

Effects of food provisioning on site use in the short-tail stingray *Bathytoshia brevicaudata*

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ABSTRACT: Food provisioning can have significant effects on marine wildlife. It is common practice for recreational anglers to discard fish waste back into waterways, yet the effects of incidental provisioning as a result of recreational fish cleaning on marine wildlife have not been assessed and are likely not being considered in fisheries management. At the Woollamia boat ramp in Jervis Bay, Australia, local anglers have been incidentally provisioning short-tail stingrays *Bathytoshia brevicaudata* through fish-cleaning activities for >30 yr. This provided an opportunity to investigate the influence of provisioning on a small scale. We used behavioural observations to assess stingray site use patterns against provisioning intensity to determine if provisioning can cause changes to the movements and behaviour of this large, marine mesopredator. Twelve female short-tail stingrays were found to use the site during observation periods for this study. Their presence was significantly correlated with the intensity of provisioning events (cumulative duration per observation session), which occurred most often in the afternoons. Significantly more stingrays visited during provisioning than pre-provisioning in simulated provisioning trials at sites where stingrays are not normally provisioned. Additionally, stingrays were considered to be exhibiting anticipatory behaviour as evidenced by increased visitation in the afternoon, irrespective of whether the fish-cleaning table was in use. These data indicate an influence of provisioning on the stingrays' movements and use of the site and has implications with respect to accepted practices for discarding fish waste.

KEY WORDS: Incidental provisioning · Recreational fishing · Human–wildlife interaction · *Bathytoshia brevicaudata* · Batoidea · Shark and ray tourism

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INTRODUCTION

While common worldwide, the topic of feeding wildlife is polarising (Orams 2002). Backyard bird feeding is considered ecologically benign (Howard & Jones 2004), for example, and the Royal Society for the Protection of Birds in the UK actively encourages bird feeding (RSPB 2009), despite research suggesting that feeding wild birds can impact almost every aspect of their ecology (Robb et al. 2008). Food provisioning (herein provisioning), however, has been used as a management tool to successfully aid the recovery of threatened species as part of broader species conservation strategies (Orams 2002, New-

some & Rodger 2008, Martinez-Abraín & Oro 2013). Further, interacting with wildlife in a natural setting can be an important educational and emotional experience for people (Marion et al. 2008, Zeppel & Muloin 2008). Benefits have also been identified for target species, including reduced energy expenditure for foraging, which can be invested into growth and/or reproduction (Orams 2002, Semeniuk & Rothley 2008, Semeniuk et al. 2009, Donaldson et al. 2010). Other benefits may exist from grouping, such as increased chance of mating and lowered individual predation risk (Semeniuk & Rothley 2008). There are also costs, however. Some animals invest significant energy into 'begging' for food (Orams 2002) or

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defending the provisioned food source (Monaghan & Metcalfe 1985). Further, higher population density can result in increased levels of aggression and disease transmission (e.g. Lewis & Newsome 2003, Semeniuk & Rothley 2008; see also Orams 2002). In addition, many perceived benefits may only be short-term, and animals who readily adjust to using provisioned resources may unknowingly incur greater long-term costs, in a phenomenon termed an 'ecological trap' (Schlaepfer et al. 2002). Importantly, there is a growing body of evidence illustrating the negative, long-term impacts that provisioning can have on wildlife and their environments (Table 1; see also Orams 2002, Oro et al. 2013).

Provisioning in the aquatic realm is becoming more popular, but by comparison to the terrestrial environment, the body of associated research is minimal (Corcoran et al. 2013). Sharks (Subdivision: Selachii) and rays (Subdivision: Batoidea) (Subclass: Elasmobranchii) in particular have increasing appeal for tourism (Cisneros-Montemayor et al. 2013). The economic benefits associated with wildlife tourism have led to the protection of some elasmobranch species and their habitats (e.g. stingrays in Hamelin Bay, Western Australia; Department of Fisheries 2012, 2015; see also Topelko & Dearden 2005). Most importantly from a conservation perspective, it is becoming apparent that elasmobranchs can be worth more to local communities alive than dead (Topelko & Dearden 2005, Gallagher & Hammerschlag 2011, Cisneros-Montemayor et al. 2013). The elusiveness of elasmobranchs has resulted in much of the shark and ray tourism sector using provisioning to facilitate

encounters. This elusiveness also imposes logistical constraints on studying these species by negating the use of classical approaches, such as comparisons with control sites, resulting in a considerable lack of baseline data on their biology and ecology to inform research (Brena et al. 2015). Provisioning activities can therefore provide a platform to not only study the impacts caused by such an activity, but also to fill gaps in our knowledge of the biology and ecology of target species (e.g. Brunnschweiler & Barnett 2013).

Brena et al. (2015) comprehensively reviewed the current literature (16 papers) investigating the impacts of provisioning on sharks and rays. Six of the papers considered ray provisioning, and only 3 provisioned populations have been assessed to date (Newsome et al. 2004, Gaspar et al. 2008, Corcoran et al. 2013). The level of impact experienced by rays appears to relate to the intensity of provisioning. For example, in Stingray City, Cayman Islands, southern stingrays *Hypanus americanus* are fed by over 1 million tourists annually (Corcoran et al. 2013), and these stingrays now exhibit dependency, high site fidelity, reduced home ranges, reversed diel activity patterns, reduced overall health and increased aggression (Semeniuk et al. 2007, 2009, Semeniuk & Rothley 2008, Corcoran et al. 2013). By contrast, targeted provisioning of short-tail stingrays *Bathytoshia brevicaudata* and brown stingrays *B. lata* at Hamelin Bay, Western Australia, has not yet resulted in severe impacts, but they were considered to be at high risk in the absence of appropriate management (Newsome et al. 2004). In both cases, provisioning began incidentally from fishermen cleaning their catches.

