Evaluating the physiological and physical consequences of capture on post-release survivorship in large pelagic fishes

G. B. SKOMAL

Martha's Vineyard Marine Fisheries Station, Massachusetts Division of Marine Fisheries, Vineyard Haven, MA, USA

Abstract Sharks, tunas and billfishes are fished extensively throughout the world. Domestic and international management measures (quotas, minimum sizes, bag limits) mandate release of a large, yet poorly quantified, number of these fishes annually. Post-release survivorship is difficult to evaluate, because standard methods are not applicable to large oceanic fishes. This paper presents information on the current approaches to characterising capture stress and survivorship in sharks, tunas and marlins. To assess mortality associated with capture stress, researchers must examine the cumulative impacts of physical trauma and physiological stress. Physical trauma, manifested as external and internal tissue and organ damage, is caused by fishing gear and handling. Gross examination and histopathological sampling have been used to assess physical trauma and to infer post-release survivorship. Exhaustive anaerobic muscular activity and time out of water cause physiological stress, which has been quantified in these fishes through the analyses of blood chemistry. Conventional, acoustic and archival tagging have been used to assess post-release survivorship in these species. Future studies relating capture stress and post-release survivorship could yield information that helps fishermen increase survivorship when practicing catch and release.

KEYWORDS: marlin, mortality, sharks, stress, survivorship, tuna.

Introduction

Sharks, tunas and billfishes are exploited by extensive recreational and commercial fisheries throughout the world. In the temperate western North Atlantic, the most commonly captured pelagic species include blue shark, *Prionace glauca* (Linnaeus), shortfin mako shark, *Isurus oxyrinchus* Rafinesque, common thresher shark, *Alopias vulpinus* (Bonnaterre), bluefin tuna, *Thunnus thynnus* (Linnaeus), yellowfin tuna, *T. alba-cares* (Bonnaterre), albacore, *T. alalunga* (Bonnaterre), bigeye tuna, *T. obesus* (Lowe), skipjack tuna, *Katsuw-onus pelamis* (Linnaeus), swordfish, *Xiphias gladius* Linnaeus, white marlin, *Tetrapterus albidus* Poey, and blue marlin, *Makaira nigricans* Lacepède [National Marine Fisheries Service (NMFS) 2005]. Off the south eastern United States coast, the diversity of offshore species increases and comprises a high number of coastal sharks, several smaller tunas including Atlantic bonito, *Sarda sarda* (Bloch), and false albacore, *Euthynnus alletteratus* (Rafinesque), dolphinfish, *Cor-*

yphaena hippurus Linnaeus, wahoo, *Acanthocybium solandri* (Cuvier), and sailfish, *Istiophorus albicans* (Latreille) (NMFS 2005).

Many of these highly migratory species are currently managed by a NMFS (2005) fishery management plan as well as international agreements (NMFS 2004). Management measures, which include minimum sizes, bag limits and quotas (NMFS 2004, 2005), have resulted in the mandated release of sharks, tunas, and marlins by both the recreational and commercial fishing sectors. This is augmented by the non-retention of bycatch species, as well as a growing conservation ethic among some fisheries participants (Radonski 2002). In general, accurate species-specific estimates of the number of these fishes released are lacking in the Atlantic because few countries collect these data. However, there are indications from US fisheries that these numbers are quite high (NMFS 2005). For example, the US pelagic longline catch of blue sharks in the western North Atlantic ranged from 50 to 120 thousand sharks annually from 1993 to 1995, with an

Correspondence: G. B. Skomal, Martha's Vineyard Marine Fisheries Station, Massachusetts Division of Marine Fisheries, PO Box 68, Vineyard Haven, MA, USA 02568 (e-mail: gregory.skomal@state.ma.us)

average of 81% released alive (Cramer 1997). In the recreational fishery, a single 2-day shark fishing tournament in Massachusetts can result in the catch of over 2000 blue sharks and 99% are typically released alive.

Little is known of the post-release mortality associated with the catch and release of sharks, tunas and marlins. Regardless of the fishing gear, captured fish are exposed to varying degrees of stress, which includes the cumulative impacts of physical trauma and physiological stress. The magnitude of either stressor depends on capture method and handling. For example, a fish hooked in the jaw and exposed to a lengthy angling event may be as vulnerable to the same level of cumulative stress as a fish hooked in the stomach and angled for a short period of time. Standard methods for assessing post-release mortality in fishes, which typically include natural or artificial confinement (Muoneke & Childress 1994), are simply not applicable to large pelagic fishes. Moreover, sharks, tunas and marlins comprise a physiologically diverse group that exhibits a broad range of aerobic and anaerobic swimming capacities (Dickson, Gregorio, Gruber, Loefler, Tran & Terrell 1993; Bernal, Sepulveda, Mathieu-Costello & Graham 2003). Hence, efforts to characterise the physiological and physical effects of capture on highly migratory species must include novel techniques across diverse phylogenetic groups.

