**Coasting of Pelagic Thresher Sharks, *Alopias pelagicus*,
in Comparison to Two Other Species of the Same
Ecomorphotype, and the Limitation of Video Capturing
in Natural Settings**

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Abstract

Burst-and-coast is a widespread swim behavior among teleosts, but not so for sharks. Coasting seems to occur only rarely among sharks and even then rather sporadically and only among non-benthic sharks. One of the shark species for which coasting seems to occur more frequently is the pelagic thresher shark, *Alopias pelagicus* (Nakamura). Compared to oceanic whitetip sharks, *Carcharhinus longimanus* (Poey), and blue sharks, *Prionace glauca* (Linnaeus), two members of the same ecomorphotype, the macropelagic sharks, pelagic threshers, coast significantly longer, $p < 0.005$ and $p < 0.0001$, respectively, averaging 29.4 seconds per coasting phase (SE = 2.8,

N = 62). The most striking feature among pelagic threshers during these gliding phases is the decrease of the tail's heterocercal angle from 36.6° to 23.3°. This tail drop brings the caudal fin's upper lobe below the level of the first dorsal fin's tip, effectively reducing drag, further enhancing energy saving while coasting. This study summarizes the first detailed information on swim habits of pelagic thresher sharks, in comparison to oceanic whitetip and blue sharks, gathered through direct observation under natural conditions, and highlights the problems of video capturing in natural settings.

Keywords: ecomorphotype, thresher shark, coasting, *Alopias pelagicus*

Introduction

Coasting, as part of the burst-and-coast pattern, is a common feature in the locomotion repertoire of many teleosts (see, for example, Fish et al., 1991; Müller et al., 2000; McHenry and Lauder, 2005). Burst-and-coast swimming consists of an acceleration phase through a variable number of tailbeat cycles, followed by a gliding phase in which the animal keeps its body still and stretched (Weihs, 1974; Videler 1981; Wu et al., 2007). Although coasting has been noticed among shark species on rare occasions, for example, in white sharks, *Carcharodon carcharias* (Linnaeus); Caribbean reef sharks, *Carcharhinus perezi* (Poey); or whale sharks, *Rhincodon typus* (Smith) (personal observation), coasting is so rare that conducting a quantitative analysis to determine whether intermittent swimming is as common for sharks as for bony fishes or whether even burst-and-coast occurs has not been feasible. However, one species, the pelagic thresher shark, seems to coast on a more regular basis. Although this species prefers off-shore habitats (Compagno, 2001; Bonfil and Abdallah, 2004; Camhi et al., 2008), it occasionally frequents sea mounts (Oliver et al., 2011) and shallow reefs, so it comes, although rarely, into contact with humans. Despite the scarcity of such encounters, I could videotape several coasting occurrences in 2005 in the Red Sea, and the first evaluations revealed that pelagic thresher sharks coast rather frequently compared to other species mentioned above. To verify these first results, I undertook additional trips between 2006 and 2012 to the Red Sea to gather more data on the locomotion patterns of this species.

This study represents the first detailed information gathered through direct observation on the intermittent swim habits of pelagic thresher sharks. Besides quantifying instances of coasting, I also summarize additional aspects of locomotion for this species. To weigh these first results, I further examined two other species of the same ecomorphotype, the blue shark, and the oceanic whitetip shark. This ecomorphotype, called 'macropelagic', calls for the same habitat, similar feeding habits, and some shared anatomical features, like long pectoral fins, slender body forms, and such (Compagno, 1990). Besides the three species mentioned, silky sharks, *C. falciformis* (Bibron), and longfin makos, *Isurus paucus* (Guitar), belong also to this group.

Material and methods

I videotaped pelagic thresher sharks around 'Al Akhawin,' commonly known as the 'Brother Islands.' All encounters occurred in the morning hours between 0600 and 0730 or late in the afternoon and early evening hours, at depths between 45m and 60m. Visibility always exceeded 30m. Current was largely absent. Data collection on the oceanic whitetip sharks happened largely around the same sites as well or farther south around 'Abu El Kizon,' commonly known as the 'Daedalus Reef,' during the same time, whereas for the blue shark I collected data between 2010 and 2012, during the summer months around the Azores in the Atlantic.