Table 1. Examples of negative impacts from food provisioning activity

	Impact	References
Human–animal interactions	Dependency and human-tolerance; nuisance animals	Burns & Howard (2003), Corcoran et al. (2013)
Behavioural changes	Altered natural behaviours, activity patterns, energy budgets	Orams (2002), Green & Giese (2004), Fitzpatrick et al. (2011), Brena et al. (2015)
	Changes in abundance and distribution; altered trophic relationships	Boutin (1990), Orams (2002), Green & Giese (2004), Corcoran et al. (2013)
	Increased conspecific aggression	Orams (2002), Newsome et al. (2004), Clua et al. (2010)
	Altered mating systems	Krause & Ruxton (2002), Green & Giese (2004), Corcoran et al. (2013), Foroughirad & Mann (2013)
Overall health	Overfeeding, malnourishment	Orams (2002), Lewis & Newsome (2003), Newsome et al. (2004)
	Higher risk of disease and parasitisation from high density	Orams (2002), Lewis & Newsome (2003), Semeniuk & Rothley (2008)
Environmental	Environment fouling	Lewis & Newsome (2003), Newsome et al. (2004), Turner & Ruhl (2007)

In Australia, an increased number of fish-cleaning facilities are being built to support recreational fishing (NSW DPI 2016). These facilities are often built at the water's edge and/or have discard pipes that run into adjacent waters, and it is accepted practice to discard recreational fish waste back into waterways. Surprisingly, the effects of incidental provisioning from fish-cleaning activity on marine life have not yet been assessed, to our knowledge, despite its widespread occurrence globally.

In Jervis Bay, New South Wales, Australia, short-tail stingrays are incidentally provisioned with fish scraps from a fish-cleaning facility at the Woollamia boat ramp. Anecdotal evidence suggests the stingrays and a range of other species, including chestnut teal *Anas castanea*, white-faced herons *Egretta novaehollandiae*, Australian pelicans *Pelecanus conspicillatus* and various fishes, have opportunistically foraged scraps here since the installation of the fish-cleaning facility in 1985 (M. Strachan pers. comm.). As yet, it is unclear how many short-tail stingrays use the site and how reliant they are on the provisioned resource. This site provided an opportunity to obtain data on the effects of small-scale, incidental provisioning on the movements of these stingrays. Here we address the impact of provisioning intensity, boating activity and tidal currents on site use by these stingrays. We hypothesised that if the stingrays were affected by provisioning activity, (1) there

would be a resident population of stingrays with high site attachment; (2) their presence would be driven by food provisioned from fish-cleaning activity, boating activity (by learned association) and by tidal currents (potential olfactory cues); and (3) they would quickly recruit to 'new' provisioning sites, reinforcing the influence of provisioned food on activity patterns and movements, and demonstrating their ability to readily alter their behaviours to use human-provisioned food sources. Importantly, we also hypothesised that (4) the stingrays would exhibit signs of anticipatory behaviour as indicated by repeated visits to the site even when food was not available.

MATERIALS AND METHODS

Study species and sites

Short-tail stingrays are among the largest species of stingray with a maximum size of 210 cm disc width (DW) and weights up to 350 kg (Last et al. 2016). They are a common neritic species with a broad distribution (Last et al. 2016). Although considered 'Least Concern' on the IUCN Red List of Threatened Species (Duffy et al. 2016), little is known about the biology and ecology of this species.

The Woollamia boat ramp (WBR) is within Currambene Creek, situated to the northwest of Jervis Bay (Fig. 1A,B). There is a 4-station cleaning table from which a discard pipe runs into the waters of the estuary (Fig. 1C). Short-tail stingrays were visually tagged at the WBR, and subsequent observations of stingray site use were undertaken in the vicinity of the mouth of the discard pipe at the WBR (the provisioning site) and at simulated provisioning sites nearby (see Fig. 2). Tagging and observations were undertaken during August 2016.

Visual tagging

Short-tail stingrays were visually tagged over 10 d, prior to the observation period, and then opportunistically during the observation period, but outside observation sessions. Every individual short-tail stingray observed during the study site was

