

*Journal of Fish Biology* (2010) **76**, 1863–1868

doi:10.1111/j.1095-8649.2010.02616.x, available online at [www.interscience.wiley.com](http://www.interscience.wiley.com)

## The functional role of the caudal fin in the feeding ecology of the common thresher shark *Alopias vulpinus*

S. A. AALBERS\*, D. BERNAL† AND C. A. SEPULVEDA\*‡

\*Pfeiffer Institute of Environmental Research, 315 N. Clementine St, Oceanside, CA 92054, U.S.A. and †Department of Biology, University of Massachusetts Dartmouth, 285 Old Westport Rd, Dartmouth, MA 02747, U.S.A.

(Received 17 March 2009, Accepted 5 February 2010)

This study tests the hypothesis that the common thresher shark *Alopias vulpinus* uses its elongate caudal fin to both produce thrust and immobilize prey during feeding. Underwater video recorded in southern California from 2007 to 2009 revealed 34 feeding events, all of which were initiated with the upper lobe of the caudal fin.

© 2010 The Authors

Journal compilation © 2010 The Fisheries Society of the British Isles

Key words: Alopiidae; behaviour; prey.

The three thresher shark species, *Alopias vulpinus* (Bonnaterre), *Alopias superciliosus* (Lowe) and *Alopias pelagicus* Nakamura, comprise a monophyletic group of pelagic elasmobranchs most commonly recognized by an elongate dorsal lobe of the caudal fin, which approaches the length of the trunk of the body (Gruber & Compagno, 1981). Despite distinct morphological and ecological differences among the three species, it has been suggested that all three alopiids utilize the elongate dorsal lobe of the caudal fin to stun prey before it is consumed (Allen, 1923; Gubanov, 1972; Stillwell & Casey, 1976; Preti *et al.*, 2001). The functional role of the caudal fin to both pursue and immobilize prey, however, has not previously been confirmed for this group of elasmobranchs (Springer, 1961; Gruber & Compagno, 1981).

Fisheries-related data show that thresher sharks are frequently hooked in the tail when captured by long-line gear, further suggesting the use of the caudal fin in the pursuit of prey (Gubanov, 1972; Stillwell & Casey, 1976; Nakano *et al.*, 2003). Similarly, a southern California recreational fishery for *A. vulpinus* predominantly captures tail-hooked individuals while slow-trolling baited lures (NOAA, 2009). Additional support comes from an observational account of a free-swimming *A. vulpinus*, which also suggests the use of the caudal fin during feeding (Allen, 1923). Furthermore, gut-content studies provide indirect evidence for the use of the tail to pursue prey by showing that the alopiid diet primarily consists of small schooling

‡Author to whom correspondence should be addressed. Tel.: +1 760 721 1404; fax: +1 760 721 1475; email: [Chugey@pier.org](mailto:Chugey@pier.org)

fishes, species that may be readily exploited with the elongate caudal fin (Bedford, 1992; Preti *et al.*, 2001).

Despite mounting evidence that alopiid sharks use their caudal fin during prey capture, there are no published accounts that substantiate this mode of predation (Springer, 1961; Gruber & Compagno, 1981). Thus, the primary objective of this work was to document the manner in which *A. vulpinus* utilizes its caudal fin during feeding.

An underwater video recording system was towed from the R.V. *Malolo* in the nearshore waters of southern California between Newport Beach and Point La Jolla from March 2007 to June 2009. Live chub mackerel *Scomber japonicus* Houttuyn were tethered to hookless, lead-headed lures and trolled 10 m behind the vessel at 3.7 to 7.4 km h<sup>-1</sup> (2–4 knots) and at a depth of *c.* 8 to 12 m (Fig. 1). An in-line video recording system (SeaViewer; www.Seaviewer.com) with a wide-angle lens was towed from 3 to 6 m (depending on water clarity) ahead of one or more of the baits to view the near-field environment surrounding the lures. Underwater images were digitally recorded at a frame rate of 30 Hz using a 30 GB hard-drive video camcorder (JVC, G2-MG155; www.jvc.com) connected to the towed camera *via* a 20 m long S-video cable.

