Sixteen years later: an updated evaluation of the impacts of chronic human interactions with bottlenose dolphins (*Tursiops truncatus truncatus*) at Panama City, Florida, USA

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ABSTRACT

Panama City, Florida is considered a notorious 'hot spot' in the southeastern United States for chronic illegal feeding and harassment of bottlenose dolphins. The nature and extent of these interactions was evaluated by Samuels and Bejder (2004); they concluded that food provisioning was the basis for human interactions with wild dolphins, and that these encounters were likely harmful to dolphins. A follow-up study was conducted in 2014 to reassess the current state of human interactions with wild dolphins. The number of conditioned dolphins ($n = 21$) tripled compared to the previous study. Both studies found conditioned dolphins engaged in human interaction events during approximately 75% of observable time points when vessels or swimmers were present. In this study, conditioned dolphins spent as much as 81% of their time begging or patrolling and significantly decreased their distance moved while doing so. Nested multinomial regression analysis revealed conditioned dolphins engaged in resting or foraging (i.e. natural) behaviour were extremely likely to switch to begging or patrolling (i.e. interaction) behaviours when vessels or swimmers were present. Numerous high risk situations were observed for both conditioned dolphins and humans during these interactions. The latest development in illegal feeding was documented: bait boats feeding dolphins to lure the animals into interactions with tour vessels and swimmers. Our observations indicate that the problem in Panama City has escalated: dolphins are being actively provisioned, often for long periods of time; the proportion of conditioned dolphins has increased; interacting dolphins and humans are both at increased risk for injury, illness, or death; and conditioned dolphin activity budgets and movement patterns continue to be negatively impacted by human behaviour. We recommend a more aggressive management strategy, such as targeted and sustained enforcement of existing regulations as well as additional restrictions that prohibit close approaches and in-water interactions for Panama City in order to curtail continued harassment of dolphins and reduce the risk of injury for both humans and dolphins.

KEYWORDS: BEHAVIOUR; BOTTLENOSE DOLPHIN; CONSERVATION; WHALE WATCHING

INTRODUCTION

Wildlife viewing in the marine environment has been growing at a rapid rate. Whale watching activities worldwide are currently estimated as a $2.1 billion USD industry and support approximately 13,000 jobs (O'Connor *et al.,* 2009) with capacity for future expansion (Cisneros-Montemayor and Sumaila, 2010). Commercial and private tours to view marine mammals range from land or vessel-based platforms observing animals to in-water swim-with activities that encourage close encounters and interactions with the animals. The impacts of tourism on bottlenose dolphins (*Tursiops* spp.) are well studied since the species is found year-round in close proximity to the shore and human populations. Dolphins are significantly affected by human interactions both at an individual and population level (Bejder *et al.,* 2006a; Bejder *et al*., 2006b; Lusseau *et al.,* 2006). Numerous studies examining the effects of viewing or swim-with tours have shown that vessels and swimmers disturb dolphins' natural behaviour patterns, causing shifts in activity budgets, changes in group cohesion and group size, deviations in swim patterns, increased travelling behaviour, and reductions in natural foraging and resting behaviours (Allen and Read, 2001; Bejder *et al.,* 2006a; Bejder *et al.,* 2006b; Constantine *et al.,* 2004; Samuels and Bejder, 2004). These short-term behavioural changes can lead to long-term biological impacts for dolphin populations such as declines in reproductive health and permanent habitat displacement or abandonment (Bejder, 2005; Bejder *et al.,* 2006b; Lusseau, 2006; Lusseau *et al*., 2006; Parsons, 2012; Tyne *et al.,* 2014). The popularity and growth of marine mammal tourism continues despite a wealth of scientific literature documenting how marine mammals are negatively impacted by such interactions (O'Connor, 2009).

In addition, activities involving provisioning (i.e. feeding) the animals have emerged either with government approval (e.g. in Australia: Foroughirad and Mann, 2013; Mann *et al*., 2000; Mann and Kemps, 2003), in violation of laws prohibiting feeding (e.g. in the United States: Cunningham-Smith *et al*., 2006; Donaldson *et al*., 2010; 2012; Finn *et al*., 2008; NMFS, 1994; Samuels and Bejder, 2004), and has been defined as 'ecologically intrusive' by the International Whaling Commission (IWC) (Parsons *et al.,* 2006). In either scenario, feeding activities seek to facilitate reliable and close interactions between people and marine mammals in the wild. However, it has been well documented for more than 20 years that feeding wild dolphins can lead to a variety of high risk situations that place both dolphins and people in danger (Cunningham-Smith *et al.,* 2006; NMFS, 1994; Orams *et al.,* 2002; Samuels and Bejder, 2004). When dolphins learn to associate people with food, unnatural behaviours such as begging for handouts disrupt their natural foraging repertoire and become an abnormal and detrimental feeding strategy (NMFS, 1994; Powell and Wells, 2011). Conditioned dolphins approach boats more readily looking for handouts, thus increasing the animals' risk for boat strike or gear entanglement (Bechdel *et al.,* 2009; Powell and

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Wells, 2011; Samuels and Bejder, 2004; Wells and Scott, 1997). Conditioned dolphins can also become targets for human acts of retaliation, often from fishers who become frustrated by dolphins begging, removing bait or catch from their lines or scavenging on undersized throw-backs (DOJ, 2006; 2007). Begging and other human-conditioned behaviours can be passed through a dolphin population via social learning, thus perpetuating and increasing the prevalence of the problem over time (Donoghue *et al.,* 2002; Wells, 2003; Whitehead *et al.,* 2004). Calves of provisioned mothers are at increased risk of compromised developmental and social learning skills, predation, and insufficient hunting experience due to neglect experienced while mothers are seeking handouts from humans (Foroughirad and Mann, 2013; Mann and Barnett, 1999; Mann and Kemps, 2003).

The Marine Mammal Commission (MMC) and the National Marine Fisheries Service (NMFS) have been concerned about the impacts of marine mammal tourism in the United States for several decades (i.e. Spradlin *et al.*, 1999)[4]. The Marine Mammal Protection Act (MMPA) and its implementing regulations prohibit the 'take'[5] and 'harassment'[6] of marine mammals. However, enforcement of those prohibitions has been challenging because of either real or perceived gaps in the scientific knowledge about the impacts of harassment, as well as varying interpretations about the legal definitions of those terms (e.g. Lewandowski, 2005). Feeding and attempting to feed a marine mammal in the wild is also included under the definition of 'take' and is prohibited under the MMPA (50 CFR 216.3). In 1998, the MMC funded a study (i.e. Samuels and Bejder, 1998) designed to systematically evaluate how chronic in-water interactions with humans affect the behaviour of free-ranging common bottlenose dolphins (*Tursiops truncatus truncatus*). From the results of Samuels and Bejder (1998), the MMC concluded that interacting with dolphins in the wild constitutes at least 'level B harassment', and recommended NMFS promulgate regulations to prohibit the activities (MMC letter to NMFS, 23 May 2000).

The problem in Panama City, Florida

Panama City, Florida has been a well-known 'hot spot' in the southeastern United States for chronic feeding and harassment of bottlenose dolphins for more than three decades. The study by Samuels and Bejder (1998; 2004), funded by the MMC, concluded that chronic levels of human interactions with wild dolphins near Panama City, Florida were likely harmful and increased animals' risk for injury, illness, or death. Currently, Panama City hosts approximately 25 dolphin viewing and swim-with vessel companies; most offering swim-with opportunities in contradiction to NMFS recommended but voluntary wildlife viewing guidelines and policies[7] and some feed the local dolphins to promote close interactions. Private recreational boaters also regularly feed and harass dolphins. Illegal feeding and conditioning of wild dolphins have been carried out for many years (Samuels and Bejder, 1998; 2004). Conditioned dolphins at Panama City are effectively trained to interact with people through 'variable reinforcement', in which reinforcement (i.e. illegal food handouts) is delivered only after an unpredictable number of behavioural responses (i.e. begging) (Zeiler, 1968). This results in a suite of maladaptive behaviours that are difficult to extinguish. Tour businesses anecdotally complained of increases in dolphin aggression towards swimmers (Orams *et al.,* 1996; Samuels and Gifford, 1997; Connor, 2000). There are safety risks for both swimmers and dolphins given the high numbers of engaged vessels (e.g. 20) maneuvring through and around dolphins and swimmers at any given time, sometimes in fast currents and narrow channels.

