Mar Biol (2009) 156:2483–2492
DOI 10.1007/s00227-009-1273-3

ORIGINAL PAPER

Determining shark size from forensic analysis of bite damage

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Received: 31 January 2009 / Accepted: 25 July 2009 / Published online: 12 August 2009

Abstract Bite damage patterns have long been used to estimate shark species and body size, with somewhat limited success. The lack of fit between damage patterns and shark size is partially due to variation in tooth size and shape within an individual. The ability to accurately predict body size from bite patterns is important for better understanding the ecological and behavioral underpinnings of shark bites/attacks on marine organisms, humans, and submarine equipment. To this end, we measured interdental distance (IDD) between the most labial teeth in the first six tooth files on both the upper and lower jaws, as well as the circumference of the portion of each jaw that bears teeth, for prepared jaw sets from fourteen shark species and regressed these data against total length. IDD is allometric as well as an accurate predictor of total length in all species examined, except *Carcharhinus acronotus*. Tooth-bearing circumference is also allometric and predictive of total length in all species. Though considerable overlap exists in IDD and circumference ranges among species for the total length ranges examined, *Carcharodon carcharias* and *Isurus* sp. can be differentiated from *Carcharhinus limbatus*, *Carcharhinus brevipinna*, and *C. acronotus* based on these values alone. When combined with knowledge of species-specific feeding behavior, geographic distribution, and habitat preferences, these simple measures from bite damage patterns allow quick, accurate assessment of shark size and potential species.

Introduction

Sharks bite both animate and inanimate objects for diverse reasons, including predation, aggression, defense, mating, and investigation of novelty (Johnson and Nelson 1973; Pratt 1979; Miller and Collier 1981; Long 1996; Heithaus et al. 2002a; Auerbach and Burgess 2007). Forensic descriptions of shark bite damage exist for submarine cables, marine turtles, pinnipeds, cetaceans, other sharks, surf boards, and humans (Alcorn and Kam 1986; Marra 1989; Long and Jones 1996; Byard et al. 2000; Caldicott et al. 2001; Woolgar et al. 2001; Heithaus et al. 2002b; Zahuranec 2003; van den Hoff and Morrice 2008). On soft objects, such as skin or blubber, shark bites are typified by a series of ragged-edged, roughly parallel lacerations that may overlap to form a crescent-shaped perimeter around a mass of tissue that may be completely excised (Byard et al. 2000; Heithaus 2001b; Woolgar et al. 2001; Auerbach and Burgess 2007) (Fig. 1, upper image). On hard or rigid

Communicated by U. Sommer.

Electronic supplementary material The online version of this article (doi:10.1007/s00227-009-1273-3) contains supplementary material, which is available to authorized users.

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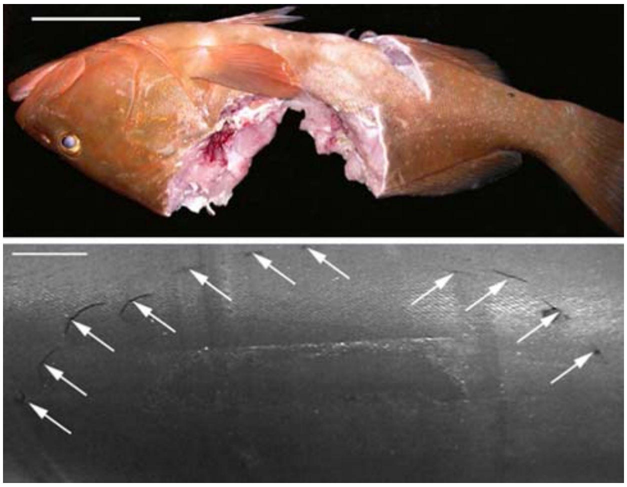

Fig. 1 Representative shark bite damage on a tough, rigid surface and a soft, pliable surface. The *upper image* shows a bite circumference on a grouper from the upper jaw of a Caribbean reef shark *Carcharhinus perezii*. The bite circumference is 282 mm. The *lower image* shows a bite impression on a nitrile butadiene hose from the lower jaw of *C. perezii*. Centers of the perforations made by each tooth are indicated by *arrows*. The mean interdental distance (IDD) is 7.6 mm. The *scale bar* in the *upper left corner* of both the images is 10 mm

objects, such as bone or metal, shark bites tend to appear as a series of roughly parallel scratches or a clearly delineated curved array of dimples or dents (Byard et al. 2000; Woolgar et al. 2001) (Fig. 1, lower image). Notable exceptions to these general descriptions are bite damage from the cookie-cutter shark *Isistius brasiliensis*, which consists of a distinct circular wound from which a plug of tissue is typically removed (Gallo-Reynoso and Figueroa-Carranza 1992; Gasparini and Sazima 1996), and bite damage from the nurse shark *Ginglymostoma cirratum*, which appears as a concave wound generated by suction feeding (GHB, unpublished data).

