C H A P T E R

27

White Shark Predation and Scavenging on Cetaceans in the Eastern North Pacific Ocean

DOUGLAS J. LONG
Department of Ichthyology
California Academy of Sciences
Golden Gate Park
San Francisco, California

ROBERT E. JONES
Museum of Vertebrate Zoology
University of California
Berkeley, California

Introduction

Cetacean remains are frequently found in the stomachs of sharks (Table I). Thus, sharks are often considered to be predators of dolphins and porpoises. To better understand the extent of predation on cetaceans, it is essential to understand how a cetacean might end up in the stomach of a shark. A fundamental distinction must be made between scavenging a dead cetacean and the act of predation—attacking and/or killing a live cetacean. Of over 350 species of sharks, only about 6, including the white shark *Carcharodon carcharias,* are known to prey on small odontocetes (Table II).

Bites, punctures, and tooth rakes have been used with some success to identify species of sharks responsible for attacks on humans (Gudger, 1950; Martini and Welch, 1981; Egaña and McCosker, 1984; Lea and Miller, 1985; Collier, 1992; Nakaya, 1993), since tooth shape, size, spacing, and variability differ among genera and species (see Chapter 3, by Hubbell, and Chapter 8, by Purdy). This method has been used in studies of shark predation on pinnipeds (Brodie and Beck, 1983; Hiruki *et al.,* 1993) and on small odontocetes (Leatherwood *et al.,* 1972; Corkeron *et al.,* 1987; Cockcroft *et al.,* 1989) and has been especially important in understanding white shark predatory dynamics along the California coast (Ames and Morejohn, 1990; Le Boeuf *et al.,* 1982; Ainley *et al.,* 1985; McCosker, 1985; Long, 1991a; Long *et al.,* Chapter 24; Ames *et al.,* Chapter 28).

Along the Atlantic seaboard of North America, the white shark sometimes preys on harbor porpoises *Phocoena phocoena* (Day and Fisher, 1954; Arnold, 1972). Off South Africa, white sharks prey on bottle-nosed dolphins *Tursiops truncatus,* common dolphins *Delphinus delphis,* and Indo-Pacific humpback dolphins *Sousa plumbea* (Cockcroft *et al.*, 1989; Cliff *et al.*, 1989). In Australian waters, white sharks are known to prey on bottle-nosed dolphins (Corkeron *et al.,* 1987; Bruce, 1992). In the Mediterranean, white sharks may also feed on cetaceans, including the Risso's dolphin *Grampus griseus* and other species (see Chapter 30, by Fergusson). In New Zealand waters, white sharks apparently attack dusky dolphins *Lagenorynchus obscurus,* based on observations of individuals with healed bite scars and shark-damaged dorsal fins (M. Webber, personal communication) (Fig. 1D).

In contrast to the above records, shark predation on cetaceans in the eastern North Pacific Ocean is poorly documented. Norris (1967) said, " . . . apparently shark predation is of importance in some areas. We almost never see this in California; at least I can-

GREAT WHITE SHARKS
The Biology of *Carcharodon carcharias*

TABLE I Shark Species Whose Diets Are Known to Include Cetaceans

Common name	Species	Reference
Pigeye shark	*Carcharhinus amboinensis*	Cliff and Dudley (1991b)
Bronze whaler shark	*Carcharhinus brachyurus*	Cliff and Dudley (1992a)
Galápagos shark	*Carcharhinus galapagensis*	Compagno (1984a)
Bull shark	*Carcharhinus leucas*	Baughman and Springer (1950); Bass *et al.* (1975); Cliff and Dudley (1991b)
Blacktip shark	*Carcharhinus limbatus*	Dudley and Cliff (1993b)
Oceanic whitetip shark	*Carcharhinus longimanus*	Compagno (1984a); Stevens (1984)
Dusky shark	*Carcharhinus obscurus*	Compagno (1984a)
Sandbar shark	*Carcharhinus plumbeus*	Cliff *et al.* (1988a); Stillwell and Kohler (1993)
White shark	*Carcharodon carcharias*	Templeman (1963); Randall (1973); Ellis (1975); Carey *et al.* (1982); Pratt *et al.* (1982); Stevens (1984); McCosker (1985); Cliff *et al.* (1989); Bruce (1992)
Portuguese shark	*Centroscymnus coelolepis*	Clark and Merrett (1972); Ebert *et al.* (1992)
Tiger shark	*Galeocerdo cuvieri*	Bell and Nichols (1921); Baughman and Springer (1950); Compagno (1984a); Stevens (1984); Stevens and McLoughlin (1991); Randall (1992); Simpfendorfer (1992)
Sixgill shark	*Hexanchus griseus*	Ebert (1986, 1994)
Shortfin mako shark	*Isurus oxyrinchus*	Stillwell and Kohler (1982); Stevens (1984); Cliff *et al.* (1990)
Sevengill shark	*Notorynchus cepedianus*	Ebert (1991); D. J. Long (unpublished observation)
Blue shark	*Prionace glauca*	Strasburg (1958); Stevens (1973, 1984)
Sleeper shark	*Somniosus microcephalus*	Williamson (1963); Beck and Mansfield (1969)
Pacific sleeper shark	*Somniosus pacificus*	Crovetto *et al.* (1992)
Hammerhead shark	*Sphyrna* sp.	Leatherwood *et al.* (1972)

not think of a case." Leatherwood *et al.* (1972) and Ridgway and Dailey (1972) observed several instances of shark-wounded dolphins and of sharks attacking living dolphins in waters off southern California and western Mexico, but such observations were scarce, and none implicated the white shark.

Stroud and Roffe (1979), from Oregon, reported a white-sided dolphin *Lagenorynchus obliquidens* in which shark attack was the primary cause of death, and Long (1991a) reported a white shark attack on a live pygmy sperm whale *Kogia breviceps* on the basis of a white shark bite on the caudal peduncle. Slipp and Wilke (1953) and Sullivan and Houck (1979) reported carcasses of Baird's beaked whale *Berardius bairdi*, and Roest (1970) reported a Cuvier's beaked whale *Ziphius cavirostris*, all having large shark bites, but they did not discuss the possibility of postmortem scavenging. Minasian *et al.* (1984) illustrated a live stranded Cuvier's beaked whale having a partially healed scar attributed to a shark, but upon examination of their photograph, we conclude that a shark was not the cause of the scar.

Examinations of white shark stomach contents collected along the West Coast of the United States from 1935 to 1984, reported by Klimley (1985b), failed to find cetacean remains. The first records of white shark

TABLE II Shark Species Identified as Predators on Small Odontocetes

Common name	Species	Reference
Bull shark	*Carcharhinus leucas*	Caldwell *et al.* (1965); Cockroft *et al.* (1989)
Oceanic whitetip shark	*Carcharhinus longimanus*	Leatherwood *et al.* (1972); D. J. Long (unpublished data)
Dusky shark	*Carcharhinus obscurus*	Cockcroft *et al.* (1989)
White shark	*Carcharodon carcharias*	Day and Fisher (1954); Arnold (1972); Cockroft *et al.* (1989); Long (1991b)
Tiger shark	*Galeocerdo cuvieri*	Cockroft *et al.* (1989)
Shortfin mako shark	*Isurus oxyrinchus*	Leatherwood *et al.* (1972); Ridgway and Dailey (1972)

