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Plasma catecholamine levels as indicators of the post-release survivorship of juvenile pelagic sharks caught on experimental drift longlines in the Southern California Bight

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Abstract. Between 1983 and 2004, nearly 12 000 shortfin mako (*Isurus oxyrinchus*), common thresher (*Alopias vulpinus*) and blue (*Prionace glauca*) sharks were tagged in the Southern California Bight; however, only 1.97% of these have been returned. One possible reason for this low return rate could be post-release mortality caused by capture stress from the experimental longline. Plasma catecholamine levels were analysed to evaluate stress levels in longline-captured, rod-and-reel-captured and unstressed docile sharks. The mean catecholamine values determined for the three tag–release species ranged from 6539 to 22 079 pg mL^{-1}. The level of adrenaline found in moribund *I. oxyrinchus* (94 807 pg mL^{-1}) was much higher than in either *P. glauca* (46 845 pg mL^{-1}) or *A. vulpinus* (36 890 pg mL^{-1}). In contrast, blood obtained from sharks that were landed within minutes had lower catecholamine values (*P. glauca*, 889 and 1347 pg mL^{-1}; *I. oxyrinchus*, 2960 and 3946 pg mL^{-1}, adrenaline and noradrenaline respectively). Among the nine *I. oxyrinchus* specimens that were recaptured long after their longline capture and release, the highest adrenaline level measured just before release was 33 352 pg mL^{-1}. Because these mako sharks survived sufficiently long to be recaptured, their time-of-release catecholamine levels provide a conservative estimate of ~80% viability on the longline-captured and released population.

Additional keywords: adrenaline, *Alopias vulpinus*, elasmobranchs, *Isurus oxyrinchus*, lactate, noradrenaline, *Prionace glauca*.

Introduction

Each year commercial and recreational fishers capture large numbers of sharks including thresher (*Alopias* spp.), shortfin mako (*Isurus oxyrinchus* Rafinesque, 1809) and blue (*Prionace glauca* (Linnaeus, 1758)) sharks within the Southern California Bight (SCB), an open embayment extending 732 km along the Pacific coast from Point Conception, CA, USA (34°33′N, 120°28′W) to Cabo Colnett, Baja California, Mexico (30°57′N, 116°20′W). This fishing pressure raised the question of whether these shark populations could be sustained (Cailliet and Bedford 1983; Hanan *et al.* 1993; O'Brien and Sunada 1994; Holts *et al.* 1998). To investigate this, the California Department of Fish and Game (CDFG) initiated a pelagic shark-tagging program in 1983. In 1992, this effort merged

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with the Southwest Fisheries Science Center (SWFSC, NOAA Fisheries) drift longline tag–release program, the objectives of which are to determine the relative abundance, spatial distribution, demographic structure, population genetics and migratory movements of the shortfin mako, the common thresher (*Alopias vulpinus* (Bonnaterre, 1788)) and the blue shark in the SCB.

Although this research has provided valuable information on the biology of all three species, only a small number of the tagged sharks have been recaptured. From 1983 to 2003, 11 321 blue, common thresher and shortfin mako sharks were tagged by recreational fishers and by the experimental drift longline surveys. Thus far, only 223 tags have been retrieved (Taylor 2003; Holts and Rasmussen 2004). This low recovery percentage (1.97%) can be attributed to tag attrition, natural mortality, emigration, reporting failure or to such a high stock size of sharks that the re-appearance of a tagged individual has a very low probability (Simpfendorfer *et al.* 2002; Eveson *et al.* 2004; Gaertner *et al.* 2004).