I recorded each encounter with either a Sony HC-9 video camera in a SeaTool housing, or a Sony DCR-TRV900 camera in a SeaDog housing. Frame rate for both cameras was 30 fps. Since pelagic thresher sharks predominantly appeared alone, I treated each encounter as an independent observation. Among oceanic whitetips and blue sharks, I was able to differ between individuals, and so videotaped each shark only once during a dive. Did I repeat dives at the same site for a few days, recognizable sharks (e.g., having wounds or scars, missing fin tips, and such) were not videotaped a second time.

Some of the problems I encountered while videotaping free-swimming thresher sharks were 1) the lack of scaling, 2) the occurrence of parallax effects, and 3) short observation periods. To overcome these problems, I only used videos in which 1) sharks swam on eye level with me, 2) I could neglect parallax effect since the animal swam far enough, and 3) the beginning and end of coasting were visible. The following factors were estimated: coasting duration, tailbeat frequency, and "tail drop" expressed through the heterocercal angle. In order to get a somewhat correct measurement on the tail drop (Fig. 1a), I estimated the heterocercal angle between vertebral column and the horizontal plane (Wilga and Lauder, 2002). I then approximated this angle by measuring the larger complementary angle α , consisting of the angle between the upper lobe's axis, identical to the vertebrate column's direction, and the longitudinal direction of the peduncle identifying the corresponding horizontal plane (Fig. 1a), and then converted to the heterocercal angle. I estimated each angle three times and then took the average. Measurements of the complementary angle α were calculated by transferring single video frames into Photoshop CS5® by Adobe® and then applying the info palette's angle function.

To get a best approximation for the tailbeat frequency from these large-amplitude species, I measured the time from a maximum lateral extension of the tail back to this position for the third time and then take the average calculated for a single cycle. Evaluation was done with the video program Final Cut Pro 6.0® by Apple®. Although I could identify gender among blue and oceanic whitetip sharks as they passed by, such was impossible for nearly all encounters with thresher sharks. Magnification of the videos taken was not clear enough—even with appropriate enhancements through Photoshop CS5®—to identify their sex. Claspers, even of mature males, are rather small, compared to the overall body length of the animal, fitting very tightly under the shark's body. Thus, I disregarded gender for all three species.

Results

Coasting

Coasting lasted significantly longer among pelagic threshers than oceanic whitetips ($p < 0.005$, $t = 3.185$, $df = 91$) and blue sharks ($p < 0.0001$, $t = 4.839$, $df = 84$) and also differed between the latter two species ($p < 0.005$, $t = 3.141$, $df = 53$) (Table 1). Thresher sharks were the only sharks among the three species in which I observed multiple occurrences of coasting. The average duration of repetitive coasting lasted 22.4 seconds ($SE = 2.6$, $N = 36$), which did not significantly differ from single coasting ($p = 0.9699$; $t = 0.03792$, $df = 76$), which averaged 29.4 seconds ($SE = 2.8$, $N = 62$). The one thresher shark that I could observe the longest, performed seven coastings over a period of 182.5 seconds, with an average coasting duration of 12.5 seconds ($SE = 4.7$, $N = 7$) and 12.7 seconds ($SD = 2.4$, $N = 6$) cruising time in between.

Heterocercal angle

The complementary angle increased from 143.4° ($SE = 1.429$; $N = 31$) to 156.7° ($SE = 1.244$; $N = 31$) during coasting, lowering the upper tip of the caudal fin below the level of the first dorsal fin's apex (Fig. 1a). Expressed in the form of the heterocercal angle, the difference between 36.6° ($SE = 1.429$; $N = 31$) and 23.3° ($SE = 1.244$; $N = 31$) was significant ($p < 0.0001$; $t = 6.892$; $df = 60$).

Tailbeat frequency

The highest tailbeat frequency I measured among blue sharks (Table 1) was significantly higher than among pelagic threshers ($p < 0.0001$; $t = 10.02$; $df = 107$) and oceanic whitetips ($p < 0.05$; $t = 2.094$; $df = 141$).

