Environmental Biology of Fishes **60:** 191–223, 2001.

Shark tagging: a review of conventional methods and studies

Nancy E. Kohler & Patricia A. Turner
NOAA/NMFS, Northeast Fisheries Science Center, 28 Tarzwell Drive, Narragansett, RI 02882, U.S.A.
(e-mail: nancy.kohler@noaa.gov)

Received 15 July 1999 Accepted 28 April 2000

Key words: elasmobranch, mark, tag, recapture, migration, movement

Synopsis

The tagging of sharks using conventional tags has long been recognized as a valuable means for studying various aspects of their life history, migrations and movements, and population structure. Conventional tags are defined as those that can be identified visually without the use of special detection equipment. Tagging studies specifically targeting sharks began in the late 1920's, and today numerous cooperative shark tagging programs exist worldwide. Cooperative programs depend on the joint participation of scientists and public volunteers to accomplish research objectives. Benefits and problems of these programs are discussed using the tagging methodologies, protocols, and results of the National Marine Fisheries Service Cooperative Shark Tagging Program. An additional 63 shark tagging studies and programs of all types are reviewed. Information useful for behavioral, biological, and fishery management studies can be derived from data resulting from these studies, including species and size composition, sex ratios, spatial and temporal distribution, migrations, movement patterns, rates of travel, delineation of pupping grounds, distribution of maturity intervals, indices of relative abundance, and recognition of individuals. Specific tagging experiments can be designed to provide additional data on age and growth, homing and site fidelity, dispersal rate, residence time, movement rates, tag shedding, and population parameters (e.g. size, mortality, recruitment, exploitation, interaction rates, and stock identity). Sources of bias inherent in tagging and recapture data include mortality, variation in tagging effort and fishing pressure, non-recovery and non-reporting of tags, and tag shedding. Recent advances in tagging methodologies that complement and extend conventional tagging studies will further our knowledge on shark movements and migrations, particularly in the areas of resource utilization and management, space utilization, and population dynamics.

Introduction

External and internal tags have been used for centuries as markers on marine and freshwater fishes for the purposes of identification and information retrieval. From the earliest application on salmonids to the more recent use on sharks, these markers can be divided into five general categories. Overall, physical tags have been used most extensively, followed by dyes and pigments, mutilation, branding, and meristic and morphometric characters including ageing structures (Arnold[1], McFarlane et al. 1990). More than twenty-five general types of physical tags (both external and internal) can be defined, as described by Rounsefell & Everhart (1953), Jakobsson (1970), and McFarlane et al. (1990). These tags are made of various materials, are sometimes designed for specific species or groups of animals, and have been used with varied success. The most common physical tag is external, with some form of anchor that penetrates the skin or other tissues, and includes a component for recognition of individuals (Bergman et al. 1992).

Tagging is a valuable technique for investigating the behavior of sharks (Sciarrotta & Nelson 1977). Oceanic and deep-water sharks are difficult to study, and most shallow water species are either large, active

[1] Arnold, D.E. 1966. Marking fish with dyes and other chemicals. Technical paper No. 10, Bureau of Sport Fisheries and Wildlife, U.S. Dept. of Interior. 44 pp.

predators not easily observed for any length of time, or are species that are rarely seen and in small numbers (McLaughlin & O'Gower 1971). Sharks in general are particularly suited to tagging studies because of their extensive movements, schooling behavior, and relatively large size which allows them to carry most tags successfully (Bonham et al. 1949).

Tagging studies provide valuable information on a wide variety of aspects of elasmobranch biology, including life history parameters, stock status, behavioral and distribution patterns, and migration patterns. The ability to account for the presence of a particular fish or group of fish in time and space by marking provides an important tool to the fishery manager (Rounsefell & Everhart 1953) and may be the most cost-effective, reliable, and direct means to obtain data for studying populations (Everhart & Youngs 1981, Gordon 1990).

The purpose of this paper is to summarize the results of the major shark tagging studies that have used conventional tags. Conventional tags are defined as those that can be identified visually without the use of special detection equipment. We review methods and data protocols used by the National Marine Fisheries Service (NMFS) Cooperative Shark Tagging Program (CSTP) which typify those of many large scale game fish tagging programs around the world. We use results from the CSTP and other tagging studies to review objectives of tagging programs, types of information derived from such programs, and possible problems and biases in these data. In addition, we explore the future use of conventional tags and tagging techniques in combination with new tagging technologies.

Materials and methods

This review contains a comprehensive compilation of 64 past and present worldwide shark tagging studies and programs. Appendix 1 includes the scientific or common name as initially reported in the study, original units for the distance data converted to kilometers and time at liberty data converted to years. Distance traveled is customarily reported as a minimum straight line distance between point of tagging and recapture. An attempt was made to keep study results discrete. It was often difficult, however, to clearly distinguish between studies from the information provided in the reports we reviewed, since multiple authors have reported results from the same studies at different times, or performed different analyses on the same data, and other authors updated results from long term studies. For some multi-year studies, we relied on personal communications from the program managers for the most current results.

Historical review

Development of tagging technology

In a comprehensive review of the historical development of external tags and marks documenting approximately 900 published studies, McFarlane et al. (1990) traced the earliest occurrence of animal marking to between 218 and 201 BC. Much of the initial fish tagging was on salmonids. As early as the 1600s, juvenile *Salmo salar* were marked with colored wool ribbons on their tails to document their return from the sea to natal rivers. In the 1800s, salmon were marked using a variety of methods including fin clipping, fin and jaw wires (ring tags), tail and opercle tags (collar tags and numbered label tags), and dangler-type tags attached through the muscles in front of the dorsal fin (Archer and Atkins tags) (Rounsefell & Everhart 1953, McFarlane et al. 1990). Pelagic herring were first tagged with barbed hooks (Jakobsson 1970) during this same time period. With the introduction of the Petersen disc tag in 1894, the range of studies that could be carried out through tagging was greatly expanded. Demersal species such as plaice were first marked using this extremely popular and successful tag type (Rounsefell & Everhart 1953, Jakobsson 1970).

Until about 1900, the tagging of fish developed very slowly and only about 100 000 fish were tagged by 1910 (Rounsefell & Everhart 1953). Between 1900 and 1929, salmonids and some demersal species such as plaice, cod, haddock, pollock, and halibut were marked with a variety of newly developed tag types. These included Lofting, safety pin, strap, wire loop, Heinicke ring and stud, and bachelor button tags attached through the muscle, fin, jaw, and opercle. By the 1930's, the number of fish tagged increased to over 400 000 as other types of markers, including body cavity, sturgeon, hydrostatic, barbed, and internal anchor, came into use primarily on anadromous and demersal marine species (see Rounsefell & Everhart 1953, Jakobsson 1970, McFarlane et al. 1990).

The first attempt to tag a pelagic species of fish was in 1893 when the Fishery Board of Scotland tagged 600 herring using barbed hooks with a rigid numbered plate on the shaft (Jakobsson 1970). In

1911, Sella tagged *Thunnus thynnus* by using a collar tag consisting of a piece of copper chain fastened around the caudal peduncle. Both methods yielded no returns (Rounsefell & Everhart 1953, Jakobsson 1970). Tuna, herring and mackerel were tagged in subsequent decades using celluloid collar and disc, opercle clip, barb, strap, Petersen disc, plastic strip, body cavity, and hook tags with varied success (Rounsefell & Everhart 1953, Jakobsson 1970, McFarlane et al. 1990).

The internal anchor tag was developed by Rounsefell in 1936 to satisfy the need for an externally visible tag that fish could carry successfully, even as they increased greatly in size, without the high shedding rate of early body cavity tags (Rounsefell & Everhart 1953). By the early 1950's, relatively inexpensive vinyl tubing was readily available in a variety of sizes and colors for use as components of new types of external tags. With the development of the spaghetti loop tag in 1952 by Wilson (Jakobsson 1970) and the dart and streamer tag in 1954 by Mather[2], tagging of pelagic species became widespread. Both tag types were composed of plastic vinyl tubing with a printed number and legend and had little drag in flowing water. Dart tags, developed for larger fish, could be applied with a minimum handling time while the fish remained in the water. The harpoon-like head of the dart tag was initially made of stainless steel and later fitted by Yamashita & Waldron (1958) with a nylon barb. This nylon and stainless steel barb was further modified in size and shape in subsequent years for specific uses on target species and life history intervals like school tuna and *Scomberomorus cavalla* (Mather[2], Bayliff & Holland[3], McFarlane et al. 1990).

The modern anchor tag, first used in the 1960's, is similar to the dart tag except that the barbed head has been replaced by a nylon T-bar. These streamer tags are used widely because of the ease with which large numbers of fish can be tagged with individual serial numbers, their low cost, and their relatively high retention rate (McFarlane et al. 1990).

Since the early 1960's, a variety of subcutaneous tags has been developed and used initially on salmonids. Many of these involve the use of magnetic and electronic detection devices. While they fall outside of our definition of conventional tags, we have included a brief description of their development here. The first of these are small magnetized stainless steel coded wire tags (CWT) that are hypodermically implanted into suitable tissue such as the snout or cheek (Monan 1982). Advantages of CWT include easy identification of large numbers of experimental groups, low tag mortality, and a high tag retention rate. Disadvantages include high initial cost of application and detection equipment, non-visibility of tags, and the necessity of having to kill the fish before removal of the tag to decipher the binary coding (etching) (Raymond 1974, Pepper & O'Connell 1983, Bergman et al. 1992). A more recent coded wire tag (rare earth) allows data to be read with x-ray fluorescent spectroscopy without killing the fish (Monan 1982). Another tag, the passive integrated transponder (PIT) tag, was developed in the early 1980s and has proven very effective. The PIT tag consists of an integrated microchip and antenna encapsulated in ceramic material. The tag is energized by an external detection decoder system to transmit a unique 10-digit alphanumeric identification code (Prentice et al. 1990). Advantages of this tag type include: *in situ* detection of individual fish through soft and hard tissue, glass, plastic, and freshwater and saltwater; no need to anesthetize, handle or restrain the fish during data gathering; and nearly 100% tag retention in the body cavity with no effect on growth, survival, or behavior for salmonids (Prentice et al. 1990). A drawback to all of these tag types is that they must be surgically inserted (which limits the number of fish that can be tagged within a given time) and must be recovered by personnel using the proper equipment to read the tag. A more recent subcutaneous tag that is individually discernable and externally visible without the use of an external device, is the visible implant (VI) tag that is implanted beneath the integument in transparent tissue (Haw et al. 1990, Bergman et al. 1992).

Early elasmobranch tagging

The successful tagging of elasmobranchs has been a relatively recent event. By 1936, 700 skates and rays were tagged and released around the British Isles, and only 1005 had been tagged in all European waters up to 1940 (Olsen 1953). Beginning in the 1940's, however, the tagging of sharks, primarily *Squalus acanthias* and *Galeorhinus galeus*, took place in both the Pacific and Atlantic Oceans.

---

[2] Mather, F.J., III. 1963. Tags and tagging techniques for large pelagic fishes. pp. 288–293. *In:* International Commission of Northwest Atlantic Fisheries Special Publication 4, North Atlantic Fish Marking Symposium.

[3] Bayliff, W.H. & K.N. Holland. 1986. Materials and methods for tagging tuna and billfishes, recovering the tags and handling the recapture data. FAO Fish. Tech. Pap. 279. 36 pp.

In the Pacific, a *G. galeus* fishery developed during World War II for the vitamin A oils from its liver. Tagging of this species in southeastern Australia commenced in 1942 when 22 fish were internally tagged (Olsen 1953). In 1947, a comprehensive tagging program was undertaken by the Commonwealth Scientific and Industrial Research Organization (CSIRO) (Olsen 1953, 1954). This program, part of the general investigations on the biology of the species, was started in response to concern about declining catches. Up until 1956 when the program ceased, a total of 6502 *G. galeus* were tagged with a combination of internal and external tag types (Olsen 1984). In addition, 587 *Mustelus antarcticus* were also released. Tagging resumed between 1973 and 1976 by the then Fisheries and Wildlife Division of Victoria and again in 1990 by the Fisheries Research and Development Corporation Southern Shark Tagging Project. By 1996, a total of 20 185 sharks of 22 species (Appendix 1) had been tagged in both the Pacific and Indian Oceans (Walker et al.[4]). A male *G. galeus* tagged with an internal plastic tag, was recaptured after 41.8 years from the early CSIRO tagging program off Southern Australia. This is the longest recorded period at large for any species of tagged fish (Coutin 1992).

Due to the demand for vitamin A in liver oil of *S. acanthias*, an intensive fishery for this species developed on the Pacific coast of the United States (US) between 1941 and 1950. The development of this fishery prompted the need for life history information (Holland 1957). A few *S. acanthias* (176) were tagged in 1940 incidental to a study of the otter-trawl fishery, but a sustained tagging program began in 1942. This was a cooperative project involving commercial fishermen, the Washington State Fisheries Department, and the Technological Laboratory of the US Fish and Wildlife Service (USFWS) at Seattle, and was designed to determine the extent and pattern of migration, rate of growth, and fishing mortality. The primary tagging areas were off the coasts of Washington and British Columbia. A total of 9705 *S. acanthias* were tagged and released by August 1946 (Bonham et al. 1949, Holland 1957). *S. acanthias* in the eastern North Pacific were tagged with celluloid Petersen-type disk tags. By the end of 1953, 6.7% of the tagged sharks had been recaptured, with a maximum time at liberty of 10 years and a maximum distance traveled of 8704 km (Appendix 1).

Additional early North American Pacific tagging included the release of 564 *S. acanthias* off British Columbia reported by Foerster[5] and 16 588 tagged *S. acanthias* off Japan between 1929 and 1957 (Taniuchi personal communication). An additional 427 tagged *G. zyopterus* were released in Oregon waters (Westrheim in Herald & Ripley 1951) and another 118 *G. zyopterus* tagged in California waters reported by Herald & Ripley (1951).

In the Atlantic, one of the first shark tagging experiments was on *Somniosus microcephalus*, carried out by the Greenland Fisheries Investigations in 1936, 1939, 1948, and 1949 to determine the growth rate of the species. Hansen (1963) reported a total of 411 sharks tagged using Petersen disc tags with silver and stainless steel wire attachments. Twenty-eight sharks were recaptured up to 1296 km away and after 16 years at liberty. While these returns yielded little or no growth information, they did provide important longevity information for this species.

Most of the initial tagging in the North Atlantic was also on *S. acanthias*. Unlike in the Pacific Ocean, however, *S. acanthias* was not fished commercially on the Atlantic coast, and its large population was considered a hindrance to cod fishing (Templeman 1954). A tagging study was initiated by the government of Newfoundland to determine if the stock was local rather than international, and thus could be locally managed. In 1942, Templeman (1944, 1954) released 279 *S. acanthias* near St. John's Newfoundland that were tagged with Petersen disc tags attached with a nickel wire. This study continued until 1965 with a total of 2855 *S. acanthias* tagged, of which 8.2% were recaptured. The longest time at liberty was 11.2 years with one trans-Atlantic recapture reported (Templeman 1976). Other early North Atlantic *S. acanthias* tagging included 907 sharks tagged in the New England–Gulf of Maine area between 1956 and 1964 and over 20 000 *S. acanthias* tagged in the northeast Atlantic between 1957 and 1963 (Aasen 1960, 1962, Holden 1965, Templeman 1976).

The first tagging of elasmobranchs off South Africa in the Indian Ocean was initiated in 1964 by the

[4] Walker, T.I., L.P. Brown & N.F. Bridge. 1997. Southern shark tagging project. Final report to Fisheries Research and Development Corporation (FRDC Project 93/066), Client report, (November 1997), Marine and Freshwater Resources Institute, Queenscliff, Victoria, Australia. 61 pp.

[5] Foerster, R.E. 1942. Dogfish tagging – preliminary results. Canada Fish. Res. Board. Pacific Coast Sta., Prog. Rep. No. 53: 12–13.

Oceanographic Research Institute (ORI) to help devise protective measures for swimmers against shark attacks in the area (Davies & Joubert 1967). A total of 1001 sharks were initially tagged off Durban with Jumbo Rototags and Petersen disc tags (39% were recaptured in the first year) and later with a modified Jumbo Rototag called the ORI tag (Davies & Joubert 1967). Bass et al. (1973) and Bass (1977) reported the further early tagging of several species of sharks off the Durban coast.