Biologists are often called upon to estimate shark size and species from investigation of bite wounds and/or damage. Having reliable estimates of size and species are key to understanding feeding and hunting behavior (Stillwell and Kohler 1982), dietary composition (Cortes 1999), and ecological interactions (Heithaus et al. 2002a), as well as making assessments of potential hazard to humans and human constructs (Burgess 2008). To date, no standardized forensic metric for making such estimates exists. Predictions are typically based on the circumstantial experience of an investigator with feeding behavior, geographic distribution, and bite damage from particular species and size ranges of sharks, or in some cases they are made by matching the wound pattern to dried jaws in museum collections (Ritter and Levine 2004). Though numerous qualitative and quantitative descriptions of shark bite damage exist, only one comprehensive effort to distinguish bites among species and sizes of bony fishes and sharks has been published and was largely confined to bites on ropes (Berteaux and Prindle 1987). In examining predation of killer whales *Orcinus orca* on bowhead whales *Balaena mysticetus*, George et al. (1994) determined that the range of the distance between consecutive tooth tips (interdental distance or IDD) in the skulls of museum specimens matched the range of the distance between slashes on the skin of *B. mysticetus* and was distinct from the IDD range of beluga whales *Delphinapterus leucas*, another known *B. mysticetus* predator. If species-specific ranges of IDD exist in sharks, identifying the species responsible for damaging an object or organism should be possible by making a few simple forensic measurements. In addition to IDD ranges potentially being species-specific, substantial differences in tooth morphology occur between the upper and lower jaws of many shark species (Compagno 1984a, b) such that tooth spacing may vary between jaws within a species. If this is the case, damage done by each jaw could be differentiated, allowing an assessment of shark position relative to prey position during a bite (Ritter and Levine 2005).

Tooth size is known to vary directly with total length in some shark species (Compagno 1984a, b; Shimada 2002, 2004; Shimada and Seigel 2005). Given that this relationship also applies to IDD and is consistent across a broad size range within a species, estimates of total length could be made after species identification. Alternatively, in the presence of overlap between IDD ranges for two or more candidate species being able to determine shark size could be combined with knowledge of total length ranges to eliminate species from consideration. The circumferential region of damage made by a shark's teeth during a single bite on a hard or rigid object, in the absence of head shaking, cannot exceed the summation of IDD measurements along the functional row of teeth (bite circumference). If the teeth penetrate to their base, the bite circumference will be slightly greater than the cumulative IDD. In the presence of a predictable relationship between IDD and shark total length, bite circumference measurements could establish the minimum size of the shark responsible for bite damage and be helpful in further narrowing candidate species.

This study has two goals: (1) introduce a method for identifying shark size and possibly species from forensic analysis of bite damage, and (2) present anatomical data for a discrete set of shark species over a broad range of sizes that can be correlated with forensic data to make informed predictions about individuals responsible for bite damage.

Materials and methods

Species were selected for consideration in this study based on a combination of three factors: (1) their known propensity to bite humans (Baldridge 1973; Burgess 2008: www.flmnh.ufl.edu/fish/sharks/statistics/species2.htm), marine mammals, and turtles (Compagno 1984a, b; Snelson et al. 1984; Heithaus et al. 2005; Martin et al. 2005); (2) their ecological role as high order predators (Compagno 1984a, b; Cortes 1999; Heithaus 2001a, b; Hoffmayer and Parsons 2003); and (3) the availability of specimens. Three lamniform species, the white shark *Carcharodon carcharias*, shortfin mako shark *Isurus oxyrinchus*, and longfin mako shark *I. paucus*, and 11 carcharhiniform species, the tiger shark *Galeocerdo cuvier*, bull shark *Carcharhinus leucas*, blacktip shark *C. limbatus*, sandbar shark *C. plumbeus*, silky shark *C. falciformis*, dusky shark *C. obscurus*, spinner shark *C. brevipinna*, blacknose shark *C. acronotus*, lemon shark *Negaprion brevirostris*, scalloped hammerhead shark *Sphyrna lewini*, and great hammerhead shark *S. mokarran*, were selected for this study.

In order to sample across the widest possible size range for these species, between 10 and 24 dried jaw sets per species were obtained from several public and private collections (Jaws Unlimited, Mote Marine Laboratory, the Florida Museum of Natural History, and the University of South Florida) (Table 1). Jaws in each collection were initially acquired by recreational and commercial fishers, as well as during scientific sampling surveys. In most cases, catch data associated with each jaw set included date, fisher or sampling expedition, shark weight, and shark sex. Only those jaws with intact, undamaged teeth and for which a verified total length was available were used. Reconstructed jaws from which teeth had been removed, cleaned, and replaced were not used except in the case of five of the larger specimens of *C. carcharias* from Jaws Unlimited. An exception was made in this case because large specimens were otherwise lacking.