Another possibility is that the tagged and released sharks did not survive the trauma of either angling or longline fishing and tagging and succumbed within a short time of release as a result of injury or a high level of stress. Severe stress can result from prolonged behavioural, physiological, biochemical or other challenges and is typified by the presence of elevated catecholamine (adrenaline and noradrenaline), cortisol, and other stress hormones in the blood (Mazeaud *et al.* 1977; Randall and Perry 1992; Iwama *et al.* 2006). The present paper reports a study of the effects of rod-and-reel and longline fishing on plasma catecholamine levels and other variables in mako, thresher and blue sharks. The objective was to assess the possibility that longline capture and tagging could result in stress levels that were sufficiently high to cause post-release mortality (Wood *et al.* 1983). We contrasted the catecholamine levels in sharks that died or were moribund at the time they were brought aboard to those that were tagged, released and did in fact completely recover from capture stress as evidenced by the subsequent tag returns by fishers. Further quantitative comparisons of catecholamine levels were made for blue and shortfin mako sharks that were caught by angling and either landed immediately (2 min for *I. oxyrinchus* and 2 to 15 min for *P. glauca*) or played on the line for 15 to 30 min (*I. oxyrinchus*). Catecholamine and lactate samples from non-stressed aquarium-held benthic sharks were also assayed to obtain additional data for resting sharks and for interspecific comparisons.

Materials and methods

Sharks were collected from 93 experimental drift longline deployments from the NOAA vessel *R. V. David Starr Jordan* at 16 stations within the SCB during the summers (June to July) of 1998, 2000, 2001, and 2002. The longline was deployed off the stern. It consisted of a series of five gangions spaced ~15 m apart with each series separated by a float. A stainless steel longline with 200 straight shank 'J' hooks (2/0 size, Mustad, Gjövik, Norway) baited with mackerel was used to target *I. oxyrinchus*. A monofilament longline with 100 circle hooks (12/0 size, Mustad, Gjövik, Norway) baited with mackerel or squid was used for *A. vulpinus*. Fishing for *I. oxyrinchus* was done further offshore than for *A. vulpinus*, but blue sharks were captured in both study areas. To maximise captured shark survival, the longline was deployed for a short period (~3 h) before recovery.

Captured sharks were maneuvered into a U-shaped cradle (245 × 60 × 60 cm) located at the stern of the vessel, which was raised to just above the water and adjacent to a processing platform. A heavy piece of blanket was placed over the shark's head and a hose with running seawater was placed in its mouth to irrigate the gills. Once the shark was restrained, morphometric measurements were made, a tissue biopsy was taken for genetic analysis and a 5-mL blood sample for catecholamine analysis was collected via the percutaneous insertion of an 18-gauge thin-walled needle into the caudal vein or artery. The shark was then given one or two identification tags, and the hook was removed or the leader cut as close to the hook as possible before release. The entire handling process required less than 10 min. Sharks that were dead or that were judged as moribund and thus unlikely to survive were kept for additional study and blood sampling.

Rod-and-reel fishing from a skiff in waters ~10-km offshore from Scripps Institution of Oceanography (SIO) was used to obtain comparative catecholamine data for blue and mako sharks. Sharks were attracted to the boat using a chum line. Blue (123 ± 3 cm) and mako (124 ± 8 cm) sharks swimming around the boat were caught on baited hooks and either landed immediately (2 min for *I. oxyrinchus* and 2 to 15 min for *P. glauca*), or played on the line for 15 to 30 min (*I. oxyrinchus*). Blood was obtained via caudal puncture.

Blood haematocrit and plasma catecholamine levels were used to assess the effects of stress on longline-captured and angled sharks. Plasma lactate level, also used to assess stress, was determined for sharks taken on longline and one aquarium species. Blood samples were immediately transferred to a glass tube and placed on ice until processing commenced. A small aliquot of blood was used to determine haematocrit and the remaining sample was cold centrifuged to separate the plasma, which was stored in a vial at −70°C. A modification of the catechol-*O*-methyltransferase (COMT) based radioenzymatic technique was used to assay noradrenaline and adrenaline concentrations (Kennedy and Ziegler 1990). A lactate analyzer (YSI 2300 Stat Plus Analyzer, Yellow Springs, OH, USA) was used for plasma lactate determinations.