Cooperative tagging programs

Most of the aforementioned tagging studies were initiated and carried out by scientists to answer specific biological questions. All tagging, and in some cases returns, were done by investigators directly involved in the study. Another type of program is a cooperative tagging program, i.e. one that depends on joint participation of scientists and public volunteers to accomplish research objectives (Scott et al.1990). One of the first cooperative marine gamefish tagging programs that utilized assistance from volunteer fishermen was initiated in the US in 1951 by Frank Mather of the Woods Hole Oceanographic Institution (Mather[2]). Since that time, numerous small and large scale programs have developed worldwide and have expanded to include a variety of shark species. Some of these cooperative programs that specifically target sharks include: the ORI Program and the Southern Shark Tagging Project mentioned previously; a tagging study begun by the Ministry of Agriculture, Fisheries and Food in England in conjunction with a local shark angling club in 1970 (Stevens 1990); the Australian cooperative game-fish tagging program begun in 1973 by the Fisheries Research Institute of the New South Wales Department of Agriculture and Fisheries (Pepperell 1990); and the Ireland Central Fisheries Board's cooperative tagging efforts primarily on *Prionace glauca* and *G. galeus*, which began in 1970 (Fitzmaurice 1994, Green personal communication). In the US, these programs include the California Department of Fish and Game Pelagic Shark Tagging Program, which was initiated in 1983 (Ugoretz[6]) the Center for Shark Research at Mote Marine Laboratory in Sarasota, Florida (Hueter personal communication), and the NMFS CSTP described in more detail below.

Numerous other cooperative fish tagging programs have also included sharks as a component of their tagged fish. These include the New Zealand Ministry of Agriculture and Fisheries highly migratory tuna and game-fish efforts (Murray 1990, Hartill & Davies[7]) the American Littoral Society in Highlands, New Jersey, and various US state tagging programs.

NMFS Cooperative Shark Tagging Program

The NMFS CSTP is an extensive Atlantic shark tagging program, which is part of continuing research directed to the study of the biology of Atlantic sharks. The CSTP was started in 1962 by John G. Casey at the Department of Interior's USFWS Sandy Hook Laboratory, Highlands, NJ, in response to several shark attacks along the New Jersey coast. Volunteer participation began with a group of 74 anglers involved in tagging feasibility studies in 1963. The program expanded in subsequent years, coming under the auspices of NMFS in 1970, and currently includes over 6500 volunteers distributed along the Atlantic and Gulf coast of North America, and Europe. An overview of the early history of the CSTP is included in Casey (1985) and Kohler et al. (1998).

Sampling procedures described below for NMFS CSTP are similar to those of other tagging studies and cooperative tagging programs worldwide (Sluczanowski 1988). The two principal tag types used in the CSTP are a fin tag and a dart tag. The fin tags are variously colored, two piece, nylon cattle ear tags (Jumbo Rototags and Rototags) inserted through the first dorsal fin. Rototags are currently in use on neonate and juvenile sharks. Jumbo Rototags were first used by staff biologists on small sharks during the early years of the CSTP when the sharks were taken on board the boat, tagged, measured and released. The fin tags are applied with an applicator through a hole punched in the leading edge of the first dorsal fin by a leather punch. Today these tags are still primarily used by NMFS or other cooperating biologists.

As the program expanded to include thousands of volunteer fishermen, the dart tag was developed to be easily and safely applied to sharks in the water. Originally developed by Frank Mather for tunas (Mather[2]), the dart tags were modified for use on sharks (Casey 1985). A variety of stainless steel dart tags were used,

[6] Ugoretz, J. 1999. Shark tagging news, a newsletter of the California Department of Fish and Game shark tagging program (January 1999). 4 pp.

[7] Hartill, B. & N.M. Davies. 1999. New Zealand billfish and gamefish tagging 1997–98. NIWA Technical Report 57. 39 pp.

beginning in 1965. These included an F1 Streamer tag, NMFS M(s) Stainless tag, a Floy F66 tag, and a NMFS M tag. Recently, a small Hallprint nylon barbed tag is being used on neonates and small sharks. The M tag is the standard dart tag used by volunteer anglers. It has a stainless steel dart head, monofilament line, and a Plexiglas capsule containing a vinyl legend with return instructions printed in English, Spanish, French, Japanese and Norwegian (Kohler et al. 1998). The dart tags are used by biologists and volunteer recreational and commercial fishermen, and are applied using a sharpened stainless steel needle that is mounted in a variable length tagging pole. The head of the dart tag fits into the slotted point of the needle and the entire tag is held in place on the pole by a rubber band near the tag capsule. The dart head is sharpened and curved so that the two rear points will face downward into the muscle when the tag is inserted. Tags are implanted in the dorsal musculature near the base of the first dorsal fin. The dart is inserted at an angle toward the head end of the shark so that the capsule assumes a trailing position on the body. Hallprint tags are also applied with a stainless steel applicator that is affixed in a pole of suitable length. The tip of the applicator is sharpened and is inserted under the first dorsal fin until the nylon barb anchors in the basal cartilage.

Numbered dart tags are sent to volunteer participants on self-addressed return post cards for recording tagging information. The information requested from the volunteers is species, size, and sex of the shark, date, location, and capture gear, as well as the tagger's name and address. A remarks section is included so that the angler can add additional biological or environmental data. Size is estimated or measured and reported in total length, fork length, and/or weight. A card is filled out immediately following a tagging episode. First time taggers are sent instructions on proper catching and handling procedures to minimize injuring the shark before releasing it. The condition of the tagged shark is assessed before and after release and noted on the tag card. The assessment is based on how lively the fish is during the tagging process and after release and whether any injuries are evident. These data are numerically coded by assigning a shark to a general fish condition category: good, fair, or poor, with a specific fish condition category enumerating more details (e.g. bleeding, gut hooked).

There was an initial one-dollar reward sent as an incentive for returning tags, which after a few years was increased to five dollars. Since 1988, a hat with an embroidered logo has been sent as a reward. The tagging program is publicized through various articles in sport fishing magazines and other venues.

Literature such as newsletters, which detail biological information on shark life history parameters, shark identification, results of scientific studies, and management issues, are sent directly to all tagging program participants. In addition, staff frequently travel to fishing centers and to fishermen's forums to further educate constituents on shark conservation and the benefits of tag and release. Most tagging program participants, in turn, are very receptive to scientific information and are gratified to help further knowledge of the various species of sharks that they encounter. Tagging studies have been mostly single release events in which recoveries are made opportunistically by recreational and commercial fishermen. When a tagged shark is re-caught, information similar to that obtained at tagging is requested from the recapturer. Minimum straight-line distance between tagging and recapture (T/R) sites (distance traveled), the number of days at liberty, and the rate of travel are determined for all tags returned. All distance data are converted to kilometers from their original reported units.

Benefits and problems of cooperative programs

The aim of cooperative tagging programs is to gather various types of information on the target species. These data fall into three general categories: (1) life history information, which can be derived from tagging data and to some extent from the results of recaptures; (2) population dynamics information, which comes primarily from the recapture data; and (3) strategies for management, which can be determined from a combination of analysis of both types of data.

The cost/benefit ratio for cooperative tagging programs is extremely low. It would be nearly impossible for an individual or an individual institution or agency to mark and recapture the large quantity of fish over the extensive areas covered by utilizing literally thousands of knowledgeable volunteer recreational and commercial fishermen. Aside from the overhead of the over-seeing institution, this research is accomplished for basically the cost of the tags.

Cooperative shark tagging programs have resulted in large numbers of fish tagged, and time at liberty and distance records for many species of sharks, including *P. glauca*, *Isurus oxyrinchus*, *Carcharhinus plumbeus*, and *Lamna nasus* (Table 1). For example, one cooperative program, the CSTP, was responsible

Table 1. Distance traveled and time at liberty maximums for 101 species of sharks from a review of 64 shark tagging studies using conventional tags (x = data unavailable).

Species	Number of studies	Number tagged	Maximum distance traveled (km)	Maximum time at liberty (yr)
Alopias pelagicus	1	18	x	x
A. superciliosus	3	429	2767	6.5
A. vulpinus	8	150	1556	8.8
Aprionodon isodon	1	127	x	x
Apristurus brunneus	1	23	x	x
Carcharhinus acronotus	2	1331	315	9.2
C. albimarginatus	4	195	< 9	0.7
C. altimus	2	175	3343	11.2
C. amblyrhynchoides	1	122	173	8.8
C. amblyrhynchos	4	202	x	4.2
C. amboinensis	3	177	242	4.7
C. brachyurus	5	6729	1320	3.1
C. brevipinna	5	1806	1665	4.5
C. dussumieri	2	81	4	1.4
C. falciformis	7	1245	1339	7.1
C. fitzroyensis	1	55	150	0.2
C. galapagensis	6	659	2859	5.1
C. isodon	1	108	6	0.8
C. leucas	7	4883	643	7.9
C. limbatus	8	6289	2146	7.3
C. longimanus	4	723	2811	3.3
C. macloti	1	1610	711	10.5
C. maculipinnis	1	183	1383	0.6
C. melanopterus	3	1049	5	3.9
C. obscurus	7	15074	3800	15.8
C. perezi	1	630	48	4.4
C. plumbeus	7	19846	3776	27.8
C. porosus	2	106	> 37	x
C. sealei	1	124	367	x
C. signatus	2	225	2669	13.8
C. sorrah	2	2941	1116	9.9
C. spallanzi	1	1	x	x
C. tilstoni	1	4846	1348	12.9
C. wheeleri	1	33	x	x
Carcharodon carcharias	8	578	1445	2.6
Centrophorus granulosus	1	3	x	x
C. uyato	1	6	x	x
Cetorhinus maximus	3	216	x	x
Chlamydoselachus anguineus	1	1	x	x
Echinorhinus brucus	1	1	x	x
Eusphyra blochii	1	34	21	1
Furgaleus macki	1	79	x	x
Galeocerdo cuvieri	9	8132	6747	10.9
Galeorhinus galeus	10	17 574	4940	41.8
G. zyopterus	5	913	2037	2.1
Ginglymostoma cirratum	4	1366	541	7.8
Haploblepharus fuscus	1	164	8	x
Hemipristis elongatus	1	4	x	x
Heterodontus francisci	2	333	19	11.2
H. portusjacksoni	3	550	850	1.8
Hexanchus griseus	1	2	x	x
H. vitulus	1	11	x	x
Isurus oxyrinchus	9	10828	4543	12.8
I. paucus	1	90	3430	5.5
Lamna nasus	7	1074	4260	13.0
Loxodon macrorhynchus	1	2	x	x
Mustelus antarcticus	2	8698	x	x
M. canis	3	425	402	4.0
M. henlei	1	1	x	x
M. lenticulatus	1	2234	1159	5.0
M. nigropunctatus	1	1	x	x
M. norrisi	2	57	x	x
M. palumbes	1	47	210	x
Nasolamia velox	1	1	x	x
Nebrius ferrugineus	2	11	43	x
Negaprion acutidens	2	132	5	3.9
N. brevirostris	3	1724	426	4.1
Notorynchus cepedianus	4	1022	539	1.4
Odontaspis taurus	5	4032	1897	11.0
Poroderma africanum	1	421	1964	x
Prionace glauca	16	115177	7871	10.7
Pristiophorus cirratus	1	376	x	x
P. nudipinnis	1	499	x	x
Pseudocarcharias kamoharai	1	21	x	x
Rhincodon typus	2	264	x	x
Rhizoprionodon acutus	3	1052	1004	1.8
R. lalandii	1	2	x	x
R. longurio	1	73	1111	x
R. porosus	1	14	x	x
R. taylori	1	119	92	0.2
R. terraenovae	3	3803	1037	7.3
Scyliorhinus retifer	1	1	x	x
Somniosus microcephalus	2	433	1296	16.0
Sphyrna lewini	11	3278	1671	9.6
S. media	1	1	x	x
S. mokarran	3	220	1180	4.2

Table 1. (*Continued*).

Species	Number of studies	Number tagged	Maximum distance traveled (km)	Maximum time at liberty (yr)
S. tiburo	3	3885	343	5.6
S. tudes	1	2	x	x
S. zygaena	6	1427	1122	2.1
Squalus acanthias	14	78386	8704	11.2
S. cubensis	1	9	x	x
S. megalops	2	664	39	0.4
S. mitsukuri	1	10	x	x
Squatina africana	1	8	x	x
S. australis	1	4	x	x
S. californica	4	615	61	6.3
S. dumerili	1	106	x	x
Stegostoma fasciatum	2	3	x	x
Triaenodon obesus	2	237	9	3.4
Triakis megalopterus	2	4550	1066	x
T. semifasciata	3	1004	140	2.1

for over 70% of *P. glauca* tagged worldwide. In this program, 142 868 sharks of more than 52 species were tagged by CSTP participants between 1962 and 1997. Most species (30) have more than 100 sharks tagged (Appendix 1). In addition to species composition, information on migrations, movement patterns and rates of travel has resulted from analysis of CSTP data. Distances traveled for 31 species of sharks in the CSTP ranged from negligible to 6926 km. Seven species traveled distances over 3000 km: *P. glauca*, *Galeocerdo cuvier*, *I. oxyrinchus*, *C. obscurus*, *C. plumbeus*, *I. paucus*, and *C. altimus*. Maximum time at liberty for any shark in the CSTP is 27.8 years. Overall, individuals of 6 species of shark have been at liberty for over 10 years (*C. plumbeus*, *C. obscurus*, *C. signatus*, *I. oxyrinchus*, *C. altimus*, and *G. cuvier*) (Figures 1,2).

There are additional educational and conservation benefits of cooperative tagging programs. Tagging is now a socially acceptable component to recreational fishing, and there are many anglers who solely practice catch and release (van der Elst 1990). The old adage 'the only good shark is a dead shark' is no longer widely accepted, due partly to the education received by shark fishermen through volunteer tagging programs. In the past, shark fishing tournaments landed every shark caught. This resulted in the capture of many small sharks that would not qualify for a prize. Through educational efforts on tag and release and the implementation of minimum sizes, far fewer sharks are landed today. Most tournaments have a tag and/or release prize, and a few closely monitored tournaments have become tag and release only.

Along with the benefits are some significant data quality issues with a large volunteer tagging program. New participants sometimes fail to report all the requested information. Since the shark is usually tagged in the water, size estimates are often exaggerated, and species identification errors, particularly of the genus *Carcharhinus*, are common. Even though volunteers are becoming more skilled observers, errors in species identification and measurement are often not discovered until the shark is recaptured. Much time is spent by tagging program personnel contacting individual taggers and recapturers to fill in missing information and to verify data, especially when the tag or recapture is a record of some sort, is on an uncommon species, or when the shark is caught at an unusual location or time of year. Another problem in many cooperative tagging programs is that as the program expands, the demand for tags often exceeds the supply available. Care must be taken to distribute a limited tag supply over as large a geographic area and season as possible, to avoid unequal distribution of tagging effort. In addition, weather, research cruises, opening or closing of a commercial fishery, commercial value of a species, and life history characteristics all play a role in the tag and recapture rates and distribution patterns (Kohler et al. 1998).

Information derived from tagging and recapture data

Historically, initial objectives of most tagging studies were to study movements and migrations, with more recent techniques developed as tools for studying population dynamics (Rounsefell & Everhart 1953). For instance, in a review of 59 marine tagging studies completed in New Zealand waters, 58% dealt with movements, 22% with age and growth, and 20% with population dynamics (Murray 1990).

