

Insights into young of the year white shark, *Carcharodon carcharias*, behavior in the Southern California Bight

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Received 9 May 2003 Accepted 2 September 2003

Key words: satellite telemetry, foraging, diving, thermoregulation

Synopsis

A young of the year female white shark, *Carcharodon carcharias*, was tagged with a pop-up satellite archival tag off Southern California in early June of 2000. The tag was recovered after 28 days, and records of temperature, depth and light intensity were extracted. Depth and temperature records indicate a number of interesting behaviors, including a strong diurnal pattern. At night the shark remained in the top 50 m, often making shallow repetitive vertical excursions. Most dives below the mixed layer were observed during the day, 91% of which occurred from 05:00 to 21:00 h, with depths extending to 240 m. Many of the dives exhibited secondary vertical movements that were consistent with the shark swimming at the bottom (at depths from 9 to 165 m) where it was most likely foraging. The white shark experienced dramatic and rapid changes in temperature, and demonstrated a considerable tolerance for cold waters. Temperatures ranged from 9°C to 22°C, and although 89% of the total time was spent in waters 16–22°C, on some days the small shark spent as much as 32% of the time in 12°C waters. The deep dives into cold waters separate the white sharks from mako sharks, which share the California Bight nursery ground but appear to remain primarily in the mixed layer and thermocline. Movement information (derived from light-based geolocation, bottom depths and sea surface temperatures) indicated that the white shark spent the 28 days in the Southern California Bight, possibly moving as far south as San Diego, California. While the abundance and diversity of prey, warm water and separation from adults make this region an ideal nursery ground, the potential for interaction with the local fisheries should be examined.

Introduction

Our understanding of the biology of adult and adolescent white sharks has advanced dramatically over the last 10–15 years (see Ellis & McCosker 1991, Klimley & Ainley 1996). Most studies have benefited from the development of a suite of new tagging technologies (Arnold & Dewar 2001) as well as the affinity of white sharks for near-shore habitats, which provides an excellent opportunity for shore-based research projects. Using a combination of photo identification, conventional tagging, visual observations, satellite technologies and acoustic telemetry, researchers have amassed a substantial global database on white shark biology. Studies have examined long-term site

fidelity (Anderson & Goldman 1996, Cliff et al. 1996, Ferreira & Ferreira 1996), foraging strategies (Tricas & McCosker 1984, Klimley et al. 2001), thermal biology (Carey et al. 1982, McCosker 1987, Goldman 1997) and general movement and activity patterns (Klimley et al. 1992, Strong et al. 1996, Goldman & Anderson 1999). While most efforts have focused on the near-shore environment, satellite telemetry is beginning to provide insights into offshore movements, reinforcing the capacity for extensive migrations in adults (Boustany et al. 2002).

These collective research efforts have provided a rough outline of the biology of white sharks, especially off the west coast of North America. In the waters off California and Mexico, white shark abundance varies

seasonally and geographically, although over a large portion of the coast they are encountered year round (Klimley 1985, Long et al. 1996). Marine mammals form a relatively large portion of the adult shark's diet (Tricas & McCosker 1984, Klimley 1985), and adult white sharks are commonly associated with pin-niped rookeries along the California coast, particularly at Año Nuevo and the South Farallon Islands. In the summer it is thought that the females move from these feeding areas to nursery grounds to give birth (Klimley 1985, Francis 1996). Pupping is thought to occur during the summer and fall in the California Bight, south of Point Conception. In this region, both pregnant females and young of the year (YOY) white sharks have been incidentally caught by a number of fishing gear types, primarily gill nets (Klimley 1985). The incidental take of young sharks both here and in other areas has provided the opportunity to examine stomach contents and it is apparent that, when compared to adult white sharks, the juveniles have a substantially different diet. While the adults feed largely on marine mammals (Tricas & McCosker 1984, Casey & Pratt 1985, Klimley 1985), juveniles have been found to feed primarily on invertebrates, demersal teleosts and elasmobranchs. Squid and epipelagic fish are also consumed but to a lesser extent. This shift in diet is matched by an ontogenetic change in dentition (Tricas & McCosker 1984, Hubbell 1996).

Although the combined global effort in the study of white sharks is rapidly elucidating adult and adolescent biology, almost nothing is known about the juveniles. Current understanding of YOY biology is based largely on the incidental take of juveniles and pregnant females, and stomach content analyses from a relatively small number of individuals (Klimley 1985, Francis 1996, Uchida et al. 1996). Given the considerable shift in diet and the differences in geographic location, inferences about juveniles based on adult behavior are questionable. With the global concern about white shark conservation (Heneman & Glazer 1996, Murphy 1996), it is critical that additional information is obtained on this poorly understood life history stage. We report here the results from one pop-up archival satellite tag (PAT) recovered after 28 days on a YOY white shark in the Southern California Bight.

Materials and methods

A juvenile female white shark, 1.4 m fork length (FL), was captured in a bottom set net off of Long Beach,

California on May 28, 2000, and then taken to the Southern California Marine Institute facility in Long Beach Harbor. Here the animal was maintained in a 6 m covered tank for 4 days where it remained alert and in good condition. Prior to its release on June 2, 2000 the shark was moved from the tank using a sling, measured and then placed in a small holding tank on a fishing vessel. While still in the vessel's holding tank, the PAT (PAT-2000, Wildlife Computers, Redmond WA, U.S.A.) was inserted at the base of the dorsal fin using a large plastic dart. The shark was then released just off shore of Long Beach, California in 24 m of water. Although the satellite tag was set to release after 6 months, it was recovered 28 days later by a second fisherman near the point of release, at Huntington Flats, on June 30, 2000. The fisherman reported that only the tag was entangled in the net and that there was no evidence of the small shark.

The PAT is a relatively new tool used to examine the large-scale movements and behaviors of pelagic fish (Lutcavage et al. 2000, Block et al. 2001, Boustany et al. 2002). These devices are secured to the fish and collect data on temperature ($\pm 0.05^{\circ}\text{C}$), depth (± 0.5 m) and light intensity (measured as irradiance at 550 nm) every 2 min. At a predetermined time, the tag releases from the fish, floats to the surface and uploads summarized data to the Argos satellites. If the tag is recovered either prior to or after its predetermined release time, the full data set (unsummarized) can be extracted.