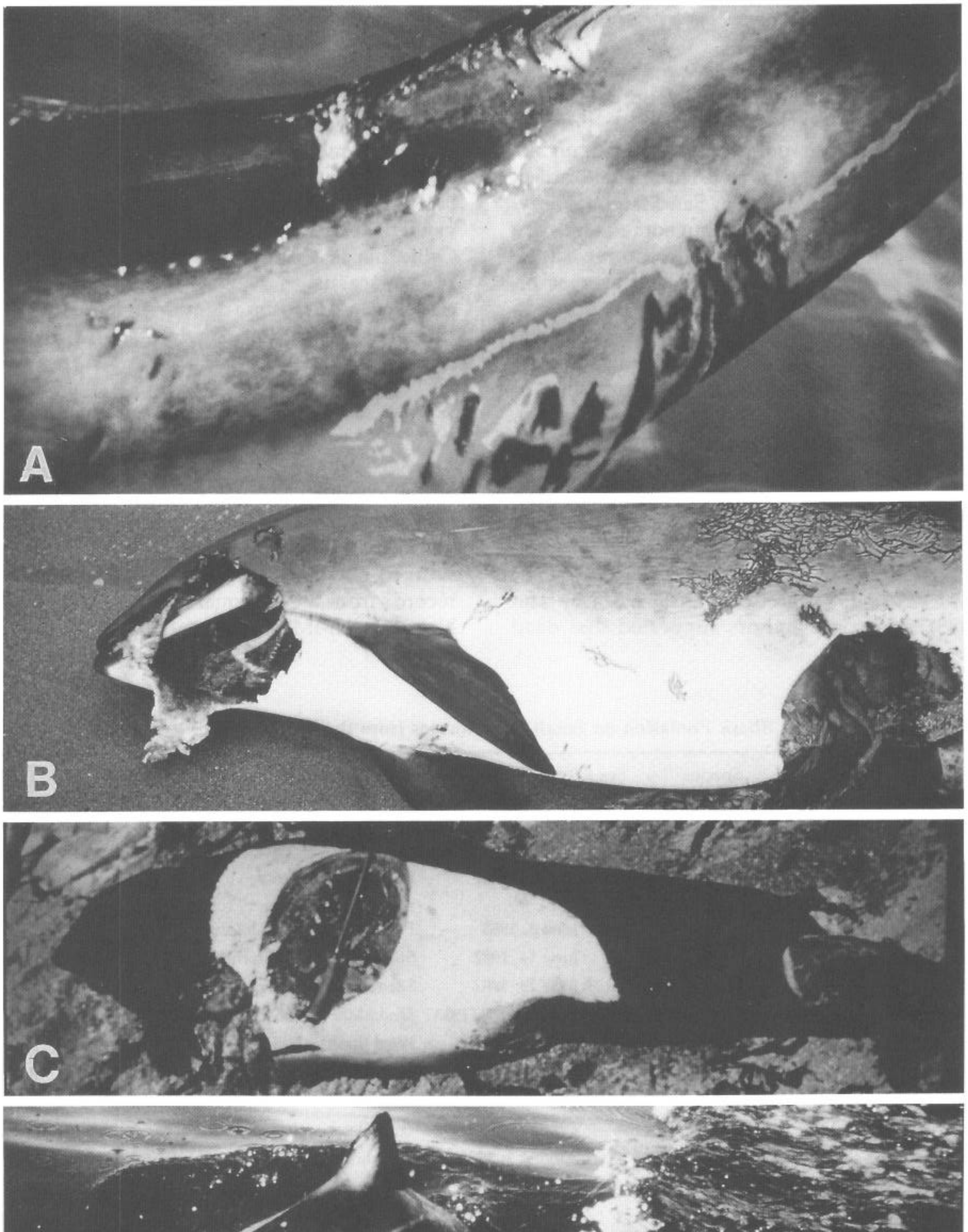

FIGURE 1 Small odontocetes wounded by white sharks. (A) The caudal peduncle of an immature pygmy sperm whale (case 15). (Photo by D. J. Long.) (B) A harbor porpoise, showing a fatal bite in the abdomen (34 cm wide) and a second bite on the lower jaw (case 19). (Photo by C. Keiper.) (C) A Dall's porpoise, showing a large (36-cm-wide) bite on the left flank and a smaller bite on the chest (case 1). (Photo by R. E. Jones.) (D) A dusky dolphin, showing healed scars from a white shark bite (southern New Zealand). (Photo by M. Webber.)

predation on cetaceans in this area were from wounded carcasses reported by Stroud and Roffe (1979) and Long (1991a). However, another possible record of predation on odontocetes, based on accounts by local fishermen, was a white shark attack on a harbor porpoise off Pacifica, San Mateo County, California on September 1, 1983, but some details are lacking (Szczepaniak, 1990). There are no records of white sharks preying on larger odontocetes or on adult mysticetes.

While predation by sharks on cetaceans is relatively rare, many sharks scavenge dead cetaceans (Long, 1991b) (Table III). Carcasses of mysticete or large odontocete whales may float for several weeks, providing a large amount of food for many species of sharks and, possibly, supply an important portion of the diet for white sharks during certain times of the year. White sharks are frequently observed feeding on carcasses of whales off Australia and the eastern United States (Randall, 1973; Ellis, 1975; Carey *et al.*, 1982; Pratt *et al.*, 1982; McCosker, 1985; Casey and Pratt, 1985), and some authors suggested that dead cetaceans may be a primary food source for white sharks in certain areas (Carey *et al.*, 1982; Castro, 1983). Scavenging by white sharks on the west coast of North America has not been well documented, but white sharks have been seen scavenging carcasses of basking sharks *Cetorhinus maximus* (Follett, 1966). Reviewed here are records collected from the coast of California of white sharks attacking and feeding on live cetaceans as well as scavenging cetacean carcasses; these accounts demonstrate the importance of cetaceans in the diet of white sharks in the eastern North Pacific.

Methods

Information about shark predation and scavenging on cetaceans in the eastern North Pacific from 1972 to 1992, spanning the entire coast from Washington state to southern California, was gathered through records from the National Marine Mammal Stranding Network (NMMSN), several museums, and scientific

TABLE III **White Shark Predation on Small Odontocetes from the West Coast of the United States**

No.	Common name	Species	Sex	Date	Locality[a]	Bite location[b]	Condition[c]
1	Dall's porpoise	*Phocoenoides dalli*	F	August 7, 1973	Bolinas Beach, California	2, 3, 6	Recently killed
2	Harbor porpoise	*Phocoena phocoena*	M	July 28, 1978	South Beach, California	1, 3	Alive
3	White-sided dolphin	*Lagenorhynchus obliquidens*	M	May 12, 1981	Fort Ord, California	1	Alive
4	Harbor porpoise	*Phocoena phocoena*	F	June 4, 1982	Pomponio Beach, California	4	Recently killed
5	Harbor porpoise	*Phocoena phocoena*	F	June 14, 1982	Stinson Beach, California	1	Recently killed
6	Harbor porpoise	*Phocoena phocoena*	F	June 23, 1982	Stinson Beach, California	1, 2	Recently killed
7	Harbor porpoise	*Phocoena phocoena*	M	September 2, 1983	Linda Mar Beach, California	1, 4	Recently killed
8	Harbor porpoise	*Phocoena phocoena*	M	October 1, 1983	Point Bonita, California	1, 3	Recently killed
9	Harbor porpoise	*Phocoena phocoena*		October 2, 1983	Fort Cronkhite, California	1, 2	Recently killed
10	Harbor porpoise	*Phocoena phocoena*	F	July 18, 1984	Dillon Beach, California	4	Recently killed
11	Harbor porpoise	*Phocoena phocoena*		December 4, 1985	Long Beach, Washington	1, 3, 4	Recently killed
12	Harbor porpoise	*Phocoena phocoena*		August 5, 1986	Franklin Point, California	2, 3	Recently killed
13	Dwarf sperm whale	*Kogia simus*	M	January 12, 1987	Stinson Beach, California	1	Alive
14	Risso's dolphin	*Grampus griseus*	F	July 8, 1989	Trinidad Beach, California	1, 2	Recently killed
15	Pygmy sperm whale	*Kogia breviceps*	M	August 31, 1989	Parjaro Dunes, California	1	Alive
16	Stejneger's beaked whale	*Mesoplodon stejnegeri*	M	May 21, 1990	Pacific Grove, California	1, 2	Alive
17	Cuvier's beaked whale	*Ziphia cavirostris*		June 19, 1990	South Beach, California	1	Recently killed
18	Harbor porpoise	*Phocoena phocoena*	F	April 4, 1991	Drake's Beach, California	3, 5	Recently killed
19	Harbor porpoise	*Phocoena phocoena*	F	February 15, 1993	Kehoe Beach, California	3, 5	Recently killed

[a]Location collected (see Fig. 2).
[b]Location of bite on the body (see Fig. 8).
[c]Condition of the animal at the time of first examination.

institutions (see Acknowledgments). All marine mammals are federally protected, and all live or dead stranded cetaceans that are found are examined. Information on species, sex, size, age, location, date, and overall condition is collected, and when possible, a gross necropsy is performed to determine the cause of death. Although the NMMSN spans the entire coastline of the western United States, and the area for California is well monitored, potential biases exist in the stranding data (see Chapter 24, by Long *et al.*).

