Feeding behavior of white sharks (*Carcharodon carcharias*) around a cage diving vessel and the implications for conservation

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Abstract

White sharks (*Carcharodon carcharias*) are marine apex predators whose top-down effects are crucial to community structure and function of marine ecosystems. White shark populations are declining around the world due to human impacts, particularly overexploitation by fisheries. The role of white sharks and their declining numbers are motivating conservation and protection efforts. Among these, cage diving ecotourism has emerged in recent years as a promising platform to inform the general public about the importance of shark conservation. However, there are concerns that cage diving operations could negatively affect shark behavior, reducing potential benefits for conservation. This study compares the behavior of white sharks toward bait around a cage diving vessel with natural predatory behavior toward seals. Sharks around the dive boat performed more investigative behaviors and fewer aggressive behaviors than the sharks hunting seals. The decision to feed on the bait after investigation varied among individuals, indicating that the bait is not inherently considered a prey item; instead, feeding decisions seem to be made on an individual basis. Therefore, I suggest that sharks do not approach cage diving vessels with the intent to feed on the bait, but rather are attracted to the boat by the chum and then become interested in the bait as a potential prey item upon arrival. Based on the results of this study, cage diving operations do not appear to have significant negative effects on white shark behavior and thus, could be a useful tool in promoting shark conservation.

Introduction

Like many other elasmobranch species, white sharks (*Carcharodon carcharias*) are currently facing dramatic declines due to human impacts (Camhi et al. 1998; Baum et al. 2003; "White shark" 2004; Dulvy et al. 2014). For instance, in the Northwest Atlantic, a 79% decrease in white shark populations was observed from 1986 to 2000 (Baum et al. 2003). In 1996, white sharks were classified as vulnerable on the International Union for Conservation of Nature Red List and their status remains unchanged (Fergusson et al. 2009). White sharks are protected in several regions of the world, including the United States, Australia, New Zealand, Malta, South Africa, and Namibia, which prohibit target commercial fisheries (Camhi et al. 1998; "White shark" 2004). Management of white shark fisheries in other regions of the world is unknown, but there is evidence of illegal trade in shark products ("White shark" 2004). Despite their protection in certain regions, white shark populations are continuing to decline due to overexploitation by fisheries, recreational angling, and bycatch mortality (Bonfil 1994; Camhi et al. 1998; "White shark" 2004; Dulvy et al. 2014).

White sharks are highly valued and exploited for their meat, fins, cartilage, liver oil, jaws, and teeth (Bonfil 1994; "White shark" 2004; Dulvy et al. 2014). The poorly-monitored market for shark fins in Asia is a major cause of overexploitation due to the popularity of shark fin soup, a cultural delicacy in Asian countries (Verlecar et al. 2007; Dulvy et al. 2014). White sharks are also a major target of recreational anglers, who consider the teeth and jaws to be prized trophies (Bonfil 1994; Camhi et al. 1998; "White shark" 2004). In addition, many are unintentionally caught in the nets and drum lines of other fisheries (Bonfil 1994; "White shark" 2004; Dulvy et al. 2014), as well as beach nets, which are used to keep sharks away from popular beaches (Paterson

1990; "White shark" 2004). Furthermore, due to their commercial value, shark bycatch is often retained and sold in illegal markets ("White shark" 2004; Dulvy et al. 2014).

The life history traits of white sharks make them particularly vulnerable to overexploitation (Cailliet et al. 1985; Camhi et al. 1998; "White shark" 2004; Dulvy et al. 2014). Like most elasmobranchs, white sharks are a slow-growing, late-maturing, long-lived species with low fecundity (Cailliet et al. 1985; Camhi et al. 1998; "White shark" 2004; Dulvy et al. 2014). Consequently, many sharks are removed from the population before they reach reproductive maturity, inhibiting population maintenance and recovery from declines (Camhi et al. 1998). White sharks also tend to aggregate in nearshore coastal areas, increasing their exposure to human exploitation (Casey & Pratt 1985; Klimley 1985; "White shark" 2004).

Reduction or extirpation of white shark populations is expected to have broad ecological impacts (McCosker 1985; Camhi et al. 1998; Baum et al. 2003; Heithaus et al. 2008). As with other large apex predators, white sharks are thought to have a significant influence on community structure and ecosystem dynamics through trophic cascades (Cailliet et al. 1985; McCosker 1985; Camhi et al. 1998; Baum et al. 2003; "White shark" 2004; Heithaus et al. 2008). Declines in white shark populations release mesopredator prey populations from predatory control, which has further consequences for prey populations (Prugh 2009). For example, Myers et al. (2007) showed that reductions in shark populations along the east coast of the United States was correlated with increases in populations of mesopredator elasmobranchs, particularly cownose rays. Increased ray abundance can diminish bivalve populations through predation, as was demonstrated in a 2003 survey that showed a substantial decrease in the commercial harvest of bivalves in Chesapeake Bay due to high cownose ray predation (Myers et al. 2007). Thus, removal of apex predators such as white sharks affects ecosystem ecology, which in turn can impact fisheries. These threats to ecosystem function and fisheries management have driven shark conservation efforts in recent years, including the use of cage diving to raise awareness of shark conservation issues.

Cage diving ecotourism was developed in 1991, shortly after legislation was passed to protect white sharks in South Africa (Johnson & Kock 2006). Cage diving operations lure white sharks to a boat using chum and bait to allow clients to view the sharks. This ecotourism activity has become a central platform for promoting the conservation of sharks. Companies, such as White Shark Africa in Mossel Bay, South Africa and Marine Dynamics in Gansbaai, South Africa, take advantage of the opportunity to educate clients about the importance of sharks in the ecosystem and the need for conservation (M. Bromilow, personal observations). Such encounters with sharks can lead to a greater understanding and awareness of ecological concerns, which could potentially increase support for conservation (Zeppel 2008).

Although cage diving ecotourism has great potential to inform the public about white sharks, there is some concern that cage diving operations can have negative effects on the sharks (Green & Higginbottom 2001; Orams 2002; Johnson & Kock 2006; Laroche 2007). One of the main concerns is that by eating the bait, sharks will become conditioned to associate boats and humans with food, and potentially create a dependency on the bait as a major food source (Green & Higginbottom 2001; Orams 2002; Johnson & Kock 2006; Laroche 2007). This could cause sharks to ignore their natural prey and result in altered ecosystem dynamics (Green & Higginbottom 2001; Orams 2002). Conservationists are also concerned that sharks may become habituated to the presence of boats and humans (Green & Higginbottom 2001; Orams 2002; Johnson & Kock 2006), which could put sharks at greater risk of human exploitation.

The primary concern about sharks interacting with cage diving operations is the potential to change natural shark behavior. This study was performed to determine if cage diving ecotourism affects the feeding behavior of white sharks. Behavioral observations of white sharks around a cage diving vessel and bait were compared to the published observations of natural predations on seals made by Martin et al. (2005). Results are evaluated in terms of potential impacts on white shark conservation.

Materials and Methods

Study site

Behavior of white sharks around a cage diving vessel was observed from 20 May to 17 June 2013 at Seal Island, Mossel Bay, South Africa. Seal Island is a small, rocky islet oriented northwest-southeast at approximately 34°09'S, 22°07'E, with a rocky outcrop on the northwestern side of the island (Fig. 1). The island is approximately 800 m from the mainland and roughly 100 m long and 50 m wide. The surrounding water is 14 m deep and transitions from rock on the island to sand or exposed reef with distance from the island. Appropriately named, Seal Island is inhabited by nearly 4,000 Cape fur seals (*Arctocephalus pusillus pusillus*), which traverse the waters around the island to offshore foraging sites. White sharks are attracted to large aggregations of seals and use the waters around the island as their primary hunting ground.

