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NOAA Technical Memorandum NMFS

SYNOPSIS OF BIOLOGICAL DATA ON THE GREEN TURTLE IN THE HAWAIIAN ISLANDS

George H. Balazs

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October 1980

U.S. DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Southwest Fisheries Center

NOAA Technical Memorandum NMFS

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U.S. DEPARTMENT OF COMMERCE
Philip M. Klutznick, Secretary
National Oceanic and Atmospheric Administration
Richard A. Frank, Administrator
National Marine Fisheries Service
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Adult female Hawaiian green turtle basking on Trig Island at French Frigate Shoals. The small depth recorder attached to the carapace was used to measure maximum diving depth during the internesting interval. (Photograph by G. H. Balazs, June 1979.)

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INTRODUCTION

The green turtle, *Chelonia mydas*, is the principal marine turtle species in the Hawaiian Islands. It has been the recipient of nearly all research conducted to date within this region of the Pacific. Although significant advances have been made during recent years in the knowledge of Hawaiian *Chelonia*, important aspects of the turtle's natural history remain to be elucidated. The purpose of this synopsis is to bring together all of the biological information presently known on the population (as of September 1979) and, in doing so, focus attention on future research needs. The unique behavioral and population characteristics of Hawaiian *Chelonia* detailed in this synopsis will also serve to emphasize the excellent research opportunities for gaining information applicable to all green turtle populations. The information presented has been derived from a comprehensive review of the literature and from unpublished original research conducted by the author.

The format used in this synopsis is patterned after the synopsis series on species and stocks issued by the Food and Agriculture Organization (FAO) of the United Nations. A synopsis of biological data dealing with the green turtle on a global basis was published in 1971 as part of this series (Hirth 265). The present synopsis complements and updates this earlier document, which dealt only in general terms with Hawaiian *Chelonia*. An additional feature of the present synopsis is the incorporation of an extensive list of references covering Hawaiian cultural and legendary aspects of marine turtles.

The two other species of marine turtles found in the Hawaiian Islands are the hawskbill, *Eretmochelys imbricata*, and the leatherback, *Dermochelys coriacea*. The hawksbill is only known to occur in small numbers exclusively at the southeastern end of the Hawaiian Archipelago where a few nestings have been recorded in recent years on the islands of Molokai and Hawaii. The leatherback is regularly sighted in offshore waters of the Hawaiian Islands, but nesting is not known to take place. The loggerhead, *Caretta caretta*, and the olive ridley, *Lepidochelys olivacea*, have also been documented in Hawaiian waters, but only as rare visitors. All of the known literature relating to these four species in the Hawaiian Islands as of September 1979 has been included in the bibliography of this synopsis.

This synopsis was originally prepared by the author under contract No. 79-ABA-02422 and constituted Working Paper No. 13 of the Joint South Pacific Commission/National Marine Fisheries Service Workshop on Marine Turtles in the Tropical Pacific Islands (11-14 December 1979, Noumea, New Caledonia).

The author's research of the Hawaiian green turtle has been funded during previous years by the University of Hawaii Sea Grant College Program, the State of Hawaii Office of the Marine Affairs Coordinator, the National Geographic Society, the U.S. Fish and Wildlife Service (USFWS), and the New York Zoological Society. The author is currently affiliated with the Southwest Fisheries Center Honolulu Laboratory under an Intergovernmental Personnel Act contract with the University of Hawaii, Hawaii Institute of Marine Biology.

This work is the result of research sponsored in part by the University of Hawaii Sea Grant College Program under Institutional Grant Nos. 04-6-158-44114, 04-7-158-44129, and 04-8-MOI-178 from NOAA Office of Sea Grant, Department of Commerce. Sea Grant Cooperative Report UNIHI-SEAGRANT CR-81-02.

I IDENTITY

1.1 Nomenclature and Taxonomy

The valid name for the green turtle is *Chelonia mydas* (Linnaeus) 1768, with the *mydas* complex consisting of a number of genetically isolated populations distributed worldwide in tropical and subtropical latitudes. Some of these populations have been assigned subspecific names on the basis of coloration, carapace morphology, and geographical location; however, for the most part detailed taxonomic studies have not been carried out.

The Atlantic green turtle, *Chelonia mydas mydas* (Linnaeus) (type locality-Ascension Island) has a predominantly brown coloration to its dorsal surfaces, a white to light yellow plastron, and a carapace displaying a low profile, especially from the middle of the lateral laminae to the periphery. At the present time there is no clear distinction between *Chelonia mydas mydas* and green turtles of the major Caribbean breeding colony at Tortuguero, Costa Rica. However, Carr (151) has expressed confidence that small morphometric, behavioral, and physiological differences exist and, once demonstrated, the name *Chelonia mydas viridis* (Schneider) will apply.

In the eastern Pacific, *Chelonia mydas agassizi* Bocourt has been described from the coasts of Central and South America and the Galapagos Islands. This subspecies is characterized by a greenish-olive dorsal coloration with the carapace at times strongly marked with black. In contrast with *mydas*, the *agassizi* carapace is highly arched with indentations over the hind flippers. *Chelonia mydas carrinegra* Caldwell, the stock of turtles with heavy black pigmentation described from the Gulf of California and Pacific coast of Baja California, is now considered by some authorities to be synonymous with *Chelonia mydas agassizi*.

The Hawaiian *Chelonia* population has thus far not been given nomenclature recognition. Based on turtles observed at French Frigate Shoals and Pearl and Hermes Reef in the Northwestern Hawaiian Islands (NWHI), Carr (150, 151) indicated that *carrinegra* or *agassizi* characteristics are present. Similar features have also been recorded by Amerson *et al.* (32) and Balazs (57, 62). In contrast, Caldwell (147) and Pritchard (418) could not distinguish the small number of Hawaiian specimens they observed from *mydas* stock. The presence and possible predominance of *mydas*-like stock in the Hawaiian Islands have also been suggested by Hirth and Carr (267). Based on zoogeographic considerations and unspecified data, Oliver and Shaw (379) thought that the Hawaiian population might represent the easternmost outpost of the western Pacific green turtle, *Chelonia mydas japonica* (Thunberg).

Since 1972 the author has observed approximately 2,000 naturally occurring Hawaiian *Chelonia* of nearly all sizes, including large samples of adult males and females at the breeding colony of French Frigate Shoals. A reference collection of color photographs including many tagged animals has been compiled along with these field observations. Findings to date show that the predominant carapace coloration of adult females is heavy black with infusions of yellowish gold and olive. In most cases, the black component comprises an estimated 80% or more of the carapace area. The head and dorsal surfaces of the flippers are also mainly black with light seams frequently outlining the scales on each side of the head. Along with these predominantly black turtles, a small number (<3%) of adult females possess a basically brown colored carapace with patterns of yellow, gold, and reddish brown. The head and dorsal surfaces of the flippers of these individuals are also lighter colored.

Within the adult females of the Hawaiian population, there is generally a highly arched appearance to the carapace. The measurement of this characteristic has been undertaken by calculating the ratio of the curved and straight carapace widths as an estimate of carapace height. Although this ratio would not be valid for comparisons between radically different carapace shapes of the same straight width (i.e. domed vs. a flat top), it nevertheless represents a simplified index of some value. In a sample of 93 females from French Frigate Shoals, this ratio was found to be 1.28 ± 0.05 with a range of 1.17-1.44. Similar measurements will be necessary in other *Chelonia* populations in order to determine if significant differences do indeed exist.

The carapace of the adult male in the Hawaiian population can also contain considerable black pigmentation, however, greater variability has been recorded. Olive and yellowish gold components consisting of several different patterns can at times prevail. In general, the head and dorsal surfaces of the flippers are similar in pigmentation to the black-phase female. The male's carapace seems to present a lower profile than the female, however, further morphometric data need to be gathered to clarify this apparent sexual dimorphism that was also a part of Caldwell's (147) description of *carrinegra*.

Plastron coloration in the adults of both sexes ranges from orange to yellowish orange. This color also encompasses the ventral surfaces of the marginals and the inframarginals, which are clearly visible during periods of land basking and nesting. A border of orange or yellowish orange often extends along the anterior edges of the second, third, and fourth marginals on both sides of the carapace. The black or gray pigmentation in the plastron described for *carrinegra* by Caldwell (147) has only been found in a few of the adult Hawaiian *Chelonia* thus far examined by the author. A photograph showing the distinctly black pigmented plastron of an adult at French Frigate Shoals appears in a 1954 article by Eagle (204).

Indentations or constrictions of the marginals over the hind flippers have been found in varying degrees in Hawaiian *Chelonia* of both sexes. For the female, such a modification may serve to lessen the injury to dorsal surfaces of the hind flippers that can result from repeated contact with the marginals during excavation of the egg chamber.

Immature green turtles observed throughout the Hawaiian Archipelago have been found to show considerable variation in carapace coloration and pattern, both between and within different size categories. Colorations include combinations of yellowish gold, brown, reddish brown, black, and olive. Like the adults, such colorations can only be properly described in conjunction with a dossier of color photographs. Preliminary evidence has been gathered indicating that some color phases, particularly those with black pigmentation, are more prevalent in certain resident foraging areas. This would suggest an environmental influence, resulting possibly from food sources or other characteristics of the habitat. Changes in the coloration of both the carapace and plastron have been recorded in Hawaiian *Chelonia* raised under captive conditions. For the plastron, extensive black pigmentation develops in juveniles by the time they reach 8 cm in straight carapace length, but fades and disappears by a size of approximately 20 cm. This has not been reported in other *Chelonia* populations and its adaptive significance is presently unknown. In addition to gradual and subtle transformations occurring during normal growth, some color changes recorded in captive specimens have been both discrete and radical with the causative factor suspected to be of an environmental nature.

With respect to carapace morphology, the highly arched characteristic has not been found to manifest itself among immature Hawaiian *Chelonia* measuring less than approximately 65 cm in straight carapace length.

The overall question of taxonomic status for Hawaiian *Chelonia* is clearly a complex matter that may prove to be difficult to resolve solely on the basis of coloration and carapace morphology. The unique land basking behavior exhibited within the population could in fact be the most valid claim for eventual designation as a separate subspecies.

1.2 Common Names

Common names used for *Chelonia* in the Hawaiian Archipelago include green turtle, green sea turtle, and honu (Hawaiian). Amerson *et al.* (32) have used the name "black turtle."

1.3 Size Categories

The size categories used for Hawaiian *Chelonia* are as follows: hatchling--umbilical scar still present; juvenile--posthatchling to 65 cm (25.5 in.) straight carapace length; subadult--65 to 81 cm (31.5 in.) straight carapace length; adult-->81 cm and reproductively mature.

These definitions are modified from the ones offered by Hirth (265) in that the division between juvenile and subadult categories is placed at 65 cm instead of 40 cm. This is justified on the basis that 65 cm is the minimum size at which sexual dimorphism (lengthening of the male's tail) has been observed to start taking place. Furthermore, human contact and research opportunities with naturally occurring posthatchling turtles <35 cm are extremely rare in the Hawaiian Archipelago. Retention of Hirth's (265) 40 cm division would consequently limit the juvenile category, for practical purposes, to a narrow 35-40 cm range.

1.4 Tagging and Measuring

The first recorded occurrence of *Chelonia* being "tagged" in the Hawaiian Archipelago involved the early 1900's cultural practice among some Japanese residents of inscribing characters on a carapace and returning the turtle to the sea (Cobb 176). The first known tags actually attached to Hawaiian green turtles occurred in June 1934 when brass tags inscribed with "*U.S.S. Itasca* 1934" were placed on three adults prior to release at sea near Laysan Island (Baylis 104; Clapp and Wirtz 171). During short visits to Laysan Island and Pearl and Hermes Reef in June 1950, Brock (133) tagged an unknown number of green turtles using small stainless steel plates fastened to the carapace (Pacific Ocean Fisheries Investigations 387; R. Brock, personal communication; Anonymous 574).

The use of size 49 cattle ear tags manufactured from Monel[1] 400 alloy by the National Band and Tag Company of Newport, Kentucky, was initiated during the early 1960's by the State of Hawaii Division of Fish and Game (HDFG) (Walker 532, 533; Woodside 554). This type of tag had already been successfully used on *Chelonia* in both Sarawak and Costa Rica. Personnel of the USFWS and the Pacific Ocean Biological Survey Program (Smithsonian Institution) subsequently also used this tag on green turtles, as well as Hawaiian monk seals, *Monachus schauinslandi*, during intermittent survey and inspection visits to the Hawaiian Islands National Wildlife Refuge. In 1967 the USFWS made these tags available to the Koral Kings Diving Club at the U.S. Navy station on Midway for use on juvenile and subadult turtles captured during recreational diving. By 1972 an approximate total of 800 turtles had been tagged as a result of these combined efforts. Nearly all of the taggings were in the NWHI, and the majority consisted of adults of both sexes captured while basking ashore (Amerson 30; Amerson *et al.* 32; Clapp and Wirtz 171; Clapp and Kridler 172; Ely and Clapp 211; Kridler 311-327; Olsen 380-385; Woodward 556).

Systematic tagging and monitoring of nesting green turtles at the French Frigate Shoals breeding colony was initiated by the author in June 1973. This research program has continued during subsequent years and has been expanded to include juveniles, subadults, and adults basking ashore and residing in foraging areas throughout the Hawaiian Archipelago. Between 1973 and September 1976, size 49, as well as the smaller size 681, Monel tags were used in this program. Since that time only size 681 Inconel 625 alloy tags, specially manufactured by the National Band and Tag Company, have been used as the primary means of individual identification. These tags weigh 3.5 g and measure 8 by 29 mm. The change to Inconel was made following a determination by the author that considerable corrosion and subsequent tag loss had occurred in many of the Monel tags placed on Hawaiian *Chelonia* (Balazs 66; Mrosovsky 363). The implications of this corrosion with respect to the introduction of heavy metals (copper and nickel) into an animal's system are potentially far-reaching. Similar corrosion has been found in Monel tags used in a number of other marine turtle populations. No signs of corrosion have thus far been found in the Inconel tags placed on Hawaiian *Chelonia*.

