Zoo Biology 21:243–251 (2002)

Notes on the Long-term Transport of the Scalloped Hammerhead Shark (*Sphyrna lewini*)

Forrest A. Young,[1]* Stephen M. Kajiura,[2] Gerard J. Visser,[3] João P.S. Correia,[4] and Mark F.L. Smith[5]

[1] *Dynasty Marine Associates, Inc., Marathon, Florida*
[2] *University of Hawaii at Manoa, Hawaii Institute of Marine Biology, Kaneohe, Hawaii*
[3] *Rotterdam Zoological and Botanical Gardens, Rotterdam, The Netherlands*
[4] *Oceanário de Lisboa, Lisboa, Portugal*
[5] *Oceanário de Lisboa/IDEA, Inc., Lisboa, Portugal*

The capture and transport of scalloped hammerhead sharks (*Sphyrna lewini* Griffith and Smith, 1834) historically has represented a difficult, expensive, and uncertain undertaking for the public aquarium community. In this study, techniques were developed to improve the successful long-term transport of *S. lewini* by mitigating some of the deleterious effects associated with hyperactivity and impaired swimming patterns. The relationship between the transport vessel size and shark sizes, numbers, and swimming behavior was considered when formulating the transport regime. By balancing these factors and adopting a comprehensive water treatment method, it was possible to extend the duration of a successful transport by up to 60 hr. Implications for the future transport of *S. lewini* and other free-swimming sharks are discussed. Zoo Biol 21:243–251, 2002.

Key words: physiology; stress; elasmobranch; aquarium

INTRODUCTION

Large obligate ram-ventilating demersal and pelagic shark species are often difficult to transport for extended periods of time with any degree of success. Some of the challenges associated with transporting these animals have been outlined in previous studies [Cliff & Thurman, 1984; Andrews & Jones, 1990; Smith, 1992; Arai, 1997]. Fortunately, developments in transport techniques have enabled workers to

*Correspondence to: Dr. Forrest A. Young, Dynasty Marine Associates, Inc., 7th Avenue, Gulf, Marathon, FL 33050. E-mail: forrestyoung@bellsouth.net

Received for publication May 21, 2001; Accepted December 17, 2001.

DOI: 10.1002/zoo.10019
Published online in Wiley InterScience (www.interscience.wiley.com).

successfully transport large shark species, such as the bull shark (*Carcharhinus leucas* Müller and Henle, 1839) and sandbar shark (*Carcharhinus plumbeus* Nardo, 1827), for longer periods of time [Andrews and Jones, 1990; Smith, 1992]. The authors have also successfully transported the blacktip shark (*Carcharhinus limbatus* Müller and Henle, 1839), the bonnethead shark (*Sphyrna tiburo* Linnaeus, 1758), and the blacknose shark (*Carcharhinus acronotus* Poey, 1860) for periods exceeding 24 hr.

Historically, the scalloped hammerhead shark (*Sphyrna lewini*) has been regarded as difficult to successfully transport for any extended period of time, and hence for any appreciable distance [Arai, 1997]. This work reports on techniques that attempt to address the unique challenges presented by this species and facilitate their successful transport for periods of up to 60 hr.

Hammerhead sharks, in the family Sphyrnidae, represent a small group of eight distinct species. They are a wide-ranging, coastal marine shark, with family representatives occurring in warm-temperate and tropical oceans throughout the world. They typically feed on teleost fishes, cephalopods, and crustaceans [Compagno, 1984]. Hammerheads are distinguished by a distinctive hammer- or mallet-shaped lateral expansion of the head, known as a cephalofoil. The function of this lateral expansion is not clear; however, it has been interpreted as a morphological development to facilitate one or more of the following: 1) improved hydrodynamic maneuverability; 2) enhanced anterior binocular vision; 3) enhanced acuity and directionality of olfaction; and 4) enhanced pressure and electroreception, through an augmentation of the lateral line canals and the ampullae of Lorenzini [Compagno, 1984].

