be noted that there is a one-to-one correspondence between the average of the exponents  $\zeta(q)$  estimated for each individual seal and the exponents  $\zeta(q)$  estimated from an ensemble average of the  $\|\Delta\omega(\tau)_{\tau}\|$  of all the seals considered; see Seuront (2005, 2010) and Seuront and Schmitt (2005*a*, *b*) for further details.

First, it is stressed that no significant differences were found between the exponents  $\zeta(q)$  estimated for distinct individuals *P. vitulina* and *H. grypus* (analysis of covariance, p > 0.05). This result suggests that despite the interindividual differences in diving and surfacing durations reported above and in the literature, the complexity of the temporal dynamics of the alternation of diving and surfacing durations did not differ between individuals. Both *P. vitulina* and *H. grypus* diving and surfacing patterns were hence consistently characterized as fractional random walks as  $\zeta(q) = qH$ , with H = 0.42 and H = 0.31 for *P. vitulina* respectively at Fort de Croy and Phare de Walde, and H = 0.31



*Figure 7.* Binary behavioral sequence z(i) of the harbor seal, *Phoca vitulina* (A, B), where z(i) = 1 (black vertical lines) and z(i) = -1 (white vertical lines) when seals were respectively diving and surfacing, and the resulting behavioral sequence random walk  $w(t) = \sum_{i=1}^{N} z(i)$  (C, D) observed at sites nonimpacted (A, C) and impacted (B, D) by anthropogenic activities.



*Figure 8.* Binary behavioral sequence z(i) of gray seals, *Halichoerus grypus* (A, B), where z(i) = 1 (black vertical lines) and z(i) = -1 (white vertical lines) when seals were respectively diving and surfacing, and the resulting behavioural sequence random walk  $w(t) = \sum_{i=1}^{N} z(i)$  (C, D) observed at sites nonimpacted (A, C) and impacted (B, D) by anthropogenic activities.

0.57 at Fort de Croy (Fig. 9A) and H = 0.61 at Phare de Walde (Fig. 9B). Specifically,  $H \le 0.5$  and  $H \ge 0.5$  for *P. vitulina* and *H. grypus*, showing that the dynamics of the alternation between diving and surfacing behaviors belong to the class of nonpersistent (or negatively correlated) and persistent (or positively correlated) fractional Brownian motion, respectively. The surfacing patterns of *P. vitulina* and *H. grypus* are then describe by two different types of fractal models. This result may suggest that behavioral complexity may be species-specific in pinnipeds, though further work is needed to validate this hypothesis. Now, no significant differences were found between sites in Hestimated for *H. grypus*, indicating that the complexity of *H. grypus* behavioral display is not affected by the differences in anthropogenic activities and coastal structures between our two sites. In contrast, we found a significant increase in the values of H for P. vitulina between Fort de Croy and Phare de Walde. This is indicative of a decrease in behavioral complexity at the most anthropogenically impacted site; *i.e.*, Fort de Croy is located in the immediate vicinity of a sailing club, along a shoreline essentially made of concrete seawalls and coastal defense structures, in contrast to the remote Phare de Walde, which is located away from any anthropogenic activities.

# CASE STUDY 3: SOUTHERN RIGHT WHALE

Southern right whales have a circumpolar distribution in the southern hemisphere, *i.e.*, from  $20^{\circ}$ S to  $60^{\circ}$ S (Townsend 1935). Annually they migrate south during



*Figure 9.* Structure function exponents  $\zeta(q)$  shown for *P. vitulina* (A) and *P. grypus* (B) at sites nonimpacted (gray) and impacted (black) by anthropogenic activities. The dashed line indicate the Brownian motion theoretical expectation, *i.e.*,  $\zeta(q) = q/2$ .

warmer months to feed and north during winter months to coastal regions for breeding (Rowntree *et al.* 2001, Pirzl *et al.* 2009). The coastal waters of Southern Australia are considered an important habitat for this species (Allen and Bejder 2003), where they are recurrently observed forming aggregations especially in Encounter Bay and at the Head of the Great Australian Bight (Burnell and Bryden 1997). Specifically, unaccompanied individuals as well as females typically return annually to these shallow, sheltered, nearshore waters to give birth, raise young, and socialize (Burnell and Bryden 1997, Carroll *et al.* 2014). The applicability of fractal methods to assess the binary temporal patterns of the diving and surfacing durations of *E. australis* was here inferred from records of the times spent underwater and at the surface by one solitary individual, and a female with a calf. Observations were conducted from a land-based





*Figure 10.* Binary behavioral sequence z(i) of southern right whale, *Eubalaena australis* female (A) and accompanying calf (B), where z(i) = 1 (black vertical lines) and z(i) = -1 (white vertical lines) when they were respectively diving and surfacing, and the resulting behavioral sequence random walk  $w(t) = \sum_{i=1}^{N} z(i)$  (C, D).

station (Freeman's Knob, Port Elliot, South Australia;  $32^{\circ}32'15''$ S,  $138^{\circ}41'52''$ E) on 10 July 2006 and 14 August 2006, respectively. In both cases, the times spent underwater and at the surface were recorded using a hand held chronometer from the beach using binoculars (magnification ×60).

Both diving and surfacing durations did not significantly (p > 0.05) differ between the two adult individuals, even though the shortest and longest surface durations of the unaccompanied individual lasted respectively 400% and 33% longer than in the accompanied adult (Table 1). Calf surface durations did not significantly differ from those of both the accompanying female and the unaccompanied individual (Table 1). In contrast, the calf diving durations were on average 2-fold shorter than in adults (Table 1). The corresponding binary behavioral sequence of diving and surfacing durations z(i) vary between an adult (Fig. 10A) and its accompanying calf (Fig. 10B), resulting in a more persistent behavioral random walk w(t) for adult (Fig. 10C) than calf (Fig. 10D). These observations result in significantly different fractal behavior, with H = 0.71 and H = 0.73 for nonaccomanying and accompanying adults, respectively, and H = 0.63 for a calf. These results suggest that while nonaccomanying and accompanying adults exhibit similar behavior, the decrease in H is indicative of a lower persistence (*i.e.*, greater complexity in the sense that the related random walks present greater fluctuations throughout the sequence) in calf behavior than in adults.