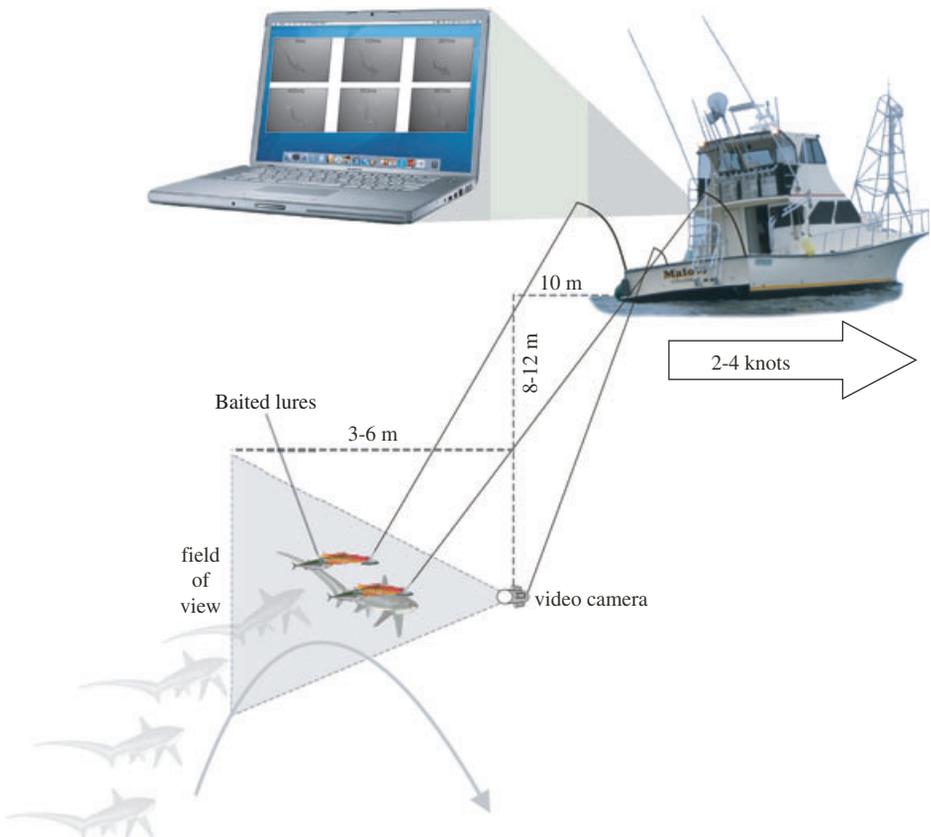


FIG. 1. A diagram of the field data collection system used to acquire *Alopias vulpinus* feeding behaviour.

Digital video was transferred to a computer hard-drive and video segments containing *A. vulpinus* feeding behaviour were selected for sequential frame-by-frame analysis. Image analyses were conducted only when ambient light level, water clarity (>3 m) and the orientation of the camera were appropriate for viewing the entire fish within the frame. A feeding event or strike was defined as any instance in which a fish made an active attempt to engage the baited lures with its mouth or caudal fin. For all feeding events, video clips were isolated beginning at a time 500 ms before the strike and ending 500 ms after the strike. Isolated images were imported into Adobe Illustrator CS4 software (Adobe Systems Inc.; www.adobe.com) to enhance the contrast of the fish and baited lure against the open-ocean background for further measurements. The silhouette of the fish and baited lure were both digitally traced within each frame throughout the entire duration of the feeding event. Feeding events were independently viewed frame-by-frame to identify specific variables, including the ratio of successful to unsuccessful strikes, strike position of the bait along the caudal fin and strike duration. Strike duration was estimated by the number of frames (*i.e.* at 30 Hz frame rate) that the bait remained in contact with the caudal fin during the feeding event. Body (*i.e.* fork length,  $L_F$ ) and caudal fin length ( $L_{CF}$ ) were estimated using a scale (*i.e.* dimension of the baited lure) within the digital images. Length estimates were performed only when the fish was positioned at a distance from the camera that was equal to that of the scale. The relative position along the caudal fin that made contact with the baited lure was also recorded for each strike and presented as a percentage of  $L_{CF}$ . These measurements started at the lower lobe (0% of  $L_{CF}$ ) and progressed to a maximum distance near the tip of the caudal fin (100%  $L_{CF}$ ). All observed fish were classified as either juvenile or adult based on the minimum size of maturity reported by Kohler *et al.* (1996) for male (184 cm  $L_F$ ) and female (226 cm  $L_F$ ) *A. vulpinus*.