The tagging sites used on Hawaiian *Chelonia* have been the trailing edges of the front flippers, both in the fold of flesh proximal to the body and between scales at a distal site. This latter location is more conducive to the visual recovery of tag numbers from basking turtles without causing disturbance. When possible and appropriate, as many as three Inconel tags are placed at the different tagging sites on each turtle.

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[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

A number of other identification techniques have been tested for possible use in conjunction with the basic tag. This has included the production of identifiable antibodies (Benedict 107, 108; Hendrickson 262), epoxy paint applied to the carapace (Kridler 324; Anonymous 579), tattooing (Balazs 77), carapace notching of juveniles, vinyl strips attached through the carapace, and plastic tags manufactured by various companies. None of these techniques have proven to be very satisfactory for long-term identification.

Numbers formed on the carapace of nesting and basking turtles with aerosol paint (DuPont Lucite) have been successfully utilized for short-term identification and monitoring of daily activities (Balazs 49, 51).

Under the present research program, a total of 1,102 *Chelonia* has thus far been tagged throughout the Hawaiian Archipelago (Table 1). This includes 444 immature turtles and 140 adult males, two categories that are not normally tagged in most other marine turtle populations.

The measurements recorded for Hawaiian *Chelonia* have consisted of: straight and curved carapace length along the midline; straight and curved carapace width at the widest point (usually the sixth marginal), head width; straight plastron length along the midline; tail length from the posterior edge of the plastron along the midline; and body weight. Since June 1973, basking and nesting turtles have not been regularly turned over or otherwise restrained in order to carry out tagging and measuring. The suspension of this previous practice has lessened the opportunities to record plastron and tail measurements, body weight and, at times, other measurements. Nevertheless, this reduction of impact on turtles from research activities was deemed necessary in order to ensure the continuation of normal basking and nesting behavior (see Wallace 535).

2. DISTRIBUTION

2.1 Total Area

Green turtles are distributed at select locations throughout the 2,450-km long Hawaiian Archipelago. This nearly linear chain consists of 132 islands, islets, and reefs extending from lat. 18°54'N, long. 154°40'W to lat. 28°15'N, long. 178°20'W in an isolated region of the North Central Pacific Ocean (Figure 1). Eight main and inhabited islands (Hawaii, Maui, Kahoolawe, Lanai, Molokai, Oahu, Kauai, and Niihau) located in the southeastern segment of the Hawaiian Archipelago comprise over 99% or 16,650 km^2 of the total land area. The remainder consists of offshore islets and the small islands extending to the northwest of Kauai and Niihau known as the Leeward Islands or the NWHI. Except for Kure and Midway, the islands and certain adjacent waters in this segment of the chain constitute the Hawaiian Islands National Wildlife Refuge.

There are 1,210 km of coastline in the Hawaiian Archipelago, with the main islands accounting for 1,165 km or 96% of the total. However, the adjacent underwater coastal shelf where most green turtles reside is generally very narrow with the 20-fathom curve (37 m) often only a few kilometers from shore. A number of large banks with little or no associated emergent land occur in the northwestern segment of the Hawaiian Archipelago. Within the 100-fathom curve (182 m), these submerged areas encompass approximately 16,000 km^2.

The closest island area to the Hawaiian Archipelago is Johnston Atoll located 820 km south of French Frigate Shoals at lat. 16°45'N, long. 169°31'W. A green turtle aggregation of undetermined composition and size occurs at Johnston, however, its relationship, if any, to Hawaiian *Chelonia* is not known at the present time. An isolated green turtle aggregation also occurs at Wake Island (lat. 19°18'N, long. 166°36'E), which is 1,900 km southwest of Midway and the closest island area located to the west of the Hawaiian Archipelago. One of the juveniles tagged at Midway was subsequently recovered at Wake, however, the weakened and apparently pathological condition of the turtle suggests that it may have passively drifted there with prevailing winds and currents (Balazs 69, 81; Anonymous 641). Nevertheless, the relationship of the Wake aggregation remains to be determined.

The distribution of green turtles in the Hawaiian Archipelago has been reduced within historical times. A breeding colony that formerly occurred at Polihua Beach on the island of Lanai no longer exists (Balazs 55; Emory 213; Kahaulelio 281; Tabrah 473). Reductions have also occurred in the distribution of green turtles in their resident foraging areas adjacent to the main islands (Balazs 46, 48; Hendrickson 262; State of Hawaii 459-463). In the NWHI, the large aggregation of green turtles that formerly occurred at Laysan Island has now nearly disappeared (Ely and Clapp 211). The aggregation at Pearl and Hermes Reef appears to be following a similar pattern and the situation at this location warrants attention.

2.2 Differential Distribution

2.21 Adults

The distribution of adult *Chelonia* in the Hawaiian Archipelago is determined primarily by the locations of acceptable breeding, feeding, and resting habitat and, of course, the existence of sufficient numbers of animals to utilize such areas.

In excess of 90% of all breeding by Hawaiian *Chelonia* occurs at French Frigate Shoals (Figure 2), a 35-km long crescent-shaped atoll situated in the middle of the Archipelago (Amerson 30; Balazs 51, 55, 57; Hendrickson 262; Hirth 265; Kridler 311-327; Olsen 380-385). Small groups of turtles and separately nesting individuals using Laysan and Lisianski Islands and Pearl and Hermes Reef account for the remaining reproductive effort. Only a few nestings have ever been recorded at Kure and Midway (Balazs 76).

Feeding and resting areas where adult Hawaiian *Chelonia* live the greater portion of their lives during nonbreeding periods are located in coastal waters of both the main islands and the NWHI. The principal food source, marine benthic algae of several genera, is restricted to shallow depths where sunlight, substrate and nutrients are conducive to plant growth. Feeding pastures used by adults are usually less than 10 m deep, and frequently not more than 3 m deep. The underwater sites where adults regularly retreat for periods of quiesence include coral recesses, the undersides of ledges, and sand bottom areas (called "nests") that are relatively free of strong currents and disturbance from natural predators and man. These resting areas for adults in the main islands usually occur at depths >20 m, but probably not normally exceeding 50 m. Available information indicates that the resting areas are in proximity to the feeding pasture. Periods of rest near the feeding pasture are also known to take place while floating at the surface during light winds and calm seas. This surface basking undoubtedly yields a thermal advantage due to solar radiation directly on the carapace and the warmer layer of water present at the surface. In addition, less energy would be expended by not having to periodically swim to the surface for respiration.

Some of the important resident areas in the main islands where adult *Chelonia* feed and rest are shown in Figure 3 and include the following: Hawaii--Kau and North Kohala Districts; Maui--Hana District and Paia; Lanai--northern and northeastern coastal areas bordering the Kalohi and Auau Channels; Molokai--southern coastal areas from Kamalo to Halena; Oahu--Kailua and Kaneohe Bays, and northwestern coastal areas from Mokuleia to Kawailoa Beach; Kauai--Princeville, northwestern coastal areas of Na Pali, and southern coastal areas from Kukuiula to Makahuena Point. Additional investigations are needed to adequately delineate these and other coastal areas.

In the NWHI, resident aggregations of adults are known to occur at Necker Island, French Frigate Shoals, Lisianski Island, Pearl and Hermes Reef, and, to a lesser extent, Laysan, Midway, and Kure Islands. Except for Midway, resting habitat at these locations also includes shoreline areas where land basking regularly takes place. Although a few random sightings have been made, it is still unknown if adults, or any other size categories, reside on or in some way utilize the submerged banks with no emergent land located in the northwestern segment of the Hawaiian Archipelago. Data are also lacking for Nihoa and Gardner Pinnacles.

While in transit during reproductive migrations, adult Hawaiian *Chelonia* are distributed at unknown locations in the pelagic environment between the islands of the Hawaiian Archipelago.

2.22 Hatchlings, juveniles, and subadults

Hatchlings emerge from their nests and enter the water at French Frigate Shoals and the other breeding sites in the NWHI between mid-July and early October. Following a rapid departure from the adjacent waters, they are lost to almost all human contact. This disappearance is consistent with what has been found to occur in other *Chelonia* populations (Hirth 265). Hawaiian green turtle hatchlings are thought to be subsequently dispersed in the pelagic environment by currents and vigorous swimming. Surface drift trajectories plotted for the theoretical movement of hatchlings leaving French Frigate Shoals suggest a predominant westerly dispersal (Figure 4). However, *Chelonia* hatchlings are strong swimmers and the distinct possibility exists that considerable movement takes place at variance with prevailing surface currents.

The 28 March 1779 log of the *Resolution* records the pelagic sighting of a posthatchling turtle of unknown species to the southwest of the Hawaiian Archipelago at lat. 20°15'N, long. 179°20'E (Beaglehole 105).

The distribution of juveniles up to 35 cm in the Hawaiian Archipelago is also unknown, due again to a nearly complete absence of human contact. Turtles of this size are almost certainly still residing in the pelagic environment where the chances of seeing them are greatly reduced. Nevertheless, predation by certain pelagic fishes such as the oceanic whitetip shark, *Carcharhinus longimanus*, could be expected to take place. Efforts are therefore being made to recover juveniles of this "lost" size from the stomachs of potential predators (Balazs 70, 79; Hendricks 261; Anonymous 658).

Juveniles larger than 35 cm as well as subadults can be found feeding and resting in coastal areas throughout the Hawaiian Archipelago. These turtles frequently reside in the same general area as the adults. There is, however, the tendency among juveniles and subadults to utilize resting habitat located at a shallower depth. In addition, only juveniles are able to use some feeding pastures due to the very shallow depths involved.

3. ECOLOGY AND LIFE HISTORY

3.1 Reproduction

3.11 Sexuality

Adult males of the Hawaiian *Chelonia* population have a 35 to 45 cm long prehensile tail that extends beyond the hind flippers while swimming and is larger in overall diameter than the tail of the adult female. The adult female's tail ranges from 20 to 25 cm in length and only extends to about the middle of the hind flippers. The single nail present on the foremargin of each front flipper is also longer in the adult male. However, in both sexes this structure can be considerably worn down, probably due mostly to abrasion with hard substrate encountered while feeding and resting underwater. Furthermore, the nails on the female receive some wear during nesting, while nails on the male may be abraded during copulation. A heavily keratinized tip is present at the end of the male's tail, but this may be missing in many individuals due to injury from other turtles or predators.

It is presently only possible to determine sex on the basis of external characteristics in individuals larger than 65 cm. Even then, caution must be exercised in that lengthening of the tail in some males does not start until a greater size is reached.

3.12 Maturity

The smallest female thus far found nesting at French Frigate Shoals measured 81 cm in straight carapace length, with 92 cm being the overall mean (Table 2). Curved carapace measurements are presented in Table 3 for comparative purposes. Data by Kridler (311-327) and Olsen (380-385) show that the mean weight of adult females is 110 kg (range 68-148 kg N=69). As noted by Hirth (265), nesting aggregations of *Chelonia* may consist of some females that grew to a large size after reaching maturity, and some that did not mature until reaching a large size. Such a phenomenon could also be expected for adult males. It is presently not possible to identify newly matured individuals (recruits) in the French Frigate Shoals breeding assemblage, however, continued tagging and collection of size-frequency data may eventually provide the basis for this determination.

The age at which green turtles mature under natural conditions has received very little research attention in most populations, although estimates based principally on captive growth rates have appeared in the literature (Hirth 265). For Hawaiian *Chelonia*, tag and recapture experiments with wild juveniles have demonstrated significant differences in the rates of growth, hence age at maturity, between resident areas throughout the Hawaiian Archipelago (Balazs 81). The projected lengths of time for 35 cm juveniles to reach the mean size of adult females range from 11 to 59 yr (Table 4). Turtles that reside in the NWHI seem to require the longest periods of time to mature.

3.13 Mating

Courtship and copulation take place in the shallow waters of French Frigate Shoals, usually within 2 km of the 11 small islands present at this location. Some observations have suggested that the greatest influx of males to the area occurs prior to the arrival of most females (Balazs 49; Olsen 382). This is complicated, however, by the presence of adult males that are known to reside for extended periods at French Frigate Shoals.

Copulation has been observed taking place at the surface, on the bottom, and at various depths within the water column. Several males are almost always in attendance with a copulating pair, circling, smelling and biting the tail and flippers of the successfully mounted male. The injuries inflicted by this behavior are frequently extensive with scales and flesh being torn away and the underlying limb bones exposed. Males that have undergone these assaults during previous seasons can often be recognized by the missing areas along the trailing edges of their front flippers and the presence of thick, nonpigmented scar tissue. These scars may eventually be useful in the identification of neophyte males at the breeding colony.

The male maintains his position during copulation by grasping the margins of the female's carapace with the distal areas of his four flippers. The nail on the front as well as the hind flippers seem to provide some assistance to this effort. The muscular prehensile tail also serves as a holding device by extending under the female to a position where the penis can be inserted into the cloaca. During copulation the female is in complete control of all movement since her four flippers are not restrained. Copulating pairs still locked together have been observed both diurnally and nocturnally in water only several centimeters deep adjacent to the islands at French Frigate Shoals. This beaching maneuver is presumably carried out by the female in an attempt to detach the male.

Most copulation at French Frigate Shoals occurs during the early portion of the breeding season, between mid-April and early June. The use of identification numbers painted on the carapace of nesting turtles has indicated that females will not copulate after laying their first clutch of eggs. Copulations recorded later in the breeding season appear to involve females that have only recently arrived at French Frigate Shoals.

Copulating turtles have been seen at Lisianski Island during April 1976 (C. Fiscus, personal communication) and at Pearl and Hermes Reef during March 1961, late May 1967 (Amerson *et al.* 32), and April 1976 (DeLong *et al.* 195). No records exist for Laysan, Kure, and Midway.