#### DISCUSSION

#### Fractality in Marine Mammal Behavior

Ş

The three case studies considered in the present work show that the complexity of (1) the dive duration patterns of the Indo-Pacific bottlenose dolphin and killer whale, and (2) the alternation between diving and surfacing times of two common seal species, the harbor seal and the gray seal and (3) the southern right whales were all quantifiable using fractal techniques. These observations indicate the presence of an underlying fractal structure, which may be independent on the species, and the type of behavior they are engaged in. The presence of fractal fluctuations in biological

systems suggests that there are biological mechanisms that are adaptive, in that these mechanisms serve as an organizing principle for highly complex, nonlinear processes, and they avoid restricting the functional response of an organism to highly periodic behavior (Goldberger et al. 2000). Fractal fluctuations are also error tolerant, as they allow organisms to cope with stress and unpredictable environments (Goldberger et al. 1990). Because behavior is the end-product of the 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 behavior of a range of marine mammals with different size, feeding habits and foraging strategies are consistent with the fractally colored environment in which they are embedded. Fractal properties have indeed been consistently found in the abiotic and biotic properties of marine mammal environments. These properties include, e.g., the topographic complexity of coral and rocky reefs (Bradbury et al. 1984), coastline (Chattopadhyay and Kumar 2007) and seafloor (Ashalatha 2007), the spatial patterns of seagrass meadows (Manzanera and Romero 2000), the architecture of sessile flora and fauna (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) and the foraging behavior of fish and fish schools (Tatsuro et al. 2001, Tikhonov et al. 2001, Medvinsky et al. 2002). A direct consequence of the aforementioned fractal properties of the marine environment is that the distribution of information needed to fulfill basic activities such as foraging and navigation are fundamentally multiscale, spanning from relatively short temporal (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 (migratory patterns of prey species) and larger spatial scales (coastline topography). 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 (Humphries et al. 2012, Sims et al. 2012) and predator-prey encounter rates (Seuront and Stanley 2014). The identification of fractal fluctuations in marine mammal behavior is hence critical to improve our understanding of marine mammal ecology, and how they interact with their spatially and temporally complex environment. More specifically, further work is needed to assess if (and eventually how) the fractal properties of the environment (both biotic and abiotic) of marine mammal may affect the fractal properties of their behavior.

#### A Note on Individual Variability and Fractality Marine Mammal Behavior

The behavior of a range of marine mammal has widely been shown to differ between individuals of the same species, *e.g.*, Perrin *et al.* (2009). These differences can either be temporally or spatially consistent (Twiss and Franklin 2010), hence the concept of personality (see Bell 2007). Alternatively, individual variability in behavior can also be related to sites, seasons, time of day, and be sex-specific, *e.g.*, Rogers and Cato (2002), Van Parijs *et al.* (2000), Wilson *et al.* (2014), and Russell and McConnell (2014). In this context, the results presented here should *a priori* be considered with caution due to the relatively limited number of distinct individuals used in our analyses (see Table 1). It is, nevertheless, stressed that no interindividual differences were ever found in the present work in the fractal properties of the observed behaviors even when significant differences were found between individuals using standard behavioral metrics such as, *e.g.*, diving and surfacing durations in harbor seal. These results suggest that the underlying fractal structure of a given behavior may be a more resilient property than the actual duration of the behavior itself, at least at the species level. The presence of a fractal structure may hence represent a fundamental property of marine mammal behavior that may have ramifications well beyond the species level, considering the inter-specific differences observed in the diving behavior of a range of marine mammals; see Hooker *et al.* (2011) for a review. The resolution of this issue is beyond the scope of the present work, but nevertheless stresses the fact that further work is needed to explore marine mammal behavior through the fractal lens through, *e.g.*, a systematic quantification of behavioral interindividual variability assessed using both standard and fractal metrics.

# May Fractals Provide More Sensitive Metrics to Assess Stress Levels in Marine Mammals?

Beyond the evidence of the presence of an underlying fractal structure in the behavioral complexity of two species of seals (harbor and gray seals), two species of odontocetes (the Indo-Pacific bottlenose dolphin and the killer whale), and one mystycete (the southern right whale), our results indicate that fractal analysis may be more sensitive than traditional behavioral metrics to detect subtle changes in behavioral complexity. The strength of the fractal methods introduced here lies in the fact that they take into account two fundamental behavioral properties that are typically ignored by traditional behavioral metrics, *i.e.*, the probability of occurrence of behavioral states and the temporal nature of behavior. These properties are explicitly embedded into the fractal methods introduced here, see Equations (2, 3) and Equations (4, 5), respectively.

No statistically significant differences were detected in the diving durations observed in the absence of boats and where boats were present for both the Indo-Pacific bottlenose dolphin and the killer whale. In contrast, the fractal exponent  $\alpha$  significantly increased (hence indicated a decrease in behavioral complexity) from 0.67 to 0.98 for the Indo-Pacific bottlenose dolphin and from 0.60 to 0.74 for the killer whale, respectively when boats were absent and present. Note, however, that these results should be taken with caution given the relatively low number of distinct individuals considered in our analyses. The higher behavioral complexity observed in the killer whale in the absence of boat also suggests that their behavioral repertoire is richer than the Indo-Pacific bottlenose dolphin, hence they may have more behavioral flexibility to respond to disturbances. This statement should be considered with caution given the lack of additional information related to the properties of the environments where the killer whale and the Indo-Pacific bottlenose dolphin were observed. Similarly, the diving and surfacing durations did not significantly differ between sites in both harbor and gray seals (Table 1). No significant differences were found for diving duration between species, though significant interspecific differences exit for surfacing durations, which were significantly shorter in the harbor seal than in the gray seal (Table 1). The fractal exponent H significantly differs (1) between species, *i.e.*, H ranges from 0.31 to 0.42 in the harbor seal, and from 0.57 to 0.61 in the gray seal, and (2) between sites for the harbor seal (H decreased from 0.42 to 0.31 from the less to the most anthropogenically impacted sites). These results suggest that standard metrics (here dive duration) typically used in marine mammal studies may not be sensitive enough to detect species-specific and disturbance-driven changes in behavioral complexity. This conclusion is consistent with previous work showing that behavioral traditional metrics are much less sensitive to changes in behavioral complexity than fractal-based methods (Motohashi et al. 1993, Rutherford et al. 2003, Seuront and Cribb 2011, Seuront 2015). This discrepancy between traditional and

fractal-based methods hence generalizes to marine mammal behavioral ecology the early claim that it creates "the need for fractal analysis" in behavioral studies (Coughlin *et al.* 1992).