Geolocation

Values for latitude and longitude are estimated using light intensity measurements and the apparent time of dawn and dusk as indicated by the exponential change in light levels recorded over these periods (Hill 1994, Klimley et al. 1994, Hill & Braun 2001). By calculating the midpoints between dawn and dusk, local noon and midnight can be determined and longitude calculated using standard astronomical equations. Day length (the time interval between dawn and dusk) changes along the earth's meridians in a predictable manner and thus estimates of day length can be used to calculate latitude assuming the date is known. It is estimated that for this model of Wildlife Computers PAT tags when archival records are recovered, latitude and longitude can be determined within $0.78\text{--}3.5^{\circ}$ and $0.15\text{--}0.25^{\circ}$, respectively (Musyl et al. 2001). Latitude estimates can however, be improved by comparing sea surface temperature (SST) measured by the tag with SST determined from Advanced Very High Resolution

Radiometry (AVHRR) imagery along a line of longitude with constraints employed on maximum movements between days (Block et al. 2001, Gunn & Block 2001). Location estimates are further improved by comparing maximum deep dives or bottom depths (see below) to regional bathymetric maps.

Vertical movements

From depth and temperature data recorded by the tag, information on habitat preferences, behavioral patterns and the thermal characteristics of the water column can be obtained. To examine vertical movements, dives longer than 4 min, where temperature changed by more than 5°C (this eliminated minor vertical movements), were characterized by their depth (D_{depth}), temperature at depth (D_{temp}), duration (D_{duration}), time of day, the surface interval between dives (S_{interval}) and the integral of the change in temperature over the dive (T_{integral}). The integral was used to estimate the magnitude of the dive from a thermal perspective and is essentially, the temperature change multiplied by the length of exposure. This was calculated by first subtracting the ambient temperature at depth from SST for each 2-min sampling interval, providing a profile of the temperature difference with time throughout each dive. To obtain the area (integral) within the temperature profile, the area for each 2-min sampling interval was calculated by first multiplying each temperature difference by 2 min, these values were then summed over the duration of the dive (Equation (1)).

$$T_{\text{integral}} = \Sigma(\text{SST} - D_{\text{temp}}^{\circ\text{C}})2 \text{ min} \quad (1)$$

The T_{integral} will be greater for longer dives or those into cooler waters. Thus, higher T_{integral} values reflect a greater level of thermal stress. Each dive was also examined to establish whether the vertical movement at depth was consistent with the shark swimming at or near the bottom (e.g. secondary vertical movements while at depth were minimal). All data were analyzed for normalcy and the average \pm SD reported unless otherwise indicated.

Results

Geolocation

Figure 1 shows the geographic region in which the white shark was located over the 28-day deployment

based on the recapture and release points, apparent benthic swimming behavior, maximum dive depths and the SST-augmented, light-based geolocation estimates. The Huntington Flats fishing area, where the white shark encountered the net both times, is located from three miles off Long Beach to the shelf break. On 12 of the recorded days, the animal displayed dive patterns suggesting that it dove to and along the seafloor, displaying minimal secondary vertical movement while at depth. During these dives, the bottom depths ranged from 9 to 165 m (see below), and placed the shark over the continental shelf or slope, within 2–22 km of shore. Based on the available information, it appears that the shark remained in the Southern California Bight (in the area delineated by the solid line) for the 28-day deployment, moving as far south as San Diego for 3 days, from June 12 through June 14. For the remainder of the days, the available data indicated that the shark was between Long Beach and Camp Pendleton. Also, shown is the 240-m contour, which is the deepest dive depth observed. Unfortunately, the errors in geolocation estimates, even with the use of SST, preclude the generation of an actual track over this spatial scale.

Depth and temperature

The vertical movements were examined for diurnal patterns, habitat preference and other behaviors. The first 8 h after the release were excluded from the analysis to allow for a recovery period following tagging (Arnold & Dewar 2001). Based on the temperature profiles, the depth of the mixed layer varied throughout June, ranging from 10 to 20 m. (A thermal lag in the thermistor makes a more precise definition of the thermal profile difficult.) Figure 2a shows a comparison of the day and night depth distributions. (Daylight hours include the period of dawn and dusk where light is detected.) At night depths were constrained to within the top 50 m with 96% of the time spent above 20 m, 39% of which was at the surface (depth = 0–1 m). During the day, depth ranged from 0 to 240 m and although 89% of the time was above 20 m, a greater percentage of time (62%) was spent at the surface with less time in the remaining portion of the mixed layer. The shark spent significantly more time in deep water during the day than at night (2-sample Kolmogorov–Smirnov Test, $p = 0.008$).

A summary of temperature measurements over the record indicated the following. Although the majority of the time (89%) was spent in waters 16–22°C

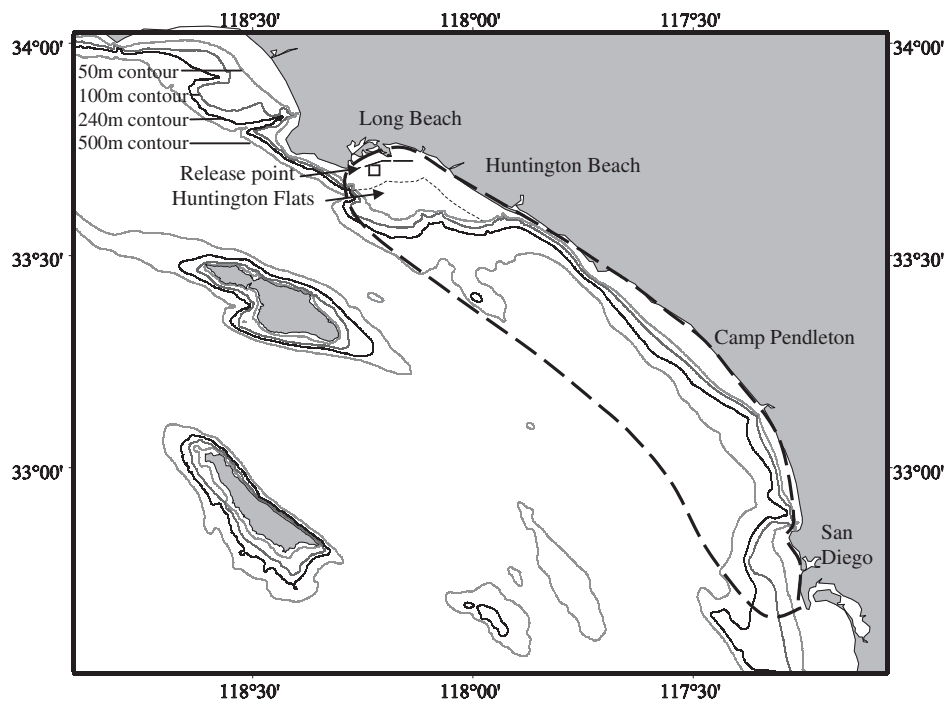


Figure 1. Map of Southern California outlining the estimated area where the white shark remained over the 28-day deployment. The black dotted line indicates the 3-mile line, which marks the eastern boundary of the fishing grounds at Huntington flats. The 240 m contour, the deepest depth the shark attained, is also indicated.