The objective of this paper is to elucidate current approaches to characterising physical trauma and physiological stress associated with the capture of sharks, tunas and marlins. Additionally, this paper evaluates the consequences of capture stress on post-release survivorship in these highly migratory species. These considerations are important, because increased capture-induced mortality will have major implications in release and quota management strategies for these species. This paper is not meant to be a comprehensive review of the literature on catch and release in these fishes, but rather an assessment of current methodologies while citing appropriate examples. After a brief discussion of the physical and physiological attributes of capture stress, the paper addresses post-release survivorship and the importance of linking stress to mortality.

Capture stress

Physical trauma

Fish can be caught using a variety of methods including rod and reel, longline, trawl and gillnet, each of which causes some degree of external and internal physical trauma. For example, hooks can cause internal tissue damage while trawl net abrasion may cause external epithelial damage. The extent of injury also depends on how the fish is handled during the capture event. While physical trauma has been quantified and qualified for several species of recreationally caught fishes (Muoneke & Childress 1994), this information is generally lacking for sharks, tunas and marlins.

Of the limited number of studies of physical injury associated with fishing in large pelagic fishes, most have focused on recreational fisheries and have largely examined hook damage relative to hook type and fishing technique. Skomal, Chase & Prince (2002) found a significant association between hook type and hooking location in recreational fisheries using natural bait for juvenile bluefin tuna. Prince, Ortiz & Venizelos (2002) conducted similar research on sailfish and blue marlin, *Makaira nigricans* Lacepède, and quantified hooking location, hook performance and the extent of bleeding relative to hook type. Comprehensive histopathology has also yielded valuable information about the chronic effects of hook damage. Postmortem pathology indicated that hook retention in blue shark stomachs caused chronic systemic disease (Borucinska, Martin & Skomal 2001; Borucinska, Kohler, Natanson & Skomal 2002).

Physical trauma caused by capture can have acute and chronic effects that are difficult to evaluate with regard to post-release survival. In the absence of tagging (see below), studies that simply characterise the extent of physical trauma yield little data about post-release mortality. Nonetheless, physical and histopathological examination of fishes after capture allows researchers to make inferences about potential post-release mortality. For example, extensive internal damage and bleeding are assumed to cause acute post-release mortality. Skomal *et al.* (2002) estimated that release mortality would have occurred in 4% of the bluefin tuna caught on circle hooks and 28% caught on 'J' hooks based on the frequency and extent of observed hook damage. Moreover, these studies provide useful information to fisheries managers and fishermen about how physical trauma caused by terminal tackle can be reduced.

Physiological stress

Fish react to the acute stress of capture, exhaustive exercise and handling with more exaggerated disruptions to their physiology and biochemistry than higher vertebrates (reviewed by Pickering 1981; Adams 1990; Wood 1991; Milligan 1996; Kieffer 2000). The

myotomal muscle mass of nearly all species of fish is dominated by anaerobic white muscle (80–95%), which allows high work output in short bursts (Driedzic & Hochachka 1978). Most fishing techniques cause high anaerobic activity, muscular fatigue and time out of water, resulting in physiological disruptions of the internal milieu of fish (Wells, Tetens & Devries 1984).

The vast majority of studies of capture stress physiology and recovery in fishes have been conducted on salmonids (e.g. Kieffer, Currie & Tufts 1994); few have described these processes in tunas, sharks and marlins. This is largely due to the difficulty of maintaining these species in captivity and applying standard clinical procedures to large, active fish, as well as to the inability to obtain unstressed animals. The few studies specifically designed to examine the physiological effects of capture stress in sharks, tunas and marlins have quantified changes in blood chemistry.

As the body mass of fish comprises more than 30% white muscle and only 3–6% blood, changes in muscle biochemistry are strongly reflected in the blood (Wells, McIntyre, Morgan & Davie 1986). Therefore, changes in blood chemistry measured relative to degree of physical exhaustion can provide quantitative information about the magnitude of the stress (Wedemeyer & Yasutake 1977; Wells et al. 1984). Early work by Barrett & Connor (1962, 1964) found interspecific differences in blood lactate and glycogen levels in yellowfin and skipjack tunas held in captivity for varying lengths of time. Wells et al. (1986) sampled the postmortem blood chemistry of a limited number of tunas, marlins and sharks after tournament capture and concluded that elevated levels of plasma electrolytes, osmolality, blood metabolites (glucose, lactate), plasma enzymes and haematocrit were useful indicators of capture stress. Similarly, Hoffmayer & Parsons (2001) found significant changes in blood glucose, lactate, haematocrit and plasma osmolality in the Atlantic sharpnose shark, *Rhizoprionodon terraenovae* (Richardson), after rod-and-reel capture. Manire, Heuter, Hull & Spieler (2001) quantified serological changes associated with gillnet capture in bonnethead sharks, *Sphyrna tiburo* (Linnaeus), blacktip sharks, *Carcharhinus limbatus* (Valenciennes), and bull sharks, *Carcharhinus leucas* (Valenciennes). They concluded that species-specific differences in gillnet mortality were likely associated with the animal's respiratory physiology and the degree of struggling. Skomal & Chase (2002) and Skomal (2006) quantified changes in blood acid–base status, metabolites, electrolytes and proteins in several species of sharks, tunas and marlin