Records of all cetaceans suspected to have been bitten by sharks were carefully reviewed, and white shark predation was determined by three criteria: (1) direct observation of an attack in which both predator and prey were positively identified (only one such encounter is known from this area), (2) observations of living cetaceans showing fresh bite wounds or healed bite scars that could be positively attributed to a white shark, or (3) necropsies on dead cetaceans indicating that white shark attack was the primary cause of death, or that bites were inflicted prior to death. Criteria included evidence of recent exsanguination from a bite area, trauma, subdermal muscular or osseous hemorrhage near a bite, or signs of blood clotting or healing around a bite area.

Jaws and tooth sets of predatory sharks from California were examined to determine the species responsible for inflicting wounds seen on odontocete and mysticete carcasses and to interpret feeding behavior. Jaws of white sharks (N = 27), shortfin mako sharks *Isurus oxyrinchus* (N = 28), blue sharks *Prionace glauca* (N = 61), sevengill sharks *Notorynchus cepedianus* (N = 15), sixgill sharks *Hexanchus griseus* (N = 8), tiger sharks *Galeocerdo cuvieri* (N = 11), bull sharks *Carcharhinus leucas* (N = 13), and dusky sharks *Carcharhinus obscurus* (N = 10) were studied (for data, see Long, 1994). Complete bite widths of white sharks (Table IV) were measured across the upper jaw behind the last posterior tooth, and behind the fifth tooth for partial bites.

Evidence of scavenging was based on direct observation of the sharks actually feeding on the carcass, or on bites and/or tooth marks left on a carcass that can be attributed to a white shark. Bites, punctures, and rake marks were measured and photographed when possible. We assessed seasonal and annual trends of white shark scavenging of large cetaceans stranded along the California coast from Del Norte County south to Monterey County, 1972–1992. The large cetacean category included all mysticete and large odontocete whales, such as sperm whales *Physeter catodon*, killer whales *Orcinus orca*, pilot whales *Globicephala macrorhynchus*, and beaked whales *Z. cavirostris* and *Mesoplodon* spp.

TABLE IV **White Shark Lengths and Bite Gapes**

Total Length (m)	Bite Width (cm)[a]	Incomplete Width (cm)[b]
1.63	11.7	10.2
1.96	17.7	13.8
2.64	23.4	19.4
2.69	27.0	22.4
3.68	32.0	30.1
5.10	48.0	39.5

[a]Measured across the upper jaw from behind the last tooth of the row.
[b]Measured across the upper jaw from behind the fifth tooth.

Results

Predation

We inspected 19 small odontocetes that showed signs of predation by white sharks (Table III). These specimens included 11 harbor porpoises, 2 Dall's porpoises *Phocoenoides dalli*, and 1 each of the white-sided dolphin, Risso's dolphin, pygmy sperm whale, dwarf sperm whale *Kogia simus*, Cuvier's beaked whale, and Stejneger's beaked whale *Mesoplodon stejnegeri*.

Bites were usually located on several areas of the body: 68% (N = 13) on the caudal peduncle, 31% (N = 6) in the urogenital region, 36% (N = 7) on the abdomen, 21% (N = 4) on the dorsum, 10% (N = 2) on the head, and 5% (N = 1) on the flanks. Of the 19 specimens, 1 was recovered from Washington state, and the others were collected from central and northern California (Humboldt, Marin, San Mateo, and Monterey counties; Fig. 2). Attacks on small odontocetes occurred year-round, but most were recorded during summer (52%), with fewer attacks reported in fall, winter, and spring (15% each; Fig. 3).

These records are the only known examples of white shark predation on odontocetes in the eastern North Pacific Ocean. For the Dall's porpoise, the dwarf sperm whale, and the Cuvier's and Stejneger's beaked whales, this report lists the first known instances of white shark predation on these species. Reported here is the first record of shark predation on the Risso's dolphin in North American waters, but Ian Fergusson (Chapter 30) believes that white sharks may prey on this species in the Mediterranean.

Scavenging

Records of shark-scavenged carcasses extended from Bandon, Oregon, and Crescent City, California,

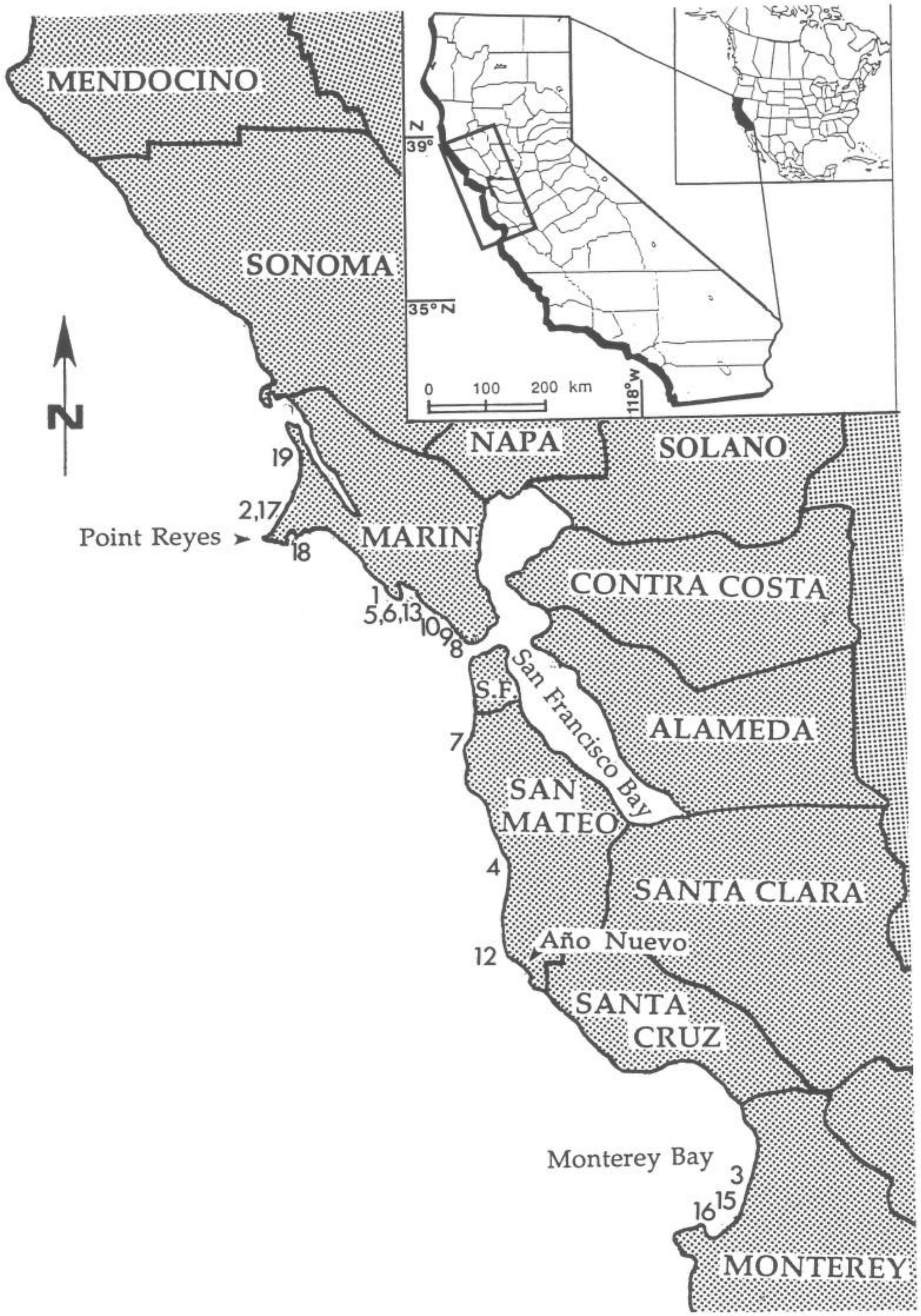

FIGURE 2 The central California coast, showing the stranding localities of small odontocetes listed in Table III; cases 11 and 14, both north of the area covered, are not shown.