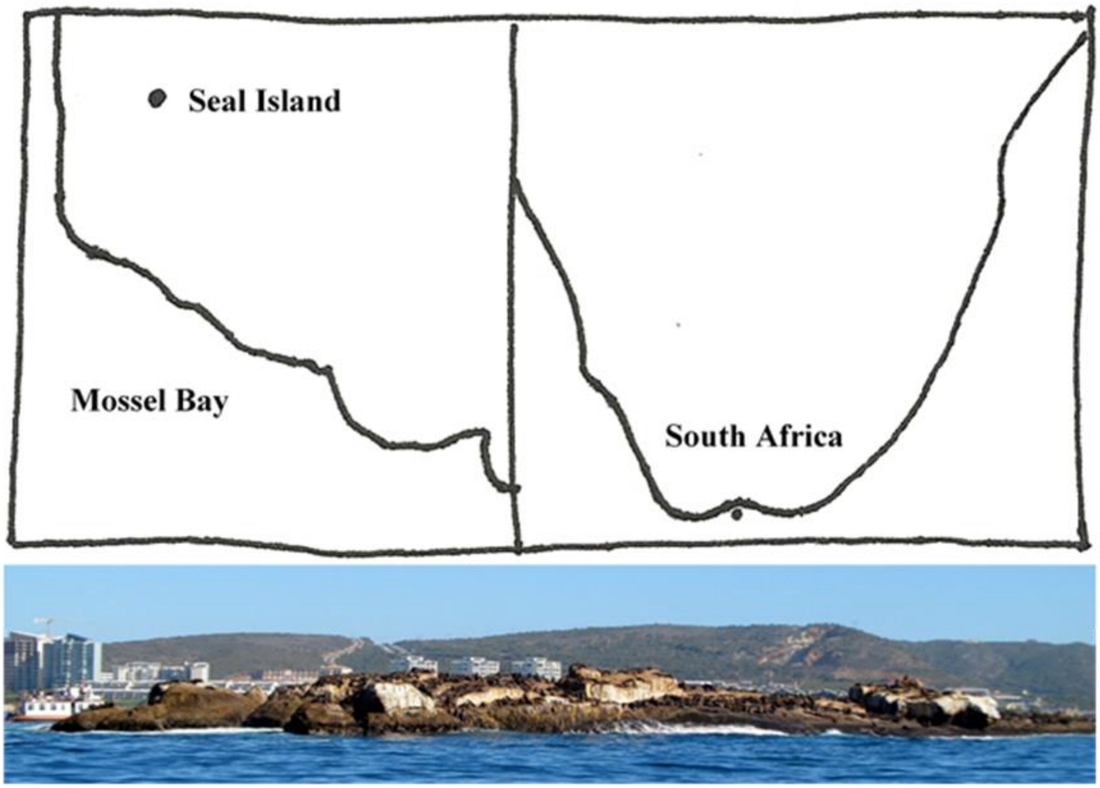

Figure 1. *Study site – Seal Island, Mossel Bay, South Africa*

Data collection

Sharks were observed from a dive vessel owned by White Shark Africa, a cage diving operation and internship program, which made daily trips to Seal Island, weather permitting. Data were collected during 17 cage diving excursions. Observations began shortly after anchoring at Seal Island. Arrival time at Seal Island depended on weather and sea conditions and ranged from 0930 h to 1600 h. All observations were made within 120 m of the eastern side of the island. As soon as the anchor was set, a member of the crew began chumming the water with a mixture of fish oils and sardines, and a dive cage was then attached to the side of the boat. A big-eye tuna head was tied to a 7 to 15 m bait line, which was then tossed into the water. Chum was added to the water throughout the trip to maintain the chum corridor, while the bait handler lured sharks to pass in front of the cage by pulling the bait line along the side of the boat. The intent was not to feed the sharks, but rather to attract sharks to the vicinity of the cage for viewing; however, a shark occasionally took the bait.

A team of two recorded shark behavior each trip: one recorded the time of shark appearances, while the other recorded shark behavioral sequences using a pre-designed data sheet with columns for each behavior. The same individual recorded the shark behavior sequences for every trip throughout this study for consistency. After the cage was put in the water and sharks began to arrive at the boat, a shark was identified that consistently interacted with the bait. Each shark was identified by both observers on the basis of unique pigmentation, deformities, and scars or scratches. Some sharks were identifiable by acoustic and/or satellite tags from other studies done in the area. Behavioral sequences were recorded every time the identified shark came within view in a roughly 25 m radius semi-circle around the cage-side of the 12 m boat. The time-keeper recorded the time of entry to the observation area, while the behavior recorder marked off the occurrence of behaviors in successive rows on the data sheet. Behaviors were recorded until the shark was no longer visible within the observation area, at which point, the time-keeper recorded the time for the end of the behavioral sequence. An individual shark was observed until it disappeared for 15 minutes, after which, a new shark was identified for observation.

Behaviors

The behaviors observed in this study were chosen and defined based on previous observations of white sharks around a cage diving vessel (M. Bromilow, personal observations) and on the behaviors seen during natural predations on seals in a study by Martin et al. (2005). Behaviors were organized into the major phases of the predation cycle: investigation, pursuit, prey capture, prey handling, feeding, and release. The variations of behaviors within these phases that were recognized by Martin et al. (2005) were condensed to facilitate a comparison of behaviors and behavioral sequences between sharks in a natural predatory setting and sharks interacting with the bait line of a cage diving operation (Table 1). Behaviors were identified and defined as follows:

Phase 1: Investigation

Slow Swimming (SLOSWM): The shark swam slowly at the surface toward the prey, or just past it.

Turn-About (TRNABT): After swimming past the prey, the shark turned back toward it slowly or moderately quickly, with little change in speed.

Phase 2: Pursuit

Jump (JUMP): The shark leapt partially or completely out of the water, attempting to attack the prey.

Horizontal Lunge (HRLUNG): The shark accelerated quickly along the surface toward the prey with its jaws open and its back partially out of the water.

Vertical Lunge (VTLUNG): The shark accelerated quickly toward the prey from below with its jaws open.

Phase 3: Prey Capture

Horizontal Surface Grasp (HSGRSP): The shark slowly approached and grasped the prey while swimming horizontally near the surface.

Vertical Surface Grasp (VSGRSP): The shark slowly approached the prey from below, grasping the prey in its mouth at the surface.

Lateral Snap (LATSNP): The shark attempted to bite the prey, either successfully or unsuccessfully, with a sudden lateral snap of its jaws as it swam along the surface.

Phase 4: Prey Handling

Carrying (CARRY): The shark held the prey in its mouth while swimming slowly with large amplitude tail beats.

Thrashing (THRASH): The shark held the prey in its mouth while shaking its head and body from side to side in an attempt to remove flesh.

Phase 5: Feeding

Feeding (FEED): The shark repeatedly bit the prey, either at the surface or underwater, consuming pieces of flesh.

Phase 6: Release

Release (RLEASE): The shark released the prey from its mouth, leaving the prey partially or completely intact.

Table 1. The classification of behaviors from Martin et al. (2005) into more generalized behaviors as defined for this study.

