Memoirs, Vol. 9, pp. 81–91

Feeding Ethology of the White Shark, *Carcharodon carcharias*

Timothy C. Tricas

Abstract.—Feeding ethology of the white shark, *Carcharodon carcharias* by Timothy C. Tricas. *Southern California Acad. Sci.,* Memoirs, Vol. 9, 1985. Approach and attack behaviors of white sharks, *Carcharodon carcharias,* to bait were documented in the field using cinematographic techniques. The five different approach behaviors were: 1) underwater approach, 2) surface approach, 3) inverted approach, 4) normal underwater pass, and 5) side roll.

Feeding attacks made on food items at the surface involved a pronounced elevation of the head and protraction of the upper jaw out of the oral cavity to inflict the bite. The components that form the feeding action are: 1) snout lift, 2) lower-jaw depression, 3) palatoquadrate protrusion, 4) lower-jaw elevation, and a bout-ending 5) head drop. Time for a complete bite (that included a snout drop) averaged .985 s for a 3.5 m (TL) shark, while a bite action (not including the snout drop) was made in a mean time of .443 s. Maximum gape and palatoquadrate protrusion occurred at mean times of .167 and .307 s, respectively. Sharks also occasionally engulfed small bait by simple depression of the lower jaw.

While feeding actions were clearly stereotyped in their sequence of occurrence, significant temporal differences exist between sharks for total feeding-bout time, between acts for each shark, and between acts among sharks. These results are discussed in light of the current paradigms used to distinguish and classify stereotypic behaviors.

A major factor for the evolutionary success of sharks as predators in marine ecosystems is the diversity of feeding mechanisms found within the group. From a morphological standpoint, this functional diversity in feeding is determined largely by the structural characteristics of the upper jaw (palatoquadrate), lower jaw (mandibular), and suspensorium (hyomandibular) cartilages. Because of the relatively simple structure of the elasmobranch jaw, the spatial arrangements of these three components and their articulations to the cranium are also important in the expression of actions that characterize different feeding modes (Moss 1972, 1977).

Almost all previous studies on feeding adaptations in sharks entailed descriptions of skeletal, connective, and muscle tissues from dead specimens (e.g., Luther 1909; Haller 1926), and few have addressed the functional morphology of the shark jaw in contexts other than those used for comparative or phylogenetic applications (e.g., Compagno 1973, 1977). From a behavioral point of view, little is known about jaw movements in relation to predation. Studies that deal with preserved specimens provide only inferential data on feeding mechanics and therefore little is known on sequential and temporal relationships of the structures involved in feeding. In the best known exception, Moss (1972) studied the feeding mechanisms of living and fresh-collected carcharhinid sharks using electrical muscle stimulation and cinematography. He showed that within a species, upper jaw protraction can occur in different ways that relate to feeding on prey of different sizes and disposition. Although the existence of variable feeding modes within species is well known (Springer 1961; Budker 1971; Tricas 1979, 1982) information on behavioral stereotypy for specific feeding patterns is tentative.

This paper presents an ethological analysis of the feeding behavior of white sharks, *Carcharodon carcharias,* and examines the sequential and temporal variability of feeding actions and their components. This species is the largest flesh-eating shark in the world and exhibits feeding displays amenable to close observation and analyses. Its predatory and attack behaviors are of particular relevance since it feeds on a variety of marine mammals (including some endangered species) and is also known to attack humans.

Methods

The feeding behavior of white sharks was documented during January 1980 in waters near Dangerous Reef, South Australia (approximately 136°13′E, 34°47′S). Topside observations were made from the deck of a 20-m-long vessel anchored in 20–30 m of water just off the north shore of the two small islands. Underwater observations were made using scuba and protective steel cages. Water surface temperature was approximately 21°C. Sharks were attracted using tuna and meat by-products as chum. Behaviors associated with feeding were photographed using Actionmaster 500 ciné cameras and 7247 Kodak color reversal film shot at either 24 (normal) or 200 (high speed) frames per second. A more general analysis of the feeding behavior is presented elsewhere (Tricas and McCosker 1984). Additional feeding behaviors were photographed with 35 mm still cameras. To determine sequential and temporal characteristics of the behaviors, frame by frame analyses of movie films were performed on a digital Moviola film editor.

