

Rapid voluntary stomach eversion in a free-living shark

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Video observation of oral gastric eversion in a free-living Caribbean reef shark (*Carcharhinus perezi*) shows voluntary gastric eversion followed by retraction not only occurs, but is extremely rapid (lasting ~ 0.3 s). Eversion may occur by stomach relaxation–oesophageal contraction coupled with increased abdominal pressures to enable prolapse, and retraction by a mechanism analogous to suction feeding. This behaviour provides a 'cleansing' function for removing indigestible food particles, parasites or mucus from the stomach lining. Sharks, and possibly other animals with similar gut morphologies, may use this technique to help maintain a healthy alimentary tract.

INTRODUCTION

Gastric eversion followed by recovery has been induced experimentally by administration of emetic (vomiting) agents in amphibians and batoid elasmobranchs (Hukuhara et al., 1973; Naitoh et al., 1989, 1991; Sims et al., 2000). It may serve to evacuate gastric contents and, hence, is functionally analogous to vomiting in mammals. However, in the batoid *Raja*, and by extrapolation, other elasmobranchs in which this occurs, it has been proposed that this is a more efficient strategy to cleanse the gastric mucosa by rinsing away small indigestible food particles, sloughed mucosa and mucus (Sims et al., 2000), which would not be cleared by the more usual gastric compression and bulk ejection mechanism involved in vomiting (Andrews & Young, 1993). However, spontaneous gastric eversion has not been observed, to our knowledge, in any free-living vertebrate in the natural environment. The absence of direct observation raises the possibility that this behaviour does not occur naturally and thus does not fulfil a cleansing function.

The ability of elasmobranchs such as sharks to exhibit stomach eversion was suspected at least 300 years ago from reports of sharks being line-caught with stomachs protruding orally (e.g. Labat, 1728 cited in Budker, 1971). Here we characterize for the first time spontaneous oral eversion of the stomach in a free-swimming Caribbean reef shark (*Carcharhinus perezi*) in its natural habitat. Based on these observations we propose a mechanism for gastric eversion, and from observations of scavenging fish following the shark, propose a function for this peculiar activity.

MATERIALS AND METHODS

An underwater video recording (SONY PC3 digital camera with Sealux housing recording at 24 frames s^{-1} ; no artificial illumination) of the Caribbean reef shark (*Carcharhinus perezi*) was taken at Walker's Cay, Bahamas

(latitude 27.240°N, longitude 78.401°W) in an open coral-reef area. More than 10 h of behaviour of different reef sharks were recorded over a few days during which a stomach eversion sequence was observed (between 1000 and 1100 h on 14 April 2003) only once in an adult female approximately 1.8 m total body length as it cruised slowly just above the sea bottom at a depth of 12 m.

A 4-s time period containing 96 frames was selected for quantitative analysis because the shark was in good lateral profile facilitating measurement of body movements. Frame-by-frame analysis of this sequence was undertaken to characterize different body movements and to determine the timing of particular activity patterns (Adobe Premiere v.6, Adobe Systems Inc., San Jose, CA, USA). Precise measurements of body movements were made from individual frames: body angle, pharyngeal depth, abdominal depth and mouth gape (Figure 1A).

RESULTS

Prior to beginning video-recording, the shark had been under observation for approximately 10 min and its swimming behaviour did not differ from conspecifics in this location. Because of the relatively brief period of video recording made prior to the eversion episodes, description of the external changes accompanying eversion are limited to approximately 1 s prior to each episode; in both cases peri-eversion behaviour was similar. Two episodes of overt oral gastric eversion lasting ~ 0.28 and 0.40 s were observed 1.52 s apart during the 4-s time period selected for detailed analysis (Figure 1B).