Finally, for the southern right whale, if diving and surfacing durations did not significantly differ between nonaccompanying and accompanying adults and calf, fractal analysis clearly shows that the complexity of the temporal alternation between diving and surfacing differ between adult (*H* in the range 0.71–0.73) and calf (H = 0.63). Attempting to provide a mechanistic explanation for the observed patterns is far beyond the scope of the present work and would be at best speculative considering the low number of individuals considered here. Our results nevertheless indicate that the temporal structure of baleen whale surfacing and diving behavior can be described as a persistent correlated random walk—it exhibits an underlying fractal structure and that the complexity of this pattern may be driven by ontogeny as previously shown in both invertebrates (Osborne *et al.* 2013) and vertebrates (Dowling *et al.* 2000).

# Fractal-based Methods and Marine Mammal Management and Conservation Strategies

Our results have potential ramification in the establishment of management and conservation strategies. Specifically, chronic exposure to even low levels of disturbance (which is typically the case when, e.g., dolphin-watching sea kayaks co-occur daily with Orcinus orca) 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 (Bejder et al. 2006). This chronic exposure has critical implications for marine mammal welfare, hence the related development and implementation of effective mitigation and management strategies. The habituation to, e.g., boat traffic reported for bottlenose dolphins (Sini et al. 2005) did not imply the absence of stress. This fact may be thought a *pernicious* threat, as suggested in a preliminary study (Seuront and Cribb 2011). The identification of even subtle changes in the behavioral complexity of marine mammals is then critical to infer their susceptibility to disturbance, in particular, for species inhabiting anthropogenically impacted coastal areas. For instance, the clear decrease in the behavioral complexity observed in the harbor seal in the environment that is the most impacted by anthropogenic activities may be indicative of a high susceptibility to disturbance. In contrast, both the higher behavioral complexity exhibited by the gray seal relative to the harbor seal and the lack of observed changes in their behavioral complexity in anthropogenically impacted environments suggest that this species may be more resistant to disturbance, as their baseline behavioral repertoire is richer, which allows them more behavioral flexibility to respond to disturbances. In this context, the assessment of the potential impacts any anthropogenic activity may have on marine mammals, hence the identification of their potential long-term ramifications, necessitates very sensitive tools to unambiguously infer the presence of behavioral changes.

#### Conclusion

This work illustrates how standard behavioral metrics may fail to identify changes in the behavioral complexity of a range of marine mammals (*i.e.*, *Tursiops aduncus*, *Orcinus orca*, *Phoca vitulina*, *Halichoerus grypus*, and *Eubalaena australis*). The fractal methods described and illustrated in the present work, beyond being relatively easy to implement, provide a powerful alternative to traditional behavioral metrics used in marine mammal studies. Specifically, the strength of these fractal methods lies in the fact that they take into account two fundamental behavioral properties that are typically ignored by traditional behavioral metrics, *i.e.*, the probability of occurrence of behavioral states and the temporal nature of behavior. Combined with land-based observations, fractal analysis provides an objective and quantitative tool to quantify subtle behavioral changes in marine mammals. The approach described in this work is suggested as a way to provide baseline information about marine mammal behavioral complexity and infer their behavioral flexibility and the related behavioral changes that may be induced by anthropogenic activities.

#### ACKNOWLEDGMENTS

This research was supported under Australian Research Council's Discovery Projects funding scheme (project numbers DP0664681 and DP0988554). Professor Seuront is the recipient of an Australian Professorial Fellowship (project number DP0988554). Krystal Jay, Trish Lavery, and J. G. Mitchell are acknowledged for stimulating discussions and preliminary studies that stimulated the present work. The authors declare no conflict of interests.

#### LITERATURE CITED

- Abraham, E. R. 2001. The fractal branching of an arborescent sponge. Marine Biology 138:503-510.
- Airoldi, L., M. Abbiati, M. W. Beck, et al. 2005. An ecological perspective on the deployment and design of low-crested and other hard coastal defence structures. Coastal Engineering 52:1073–1087.
- Alados, C. L., and M. A. Huffman. 2000. Fractal long-range correlations in behavioural sequences of wild chimpanzees: A non-invasive analytical tool for the evaluation of Health. Ethology 106:105–116.
- Alados, C. L., J. M. Escos and J. M. Emlen. 1996. Fractal structure of sequential behaviour patterns: An indicator of stress. Animal Behaviour 51:437–443.
- Allen, S., and L. Bejder, 2003. Southern right whale *Eubalaena australis* sightings on the Australian coast and the increasing potential for entanglement. Pacific Conservation Biology 9:228–233.
- Andersen, M., A. E. Derocher, Ø. Wiig and J. Aars. 2008. Movement of two Swalbard polar bears recorded using geographical positioning system satellite transmitters. Polar Biology 31:905–911.
- Andersen, S. M., J. Teilmann, R. Dietz, N. M. Schmidt and L. A. Miller. 2012. Behavioural responses of harbour seals to human-induced disturbances. Aquatic Conservation: Marine and Freshwater Ecosystems 22:113–121.
- Ashalatha, B. 2007. Fractal analysis of gravity and bathymetry profiles across ridges in Indian Ocean. Indian Journal of Marine Sciences 36:110–116.
- Asher, L., L. M. Collins, A. Ortiz-Pelaez, J. A. Drewe, C. J. Nicol and D. U. Pfeiffer. 2009. Recent advances in the analysis of behavioural organization and interpretation as indicators of animal welfare. Journal of the Royal Society Interface 6:1103–1119.
- Austin, D., W. D. Bowen and J. McMillan, 2004. Intraspecific variation in movement patterns: Modelling individual behaviour in a large marine predator. Oikos 105:15–30.
- Balmer, B. C., L. H. Schwacke, R. S. Wells, et al. 2013. Comparison of abundance and habitat usage for common bottlenose dolphins between sites exposed to differential anthropogenic stressors within the estuaries of southern Georgia, U.S.A. Marine Mammal Science 29:114–135.
- Barnsley, M. F. 2014. Fractals everywhere. Morgan Kaufmann, Burlington, MA.

