

REVIEW

Shark and ray provisioning: functional insights into behavioral, ecological and physiological responses across multiple scales

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ABSTRACT: The use of olfactory stimuli and the provision of food are a common practice to prompt artificial aggregations of emblematic wild species and ensure the economic viability of the wildlife-watching industry. Several elasmobranch species have been targeted by such operations in a variety of locations for over 4 decades. A recent review succinctly addressed the potential effects of shark diving tourism, including shark provisioning, on shark individual behavior and ecology, but the paucity of data on the ecology of elasmobranchs precluded general statements. By using a functional framework, we reviewed the findings of the 22 available studies that investigated the behavioral, physiological, and ecological response of 14 shark and 3 ray species targeted by artificial provisioning. Focusing on the underlying processes that rule the response of targeted elasmobranch species, we report further effects acting beyond the individual scale. We suggest that the most commonly described alterations of individual movement patterns have cascading effects through the group and community scales, ultimately resulting in altered health condition and individual behavior toward humans. We conclude by stressing the potential for provisioning activities to support the investigation of complex ecological and behavioral processes in elasmobranchs.

KEY WORDS: Anthropogenic disturbance · Ecological effects · Management · Non-consumptive exploitation · Shark conservation · Wildlife provisioning

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INTRODUCTION

The flourishing growth of nature-based tourism can partly be explained by the need for current generations to reconnect with nature (Miller 2005). Specifically, the viewing of emblematic wildlife has increased in popularity (Knight 2009), and the promoters of wildlife-watching point out various benefits, ranging from financial inputs to local economies to enhancing education and environmental awareness (Orams 2002), that contribute towards the conservation of showcased species and their environments (Walpole & Thouless 2005). The economic viability of commercial wildlife viewing depends on

the predictable and constant sightings of wild animals (Whittaker 1997), which can be enhanced by attracting them. In particular, the use of appetitive stimuli is a common practice to ensure animals are viewable to tourists (Knight 2009), but there are concerns regarding possible negative consequences for the targeted animals and their ecosystems. Orams (2002), Newsome & Rodger (2008) and Burgin & Hardiman (2015) reviewed a number of studies that characterized the alteration of behavioral and physiological parameters in terrestrial vertebrates, cetaceans, and fish, including but not limited to altered health condition and increased aggression toward humans.

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Shark and ray provisioning is an umbrella term encompassing various practices (Richards et al. 2015) ranging from solely using an olfactory stimulus to feeding varying amounts of food, in order to facilitate encounters between tourists and elusive elasmobranch species. These activities generate large revenues for tourist operators and related businesses worldwide (Gallagher & Hammerschlag 2011, Cisneros-Montemayor et al. 2013) and promote the non-extractive value of elasmobranchs (Brunnschweiler 2010, Clua et al. 2011, Vianna et al. 2012). They are also assumed to increase environmental awareness and enhance positive attitudes toward this threatened taxon, thereby promoting its conservation (Topelko & Dearden 2005).

The ecological consequences of elasmobranch provisioning activities have received relatively little attention to date. A recent review by Gallagher et al. (2015) on the effects of shark diving tourism succinctly describe some impacts of artificial provisioning on shark individual behavior, but does not include the responses of rays, nor cover the effects of provisioning beyond the individual scale. Few ecological aspects have been studied across enough species to allow comparison and establish common effects (Table 1). This patchy information prevents general conclusions being drawn from findings that depend on the interplay between (1) the frequency and type of activities, (2) the focal species, characterized by a wide variety of site-dependent natural behaviors and ecology, and (3) the general ecology of the viewing site (Duffus & Dearden 1990). Moreover, logistical constraints imposed by the study of elusive species often preclude classical approaches: control sites and baseline data on the ecology of the target population are seldom available. Therefore, focusing on the underlying processes that rule the response of targeted species is crucial to characterizing the impact of provisioning activities.

Here, we adopt a functional framework to synthesize the effects of provisioning operations on the ecology, behavior and physiology of elasmobranchs beyond the individual scale. We gathered the 22 available studies that investigated the behavioral, physiological, and ecological response of 14 shark and 3 ray species at 11 sites around the world where aggregations were conducted using appetitive stimuli (Fig. 1). Given the shared ecological and biological features of sharks and rays (Carrier et al. 2012), an exhaustive review of elasmobranch responses to provisioning ought to benefit our understanding of the underpinning mechanisms in action. This procedure allows us to (1) suggest a complementary ap-

proach to the review provided by Gallagher et al. (2015), that includes additional references and discusses further described impacts; (2) to highlight the putative connections between every impact described in isolation, across the individual, group and community scales; and (3) to illustrate the potential for provisioning activities to support the investigation of key ecological and behavioral processes in elasmobranchs.

