

Insights into the life history and ecology of a large shortfin mako shark *Isurus oxyrinchus* captured in southern California

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In June 2013, a record-breaking female *Isurus oxyrinchus* (total length 373 cm, mass 600 kg) was captured by rod and reel off Huntington Beach, California, where it was subsequently donated to research and provided a rare opportunity to collect the first data for a female *I. oxyrinchus* of this size. Counts of vertebral band pairs estimate the shark to have been *c.* 22 years old, depending upon assumptions of band-pair deposition rates, and the distended uteri and spent ovaries indicated that this shark had recently given birth. The stomach contained a *c.* 4 year-old female California sea lion *Zalophus californianus* that confirmed the high trophic position of this large *I. oxyrinchus*, which was corroborated with the high levels of measured contaminants and tissue isotope analyses.

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In the northeastern Pacific Ocean (NEP), shortfin mako sharks *Isurus oxyrinchus* (Rafinesque 1810) are prominent, widespread predators that utilize both coastal and oceanic habitats (Compagno, 2001; Block *et al.*, 2011). While considerable data have been collected on immature specimens, little is known about mature animals,

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particularly females. Data collection on large, mature *I. oxyrinchus* females (280 cm total length, L_T ; Joung & Hsu, 2005) is often difficult because these specimens are typically less prevalent, harder to capture, unable to be held in captivity and, unlike the great white shark *Carcharodon carcharias* (L. 1758), they do not form known aggregations. Despite the importance of large females to the reproductive potential of the population (Tsai *et al.*, 2014), very little basic information about mature female *I. oxyrinchus* is available, particularly with regard to morphometrics, reproductive biology, foraging ecology, contaminant loads and age and growth. In the summer of 2013, a 373 cm L_T *I. oxyrinchus* was captured recreationally by hook and line off the coastline of the Southern California Bight (SCB) and subsequently donated to research. The purpose of this paper is to provide insights into aspects of the life history and ecology of *I. oxyrinchus* obtained from this rare specimen.

On 3 June 2013, a female *I. oxyrinchus* was captured by a recreational angler fishing c. 24 km off Huntington Beach, California (33.48° N; 118.15° W). The shark was transported to New Fishall Bait Co. (<https://www.facebook.com/NewFishallBaitCo>) where it was stored chilled (*i.e.* not fully frozen) until necropsy on 9 June 2013. External measurements (straight line and curve lengths) were taken as well as masses of organs at the time of dissection (Tables I and II).

The stomach was cut anteriorly and the fluid inside the stomach was removed, weighed on-site and filtered through a 0.5 mm mesh sieve. The whole stomach and contents were then transported to the National Oceanic and Atmospheric Administration (NOAA) Southwest Fisheries Science Center (SWFSC), La Jolla, CA, for examination. Materials and fluid were rinsed and sorted through a series of screen sieves with mesh sizes of 9.5, 1.4 and 0.5 mm. The stomach was distended and contained the remains of a California sea lion *Zalophus californianus* (CSL; Fig. 1). By using the skull morphology and teeth annuli, it was possible to determine that the CSL was a juvenile female c. 4 years of age (Lowry & Folk, 1990). The mean \pm 95% c.i. mass was estimated at 67.6 ± 17.0 kg based on a linear age growth model constructed from wild female CSLs ($n = 26$) that ranged from 2.00 to 3.41 years of age (National Marine Mammal Laboratory, Seattle, WA).

To investigate long-term feeding ecology, stable-isotope analysis (SIA) on white muscle tissue was performed, which in large sharks provides information on the diet over the past year or more (Carlisle *et al.*, 2012). Dorsal muscle tissue was sampled and frozen at -20° C and prepared for analysis (including urea extraction) following the methods of Madigan *et al.* (2012). $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from this *I. oxyrinchus* were compared with regional prey and predator values from Carlisle *et al.* (2012) and Madigan *et al.* (2012) to subjectively assess whether this individual appeared to largely reflect feeding in the California Current Large Marine Ecosystem (CCLME).