- Baş, A. A., A. Öztürk and B. Öztürk. 2015. Selection of critical habitats for bottlenose dolphins (*Tursiops truncatus*) based on behavioral data, in relation to marine traffic in the Istanbul Strait, Turkey. Marine Mammal Science 31:979–997.
- Bejder, L., A. Samuels, H. Whitehead and N. Gales. 2006. Interpreting short-term behavioural responses to disturbance within a longitudinal perspective. Animal Behaviour 72:1149–1158.
- Bejder, L., A. Samuels, H. Whitehead, H. Finn and S. Allen. 2009. Impact assessment research: Use and misuse of habituation, sensitisation and tolerance in describing wildlife responses to anthropogenic stimuli. Marine Ecology Progress Series 395:177–185.
- Bell, A. M., 2007. Future directions in behavioural syndromes research. Proceedings of the Royal Society of London B: Biological Sicences 274:755–761.
- ben-Avraham, D., and S. Havlin. 2000. Diffusion and reactions in fractals and disordered systems. Cambridge University Press, Cambridge, U.K.
- Bradbury, R. H., R. E. Reichelt and D. G. Green. 1984. Fractals in ecology: Methods and interpretation. Marine Ecology Progress Series 14:295–296.
- Brandt, M. J., A. Diederichs, K. Betke and G. Nehls. 2011. Responses of harbour porpoises to pile driving at the Horns Rev II offshore wind farm in the Danish North Sea. Marine Ecology Progress Series 421:205–216.
- Buckstaff, K. C. 2006. Effects of watercraft noise on the acoustic behavior of bottlenose dolphins, *Tursiops truncatus*, in Sarasota Bay, Florida. Marine Mammal Science 20:709– 725.
- Burnell, S. R., and M. M. Bryden. 1997. Coastal residence periods and reproductive timing in Southern right whales, *Eubalaena australis*. Journal of Zoology 241:613–621.
- Chattopadhyay, S., and S. S. Kumar. 2007. Fractal dimensions of selected coastal water bodies in Kerala, SW coast of India – A case study. Indian Journal of Marine Sciences 36:162– 166.
- Carroll, E. L., W. J. Rayment, A. M. Alexander, et al. 2014. Reestablishment of former wintering grounds by New Zealand southern right whales. Marine Mammal Science 30:206–220.
- Clark, C. W., W. T. Ellison and B. L. Southall, et al. 2009. Acoustic masking in marine ecosystems: Intuitions, analysis, and implication. Marine Ecology Progress Series 395:201–222.
- Commito, J. A., and B. R. Rusignuolo. 2000. Structural complexity in mussel beds: The fractal geometry of surface topography. Journal of Experimental Marine Biology and Ecology 255:133–152.
- Constantine, R., D. H. Brunton and T. Dennis. 2004. Dolphin-watching tour boats change bottlenose dolphin (*Tursiops truncatus*) behaviour. Biological Conservation 117:299–307.
- Coughlin, D. J., J. R. Strickler and B. Sanderson. 1992. Swimming and search behaviour in clownfish, *Amphiprion perideraion*, larvae. Animal Behaviour 44:427–440.
- Cribb, N., and L. Seuront. 2016. 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. Journal of Experimental Marine Biology and Ecology 482:118–127.
- Dimri, V. P., and K. Srivastava. 2007. Tsunami propagation of the 2004 Sumatra earthquake and the fractal analysis of the aftershock activity. Indian Journal of Marine Sciences 36:128–135.
- Dowling, N. A., S. J. Hall and J. G. Mitchell. 2000. Foraging kinematics of barramundi during early stages of development. Journal of Fish Biology 57:337–353.
- Edgar, G., 2004. Classics on fractals. Westview Press, Boulder, CO.
- Edwards, A. M., 2011. Overturning conclusions of Lévy flight movement patterns by fishing boats and foraging animals. Ecology 92:1247–1257.

- Ellison, W. T., B. L. Southall, C. W. Clark and A. S. Frankel. 2012. A new context-based approach to assess marine mammal behavioural responses to anthropogenic sounds. Conservation Biology 26:21–28.
- Falconer, K. 1985. The geometry of fractal sets. Cambridge University Press, Cambridge, U.K.
- Falconer, K. J. 1993. Fractal geometry. Mathematical foundations and applications. Wiley, Chichester, U.K.
- Feder, J. 1988. Fractals. Plenum Press, New York, NY.
- Ferguson, S. H., M. K. Taylor, E. W. Born and F. Messier. 1998. Fractals, sea ice landscape and spatial patterns of polar bears. Journal of Biogeography 25:1081–1092.
- Firth, L. B., and S. J. Hawkins. 2011. Introductory comments Global change in marine ecosystems: Patterns, processes and interactions with regional and local scale impacts. Journal of Experimental Marine Biology and Ecology 400:1–6.
- Frontier, S. 1987. Applications of fractal theory to ecology. Pages 335–378 in P. Legendre and L. Legendre, eds. Developments in numerical ecology. Springer Verlag, Berlin, Germany.
- Gill, J. A., K. Norris and W. J. Sutherland. 2001. Why behavioural responses may not reflect the population consequences of human disturbance. Biology of Conservation 97:265– 268.
- Glavovic, B. C., and G. P. Smith. 2014. Adapting to climate change. Springer, New York, NY.
- Goldberger, A. L., and B. J. West. 1990. Fractals in physiology and medicine. Yale Journal of Biology and Medicine 60:421–435.
- Goldberger, A. L., D. R. Rigney and B. J. West. 1990. Chaos and fractal in human physiology. Scientific American 363:43–49.
- Goldberger, A. L., L. A. N. Amaral, L. Glass, *et al.* 2000. Physiobank, physiotookit and physionet. Components of a new research resource for complex physiologic signals. Circulation 101:e215–e220.
- Gordon, N. 2000. Introducing fractal geometry. Duxford, U.K.
- Greer, K., S. Harper, D. Zeller and D. Pauly. 2014. Evidence for overfishing on pristine coral reefs: Reconstructing coastal catches in the Australian Indian Ocean Territories. Journal of the Indian Ocean Region 10:67–80.
- Hastings, H. M., and G. Sugihara. 1993. Fractals. A user's guide for the natural sciences. Oxford University Press, Oxford, U.K.
- Hausdorff, J. M., C. K. Peng, Z. Ladin, J. Y. Wei and A. R. Goldberger. 1995. Is walking a random walk? Evidence for long-range correlations in stride interval of human gait. Journal of Applied Physiology 78:349–358.
- Hausdorff, J. M., S. L. Mitchell, R. Firtion, et al. 1997. Altered fractal dynamics of gait: Reduced stride-interval correlations with aging and Huntington's disease. Journal of Applied Physiology 82:262–269.
- Hausdorff, J. M., D. A. Rios and H. K. Edelberg. 2001. Gait variability and fall risk in community-living older adults: A 1-year prospective study. Archives of Physical Medicine and Rehabilitation 82:1050–6105.
- Havsteen, B. H. 2002. Evidence of quasi-linear gas transport through sperm whale myoglobin. European Biophysics Journal with Biophysics Letters 31:549–553.
- Hildebrand, J. A. 2009. Anthropogenic and natural sources of ambient noise in the ocean. Marine Ecology Progress Series 395:5–20.
- Hill, R. A., A. Bentley and R. I. M. Dunbar. 2008. Network scaling reveals consistent fractal pattern in hierarchical mammalian societies. Biology Letters 4:748–751.
- Hocking, P. M., K. M. D. Rutherford and M. Picard. 2007. Comparison of time-based frequencies, fractal analysis and T-patterns for assessing behavioural changes in broiler breeders fed on two diets at two levels of feed restriction: A case study. Applied Animal Behaviour Science 104:37–48.