(Figure 2b), on some days the shark spent as much as 32% of the time in 12°C waters (see below). The lowest temperatures encountered by the shark, down to 9°C, were associated with vertical excursions. On average, the minimum temperature encountered on a given day was lower than SST by 8.6°C (± 3.0 , ranging from 2.4°C to 13.4°C). SST varied by only 3.8°C (18.2–22°C; average = 20 ± 1). Examination of SST in relation to daily AVHRR imagery indicated that the white shark was detected primarily in the warmer water masses found closer to shore.

While the behaviors and vertical distributions observed during the night were relatively consistent over the 28-day record, there was a considerable degree of variation observed among behaviors during the daylight hours as evidenced in Figure 3a,b. On June 8 (Figure 3a) during both the day and night hours, the shark remained in the mixed layer making regular vertical movements between the surface and ~25 m. On 20 June (Figure 3b) a very different pattern was observed. Although the shark generally remained in the top 25 m at night, during the day she was either at the surface (depth = 0–1 m) or made rapid dives below

the thermocline to an average depth of 71 m (± 7 m). She remained at depth for 26–76 min and had surface intervals ranging from 52 to 122 min. During the daylight hours on this day, the shark spent 32% of its time between 50 and 75 m in 12°C water and 65% of its time at the surface at between 20°C and 21°C.

A similar pattern of only shallow excursions at night and deep dives during the day was observed during 20 of the 28 days. Most of the remaining 8 days occurred at the beginning of the record; for 5 days immediately following its release, the shark remained above 30 m in the mixed layer. For the 20 days where deep dives were documented, a closer examination of the temporal occurrence of these dives confirms the diurnal pattern observed in Figure 3b. Of the 82 dives documented, only seven (8.5%) occurred at night and six of the seven were on two nights (June 19 and 21, 2000) shortly after the full moon (June 17, 2000). The timing of dives (Figure 4) is bi-modally distributed with peaks from 05:00 to 07:00 h and 13:00 to 19:00 h when 21% and 41% of the dives were made, respectively. When comparing 1-h blocks, the largest percentage of dives occurred before the sun reached the horizon from

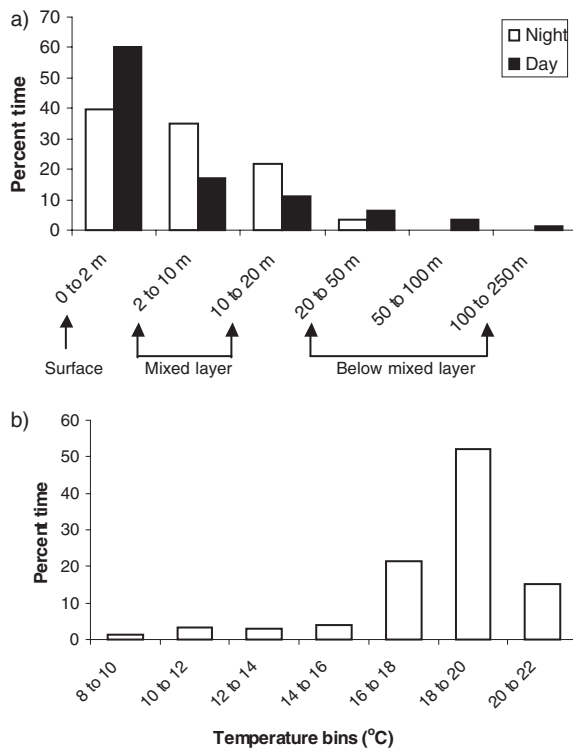


Figure 2. The percentage of time spent at different (a) depths, for both day and night, and (b) temperature for the entire 28-day record.

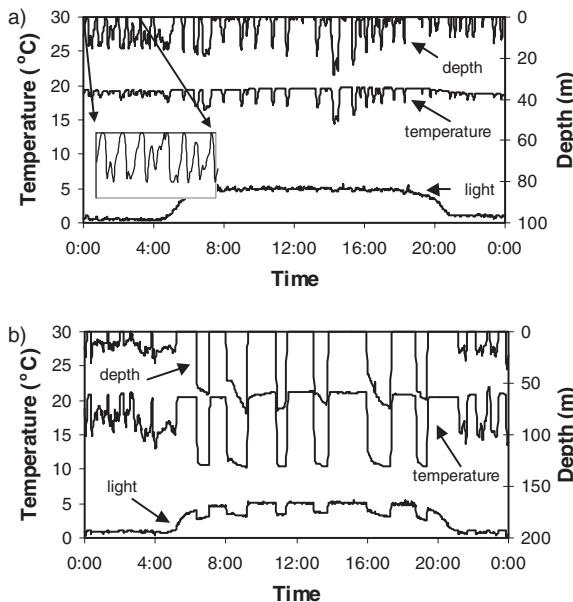


Figure 3. Temperature, depth and light level data recorded every 2 min over a 24-h period for (a) 8 June and (b) 20 June.

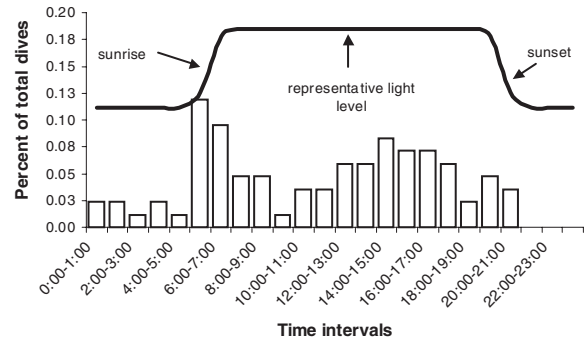


Figure 4. Percentage of dives at different hourly intervals over a 24-h day. Only dives longer than 4 min where temperature changed by at least 5°C are included. Also indicated is a representative light curve for a 24-h period.

05:00 to 06:00 h. The most extreme dive to 240 m at 9°C occurred at 05:19 h and was for 80 min.

For all dives D_{depth} ranged from 18 to 240 m (median 48 m). D_{temp} ranged from 9°C to 15°C (average $11.7 \pm 1.5^\circ\text{C}$). D_{duration} ranged from 6 to 110 min (average 39 ± 23 min). S_{interval} ranged from 0 to 716 min (median 63). The T_{interval} ranged from 27 to 900 min °C (average 296 ± 219). Although there is a large degree of variability in the data, regression analysis indicates a significant increase in S_{interval} as a function of T_{interval} ($p < 0.05$, $r^2 = 0.15$). More time in cold water was associated with longer surface intervals. Up to T_{interval} values of 444 min °C, S_{interval} ranged from 0 to 216 min, at higher values S_{interval} increased, ranging from 26 to 310 min. The shark was able to make dives into relatively cool waters (10.8°C) for up to 58 min with little time at the surface prior to subsequent dives.

