EXPERIMENTAL SCAVENGING PREFERENCE FOR THE ADULT WHITE SHARK, CARCHARODON CARCHARIAS

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INTRODUCTION

White sharks, Carcharodon carcharias, are opportunistic predators and scavengers, consuming a wide variety of prey to meet their caloric requirements. As juveniles, the white shark diet consists mainly of nearshore fishes while marine mammals make up a significant portion of the adult diet (Ainley et al. 1981, Tricas and McCosker 1984, McCosker 1985, Klimley 1985, Klimley et al. 1996, Estrada et al. 2006). In addition to predation on live mammals, adult white sharks are known to scavenge marine mammal carcasses (Carey et al. 1982; Pratt et al. 1982; Casey and Pratt 1985; Long and Jones 1996; Curtis et al. 2006; Dicken 2008); an event thought to be an important part of the ecology of these large predators (Carey et al. 1982, Long and Jones 1996). Although marine mammals have long been considered important only to adult white sharks, young of the year and juvenile white sharks have recently been observed scavenging a decomposing humpback whale carcass (Dicken 2008).

Guadalupe Island is known for its seasonal white shark population, which is present from August to February, with some sharks remaining into May (Domeier and Nasby-Lucas 2007, Domeier and Nasby-Lucas in press). The Island is host to several potential white shark prey species, including seasonal and resident populations of both large pelagic teleosts and marine mammals. Fishes include yellowfin tuna, Thunnus albacares, bluefin tuna (historically but not presently), Thunnus thynnus, and yellowtail, Seriola lalandi; marine mammals include California sea lion, Zalophus californianus, Guadalupe fur seal, Arctocephalus townsendi, and northern elephant seal, Mirounga angustirostris (Walford 1974, Hanan and Sisson 2001). Beaked whales (likely Beradius bairdii, but unconfirmed) and the large squid, Dosidicus gigas, have also been routinely observed at the island (this study).

A research expedition to study the white shark population off of Isla Guadalupe, Mexico (412 km south of San Diego, California) provided a unique opportunity to study the scavenging preferences and feeding behavior of adult white sharks. The opportunistic discovery of a decomposing, but otherwise intact, sea lion carcass enabled us to devise an experiment that allowed adult white sharks to choose between the carcasses of two prey types common to Guadalupe Island: the California sea lion and yellowfin tuna. This brief communication reports on observations made during

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repeated, controlled white shark scavenging events.

MATERIALS AND METHODS

Carcass preference experiments were performed on 24 August 2004, near the northeast end of Guadalupe Island in 45 m of water. White sharks were attracted to the anchored 15m R/V Malolo by chumming with beef blood and tuna carcasses. Blood was poured into a flow-through seawater system where it was diluted and pumped into the surrounding water, while the tuna carcasses were tethered by the caudle peduncle and buoyed near the vessel.

Upon the appearance of the first white shark, a fresh tuna carcass and the decomposing sea lion carcass were placed in the water. Each carcass was tethered to opposite corners of the vessel’s stern, using 6 m of 6 mm diameter polypropylene line; the strong current held each bait approximately the same distance from the boat. Scavenging behavior was scored by documenting all interactions sharks had with the carcasses. Klimley et al. (1996) defined many white shark behaviors associated with feeding events and here we attempt to use some of his terminology for the purpose of clarity and continuity. Directed movements in which a shark came within 1 m of a carcass were defined as investigations. Physical contact between a shark’s mouth and a carcass was defined as contact. Grasping of the carcass in the shark’s mouth without the removal of flesh was defined as mouthing (per Klimely 1996), and events that resulted in flesh being separated from the carcass and swallowed was defined as a feeding event.

RESULTS

Four adult white sharks, ranging in size from approximately 3.5 to 4 m, were attracted to the experiment over a period of 4 hours. The sharks approached from the down current direction until they discovered the source of the attractant, after which they circled the boat and carcasses both at the surface and below the surface. Swimming was deliberate and relatively slow, even when approaching the carcasses to feed. Thirty-eight interactions between sharks and carcasses were observed. The tuna carcass solicited twice as many investigations as the sea lion carcass and a higher percentage of investigations that resulted in physical contact between the shark’s mouth and the carcass (Table 1). All physical contact between a shark and a tuna carcass resulted in a feeding event, while the sea lion carcass solicited mouthing but never a feeding event (Table 1; Figures 1 and 2).