south to San Diego, California. At least half of the strandings occurred off the central California coast, and these were the ones considered in this study. Three to 12 (average, 6.2) large cetaceans have stranded along the central California coast annually (Fig. 4), but many more probably sank or floated out to sea. Cetacean carcasses were available all year, but the abundance of cetacean carcasses increased mark-

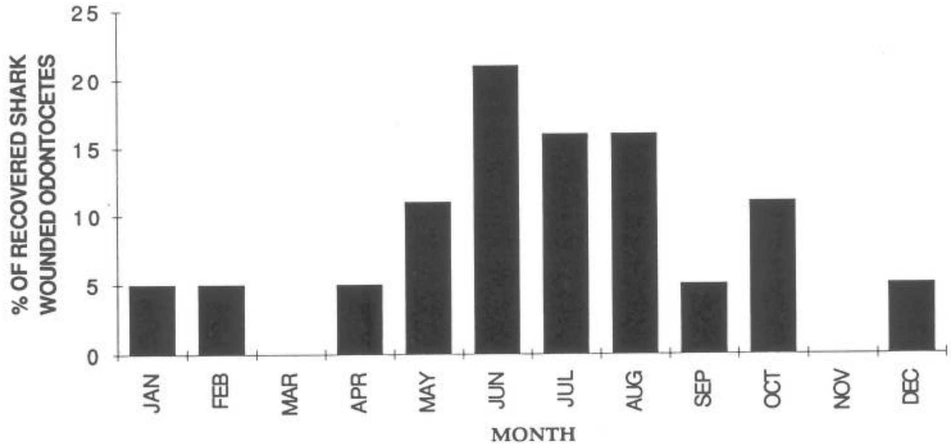

FIGURE 3 The seasonal distribution (by month) of odontocetes wounded by white sharks (N = 19).

edly during spring (Fig. 5). About 70% of carcasses were from gray whales *Eschrichtius robustus*.

It was difficult to estimate the percentage of cetacean carcasses that were scavenged by white sharks, because earlier stranding reports sometimes did not identify the species of shark that inflicted the bites. However, of the 37 large carcasses we examined, 56% (N = 21) were scavenged by white sharks; 21% (N = 8), by blue sharks; and 2% (N = 1), by sevengill sharks. Only 8% (N = 3) showed evidence of scavenging by both white and blue sharks.

Discussion

Proper Identification and Practical Uses of Shark Bites

Without firsthand observation of sharks feeding on marine mammals, it is difficult to correctly identify what species of shark may be involved when examining bites on a live or dead mammal. However, most species of large predatory sharks have a distinct dental morphology that, if properly examined, can lead

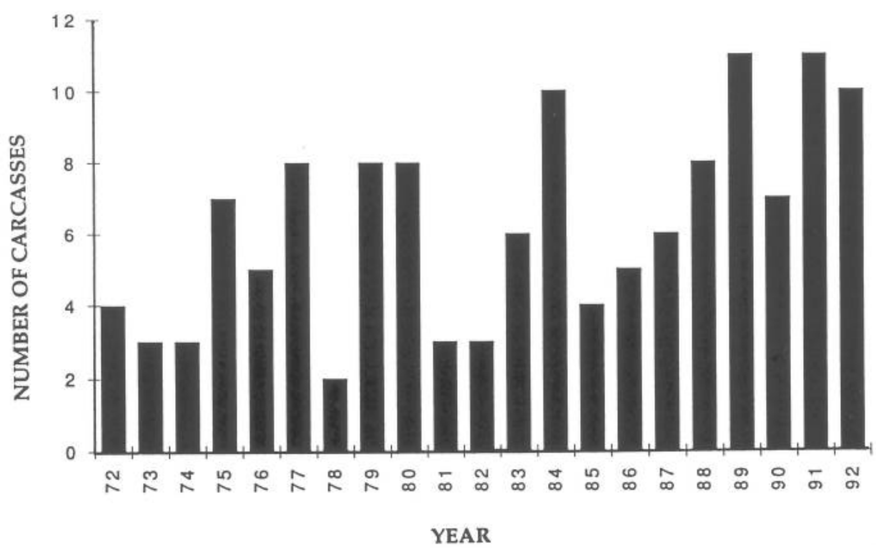

FIGURE 4 The annual numbers of large cetacean carcasses stranded along central California, 1972–1992.

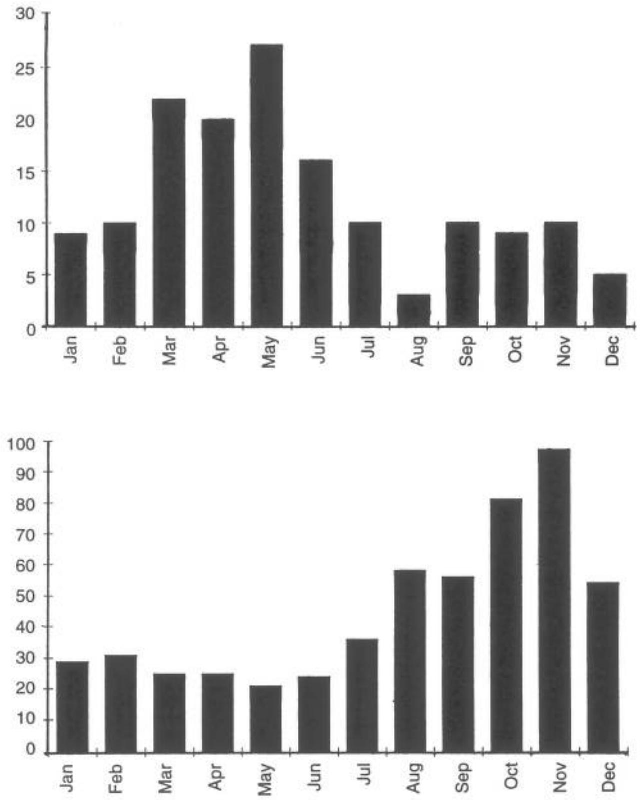

FIGURE 5 (A) The seasonal (by month) distribution of large cetacean carcasses stranded along central California, and (B) the seasonal occurrence of stranded pinnipeds showing white shark bites (after Chapter 24, by Long *et al.*).

to accurate specific or generic identification (see Chapter 3, by Hubbell). In special cases, tooth fragments recovered from a body or carcass provide an unquestionable identification of the shark species involved (Orr, 1959; Collier, 1964; Ames and Morejohn, 1980; Nakaya, 1993); identification can also be provided by serration marks left on bone and other hard objects (Deméré and Cerutti, 1982; Ames and Morejohn, 1980; Cigala-Fulgosi, 1990; Nakaya, 1993).

The size, shape, and condition of bites on carcasses can also be diagnostic for shark identification. White shark bites show several unique characteristics: the bite area is wide (usually 20–60 cm; see Table IV); the teeth are relatively large, proportionately long, and coarsely serrated; the upper teeth are wide and thin, and the lower teeth are slender and more conical; they have relatively few (12–13) teeth in the tooth row; and there is no overlap between adjacent teeth. Carcharhinid sharks (including *Carcharhinus* and *Prionace*) have smaller bite widths (usually <30 cm), smaller and more numerous overlapping teeth having finer serrations, and lower teeth that are very narrow and lack serrations; bites on cetaceans are usually small and clean-cut (Fig. 6C and D). Tiger sharks have wide but relatively short teeth that are heavily serrated and show no difference between uppers and lowers. Mako sharks have unserrated, long, and thin anterior teeth, and shorter lateral teeth in both the upper and lower jaws; unlike other predatory sharks, they have more than one tooth row functional at a time. Thus, white shark bites can be determined by wide parabolic or arc-shaped wounds, showing a single row of large punctures that exhibit a difference between the upper and lower jaws, or else a wide, deep, continuous cut or circular bite (Figs. 1, 6, and 7). For more detailed descriptions of shark dentition, see the work of Bass *et al.* (1975), Compagno (1988), Long (1994), Hubbell (Chapter 3), Applegate and Espinosa-Arrubarrena (Chapter 4), and Purdy (Chapter 8).