Data collected in a tagging program can be used to develop information on behavior, species composition, size composition, sex ratios, spatial and temporal distribution, delineation of nursery and pupping areas, distribution of maturity intervals, indices of relative abundance, and recognition of individuals. External tags can be used to readily identify specific sharks

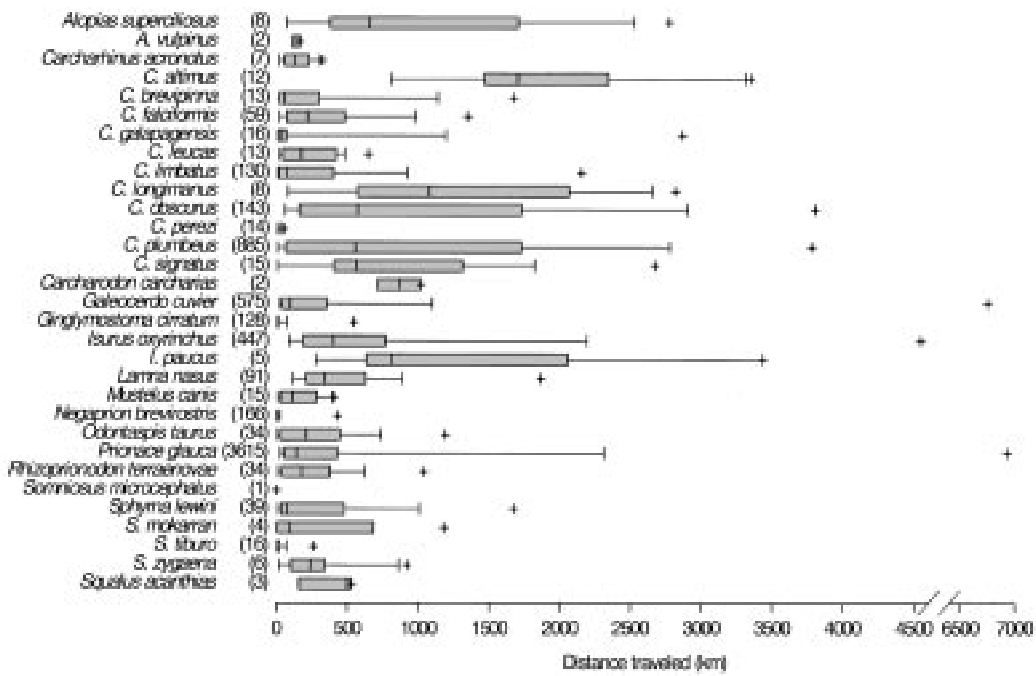


Figure 1. Box and whisker plots of distances traveled for 31 species of sharks from the CSTP, 1962–1997. The box indicates the 25th and 75th percentiles, the line within the box marks the median. Whiskers indicate the 10th and 90th percentiles. Maximum reported value for distance traveled by a species is indicated by +. Sample size in parentheses.

in behavioral studies (Compagno & Fergusson[8]), to determine the stability of a school, and to follow changes in group composition and size over a period of time (Klimley & Nelson 1984). Combinations of tag types, colors, and patterns can be used to distinguish individuals and a particular tagging year or location (Pratt & Carrier 2000). Tagging experiments can also be designed to examine age validation and growth parameters, homing and site fidelity, dispersal rates, residence times, identification and composition of fisheries, fisheries interactions, changes in fishing patterns, gear selectivity and catchability, stock identity, movement rates, population size, abundance, mortality and survival rates, recruitment, interaction rates between areas, catch (harvest) estimates, exploitation rates, tag shedding, survival and growth of hatchery and transplanted fish, and environmental data.

Age and growth studies

A T/R study provides an excellent means for obtaining empirical growth data when the fish are measured at tagging and recapture and the time at liberty is known (Jensen[9], Cailliet 1990). Growth in sharks calculated from tagging experiments is well documented (e.g. Bonham et al. 1949, Holland 1957, Jensen et al. 1961, Hansen 1963, Kato & Carvallo 1967, Tester[10], Clarke 1971, Gubanov 1976, Stevens 1976, 1984, 1990, Bass 1977, Randall 1977, Thorson & Lacy 1982, Pratt & Casey 1983, Pittenger 1984, Tucker 1985). Data from recaptures have been used to determine longevity,

[8] Compagno, L.J.V. & I.K. Fergusson. 1994. Field studies and tagging of great white sharks, *Carcharodon carcharias* (Linnaeus, 1758) off Cape Province, South Africa: a synopsis for 1992–1993. pp. 18–21. *In:* S.L. Fowler & R.C. Earll (ed.) Proceedings of the Second European Shark and Ray Workshop, 15–16 February 1994, Tag and Release Schemes and Shark and Ray Management Plans, Unpublished report.

[9] Jensen, A.C. 1963. Further field experiments with tags for haddock. pp. 194–203. *In:* International Commission of Northwest Atlantic Fisheries Special Publication 4, North Atlantic Fish Marking Symposium.

[10] Tester, A.L. 1969. Cooperative shark research and control program final report 1967–1969. University of Hawaii, Honolulu. 47 pp.

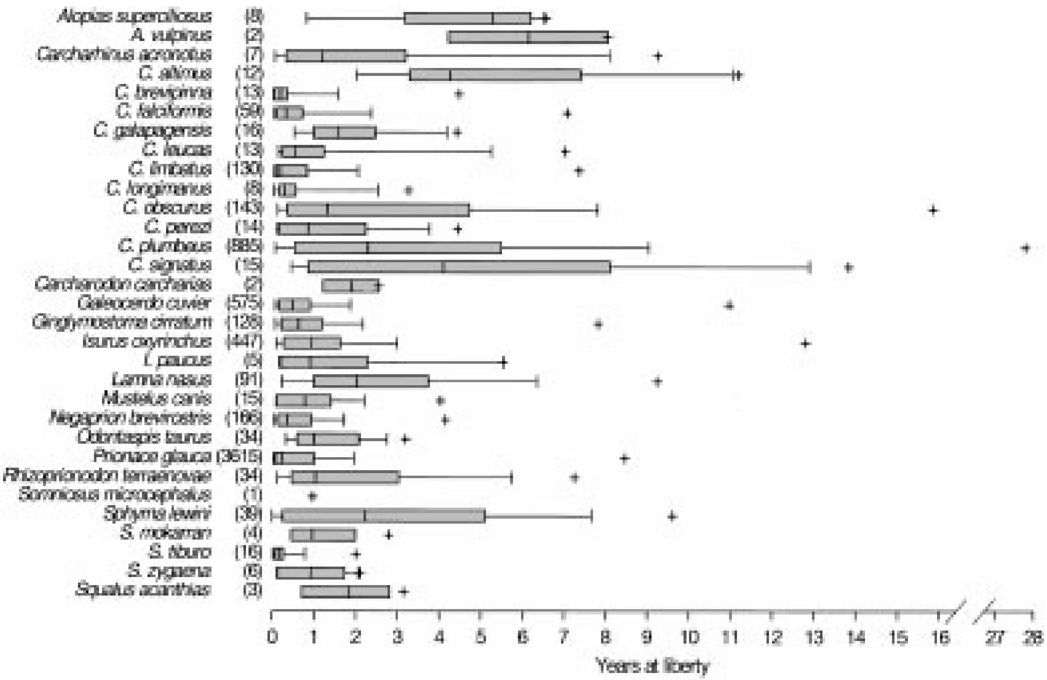


Figure 2. Box and whisker plots of time at liberty for 31 species of sharks from the CSTP, 1962-1997. The box indicates the 25th and 75th percentiles, the line within the box marks the median. Whiskers indicate the 10th and 90th percentiles. Maximum reported value for time at liberty for a species is indicated by +. Sample size in parentheses.

growth rates, and von Bertalanffy growth parameters (Gulland & Holt 1959, Fabens 1965, Francis 1988b,c). In sharks, calculation of growth parameters and/or age verification using T/R data have been accomplished for *C. plumbeus* (Casey & Natanson 1992), *Negaprion brevirostris* (Gruber & Stout 1983), *S. tiburo* (Parsons 1987), *G. cuvier* (Natanson et al. 1999), *Rhizoprionodon terraenovae* (Branstetter 1987), *G. galeus* (Grant et al. 1979, Olsen 1984, Moulton et al. 1992, Francis & Mulligan 1998), *Squatina californica* (Cailliet et al. 1992), *P. glauca* (Skomal 1990), *S. acanthias* (Ketchen 1975, Tucker 1985, McFarlane & Beamish 1987), *Triakis semifasciata* (Smith 1984, Kusher et al. 1992), *M. lenticulatus* (Francis & Francis 1992), *M. antarcticus* (Moulton et al. 1992), *C. tilstoni* and *C. sorrah* (Davenport & Stevens 1988).

Population size

Although marking fish has long been recognized as the most direct means of studying populations for calculation of abundance and size (Ricker 1975, Everhart & Youngs 1981, Jensen 1981), these techniques have infrequently been applied to sharks. Indications of relative population size for juvenile and neonate *Sphyrna lewini* have been inferred from the recapture rate and by the method of Jolly (1965) (Clarke 1971). An estimate of population size from the Jolly-Seber and Peterson methods and an abundance index based on resightings was calculated for *Carcharodon carcharias* (Cliff et al. 1996, Strong et al. 1996). Resighting data were also used to estimate the population size of *S. californica* with the Lincoln–Peterson index, and to calculate size from a simple assumption of proportionality in the numbers of tagged/resighted and untagged/resighted sharks for *Heterodontus portusjacksoni* (McLaughlin & O'Gower 1971, O'Gower & Nash 1978). In addition, population size (Stevens & West[11]) and a framework established for estimating rate of movement (Hilborn 1988, Xiao 1996) were determined for *G. galeus*, and

[11] Stevens, J.D. & G.J. West. 1997. Investigation of school and gummy shark nursery areas in south eastern Australia. Fisheries Research and Development Corporation Project Final Report: Project 93/061. 76 pp.

population density and size have been calculated for *C. melanopterus* (Stevens 1984).

Other life history information

Tag returns from a commercial or recreational fishery in conjunction with tag-recovery and capture–recapture models can be used to determine other life history parameters (Jones 1976, Brownie et al. 1978, Schwarz & Arnason 1990, Pollock et al. 1991, Myers et al. 1997, Brooks et al. 1998, Hoenig et al. 1998a,b). Mortality rates based on recapture data have been calculated for *G. galeus* (Grant et al. 1979, Olsen 1984, Xiao et al. 1999b), *T. semifasciata* (Smith & Abramson 1990, Cailliet 1992), and *C. carcharias* (Cliff et al. 1996). Other fishery parameters derived from shark T/R data include an interaction rate between areas for *M. lenticulatus* (Francis 1988a), an exploitation rate for *M. lenticulatus* (Francis 1989) and *T. semifasciata* (Smith & Abramson 1990, Cailliet 1992), yield per recruit for *G. galeus* (Grant et al. 1979, Olsen 1984) and *T. semifasciata* (Smith & Abramson 1990, Cailliet 1992), gear catchability for *M. antarcticus* (Walker 1992), and stock replacement values for *T. semifasciata* (Smith & Abramson 1990, Cailliet 1992).

Environmental data that are collected ancillary to the tagging of fishes either in a directed study or opportunistically by volunteer taggers can be used for the characterization of pupping areas, definition of essential fish habitat, and habitat preferences of a species or life interval of that species or to determine the causative factors for a particular behavior or movement pattern. Seasonal changes in environmental conditions and fluctuations in temperature, in general, are thought to be chief factors influencing movements of highly migratory species including sharks (e.g. Backus et al. 1956, Strasburg 1958, Springer 1960, Jensen et al. 1961, Kato & Carvallo 1967, Hoey 1983, Talent 1985, Pyle et al. 1996).

There is considerable evidence of seasonal movements by sharks discerned through the use of T/R data. Movement patterns include latitudinal and inshore–offshore migrations in response to increasing water temperatures (Francis 1988a) and have been shown for almost all families of tagged sharks, e.g. heterodontids (McLaughlin & O'Gower 1971), lamnids (Bruce 1992, Casey & Kohler 1992), carcharhinids (Stevens 1976, Tricas 1977, Olsen 1984, Francis 1988a), sphyrnids (Clarke 1971), and squalids (Holland 1957, Jensen et al. 1961, Templeman 1976).

The dispersal rate, residence time, movement patterns, and behavior of tagged fishes can be used to determine the extent of their home range (Harden Jones 1968). Site affinity, homing ability, and/or a home range for sharks have been demonstrated using conventional tagging methods alone or in combination with acoustic tagging techniques for the following species: *N. brevirostris* (Gruber et al. 1988, Morrissey & Gruber 1993), *H. portusjacksoni* (McLaughlin & O'Gower 1971, O'Gower & Nash 1978), *S. californica* (Pittenger 1984), and *C. carcharias* (Strong et al. 1992, Compagno & Fergusson[8]).

Sources of bias in tagging and recapture data

In an ideal world, tagging would be an excellent means to derive the life history and population dynamics information described above. In practice, however, there are a variety of factors that influence the rate of tag returns and limit the validity of the inferences that may be drawn from these data. More than half (55%) of the 191 reported recapture rates for 72 species of sharks from 52 shark tagging studies reviewed in this study reported return rates of less than 5% (Figure 3). Factors that influence this tag return rate include natural mortality of tagged fish (which may differ from year to year and among migration destinations), tagging induced mortality (which includes mortality associated with capture), variation in fishing pressure, emigration out of the principal tagging and fishing area, immigration from non-tagging areas, variation in tagging location and time of release and recovery, changes in the susceptibility to capture over time, experience level of tagging personnel, incorrect species identification, incorrect recording of tag or recapture data, failure to receive recovered tags (including non-recognition, non-recovery, and non-reporting of tags), and tag shedding or loss (Holland 1957, Ricker 1975, Buchanan et al.[12], Grant et al. 1979, Porter 1979, Gulland 1983, Francis 1989, Pepperell 1990, Schwarz & Arnason 1990).

Insuring the reporting of recovered tags in a voluntary program is difficult. The magnitude of this

[12] Buchanan, C.C., F.J. Mather, III & J.M. Mason, Jr. 1977. An overview: cooperative game fish tagging program (Atlantic Ocean). pp. 181–206. *In:* R.A. Barnhart & T.D. Roelofs (ed.) Catch-and-Release Fishing as a Management Tool – A National Sport Fishing Symposium, September 7–8, 1977, Humboldt State University, California.

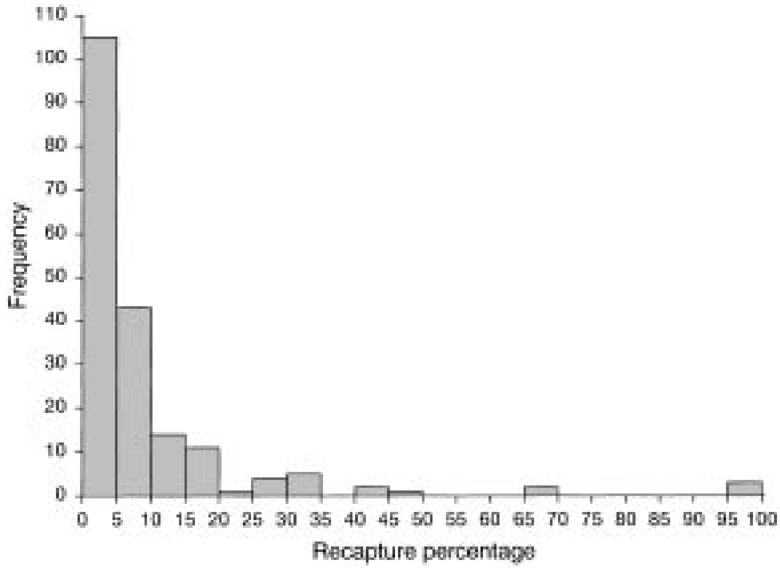


Figure 3. Frequency distribution of 191 reported recapture rates for 72 species of sharks from 52 shark tagging studies using conventional tags.

factor may vary among fisheries and from year to year (Eisner & Ritter 1979). A well-publicized reward and/or lottery system and an easily recognizable tag legend will encourage returns. Stricter management regulations in some fisheries, however, may decrease the likelihood of commercial fishermen sending in information on a recovered tag and cause differences in under-reporting among fisheries (e.g. Harden Jones 1968, Murray 1990). For example, data from the *G. galeus* fishery in Australia showed that only about half of the recaptured sharks have been recorded due to deliberate suppression of information by some fishermen, as well as the fact that some internal tags were accidentally lost during gutting and cleaning operations at sea (Olsen 1984). In contrast, it was found, on average, that only 3% of recreational anglers participating in a cooperative tagging program off Natal, South Africa, did not return tags (van der Elst 1990). Olsen (1953) reported that the return percentage increased three fold after the practice of double tagging was instituted, suggesting that many tags were either shed or missed by fishermen. The color of the tags, however, made no difference in reporting rates (Olsen 1953, Stevens et al. 2000). Various methods have been derived to assess the probability that a tag is returned by fishermen or processors and to calculate the tag reporting rate (Jakobsson 1970, Hilborn 1988, Hoenig et al. 1998a).