The uniqueness, notoriety, and sheer visual presence of *S. lewini* make them a very interesting candidate for public display. Unfortunately, the very morphological feature that makes *S. lewini* so popular—the cephalofoil—also presents a challenge to workers in relation to the successful capture, transport, and maintenance of this shark. During these processes, specimens are often observed damaging their head and eyes by impacting the physical boundaries of the transport vessel or the holding facility [Arai, 1997; Howe, 1998]. In addition, experience has demonstrated that *S. lewini* appears to be highly susceptible to the same physiological changes observed in other Carcharhiniformes during capture and transport, confounding an already difficult recovery process [Cliff and Thurman, 1984; Smith, 1992; Howe, 1998]. Based on a number of previous studies, it was hypothesized that these changes could be linked to a number of mechanisms. These include: 1) impaired ram ventilation, which occurs when the shark cannot pass sufficient water over its gills, and effective ventilation and respiration is compromised [Gruber and Keyes, 1981; Hewitt, 1984]; 2) an interrupted swimming pattern and associated decreased muscular pumping activity, resulting in reduced circulation of vascular and lymphatic fluids [Gruber and Keyes, 1981; Lowe, 1996]; 3) elevated energy expenditure from increased turning frequency to avoid tight corners and interactions with conspecifics [Weihs, 1973; Klay, 1977]; and 4) anaerobic metabolism and blood acidosis induced by periods of extended hyperactivity [Murdaugh and Robin, 1967; Albers, 1970; Bennett, 1978].

The capture, transport, and display of *S. lewini* have been attempted by a number of public aquaria, with varying degrees of success. An historical overview of these attempts is summarized in Table 1a. Any attempt to transport *S. lewini* for periods approaching 36 hr has resulted in increased levels of mortality.

It is possible that previous attempts to transport *S. lewini* may not have entirely addressed the important spatiodynamic requirements of the species, and hence the physi-

TABLE 1a. Historical overview of previous attempts to transport the scalloped hammerhead shark, *Sphyrna lewini*

Institution	Date of transport	Handling technique	Number of sharks	Size of sharks TL (cm)	Transport duration (hrs)	Transport mode	Number of sharks per container	Container shape	Container dimensions (cm)	Container construction material	Water exchanges (%)
SeaWorld, San Diego[a]	1980	Shark dish	15–20	25–40	35.0	Flat-bed truck	15–20	Rectangular	610 × 230 × 180	FRP	None
SeaWorld, San Diego[a]	1982	Shark dish	15–20	25–40	35.0	Flat-bed truck	15–20	Rectangular	610 × 230 × 180	FRP	None
SeaWorld, San Diego[a]	1983	Shark dish	15–20	25–40	35.0	Flat-bed truck	15–20	Rectangular	610 × 230 × 180	FRP	None
Waikiki Aquarium, Hawaii[b]	1984–1986	Scoop net	> 6	45–55	1.0	Truck	1	Square	120 × 120 × 40	FRP	None
Sealife Park, Hawaii[b]	1985	Scoop net	3	45–55	1.0	Truck	3	Cylindrical	120 D × 60	FRP	None
Sealife Park, Tokyo[c]	1987–1988	Hand	~ 4	50–60	36.0	Boat + truck	~ 4	Rectangular	320 × 180 × 100	FRP	Continuous
SeaWorld, Texas[d]	1988	Shark dish	15	55–65	>26.0	Tractor-trailer	1–10	Rectangular	640 × 240 × 120	FRP	None
SeaWorld, Texas[d]	1989	Shark dish	20	55–65	> 26.0	Tractor-trailer	1–10	Rectangular	640 × 240 × 120	FRP	None
Sealife Park, Tokyo[c]	1989	Hand	~ 38	50–60	36.0	Boat + truck	~ 5–6	Rectangular	320 × 180 × 100	FRP	Continuous
Aquarium of the Americas, Louisiana[b]	1989	Scoop net	1	25–40	60.0	Truck	1	Square	360 × 90 × 120	FRP	None
Point Defiance Aquarium, Washington[e]	1990	Plastic containers	2	~45	13.7	Air + truck	1	Square	120 × 110 × 80	Polypropylene	None
Point Defiance Aquarium, Washington[e]	1990	Plastic containers	2	~ 45	14.7	Air + truck	2	Rectangular	120 × 60 × 60	FRP	None
SeaWorld, Texas[d]	1990	Shark dish	20	55–65	>26.0	Tractor-trailer	1–10	Rectangular	640 × 240 × 120	FRP	None
Sealife Park, Tokyo[c]	1990–1992	Hand	~ 95	50–60	36.0	Boat + truck	~ 5–13	Rectangular	320 × 180 × 100	FRP	Continuous
SeaWorld, Texas[d]	1992	Shark dish	23	55–65	3.0	Tractor-trailer	10–15	Rectangular	640 × 240 × 120	FRP	None
Point Defiance Aquarium, Washington[e]	1993	Plastic containers	2	~45	13.5	Air + truck	1	Square	120 × 110 × 80	Polypropylene	None
Sealife Park, Tokyo[c]	1993–1995	Hand	~ 10	70–110	36.0	Boat + truck	~ 2–5	Rectangular	320 × 180 × 100	FRP	Continuous
Waikiki Aquarium, Hawaii[b]	1994	Scoop net	3	30–45	1.5	Truck	1	Cylindrical	90 D × 40	FRP	None
Monterey Bay Aquarium, California[f]	2000	Hand	2	45–55	20.5	Air + truck	1	Cylindrical	107 D × 60	Polyethylene	1
Monterey Bay Aquarium, California[f]	2000	Hand	2	45–55	20.5	Air + truck	1	Cylindrical	107 D × 60	Polyethylene	1