Documented feeding behavior was separated into two groups: 1) behaviors used to approach, and 2) attack patterns used to bite and engulf baits. Qualitative descriptions of approach patterns were obtained by direct observation and review of film footage. Attack behavior was further analyzed by subdivision into acts that composed an attack pattern. The definition of these behavioral subunits was based upon two criteria. First, an act must show points of initiation and termination that could be measured on a temporal scale. Second, and more subjective, was that each act must have appeared to characterize individual neuro-muscular actions. This qualification was based largely on descriptions of muscle control of jaw movements from other studies (e.g., Moss 1972).

Standard parametric and non-parametric statistical tests were performed on data from the film analyses for time durations of the attack behavior and its component acts. For estimates of variability, a coefficient of variation (CV) was generated for durations of feeding bouts and each act.

$$CV = \frac{SD \times 100}{\bar{X}},$$

where $\bar{X}$ = mean duration and SD = standard deviation. A high CV value indicates a relatively high degree of temporal variability for a behavior.

An index of stereotypy (ST) was also determined for feeding action patterns and component acts where,

$$ST = \frac{100}{CV + 1}.$$

This index described the relative degree of temporal constancy for the act or action pattern considered. High values indicate a relatively high degree of stereotypy. The use and limitations of these indices were discussed by Barlow (1977).

Results

Approach Behaviors

Sharks approached baits in five distinct ways depending on bait size, location relative to the surface, and motivational state of the sharks. Three modes were most commonly used to advance on bait floating on the surface.

1) Underwater approach.—Most attacks at the surface were made from this approach pattern. In this behavior, sharks swam just below the surface until approximately 1 m from the bait and then attacked by deflecting the head upward and emerging out of the water to either swallow or bite baits.

2) Surface-charge.—Sharks often approached bait by swimming partially above the surface. This approach was characterized by a rapid rush towards the bait and created considerable surface disturbance (i.e., splashing) before the attack was actually made.

3) Inverted approach.—When advancing towards bait at the surface, sharks often rolled over 180 degrees and swam with ventral side up. Generally, sharks that showed this type of approach were in relatively low states of excitement and had been feeding in the area for some time.

Sharks took submerged bait in two additional approach modes.

4) Normal underwater pass.—This approach pattern consisted of swimming below the surface (>1 m) towards the bait at a normal speed.

5) Side roll.—Sharks directly approached baits under the surface, but rolled approximately 60 degrees from normal, took the prey, and returned to an upright swimming attitude.

Ethology of the Attack

Underwater attacks.—Within the various approach modes, sharks exhibited different patterns of attacks on food items once within striking range. In attacks made from approaches to bait suspended beneath the surface (approximately >1 m), the mouth was opened by a slight elevation of the snout and full depression of the lower jaw. This feeding pattern was relatively subtle and involved no protrusion of the upper jaw. Although most commonly observed underwater, this form of attack was coupled at times with all five different approach modes. Some sharks occasionally displayed upper jaw protrusion during bites made underwater. These usually occurred when sharks vigorously bit large pieces of bait, or snapped their jaws while abreast of the cages.

Surface attacks.—The most aggressive and observable attack behavior occurred when sharks took bait at the surface from underwater or surface-charge approaches. Sharks approached just below the surface until approximately 1 m away