Although analysis of bites can provide insight into the feeding activities of sharks, some caution is warranted. Several workers have measured the sizes of bites on carcasses as a way to estimate the relative size of the shark. Theoretically, the size of a white shark's gape increases with the total length of the shark, and the size of the bite is about equal to the size of the gape. Randall (1973) and Castro (1983) suggested that some white sharks may reach a maximum size of 750 cm, even though the largest reliably recorded white shark was about 720 cm (see Chapter 10, by Mollet *et al.*).

Size estimates based on bite sizes can be misleading due to several sources of error, detailed here.

Original Estimates of Bite Size and Total Length

Estimates of shark bite–body length relationships are based largely on the review by Randall (1973). In this, he cites bite–length estimates based on general observations from a personal communication: a bite width of a 441- to 457-cm shark is about 30.5 cm wide, and that of a 487-cm shark is 33 cm wide. Apparently, Randall did not actually measure the gapes of fresh specimens or jaws from sharks of known lengths. These estimates are likely disproportionate, and probably lead to an overestimation in the total length of the shark.

From our measurements of white shark jaws and from fresh bites on pinnipeds and cetaceans, the size of white shark bites appears to be proportionately larger in relation to the total length of the shark than was reported by Randall (1973). Mouth width–total length relationships of white sharks reported by Bass *et al.* (1975) also support this: a 170-cm shark had a mouth width of 16.3 cm, and a 391-cm specimen had a mouth width of 37.6 cm. Additionally, we measured a bite-sized piece of blubber, 40 cm across, that was

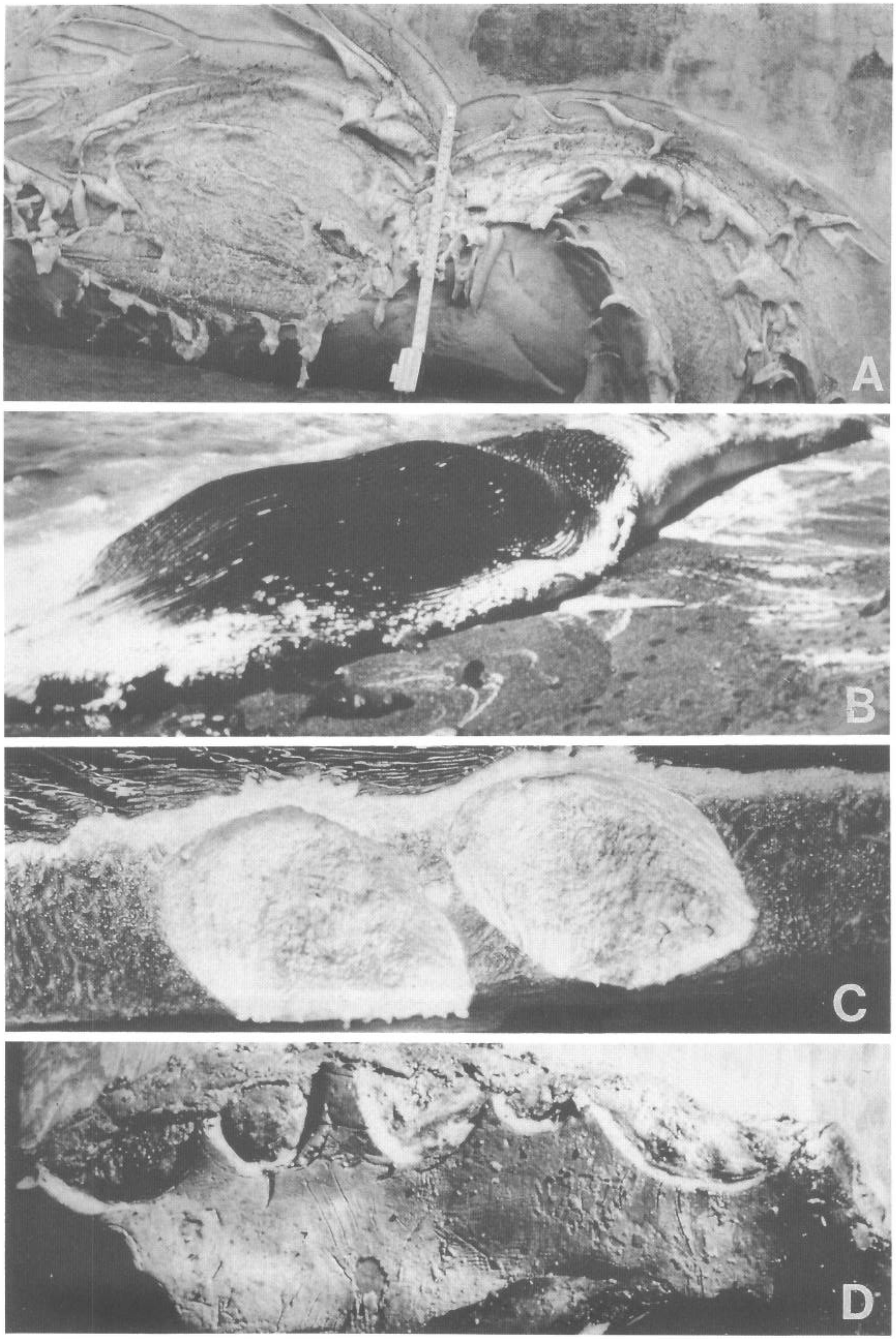

FIGURE 6 Shark bites on cetacean carcasses. (A) Two large bites on a mysticete carcass, showing the large size and often ragged edges made by white sharks (the measuring tape shows a 30-cm section for scale). (Photo by D. J. Long.) (B) A blue whale carcass, showing white shark scavenging on the entire lateral margin of the blubber layer. (Photo by R. E. Jones.) (C) Two small (16- to 18-cm-wide) blue shark bites on a mysticete carcass, showing the characteristic small circumference and clean bite edges. (Photo by K. Beckmann.) (D) A harbor porpoise carcass scavenged by a blue shark, showing clean-edged bites and selective feeding on the blubber layer. (Photo by D. J. Long.)