Since the Samuels and Bejder (1998; 2004) study, NMFS has invested significant resources in research, education and outreach[8], and enforcement at Panama City to address the problem. Outreach efforts have included public service announcements, brochures, signage, and educational letters distributed throughout the community (Vail, 2016), although the extent to which this approach is effective is unknown. In addition, NMFS commissioned human dimension surveys and focus groups to better design outreach and education projects (Duda *et al.,* 2013a; 2013b). Targeted, pulsed enforcement and the issuance of citations for violations of the MMPA feeding prohibition have also increased in the Panama City area. Despite these efforts, illegal feeding and harassment of wild dolphins continues on a larger and more surreptitious scale than in the past.

This study aimed to understand how human-dolphin interactions at Panama City have progressed specifically in the absence of viewing or swim-with regulations. This study replicates the methods of Samuels and Bejder (1998; 2004) and compares the current and past results to track how dolphin behaviour, the number of dolphins affected, and the potential impacts and risk to dolphins (and people) have changed over the past 16 years and recommends an improved management strategy. The goal of this study was to provide quantitative, longitudinal results to assist managers in designing, justifying, and implementing management strategies to protect populations of dolphins from commercial and recreational activities of concern.

METHODS

Samuels and Bejder (1998; 2004) focused effort around 'Interaction Beach' offshore of Shell Island and St. Andrew

[4] The National Marine Fisheries Service (NMFS) is charged with managing cetaceans in the United States by implementing the Marine Mammal Protection Act (MMPA). The Marine Mammal Commission (MMC) is an independent government agency charged by the MMPA to provide oversight and advise the National Marine Fisheries Service (NMFS).

[5] 'Take' as defined by the MMPA implementing regulations (50 CFR 216.3) means 'to harass, hunt, capture, collect, or kill, or attempt to harass, hunt, capture or kill any marine mammal. This includes, without limitation, any of the following: the collection of dead animals, or parts thereof; the restraint or detention of a marine mammal, no matter how temporary; tagging a marine mammal; the negligent or intentional operation of an aircraft or vessel; the doing of any other negligent or intentional act which results in disturbing or molesting a marine mammal; or feeding or attempting to feed a marine mammal in the wild'.

[6] Harassment is defined in the 1994 amendments to the MMPA (16 U.S.C. 1362) as any act of pursuit, torment, or annoyance that has the *potential to injure* a marine mammal or marine mammal stock in the wild (Level A harassment); or that has the *potential to disturb* a marine mammal or marine mammal stock in the wild by causing disruption of behavioural patterns, including, but not limited to, migration, breathing, nursing, breeding, feeding, or sheltering, but does not have the potential to injure a marine mammal or marine mammal stock in the wild (Level B harassment).

[7] NOAA Fisheries policy on human interactions with wild marine mammals and suite of viewing guidelines is available at *http://www.nmfs.noaa.gov/topic/marine-life-viewing-guidelines*

[8] Examples of education and outreach materials can be found at *http://sero.nmfs.noaa.gov/protected_resources/outreach_and_education/index.html*.

Fig. 1. The approximate perimeter of the study area near Panama City, Florida is shown in red and green. The original study area by Samuels and Bejder (1998; 2004) is outlined in red. Most human-interactions were documented on the beach side of Shell Island, known as 'Interaction Beach' and at the 'Bait Barge' located inside the northwest shore of the pass (highlighted by the star).

Bay near Panama City, Florida, USA (Fig. 1). The methodologies and survey design for this study mirrored those of Samuels and Bejder (1998; 2004) to the extent possible (Table 7). Between 15–27 June 2014, 78hrs 44min of on-water observations were conducted within 30 n.m.^{2} around 'Interaction Beach', St. Andrew Bay, Grand Lagoon (including the 'Bait Barge' located inside this area), East Bay, and West Bay (Fig. 1).

The analyses of Samuels and Bejder (1998; 2004) were repeated to facilitate longitudinal comparison and additional analyses were performed to more fully elucidate the progression of human-dolphin interactions in this area (Table 7).

Photo-identification and sightings

Photo-identification surveys were conducted throughout the study area (Fig. 1) using an unmarked 6.4m vessel with a 150hp 4-stroke engine. Although the vessel was unmarked, if asked by a tour business about our intentions, we identified ourselves and stated that we were studying the dolphins' behaviour. Tour businesses were not informed of our presence prior to the study.

The goals of photo-identification surveys were to determine the number of individual dolphins that engaged in human interactions and to locate prospective animals for focal follows. Surveys were expanded outside of areas studied by Samuels and Bejder (1998; 2004) to locate non-conditioned dolphins (i.e. animals that did not engage in human interactions) for focal follows and to document any new human interaction hot-spots. Survey effort was measured by recording the GPS location of the research vessel every 3mins when 'on effort', that is, actively searching for dolphins during surveys. Surveys were discontinued if the wind reached ≥ 4 on the Beaufort scale.

For each dolphin sighting, date, time, location, GPS coordinates, environmental parameters, number of dolphins, and behaviour of all dolphins were recorded (Tables 1 and 2). Whenever possible, all dolphins within the group were photographed. If a dolphin was seen engaging in human interactions (Table 2) during a sighting, the behaviour(s) and the corresponding photograph frame numbers were recorded. Photographs were analysed and identified in accordance with the standards defined in Urian *et al.* (1999) and Rosel *et al.* (2011) and assigned to a catalogue if of sufficient quality.

Samuels and Bejder (2004) defined 'conditioned' dolphins as those that were sighted accepting food and repeatedly exhibiting behaviours listed in Table 2. However, feeding was anticipated to be more clandestine than it was in the previous study based on increased enforcement presence and citations in recent years. Therefore, 'conditioned' dolphins were defined as those documented engaging in two or more

Table 1

Definitions of behaviours used for this study (adapted from Shane *et al.*, 1986).

Behaviour	Description
Mill	Non-directional movement; frequent changes in heading.
Forage	Characterised by efforts to capture prey, such as active diving, chasing fish, or pinwheeling.
Travel	Persistent, directional movement.
Rest	Involves slow movement as a tight group and in the absence of other identifiable activities.
Socialise	Includes all active interactions between dolphins, such as contact, chasing, rubbing, sexual interactions, etc.

Table 2

Dolphin behaviour event definitions indicative of chronic human interactions (adapted from Perrtree *et al*., 2014; Powell and Wells, 2011; and Samuels and Bejder, 2004).

Behaviour	Description
Remain close	Remain within touching distance of one or more humans that are in the water or in a vessel.
Head up	Approach with head out of water (either vertically or horizontally) to within 2m of vessel or human.
Beg	Approach with head out of water and open mouth to within 2m of vessel or human.
Lunge at vessel	Vertical lunge with open mouth and head and flippers out of water within 2m of a vessel.
Follow vessel	Rapid travel within 2m of the side or stern of a vessel that is moving at speed (but not riding the bow wave).
Accept food	Accept (or attempts to accept) food or non-food items from humans.
Patrol	Dolphin travels in repeated directions around fishing gear, vessel, or dock.

of the behaviours listed in Table 2 regardless of whether, or not, they were observed to accept food.

Focal follows

Methodology for focal follows was adapted from Samuels and Bejder (1998; 2004) with only minor adjustments to account for expanded dolphin behavioural repertoires, difficulty locating non-conditioned dolphins, and unsafe boating conditions due to waters crowded with vessels, personal watercrafts, and swimmers. During focal follows, 50m distance from the dolphin was maintained when possible; however, this distance was reduced when necessary to maintain a clear view of the focal animal. Dolphins were always approached at idle speed from the side and slightly behind. Given the presence and behaviour of the research vessel was a constant variable and minimally invasive, we presumed that observed dolphin behavioural responses were a result of other variables such as tour vessels or swimmers; however, the research vessel may potentially have been a confounding variable.