When applying conclusions drawn from tagged fish to the overall population, it is often assumed that: tagged fish mix rapidly with the untagged part of a population; tagged fish are as likely to be caught as untagged fish; and the act of catching or tagging has no effect on behavior, growth, migration patterns, or subsequent survival (Gulland 1983, Schwarz & Arnason 1990). The effect of capture and tagging of sharks on growth has been investigated by a number of researchers. Some studies have concluded that the normal growth rate of some shark species may be interrupted by the effects of tagging for various periods of time, depending on injuries received by the fish during tagging operations and the amount of irritation inflicted by various types of tags. This has been shown for *Ginglymostoma cirratum* (Carrier 1985), *S. acanthias* (Bonham et al. 1949, Holland 1957, Ketchen 1975, Templeman 1984), *S. tiburo* (Parsons 1987), *N. brevirostris* (Manire & Gruber 1991), *M. lenticulatus* (Francis & Francis 1992), *C. tilstoni* and *C. sorrah* (Davenport & Stevens 1988). Another *N. brevirostris* tagging study by Gruber & Stout (1983), however, showed that tagging per se did not greatly affect the growth rate when food is not limiting. No effect of tagging on growth was found for *G. cuvier* (Natanson et al. 1999) and *I. oxyrinchus* (Pratt & Casey 1983) and no detrimental effect on body size was found for *Hemiscyllium ocellatum* (Heupel & Bennett 1997).

The tagging process may alter behavior patterns. Underwater observations indicate that adult *G. cirratum* tagged with a spear gun did not leave the tagging area or left only briefly to return the next day (Pratt & Carrier 2001). In another study, approximately 50% of *S. californica* tagged in situ near the base of the tail did not flee after tagging (Pittenger 1984). Some tagging disturbance was noted when *H. portusjacksoni* were banded with caudal peduncle tags, in situ, and seen to move away from their initial site of tagging within their reef environment (McLaughlin & O'Gower 1971). It was determined, however, that no marked change in behavior had occurred (McLaughlin & O'Gower 1970).

In addition to direct observations, volunteer taggers in the CSTP often report that tagged *P. glauca* return immediately to the boat after tagging and/or are subsequently recaught on another line. While this anecdotal information does not address any long term effects, multiple recaptures of individual tagged *G. cuvier* over time (Natanson et al. 1999) suggest that the act of capture and tagging produces a minimum of trauma for some species.

An indirect method of determining initial mortality from the tagging operation is to compare the proportion of sharks of different release conditions that have been recaptured. If there were no differences between groups, this would suggest low tagging mortality (Beverton et al. 1959, Jakobsson 1970, Ricker 1975, Gulland 1983). A quantitative assessment of fish condition is commonly recorded in shark studies (e.g. Bonham et al. 1949, Holland 1957, Clarke 1971, Smith & Abramson 1990, Stevens et al. 2000). Results from some studies show that recovery rates are similar for all sharks released except for those released in what is judged to be the poorest condition category (e.g. Holland 1957, Clarke 1971, Francis 1989). Stevens et al. (2000) reported that recapture rates were not related to condition for *C. sorrah* and *C. macloti*, but there were fewer returns from *C. tilstoni* originally released in fair or poor condition. In addition, it has been suggested that shark length (Francis 1989) and capture gear (Stevens et al. 2000) can affect recapture rates.

The mortality of tagged sharks may vary by gear type. Reported recapture rates of trawl caught and tagged *M. lenticulatus* were less than those of set net caught and tagged *M. lenticulatus*, suggesting that trawl caught fish had significant initial mortality (Francis 1989). For *S. lewini* tagged in the laboratory, there were no deaths directly attributable to tagging, even though these sharks had been handled more and had been held in a small container en route to the laboratory (Clarke 1971). Other evidence that tagging-induced mortality may be low in sharks is derived from sonic tagging experiments. Results from these studies suggest that sharks survive the stress of capture, tagging, and release, and have been tracked successfully up to 90 days (Nelson 1990).

A final influence on the rate of tag returns is tag shedding or loss. Tag loss is possibly the most critical issue that must be considered in the evaluation of results from tagging experiments (McFarlane et al. 1990). In many studies, a tagged animal is assumed to retain its tag permanently, which is clearly not a valid assumption for certain types of tags (Xiao et al. 1999a). Double tagging experiments (e.g. Kato & Carvallo 1967, Francis 1989, Xiao et al. 1999a, Stevens et al. 2000) and aquarium studies (Davies & Joubert 1967) are two ways to estimate tag loss (Harden Jones 1968, Bayliff & Holland[3], McFarlane et al. 1990). The presence or absence of wounds or scars left from shed tags may also give some anecdotal information on tag shedding (Clarke 1971, Randall 1977, Klimley & Nelson 1984, Pittenger 1984).

Tag shedding information in the literature is published in two forms, percentages and rates. Early studies used a tag shed loss percentage to evaluate the effectiveness of various tag types (e.g. Davies & Joubert 1967, Kato & Carvallo 1967). One very recent study has calculated an instantaneous rate of tag shedding for *G. galeus* (range $= 0.2829 - 4.5992$) (Xiao et al. 1999). Tag shedding rates in sharks, however, must be evaluated by species (Pepperell 1990, Walker et al.[4]) and within species (Holden & Horrod 1979). Tag shedding rates have been found to vary with tag type (e.g. Davies & Joubert 1967, Xiao et al. 1999a), sex (e.g. Xiao et al. 1999a), capture gear (e.g. Hurst et al. 1999), and tagging position (e.g. Davies & Joubert 1967, Kato & Carvallo 1967, Xiao et al. 1999a). For example, spaghetti loop tags placed in front of the first dorsal fin of *M. lenticulatus* were shed more often than those placed between the dorsal fins (18% and 6%, respectively) (Francis 1989). Rototags applied closer to the tip of the first dorsal fin were lost more frequently than those placed towards the base of the leading edge of the fin (Stevens et al. 2000). The shedding rate of dart tags anchored in the basal cartilage of the dorsal fin was about half that of dart tags anchored in the dorsal musculature for *G. galeus* and *M. antarcticus*.

In addition, tag shedding rates for these two species did not vary with length at release or time at liberty (Xiao et al. 1999a).

Tissue irritation was found in some species of sharks marked with dart tags (Davies & Joubert 1967, Manire & Gruber 1991). These studies, however, looked at the external appearance of the wound. When tissue response and healing rates were investigated, it was reported that a spaghetti dart tag inserted into the dorsal musculature of *H. ocellatum* produced only localized tissue disruption and was not detrimental to long term health. In addition, tagging did not appear to predispose the sharks to infection (Heupel & Bennett 1997). A similar result was found using fin tags on juvenile *C. melanopterus*, *C. plumbeus*, and *C. obscurus* (Heupel et al. 1998). The authors caution that the fin tags should be large enough to allow for fin growth over time.

Tag choice

Many of the early shark tagging studies utilized Petersen discs (e.g. Holland 1957, Kato & Carvallo 1967, Bane 1968) or Rototags (e.g. Davies & Joubert 1967, Kato & Carvallo 1967) as their primary tags. Petersen disc tags were found to have a higher return percentage than dangler tags for *S. acanthias* (Holden 1965, Templeman 1984) but have been replaced by Rototags as the principal fin tag used on sharks because of their much lower shedding rate (Kato & Carvallo 1967, Thorson 1971, Holden & Horrod 1979, Walker et al.[4], Xiao et al. 1999a). Other tagging studies on sharks have used internal tags (Olsen 1953) and miscellaneous dangler, collar, loop, and hydrostatic tags and, in some cases, multiple tagging protocols on each fish (Gruber 1982, Gruber & Stout 1983, Pratt & Carrier 2001). These general tag types have been used in a variety of shapes, sizes, materials, and colors and have had varying success rates. With the advent of cooperative shark tagging programs, nylon and stainless steel dart tags were more commonly used (Casey 1985, Pepperell 1990, van der Elst 1990, Hartill & Davies[7], Ugoretz[6]). Overall, of the 54 studies reviewed that included information on tag type, the dart tag was the most widely used, followed by the Rototag (Figure 4).

There are disadvantages to using all of these tag types. External tags generally have a shorter life expectancy, while internal tags have been recovered after many years (Olsen 1953, Grant et al. 1979, Hurst et al. 1999). For recovery purposes, however, an internal tag is not highly visible to fishermen and may be difficult and time consuming to insert (Walker et al.[4]). In general, dart tags have an incidence of higher shedding than fin tags (Davies & Joubert 1967, Kato & Carvallo 1967, Walker et al.[4], Xiao et al. 1999a) but have been retained for longer periods on sharks than other tag types (Carrier 1985). A drawback to fin tags (Rototags, Petersen disc, and strap tags) is their increased susceptibility to fouling in capture gear and vegetation (Olsen 1953, Davies & Joubert 1967, van der Elst 1990) and the restriction of substantial growth in body and fin thickness during long-term experiments (Davies & Joubert 1967, Carrier 1985, McFarlane et al. 1990, Stevens et al. 2000). This can lead to subsequent splitting and deterioration of the fin and is especially true when used on immature sharks (Kato & Carvallo 1967, Carrier 1985) whose cartilaginous dorsal rays are softer (Olsen 1953) and the shark has more dramatic growth over time.

Many sources of bias can be associated with, or mitigated by, the choice of tags. The performance of various tags can be evaluated by comparing the differences in recovery rate and in the rate of decline of reported recoveries among different tags over time. Results from the Australian Cooperative Gamefish Program from 1973 to 1987 showed that higher proportions of sharks tagged with steel anchor tags were likely to be recaptured after long periods compared with various nylon barbed tuna dart tags, which suggests a slower shedding rate for the steel anchor tags. The longest times at liberty were also from fish tagged with this tag type (Pepperell 1990). Results from other studies on pelagic teleosts and some shark species have shown that return rates were similar for the nylon head and stainless steel barb (Mather[2], Lenarz et al. 1973, Baglin et al. 1980) or higher for the stainless steel dart (Beckett[13], Mather et al. 1974, Carrier 1985) depending on the species of fish (McFarlane et al. 1990, Pepperell 1990) and the method of tagging used (Bayliff & Holland[3]). The ORI fin tag was returned after longer times at liberty than the dart tag and the sheep ear tag when different tag types were tested on sharks in the ORI Tagging Program in South Africa (van der Elst 1990). In the NMFS CSTP, sharks have been at liberty for a maximum of 22.6 and 27.8 years for stainless steel dart and Jumbo Rototags, respectively, with similar overall return rates (5.2%, 6%).

[13] Beckett, J.S. 1970. Swordfish, shark and tuna tagging 1961–1969. Fish. Res. Board Can. Tech. Rep. 193: 1–32.

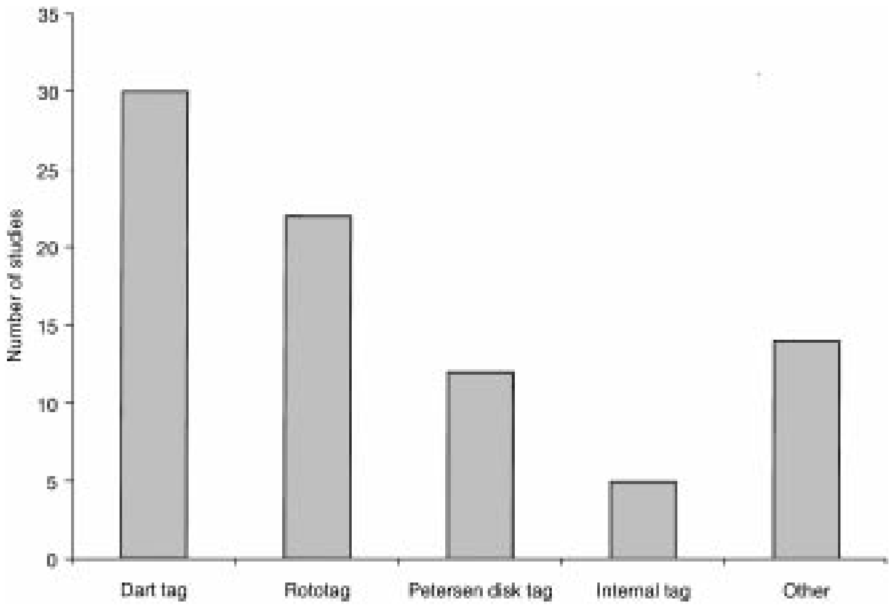


Figure 4. Relative uses of tag types from 54 shark tagging studies using conventional tags. Some studies used more than one tag type. Other tag category includes hydrostatic, freeze brand, loop, dangler, strap, Carlin disc, stainless steel bridle, caudal, and disk.

Choosing a tag type is thus a major factor to consider when a tagging program is planned. No single tag type is appropriate for all shark species or even for all life intervals of a species. No single technique is completely acceptable from a biological or technical standpoint (Prentice et al. 1990). It is, therefore, critical to consider any known life history information about the species to be marked in determining what form of tag to use (McFarlane et al. 1990). Factors determining the selection of an external tag are: the objectives of the study; the effect of the tag on behavior, survival, growth, or other life history characteristics; the stability of the mark; the number and size of the fish to be tagged; the stress of capture, handling, and marking of the fish; the ease of skin penetration or application of the tag; the length of time that the tag should remain on the fish; the availability and skills required by tagging personnel; the cost of conducting the experiment and recovery of tagged fish; the amount of coordination required among agencies, states, or countries; the species of fish the tag is to be used on; and the methods of recovery and reporting of the tags (Rounsefell & Everhart 1953, Arnold[1], Jakobsson 1970, McFarlane et al. 1990). The most important concerns in selecting a tag type for the CSTP (and for most cooperative programs) were that the external tag must be visible, be simple to use with inexpensive equipment, be easily and safely applied by volunteer fishermen, and contain detailed return instructions in several languages (Casey 1985).

Beyond conventional tagging studies: future directions

Historically, data analyses from tagging programs primarily involved descriptions of distributions and movements. Reports on these programs generally relied on descriptive statistics, such as averages (numbers tagged, recapture percentages), and maximums (days free, distances traveled), length frequencies, and distributions by species. Though some current researchers have begun to move beyond conventional data analyses, the time has come to more thoroughly investigate the practical application of T/R data to crucial management issues. Future tagging programs should include studies designed to investigate research questions in the following areas: resource utilization, space utilization, and population dynamics. In addition, the wealth of information from existing programs provides an opportunity for further critical analysis of these research areas.

Resource utilization and management hypotheses

Currently, one of the major challenges to fishery managers is the management and allocation of transboundary or migratory stocks (Hilborn et al. 1990). The migratory (nomadic) nature of many shark species requires international cooperation for management. For example, mating grounds for *P. glauca* occur in the western North Atlantic, whereas pupping grounds exist in the eastern North Atlantic (Casey 1985). Tagging programs can continue to provide data on stock structure, distribution of life history intervals, the exploitation of a resource by multinational fisheries, and direct evidence of fish movements across national and international boundaries. Traditional tagging techniques can be effective tools to test predicted migratory pathways and determine utilization of the resource.

Space utilization hypotheses

Another challenge to fishery managers is developing strategies for the recovery of over fished stocks including establishing minimum sizes, delineating known pupping areas, and determining essential fish habitat. For example, a directed tagging study on juvenile *C. plumbeus* in Delaware Bay has delineated the extent of the pupping area and established baseline neonate life history parameters (Merson 1999). Conventional tag data can serve as a cost-effective research tool (Smith & Abramson 1990) to test the predictions of management models that assume specific movement patterns or space utilization of the study species. Answers to these questions can then provide important information to develop stock maintenance strategies and test the success of these management initiatives.

