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*Comment*¹ —

Brunnschweiler, J. M. and J. McKenzie. 2010. Baiting sharks for marine tourism: Comment on Clua et al. (2010). *Marine Ecology Progress Series* 420 : 283-284.

Reply —

Clua, E., N. Buray, P. Legendre, J. Mourier and S. Planes. 2010. Effects of provisioning on shark behaviour: Reply to Brunnschweiler & McKenzie (2010). *Marine Ecology Progress Series* 420 : 285-288.

¹ Comment on the following paper:

Clua, E., N. Buray, P. Legendre, J. Mourier and S. Planes. 2010. Behavioural response of sicklefin lemon sharks *Negaprion acutidens* to underwater feeding for ecotourism purposes. *Marine Ecology Progress Series* 414 : 257-266.

COMMENT

Baiting sharks for marine tourism: Comment on Clua et al. (2010)

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ABSTRACT: A recent study by Clua et al. (2010; Mar Ecol Prog Ser 414:257–266) that looks at the behavioural response of sicklefin lemon sharks *Negaprion acutidens* to underwater feeding for eco-tourism purposes has a number of methodological and semantic problems that complicate the evaluation of the results and raise questions about the conclusions. Main issues are the lack of a control, the use of non-defined terms to characterize observed behaviours, and statements not supported by data. Unwarranted conclusions include the notion that behavioural changes were caused by the human interference, the link between intraspecific aggression and the feeding process, and the loss of genetic variability as a consequence of the aggregating effect of shark feeding.

KEY WORDS: Shark feeding · Behaviour · Intraspecific aggression · Marine tourism · Food provisioning

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Attracting elasmobranchs with food for the purpose of marine tourism is a highly controversial issue. There is general agreement that feeding or attracting wildlife with food can have a variety of effects (Orams 2002). In the case of sharks, quantifying the magnitude of these effects has proven difficult because critical baseline data remain scarce (Laroche et al. 2007, Meyer et al. 2009). Whereas using biomarkers to measure physiological responses to provisioning-tourism and effects on health is relatively straightforward (Semeniuk & Rothley 2008, Semeniuk et al. 2009), measuring behavioural responses by directly observing the animals is much more challenging. Clua et al. (2010) have taken on this challenge and present data from a group of sicklefin lemon sharks *Negaprion acutidens* in the South Pacific. Here we point out fundamental methodological and semantic issues with this study that we think complicate the evaluation of the study's results and raise questions about the conclusions.

(1) The collection of presence/absence, abundance or behavioural data of mobile fish using underwater

visual census and observation techniques is prone to bias (Samoilys & Carlos 2000, Edgar et al. 2004, Ward-Paige et al. 2010), but this is not acknowledged in Clua et al. (2010). For example, direct observation data of shark behaviour can typically only be collected during a few hours each day, and therefore the majority of the behaviour is not recorded. The use of proxies such as mating scars or bite wounds to measure or quantify behaviour is possible (e.g. Porcher 2005), but relating these proxies with confidence to spatio-temporal causative intra- and interspecific behaviours is challenging, requiring adequate caution when interpreting the results.

(2) The frequent and arbitrary use of non-defined terms is a problem in Clua et al. (2010). Terms such as 'natural behaviour' (p. 257, 258), 'real provisioning' (p. 258), 'atypical dominance behaviour' (p. 262), 'pivotal role' (p. 262), 'exacerbated competition' (p. 263), 'dominant' (p. 263), and 'natural conditions' (p. 263) are neither defined nor referenced. It remains unknown, for example, what the authors consider typical

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dominance behaviour and, as a consequence, irreproducible why an observation should be 'atypical dominance behaviour' (p. 262).

(3) It remains unclear how Clua et al. (2010) measured and quantified 'increased aggression' (p. 262), 'M05, which appeared to be old' (p. 262), 'Since males M07 and M18 were dominant in 2005' (p. 263), and 'Aggression increased significantly' (p. 263) and, if at all, against what baseline they compared their observations.

(4) A fundamental problem in Clua et al. (2010) is the lack of a control. Without a comparable group of sharks that are not being fed the authors cannot postulate with confidence that any observed behavioural changes were caused directly by the human interference.

(5) Several statements and conclusions in Clua et al. (2010) are based on anecdotal observations and not evidenced. (a) There are no data that 'link' intraspecific aggression to the feeding process (p. 263). Therefore, the anecdotal observation of intraspecific aggression cannot be interpreted as 'deviant behaviour' (p. 263). (b) The statement of 'an increase in shark abundance over time' (p. 263) is not supported by results. (c) The authors repeatedly mention that there may be loss of genetic variability as a consequence of the aggregating effect of shark-feeding (p. 263, 264). However, these speculations are unsupported; the data do not address any such link. In fact, the authors themselves state that the number of males decreased during the reproductive season (p. 259), suggesting 'temporary migration for mating with females that do not belong to the studied population' (p. 262).