Defined behaviors	Martin behaviors
SLOSWM	DIR
TRNABT	ARC
JUMP	POL
	BRS
	BRL
	BRI
HRLUNG	LUN
	KIL
	INA
VTLUNG	INU
HSGRSP	GRH
VSGRSP	GRV
LATSNP	SNL
CARRY	CAR
THRASH	LHS
FEED	FDS
	FDU
	REP
RLEASE	REL

Data analysis

Based on the observations around the cage diving vessel, there was a clear distinction between two sets of sharks: those that did not consume the bait and those that did, designated "unfed" and "fed" respectively. These were compared with the shark behavioral data for natural predations from Martin et al. (2005), referred to as the "Martin" data set.

Proportions of observed behavioral phases and individual behaviors were calculated for each of the unfed, fed, and Martin data sets. Frequency distributions for the occurrence of each behavioral phase and behavior were compared using Chi-square analysis. Some behaviors were rare. Only those that occurred at least once across all the three data sets were included in the analyses, i.e. behaviors that had a frequency of zero in any data set were excluded from the statistical analyses. Tukey post-hoc tests for multiple comparisons of proportions were used to determine the underlying differences in behavioral phase and behavior frequencies between the three data sets (Zar 2010).

Results

A total of 28 white sharks were observed around the cage diving vessel over 15 days. Of these 28 sharks, eight successfully fed on the bait. A total of 502 behaviors were recorded in 140 behavioral sequences; 309 of these behaviors were observed for the unfed sharks and 193 for the fed sharks. The 502 observed behaviors around the cage diving vessel were compared to the 784 natural predatory behaviors observed by Martin et al. (2005) (Table 2).

Table 2. Frequency of behaviors in various behavioral phases of the predation cycle for unfed, fed, and Martin sharks.

		Unfed sharks		Fed sharks		Martin sharks	
Behavioral phase	Behavior	Frequency	Proportion	Frequency	Proportion	Frequency	Proportion
Investigation	SLOSWM	155	0.5016	77	0.3990	7	0.0089
	TRNABT	74	0.2395	26	0.1347	11	0.0140
Pursuit	JUMP	0	0.0000	0	0.0000	216	0.2755
	HRLUNG	11	0.0356	4	0.0207	160	0.2041
	VTLUNG	5	0.0162	7	0.0363	2	0.0026
Prey capture	LATSNP	3	0.0097	2	0.0104	110	0.1403
	HSGRSP	41	0.1327	26	0.1347	14	0.0179
	VSGRSP	13	0.0421	12	0.0622	8	0.0102
Prey handling	CARRY	4	0.0129	6	0.0311	56	0.0714
	THRASH	0	0.0000	3	0.0155	53	0.0676
Feeding	FEED	0	0.0000	15	0.0777	98	0.1250
Release	RLEASE	3	0.0097	15	0.0777	49	0.0625
	TOTAL	309	1.0000	193	1.0000	784	1.0000

**SLOSWM = Slow Swimming, TRNABT = Turn-About, JUMP = Jump, HRLUNG = Horizontal Lunge, VTLUNG = Vertical Lunge, LATSNP = Lateral Snap, HSGRSP = Horizontal Surface Grasp, VSGRSP = Vertical Surface Grasp, CARRY = Carrying, THRASH = Thrashing, FEED = Feeding, RLEASE = Release*

General behavior

Predation typically follows a general sequence composed of major behavioral phases (Helfman et al. 2009). Around the cage diving vessel, the first phase observed was investigation of the bait, in which a shark approached the tuna head slowly, usually swimming past it before turning back to inspect the potential prey again. In the next major phase, pursuit, sharks became more aggressive and attempted to take the bait. Pursuit generally resulted in prey capture, which involved sharks successfully seizing the bait in their mouths. Once captured, sharks manipulated the bait by attempting to swim away with the tuna head or by thrashing their bodies in an attempt to remove pieces of flesh. This was termed the prey handling phase. Some sharks successfully swallowed pieces of the bait, defining the feeding phase, which was usually followed by release. Generally, the whole tuna head was not consumed. Other sharks released the bait without eating any flesh.

These major phases describe generalized predation cycles, but not all steps occurred in every predator-prey interaction. When subsequent steps were absent or failed, sharks returned to the interaction at an earlier phase and some previous steps were repeated. For example, the more aggressive pursuit phase generally led to prey capture, but, if unsuccessful, sharks usually returned to investigation.

Comparison of general behavior patterns of unfed, fed, and Martin sharks showed similar behavioral phases, but within these phases, behavioral sequences of Martin sharks in a natural setting were more complicated than unfed and fed sharks, having greater diversity in the occurrence and succession of behaviors (Fig. 2). Differences found in the distributions of behavioral phases were significant between all three data sets ($\chi^2 = 1764.464$, df = 12, $p < 0.05$).