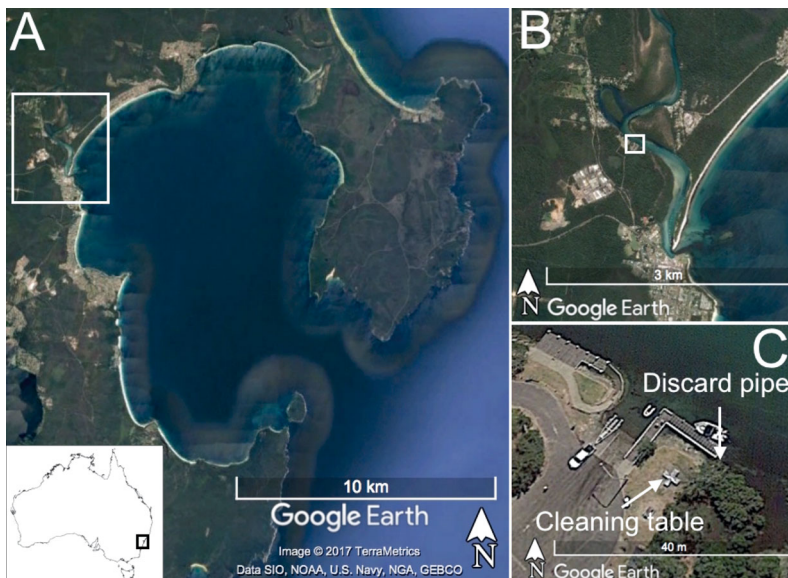


Fig. 1. Study location in New South Wales, Australia. (A) Jervis Bay; white box indicates area enlarged in panel B, inset: geographic location within Australia. (B) Lower Currambene Creek; white box indicates area enlarged in panel C. (C) Aerial photograph of the Woollamia boat ramp indicating the location of the fish-cleaning table and discard pipe (source: Google Earth)

tagged. The stingrays were tagged using stainless steel dart tags (Hallprint), with colour-coded vinyl streamers for individual identification, administered into the dorsal musculature using a 3 m handheld spear. DW was measured from fin tip to fin tip (*sensu* Yearsley & Last 2016), and sex was determined by the presence (male) or absence (female) of claspers.

Provisioning site use

Site attachment

Site fidelity was estimated as the proportion of days an individual was observed at the provisioning site during the study period (22 d = 10 tagging days + 12 observation days). A residency period was defined as the total number of days an individual was seen over the same observation period, provided the gaps between consecutive days sighted did not exceed 1 d (*sensu* Bruce & Bradford 2013). A 1 d period was chosen to account for potentially missed visits between observation sessions (see below). Maximum residency was used as the measure of residency and was the longest residency period for each individual.

Influence of cleaning events and boating activity

Observations of stingray presence, provisioning intensity and the number of boats were undertaken during two 3 h observation sessions (09:00–12:00 h, 14:00–17:00 h AEST) each day over 12 d, as time and personnel constraints did not allow full-day observations (*sensu* Gaspar et al. 2008). A stingray was considered present if observed within the 10 m radius from the mouth of the discard pipe (stingray visitation area; Fig. 2) within an observation session. We considered stingrays present within the small observation area to be there for the purposes of obtaining provisioned food. A provisioning event was classed as any event where fish were cleaned, rinsed and/or disposed of at the cleaning table. The start ('tap on' or cleaning began) and end ('tap off' or cleaning ceased) times of each provisioning event were recorded, and the cumulative lengths of cleaning events (in minutes) per observation session (*clean_length*) were used as a proxy for the level of provisioning. The observation boundary for boating activity extended to 50 m either side of the observation point (wharf) and was inclusive of the entire width of the estuary (Fig. 2). Every vessel that entered this boundary during the observation session was counted, and

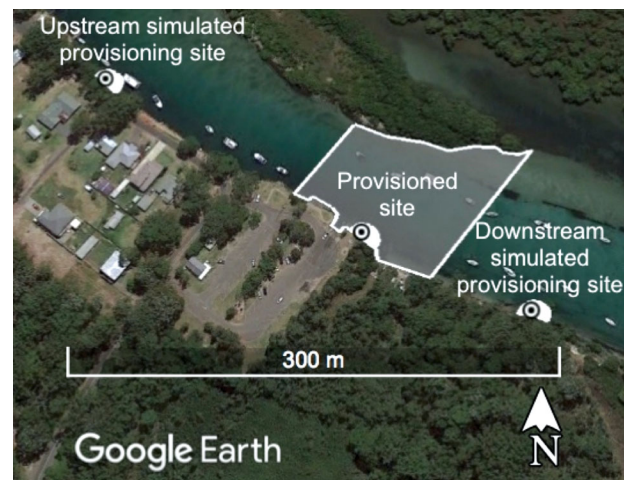


Fig. 2. Location of the provisioning (Woollamia boat ramp) and simulated provisioning sites. The grey shaded area indicates the observation boundary for boating activity at the provisioned site; the white shaded areas indicate the boundary for stingray visitation observations (10 m radius) and black circles denote the observation points

the number of vessels (*n_boats*) provided a proxy for the intensity of boating activity to determine whether stingrays had learned an association between boating and provisioning activity.

A generalised linear mixed effects model (GLMM) was used to determine the influence of provisioning (*clean_length*) and boating activity (*n_boats*) on the presence/absence of individual short-tail stingrays (presence) within each observation session (AM/PM), using the following formula:

$$\text{glmm}(\text{presence} \sim \text{scale}(\text{clean_length}) \times \text{scale}(\text{n_boats}) + (1 \mid \text{ID})) \quad (1)$$

where the dependent variable (presence) was binomial (1 = individual was present, 0 = absent). Stingray ID was used as the random effect (1 | ID) to avoid pseudoreplication. The fixed effects (*clean_length* and *n_boats*) were scaled to resolve scaling errors, and the number of iterations was set to 100 000 using the BOBYQA Optimisation (Powell 2009) to resolve optimisation errors.