To determine resting catecholamine levels in sharks, blood samples taken from unstressed sharks in holding tanks in the Hubbs Hall experimental aquarium at SIO were analysed as above. Sharks used in this comparison study included 18 horn sharks (*Heterodontus francisci* (Girard, 1854)) and eight swell sharks (*Cephaloscyllium ventriosum* Garman, 1880), both of which are benthic and nocturnal. These sharks were long-term residents of the experimental aquarium and accustomed to human activity in and around their holding tank. Blood samples were obtained by rapidly dip-netting the shark and withdrawing blood via caudal puncture within 30 s.

Results and discussion

In this 4-year survey, a grand total of 408 *I. oxyrinchus* specimens, 45 *A. vulpinus* specimens and 1341 *P. glauca* specimens were captured on the longline. Blood analyses were done on

149 (83 males, 62 females, 4 sex not determined) *I. oxyrinchus* specimens. Of these, 110 (size range 75–205-cm total length, TL) were tagged and released and the remaining 39 (83–162-cm TL) were either dead or moribund. Of the 43 *A. vulpinus* specimens caught for blood analyses (26 males, 17 females), two (135–262-cm fork length, FL) were dead, but the remaining 41 (114–255-cm FL) were tagged and released. For the 79 *P. glauca* specimens caught for blood analyses (45 males, 30 females, 4 not determined), 19 (75–229-cm TL) were either dead or moribund and 60 (80–270-cm TL) were tagged and released.

Most of the tag–release sharks were observed to swim steadily away from the vessel, but a few did not exhibit steady swimming. Longline-captured sharks that were judged moribund typically showed little vigour, had a tight jaw tone and a stiff body, exhibited shallow branchial movements and had lost the normally brilliant coloration. In some cases, death or moribund state was caused by a fatal hook wound (into a vital organ or major blood vessel) and this could be verified by necropsy. Other dead and moribund sharks lacked lethal hook wounds, suggesting they either suffocated or were severely weakened and moribund as a result of struggling and becoming tangled in the fishing gear. The percentages of each species of captured sharks affected in this way were *I. oxyrinchus* 10%, *A. vulpinus* 5% and *P. glauca* 6%.

Capture stress effects: lactate and haematocrit

Table 1 shows the lactate values for sharks in this study. Lactate forms during anaerobic respiration, concentrates in tissues with a high anaerobic potential (e.g. shark white myotomal muscle) and also becomes elevated within the plasma (Dickson *et al.* 1989; Wendelaar Bonga 1997; Manire *et al.* 2001). The plasma lactate levels of tag–release and moribund *I. oxyrinchus* specimens were similar to the values reported for sharks of this species (16 mM, $n = 9$) that had been stressed by recreational angling (Wells and Davie 1985). The mean lactate levels of tag–release *I. oxyrinchus* and *A. vulpinus* are comparable with other active shark species that had been stressed (bonnethead shark, *Sphyrna tiburo*: 12 mM; blacktip shark, *Carcharhinus limbatus*: 12 mM; bull shark, *C. leucas*: 12 mM (Manire *et al.* 2001); sharpnose shark, *Rhizoprionodon terraenovae*: 28.9 mM (Hoffmayer and Parsons 2001)). The mean lactate level of the moribund group of *P. glauca* is also within this range; however, the value for the released blue sharks is lower (Table 1). Relative to the resting lactates measured for unstressed *H. francisci*, the mean lactate levels of *I. oxyrinchus*, *A. vulpinus* and *P. glauca* are 14, 17 and 5 times higher respectively (Table 1). This indicates that anaerobic metabolism becomes greatly elevated as a result of longline capture.