All specimens were reported captured by hand-cast hook and line. Shark dish, hemispherical fiberglass transfer vessel; FRP, fiberglass reinforced polymer.
[a]Keyes, R. 2000. SeaWorld, 500 SeaWorld Drive, San Diego, CA 92109, USA. Personal communication.
[b]Wisner, M. 2000. Mauna Lani Bay Hotel, 68-1400 Mauna Lani Drive, Kohala Coast, HI 96743-9796, USA. Personal communication.
[c]Arai [1997].
[d]Violetta, G. 2000. SeaWorld, 7007 SeaWorld Drive, Orlando, FL 32821, USA. Personal communication.
[e]Rupp, J. 2000. Point Defiance Zoo and Aquarium, 5400 North Pearl Street, Tacoma, WA 98407-3218, USA. Personal communication.
[f]O'Sullivan, J. Monterey Bay Aquarium, 886 Cannery Row, CA 93940, USA. Personal communication.

ological changes induced by transport. It was hypothesized that any future attempts at long-term transport of this species must consider the following important challenges: 1) physical injury to the head and eyes; 2) compromised ram ventilation; 3) compromised systemic circulation through impaired muscular pumping; 4) elevated energy expenditure; 5) anaerobic respiration and blood acidosis; 6) declining water quality, resulting from the excretion of ammonia; and 7) decreasing pH of the transport water, resulting from the excretion of CO_2 and H^+ ions [Cliff and Thurman, 1984; Smith, 1992].

In the light of these concerns, several parameters were considered during the formulation of the transport regime for this study, specifically: 1) transport vessel size, 2) transport vessel shape, 3) number of obstructions within the transport vessel, 4) size of the specimens transported, 5) number of specimens transported, and 6) the water treatment regime.

METHODS

All *S. lewini* specimens were caught in Kaneohe Bay, Oahu, Hawaii, using hand-cast hook and line. Time between hooking and boating specimens was minimized (i.e., < 1 min). Sharks were subjected to tonic immobility during manual handling according to the method of Watsky and Gruber [1990]. Following the advice of Keyes (personal communication), the animals were transferred by boat in a 1.3-m-diameter, hemispherical, fiberglass, water-filled vessel, avoiding damage to their eyes and cephalofoil. Within 15 min the animals were recuperating in a calm-water holding pen (20.0 m long × 10.0 m wide × 1.3 m deep) adjacent to the shoreline of the bay. Specimens were maintained in the pen for 2–3 weeks before long-term transport commenced.