- Hodgson, A. J., and H. Marsh. 2007. Response of dugongs to boat traffic: The risk of disturbance and displacement. Journal of Experimental Marine Biology and Ecology 340:50–61.
- Hooker, S. K., A. Fahlman, M. J. Moore, *et al.* 2011. Deadly diving? Physiological and behavioral management of decompression stress in diving mammals. Proceedings of the Royal Society B: Biological Sciences 279:1041–1050.
- Hu, S., C. Zhiyu, C. Cunqiang and J. Zhang. 2009. Risk prediction of marine traffic based on Fractal interpolation algorithm. IEEE International Conference on Industrial Engineering and Engineering Management 330–334.
- Humphries, N. E., N. Queiroz, J. R. M. Dyer, *et al.* 2010. Environmental context explains Lévy and Brownian movement patterns of marine predators. Nature 465:1066–1069.
- Humphries, N. E., H. Weimerskirch, N. Queiroz, E. J. Southall and D. W. Sims. 2012. Foraging success of biological Lévy flights recorded in situ. Proceedings of the National Academy of Science of the United States of America 109:7169–7174.
- Isojunno, S., and P. J. O. Miller. 2015. Sperm whale response to tag boat presence: Biologically informed hidden state models quantify lost feeding opportunities. Ecosphere 6:1–46.
- Ivanov, P. Ch., L. A. Nunes Amaral, A. L. Golberger, S. Havlin, M. G. Rosenblum, Z. R. Struzik and H. E. Stanley. 1999. Multifractacilty in human heartbeat dynamics. Nature 399:461–465.
- Jefferson, T. A. 2000. Population biology of the Indo-Pacific humpbacked dolphin in Hong Kong waters. Wildlife Monographs 144:1–65.
- Kelly, C., G. A. Glegg and C. D. Speedie. 2004. Management of marine life disturbance. Ocean & Coastal Management 47:1–19.
- Kembro, M. A., R. H. Marin, J. A. Zygaldo and R. M. Gleiser. 2009a. Effects of the essential oils of *Lippia turbinata* and *Lippia polystacha* (Verbenaceae) on the temporal pattern of locomotion of the mosquito *Culex quinquefasciatus* (Diptera:Culicidae) larvae. Parasitology Research 104:1119–1127.
- Kembro, M. A., P. A. Perillo, D. G. Pury and R. H. Satterlee. 2009/. Fractal analysis of the ambulation pattern of Japanese quail. British Poultry Science 50:161–170.
- Kenkel, N. C., and D. J. Walker. 1993. Fractals and ecology. Abstracta Botanica 17:53-70.
- Kuikka, J. T. 2003. Scaling laws in physiology: Relationship between size, function, metabolism and life expectancy. International Journal of Nonlinear Sciences and Numerical Simulation 4:317–327.
- Laidre, K. L., M. P. Heide-Jørgensen, M. L. Logsdon, R. C. Hobbs, R. Dietz and G. R. VanBlaricom. 2004. Fractal analysis of narwhal space use patterns. Zoology 107:3–11.
- La Manna, G., M. Manghi, G. Pavan, F. Lo Mascolo and G. Sara. 2013. Behavioural strategy of common bottlenose dolphins (*Tursiops truncatus*) in response to different kinds of boats in the waters of Lampedusa Island (Italy). Aquatic Conservation 23:745–757.
- Lemon, M., T. P. Lynch, D. H. Cato and R. G. Harcourt. 2006. Response of travelling bottlenose dolphins (*Tursiops aduncus*) to experimental approaches by a powerboat in Jervis Bay, New South Wales, Australia. Biological Conservation 127:363–372.
- Lesmoir-Gordon, N., W. Rood and R. Rodney. 2000. Introducing fractal geometry. Icon Books, Cambridge, U.K.
- Lessage, V., C. Barrette, M. C. S. Kingsley and B. Sjare. 1999. The effect of vessel noise on the vocal behavior of belugas in the St. Lawrence River Estuary, Canada. Marine Mammal Science 15:65–84.
- Li, Y., C. Ortiz and M. C. Boyce. 2012. Bioinspired, mechanical, deterministic fractal model for hierarchical suture joints. Physical Review E 85:031901.
- Lusseau, D. 2003*a*. Effects of tour boats on the behavior of bottlenose dolphins: Using Markov chains to model anthropogenic impacts. Conservation Biology 17:1785–1793.
- Lusseau, D. 2003b. Male and female bottlenose dolphins *Tursiops* spp. have different strategies to avoid interactions with tour boats in Doubtful Sound, New Zealand. Marine Ecology Progress Series 257:267–274.

- Lusseau, D. 2004. The hidden cost of tourism: Effects of interactions with tour boats on the behavioral budget of two populations of bottlenose dolphins in Fiordland, New Zealand. Ecological and Society 9(1):2.
- Lusseau, D. 2005. Residency patterns of bottlenose dolphins *Tursiops* spp. in Milford Sound, New Zealand, is related to boat traffic. Marine Ecology Progress Series 295:265–272.
- Lusseau, D. 2006. The short-term behavioral reactions of bottlenose dolphins to interactions with boats in Doubtful Sound, New Zealand. Marine Mammal Science 22:802–818.
- Lusseau, D., and L. Bejder. 2007. The long-term consequences of short-term responses to disturbance experiences from whalewatching impact assessment. International Journal of Comparative Physiology 20:228–236.
- MacIntosh, A. J. J. 2014. The fractal primate: Interdisciplinary science and the math behind the monkey. Primate Research 30:95–119.
- MacIntosh, A. J. J., C. L. Alados and M. A. Huffman. 2011. Fractal analysis of behaviour in a wild primate: Behavioral complexity in health and disease. Journal of the Royal Society Interface 8:1497–1509.
- MacIntosh, A. J. J., L. Pelletier, A. Chiaradia, A. Kato and Y. Ropert-Coudert. 2013. Temporal fractals in seabird foraging behaviour: Diving through the scales of time. Scientific Reports 3:1884.
- Mandelbrot, B. B. 1967. How long is the coast of Britain? Statistical self-similarity and fractional dimension. Science 156:636–638.
- Mandelbrot, B. B. 1977. Fractals. Form, chance, and dimension. Freeman, San Francisco, CA.