Data collection

Beginning with the tip of the most labial tooth in the anterior tooth file on the left side of the lower jaw, the distance to the tip of the tooth in the next consecutive tooth file (IDD) was measured to the nearest 0.1 mm using Vernier calipers (Fig. 2). Symphyseal tooth files were not considered in these measurements because these teeth are often small, misshapen, and randomly arranged. Moving posterolaterally, the IDD was then measured for the next four pairs of consecutive tooth files, ending with the sixth tooth file. These measurements were then repeated on the right side of the lower jaw and both sides of the upper jaw, producing a total of 20 measurements per jaw set. The IDD was then measured between the tips of the most labial teeth in the first tooth file on each side of the symphysis in the lower and upper jaws. Finally, bite circumference was measured by placing one end of a piece of inelastic twine at the base of the most posterior tooth in the functional row on one side of each jaw and contouring it under tension along consecutive tooth bases until reaching the most posterior tooth base

Table 1 Summary of shark species sampled, including the number of jaw sets from which measurements were taken

Family Common name	Scientific name	Species code	IDD sample size (*n*)	Circumference sample size (*n*)
Lamnidae	–	–	–	–
White shark	*Carcharodon carcharias*	CC	18	20
Shortfin mako shark	*Isurus oxyrinchus*	IO	24	23
Longfin mako shark	*Isurus paucus*	IP	19	19
Carcharhinidae	–	–	–	–
Tiger shark	*Galeocerdo cuvier*	GC	10	22
Bull shark	*Carcharhinus leucas*	CLE	17	22
Blacktip shark	*Carcharhinus limbatus*	CLI	18	20
Sandbar shark	*Carcharhinus plumbeus*	CP	21	23
Silky shark	*Carcharhinus falciformis*	CF	6	10
Dusky shark	*Carcharhinus obscurus*	CO	14	17
Spinner shark	*Carcharhinus brevipinna*	CB	11	12
Blacknose shark	*Carcharhinus acronotus*	CA	17	20
Lemon shark	*Negaprion brevirostris*	NB	7	10
Sphyrnidae	–	–	–	–
Scalloped hammerhead shark	*Sphyrna lewini*	SI	6	14
Great hammerhead shark	*Sphyrna mokarran*	SM	7	13

IDD interdental distance, the distance between the tips of the most labial teeth in adjacent tooth files. *Circumference* the distance along the tooth bases from the last tooth on one side to the last tooth on the other side in the upper or lower jaw of a jaw set

Fig. 2 Oblique anterior view of a cleaned and prepared bull shark *Carcharhinus leucas* lower jaw depicting the measurement of interdental distance (IDD) (*short line*) and bite circumference (BC) (*long line*). Bite circumference is slightly larger than the summation of all IDD measures in a jaw because it is measured along the tooth bases. IDD was measured between the most labial teeth of the first six tooth files on each side of the symphysis, excluding symphyseal teeth (if present). *S* Symphyseal tooth. *Numbers* indicate tooth position counting from the symphysis

on the other side of the jaw (Fig. 2). This measure simulates a total bite circumference of the upper and lower jaws provided the teeth penetrate to their bases. The length of this twine was then measured with a ruler to the nearest millimeter. The arc of curvature of the bite circumference was not measured for two reasons: (1) the dried position of the jaws was often anatomically incorrect, and (2) this measurement is known to change during biting due to torsion of the jaw cartilages in at least some shark species (Wu 1994).

Data analysis

Two average IDD values were calculated for each jaw set, one for the upper and one for the lower jaw, and the range of these values was determined for each species. Paired *t*-tests were then performed for each species to determine whether IDD differed between the upper and lower jaw within individuals. If the paired *t*-test for a species indicated no difference between jaws, all IDD values for each individual were averaged, this value was log-transformed, and then average IDD values for all individuals were regressed against the logarithm of total length using Model I linear regressions. If the paired *t*-test for a species indicated a difference between the upper and lower jaws within individuals, however, the log-transformed average IDD values for the upper and lower jaws were regressed independently against the logarithm of total length using Model I linear regressions. Significance of each regression was assessed via ANOVA ($P = 0.05$). The slope of each regression was compared against an isometric slope of one using a modified *t*-test (Zar 1999).

The range of bite circumference values was determined for the upper and lower jaws of each species independently. Paired *t*-tests were then performed for each species to determine whether bite circumference differed systematically between the upper and lower jaws. In all species *t*-test results indicated a difference between the upper and lower jaws, so the log-transformed bite circumference values for the upper and lower jaws were regressed independently against the logarithm of total length. Significance of each regression was assessed via ANOVA ($P = 0.05$).

Effects of shrinkage

To determine to what degree using dried jaws influenced the measurements made during this study, a sample of ten fresh sets of jaws was obtained from *Carcharhinus plumbeus* spanning the total length range of dried jaws already used. Jaws from *C. plumbeus* were used because this species is a moderate to large carcharhinid (Compagno 1984b), was already included in the IDD analysis, and fresh jaws were readily obtainable. Measurements of IDD and bite circumference were taken while the jaws were still fresh, as described above. The jaws were then dried completely over 3 months, and the same measurements were taken a second time. Average IDD was calculated for each set of jaws as a whole, as well as for the upper and lower jaws in each set independently. Paired *t*-tests were then performed for pre- and postdrying IDD and circumference measurements to assess the effects of shrinkage.