Two adult males locked together in a copulatory position have been observed on several occasions at French Frigate Shoals, both during the breeding season and in the month of December. During one of these encounters, the position was maintained for at least 20 min. Similar behavior among males has also been documented at Necker, a small rock island with no sand beaches located 155 km east of French Frigate Shoals (Balazs 72).

3.14 Fertilization

It is uncertain if the eggs of *Chelonia* (and other marine turtles) are fertilized as a result of copulation that occurs within the same breeding season, or from spermatozoa stored in the reproductive tract resulting from copulation during a previous season. If storage is a prerequisite for the fertilization, and copulation only occurs near the nesting beaches, then the neophyte female would have to make her first visit to French Frigate Shoals solely for mating purposes. Such a trip could, however, also involve nesting excursions ashore, but with only infertile eggs or no eggs at all being laid. Although both of these occurrences have been documented at French Frigate Shoals, other factors could very well be responsible.

In an effort to determine if fertility decreases at French Frigate Shoals as the breeding season progresses, 40 precounted egg clutches laid over a 72-day period (June-August 1974) were excavated and examined following the natural emergence of hatchlings. Regression analysis of these data showed a tendency toward decreased fertility with time, however, this was not found to be significant ($P=0.08$).

3.15 Nesting and habitat charactersitics

Nesting takes place at French Frigate Shoals only on the islands of East, Whale-Skate, Trig, Tern, Gin, and Little Gin (Figure 2). Of the females present for each breeding season, approximately 55% nest on East and 35% nest on Whale-Skate. East Island has consequently been the site of intensive research during each breeding season since 1973 with surveys being made at regular intervals on the other islands. Nesting commences during the middle of May, reaches its peak during late June, and declines to a very low level by early August. Some sporadic nesting may occur until mid-September. Although actual egg deposition takes place at night, or at least by sunrise, females have been recorded ashore excavating a nest site as early as 2 h prior to sunset.

East and Whale-Skate are the two largest naturally occurring islands at French Frigate Shoals, consisting of 4.0 and 6.8 ha, respectively, with elevations not exceeding 2 m. Both islands have a calcareous substrate composed of fine to coarse fragments of corals, coralline algae, molluscs, and barnacles. The interiors of both islands have low vegetation (*Tribulus, Chenopodium, Portulaca, Boerhavia*) and are rich with humus originating from nesting seabird colonies. From 1944 to 1952 East Island was the site of a 26-man U.S. Coast Guard navigation (LORAN) station. Although some clean-up activities took place in 1965 and 1973, remains of this abandoned facility are still prominent on the island. Tern Island, located 11 km to the northwest of East Island, is a reconstructed island that was enlarged by dredging and landfill from 4.5 to 23 ha for military purposes in 1942 (Amerson 30; Berger 125; Olsen 383). From 1952 to 1979, a U.S. Coast Guard LORAN station was also present on Tern Island.

Mean monthly sea-surface temperatures recorded at French Frigate Shoals between 1974 and 1976 were found to range from 23.8° to 28.3°C, with the warmest water generally occurring from June through October (Figure 5). This is similar to sea-surface temperatures found in the main Hawaiian Islands. The mean annual rainfall at French Frigate Shoals is 115 cm with the driest months being April through November. Additional climatic data for the area are presented by Amerson (30).

Green turtles nesting at East Island have been recorded laying as many as six egg clutches within a season, however, the mean number is only 1.8 (Table 5). Approximately 40% of the turtles lay only once in a season. Almost 10% make nesting attempts on several consecutive nights, but do not lay eggs and often are not seen again. Only a few turtles (<5%) have been recorded each season changing islands once nesting has started. This factor alone would, therefore, not fully explain the absence of oviposition by some individuals. It is plausible that some of these turtles are releasing their eggs in the water due to a nesting dysfunction, while others could be mortalities due to predation by tiger sharks, *Galeocerdo cuvier*.

The length of time between oviposition in turtles that lay more than once in a season ranges from 11 to 18 days, with the mean being 13 days (Table 6). During this internesting interval, turtles identified by painted numbers are regularly seen basking at East Island and swimming in the adjacent waters. The undersides of reefs that extend both to the southeast and northwest of the island are also known to be utilized during the internesting period. In a preliminary experiment conducted during June 1979, the maximum diving depth recorded with small depth gauges attached to two females at Trig and Whale-Skate Islands was 12.8 m. This suggests that movement to deeper waters outside the lagoon may not be taking place during the breeding season.

The degree of site fidelity displayed by green turtles nesting at East Island within each season has been examined by dividing the shoreline into seventeen 50-m long reference areas. Observations made over the 1973, 1974, and 1975 seasons revealed that 32% of the egg clutches laid during renestings were in the same 50-m area as earlier nestings. Approximately 60% were in the same or an adjacent 50-m area, while 83% of the turtles emerged on the same side of the island as the earlier nestings. Some individuals showed considerable site fixity, as demonstrated by two turtles in 1974 that each nested four times in the same 50-m area, and a turtle that nested six times, alternating regularly between the same two areas (1 and 6). Also during 1974, renestings by five turtles involved egg clutches that were laid only 1.5 to 3.5 m from an earlier clutch.

The locations of 220 egg clutches laid at East Island during the 1974 season are presented in Figure 6. The unutilized portions of the interior of areas 2-3 and 14-16 contain several low concrete foundations from the abandoned Coast Guard facility. Although suitable substrate for nesting is also present, very few turtles have ever been recorded entering this region of the island.

Usually less than half of the turtles that emerge for nesting on any one night successfully lay eggs (Figure 7). The remaining turtles continue to emerge on subsequent nights until oviposition is achieved or, as previously described, the turtle is no longer present. Many of these nesting attempts involve the nearly complete excavation of an egg chamber before abandonment takes place and another site is selected on the island. In other cases, only rudimentary body pits are dug before a site is abandoned. Three factors that contribute to the incomplete excavation of a nest include injuries or amputations of a turtle's hind flippers, insufficient moisture in the substrate due to low rainfall, and contact with buried antenna wire and other debris present on East Island. It is also possible that some of these nesting attempts are unsuccessful because the complement of eggs has not yet developed to a stage for oviposition to occur. The tendency of some green turtles to make short, nonegg-laying emergences in which the tracks form a parabolic curve (Carr *et al.* 153; Hirth 265) has only rarely been recorded in Hawaiian *Chelonia*. The "sand-smelling" behavior exhibited by newly emerged females in some green turtle populations has never been observed at French Frigate Shoals.

During the nesting process, Hawaiian *Chelonia* are least susceptible to disturbance immediately following oviposition when nest covering has just started to take place. Carapace measurements and tagging are therefore usually carried out during this period.

A sample of 50 egg clutches counted during oviposition over a 75-day period (June-August 1974) at East Island revealed a mean of 104 eggs per clutch with a range of 38 to 145 eggs. Multiple regression analysis of these data was conducted to determine if significant relationships exist between the number of eggs in a clutch and the independent variables of: time of oviposition within the season (x_1), ratio of the curved and straight carapace widths of the female (x_2), and straight carapace length of the female (x_3). Larger females were found to lay significantly ($P<0.05$) more eggs per clutch. Although there was a tendency for fewer eggs per clutch to be laid as the season progressed, this was not significant ($P=0.10$). The relationship between the curved-straight width ratio and number of eggs per clutch was also not found to be significant ($P=0.30$). This suggests that body thickness alone is not an adaptation for the storage of greater numbers of eggs. The resulting formula for predicting the number of eggs in a clutch (y) is $y = -268.704 + (-0.271)x_1 + 93.768x_2 + 2.819x_3$.

The mean incubation period (days to hatchling emergence at the surface) of 38 nests laid at East Island from June to August 1974 was found to be 64.5 days with a range of 54 to 88 days. Multiple regression analysis of these data found no significant relationships between incubation period and time of oviposition within the season, coarseness of the nest substrate, or depth of the egg chamber. The mean egg chamber depth was 60 cm (range 48-74 cm). A significant relationship ($P<0.05$) was found between depth of the egg chamber and coarseness of substrate, with shallower chambers being excavated in coarser substrate. No significant relationship was found between egg chamber depth and size of the nesting female.

The mean width and length of the surface area excavated by 19 turtles that successfully nested on East Island was 2.0 m (range 1.7-2.7 m) and 3.8 m (range 2.3-5.0 m), respectively. No significant relationship was found between these measurements and the size of the nesting female.

Turtles on both East and Whale-Skate Islands regularly come into contact with 10 species of nesting seabirds, the most abundant of which are sooty terns, *Sterna fuscata*, and wedge-tailed shearwaters, *Puffinus pacificus*. The crushing of eggs and young chicks by nesting turtles consequently takes place to varying degrees depending on the time of the season. In addition, adult shearwaters occasionally become buried in their underground burrows as a result of turtle activity. Monk seals hauled out along the shoreline and in the vegetation zone are also encountered at times by nesting turtles, but with the exception of mothers with pups, usually little if any interaction takes place.

Table 7 presents the results of 40 precounted egg clutches laid at East Island from June to August 1974 that were excavated and examined following the natural emergence of hatchlings. Multiple regression analyses of these data were conducted to determine if significant relationships exist between 1) percent of eggs hatched, 2) percent of hatchling emergence, 3) percent of dead hatchlings, 4) percent of partially developed but dead embryos, 5) percent of eggs with no apparent development, and the independent variables of 1) time of oviposition within the season, 2) coarseness of the nest substrate, 3) depth of nest, and 4) straight carapace length of the female. The only significant relationship ($P<0.05$) found was that the percent of hatchlings emerging at the surface decreases in egg clutches that are laid as the season progresses.

3.16 Reproductive cycles

Reproductive cycles, as measured by remigration intervals, have been documented in 21 nesting females at East Island since June 1973 (Table 8). Fourteen of these turtles (66.7%) displayed a 2-yr cycle, six (28.6%) a 3-yr cycle, and one turtle (4.7%) was not seen again until 6 yr after being tagged. Thus far, no nesting turtles have been recovered at French Frigate Shoals after only a 1 yr absence. The present predominance in recordings of 2-yr nesting cycles is due to the significant increase in recoveries made during the 1979 breeding season of turtles tagged 2 yr earlier in the 1977 season (Table 8). Because 1977 was the first season in which the more durable Inconel tags were used at French Frigate Shoals, continued monitoring and tagging will be necessary during future breeding seasons (particularly 1980 and 1981) in order to accurately determine the most common nesting cycle. In view of the long time periods apparently required for Hawaiian *Chelonia* to reach maturity at certain resident foraging areas (section 3.12), it is reasonable to assume that the same controlling ecological factors would also cause protracted periods for reproductive readiness to be reached between remigrations. The occurrence of some nesting cycles far greater than 3 or even 6 yr should therefore be considered as a distinct possibility. Furthermore, the low recovery rates of tagged adult females in both the Hawaiian and Caribbean (Carr *et al.* 153) *Chelonia* populations suggest the possibility that many turtles may only be involved in a single breeding season during the course of their entire lifetime.

The reproductive cycles of males at French Frigate Shoals have been documented in 16 cases. Nine (56.2%) of these represented a 1-yr cycle, five (31.3%) a 2-yr cycle, and two (12.5%) a 3-yr cycle. The nature of these tag recoveries indicates that the 1-yr cycle involves remigrations rather than simply a residency at French Frigate Shoals. The apparent predominance of a 1-yr cycle in males may be due to a lower energy requirement for reaching reproductive readiness between remigrations in comparison to females. Although the occurrence of 2- and 3-yr cycles is believed to be valid, it should be noted that greater difficulties are encountered in reliably determining male reproductive cycles that are longer than 1 yr. This is due to the fact that there is no assurance that all males will come ashore to bask during a given season and, therefore, be available for tagging and tag recovery.

The modulation of reproductive cycles (see Carr *et al.* 153) has thus far been recorded in two turtles at French Frigate Shoals. This involved a phase change from a 3- to a 2-yr cycle in a female, and a change from a 2- to a 1-yr cycle in a male. The extent and significance of such shifts in Hawaiian *Chelonia* are presently unknown. Modulation of reproductive cycles may be a reflection of periodic changes in productivity or other ecological conditions of the turtle's resident foraging area.

3.17 Eggs

The mean weight of eggs laid at East Island by a 96 cm straight carapace length female was 50 g (range 45-54 g, N=99). The mean diameter of these eggs was 44 mm with a range of 43 to 46 mm. Three of 50 egg clutches observed during oviposition at East Island were found to contain a few of the abnormally small or nonspherical eggs that have been reported in other *Chelonia* populations. The time required for an egg clutch to be deposited into a successfully excavated egg chamber ranges from approximately 20 to 30 min. This is considerably longer than the 10 min reported by Hirth (265) for other *Chelonia* populations.

Predation on eggs does not normally take place at French Frigate Shoals. Although two species of ghost crabs (*Ocypode ceratophthalmus* and *O. laevis*) are present in relatively small numbers, neither of these crustaceans have been found burrowing into a nest. Although it is a rare occurrence at French Frigate Shoals, nesting turtles will at times inadvertently dig into an existing clutch of eggs. Broken and exposed eggs from nests that have been disturbed in this manner have been observed being eaten by *O. laevis*, as well as migratory shore birds (ruddy turnstones, *Arenaria interpres* and golden plovers, *Pluvialis dominica*). On a single occasion, a wedge-tailed shearwater was recorded as having accidently burrowed into a clutch of eggs at East Island. In a few instances, egg clutches have been laid too close to the shoreline, thereby being uncovered and washed away by subsequent wave action. Also a few turtles have been observed breaking large numbers of their own eggs as a result of harsh contact by a partially amputated hind flipper during the nest covering process.

From 1973 to 1979, an estimated 500 kg of unhatched green turtle eggs and dead hatchlings have remained buried in the ground each season at French

Frigate Shoals and undergone decomposition. Although probably small in comparison to deposits from nesting seabirds, this chelonian organic matter nevertheless represents a valuable contribution to the soil fertility of the islands.