The haematocrit values (Table 1) do not show a clear relationship with capture stress. Both baseline (2 min capture) and stressed (tag–release) *I. oxyrinchus* and *P. glauca* did not undergo haematocrit changes. Although the haematocrits of both tag–release and moribund sharks are comparable with literature values (Wells and Davie 1985; Emery 1986; Lai *et al.* 1997), uncertainties in the tag–release sharks, such as the amount of blood loss and the rate of fluid–volume change between the vascular and interstitial spaces lessen the clarity of haematocrit as a marker for stress. Other studies report a range of stress effects on

Table 1. Adrenaline, noradrenaline, lactate and haematocrit (Hct) values for the moribund and tag–release groups of *Isurus oxyrinchus*, *Prionace glauca* and *Alopias vulpinus*

Asterisks denote significant differences between moribund and tag–release groups (unpaired *t*-test, two tails, $P < 0.05$). ND denotes no data

	Adrenaline ($pg\ mL^{-1}$)			Noradrenaline ($pg\ mL^{-1}$)			Lactate (mM)			Hct (%)		
	Mean ± s.e.	Range	*n*	Mean ± s.e.	Range	*n*	Mean ± s.e.	Range	*n*	Mean ± s.e.	Range	*n*
Isurus oxyrinchus												
Moribund	94 807 ± 13 142	5618–335 439	39	97 028 ± 14 098	5352–318 828	39	20 ± 2	9–26	7	36 ± 2	8–70	32
Tag–release	20 331 ± 1586*	614–85 589	110	22 079 ± 2334*	1439–197 642	110	18 ± 1	2–37	48	36 ± 1	7–60	92
2-min 'routine'	2960 ± 1165	30–5389	4	3946 ± 2320	518–10 791	4	ND			31 ± 2	27–35	3
15–30-min 'stress'	54 509 ± 39 110	2644–131 149	3	26 629 ± 8572	10 955–40 480	3	ND			25 ± 5	15–30	3
Prionace glauca												
Moribund	46 845 ± 8906	4305–131 988	19	34 647 ± 6016	5232–97 418	19	16 ± 2	1–40	18	13 ± 1	4–20	15
Tag–release	10 098 ± 1854*	558–75 625	60	9312 ± 1184*	463–51 715	60	6 ± 1*	1–26	55	20 ± 1*	4–31	58
2–15-min 'routine'	889 ± 187	432–1349	4	1347 ± 321	678–2199	4	ND			23 ± 4	19–26	2
Alopias vulpinus												
Moribund	36 890 ± 23 185	13 705–60 075	2	5129 ± 3073	2056–8203	2	19 ± 2	17–21	2	35 ± 2	34–37	2
Tag–release	9801 ± 1131	1980–34 839	41	6539 ± 2019	340–72 986	41	22 ± 2	0.5–39	36	37 ± 1	18–52	39
Heterodontus francisci												
Resting	615 ± 124	60–1977	18	666 ± 249	48–4211	18	1.3 ± 0.2	0.8–1.7	4	ND		
Cephaloscyllium ventriosum												
Resting	375 ± 92	20–779	8	428 ± 119	7–1025	8	ND			ND		

haematocrit; from no change to both haemodilution and haemoconcentration. Cooper and Morris (2004) found that lowered salinity caused haemodilution in the horn shark (*Heterodontus portusjacksoni*). Wood *et al.* (1983) observed a short-lived haemoconcentration in exercised trout (*Salmo gairdneri*) and Opdyke *et al.* (1982) did not see a change in haematocrit between exercised and non-exercised sharks (*Squalus acanthias*).