WHY INCLUDE SHARKS AND RAYS?

Our review covers the effects of provisioning of both sharks and rays. Like most shark species, some ray species are carnivorous and are privileged targets for artificial provisioning activities. Most of the individual responses by sharks to provisioning reported in Gallagher et al. (2015) have also been described in rays. In this section, we briefly justify the inclusion of both sharks and rays in our review by (1) highlighting their key similar responses to provisioning, and (2) discussing how the comparison of different responses can help address key research questions on the impact of provisioning.

Similar individual responses by sharks and rays

Horizontal movement patterns in fed sharks and rays are affected by provisioning at both local spatial and short-term temporal scales. Sharks and rays exposed to provisioning operations generally show a reduced horizontal activity. By tracking the fine-scale distribution of great white sharks *Carcharodon carcharias* in the vicinity of cage-diving operations at Neptune Islands, South Australia, Huveneers et al. (2013) showed that the area where individuals spend 50% of their time decreased by 28% during berleying operations. Similarly, female southern stingrays *Dasyatis americana* fed at a tourist site in Grand Cayman displayed smaller activity spaces than non-fed rays, in addition to reversed diel activity patterns (Corcoran et al. 2013). Furthermore, several studies report that the centers of activity of tracked sharks and rays align with areas and hours of active provisioning (Newsome et al. 2004, Clarke et al. 2011, Bruce & Bradford 2013, Huveneers et al. 2013).

Some studies describe the emergence of an anticipatory response by fed sharks and rays. The learning capabilities of elasmobranchs are now widely recognized (Guttridge et al. 2009), and the regular exposure to an olfactory stimulus, sometimes followed by

Table 1. Overview of the ecological concepts investigated in the literature on shark and ray feeding. nys: not yet studied

Model species	Studied concept						Individual health	Behavior to humans
	Individual horizontal distribution	Individual vertical distribution	Site occupancy patterns	Dietary habits	Abundance	Community composition		
<i>C. albimarginatus</i>	nys	nys	Brunnschweiler et al. (2014)	nys	nys	Brunnschweiler et al. (2014)	nys	nys
<i>C. amblyrhynchos</i>	nys	nys	Brunnschweiler et al. (2014)	nys	Clarke et al. (2013)	Brunnschweiler et al. (2014)	nys	nys
<i>C. carcharias</i>	Bruce & Bradford (2013)	Bruce & Bradford (2013)	Bruce & Bradford (2013)	nys	Bruce & Bradford (2013)	Brunnschweiler et al. (2013)	nys	nys
	Huvaneers et al. (2013)	Laroche et al. (2007)	Laroche et al. (2013)		Bruce & Bradford (2013)	Brunnschweiler et al. (2013)		
<i>C. falciformis</i>	Clarke et al. (2011)	nys	Clarke et al. (2011)	nys	Clarke et al. (2013)	Clarke et al. (2013)	nys	Clarke et al. (2013)
<i>C. galapagensis</i>	nys	nys	Meyer et al. (2009)	nys	Meyer et al. (2009)	Meyer et al. (2009)	nys	nys
<i>C. leucas</i>	Brunnschweiler & Barnett (2013)	nys	Brunnschweiler & Barnett (2013)	nys	Brunnschweiler & Baensch (2011)	Brunnschweiler & Baensch (2011)	nys	nys
<i>C. melanopterus</i>	nys	nys	Brunnschweiler et al. (2014)	nys	Brunnschweiler et al. (2014)	Brunnschweiler et al. (2014)	nys	nys
<i>C. perezi</i>	nys	nys	Malkov & Côté (2011)	nys	Malkov & Côté (2011)	Brunnschweiler et al. (2014)	Mounier et al. (2013b)	nys
<i>C. plumbeus</i>	nys	nys	Meyer et al. (2009)	nys	Meyer et al. (2009)	Meyer et al. (2011)	Malkovi & Côté (2011)	nys
<i>G. cuvier</i>	nys	nys	Brunnschweiler et al. (2014)	nys	Brunnschweiler et al. (2014)	Brunnschweiler et al. (2014)	Mounier et al. (2013b)	nys
<i>N. acutidens</i>	nys	nys	Brunnschweiler et al. (2014)	nys	Brunnschweiler et al. (2014)	Brunnschweiler et al. (2014)	Mounier et al. (2013b)	nys
<i>N. ferrugineus</i>	nys	nys	Brunnschweiler et al. (2014)	nys	Brunnschweiler et al. (2014)	Brunnschweiler et al. (2014)	Mounier et al. (2013b)	nys
<i>R. typus</i>	nys	nys	Araujo et al. (2014)	nys	Araujo et al. (2014)	Brunnschweiler et al. (2014)	Araujo et al. (2014)	nys
<i>T. obesus</i>	nys	Fitzpatrick et al. (2011)	Brunnschweiler et al. (2014)	nys	Brunnschweiler et al. (2014)	Brunnschweiler et al. (2014)	Araujo et al. (2014)	nys
<i>D. americana</i>	Corcoran et al. (2013)	nys	Corcoran et al. (2013)	nys	Semeniuk et al. (2007)	Brunnschweiler et al. (2014)	Newsome et al. (2004)	Semeniuk & Rothley (2008)
<i>H. fai</i>	Gaspar et al. (2008)	nys	Gaspar et al. (2008)	nys	Gaspar et al. (2008)	Brunnschweiler et al. (2014)	Newsome et al. (2004)	Semeniuk & Rothley (2008)
<i>M. australis</i>	nys	nys	Newsome et al. (2004)	nys	Newsome et al. (2004)	Brunnschweiler et al. (2014)	Newsome et al. (2004)	Semeniuk & Rothley (2008)