3.2 Hatchling Phase

Newly emerged hatchlings at French Frigate Shoals measure 53 mm in straight carapace length (range 48-59 mm, N=556) and weigh 31 g (range 25-35 mm, N=120). The dorsal surfaces of the hatchlings are black with white edges 2- to 3-mm wide on the flippers and a 1-mm wide white edge along the periphery of the marginal laminae. The ventral surfaces of the hatchlings are white with areas of black located on the flippers (see Balazs 55, 62 for color photographs).

Prior to emergence from the nest, Hawaiian green turtle hatchlings have been found to exhibit sudden bursts of activity when subjected to loud sound, such as produced by jet aircraft (Balazs and Ross 89; Barr 101). The biological effects of such noise on hatchlings, as well as developing embryos, are presently unknown.

The emergence of hatchlings at French Frigate Shoals is only known to occur at night, usually within a few hours after sunset. A firsthand observation of natural departure from the underground nest was made by the author during August 1974. Once emergence was initiated, the hatchlings crawled out singularly or in pairs in a moderately slow but continuous stream over a 4- to 5-min period. This was followed by very slow circular movements in the immediate area of the nest site. During this period, which lasted for about 2 to 3 min, the hatchlings' heads were extended upward giving the appearance of intently observing some feature of the sky or horizon. Following these distinct movements, the hatchlings moved rapidly to the water in a number of different directions.

Although most hatchlings seem to enter the water at the shoreline closest to their nest site, all directions (except on Tern Island) will ultimately result in success due to the small land areas involved. Unnecessary terrestrial excursions would, however, result in an increased energy expenditure that could conceivably lessen the hatchlings' survival capabilities during the first few days in the pelagic environment. Groups of hatchlings on East Island have been recorded traveling in the direction of a bright moon, thereby considerably increasing the distance covered to reach the water.

Predation on hatchlings at French Frigate Shoals takes place by both species of ghost crabs, but *O. ceratophthalmus* is consistently more successful due to its larger size. Predation only occurs in or immediately above the narrow intertidal zone where both crabs periodically dig their burrows. Hatchlings are seized by the head, neck, or front flippers and eaten either on the surface or inside a burrow. The internal organs and portions of the head, neck, and pectoral muscles are usually the only parts consumed. The number of hatchlings eliminated from the population by ghost crabs probably does not exceed 5% or an estimated seasonal average of 1,200 individuals. Reducing the number of ghost crabs during the course of tagging and other research activities offers some potential as a management practice.

Although frigatebirds, *Fregata minor*, are among the seabirds present at French Frigate Shoals, they are not known to prey on hatchlings on land or in the inshore waters such as reported in certain other *Chelonia* populations (Hirth 265). Nocturnal emergence undoubtedly serves as a protective mechanism against such predation. Examinations of fecal matter at the nesting and roosting sites of frigatebirds have not resulted in the recovery of laminae or other indigestible particles of hatchlings. This suggests that predation is also not occurring in the pelagic waters surrounding French Frigate Shoals where frigatebirds periodically forage.

During the U.S. Coast Guard tenure at East and Tern Islands, newly emerged hatchlings were regularly disoriented and attracted to artificial lights and possibly vibrations from diesel generators associated with station facilities. Mortalities from thermal exposure subsequently resulted in those hatchlings that were not discovered by Coast Guard personnel and transported to the water.

Predation on hatchlings by carnivorous fishes at French Frigate Shoals does not appear to be significant. It is difficult, however, to assess such impacts within the marine environment. From July to October 1974, 101 ulua, *Caranx ignobilis*, *C. melampygus*; 16 wrasses, *Thalassoma purpureum*, *Bodianus bilunulatus*; and 13 gray reef sharks, *Carcharhinus amblyrhynchos*; were captured in the vicinity of East Island to examine stomach and intestinal contents for the presence of hatchlings. Major food items recovered included filefish, *Pervagor spilosoma*, and pieces of unidentified crabs and cephalopods, but no evidence of hatchling predation was found.

Hatchlings that emerge from nests in the center of East Island are coated with particles of humus, while those originating from pure calcareous sand areas along the periphery and at the west end emerge perfectly clean. For an unknown period of time after entering the water, hatchlings coated with humus emit a trail of organic material. It would be of value to know if this provides olfactory cues to potential fish predators, or somehow possibly serves as a deterrent to predation.

The types and levels of predation on hatchlings that emerge from nests at other islands in the northwestern segment of the Hawaiian Archipelago are presently unknown. Both species of ghost crabs as well as many of the same carnivorous fishes are also present at these locations.

Hawaiian *Chelonia* hatchlings that emerged from a captive nest at Sea Life Park on Oahu in 1976 were extensively preyed upon by wild mongoose, *Herpestes auropunctatus*, (Bourke *et al.* 131). This mammal was first introduced to Hawaii in 1883 and is now present on all of the main islands except Kahoolawe, Lanai, and Niihau.

3.3 Juveniles, Subadults, and Adults

3.31 Longevity

There is virtually no information on the life spans of Hawaiian *Chelonia* or marine turtles of any other population. The maximum age obtained could, however, be considerable in view of the findings that turtles at certain resident foraging areas may require more than 59 yr to reach maturity (Table 4), Tag recoveries of four females and eight males have been made in the Hawaiian Archipelago after periods exceeding 9 yr. All of these turtles were recorded as being adults when originally tagged. The longest time between initial tagging and last recovery for a female is 12.1 yr, while the longest for a male is 14.3 yr. In a 22-yr old research program at Tortuguero, Costa Rica, the longest elapsed time reported for the recovery of a tagged nesting green turtle was 19 yr (Carr *et al.* 153).

Investigations by the author are currently underway to develop a method of estimating the age of Hawaiian *Chelonia* based on annuli discovered in the plastral and limb bones. These bands are most prominent in the dorsal segments of the hyoplastrons. Preliminary results have indicated a positive correlation between the number of bands and the size of the turtle. To supplement this research, autoradiographs are being attempted with sections of bones and laminae obtained from *Chelonia* at Enewetak Atoll (Marshall Islands) where nuclear devices were detonated during the 1950's.

3.32 Competitors

Monk seals with pups at times compete with green turtles for preferred basking space along the shorelines at French Frigate Shoals. Competition for basking space with this species has also been documented at the small sloping rock ledge at Necker Island (Balazs 72). Humans in the NWHI have periodically competed with *Chelonia* for terrestrial space. This has principally been in the form of military exercises, construction of facilities, commercial fishing, wildlife research, and pursuit of ornamental glass fishing floats (Amerson 30; Amerson *et al.* 32; Clapp and Wirtz 171; Clapp and Kridler 172; Ely and Clapp 211; Woodward 556).

At some of the resident foraging areas in the main islands, humans compete with green turtles for space by setting gill nets and baited hooks, and by repeatedly intruding into habitat with boats and scuba. Although probably not a significant factor at the present time, competition also exists for certain kinds of benthic algae (*Codium, Ulva, Gracilaria*) that are eaten by both green turtles and humans (Abbott and Williamson 1; Fortner 228). Herbivorous fishes and some invertebrates in the Hawaiian Archipelago also utilize benthic algae as food sources, but the extent of this competition is not known.

3.33 Predators

Tiger sharks are virtually the only known natural predators of juvenile, subadult and adult Hawaiian *Chelonia*. Considering just the marine environment, this is essentially the case for all populations of Cheloniidae. Intensive shark research and eradication programs periodically conducted around the main Hawaiian Islands found that 18% (Ikehara 275), 10.8% (Fujimoto and Sakuda 230), and 12.7% (Tester 487) of the tiger sharks examined with food in their stomachs had been feeding on turtles. During 1974 the author captured four tiger sharks at French Frigate Shoals ranging from 1.6 to 3.4 m in length. Two of these sharks contained pieces of turtles representing three individuals, one of which was an adult. At French Frigate Shoals and Pearl and Hermes Reef, green turtles were recorded by Taylor and Naftel (481, 482) in 31% and 36%, respectively, of the tiger sharks captured that contained food. An analysis of the recovered bones, laminae and beaks revealed the presence of nine different turtles in the five tiger sharks from French Frigate Shoals, and eight different turtles in the four tiger sharks from Pearl and Hermes Reef (Balazs 70). A single shark at Pearl and Hermes Reef accounted for five turtles that ranged from an estimated 53 to 64 cm in straight carapace length. Four of the turtles recovered from sharks at French Frigate Shoals were found to be adults of unknown sex ranging from an estimated 81 to 94 cm in straight carapace length. The sizes of the tiger sharks captured ranged from 2.8 to 4.3 m, but significant relationships ($P<0.05$) were not found between size of the turtles eaten and the shark's length or mouth width, which ranged from 26 to 51 cm. Based on these findings, it may be necessary to revise the prevalent belief that natural predation on adult green turtles is minimal (Hirth 265). The digestion rates of green turtle parts in tiger sharks are unknown, therefore it is not possible to determine how long this material may have been retained in each stomach. Due to the comparatively large quantity of laminae and beaks present among the recovered items, it seems likely that keratinized structures are the most difficult to digest, if in fact they can be digested at all. It has been suggested that indigestible items eaten by tiger sharks may be periodically eliminated by regurgitation.

The feeding mechanism of the tiger shark includes heavy sawing actions by both jaws which can effectively cut up large green turtles into pieces suitable to swallow. However, for smaller size turtles this is apparently not necessary. On numerous occasions juvenile Hawaiian *Chelonia* ranging from 35 to 50 cm in straight carapace length have been recovered whole from tiger shark stomachs (Taylor and Naftel 481, 482; Tester 487; C. Chiswick and D. Hertz, personal communications). Tinker (490, 492) reported that a 23 kg turtle was found in a large tiger shark caught off Oahu in 1935.

Tiger sharks have been regularly recorded at French Frigate Shoals in water only a few meters deep adjacent to the various islands (Balazs and Whittow 90). In April 1956, a 3-m shark was observed attacking a large turtle off Whale-Skate Island (Pacific Ocean Fisheries Investigations 392). In June 1974, the author watched a 2-m tiger shark beach itself momentarily on East Island during the unsuccessful pursuit of a juvenile green turtle that had fled to the shoreline. Two tiger sharks were also recorded swimming close to a copulating pair of turtles and three male escorts, but no attack resulted. In August 1978, a large tiger shark was observed for 2 h repeatedly trying to reach a dead adult turtle with a missing head and flippers that had become beached in the wavewash at Trig Island (G. C. Whittow, personal communication). In view of these sightings, it is significant to note that during an 11-mo period on East Island in 1946, former Coast Guardsman H. E. Finch (personal communication) never saw a tiger shark, even though he regularly set baited hooks and caught numerous *Carcharhinus amblyrhynchos*.

Approximately 10% of the turtles nesting on East Island have healed or fresh injuries or amputations of their hind flippers that are suggestive of shark attack. A tagged female released from captivity off Oahu in December 1973 (Anonymous 611, 613, 616) was observed 25 mo later basking on Whale-Skate Island with a front flipper freshly amputated at the humerus. An adult male with a freshly amputated front flipper was seen basking at East Island during July 1976. Two other adult males with a completely missing but healed front flipper have also been recorded while basking. A tagged adult female with one front and both hind flippers missing, but partially healed, was seen basking at Trig Island in June 1973 (Olsen 384). An adult female tagged at East Island in 1973 was recovered 13 mo later off Maui and found to have a recently amputated front flipper (Balazs 57). A turtle with a missing front flipper was seen at Gin Island in 1923 (Wetmore 541). At Lisianski Island, Taylor (475) recorded an adult male in a moribund condition with its tail freshly amputated.

In a trial calculation of the depletion rate in the Hawaiian *Chelonia* population, Hendrickson (262) speculated that no less than 100 and possibly as many as 1,000 turtles per year of 23 kg and above were lost to tiger shark predation.

The only other natural predator of posthatchling green turtles documented in the Hawaiian Archipelago is the large grouper, *Epinephelus tauvina*. In October 1974, a 205 kg specimen caught off Molokai was found to contain a partially digested but whole juvenile turtle measuring approximately 52 cm in straight carapace length (K. Mench, personal communication). Sightings and captures of these groupers are rare in the Hawaiian Archipelago, but specimens as large as 365 kg have been documented.

3.34 Epizoics, diseases, abnormalities, and injuries

Barnacles commonly found on Hawaiian *Chelonia* include *Chelonibia testudinaria* (Bryan 143; Edmondson 205; Gordon 237) and *Platylepas hexastylos* (identified by W. J. Cooke). *Chelonibia* is usually confined to the carapace, plastron and head, while *Platylepas* attaches itself principally to the skin regions, occasionally in large numbers. Large specimens of *Chelonibia* can measure 50 mm in diameter at the base, while *Platylepas* usually does not exceed 6 mm. Adult turtles consistently host larger specimens of these two barnacles than the juvenile or subadult turtles. The burrowing barnacle, *Stephanolepas muricata*, (identified by W. J. Cooke) has been recovered from the front flipper of a juvenile in Kaneohe Bay, Oahu, but is apparently a rare species in Hawaiian *Chelonia*.

Two specimens of the piscicolid leech, *Ozobranchus branchiatus*, (identified by M. D. Dailey) have been recovered from a juvenile green turtle at Necker Island. During 1978 green, hawksbill and loggerhead turtles on display at Sea Life Park (Oahu) became heavily parasitized with *O. margoi* (identified by M. D. Dailey). This infestation is thought to have originated from a stray loggerhead that had been found off Molokai and brought into captivity (Altonn 20; McKinney 351). At present, no other records exist for *Ozobranchus* in the Hawaiian Archipelago.

The buccal cavity of Hawaiian *Chelonia* occasionally contains one or two specimens of the talitroidean amphipod, *Hyachelia tortugae* (identified by W. J. Cooke). This crustacean has also been found on the neck and hind flippers living in association with superficial skin lesions.

In June of 1974, the author observed a remora, *Echeneis* sp., attached to the plastron of an adult female off East Island.