after rod-and-reel capture and found significant interspecific differences relative to the magnitude and nature of these disturbances; disruption was greatest in the tunas (Fig. 1). Blood gas data indicated that blood acidoses associated with exhaustive exercise were of metabolic and respiratory origin in the bluefin and yellowfin tunas, but only of metabolic origin in the blue shark (Skomal & Chase 2002). By quantifying changes in various blood constituents relative to angling time, Dobson, Wood, Daxboeck & Perry (1986) and Skomal (2006) developed regression models that directly relate physiological changes to the capture event. As an example, Fig. 2 shows changes in blood pH with angling time for the blue shark (Skomal 2006).
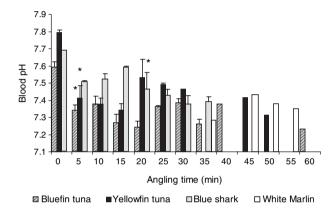

Figure 1. Changes in blood pH relative to angling (fight) time in rod-and-reel caught bluefin tuna ($n = 69$), yellowfin tuna ($n = 46$), blue sharks ($n = 40$), and white marlin ($n = 4$). For the purpose of statistical comparison, pH values (mean $+$ SEM) are averaged at 5-min intervals of angling time and *significant change in blood pH relative to angling time $= 0$ (ANOVA, $P < 0.05$). Results from Skomal & Chase (2002).
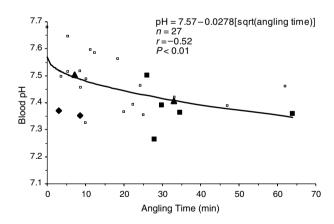

Figure 2. Relationship between blood pH and angling time of rod-and-reel-caught blue sharks ($n = 27$). Each point represents individual fish (small open squares); post-release survivorship is indicated by fish that were later recaptured (filled triangle), tagged with pop-up satellite archival tags (filled diamond), or acoustically tracked (filled square). Results from Skomal (2006).

Studies that quantify the physiological effects of capture stress in large pelagic fishes can only provide information about post-release survivorship if conducted on captive fishes or coupled with tagging (see below). While most sharks, tunas and marlins are not suited for captive studies, smaller (or younger) specimens of tunas and sharks have been maintained in captivity to assess physiological recovery from exhaustive exercise and draw inferences about post-release survivorship. Perry, Daxboeck, Emmett, Hochachka & Brill (1985) found that skipjack tuna displayed a mixed blood acidosis of respiratory and metabolic origin after induced exhaustive exercise; lactate clearance was rapid, resulting in recovery after 50 min. Weber, Brill & Hochachka (1986) confirmed that lactate turnover in this species was as great as or greater than those recorded for mammals. This sharply contrasts with laboratory studies of sharks that indicate physiological recovery periods as long as 24 h. Piiper, Meyer & Drees (1972) and Holeton & Heisler (1978) found that spotted dogfish, *Scyliorhinus stellaris* (Linnaeus), required up to 24 h to physiologically recover from exhaustive activity. Barham & Schwartz (1992) reported that blood glucose and haematocrit levels required 24 h to return to normal in neonatal smooth dogfish, *Mustelus canis* (Mitchill). Similarly, capture-induced blood chemistry changes in the dusky shark, *Carcharhinus obscurus* (LeSueur), required 24 h for recovery (Cliff & Thurman 1984). However, Spargo (2001) and Skomal (2006) found that acid–base blood chemistry in rod-and-reel-caught sandbar sharks, *Carcharhinus plumbeus* (Nardo), recovered to pre-stress levels in < 3 h, thereby emphasising the need for species-specific studies.

A major problem confronting many field-based studies is the determination of baseline pre-stress levels of physiological indicators (i.e. controls). Any attempt to sample fishes, particularly larger species, requires handling to some degree. In most cases, researchers consider those samples taken from fishes that were handled minimally or for the shortest amount of time to be baseline (e.g. Hoffmayer & Parsons 2001). Skomal & Chase (2002) and Skomal (2006) estimated baseline blood chemistry values using blood drawn quickly from free-swimming blue sharks that were tail-roped and from free-swimming bluefin tuna that were harpooned and electroshocked. However, minimal handling may not produce true baseline estimates because changes in some blood chemistry parameters, like acid–base, are manifested rapidly (< 5 min). Alternatively, theoretical baselines may be mathematically derived if a significant statistical relationship is found between physiological indicators and the magnitude of the stressor (e.g. angling time). For example, Skomal (2006) collected blood gas data from 27 blue sharks captured on rod and reel over a broad range of angling times and found a significant negative relationship between blood pH and angling time (Fig. 2). As the relationship was statistically significant, the value of blood pH at angling time $= 0$ represents a theoretical baseline. Unfortunately, this is not necessarily possible for multiple fishing gear types. As an alternative, Manire *at al.* (2002) used a subjective behavioural scale to categorise minimally stressed bull, blacktip and bonnethead sharks taken in gillnets.