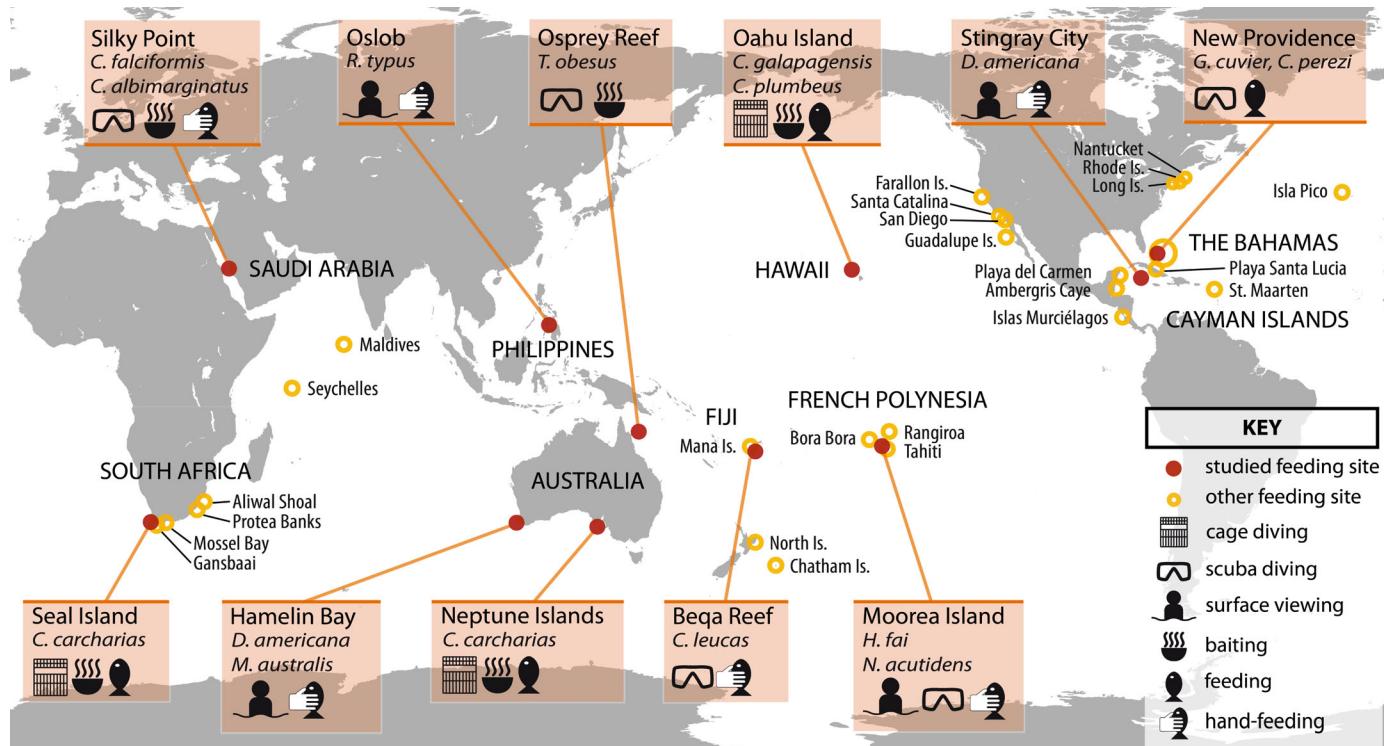


Fig. 1. Distribution of provisioning operations targeting sharks and rays. Map shows the countries/states where the impact of shark and ray provisioning operations have been studied

easy access to food, can drive individuals into a repeated and predictable use of the provisioning site. At locations where provisioning operations take place daily at regular times, several authors witnessed sharks and rays arriving at provisioning sites in anticipation of the process, even before bait is supplied or with no bait at all (Gaspar et al. 2008, Meyer et al. 2009, Bruce & Bradford 2013, Clarke et al. 2013, Corcoran et al. 2013). In cases when no anticipatory response is reported, individuals responded much faster to the stimulus after baiting was initiated (Newsome et al. 2004, Johnson et al. 2006).