A conditioned focal dolphin was selected if it was observed engaging in at least two human interaction behaviours (Table 2) during the initial sighting and ideally, had distinctive dorsal fin markings. Non-conditioned dolphins were selected if the animal and no others in the group displayed behaviours indicative of human interactions during the initial sighting. In only one instance, did an originally selected non-conditioned animal begin to display human interaction behaviours shortly after beginning a follow. That animal was re-categorised as a conditioned focal dolphin. Focal follows were conducted throughout the study area, although the majority were concentrated near ‘Interaction Beach’ to maintain consistency with Samuels and Bejder’s (1998; 2004) methodology (Fig. 2).

Standard behavioural sampling techniques were applied (Altmann, 1974). Nearly all data were collected via 3min point samples including: GPS location, group size, number of subgroups, group cohesion, presence/absence of dolphin behaviour events indicative of human interaction (Table 2), number of vessels within 10m and 50m (not including the research vessel), number of swimmers within 10m and 50m, and any notable comments. Focal dolphin activity as well as the overall group activity were recorded as the most predominant activity observed over the 3min interval (Tables 1 and 2). All human-dolphin interactions were documented that presented potential risk to either humans or dolphins during each point sample (Table 3). Samuels and Bejder (1998; 2004) collected point samples at 1min intervals when focal dolphins were in close proximity to human activity. However, a 3min interval was maintained when focal dolphins were in close proximity to humans due to the difficulties of safely manoeuvring the research vessel amongst the large number of vessels and swimmers present while also monitoring the focal animal.

Statistical analyses

Replication of Samuels and Bejder methodologies

Behavioural data from focal follows were compiled and summarised according to conditioned or non-conditioned status (Samuels and Bejder, 1998; 2004). The percent time during a follow that a focal dolphin was within 10m or 50m of a swimmer or vessel, the percent time the focal dolphin engaged in human interaction events, the percent time the focal dolphin was fed or attempted to be fed, and the percent time the focal dolphin or interacting human was at risk were all quantified.

Supplementary analysis: Markov chains

First-order discrete-time Markov chains were used to build transition matrices of proceeding to succeeding behaviour

Table 3

Human-dolphin interactions that present risk of injury, illness, or death (adapted from Samuels and Bejder, 2004).

Interaction risk code	Type of interaction	Sources of risk
D1	Human and dolphin make physical contact (or within touching distance).	Human may inadvertently touch vulnerable body parts of dolphin; human may be aggressive and injure dolphin; human attempts to ride dolphin; potential for disease transmission.
D2	Dolphin is in close proximity to vessels.	Dolphin may be injured by propeller, hit by moving vessel, crushed or trapped between two vessels, or injured by an object that falls or is dropped form a vessel.
D3	Dolphin is in close proximity to deployed fishing gear.	Dolphin may be entangled, hooked, or ingest fishing gear; dolphin may learn to steal fish from fishers; dolphin may be injured by retaliatory action by fisher.
D4	Human feeds dolphin.	Dolphin may ingest tainted fish or inappropriate food; young dolphins may not learn appropriate foraging skills; dolphin less vigilant and prone to predation; conspecific aggression.
D5	Human offers object to dolphin.	Dolphin may ingest object and sustain internal injuries.
H1	Human and dolphin make physical contact (or within touching distance).	Dolphin may inadvertently touch vulnerable body parts of human; dolphin may be aggressive and injure human; potential for disease transmission.

states. Separate chains were constructed for the presence and absence of human stimuli (i.e. vessels or swimmers) within 10m and 50m. Both conditioned and non-conditioned dolphins were included in this analysis. The use of Markov chains is well described in the literature and is typically used to quantify disturbance impacts to marine mammals from anthropogenic sources (e.g. Dans *et al.,* 2008; Lusseau, 2003; Lusseau, 2004; Meissner *et al.,* 2015; Peters *et al*., 2013; Stockin *et al.,* 2008). These chains quantify the dependence of a behaviour on the preceding ones and provide probabilities of transition from one behaviour to another (Lusseau, 2003). This method allows for a direct comparison to other marine mammal behavioural studies.

Data were compiled into two-way contingency tables as described in Lusseau (2003) using *Proc Freq* in SAS v9.3 (SAS Institute, Inc., Cary, NC). Intra-specific socialising was never observed and resting only observed once as the dominant activity state over a 3min period; therefore, these behaviours were excluded from the analysis. Begging and patrolling behaviour states were combined into an 'Interaction' behaviour category because the sample size for begging was small ($n = 13$). Begging was not often witnessed as a dominant behavioural state over a 3min interval but was typically an event that occurred while the dolphin was patrolling near vessels or swimmers. The transition probabilities were calculated for all Markov chains as:

$$p_{i,j} = \frac{a_{i,j}}{\sum_{j=1}^{4} a_{i,j}}, \sum_{j=1}^{4} p_{i,j} = 1$$

where $p_{i,j}$ is the transition probability from preceding behaviour i to succeeding behaviour j and $a_{i,j}$ is the number of observed transitions from behaviour i to behaviour j. Transition probabilities were compared using an exact test for Pearson chi-square for proportions (Pearson, 1900).

Following the Perron-Frobenius Theorom and ergodic theorem (Caswell, 2001), the dominant left eigenvector of the dominant eigenvalue for each transitional matrix corresponds to a stationary behavioural state distribution (Lusseau, 2003). Eigenanalyses were conducted using the library *popdemo* (Stott *et al.,* 2012) in R (R Core Team, 2013). Stationary behavioural states (i.e. activity budgets) between presence and absence of human stimuli at 10m and 50m, respectively, were compared using a z-test for proportions (Zar, 1996).

Supplementary analysis: multinomial logistic regression

To evaluate the likelihood and significance of specific behavioural transitions in the presence or absence of a human stimulus, odds ratios were generated from a multinomial logistic regression with a cumulative logit link using *Proc Genmod* in SAS v9.3. Unlike the Markov chain approach, this modelling approach controlled for the effects of individual variability by using focal dolphin as an aggregating (i.e. repeated measures) variable. Specifically, group activity, focal activity, change in number of dolphins, increase in number of dolphins, change in number of subgroups, increase in number of subgroups, change in cohesion, and increase in cohesion were examined as responses to the presence or absence of a human stimulus.

For this analysis, focal activities were aggregated into three categories: interaction (begging and patrolling), natural (foraging and one period of resting), and transitional (travelling and milling). Aggregation into three categories greatly simplified interpretation of the response profiles from the multinomial logistic regression analysis. Travelling was considered a transitional state because conditioned dolphins moved between vessels or swimmers and successively engaged in human interaction events. The behaviour of moving between vessels was often documented as travel rather than patrol since it was not possible to distinguish when the focal dolphin was deliberately travelling while opportunistically happening upon a vessel/swimmer to interact with, versus deliberately patrolling for provisions. This is similar to Samuels and Bejder's (1998; 2004) findings in which all recorded travel by conditioned dolphins was from vessel to vessel. Milling was combined with travelling because it was infrequently observed and other studies have suggested it may be a transitional state (Constantine *et al.,* 2004; Peters *et al.,* 2013).

Any missed point samples in which the focal animal was temporarily out of sight were excluded from the analysis. Regression models incorporated single time step lagged response variables as covariates to control for autocorrelation inherent in time series data. Three human stimuli covariates were evaluated at each distance: presence of a human stimulus in the current time step, presence of a human stimulus in the previous time step, and persistence of a human stimulus from the previous to the current time step. Separate regressions were performed for human stimuli at 10m and 50m to examine the differential impacts of proximity of human stimuli upon dolphin behaviour.