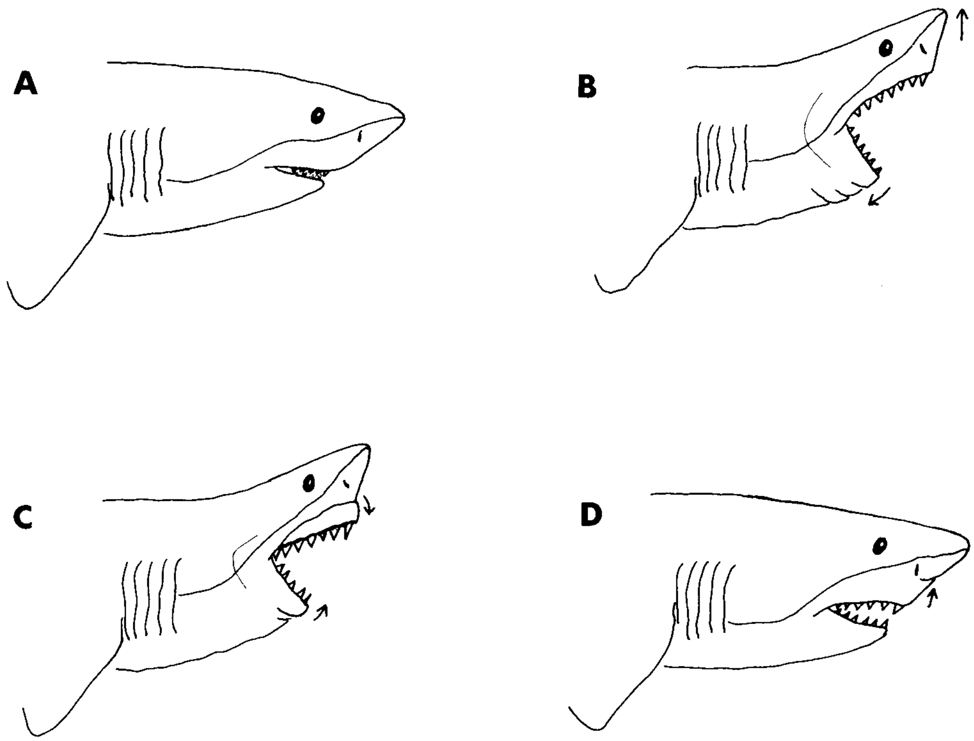

Fig. 1. The surface attack behavior pattern. A) Shark just prior to initiation of feeding action. Snout and lower jaw are at normal resting position. B) Snout lift and lower jaw depression result in maximum gape. C) Palatoquadrate protrusion rotates upper jaw forward and downward exposing upper teeth. Lower jaw moves forward and upward. D) Snout drop, which occurs at the end of a feeding bout, results in return of upper jaw to its normal juxtaposition beneath the cranium. Arrows indicate direction of jaw movements.

from the bait and lunged out of the water to attack. The most frequent and vigorous attacks involved elevation of the head and protrusion of the upper jaw from the oral cavity thus swallowing (small) or biting (large) baits with its jaws. This pattern has been observed when sharks attacked pinnipeds and humans (Tricas and McCosker 1984).

The "surface attack" involved five discrete behavioral acts coupled in a fixed sequence of occurrence (Figs. 1 and 2).

1) Snout lift.—The initiation of a feeding action was marked by elevation of the head by flexion just posterior to the occiput.

2) Lower-jaw depression.—This act involved a drop of the lower jaw, occurred concurrently with the snout lift, and resulted in expansion of the mouth.

3) Palatoquadrate protrusion.—Once the mouth was fully opened, the upper jaw disassociated from its sub-cranial position and rotated forward and downward out of the oral cavity. This initiated the closing action of the mouth and fully exposed the teeth of the upper jaw.

4) Lower-jaw elevation.—Concurrent with palatoquadrate protrusion, the lower jaw began an antero-dorsal (upward) motion. These two acts collectively closed the jaws.