The debate over baiting sharks for marine tourism is largely based on inference, opinion and anecdote, and therefore research on the effects of food-provisioning tourism is much needed. Thus Clua and his coworkers are to be acknowledged for bringing science to this

controversial topic. In our opinion, however, the presentation and discussion of the results in Clua et al. (2010) adds more to the debate than to the objectification of the public discourse.

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REPLY COMMENT

Effects of provisioning on shark behaviour: Reply to Brunnschweiler & McKenzie (2010)

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ABSTRACT: Brunnschweiler & McKenzie (2010; Mar Ecol Prog Ser 420:283–284) expressed reservations over the findings of Clua et al. (2010; Mar Ecol Prog Ser 414:257–266), mostly related to the lack of a reference site or a control group in the methodology. In our study, we distinguished between 39 individuals of sicklefin lemon sharks *Negaprion acutidens*, mainly based on photo-identification. Our study was based on the field-survey approach, with time (a continuous variable) as the source of variation, and thus a control group was not necessary. We provide here additional data that support the notion that abundance of lemon sharks on the provisioning site was increasing, both in their number and fidelity. We maintain our conclusion that sicklefin lemon shark provisioning off Moorea Island can continue, but should be more intensely controlled.

KEY WORDS: Field survey approach · Lack of control site · Shark abundance · Site fidelity · Shark conservation

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We are grateful to our colleagues J. M. Brunnschweiler and J. McKenzie for their interest in our article about the behavioural response of sicklefin lemon sharks *Negaprion acutidens* to underwater provisioning in French Polynesia (Clua et al. 2010). To their major issues we respond as follows.

(1) Methodology for assessing shark behaviour

Applying reliable methods for assessing shark behaviour is a challenge. We assured the quality of our observations by identifying each individual lemon shark through photo-identification, as detailed in a separate paper (Buray et al. 2009). Our study com-

prised a relatively low number of sharks (39), while photo-identification allows independent and reliable diagnoses for much larger numbers, e.g. 159 whale sharks *Rhincodon typus* (Meekan et al. 2006) or 194 nurse sharks *Ginglymostoma cirratum* (Castro & Rosa 2005). In that context, the references to Samoily & Carlos (2000) and Edgar et al. (2004) made by Brunnschweiler & McKenzie (2010, p. X) are irrelevant as those authors discuss biases linked to underwater visual censuses (UVC) of several small-sized, highly mobile and hard to distinguish coral reef finfishes. There is no logical or factual link between the potential biases discussed in these studies and the individual identification of large sharks moving in a restricted area, as in our study. When discussing the biases in

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shark observation methodology, Ward-Paige et al. (2010, p.5) even state 'When the goal of a scientific study is to examine relative spatial and temporal differences in the density of a single species surveyed under homogenous sampling conditions, non-instantaneous UVC count data may produce satisfactory information'. This is actually the case for our study.

(2) Arbitrary use of non-defined terms

'Real provisioning' refers to any anthropogenic provisioning of sharks with a sizeable amount of food that they can acquire, and does not rely only on the olfactory attraction of food, usually described as 'chumming' or 'baiting'.

We anticipated difficulties in understanding of some of our statements, when no previous references are available. Therefore, we defined what we considered to be 'atypical dominance behaviour' (Clua et al. 2010, p. 262) with the following sentence: 'As the study progressed, in addition to a strong residency pattern, this shark showed increasing aggression towards its male and female conspecifics and, to a lesser degree, toward divers (N. Buray pers. obs.).' We think this explanation is clear.

For a better understanding of the imminent risk of long-term feeding, we referred to the observed behaviour of lemon sharks over time, see Section (4). Unfortunately, there are no scientific studies fully describing the natural behaviour of lemon sharks, so we had to rely on statements by our team of experienced scientific divers who have accumulated thousands of hours of underwater observations.

(3) Justifying and quantifying 'increased aggression'

At its adult stage, *Negaprion acutidens* cannot be considered to be a gregarious species (Stevens 1984). In contrast to other sharks with a solitary behaviour but a capacity to aggregate and compete, such as white shark *Carcharodon carcharias* (McCosker 1985) or tiger shark *Galeocerdo cuvier* (E. Clua pers. obs.), aggressiveness over food does not occur in the wild for lemon sharks (see Nelson & Johnson 1980). Therefore, we maintain that provisioning sicklefin lemon sharks may create a non-natural source of intra-specific aggressiveness (Clua et al. 2010, p. 263). We are willing to modify this statement only if evidence is presented that *N. acutidens* are prone to natural intra-specific aggressiveness by reason of food in the wild.

The 'lack' of a base line for assessing and quantifying the increasing aggression is a particular aspect of the critique discussed in Section (4) below.