<table>
<thead>
<tr>
<th>Carcass Type</th>
<th>Investigations</th>
<th>Contacts</th>
<th>Mouthings</th>
<th>Feeding Events</th>
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<td>Yellowfin tuna</td>
<td>16</td>
<td>10</td>
<td>0</td>
<td>10</td>
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<tr>
<td>Sea lion</td>
<td>8</td>
<td>4</td>
<td>4</td>
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Table 1. White shark carcass preference data.
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BIOENERGETIC MODELING EVIDENCE FOR A CONTEXT-DEPENDENT ROLE OF FOOD LIMITATION IN CALIFORNIA'S SACRAMENTO-SAN JOAQUIN DELTA

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Striped bass, *Morone saxatilis*, and largemouth bass, *Micropterus salmoides*, are two of the top piscivores in California's San Francisco Estuary. The relative abundance of age-0 striped bass has plummeted since the late 1960s, whereas the abundance of largemouth bass has increased since the early 1990s. Major changes to the estuarine food web have made it a likely place for significant striped bass food limitation, and despite their population increase, there is evidence that young largemouth bass might also be chronically food-limited. Food limitation can be thought of as a context-dependent stressor, meaning that population-level consequences of food limitation are discernable only when they are severe enough to override other factors influencing the growth and mortality of young fishes. The purpose of this study was to clarify the role that food limitation plays in the early life history of striped bass and largemouth bass. I used a combination of previously published beach seine data and bioenergetic modeling (BEM) to evaluate the question, which species is likely more food-limited during its first growing season? I hypothesized that age-0 striped bass would show evidence of greater food limitation than largemouth bass (as indexed by realized vs. potential growth). The BEM simulations predicted that largemouth bass would grow larger than striped bass given the water temperature histories these fish experienced in the Sacramento-San Joaquin Delta during summer-autumn 2001 and 2003. However, the striped bass collected during autumn were larger than the largemouth bass and had thus performed better relative to BEM predictions. I conclude that age-0 striped bass were less food limited than age-0 largemouth bass in these recent years. As discussed, the upsurge of largemouth bass is likely the outcome of low survival in an expanding area of suitable habitat, whereas striped bass food limitation covaries in time with high entrainment loss and declining abiotic habitat suitability. This contrast provides a counter-intuitive example of the context-dependence of food limitation.

Figure 1: White shark feeding on a yellowfin tuna carcass.

Figure 2: White shark investigating, but not feeding on a California sea lion carcass.
The sharks that participated in this study showed a clear preference for yellowfin tuna carcass over California sea lion carcass, a result that is contrary to the accepted theory that adult white sharks preferentially prey upon marine mammals. Although white sharks are known to scavenge on marine mammal carcasses (cetaceans) in a very advanced state of decomposition (Pratt et al. 1982, Long and Jones 1996, Curtis et al. 2006, Dicken 2008), a record also exist in which a shark mouthed a decomposed sea lion several times before taking and swallowing a single bite (Klimley et al. 1996). Although not always the case, sharks feeding on large cetacean carcasses have been noted to preferentially scavenge the blubber, leaving behind the muscle tissue (Pratt et al. 1982). If it is the case that white sharks prefer blubber to other tissues (i.e., muscle, bone and connective tissue), perhaps decomposing pinnipeds do not offer enough blubber to elicit a feeding event. However, white sharks have become notorious within the public media for their aggressive feeding on small species of pinnipeds while alive (e.g. fur seals in South Africa).

Guadalupe Island is a frequent seasonal destination for the San Diego recreational dive and sportfishing fleets. The dive charters are dedicated specifically to white shark observation while the anglers target the seasonally abundant yellowfin tuna and yellowtail populations. Guadalupe Island white sharks are routinely fed by both of these recreational fleets. The dive charters directly feed the sharks by deploying tuna carcasses (in a similar manner to this study), while anglers aboard the fishing vessels indirectly feed the sharks through predation events on fish that are being fought on rod and reel. The author found it extremely difficult to bring tuna to the research vessel via rod and reel once the sharks were attracted to the boat; the sharks exhibited great speed and agility in chasing and capturing the hooked tuna. Have the white sharks of Guadalupe Island been habitually trained to consume fish despite their presumed role as a predator of marine mammals? Or do the Guadalupe white sharks regularly prey upon the pelagic teleosts seasonally abundant around the island?

Future research focusing on determining the relative importance of fish in the diet of adult white sharks is needed. Eastern Pacific white sharks are known to spend protracted times in a Shared Offshore Foraging Area (SOFA), far from any land (Boustany et al. 2001, Weng et al. 2008, Domeier and Nasby-Lucas in press). Swordfish, tuna, and other shark species are likely present in the SOFA, and it is possible that pelagic fish are an important part of the white shark diet while they occupy the deep pelagic environment. Studies directed at comparing the diet of the Guadalupe sharks at the island compared to when they are at sea could be revealing. Also, comparing the diet of Guadalupe white sharks to those of other white shark populations could indicate habitat differences or an anthropomorphic effect on the diet of Guadalupe sharks. Isotope analyses may be a means of addressing these questions.

The recent Convention on International Trade of Endangered Species (CITES) protection granted to white sharks is raising the awareness of the conservation issues surrounding this species. White shark-based tourism is a growing industry which is increasing the interaction between humans and sharks. The effects these interac-
tions may have on the behavior and diet of white sharks should be studied to prevent deleterious consequences.

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