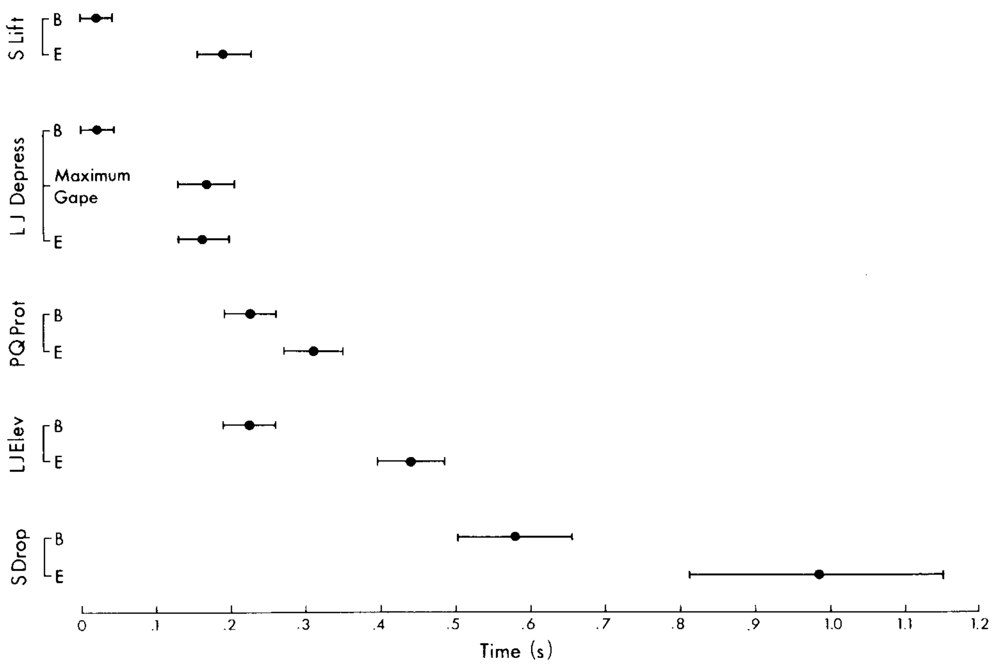

Fig. 2. Timing of feeding actions for eleven bites made by a 3.5 m (TL) white shark (#2). Mean times indicated by points. Horizontal lines show 95% confidence limits. Legend: B = begin, Depress = depression, E = end, Elev = elevation, LJ = lower jaw, Max = maximum, PQ Prot = palatoquadrate (upper jaw) protrusion, S = snout.

5) Snout drop.—The occurrence of this act marked the termination of a feeding bout. The snout drop was characterized by lowering of the head and snout, and a retraction of the palatoquadrate cartilage to its original position ventral to the cranium. During multiple-bite bouts, the snout remained elevated until the last bite was inflicted.

Variability in durations for a complete bite action between three sharks is shown in Table 1. Mean times ranged from .264 to .740 s and were significantly different (Kruskal-Wallis non-parametric one-way analysis of variance test, $P < .005$). These subjects also showed different levels of stereotypy with the smallest shark being the least variable in duration for a complete bite. Comparisons of mean durations and stereotypy for each act for two sharks are given in Table 2. The ranked sequence for mean duration of each act is shown in Figure 3, and was the same for both sharks. The act of shortest duration was palatoquadrate protrusion, while snout drop was the longest. Variability within acts however was not similar between individual sharks as indicated by index of stereotypy ranks shown in Figure 3. Of the four sequence-linked acts (exclusive of the snout drop), palatoquadrate protrusion showed the least variability for shark #2, while the most for shark #4. Snout drop showed the greatest variability thus lowest stereotypy in duration for both sharks, which reflects its non-integral part in a bite action.

While the sequence of acts did not vary among different sharks, significant durational differences exist between acts within each shark (Table 2) and between

Table 1. Stereotypy (ST) of "surface attack" feeding pattern for 3 white sharks. Snout drop act not included in analysis due to variability in its occurrence. Shark total lengths (TL) are estimates.

Shark ID no. and (TL)	Number of bites	Range	Mean	SD	CV%	ST
2 (3.5)	20	.210–1.540	.540	.331	58.5	1.7
4 (3.0)	7	.225–.295	.264	.028	10.8	8.5
5 (3.5)	4	.542–1.083	.740	.239	32.3	3.0

some acts among sharks as seen in Table 3. In the latter case, no significant differences were detected in mean duration for the lower jaw depression or palatoquadrate protrusion acts.