A Bayesian mixing model MixSir (Moore & Semmens, 2008) was used to estimate the relative importance of prey contributions in the CCLME to the diet of this *I. oxyrinchus*. Trophic groupings from Madigan *et al.* (2012) as well as $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ from selected marine mammals (Carlisle *et al.*, 2012) were used to assess the contributions of marine mammals, large predators, smaller predators and forage fish to the diet of this *I. oxyrinchus*. One million iterations were run where shark and diet–tissue discrimination factors (DTDF: the difference between shark diet $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values) from large active sharks were used [mean \pm s.d. $\Delta^{15}\text{N} = 2.29 \pm 0.22$, $\Delta^{13}\text{C} = 0.90 \pm 0.33$; Hussey *et al.* (2010)]. White muscle $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for this *I. oxyrinchus* were -16.3 and 17.1‰ , respectively (C:N = 3.3). Assuming predation

TABLE I. Various morphometrics of the *Isurus oxyrinchus* taken upon dissection. External measurements were taken over the curve of the body and as a straight line

Measurements	Curve length (cm)	Straight-line length (cm)
Body		
Total stretch	386	383
Total natural	373.5	373
Fork		
Precaudal (to notch)	313	310
Snout to last gill slit	111	101
Snout to dorsal origin	144	139
Snout to vent	244	227
Snout to second dorsal-fin origin		270
First dorsal-fin origin to second origin	132	130
Snout to anal-fin origin	290	275
Snout to left pectoral-fin origin	100	89
Snout to orbit	25	
Snout to nare	16	
Nare to nare	17.2	
Girths		
Anterior to dorsal origin	238	
Posterior to pectoral-fin insertion	209	
Anterior to pelvic-fin origin	150	
Fins		
Width across keel	32	
Dorsal fin		
Height from midline	35.5	
Height from origin	44	
Origin to free rear tip width	43	
Origin to insertion width	37	
Pectoral fin		
Origin to tip	65	
Widest width	39	
Origin to insertion width	30	
Caudal fin		
Width (origin to fork)	26	
End of keel to fork	23	
Length of superior caudal fin	66	
Length of inferior caudal fin	52	
Height (tip to tip of caudal)	98	
Pelvic fin		
Origin to insertion	22	
Origin to free rear tip	26	
Width of left pelvic fin	10	
Gill slits		
Length of fifth gill slit	35	
Length of fourth gill slit	32	
Length of third gill slit	31	
Jaws		
Midline of upper jaw to left joint	29.8	
Gape (joint to joint)	25	
Eye diameter	4.6	
Reproductive		
Uteri length (R, L)	90, 89	
Uteri width (R, L)	15, 15	
Shell gland length (R, L)	8, 8	
Shell gland width (R, L)	5.3, 5	

R, right; L, left.

TABLE II. Mass of internal organs of *Isurus oxyrinchus* taken at the time of dissection. Total mass of the animal was obtained from an International Game Fish Association (www.igfa.org) certified scale at the time of landing

Organ	Mass (kg)
Total	600.11
Liver	56.70
Left liver lobe	29.03
Right liver lobe	27.67
Reproductive tract (ovaries and uterus)	4.97
Heart	0.73
Pancreas	0.39
Total mass of stomach and contents	95.30
Stomach fluid removed	67

primarily in the CCLME, these values indicate a high trophic level for this *I. oxyrinchus* based on comparison of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values with other CCLME predators (Madigan *et al.*, 2012). $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were higher than those of other pelagic predators (billfish, tunas, jacks and small sharks) in the CCLME (Madigan *et al.*, 2012) but lower than those of marine mammals and *C. carcharias* in the CCLME (Carlisle *et al.*, 2012; Fig. 2). Estimated prey (with ranges) contributions to the *I. oxyrinchus* diet were marine mammals 29% (5–55%), large predators 24% (2–70%), smaller predators 18% (2–56%) and forage fishes and squids 18% (2–47%).



FIG. 1. Remains of the *Zalophus californianus* found in the *Isurus oxyrinchus* stomach. Photo credit: Rocky Kasler