Influence of tidal currents

Hourly tide height data obtained from the Bureau of Meteorology (BOM 2017) were adjusted to reflect local tide times for Huskisson, Jervis Bay (Port Kembla AEST +13 min; Australian Hydrographic Service 2016) and used to determine the predominant tidal direction for each observation session. A GLMM was

used to determine the influence of tide direction (tide_direction) and in turn, scent trails as olfactory cues, and/or observation session (AM/PM; session) on the presence/absence (presence) of individual short-tail stingrays using the following model:

$$\text{glmm}(\text{presence} \sim \text{tide_direction} \times \text{session} + (1 \mid \text{ID})) \quad (2)$$

where the dependent variable (presence) was binomial (1 = individual was present, 0 = absent). Stingray ID was used as the random effect (1 | ID) to avoid pseudoreplication. The fixed effect, tide_direction, was an integer where 1 = outgoing, 2 = low, 3 = incoming and 4 = high. The fixed effect, session, was an integer where 1 = AM and 2 = PM. The BOBYQA Optimisation (Powell 2009) was used to resolve optimisation errors.

Anticipation

To determine if stingrays at WBR exhibited anticipatory behaviour, the number of individual stingrays present (n_rays) and the cumulative length of cleaning events (in minutes) (clean_length) within each observation session (AM/PM; session) were compared using a 1-way ANOVA. Session was an integer for which AM = 1 and PM = 2, and the following model was used:

$$\text{ANOVA}(\text{session} \sim \text{n_rays} \times \text{clean_length}) \quad (3)$$

We found that cleaning events were longer and significantly more stingrays used the site in the afternoon (see 'Results'); therefore, a 2-way ANOVA was used to determine if the stingrays used the site during this time regardless of provisioning activity. Stingray visitation rates (number of visits h⁻¹) were calculated for when the cleaning table was in use or not (cleaning), within each observation session (AM/PM; session) per day. Visitation rates were log transformed for normality (LogRate), and analysed using the following model:

$$\text{ANOVA}(\text{LogRate} \sim \text{session} \times \text{cleaning}) \quad (4)$$

Simulated provisioning

To further investigate the link between provisioning and stingray movements at the WBR, simulated provisioning experiments were run at different locations upstream and downstream of the provisioning site where the stingrays were not provisioned, nor frequently observed (Fig. 2). During two 3 h observation sessions (09:00–12:00 h, 14:00–17:00 h AEST)

each day for 6 d, baseline observations of short-tail stingray visitation (each entry into the 10 m visitation radius was classed as a new visit) to the 2 simulated provisioning sites were recorded to confirm that the stingrays were not frequently using these sites. Over the subsequent 6 d period, assorted locally sourced fish frames were placed in the water to simulate a provisioning event. Observations of stingray visitation were then repeated during this period to determine if short-tail stingray visitation increased relative to background levels.

We expected that stingrays from the provisioned site would visit these 'new' provisioning sites post-provisioning, indicating that their movements and use of the surrounding Currumbene Creek were strongly driven by provisioned food. We also expected their response to provisioning at these sites to be slower than that at the provisioning site, reinforcing the association formed with provisioned food at the provisioning site.

A 1-way ANOVA was used to compare visitation (visits) before and during simulated provisioning observations (provision), between the two 3 h observation sessions each day (AM/PM; session) and between the 2 simulated provisioning locations (upstream or downstream; location). Visitation data were binned into half hour segments and then negative square root transformed for normality (visits_negsqrt). The following model was used:

$$\text{ANOVA}(\text{visits_negsqrt} \sim \text{location} \times \text{session} \times \text{provision}) \quad (5)$$

A Tukey's HSD post hoc analysis was used to determine where significant interactions occurred.

Time to first arrival

The time taken for an individual to arrive after the introduction of a food resource is indicative of the strength of the learned association (e.g. Reeb 1993); however, it should be noted that initial proximity to the resource is also an important factor. To determine if the time to first arrival differed between the provisioning and simulated provisioning sites, a 1-way ANOVA was used, following the formula ANOVA (time_difference ~ site), where time_difference was the time to first arrival after a provisioning (provisioning site) or simulated provisioning (simulated provisioning sites) event and site was the site at which it occurred. A pairwise (*t*-test) post hoc analysis was used to determine where significant interactions occurred.

Data analysis

All statistical analyses were conducted using R V.3.3.1 (R Core Team 2015) with the R Studio interface V.0.99.903 (RStudio Team 2015). All datasets and code used for analyses are available in Supplements 1 & 2 at www.int-res.com/articles/suppl/m600p099_supp/.

RESULTS

Population structure

A total of 12 short-tail stingrays were tagged during this study, with 11 tagged during the initial 10 d tagging period and 1 tagged during the observation period but after the day's observations had ceased (18/08/16, 17:10 h; see Table A1 in the Appendix). Individual stingrays showed varied responses to tagging, but all rapidly returned to the provisioning site, thus we consider tagging to have had no impact on our observations. All 12 tagged individuals were female and ranged in DW from 110 to 165 cm (mean = 143 cm). Seven individuals were considered adults (based on size, i.e. >150 cm DW, sensu Le Port et al. 2012, or they were obviously gravid [n = 5]; see Le Port et al. 2012). Five were considered sub-adults (70–150 cm DW; Le Port et al. 2012). For more detailed information see Table A1 in the Appendix.