Discussion

This study focuses on two aspects of white shark predatory behavior that deal with interactions after prey detection. The first classifies different modes of approach in terms of the shark's spatial orientation to the location of the prey. The second addresses proximate patterns of prey capture and consumption, and describes different behavioral, spatial, and temporal characteristics of biting. A complete understanding of white shark predatory behavior must include other relevant aspects that relate to motivation, search patterns, prey detection and recognition, prey selection, and capture. Some of these were addressed by Tricas and McCosker (1984).

Although approach and capture patterns are intimately linked, it is appropriate to separate them for analysis since each is composed of distinct independent behaviors. For example, sharks that took bait by the highly aggressive 'surface attack' pattern, often advanced on prey from either surface charges or underwater approaches. Similarly, different capture behaviors were observed among sharks

Table 2. Comparisons of stereotypy for individual feeding acts for two white sharks. Mean act durations for each shark are significantly different (Kruskal-Wallis test).

Act	Range (s)	Mean (s)	SD	CV	ST
Shark #2 (TL = 3.5 m, n = 11)					
Snout Lift	.083–.208	.171	.054	31.9	3.1
LJ Depress	.083–.292	.140	.057	40.7	2.4
PQ Prot	.083–.125	.084	.001	.8	54.9
LJ Elev	.167–.292	.220	.046	20.9	4.6
Snout Drop	.292–1.041	.405	.230	56.8	1.7
				$P < .001$	
Shark #4 (TL = 3.0 m, n = 7)					
Snout Lift	.090–.170	.118	.027	22.7	4.2
LJ Depress	.070–.145	.113	.029	25.3	3.8
PQ Prot	.040–.085	.064	.019	29.6	3.2
LJ Elev	.095–.150	.121	.020	16.3	5.8
Snout Drop	.055–.240	.159	.073	45.7	2.1
				$P < .025$	

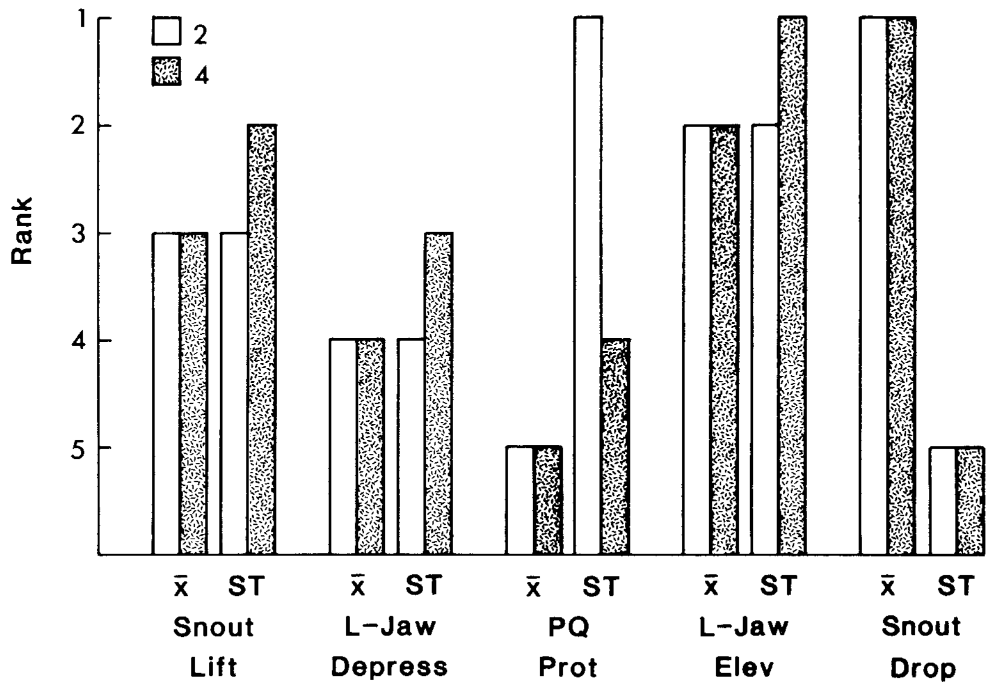

Fig. 3. Comparison of ranked mean durations (x̄) and indices of stereotypy (ST) for acts that compose the surface feeding attack behavior. Shark #2 = open bars; shark #4 = shaded bars.

that used the same approach mode. This was evident when some sharks approached from underwater but engulfed prey by either a slight opening of the mouth or a full surface attack.