The transport regime was based on a feasibility study undertaken by Kajiura (unpublished results). Eighteen juvenile *S. lewini* (45.0–68.0 cm TL) were transported in six containers (three sharks per container). Each container was a white, smooth-walled, cylindrical fiberglass tank, 250.0 cm in diameter × 65.0 cm high. In addition, a live-well (112.0 cm long × 112.0 cm wide × 46.0 cm high) was mounted on the top of each tank. A perforated plexiglas plate was fitted into the base of the live-well, which served as a lid (Fig. 1). A pump (model 27D; Rule ITT Industries, Gloucester, MA) of 4.16 $m^3.h^{-1}$ capacity was mounted on the underside of the lid, keeping it off the floor where it could potentially interrupt the swimming pattern of the sharks. This pump was responsible for driving a filtration system consisting of a canister filter filled with activated carbon, which was mounted on the top of the lid. Once the water was filtered, it was sprayed onto the perforated plate and allowed to trickle back into the transport container. This was done to enhance gas exchange and CO_2 liberation. A second small pump (model 24; Rule ITT Industries, Gloucester, MA) of 1.36 $m^3.h^{-1}$ capacity was used to provide a very gentle circulation within the body of the transport vessel. To prevent sloshing, each transport container was filled with seawater to just below the base of the live-well. Hence, each vessel contained approximately 3.20 m^3 of seawater. Each container was packed onto a single aircraft pallet with two 12 V sealed batteries (model 800 S; Optima, Denver, CO) and two pressurized oxygen cylinders, each of 7.98 m^3 capacity. Oxygen was injected into the impeller of the circulation pump to facilitate its dissolution and dispersion. Two days before each transport, fasting was initiated; it was then maintained throughout the entire operation. No anesthesia or other chemicotherapeutics were administered during the transport.

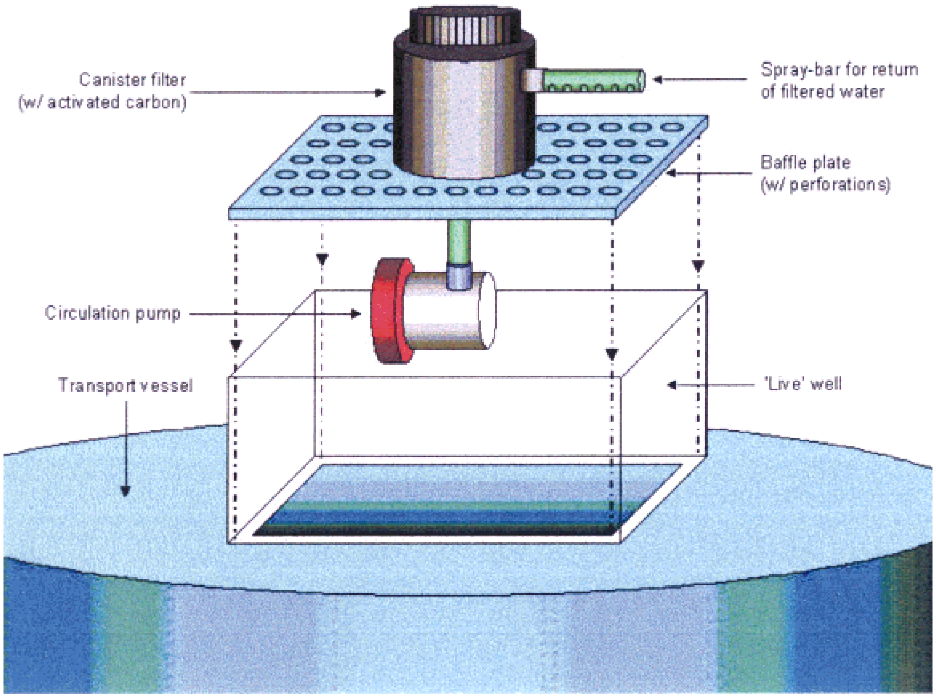

Fig. 1. Diagram of container used for the long-term transport of scalloped hammerhead sharks (*Sphyrna lewini*), showing water treatment system mounted on a plexiglas baffle-plate, and situation of the same in a live-well. The tank is 2.50 m in diameter. [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