Provisioning site use

Site fidelity and residency

Site fidelity and maximum residency periods at the provisioning site varied greatly among individuals (Fig. 3). Mean \pm SE site fidelity was 0.322 ± 0.056 (proportion of days sighted; min = 0.045; max =

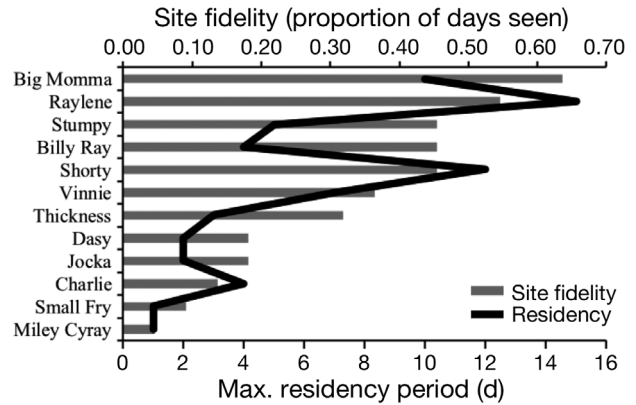
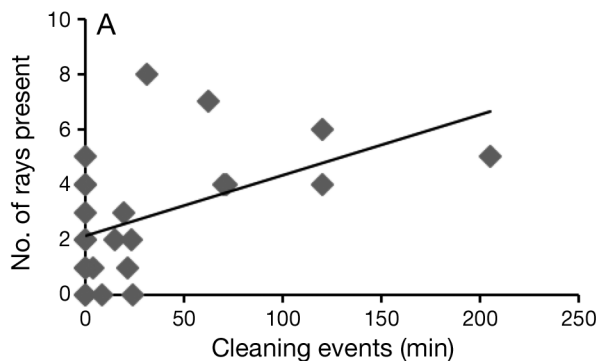


Fig. 3. Site fidelity (proportion of days seen out of 12 observation days) and maximum residency period (days) for each individual stingray at the provisioning site

0.636). The mean maximum residency period was 5.5 ± 1.3 d (min = 1; max = 15).

Influence of cleaning events and boating activity

Stingray presence was significantly correlated with the cumulative length of cleaning events (GLMM: coefficient estimate $[\beta] \pm SE = 0.60 \pm 0.17$, N = 288, $p < 0.001$; Fig. 4A), but not with the total number of boats (GLMM: $\beta = -0.27 \pm 0.17$, N = 288, $p = 0.11$; Fig. 4B). However, the cumulative length of cleaning events and the number of boats were significantly negatively correlated (Pearson product-moment correlation: $r = -0.15$, N = 288, $p = 0.01$).

Influence of tidal currents

Individual stingray presence was significantly correlated with tide direction (GLMM: $\beta = 1.32 \pm 0.40$, N = 288, $p < 0.001$), observation session (GLMM: $\beta = 4.92 \pm 1.18$, N = 288, $p < 0.001$) and the interaction

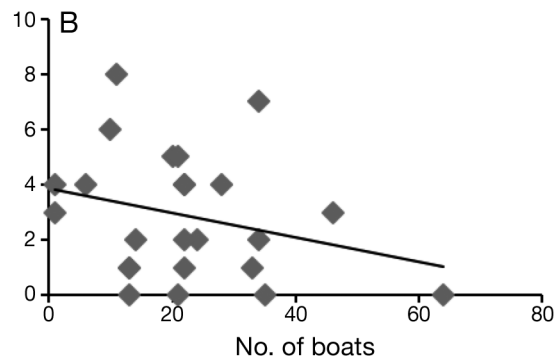


Fig. 4. Number of stingrays present in comparison with (A) the cumulative length of cleaning events (in min) ($p < 0.001$) and (B) the number of boats ($p = 0.11$) per observation session (N = 288 observations)

between the 2 (GLMM: $\beta = -1.48 \pm 0.44$, $N = 288$, $p < 0.001$). There were significantly more individuals present in the afternoons, although this was most apparent during the low tidal phase (Fig. 5).

Anticipation

The cumulative length of fish-cleaning events tended to be longer during afternoon observation sessions (1-way ANOVA: $F_{1,60} = 3.401$, $p = 0.08$), and significantly more individual stingrays were present in the afternoon throughout the study period (1-way ANOVA: $F_{1,60} = 11.796$, $p = 0.0027$). Observation session had a significant effect on stingray visitation (2-way ANOVA: $F_{1,44} = 8.117$, $p = 0.007$), with visitation being higher in the afternoon irrespective of whether or not the cleaning table was in use (2-way ANOVA: $F_{1,44} = 0.34$, $p = 0.563$; Fig. 6).

Simulated provisioning

There was a significant effect of provisioning on stingray visitation (1-way ANOVA: $F_{1,280} = 14.784$, $p < 0.001$), with more visits during than before provisioning (Fig. 7). There was a marginal but non-significant effect of sampling session (AM or PM) (1-way ANOVA: $F_{1,280} = 3.122$, $p = 0.078$), with a tendency for more stingrays in the afternoon, and a marginal but non-significant effect of location (1-way ANOVA: $F_{1,280} = 3.499$, $p = 0.063$) with a tendency for more stingrays at the downstream location. There was a significant interaction between session and provisioning (before vs. during) (1-way ANOVA: $F_{1,280} = 4.089$, $p < 0.05$; Fig. 7), with a greater increase in visitation while the bait was present in the morning relative to the afternoon (pairwise comparisons, Tukey HSD post hoc: AM×Provisioned vs. AM×Non-provisioned, $p < 0.001$; PM×Provisioned vs. AM×Non-provisioned, $p < 0.001$). There were no further significant interactions.