Sets of these behaviors were shown both among different sharks and within the same individuals. Generally, the most vigorous attacks were made when sharks first arrived at the baiting site and were probably in a hunger-motivated state. After numerous feedings by an individual, the active bite attack behavior (that involved upper jaw protrusion) often transgressed to the simple swallowing of pieces of bait. This change in attack behavior may be due to satiation. Some of the same sharks also rolled ventrally to approach and ingest small pieces of bait ingested by lower-jaw depression alone. Pratt et al. (1982) observed white sharks feeding on a large whale carcass by first turning (= approaching) ventral-surface-up to set the teeth and then rolling upright to cut a clean mouthful of blubber. This behavior was observed three times (probably among different sharks) and was seen only during attacks at the waterline. They also observed an attack from an upright swimming position (= the surface attack). Unfortunately, very large baits were not available in the present study to experimentally scrutinize differences in feeding actions between large and small prey. It appears however that specific approach and attack behaviors may be a function of motivational, prey size, and prey position factors.

In spite of the variability in linkage of specific approach and attack behaviors, some associations were more frequent than others. The most common co-occurrence was the underwater approach and the surface attack. A similar recurrent

Table 3. Comparison of mean durations of feeding acts that comprise a "surface attack" in two white sharks (#2 and #4). Probabilities given for parametric (analysis of variance) and non-parametric (Mann-Whitney U-test) tests. Observations: shark #2, n = 11; shark #4, n = 7. Legend: ns = not significant; * = $P < .05$, ** = $P < .025$, *** = $P < .001$; m = modified analysis of variance for unequal means (see Sokal and Rohlf, 1969). Act legend as for Figure 2.

Act	F	Probability	
		Anova	U-test
S Lift	7.72 m	*	**
LJ Depress	.84	ns	ns
PQ Prot	2.63 m	ns	ns
LJ Elev	39.51 m	*	***
S Drop	10.91 m	**	***
Max Gape	6.29 m	*	**

association was observed when sharks fed on submerged baits after approaching by normal underwater passes and using a simple lowering of the jaw to engulf the bait.

The Surface Attack—A Patterned Behavior

The need for defining shark behaviors is clear, but because they are rarely addressed in quantified ways they are often difficult to characterize and compare. The problems associated with identification of action patterns and their behavioral "units" are not new and the solutions still in debate. Barlow (1968, 1977) reviewed the terminological problems and proposed the term "modal action pattern" (MAP) which avoids the interpretive and semantic constraints inherent in the long-used term "fixed action pattern" and other classifications that infer instinctive or innate origins of behaviors. Of the many properties proposed by behaviorists to identify motor patterns, a set of major criteria can be defined (see Schleidt 1974; Barlow 1977 for review). The action pattern must 1) appear stereotyped, 2) be a product of central nervous system processes rather than a simple reflex, 3) once triggered be independent of environmental feedback, 4) generally have a more variable taxic component used for orientation prior to expression of the action pattern, and 5) be widely distributed among individuals of a population (i.e., be heritable).

The surface attack behavior and its components are clearly stereotyped in nature. The sequence of each act was invariably linked to the preceding one, and the order of occurrence was fixed. Within individual sharks, each component had a narrow range of non-overlapping temporal limits. Strict spatial relationships between acts also exist, although it was not possible to measure these because of varying observational perspectives and the lack of suitable scaling during film analyses.