Discussion

All three shark species showed coasting but lacked the speed bursts in between, which commonly occurs among teleosts during burst-and-coast (Videler and Weihs, 1982; McHenry and Lauder, 2005) and just cease their active motion. Since pelagic threshers, oceanic whitetips, and blue sharks belong to the same ecomorphotype, it can be assumed that coasting is a common locomotion trait of macropelagic sharks.

Coasting and energy saving

The most obvious gain from coasting is energy saving (Videler and Weihs, 1982; Fish et al., 1991), which could be greatly enhanced should the coasting animals glide along currents. During the entire data collection for thresher sharks, as well as oceanic whitetips, current was largely absent, and I can not make any conclusion to whether coasting is indeed preferred while swimming with a current. However, because it is well documented that sharks often follow large ocean currents while, for example, migrating (Carey and Scharold, 1990; Montgomery and

Walker, 2001), such a pattern likely fits these pelagic species too since all three species are known to migrate (Kohler et al., 1998; Nakano and Stevens, 2009). Weihs (1974) estimated that an energy saving of over 50% could be attained using burst-and-coast among teleosts, but to what extent energy saving might occur among sharks without prior bursts and gliding along a current needs to be determined.

Beside currents as an hydrodynamic force to support a shark's motion, thermoclines were infrequently noticed close to the sharks cruising and coasting depths in the Red Sea. In such cases, thresher sharks might stay right on top of thermoclines and use the higher density below to enhance gliding. Beside such potential use of currents and thermoclines, it is quite likely that other fluid dynamic related factors support coasting as well.

One thresher shark performed seven coastings in which the average durations of coasting and cruising were identical. Although observed only once and the cruising and coasting were rather brief, 12.5 seconds and 12.7 seconds, respectively, these equal times might not have happened by chance but could indicate a more preferred ratio between coasting and cruising for this species if performed over longer periods of time. Further observations are needed to determine whether such multiple coastings are indeed a more frequent form of intermittent swimming for thresher sharks than the occasional singular coasting.

Coasting and ecomorphotype

Among these three macropelagic species, thresher sharks seem to coast more and longer on an individual basis than oceanic whitetip and blue sharks. However, since the number of animals and observations for each species differed, this observation may not be factual.

Macropelagic shark species differ from the second pelagic shark group, the tachypelagic species, largely in the faster speed with which the latter group cruises. That group includes the shortfin mako, *I. oxyrinchus* (Rafinesque), the salmon shark, *Lamna ditropis* (Hubbs and Follett), and the porbeagle shark, *L. nasus* (Bonnaterre). Some tachypelagic sharks have been observed (personal observation), but I never noticed coasting. If these species do not coast at all, considering their rather high-energy lifestyle, remains unknown but gliding might not be a preferred feature of their locomotion repertoire. If absent, then coasting could indeed reflect a more typical characteristic behavior for macropelagic sharks. In contrast, lepto- and platybenthic littoral sharks (Compagno, 1990), represented by different catshark families, angel sharks, or wobbegong species, have never been seen coasting (personal observation), but it does not seem necessary considering that they spend a large part of their time resting on the bottom (Farina and Patricio Ojeda, 1993; Gaida, 1997; Carraro and Gladstone, 2006) and do not show the typical migration patterns of non-benthic oriented shark species.

Tail drop

The only comparison available for a heterocercal angle on a pelagic thresher to the data presented here was offered by Kim (2002). His measurement, taken from a single, preserved, and, based on the total length given, juvenile animal, indicated an angle of 11°. This value is less than half of what I measured in this study for the dropped configuration. No living shark came

close to having such a low angle, and it seems that Kim's measurement reflects an artefact of preservation rather than a true position.

It remains unclear what causes the tail drop and its potential value. The phenomenon is likely an active process of depressing the vertebral column by contracting the radialis muscle (Flammang, 2010) to streamline the body while gliding. It is possible that the pure weight of the upper lobe might also have an effect, but considering that the most anterior part of the upper lobe is also bent suggests that an active process is mostly responsible. Although a drag reduction during the tail drop seems to occur, due to the vortex production behind the tail some tail drag remains (Zhu et al., 2002). Nevertheless, the overall reduction of the frictional drag must be beneficial when coasting (e.g., Blake, 2004).