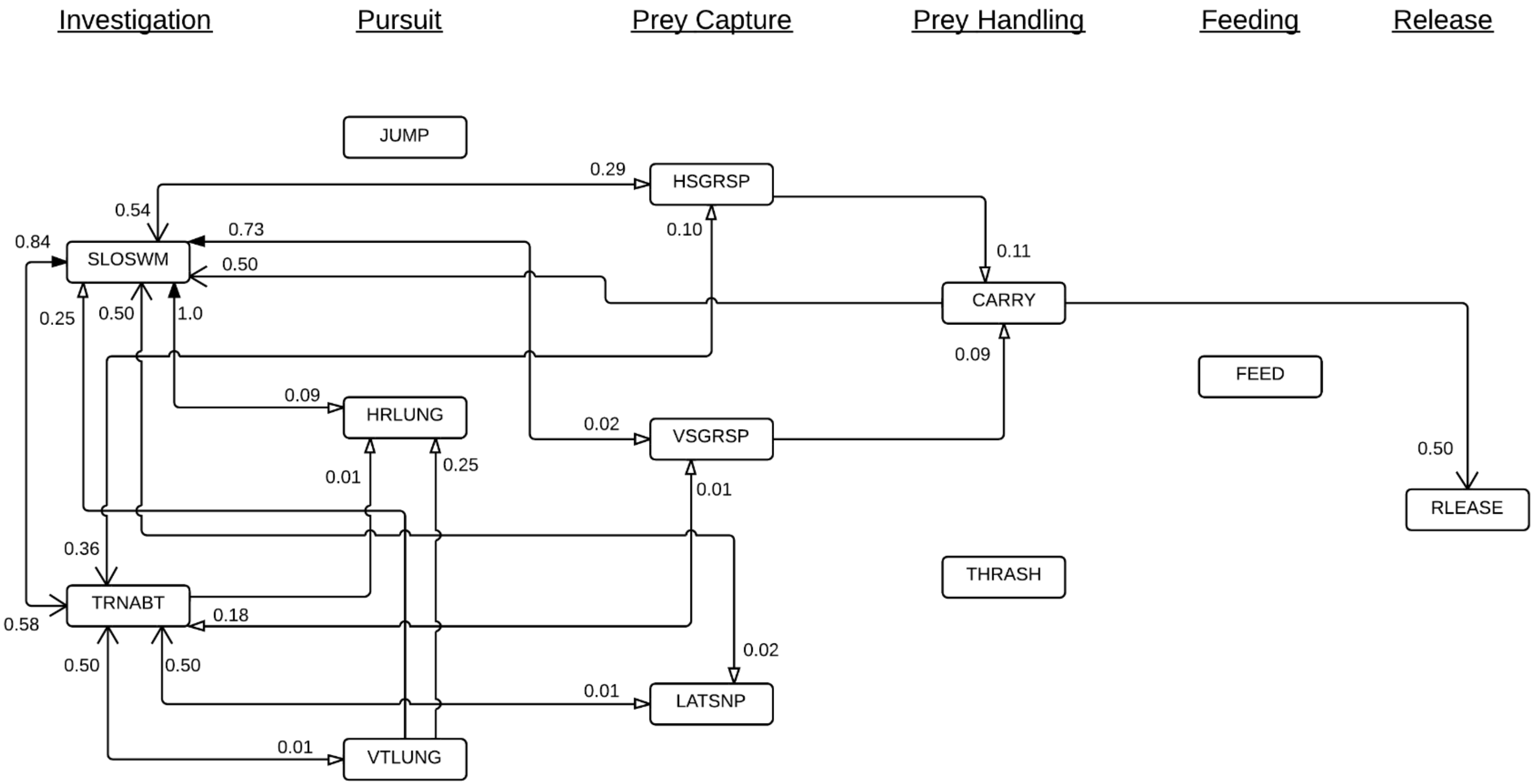

Figure 2A. *Flow diagram of observed behavioral sequences for sharks around the cage diving vessel that did not consume bait. Numbers are the probabilities that a behavior will follow the preceding behavior.*

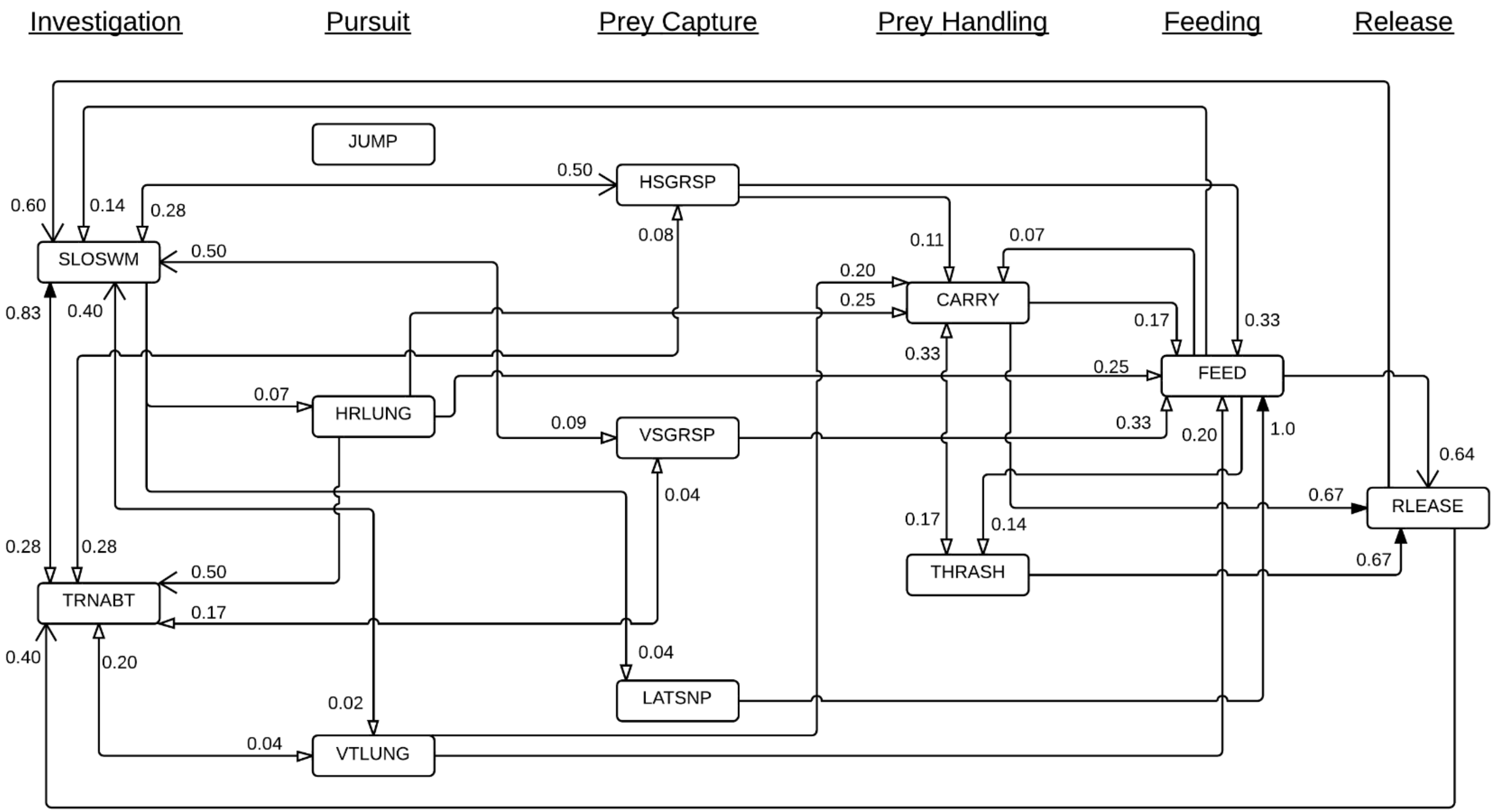

Figure 2B. *Flow diagram of observed behavioral sequences for sharks around the cage diving vessel that consumed bait. Numbers are the probabilities that a behavior will follow the preceding behavior.*