Population dynamics hypotheses

An important application of conventional tagging methods includes the design of specific studies with experimental components to estimate critical population parameters (e.g. population size, exploitation/recruitment rates), develop fishery models (Xiao et al. 1999a), and to further investigate the possible bias in T/R data (Xiao 1994). Many of the questions and hypotheses on which these experimental studies are based can be answered best by conventional tagging techniques. In addition, quantitative evaluation of the potential bias and errors inherent in tagging data and assuring that the tagged fish are representative of the entire population would vastly improve the analysis of data available from tagging programs worldwide. Although techniques for estimating these parameters from tag data have existed for some time, relatively few programs have focused on experimental studies to investigate the population dynamics of large sharks.

The study of fish migrations includes both the description of movements, and the determination of the causative factors for the movements (Harden Jones 1968). Detailed examination of tag-recapture data can add significantly to both of these kinds of studies. While conventional tagging studies have traditionally described movement patterns, the next step in many programs is to determine what influences these migrations or behaviors through use of a combination of tagging methodologies and state of the art technology. New developments in internal, chemical, electronic, satellite, and archival tags, and genetic and biochemical stock analysis methods have occurred (McFarlane et al. 1990, Eckert & Stewart 2001, West & Stevens 2001). The future of tagging studies lies in the integration of these techniques with traditional methods to help answer some of these questions and further our knowledge on the movements and migrations of these highly migratory sharks.

Acknowledgements

We are indebted to the personnel of the Apex Predators Program, in particular, to L. Natanson who provided vital and timely assistance to B. Wetherbee who provided us with many tagging references and a valuable review of the manuscript, to W. Pratt who made additional comments, to J. Mello who assisted in preliminary preparations and ongoing research, and to R. Briggs for continued support in the NMFS CSTP. Our sincere thanks to the many researchers who contributed unpublished results from their shark tagging programs to render a more comprehensive review of worldwide programs. We apologize if some studies were inadvertently omitted. We are also grateful for critical reviews by T. Tricas, F. Almeida, W. Gabriel, and J. Kocik, and to K. Zewinski for providing valuable technical assistance.

References cited

Aasen, O. 1960. The Norwegian taggings of spiny dogfish (*Squalus acanthias*). Annales Biologiques 17: 85–95.
Aasen, O. 1961. Pigghaundersokelsene. Fisken Havet 1: 1–9.

Aasen, O. 1962. Norwegian dogfish tagging. Annales Biologiques 18: 106–107.

Backus, R.H., S. Springer & E.L. Arnold, Jr. 1956. A contribution to the natural history of the white-tip shark, *Pterolamiops longimanus* (Poey). Deep-Sea Res. 3: 178–188.

Baglin, R.E., Jr., M.I. Farber, W.H. Lenarz & J.M. Mason, Jr. 1980. Shedding rates of plastic and metal dart tags from Atlantic bluefin tuna, *Thunnus thynnus*. U.S. Fish. Bull. 78: 179–185.

Bane, G.W. 1968. The great blue shark. Calif. Currents 1: 3–4.

Bass, A.J. 1977. Long-term recoveries of tagged sharks. Copeia 1977: 574–575.

Bass, A.J., J.D. D'Aubrey & N. Kistnasamy. 1973. Sharks of the east coast of southern Africa. I. The genus *Carcharhinus* (Carcharhinidae). Invest. Rep. Oceanogr. Res. Inst. Durban 33. 168 pp.

Bergman, P.K., F. Haw, H.L. Blankenship & R.M. Buckley. 1992. Perspectives on design, use, and misuse of fish tags. Fisheries 17: 20–25.

Beverton, R.J.H., J.A. Gulland & A.R. Margetts. 1959. Whiting tagging: how the tag return rate is affected by the condition of fish when tagged. J. du Cons. 25: 53–57.

Bonham, K., F.B. Sanford, W. Clegg & G.C. Butcher. 1949. Biological and vitamin A studies of dogfish landed in the State of Washington (*Squalus suckleyi*). Wash. Dept. Fish. Biol. Bull. 49A: 83–114.

Branstetter, S. 1987. Age and growth validation of newborn sharks held in laboratory aquaria, with comments on the life history of the Atlantic sharpnose shark, *Rhizoprionodon terraenovae*. Copeia 1987: 291–300.

Brooks, E.N., K.H. Pollock, J.M. Hoenig & W.S. Hearn. 1998. Estimation of fishing and natural mortality from tagging studies on fisheries with two user groups. Can. J. Fish. Aquat. Sci. 55: 2001–2010.

Brownie, C., D.R. Anderson, K.P. Burnham & D.S. Robson. 1978. Statistical inference from band recovery data – a handbook. U.S. Fish and Wildl. Serv. Resour. Publ. No. 131. 212 pp.

Bruce, B.D. 1992. Preliminary observations on the biology of the white shark, *Carcharodon carcharias*, in South Australian waters. Aust. J. Mar. Freshwater Res. 43: 1–11.

Burnett, C.D., J.S. Beckett, C.A. Dickson, P.C.F. Hurley & T.D. Iles. 1987. A summary of releases and recaptures in the Canadian large pelagic fish tagging program 1961–1986. Can. Data Rep. Fish. Aquat. Sci. 673: 1–99.

Cailliet, G.M. 1990. Elasmobranch age determination and verification: an updated review. pp. 157–165. *In:* H.L. Pratt, Jr., S.H. Gruber & T. Taniuchi (ed.) Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics, and the Status of the Fisheries, NOAA Tech. Rep. NMFS 90.

Cailliet, G.M. 1992. Demography of the central California population of the leopard shark (*Triakis semifasciata*). Aust. J. Mar. Freshwater Res. 43: 183–193.

Cailliet, G.M., H.F. Mollet, G.C. Pittenger, D. Bedford & L.J. Natanson. 1992. Growth and demography of the Pacific angel shark (*Squatina californica*), based upon tag returns off California. Aust. J. Mar. Freshwater Res. 43: 1313–1330.

Carrier, J.C. 1985. Nurse sharks of Big Pine Key: comparative success of three types of external tags. Florida Sci. 48: 146–154.

Casey, J.G. 1985. Transatlantic migrations of the blue shark: a case history of cooperative shark tagging. pp. 253–68. *In:* R.H. Stroud (ed.) World Angling Resources and Challenges: Proceedings of the First World Angling Conference, Cap d'Agde, France, September 12–18, 1984, International Game Fish Association, Ft. Lauderdale.

Casey, J.G. & N.E. Kohler. 1992. Tagging studies on the shortfin mako shark (*Isurus oxyrinchus*) in the Western North Atlantic. Aust. J. Mar. Freshwater Res. 43: 45–60.

Casey, J.G. & L.J. Natanson. 1992. Revised estimates of age and growth of the sandbar shark (*Carcharhinus plumbeus*) from the western North Atlantic. Can. J. Fish. Aquat. Sci. 49: 1474–1477.

Clarke, T.A. 1971. The ecology of the scalloped hammerhead shark, *Sphyrna lewini*, in Hawaii. Pac. Sci. 25: 133–144.

Cliff, G., R.P. van der Elst, A. Govender, T.K. Witthuhn & E.M. Bullen. 1996. First estimates of mortality and population size of white sharks on the South African coast. pp. 393–400. *In:* A.P. Klimley & D.G. Ainley (ed.) Great White Sharks: the Biology of *Carcharodon carcharias*, Academic Press, San Diego.

Coutin, P. 1992. Sharks… and more sharks. Australian Fisheries 51: 41–42.

Davenport, S. & J.D. Stevens. 1988. Age and growth of two commercially important sharks (*Carcharhinus tilstoni* and *C. sorrah*) from Northern Australia. Aust. J. Mar. Freshwater Res. 39: 417–433.

Davies, D.H. & L.S. Joubert. 1967. Tag evaluation and shark tagging in South African waters, 1964–65. pp. 111–140. *In:* P.W. Gilbert, R. F. Mathewson & D.P. Rall (ed.) Sharks, Skates, and Rays, Johns Hopkins Press, Baltimore.

Ebert, D.A. 1996. Biology of the sevengill shark, *Notorynchus cepedianus* (Peron, 1807) in the temperate coastal waters of southern Africa. S. Afr. J. Mar. Sci. 17: 93–103.

Eckert, S.A. & B.S. Stewart. 2001. Telemetry and satellite tracking of whale sharks, *Rhincodon typus*, in the Sea of Cortez, Mexico, and the north Pacific Ocean. Env. Biol. Fish. 60: 299–308 (this volume).

Eisner, R.A. & J.A. Ritter. 1979. The Canadian Atlantic salmon (*Salmo salar*) smolt tag and its recovery system: a review. ICES, C.M. 1979/M: 24. 12 pp.

Everhart, W.H. & W.D. Youngs. 1981. Principles of fishery science. Cornell University Press, Ithaca. 349 pp.

Fabens, A.J. 1965. Properties and fitting of the von Bertalanffy growth curve. Growth 29: 265–289.

Ferreira, C.A. & T.P. Ferreira. 1996. Population dynamics of white sharks in South Africa. pp. 381–391. *In:* A.P. Klimley & D.G. Ainley (ed.) Great White Sharks: the Biology of *Carcharodon carcharias*, Academic Press, San Diego.

Fitzmaurice, P. 1994. Tagging studies of blue sharks and tope off the Irish coast. p. 17. *In:* S.L. Fowler & R.C. Earll (ed.) Proceedings of the Second European Shark and Ray Workshop, 15–16 February 1994, Tag and Release Schemes and Shark and Ray Management Plans.

Francis, M.P. 1988a. Movement patterns of rig (*Mustelus lenticulatus*) tagged in southern New Zealand. N.Z. J. Mar. Freshwater Res. 22: 259–272.

Francis, M.P. 1989. Exploitation rates of rig (*Mustelus lenticulatus*) around the South Island of New Zealand. N.Z. J. Mar. Freshwater Res. 23: 239–245.

Francis, M.P. & R.I.C.C. Francis. 1992. Growth rate estimates for New Zealand rig (*Mustelus lenticulatus*). Aust. J. Mar. Freshwater Res. 43: 1157–1176.

Francis, M.P. & K.P. Mulligan. 1998. Age and growth of New Zealand school shark, *Galeorhinus galeus*. N.Z. J. Mar. Freshwater Res. 32: 427–440.

Francis, R.I.C.C. 1988b. Are growth parameters estimated from tagging and age-length data comparable? Can. J. Fish. Aquatic Sci. 45: 936–942.

Francis, R.I.C.C. 1988c. Maximum likelihood estimation of growth and growth variability from tagging data. N.Z. J. Mar. Freshwater Res. 22: 42–51.

Gordon, W.G. 1990. Fish marking and the Magnuson Act. Amer. Fish. Soc. Symp. 7: 1–4.

Grant, C.J., R.L. Sandland & A.M. Olsen. 1979. Estimation of growth, mortality, and yield per recruit of the Australian school shark, *Galeorhinus australis* (Macleay), from tag recoveries. Aust. J. Mar. Freshwater Res. 30: 625–637.

Gruber, S.H. 1982. Role of the lemon shark, *Negaprion brevirostris* as a predator in the tropical marine environment: a multidisciplinary study. Florida Sci. 45: 46–75.

Gruber, S.H., D.R. Nelson & J.F. Morrissey. 1988. Patterns of activity and space utilization of lemon sharks, *Negaprion brevirostris*, in a shallow Bahamian lagoon. Bull. Mar. Sci. 43: 61–76.

Gruber, S.H. & R.G. Stout. 1983. Biological materials for the study of age and growth in a tropical marine elasmobranch, the lemon shark, *Negaprion brevirostris* (Poey). pp. 193–205. *In:* E.D. Prince & L.M. Pulos (ed.) Proceedings of the International Workshop on Age Determination of Oceanic Pelagic Fishes: Tunas, Billfishes, and Sharks, NOAA Tech. Rep. NMFS 8.

Gubanov, Y.P. 1976. The first catch of a tagged thresher shark (*Alopias vulpinus*). J. Ichthyol. 16: 497–498.

Gulland, J.A. 1983. Fish stock assessment. FAO/Wiley Series on Food and Agriculture, New York. 223 pp.

Gulland, J.A. & S.J. Holt. 1959. Estimation of growth parameters for data at unequal time intervals. J. Con. Explor. Mer 25: 47–49.

Hansen, P.M. 1963. Tagging experiments with the Greenland shark (*Somniosus microcephalus* (Bloch and Schneider)) in subarea 1. pp. 172–175. *In:* International Commission of Northwest Atlantic Fisheries Special Publication 4, North Atlantic Fish Marking Symposium.

Harden Jones, F.R. 1968. Fish migration. Edward Arnold, London. 325 pp.

Haw, F., P.K. Bergman, R.D., Fralick, R.M. Buckley & H.L. Blankenship. 1990. Visible implanted fish tag. Amer. Fish. Soc. Symp. 7: 311–315.

Herald, E.S. & W.E. Ripley. 1951. The relative abundance of sharks and bat stingrays in San Francisco Bay. Calif. Fish Game 37: 315–329.

Heupel, M.R. & M.B. Bennett. 1997. Histology of dart tag insertion sites in the epaulette shark. J. Fish Biol. 50: 1034–1041.

Heupel, M.R., C.A. Simpfendorfer & M.B. Bennett. 1998. Analysis of tissue responses to fin tagging in Australian carcharhinids. J. Fish Biol. 52: 610–620.

Hilborn, R. 1988. Determination of tag return from recaptured fish by sequential examination for tags. Trans. Amer. Fish. Soc. 117: 510–514.

Hilborn, R., C.J. Walters & D.B. Jester, Jr. 1990. Value of fish marking in fisheries management. Amer. Fish. Soc. Symp. 7: 5–8.

Hoenig, J.M., N.J. Barrowman, W.S. Hearn & K.H. Pollock. 1998a. Multiyear tagging studies incorporating fishing effort data. Can. J. Fish. Aquat. Sci. 55: 1466–1476.

Hoenig, J.M., N.J. Barrowman, K.H. Pollock, E.N. Brooks, W.S. Hearn & T. Polachek. 1998b. Models for tagging data that allow for incomplete mixing of newly tagged animals. Can. J. Fish. Aquat. Sci. 55: 1477–1483.

Hoey, J.J. 1983. Analysis of longline fishing effort for apex predators (swordfish, shark, and tuna) in the western North Atlantic and Gulf of Mexico. Ph.D. Thesis, University of Rhode Island, Kingston, 288 pp.

Holden, M.J. 1962. English spurdogfish tagging. Annales Biologiques 18: 107–108.

Holden, M.J. 1965. The stocks of spurdogs (*Squalus acanthias* L.) in British waters, and their migrations. Fish. Invest. Minist. Agric. Fish. Food G.B. Ser. II Salmon Freshwater Fish. 244: 1–20.

Holden, M.J. 1967. Transatlantic movement of a tagged spurdogfish. Nature 214: 1140–1141.

Holden, M.J. & R.G. Horrod. 1979. The migrations of tope, *Galeorhinus galeus* (L), in the eastern North Atlantic as determined by tagging. J. Cons. Int. Explor. Mer 38: 314–317.

Holland, G.A. 1957. Migration and growth of the dogfish shark, *Squalus acanthias* (Linnaeus), of the eastern North Pacific. Wash. Dept. Fish. Fish. Res. Pap. 2: 43–59.

Hurst, R.J., N.W. Bagley, G.E. McGregor & M.P. Francis. 1999. Movements of the New Zealand school shark, *Galeorhinus galeus*, from tag returns. N. Z. J. Mar. Freshwater Res. 33: 29–48.

Jackobsson, J. 1970. On fish tags and tagging. Oceanogr. Mar. Biol. Ann. Rev. 8: 457–499.

Jensen, A.L. 1981. Sample sizes for single mark and single recapture experiments. Trans. Amer. Fish. Soc. 110: 455–458.

Jensen, A.C., R.L. Edwards & G.C. Matthiessen. 1961. The spiny dogfish – a review. Woods Hole Lab Report No. 61–7: 1–42.

Jolly, G.M. 1965. Explicit estimates from capture–recapture data with both death and immigration-stochastic model. Biometrika 52: 225–247.