The apparent positive relationship between shark size and increasing time duration of bites and individual acts (Tables I and II) may be a result of biomechanical phenomena related to movements of increasing mass, and such physical limiting factors may set constraints on the evolution of certain predatory modes. It is also possible that durational differences between sharks for specific acts were due to the use of different muscle groups that cause the same feeding expression. For example, palatoquadrate protraction could result from various combinations of quadratomandibularis, preorbitalis, and levator hyomandibuli/palatoquadratii muscle actions in relation to food position, size, or density (see Moss 1972). Electromyographic monitoring during feeding would provide information on muscle activity involved in specific feeding actions.

The complete attack action pattern involved sets of numerous muscles (see Moss 1972) and is not a simple reflex. Once elicited, the behavior continued to its completion often in the presence of obstructions (e.g., cages, boat, poles, lines) and there was no overt indication of guidance of the behavior by sensory feedback. This observation by itself however does not eliminate possible involvement of proprioceptive feedback. Possible input by proprioceptors on the patterning of acts could be tested by local narcotization of these sites around the mouth and snout, and changes in feeding action patterns observed.

Additional arguments for designation as a MAP could be made if the action pattern could be evoked by direct stimulation of a releasing center in the shark's brain. Demski (1977) showed that biting and mouthing were produced by electrical stimulation of the inferior lobe of the hypothalamus in the nurse shark, *Ginglymostoma cirratum*. Unfortunately, no ethological description of the behavior was provided.

Action patterns are generally associated with orientation movements or taxes that serve to position the animal for delivery of the behavior (see Eibl-Eibesfeldt 1970). Much of the variability for the behavior is expressed in the taxic phase and often is the primary means of adapting to various environmental situations. For the white shark, the orienting movement is seen in the various approach behaviors to the prey, each of which has particular advantages in different situations. For example, the underwater approach is much more likely to result in a surprise attack on a basking pinniped than is a thrashing surface approach. Use of the most appropriate mode also allows the shark to position the head to deliver the most effective bite.

The surface attack behavior was observed in at least six different sharks in this study, in different white sharks by Pratt et al. (1982), and has also been widely recorded (although not analyzed) by commercial and popular cinematographers. Based upon the widespread documentation, it is very likely that this attack behavior occurs in all members of the species (i.e., is "species typical").

Adaptiveness of Predatory Behaviors

The diversity of approach and attack behaviors seen in *Carcharodon* may serve an ontogenetic function to maximize predatory success. In their summary of the food habits of white sharks, Tricas and McCosker (1984) found that individuals less than about 3 m (TL) fed primarily on fish prey while larger sharks preferred marine mammals. The authors attributed this separation of food habits to differences in tooth morphology and suggested that each tooth shape was better adapted for feeding on the different prey types. Correlations of specific attack behaviors with various prey might also be predicted. The predominant posterior-ventral location of bite wounds on pinnipeds (Tricas and McCosker 1984; McCosker, 1985) suggest attacks to be directed from beneath and behind a floating or basking prey. Similar approach patterns were reported on humans (Miller and Collier 1980) and porpoises (Arnold 1972), and generally involve jaw protrusion as in the surface attack behavior. For smaller sharks, protrusion of the upper jaw may be less efficient than a quick drop of the lower jaw to engulf small fish prey. Rapid depression of the lower jaw may also function to engulf benthic prey through suction created by buccal expansion. Suction feeding has been reported for other species of sharks (Moss 1977; Tricas 1982), and may be the primary means by which small white sharks engulf benthic fish like the cabezon *Scorpaenichthys marmoratus* (see Tricas and McCosker 1984).

There is evidence that first attacks on large mammals function to wound or kill rather than feed, and reduce risk of injury to the shark from a struggling or fighting prey (Tricas and McCosker 1984; McCosker 1985). Once prey is rendered harmless, subsequent feeding attacks often involve behaviors of prolonged contact like head shaking or twisting. Selective pressures to maximize predatory success must also direct evolution of these ancillary behaviors and undoubtedly contribute to the overall pattern and strategy of the feeding attack for white sharks.