Overall, all studies demonstrate that the propensity to respond to provisioning operations varies both among elasmobranch species and among individuals within each species (Laroche et al. 2007, Gaspar et al. 2008, Brunnenschweiler & Barnett 2013, Huveneers et al. 2013, Brunnenschweiler et al. 2014). Sharks and rays display inter-individual variation in patterns of residency and habitat use: while some individuals show year-round site attachment, others are only opportunistic visitors and are consequently less likely to be affected by provisioning operations (Clua et al. 2010a, Clarke et al. 2011, Maljković & Côté 2011, Araujo et al. 2014).

Insights provided by different responses: diet and foraging behavior

In their list of recommended research questions for the field of shark diving tourism, Gallagher et al. (2015) stress the need to better understand the impact of provisioning on sharks' trophic features but deplore the paucity of data available on the topic. Although the amount of food distributed is seldom reliably reported, the inclusion of the ray literature gives a broader perspective on the effects of provisioning regimes on the dietary habits of elasmobranchs.

To our knowledge, only 2 studies have investigated possible disturbances to dietary habits of elasmobranchs resulting from provisioning operations. Maljković and Côté (2011) used stable isotope analysis to investigate isotopic signatures of fed Caribbean reef sharks *Carcharhinus perezi* in the Bahamas and detected a putative change in their dietary habits. A small number of large individuals accessed more than 50 % of the bait offered and showed a ^{15}N tissue enrichment, which can be explained by their frequent access to high-trophic level food. Nevertheless, some authors extrapolated the energy requirements of free-ranging sharks from simple bioenergetic models de-

veloped from similar species, and concluded that provisioning was unlikely to constitute the sole source of energy for fed sharks (Maljkovi & Côté 2011, Hammerschlag et al. 2012). Conversely, Semeniuk et al. (2007) used fatty acid (FA) profile analysis to investigate human-induced physiological changes in southern stingrays fed with squid in the Caribbean. The FA profiles of fed individuals turned out to be markedly distinct from those of unfed stingrays and showed a strong similarity with the FA compositions of squid, suggesting that conditioned stingrays rely on provisioning operations as their main food source. They also showed that provisioned squid does not provide a similar nutritional lipid composition to the stingrays' natural prey. Still, the detrimental consequences of depending on provisioned food on the ability of individuals to feed independently (Orams 2002) remain undetermined. However, Newsome et al. (2004) observed that regularly fed southern stingrays maintain active foraging and natural hunting behaviors when provisioning operations do not occur, even though their rate of success in predatory actions is unknown.

These findings suggest that the extent to which fed individuals rely on provisioned food is linked to the practices involved (Richards et al. 2015). Moreover, comparing the response of elasmobranch species to different feeding regimes (i.e. whether the amount of food is restricted or not) can contribute to determining not only how they are impacted by provisioning activities, but also how they tune their feeding strategies according to fluctuating contexts.

GROUP-SCALE EFFECTS

Aggregation effects

The primary purpose of provisioning operations is to aggregate sharks and rays at a particular location, sometimes where the target species are already naturally abundant (e.g. Vianna et al. 2012). A number of studies report that tour operators have achieved the goal of increasing abundances of targeted species at the provisioning sites over prolonged periods (Meyer et al. 2009, Clua et al. 2010b, Brunnschweiler & Baensch 2011, Bruce & Bradford 2013, Clarke et al. 2013). Most notably, Brunnschweiler & Baensch (2011) noticed a 6-fold increase in the bull shark *Carcharhinus leucas* population in Fiji over 7 yr. Indeed, Bruce & Bradford (2013) state that the changes described in fed elasmobranch groups can be directly linked to provisioning operations. The authors observed that great white shark sightings near Neptune

Islands, South Australia, significantly increased following the growth of shark cage diving operations.

Provisioning operations can influence group composition in terms of species and genders that are aggregated. Using an olfactory stimulus can lead to the gathering of both gregarious and solitary species. Aggregations of naturally sociable blacktip *Carcharhinus melanopterus* (Mourier et al. 2012) or whitetip *Triaenodon obesus* (Fitzpatrick et al. 2011) reef sharks and silky sharks *Carcharhinus falciformis* (Clarke et al. 2011) are described in the literature. Likewise, gatherings of solitary tiger shark *Galeocerdo cuvier* (Hammerschlag et al. 2012), whale (Araujo et al. 2014), bull (Brunnschweiler & Baensch 2011), and great white sharks (Bruce & Bradford 2013), sicklefin lemon sharks *Negaprion acutidens* (Clua et al. 2010a) and southern stingrays (Semeniuk & Rothley 2008) have been reported. Moreover, Mourier et al. (2013b) show that the sexual segregation of blacktip reef sharks around Moorea, French Polynesia does not occur on the northern coast of the island, where feeding operations regularly take place, although this pattern could not be clearly linked to provisioning activities.