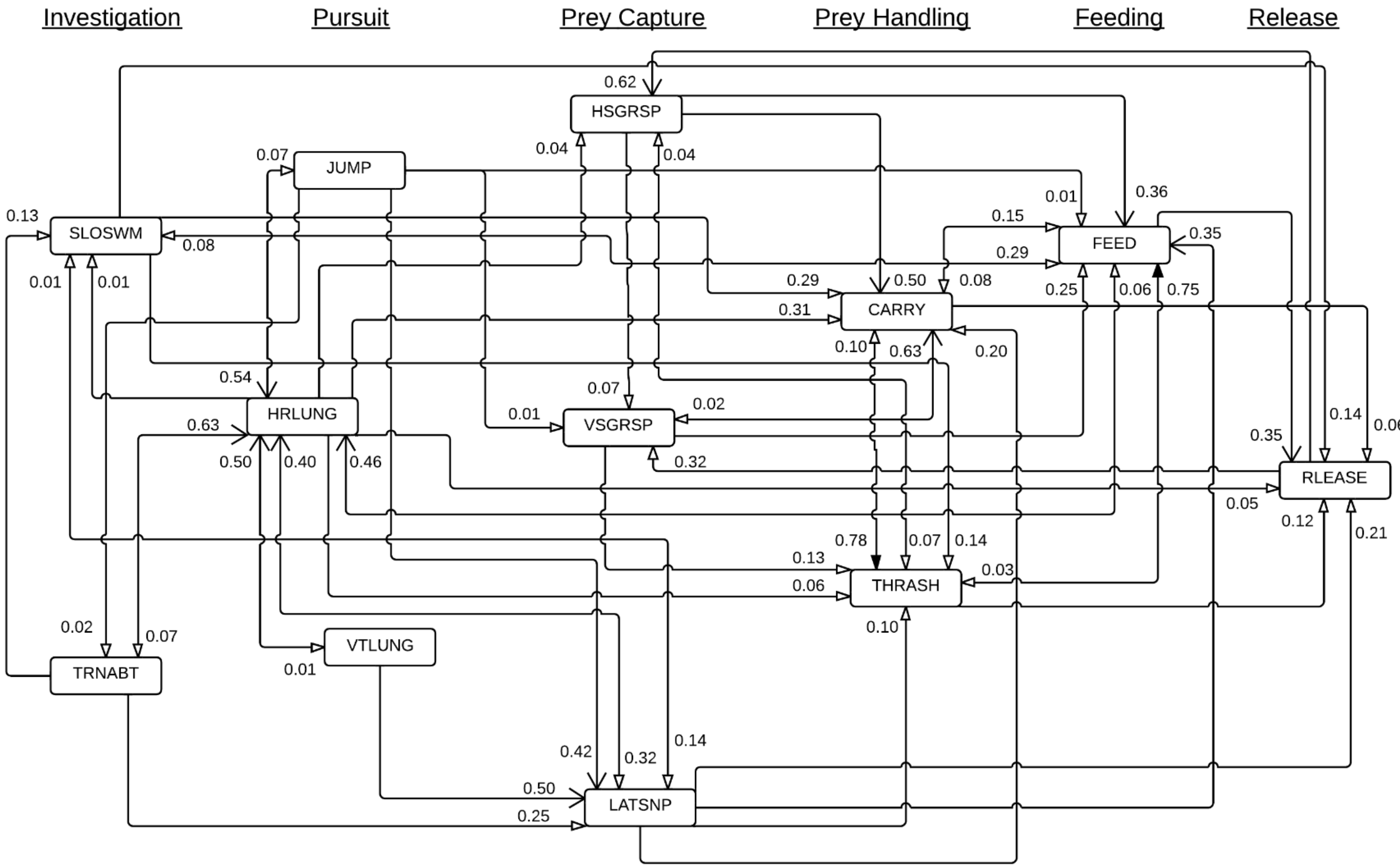

Figure 2C. *Flow diagram of observed behavioral sequences for sharks that preyed upon seals as observed by Martin et al. (2005). Numbers are the probabilities that a behavior will follow the preceding behavior.*

Investigation

During the investigation phase, sharks inspected potential prey with two behaviors: SLOSWM and TRNABT. These behaviors occurred more frequently than any others for both unfed and fed sharks around the cage diving vessel (Fig. 3), with SLOSWM occurring more frequently than TRNABT (Fig. 4). Unfed sharks exhibited TRNABT significantly more often than those that eventually consumed the bait ($q = 6.817$, $p < 0.05$). Regardless of their progress in the predation cycle, unfed and fed sharks frequently returned to investigation behaviors (Fig. 2A, B). Both unfed and fed sharks occasionally mouthed the bait while slowly swimming by at the surface. Investigation behaviors were rarely seen in the natural predatory sequences of Martin sharks, and significantly less often than for both unfed sharks ($q = 74.327$, $p < 0.05$) and fed sharks ($q = 46.853$, $p < 0.05$).

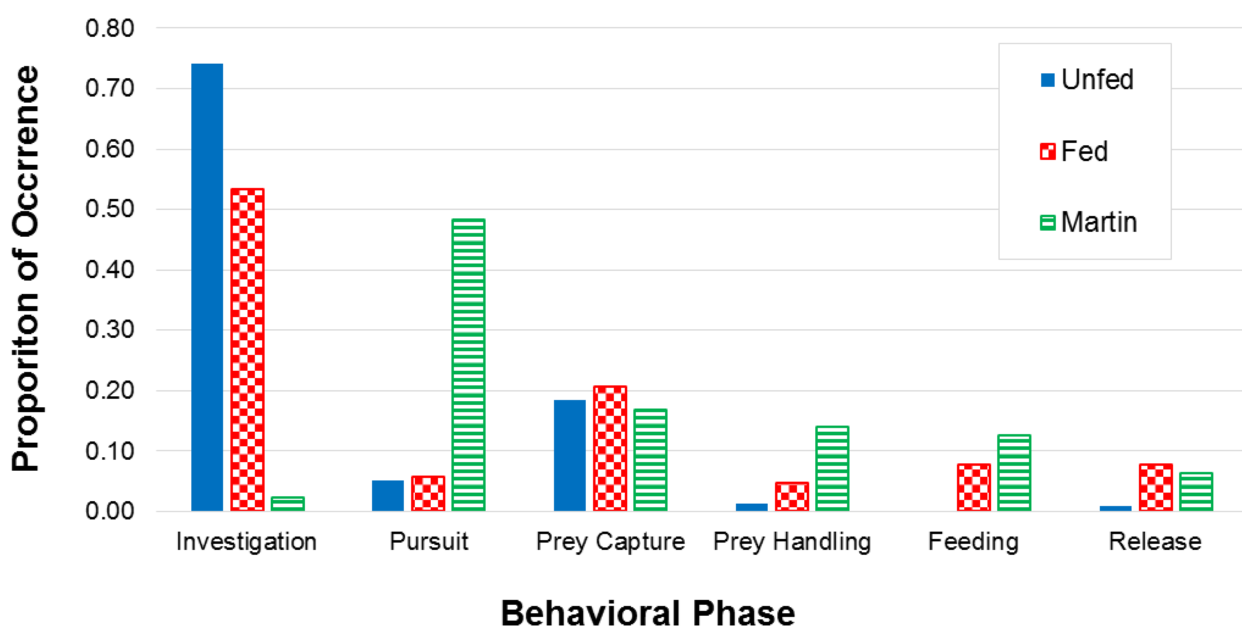

Figure 3. *Proportions of observed behavioral phases in the predation cycles of unfed, fed, and Martin sharks.*