Clearly, the physiological consequences of capture stress are poorly understood in most pelagic species captured and released by many fisheries. Adequate information about post-exercise recovery is lacking and little is known of the role that the environment may play in pelagic teleosts and elasmobranchs subjected to exhaustive exercise. Available evidence supports the notion that high anaerobic muscular activity in these species causes extreme homeostatic disruptions that may impede normal physiological and behavioural function.

Post-release survivorship

Qualitative and quantitative information about physiological stress and physical trauma allows researchers to examine factors that may contribute to post-release mortality. This information is particularly useful if it is correlated with empirical data on post-release survivorship. However, to derive numerical estimates of post-release mortality rates, it is essential to conduct quantitative studies of the fate of released fish. For smaller fishes, estimates of release mortality are typically derived from studies involving high numbers of fish maintained in confinement, but this is not possible for most highly migratory species. Although estimates for most sharks, tunas and marlins are still lacking, recent methods for assessing mortality include tagging with conventional, acoustic and high-technology tags.

Conventional tagging

Total mortality, and in some cases, natural and fishing mortality rates can be calculated from tag return data (Pine, Pollock, Hightower, Kwak & Rice 2003), but estimates of catch-and-release mortality rates are more difficult to derive from tag data. Recapture rates from NMFS tagging programmes range from 1.7% in billfishes (Prince, Ortiz, Rosenthal, Venizelos & Davy 2001) to 5.1% in sharks (Kohler & Turner 2001). Unfortunately, recapture rates alone provide very little

information about release mortality, because variables including tag shedding, emigration, stock size, tag reporting rate and fishing or natural mortality are difficult to define and affect estimates of recapture rates. Nonetheless, recapture rates do allow researchers to investigate potential sources of release mortality. For example, Francis (1989) found that recapture rates of the gummy shark, *Mustelus lenticulatus* Phillipps, were less in sharks taken in trawls than in set nets, thereby suggesting that trawl-caught fish had significantly greater release mortality.

Acoustic tracking

Survivorship and post-release recovery of pelagic fishes can be observed directly with acoustic telemetry, which provides behavioural information and, with adequate sample size, estimates of release mortality rates. Published tracking studies of sharks (reviewed in Sundstrom, Gruber, Clermont, Correia, de Marignac, Morrissey, Lowrance, Thomassen & Oliveira 2001) indicate that sharks survive the acute stress associated with hooking and tagging. Similarly, skipjack (Yuen 1970), yellowfin and bigeye (Holland, Brill & Chang 1990b), albacore (Laurs, Yuen & Johnson 1977) and giant (>140 kg) bluefin (Carey & Lawson 1973) tunas appear to recover from post-angling stress and handling practices. The limited number of billfish tracking studies produced variable mortality rates, which are dependent on species and size. Attempts to track blue marlin by Yuen, Dizon & Uchiyama (1974) resulted in 60% failure because of post-angling mortality. In contrast, Holland, Brill & Chang (1990a) reported 100% survivorship of six blue marlin tracked for 7–42 h after angling bouts of 20–35 min. Holts & Bedford (1990) tracked 11 striped marlin, *Tetrapterus audax* (Philippi), for up to 48 h and no short-term post-angling mortality was noted. Jolley & Irby (1979) assessed the immediate mortality of tagged and released Atlantic sailfish and found that seven of eight survived over tracking periods up to 28 h.

The use of acoustic tracking to assess post-release mortality has its shortcomings. Acoustic tracking studies of large pelagic fishes are labour intensive, costly in terms of personnel and ship time and provide only short-term information (hours to days). Moreover, many of the tracking studies conducted to date were designed to investigate movements and not to evaluate post-release survivorship. In most cases, great care was taken to minimise physical trauma, physiological stress and handling; this is not necessarily the case during normal fishing.

Archival tagging

The advent of new tagging technologies allows for the assessment of short- and long-term post-release survivorship. Like acoustic tags, archival tags and pop-up satellite archival tags (PSATs) allow researchers to examine movements and habitat preferences in large pelagic fishes (Lutcavage, Brill, Skomal, Chase & Howey 1999; Block, Dewar, Blackwell, Williams, Prince, Farwell, Boustany, Teo, Seitz, Walli & Fudge 2001). However, these tools are also ideal for investigating long-term (up to 1 year) post-release behaviour, recovery and survivorship.

In addition, archival tagging, with adequate sample sizes, can be used to derive post-release mortality estimates. Graves, Luckhurst & Prince (2002) investigated short-term (5 days) post-release mortality of blue marlin using pop-up satellite tag technology and found that at least eight of the nine blue marlin (89%) survived after tagging. Similarly, Kerstetter, Luckhurst, Prince & Graves (2003) tagged nine blue marlin taken on longline and found survival rate was 78%. Both these studies had to assume that non-reporting tags were mortalities, which may not have been the case. More recent generations of tags are now equipped with algorithms and hardware for the early detection of post-release mortality. The PSAT technology has limitations including tag and deployment costs ($>$ US $4000), tag retention, tag failure and tagging-induced mortality. Also a large number of tags per fishery (>100) are needed for meaningful release mortality estimation (Goodyear 2002).