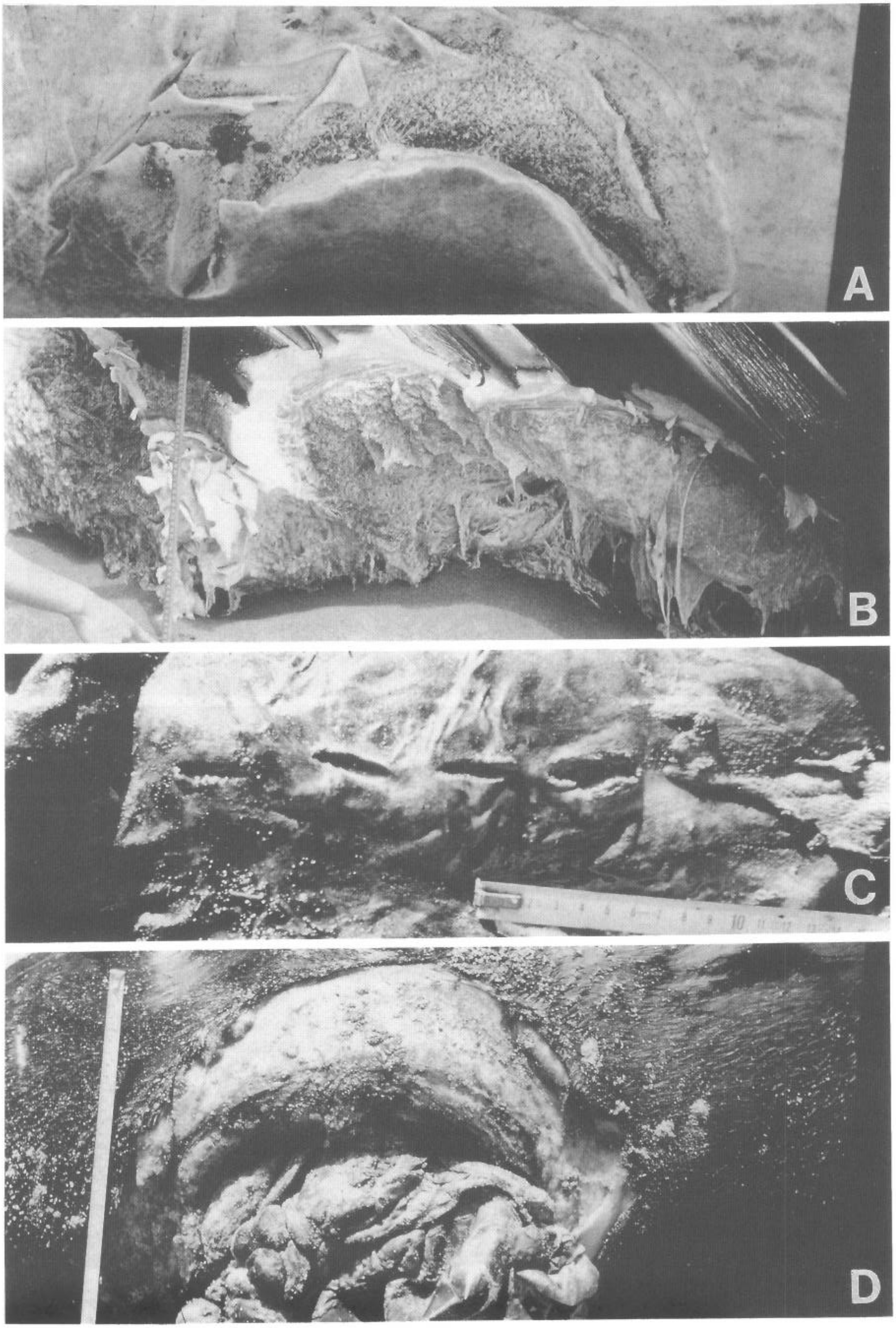

FIGURE 7 White shark bites on marine mammals, showing possible sources of interpretation error. (A) An incomplete bite on a mysticete carcass (the 23-cm-wide bite encompasses only the first half of the gape). (B) Three overlapping bites on a mysticete carcass, creating the illusion of a single bite >110 cm wide. (C) Tooth punctures on the hindflipper of an elephant seal that was curved when bitten (the flipper returned to its normal shape, but the punctures are linear and do not show the normal arc shape). (D) A large bite on a California sea lion *Zalophus californianus*, showing distortion and stretching of the bite area of the epidermis and a smaller bite arc in the blubber layer. (Photos by D. J. Long.)

regurgitated by a shark estimated to be about 450 cm. Similarly, we measured a fresh bite on an adult northern elephant seal *Mirounga angustirostris* that was 58 cm wide, even though the size of the attacking shark was <540 cm (for gape measurements, see Table IV).

Completeness of Single Bites

The width of the gape depends on where the measurements are taken. The gape is widest at the posterior of the jaw, and the gape becomes relatively smaller anterior to this. Accordingly, the size of the bite corresponds to the areal proportion of the bite, or simply, the amount of flesh that is within the gape (Table IV). If a white shark bites a carcass using only the anterior half of the gape, then the shark's total length would appear to be small (Fig. 7A). For an accurate estimate, the bite must encompass the whole of the gape, and data gathered should include a count of tooth punctures involved in the bite.

Angle and Force of Attack

Even parabolic bites were usually seen in cases in which the bite direction was relatively perpendicular to the body of the mammal. Single large uneven bites, however, were sometimes seen in some marine mammals that indicated a different direction in bite angle and/or force of bite impact against the body. The orientation of these abnormally large bites suggested that they could be inflicted if the attack angle was more oblique, or if the force of impact caused a "sliding" of the bite along the body. Tooth rakes, long cuts, and uncharacteristically wide bite parabolas were evidence of this phenomenon.

Overlapping Multiple Bites

We frequently encountered shark-scavenged cetacean carcasses that had seemingly huge single bites, but actually had two or three smaller bites that overlapped. This created the illusion of a single bite from a very large shark (Fig. 7B). Often, these bites overlapped in such a way that they created an even-looking parabola, a shape characteristic of a large single bite. More commonly, the large "bite" created by overlapping bites usually had a wide unnatural parabolic shape.

Increase of Bite Size by Scavengers

On several occasions, we have seen that the size of a single white shark bite had been increased by scavengers picking around the inner margin of the original bite, often feeding neatly without leaving evidence of their activity. On land, gulls *Larus* spp. and turkey vultures *Cathartes aura* often eat around a bite area, and in the water, blue sharks can do the same. As with overlapping bites, this creates the illusion of a single large bite.

Postmortem Gassing and Expansion

When a carcass begins to decompose, gasses fill and expand the body cavity, blubber, and dermal tissues. This results is stretching and bloating of the outer tissues; a bite on the outer wall of the body can stretch as much as 25% larger than its original size in this way (Fig. 7D). On the basis of such bites, total length estimations of sharks would be exaggerated.

Decomposition around the Bite

As marine mammal carcasses decompose, tissue is sloughed off around exposed margins, including those of the bite. Advanced decomposition increases the apparent size of the bite area. Thus, any size estimates would be greater than the original.

Drying

In cases in which stranded carcasses are exposed to heat or sunlight for extended periods, portions may dry at different rates, causing shrinkage, stretching, and distortion. The epidermis, flippers, and fins usually dry first, and in some cases, different levels of tissue dry and distort at different rates (Fig. 7D). Therefore, sizes and shapes of bites on the body may be altered due to differential drying of tissues.

Flexion and Distortion

In some cases of predation on live animals or on moving carcasses, the shark may inflict a bite on a portion of the body that is flexed into a concave position. When the animal or carcass returns to a more linear shape, the typical parabolic shape of the bite stretches much wider (Figs. 1A and 7C). If the body or carcass had been arched in a convex direction, the size of the bite arc would decrease when the body returned to its natural shape.

To use shark bites as a valid estimate of shark size, bites and scars should (1) be on fresh carcasses that show little sign of gassing, bloating, decomposition, or scavenging; (2) be an even parabolic shape, to eliminate errors associated with overlapping bites and flexion and distortion; and (3) include individual tooth marks, to judge the areal proportion of the gape actually used in the bite.

Size Relationships of White Sharks and Cetacean Prey

General estimations of shark size based on measurements of bites from the carcasses, and comparisons of bites with gape measurements of known-length white sharks, show that large, but not small (<350-cm), white sharks prey on small odontocetes. This observation is supported by Arnold (1972), Stevens (1984), Cliff *et al.* (1989), and Bruce (1992), all of whom found cetacean remains to be more common in the stomachs of adult white sharks. This also agrees with Klimley's (1985b) and others' suggestion of a size-related ontogenetic shift in prey type, with small young white sharks feeding on fish and large adult white sharks preying more frequently on pinnipeds and cetaceans (Fig. 9).

Also, there seems to be a relationship between the size of the predator and the size of the prey. The largest shark-wounded animals in this study were juvenile Cuvier's and Stejneger's beaked whales, about 300 cm long, and the size of the attacking shark, estimated from the size and width of tooth punctures to be about 500 cm long. In all other specimens examined, the size of the shark was considerably larger than that of the prey, and in no cases have we seen premortem bites on a cetacean that was larger than the attacking shark. This implies an upper size limit to the prey of white sharks and may explain why larger cetaceans are not attacked.