Results

Sufficient data were collected to examine IDD ranges and size trends in ten species (Table 2). Among species, there was substantial overlap in IDD range, however, the ranges for *Carcharodon carcharias*, *Isurus oxyrinchus*, and *I. paucus* did not overlap the ranges of *Carcharhinus limbatus*, *C. brevipinna*, or *C. acronotus*, despite overlap at the extremes of total length (except between *I. oxyrinchus* and *C. acronotus*) (Table 2; Fig. 3). Additionally, there was minimal overlap in IDD range between *C. carcharias*, *I. oxyrinchus*, and *I. paucus* as a group and *C. plumbeus*, despite substantial overlap in total length.

In six species, significant differences in IDD were detected between the upper and lower jaws, and these data were regressed separately (Table 2). Slopes ranged from 0.745 for *C. brevipinna*, indicating that IDD becomes relatively smaller with size (TL), to 1.112 for *Galeocerdo cuvier*, indicating larger *G. cuvier* have relatively larger IDD values. In half of the species, where the upper and lower jaw IDD exhibited different trends the slope was larger for the upper jaw. In all ten species, a significant

Table 2 Log-log regression parameters for average interdental distance (IDD, dependent variable) against total length (TL, independent variable)

Species	Total length range (mm)	t	Jaw	IDD range (mm)	Regression	r^2	P	P-Isom
Carcharodon carcharias	1,245–5,632	2.80**	Upper	10.9–48.9	$y = 1.005x - 2.111$	0.98	<0.001	<0.001
			Lower	10.8–47.2	$y = 0.925x - 1.808$	0.97	<0.001	<0.001
Isurus oxyrinchus	1,360–3,200	0.11	–	12.1–31.5	$y = 0.943x - 1.841$	0.88	<0.001	<0.001
Isurus paucus	1,261–3,848	3.05**	Upper	13.5–36.8	$y = 0.930x - 1.788$	0.93	<0.001	<0.001
			Lower	12.1–36.9	$y = 0.969x - 1.939$	0.93	<0.001	<0.001
Galeocerdo cuvier	711–3,581	0.67	–	3.9–25.8	$y = 1.111x - 2.563$	0.98	<0.001	<0.001
Carcharhinus leucas	1,380–2,845	3.34**	Upper	7.7–18.3	$y = 1.023x - 2.276$	0.90	<0.001	<0.001
			Lower	8.0–17.4	$y = 0.931x - 1.996$	0.92	<0.001	<0.001
Carcharhinus limbatus	780–1,935	3.55**	Upper	3.6–9.9	$y = 0.949x - 2.150$	0.86	<0.001	<0.001
			Lower	4.6–10.1	$y = 0.808x - 1.660$	0.87	<0.001	<0.001
Carcharhinus plumbeus	868–2,120	3.06**	Upper	4.4–11.9	$y = 1.040x - 2.400$	0.80	<0.001	<0.001
			Lower	4.0–11.4	$y = 1.079x - 2.549$	0.90	<0.001	<0.001
Carcharhinus obscurus	1,530–3,861	0.68	–	7.1–16.4	$y = 0.866x - 1.883$	0.93	0.001	<0.001
Carcharhinus brevipinna	1,410–2,438	1.60	–	5.7–9.7	$y = 0.742x - 1.542$	0.74	0.001	<0.001
Carcharhinus acronotus	760–1,320	7.03**	Upper	3.7–6.5	$y = 0.722x - 1.520$	0.53	0.006	<0.001
			Lower	4.0–7.8	$y = 1.016x - 2.333$	0.86	<0.001	<0.001

Pretransformed values of both the variables are in millimeters. t = values of the t statistic from paired t-tests between upper and lower jaws within a species. ** highly statistically significant ($P \leq 0.01$). Data were regressed separately by jaw for species with a significant t statistic. P = significance level of regression when compared against an expected slope of zero. A P value less than 0.05 indicates a relationship between IDD and TL. P-Isom = significance level of regression when compared against an expected slope of one (isometry)