Approximately 0.20 s before the first episode of gastric eversion the abdominal depth began to increase coincident with a decrease in pharyngeal depth and wide gaping of the mouth (Figure 1B). At this point the body was straight, but the head and body (caudal of the dorsal fin) began to ventroflex and this continued as the stomach was externalized, reaching a maximum while the stomach was still

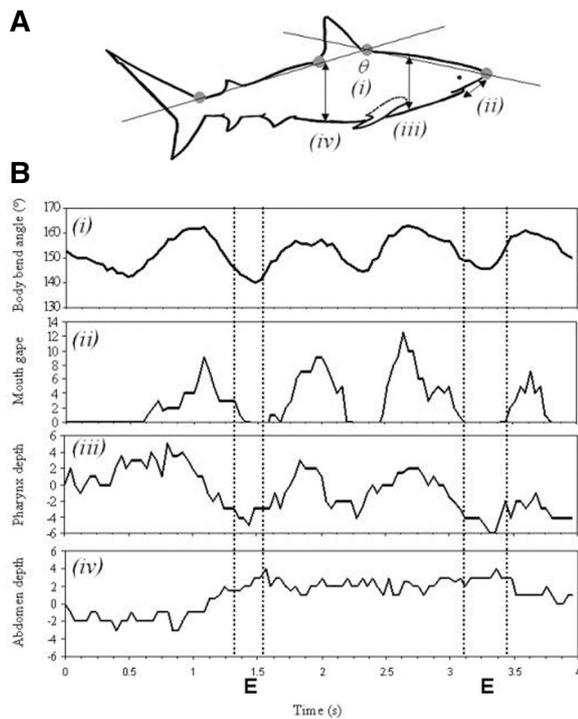


Figure 1. (A) Body movement measurements and (B) dynamics of a free-swimming *Carcharhinus perezi* during two episodes of gastric eversion (E). Body measurements *i-iv* in (A) correspond to changes in movements shown in (B) *i-iv*. The y-axis units in (B) *ii-iv* are arbitrary and denote relative changes in the body movements shown in (A).

visible. The head assumed a noticeably convex 'bulging' outline which was sustained while the stomach was everted. Pharyngeal depth reached a nadir and abdominal depth a plateau while the stomach was everted. The

stomach appeared while the mouth was still closing and was accompanied by opening of the gill slits. The stomach reached its maximum visibility 0.12 s after its appearance and remained at maximum exposure for a further 0.04 s, with retraction taking a further 0.12 s (Figure 1B). Retraction occurred while the mouth appeared closed around the stomach and when the gill slits were closed. Immediately after disappearance of the stomach the caudal body became convex over ~ 0.40 s and a cycle of mouth gaping and closure occurred, accompanied by increased pharyngeal depth and body straightening. While this cycle of activity in the inter-ejection period was broadly similar to that during gastric eversion, it differed because the gill slits were closed.

Similar events characterized the second eversion, namely a decrease in pharyngeal depth, mouth closing after a gape, body straightening and caudal body concavity (Figure 1B). The stomach was expelled forcibly and progressively over a period of 0.12 s and appeared to 'balloon' as if inflated (Figure 2E). It remained maximally exposed for 0.16 s and was retracted over 0.12 s. Gill slit opening accompanied stomach eversion. Once again, retraction began while the mouth was still closed around the stomach, but gaping followed full retraction. The gill slits were closed during retraction and afterwards the abdominal depth decreased towards the value measured prior to the onset of eversion behaviour (Figure 1B).

It was not possible to see whether any particulate material was expelled from the stomach during eversion because video images were of insufficient resolution. However, the behaviour of accompanying fish suggests that particles were ejected. Prior to oral eversion a horse-eye jack (*Caranx latus*) swam parallel to the shark in a lateral position between the first and second dorsal fins (Figure 2). During ventroflexion, when the shark's snout visibly dropped towards the seabed, the jack rapidly