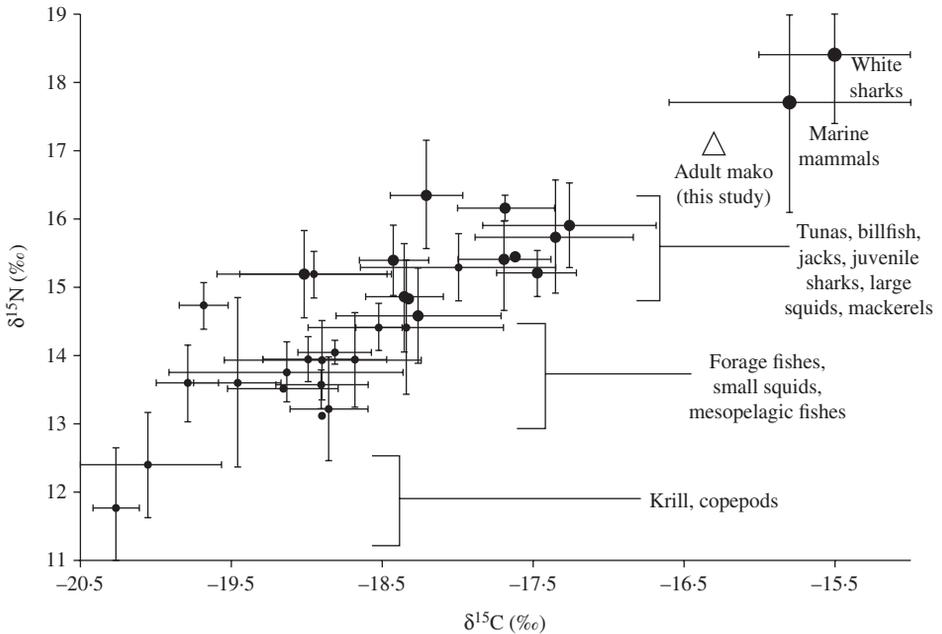


FIG. 2. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (mean \pm s.d.) for pelagic predators (●) and prey (●) in the California Current Large Marine Ecosystem. The large adult *Isurus oxyrinchus* of this study is represented (Δ). Pelagic predator and prey data from Madigan *et al.* (2012); *Carcharodon carcharias* data from Carlisle *et al.* (2012); marine mammal data are for *Phocoena phocoena* (Toperoff, 2002) and *Mirounga angustirostris*, *Phoca vitulina* and *Zalophus californianus* (Burton & Koch, 1999).

Spiral valve parasites are generally diet related and can also provide information on the diet of a shark over a longer period than the classification of identifiable food items in the gut. The spiral valve was cut open longitudinally along the line of the main blood vessel to reveal the inner lumen. All parasites found were fixed in 10% formalin and sent to the University of Aberdeen, Scotland, U.K., for identification. Three types of helminth parasite were found: 20 specimens of the tetraphyllidean tapeworm *Ceratomyxum xanthocephalum*, two of a trypanorhynch tapeworm of the family Tentaculariidae and some fragments of *Capillaria* spp. nematodes. *Ceratomyxum xanthocephalum* has been previously reported from an *I. oxyrinchus* caught off Montauk, New York (Olson *et al.*, 1999), but this is the first record from *I. oxyrinchus* for the Pacific Coast of North America. Nematodes of the genus *Capillaria* are parasites of teleosts and thus indicate predation on bony fishes.

Vertebral band-pair counts were used to estimate the age of this *I. oxyrinchus*. Vertebral centra were extracted from between the gills and the first dorsal fin and sectioned through the middle along the sagittal plane into bow-tie sections. Two methods were used to identify band pairs in the centra: (1) high frequency x-radiography (Cailliet & Bedford, 1983; Wells *et al.*, 2013) and (2) light microscopy (Bishop *et al.*, 2006; Natanson *et al.*, 2006). Both the x-radiography and light microscopy methods yielded similar counts of 26–28 band pairs (post-birth band), and all readers collectively discussed the images and agreed to a consensus count of 27 band pairs (Fig. 3). The periodicity of band-pair deposition for *I. oxyrinchus* in the NEP up to age 5 years has been validated