Closer examination of Figure 3a,b illustrates two additional behaviors of interest. First, in Figure 3a inset, note the regular vertical excursions between the surface and the bottom of the mixed layer. The rates of ascent and descent were calculated over portions of the record when similar patterns were observed (only depth changes greater than 10 m were examined). The mean rate of ascent ($1.2 \text{ m min}^{-1} \pm 0.4$) was significantly slower than the mean rate of descent ($2.5 \text{ m min}^{-1} \pm 0.6$) (two sample t-test, $p = 0.001$). The second pattern is seen in Figure 3b. Note that at depth there is very little secondary vertical fluctuation. The profile is consistent with the shark swimming near a sloping bottom. Dives of this nature occurred on 12 days and ranged from 8 to 110 min in duration (average 44 ± 26 min) over depth from 9 to 165 m (average 51 ± 28 m).

Discussion

The archival record obtained from the pop-up satellite tag represents the most detailed dataset available on the movements and behaviors of a juvenile white shark in the Southern California Bight, a key nursery ground for this species. This white shark was likely born in the spring of 2000. The reported size at birth for white sharks is 1.2–1.5 m total length (TL) (Francis 1996). Using the conversion factors provided by Mollet and Cailliet (1996), the 1.4 m FL for the small female equals a 1.54 m TL. The record obtained provides important information over a time period in the life-history of white sharks when they are least understood and vulnerable to predation and incidental take by fisheries. Additional studies are necessary to confirm results and address a suite of additional questions.

Examination of the vertical movements, especially in relation to temperature, provides important insights into foraging strategies, thermal biology and habitat preferences of the YOY white shark. The range of depth and temperature experienced by this white shark are more extensive than might have been expected based on the limited and potentially biased data available. Catch records in the California Bight for white sharks smaller than 2 m have primarily occurred in less than 25 m of water (Klimley 1985). Also, given the size of the juvenile white shark, one would expect a lower tolerance for cold waters due to a relatively low thermal inertia. Although the majority of time was spent in the warm waters of the mixed layer, movement into deeper waters was prevalent throughout the record and on some days time spent below the thermocline exceeded 30%. This indicates that ambient temperature does not prohibit the young white sharks from using the entire water column when the animal is over the continental shelf. If the shallow vertical distribution observed primarily on the days shortly after release represents a recovery period, then the summarized data are a conservative estimate of time at depth. Note however, that the shark was released in relatively shallow water (~20 m). Recent data on adult white sharks indicate that they are also not constrained to the mixed layer but spend large portions of time below the thermocline when offshore (Boustany et al. 2002).

Detailed examination of the depth records revealed a number of interesting patterns that may be related to foraging. Although at first glance the shallow cyclic excursions (Figure 3a) appear similar to the burst-glide swimming observed in many pelagic animals (Carey & Olson 1982, Holland et al. 1990, Block et al. 1997)

to reduce transport costs (Weiss 1973), this proved not to be the case. Theoretical analysis conducted by Weiss indicates that for energy savings to be realized for negatively buoyant fish, the rate of ascent must be greater than descent and specific angles of inclination are required. Although with no information on movement over ground it was not possible to quantify angles of ascent and descent, the relative rates of ascent and descent for the small white shark are opposite that required for energy savings. A similar pattern was observed for blue sharks tracked acoustically by Carey and Scharold (1990); the rates of descent were faster than for ascent. Carey and Scharold reported that the angles of ascent and descent were also not consistent with burst-glide swimming. The fact that sharks tend to be only slightly negatively buoyant might preclude their use of burst glide as an energy saving mechanism.

The shallow, repetitive vertical excursions, which were observed predominantly at night, could be associated with nocturnal foraging. The sharks may swim down and then slowly swim up while searching for profiles against any down-welling light. The presence of sufficient light at night against which to observe profiles is supported by the dive-associated variations in light that were apparent in the tag's light record two nights away from the new moon. That is, even two nights before the new moon the light level recorded by the tag increased as the shark approached the surface. The tags are sensitive to 10 log units of light, which is similar to sharks' eyes (Gruber & Cohen 1978). It should be mentioned that while feeding may occur at night in the mixed layer, stomach content data indicate benthic foraging is more important (Tricas & McCosker 1984, Casey & Pratt 1985, Klimley 1985).

Other potential explanations for shallow repetitive vertical excursions include thermoregulation, orienting to the earth's magnetic field or searching the water column for chemical cues (Carey & Scharold 1990, Klimley et al. 2002). Chemical cues might either indicate the presence of prey or be used to navigate, as with salmon returning to their natal stream (Carey & Scharold 1990, Klimley et al. 2002). However, most of these excursions were constrained to the mixed layer and top of the thermocline and the chemical stratification and temperature fluctuations will be minimal in this region.

There are a number of diurnal migrators present in the surface waters at night that are potential prey for a small white shark including squid and teleosts such as mackerel, anchovies, sardines and hake. In fact, the California Bight is an important spawning ground

for a number of species that have been documented in white shark stomach contents (Tricas & McCosker 1984, Casey & Pratt 1985, Klimley 1985). Chub mackerel, *Scomber japonicus*, is most abundant south of Point Conception within 20 miles of shore and spawning occurs in near-shore surface waters from April to August (Hernandez & Ortega 2000, Konno et al. 2001). For the Pacific sardine, *Sardinops sagax*, the peak in spawning occurs south of Point Conception from April to August in the top 50 m of the water column (Wolf et al. 2001). Pacific hake, *Merluccius productus*, also common off Southern California, move inshore after spawning in May and follow their prey (krill) to the surface each night (MBC Applied Environmental Sciences 1987, Quirollo et al. 2001). A large squid fishery exists in Southern California, and although the peak occurs earlier in the year, the fishery can extend into the summer months (Yaremco 2001).

While foraging may occur in the mixed layer and near the surface at night, the daytime dive patterns suggest that diurnal feeding occurs at or near the bottom. The deep profiles with minimal vertical excursions in Figure 3b are similar to those observed for other species documented to be at the bottom including adult white sharks (Goldman & Anderson 1999) and tiger sharks (Holland et al. 1999). An affinity for the benthic habitats is confirmed by the occurrence of white sharks as by-catch in the bottom set net fishery as well as their diet, which consists primarily of demersal species (Tricas & McCosker 1984, Casey & Pratt 1985, Klimley 1985). The range of bottom depths observed indicates that demersal feeding occurs from relatively shallow, near-shore waters to the continental slope at 165 m, although most bottom dives were from 30 to 60 m. It is likely that this benthic foraging is primarily restricted to daylight hours due to visibility. White sharks are suggested to have retinal structure most consistent with a diurnal lifestyle (Gruber & Cohen 1985).