Linking stress and survivorship

There are great benefits to assessing the sublethal effects of catch and release and the causative factors associated with post-release mortality (Cooke, Schreer, Dunmall & Philipp 2002). Information derived from acoustic tracking and archival tagging can be used by fisherman (or mandated by managers) to reduce physical trauma and physiological stress associated with catch and release.

Physical trauma and survivorship

Acoustic telemetry and PSAT tagging can be used effectively to examine the effects of fishing gear on survivorship and the effectiveness of catch and release. As noted above, acoustic tracking studies designed to examine the physical impacts of fishing gear on post-release survival in sharks, tunas and marlins are generally lacking. Gurshin & Szedlmayer (2004) used

the ultrasonic tracking of 10 Atlantic sharpnose sharks to derive a 90% short-term survival rate. They found that movement patterns did not differ between jaw and internally hooked fish.

Researchers are beginning to deploy PSAT technology to tease out the effects of physical injury on post-release behaviour and mortality. Horodysky & Graves (2005) used PSATs to compare survivorship of white marlin caught on circle hooks ($n = 20$) with those taken on straight-shank ('J') hooks ($n = 21$) and found that survival was significantly higher in marlin caught by the circle hook type (100% vs 65%). These results suggest that a simple change in hook type can significantly increase the survival of white marlin released from recreational fishing gear. Domeier, Dewar & Nasby-Lucas (2003) deployed 80 PSAT tags to derive a post-release mortality rate of 26.2% in striped marlin. Although they found no statistical differences between mortality rates of marlin caught on circle and J hooks, the degree of physical trauma was a predictor of mortality, with mortality rates of 100% for fish with gill bleeding, 63% for those hooked deep and only 9% for those in 'good condition'. Kerstetter, Polovina & Graves (2004) analysed PSAT data and attributed the post-release mortality of two white marlin to shark predation.

Physiological stress and survivorship

In an effort to link stress physiology with post-release recovery and behaviour, Skomal & Chase (2002) and Skomal (2006) sampled blood, tagged and tracked bluefin tuna, yellowfin tuna, blue sharks and white marlin after rod-and-reel capture over a broad range of angling times (0–229 min). Levels of stress were quantified by examining relative changes in various blood parameters (e.g. pH, blood gases). Survivorship, given known levels of physiological stress at the time of release, was assessed with conventional tagging, PSAT tagging and acoustic tracking. PSAT data coupled with the recapture of blood-sampled fish provided long-term recovery information, while short-term survivorship was examined with acoustic telemetry. Regression models derived from the relationship between blood chemistry and quantifiable aspects of the capture event (e.g. angling time) were used to test hypotheses on post-release survivorship. As an example, Figure 2 shows the relationship of blood pH to angling time in the blue shark; sharks that were recaptured, PSAT tagged, or tracked are identified to illustrate short and long-term post-release survivorship given the magnitude of pH change (Skomal 2006).

In addition to direct observations of mortality, acoustic tracking provides behavioural information that may be used to characterise recovery. Skomal & Chase (2002) noted that all surviving fish exhibited post-release recovery periods of 2 h or less, characterised by limited vertical activity. It was hypothesised that physiological disturbances were corrected during that period. By coupling blood chemistry data with tagging or tracking data, it may be possible to determine the probable cause of death in fish that do not survive. This, in turn, may be linked back to the capture event, thereby yielding information that may enhance survivorship. In the Skomal & Chase (2002) and Skomal (2006) studies, the single bluefin tuna that died immediately after release had low blood pH and high blood lactate levels indicative of a severe acidemia. However, two other bluefin tuna exposed to longer angling bouts exhibited more extreme acid–base disruptions and survived. A notable difference was that the fish that died had not been resuscitated at the side of the vessel before release. It is speculated that the 5–7 min of resuscitation given to the latter two fish allowed for carbon dioxide offloading and oxygen delivery. In the single mortality, it is possible that muscular fatigue associated with the angling bout precluded obligatory ram ventilation after release, leading to respiratory failure. Notably, in their archival tagging study, Graves et al. (2002) found it necessary to resuscitate three blue marlin for 3–10 min following angling bouts of 15–30 min.

Conclusions

Sharks, tunas and marlins exposed to capture stress and released must recover from physical trauma and physiological homeostatic disruptions. Given the large size and pelagic nature of these fishes, assessing post-release mortality is difficult and should include multiple approaches that quantify the extent of physical damage and the level of physiological disruption. These fishes interact with multiple gear types, which impose varying levels of stress. Hence, studies must be conducted on a fishery-specific basis.

The characterisation of physical trauma and physiological stress is not sufficient for estimating post-release mortality rates of highly migratory species. Survivorship studies utilising acoustic tracking and PSAT tagging allow researchers to examine sublethal effects on behaviour and to derive estimates of mortality associated with capture. These studies should be specifically designed to assess post-release mortality and great efforts should be taken to mimic actual fishing operations.