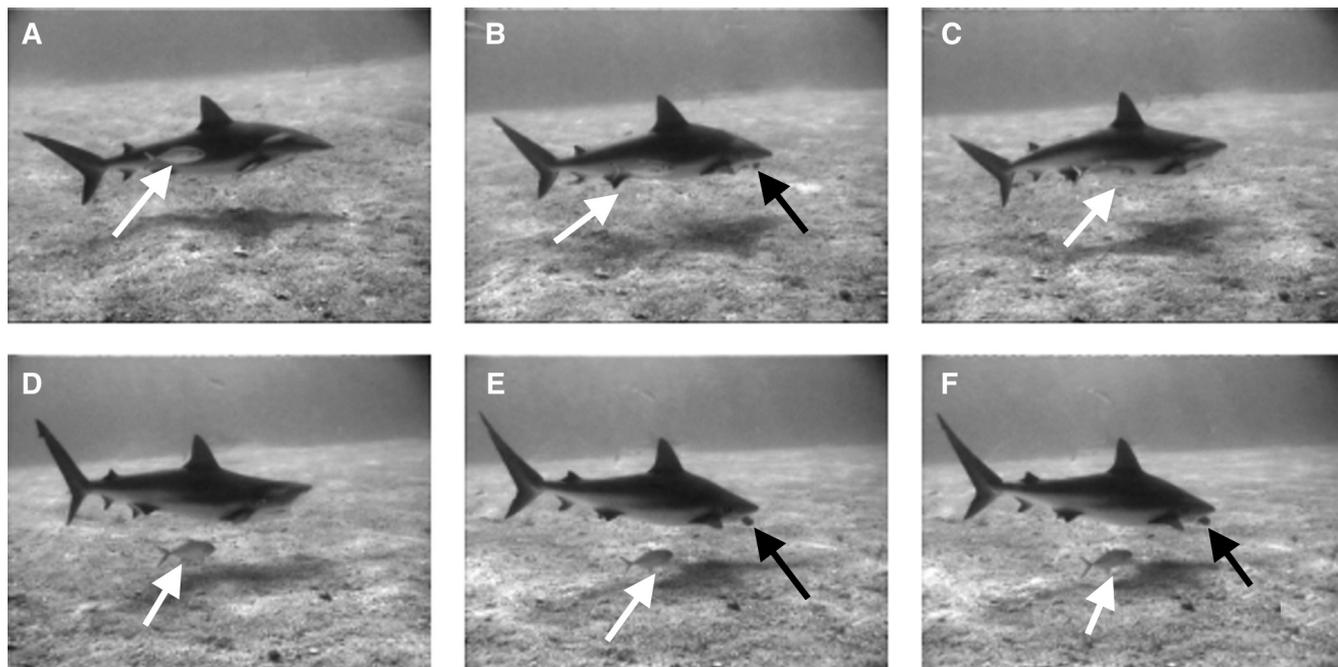


Figure 2. Episode 1 (A-C) and 2 (D-F) of oral gastric eversion. White arrows indicate position of the accompanying horse-eye jack (*Caranx latus*). Black arrows indicate the everted stomach.

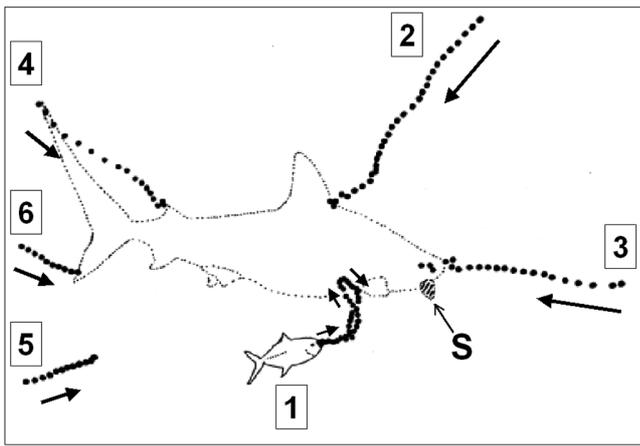


Figure 3. Behaviour and movements of six scavenging jacks (numbered 1–6) responding to gastric eversion (prolapsed stomach, S) in *Carcharhinus perezii*. Fish numbered in the order they responded to gastric eversion. Black dots represent successive positions of each fish's snout tip (0.04 s apart) over the entire sequence. Arrows give forward movement direction.

moved away from the shark, before returning to the same position. Approximately 0.75 s later the shark's stomach was visible externally for the first time and the jack moved downwards and forward to just behind the shark's right pectoral fin (Figure 2B). The second episode of gastric eversion was followed 0.37 s later by the jack rapidly turning upwards toward the shark's midline, where it lunged forward (Figure 3). This jack then returned to its previous position. Five other jacks swam towards the shark immediately after the second eversion. The first and last individuals moved into the video frame some 0.54 and 1.62 s respectively, after the first jack began moving (Figure 3).