There were a number of deep dives during the daylight hours where the plateau in vertical movements at depth was not observed. These dives may be associated with swimming near the bottom but along the steep relief of the shelf slope, possibly indicating search behavior to locate the bottom. It is also possible that the shark was orienting to the earth's magnetic field or searching for chemical cues as discussed above (Carey & Scharold 1990, Klimley et al. 2002).

There are numerous potential prey items that the YOY white shark would encounter at depth during daylight hours over the California continental shelf

including a number of flatfish, Pacific hake and a large range of smaller elasmobranchs. California halibut, *Paralichthys californicus*, are found primarily from the surf zone to 60 m overlapping with the apparent foraging depth of the white shark (MBC Applied Environmental Sciences 1987). Additional flatfish common in the area include sanddabs, *Citharichthys* spp. (Allen & Leos 2001) and turbot, *Pleuronichthys* spp. (Leos 2001). The cabezon, *Scorpaenichthys marmoratus*, occurs from the intertidal zone to 80 m (Wilson-Vandenberg & Hardy 2001). Also, a number of small elasmobranchs including the round stingray, *Urolophus halleri*, the California skate, *Raja inornata*, (Zorzi et al. 2001), the leopard shark, *Triakis semifasciata* and the smooth dogfish, *Mustelus canis*, (Castro 1983, Smith 2001) are found in high numbers off Southern California in shallow, near-shore habitats.

The vertical movement patterns of this young female differ considerably from published data for adult white sharks. Acoustic telemetry studies conducted near the Farallon Islands with adults showed a significant correlation between swimming depth and the bottom in waters less than 30 m. When depths were greater, sharks strayed from the bottom remaining within ~30 m of the surface, seldom venturing to the surface (Goldman & Anderson 1999). One large white shark tracked offshore in the western Atlantic (Carey et al. 1982) spent most of its time in the thermocline, making only infrequent excursions to the surface or below the thermocline to ~50 m. There was no diurnal pattern apparent in the depth records and the larger sharks did not spend protracted periods at the surface. Only one acoustic track has been conducted with a juvenile white shark (Klimley et al. 2002), however, the short track duration (3.6 h) makes comparisons difficult. The behavior of fish following release is often aberrant for a matter of hours (Arnold & Dewar 2001).

The patterns observed for the small white shark were similar to those observed for blue sharks acoustically tracked by Carey & Scharold (1990). At night the blue sharks tended to remain in the thermocline or mixed layer but made deep dives during the day into water as cool as 7°C. The deep dives were punctuated by periods either at the surface or in the mixed layer that served to prevent muscle temperature from dropping too low, which was evident through the use of muscle thermistors in a number of sharks. The durations in warmer waters varied from only a few minutes to 30 min before subsequent dives. The blue sharks were reported to be feeding on cephalopods in the deep scattering layer during daylight hours. Thus, the diurnal

pattern was associated with prey availability and not a difference in visibility, which appears to be a contributing factor for the small white shark when feeding on the bottom.

In addition to the white shark, the California Bight is an important nursery ground for the short-fin mako, *Isurus oxyrinchus*, another endothermic lamnid (Holts & Bedford 1993, Taylor & Bedford 2001). The two species, however, appear to be differentiated by niche separation as indicated both by diet and behavior. Juvenile mako sharks feed primarily on small schooling pelagics such as mackerel, anchovies and sardines (Holts 1988, Taylor & Bedford, 2001) where as the white sharks focus mainly on demersal species. Acoustic tracks for three 2-year-old mako sharks (Holts & Bedford 1993) indicated that they remained in the mixed layer for 90% of the time making only short excursions below the thermocline to less than 40 m. The coldest temperature encountered was 12°C, and then only for a brief period of time. Also, no diurnal pattern was observed (although the tracks were relatively short). In a second study by Klimley et al. (2002), three additional juvenile mako sharks were tracked near a submarine canyon. Although these sharks spent most of their time near the bottom of the thermocline below the mixed layer, they did appear to be constrained to waters above 14°C and never ventured below 65 m. The available data suggest that the juvenile mako forages primarily in the thermocline and above.

The differences between temperatures encountered by the mako and white shark may reflect an enhanced ability of the white shark to tolerate cold water while foraging at depth. This thermal tolerance is likely linked to the white shark's greater endothermic capacity in comparison to mako sharks, as suggested by the higher elevation in stomach temperatures reported for adults. The maximum elevation of stomach temperature above ambient temperature reported from adult white sharks is 14.3°C (Goldman 1997) where as for mako sharks it is 8°C (Carey et al. 1981).

The YOY white shark exhibited a surprising tolerance for large changes in ambient water temperature despite her small size. This is particularly impressive when one considers that although white sharks are endothermic, not all body regions are supported by countercurrent heat exchangers. The temperature of tissues, such as the heart will parallel water temperature, but must continue to function and support systems that are thermo-conserving. This small female was able to spend up to 80 min in waters at 9°C, which is

11°C cooler than surface waters. A number of surface-oriented, pelagic fish including yellowfin tuna, striped marlin and blue marlin have been demonstrated to be limited to temperature ranges from SST to 8°C cooler than SST (Brill et al. 1993, 1999, Block et al. 1997). This is a narrower temperature range than observed in this study.

Although this juvenile white shark showed a considerable tolerance for cold waters, vertical movement patterns indicated some thermal constraints on behavior. The positive relationship between thermal dive magnitude (as indicated by T_{integral}) and the subsequent surface interval as well as the pattern of regular vertical excursions are indicative of behavioral thermal regulation (Carey & Scharold 1990, Holland et al. 1992). During longer dives a greater thermal debt was incurred presumably requiring a more extensive surface interval to thermally recharge prior to subsequent dives. The variation in S_{interval} is likely explained by the multitude of factors that will influence behavior including the presence of predators, feeding and digestion. As well as influencing subsequent behaviors, feeding has a direct impact on thermal biology. Because prey consumed is at ambient temperature, feeding can cause a drop in visceral temperature (McCosker 1987, Goldman 1997, Lowe & Goldman 2001). Some sharks may also exhibit an elevation in stomach temperature with feeding as has been observed in a number of teleosts (Carey et al. 1984, McCosker 1987). Thus, successful foraging will complicate interpretation of the link between time at depth and subsequent surface intervals.