Six hundred and fifty minutes of digital video were recorded on 27 sampling dates from 2007 to 2009, yielding footage from a total of 33 individual *A. vulpinus*. Although it was not possible to determine the exact size or sex ratio of all fish in this study, juvenile and adult *A. vulpinus* of both sexes (size range *c.* 110–244 cm  $L_F$ ) were observed on video recordings. Of all *A. vulpinus* identified within the camera field of view, 58% ( $n = 19$ ) approached or followed the baited lures without initiating a strike, while 42% ( $n = 14$ ) made active attempts to strike the baited lures using either their caudal fin or mouth. A total of 29 caudal fin strikes were initiated by 14 individuals, with a 65% strike success rate ( $n = 19$ ; Table I). All fish initiated feeding events with their caudal fin, while only one fish attempted to bite the trolled lure after striking first with its tail. Prey contact with the caudal fin was observed to occur from near the base of the dorsal lobe to the uppermost tip of the tail with strike locations ranging from 17 to 100%  $L_{CF}$ . The maximum strike duration was 667 ms with a mean  $\pm$  S.E. of  $237 \pm 43$  ms. Six fish made repetitive caudal fin strikes with an individual making up to seven caudal fin strikes during a 45 s period.

In general, fish remained in the field of view from 5 to 65 s, with a total of 63 distinct approaches recorded over the course of the study. Despite observations of various feeding behaviours, video records identified two predominant tail-feeding strategies. The most prevalent feeding behaviour was initiated by a rapid forward undulation (FU) of the anterior body, which resulted in a posterior-travelling sinusoidal wave that consequently advanced along the body towards the uppermost tip of the caudal fin (Fig. 2 and Table I). This feeding behaviour was observed in 59%

TABLE I. Summary of *Alopias vulpinus* caudal-fin strike variables

Strike number	Shark number	Strike duration		% $L_{CF}$	Estimated $L_F$ (cm)†
		(ms)	Strike type*		
1	2	166	LS right	67	135
2	2	333	LS right	33	135
3	2	33	LS right	83	135
4	2	33	LS right	17	135
5	2	66	LS left	83	135
6	4	100	LS right	67	152
7	5	200	LS left	40	140
8	6	200	FU	88	142
9	7	666	FU	40	192
10	16	400	LS right	33	NA
11	18	333	LS right	36	186
12	19		FU		190
13	19	233	FU	71	190
14	24	133	LS right	50	186
15	26		FU		182
16	30	366	FU	50	190
17	31	100	FU	73	151
18	33	433	FU	44	213
19	33	33	LS left	100	213
Minimum		33		17	135
Maximum		666		100	213
Mean $\pm$ S.E.		237 $\pm$ 45		57 $\pm$ 5	

\*Strike type: lateral strike (LS) or forward undulation (FU).

†Estimated fork length ( $L_F$ ) based on lure dimensions and image digitization.

$L_{CF}$ , caudal fin length.