The red alga, *Polysiphonia tsudana*, (identified by D. J. Russell), commonly occurs on the skin of Hawaiian *Chelonia* and occasionally on the plastron and Inconel tags (see Newbert *et al.* 375 for color photograph). This species was first described from the neck of a green turtle at Laysan Island (Hollenberg 270). Other algae that have been periodically found by the author on the skin, carapace and plastron of Hawaiian green turtles include the following (identified by D. J. Russell): Rhodophyta (red) - *Polysiphonia dotyi*, *Acrochaetium gracile*, *Falkenbergia rufolanosa*, *Melobesia* sp. (encrusting); Phaeophyta (brown) - *Sphacelaria furcigeria*, *S. novae-hollandiae*, *Ectocarpus indicus;* chlorophyta (green) - *Enteromorpha clathrata;* Cyanophyta (blue-green) - *Lyngbya majuscula*, *L. cinerescens*, *Oscillatoria* sp. At Necker Island, intertidal crabs, *Grapsus grapsus*, have been observed on the carapace and flippers of basking turtles feeding on algal mats. When the turtles return to the water, surgeonfish, *Acanthurus sandvicensis*, are also attracted to these epizoics for grazing purposes (Balazs 72). At French Frigate Shoals, discrete underwater sites have been identified where green turtles regularly position themselves while wrasses and surgeonfish feed on epizoics. A color photograph showing this symbiotic behavior off the north shore of Tern Island appears in an article by Eliot (208).

Neoplastic growths ranging from small warts to huge masses 25 cm in diameter occur on 5% to 10% of the green turtles observed during each breeding season at French Frigate Shoals. Common sites of these neoplasms include the neck (Kridler 322), flippers, tail, and fold of flesh where the tags are attached. In many of the affected turtles small growths also occur in association with the eyes, apparently originating from the conjunctiva and sclera. Two adult males seen basking at East Island had eye growths so extensive that most vision was eliminated. However, except for the presence of these growths, the turtles appeared healthy. An array of growths has been obtained from moribund juvenile, subadult, and adult turtles found off Oahu since 1977, as well as from an individual held in captivity for more than 5 yr. These specimens were submitted to the Registry of Tumors in Lower Animals (Smithsonian Institution) where they were analyzed and subsequently identified as benign fibropapillomas that have been occasionally reported in other marine turtle populations. The formation of these growths in Hawaiian *Chelonia* is described as follows. The epidermis proliferates and forms pegs extending into the dermal connective tissue. At the same time, dermal papillae containing connective tissue, vascular channels, and associated melanophores grow between the epidermal pegs to provide nourishment. The surface epidermis produces abundant layers of keratin and occasionally trapped cells within the dermis form pearls or epidermal cysts containing concentric rings of keratin. Subsequent enlargement results to an increasing extent with expansion of the fibrous component. Larger tumors are therefore mostly a monotonous field of fibrocytes with some interspersed melanophores and a few epidermal pegs near the surface. Invasion of the underlying muscle does not usually take place (J. C. Harshbarger, personal communication and 255, 256, 257). The etiology of fibropapillomas is unknown. In Hawaiian *Chelonia*, they are not associated with the foreign organic materials (leeches, barnacles, algae) that have been suggested as possible causes in other marine turtle populations. The possibility of a viral origin is presently being investigated by electron microscopy of tissue biopsies from the prickle cell layer of the epidermis of early growths on Hawaiian *Chelonia* (J. C. Harshbarger, personal communication). Other possible causes include repeated contact with carcinogenic substances, such as might occur at sewage discharges or from corroding Monel tags and excessive exposure to solar radiation while floating at the surface or basking. Fibropapillomas on green turtles may not, however, be a new occurrence in the Hawaiian population. A photograph taken in 1923 at French Frigate Shoals shows a basking turtle with what appears to be a growth on the dorsal surface of its left front flipper (Tinker 492; Anonymous 568). It is likely that some turtles with fibropapillomas are more susceptible to tiger shark predation due to decreased vision and maneuverability while swimming.

A salt crystal deposit weighing 8 g and measuring 20 mm in diameter was extracted from the corner of the left eye of a juvenile green turtle at Lisianski Island. This condition probably represented some dysfunction of the lacrimal gland or blockage of the duct that transports the hypersaline secretion.

During July 1978, a turtle that nested on Laysan Island approximately 285 m inland became disoriented during her return to the ocean and died the following morning from thermal exposure (P. and B. Johnson, personal communication). There were no growths on the turtle's eyes or other external signs to explain this abnormal behavior. Similar orientation problems by nesting *Chelonia* have also been recorded by the author at Canton, a large low coral atoll at lat. 2°50'S, long. 171°43'W (see Pritchard 418).

Captive growth studies conducted with 120 green turtles collected as hatchlings at French Frigate Shoals resulted in 31 mortalities from various causes by 7 mo of age (Bardach 98; Bardach and Helfrich 99, 100). Postmortem examinations revealed that six of these turtles had lesions consisting of focal granulomas characteristic of tuberculosis. Bacilli identified as *Mycobacterium avium* Serotype 8 were isolated from one of the two specimens subsequently cultured (Brock *et al.* 134). The *M. avium* complex is usually associated with poultry, cattle, and swine, and this isolation from *Chelonia* apparently represented the first record for a poikilotherm. The source of the infection was not determined, however neonatal contact in the underground nest with substrate contaminated by seabirds would appear to be a plausible route. No information presently exists on the occurrence of *Mycobacterium* in naturally occurring seabirds or green turtles in the Hawaiian Archipelago.

Salmonella weltevreden (identified by R. M. Nakamura) and *S. san-diego* Type B (identified by M. H. Crumrine) have been isolated from the feces of captive reared Hawaiian *Chelonia*, but again nothing is known of occurrence in the wild.

Paralysis of a front flipper due to aseptic necrosis of the head of the humerus has been observed in two captive reared Hawaiian *Chelonia*. The etiology of this affliction could not be determined (M. H. Crumrine, M. W. Balk, N. E. Palumbo, and G. Liese, personal communications). Necrosis of unknown origin has also been found in the terminal scales of the front flippers of juveniles at Kure (Balazs 73).

Injuries to the carapace and plastron of Hawaiian *Chelonia* are known to result from violent contact with rocks and other underwater substrate accidentally encountered while foraging in rough surf close to shore (Wright *et al.* 557). At certain coastal areas on the island of Hawaii, tsunamis have carried juvenile and subadult green turtles over 100 m inland where they became stranded and unable to return to the water without human assistance (A. L. Howard, personal communication). It is unknown how extensive these strandings may be along remote coastal areas of the Hawaiian Archipelago following a large tsunami.

Both injuries and mortalities of Hawaiian green turtles are known to occur incidental to fishing activities directed at other species (Anonymous 570, 583). This can result from contact with fishhooks and from entanglement in gill nets, rope, and monofilament fishing line. In addition, discarded items can at times be hazardous to turtles, as evidenced by a juvenile captured off Oahu that had a part from a plastic container stuck around its neck.

3.4 Nutrition and Growth

3.41 Food sources

Green turtles that reside in coastal areas of the Hawaiian Archipelago have been documented by the author feeding on 56 species of algae, 1 marine angiosperm and 9 types of invertebrates (Table 9). However, 9 species of algae out of the approximately 400 species present in the Hawaiian Archipelago account for the major food sources utilized (Table 10). *Codium* and *Ulva* are major dietary components of juveniles, subadults, and adults in both segments of the Hawaiian Archipelago, joined by *Pterocladia* and *Amansia* in the main islands, and *Caulerpa, Turbinaria* and *Spyridia* in the NWHI (Balazs 71, 72, 75, 81, 82). In 1933 Galtsoff (231), quoted by Amerson *et al.* (32), noted that the stomachs of green turtles examined at Pearl and Hermes Reef contained large amounts of *Codium*. Abbott and Williamson (1) indicated that Hawaiian green turtles are known to eat *Sargassum*, thereby probably accounting for its native name of limu honu. Fortner (228) listed "turtle limu" as an alternate common name for *Ulva*. Hirth (265) stated that "green algae" was the food of adult turtles off Maui. Wetmore (542), quoted by Mellen (353), stated that green turtles in the NWHI "browse in submarine fields of algae." Prior to the author's research program, these references constituted the only published information on the food sources of Hawaiian *Chelonia*.

The methods used to determine the food sources of Hawaiian *Chelonia* listed in Tables 9 and 10 have included: 1) analysis of gastrointestinal contents salvaged from mortalities due to tiger shark predation, accidental and intentional human capture, and strandings of unknown causes; 2) direct observations of foraging made from shore and underwater with scuba; 3) recovery of incompletely digested food from fecal pellets found at resident foraging areas; 4) recovery of food directly from the mouths of turtles captured uninjured while actively feeding; and 5) sampling of stomach contents using a flexible plastic tube (Balazs 86) and a small diameter flexible grasping tool (Kam and Balazs 286) inserted through the esophagus.

The distribution and abundance of benthic algae in the Hawaiian Archipelago are not well known, however standing crop densities of the species preferred by green turtles appear to be far greater in the main islands. For example, certain foraging areas around the islands of Hawaii, Maui, Oahu, and Kauai have dense growths of the red alga, *Pterocladia capillacea*; while in the NWHI, this is a rare species only known to occur in small quantities at Lisianski Island. Concomitantly, *Amansia glomerata* is abundant at many main island foraging areas, but relatively scarce in the northwestern segment of the

Hawaiian Archipelago. *Caulerpa racemosa*, a green alga regularly eaten by *Chelonia* at certain sites in the NWHI, has never been found as a dietary component in the main islands even though it occurs at a number of locations. It is significant to note that the genus *Caulerpa*, and particularly the species *racemosa*, contain the toxic constituent "caulerpicin" which can produce symptoms in humans similar to ciguatera fish poisoning (Doty and Aguilar-Santos 203). It is unknown what effects, if any, caulerpicin may have on green turtles. *Turbinaria ornata* and *Spyridia filamentosa*, dietary components in the NWHI, are also not eaten in the main islands where they at times grow in the same general area as the favored *Pterocladia capillacea* and *Amansia glomerata*.

Marine angiosperms, such as turtle grass, *Thalassia testudinum*, constitute the principal food source for a number of *Chelonia* populations (Hirth 265), however the only species represented in the Hawaiian Archipelago is *Halophila hawaiiana*. This seagrass has oval blades 1 to 3 cm long and only occurs in small meadows of low densities around the main islands and at Midway.

It is of interest to note that two species of red algae, *Acanthophora spicifera* and *Hynea musciformis*, recorded in the diets of green turtles in the main islands are introductions to Hawaiian waters from Guam and Florida, respectively. In addition, the recovery of *Polysiphonia tsudana* from the stomach of a juvenile at Kure suggests that this turtle was grazing on either its own or another turtle's epizoic algal mat.

Juvenile and subadult turtles in the NWHI, particularly at Midway and Kure, have been observed voraciously feeding on the invertebrates *Physalia*, *Velella*, and *Janthina* that periodically drift into the coastal areas. The eyes and gastrointestinal tracts of these turtles are apparently not adversely affected by the nematocysts present in both *Physalia* and *Velella*. In the main islands the small black sponge, *Chondrosia chucalla*, is also periodically eaten by green turtles, usually in association with *Codium edule*. Examinations of fecal pellets have shown that these sponges, as well as pieces of *Codium* and other algal species, are able to pass through the gastrointestinal tract in a relatively undigested state. Although small crustaceans can sometimes be found living on algal filaments, these animals have not been present in the stomach samples examined.

Synthetic items such as plastic fragments, pieces of plastic bags, cloth, string, and small diameter polypropylene line have occasionally been found in Hawaiian *Chelonia*. An adult female captured by a fisherman in November 1978 off the north shore of Lanai contained large pieces of both black and clear plastic bags throughout its intestines. This material was also present in fecal matter in the rectum, thereby indicating that blockage of the tract had not taken place. Plastic items of this nature found floating at the surface appear to be mistaken by some turtles for coelenterates or other edible invertebrates. Fragments of terrestrial vegetation in the stomach as well as tar stains in the mouth have also been occasionally found in Hawaiian *Chelonia*.

The food sources of Hawaiian *Chelonia* <35 cm living in the pelagic environment are completely unknown due to the absence of human contact (section 2.22). It is logical to assume that during this period the turtles are carnivores feeding on invertebrates that occur at or near the surface. In pelagic waters surrounding the Hawaiian Archipelago, this could include *Physalia*, *Velella*, *Janthina*, the megalops stage of some portunid crabs, and immature individuals of certain oceanic squids that come to the surface at night in large numbers (i.e. *Symplectoteuthis oualaniensis*, *Onychoteuthis banksi* and *Hyaloteuthis pelagica*). Light organs present in these squids could conceivably serve as attractants to the young turtles.

3.42 Feeding behavior

Hawaiian *Chelonia* spend most of their lives residing in coastal areas where they alternate between periods of feeding and quiescence (sections 2.21, 2.22). The habitat characteristics of these resident areas can differ throughout the Hawaiian Archipelago, consequently variations exist in feeding strategy and behavior.