The punctuated vertical excursions observed in Figure 3b are similar to patterns that have been observed in a number of species employing both behavioral (blue sharks, Carey & Scharold 1990) and physiological (bigeye tuna, Holland et al. 1992, Dagorn et al. 2000) thermoregulation. Measurements of body temperature are necessary to verify the behavioral thermoregulation as well as to document the white shark's capacity for modifying the efficiency of their countercurrent heat exchangers and physiological thermoregulation (Holland et al. 1992, Dewar et al. 1994). Recent evidence indicating that both salmon sharks (Goldman pers. comm.) and mako sharks (Bernal et al. 2001) can modify heat transfer suggests that their close relative the white shark will be capable of the same. In fact, it has been suggested that adult white sharks may be homeothermic given their relatively constant body temperature over a broad range of ambient temperatures (Lowe & Goldman 2001). While this may hold true for

the adults, the apparent thermal constraints to diving suggest this may not be the case for the juveniles. Both the thermal inertia and absolute heat production will be less for these smaller animals. Further research on the thermal physiology of juvenile white sharks will elucidate ontogenetic changes in thermoregulatory abilities and as well as thermal tolerances.

The YOY white shark stayed within the Southern California Bight over the 28-day record moving between Long Beach and San Diego, California and spent a large portion of its time in near-shore waters over the continental shelf and slope. The occurrence of sharks in these areas is confirmed by both the by-catch data and strandings that occur from Point Conception to San Diego (Klimley 1985, Klimley et al. 2002, California Department of Fish and Game, unpubl. data). The Southern California Bight appears to be an ideal nursery ground. The juveniles are separated from the adults and are in warmer waters, which may help to maximize growth. Additionally, their occurrence in these waters coincides with the high abundance of a number of important and diverse prey items.

While the risk from adult predation may be reduced in the Southern California Bight, the local bottom set net fishery is an added source of mortality, although reported catch rates are low (Klimley 1985). Klimley reported that 44 white sharks smaller than 2 m had been caught between 1955 and 1985. From 1985 to 2000 the California Department of Fish and Game reports that approximately 59 white sharks over a similar size range were reported in the landings. Certainly, the reported landings under-represent the actual rate of fishery mortality; there is no market for white shark and no incentive for white shark by-catch to be reported. Logbook compliance in general is a recognized problem in fishery management. This one shark apparently encountered a net twice in 32 days indicating the potential for a high level of interaction. Based on the diurnal patterns observed in this study, it appears that bottom nets would have the highest catch rates during daylight hours. This particular shark encountered the second net at 17:00. The movement of this shark to San Diego, California indicates the potential for movement into Mexican waters, highlighting the need for a multinational management effort.

The data obtained in this study provide exciting new insights into the movements and behaviors of YOY white sharks. Up to this point our understanding of this important life-history phase has been based primarily on catch data and stomach contents leaving considerable gaps in our knowledge. While this represents

a good start, more effort is needed to increase the sample size and to address a number of important questions. What is the rate of encounter with fishing nets and the associated mortality? What are the larger-scale movement patterns and what is the southern extent of their range? What are the fine-scale geographic movements? Do the juvenile white sharks exhibit diurnal onshore/offshore movements apparent for some blue sharks? When and where are the sharks feeding? One additional tool that could be useful is an acoustic stomach temperature or pH sensor, which is currently under development (Y. Papastamatiou & C. Lowe pers. comm.). Measurements of muscle temperature during diving will further illuminate potential thermoregulatory mechanisms and thermal constraints on behavior. This information is not only important for improving our understanding of white shark biology but also for their long-term conservation and management.

Acknowledgements

We express our thanks to C. Winkler of the Southern Californian Marine Institute as well as the fishermen that caught and released the white shark and returned the PAT tag. Thanks also go to Ken Goldman for his valuable comments on this manuscript.

References

- Allen, M.J. & R. Leos. 2001. Sanddabs. pp. 201–202. *In*: W.S. Leet, C.M. Dewees, R. Klingbeil & E.J. Larson (ed.) California Living Marine Resources: A Status Report, University of California Agriculture and Natural Resources, Davis.
- Anderson, S.D. & K.J. Goldman. 1996. Photographic evidence of white shark movements in California waters. *Calif. Fish. Game* 82(4): 182–186.
- Arnold, G. & H. Dewar. 2001. Electronic tags in marine fisheries research: A 30-year perspective. pp. 7–64. *In*: J. Seibert & J. Nielsen (ed.) Electronic Tagging and Tracking in Marine Fisheries. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Bernal, D., C. Sepulveda & J.B. Graham. 2001. Water-tunnel studies of heat balance in swimming mako sharks. *J. Exp. Biol.* 204: 4043–4054.
- Block, B.A., J.E. Keen, B. Castillo, H. Dewar, E.V. Freund, D.J. Marcinek, R.W. Brill & C. Farwell. 1997. Environmental preferences of yellowfin tuna (*Thunnus albacares*) at the northern extent of its range. *Mar. Biol.* 130: 119–132.
- Block, B.A., H. Dewar, S.B. Blackwell, T.D. Williams, E.D. Prince, C.J. Farwell, A. Boustany, S.L.H. Teo, A. Seitz, A. Walli & D. Fudge. 2001. Migratory movements, depth preferences and thermal biology of Atlantic bluefin tuna. *Science* 293: 1310–1314.