DISCUSSION

This analysis of a serendipitously recorded novel behaviour in a wild shark provides the first quantitative description of this behaviour although the results must be treated with some caution because of the unknown health status of the animal, the brief period of observation and the sub-optimal position of the shark during parts of the recording. However, there were no obvious indications that the animal was other than healthy although it is impossible to know if the behaviour was induced by some recently ingested material or is a spontaneous behaviour (see below). Despite these limitations based upon the video analysis and studies of feeding and vomiting in carcharhiniform sharks we propose a mechanism for eversion which requires confirmation by more direct methods.

For the stomach to be externalized requires part of it to be everted, passed through the pectoral girdle to the pharynx and then the jaws. It is clear from the recording that this is a forceful act. It is unlikely that this could be achieved if the stomach was in a contracted state so we propose that the first step is relaxation of the cardiac (proximal) stomach mediated by the autonomic nervous system (Young, 1983; Jensen & Holmgren, 1994). The point at which the animal is at its straightest, but with the

caudal body slightly concave, a few hundred milliseconds prior to eversion, may be the point at which the stomach passes through the pectoral girdle. The apposition of the mucus-coated oesophageal and gastric mucosae would facilitate oral passage. Assuming that this is correct, how then is the relaxed stomach propelled orally?

A sustained increase in abdominal depth was recorded which could be consistent with an increase in abdominal pressure driven by lateral muscle groups. Circumstantial evidence implicated abdominal muscle contraction in oral eversion of the stomach in rays (Sims et al., 2000) and abdominal muscle contraction has been implicated in oral eversion of the stomach in frogs and toads (Naitoh et al., 1991). In the second eversion episode it is clear the stomach balloons out of the mouth and is 'inflated' from inside, which must be due to abdominal contraction. The reduction in pharyngeal depth and opening of the proximal gills is not consistent with a lowering of pharyngeal pressure needed to 'suck' the stomach into the pharynx and mouth. It is important to note that the stomach disappears from view before the mouth begins to open and that retraction, which takes only 0.12 s, occurs when the head and caudal body are at maximum ventroflexion with the gill slits closed. The mechanism by which retraction is brought about is unclear but could be facilitated by induction of a swallow indicated by the wide gaping and elevation of the snout. The entire eversion sequence is similar in duration (0.28 s and 0.40 s) to bite duration (0.38 s) in this species (Motta, 2004).

There are two main observations that support a 'cleansing' function for gastric eversion in sharks. Firstly, horse-eye jack and bar jack (*Carangoides ruber*) routinely school around Caribbean reef sharks and the behaviour of the horse-eye jack we observed following the shark during stomach eversion was characteristic of scavenging behaviour shown by these bony fish. The fast, directed movement of the jack towards the shark's body when the stomach was protruded, followed by a characteristic feeding lunge indicates orientation to items assumed to be sloughed from the gastric surface during eversion. The movements toward the shark by other jacks probably arose as a result of them detecting the first jack's movement.

Our second observation consistent with stomach eversion serving as a 'cleansing' mechanism was the gastric lining appeared to be retracted between the fleshy parts of the jaws between which the teeth are embedded although we recognize that the position of the animal was not optimal for observing the mouth. If this action occurs as we describe it could wipe away any residual mucosa or mucus not removed by the forward momentum of the stomach itself when everted, or by forward swimming. By comparison, the frog uses its forelimbs to wipe away material from the gastric surface of a prolapsed stomach (Naitoh & Wassersug, 1996). The trigger for this complex behaviour involving coordination between the gut, respiratory and locomotor systems remains to be identified but arguably differs from that which induces vomiting used to remove indigestible material in bulk from the stomach.

Our results show gastric eversion occurs in a free-living shark and, by extension, may be widespread among animals with gut morphologies facilitating this behaviour

(i.e. short, wide oesophagus; relatively untethered, mobile gut). Moreover, its function may be related to removal of indigestible food particles and mucus from the inner surface. It is known that captive Carcharhinid sharks can externalize their lower intestine by cloacal protrusion (Crow et al., 1990). Therefore, sharks, and possibly rays, appear able to externalize the major proportion of their alimentary canal. We speculate that sharks keep healthy alimentary tracts partly due to this periodic process of maintenance but this proposal requires more detailed study of this elusive behaviour in free-living animals.

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