Water quality was monitored throughout the transport. Dissolved oxygen concentrations, ammonia concentrations, and pH of transport water were measured every hour for each container. Oxygen saturation within the vessels was maintained between 80% and 120% by adjusting the flow of oxygen from the accompanying cylinders. If the concentration of ammonia was found to be higher than 0.5 $mg.l^{-1}$ a 420.0 ml dose of an ammonia detoxifier (AmQuel, Kordon-Novalek Inc., Hayward, CA) was added to the water. This amount of AmQuel had been precalculated to neutralize 1.0 $mg.l^{-1}$ of ammonia in 3.20 m^3 of water (i.e., the volume of the transport containers). If the pH was found to be lower than 8.0, a 50.0 g dose of sodium bicarbonate was also added to the water. Approximately halfway through the transport, a 60% water exchange was performed using fresh seawater taken from the point of origin. Water temperature was not monitored during the transport, although ambient temperature was regulated using the aircraft air-conditioning systems and maintained at approximately 15.0°C.

Upon arrival, the sharks were acclimated to the water parameters of their new holding facility by slowly replacing 50% of the water in the transport vessel with water from their destination tank. The sharks were then transferred from the transport container to the holding tank by hand, while they were subjected to tonic immobility.

No prophylaxis of any kind was administered to the sharks during the week following the completion of the shipments.

RESULTS

Two intercontinental shipments of *S. lewini* were undertaken, the first on 28 April 1999 and the second on 17 August 1999. Both transports used Honolulu as the point of departure and Los Angeles as the first stop. Thereafter, the first shipment continued on to its final destination of Beijing. The second shipment continued to Lisbon via Fort Worth and Miami. Half of the shipment remained in Lisbon, while the other half continued on to Rotterdam (see Table 1b).

The shortest-duration transport of 42 hr yielded an 83% survival rate 2 weeks after the arrival of the sharks in Beijing. The longest-duration transport to Rotterdam of 70 hr yielded a 33% survival rate, while the transport to Lisbon of 60 hr yielded an 83% survival rate.

Throughout the shipments, the sharks appeared to be able to avoid both the walls of the containers and the conspecifics with ease, sustaining no external physical injuries through repeated collisions.

In general, water quality was regulated and remained high throughout the early stages of the shipments. However, during the latter stages the water-quality control measures appeared to be less effective. This was evidenced by one or more of the animals exhibiting signs of distress (i.e., lying on the bottom of the vessel, increased disorientation, decreased ability to avoid the walls or conspecifics, etc.). Rectification of the water parameters, specifically ammonia and pH, regularly arrested these symptoms. During the Miami-to-Lisbon leg of the second transport, pH reached a low of 7.6 despite attempts to reverse the decline. It is conceivable that other water parameters had correspondingly deteriorated and may have contributed to the single mortality observed during that shipment after approximately 50 hr.

Upon introduction to their respective holding tanks, all surviving animals (i.e., 17 of 18) appeared in good health and commenced feeding within 2–3 days. Nevertheless, two of the six sharks in Lisbon exhibited a slight disorientation and discoloration in the hours immediately following the transport.

Manual handling of the sharks appeared to leave slightly discolored bruises on the skin of the animals, which persisted during the ensuing months. In some cases, these bruises acted as the foci for bacterial infection and required treatment with antibiotics.

DISCUSSION

This study was limited by small sample sizes, and the results should be interpreted with caution.