Supplementary analyses: ranging patterns and space use

Spatial data were projected in ARC GIS 10.1 (ESRI, Redlands, CA) to create a map of all observed human interaction events (Table 2) from focal follows and sightings. To determine whether conditioned and non-conditioned dolphins exhibit differences in ranging patterns, both linear distance moved per 3min point sample and overall space use were examined. General linear modeling (GLM) in SPSS v17.0 (IBM Corp., Armonk, NY) was used to test for differences in distance moved. GLMs controlled for the random effects of the focal individual and interaction behaviour while evaluating differences in the marginal means of distance moved per minute of observation by conditioned versus non-conditioned focal dolphins. To test for differences in space use, minimum convex polygons (MCPs) were developed for each focal dolphin using Geospatial Modeling Environment (Beyer, 2012). After the shoreline was clipped out of each MCP using existing county maps and satellite imagery, MCP areas were computed in a NAD UTM83 Zone 17N projection. Minimum convex polygon sizes for conditioned and non-conditioned dolphins were compared in Microsoft Excel (Microsoft Corp., Redmond, WA) using a two-sample t-test assuming unequal variances. To ensure that track duration did not have an impact upon the estimated MCP, mean MCP sizes for conditioned and non-conditioned dolphins were estimated to include and exclude tracks of less than 1hr duration.

RESULTS

Photo-identification and sightings

A total of 56 sightings of bottlenose dolphins were recorded; of these, 28 (50%) included a dolphin engaging in a behaviour event indicative of chronic human interaction (Fig. 2). A minimum of 57 individual, identifiable dolphins were sighted; of these, 21 (36.8%) were identified as conditioned. Photo-identification data from the original study was not available for comparison of fins.

Fourteen of the 21 conditioned dolphins (66.7%) were sighted near ‘Interaction Beach’; of these, five (23.8%) were seen there on multiple days (Fig. 2). Seven of the 21 conditioned dolphins (33.3%) were sighted at the ‘Bait Barge’ near the northwest shore of the pass; of these, four (19.0%) were seen there on multiple days (Fig. 2). One conditioned dolphin (4.8%) was sighted at both ‘Interaction Beach’ and the ‘Bait Barge’. Ten of the 21 conditioned dolphins (47.6%) were documented to ‘accept food’ from a person; five conditioned dolphins were fed at ‘Interaction Beach’, four were fed at the ‘Bait Barge’ (on three different days), and one was fed in the channel of St. Andrew’s Pass.

Focal follows: evaluating impacts of human stimuli on dolphin behaviour

During this study, focal follows were conducted for 11 individual dolphins and a male pair, for a total of 12 follows. Six conditioned dolphins were followed for a total of 9hrs 39mins and seven non-conditioned dolphins (including the male pair) were followed for a total of 8hrs 48mins. Focal follows ranged from 48mins to 2hrs 25mins. Conditioned focal dolphins followed included one juvenile/sub-adult and five adults (including one female with a calf). Non-conditioned focal dolphins included two juveniles, one sub-adult/adult, and four adults (including two females with calves and a male pair).

Replication of Samuels and Bejder methodologies

On average, conditioned focal dolphins (n = 6) were observed engaging in chronic human interaction events in 52.85% (range: 5.25–100%) of point samples observed. On average, conditioned dolphins were within 50m of a vessel or swimmer in 56.48% (range: 10.53–75%) of observed point samples, and within 10m in 45.08% (range: 10.53–70.91%) of observed point samples. Furthermore, when a vessel or swimmer was within 50m or 10m of a conditioned focal dolphin, the focal animal engaged in chronic human interaction events during 73.39% (range: 0–100%) and 80.46% (0–100%) of observations, respectively. One conditioned dolphin was fed while being followed. This particular conditioned dolphin was fed (or attempts were made to feed) during 65.45% observed point samples. Non-conditioned dolphins were observed within 50m and 10m of a vessel or a swimmer on average during 4.55% (range: 0–17.24%) and 1.14% (range: 0–4.88%) of observed point samples, respectively.

During a follow, conditioned dolphins were at risk of injury, illness, or death as a result of human-interactions (Table 3) during an average 45.60% (range: 0–74.55%) of observations (or at least 9.2 times per 1hr) whereas non-conditioned dolphins were at risk during an average of 1.7%

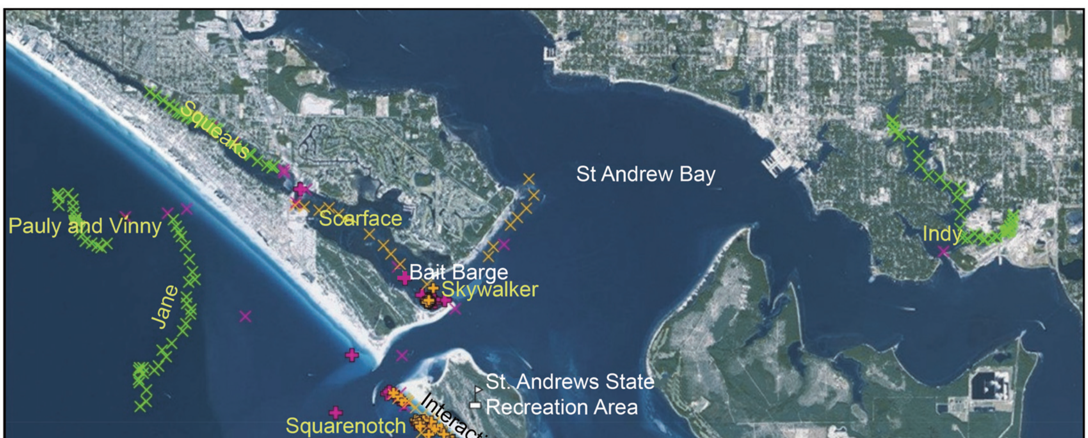

Fig. 2. Sightings (pink) and focal follow point samples for conditioned (orange) and non-conditioned (green) dolphins, highlighting locations of recorded human-dolphin interactions (crosses) in waters near Panama City, Florida. Human-dolphin interactions are clustered around ‘Interaction Beach’ and the ‘Bait Barge’ due to food provisioning of dolphins in these areas.

(range: 0–10.34%) of observations (or at least one time per 3.21hrs). Humans interacting with conditioned dolphins were at risk of injury (Table 3) during 18.13% (range: 0–32.73%) of observations or at least 3.75 times per 1hr. No direct injury for either humans or dolphins was observed as a result of an interaction, however, this was difficult to confirm given the number of vessels and swimmers in the water with an animal at one time.

Supplementary analysis: Markov chains

The use of first-order Markov chains revealed considerable differences in dolphin activity budgets in the presence versus in the absence of human stimuli (i.e. vessel or swimmer) at both 50m and 10m (Table 4, Fig. 3). In the absence of a human stimulus, dolphins spent significantly more time travelling and foraging. When a human stimulus was present, dolphins spent significantly more time interacting (i.e. begging or patrolling) with swimmers or vessels. When a human stimulus was within 50m, dolphins spent 64% of their time interacting with swimmers or vessels; with a human stimulus present within 10m, dolphins spent 81% of their time interacting with swimmers or vessels. There were no significant differences detected for the time spent milling with or without a human stimulus present.

Table 4

Detailed activity budgets (a); and corresponding *Z* and *p* values calculated based on first order Markov chain analyses (b). Milling was the only behaviour found not to be significantly different when in the presence or absence of a human stimulus at either 50 or 10m.

(a)		Activity budget			
Distance	Human stimulus	Forage	Interaction	Mill	Travel
50m	No	15%	4%	11%	70%
	Yes	3%	64%	7%	26%
10m	No	14%	4%	11%	71%
	Yes	3%	81%	4%	12%

(b)			Forage		Interaction		Mill		Travel	
Distance	Human stimulus	*N*	*Z*	*p*	*Z*	*p*	*Z*	*p*	*Z*	*p*
50m	No	210	2.97	< 0.0001	–11.84	< 0.0001	1.04	0.30	7.40	< 0.0001
	Yes	103								
10m	No	235	2.59	< 0.0001	–14.00	< 0.0001	1.86	0.06	9.09	< 0.0001
	Yes	78								