Time to first arrival

On average, short-tail stingrays arrived at the provisioning site within 9 ± 2.63 min (\pm SE, $N = 29$) of the beginning of a provisioning event. The time to first arrival of a stingray after the beginning of a provisioning event significantly differed between the upstream and downstream simulated provisioning sites and the provisioning site at the WBR (1-way ANOVA: $F_{1,49} = 9.761$, $p = 0.003$), with stingrays tak-

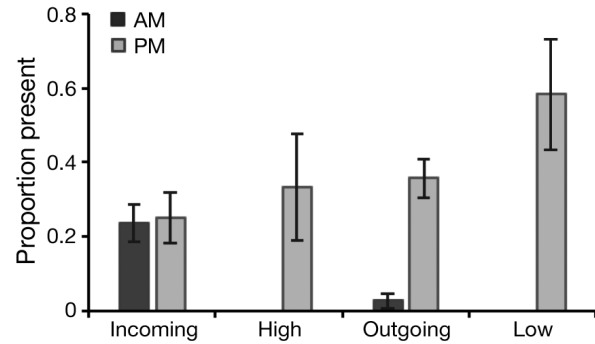


Fig. 5. Mean \pm SE proportion of stingrays present per observation session and tidal phase ($N = 288$ observations)

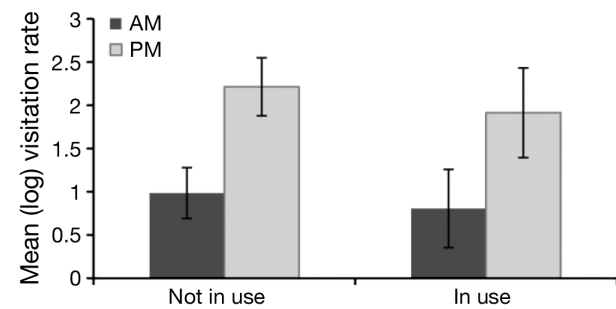


Fig. 6. Mean \pm SE (log) stingray visitation rates when the cleaning table at the Woollamia boat ramp was in use and not in use during each observation session (AM/PM) ($N = 288$ observations)

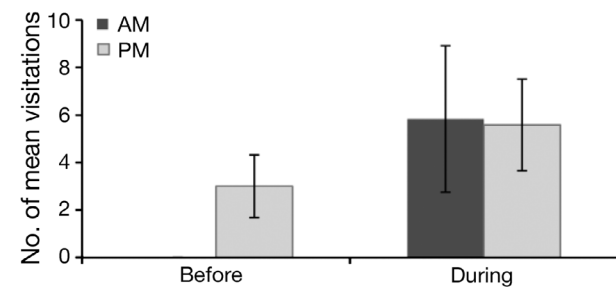


Fig. 7. Mean \pm SE stingray visitations before and during simulated provisioning during each observation session (AM/PM). Based on 6 observation sessions per trial (before vs. during) per time of day (AM vs. PM)

ing significantly longer to approach the upstream and downstream sites than the provisioning site at the WBR (pairwise t -test: upstream vs. WBR, $p < 0.001$; downstream vs. WBR, $p = 0.009$; upstream vs. downstream, $p = 0.142$).

DISCUSSION

We hypothesised that if short-tail stingrays at the WBR, Jervis Bay, Australia, were affected by provisioning activity, (1) there would be a resident popula-

tion of stingrays with high site attachment; (2) their presence would be driven by provisioning activity, boating activity (learned association) and tidal currents (olfactory cues); (3) they would recruit quickly to 'new' provisioning sites, reinforcing the influence of provisioning; and (4) they would exhibit signs of anticipation as indicated by repeated visits to the WBR even when food was not available. Site attachment was moderate; however, it may be high within the estuary generally, with mean recruitment time to the provisioning site being just 9 min post-provisioning. Tidal currents likely play an important role in the distribution of scent trails used as an olfactory cue, with outgoing and low tides eliciting higher visitation. The data suggest that the stingrays spend most of their time in the lower reaches of the estuary and visit the provisioning site in the afternoons, coinciding with higher levels of fish-cleaning activity. Critically, stingrays visit the provisioning site in the afternoons irrespective of whether the cleaning table is in use, which may indicate learned anticipatory behaviour (i.e. time–place learning). Stingrays rapidly recruited to newly provisioned locations (simulated provisioning), although their time of first arrival was significantly slower than that at the WBR, providing additional evidence of a learned association between the provisioning site and food. Contrary to previous studies, the relationship between boating activity and stingray site use was weak; thus, boating activity is not a good predictor for food provisioning for this population. Based on our results, we consider short-tail stingray movements to be influenced by food provisioning at the WBR, Jervis Bay.

Anticipation

Anticipation of feeding has been observed in a wide range of taxa (rodents: Mistlberger 1994; birds: Rijnsdorp et al. 1981; carnivores: Carlstead 1998; primates: Waitt & Buchanan-Smith 2001, teleosts: Chen & Tabata 2002, Brännäs et al. 2005; and elasmobranchs: e.g. Bruce & Bradford 2013). Time–place learning, i.e. the process by which animals link events with a particular time and place (Mulder et al. 2013), is the likely mechanism by which this behaviour develops. Indeed, many fish species are capable of anticipating up to 3 feeding events daily via this mechanism (see Mulder et al. 2013 for review). Importantly, animals still show anticipatory behaviour even in the absence of a food reward (see Schatz et al. 1999 for an example). As such, anticipation can be considered a precursor to the development of dependency on provisioned food. In fact, all studied

populations of provisioned stingrays show a level of dependency on provisioning initially manifested as anticipatory behaviour (Newsome et al. 2004, Gaspar et al. 2008, Corcoran et al. 2013). This can have many and varied implications both for the species and for the ecosystem generally (see Brena et al. 2015).