TABLE 1b. Summary of recent attempts to transport the scalloped hammerhead shark, *Sphyrna lewini*, as undertaken in this study

Institution	Date of transport	Size of sharks TL (cm)	Transport duration (hrs)	Water exchanges (%)	Survival rate at 2 wks
Beijing Landa Aquarium	28-Apr-99	50–68	42	30%	83%
Oceanário de Lisboa	17-Aug-99	50–60	60	60%	83%
Rotterdam Zoo Oceanium	17-Aug-99	50–60	70	60%	33%

All specimens were captured by hand-cast hook and line; tonic immobility was applied during handling; each transport consisted of six animals, three per container; transport tanks were cylindrical, fiber reinforced polymer, measuring 2.50 m in diameter × 0.65 m high.

The techniques used to capture, handle, and transfer the sharks to the holding facility in Hawaii provided very suitable and healthy specimens for transport. Hook and line (rather than netting) is the preferred technique for capturing *S. lewini* (Table 1a). This reflects a general understanding of the delicate integument of this species and the profound biochemical changes that may take place during a long struggle (Wisner and Violetta, personal communications). Hooking and very quickly landing these sharks, without the use of nets, helps to avoid these problems.

The hemispherical fiberglass transfer vessel proved to be a good means of moving the sharks during the critical minutes following their initial capture. The tapered walls of the vessel reduced the possibility of injury from impact and reduced the risks of physical damage to the eyes and cephalofoil (Keyes, personal communication).

The 2–3-week staging period within the holding facility at Kaneohe Bay was considered to be a critical factor in ensuring that the animals were optimally prepared for transport. Staging for at least 24 hr following capture is considered essential for the successful long-term transport of the species (Wisner, personal communication).

Manual handling, in conjunction with tonic immobility, provided a convenient method for manipulating the sharks. However, bruising that resulted from manual handling, and possible bacterial infection, indicated that physically touching the sharks should be avoided if at all possible (Kaiser, personal communications).

The dimensions of the transport container were appropriate for the size of the specimens shipped. The animals swam in a continuous manner and exhibited no signs of difficulty in avoiding the walls of the vessel. This was enhanced by the fact that the level of the water relative to the live-well helped reduce water movement within the vessel during transport [Arai, 1997]. In addition, as the circulation pump was mounted on the bottom of the baffle plate it did not obstruct the normal swimming pattern of the sharks, which remained close to the bottom of the tank. Transporting no more than three animals per container minimized stalling or turning abruptly to avoid conspecifics. The relatively unencumbered environment within the vessel may have reduced the consumption of vital energy reserves, the production of toxic metabolites, and the risks of metabolic shock. This is consistent with observations by previous workers that obligate ram-ventilating sharks need to continuously swim to facilitate systemic circulation, and will consume excess energy reserves by frequently turning to avoid conspecifics (Powell, personal communication).

It was difficult to conclude anything regarding the appropriateness of the shape of the transport container. It seems likely that the large dimensions of the vessel relative to the size of the sharks, coupled with the lack of directed current, meant that shape did not play a major role. Some workers have found that circular tanks work well with *S. lewini* for relatively short shipments, in which injury from impact is an important issue (Wisner, personal communication). However, for longer transports, in which physiological changes become increasingly important, there is some thought that short, quick turns may be less energetically challenging than continuous turning. In these cases, small circular vessels may not be so advantageous (Powell, personal communication).

Activated carbon appeared to maintain a high water quality within the vessels throughout the early stages of the transport. The spray bar positioned above the baffle plate provided a good means of gas exchange and minimized pH decline through CO_2 accumulation. Similarly, the accumulation of H^+ ions and the subsequent pH decline appeared to be alleviated to some degree by water exchanges and the periodic addition of sodium bicarbonate. Water exchanges also helped reduce the concentration of the constantly accumulating toxic ammonia. The deleterious effects of ammonia were further mitigated by the periodic additions of the detoxifier, AmQuel.

Despite every effort, water quality control measures started to become less effective during the latter stages of the shipments, i.e., after 60 hr. Probably weakened by the biochemical changes induced by hyperactivity and exposure to poorer water quality, some of the sharks suffered irreversible damage and succumbed during the latter stages of the longer transports, or during the days thereafter. Clearly, water quality is paramount during any shark transport, and water treatment mechanisms must be able to provide optimal conditions throughout the entire process. The water treatment regime adopted for this study appeared to be effective until approximately 60 hr. For longer transports, further water treatment mechanisms should be considered (e.g., additional water exchanges, replacement of activated carbon, staging at an intermediate facility, etc.).