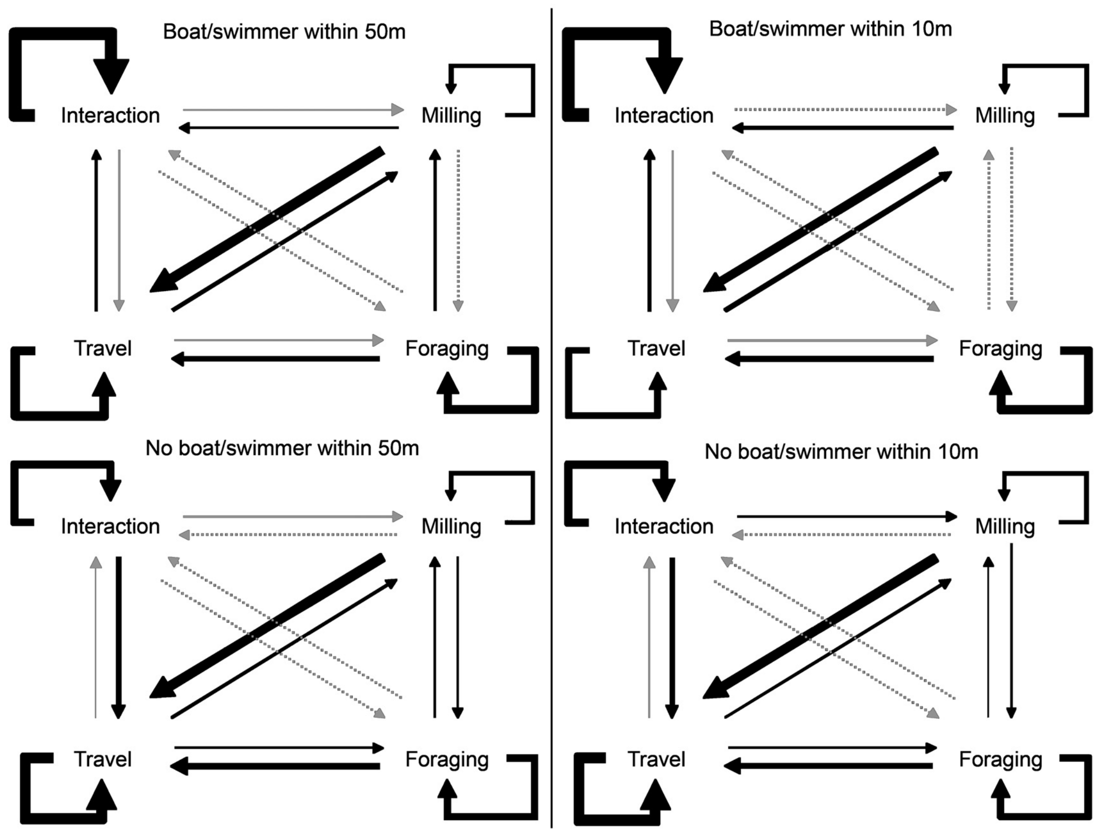

Fig. 3. Behavioural transitions by focal animals in four observed scenarios (1. Vessel/swimmer within 50m; 2. No vessel/swimmer within 50m; 3. Vessel/swimmer within 10m; 4. No vessel/swimmer within 10m). Thickness of arrows corresponds to transitional probabilities from first-order Markov chains (Table 4) with insignificant results denoted by grey dashed lines.

Table 5

Likelihood ratio model fit summary statistics for Type 3 analysis for multinomial regression analysis of human stimulus impacts on dolphin behaviour in waters near Panama City, Florida. Significant human stimulus effects in **bold**. Subscripts denote lagged variables.

Response	Human stimulus	Parameter	DF	Chi-square	Pr > ChiSq
Change in group activity	50m	Individual	9	45.87	< 0.0001
		Group activity$_{-1}$	2	71.45	< 0.0001
		Human stimulus	1	3.24	0.072
	10m	Individual	9	43.22	< 0.0001
		Group activity$_{-1}$	2	9.36	0.0093
		Human stimulus	1	2.07	0.15
Change in focal activity	50m	Individual	10	46.41	< 0.0001
		Focal activity$_{-1}$	2	20.64	< 0.0001
		Human stimulus	**1**	**6.68**	**0.0098**
	10m	Individual	10	47.49	< 0.0001
		Focal activity$_{-1}$	2	18.69	< 0.0001
		Human stimulus	**1**	**17.8**	**< 0.0001**
Change in no. dolphins	50m	Individual	10	38.27	< 0.0001
		Number of dolphins$_{-1}$	1	0.11	0.7351
		Human stimulus	1	3.25	0.0714
	10m	Individual	10	52.45	< 0.0001
		Number of dolphins$_{-1}$	1	0.11	0.7351
		Human stimulus	**1**	**11.98**	**0.0005**
Increase in no. dolphins	50m	Individual	No significant results		
		Number of dolphins$_{-1}$			
		Human stimulus			
	10m	Individual	10	53.71	< 0.0001
		Number of dolphins$_{-1}$	1	0.05	0.8207
		Human stimulus	1	0.33	0.5645
Change in no. subgroups	50m	Individual	10	41.1	< 0.0001
		Number of groups$_{-1}$	1	38.86	< 0.0001
		Human stimulus	1	1.55	0.2126
	10m	Individual	No significant results		
		Number of groups$_{-1}$			
		Human stimulus			
Increase in no. subgroups	50m	Individual	10	39.64	< 0.0001
		Number of groups$_{-1}$	1	9.04	0.0026
		Human stimulus	1	1.15	0.2845
	10m	Individual	10	38.15	< 0.0001
		Number of groups$_{-1}$	1	10.25	0.0014
		Human stimulus	1	0.02	0.9003
Change in cohesion	50m	Individual	8	25.72	0.0012
		Cohesion$_{-1}$	1	16.97	< 0.0001
		Human stimulus	1	0.78	0.3783
	10m	Individual	8	21.98	0.005
		Cohesion$_{-1}$	1	16.92	< 0.0001
		Human stimulus	1	0.18	0.6744
Increase in cohesion	50m	Individual	8	11.39	0.1808
		Cohesion$_{-1}$	1	17.57	< 0.0001
		Human stimulus	1	0.01	0.9152
	10m	Individual	8	11.56	0.1717
		Cohesion$_{-1}$	1	17.96	< 0.0001
		Human stimulus	1	0.89	0.3459

Supplementary analysis: multinomial logistic regression

Odds ratio (OR) contrast estimation within the nested multinomial regression framework revealed significant trends in how dolphins react to the presence/absence of human stimuli (Table 6, Fig. 4). When a human stimulus was within 50m, odds of switching from resting or foraging to interaction behaviour substantially increased ($OR_{natural \rightarrow interaction}$: 12.31); when a human stimulus was within 10m, these odds more than doubled ($OR_{natural \rightarrow interaction}$: 32.17). Similarly, odds of remaining engaged in interaction behaviour when there was a human stimulus within 50m were high ($OR_{interaction \rightarrow interaction}$: 3.62); when there was a human stimulus within 10m, these odds nearly tripled ($OR_{interaction \rightarrow interaction}$: 9.24). When a human stimulus was present within 10 or 50m, odds of dolphins remaining in a travel/milling behaviour or transitioning to a foraging or resting behaviour were extremely low. In the absence of a human stimulus within 10 or 50m, dolphins were likely to remain in or switch to a travel/milling behaviour.

The logistic regression analysis indicated dolphins sometimes transitioned to interaction behaviour when a