Effects on natural cycles

As shown in Gallagher et al. (2015), the impact of provisioning operations on natural cycles and behavior is hard to assess in elasmobranchs because of the general lack of baseline data on reproductive cycles and migrations for most of the species involved (Brunnschweiler & Baensch 2011). Nevertheless, provisioning platforms can represent useful tools for investigating such aspects (Meyer et al. 2009, Clua et al. 2010a, Brunnschweiler & Baensch 2011, Araujo et al. 2014). The observed seasonality in the abundance of sharks at several provisioning sites indicates that individuals maintain their natural migrations and that provisioning activities are unlikely to permanently alter them (Laroche et al. 2007, Meyer et al. 2009, Clua et al. 2010a, Brunnschweiler & Baensch 2011). The seasonal changes in abundance at the provisioning site and the patterns of habitat use described in long-term surveys are attributed to breeding migrations (Meyer et al. 2009, Clua et al. 2010a, Brunnschweiler & Baensch 2011, Hammerschlag et al. 2012). On the north shore of Moorea, French Polynesia, female resident blacktip reef sharks that are exposed to provisioning migrate to breeding grounds located on distant islands, showing that provisioning activities do not seem to alter short-term reproductive migrations (Mourier & Planes 2013).

Effects on competitive interference

Multi-species aggregations can lead to interspecific interactions in the form of bites, chases and other forms of aggression, as has been reported between eagle rays *Myliobatis australis* and southern stingrays (Newsome et al. 2004). Individuals are likely to display dominance signaling in the presence of competitors, as agonistic interactions constitute an important factor in hierarchy establishment (Martin 2007, Clua et al. 2013). Group hierarchies described in fed elasmobranch aggregations are thought to be size-dependent (Newsome et al. 2004, Clua et al. 2010a, Maljkovi & Côté 2011), as has been stated in past studies on shark social behavior (Allee & Dickinson 1954, Myrberg & Gruber 1974). Provision of a limited amount of food is therefore thought to generate inter- and intraspecific dominance interactions between competing individuals (Ritter 2001, Clua et al. 2010a). However, Semeniuk & Rothley (2008) also reported a significant increase of conspecific bite marks in southern stingrays when unlimited food was distributed, presumably linked to indiscriminate biting in a high density population. The potential for simultaneous competition related to food and reproduction is also discussed in the case of sicklefin lemon sharks in French Polynesia (Clua et al. 2010a) and southern stingrays in the Caribbean (Semeniuk & Rothley 2008) to explain the rise in seasonal intra-specific agonistic behaviors.

COMMUNITY-SCALE EFFECTS

Effects on distribution of predators and prey

It is now recognized that predators affect prey demography and trophic interactions through both direct predation and induced behavior (i.e. non-consumptive effects) that may cascade through communities (e.g. Preisser et al. 2005, Creel & Christianson 2008, Heithaus et al. 2008). In this regard, some authors discuss the potential consequences of provisioning operations on the distribution of the elasmobranch predators and prey.

As reported in Gallagher et al. (2015), it has been hypothesized that the provisioning of sharks and rays is likely to reduce predation pressure on their natural prey. On the other hand, even when predation efforts are limited in clustered predators, the structure of local prey communities can be affected if predators are not fed to satiation (Clarke et al. 2011, Corcoran et al. 2013). However, there is currently no empirical data

to support either hypothesis, and Maljkovi & Côté (2010) showed no evidence that long-term baiting affects the feeding ecology of Caribbean reef sharks.

Moreover, provisioning operations may also influence the ecology of predators that prey on the targeted fed species. For example, Corcoran et al. (2013) noted increased sightings of great hammerhead sharks *Sphyrna mokarran* in the vicinity of a southern stingray feeding site in the Cayman Islands, and suggest that the sharks are attracted by unnatural aggregations of their habitual prey. Aggregated elasmobranchs are therefore likely to influence the distribution of other species, either through consumptive or non-consumptive effects, or by attracting them as potential prey.

Effects on elasmobranch communities

A handful of studies discuss modifications of local elasmobranch community composition as another putative consequence of regular provisioning, as competitive interference is known to influence distribution of sharks over small spatial scales through competitive exclusion (Papastamatiou et al. 2006) and behaviorally mediated indirect interactions (Heithaus et al. 2008).