In conclusion, it is suggested that the interaction of several parameters should be taken into consideration when formulating a transport regime for this species. They include: 1) the swimming behavior of the species; 2) the size of the transport container; 3) the number of obstructions within the container; 4) the size of the specimens; and 5) the number of specimens. These factors will determine the turning frequency, consumption of important energy reserves, and risks of physical injury. In addition, transport duration appeared to influence shark survival rates. This may have been the result of decreasing water quality and/or the biochemical changes induced by hyperactivity and depleted energy reserves, for although turning frequency was reduced, it was not eliminated altogether. The techniques adopted in this study appear to have extended the possible duration for the transport of *S. lewini* by up to 60 hr. Similar techniques may be cautiously adopted for species with a comparable morphology and behavior. Further refinements, especially to the management of water quality, may extend transport times even further. However, 60 hr should be sufficient to transport these animals to almost any destination in the world.

ACKNOWLEDGMENTS

We gratefully acknowledge the assistance and advice of Hiroshi Arai, Angus Barnhart, Jerry Crow, Christopher Daughtry, Steve Kaiser, Ray Keyes, Allan Marshall, Frank McHugh, Miguel Oliveira, John O'Sullivan, Dave Powell, Peter van Putten, John Rupp, Gary Violetta, and Marty Wisner.

REFERENCES

Albers C. 1970. Acid-base balance. In: Hoar WS, Randall DJ, editors. Fish physiology. Vol. IV. New York: Academic Press. p 173–208.

Andrews JC, Jones RT. 1990. A method for the transport of sharks for captivity. J Aquar Aquat Sci 5:70–72.

Arai H. 1997. Collecting, transporting and rearing of the scalloped hammerhead. In: Proceedings of the Fourth International Aquarium Congress. p 87–89.

Bennett AF. 1978. Activity metabolism of the lower vertebrates. Ann Rev Physiol 408:447–469.

Cliff G, Thurman GD. 1984. Pathological and physiological effects of stress during capture and transport in the juvenile dusky shark, *Carcharhinus obscurus*. Comp Biochem Physiol 78A:167–173.

Compagno LJ. 1984. FAO species catalogue—sharks of the world. FAO Fish Syn 125 4:538–554.

Gruber SH, Keyes RA. 1981. Keeping sharks for research. In: Hawkins AD, editor. Aquarium systems. New York: Academic Press. p 373–402.

Hewitt JC. 1984. The great white shark in captivity: a history and prognosis. Ann Proc Am Assoc Zool Parks Aquar 1984:317–323.

Howe JC. 1998. Oxygen consumption rate in juvenile scalloped hammerhead sharks [*Sphyrna lewini* Griffith and Smith, 1834]: a preliminary study. J Aquar Aquat Sci 5:28–31.

Klay G. 1977. Shark dynamics and aquarium design. Drum & Croaker 17:29–32.

Lowe CG. 1996. Kinematics and critical swimming speed of juvenile scalloped hammerhead sharks. J Exp Biol 199:2605–2610.

Murdaugh VH, Robin ED. 1967. Acid-base metabolism in the dogfish shark. In: Gilbert PW, Matheson RF, Rall DP, editors. Sharks, skates and rays. Baltimore: Johns Hopkins Press. p 249–264.

Smith MFL. 1992. Capture and transport of elasmobranchs, with emphasis on the grey nurse shark [*Carcharias taurus* Rafinesque, 1810]. Aust J Mar Freshw Res 43:325–343.

Watsky MA, Gruber SH. 1990. Induction and duration of tonic immobility in the lemon shark, *Negaprion brevirostris*. Fish Physiol Biochem 8:207–210.

Weihs D. 1973. Mechanically efficient swimming techniques for fish with negative buoyancy. J Mar Res 31:194–209.