Jones, R. 1976. The use of marking data in fish population analysis. FAO Fish. Tech. Pap. 153: 1–42.

Kato, S. & A.H. Carvallo. 1967. Shark tagging in the eastern Pacific Ocean, 1962–65. pp. 93–109. *In:* P.W. Gilbert, R.F. Mathewson & D.P. Rall (ed.) Sharks, Skates, and Rays, Johns Hopkins Press, Baltimore.

Ketchen, K.S. 1975. Age and growth of dogfish *Squalus acanthias* in British Columbia waters. J. Fish. Res. Board Can. 32: 43–59.

Ketchen, K.S. 1986. The spiny dogfish (*Squalus acanthias*) in the northeast Pacific and a history of its utilization. Canadian Special Publication of Fisheries and Aquatic Sciences 88: 1–78.

Klimley, P.A. & D.R. Nelson. 1984. Diel movement patterns of the scalloped hammerhead shark (*Sphyrna lewini*) in relation to El Bajo Espiritu Santo: a refuging central-position social system. Behav. Ecol. Sociobiol. 15: 45–54.

Kohler, N.E., J.G. Casey & P.A. Turner. 1998. NMFS cooperative shark tagging program, 1962–1993: an atlas of shark tag and recapture data. Mar. Fish. Rev. 60: 1–87.

Kusher, D.I., S.E. Smith & G.M. Cailliet. 1992. Validated age and growth of the leopard shark, *Triakis semifasciata*, with comments on reproduction. Env. Biol. Fish. 35: 187–203.

Lenarz, W.H., F.J. Mather, III, J.S. Beckett, A.C. Jones & J.M. Mason, Jr. 1973. Estimation of rates of tag shedding by northwest Atlantic bluefin tuna. U.S. Fish. Bull. 71: 1103–1105.

Manire, C.A. & S.H. Gruber. 1991. Effect of M-type dart tags on field growth of juvenile lemon sharks. Trans. Amer. Fish. Soc. 120: 776–780.

Mather, F.J., III, D.C. Tabb, J.M. Mason, Jr. & H.L. Clark. 1974. Results of sailfish tagging in the western North Atlantic Ocean. pp. 194–210. *In:* R.S. Shomura & F. Williams (ed.) Proceedings of the International Billfish Symposium, Kailua-Kona, Hawaii, 9–12 August 1972, Part 2, Review and Contributed Papers, U.S. Dep. Comm. NOAA Tech. Rep. NMFS SSRF-675.

McFarlane, G.A. & R.J. Beamish. 1987. Validation of the dorsal spine method of age determination for spiny dogfish. pp. 287–300. *In:* R.C. Summerfelt & G.E. Hall (ed.) Age and Growth of Fish, Iowa State University Press, Ames.

McFarlane, G.A., R.S. Wydoski & E.D. Prince. 1990. Historical review of the development of external tags and marks. Amer. Fish. Soc. Symp. 7: 9–29.

McLaughlin, R.H. & A.K. O'Gower. 1970. Underwater tagging of the Port-Jackson shark Heterodontus portusjacksoni. Bull. Inst. Oceanogr. (Monaco) 69: 3–10.

McLaughlin, R.H. & A.K. O'Gower. 1971. Life history and underwater studies of a heterodont shark. Ecol. Monogr. 41: 271–289.

Merson, R.R. 1998. Nursery grounds and maturation in the sandbar shark in the Western North Atlantic. Ph.D. Thesis, University of Rhode Island, Kingston, 150 pp.

Monan, G.E. 1982. Advances in tagging and tracking hatchery salmonids: coded wire tags, multiple-coded and miniature radio tags, and the passive integrated transponder tag. pp. 33–37. *In:* C.J. Sindermann (ed.) Proceedings of the Eleventh U.S.–Japan Meeting on Aquaculture, Salmon Enhancement, Tokyo, Japan, October 19–20, 1982, NOAA Tech. Rep. NMFS 27.

Morrissey, J.F. & S.H. Gruber. 1993. Home range of juvenile lemon sharks, *Negaprion brevirostris*. Copeia 1993: 425–434.

Moulton, P.L., T.I. Walker & S. Saddlier. 1992. Age and growth studies of gummy shark, *Mustelus antarcticus* Gunther, and school shark, *Galeorhinus galeus* (Linnaeus), from southern Australian waters. Aust. J. Mar. Freshwater Res. 43: 1241–1267.

Murray, T. 1990. Fish-marking techniques in New Zealand. Amer. Fish. Soc. Symp. 7: 737–745.

Myers, R.A., M.O. Hammill & G.B. Stenson. 1997. Using mark-recapture to estimate the numbers of a migrating stage-structured population. Can. J. Fish. Aquat. Sci. 54: 2097–2104.

Natanson, L.J. & G.M. Cailliet. 1990. Vertebral growth zone deposition in Pacific angel sharks. Copeia 1990: 1133–1145.

Natanson, L.J., J.G. Casey, N.E. Kohler & T. Colket, IV. 1999. Growth of the tiger shark (*Galeocerdo cuvier*) in the western North Atlantic, based on tag returns and length-frequencies; and a note on the effects of tagging. U.S. Fish. Bull. 97: 944–953.

Nelson, D.R. 1990. Telemetry studies in sharks: a review, with applications in resource management. pp. 239–256. *In:* H.L. Pratt, Jr., S.H. Gruber & T. Taniuchi (ed.) Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics, and the Status of the Fisheries, NOAA Tech. Rep. NMFS 90.

O'Gower, A.K. & A.R. Nash. 1978. Dispersion of the Port Jackson shark in Australian waters. pp. 529–544. *In:* E.S. Hodgson & R.F. Mathewson (ed.) Sensory Biology of Sharks, Skates, and Rays, Office of Naval Research, Department of the Navy, Arlington.

Olsen, A.M. 1953. Tagging of school shark, *Galeorhinus australis* (Macleay) (Carcharhanidae) in south-eastern Australian waters. Aust. J. Mar. Freshwater Res. 4: 95–104.

Olsen, A.M. 1954. The biology, migration, and growth rate of the school shark, *Galeorhinus australis* (Macleay) (Carcharhanidae) in south-eastern Australian waters. Aust. J. Mar. Freshwater Res. 5: 353–410.

Olsen, A.M. 1984. Synopsis of biological data on the school shark *Galeorhinus australis* (Macleay 1881). FAO Fisheries Synopsis No. 139, FIR/S139. 42 pp.

Parsons, G.R. 1987. Life history and bioenergetics of the bonnethead shark, *Sphyrna tiburo* (Linnaeus): a comparison of two populations. Ph.D., University of South Florida, Tampa. 51 pp.

Pepper, V.A. & M.F. O'Connell. 1983. Coded wire microtag applications in Newfoundland, the first three years. ICES C.M. 1983/M 15: 1–14.

Pepperell, J.G. 1990. Australian cooperative game-fish tagging program, 1973–1987: status and evaluation of tags. Amer. Fish. Soc. Symp. 7: 765–774.

Pittenger, G.G. 1984. Movements, distribution, feeding and growth of the Pacific angel shark, *Squatina californica*, at Catalina Island, California. M.S. Thesis, California State University, Long Beach. 83 pp.

Pollock, K.H., J.M. Hoenig & C.M. Jones. 1991. Estimation of fishing and natural mortality when a tagging study is combined with a creel survey or port sampling. Amer. Fish. Soc. Symp. 12: 423–434.

Porter, T.R. 1979. A review of factors affecting the rate of return of tagged Atlantic salmon and effects of tagging. ICES C.M. 1979/M 15: 1–17.

Pratt, H.L., Jr. & J.C. Carrier. 2001. A review of elasmobranch reproductive behavior with a case study on the nurse shark, *Ginglymostoma cirratum*. Env. Biol. Fish. 60: 157–188 (this volume).

Pratt, H.L., Jr. & J.G. Casey. 1983. Age and growth of the shortfin mako, *Isurus oxyrinchus*, using four methods. Can. J. Fish. Aquat. Sci. 40: 1944–1957.

Prentice, E.F., T.A. Flagg, C.S. McCutcheon, D.F. Brastow & D.C. Cross. 1990. Equipment, methods, and an automated data-entry station for PIT tagging. Amer. Fish. Soc. Symp. 7: 335–340.

Pyle, P., S.D. Anderson, A.P. Klimley & R.P. Henderson. 1996. Environmental factors affecting the occurrence and behavior of white sharks at the Farallon Islands, California. pp. 281–291. *In:* A.P. Klimley & D.G. Ainley (ed.) Great White Sharks: the Biology of *Carcharodon carcharias*, Academic Press, San Diego.

Randall, J. E. 1977. Contribution to the biology of the whitetip reef shark (*Triaenodon obesus*). Pacific Sci. 31: 143–164.

Raymond, H.L. 1974. Marking fishes and invertebrates. I. State of the art of fish branding. Mar. Fish. Rev. 36: 1–6.
Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191. 382 pp.
Rounsefell, G.A. & W.H. Everhart. 1953. Fishery science – its methods and applications. John Wiley & Sons, New York. 444 pp.
Schwarz, C.J. & A.N. Arnason. 1990. Use of tag-recovery information in migration and movement studies. Amer. Fish. Soc. Symp. 7: 588–603.
Sciarrotta, T.C. & D.R. Nelson. 1977. Diel behavior of the blue shark, *Prionace glauca*, near Santa Catalina Island, California. U.S. Fish Bull. 75: 519–528.
Scott, E.L, E.D. Prince & C.D. Goodyear. 1990. History of the cooperative game fish tagging program in the Atlantic Ocean, Gulf of Mexico, and Caribbean Sea, 1954–1987. Amer. Fish. Soc. Symp. 7: 841–853.
Shafer, T.C. 1970. Migration and distribution of the spiny dogfish (*Squalus acanthias* L.) in the western North Atlantic. M.S. Thesis, University of Rhode Island, Kingston, 45 pp.
Skomal, G.B. 1990. Age and growth of the blue shark, *Prionace glauca*, in the North Atlantic. M.S. Thesis, University of Rhode Island, Kingston, 103 pp.
Sluczanowski, P.W.R. 1988. The development of fish tagging projects. pp. 134–140. *In:* D.A. Hancock (ed.) Australian Society for Fish Biology Tagging Workshop, Sydney, 21–22 July 1988, Bureau of Rural Resources Proceedings No. 5.
Smith, S.E. 1984. Timing of vertebral-band deposition in tetracycline-injected leopard sharks. Trans. Amer. Fish. Soc. 113: 308–313.
Smith, S.E. & N.J. Abramson. 1990. Leopard shark *Triakis semifasciata* distribution, mortality rate, yield, and stock replenishment estimates based on a tagging study in San Francisco Bay. U.S. Fish. Bull. 88: 371–381.
Springer, S. 1960. Natural history of the sandbar shark *Eulamia milberti*. U.S. Fish. Bull. 61: 1–38.
Stevens, J.D. 1976. First results of shark tagging in the north-east Atlantic, 1972- 1975. J. Mar. Biol. Ass. U.K. 56: 929–937.
Stevens, J.D. 1984. Life-history and ecology of sharks at Aldabra atoll, Indian Ocean. Proc. R. Soc. Lond. B222: 79–106.
Stevens, J.D. 1990. Further results from a tagging study of pelagic sharks in the north-east Atlantic. J. Mar. Biol. Ass. U.K. 70: 707–720.
Stevens, J.D., G.J. West & K.J. McLoughlin. 2000. Movements, recapture patterns, and factors affecting the return rate of carcharhinid and other sharks tagged off northern Australia. Mar. Freshwater Res. 51: 127–141.
Strasburg, D.W. 1958. Distribution, abundance, and habits of pelagic sharks in the central Pacific Ocean. 1958. U.S. Fish. Bull. 58: 335–361.
Strong, W.R., Jr., R.C. Murphy, B.D. Bruce & D.R. Nelson. 1992. Movements and associated observations of bait-attracted white sharks, *Carcharodon carcharias*: a preliminary report. Aust. J. Mar. Freshwater Res. 43: 13–20.
Strong, W.R., Jr., B.D. Bruce, D.R. Nelson & R.D. Murphy. 1996. Population dynamics of white sharks in Spencer Gulf, South Australia. pp. 401–414. *In:* A.P. Klimley & D.G. Ainley (ed.) Great White Sharks: the Biology of *Carcharodon carcharias*, Academic Press, San Diego.
Talent, L.G. 1985. The occurrence, seasonal distribution, and reproductive condition of elasmobranch fishes in Elkhorn Slough, California. Calif. Fish Game 71: 210–219.
Templeman, W. 1944. The life-history of the spiny dogfish (*Squalus acanthias*) and the vitamin A values of dogfish liver oil. Newfoundl. Dept. Nat. Res. Bull. (Fish.) 15: 1–102.
Templeman, W. 1954. Migrations of spiny dogfish tagged in Newfoundland waters. J. Fish. Res. Board. Can. 11: 351–354.
Templeman, W. 1976. Transatlantic migrations of spiny dogfish (*Squalus acanthias*). J. Fish. Res. Board Can. 33: 2605–2609.
Templeman, W. 1984. Migrations of spiny dogfish, *Squalus acanthias*, and recapture success from tagging in the Newfoundland area, 1963–65. J. Northw. Atl. Fish. Sci. 5: 47–53.
Thorson, T.B. 1971. Movement of bull sharks, *Carcharhinus leucas*, between Caribbean Sea and Lake Nicaragua demonstrated by tagging. Copeia 1971: 336–338.
Thorson, T.B. & E.J. Lacy, Jr. 1982. Age, growth rate and longevity of *Carcharhinus leucas* estimated from tagging and vertebral rings. Copeia 1982: 110–116.
Tricas, T.C. 1977. Food habits, movements, and seasonal abundance of the blue shark, *Prionace glauca* (Carcharhinidae), in southern California waters. M.S. Thesis, California State University, Long Beach. 79 pp.
Tucker, R. 1985. Age validation studies on the spines of the spurdog (*Squalus acanthias*) using tetracycline. J. Mar. Biol. Assoc., U.K. 65: 641–651.
van der Elst, R.P. 1990. Marine fish tagging in South Africa. Amer. Fish. Soc. Symp. 7: 854–862.
Walker, T.I. 1992. Fishery simulation model for sharks applied to the gummy shark, *Mustelus antarcticus* Gunther, from southern Australian waters. Aust. J. Mar. Freshwater Res. 43: 195–212.
West, G.J. & J.D. Stevens. 2001. Archival tagging of school sharks, *Galeorhinus galeus*, in Australia: initial results. Env. Biol. Fish. 60: 283–298 (this volume).
Williams, H. & A.H. Schaap. 1992. Preliminary results of a study into the incidental mortality of sharks in gill-nets in two Tasmanian shark nursery areas. Aust. J. Mar. Freshwater Res. 43: 237–250.
Xiao, Y. 1994. Growth models with corrections for the retardative effects of tagging. Can. J. Fish. Aquat. Sci. 51: 263–267.
Xiao, Y. 1996. A framework for evaluating experimental designs for estimating rates of fish movement from tag recoveries. Can. J. Fish. Aquat. Sci. 53: 1272–1280.
Xiao, Y., L.P. Brown, T.I. Walker & A.E. Punt. 1999a. Estimation of instantaneous rates of tag shedding for school shark, *Galeorhinus galeus*, and gummy shark, *Mustelus antarcticus*, by conditional likelihood. U.S. Fish. Bull. 97: 170–184.
Xiao, Y., J.D. Stevens & G.J. West. 1999b. Estimation of fishing and natural mortalities from tag experiments with exact or grouped times at liberty. Can. J. Fish. Aquat. Sci. 56: 868–874.
Yamashita, D.T. & K.D. Waldron. 1958. An all-plastic dart-type fish tag. Calif. Fish Game 44: 311–317.

Appendix 1. A summary of 64 past and present worldwide shark tagging studies and programs using conventional tags. For studies not including scientific names, the reported common names were used.