Capture-stress effects: catecholamines

For most fishes the typical circulating plasma catecholamine levels required for tonic regulation of cardiovascular function and metabolism are on the order of 1 to 10 nM (169–1690 pg mL^{-1} for noradrenaline and 183–1830 pg mL^{-1} for adrenaline) and severe stress can increase this level by 10 to 100 fold (Olson and Farrell 2006). Stress-related catecholamine increases alter cardiodynamics, affect branchial and systemic vascular resistances, augment respiratory gas transfer and transport efficiencies, and can also increase both aerobic and anaerobic metabolic performance (Opdyke *et al.* 1982; Butler *et al.* 1986; Hart *et al.* 1989; Wendelaar Bonga 1997; Iwama *et al.* 2006). Adrenaline, for example, increases glycogenolysis, plasma glucose and skeletal muscle response to nerve stimulation, and decreases insulin levels; all of which increase anaerobic metabolism (Hoffman 2001) and results in higher levels of blood lactate (Lai *et al.* 1990; Hoffmayer and Parsons 2001; Manire *et al.* 2001; Routley *et al.* 2002). Extremely high catecholamine levels can also cause intense vasoconstriction, which can result in irreversible organ and tissue damage through acidosis or anoxia. Catecholamine levels therefore indicate the magnitude of a stress effect on organism physiology and, by comparing levels in moribund and tag–release sharks in sharks landed within 2–15 min of being hooked ('routinely swimming'), in sharks that fought on the fishing line (30 min stress) and in resting sharks (unstressed), the effects of longline capture and release can be quantified and interpreted in terms of their indications for long-term (post release) survival. This study shows that some of the longlined sharks had catecholamines as high as 335 439 pg mL^{-1}, which could be as much as 1600 times above 'routinely swimming' levels. These values are extraordinarily high from the perspective of both physiology and pharmacology.

Sharks captured on longline undergo significant increases in their plasma catecholamines (Table 1). The adrenaline and noradrenaline concentrations for the tag–release specimens of each species are positively correlated (Pearson r range 0.3–0.7, P value range 0.005–0.0001), suggesting that either or both of these catecholamines can serve to indicate the magnitude of the stress response. Except for the noradrenaline level in moribund *A. vulpinus*, the catecholamine levels in moribund sharks greatly exceed those of tag–release, 'routinely swimming' and resting sharks (Table 1). Although the sample size for moribund *A. vulpinus* is too small to assess statistical significance, Table 1 shows that the two moribund *A. vulpinus* specimens had a greater adrenaline concentration than, but a comparable noradrenaline level with, the tag–release group.

Interspecific differences: moribund catecholamine levels

Table 1 also documents interspecific differences in the catecholamine levels for the moribund, tag–release, 'routinely swimming' and resting groups. Mean values for moribund *I. oxyrinchus* (94 807 pg mL^{-1} for adrenaline; 97 028 pg mL^{-1} for noradrenaline) are much greater than those of *P. glauca* (46 845 pg mL^{-1} for adrenaline; 34 647 pg mL^{-1} for noradrenaline) and *A. vulpinus* (36 890 pg mL^{-1} for adrenaline; 5129 pg mL^{-1} for noradrenaline). These catecholamine values suggest possible upper limits for longline-capture stress in both *I. oxyrinchus* and *P. glauca*. *Isurus oxyrinchus* specimens that were stressed sufficiently to result in catecholamine values above 95 000 pg mL^{-1} are unlikely to survive. For *P. glauca*, stress responses causing catecholamine levels greater than 40 000 pg mL^{-1} are also likely to be fatal. We emphasise that the high catecholamine levels are unlikely to be the direct cause of death in these sharks. Rather, they are symptomatic of the very high stress levels associated with capture. Also, because catecholamines are released into the bloodstream by depolarisation of sympathetic nerves, an activity that would cease at death, the high levels measured in these sharks does not reflect post-mortem changes. Although we know of no comparative study of catecholamine levels in sharks that struggled and then died *v.* sharks that simply died, we believe the physiologic mechanism in which catecholamines reach the bloodstream in sharks is similar to that of humans. In the case of humans, plasma catecholamine levels are not elevated in individuals that die suddenly, but are high when death is preceded by a stressful period (Hausdorfer *et al.* 1995).