At the WBR, short-tail stingrays appeared to show anticipation of provisioning in the afternoons. Significantly more short-tail stingrays were observed in the afternoon regardless of whether the cleaning table was in use (Fig. 6). It could be argued that this increase in visitation is part of natural diurnal movements and does not reflect an influence of provisioning. Indeed, the significant lack of baseline data on the natural behaviour of short-tail stingrays makes interpretation difficult. However, the time to first arrival at the provisioning site when food was available was significantly shorter than to either of the simulated provisioning sites even though they had to pass the downstream simulation site to get to the provisioned site. This rapid recruitment to the provisioning site suggests a learned association with this site and food. We therefore consider it very likely that the increased visitation in the afternoon at this site (see Results) regardless of fish-cleaning activity reflects an anticipatory response as opposed to natural diurnal movements. It is also important to note that visitation was counted within the 10 m radius of the discard pipe and not the general vicinity. Therefore, it is unlikely that entering this specific and small space is part of the natural movements of these animals, especially at the rates observed in this study. Long-term monitoring of the population would allow for quantitative assessment of the extent to which the stingrays are anticipating food and the dependency risk. Further, feeding experiments on captive stingrays would allow assessment of their ability to anticipate feeds.

Influence of provisioning, boating activity and tidal currents

Short-tail stingray use of the WBR appeared to be influenced by provisioning, as shown by a significant correlation between the length of cleaning events and the number of stingrays present (Fig. 4A), and stingrays arriving at the provisioning site on average just 9 min after provisioning began. Further, during simulated provisioning experiments, significantly more short-tail stingrays were observed when provisioned food was made available, particularly in the morning when stingrays are not normally present (Fig. 7). This does not mean that the stingrays would

not be using the estuary in the absence of provisioning, but rather that the stingrays would likely not use the immediate boat ramp area due to the high risks associated with interactions with people, boats and fishing gear. The observed negative, though non-significant, relationship between stingray visitation and boating activity (Fig. 4B) supports this. In addition, grouping at the provisioning site results in individuals entering into potentially costly agonistic interactions (Pini-Fitzsimmons et al. unpubl.). The benefits gained by accessing provisioned food therefore must outweigh these potential costs. The extent to which this behaviour impacts their long-term fitness is unclear, but evidence from other provisioned populations (e.g. Stingray City, Cayman Islands) suggests that dependency can lead to an ecological trap (Semeniuk & Rothley 2008). Future research should be aimed at quantifying potential fitness implications of human–stingray interactions at the WBR.

Non-natural food items often exhibit differences in macronutrients and essential fatty acids, which are important for immune function and disease resistance, stress management and reproduction (e.g. Semeniuk et al. 2007). Research suggests that this can impact the health of provisioned stingrays (Semeniuk et al. 2007, 2009, Semeniuk & Rothley 2008), but the impact on short-tail stingrays may not be as great. This species forages on juvenile fish, squid, invertebrates and macroinfauna (Le Port et al. 2008), and while the provisioned food consists of large, pelagic species (J. Pini-Fitzsimmons pers. obs.) they are locally caught. It remains unclear what proportion of the short-tail stingrays' diet comes from provisioning at the WBR. Isotopic analysis of non-provisioned and provisioned short-tail stingrays is currently being employed to help elucidate the dietary impacts of provisioning on this population.

The strong associations between stingray presence and boating activity described by Newsome et al. (2004), Gaspar et al. (2008) and Corcoran et al. (2013) were not observed in the present study. The associations described in these studies are likely related to the history of the provisioning activity and its contemporary manifestation. Provisioning of these populations began offshore from boats that were specifically entering these sites to either clean their catches (Newsome et al. 2004, Corcoran et al. 2013) or directly provision the rays (Gaspar et al. 2008). By comparison, boats that enter the WBR area usually dock at the wharf before being retrieved via the boat ramp, after which anglers begin cleaning their catches at the cleaning table. The time between the boat entering the site and cleaning catches is there-

fore highly unpredictable, impeding the stingrays' ability to learn an association between boat noise and the appearance of food.

Olfaction is a key sense used by elasmobranchs for locating prey (Hodgson & Mathewson 1971, Collin 2012), and the link between stingray presence with outgoing and low tide (Fig. 5) is perhaps unsurprising. Short-tail stingrays have been observed resting on shallow mudflats just downstream from the WBR during the day (R. Simpson pers. comm.), and olfactory stimuli have been used in Mo'orea, French Polynesia, to facilitate encounters between people and pink whiprays *Pateobatis fai* with good success (Gaspar et al. 2008). We observed that on average, the first visit of a short-tail stingray occurred after just 9 min post-provisioning, suggesting that short-tail stingrays must be reasonably close by. The fact that significantly more stingrays were observed at the downstream site during simulated provisioning trials further supports this supposition. Acoustic telemetry is currently being employed to shed further light on the movements of these animals.

Residency

Short-tail stingray habitat use and site attachment has not been comprehensively assessed. In the present study, 6 individuals exhibited above-average site fidelity, with 4 exhibiting above-average maximum residency periods (Fig. 3). However, as individuals responded quickly to provisioning events, their site fidelity and residency within the estuary is likely higher. Increases in elasmobranch site fidelity and residency patterns at provisioning sites are common (e.g. Clarke et al. 2011, Bruce & Bradford 2013, Brunnenschweiler & Barnett 2013, Huveneers et al. 2013) and can provide the first indication that provisioning activities may be influencing natural movements. As we have shown here, increases in the intensity of provisioning can lead to increases in group size (Fig. 4A). In turn, this can lead to increases in competition for access to the provisioned resource (Pini-Fitzsimmons et al. unpubl.) and disease transmission (Semeniuk & Rothley 2008, Bruce & Bradford 2013).