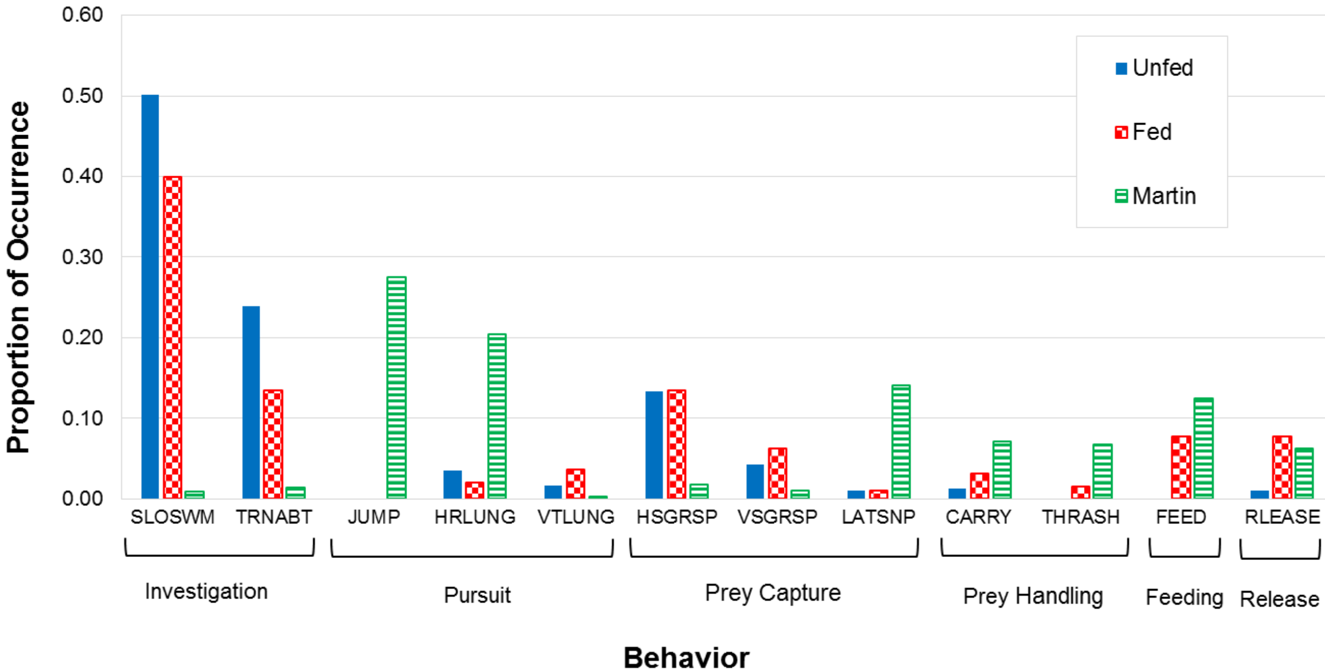

Figure 4. *Proportions of observed behaviors comprising the phases in the predation cycles of unfed, fed, and Martin sharks.*

Pursuit

The pursuit phase of the predation cycle involved an aggressive attack on the potential prey item. This phase included the behaviors JUMP, HRLUNG, and VTLUNG. Unlike the investigation phase, pursuit behaviors occurred most frequently among Martin sharks, and occurred significantly more often than for unfed sharks (q = 45.068, $p < 0.05$) and fed sharks (q = 36.765, $p < 0.05$; Fig. 3). Among pursuit behaviors, JUMP and HRLUNG were the two most frequently observed behaviors in natural predatory sequences of Martin sharks (Fig. 4). Neither unfed sharks nor fed sharks performed JUMP. HRLUNG occurred significantly more often in Martin sharks than both unfed sharks (q = 35.787, $p < 0.05$) and fed sharks (q = 31.940, $p < 0.05$). VTLUNG was rare for all sharks, but fed sharks exhibited the behavior significantly more often than unfed sharks (q = 4.451, $p < 0.05$) and Martin sharks (q = 8.224, $p < 0.05$).

Unfed sharks were generally unsuccessful using pursuit behaviors and often resulted in further investigation (Table 3). Fed sharks that were initially unsuccessful in capturing prey in the pursuit phase also often returned to investigation behaviors. Successful pursuit behaviors led to manipulation of or feeding on the tuna head by fed sharks (Table 4). Martin sharks often followed pursuit behaviors with prey capture behaviors; if unsuccessful, Martin sharks usually continued with additional pursuit behaviors (Table 5).

Prey capture

The prey capture phase resulted in the successful capture of a prey item, and was observed as HSGRSP, VSGRSP, and LATSNP. HSGRSP was the most frequently observed prey capture behavior around the cage diving vessel, and thus was seen more often in both unfed sharks (q = 14.122, $p < 0.05$) and fed sharks (q = 13.278, $p < 0.05$) than Martin sharks (Fig. 4). Martin sharks, however, performed LATSNP significantly more often than both unfed sharks (q = 32.718, $p <$ 0.05) and fed sharks (q = 26.481, $p < 0.05$). VSGRSP was rare in all data sets with the lowest frequency occurring in the Martin sharks; both unfed sharks (q = 5.065, $p < 0.05$) and fed sharks (q = 7.966, $p < 0.05$) performed VSGRSP significantly more often than Martin sharks.

Although the frequency of prey capture behaviors was similar across all shark data sets (Fig. 3), there were distinct differences within the behavioral observations. The low frequency of pursuit behaviors in unfed and fed sharks resulted in these sharks taking the bait while slowly swimming by (SLOSWM) during investigation. For unfed sharks, the mouthing of the tuna head was followed by further investigation behaviors (Table 3). Fed sharks occasionally released the bait, having fed on the bait during a different sequence, and performed further investigation behaviors. In other instances, sharks immediately fed on the bait (Table 4). Martin sharks generally captured the prey following a pursuit behavior and then continued to manipulate or feed upon the prey (Table 5).

Prey handling

The prey handling phase of the predation cycle involved the manipulation of the prey item after capture and was comprised of two behaviors: CARRY and THRASH. Prey handling behaviors were seen more frequently in Martin sharks than both unfed (q = 22.094, $p < 0.05$) and fed sharks (q = 11.255, $p < 0.05$; Fig. 3). Sharks interacting with the bait usually only performed CARRY, but Martin sharks performed CARRY more frequently than both unfed sharks (q = 19.298, $p < 0.05$) and fed sharks (q = 11.522, $p < 0.05$; Fig. 4). THRASH was rarely seen in fed sharks and not at all in unfed sharks.

Martin sharks usually exhibited prey handling behaviors after prey capture, with CARRY often preceding THRASH (Table 5). Fed sharks that managed to grab the bait with a lunge (pursuit behavior) occasionally carried the bait a short distance in their mouths before releasing it (Table 4). Unfed sharks rarely exhibited prey handling behaviors, only occasionally performing CARRY after successful prey capture before releasing the bait (Table 3; Fig. 2A).

Table 3. Probabilities that each individual behavior precedes or follows each other individual behavior for sharks around the cage diving vessel that did not consume bait.

		Subsequent behavior											
		Investigation		Pursuit			Prey Capture			Prey Handling		Feeding	Release
		SLOSWM	TRNABT	JUMP	HRLUNG	VTLUNG	HSGRSP	VSGRSP	LATSNP	CARRY	THRASH	FEED	RLEASE
Behavior	N	84	70	0	11	1	36	3	3	4	0	0	15
Preceding behavior SLOSWM	99		0.58		0.09		0.29	0.02	0.02				
TRNABT	67	0.84			0.01	0.01	0.10	0.01	0.01				
JUMP	0												
HRLUNG	1	1.00											
VTLUNG	4	0.25	0.50		0.25								
HSGRSP	28	0.54	0.36							0.11			
VSGRSP	11	0.73	0.18							0.09			
LATSNP	2	0.50	0.50										
CARRY	4	0.50											0.67
THRASH	0												0.67
FEED	0												0.64
RLEASE	0												

Table 4. Probabilities that each individual behavior precedes or follows each other individual behavior for sharks around the cage diving vessel that consumed bait.

			Subsequent behavior											
			Investigation		Pursuit			Prey Capture			Prey Handling		Feeding	Release
			SLOSWM	TRNABT	JUMP	HRLUNG	VTLUNG	HSGRSP	VSGRSP	LATSNP	CARRY	THRASH	FEED	RLEASE
	Behavior	N	38	25	0	3	2	25	5	2	6	3	15	15
Preceding behavior	SLOSWM	46		0.28		0.07	0.02	0.50	0.09	0.04				
	TRNABT	24	0.83				0.04	0.08	0.04					
	JUMP	0												
	HRLUNG	4		0.50							0.25		0.25	
	VTLUNG	5	0.40	0.20							0.20		0.20	
	HSGRSP	18	0.28	0.28							0.11		0.33	
	VSGRSP	12	0.50	0.17									0.33	
	LATSNP	1											1.00	
	CARRY	6										0.17	0.17	0.67
	THRASH	3									0.33			0.67
	FEED	14	0.14								0.07	0.14		0.64
	RLEASE	5	0.60	0.40										

Table 5. Probabilities that each individual behavior precedes or follows each other individual behavior during predatory attacks on seals (Martin et al. 2005).