Interspecific differences: stressed catecholamine levels

The catecholamine levels for tag–release *I. oxyrinchus* were twice those of tag–release *P. glauca* and *A. vulpinus* (Table 1). For sharks that were landed within 2–15 min, the difference in the 'routine' adrenaline and noradrenaline levels were 3.3 and 2.9 times higher in *I. oxyrinchus* when compared with *P. glauca* (Table 1). Catecholamine levels from the three *I. oxyrinchus* specimens that were played on the fishing line for 15–30 min showed a mean noradrenaline load of 26 629 ± 8572 pg mL^{-1} and a mean adrenaline concentration of 54 509 ± 39 110 pg mL^{-1}, both of which exceeded the tag–release level. This suggests that *I. oxyrinchus* sharks are capable of releasing a huge amount of catecholamines rapidly into their circulation to enhance cardiac and vascular performance and that their mean tonic level may be near 3000 pg mL^{-1} as indicated by the 'routinely swimming' specimens (Table 1).

The mean catecholamine values (range: 6539–22 079 pg mL^{-1}) determined for the three tag–release species in this study are also equivalent to stress-induced values reported for sedentary and moderately active sharks (lesser spotted dogfish, *Scyliorhinus canicula*: 17 000 pg mL^{-1} (Butler *et al.* 1986); spiny dogfish, *Squalus acanthias*: 11 000 pg mL^{-1} (Opdyke *et al.* 1982)). Thus, although a total catecholamine load of up to 17 000 pg mL^{-1} may be within the normal functional range of less active sharks, catecholamine levels in pelagic sharks caught by longline or that were played on the fishing line (15–30 min) exceed this quantity (Table 1). Specifically, the number of sharks in the tag–release group of each species having a catecholamine level of above 17 000 pg mL^{-1} are: 49 of 110 *I. oxyrinchus* specimens, 9 of 60 *P. glauca* specimens and 6 of 41 *A. vulpinus* specimens. The higher catecholamine level of *I. oxyrinchus*

Table 2. Recapture data for nine *Isurus oxyrinchus* specimens and one *Alopias vulpinus* specimen that were tagged and released in the Southern California Bight

Data presented are each shark's tag number, its sex and total length (TL; fork length for *Alopias vulpinus*). Pre-release blood values include: haematocrit (Hct), adrenaline (Adr), noradrenaline (Noradr) and lactate (Lac) concentrations. Recapture information includes: days at liberty (Lib), distance (Dist; Nm, nautical mile) between tagged–released and recaptured site and recaptured location. ND denotes no data

Tag no.	Sex	TL (cm)	Pre-release blood values				Recapture information		
			Hct (%)	Adr (pg mL^{-1})	Noradr (pg mL^{-1})	Lac (mM)	Lib (days)	Dist (Nm)	Location
Isurus oxyrinchus									
A058923	M	118	ND	26 830	24 230	ND	463	55	San Clemente I., CA
SH021042	M	102	45	25 254	19 406	ND	104	69	La Jolla, CA
A033445	F	106	31	17 986	15 528	12.7	149	157	Ensenada, Mexico
A058942	F	110	43	14 150	14 908	ND	196	122	S. Cortes Bank, CA
A037789	F	116	22	12 180	33 352	ND	1594	2014	Hawaii
A058944	F	98	ND	11 639	13 076	ND	405	50	San Diego, CA
A037763	F	156	30	5805	1913	10.3	34	383	S. Ensenada, Mexico
A037790	M	123	35	3719	3813	14.7	1013	2648	Midway I.
A058918	F	124	ND	3590	13 181	ND	382	46	San Clemente I., CA
Mean		117	34	13 461	15 490	13	482	616	
s.d.		17	9	8622	9637	2	509	991	
Alopias vulpinus									
A033475	M	215	49	7426	960	23	146	ND	Santa Monica, CA

observed in these circumstances is consistent with other findings indicating a greater metabolic capacity relative to *P. glauca* (Dickson *et al.* 1989; Graham *et al.* 1990; Lai *et al.* 1997, 2003, 2004).