In the Kau District on the island of Hawaii, feeding takes place along lava coastlines that lack protective reefs. The major food source, *Pterocladia capillacea*, grows in shallow water close to shore, often on rocks just below the low tide line and in areas where freshwater enters the ocean from underground springs. Although a few partially sheltered bays are present, most foraging occurs under turbulent conditions resulting from exposure to ocean swells and tradewind waves. Observations of turtles made from adjacent coastal cliffs have indicated that considerable swimming and maneuvering are required while foraging in order to prevent contact with the bottom, and to travel to the surface at regular intervals for respiration. Under these rough surf conditions, only a single rapid breath is usually taken before returning to the bottom. If human activity is observed on land during the surface interval, a turtle will frequently terminate feeding and retreat to deeper water. Along Bellows Beach on Oahu, the feeding areas used by *Chelonia* consist of sand bottoms 25 to 100 m from shore where detached pieces of *Codium*, *Ulva*, and other algae periodically collect as a result of wave action and currents. Subtidal reefs located further offshore buffer the coastline from large surf, thereby making it possible for turtles to forage with comparatively little effort. A greater tolerance is displayed in this area to human activities, such as recreational swimming and beach use. This is probably due to the fact that turtles are seldom pursued or killed at Bellows, while along the Kau coastline such activities are a periodic occurrence. French Frigate Shoals is another representative foraging area for Hawaiian *Chelonia* in which feeding behavior displays some adaptation to the characteristics of the habitat. At this location, aggregations of juveniles 37 to 55 cm in straight carapace length feed on *Caulerpa*, *Codium* and at times small anthrozoans that grow on calcareous reef structures near the islands of East, Whale-Skate, and Tern. Although the tidal difference at French Frigate Shoals is only about 1 m, foraging is generally restricted to periods of high tide due to the shallow depths present at these sites. Furthermore, many of the recesses in the substrate where the food sources grow are only large enough for juvenile turtles to reach into with their heads and beaks. Turtles foraging within French Frigate Shoals are not usually subjected to rough surf conditions. Surface intervals for respiration therefore frequently last 2 min or longer, during which time from three to eight deep breaths may be taken. The subsequent submergence times while feeding range from approximately 5 to 15 min. While grazing on a food source, juveniles will frequently place themselves in an almost vertical position with the head down and the hind flippers extending at right angles. This appears to help stabilize the turtle directly over the desired feeding site.

Stomach samples from adults of both sexes at French Frigate Shoals have shown that feeding takes place during the breeding season. This is usually not thought to occur in other *Chelonia* populations (Hirth 265), probably due to the scarcity of food at many breeding sites.

At all of the resident foraging areas thus far investigated, tagged Hawaiian *Chelonia* have been found to repeatedly feed at the same locations. This fixation has been documented on both a short-term basis (daily and weekly), and for longer periods ranging up to 37 mo (Balazs 81).

At resident foraging areas in the main islands, research techniques for tagging turtles have involved the use of carefully monitored large-mesh tangle nets (Balazs 64, 81; Kam and Balazs 286). Most of these captures have involved turtles that entered the net at night, frequently from 1 to 3 h before sunrise during periods of incoming tides. This has occurred in total darkness from heavy cloud cover, as well as during various phases of the moon with some illumination present. Mouth and stomach samples from many of these turtles have shown that active feeding was taking place. Sensory cues to supplement vision would appear to be necessary for commuting at night from resting sites to feeding areas. Olfactory cues may aid in this short-range navigation due to the fact that many of the algae eaten by turtles have pronounced odors. In addition, freshwater seepage associated with pastures of *Pterocladia* could provide a traceable salinity gradient. Tactile cues with the flippers while slowly swimming along the bottom would also seem to be a plausible orientation component for any short-range movement in the dark. Ridgeway *et al.* (433) found that Hawaiian *Chelonia*, and presumably all green turtles, are able to hear low frequency sound (60-1,000 Hz), with maximum sensitivity occurring in the range of 300 to 400 Hz. Hirth (265) has even suggested the possibility that green turtles may possess some sonar capabilities. Nevertheless, the simple detection of sounds originating from certain fish, invertebrates, and the surf could be of some navigational value at night. With respect to foraging without the benefit of vision, it is also of interest to note that a moribund juvenile with massive fibropapillomas on both eyes recovered from Kaneohe Bay was found to have relatively fresh algae in its stomach.

Examinations of stomach contents have revealed that Hawaiian *Chelonia* of all sizes generally bite off only small pieces of algae while foraging. The deeply grooved and serrated cutting edges of the beaks appear to be well adapted for this purpose. The foremargin of a front flipper rubbed against the beaks also aids in shearing food, as evidenced by an underwater observation of a juvenile feeding on *Codium edule* at Kure. In shallow water off Kahoolawe in the main islands, a juvenile was observed using its upper beak to scrape off an algal mat of *Gelidium* sp. growing on a rock. Approximately 10% of the stomach contents of an adult from Lanai was found to consist of *Halophila* blades. The cropping of this small seagrass apparently took place in a delicate manner in that no sand or other fine substrate in which *Halophila* grows was found in the stomach contents.

Short-term changes in the food preferences of some turtles have been detected by examining the complete contents of excised gastrointestinal tracts.

Differences have at times been found in the species of algae present at various distances along the intestines, and in the two compartments that comprise the stomach. Periodic dietary shifts of this nature probably help Hawaiian *Chelonia* meet their requirements for essential nutrients (i.e. amino acids, fatty acids, vitamins, minerals) that may be more concentrated in some species of algae. Certain of these nutrients may also be synthesized by microbial action within the intestine. As with other vertebrates, the nutritional requirements of green turtles in the wild would vary with age, activity, and reproductive condition.

It is not unusual for juvenile and subadult green turtles in the Hawaiian Archipelago to bite on hooks baited with squid, shrimp, and fish flesh (Carter 158; Anonymous 583). These carnivorous interludes probably represent regressions to the feeding habits exhibited while living in the pelagic environment.

3.43 Growth rates

The mean rates of growth of immature green turtles (37-59 cm) occurring naturally at seven resident areas in the Hawaiian Archipelago have been found to range from 0.08 to 0.44 cm/mo in straight carapace length (Table 4). The most rapid growth takes place along the Kau coastline of Hawaii (0.38-0.52 cm/mo), while the slowest occurs at French Frigate Shoals (0.02-0.13 cm/mo) and Kure (0.04-0.12 cm/mo). In addition to the growth data presented in Table 4, 34 healthy appearing immature turtles have been recovered after periods ranging from 2 to 20 mo in which no measurable growth could be detected. This has included 6 turtles at Midway, 3 at Lisianski, 24 at French Frigate Shoals, and 1 at Necker. One of the turtles at French Frigate Shoals was a 68 cm subadult that showed no increase in straight carapace length after an interval of 20 mo. The turtle at Necker was a 42.5 cm juvenile that was recaptured after a 17-mo interval. Although the apparent absence of growth could, in some cases, possibly be attributed to measuring errors, this is not believed to be a significant factor in that the author has personally taken most of the inital and recovery measurements. The causes and implications of cessation of growth among some turtles are unknown and further investigations are warranted.

In addition to utilizing large-mesh tangle nets, the capture of immature turtles for growth studies in the Hawaiian Archipelago has been accomplished with long-handled scoop nets and by hand while diving with scuba. In the NWHI, particularly at Lisianski, periodic basking also provides access to these turtles. The use of curved carapace length for detecting growth has been found to be generally unreliable due to variations in positioning the flexible measuring tape (see Kridler 322), and changes in the curvature of the carapace that appear to be independent of an increase in size. The use of body weight has also been found to be unreliable. This is probably due to differences in the amount of food material in the gastrointestinal tract, a component that can comprise up to 18% of the weight of juvenile Hawaiian *Chelonia* (Balazs 81).

The different rates of growth exhibited by immature turtles at various locations in the Hawaiian Archipelago are most likely a function of the sources and abundance of food at the resident areas (section 3.41). Seawater temperature would be expected to have some influence, but this is not evident based on the available data. At Kure and Midway, and probably extending to the southeast as far as Lisianski Island, mean monthly sea-surface temperatures range from a low of 20.5°C during February, to a high of 26.2°C during August and September (Clapp and Wirtz 172; Galtsoff 231). This is 2° to 3°C cooler than French Frigate Shoals (Figure 5) where essentially the same growth rates have been recorded. Temperatures at French Frigate Shoals are similar to the main islands where considerably faster growth occurs. It is unlikely that a genetic basis accounts for the differences in growth considering the polygamous behavior displayed by adults during each breeding season at French Frigate Shoals (Balazs 57).

A growth rate of 0.18 cm/mo was recorded at French Frigate Shoals for a subadult female released off Oahu 28 mo earlier after an extended period in captivity (Table 11). A 42.5 cm juvenile raised in captivity from a hatchling was found to be the same size when recovered by the author 11 mo later while diving along the Kau coastline. Two of 26 other juveniles raised from hatchlings and released at French Frigate Shoals (Altonn 15) established residency around an iron seawall off the northwestern corner of Tern Island. U.S. Coast Guard personnel regularly fed these turtles fresh fish scraps and the author was subsequently able to capture them for growth measurements (Table 11). One of the turtles grew 0.71 cm/mo over an 8-mo period, thereby constituting the most rapid growth rate thus far documented for a Hawaiian green turtle living in the wild. This turtle subsequently disappeared, while the other one was found washed up on the beach dead of unknown causes.

For comparative purposes, growth data are also presented in Table 11 for four Hawaiian *Chelonia* raised in captivity from hatchlings for periods ranging from 57 to 81 mo. The diets fed to these turtles consisted of various combinations of pelleted dry feed ingredients (i.e. fish meal, meat and bone meal, soybean meal, and corn), as well as fresh frozen squid and fish. These data show that at least 19 mo were required to reach a size of 35 cm, after which the rate of growth declined considerably. Bourke *et al.* (131) present growth data in the form of weight increases for 46 Hawaiian *Chelonia* hatched in captivity and raised to 6 mo of age.

The growth rates of Hawaiian *Chelonia* after maturation have been documented through the remeasurement of adults during each breeding season at French Frigate Shoals. Increases for 17 females and 1 male ranged from 0.01 to 0.12 cm/mo (24-75 mo), with a mean of 0.04 cm/mo (Table 12). This suggests that the rates of growth for at least some Hawaiian *Chelonia* decline significantly once maturity has been reached. A considerable length of time would therefore be required for a turtle that matured at a small size (81 cm) to grow to a large size (see sections 3.12, 3.31 and Hirth 265). The differences in growth rates recorded for mature turtles (0.01-0.12 cm/mo) may also be a function of the sources and abundance of food at the resident area (section 3.16). If this is indeed the case, mature turtles that show the most rapid growth could be identified as having remigrated from areas in the main islands. Data presented in Table 12 provide some support for this proposition in that female 5016 exhibited one of the most rapid growth rates (0.09 cm/mo) and is known to have originated from the Kau District on the island of Hawaii (section 3.52).

Table 13 presents growth rates for both immature and adult Hawaiian *Chelonia* captured from the wild and held for extended periods in captivity at Sea Life Park on Oahu. The diets of these turtles consisted of fresh frozen squid and fish.

3.5 Posthatchling Movements

3.51 Dispersal and developmental migrations

The dispersal of green turtle hatchlings from French Frigate Shoals into the pelagic environment takes place by surface currents and vigorous swimming (section 2.22). After an undetermined period of time in the open ocean, during which unknown routes are followed, juveniles of approximately 35 cm arrive at coastal areas throughout the Hawaiian Archipelago. The recruitment of these turtles at islands to the northwest of French Frigate Shoals could be a direct result of northwesterly currents that prevail for hatchlings entering the water during the month of July (Figure 4). In addition, the low level of breeding that occurs principally at Laysan and Lisianski Islands and Pearl and Hermes Reef may be a further source of juveniles in this segment of the Archipelago. The recruitment of juveniles in the main islands is more difficult to theorize. One possibility is that during the peak hatching month of August, prevailing surface currents transport hatchlings in a northerly direction for a 2-mo period to approximately lat. 28°40'N (Figure 4). At this point instead of turning to the southwest along with the same current system, the turtles swim to the vicinity of lat. 30° to 31°N where winter surface currents of 19° to 20°C travel eastward. Over an ensuing period of 6 mo or longer, the turtles could be carried by a gyre that ultimately delivers them to the main islands. Another possibility is that a far larger circular transport system is involved in which hatchlings are carried well to the west of the Hawaiian Archipelago and around a vast area of the North Pacific back to the main islands. Of course it is also conceivable that some of the turtles leaving French Frigate Shoals are not carried by the currents, but rather swim against the currents on a course directly toward the main islands. Nevertheless, whatever oceanic routes of dispersal are involved, there is little doubt that juveniles <35 cm are residing somewhere outside of the coastal areas where larger turtles feed and rest. This is supported by the dearth of direct sightings, as well as by the absence of juveniles <35 cm in the stomachs of tiger sharks. The single observation of a 20 to 25 cm juvenile reported at French Frigate Shoals (Balazs 57) was undoubtedly a rare occurrence involving a stray individual.

Juveniles measuring 35 to 40 cm that are believed to be recent arrivals to coastal areas have, on a few occasions, been observed by the author at Kure, Midway, Oahu, and along the Kau District (Wright *et al.* 557). These new recruits were discernible by an absence of epizoics and superficial scratches, and by the presence of thin translucent edges to the periphery of the marginal laminae and terminal scales on the flippers. In addition, the cutting edges of the lower beak had more pronounced serrations than other juveniles of the same or a slightly larger size. All of these characteristics could be expected to disappear rapidly after establishing resting and herbivorous foraging habits in a coastal area.

Most evidence accumulated to date indicates that after leaving the pelagic environment, Hawaiian *Chelonia* reside in the same general coastal area for extended periods, possibly throughout their entire lifetime except for remigrations for reproduction. This extended residency concept is at least partially supported by the fact that all sizes of turtles from 35 cm juveniles to mature adults are frequently present along a given coastal area. Some specific foraging sites have been identified that can only be used by juveniles (section 3.42), however habitat employed by larger turtles is usually only a short distance away. The recovery of tagged immature turtles after periods ranging up to 37 mo has also provided evidence for extended residency. With the exception of two turtles, all recaptures (146 out of 524--Table 4) have been made in the same foraging and resting areas where initial tagging occurred. At French Frigate Shoals, recoveries have shown that no movement takes place between sites separated by as short a distance as 8 km. At Kure a tagged turtle was found resting under the same coral ledge where it had been captured 13 mo earlier (Balazs 81). The only two recoveries that indicated movement of any distance involved the weak 38 cm juvenile tagged at Midway and found downwind at Wake Island (section 2.1), and a 40 cm juvenile also tagged at Midway that was reported to the author 7 mo later as having been recovered and released alive in Hilo Bay on the island of Hawaii. This latter case involves an ocean distance of approximately 2,300 km against the prevailing winds and currents in the latitudes of the Hawaiian Archipelago. Although two Monel tags were originally placed on this turtle, only one tag was found and recorded at the time of recovery. The possibility must therefore be considered that the tag number was misread due to corrosion or other causes. If such movements can, in fact, be substantiated through additional recoveries, immature turtles residing in the northwestern segment of the Hawaiian Archipelago would constitute a significant factor in recruitment to the main islands. Such a recruitment system was theorized by the author (Balazs 57) prior to the accumulation of existing data which supports the concept of an extended residency at the coastal area entered from the pelagic environment. This theory was based, in part, on observations of groups of juveniles 35 to 60 cm periodically occurring at French Frigate Shoals. These sightings suggested that developmental migrations of some nature were taking place (Balazs 57). However, subsequent tagging revealed that the same turtles were involved, and not new aggregations as originally speculated. The regular disappearance of these turtles for several weeks and possibly even months at a time has still not been resolved. One explanation would be that a form of dormancy is periodically being undertaken at sheltered underwater locations. Such behavior has been documented for *carrinegra* in the Gulf of California, but is presently unknown for Hawaiian *Chelonia*.