			Subsequent behavior											
			Investigation		Pursuit			Prey Capture			Prey Handling		Feeding	Release
			SLOSWM	TRNABT	JUMP	HRLUNG	VTLUNG	HSGRSP	VSGRSP	LATSNP	CARRY	THRASH	FEED	RLEASE
	Behavior	N	6	11	7	156	1	14	8	109	56	53	88	49
Preceding behavior	SLOSWM	7								0.14	0.29	0.14	0.29	0.14
	TRNABT	8	0.13			0.63				0.25				
	JUMP	171		0.02		0.54			0.01	0.42			0.01	
	HRLUNG	102	0.01	0.07	0.07		0.01	0.04		0.32	0.31	0.06	0.06	0.05
	VTLUNG	2				0.50				0.50				
	HSGRSP	14							0.07		0.50	0.07	0.36	
	VSGRSP	8									0.63	0.13	0.25	
	LATSNP	100	0.01			0.40					0.20	0.10	0.35	0.21
	CARRY	54							0.02			0.78	0.15	0.06
	THRASH	52						0.04			0.10		0.75	0.12
	FEED	37	0.08			0.46					0.08	0.03		0.35
	RLEASE	13						0.62	0.38					

Feeding

The feeding phase occurred after a shark captured the prey item, and consisted of successfully removing and ingesting pieces of flesh. Martin sharks most often fed on seals following prey capture and handling behaviors; however, FEED was observed to occur after every behavioral phase except RLEASE, i.e. sharks also fed on seals following investigation and pursuit behaviors (Table 5). FEED frequently preceded HRLUNG and RLEASE. HRLUNG may have occurred during and after feeding due to the seal's attempts to escape. Fed sharks performed FEED less frequently than Martin sharks (Fig. 4) and were likely to feed after prey capture and handling behaviors or lunges (Table 4). Fed sharks generally released the bait after taking a few bites. Occasionally, sharks succeeded in completely removing the tuna head from the bait line and swam away chewing on the bait. Unfed sharks, by definition, did not ingest the bait.

Release

After obtaining the prey item, sharks released the prey, with or without feeding. RLEASE occurred more frequently in fed sharks ($q = 11.678$, $p < 0.05$) and Martin sharks ($q = 18.486$, $p < 0.05$) than unfed sharks (Fig. 4), despite similar frequencies of prey capture. Unfed sharks only released the bait after CARRY (Table 3). For unfed sharks, RLEASE was always the final behavior within a behavioral sequence, i.e. the shark swam away, ending that behavioral sequence after performing RLEASE. Fed sharks released the bait after prey handling behaviors and feeding, and usually returned to investigation behaviors, regardless of consumption (Table 4). Martin sharks most often released seals after feeding, but sometimes RLEASE was observed after LATSNP, which may be due to seal escape during repurchase. Martin sharks always performed prey capture behaviors after RLEASE, supporting this idea (Table 5).

Discussion

Cage diving ecotourism has created an opportunity for people to view sharks in close proximity, while also providing a platform for shark conservation education. However, many people are concerned that cage diving operations may have negative effects on the sharks (Green & Higginbottom 2001; Orams 2002; Johnson & Kock 2006; Laroche 2007). The main concern is that by provisioning bait, sharks will be conditioned to associate boats and humans with food (Green & Higginbottom 2001; Orams 2002; Johnson & Kock 2007; Laroche 2007), potentially fostering aggression toward humans (Green & Higginbottom 2001; Orams 2002). Conversely, sharks may become habituated to the presence of boats and humans, which could make sharks more vulnerable to human impacts and exploitation (Green & Higginbottom 2001; Orams 2002). Furthermore, food provisioning could create a dependence on the bait as an important food source, altering natural predator-prey dynamics within the ecosystem (Green & Higginbottom 2001; Orams 2002). The purpose of this study was to compare the behavior of white sharks around a cage diving vessel in the presence of bait with published observations of natural predatory behavior to determine how cage diving operations impact shark behavior and the implications this may have for shark conservation.

Behavioral differences

Overall, the behavior of white sharks around the cage diving vessel differed from the natural predatory behavior of white sharks hunting seals as observed by Martin et al. (2005) (Fig. 3, 4). The most notable difference was the degree of investigation performed by the sharks. Investigation behaviors were common for sharks around the dive vessel, but rare for sharks actively hunting seals. In addition, sharks interacting with the bait were less aggressive than those hunting seals. The latter commonly initiated an attack with a sudden, vertical breach (JUMP), generally launching the seal into the air as well as the shark itself (Martin et al. 2005). Although sharks hunting seals continued the attack at the surface (e.g. HRLUNG, LATSNP) after the initial breach (Martin et al. 2005), sharks around the cage diving vessel commonly captured the bait with surface grasps, often following investigation behaviors.

Investigation behaviors may dominate around the cage diving vessel as sharks collect sensory cues to determine the potential food value of the bait, as suggested by Strong (1996). Fishes are a common item in a white shark's diet, particularly for juvenile white sharks (Casey & Pratt 1985; Klimley 1985; Fergusson 1996; Hussey et al. 2012), such that investigation of the tuna head bait is not unexpected. Other studies that focused on prey discrimination in white sharks reported observations of similar behavior, with sharks making frequent passes at or near the surface of the water around decoys (Anderson et al. 1996; Strong 1996). Collier et al. (1996) suggested that mouthing (or grasping) is the most practical way for sharks to determine the palatability of a potential prey item, which was commonly observed in this study. Sharks often briefly grasped the bait in their mouths while swimming by (SLOSWM) during investigation. Sharks around the cage diving vessel also frequently returned to investigation behaviors regardless of their progress in the generalized predation cycle.

In the study done by Martin et al. (2005), pursuit behaviors (e.g. JUMP) cued the observers to the occurrence of a predation event. As a result, Martin et al. (2005) reported few investigation behaviors. Natural predatory acts as described by Martin et al. (2005) were initiated by the shark vertically breaching (JUMP) on a seal at the surface, which is consistent with other observations of white shark predation (McCosker 1985; Anderson et al. 1996; Klimley et al. 1996a; Domeier et al. 2012). White sharks generally stalk a seal from below (Anderson et al. 1996; Klimley et al. 1996a; Domeier et al. 2012), recognizing the seal's silhouette as a visual cue for prey (McCosker

1985). Sharks then accelerate toward the seal at the surface, attempting to catch the seal by surprise from behind and below (Ainley et al. 1985; McCosker 1985; Klimley et al. 1996a; Strong 1996). Investigation behaviors may be limited in natural predatory attacks on seals because seals are maneuverable and capable of escaping with sustained rapid porpoising once made aware of the danger (Martin et al. 2005). Investigation behaviors would alert the seal of the shark's presence, reducing the shark's probability of successful prey capture (McCosker 1985; Strong 1996; Martin et al. 2005). The few investigation behaviors observed by Martin et al. (2005) occurred when a shark approached a dead or severely injured seal, which always resulted in feeding.