( $n = 17$ ) of the recorded strikes and resulted in a success rate (determined by the contact with the lure) of 47% ( $n = 8$ ). The second predominant feeding pattern occurred when the fish positioned itself in close proximity and parallel to the prey item before initiating a lateral strike (LS) of the dorsal lobe (Table I). This feeding behaviour was observed on 12 occasions and entailed rapid, whipping movements of the caudal fin and yielded a strike success rate of 92% ( $n = 11$ ). Collectively, when all successful strikes are considered, the mean  $\pm$  S.E. caudal fin position was estimated to be  $57 \pm 5\%$   $L_{CF}$  ( $n = 19$ ), and there was no significant differences in strike location from the FU ( $61 \pm 8\%$   $L_{CF}$ ) and LS ( $55 \pm 8\%$   $L_{CF}$ ) feeding behaviours.

The observations confirm the hypothesis that the caudal fin of *A. vulpinus* is used in the pursuit and capture of prey. The results offer evidence that predation events are initiated with the caudal fin in an attempt to immobilize prey before it is consumed. These findings corroborate previous reports of this feeding strategy in this group of pelagic sharks (Allen, 1923; Springer, 1961; Gruber & Compagno, 1981; Nakano *et al.*, 2003). The use of the caudal fin during feeding probably contributes to the effectiveness of alopiid sharks as a predator of lower trophic level organisms. Bedford (1992) and Preti *et al.* (2001) concluded that the northern anchovy *Engraulis mordax* Girard is the most abundant prey item in the diet of both juvenile and adult

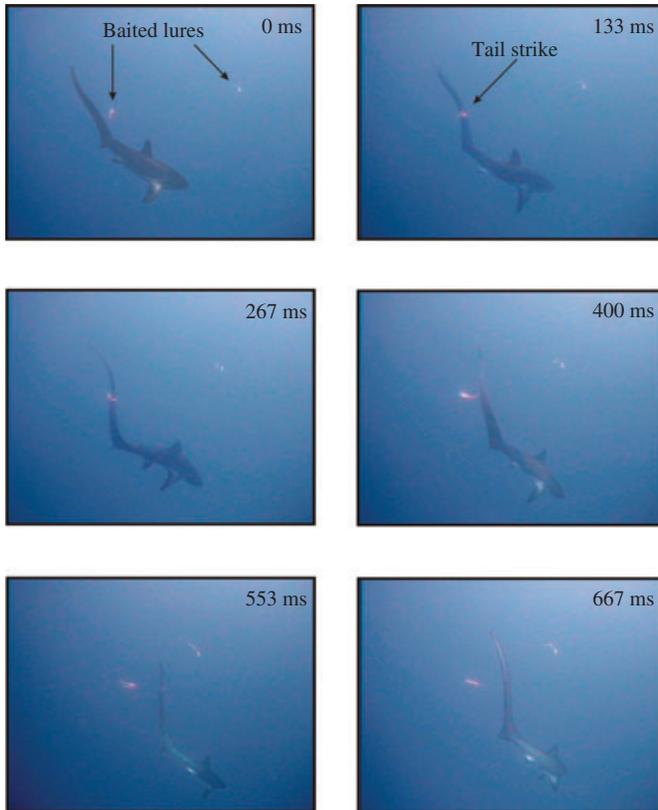


FIG. 2. Individual frames from a video sequence of a *Alopias vulpinus* (c. 151 cm  $L_F$ ) using its caudal fin to strike a baited lure.

*A. vulpinus* in the eastern Pacific, further supporting the utility of the caudal-based predation strategy on small schooling fishes.

Field observations revealed that *A. vulpinus* maintains remarkable control of the elongate caudal lobe during feeding events. The inherent logistical difficulties associated with recording underwater video in an uncontrolled environment (*i.e.* open ocean, camera orientation and scale) precluded any detailed kinematic analyses of swimming. Further observations include considerable caudal fin flexibility despite its rigid morphology (Sepulveda *et al.*, 2005). Observed adjustments in the orientation of the caudal fin may, in turn, reduce drag and increase tail speed during predatory strikes. Future kinematic analyses of swimming and feeding are needed to better understand the precise movements of the disproportionately long caudal fin in this group.