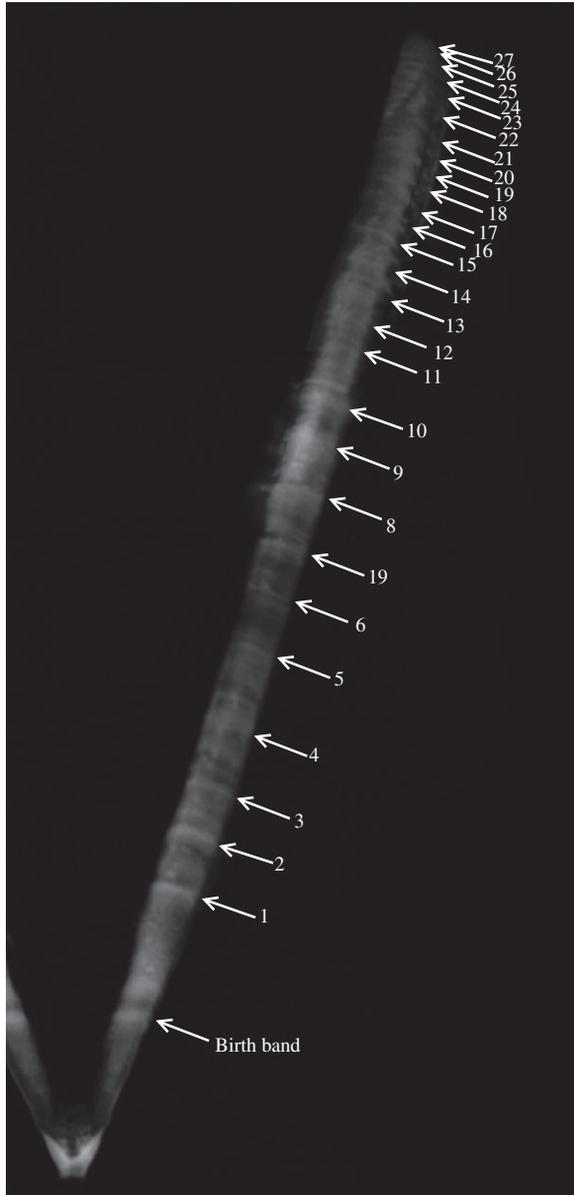


FIG. 3. Cross section of vertebra from the *Isurus oxyrinchus* with band pairs indicated by arrows.

at two band pairs per year based on oxytetracycline tagging (Wells *et al.*, 2013). In the Atlantic, bomb radiocarbon dating has shown that *I. oxyrinchus* probably deposits a single band pair per year, although the data did not preclude two band pairs being deposited in the first few years (Campana *et al.*, 2002; Ardizzone *et al.*, 2006). As this large *I. oxyrinchus* was caught in southern California waters, a band-pair deposition rate of two per year was assumed for the first 5 years switching to one per year thereafter; hence, the age was provisionally estimated to be 22 years.

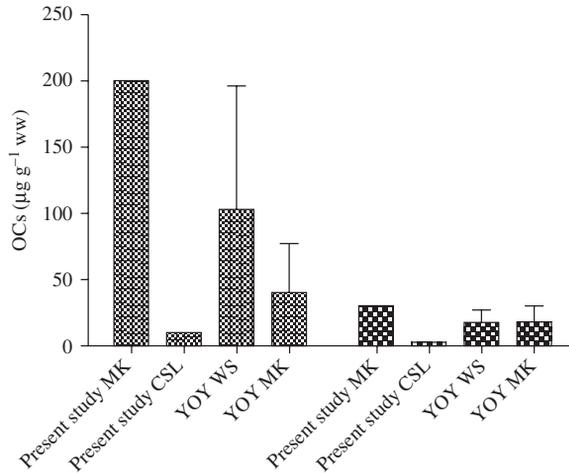


FIG. 4. Organochlorine (OC) concentrations (wet mass) for dichlorodiphenyltrichloroethanes (DDT) (▩) and polychlorinated biphenyls (PCB) (▣) measured in the liver of the *Isurus oxyrinchus* (present study MK) and the blubber of the ingested *Zalophus californianus* (present study CSL) compared with levels previously measured in young-of-the-year (YOY) *Carcharodon carcharias* (WS) and *I. oxyrinchus* (MK; Lyons *et al.*, 2013).

The reproductive organs were removed from the animal, weighed and various lengths and widths were measured (Table I). The uteri were distended and flaccid and contained a small volume of a thick, yellowish fluid. Uterine widths were similar to those reported for post-partum females in other studies (Mollet *et al.*, 2000). The internal linings of the uteri were enfolded. The ovaries contained many small (*c.* 0.5 cm) atretic ova and appeared to be recently post-partum (L. Natanson, pers. comm.).

Dichlorodiphenyltrichloroethane (DDT) and its metabolites (dichlorodiphenyl dichloroethylene, DDE and dichlorodiphenyldichloroethane, DDD), along with 54 congeners of polychlorinated biphenyls (PCB), and chlorinated pesticides were measured in the liver (distal part of left lobe) of the shark and blubber (cervical region) from the CSL following methods of Lyons *et al.* (2013). Because of the high concentration of 4,4'-DDE initially measured in the hepatic tissue, the sample was diluted 1:40 for comparison with the standard curve. Two pairs of blank spikes, one pair of sample replicates, one certified reference material (CRM; Lake Trout Tissue 1947) and one blank were run in tandem with samples to ensure accuracy and precision. The per cent recovery of compounds was high (mean \pm s.d.) in the blank spikes ($96 \pm 17\%$), CRM ($102 \pm 13\%$) and recovery surrogates ($100 \pm 21\%$), and the relative s.d. among all replicates was low ($3 \pm 3\%$). Approximately 0.5 g of white muscle was analysed for mercury following the methods of Lyons *et al.* (2013).