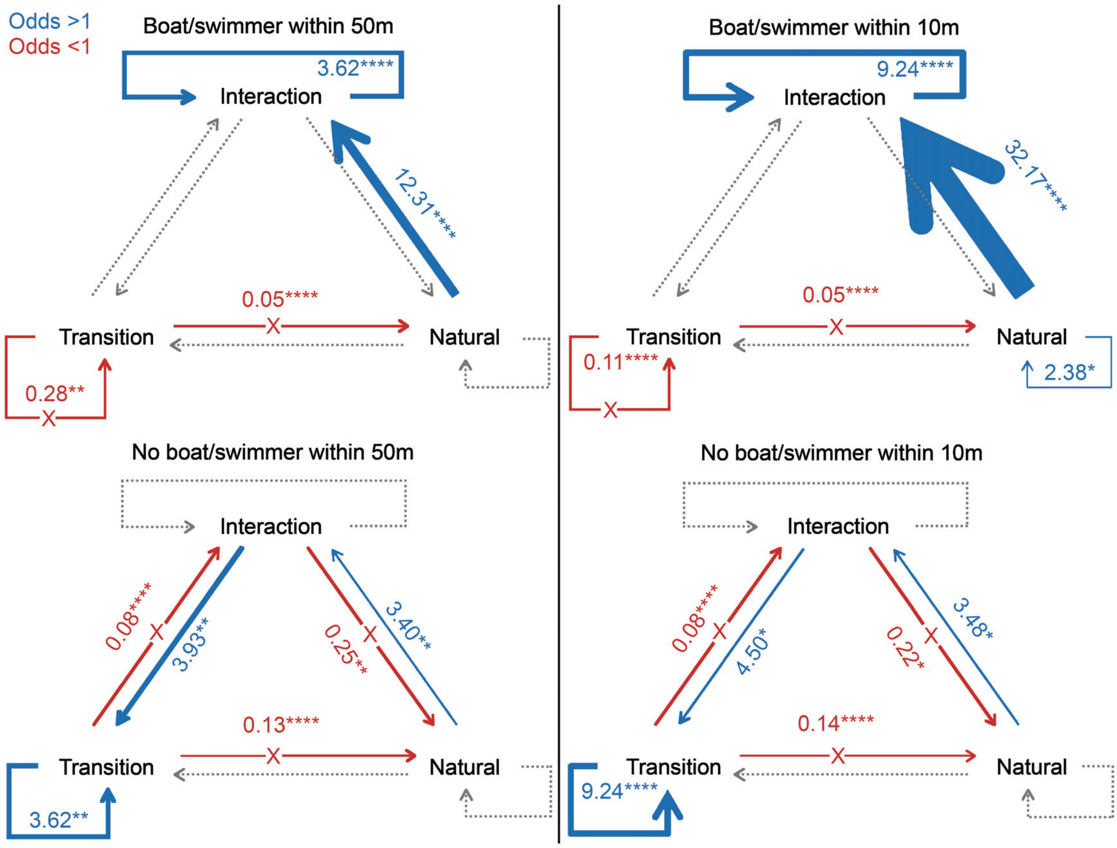

Fig. 4. Odds of specific behaviour transitions by focal animals in four observed scenarios (1. Vessel/swimmer within 50m; 2. No vessel/swimmer within 50m; 3. Vessel/swimmer within 10m; 4. No vessel/swimmer within 10m). Focal activity was aggregated into three categories: interaction (begging and patrolling), natural (resting and foraging), or transitional (travelling and milling). Thickness of arrows corresponds to transitional probabilities from nested multinomial logistic regression analysis (Table 6) with insignificant results denoted by grey dashed lines. Blue lines denote trends with odds greater than one (i.e. more likely to happen); red lines with 'X' denote trends with odds less than one (i.e. less likely to happen).

Table 6

Odds ratio statistics from contrast estimation for significant multinomial logistic regression model fits for the impacts of human stimuli (i.e. vessels or swimmers) upon dolphin behaviour in waters near Panama City, Florida. Significant contrasts in **bold**. The range following the 'mean' represents the 95% confidence limits.

Response	Human stimulus	10m Mean	10m χ^2	10m Pr > χ^2	50m Mean	50m χ^2	50m Pr > χ^2
Change in focal activity							
Travel→Travel	No	9.24 (3.19–26.81)	16.78	**< 0.0001**	3.62 (1.37–9.59)	6.69	**0.01**
Natural→Natural	No	3.08 (1.00–9.51)	3.84	0.05	2.74 (0.98–7.66)	3.67	0.06
Interaction→Interaction	No	0.32 (0.11–1.00)	3.84	0.05	0.37 (0.13–1.02)	3.67	0.06
Interaction→Natural	No	0.22 (0.06–0.78)	5.56	**0.02**	0.25 (0.07–0.87)	4.75	**0.03**
Interaction→Travel	No	4.50 (1.29–15.71)	5.56	**0.02**	3.93 (1.15–13.44)	4.75	**0.03**
Natural→Interaction	No	3.48 (1.56–7.78)	9.24	**0.00**	3.40 (1.53–7.58)	9.00	**0.00**
Natural→Travel	No	2.18 (0.59–8.09)	1.36	0.24	2.52 (0.71–9.02)	2.03	0.15
Travel→Interaction	No	0.08 (0.02–0.29)	15.02	**0.00**	0.08 (0.02–0.27)	16.06	**< 0.0001**
Travel→Natural	No	0.14 (0.06–0.33)	19.73	**< 0.0001**	0.13 (0.06–0.32)	20.41	**< 0.0001**
Travel→Travel	Yes	0.11 (0.04–0.31)	16.78	**< 0.0001**	0.28 (0.10–0.73)	6.69	**0.01**
Natural→Natural	Yes	2.38 (1.11–5.12)	4.94	**0.03**	1.55 (0.73–3.27)	1.32	0.25
Interaction→Interaction	Yes	9.24 (3.19–26.81)	16.78	**< 0.0001**	3.62 (1.37–9.59)	6.69	**0.01**
Interaction→Natural	Yes	0.53 (0.13–2.08)	0.83	0.36	0.39 (0.10–1.56)	1.76	0.18
Interaction→Travel	Yes	1.89 (0.48–7.43)	0.83	0.36	2.53 (0.64–9.99)	1.76	0.18
Natural→Interaction	Yes	32.17 (8.73–118.55)	27.21	**< 0.0001**	12.31 (3.74–40.51)	17.07	**< 0.0001**
Natural→Travel	Yes	0.24 (0.04–1.32)	2.71	0.10	0.70 (0.13–3.64)	0.18	0.67
Travel→Interaction	Yes	0.25 (0.04–1.57)	2.18	0.14	0.21 (0.04–1.18)	3.14	0.08
Travel→Natural	Yes	0.05 (0.01–0.20)	17.13	**< 0.0001**	0.05 (0.01–0.21)	16.85	**< 0.0001**
Change in no. dolphins							
	Yes	0.11 (0.03–0.42)	10.82	**0.00**			

human stimulus was absent (Table 6, Fig. 4); this result is explained by differences in sampling methodologies – focal dolphin behaviour was recorded as the dominant state over a 3min period, whereas vessel and swimmer counts were recorded as point samples. Therefore, at times, the dominant behaviour over the 3min interval was a form of interaction behaviour, but a human stimulus was not recorded for the point sample because it had just moved beyond a 10 to 50m radius of the dolphin.

Supplementary analyses: ranging patterns and space use
When movements were considered in aggregate, there were no significant differences of movement between conditioned and non-conditioned focal dolphins; however, significant differences were apparent when distance moved was compared between times focal dolphins were interacting with a vessel or swimmer versus times they were not. Mean distance moved per minute of observation was 56 ± 1m for dolphins not interacting; interacting dolphins moved significantly less (16 ± 5m less, $F_{1,333} = 12.8$, $p < 0.001$) per minute of observation. The overall space use of conditioned and non-conditioned focal dolphins, as measured by MCPs, was not significantly different ($p > 0.05$).

DISCUSSION

In the original study near Panama City, Samuels and Bejder (1998; 2004) documented 7 of 89 (8%) dolphins encountered as conditioned. In 2014, 21 of 57 (37%) dolphins encountered were conditioned. The number of conditioned dolphins identified in this study is likely underestimated. Due to the crowding and collision risk from vessels and swimmers surrounding groups of conditioned dolphins, it was sometimes difficult to monitor and acquire photographs of all individual group members during a sighting. In order to adjust for this constraint, surveys along 'Interaction Beach' were sometimes timed just prior to the arrival of tour vessels so that photo-identification data could be collected more completely, however, this was not always possible. Furthermore, there were a number of dolphins that were observed engaging in human interaction events but could not be individually identified due to lack of distinguishing dorsal fin markings.