If significant levels of recruitment to the main islands occur through developmental migrations from the northwestern segment of the Hawaiian Archipelago, then revisions would be necessary in the projected number of years needed for Hawaiian green turtles to reach maturity (section 3.12 and Table 4).

Since January 1973, 10 adult and 31 subadult green turtles have been returned to the wild after extended periods in captivity. The dispersal patterns of the five turtles that have been recaptured in the main islands are presented in Table 14 and Figure 8.

An experimental model for the life history and habitats of Hawaiian *Chelonia* is presented in Figure 9.

3.52 Remigrations

Adult Hawaiian *Chelonia* periodically travel between their resident foraging areas and French Frigate Shoals for reproduction (sections 2.21, 3.16). These remigrations have been documented for both males and females through 52 long distance tag receoveries, 31 of which involved French Frigate Shoals and the main islands, and 21 that involved French Frigate Shoals and the northwestern locations of Laysan and Lisianski Islands and Pearl and Hermes Reef (Table 15, Figure 10). Details of the 16 female and 4 male tag recoveries that have been made since June 1973 are presented in Table 16.

The recoveries in the main islands, of turtles that were tagged while at French Frigate Shoals, mostly represent mortalities resulting from direct capture by fishermen. However, recoveries at Laysan and Lisianski Islands and Pearl and Hermes Reef were of basking turtles that remained viable members of the population and, in several cases, were recovered again at later dates. Records of remigrations in the Hawaiian Archipelago are unique among marine turtle populations due to the two-way tagging opportunities afforded by the basking behavior, and by the research emphasis placed on turtles in their resident foraging areas. These factors have made it possible to document movements from the resident areas back to the breeding grounds, a missing segment in all one-way tagging programs where it is only feasible to tag nesting turtles. The documentation of long-distance movements by adult males is, of course, in itself a rare research occurrence. The results of these various opportunities with Hawaiian *Chelonia* are dramatically illustrated by male 1060 in Table 16 which was tagged at Pearl and Hermes Reef in 1964, recovered at East Island, French Frigate Shoals in 1976, and recorded back at Pearl Hermes Reef 1 yr later in 1977.

Tag recoveries demonstrate that the breeding assemblage at French Frigate Shoals is comprised of adults that remigrate from widely separated resident areas. The longest voyages thus far recorded are from French Frigate Shoals to Hilo Bay (tag 2229, Table 16), and from the Kau District to French Frigate Shoals (tag 5016, Table 16), both of which represent one-way ocean distances of approximately 1,100 km. Fourteen other recoveries (4 males, 10 females) have been made between Pearl and Hermes Reef and French Frigate Shoals, a distance of 1,050 km. Mating is therefore taking place between some males and females that live in areas separated by as many as 2,150 km. A minimum rate of travel of 23 km/day during these remigrations has been computed from a relatively short-term recovery between French Frigate Shoals and Kauai (tag 853, Table 16). If the contour of the adult female's carapace is indeed more highly arched (less streamline) in Hawaiian *Chelonia* as suspected (section 1.1), then a greater expenditure of energy, and perhaps even slower swimming speeds, would be expected to occur in comparison to Atlantic and Caribbean *Chelonia* populations.

It is significant to note that adults from the main islands, as well as from Laysan and Lisianski Islands and Pearl and Hermes Reef have only been recorded traveling from their respective segments of the Hawaiian Archipelago as far as French Frigate Shoals, and not beyond. This further supports the belief that Hawaiian *Chelonia* return to their same resident foraging area at the end of each breeding season. Although a homing instinct for the breeding grounds is widely recognized for *Chelonia* populations, far less attention has been given to the pronounced fixation which also appears to exist for the resident area (Balazs 57; Hirth 266). It is also significant to note that, except for the weak juvenile found at Wake Island, none of the turtles tagged in the Hawaiian Archipelago have been recovered at any other location in the Pacific.

It is unknown if the low level of breeding that occurs at islands to the northwest of French Frigate Shoals involves nonmigratory residents of these areas, or adults that have remigrated from other locations in the Hawaiian Archipelago. The occurrence of remigrations would suggest that these turtles are genetic remnants of what at one time may have been far larger breeding colonies. Such reproductive voyages could conceivably be taking place from resident areas anywhere in the Hawaiian Archipelago. This could even include French Frigate Shoals, where tagged adult females known to live in the area have never been recorded nesting at that location. Although migrations from French Frigate Shoals to other areas for breeding purposes would seem to be totally unnecessary, this form of cycle is taking place when adults travel from the breeding areas of Laysan and Lisianski Islands and Pearl and Hermes Reef to reproduce at French Frigate Shoals. Another possible explanation to account for nesting at islands to the northwest of French Frigate Shoals is that some of the females are returning to their resident area from French Frigate Shoals with an unlaid clutch or partial clutch of eggs. The presence of eggs in a female shortly after her return to Kauai has been reported by a fisherman (tag 853, Table 16), but details could not be obtained and no recent nestings have been recorded for this island.

It is unknown what motivating factors may have been involved in the 440 km movement of an adult female tagged while basking at Pearl and Hermes Reef in March 1965, and recovered while basking at Laysan Island in December 1967 (Kridler 324, Figure 10).

3.53 Navigation and orientation

The periodic migrations carried out in *Chelonia* populations between resident foraging areas and distant breeding grounds require some form of navigational ability. Furthermore, a highly refined guidance system would have to be in use for long distance movements involving small oceanic islands, such as from the coast of Brazil 2,000 km to Ascension Island (Carr 150, 151). Hirth (265) has suggested that navigation by green turtles is likely to be a composite process employing different senses that are based on a multiplicity of cues. The various mechanisms thus far suggested to explain this ability have also been summarized by Hirth (265) and include bicoordinate celestial navigation, light-compass sense, olfactory cues, perception of Coriolis force, magnetic sense, inertial guidance, sonar sense, and subtle oceanographic cues such as currents and wave patterns. However, the actual system or systems utilized remain totally unknown. This is mostly due to the unresolved problems of tracking a turtle over long distances of open ocean using boats, airplanes, or land-based monitoring techniques. The successful tracking of a turtle would reveal the actual routes taken, thereby aiding greatly in determining what cues are being employed. The recent availability of earth-orbiting satellites for wildlife telemetry offers considerable potential for answering this navigational question for a green turtle population.

A basic assumption in the migrations and navigation of *Chelonia* is that the adults return to breed at the same location where they originated as hatchlings. This fixation on the natal beach, which is supported by considerable indirect evidence, is thought to result from some form of "imprinting" that takes place when the hatchlings emerge from the nest or depart through adjacent waters. However, nothing is known about this process, if indeed one exists. If adults remigrate in groups to improve their accuracy of orientation, as has been suggested (Hirth 265), this could also serve the purpose of providing a learning mechanism for newly matured turtles to find their way back to the breeding grounds.

For Hawaiian *Chelonia*, the least complex system for finding French Frigate Shoals when remigrating from resident foraging areas would appear to be one in which the various islands and submerged areas with no emergent land are followed and used as navigational guideposts. Turtles residing in the main islands could follow the coastlines in a northwesterly direction, crossing the relatively narrow interisland channels of 15 to 120 km until reaching Kauai or Niihau. The next island guidepost could then be Nihoa (area 63 ha, elevation 273 m) located 225 km to the northwest, with a 19 fathom (35 m) shoal occurring at 125 km along this course. The distance from Nihoa to Necker (area 17 ha, elevation 85 m) is 295 km, but three small shoals are located at about the midpoint between the two islands. In addition, Necker itself is situated on a large 28 by 74 km bank with depths ranging from 8 to 23 fathoms (15-42 m). One of the few reported sightings in the Hawaiian Archipelago of a green turtle away from land was made in March 1979 along the southern edge of the Necker Bank. This involved an adult, but it could not be determined if the turtle was in transit or a resident of the area (G. L. Naftel, personal communication). From Necker, the final goal of French Frigate Shoals for a remigrating turtle is 155 km directly to the west.

Turtles at resident foraging areas to the northwest of French Frigate Shoals would have to follow the Hawaiian Archipelago in a southeasterly direction during remigrations. Along this route, the maximum span between an island and a submerged area, or two separate submerged areas, would be 155 km, the distance between Raita Bank and Gardner Pinnacles (area 1 ha, elevation 45 m). Between Pearl and Hermes Reef and French Frigate Shoals, there are 14 submerged areas and three islands with associated banks. The largest of these is Gardner Pinnacles bank which is 37 by 93 km, with depths of 10 to 25 fathoms (18-46 m).

Turtles traveling from resident foraging areas in the main islands to French Frigate Shoals would be moving generally with the prevailing currents and therefore would not be able to directly utilize chemical cues or plumes that may emanate from the various islands and submerged areas. Indirect use could result, however, by sensing the position of these areas once they have been passed and are upstream. Turtles traveling from the northwestern resident foraging areas to French Frigate Shoals would be moving generally against the prevailing currents and therefore could conceivably make direct use of chemical cues. During the return trip from French Frigate Shoals back to the resident areas, turtles from each segment of the Hawaiian Archipelago would be confronted with an opposite set of current conditions from their earlier voyage.

In the latitudes of the main islands, the sun is at the zenith during late May as it travels to its farthest point north, and again in late July as it returns south. Turtles departing from French Frigate Shoals to return to the main islands during July could therefore set a course each morning directly into the rising sun.

Another navigational aid that could possibly be used by Hawaiian *Chelonia* is the subtle color differences that are present in clouds due to reflections from shallower ocean depths where banks occur. However, the use of visual cues may not be essential considering that two males found with extensive fibropapillomas on their eyes were believed to have been recent migrants to French Frigate Shoals (section 3.34).

The evolution of reproductive migrations by *Chelonia* to midocean Ascension Island is thought to be an adaptation to the gradual separation of South America and West Africa resulting from seafloor spreading (Carr 150, 151; Hirth 265). Similar geophysical mechanisms may also help to account for evolution of the Hawaiian *Chelonia* pattern with respect to voyages occurring between the geologically older northwestern areas of the Hawaiian Archipelago and the more recently formed French Frigate Shoals. This migratory component appears to be equivalent to the Ascension Island pattern. As new islands progressively appeared and disappeared, ancestors of Hawaiian *Chelonia* may also have gradually extended their traveling distances between resident foraging areas and aggregate breeding grounds. This theory does not, however, provide an explanation for reproductive migrations occurring from the main islands, which are known to be geologically younger than French Frigate Shoals.

While at French Frigate Shoals, nesting turtles demonstrate a distinct preference for a certain island and, to a lesser extent, show some favoritism for certain areas on that island (section 3.15). The retention of this island fixity between breeding seasons in the 21 remigrations of females thus far documented (section 3.16) suggests the presence of a refined memory system for short-range orientation. Direct vision as well as olfactory cues are undoubtedly major components of this discrimination process. The orientation of turtles underwater at night prior to emergence for nesting could be expected to involve some of the same sensory cues used by turtles foraging at night in the resident areas (section 3.42).

3.6 Basking

Hawaiian green turtles exhibit the behavioral trait of coming ashore to bask or rest at certain undisturbed sites in the NWHI. This includes adults of both sexes and, to a lesser extent, immature turtles of all sizes larger than 35 cm. The land basking habit is rare among marine turtles, with Hawaiian and Galapagos *Chelonia* being the only two populations in which it has been well documented in the historical literature. However, basking in the Galapagos Archipelago has not been observed for a number of years and therefore may no longer be a characteristic of the population. There is no historical evidence of Hawaiian *Chelonia* basking on any of the main islands. However, an observation made at Johnston Atoll suggests that on rare occasions green turtles may bask at this location (Amerson and Shelton 31; Balazs 78). At the Wellesley Isles in Australia's Gulf of Carpentaria, female green turtles alone are known to come ashore during the breeding season to avoid males. The 27 December 1777 log of the *Resolution* states that at Christmas Island green turtles were turned on their backs while "asleep," and that this was a common method of capture (Beaglehole 105). In addition, previously unreported basking behavior by green turtles has been observed at Lizard Island on the Great Barrier Reef (W. Anderson and J. Leis, personal communications) and at North West Cape, Western Australia (J. Bradley, personal communication).