Brunnschweiler et al. (2014) monitored the abundance of 8 shark species at a feeding site in Fiji over several years. They observed a rapid increase in the population of bull sharks, whitetip and blacktip reef sharks, along with a decrease in nurse *Nebrius ferrugineus*, silvertip *Carcharhinus albimarginatus*, tiger and sicklefin lemon sharks. In this case, the rapidly expanding population of bull sharks is thought to exclude all other species through competitive exclusion. Similarly, it has been suggested that increasingly abundant large sharks exclude smaller species from provisioning sites at several other locations (Meyer et al. 2009, Clarke et al. 2013), but no clear cause-and-effect relationships have been established so far. The extent to which accumulations of large predatory sharks play a role in altering community dynamics remains undetermined (Clarke et al. 2011) and deserves further attention, given the fundamental role of elasmobranchs in structuring and maintaining healthy marine ecosystems (Ruppert et al. 2013). Moreover, the use of olfactory stimuli and/or food items can also aggregate non-targeted marine species, such as predatory fish, and potentially contribute to local community changes.

The effects of artificial provisioning on the fertility of exposed populations remains unknown. Some authors suggest that sedentary behaviors of sharks

and rays could favor inbreeding on the long term (Clua et al. 2010a), especially in small populations with naturally low genetic diversity (Mourier et al. 2013a, Mourier & Planes 2013). On the other hand, the potential role of repeated artificial aggregations in promoting mating has yet to be addressed.

CASCADING EFFECTS ON INDIVIDUAL HEALTH AND BEHAVIOR

In this section, we treat altered health condition and behavior of fed species separately, since they are considered as potential end results of several effects discussed earlier. Whereas impacts on individual health have mainly been documented in rays, with several altered health parameters described, all resulting in lowered body condition, the emergence of inquisitive behaviors towards humans is described for both sharks and rays.

Altered health condition

Rays exposed to regular provisioning have a higher probability of being injured. Semeniuk & Rothley (2008) compared the prevalence of injured southern stingrays between a routine feeding spot and a control site in the Cayman Islands and demonstrated that 85 % of fed rays were injured, compared to 30 % of non-fed rays. At the feeding site, injuries included conspecific bite marks, predator wounds (interpreted as an increased predation risk), and a wide range of boat-related injuries caused by anchors, chains and propellers (Semeniuk & Rothley 2008). Similarly, Araujo et al. (2014) reported a 47 % incidence of boat-propeller scars in whale sharks, although these were not attributable solely to provisioning operations.

Increased parasite transmission has been noticed among fed rays (Semeniuk & Rothley 2008, Semeniuk et al. 2009). High group densities during feeding events are likely to favor parasite transmission, resulting in a higher number of parasites per ray (Semeniuk & Rothley 2008). This issue has also been suggested to affect surrounding fish communities and possibly sharks as secondary hosts (Vignon et al. 2010).

While investigating a range of physiological parameters in regularly fed rays, Semeniuk et al. (2009) reported decreased hematocrit and total serum proteins, which were related to increased parasites and infection as well as to differential leukocrit/leukocyte reactions, indicating oxidative stress. According to the authors, these multiple degraded physiological

parameters in fed rays are likely to lead to a decrease in survival (Semeniuk et al. 2009), but no long-term investigation of putative detrimental effects of feeding on individual fitness has been undertaken so far.

Effects on behavior to humans

Although no correlation has been demonstrated so far between provisioning operations and unprovoked shark and ray bites (Meyer et al. 2009), the dense aggregations of sharks and rays targeted by tourist operations lead to increased interactions with humans, sometimes resulting in bites (Levine et al. 2014). While the Shark Attacks and Related Incidents File (SARIF) database (2014; http://sharkattacksurvivors.com/shark_attack/) provides 10 cases of shark bite occurring during shark provisioning operations between 1968 and 2014, these incidents are significantly unreported and must be treated with caution. In fact, Maillaud & Van Grevelinghe (2005) reviewed 54 cases of shark bite that occurred between 1979 and 2001 in French Polynesia (none of which were reported in the SARIF database) and reported that up to 25 cases (45 %) were linked to shark provisioning operations involving fish blood or flesh close to the victim. Likewise, the practice of hand-feeding seems to enhance the risk of a bite, and most victims in this case review were the feeding operators themselves (Maillaud & Van Grevelinghe 2005).