Despite the expanded study area and increased field time compared to the previous study, only 57 distinct conditioned and non-conditioned dolphins were identified, versus the 89 individuals identified by Samuels and Bejder (1998; 2004) in 1998 (Table 7). The number of identifications documented here are not representative of the entire St. Andrew Bay stock population, but rather a sub-set of the population. However, the reduction in identifications between the two studies warrants further exploration. Numerous studies have documented declines in the abundance of dolphin populations exposed to intensive tourism pressure as a result of diminished reproductive health or permanent habitat displacement or abandonment (Bejder, 2005; Bejder *et al.,* 2006b; Lusseau, 2006; Lusseau *et al*., 2006; Tyne *et al.,* 2014). Additionally, an increase in the number of dolphin deaths in this area was documented between 1999 and 2006. The Panhandle region of Florida experienced three bottlenose dolphin Unusual Mortality Events (1999–2000, 2004 and 2005–2006), which had an unknown impact on the population of resident dolphins (Balmer *et al.,* 2008; Schwacke *et al.,* 2010). The observations of focal dolphin 'X02', examined and freeze-branded during NMFS' 2005 bottlenose dolphin health assessment project in nearby St. Joseph Bay (43km to the east), demonstrates some dolphins move between and utilise different habitat areas along the Florida Panhandle. Baseline population data will be important in helping to understand the status of this population and the impacts of human interactions.

Impacts of human stimuli on dolphin behaviour
When a human stimulus was present within 50m, conditioned focal dolphins engaged in human interactions

Table 7

Comparison of results between this project (2014) and Samuels and Bejder (1998; 2004) specifically related to human-dolphin interactions near Panama City, Florida.

	2014 study	Samuels and Bejder (1998; 2004)
Study length	12 days (15-27 June 2014)	5 days (4-9 August 1998)
Study area	30 n.miles^2	24 n.miles^2
Field methods	Photo-identification, focal follows	Photo-identification, focal follows
Statistical analysis	Descriptive statistics, Markov chains, multinomial logistic regression, spatial analysis	Descriptive statistics
Conditioned dolphins identified	21/57 (37%)	7/89 (8%)
Hot spot locations	Interaction Beach and Bait Barge	Interaction Beach
Non-conditioned dolphins focal follows:		
No. of follows	6 (8h, 48min.)	5 (5h, 28min.)
Age/sex class	1 juvenile,1 adult/sub-adult; 4 adults (2 females with calves and male pair)	Single dolphin (unknown sex/age); mixed groups
Conditioned dolphins focal follows:		
No. of follows	6 (9h, 39min.)	4 (6h, 32min.)
Age/sex class	1 juvenile/sub-adult; 5 adults (including 1 female with calf)	1 juvenile; 1 adult
Time engaged in chronic human interactions	73% of 3min. samples	77% of 1 min. samples
Risk	Dolphins: 9.2x/hr; humans: 3.75x/hr	e.g. HiMidLo-5x/hr; humans-2x/hr
Ranging patterns	No sig. diff. overall from non-conditioned; sig. less movement when begging/patrolling	<1 n.mile of Interaction Beach; travel less than non-conditioned
Activity budgets	Atypical behavior: 64-81% of time begging/ patrolling; no social; 1 period of resting	e.g. HiMidLo-atypical behavior (2 incidents of social; 1 incident of forage)

events during 73% of observation points (Table 7), similar to the 77% interaction rate documented by Samuels and Bejder (1998; 2004). The well-established ability of dolphins to learn by observation (i.e. social learning) likely contributed to the increase in number of individual dolphins that engage in human interaction behaviours over time (Cunningham-Smith *et al*., 2006; Donoghue *et al.,* 2002; Wells, 2003; Whitehead *et al.,* 2004). Also, dolphins in Panama City are now routinely fed in at least two locations: 'Interaction Beach' and the 'Bait Barge' versus the one location ('Interaction Beach') as described in Samuels and Bejder (1998; 2004) (see Fig. 2). In general, this highlights how unnatural foraging strategies, including begging, may increase in frequency given high rates of reinforcement by humans.

Activity budgets, a standard measure of animals' behavioural states, are particularly useful in understanding how energy expenditure or acquisition is impacted by human activities (Christiansen *et al.,* 2014; Lusseau *et al.,* 2009; Williams *et al.,* 2006). Samuels and Bejder (1998; 2004) profiled the behaviour of a specific juvenile animal 'HiMidLo' to show that the activity budget of a conditioned dolphin is not representative of unconditioned dolphin behaviour (Table 7). For example, the conditioned dolphin, 'HiMidLo', was followed over three days for a total of 5hrs and 53mins and was only observed socialising with other dolphins twice and foraging naturally once (Samuels and Bejder, 1998; 2004). In the 2014 study, the activity budgets of focal conditioned dolphins were also atypical when a human stimulus was present within 10 or 50m (Table 7). In these circumstances, conditioned focal dolphins spent the majority of their time (stimulus within 50m: 64%, stimulus within 10m: 81%) begging or patrolling near vessels and people, which meant less time was devoted to natural behaviours such as resting, foraging, and socialising. Additionally, there were extremely high statistical odds that dolphins engaged in natural behaviour would switch to an interaction behaviour when a human stimulus was present.

In the absence of a human stimulus within 50m, focal dolphin activity budgets (conditioned and non-conditioned combined) were somewhat comparable to activity budgets for other dolphins on Florida's West coast, especially in terms of time spent travelling, foraging, and milling (Waples, 1995). However, in Panama City, major differences included no social behaviour and only a single sample of resting behaviour. The lack of observed intra-specific social behaviour in the presence of high boat traffic has also been documented for other cetacean species (Constantine, 2001; Dans *et al.,* 2008; Lundquist *et al.,* 2008; Williams *et al.,* 2006). It is also possible that conditioned dolphins are re-allocating their energy to begging or patrolling to seek provisions, thus decreasing the amount of time interacting with conspecifics. Considering that the development of play is crucial for animal social skills, less interaction with conspecifics particularly for conditioned juveniles or calves could result in developmental delays or associated problems (Foroughirad and Mann, 2013; Mann and Barnett, 1999; Mann and Kemps, 2003; Samuels and Bejder, 2004). Resting is one of the most easily disturbed natural behaviours; the lack of observed resting behaviour was consistent with numerous studies, which documented declines in bottlenose dolphin resting behaviour in the presence of vessels (Arcangeli *et al*., 2009; Constantine *et al.,* 2003; Constantine *et al.,* 2004; Lusseau, 2003; Yazdi, 2007).

Once a conditioned dolphin began to engage in an interaction behaviour state, the animal tended to continue to do so. If the stimulus was removed, the dolphin would often switch to travel behaviour, but travel behaviour was often terminated when the animal arrived at another vessel or swimmer, highlighting the likelihood that the animal was travelling in search of provisions. Overall, the conditioned dolphin activity budgets found here are somewhat similar to other dolphin disturbance studies, with one key difference. Most of the literature supports that dolphins spend less time foraging and resting and more time milling and travelling in the presence of vessels and swimmers (Arcangeli *et al.,* 2009; Lusseau, 2004; Lundquist *et al.,* 2012; Meissner *et al.,* 2015; Montero-Cordero and Lobo, 2010; Steckenreuter *et al.,* 2012; Stockin *et al.,* 2008). In these cited studies, responses are likely disturbance responses from non-conditioned dolphins and attributed to animals' efforts to avoid human stimuli. However, in this study, dolphins increased their time travelling and decreased time milling because they were conditioned and actively sought out additional provisioning opportunities from vessels/ swimmers, rather than avoiding the stimuli.

Samuels and Bejder (1998; 2004) found dramatically different ranging patterns between conditioned and non-conditioned dolphins (Table 7). Conditioned dolphins stayed within < 1 n. mile^2 area around 'Interaction Beach' and the adjacent pass, whereas, non-conditioned dolphins travelled distances of several nautical miles (Samuels and Bejder, 1998; 2004). In this 2014 study, conditioned animals were mainly observed around 'Interaction Beach', the adjacent pass, and inside the bay near the 'Bait Barge'. Conditioned dolphins moved significantly less only when engaged in interaction behaviours. Distance traveled and space use by conditioned dolphins when not interacting was likely comparable to non-conditioned animals because conditioned dolphins travelled from one vessel/swimmer to another in search of food. In addition, in a few instances, conditioned dolphins moved to deeper water away from the beach at times when the number of vessels and swimmers peaked during an interaction. The swim-with tour vessels would typically not follow the dolphins into the deeper water presumably due to the decline in water clarity. This type of vertical and horizontal avoidance strategy exhibited by conditioned animals is frequently utilised by non-conditioned bottlenose dolphins potentially as a way to avoid tourism pressure (Latusek, 2002; Lemon *et al.,* 2006; Lusseau, 2004; Lusseau, 2006).