Elasmobranchs exhibit a broad spectrum of caudal fin morphologies ranging from the extremely heterocercal fin in the alopiid sharks to the lunate, nearly homocercal caudal fin in the lamnid sharks (Lauder, 2000). Because the locomotor efficiency of the disproportionately long caudal fin of the alopiid sharks has not been quantified, it is not possible to fully assess the driving forces behind the evolution of the unique alopiid design. Based on the documented use of the tail to immobilize prey, there

may be selection pressures other than locomotion driving the evolution of caudal fin morphology in this group of sharks.

This material is based on work supported by the National Science Foundation under grants IOS-0617384 and IOS-0617403. Any opinions, findings or conclusions expressed in this material are those of the authors and do not necessarily reflect the views of the National Science Foundation. Additional support was provided by the George T. Pflieger Foundation, the William H. and Mattie Wattis Harris Foundation and the National Oceanic and Atmospheric Administration Bycatch Reduction and Engineering Program. Special thanks are offered to J. Donley, K. Lafferty, N. Wegner, T. Fullam, V. Wintrode, L. Bohnet, D. McGillivray, D. Syme, C. Heberer, J. Ness, T. Young, D. Lewis, C. Albright, T. Tazo, J. Valdez and J. Albright for logistical and field support. We sincerely owe gratitude to T. Pflieger and the Pflieger family for their continued dedication towards the marine environment. This work was performed under the guidelines of the Animal Care and Use Committee of the University of Massachusetts, Dartmouth, Protocol # 05-06.

### References

- Allen, W. E. (1923). Behavior of the thresher shark. *Science* **63**, 31–32.
- Bedford, D. (1992). Thresher shark. In *California's Living Marine Resources and Their Utilization* (Leet, W. S., Dewees, C. M. & Haugen, C. W., eds), pp. 49–51. *California Sea Grant Publication UCSGEP-92-12*.
- Gruber, S. H. & Compagno, L. J. V. (1981). Taxonomic status and biology of the bigeye thresher, *Alopias superciliosus* (Lowe, 1839). *Fishery Bulletin* **79**, 617–640.
- Gubanov, Y. P. (1972). On the biology of the thresher shark, *Alopias vulpinus* (Bonnaterre), in the northwest Indian Ocean. *Journal of Ichthyology* **12**, 591–600.
- Kohler, N. E., Casey, J. G. & Turner, P. A. (1996). Length–length and length–weight relationships for 13 shark species from the Western North Atlantic. *NOAA Technical Memorandum NMFS-NE-110*, 1–29.
- Lauder, G. V. (2000). Function of the caudal fin during locomotion in fishes: kinematics, flow visualization, and evolutionary patterns. *American Zoologist* **40**, 101–122.
- Nakano, H., Matsunaga, H., Okamoto, H. & Okazaki, M. (2003). Acoustic tracking of bigeye thresher shark *Alopias superciliosus* in the Eastern Pacific Ocean. *Marine Ecology Progress Series* **265**, 255–261.
- Preti, A., Smith, S. E. & Ramon, D. A. (2001). Feeding habits of the common thresher shark (*Alopias vulpinus*) sampled from the California-based drift gill net fishery, 1998–1999. *California Cooperative Oceanic Fisheries Investigations Report* **42**, 145–152.
- Sepulveda C. A., Wegner N. C., Bernal, D. & Graham J. B. (2005). The red muscle morphology of the thresher sharks (family Alopiidae). *Journal of Experimental Biology* **208**, 4255–4261.
- Springer, S. (1961). Dynamics of the feeding mechanism of large galeoid sharks. *American Zoologist* **1**, 183–185.
- Stillwell, C. E. & Casey, J. G. (1976). Observations on the bigeye thresher shark, *Alopias superciliosus*, in the western North Atlantic. *Fishery Bulletin* **74**, 221–225.

### Electronic Reference

- NOAA (2009). *Annual Report to Congress on the Bycatch Reduction and Engineering Program*. 31–33. Available at [http://www.nmfs.noaa.gov/by\\_catch/docs/brep\\_report\\_final.pdf](http://www.nmfs.noaa.gov/by_catch/docs/brep_report_final.pdf)