Interspecific differences: resting catecholamine levels

The mean catecholamine levels determined for undisturbed *H. francisci* and *C. ventriosum* were markedly lower than those of tag–release and 'routinely swimming' *I. oxyrinchus* and, to a lesser degree, *P. glauca* (Table 1). The maximum adrenaline level for *Cephaloscyllium ventriosum* was 779 pg mL^{-1} and 1977 pg mL^{-1} for *Heterodontus francisci*, whereas maximum noradrenaline levels were 1025 and 4211 pg mL^{-1} respectively. These catecholamine levels are comparable with those measured in other unstressed elasmobranchs (*Squalus* and *Scyliorhinus* noradrenaline: 1200–8612 pg mL^{-1}, adrenaline: 400–7609 pg mL^{-1} (Hart *et al.* 1989)). In comparison, the catecholamine concentration for the tag–release *I. oxyrinchus* is 50 times higher than that of unstressed *C. ventriosum* and 33 times greater than in *H. francisci*. The values for *A. vulpinus* and *P. glauca* are 10 to 26 times higher. Comparing *H. francisci* with the 'routinely swimming' *P. glauca* and *I. oxyrinchus*, the adrenaline levels were 1.4 and 4.8 times higher and noradrenaline levels were 2 and 6 times higher respectively. Although these levels no doubt reflect stress associated with being on the fishing line for 2–15 min, they may not be too much above normal circulating catecholamine levels.

Inferences about the post-release survival of Isurus oxyrinchus *based on catecholamine levels and recapture*

Since the mid 1980s, the shark census programs run by the SWFSC and CDFG tagged and released 3094 *I. oxyrinchus* specimens, 157 *A. vulpinus* specimens and 8070 *P. glauca* specimens. The recapture results for these sharks are: 152 *I. oxyrinchus* (5.1%), 6 *A. vulpinus* (3.8%) and 65 *P. glauca* (0.8%) (Holts 2004). In the present study, out of the 110 tag–release *I. oxyrinchus* specimens for which catecholamine data were obtained, nine have now been recaptured (8.1%). Also, one of the 41 tag–release *A. vulpinus* specimens has been recaptured (2.5%). Although none of our tag–release *P. glauca* specimens have been caught again, our recapture percentages for *I. oxyrinchus* (8.1%) and *A. vulpinus* (2.5%) approximate the 20-year total returns.

Table 2 provides information on the recaptured *I. oxyrinchus* and *A. vulpinus* specimens, including catecholamine levels at the time of release. The single recaptured *A. vulpinus* specimen and seven of the recaptured *I. oxyrinchus* specimens were all caught within the SCB, where they had been at large for 34–463 days. This further documents the importance of the SCB as a nursery ground for these two species (Cailliet and Bedford 1983; O'Brien and Sunada 1994) and supports survey findings of high numbers of the young-of-the-year and older juveniles within this region. Recent satellite track data show that *I. oxyrinchus* moves out of the SCB (D. B. Holts, personal communication), which is consistent with two of the recaptures reported in Table 2. These sharks (tag numbers A037789 and A037790) were caught in the central Pacific and had been at large for 4.4 and 2.8 years respectively. They had been tagged on successive days in 2000 when both were ~1.2-m TL; the recapture length data for one of these indicates a 0.85-m increase over 4.4 years.