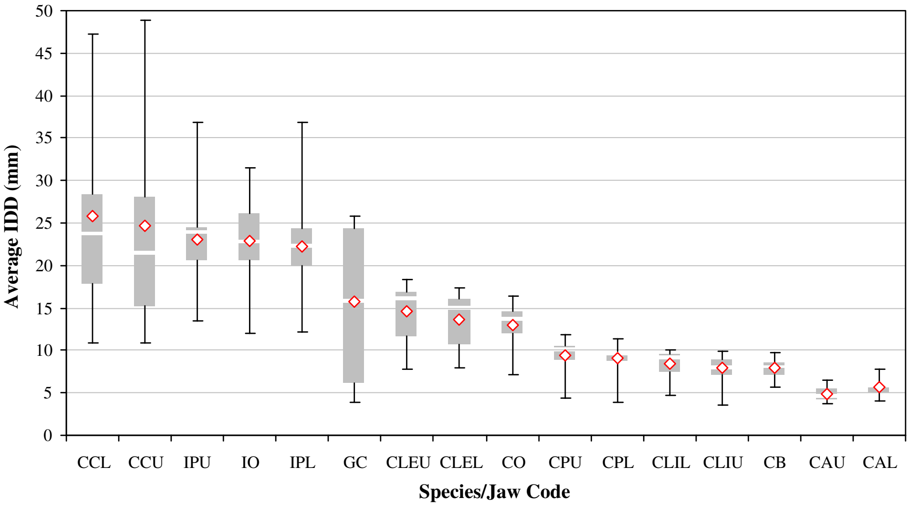

Fig. 3 *Box plots* showing the distribution of average interdental distances (IDD) for each species. Where differences between jaws were detected with paired *t*-tests the distributions for each jaw are shown separately. *X*-axis labels are a combination of genus, species (see Table 1), and jaw (upper [U] vs. lower [L], or combined [no jaw code]). *Error bars* indicate the upper and lower bounds of each range, *grey bars* represent the 25th and 75th quartiles, *white horizontal lines* indicate the median, and *diamonds* indicate the mean

allometric relationship was detected between average IDD and TL (Table 2). This relationship was positively allometric for *G. cuvier*, the upper jaw of *C. leucas*, both jaws of *C. plumbeus* separately, and the lower jaw of *C. acronotus* and negatively allometric for the remainder of the species. On an individual basis, average IDD was always greater in the lower jaw than in the upper jaw for *C. acronotus*. This relationship was also prevalent in *C. carcharias* (83% of individuals) and *C. limbatus* (82%). In *C. taurus*, *C. plumbeus*, and *I. paucus* average IDD was larger in the upper jaw in 29, 16, and 33% of individuals, respectively. In no species was there a clear tendency for the relationship between upper and lower jaw average IDD to reverse with growth.

Sufficient data were collected to examine bite circumference ranges and size trends in fourteen species (Table 3). The only species for which the bite circumference range of either jaw separated completely from at least one other species was *C. acronotus*. The ranges for both jaws in this species separated from both jaws of *C. carcharias*, *I. oxyrinchus*, *I. paucus*, *C. obscurus*, *C. taurus*, *C. brevipinna*, and *Sphyrna mokarran* (Fig. 4).

Significant differences in bite circumference were detected between upper and lower jaws in all species and

Table 3 Log-log regression parameters for bite circumference (dependent variable) against total length (TL, independent variable)

Species	Total length range (mm)	t	Jaw	Bite circumference range (mm)	Regression	r^2	P	P-Isom
Carcharodon carcharias	1,245–5,632	16.65**	Upper	224–990	$y = 1.007x - 0.800$	0.98	<0.001	<0.001
			Lower	180–760	$y = 0.966x - 0.743$	0.99	<0.001	<0.001
Isurus oxyrinchus	1,360–3,200	21.46**	Upper	239–580	$y = 1.009x - 0.778$	0.96	<0.001	<0.001
			Lower	203–505	$y = 0.924x - 0.571$	0.90	<0.001	<0.001
Isurus paucus	1,261–3,848	24.51**	Upper	231–645	$y = 0.954x - 0.607$	0.98	<0.001	<0.001
			Lower	174–570	$y = 1.051x - 1.024$	0.98	<0.001	<0.001
Galeocerdo cuvier	711–3,581	3.81**	Upper	98–540	$y = 1.085x - 1.153$	0.98	<0.001	<0.001
			Lower	97–532	$y = 1.100x - 1.215$	0.98	<0.001	<0.001
Carcharhinus leucas	1,380–2,845	18.90**	Upper	199–443	$y = 1.118x - 1.208$	0.95	<0.001	<0.001
			Lower	172–389	$y = 1.101x - 1.203$	0.94	<0.001	<0.001
Carcharhinus limbatus	780–1,935	15.94**	Upper	123–285	$y = 0.879x - 0.435$	0.92	<0.001	<0.001
			Lower	112–260	$y = 0.824x - 0.305$	0.90	<0.001	<0.001
Carcharhinus plumbeus	868–2,120	9.53**	Upper	110–307	$y = 1.163x - 1.366$	0.93	<0.001	<0.001
			Lower	102–271	$y = 1.122x - 1.279$	0.92	<0.001	<0.001
Carcharhinus falciformis	735–2,650	2.79**	Upper	96–320	$y = 0.865x - 0.477$	0.95	<0.001	<0.001
			Lower	85–299	$y = 0.912x - 0.645$	0.97	<0.001	<0.001
Carcharhinus obscurus	1,530–3,861	7.95**	Upper	212–465	$y = 0.930x - 0.629$	0.93	<0.001	<0.001
			Lower	197–435	$y = 0.935x - 0.687$	0.91	<0.001	<0.001
Carcharhinus brevipinna	1,410–2,438	9.21**	Upper	179–282	$y = 0.678x + 0.159$	0.79	<0.001	<0.001
			Lower	164–267	$y = 0.700x + 0.056$	0.76	<0.001	<0.001
Carcharhinus acronotus	760–1,320	9.17**	Upper	85–161	$y = 1.092x - 1.210$	0.96	<0.001	<0.001
			Lower	81–148	$y = 1.060x - 1.146$	0.93	<0.001	<0.001
Negaprion brevirostris	685–2,680	10.16**	Upper	103–406	$y = 0.991x - 0.776$	0.96	<0.001	<0.001
			Lower	93–389	$y = 1.026x - 0.931$	0.96	<0.001	<0.001
Sphyrna lewini	1,000–3,260	10.41**	Upper	106–298	$y = 0.879x - 0.610$	1.00	<0.001	<0.001
			Lower	95–281	$y = 0.898x - 0.708$	0.99	<0.001	<0.001
Sphyrna mokarran	2,050–4,140	9.16**	Upper	227–582	$y = 1.244x - 1.780$	0.91	<0.001	<0.001
			Lower	201–504	$y = 1.245x - 1.832$	0.88	<0.001	<0.001