Since the tail's lift is eliminated while coasting, the angle of the pectoral fins' axes possibly increases to compensate for the loss of lift (Fish and Shannahan, 2000). While some actively swimming pelagic thresher sharks passed rather close (Fig. 1b), coasting animals avoided me all together, making a measurement for comparison between the possible pectoral fins' axes angle differences impossible. However, should there be no compensation, the following cruising period where the sharks then swim "upward" again for short periods of time would be a method of compensation (e.g., Klimley et al., 2002). This up and down motion for sharks, sometimes called "yo-yo diving" (e.g., Carey and Scharold, 1990; Iosilevskii et al., 2012) would then be comparable to burst-and-coast found in teleosts (e.g., Fish and Shannahan, 2000; Fish et al., 1991; Kramer and McLaughlin, 2001). That some shark species show bursts of speed with some gliding afterwards is known (e.g., Klimley et al., 2002), but this is different from the pelagic thresher sharks' rather continuous cruise-and-coast locomotion.

Tailbeat frequency

Tailbeat frequency does not carry a lot of meaning if measured without other parameters e.g., swim speed or the tail's amplitude, since it could easily be affected by either of these two parameters (e.g., Brainbridge, 1958) hence the estimation here is rather seen as a first reference for further studies related to this shark species.

Tailbeat frequency is a relative indicator for the speed of an aquatic animal while actively moving forward (Graham et al., 1990; Steinhausen et al., 2005). The rather increased tailbeat frequency of blue sharks in comparison to pelagic threshers and oceanic whitetips resembles the tachypelagic type more than the slower macropelagic sharks, the group to which the blue sharks belong (Graham et al., 1990). However, the videotaped blue sharks were largely juveniles in which higher tailbeat frequencies likely reflect the animals' smaller sizes. Brainbridge (1958), Graham et al. (1990), and others mentioned that a decrease in the tailbeat frequency can be assumed in larger specimen of the same species. Hence, this observation for blue sharks might be due to their younger age and smaller size, and only mature blue sharks should be used to make a factual comparison. The smaller size of these blue sharks could also have had another effect on the comparison between this species with the other two. A model by McHenry and Lauder (2006) suggests that longer bodies have a positive effect on the duration of coasting, possibly indicating that the measured coasting duration for blue sharks might be longer for adults, hence

more comparable to the pelagic threshers and oceanic whitetips, which, according to their sizes, were probably mature animals.

A necessity of field observation concerning large sharks

Direct observation of sharks in unrestricted places has merit over behavioral and locomotion studies in flume or flow tanks, or even aquaria (e.g., Graham et al., 1990; Videler and Wardle, 1991; Lowe, 1996). Nevertheless, targeted species often live in hard to access habitats, making tests in confined spaces the only alternative for obtaining a glimpse of how life might be in their natural environment. However, some shark species are too big to be examined in tanks, so the only way of shedding some light onto their behavior is to find and study them in their natural habitats. The pelagic thresher shark is such a species, and while some parameters presented in this study represent mere estimations, the quantification of cruising and coasting of this species offers a first glimpse of the undulatory locomotion of a shark species with an exceptionally long, heterocercal caudal fin.

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Table 1. Average coasting duration and tailbeat frequency of observed species.

N = number of observations; $\emptyset$ = average duration in seconds, SE = Standard error; tbs = tailbeats per second

Species	Coasting (N)	Duration ($\emptyset \pm \text{SE}$)	Cruising (N)	tbs ($\emptyset \pm \text{SE}$)
<i>Alopias pelagicus</i>	62	29.4 $\pm$ 2.8	43	0.5 $\pm$ 0.01
<i>Carcharhinus longimanus</i>	29	15.4 $\pm$ 2.3	100	0.6 $\pm$ 0.01
<i>Prionace glauca</i>	24	7.2 $\pm$ 1.1	66	1.0 $\pm$ 0.03

Figure 1. Heterocercal angle α of a coasting and cruising pelagic thresher shark.

a) lateral view, coasting; b) lateral view, cruising.

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