DDTs were the most prominent class of organic contaminants measured in the liver, comprising 86% of the total, with the 4,4'-DDE being the most concentrated compound [200 and 250 $\mu\text{g g}^{-1}$ wet (ww) and lipid (lw) mass, respectively]. Assuming homogenous concentrations of organic contaminants throughout the liver, *c.* 11.4 g of DDT compounds were estimated to be in the liver. PCBs (30 and 37 $\mu\text{g g}^{-1}$ ww and lw,

respectively) comprised 13% of the total contaminant load. The contaminant concentrations in the CSL blubber were lower than those found in the liver when compared on a wet-mass basis (Fig. 4), but not on a lipid-mass basis. The ratio of [DDTs]:[PCBs] can be used to describe the relative proximity of an animal's food source to coastal California contamination point sources (e.g. the Palos Verdes Shelf Superfund site located 3 km offshore in Los Angeles County, CA) with higher ratios indicating closer proximity to the site. The DDT:PCB ratio was higher in the *I. oxyrinchus* (6.6) than it was in the sea lion (4.0). Mean \pm s.d. total mercury measured in the muscle tissue of the *I. oxyrinchus* was $20.8 \pm 0.8 \mu\text{g g}^{-1}$ wet mass, averaging across three replicates.

The trophic ecology of this large *I. oxyrinchus* was examined using stomach content analysis, SIA and contaminant signatures. These three methods consistently indicated that the *I. oxyrinchus* foraged at a high trophic level and that marine mammals were part of its diet. These results are not uncommon for large *I. oxyrinchus* in the NEP as previous examinations have documented the presence of pinnipeds in the stomachs of large female sharks in this region. In a separate series of studies conducted at the SWFSC, A. Preti and D. Kacev (unpubl. data) documented the presence of pinnipeds in the stomachs of five large (>296 cm) female *I. oxyrinchus*, and D. B. Holts and D. A. Ramon (unpubl. data) found the remains of a harbour seal *Phoca vitulina* and small odontocete in a large *I. oxyrinchus* caught near Santa Barbara Island, California. While it is difficult to determine whether the consumed CSL was the result of an attack or scavenging event, long streaking lesions on the CSL remains suggest an active attack. The rise in NEP pinniped populations probably provides a high quality food source for these large *I. oxyrinchus* (Carretta *et al.*, 2014). As smaller-sized *I. oxyrinchus* (<280 cm L_T) feed primarily on teleosts and squids (Preti *et al.*, 2012), it is possible that the role this species plays in local ecosystems may change with ontogeny as different food items are incorporated into the diet.

Mixing model estimates, by using prey data from the CCLME, rely on the assumption that this *I. oxyrinchus* was primarily a CCLME predator. It had higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values than other pelagic predators in the CCLME (Madigan *et al.*, 2012), but lower values than marine mammals and adult *C. carcharias* (Carlisle *et al.*, 2012). Based on tagging data of other large *I. oxyrinchus* (Kohler *et al.*, 2002; Block *et al.*, 2011), it is likely that this *I. oxyrinchus* made seasonal forays into oligotrophic waters as do adult *C. carcharias* (Carlisle *et al.*, 2012). The relative influence of prey type and foraging locations cannot be determined as prior movements are unknown. Off-shore feeding in oligotrophic regions, however, would decrease $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of this *I. oxyrinchus*; thus, the SIA-based trophic position of this *I. oxyrinchus* is a conservative estimate (Fig. 2).

Southern California's unique DDT signature can be used to infer proximity of feeding to this coastal location. The higher DDT:PCB in this *I. oxyrinchus* than the consumed CSL and young-of-the-year *C. carcharias* (which acquire their signal maternally; Lyons *et al.*, 2013) was unexpected. Typically, CSLs and juvenile *C. carcharias* are nearshore and would thus be expected to have higher ratios than the generally more pelagic *I. oxyrinchus*. The ratio in the *I. oxyrinchus*, however, was lower than that found in white croaker *Genyonemus lineatus* (Ayres 1855) sampled directly from the Palos Verdes Shelf Superfund Site where ratios ranged from 15 to 22 (Gossett *et al.*, 1983). This strong coastal SCB DDT:PCB signature in the *I. oxyrinchus* could be explained by greater utilization of inshore waters than previously thought or by consumption of coastally associated prey that had ventured offshore.