Mandelbrot, B. B. 1983. The fractal geometry of nature. Freeman, San Francisco, CA.

- Manzanera, M., and J. Romero. 2000. Multifractal structure in *Posidonia oceanica* meadows. Biologia Marina Mediterranea 7:389–392.
- María, G. A., J. Escós and C. L. Alados. 2004. Complexity of behavioural sequences and their relation to stress conditions in chickens (*Gallus gallus domesticus*): A non-invasive technique to evaluate animal welfare. Applied Animal Behaviour 86:93–104.
- Matias, M. G., A. J. Underwood, D. F. Hochuli and R. A. Coleman. 2010. Independent effects of patch size and structural complexity on diversity of benthic macroinvertebrates. Ecology 10:1908–1915.
- Mathews, E. A., L. A. Jemison, G. W. Pendleton, K. M. Blejwas, K. E. Hood and K. L. Raum-Suryan. 2016. Haul-out patterns and effects of vessel disturbance on harbor seals (*Phoca vitulina*) on glacial ice in Tracy Arm, Alaska. Fishery Bulletin 114:186–202.
- Matson, M. C., J. A. Thomas and D. St. Aubin. 2005. Effects of boat activity on the behaviour of bottlenose dolphins (*Tursiops truncatus*) in waters surrounding Hilton Head island, South Carolina. Aquatic Mammals 31:133–140.
- Mazgalev, T. N. 2005. The Sisyphean task of atrioventricular nodal scaling: Is the stone at the top of the mountain? Editorial commentary. Heart Rhythm 2:197–200.
- McCarthy, E. 2004. International regulation of underwater sound: Establishing rules and standards to address ocean noise pollution. Kluwer Academic Publishers, Boston, MA.
- Meager, J. J., T. A. Schlacher and M. Green. 2011. Topographic complexity and landscape temperature patterns create a dynamic habitat structure on a rocky intertidal shore. Marine Ecology Progress Series 428:1–12.
- Medvinsky, A. B., S. V. Petrovskii, I. A. Tikhonova, H. Malchow and B. Li. 2002. Spatiotemporal complexity of plankton and fish dynamics. Society for Industrial and Applied Mathematics Review 44:311–370.
- Méndez, V., D. Campos and F. Bartumeus. 2014. Stochastic foundations in movement ecology. Springer, New York, NY.
- Mishima, M., T. Hirai, H. Itoh, et al. 1999. Complexity of terminal airspace geometry assessed by lung computed tomography in normal subjects and patients with chronic obstructive pulmonary disease. Proceedings of the National Academy of Sciences of the United States of America 96:8829–8834.
- Monnahan, C. C., T. A. Branch and A. E. Punt. 2015. Do ship strikes threaten the recovery of endangered eastern North Pacific blue whales? Marine Mammal Science 31:279–297.

- Motohashi, Y., Y. Miyazaki and T. Takano. 1993. Assessment of behavioural effects of tetrachloroethylene using a set of time-series analyses. Neurotoxicology and Teratology 15:3–10.
- Mouillot, D., and D. Viale. 2001. Satellite tracking of a fin whale (*Balaenoptera physalus*) in the northwestern Mediterranean Sea and fractal analysis of its trajectory. Hydrobiologia 452:163–171.
- Mustika, P. L. K., A. Birtles, Y. Everingham and H. Marsh. 2015. Evaluating the potential disturbance from dolphin watching in Lovina, north Bali, Indonesia. Marine Mammal Science 31:808–817.
- New, L. F., J. Harwood, L. Thomas, *et al.* 2013. Modelling the biological significance of behavioural change in coastal bottlenose dolphins in response to disturbance. Functional Ecology 27:314–322.
- Noujaim, S. F., E. Lucca, V. Munoz, et al. 2004. From mouse to whale: A universal scaling relation for the PR interval of the electrocardiogram of mammals. Circulation 110:2802–2808.
- Nowacek, S. M., R. S. Wells and A. R. Sollow. 2001. Short-term effects of boat traffic on bottlenose dolphins, *Tursiops truncatus*, in Sarasota Bay, Florida. Marine Mammal Science 17:673–688.
- O'Connor, S., R. Campbell, H. Cortez and T. Knowles. 2009. Whale watching worldwide: Tourism numbers, expenditures and expanding economic benefits. A special report from the International Fund for Animal Welfare, Yarmouth, MA, prepared by Economists at Large. 295 pp.
- Ordnance Survey. 2016. Geography and maps. Available at https://www.ordnancesurvey.co. uk/support/geography-map-facts.html.
- Osborne, J. L., A. Smith, S. J. Clark, D. R. Reynolds, M. C. Baron, K. S. Lim and A. M. Reynolds. 2013. The ontogeny of bumblebee flight trajectories: From naïve explorers to experienced foragers. PLoS ONE 8:e78681.
- Parsons, E. C. M. 1998. The behaviour of Hong Kong's resident cetaceans: The Indo-Pacific humpbacked dolphin and the finless porpoise. Aquatic Mammals 24:91–98.
- Patenaude, N. J., W. J. Richardson, M. A. Smultea, W. R. Koski, G. W. Miller, B. Würsig and C. R. Greene. 2006. Aircraft sound and disturbance to bowhead and beluga whales during spring migration in the Alaskan Beaufort Sea. Marine Mammal Science 18:309– 335.
- Peng, C. K., S. Havlin, H. E. Stanley and A. L. Goldberger. 1995. Quantification of scaling exponents and crossover phenomena in nonstationary heartbeat time series. Chaos 5:82– 87.
- Peters, K. J., G. J. Parra, P. P. Skuza and L. M. Möller. 2013. First insights into the effects of swim-with-dolphin tourism on the behavior, response, and group structure of southern Australian bottlenose dolphins. Marine Mammal Science 29:484–497.
- Pirotta, E., B. E. Laesser, A. Hardaker, N. Riddoch, M. Marcoux and D. Lusseau. 2013. Dredging displaces bottlenose dolphins from an urbanised foraging patch. Marine Pollution Bulletin 74:396–402.
- Pirzl, R., N. J. Patenaude, S. Burnell and J. Bannister. 2009. Movements of southern right whales (*Eubalaena australis*) between Australian and subantarctic New Zealand populations. Marine Mammal Science 25:455–461.
- Popper, A. N., J. Fewtrell, M. E. Smith and R. D. McCauley. 2003. Anthropogenic sound: Effects on the behaviour and physiology of fishes. Marine Technology Society Journal 37:35–40.
- Powell, J. R., and R. S. Wells. 2010. Recreational fishing depredation and associated behaviors involving common bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida. Marine Mammal Science 27:111–129.
- Pyke, G. H., 2015. Understanding movements of organisms: It's time to abandon the Lévy foraging hypothesis. Methods in Ecology and Evolution 6:1–16.