- Brill, R.W., D.B. Holts, R.K.C. Chang, S. Sullivan, H. Dewar & F.G. Carey. 1993. Vertical and horizontal movements of striped marlin (*Tetrapturus audax*) near the Hawaiian Islands, determined by ultrasonic telemetry, with simultaneous measurements of oceanic currents. *Mar. Biol.* 117: 567–574.
- Brill, R.W., B.A. Block, C.H. Boggs, K.A. Bigelow, E.V. Freund & D.J. Marcinek. 1999. Horizontal movements and depth distribution of large adult yellowfin tuna (*Thunnus albacares*) near the Hawaiian Islands, recorded using ultrasonic telemetry: Implications for the physiological ecology of pelagic fishes. *Mar. Biol.* 133: 395–408.
- Boustany, A.M., S.F. Davis, P. Pyle, S.D. Anderson, B.J. Le Boeuf & B.A. Block. 2002. Expanded niche for white sharks. *Nature* 415: 35–36.
- Carey, F.G. & R.J. Olson. 1982. Sonic tracking experiments with tuna. *Collect. Vol. Sci. Paper. ICCAT* 17: 458–466.
- Carey, F.G. & J.V. Scharold. 1990. Movements of blue sharks (*Prionace glauca*) in depth and course. *Mar. Biol.* 106: 329–342.
- Carey, F.G., J.M. Teal & J.W. Kanwisher. 1981. The visceral temperatures of mackerel sharks (Lamnidae). *Physiol. Zool.* 54: 334–343.
- Carey, F.G., J.W. Kanwisher, O. Brazier, G. Gabrielson, J.G. Casey & H.L. Pratt. 1982. Temperature and activities of a white shark, *Carcharodon carcharias*. *Copeia* 1982(2): 254–260.
- Carey, F.G., J.W. Kanwisher & E.D. Stevens. 1984. Bluefin tuna warm their viscera during digestion. *J. Exp. Biol.* 109: 1–20.
- Casey, J.G. & H.L. Pratt Jr. 1985. Distribution of the white shark, *Carcharodon carcharias*, in the western North Atlantic. *Mem. Southern Calif. Acad. Sci.* 9: 2–14.
- Castro, J.I. 1983. *Sharks of North American Waters*, Texas A&M University Press, College Station, Texas. 180 pp.
- Cliff, G., R.P. Van Der Elst, A. Govender, T.K. Witthuhn & E.M. Bullen. 1996. First estimates of mortality and population size of white sharks on the South African coast. pp. 393–400. *In: A.P. Klimley & D.G. Ainley (ed.) Great White Sharks: The Biology of Carcharodon carcharias*, Academic Press, San Diego.
- Dagorn, L., P. Bach & E. Josse. 2000. Movement patterns of large bigeye tuna (*Thunnus obesus*) in the open ocean, determined using acoustic telemetry. *Mar. Biol.* 136: 361–371.
- Dewar, H., J.B. Graham & R.W. Brill. 1994. Studies of tropical tuna swimming performance in a large water tunnel II. Thermoregulation. *J. Exp. Biol.* 192: 33–44.
- Ellis, R. & J.E. McCosker. 1991. *Great White Shark*, Stanford University Press, Stanford, California. 270 pp.
- Ferreira, C.A. & T.P. Ferreira. 1996. Population dynamics of white sharks in South Africa. pp. 381–391. *In: A.P. Klimley & D.G. Ainley (ed.) Great White Sharks: The Biology of Carcharodon carcharias*, Academic Press, San Diego.
- Francis, M.P. 1996. Observations on a pregnant white shark with a review of reproductive biology. pp. 157–172. *In: A.P. Klimley & D.G. Ainley (ed.) Great White Sharks: The Biology of Carcharodon carcharias*, Academic Press, San Diego.
- Goldman, K.J. 1997. Regulation of body temperature in the white shark, *Carcharodon carcharias*. *J. Comp. Physiol. B* 167: 423–429.
- Goldman, K.J. & S.D. Anderson. 1999. Space utilization and swimming depth of white sharks, *Carcharodon carcharias*, at the South Farallon Islands, central California. *Env. Biol. Fish.* 56: 351–364.
- Gruber, S.H. & J.L. Cohen. 1978. Visual systems of elasmobranchs: state of the art 1960–1975. pp. 11–116. *In: E.S. Hodgson & R.F. Mathewson (ed.) Sensory Biology of Sharks Sakes and Rays*, Office of Naval Research, Arlington Virginia.
- Gruber, S.H. & J.L. Cohen. 1985. Visual systems of the white shark *Carcharodon carcharias*, with emphasis on Retinal Structure. *Mem. South. Calif. Acad. Sci.* 9: 61–72.
- Gunn, J.S. & B.A. Block. 2001. Advances in acoustic, archival and satellite tagging of tunas. pp. 167–224. *In: B.A. Block & E.D. Stevens (ed.) Tuna: Physiological Ecology and Evolution*, Academic Press, San Diego.
- Heneman, B. & M. Glazer. 1996. More rare than dangerous: A case study of white shark conservation in California. pp. 481–491. *In: A.P. Klimley & D.G. Ainley (ed.) Great White Sharks: The Biology of Carcharodon carcharias*, Academic Press, San Diego.
- Hernandez, J.J.C. & A.T.S. Ortega. 2000. Synopsis of biological data on the chub mackerel (*Scomber japonicus*, Houttuyn, 1782) FAO fisheries synopsis, 157.
- Hill, R.D. 1994. Theory of geolocation by light levels. pp. 227–236. *In: B.J. Le Boeuf & R.M. Laws (ed.) Elephant Seals: Population Ecology, Behavior, and Physiology*, University of California Press, Berkeley.
- Hill, R.D. & M.J. Braun. 2001. Geolocation by light levels – the next step: Latitude. pp. 89–108. *In: J. Seibert & J. Nielsen (ed.) Electronic Tagging and Tracking in Marine Fisheries*, Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Holland, K.N., R.W. Brill & R.K.C. Chang. 1990. Horizontal and vertical movements of yellowfin and bigeye tuna associated with fish aggregating devices. *Fish. Bull. US* 88: 493–507.
- Holland, K.N., R.W. Brill, R.K.C. Chang, J.R. Sibert & D.A. Fournier. 1992. Physiological and behavioural thermoregulation in bigeye tuna, *Thunnus obesus*. *Nature* 358: 410–412.
- Holland, K.N., B.M. Wetherbee, C.G. Lowe & C.G. Meyer. 1999. Movements of tiger sharks (*Galeocerdo cuvier*) in coastal Hawaiian waters. *Mar. Biol.* 134: 665–673.
- Holts, D.B. 1988. Review of US west coast commercial shark fisheries. *Mar. Fish. Rev.* 50(1): 1–8.
- Holts, D.B. & D.W. Bedford. 1993. Horizontal and vertical movements of the shortfin mako shark, *Isurus oxyrinchus*, in the Southern California Bight. *Aust. J. Mar. Freshw. Res.* 44: 901–909.
- Hubbell, G. 1996. Using tooth structure to determine the evolutionary history of the white shark. pp. 9–18. *In: A.P. Klimley & D.G. Ainley (ed.) Great White Sharks: The Biology of Carcharodon carcharias*, Academic Press, San Diego.
- Klimley, A.P. 1985. The aerial distribution and autecology of the white shark (*Carcharodon carcharias*), off the west coast of North America. *Mem. South. Calif. Acad. Sci.* 9: 15–40.
- Klimley, A.P. & D.G. Ainley. 1996. *Great White Sharks: The Biology of Carcharodon carcharias*, Academic Press, San Diego. 517 pp.