Age and growth studies have generally been limited to smaller, younger specimens, which has made it difficult to estimate life span of the long-lived *I. oxyrinchus*. The large size of this *I. oxyrinchus* has provided a valuable data point that will give greater certainty to the upper end of growth curves, which is important for assessing the species' productivity and abundance and implementing appropriate management practices (Hoenig & Gruber, 1990). The exact age of this animal was uncertain due to the unresolved band-pair deposition rates across regions, ages and sexes for NEP *I. oxyrinchus*. Given the uncertainty in band-pair deposition rates for adults in the NEP, the specimen examined could be as young as 13.5 years if biannual band-pair deposition continues throughout life, or could be between the estimated ages of 13.5 and 22.0 years if an ontogenetic shift in banding periodicity occurs sometime after 5 years (Wells *et al.*, 2013). The size and estimated age range of this *I. oxyrinchus* fall near the top of the previously aged *I. oxyrinchus* in the Pacific Ocean as does the number of band pairs counted; however, some similarly sized sharks in the Atlantic have had as many as 32 vertebral band pairs, which were thought to be reflective of an annual deposition pattern based on bomb radiocarbon dating, suggesting a difference in growth rates and size at age between oceans (Cailliet & Bedford, 1983; Ardizzone *et al.*, 2006; Bishop *et al.*, 2006; Natanson *et al.*, 2006; Semba *et al.*, 2009; Doño *et al.*, 2015; H. H. Hsu, unpubl. data).

Previous reproductive studies of *I. oxyrinchus* have suggested that they reproduce every 2–3 years, with an estimated gestation of 12–25 months (Pratt & Casey, 1983; Mollet *et al.*, 2000, 2002; Joung & Hsu, 2005) followed by a rest period before the next pregnancy begins (Stevens, 2008). The lack of ovarian activity (*i.e.* ripe or developing ova 0.6–0.8 cm; Mollet *et al.*, 2000), presence of yellowish fluid in the distended uteri, spent ovaries with many atretic ova and the enfolded rather than smooth uterine lining suggest that this *I. oxyrinchus* had recently given birth and had not started her resting period at the time of capture. *Isurus oxyrinchus* are thought to pup from late winter to mid spring (Mollet *et al.*, 2000; Joung & Hsu, 2005). This post-partum female was caught in early June in the SCB, near the end of the purported pupping season. Since the SCB is a putative nursery, her presence in this area could have been for reproductive reasons in addition to feeding.

While the potential health effects of contaminants on sharks are not known, there are known concerns about human consumption of contaminants. The DDT and PCB concentrations present in the liver of the present specimen were nearly 100 and 250 times greater, respectively, than the no-consumption limit based on values developed by the US Environmental Protection Agency (Klasing *et al.*, 2009). Also, the high mercury loads measured in the muscle greatly surpass by *c.* 20-fold the US Food and Drug Administration's action level of $1.0 \mu\text{g g}^{-1}$ ww (USFDA, 2000), above which legal action will be taken to remove products from the market. Based on a 227 g (8 oz) serving size and using advisory tissue levels from Klasing *et al.* (2009), the levels measured in the *I. oxyrinchus* were *c.* 45 times greater than the no consumption level for women of child-bearing age and children and *c.* 15 times greater for women over 45 and men.

Valuable information was obtained from this animal on age and growth, reproduction, morphometrics and foraging ecology. This single specimen provided insights into the behaviour and ecology of large *I. oxyrinchus* in southern California ecosystems. Results from feeding ecology analysis suggest that both pinnipeds and coastal prey were components of the diet. High trophic level feeding coupled with a relatively old age contributed to high contaminant levels in this *I. oxyrinchus*. Although considered

rare, large *I. oxyrinchus* are caught in recreational fisheries in southern California, a fishery with considerable effort. Based on the present findings, large sharks like the specimen studied may spend protracted periods in coastal pelagic habitats (<20 km from the shore) where they may be vulnerable to capture in recreational fisheries. By understanding their habitat use and potential sources of mortality, especially for larger females, more reliable population assessments and appropriate management efforts can be achieved.

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