Geographic Distribution of Predation

The majority of white shark-bitten odontocetes were recorded along the central California coast (Fig. 2); this is a pattern similar to that of shark-wounded pinnipeds (see Chapter 24, by Long *et al.*). Only one new record was from north of this area, that of a harbor porpoise from Long Beach, Pacific County, Washington, which is the only area north of California where white sharks have been recorded in significant numbers (Klimley, 1985b). Few reliable records of shark-bitten odontocetes have been confirmed south of central California, one being an adult female common dolphin collected at La Jolla, San Diego County, California, on May 27, 1989. This specimen had shark bites on the tail and caudal peduncle, but the species of shark was not determined.

It is possible that predation on odontocetes is more frequent than records indicate. White sharks feed heavily on pinnipeds, but pinnipeds can haul out onto land to heal from a shark injury without risk of another immediate attack (Klimley *et al.*, 1992; Long *et al.*, Chapter 24). On the other hand, cetaceans cannot retreat to shark-free areas, so they are more vulnerable to subsequent attacks. Most would be consumed, and few would be recorded by investigators. White sharks are known to hunt in nearshore waters (Klimley, 1985b; Klimley *et al.*, 1992), but most of the species of cetaceans discussed here are found further offshore (Leatherwood *et al.*, 1982; Dohl *et al.*, 1983). The exception is the harbor porpoise, which is the most common inshore odontocete (Huber *et al.*, 1980; Dohl *et al.*, 1983; Szczepaniak, 1990). This may account for the relatively high incidence of predation on this species in comparison to the other small odontocete species found in the area, but offshore data are required to resolve this matter.

Another reason for the low number of shark attacks on cetaceans also relates to the availability and abundance of different species of pinnipeds, the primary prey items of white sharks in this area. In areas where white shark predation on odontocetes is more frequent (e.g., South Africa, Australia, and the Mediterranean), the abundance and diversity of pinnipeds are lower (Corkeron *et al.*, 1987; Cliff *et al.*, 1989; Cockcroft *et al.*, 1989; Bruce, 1992; Fergusson, Chapter 30). Last, the incidence of shark attack in eastern North Pacific waters may be low because only one species of shark is involved. In other areas, where predation levels on odontocetes are higher (as much as 30% or more), white sharks, as well as tiger sharks, bull sharks, and dusky sharks, may be involved (Wood *et al.*, 1970; Corkeron *et al.*, 1987; Cockcroft *et al.*, 1989). None of these other species live in the cooler waters off the central and northern California coast (Compagno, 1984a; Long, 1994; Seigel *et al.*, 1996). Overall, shark predation on small cetaceans along the North American west coast appears to be low.

Seasonality of Attacks

White shark attacks on cetaceans were documented year-round, but most wounded odontocetes were recorded during summer and autumn (Fig. 3). The timing of these attacks corresponded to the seasonal peak of shark-wounded pinnipeds along the central California mainland (see Chapter 24, by Long *et al.*). This indicates that during summer and early fall, a greater number of sharks may be feeding along this coast. The majority of records were from harbor porpoises, but this species is most abundant during autumn, and least abundant during summer (Szczepaniak, 1990). Additionally, harbor porpoises are most abundant in California waters north of Point Reyes (Dohl *et al.*, 1983), but all of the California records of white shark-bitten harbor porpoises were south of there. The same geographic patterns are exhibited among white shark-wounded pinnipeds (see Chapter 24, by Long *et al.*). This evidence indicates that seasonal trends of attacks are related to predator abundance, rather than prey abundance.

Method of Attack

White sharks may attack small odontocetes in relatively the same way that they attack pinnipeds and humans: by a swift initial bite that surprises and kills or disables the animal (Tricas and McCosker, 1984; Klimley, 1994). The usual attack pattern may vary when hunting dolphins and porpoises. Odontocetes have an anteriorly directed sonar and a lateral visual field, so a surprise attack must be in the "blind area" either from above, below, or behind to avoid visual detection or detection from the sonar (Fig. 8). To avoid detection, white sharks seem to focus their bites on particular areas of the cetacean body. On the basis of bite orientation on live and dead shark-wounded cetaceans, it appears that sharks attack four major areas of the body: (1) the caudal peduncle, (2) the urogenital region, (3) the abdominal area, and (4) the dorsum; bites on the head and the flanks are less common (Table III and Fig. 8). An ineffective initial attack, or "bite-and-spit" behavior (Tricas and McCosker, 1984; Klimley, 1994), would allow some animals to survive and escape with minor wounds, but this attack behavior has since been discounted (see Chapter 22, by Klimley *et al.*).

The caudal peduncle is a vulnerable area, because a single well-placed bite can sever swimming muscles, the spinal column, and major blood vessels (Burne, 1952), thus effectively immobilizing the cetacean. Previous accounts of shark predation on cetaceans confirm that this area is frequently attacked. Arnold (1972) reported that three harbor porpoises, in the stomach of a single white shark, each had the flukes severed from the tail stock. Previous studies on Hawaiian spinner dolphins *Stenella longirostris* (Norris and Dohl, 1980), bottle-nosed dolphins (Cockcroft *et al.*, 1989), and the pygmy sperm whale (Long, 1991a) also noted a high prevalence of bites in this area. Results of our investigation confirm the vulnerability of the caudal peduncle in odontocetes, 68% of the animals in this study showing bite wounds there.

Bites in the urogenital and abdominal regions can also be serious since these areas have dense networks of nerves, blood vessels, and vital organs (Burne, 1952). Many of the shark-wounded animals inspected in this study had bites in these areas. The dorsal areas have a much thicker blubber and muscle mass, and attacks in these areas would less likely cause death. This may be why healed shark wounds are more frequently seen on the backs of living dolphins and porpoises (Norris and Dohl, 1980; Corkeron *et al.*, 1987).

Scavenging

Whale carcasses are available off northern California throughout the year, but are particularly abun-

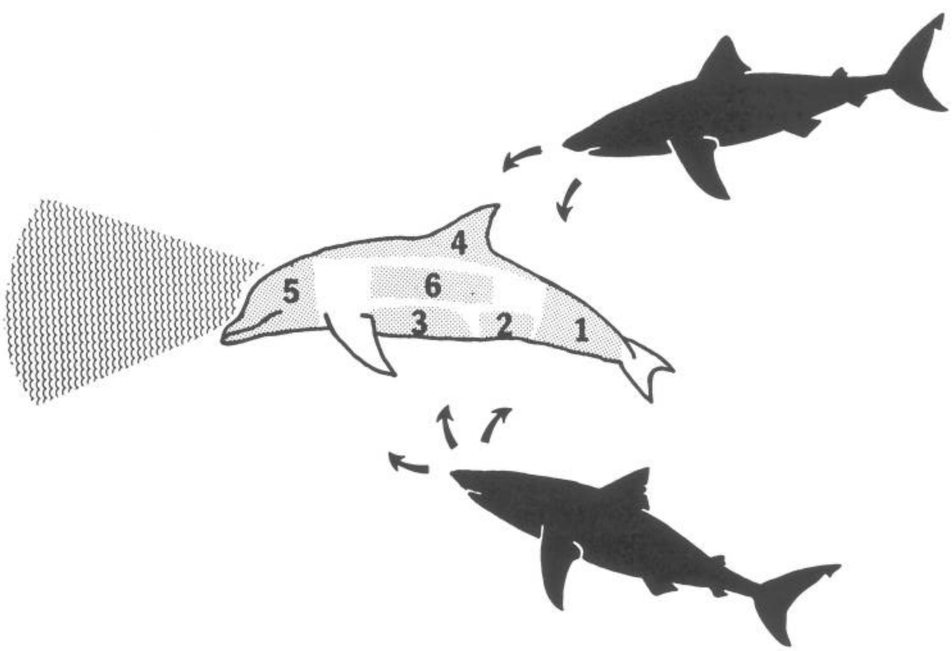

FIGURE 8 The major areas where white sharks bite small odontocetes: (1) the caudal peduncle, (2) the urogenital region, (3) the abdominal region, (4) the dorsal region, (5) the head, and (6) the flanks. Also illustrated is how white sharks probably attack from below, above, or behind, out of the range of the sonar field (wavy lines).

dant during spring (Fig. 5). Nearly 70% of carcasses are of the gray whale, which experience their peak natural mortality during their northward migration in spring (Poole, 1981). A smaller mortality peak among other large cetaceans occurs during fall and winter. Although the periodicity and locality of whale carcasses are unpredictable, they nonetheless are a regular food source for sharks in the area. The timing in abundance of cetacean carcasses corresponds to the time of the year that white shark predation on pinnipeds is low (see Chapter 24, by Long *et al.*) (Fig. 6). It is possible that white sharks shift from hunting pinnipeds in late summer and fall to scavenging large cetaceans in spring and early summer (Fig. 9).