- Qian, Z. W. 1996. Fractal dimensions of sediments in nature. Physical Review E 53:2304– 2308.
- Redondo, J. M., and A. K. Platonov. 2009. Self-similar distribution of oil spills in European coastal waters. Environmental Research Letters 4:014008.
- Reynolds, A. M. 2015*a*. Liberating Lévy walk research from the shackles of optimal foraging. Physics of Life Reviews 14:59–83.
- Reynolds, A. M., 2015*b*. Venturing beyond the Lévy flight foraging hypothesis. Physics of Life Reviews 14:115–119.
- Reynolds, A. M., and C. J. Rhodes. 2009. The Lévy flight paradigm: Random search patterns and mechanisms. Ecology 90:877–887.
- Rogers, T. L., and D. H. Cato. 2002. Individual variation in the acoustic behaviour of the adult male leopard seal, *Hydrurga leptonyx*. Behaviour 139:1267–1286.
- Rossman, S., N. B. Barros, P. H. Ostrom, C. A. Stricker, A. A. Hohn, H. Gandhi and R. S. Wells. 2013. Retrospective analysis of bottlenose dolphin foraging: A legacy of anthropogenic ecosystem disturbance. Marine Mammal Science 29:705–718.
- Rowntree, V. J., R. S. Payne and D. M. Schell. 2001. Changing patterns of habitat use by southern right whales (*Eubalaena australis*) on their nursery ground at Península Valdés, Argentina, and their long-range movements. Journal of Cetacean Research and management 2:133–143.
- Russell, D. J. F., and B. McConnell. 2014. Seal at-sea distribution, movements and behaviour. Report to DECC as part of the UK Department of Energy and Climate Change's offshore energy Strategic Environmental Assessment programme. 12 pp.
- Rutherford, K. M. D., M. J. Haskell, C. Glasbey, R. B. Jones and A. B. Lawrence. 2003. Detrended fluctuation analysis of behavioural responses to mild acute stressors in domestic hens. Applied Animal Behaviour Science 83:125–139.
- Rutherford, K. M. D., M. J. Haskell, C. Glasbey, R. B. Jones and A. B. Lawrence. 2004. Fractal analysis of animal behaviour as an indicator of animal welfare. Animal Welfare 13:99–103.
- Rutherford, K. M. D., M. J. Haskell, C. Glasbey and A. B. Lawrence. 2006. The response of growing pigs to chronic-intermittent stress treatment. Physiology and Behavior 89:670– 680.
- Sagan, H. 1994. Space-filling curves. Springer Verlarg, New York, NY.
- Santhaseelan, V., and V. K. Asari. 2013. Whale blow detection in infrared video using fractal analysis as tool for representing dynamic shape variation. 2013 IEEE Workshop on Applications of Computer Vision. Pp. 520–525.
- Scheidat, M., C. Castro, J. Gonzalez and R. Williams. 2004. Behavioural responses of humpback whales (*Megaptera novaeangliae*) to whalewatching boats near Isla de la Plata, Machalilla National Park, Ecuador. Journal of Cetacean Research and Management 6:63–68.
- Seuront, L. 2005. Hydrodynamical and tidal controls of small-scale phytoplankton patchiness. Marine Ecology Progress Series 302:93–101.
- Seuront, L. 2010. Fractals and multifractals in ecology and aquatic science. CRC Press, Boca Raton, FL.
- Seuront, L. 2011. Behavioral fractality in marine copepods: Endogenous rhythms vs. exogenous stressors. Physica A 309:250–256.
- Seuront, L. 2015. On uses, misuses and potential abuses of fractal analysis in zooplankton behavioral studies: A review, a critique and a few recommendations. Physica A 432:410– 434.
- Seuront, L., and N. Cribb. 2011. Fractal analysis reveals pernicious stress levels related to boat presence and type in the Indo-Pacific bottlenose dolphin, *Tursiops aduncus*. Physica A 390:2333–2339.
- Seuront, L., and S. C. Leterme. 2007. Increased zooplankton behavioural stress in response to short-term exposure to hydrocarbon contamination. The Open Oceanography Journal 1:1–7.