Currently, there is a paucity of information about post-release mortality in sharks, tunas and marlins. There is some evidence from the physiological and tagging (conventional, acoustic, PSAT) studies noted above that these fishes are capable of recovery from physiological stress and that mortality is more closely linked to the extent of physical injury. Future studies that correlate physical and physiological capture stress to survivorship are important for the development of management measures that increase post-release survivorship. The coupling of stress indicators with quantifiable aspects of the capture event allows researchers to test hypotheses on post-release survivorship and, ultimately, derive models that effectively link physiology to mortality.

Although most studies of post-release mortality in fishes have focused on survival of individuals, catch and release may have sublethal population level consequences (Cooke *et al.* 2002), which are more difficult to assess, particularly for highly migratory species with poorly understood life histories. As tagging technology improves and becomes more cost effective, it is anticipated that population level studies will become more feasible. With larger sample sizes and longer tag deployments, researchers may begin to investigate the extent to which catch and release reduces individual fitness and, thereby, has population impacts in sharks, tunas and marlins.

Acknowledgments

References

Adams S.M. (1990) *Biological Indicators of Stress in Fish.* Bethesda, USA: American Fisheries Society, Symposium 8, 191 pp.

Barham W.T. & Schwartz F.J. (1992) Physiological responses of newborn smooth dogfish, *Mustelus canis*, during and following temperature and exercise stress. *The Journal of the Elisha Mitchell Scientific Society* **108,** 64–69.

Barrett I. & Connor A.R. (1962) Blood lactate in yellowfin tuna, *Neothunnus macropterus*, and skipjack, *Katsuwonus pelamis*, following capture and tagging. *Inter-American Tropical Tuna Commission Bulletin* **6,** 231–280.

Barrett I. & Connor A.R. (1964) Muscle glycogen and blood lactate in yellowfin tuna, *Thunnus albacares*, and skipjack, *Katsuwonus pelamis*, following capture and tagging. *Inter-American Tropical Tuna Commission Bulletin* **9,** 219–268.

Bernal D., Sepulveda C., Mathieu-Costello O. & Graham J.B. (2003) Comparative studies of high performance swimming in sharks I. Red muscle morphometrics, vascularization and ultrastructure. *Journal of Experimental Biology* **206,** 2831–2843.

Block B.A., Dewar H., Blackwell S.B., Williams T.D., Prince E.D., Farwell C.J., Boustany A., Teo S.L.H., Seitz A., Walli A. & Fudge D. (2001) Migratory movements, depth preferences, and thermal biology of Atlantic bluefin tuna. *Science* **293,** 1310–1314.

Borucinska J., Martin J. & Skomal G. (2001) Peritonitis and pericarditis associated with gastric perforation by a retained fishing hook in a blue shark. *Journal of Aquatic Animal Health* **13,** 347–354.

Borucinska J., Kohler N., Natanson L. & Skomal G. (2002) Pathology associated with retained fishing hooks in blue sharks, *Prionace glauca* (L.), with implications for their conservation. *Journal of Fish Diseases* **25,** 515–521.

Carey F.G. & Lawson K.D. (1973) Temperature regulation in free-swimming bluefin tuna. *Comparative Biochemistry and Physiology* **44A,** 375–392.

Cliff G. & Thurman G.D. (1984) Pathological effects of stress during capture and transport in the juvenile dusky shark, *Carcharhinus obscurus*. *Comparative Biochemistry and Physiology* **78A,** 167–173.

Cooke S.J., Schreer J.F., Dunmall K.M. & Philipp D.P. (2002) Strategies for quantifying sublethal effects of marine catch-and-release angling: insights from novel freshwater applications. In: J.A. Lucy & A.L. Studholme (eds) *Catch and Release in Marine Recreational Fisheries.* Bethesda, USA: American Fisheries Society, Symposium 30, pp. 121–134.

Cramer J. (1997) By-catch of blue sharks (*Prionace glauca*) reported by U.S. pelagic longline vessels from 1987–1995. *International Committee for the Conservation of Atlantic Tunas, Collective Volume of Scientific Papers* **46,** 456–464.

Dickson K.A., Gregorio M.O., Gruber S.J., Loefler K.L., Tran M. & Terrell C. (1993) Biochemical indices of aerobic and anaerobic capacity in muscle tissues of California elasmobranch fishes differing in typical activity level. *Marine Biology* **117,** 185–193.

Dobson G.P., Wood S.C., Daxboeck C. & Perry S.F. (1986) Intracellular buffering and oxygen transport in the Pacific blue marlin (*Makaira nigricans*): adaptations to high-speed swimming. *Physiological Zoology* **59,** 150–156.

Domeier M.L., Dewar H. & Nasby-Lucas N. (2003) Mortality rate of striped marlin (*Tetrapturus audax*) caught with recreational tackle. *Marine and Freshwater Research* **54,** 435–445.

Driedzic W.R. & Hochachka P.W. (1978) Metabolism in fish during exercise. In: W.S. Hoar & D.J. Randall (eds) *Fish Physiology, Volume VII, Locomotion.* New York, USA: Academic Press, pp. 503–543.