Source	Species	Tagged number	Recaptured number	%	Max. speed (km day^{-1})	Max. distance (km)	Max. time (yr)	Number of species tag	recap.	Location	Tag type
Aasen in Templeman (1976), Aasen (1961)	*Squalus acanthias*	8122		10.8				1	1	Norway, Shetland Islands	yellow polyethylene film with stainless steel bridle
Bane (1968), Bane (unpublished) in Tricas (1977)	*Prionace glauca*	250	3	1.2		2561	2.1	1	1	California	Petersen disc tag, roto snap tag, stainless steel cattle tag
Bass (1977)	Summary information									South Africa – Durban	
	Carcharhinus galapagensis						5.1				
	Carcharhinus leucas						7.7				
Bass et al. (1973)	Summary information									South Africa – Durban	
	Carcharhinus obscurus	2174	98	4.5							
	Carcharhinus brevipinna	960	31	3.2							
Beverton et al. (1959)	*Squalus acanthias*	75	2	2.7			0.6	1	1	Irish Sea	yellow plastic flag on braided nylon loop
Burnett et al. (1987)	Summary information	2514	25	1.0		2228	9.5	> 1.3	5	Atlantic ocean	dart dag
	Prionace glauca	2003	17	0.8		1072					
	Isurus oxyrinchus	110	5	4.5		1028					
	Carcharhinus obscurus	80	1	1.3		6					
	Carcharhinus falciformis	74	0	0.0							
	Carcharhinus longimanus	73	0	0.0							
	Sphyrna lewini	60	0	0.0							
	Carcharhinus plumbeus	34	1	2.9		2228					
	Carcharhinidae	18	0	0.0							
	Galeocerdo cuvieri	18	1	5.6							
	Sphyrnidae	16	0	0.0							
	Lamnidae	11	0	0.0							
	Lamna nasus	8	0	0.0							
	Carcharhinus signatus	5	0	0.0							
	Cetorhinus maximus	2	0	0.0							
	Alopias superciliosus	1	0	0.0							
	Rhizoprionodon terraenovae	1	0	0.0							
Carrier (1985)	*Ginglymostoma cirratum*	70	14	20.0			2.2	1	1	Big Pine Key, Florida	stainless steel barb, plastic barb, Carlin disc

Appendix 1. (*continued*).

Source	Species	Tagged number	Recaptured number	%	Max. speed (km day^{-1})	Max. distance (km)	Max. time (yr)	Number of species tag	recap.	Location	Tag type
Caunter in Stevens (1976)	*Prionace glauca*	200+	1					1	1	Great Britain	
Clarke (1971)	*Sphyrna lewini*	410	76	18.5			0.3	1	1	Hawaii	numbered plastic dart tag
Davies & Joubert (1967)	Summary information	1062	385	36.3	59.1	1383	0.6	16	5	South Africa – Durban, Port Elizabeth	Petersen disc, WHOI nylon barb, WHOI stainless dart, Rototag, Jumbo Rototag, ORI tag
	Carcharhinus obscurus	727	322	44.3	59.1		0.6				
	Carcharhinus maculipinnis	183	47	25.7		1383	0.6				
	Rhizoprionodon acutus	83	6	7.2		14	0.3				
	Carcharhinus sorrah	22	0	0.0							
	Mustelus canis	13	9	69.2		< 2	0.3				
	Carcharhinus albimarginatus	11	0	0.0							
	Squalus cubensis	9	0	0.0							
	Carcharhinus limbatus	3	0	0.0							
	Carcharhinus tjutjot	2	0	0.0							
	Galeocerdo cuvieri	2	0	0.0							
	Loxodon macrorhynchus	2	0	0.0							
	Carcharhinus galapagensis	1	0	0.0							
	Carcharhinus leucas	1	1	100.0			1 day				
	Carcharhinus spallanzi	1	0	0.0							
	Mustelus nigropunctatus	1	0	0.0							
	Sphyrna lewini	1	0	0.0							
Ebert (1996)	*Notorynchus cepedianus*	614	26	4.2	3.5	539	1.4	1	1	Southern Africa	rototag (ORI tag)
Ferreira & Ferreira (1996)	*Carcharodon carcharias*	147						1		South Africa, Dyer Island	plaque attached to ORI spaghetti dart tag
Foerster[1]	dogfish (grayfish)	564	34	6.0				1	1	British Columbia	colored celluloid disk
Francis (1988, 1989)	*Mustelus lenticulatus*	2234	382	17.1	21.0	1159	> 5	1	1	Southern New Zealand – South Island & SW North Island	Floy FT4, 12 cm tube length (yellow plastic)

Govender et al.[2]	Summary information	29 564	1451	4.9	1964	> 36	> 33	South Africa	steel head dart tag, round cattle ear tag
	dusky shark	5065	422	8.3	1835				
	blacktail	4976	148	3.0	788				
	spotted gulley shark	4548	299	6.6	1066				
	copper/bronze shark	3958	137	3.5	1320				
	smooth blackspot houndshark	2158	80	3.7	1407				
	spotted ragged-tooth	1637	79	4.8	1416				
	smooth hammerhead	1216	31	2.5	1122				
	cow and frill sharks	784	29	3.7	497				
	milk shark	692	31	4.5	1004				
	soupfin shark	459	17	3.7	453				
	striped/pyjama catshark	421	20	4.8	1964				
	blacktip shark	402	21	5.2	380				
	hammerhead sharks	384	4	1.0	233				
	sandbar shark	295	6	2.0	347				
	broadnose sevengill shark	284	8	2.8	539				
	scalloped/bronze hammerhead	278	7	2.5	254				
	bluntnose/spiny dogfish	262	4	1.5	87				
	longnose/spinner shark	222	11	5.0	164				
	shorttail catshark	215	24	11.2	1010				
	tiger shark	168	8	4.8	145				
	great white shark	165	7	4.2	1445				
	brown shyshark	164	4	2.4	8				
	Zambezi shark	158	11	7.0	125				
	blackspot shark	124	8	6.5	367				
	flapnose shark	85	5	5.9	54				
	sliteye shark	70	4	5.7	575				
	banded catshark	53	10	18.9	63				
	hardnose/smooth houndshark	53	1	1.9	228				
	whitespotted/smooth houndshark	47	4	8.5	210				
	spotted/spiny dogfish	43	1	2.3	47				
	catsharks	29	2	6.9	0				
	shortfin/mako shark	28	1	3.6	6				
	brown catshark	23	1	4.3	0				
	blue shark	19	0	0.0	0				
	Java shark	15	2	13.3	61				
	blackspot catshark	14	2	14.3	38				

[1]Foerster, R.E. 1942. Dogfish Tagging – preliminary results. Canada Fish. Res. Bd. Pacific Coast Sta., Prog. Rep. No. 53: 12–13.
[2]Govender, A., E. Bullen & R. van der Elst. 1995. Tagging news No. 11 Newsletter from the Oceanographic Research Institute, Durban, South Africa.

Appendix 1. (*continued*).

Source	Species	Tagged number	Recaptured number	%	Max. speed ($km\ day^{-1}$)	Max. distance (km)	Max. time (yr)	Number of species tag	recap.	Location	Tag type
	Galapagos shark	14	0	0.0		0					
	thintail/thresher shark	13	0	0.0		0					
	grey reef shark	12	1	8.3		0					
	requiem sharks	11	1	9.1		568					
Green (personal communication)	Summary information	17 768	763	4.3		7871	15.2	4	3	Ireland	Jumbo Rototag, dart tags, Petersen disc
	blue shark	14 990	511	3.4		7871	3.9				
	tope	2722	246	9.0		4047	15.2				
	porbeagle shark	55	6	10.9		4260	10.8				
	thresher shark	1	0	0.0							
Gruber & Stout (1983)	*Negaprion brevirostris*	~1500	70+	5.0				1	1	Florida Keys, Bahamas	freeze band, mini-rototag, plastic dart tag, internal tag
Gubanov (1976)	Summary information	225	2	0.9				12		Sumatra	hydrostatic tag (polyethylene cylindrical ampule)
	Alopias vulpinus					1556	2.0				
Hansen (1963)	*Somniosus microcephalus*	411	28	6.8		1296	16.0	1	1	Greenland	Petersen disc
Hartill & Davies[3]	Summary information	11 986	285	2.4	42.4		11.9	10	5	New Zealand waters	stainless steel dart tag
	mako	9143	224	2.4	42.4		6.5				
	blue shark	2411	30	1.2	27.0		1.7				
	hammerhead	165	0	0.0							
	school shark	95	25	26.3	8.0		11.9				
	bronze whaler	75	3	4.0	14.1		3.1				
	thresher	55	0	0.0							
	sevengill	24	3	12.5	9.8		1.9				
	porbeagle	16	0	0.0							
	carpet	1	0	0.0							
	white tip	1	0	0.0							
Herald & Ripley (1951)	*Galeorhinus zyopterus*	118	4	3.4	44.0	2037	2.1	1	1	California waters	
Holden (1962, 1965, 1967)	*Squalus acanthias*	11 996	1044	8.7			3.8	1	1	England, Scotland, Norway, Faroe Islands	Petersen disc, internal and external polythene flag tag

Holden & Horrod (1979)	*Galeorhinus galeus*	491	32	6.5		2526	10.8	1	1	England	Petersen disc, Rototag
Holland (1957)	*Squalus acanthias*	9705	655	6.7		8704	10.0	1	1	Washington	celluloid Petersen tag
Hueter (personal communication)	Summary information	8028	350	4.4	13.9	519	5.6	16	11	Gulf of Mexico	Hallprint PDB plastic-tipped dart tag
	Sphyrna tiburo	2966	96	3.2	3.2	343	5.6				
	Carcharhinus limbatus	2375	184	7.7	13.9	519	2.9				
	Rhizoprionodon terraenovae	1263	17	1.3	3.2	102	4.0				
	Carcharhinus acronotus	805	22	2.7	0.9	111	4.0				
	Carcharhinus brevipinna	150	7	4.7	1.3	370	0.8				
	Carcharhinus leucas	131	14	10.7	1.5	194	0.5				
	Carcharhinus isodon	108	2	1.9	< 0.1	6	0.8				
	Mustelus norrisi	42	0	0.0							
	Carcharhinus plumbeus	41	1	2.4	0.1	7	0.2				
	Sphyrna mokarran	39	2	5.1	0.4	213	2.0				
	Negaprion brevirostris	34	3	8.8	0.1	4	0.4				
	Sphyrna lewini	28	0	0.0							
	Ginglymostoma cirratum	25	0	0.0							
	Galeocerdo cuvier	11	2	18.2	1.4	482	1.0				
	Mustelus canis	8	0	0.0							
	Carcharhinus falciformis	2	0	0.0							
Hurst et al. (1999)	*Galeorhinus galeus*	3950	207	5.2	22.8	4940	9.6	1	1	New Zealand	Floy dart tag, loop tag, plastic Nesbit internal tag
Jensen in Templeman (1976)	*Squalus acanthias*	907		3.0				1	1		
Kato & Carvallo (1967)	Summary information	860	83	9.7		1111	> 0.6	> 14	> 8	Mexican coast, Revillagigedo Islands, offshore Southern California to Peru	Petersen disc, Jumbo Rototag, strap (cattle size ear tag), Floy dart tag
	Carcharhinus galapagensis	215	29	13.5		> 59					
	Carcharhinus limbatus	184	19	10.3		> 37					
	Carcharhinus albimarginatus	139	19	13.7		< 9					
	Carcharhinus falciformis	123	5	4.1		176					
	Carcharhinus porosus	77	6	7.8		> 37					
	Rhizoprionodon longurio	73	2	2.7		1111					

[3]Hartill, B. & N.M. Davies. 1999. New Zealand billfish and gamefish tagging 1997–98. NIWA Technical Report 57. 39 pp.

Appendix 1. (*continued*).

Source	Species	Tagged number	Recaptured number	%	Max. speed (km day^{-1})	Max. distance (km)	Max. time (yr)	Number of species tag	recap.	Location	Tag type
	Sphyrna lewini	25	1	4.0		> 37					
	Prionace glauca	5	0	0.0							
	Carcharhinus altimus	4	0	0.0							
	Sphyrna zygaena	4	0	0.0							
	Carcharhinus longimanus	3	0	0.0							
	Alopias vulpinus	2	0	0.0							
	Mustelus spp.	2	0	0.0							
	Carcharhinus velox	1	0	0.0							
	Ginglymostoma cirratum	1	1	100.0		> 37					
	other	2	1	50.0							
Ketchen (1986)	*Squalus acanthias*	24 079	1150	4.8		7890		1	1	Straits of Georgia, Canada, Puget Sound	
Klimley & Nelson (1984)	*Sphyrna lewini*	100						1	1	Gulf of California	color coded plastic streamer (dart tip)
Kohler & Turner (this study)	Summary information	142 868	7352	5.1	82.4	6926	27.8	> 52	> 31	Atlantic Ocean, Mediterranean Sea, Gulf of Mexico	stainless steel dart tag, Jumbo Rototag, Rototag
	Prionace glauca	82 080	4001	4.9	82.4	6926	8.5				
	Carcharhinus plumbeus	19 344	987	5.1	21.6	3776	27.8				
	Galeocerdo cuvier	7161	620	8.7	61.4	6747	10.9				
	Carcharhinus obscurus	6707	155	2.3	41.3	3800	15.8				
	Isurus oxyrinchus	4419	483	10.9	66.1	4543	12.8				
	Carcharhinus limbatus	3239	142	4.4	30.4	2146	7.3				
	Rhizoprionodon terraenovae	2539	39	1.5	10.6	1037	7.3				
	Sphyrna lewini	2240	45	2.0	11.1	1671	9.6				
	Negaprion brevirostris	1690	171	10.1	7.4	426	4.1				
	Ginglymostoma cirratum	1270	134	10.6	13.6	541	7.8				
	Carcharhinid sharks	1182	101	8.5							
	Carcharhinus falciformis	974	61	6.3	59.7	1339	7.1				
	Lamna nasus	942	96	10.2	40.7	1861	9.2				
	Hammerhead sharks	867	20	2.3							
	Sphyrna tiburo	849	19	2.2	5.8	261	2.0				
	Misc. sharks	784	83	10.6							
	Odontaspis taurus	684	39	5.7	5.4	1187	3.2				

Carcharhinus perezi	630	16	2.5	1.5	48	4.4
Carcharhinus leucas	621	15	2.4	20.1	643	7.0
Carcharhinus longimanus	597	8	1.3	32.4	2811	3.3
Carcharhinus acronotus	526	9	1.7	1.5	315	9.2
Carcharhinus brevipinna	494	14	2.8	6.1	1665	4.5
Mustelus canis	404	15	3.7	9.7	402	4.0
Carcharhinus galapagensis	403	16	4.0	1.8	2859	4.4
Alopias superciliosus	346	8	2.3	17.3	2767	6.5
Squalus acanthias	237	5	2.1	0.8	532	3.2
Carcharhinus signatus	220	16	7.3	11.2	2669	13.8
Sphyrna zygaena	185	6	3.2	4.8	919	2.1
Carcharhinus altimus	171	12	7.0	4.6	3343	11.2
Cetorhinus maximus	157	0	0.0			
thresher sharks	144	0	0.0			
Sphyrna mokarran	133	4	3.0	1.2	1180	2.8
Aprionodon isodon	127	0	0.0			
Squatina dumerili	106	0	0.0			
Isurus paucus	90	5	5.6	9.6	3430	5.5
Alopias vulpinus	72	3	4.2	0.1	159	8.0
mackerel sharks	42	1	2.4			
Carcharodon carcharias	38	2	5.3	1.6	1011	2.5
Carcharhinus porosus	29	0	0.0			
Somniosus microcephalus	22	1	4.5		0	1.0
Pseudocarcharias kamoharai	21	0	0.0			
Galeorhinus galeus	16	0	0.0			
Mustelus norrisi	15	0	0.0			
Rhizoprionodon porosus	14	0	0.0			
Hexanchus vitulus	11	0	0.0			
Triakis semifasciata	5	0	0.0			
Centrophorus granulosus	3	0	0.0			
Hexanchus spp.	3	0	0.0			
Rhincodon typus	3	0	0.0			
Hexanchus griseus	2	0	0.0			
Rhizoprionodon lalandii	2	0	0.0			
Sphyrna tudes	2	0	0.0			
Chlamydoselachus anguineus	1	0	0.0			
Echinorhinus brucus	1	0	0.0			

Appendix 1. (*continued*).