Pretransformed values of both the variables are in millimeters. t = values of the t statistic from paired t-tests between upper and lower jaws within a species. ** highly statistically significant ($P = 0.01$). Data were regressed separately by jaw for species with a significant t statistic. P = significance level of regression when compared against an expected slope of zero. A P value less than 0.05 indicates a relationship between bite circumference and TL. P-Isom = significance level of regression when compared against an expected slope of one (isometry)

data were regressed separately (Table 3). Slopes ranged from 0.678 for the upper jaw of *C. brevipinna* to 1.245 for the lower jaw of *S. mokarran* and were allometric in all cases (Table 3). Upper jaw bite circumference was larger than lower jaw bite circumference in 99% of individuals sampled (demonstrated by higher y-intercept values), regardless of species. Within the size ranges sampled, the upper and lower jaw regressions did not intersect for any species sampled, indicating that despite allometric variation the upper jaw has larger bite circumference values than the lower jaw, regardless of species.

Based on measurements made on *C. plumbeus* jaws, drying does not significantly change average IDD for an entire jaw set ($P = 0.38$), or the upper ($P = 0.47$) or lower jaw ($P = 0.39$) in isolation. On average, any single IDD measurement varied by 0.35 ± 3.01% (mean ± SD), or approximately 0.31 mm, before and after drying. Shrinkage was similarly insignificant for measurements of upper ($P = 0.47$) and lower jaw ($P = 0.39$) bite circumference, for which measurements varied by 2.13 ± 1.22 and 1.78 ± 3.48%, respectively. Based on these results, the data from dried jaws presented here are thought to be accurate reflections of trends in live animals.

Figures for all regression equations presented herein and an Excel spreadsheet programmed to estimate shark size from measurements of bite damage patterns are available as digital appendices to this manuscript. Supplemental data for additional shark species can be found at (http://www.flmnh.ufl.edu/fish/Sharks/Research/Bite_Circumference.html).

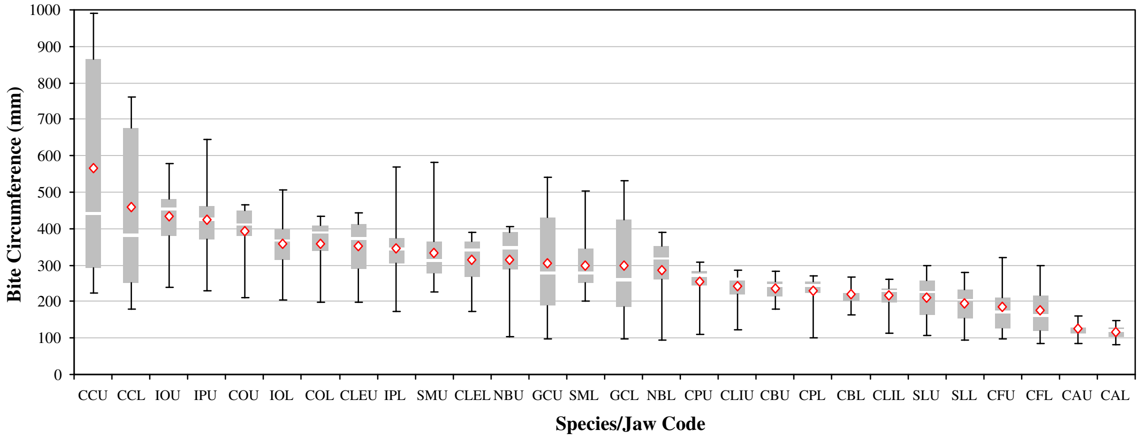

Fig. 4 *Box plots* showing the distribution of average bite circumferences for each species. *X*-axis labels are a combination of genus, species (see Table 1), and jaw (upper [U] vs. lower [L]). *Error bars* indicate the upper and lower bounds of each range, *grey bars* represent the 25th and 75th quartiles, *white horizontal lines* indicate the median, and *diamonds* indicate the mean