Food provisioning

As described 16 years earlier in Samuels and Bejder (1998), illegal food provisioning still facilitates swim-with activities with dolphins in Panama City. Ten dolphins were documented being provisioned during this study. In one case, a focal animal, 'X02', and two other dolphins in his group were fed repeatedly by the captain of a bait boat (a vessel that fishes for and then holds live bait fish to sell to recreational fishers) anchored off 'Interaction Beach' for nearly two hours (Fig. 5). The captain would throw handfuls of bait at the dolphins and then cast his net on top of or near the bait while the dolphins scavenged under the guise that to protect his nets, he had to feed the dolphins. The captain also began radio communication as soon as the dolphins arrived, and dolphin tour vessels arrived on site within 15 minutes of the call. The bait boat captain was then observed throwing handfuls of bait into the middle of the group of swimmers, attracting the scavenging dolphins close enough for swimmers to closely approach and touch the animals (Fig. 5). X02 and his companions displayed aggressive behaviours such as bubble-blowing and tail-slapping directed at swimmers during these interactions.

The 'Bait Barge' has emerged as a new provisioning location. The 'Bait Barge' is an anchored barge where fishermen can purchase live bait fish. Dolphins were observed being fed there on four different dates. At the 'Bait Barge', an attendant was observed using a boat hook to slap the water, essentially training a dolphin through variable food reinforcement to station near the barge where swimmers were dropped off by commercial vessels to swim and interact with the animal (Fig. 6). This technique is very similar to how marine mammal trainers work with dolphins at zoos/aquariums (Ramirez, 1999). An individual on the commercial vessel then passed a small object with a dip net to the barge attendant after the swimmers were finished with the interaction. Based on the size of the object and the nature of interaction, this 'object' may have been monetary compensation; however, this could not be confirmed.

In multiple incidences, dolphins displayed aggressive behaviour (i.e. tail-slapping, bubble-blowing, chuffing) when swimmers entered the water near dolphins (Orams *et al.,* 1996; Samuels and Gifford, 1997; Connor, 2000). Dolphins were also aggressive when they anticipated a boater may have a food provision on board, but were not fed. In one instance, '90050' reached its head over the vessel's gunwale in an attempt to bite the data clipboard out of the hand of a field assistant, apparently perceiving it as food. Food provisioning and animal aggression causing injuries to humans have been documented in a variety of other species including baboons (Kamal *et al*., 1997; Wrangham, 1974), macaques (Aggimarangsee, 1993; Fa, 1992), chimpanzees (Goodall, 1986), bears (Gunther, 1992), and larger fishes

Fig. 5. The captain of the bait boat reaches for more bait to feed the begging bottlenose dolphins to keep the animals nearby as a tour boat puts swimmers in the water. The photo was taken on 21 June 2014 at 'Interaction Beach', Panama City, Florida.

Fig. 6. An attendant at the 'Bait Barge' in Panama City, Florida uses a boat hook to slap the water to attract a bottlenose dolphin towards swimmers that were dropped off by tour vessels to swim and interact with the animal. This dolphin was provisioned during this incident. The photo was taken on 23 June 2014.

(Perrine, 1989). NMFS Southeast Regional Office has recorded 18 cases of dolphins biting people in the Southeastern United States since 1997; these injuries typically occurred while the person was feeding, swimming, or harassing a dolphin. Furthermore, intra-species aggression is also a consequence of provisioning by humans, which tends to increase when animals are aggregated more densely as a result of human provisioning (Orams, 2002) or when adult males are present (Orams *et al.*, 1996).

Provisioning wild dolphins may have other unanticipated consequences. Once dolphins learn to associate humans with food through provisioning, the animals may be more likely to engage in more risky behaviours such as depredating or scavenging from fishermen (Powell, 2010). In Panama City, two conditioned dolphins previously observed begging, were also sighted patrolling and attempting to depredate from recreational fishermen off 'Interaction Beach'. Interacting with recreational fishermen presents increased risks of injury or death for conditioned dolphins due to acts of retaliation by fishers or entanglement and ingestion in fishing gear (Adimey *et al*., 2014; DOJ 2006, 2007; Read, 2008; Stolen *et al*., 2013; Wells *et al*., 2008).

CONCLUSION

This study confirms that the problem in Panama City has escalated over the last 16 years: dolphins are actively provisioned; the proportion of conditioned dolphins has increased substantially; conditioned dolphin activity budgets, behaviours, and movement patterns continue to be impacted by human interactions; and the risk of injury or mortality for both dolphins and humans from their interactions occurs multiple times per hour. NMFS has attempted to address the harassment to and illegal provisioning of dolphins in this area with outreach and educational campaigns, as well as intermittent law enforcement, including undercover operations. Unfortunately, it appears that the tour operators have adapted surreptitious provisioning methods over time to hide from enforcement efforts. Dolphin provisioning in Panama City by local tour businesses has progressed from: (1) tour operators provisioning dolphins directly from vessels; (2) tour operators disguising feeding by provisioning animals underwater; (3) tour operators throwing a metal bucket (sometimes containing fish) over the side of the vessel when dolphins were near; to (4) tour operators capitalising on local bait fishermen and barge operators who feed dolphins under the guise that they are throwing back unwanted fish or feeding the animals to keep them from damaging their gear (Samuels and Bejder, 1998; 2004).

A more aggressive management strategy is recommended for Panama City to reduce and eliminate high risk human-dolphin interactions. Given that long-term, high profile outreach/education and pulsed enforcement efforts have proven unsuccessful, we suggest a targeted and sustained enforcement campaign based on the existing regulations at 50 CFR 216 that prohibit feeding and other forms of 'take' and 'harassment'. Additional regulations should also be developed as soon as possible to clearly restrict close approaches and in-water interactions. All efforts will require a consistent enforcement effort for effectiveness. Lessons learned from immediate enforcement efforts will better inform the development of potential future proposed rulemakings.

In addition, long-term and consistent monitoring studies throughout the year would be ideal to evaluate seasonal and long-term population-level impacts resulting from human interactions. Minimally, we recommend repeating this study in the off-season months when tourism pressure subsides so that both conditioned and non-conditioned dolphin behaviour can be re-examined and compared with the summer tourism peak to allow for a more complete understanding of how human interactions affect dolphin behaviour. Human dimension studies on the motivation and incentives for both businesses and tourists to engage in close interactions with wild dolphins may also provide insight on social expectations (e.g. Filby *et al.,* 2015) and could help guide management actions to maximise safe and enjoyable wild dolphin viewing opportunities.

ACKNOWLEDGEMENTS

We thank Kristen Spzak and Sam Beck for their assistance in the field, Maddie Evans for photo-id assistance, and Brian Balmer for providing information on focal animal, 'X02', and other suspected dorsal fin matches between the Panama City and St. Joseph Bay catalogs. We also thank Lars Bejder and Stacey Horstman for providing advice and assistance. We appreciate the reviews of this manuscript provided by David Laist and Dee Allen (Marine Mammal Commission) and Randall Wells (Sarasota Dolphin Research Program). This research was funded by MMC contract MMC14-193, and conducted under the NMFS Office of Protected Resources Permit No.14450-0

Dedication: This study is dedicated to Dr Amy Samuels (1950–2008) who conducted the original research on human-dolphin interactions in Panama City, Florida in 1998. Amy was a rigorous scientist, passionate conservation biologist, and great mentor who pioneered the application of quantitative behavioural research methods in the marine mammal science field. She devoted her life to collecting detailed behavioural observations of animals that provided important new insights into the social behaviour of both cetaceans and primates. Amy worked on several research projects to assess human impacts on dolphins, both in the wild and at public display facilities, and the data she collected enabled government agencies around the world to make informed management decisions to protect the health and welfare of both animals and the public. In replicating her ground-breaking research project in Panama City, we humbly aspired to honour Amy's life work and legacy, and hopefully have provided additional new information that will inform future management efforts to further protect dolphin and human safety.

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