A possible association between tourist presence, food rewards and subsequent attraction to humans has been described in southern stingrays in Hamelin Bay, Western Australia (Newsome et al. 2004). Moreover, fed individuals can develop very inquisitive attitudes (Clua et al. 2010a), sometimes displaying pushy behaviors or ramming toward tourists with food (Semeniuk & Rothley 2008). Similarly, group size and corresponding competition could be a potential factor leading to aggression toward tourists. For example, Clarke et al. (2013) described context-dependent behavior of fed silky sharks toward humans, with individuals acting more boldly as group size increased. Overall, the relationship between shark provisioning operations and increased risk of shark bites on recreational ocean users is still being discussed (Meyer et al. 2009). However, naturally increased aggression between individuals in the breeding season, combined with competition for provisioned food, can be an important factor contributing to bites on humans during provisioning events, as reported in male sicklefin lemon sharks (Clua et al. 2010a), and should therefore be taken into account in managing the activity.

DISCUSSION

Exhaustively reviewing the available literature on the response of elasmobranchs to provisioning activities not only allowed us to report group-scale and community-scale effects, but also to highlight putative cross-scale relationships between the described effects and to discuss potential underlying mechanisms. The synoptic functional framework (Fig. 2) presented here illustrates the potential for provisioning activities to support the investigation of complex ecological and behavioral processes in elasmobranchs.

A frame of bound multiple-scale effects

The described effects of provisioning on elasmobranchs occur across individual, group, and community scales, and interact in a framework of theoretical relationships (Fig. 2). Modification of local-scale activity patterns is the most frequently described impact. In particular, reduced horizontal activity and increased residency of fed elasmobranchs are common features. At the individual scale, the disruption of natural movement patterns is likely to have negative effects on animals' energy budgets and overall health, as reported in whales (Lusseau 2004).

The impact of provisioning on individual activity patterns can also have group-scale repercussions, including increased abundances over both short and long time scales, and the aggregation of both natu-

rally solitary and gregarious species. Seasonal reproductive cycles do not seem to be impacted in the short term, although this aspect has only been studied in a few species. Long-term studies are needed to better address this question, as it is already known in terrestrial species that disruptions in natural cycles can influence the fertility and demography of the focal species (Boutin 1990, Orams 2002).

The potential community-scale effects of provisioning operations have not been expressly studied, but investigation of the relative abundance of species at provisioning sites may help to elucidate this topic. The influence of regular provisioning on the dietary habits of elasmobranchs depends in all likelihood on the focal species and practices. Although the lack of data precludes cross-study comparisons or general conclusions, one striking case among the few available studies on the subject shows that stingrays rely heavily on unnatural food items provided by tourists (Semeniuk et al. 2007).

Moreover, although the sanitary implications of provisioning operations remain insufficiently investigated, individual health appears to be negatively affected as a potential end-result of several impacts listed above. Repetitive gathering of regularly fed large groups is likely to favor parasite transmission and injuries resulting from competition, predation, and interactions with humans. Physiological costs of artificially enhanced group living have been clearly established in one study (Semeniuk et al. 2009) on stingrays, which should encourage similar studies of more species in different contexts. Finally, the rise in competition for food in multi-species aggregations and the elicitation of conditioned responses to tourist presence can alter the natural behavior of the target species, potentially leading to inquisitive attitudes toward humans and accidental bites.

A case of ecological trap?

Various hypotheses have been proposed to explain persisting aggregating behaviors in spite of the deleterious effects described. Instinctive behavior drives an individual's response to appetitive stimuli (i.e. the bait scent). Operant conditioning can happen when individuals access food and the response to the stimulus is positively reinforced with a reward (Skin-

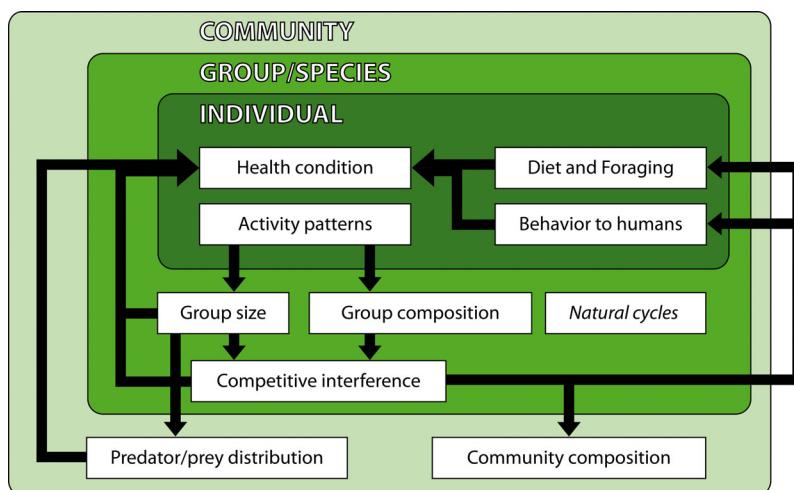


Fig. 2. Multi-scale framework of concepts investigated in impact assessment studies of shark and ray feeding. Arrows show theoretical relationships between impacted concepts at the individual, group/species and community-scale. Data collected so far do not indicate that natural cycles are impacted