Francis M.P. (1989) Exploitation rates of rig (*Mustelus lenticulatus*) around the South Island of New Zealand. *New Zealand Journal of Marine and Freshwater Research* **23,** 239–245.

Goodyear C.P. (2002) Factors affecting robust estimates of the catch-and-release mortality using pop-off tag technology. In: J.A. Lucy & A.L. Studholme (eds) *Catch and Release in Marine Recreational Fisheries.* Bethesda, MD, USA: American Fisheries Society, Symposium 30, pp. 172–179.

Graves J.E., Luckhurst B.E. & Prince E.D. (2002) An evaluation of pop-up satellite tags for estimating postrelease survival of blue marlin (*Makaira nigricans*) from a recreational fishery. *Fishery Bulletin* **100,** 134–142.

Gurshin C.W.D. & Szedlmayer S.T. (2004) Short-term survival and movements of Atlantic sharpnose sharks captured by hook-and-line in the northeast Gulf of Mexico. *Journal of Fish Biology* **65,** 973–986.

Hoffmayer E.R. & Parsons G.R. (2001) The physiological response to capture and handling stress in the Atlantic sharpnose shark, *Rhizoprionodon terraenovae. Fish Physiology and Biochemistry* **25,** 277–285.

Holeton G. & Heisler N. (1978) Acid–base regulation by bicarbonate exchange in the gills after exhausting activity in the larger spotted dogfish *Scyliorhinus stellaris. Physiologist* **21,** 56.

Holland K., Brill R. & Chang R.K.C. (1990a) Horizontal and vertical movements of Pacific blue marlin captured and released using sportfishing gear. *Fishery Bulletin* **88,** 397–402.

Holland K., Brill R. & Chang R.K.C. (1990b) Horizontal and vertical movements of yellowfin and bigeye tuna associated with fish aggregating devices. *Fishery Bulletin* **88,** 493–507.

Holts D. & Bedford D. (1990) Activity patterns of striped marlin in the southern California bight. In: R.H. Stroud (ed.) *Planning the Future of Billfishes.* Savannah, GA, USA: National Coalition for Marine Conservation, pp. 81–93.

Horodysky A.Z. & Graves J.E. (2005) Application of pop-up satellite archival tag technology to estimate postrelease survival of white marlin (*Tetrapturus albidus*) caught on circle and straight-shank ('J') hooks in the western North Atlantic recreational fishery. *Fishery Bulletin* **103,** 84–96.

Jolley J.W. & Irby E.W. Jr (1979) Survival of tagged and released sailfish (*Istiophorus platypterus*: Istiophoridae) determined with acoustical telemetry. *Bulletin of Marine Science* **29,** 155–169.

Kerstetter D.W., Luckhurst B.E., Prince E.D. & Graves J.E. (2003) Use of pop-up satellite archival tags to demonstrate survival of blue marlin (*Makaira nigricans*) released from pelagic longline gear. *Fishery Bulletin* **101,** 939–948.

Kerstetter D.W., Polovina J.J. & Graves J.E. (2004) Evidence of shark predation and scavenging on fishes equipped with pop-up satellite archival tags. *Fishery Bulletin* **102,** 750–756.

Kieffer J.D. (2000) Limits to exhaustive exercise in fish. *Comparative Biochemistry and Physiology* **126A,** 161–179.

Kieffer J.D., Currie S. & Tufts B.L. (1994) Effects of environmental temperature on the metabolic and acid–base responses of rainbow trout to exhaustive exercise. *Journal of Experimental Biology* **194,** 299–317.

Kohler N.E. & Turner P.A. (2001) Shark tagging: a review of conventional methods and studies. *Environmental Biology of Fishes* **60,** 191–223.

Laurs R.M., Yuen H.S.H. & Johnson J.H. (1977) Small-scale movements of albacore, *Thunnus alalunga*, in relation to ocean features as indicated by ultrasonic tracking and oceanographic sampling. *Fishery Bulletin* **75,** 347–355.

Lutcavage M., Brill R., Skomal G., Chase B. & Howey P.W. (1999) Results of pop-up satellite tagging of spawning size class fish in the Gulf of Maine: do North Atlantic Atlantic bluefin tuna spawn in the mid-Atlantic? *Canadian Journal of Fisheries and Aquatic Sciences* **56,** 173–177.

Manire C., Heuter R., Hull E. & Spieler R. (2001) Serological changes associated with gillnet capture and restraint in three species of sharks. *Transactions of the American Fisheries Society* **130,** 1038–1048.

Milligan C.L. (1996) Metabolic recovery from exhaustive exercise in rainbow trout. *Comparative Biochemistry and Physiology* **113A,** 51–60.

Muoneke M.I. & Childress W.M. (1994) Hooking mortality: a review for recreational fisheries. *Reviews in Fishery Science* **2,** 123–156.

National Marine Fisheries Service (NMFS) (2004) *International Agreements Concerning Living Marine Resources of Interest to NOAA Fisheries.* Silver Spring, USA: U.S. Department of Commerce, 198 pp.

National Marine Fisheries Service (NMFS) (2005) *Draft Consolidated Atlantic Highly Migratory Species Fishery Management Plan.* Silver Spring, MD, USA: U.S. Department of Commerce, 1165 pp.