- Klimley A.P., S.D. Anderson, P. Pyle & R.P. Henderson. 1992. Spatiotemporal patterns of white shark (*Carcharodon carcharias*) predation at the south Farallon Islands, California. *Copeia*. 1992: 680–690.
- Klimley, A.P., E.D. Prince, R.W. Brill & K. Holland. 1994. Archival Tags 1994: Present and Future. US Department of Commerce, NOAA Technical Memorandum NMFS-SEFSC 357. 42 pp.
- Klimley, A.P., B.J. Le Boeuf, K.M. Cantara, J.E. Richert, S.F. Davis & S. Van Sommeran. 2001. Radio-acoustic positioning as a tool for studying site-specific behavior of the white shark and other large marine species. *Mar. Biol.* 138: 429–446.
- Klimley, A.P., S.C. Beavers, T.H. Curtis & S.J. Jorgensen. 2002. Movements and swimming behavior of three species of sharks in the La Jolla Canyon, California. *Env. Biol. Fish.* 63: 117–135.
- Konno, E.S., P. Wolf & D.R. Bergen. 2001. Pacific mackerel. pp. 306–308. *In*: W.S. Leet, C.M. Dewees, R. Klingbeil & E.J. Larson (ed.) California Living Marine Resources: A Status Report, University of California Agriculture and Natural Resources, Davis.
- Leos, R. 2001. Other flatfishes. pp. 203–205. *In*: W.S. Leet, C.M. Dewees, R. Klingbeil & E.J. Larson (ed.) California Living Marine Resources: A Status Report, University of California Agriculture and Natural Resources, Davis.
- Long, D.J., K.D. Hanni, P. Pyle, J. Roletto, R.E. Jones & R. Bandar. 1996. White shark predation on four pinniped species in central California waters: Geographic and temporal patterns inferred from wounded carcasses. pp. 263–274. *In*: A.P. Klimley & D.G. Ainley (ed.) Great White Sharks: The Biology of *Carcharodon carcharias*, Academic Press, San Diego.
- Lowe, C.G. & K.J. Goldman. 2001. Thermal and bioenergetics of elasmobranchs: Bridging the gap. *Environ. Biol. Fish.* 60: 251–266.
- Lutcavage, M., R. Brill, J. Porter, P. Howey, E. Murray, A. Mendillo, W. Chaprales, M. Genovese & T. Rollins. 2000. Summary of pop-up satellite tagging of giant blue-fin tuna in the joint US-Canadian program, Gulf of Maine and Canadian Atlantic. ICCAT, SCRS/00/95. 9 pp.
- MBC Applied Environmental Sciences. 1987. Ecology of important fisheries species offshore California. OCS Study MMS 86-0093. Rep. To Minerals Management Serv., U.S. Dept. Int., Contract No. MMS 14-12-0001-30294. 251 pp.
- McCosker, J.E. 1987. The white shark, *Carcharodon carcharias*, has a warm stomach. *Copeia* 1987(1): 195–197.
- Mollett, H.F. & G.M. Cailliet. 1996. Using allometry to predict body mass from linear measurements of the white shark. pp. 81–89. *In*: A.P. Klimley & D.G. Ainley (ed.) Great White Sharks: The Biology of *Carcharodon carcharias*, Academic Press, San Diego.
- Murphy, R.C. 1996. A plea for white shark conservation. pp. 5–6. *In*: A.P. Klimley & D.G. Ainley (ed.) Great White Sharks: The Biology of *Carcharodon carcharias*, Academic Press, San Diego.
- Musyl, M.K., R.W. Brill, D.S. Curran, J.S. Gunn, J.R. Hartog, R.D. Hill, R.W. Welch, J.P. Eveson, C.H. Boggs & R.E. Brainard. 2001. Ability of electronic archival tags to provide estimates of geographical position based on light intensity. pp. 343–367. *In*: J. Seibert & J. Nielsen (ed.) Electronic Tagging and Tracking in Marine Fisheries, Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Quirolo, L.F., V.G. Wespestad & M.W. Dorn. 2001. Pacific Hake. pp. 393–397. *In*: W.S. Leet, C.M. Dewees, R. Klingbeil & E.J. Larson (ed.) California Living Marine Resources: A Status Report, University of California Agriculture and Natural Resources, Davis.
- Smith, S.E. 2001. Leopard shark. pp. 252–254. *In*: W.S. Leet, C.M. Dewees, R. Klingbeil & E.J. Larson (ed.) California Living Marine Resources: A Status Report, University of California Agriculture and Natural Resources, Davis.
- Strong, W.R., B.D. Bruce, D.R. Nelson & R.D. Murphy. 1996. Population dynamics of white sharks in Spencer Gulf, South Australia. pp. 401–414. *In*: A.P. Klimley & D.G. Ainley (ed.) Great White Sharks: The Biology of *Carcharodon carcharias*, Academic Press, San Diego.
- Taylor, V.B. & D.W. Bedford. 2001. Shortfin mako shark. pp. 336–338. *In*: W.S. Leet, C.M. Dewees, R. Klingbeil & E.J. Larson (ed.) California Living Marine Resources: A Status Report, University of California Agriculture and Natural Resources, Davis.
- Tricas, T.C. & J.E. McCosker. 1984. Predatory behavior of the white shark (*Carcharodon carcharias*), with notes on its biology. *Proc. Calif. Acad. Sci.* 43: 221–238.
- Uchida, S., M. Toda, K. Teshima & K. Yano. 1996. Pregnant white sharks and full-term embryos from Japan. pp. 139–155. *In*: A.P. Klimley & D.G. Ainley (ed.) Great White Sharks: The Biology of *Carcharodon carcharias*, Academic Press, San Diego.
- Weiss, D. 1973. Mechanically efficient swimming techniques for fish with negative buoyancy. *J. Mar. Res.* 31: 194–209.
- Wilson-Vandenberg, D. & R. Hardy. 2001. Cabezon. pp. 157–159. *In*: W.S. Leet, C.M. Dewees, R. Klingbeil & E.J. Larson (ed.) California Living Marine Resources: A Status Report, University of California Agriculture and Natural Resources, Davis.
- Wolf, P., P.E. Smith & D.R. Bergen. 2001. Pacific Sardine. pp. 299–302. *In*: W.S. Leet, C.M. Dewees, R. Klingbeil & E.J. Larson (ed.) California Living Marine Resources: A Status Report, University of California Agriculture and Natural Resources, Davis.
- Yaremko, M. 2001. California market squid. pp. 295–298. *In*: W.S. Leet, C.M. Dewees, R. Klingbeil & E.J. Larson (ed.) California Living Marine Resources: A Status Report, University of California Agriculture and Natural Resources, Davis.
- Zorzi, G.D., L.K. Martin & J. Ugoretz. 2001. Skates and rays. pp. 257–261. *In*: W.S. Leet, C.M. Dewees, R. Klingbeil & E.J. Larson (ed.) California Living Marine Resources: A Status Report, University of California Agriculture and Natural Resources, Davis.