Source	Species	Tagged number	Recaptured number	%	Max. speed (km day^{-1})	Max. distance (km)	Max. time (yr)	Number of species tag	recap.	Location	Tag type
	Mustelus henlei	1	0	0.0							
	Scyliorhinus retifer	1	0	0.0							
	Sphyrna media	1	0	0.0							
	Squatina californica	1	0	0.0							
Levine (personal communication)	*Rhincodon typus*	261						1		Indian Ocean, Caribbean Sea	custom dart tag applied *in situ*
Matsunaga (personal communication)	Summary information	1670	14	0.8	35.2	1550	0.4	> 7	1	North Pacific	Floy stainless dart
	blue shark	1394	14	1.0	35.2	1550	0.4				
	bigeye thresher	82	0	0.0							
	silky shark	69	0	0.0							
	oceanic whitetip	50	0	0.0							
	porbeagle	24	0	0.0							
	pelagic thresher	18	0	0.0							
	mako shark	14	0	0.0							
	other	19	0	0.0							
McLaughlin & O'Gower (1971)	*Heterodontus portusjacksoni*	295	4	1.4	1.8	400	0.6	1	1	Bondi, Sydney, Australia	caudal peduncle collar tag applied *in situ*
Natanson & Cailliet (1990)	*Squatina californica*	105	6	5.7				1	1		Jumbo Rototag
Nelson (personal communication), Nelson (unpublished) in Tricas (1977), Sciarrotta & Nelson (1977)	*Prionace glauca*	16	2	12.5		3589	3.2	1	1		Floy FH-69 stainless steel dart tag
Nelson (personal communication)	*Heterodontus francisci*	21	7	33.3		19	11.2	1	1		
Nelson (personal communication)	Summary information	218	117	53.7				3	3		
	Triakis obesus	113	78	69.0		9	3.4				
	Carcharhinus amblyrhynchos	65	28	43.1			4.2				
	Carcharhinus melanopterus	40	11	27.5			0.3				
O'Gower & Nash (1978)	*Heterodontus portusjacksoni*	230	14	6.1	6.5	850	1.8	1	1	Bondi, Sydney, Australia	caudal peduncle collar tag applied *in situ*
Parsons (1987)	*Sphyrna tiburo*	70	5	7.1				1	1	Tampa Bay, Florida	Dalton Rototag

Pepperell (1990), Henry (personal communication)	Summary information	17 401	351	2.0	24.1	5504	7.3	> 6	> 6	Australia	plastic streamer, nylon barbed dart, T-anchor, steel anchor dart
	Isurus oxyrinchus	3581	69	1.9	13.0	3293	5.0				
	Sphyrna spp.	3542	37	1.0	13.0	556	2.7				
	Carcharhinus spp.	3188	57	1.8	9.3	1796	7.3				
	Carcharhinus brachyurus	2518	50	2.0							
	Prionace glauca	2308	40	1.7	24.1	5504	1.6				
	Galeocerdo cuvier	452	14	3.1							
	Carcharodon carcharias	96	7	7.3							
	Eugomphodus taurus	76	4	5.3							
	Alopias spp.	75	1	1.3							
	Misc. sharks	1565	72	4.6			6.0				
Pittenger (1984)	*Squatina californica*	402	111	27.6		24	3.0	1	1	Catalina Island, California	Floy FH-69 stainless steel dart tag applied *in situ*
Randall (1977)	*Triaenodon obesus*	124	7	5.6	< 0.1	3	2.0	1	1	Johnston Island	monel cattle ear tag, streamer dart tag with bright yellow vinyl
Schwartz (personal communication)	Misc. sharks	203 000	3103	1.5		2126	1.5	28	10	North Carolina	metal strap, Petersen, Hallprint dart tag
Shafer (1970)	*Squalus acanthias*	3583	61	1.7	21.1	1578	1.9	1	1	Rhode Island, North Carolina, Maine	Jumbo Rototag
Smith & Abramson (1990)	*Triakis semifasciata*	948	108	11.4		140				San Francisco Bay, California	plastic Rototag
Stevens (1984)	Summary information	1218	274	22.5		11	3.9	6	5	Aldabra Atoll	Jumbo Rototag
	Carcharhinus melanopterus	1003	233	23.2		5	3.9				
	Negaprion acutidens	131	19	14.5		5	3.9				
	Carcharhinus albimarginatus	44	15	34.1		7	0.7				
	Carcharhinus wheeleri	33	6	18.2							
	Nebrius concolor	5	0	0.0							
	Carcharhinus falciformis	2	1	50.0		11	0.4				
Stevens (1990)	Summary information	2883	102	3.5	7.5	7176	13.0	4	4	North East Atlantic	Jumbo Rototag
	Prionace glauca	2585	51	2.0	7.5	7176	10.7				
	Galeorhinus galeus	271	42	15.5	3.0	2461	6.7				
	Lamna nasus	26	8	30.8		2370	13.0				
	Isurus oxyrinchus	1	1	100.0		390	4.6				

Appendix 1. (*continued*).

Source	Species	Tagged number	Recaptured number	%	Max. speed (km day^{-1})	Max. distance (km)	Max. time (yr)	Number of species tag	recap.	Location	Tag type
Stevens et al. (2000)	Summary information	10 489	579	5.5	18.6	1348	12.9	23	16	Northern Australia	Jumbo Rototag, Rototag
	Carcharhinus tilstoni	4846	402	8.3	24.7	1348	12.9				
	Carcharhinus sorrah	2919	83	2.8	6.8	1116	9.9				
	Carcharhinus macloti	1610	52	3.2	18.6	711	10.5				
	Rhizoprionodon acutus	277	4	1.4	0.1	45	1.8				
	Carcharhinus amboinensis	131	13	9.9	18.3	242	4.7				
	Carcharhinus amblyrhynchoides	122	13	10.7	8.3	173	8.8				
	Rhizoprionodon taylori	119	1	0.8		92	0.2				
	Sphyrna lewini	93	1	1.1		113	< 0.1				
	Carcharhinus dussumieri	79	1	1.3		4	1.4				
	Carcharhinus brevipinna	59	1	1.7		19	1.7				
	Carcharhinus fitzroyensis	55	1	1.8		150	0.2				
	Galeocerdo cuvier	55	2	3.6	3.3	156	5.7				
	Sphyrna mokarran	48	2	4.2	0.8	385	4.2				
	Eusphyra blochii	34	1	2.9		21	1.0				
	Carcharhinus amblyrhynchos	12	0	0.0							
	Carcharhinus melanopterus	6	0	0.0							
	Nebrius ferrugineus	6	1	16.7		43					
	Carcharhinus limbatus	5	1	20.0							
	Carcharhinus plumbeus	5	0	0.0							
	Hemipristis elongatus	4	0	0.0							
	Stegostoma fasciatum	2	0	0.0							
	Carcharhinus falciformis	1	0	0.0							
	Negaprion acutidens	1	0	0.0							
Strong et al. (1992, 1996), Bruce (1992)	*Carcharodon carcharias*	40	4	10.0		220	0.2	1	1	South Australia	Hallprint stainless steel dart tag
Strong in Nelson (personal communication)	*Heterodontus francisci*	312	46	14.7		4	2.1	1	1		
Sutcliffe[4]	*Galeorhinus galeus*	74	12	16.2		3200	12.0	1	1	Scotland	Dalton Rototag, Floy FT-1 dart tag

Taniuchi (personal communication)	*Squalus acanthias*	16 588	340	2.0	25.9		5.9	1	1	Tail region of Tsushima Warm Current, Japan	caudal tags
Templeman (1976)	*Squalus acanthias*	2855		8.2			11.2	1	1	Newfoundland	Petersen disc, flat dangler tag, hydrostatic tag
Tester[5]	Summary information	279	17	6.1		83	1.6	7	4	Hawaii	metal strap tag (small & large), internal plastic tag
	gray reef	113	11	9.7			1.5				
	sandbar	86	1	1.2			1.6				
	tiger	41	4	9.8		83	0.8				
	galapagensis	26	1	3.8			0.5				
	scalloped hammerhead	11	0	0.0							
	blacktip	1	0	0.0							
	smooth hammerhead	1	0	0.0							
Thorson & Lacy (1982), Thorson (1971)	*Carcharhinus leucas*	3859	623	16.1			7.9	1	1	Nicaragua, Costa Rica	Petersen disc, Jumbo Rototag
Tricas (1977)	Summary information	123	4	3.2	2.8	~160	0.9	2	2	Santa Catalina Island, California	Floy FH-9 stainless steel dart tag with plastic spaghetti streamer, telemetry tag
	Prionace glauca	120	3	2.5	2.8	119	0.9				
	Isurus oxyrinchus	3	1	33.3		~160	3 days				
Ugoretz[6] , Ugoretz (personal communication)	Summary information	10 105	172	1.7		6147	6.3	> 9	> 5	California – Monterey Bay to Cabo San Lucas, Baja	Floy FH-69 steel dart tag, yellow and red
	Prionace glauca	6958	49	0.7		6147	3.8				
	Isurus oxyrinchus	2674	108	4.0		3728	2.6				
	Alopias spp.	143	2	1.4		19	0.2				
	Squatina californica	107	6	5.6		61	6.3				
	sevengill	65	6	9.2		352	2.1				
	basking shark	57	0	0.0							
	leopard	51	1	2.0		6	2.1				
	Carcharodon carcharias	16	0	0.0							
	soupfin	5	0	0.0							
	Squalus acanthias	4	0	0.0							
	Mustelus spp.	3	0	0.0							
	other	22	0	0.0							

[4]Sutcliffe, R. 1994. Twenty years of tagging common skate and tope off the west coast of Scotland. pp. 14–16. In: S.L. Fowler & R.C. Earll (ed.) Proceedings of the Second European Shark and Ray Workshop, 15–16 February 1994. Tag and Release Schemes and Shark and Ray Management Plans. Unpublished report.

[5]Tester, A.L. 1969. Cooperative shark research and control program final report 1967–69. University of Hawaii, Honolulu. 47 pp.

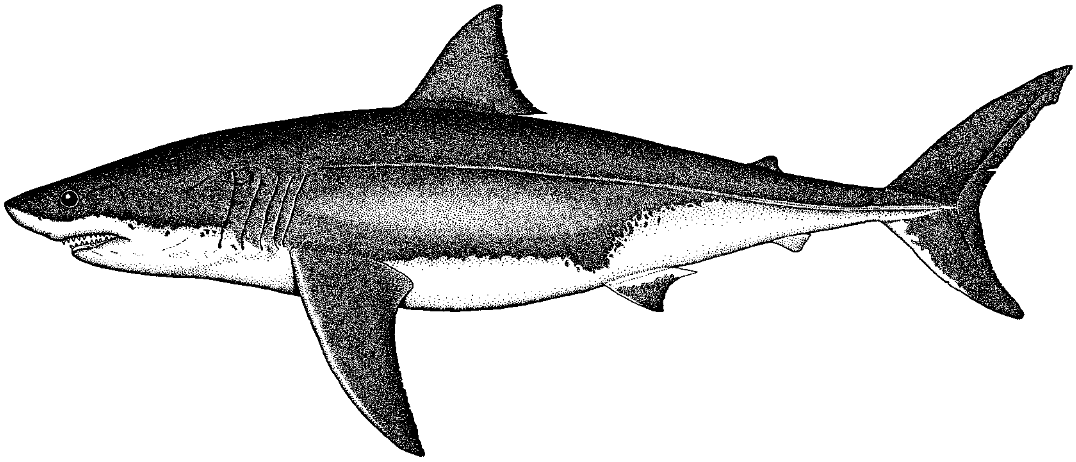
[6]Ugoretz, J. 1999. Shark tagging news, a newsletter of the California Department of Fish and Game shark tagging program (January 1999). 4 pp.

Appendix 1. (*continued*).

Source	Species	Tagged number	Recaptured number	%	Max. speed (km day^{-1})	Max. distance (km)	Max. time (yr)	Number of species tag	recap.	Location	Tag type
Vas (personal communication)	Summary information	337	0	0.0				3	0	Southern coast of England	Floy dart tag
	Galeorhinus galeus	298	0	0.0							
	Prionace glauca	36	0	0.0							
	Lamna nasus	3	0	0.0							
Walker et al.[7], Coutin (1992)	Summary information	20 185	2753	13.6				>21	12	Australia	Rototag, Jumbo Rototag, nylon-headed dart tag, Petersen fin tag, internal Nesbit tag, T-bar tag
	Galeorhinus galeus	9638	1011	10.5			41.8				
	Mustelus antarcticus	8647	1659	19.2							
	Squalus megalops	617	9	1.5							
	Pristiophorus nudipinnis	499	21	4.2							
	Pristiophorus cirratus	376	30	8.0							
	Notorynchus cepedianus	116	8	6.9							
	Furgaleus macki	79	0	0.0							
	Carcharhinus obscurus	75	7	9.3							
	Carcharhinus brachyurus	46	2	4.3							
	Heterodontus portusjacksoni	25	3	12.0							
	Cephaloscyllium sp.	16	1	6.3							
	Squalus mitsukuri	10	1	10.0							
	Sphyrna zygaena	7	0	0.0							
	Squalus acanthias	7	0	0.0							
	Centrophorus uyato	6	0	0.0							
	Alopias vulpinus	5	0	0.0							
	Squalus sp.	4	0	0.0							
	Squatina australis	4	0	0.0							
	Carcharodon carcharias	3	1	33.3							
	Carcharias taurus	2	0	0.0							
	Prionace glauca	2	0	0.0							
	Isurus oxyrinchus	1	0	0.0							
Westrheim in Herald & Ripley (1951)	*Galeorhinus zyopterus*	309				167	0.2		1	Oregon Waters	
G.P. Whitley in Olsen (1953)	*Galeorhinus zyopterus*	22							1	Tasmanian waters	internal tag
Williams & Schaap (1992)	Summary information	302	2	0.7		39	~ 0.4	4	1	Tasmania	cattle ear tag, T-bar tag with streamer

	Squalus acanthias	185	0	0.0							
	Mustelus antarcticus	51	0	0.0							
	Squalus megalops	47	2	4.3		39	~0.4				
	Galeorhinus galeus	19	0	0.0							
Wintner (personal communication), Cliff et al. (1996)	Summary information	2799	159	5.7	39.4	1897	11.0	> 19	> 11	South Africa, KwaZulu-Natal	steel head dart tag, round cattle ear tag (ORI tag)
	Carcharias taurus	1633	121	7.4	39.4	1897	11.0				
	Carcharhinus obscurus	246	6	2.4	10.6	360	4.8				
	Galeocerdo cuvier	224	9	4.0	1.2	143	2.2				
	Carcharhinus brevipinna	143	2	1.4	9.0	45	5 days				
	Carcharhinus brachyurus	132	2	1.5	53.0	53	1.2				
	Carcharhinus leucas	113	4	3.5	14.0	123	0.6				
	Carcharhinus limbatus	80	3	3.8	0.9	6	2.8				
	Carcharodon carcharias	73	6	8.2	28.7	1409	2.6				
	Carcharhinus plumbeus	41	0	0.0							
	Sphyrna lewini	32	2	6.3	1.7	267	0.4				
	Carcharhinus amboinensis	31	2	6.5	0.3	84	4.4				
	Sphyrna zygaena	14	0	0.0							
	Isurus oxyrinchus	11	2	18.2	1.5	6	2.2				
	Notorynchus cepedianus	8	0	0.0							
	Squatina africana	8	0	0.0							
	Mustelus sp.	4	1	25.0							
	Alopias vulpinus	2	0	0.0							
	Triakis megalopterus	2	0	0.0							
	Carcharhinus albimarginatus	1	0	0.0							
	Stegostoma fasciatum	1	0	0.0							

[7] Walker, T.I., L.P. Brown & N.F. Bridge. 1997. Southern shark tagging project. Final report to Fisheries Research and Development Corporation (FRDC Project 93/066). Client report. (November 1997). Marine and Freshwater Resources Institute, Queenscliff, Victoria, Australia. 61 pp.



A female of the great white shark, *Carcharodon carcharias*, 3 m long (PV).