A single large cetacean is a huge food source. A carcass may float for several weeks and exude a continuous slick of blood and oil that can attract sharks from long distances. Pratt *et al.* (1982) observed four to nine white sharks feeding on the carcass of a dead fin whale *Baleanoptera physalus* off New York, but they saw only one shark feeding at a time. One of us (D.J.L.) had the chance to observe a similar situation when the carcass of a blue whale *Baleanoptera musculus* was floating off San Francisco, California, in August 1988. About five different white sharks fed on the carcass, but only one individual fed at a time. Even though blue sharks were in the area, none fed when the white sharks were feeding. Accordingly, we have found few carcasses on which bites from both white and blue sharks were evident (8% of 37 carcasses examined). All of this indicates, as noted by Pratt *et al.* (1982), that a feeding hierarchy exists among white sharks, and between white sharks and other species of sharks.

On the basis of relative sizes of bites on the whale carcasses we examined, it appears that only large (>350-cm) white sharks scavenge carcasses. Pratt *et al.* (1982) and Casey and Pratt (1985) observed only adult white sharks feeding on whale carcasses off the eastern United States, and Klimley (1985b) noted that only large white sharks scavenge basking shark carcasses off California. As with predation on small odontocetes, scavenging large carcasses may also be a form of ontogenetic dietary change (Fig. 9).

The stomach contents of one of the feeding sharks in the study by Pratt *et al.* (1982) weighed 28 kg, but our observations and estimates from examination and measurements of carcasses, based on the amount of

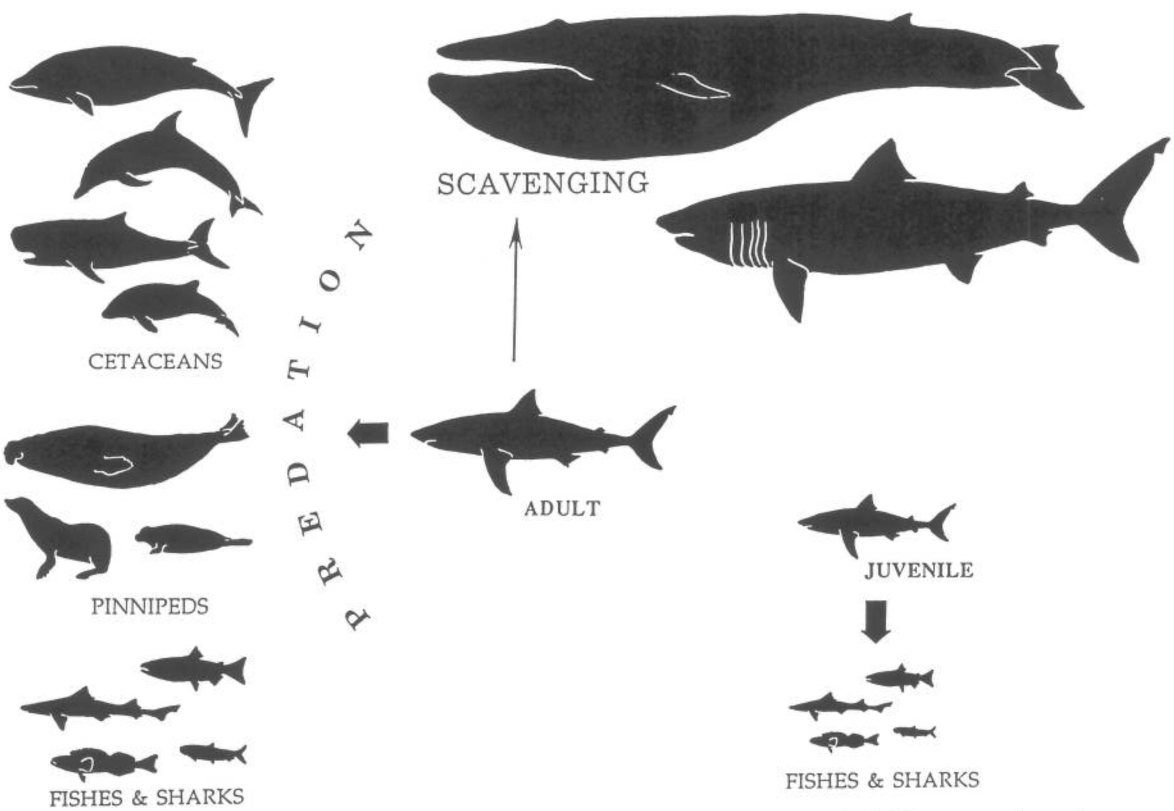

FIGURE 9 The ontogenetic prey shift in the white shark, from a diet consisting mainly of fishes among juveniles to one of mammals and larger fish among adults.

flesh removed by single white shark bites, show that large white sharks can easily consume at least 20 kg of flesh in a single bite. Pratt *et al.* (1982) also noted that the same individuals were seen around the carcass for at least 1 week. Both white and blue sharks seem to feed selectively on the blubber layer of a carcass (see Klimley, 1994); they move along the carcass and strip off and eat the outer layer (Fig. 6B and D). Carey *et al.* (1982) estimated that 30 kg of blubber may provide enough food to satisfy the energy needs of an average-sized white shark for 1.5 months. It seems, then, that the sharks may maximize their energy intake by preferentially feeding on cetacean blubber.

Summary

Nineteen specimens of odontocetes found stranded alive or recently dead on beaches along the West Coast of the United States, mostly from central California, showed bite wounds attributable to white sharks *C. carcharias*. Bites inflicted prior to death confirm that the white shark occasionally preys on small odontocetes in the eastern North Pacific Ocean. These prey include the harbor porpoise *P. phocoena*, Dall's porpoise *P. dalli*, Pacific white-sided dolphin *L. obliquidens*, Risso's dolphin *G. griseus*, pygmy sperm whale *K. breviceps*, dwarf sperm whale *K. simus*, Cuvier's beaked whale *Z. cavirostris*, and Stejneger's beaked whale *M. stejnegeri*. On the basis of stranding records, white shark predation on cetaceans in the region seems uncommon. Most wounded odontocetes were recovered during summer and early fall, and seasonal trends were likely due to white shark, not cetacean, abundance. Usually, large (>350-cm) white sharks attack cetaceans, and most bites on recovered carcasses are on the caudal peduncle or the abdomen. White sharks also commonly scavenge on carcasses of large cetaceans. Up to a dozen such carcasses are beached along the central California coast each year, and many show evidence of scavenging by sharks. In the eastern North Pacific, the natural mortality of large cetaceans offers a potential food source for white sharks during spring and early summer.

Acknowledgments

Thanks go to the Museum of Vertebrate Zoology, University of California, Berkeley; R. Bandar, I. D. Szczepaniak, L. Thomsen, D. Catania, B. Cutler, and T. Iwamoto of the California Academy of Sciences; K. D. Hanni, K. Beckmann, and M. Webber of the Marine Mammal Center, Sausalito; J. A. Seigel and J. Heyning of the Los Angeles County Museum of Natural History; H. J. Walker, Jr., of the Scripps Institution of Oceanography, La Jolla; and C. Keiper, J. Cordaro, and field volunteers of the NMMSN, National Marine Fisheries Service. The comments by anonymous reviewers and the editors certainly improved this chapter.