White shark attacks on seals involved aggressive pursuit behaviors such as breaching (JUMP) and lunging (HRLUNG). Sharks were also more aggressive when handling prey, often thrashing its body from side to side with a seal in its mouth (THRASH). In contrast, interactions with the bait were less common and less aggressive (Fig. 3). Sharks around the cage diving vessel exhibited fewer pursuit behaviors and often did not feed on the bait even when the opportunity was present. For example, there were instances when unfed sharks had the bait in their mouths but did not feed. Fed sharks also often released the bait (RLEASE) after taking a few bites. The lack of aggression in sharks around the cage diving vessel might be attributed to more active hunting at dawn, as described by Martin et al. (2005). Cage diving trips occurred between mid-morning and late afternoon. However, Martin et al. (2005) observed predations throughout the day, until 1830 h, suggesting that the time of behavioral observations is not sufficient to explain the differences between behavior around the dive vessel and natural predations.

Additionally, throughout the cage diving operation, a crew member pulled the bait away from the sharks to try to prevent them from capturing the bait (M. Bromilow, personal observations). Although bait movements were less vigorous than those of a seal, successful capture of the bait would be expected to necessitate a more aggressive attack than observed.

Sharks around the dive vessel most frequently captured the bait using a horizontal grasp (HSGRSP) while swimming past the bait at the surface (SLOSWM). Grasping is not an aggressive behavior, especially when compared to lateral snap. In addition, the frequency at which the bait was released suggests that these grasping behaviors play a role in investigation as opposed to feeding. Strong (1996) also observed a majority of horizontal approaches as white sharks investigated multiple decoys.

White sharks are known to be opportunistic generalist predators (Fergusson 1996; Hussey et al. 2012) for which fishes are an important dietary component (Casey & Pratt 1985; Klimley 1985; Fergusson 1996; Hussey et al. 2012). Nevertheless, the frequent release of the bait (RLEASE) may suggest that the tuna head was unpalatable or undesirable. Observations from previous studies have shown that sharks may reject food thought to be unpalatable. In a behavioral study similar to Martin et al. (2005), Klimley et al. (1996a) observed a white shark approach a decomposed sea lion carcass and take a single bite before rejecting the prey and swimming away, similar to the behavior pattern seen around the cage diving vessel.

In addition, a natural prey population of seals was close to the dive vessel during operation. Pinnipeds are a preferred prey item for white sharks and many studies in different regions of the world have shown that sharks naturally aggregate near seal rookeries to hunt (Ainley et al. 1985; Casey & Pratt 1985; Klimley 1985; Ferreira & Ferreira 1996; Goldman et al. 1996; Klimley & Anderson 1996; Long et al. 1996; Johnson 2003; Domeier et al. 2012; Duffy et al. 2012). Marine mammals, such as pinnipeds, are considered high quality prey due to their high, energy-rich fat content (Klimley et al. 1996a; Le Boeuf & Crocker 1996; Hussey et al. 2012). During this study, a natural predation on a seal was observed from the cage diving vessel, indicating that white sharks continue to feed on these natural prey, even in the presence of cage diving activity and bait that may be easier to catch but of lower quality.

Sharks seek prey using a variety of olfactory, visual, and auditory cues (Gruber & Cohen 1985; McCosker 1985; Anderson et al. 1996; Demski & Northcutt 1996; Strong 1996). Thus, sharks would be expected to explore the vicinity of the cage diving vessel given the large quantities of chum released. However, sharks spent a majority of their time investigating the bait rather than performing aggressive attacking behaviors. Given the results of this study, white sharks were probably attracted to the boat by the chum and then inspected the bait out of curiosity. Interactions with the bait varied among sharks, suggesting that the bait is not an inherent prey item. Sharks appear to make informed decisions about potential prey items on an individual, case-by-case basis.

Cage diving operations as platforms for studying shark behavior

The results of this study indicate significant differences in the predatory behavior of sharks around a cage diving vessel compared to the behavior of sharks in a natural setting. Consequently, studying the predatory behavior of sharks from a cage diving vessel would provide little understanding of the natural predatory behavior of white sharks, aside from illustrating that investigation is presumably a large behavioral component when a new food source is introduced. However, cage diving operations could provide a platform for other behavioral studies of white sharks. Klimley et al. (1996a) observed agonistic interactions between sharks that included a behavior ("side by side") in which sharks swam side by side to size each other up and establish dominance. Generally, the subordinate shark would yield to the larger or more aggressive shark and dart off in another direction. Klimley et al. (1996b) also described "tail slap," a behavior in which a shark slapped its caudal fin at the surface of the water in the direction of another shark, which appeared to discourage the other shark from feeding on the prey. Both of these behaviors were seen from the cage diving vessel throughout this study, suggesting that cage diving operations could provide a platform for studying intraspecific interactions between sharks, such as agonism.

Conservation implications

There are some concerns that cage diving operations can have negative impacts on sharks and the ecosystem in which they live (Green & Higginbottom 2001; Orams 2002; Johnson & Kock 2006; Laroche 2007). First, sharks may become conditioned to the bait used by cage diving operations and as a result, may display more aggression toward humans (Green & Higginbottom 2001; Orams 2002). However, for such conditioning to occur, the reward must be presented often and in a predictable manner (Johnson & Kock 2006), which is generally not the case in cage diving ecotourism. Cage diving companies have to apply for a permit to operate, which prohibits the intentional feeding of sharks and sets a limit on the amount of bait allowed on the boat per trip (DEAT). Therefore, allowing sharks to take the bait is not legal nor is it economical for cage diving companies. In addition, previous studies have shown that sharks adapt to the presence of chum and bait, with responses decreasing over time (Johnson & Kock 2006; Laroche 2007). Other studies have shown that feeding on bait did not increase the amount of time sharks spent around a boat (Johnson & Kock 2006; Laroche 2007). The general lack of interest in the bait in this study also suggests that conditioning is unlikely. Furthermore, sharks around the cage diving vessel were less aggressive toward the bait, suggesting that sharks are not likely to become more aggressive toward humans as a result of cage diving operations. The results of this study do not provide evidence for or against the habituation of white sharks in a cage diving setting.

In terms of broader ecological impacts, white sharks are apex predators that effectively control pinniped populations by predation (McCosker 1985). Orams (2002) suggested that provisioning wildlife tourism, such as cage diving, could negatively affect the ecosystem by diverting sharks from their natural prey and creating a dependency on the bait. The current study provides no evidence to support this idea. The low capture rates and even lower occurrence of feeding on the bait indicate that this food source plays a small role in the diet of the sharks. Thus, as long as cage diving companies prevent sharks from feeding on the bait as much as possible and operate in areas where sharks are naturally present, this tourist attraction appears to have little impact on the sharks. Moreover, cage diving operations could increasingly contribute to the conservation of white sharks as a platform for education and tourism.

Conclusion

The results of this study reveal clear differences in the behavior of white sharks around a cage diving vessel and white sharks in a natural predation setting involving Cape fur seals. Sharks around the dive vessel were less aggressive toward the bait and performed more investigation behaviors than white sharks hunting seals. This suggests that white sharks do not approach cage diving vessels with the intent to feed on the bait, but rather are attracted to the smell of the chum released and then remain around the boat to examine the bait as a potential prey item. Therefore, sharks appear to make a decision to feed on the bait on an individual basis based on their investigation. Sharks were generally uninterested in feeding on the bait, which suggests that conditioning by cage diving operations is unlikely. Additionally, sharks continued to prey upon seals in the midst of cage diving activity, indicating that cage diving does not affect natural predator-prey interactions. Cage diving operations appear to have limited effects on sharks, and can even provide a platform for conservation education and future studies of white sharks, given that government regulations are obeyed and that companies only operate in areas where white sharks are naturally present.

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