(4) Lack of a control site

Many experimenters compare their 'treatments' with 'controls' and evaluate their data by analysis of variance (ANOVA). Field survey ecologists may use another approach: the observations are carried out along one or several gradients represented by continuous variables, so that there is no need for an independently-set control to draw conclusions (Hurlbert 1984, Legendre & Legendre 1998). In our study, we used this field survey approach with 'time' as a continuous variable. We demonstrated an increase in shark aggregation by plotting the number of shark sightings as a function of time and computing linear regressions (see Fig. 4 in Clua et al. 2010). There is a significant increase in the number of sightings of individual sharks in Groups A, C and D across the 44 mo of the study. As natural aggregation of sicklefin lemon sharks does not exist in the wild (see Section 3), it was not possible to carry out a study at a control site.

(5a) Provisioning and intraspecific aggression

As stated in Section (3), there is no evidence that lemon sharks are aggressive over food in the wild. Therefore, artificial provisioning is most likely adding another cause for intraspecific aggression to the existing competition for mating. Clua et al. (2010) do not directly link the feeding process to an increased competition for mating. However, provisioning, which produces artificial aggregation, during or right after the mating season may raise the level of intra-specific aggression, and may be the cause of obvious wounds on male lemon sharks which are more likely to fight for dominance (N. Buray pers. obs.). Fig 5b in Clua et al. (2010) gives an example of a wounded male; the total number of such wounds, however, was not anecdotal. In the context of our study over 44 mo, which did not focus on intra-specific dominance, we presented the accumulated information on the increased aggression amongst males after the mating season as an incidental result. It was a qualitative analysis that compared observations from different seasons, rather than a conclusion based on quantitative data.

(5b) Increase in shark abundance

In the context of Clua et al. (2010), the term 'abundance' can be understood in different ways: (1) as a purely quantitative term (number of shark sightings, not regarding the number of different individuals); (2)

as a purely qualitative concept (number of *different* sharks involved in a given number of sightings); and (3) as a mix of these 2 concepts. We agree that the accuracy of our data does not allow us to use the term 'abundance' in the second or third sense. However, our results (see Fig. 4 in Clua et al. 2010) allow us to use the term for the number of shark sightings. We are pleased to provide here complementary data, not included in our original article, showing that, in addition to an increase in site fidelity, our data also support our hypothesis of a significant increase with time in the number of distinct sharks involved in the sightings (Fig. 1). Both graphs show that the provisioning site was increasingly frequented. From this observation we derived our statement that 'In the case of lemon sharks, their increased site fidelity can have a negative effect on gene flow' (Clua et al. 2010, p. 263).

(5c) Loss of genetic variability

At the end of our discussion (Clua et al. 2010, p. 264), we cautiously stated that 'Because the studied population is small, daily aggregations at the same location could result in increased social interactions and increased mating between close relatives, reinforcing the risk of inbreeding.' We were not saying that there was any present loss. We think readers will be able to appreciate the difference between a 'risk', which includes a probability for not happening, and a 'fact', which does not allow any room for an alternative, and needs to be supported.

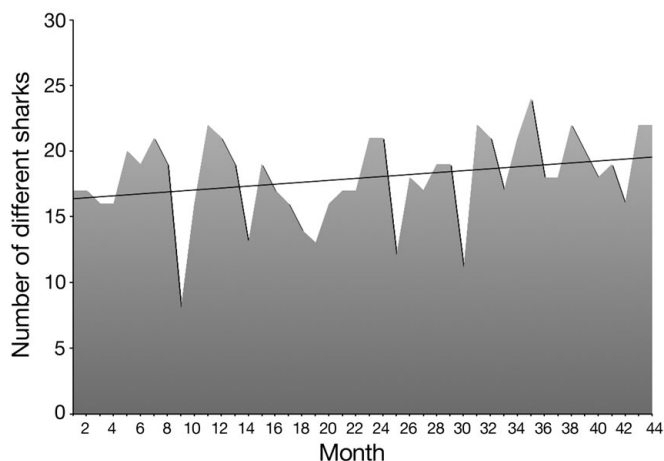


Fig. 1. *Negaprion acutidens*. Number of different sharks contributing to the sightings during the course of the study (44 mo). The line representing the linear trend supports the hypothesis of a significant increase (at the usual 5% significance level) in the number of sharks at the feeding site (1-tailed *t*-test of significance of the slope, $p = 0.029$).

CONCLUSIONS

Clua et al. (2010) provided (1) reliable information (2) in a specific case (3) about a controversial subject. The consideration of provisioning as an asset for conservation of endangered species (Bookbinder et al. 1998, Halpenny 2003), however, does not automatically allow the results of Clua et al. (2010) to be generalised to other feeding sites or shark species. We concluded that sicklefin lemon shark provisioning off Moorea Island can continue but should be better controlled. Our recommendations were specifically addressed to the French Polynesian management authorities (Clua et al. 2010, p. 266). At this stage, we are not advocating a ban on shark feeding. We are currently assessing the direct income generated by lemon shark ecotourism and its importance for the local economy of Moorea Island. This information should convince fishermen of the benefits of shark conservation (Clua et al. unpubl.). However, shark-feeding management still requires studies addressing a variety of subjects and situations, hopefully including further contributions by our colleagues J. M. Brunnschweiler and J. McKenzie.

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