Perry S.F., Daxboeck C., Emmett B., Hochachka P.W. & Brill R.W. (1985) Effects of exhausting exercise on acid–base regulation in skipjack tuna (*Katsuwonus pelamis*) blood. *Physiological Zoology* **58,** 421–429.

Pickering A.D. (1981) *Stress and Fish.* New York, USA: Academic Press, 367 pp.

Piiper J., Meyer M. & Drees F. (1972) Hydrogen ion balance in the elasmobranch *Scyliorhinus stellaris* after exhausting exercise. *Respiration Physiology* **16,** 290–303.

Pine W.E., Pollock K.H., Hightower J.E., Kwak T.J. & Rice J.A. (2003) A review of tagging methods for estimating fish population size and components of mortality. *Fisheries* **28,** 10–23.

Prince E.D., Ortiz M.A., Rosenthal D., Venizelos A. & Davy K. (2001) An update of the tag release and recapture files for Atlantic Istiophoridae. *International Commission for the Conservation of Atlantic Tunas, Collective Volume of Scientific Papers* **53,** 198–204.

Prince E.D., Ortiz M.A. & Venizelos A. (2002) A comparison of circle hook and 'J' hook performance in recreational catch-and-release fisheries for billfish. In: J.A. Lucy & A.L. Studholme (eds) *Catch and Release in Marine Recreational Fisheries*. Bethesda, MD, USA: American Fisheries Society, Symposium 30, pp. 66–79.

Radonski G.C. (2002) History and application of catch-and-release fishing: the good, the bad, and the ugly. In: J.A. Lucy & A.L. Studholme (eds) *Catch and Release in Marine Recreational Fisheries*. Bethesda, MD, USA: American Fisheries Society, Symposium 30, pp. 3–10.

Skomal G. (2006) *The Physiological Effects of Capture Stress on Post-release Survivorship of Sharks, Tunas, and Marlin*. PhD Dissertation, Boston, MD, USA: Boston University, 304 pp.

Skomal G. & Chase B. (2002) The physiological effects of angling on post-release surviorship in tunas, sharks, and marlin. In: J.A. Lucy & A.L. Studholme (eds) *Catch and Release in Marine Recreational Fisheries*. Bethesda, MD, USA: American Fisheries Society, Symposium 30, pp. 135–138.

Skomal G., Chase B. & Prince E.D. (2002) A comparison of circle hook and straight hook performance in recreational fisheries for juvenile Atlantic bluefin tuna. In: J.A. Lucy & A.L. Studholme (eds) *Catch and Release in Marine Recreational Fisheries*. Bethesda, MD, USA: American Fisheries Society, Symposium 30, pp. 57–65.

Spargo A. (2001) The physiological effects of catch and release angling on the post-release survivorship of juvenile sandbar sharks (*Carcharhinus plumbeus*). MSc thesis, Kingston, RI, USA: University of Rhode Island, 99 pp.

Sundstrom L.F., Gruber S.H., Clermont S.M., Correia J.P.S., de Marignac J.R.C., Morrissey J.F., Lowrance C.R., Thomassen L. & Oliveira M.T. (2001) Review of elasmobranch behavioral studies using ultrasonic telemetry with special reference to the lemon shark, *Negaprion brevirostris*, around Bimini Islands, Bahamas. *Environmental Biology of Fishes* **60,** 225–250.

Weber J.M., Brill R.W. & Hochachka P.W. (1986) Mammalian metabolic flux rates in a teleost: lactate and glucose turnover in tuna. *American Journal of Physiology* **250,** R452–R458.

Wedemeyer G.A. & Yasutake W.T. (1977) Clinical methods for the assessment of the effects of environmental stress on fish health. *Technical Papers of the U.S. Fish and Wildlife Service* **89,** 1–18.

Wells R.M.G., Tetens V. & Devries A.L. (1984) Recovery from stress following capture and anaesthesia of antarctic fish: hematology and blood chemistry. *Journal of Fish Biology* **25,** 567–576.

Wells R.M.G., McIntyre R.H., Morgan A.K. & Davie P.S. (1986) Physiological stress responses in big gamefish after capture: observations on plasma chemistry and blood factors. *Comparative Biochemistry and Physiology* **84A,** 565–571.

Wood C.M. (1991) Acid–base and ion balance, metabolism, and their interactions after exhaustive exercise in fish. *Journal of Experimental Biology* **160,** 285–308.

Yuen H.S.H. (1970) Behavior of skipjack tuna, *Katsuwonus pelamis*, as determined by tracking with ultrasonic devices. *Journal of the Fisheries Research Board of Canada* **27,** 2071–2079.

Yuen H.S.H., Dizon A.E. & Uchiyama J.H. (1974) Notes on the tracking of the Pacific blue marlin, *Makaira nigricans*. In: R.S. Shomura & F. Williams (eds) *Proceedings of the International Billfish Symposium, Part II*. U.S. Department of Commerce, NOAA Technical Report, NMFS, SSRF-675, pp. 265–268.