ner 1938). In this case, fed individuals only perceive the short-term benefits of responding to the stimulus, but incur greater costs in the long term, a phenomenon defined as an ecological trap (Schlaepfer et al. 2002). However, the extent to which provisioning activities provide an easy-to-access resource greatly depends on the ratio between food amount and number of competitors. When the amount of food is limited, only a few individuals will benefit, and we suggest that aggregating behaviors may persist due to social amplification. Indeed, social information can be vicariously acquired and used as an indirect means to evaluate environmental cues (Danchin et al. 2004). It is reasonable to assume that individuals interpret the presence of conspecifics as positive feedback, adding to their individual instinctive response to the appetitive stimulus. As more conspecifics aggregate at the provisioning site, the probability of another individual coming increases (Sumpter 2006). From this perspective, Bejder et al. (2009) suggests the need for integrated models incorporating individual decision making as the theoretical basis for understanding how human disturbances influence animal behavior.

Unveiling natural processes and informing sustainability

The mitigation of shark–human conflicts is critical to the promotion of shark conservation, and includes (1) implementing the sustainable exploitation of shark species and (2) the prevention of shark bites on humans (Neff & Yang 2013). The popularity of shark and ray provisioning operations among the public provides an incentive to preserve the targeted species from commercial exploitation by fisheries in areas where sharks and rays are not protected. Supplementary feeding can also be perceived as an artificial support to the targeted species by providing easy-to-access resources (Clua et al. 2010a, Laroche et al. 2007), allowing individuals to allocate more energy to other activities such as reproduction (Orams 2002). However, most effects of provisioning appear to be either neutral or detrimental. The implementation of sustainable practices in elasmobranch tourist provisioning, as well as in other forms of elasmobranch exploitation, requires a solid body of knowledge on how elasmobranch species interact with their environment.

As stated in most of the studies reviewed here, including the recent summary on individual-scale effects of shark provisioning by Gallagher et al. (2015), the general lack of baseline data on the biology, eco-

logy and physiology of elasmobranchs complicates the interpretation of available findings on the effects of artificial provisioning. Here, we considered the literature on both shark and ray responses to provisioning and used the findings to develop a functional framework showing the interactions of the described effects across multiple scales. This procedure ought to benefit our understanding of the natural mechanisms underpinning the response of elasmobranchs to provisioning activities, and to a broader extent, the interaction between elasmobranch individuals and their environment. Shark and ray provisioning activities could therefore provide opportunities to support the investigation of several fundamental concepts in elasmobranch ecology. Such investigations are usually curbed by practical and financial constraints that restrict the number of individuals and the type of response variables that can be sampled (Bejder et al. 2009). We suggest that provisioning operations could support studies on short-term behavioral features at both the individual and group scales (Beale & Monaghan 2004, Higham & Shelton 2011), as well as on long-term ecological and physiological processes that may affect the response of the focus species not only to provisioning, but also to other environmental cues, provided that the necessary precautions are adopted when interpreting the findings.

More specifically, the phenomena determining shark behavior toward humans are of great concern for the mitigation of shark–human conflicts, and shark conservation more generally. Indeed, shark bites receive tremendous coverage in the media, which can lead to any or all of the following: (1) negative perceptions and attitudes among the public; (2) reduced compliance with conservation policies; and (3) populist political decisions that may not be effective. In addition to putative impacts on individual fitness, actively feeding elasmobranchs can influence their behavior toward humans. Excited and competing individuals can become less wary of people and eventually cause an accident, as has been described in a range of other fed terrestrial wildlife species (Aggimarangsee 1993, Kamal et al. 1997). Levine et al. (2014) recently suggested a possible connection between hand-feeding practices by scuba divers and a series of unprovoked attacks in the Red Sea. However, based on the partial data provided, their conclusions seem highly speculative, and we suggest that more evidence is needed before feeding practices can be reliably linked to unprovoked shark bite incidents. As previously discussed in this review, sharks' individual behavior to humans can be viewed as the consequence of several ecological and physio-

logical features occurring at multiple scales, investigation of which should be deepened to inform sustainable practices, and promote the role of shark and ray provisioning toward their conservation.

Acknowledgements. This study benefited from the financial support of the Ministère de l'Ecologie, du Développement durable et de l'Energie (MEDDE) of France, the Fonds Français pour l'Environnement Mondial (FFEM) and the Délégation Régionale à la Recherche et à la Technologie (DRRT) of French Polynesia. We also thank R. Dixon, L. Minetti and J. L. Rummer for their help in improving the manuscript.

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