How might data on catecholamine levels at the time of release be used to assess the prospects for survival of the other 101 tagged and released *I. oxyrinchus* specimens? Figure 1 plots the frequency distributions of plasma adrenaline and noradrenaline levels determined for both the moribund and tag–release groups of *I. oxyrinchus* and indicates the position

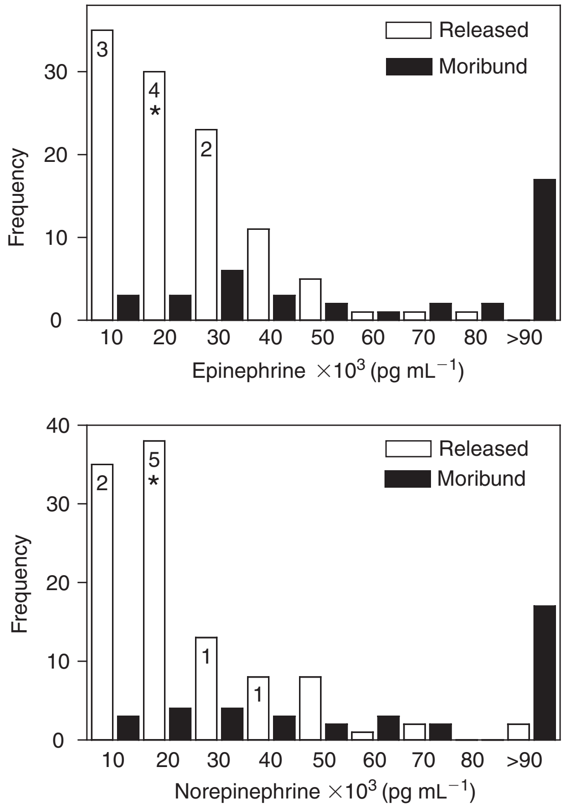

Fig. 1. Frequency distributions of plasma catecholamine levels in moribund and tag–released *Isurus oxyrinchus* specimens. Asterisk denotes mean catecholamine value of the tag–release group. Numbers within histogram bars indicate the number of recaptured sharks with the specified catecholamine level at the time of release.

of each of the recaptured sharks within the frequency distribution. This shows that most of the tag–release sharks had catecholamine levels below the average determined for the entire group (~20 000 pg mL^{-1}; asterisks in the histogram). Even though some sharks in the moribund group had catecholamine concentrations that were below the tag–release average, most of the moribund sharks had values close to the maximum measurements (>90 000 pg mL^{-1}).

The numbers on the histogram bars (Fig. 1) show that most of the nine recaptured *I. oxyrinchus* specimens had catecholamine levels that were at or below the average for the tag–release group (cf. Tables 1 and 2). Only one of these sharks had adrenaline and noradrenaline levels that exceeded the average values for the tag–release group. The highest adrenaline and noradrenaline concentrations measured in the nine recaptured sharks were 26 830 and 33 352 pg mL^{-1}. Because these sharks survived sufficiently long to be recaptured, their time-of-release catecholamine levels provide a conservative estimate of the potential long-term viability of longline-captured and released *I. oxyrinchus*. Applying these survival threshold values to our 110 released sharks shows that 81of them (74%) would be expected to survive because their adrenaline levels were below 26 830 pg mL^{-1}. For noradrenaline, 89 (81%) of the released sharks would survive.

In conclusion, experimental longline fishing and the tag–release survey methods are essential tools for determining the relative abundance, spatial distribution, demography, population genetics and migratory movement patterns of pelagic sharks in the SCB. Even with the use of short longline fishing times, the sharks that are captured are severely traumatised and, as a result, as many as 10% of them may be dead or near death when they come aboard the vessel. Also, nearly all of the sharks judged healthy enough to be tagged and released reflect the stress of capture through elevated levels of plasma lactate and catecholamines. This suggests that the relatively low return rates for tagged and released sharks in the SCB may be partially attributable to post-release death resulting from the stress of longline capture and tagging. However, based on the release catecholamine levels determined for the nine *I. oxyrinchus* specimens that were subsequently recaptured, we posit that most of the tag–release sharks do survive. A large percentage of the SCB shark censusing has been done by recreational anglers using hook and line and not longlines. Although this sampling method would preclude the shark mortality and stress factors associated with longlining, it may also have an adverse effect on long-term post-release survival because of the stress associated with a prolonged time of play on the fishing line before tag and release; additional work on this is needed.

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