Acknowledgments

I thank Al Giddings (Ocean Films, Ltd.) for the opportunity to work with these sharks in Australia, and for his films used in the behavioral analyses. John E. McCosker (California Academy of Sciences) provided helpful field assistance and many stimulating discussions on the behavior of white sharks. I also thank an anonymous reviewer for helpful comments on the manuscript. S. Nakamura (University of Hawaii) patiently prepared Figure 1, and my wife, Helen, provided endless encouragement, editing, and understanding.

Literature Cited

Arnold, P. W. 1972. Predation on harbour porpoise, *Phocoena phocoena,* by a white shark, *Carcharodon carcharias.* J. Fish. Res. Bd. Canada, 29(8):1213–1214.

Barlow, G. W. 1977. Modal action patterns. *In* How animals communicate. (T. A. Sebeok, ed.), Indiana Univ. Press, Bloomington.

———. 1968. Ethological units of behavior. Pp. 217–232 *in* The central nervous system and fish behavior. (D. Ingle, ed.), Univ. Chicago Press, Chicago.

Budker, P. 1971. The life of sharks. Columbia Univ. Press, New York, 222 pp.

Compagno, L. J. V. 1973. Interrelationships of living elasmobranchs. *In* Interrelationships of fishes. (P. H. Greenwood, R. S. Miles, and C. Patterson, eds.), supp. 1, Zool. J. Linnean Soc., 53: 15–61.

———. 1977. Phyletic relationships of living sharks and rays. Amer. Zool., 17:303–322.

Demski, L. S. 1977. Electrical stimulation of the shark brain. Amer. Zool., 17:487–500.

Eibl-Eibesfeldt, I. 1970. Ethology: the biology of behavior. Holt, Rinehart and Winston, New York, 530 pp.

Haller, G. 1926. Uber die Entwichlung, den Bau und die Mechanik des Kieferapparates des Dornhais (*Acanthias vulgaris*). Z. Mikrosk. Anat. Forsch., 5:389–411.

Luther, A. F. 1909. Untersuchungen über die vom N. trigeminus innervierte Musculator der Selachier (Haie und Rochen) unter Berücksichtigung ihrer Beziehungen zu benachbarten Organen. Acta Soc. Sci. Fenn., 36:1–176.

McCosker, John E. 1985. White Shark Attack Behavior: Observations of and Speculations About Predator and Prey Strategies. Southern California Acad. Sci., Memoirs #9. Pp. 123–135.

Miller, D. J., and R. S. Collier. 1980. Shark attacks in California and Oregon, 1926–1979. Calif. Fish Game, 67:76–104.

Moss, S. A. 1972. The feeding mechanisms of sharks of the family Carcharhinidae. J. Zool. Lond., 167:423–436.

———. 1977. Feeding mechanism of sharks. Am. Zool., 17:355–364.

Pratt, H. L., J. G. Casey, and R. B. Conklin. 1982. Observations on large white sharks, *Carcharodon carcharias,* off Long Island, New York. Fish Bull., U.S., 80:153–156.

Schleidt, W. M. 1974. How "fixed" is the fixed action pattern? Z. Tierpsychol., 36:184–211.

Sokal, R. R., and F. J. Rohlf. 1969. Biometry. Freeman and Co., San Francisco, 776 pp.

Springer, S. 1961. Dynamics of the feeding mechanism of large galeoid sharks. Am. Zool., 1:183–185.

Tricas, T. C. 1979. Relationships of the blue shark, *Prionace glauca,* and its prey species near Santa Catalina Island, California. Fish Bull., U.S., 77:175–182.

———. 1982. Bioelectric-mediated predation by swell sharks, *Cephaloscyllium ventriosum.* Copeia, 1982(4):948–952.

Tricas, T. C., and J. E. McCosker. 1984. Predatory behavior of the white shark, *Carcharodon carcharias,* with notes on its biology. Proc. Calif. Acad. Sci., 14:221–238.

Accepted for publication 14 May 1984.

Department of Zoology, University of Hawaii at Manoa, Honolulu, Hawaii 96822.