Discussion

Shark size directly influences swimming speed, bite force capacity, hunting behavior, and numerous ecological relationships (Snodgrass and Gilbert 1967; Graham et al. 1990; Heithaus 2001b; Heithaus et al 2002a, b; Huber et al. 2006; Hazin et al. 2008). Quantifying shark size from forensic examination of bitten organisms or objects can increase understanding of predator–prey interactions and feeding ethology and provide useful data on the size and species of shark attacking humans. Additionally, this analysis may help reduce the risk of attacks by informing the use of specific safety measures both for humans [e.g., protecting swimming beaches with nets of a specific mesh size to reduce indiscriminant catches (Dudley and Simpfendorfer 2006)] and inanimate submarine equipment [e.g., protecting cables with steel mesh that is sufficiently thick but not too heavy (Marra 1989)]. The method presented here provides a way in which shark size, and in some cases species, can be determined from a few easily collected forensic measurements. Though substantial overlap exists among the ranges of both IDD and bite circumference for the species considered, complete separation occurs between some species pairings. These species-specific ranges can be used to eliminate certain species during the course of an investigation. Regressions can then be used to generate size estimates for selected species. Where IDD relationships differ with size between the upper and lower jaws of a species, the total length estimates from each regression can be compared to identify mismatches and eliminate these species from further consideration. Bite circumference regressions generate minimum predictions of total length because unfavorable angles of attack or use of only a portion of the jaw during the bite may lead to less than a full bite circumference being present on the damaged object/organism. Preliminary field testing of this method with various species shows model predictions match well with measured shark size in baited, seminatural situations (PM and DL, unpublished data), though considerable additional testing is warranted.

The utility of the size and species estimation method presented may be detrimentally affected by at least two important factors. The first of these is that soft tissue deforms when bitten, rebounds elastically when released, and knits back together in a manner that is highly dependent on organism age (Mays et al. 1991; Mutsaers et al. 1997), mechanical loading in the vicinity of the wound (Bishop et al. 1993; Butt et al. 1995), and other individual-specific factors (Mutsaers et al. 1997; Auerbach and Burgess 2007). This means that in cases where multiple overlapping bites (i.e., ‘chewing’) occur exclusively on soft tissue, the capacity to estimate shark size and species may be substantially limited. In cases where soft tissue damage is not extensive, however, it may be possible to surgically reconstruct the tissue and obtain discernable bite patterns (Byard et al. 2000). The second major factor affecting the utility of IDD and bite circumference data is that all materials degrade with time. This issue is most pertinent when examining biological tissues, as noted above, but is also applicable to man-made objects that may rust or corrode over time causing damage patterns to become obscured. To maximize predictive capacity, measurements of IDD and bite circumference should be taken from the least malleable or elastic material within a damaged object or organism (e.g., bone, shell, metal) and as quickly as possible after damage occurs.

To maximize the accuracy of predictions of shark species and size made using the method presented, several additional pieces of information associated with a specific bite/attack must be taken into consideration. First, the distribution of potential species within a geographic and oceanographic framework must be considered. Though many shark species are cosmopolitan, some occur only in a single ocean basin (e.g., *Carcharhinus acronotus*) (Compagno 1984a, b) or are ecologically separated within a geographic region. Parameters such as water depth, temperature, and salinity are important in determining species distribution because of physiological limitations, novelties, and/or preferences (Compagno 1984a, b; Pyle et al. 1996; Wintner et al. 2002; Hopkins and Cech 2003; Campana and Joyce 2004). Another important factor in making accurate predictions of species and size is knowledge of the feeding ethology and diet of candidate species. *Carcharodon carcharias* is a well-documented seasonal hunter of pinnipeds in the vicinity of breeding colonies and patrols the deep waters adjacent to beaches (Tricas 1985; Klimley et al. 1996, 2001; Kirkwood and Dickie 2005). In contrast *Isurus oxyrinchus*, which geographically co-occurs with *C. carcharias* and has overlapping IDD and bite circumference ranges, tends to inhabit deeper waters and consume a diet primarily of bony fish and cephalopods, though marine mammals and turtles are occasionally taken by large specimens (Stillwell and Kohler 1982; Compagno 1984a). Based on these disparities in behavior and diet, bites on pinnipeds near breeding colonies are much more likely to be from *C. carcharias*.