Population structure

Our study population is female biased, with many in breeding condition, which is consistent with other studies on provisioned elasmobranchs (Newsome et al. 2004, Clua et al. 2010, Brunnenschweiler & Baensch

2011, Brunnschweiler & Barnett 2013, Corcoran et al. 2013, but see Gaspar et al. 2008). The observed sex ratio may be explained by the increased female energy requirements associated with breeding (Wearmouth & Sims 2008). Alternatively, females, being larger than males in this species, may be competitively excluding males from the site (Newsome et al. 2004, Corcoran et al. 2013). This would also explain the lack of juveniles. Spatial sexual segregation is common in elasmobranchs (Wearmouth & Sims 2008) and may provide another possible explanation for the absence of males at the WBR. A lack of behavioural and habitat preference data for short-tail stingrays makes interpretation difficult.

Implications

We have provided the first assessment of incidental provisioning from a fish-cleaning facility on Australia's coast, and we have shown that this activity likely influences the movements of a large mesopredator as indicated by residency patterns and potential anticipatory behaviour. The results are consistent with a number of studies in terrestrial and aquatic ecosystems (e.g. Schatz et al. 1999, Waitt & Buchanan-Smith 2001, Brena et al. 2015). As such, we suggest that the population of short-tail stingrays provisioned at the WBR may be at risk of experiencing negative impacts (e.g. dependency on provisioned food, reduced fitness) in the absence of appropriate management regarding the discarding of recreational fish waste. Additional research over longer temporal and larger spatial scales is required to quantify these risks and inform future management of this activity.

An increasing number of fish-cleaning facilities are being built around Australia to support recreational fishing (NSW DPI 2016). It is commonplace and accepted practice for anglers to discard fish waste into waterways at these facilities (C. Mercier pers. comm.). In Tasmania, it is stipulated that fish waste must be discarded where the fish was caught or in household rubbish (Wild Fisheries Management Branch 2015). New South Wales legislation vaguely stipulates that recreational fish waste is disposed of 'responsibly' (NSW DPI 2015). No such regulations exist in any other Australian state or territory, nor could we find clearly stipulated regulations for the USA or the European Union. Given the known effects of provisioning on wildlife, these management gaps need addressing as a matter of some urgency.

Some social and economic benefits have been identified from provisioning activities, which may have

importance for Jervis Bay, as tourism is a primary pillar of the local economy. Wildlife provisioning can add value to a tourism experience, leading to greater visitor satisfaction and in turn greater economic benefit (Newsome & Rodger 2008). Many people feel joy during the experience, which can lead to increased awareness and improved attitudes towards nature, the environment and conservation (Green & Higginbottom 2000, Hammerschlag et al. 2012, Burgin & Hardiman 2015). It is possible, however, for involvement in provisioning to lead to a misunderstanding of the actual risks and impacts of wildlife provisioning (Green & Giese 2004, Dubois & Fraser 2013). Education is key for a well-structured wildlife provisioning activity and can heighten awareness and satisfaction with an experience (Shackley 1998, Newsome & Rodger 2008), and we recommend that this be considered in future management of this activity.

Ethical note. This study was carried out under approval from the Macquarie University Animal Ethics Committee (ARA – 2014/015-7) and NSW DPI Fisheries Scientific Collection Permit P08/0010-4.4. To the best of our knowledge, there were no negative impacts on the welfare of the animals used in this study.

Acknowledgements. J.P.F. was supported by the Macquarie University RTP Scholarship, and the project benefited greatly from funding provided by Macquarie University and the New South Wales Department of Primary Industries. We thank the Macquarie University's Behaviour, Ecology and Evolution of Fishes laboratory and volunteers for their assistance with fieldwork for this project, and the 'World Famous Fish and Chip Shop', Huskisson, for their donation of fish frames and offal. Special thanks to local anglers at the WBR, also known as the 'Table of Knowledge', who shared their vast local knowledge of fishing, boating and the 'local' stingrays.

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APPENDIX. Additional data

Table A1. Summary table of individual short-tail stingrays tagged in this study. All individuals were females. All PIT tags begin with the number 900032002394-

Date (dd/mm/yy) and time tagged (h, AEST)	— Tag colour —		PIT tag number	Disc width (cm)	Size class
	Proximal	Distal			
01/08/16, 15:51	Pink	Blue	989	135	Subadult
01/08/16, 16:08	Green	Grey	834	135	Subadult
02/08/16, 16:55	Green	Red	848	135	Subadult
03/08/16, 14:15	Green	White	0983	140	Adult (gravid)
06/08/16, 15:41	Grey	Red	976	145	Adult (gravid)
07/08/16, 10:36	Green	Green	987	155	Adult (gravid)
07/08/16, 13:28	Pink	Grey	977	155	Adult (gravid)
08/08/16, 12:44	White	Red	990	155	Adult
08/08/16, 15:51	Pink	Green	984	135	Subadult
09/08/16, 09:51	Pink	Pink	971	155	Adult (gravid)
09/08/16, 10:14	Grey	Grey	846	165	Adult
18/08/16, 17:10	Pink	Red	975	110	Subadult