- Seuront, L., and J. G. Mitchell. 2008. Towards a seascape typology. I. Zipf versus Pareto laws. Journal of Marine Systems 69:310–327.
- Seuront, L., and F. G. Schmitt. 2005a. Multiscaling statistical procedures for the exploration of biophysical couplings in intermittent turbulence. Part I. Theory. Deep-Sea Research II 52:1308–1324.
- Seuront, L., and F. G. Schmitt. 2005b. Multiscaling statistical procedures for the exploration of biophysical couplings in intermittent turbulence. Part II. Applications. Deep-Sea Research II 52:1325–1343.
- Seuront, L., and H. E. Stanley. 2014. Anomalous diffusion and multifractality optimises mating encounters in the ocean. Proceedings of the National Academy of Science of the United States of America 111:2206–2211.
- Seuront, L., F. Schmitt, D. Schertzer, Y. Lagadeuc and S. Lovejoy. 1996a. Multifractal intermittency of Eulerian and Lagrangian turbulence of ocean temperature and plankton fields. Nonlinear Processes in Geophysics 3:236–246.
- Seuront, L., F. Schmitt, Y. Lagadeuc, D. Schertzer, S. Lovejoy and S. Frontier. 1996b. Multifractal structure of phytoplankton biomass and temperature in the ocean. Geophysical Research Letters 23:3591–3594.
- Seuront, L., F. Schmitt, Y. Lagadeuc, D. Schertzer and S. Lovejoy. 1999. Multifractal analysis as a tool to characterize multiscale inhomogeneous patterns. Example of phytoplankton distribution in turbulent coastal waters. Journal of Plankton Research 21:877–922.
- Sims, D. W., E. J. Southall, N. E. Humphries, *et al.* 2008. Scaling laws of marine predator search behaviour. Nature 451:1098–1102.
- Sims, D. W., N. E. Humphries, R. W. Bradford and B. D. Bruce. 2012. Lévy flight and Brownian search patterns of a free-ranging predator reflect different prey field characteristics. Journal of Animal Ecology 81:432–442.
- Sims, D. W., A. M. Reynolds, N. E. Humphries, E. J. Southall, V. J. Wearmouth, B. Metcalfe and R. J. Twitchett. 2014. Hierarchical random walks in trace fossils and the origin of optimal search behavior. Proceedings of the National Academy of Sciences of the United States of America 111:11073–11078.
- Sini, M. I., S. J. Canning, K. A. Stockin and G. J. Pierce. 2005. Bottlenose dolphins around Aberdeen harbour, north-east Scotland: A short study of habitat utilization and the potential effects of boat traffic. Journal of the Marine Biological Association of the United Kingdom 85:1547–1554.
- Stamation, K., P. Shaughnessy, K. Waples and S. Briggs. 2010. Behaviopral responses of humpback whales (*Megaptera novaeangliae*) to whale-watching vessels on the southeastern coast of Australia. Marine Mammal Science 26:98–122.
- Sturmberg, J. P., and B. J. West. 2013. Fractals in physiology and medicine. Pages 171–192 in J. P. Sturmberg and C. M. Martin, eds. Handbook of systems and complexity in health. Springer, New York, NY.
- Tatsuro, S., N. Haruhiko and K. Tetsuro. 2001. A fractal evaluation of school movement patterns using fish behavior models. Transactions-Information Processing Society of Japan 42:1592–1600.
- Tikhonov, D. A., J. Enderlein, H. Malchow and A. B. Medvinsky. 2001. Chaos and fractals in fish school motion. Chaos, Solitons & Fractals 12:277–288.
- Thompson, R. C., Y. Olsen, R. P. Mitchell, et al. 2004. Lost at sea: Where is all the plastic? Science 304:838.
- Thompson, R. C., S. H. Swan, C. J. Moore and F. S. von Saal. 2009. Our plastic age. Philosophical Transactions of the Royal Society B 364:1973–1976.
- Thompson, P. M., K. L. Brookes, I. M. Graham, T. R. Barton, K. Needham, G. Bradbury and N. D. Merchant. 2013. Short-term disturbance by a commercial two-dimensional seismic survey does not lead to long-term displacement of harbour porpoises. Proceedings of the Royal Society B: Biological Sciences 280:20132001.
- Townsend, C. H. 1935. The distribution of certain whales as shown by logbook records of American whaleships. Zoologica 19:1–50.

- Trathan, P. N., M. A. Collins, S. M. Grant, M. Belchier, D. K. A. Barnes, J. Brown and I. J. Staniland. 2014. The South Georgia and the South Sandwich Islands MPA: Protecting a biodiverse oceanic island chain situated in the flow of the Antarctic Circumpolar Current. Advances in Marine Biology 69:15–78.
- Twiss, S. D., and J. Franklin. 2010. Individually consistent behavioural patterns in wild, breeding male grey seals (*Halichoerus grypus*). Aquatic Mammals 36:234–238.
- Van Parijs, S. M., G. D. Hastie and P. M. Thompson. 2000. Individual and geographical variation in display behaviour of male harbour seals in Scotland. Animal Behaviour 59:559–568.
- Viswanathan, G. M., S. V. Buldyrev, S. Havlin, et al. 1999. Optimizing the success of random searches. Nature 401:911–914.
- Viswanathan, G. M., M. G. E. da Luz, E. P. Raposo and H. E. Stanley. 2011. The physics of foraging: An introduction to random searches and biological encounters. Cambridge University Press, Cambridge, U.K.
- Wang, Q. L., J. H. He and Z. B. Li. 2012. Fractional model for heat conduction in polar bear hairs. Thermal Science 16:339–342.
- Wartzok, D., A. N. Popper, J. Gordo and J. Merrill. 2003. Factors affecting the responses of marine mammals to acoustic disturbance. Marine Technology Society Journal 37:6–15.
- Waycott, M., C. M. Duarte, T. J. N. Carruthers, et al. 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. Proceedings of the National Academy of Sciences of the United States of America 106:12377–12381.
- West, B. J. 2010. Fractal physiology and the fractional calculus: A perspective. Frontiers in Physiology 1:12.
- West, B. J., M. Bologna and P. Grigolini. 2008. Maximizing information exchange between complex networks. Physics Reports 468:1–99.
- Williams, R., D. E. Bain, J. K. B. Ford and A. W. Trites. 2002a. Behavioural responses of male killer whales to a "leapfrogging" vessel. Journal of Cetaceans Research and Management 4:305–310.
- Williams, R., A. W. Trites and D. E. Bain. 2002b. Behavioural responses of killer whales (Orcinus orca) to whale-watching boats: Opportunistic observations and experimental approaches. Journal of Zoology 256:255–270.
- Williams, R., D. Lusseau and P. S. Hammond. 2006. Estimating relative energetic costs of human disturbance to killer whales (*Orcinus orca*). Biological Conservation 133:301–311.
- Williams, R., E. Ashe, D. Sandilands and D. Lusseau. 2011. Stimulus-dependent response to disturbance affecting the activity of killer whales. Scientific Committee of the International Whaling Commission. Document: SC/63/WW5 1–27.
- Wilson, K., M. Lance, S. Jeffries and A. Acevedo-Gutiérrez. 2014. Fine-scale vriability in harbor seal foraging behavior. PLoS ONE 9(4):e92838.
- Wright, A. J., N. A. Soto, A. L. Baldwin, et al. 2007. Do marine mammals experience stress related to anthropogenic noise? International Journal of Comparative Psychology 20:274–316.
- Yang, W. J., and D. Baleanu. 2013. Fractal heat conduction problem solved by local fractional variation iteration methods. Thermal Science 17:625–628.
- Zar, J. H. 1999. Biostatistical analysis. Prentice Hall, Englewood Cliffs, NJ.

Received: 6 August 2015 Accepted: 16 December 2016