Two additional, though rare, sources of information that may be combined with IDD and bite circumference data to narrow predictions of shark species and size are whole teeth/tooth fragments imbedded in the object/organism and eyewitness accounts of damage being inflicted. By virtue of the violent, forceful nature of shark bites, and because teeth are flexibly attached to the jaw with collagen fibers, whole teeth or fragments thereof may become imbedded in a target object/organism (Berteaux and Prindle 1987; Byard et al. 2000; Woolgar et al. 2001; Auerbach and Burgess 2007). These can then be compared to catalogues of shark tooth shape (e.g., Compagno 1984a, b) or preserved specimens, X-rayed (Gafner et al. 1985), or subjected to radiological analysis (Davies and Campbell 1962) to determine species. Once species has been determined estimates of total length can be made. Eyewitness accounts of shark bites are most common when humans are the target (Woolgar et al. 2001; Ritter and Levine 2004), though reports of observed attacks on marine mammals also exist (Alcorn and Kam 1986; Mann and Barnett 1999; Maldini 2003; Gibson 2006). Eyewitness accounts vary substantially in their reliability and are influenced by environmental conditions, distance from the incident, and psychological state of the reporting party (Burgess 2008 unpublished data: www.flmnh.ufl.edu/fish/sharks/statistics/species2.htm). Despite these shortcomings, valuable information may be gleaned by comparing multiple accounts and elucidating similarities that identify diagnostic features of a candidate species.

It should be noted that the data used to construct the regressions here were taken largely from adult and/or subadult specimens due to the availability of prepared jaws. Allometric changes in tooth shape and/or spacing that occur over early ontogeny were, therefore, likely excluded from this analysis. Isolating variation in these parameters caused by such developmental factors will require collection of data over the entire size range of a species, as well as having detailed information on capture site and condition.

Case study/example

On October 31, 2003, a 13-year-old female was attacked while surfing off Makua Beach, Haena, Hawaii. Most attacks on surfers in Hawaii are attributed to *Galeocerdo cuvier* (Burgess 2008 unpublished data). The severe nature of the attack, which resulted in traumatic amputation of the victim's left arm and removal of a large semicircular portion of the victim's surfboard (Fig. 5), resulted in widely reported speculation about the involvement of a 14–15 ft (4.4–4.7 m) TL-sized shark. The bite circumference on the surfboard measured 645 mm. The surfer was lying prone on her surfboard when the attack occurred, and the shark was observed to be in an upright position. The logarithm (base ten) of the measured bite circumference (2.810) was inserted as the dependent variable (Y) into the upper jaw regression equation for *G. cuvier* ($y = 1.085x - 1.153$) (Table 3), the base-ten logarithm of TL (x) was solved for, and the antilog was calculated to yield a minimum length estimate of 4,493 mm. This estimate falls well within the known total length range for *G. cuvier* (Compagno 1984b) and corroborates estimates made by scientists at the time of the incident.

Fig. 5 Bite damage to a surfboard produced by a large tiger shark (*Galeocerdo cuvier*) during a traumatic injury attack upon a human in Hawaii. The bite circumference (ends shown by *arrows*) was measured on the photograph to be 645 mm. The size of the shark responsible for the damage was predicted, using the upper jaw circumference equation in Table 3, to be 4,486 mm in total length. See text for additional details (Case Study). Photograph: R. Honebrink

Conclusions

Considerable ability exists to determine shark size from easily quantified forensic measurements of bite damage. Average IDD can provide a robust estimate of total length in most cases because high-fidelity linear relationships exist between these variables. For some species the ability exists to discriminate upper from lower jaw damage, providing knowledge of the shark's position during a bite. Bite circumference measurements can be used to generate a minimum estimate of shark size but are substantially less informative than average IDD when only a portion of the jaw is employed during biting. In nearly all cases, for the species surveyed, upper jaw bite circumference is larger than lower jaw bite circumference, again facilitating determination of shark position during a bite. It should be noted, however, that this relationship is reversed for some shark species (e.g., the bluntnose sixgill shark *Hexanchus griseus*) (DL, unpublished data). When combined with knowledge of shark feeding behavior, geographic distribution, and other circumstantial evidence, measurements of IDD and bite circumference can be used to narrow the list of candidate species and make informed predictions of shark species and size from bite damage patterns. Additional resources to aid in the process of shark identification are available through the Florida Museum of Natural History at (http://www.flmnh.ufl.edu/fish/Sharks/Research/Bite_Circumference.html). Data collection from species not included here is ongoing and will be available upon final analysis and the website mentioned above.

Acknowledgments The authors are indebted to G. Hubbell, E. Clarke, J. Castro, and R. Hueter for access to their scientific collections of shark jaws, without which this project would not have been possible. Our sincere thanks to H. Hughes for assisting with preliminary data collection. Two anonymous reviewers contributed substantially to the final format of the manuscript. Funding for this project was provided in part by CAPES fellowship (BEX 1277-02/2) to A.L.F.C. The photograph in Fig. 5 was contributed by R. Honebrink. All procedures described herein comply with current laws of the United States of America.

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