The presence of basking turtles in the NWHI was noted by many of the early visitors during the 1800's (Brooks, 135, 136; Farrell 220; Hornell 271; Lisiansky 335; Morrell 360; Munro 365-370; Paty 402; Read 429; Rothschild 435; Walker 531; Anonymous 564, 566). However, widespread knowledge of this behavior did not occur until publication of an account of the 1923 Tanager Expedition in a 1925 issue of *National Geographic Magazine* (Wetmore 542). A photograph from this article of a basking turtle at Lisianski Island was republished shortly thereafter in the *New York Zoological Society Bulletin*, along with further descriptive information by Dr. Alexander Wetmore (Mellen 353). Several other authors subsequently mentioned the occurrence of basking by Hawaiian *Chelonia* as a rarity among marine turtles (Carr 150, 152; Grant 238; Loveridge 336; Pope 415). During aerial censuses of Hawaiian monk seals in 1957 and 1958, Kenyon and Rice (288) regularly observed turtles basking along the shorelines of the NWHI (see also Parsons 400). From 1950 to 1973, basking turtles were at various times recorded and counted in conjunction with biological surveys by the Pacific Ocean Fisheries Investigation (386-398), the HDFG (Brock 133; Kramer 308, 309; Kramer and Beardley 310; Walker 532, 533; Woodside 554; Woodside and Kramer 555), the Pacific Ocean Biological Survey Program (see Subject Index), and the USFWS (Kridler 311-327; Olsen 380-385). Summaries of these observations and censuses have been published by Amerson (30); Amerson *et al.* (32); Clapp and Wirtz (171); Clapp and Kridler (172); Clapp *et al.* (173); Ely and Clapp (211); and Woodward (556). During recent years, photographs of basking Hawaiian *Chelonia* have appeared along with articles and reports by Altonn (6); Balazs (55 with *Monachus*, 57, 61 with *Ocypode*, 62, 78); Eliot (208); Hirth (265); Lipman (333); Moake (358 with *Chelonibia*); and Anonymous (642, 657, 667).

Basking in the NWHI takes place on calcareous sand beaches of varying particle size and composition located at French Frigate Shoals, Laysan and Lisianski Islands, Pearl and Hermes Reef, Kure and, on a single reported occasion, Midway (Balazs 78). At Laysan (P. and B. Johnson, personal communication) and Lisianski Islands, some turtles also emerge on calcareous beachrock slabs. At Nihoa, two turtles have been seen on a single occasion basking on a rock at the base of the island's northwest cliff (Clapp *et al.* 173; Kridler 326). At Necker Island, basking turtles regularly use a small sloping rock ledge measuring approximately 4 by 5 m. During periods of large westerly and northwesterly ocean swells, some turtles bask at an alternate protected shoreline area a short distance away that is comprised of smooth waterworn boulders. The resident aggregation of green turtles that basks and feeds at Necker Island is undoubtedly one of the most interesting, unusual, and fragile components of the Hawaiian *Chelonia* population (Balazs 72).

Although basking occurs principally in the daytime between approximately 1000 and 1830 h (variable with season), turtles at Necker Island have been found to also commonly emerge at night. At times this nocturnal emergence appears to be correlated with the setting of a bright moon (Balazs 72). The author has also observed small numbers of turtles resting along the shoreline at night at French Frigate Shoals and Laysan Island, but not at Lisianski Island. Amerman (24), Kridler (319), and Sibley (444, 445) frequently found turtles resting at night on Southeast Island at Pearl and Hermes Reef. Amerson *et al.* (32) attributed nighttime emergence to the disturbing activities of research personnel during the daytime. However, this seems unlikely in view of the fact that, for the September 1967 visit to Southeast Island by USFWS personnel, Kridler (319) stated "When the island was first landed upon, there were no turtles present on the beach. At dusk the first day, however, one after another hauled up on the beach on the lagoon side near camp until 19 were present."

With the exception of La Perouse Pinnacle, basking occurs on all of the islands at French Frigate Shoals (Figure 2), as well as on several unnamed seasonally occurring sandbars. The northern shore of Trig Island and the northeastern shore of Whale-Skate Island are the most heavily utilized during all months of the year by the resident aggregation. At East Island, basking tends to coincide more with the breeding season (April-September). Turtles use the entire coastline, but higher concentrations consistently occur at the southeastern end (Figure 6, areas 8-9). As with nesting, turtles display a fixity for basking on a particular island and, to a lesser extent, for regularly basking at the same site on that island. The greatest numbers of basking turtles are found throughout French Frigate Shoals during late May and June due to the presence of the migratory breeding assemblage. The incidence of basking then declines as the breeding season progresses (Figure 11). The greatest number of basking turtles seen by the author at any one time was 52 (18 males, 18 females, and 16 unknown) along the northeastern shore of Whale-Skate on 12 June 1978 at 1630 h. It is of interest to note that turtles have never been observed entering into nesting activity directly from a basking position.

Some adult Hawaiian *Chelonia* apparently do not bask. During each breeding season at French Frigate Shoals since 1973, approximately 46% (range 32.7%-56.2%) of the turtles identified with painted numbers on their carapace while nesting were subsequently never seen basking. Some of these females are undoubtedly among the 40% that only lay a single clutch of eggs in a breeding season (section 3.15). Consequently, after nesting the turtles may not be present to bask because they have either departed on the return trip to their resident area, or have been eliminated by tiger sharks. Females that attempt to nest but no not lay eggs and are subsequently not seen again (section 3.15) also constitute some of the turtles that are not seen basking. It is possible, however, that turtles in both of these categories do bask, but only during the time prior to first coming ashore to nest or make nesting attempts.

No differences were found between the lengths of the internesting intervals of basking and nonbasking turtles observed during the 1974 and 1975 breeding seasons. This indicates that basking does not significantly hasten the *in vivo* development of eggs for oviposition as might be expected.

It is important to note that at least some members of the seasonal breeding aggregation that are from resident areas in the main islands do, in fact, bask while they are at French Frigate Shoals. This is a significant point in that the 54% recorded basking each season could conceivably consist of only those females from Laysan and Lisianski Islands and Pearl and Hermes Reef where basking is a regular occurrence. Both males and females observed basking at French Frigate Shoals have been among the tagged turtles recovered in the main islands (Table 15). In addition, basking has been displayed at French Frigate Shoals by three turtles that were returned to the wild after extended periods in captive facilities where emergence for basking was not possible (Table 16).

Investigations of the thermal ecology of basking Hawaiian *Chelonia* are currently being conducted by Whittow and Balazs (549). Results of this work to date have shown that the surface temperature of the carapace measured with a radiometer can attain values as great as 42°C. The large areas of black pigmentation present in most adult Hawaiian *Chelonia* undoubtedly contribute to high surface temperatures during periods of intense solar radiation. The greatest internal body temperature recorded through the cloaca was 31.3°C at a time when the ambient seawater temperature was 26.3°C. Shortly after coming ashore to bask, some turtles open their mouth to a wide position and regurgitate small amounts of liquid (see Anonymous 670 for photograph). This is probably a result of compression of the stomach due to the body weight pressing on the plastron while on land. Turtles exhibit very little activity while basking except for occasionally flipping sand on their carapace for thermoregulation (see Tinker 492 for photograph). They do not, however, seem to orient their position in relation to the sun. In males, the tail will frequently be curled close to the body rather than fully extended. The length of time spent basking appears to be inversely related to the black-globe temperature. Respiration patterns while basking have been found to consist of breath-holds averaging 3.6 min, followed by a single shallow breath.

Basking in freshwater turtles (and other poikilotherms) is principally a behavioral strategy to raise body temperature and accelerate metabolic processes such as digestion and growth. Other motivating factors or benefits that have been suggested include synthesis of Vitamin D from skin sterols (Pritchard and Greenhood 419), removal of epizoics through drying, and social interaction (Boyer 132). These factors could also be applicable to basking by Hawaiian green turtles.

With respect to socialization (Hirth 265), considerable gregarious behavior is displayed while basking at French Frigate Shoals, with turtles often in direct contact or even partially on top of one another (Balazs 57). This is, of course, consistent with the other life activities of *Chelonia* such as feeding together, breeding together in large aggregations, and probably even traveling together across the open ocean. Hawaiian monk seals sometimes show gregarious tendencies toward basking turtles, both at French Frigate Shoals and at Necker. This has involved seals of all sizes from young pups to adults. Mothers with newborn pups may, however, make aggressive gestures and vocalizations at turtles emerging to bask in the immediate shoreline area.

One of the advantages to Hawaiian *Chelonia* obtained from basking is the reduction in exposure to predation by tiger sharks. In some cases, this could even be the motivating factor for basking (section 3.33). Emergence to land at night may be especially advantageous, considering that tiger sharks are believed to be principally nocturnal predators. Resting along the shoreline at night could, however, also be due to a scarcity of acceptable resting sites located underwater. A further advantage to resting on land would be the conservation of energy by not having to periodically swim to the surface for respiration.

Hawaiian *Chelonia* will bask under captive conditions if they are provided with a sloping area suitable for emergence (Balazs and Ross 88). Both Sea Life Park and the Kahala Hilton Hotel on Oahu have display facilities in which Hawaiian green turtles regularly bask. However, hawksbills and loggerheads in the same pool at Sea Life Park never exhibit this behavior. A subadult green turtle of Hawaiian origin at the Kewalo Marine Laboratory, University of Hawaii, also regularly basks on a wooden ramp installed in its concrete tank (Whittow and Balazs 549). There are no reports in the literature of green turtles from other populations basking in captivity. However, most facilities where marine turtles are maintained do not have sloping areas where emergence can occur.

The basking behavior of Hawaiian *Chelonia* could very well be an inherited characteristic that evolved as a protective mechanism against tiger sharks and as a method for gaining body heat at locations where seawater temperatures were marginal. The mean temperature of 20.5°C in February at the northwestern end of the Hawaiian Archipelago (section 3.43) could consitute such an environment at the present time, and perhaps cooler ocean conditions prevailed during the early development of the population. The survival value of basking, however, declined significantly with the first arrival of humans in the NWHI in the late 1700's. The extensive exploitation of turtles that subsequently took place can be attributed mostly to the basking behavior which provides accessibility for easy harvesting in the terrestrial environment.

In addition to the unique research opportunities for tagging (section 3.52) and depth recordings (section 3.15), the basking behavior of Hawaiian *Chelonia* offers considerable potential for investigations of hearing and vision on land under natural conditions. The author is particularly interested in the aspect of vision, due to the fact that green turtles are believed to be myoptic when out of the water (see Hirth 265). This would appear to be an unusual evolutionary development considering that the turtle's eyes leave the water each time a breath is taken. Observations to date have indicated that Hawaiian *Chelonia* display considerable visual sensitivity while basking.

4. POPULATION

4.1 Structure

4.11 Sex ratio

The inability to distinguish immature males from females on the basis of external characteristics is a limiting factor in determining natural sex ratios in populations of *Chelonia* and other marine turtles. Observations at French Frigate Shoals during June of 1973, 1978, and 1979 on days when relatively large numbers of adult basking turtles were ashore revealed a sex ratio of 66% females and 34% males (range 50%-81% females, 23%-50% males). As the breeding season progresses, the percent of basking males has been found to decline considerably. Of the 33 basking adults tagged by Amerson (28) at French Frigate Shoals during May and June of 1967, 73% were females and 27% were males. During May of 1972, Olsen (382) tagged 52 basking adults at French Frigate Shoals, with the resulting sex ratio of 54% females and 46% males. These various counts at the breeding colony would, however, be biased if a differential exists in the levels of basking undertaken by each sex. For example, males might be less inclined to bask when sexually receptive females are in the surrounding waters. At the same time, females that have already laid their first clutch of eggs for the season may be more inclined to bask in order to avoid the attention of males. An additional complicating factor is the occurrence of shorter reproductive cycles in males (section 3.16). This would cause the breeding aggregation to be an unrepresentative sample of the adults present in the total population, with the bias in favor of males.

Observations of adults basking at other locations in the NWHI have resulted in the following sex ratios: Necker Island - 71% females, 29% males; Lisianski Island - 62% females, 38% males; Pearl and Hermes Reef - 60% females, 40% males.

In the main islands, 48 adult green turtles were reported to the HDFG as being captured by fishermen for noncommercial purposes from 1974 to 1977. Approximately 52% were listed as females and 48% as males. However, it is unknown if these determinations were made on the basis of external characteristics, or an internal examination of the reproductive tract. The reports for each island are listed as follows: Hawaii - 4 females, 0 male, Maui - 3 females, 1 male; Lanai - 0 female, 1 male; Molokai - 0 female, 3 males; Kauai - 10 females, 7 males; Oahu - 8 females, 11 males. The reports on file with the HDFG for turtles commercially captured prior to the prohibition of 1974 do not contain information on sex.

The underwater sampling of green turtles with scuba along the Kau coastline from July to September of 1976 resulted in the capture of one adult female, 8 subadults, and 29 juveniles. None of the subadults showed evidence of tail enlargement (Wright *et al.* 557). Subsequent samplings along this resident foraging area using scuba, as well as large-mesh tangle nets, have resulted in the capture of 5 more adult females, 9 subadults, and 26 juveniles. One of the subadults showed initial signs of tail enlargement (Balazs 64, Kam and Balazs 286).

The greater number of adult females that appear to exist in the Hawaiian green turtle population is consistent with the limited data on sex ratios summarized by Hirth (265) for several other *Chelonia* populations. However, further investigations are necessary to determine if tail enlargement among some males may be occurring after an "adult" size has been reached. It is also plausible that mortality rates may be higher in males than in females (section 4.4).

4.12 Size composition

The size composition of Hawaiian *Chelonia*, based on a sample of 77 turtles captured along the Kau coastline, has been found to be 71.4% juveniles, 22.1% subadults, and 6.5% adults. These values are generally in agreement with sightings of turtles made during underwater surveys at Kau and other areas in the main islands.

Estimations of the weight composition of turtles reported as being commercially captured in the main islands from 1948 to 1973 are presented in Table 17. These data were calculated from reports submitted each year that listed the number of turtles captured along with the total weight. The resulting yearly average weights range from 4.5 to 115.7 kg, with the overall averages for each island ranging from 38.8 kg for Hawaii to 50.0 kg for both Molokai and Oahu. The standard deviations for the yearly weights indicate that most of the turtles captured were immature, since the minimum weight for an adult female is 68 kg (section 3.12).

Caldwell and Caldwell (148), quoted by Hirth (265), theorized that green turtle populations may consist of mostly larger turtles due to high mortality of the very young, rapid growth of those that survive, and long life after reaching maturity. This is not in agreement with the findings to date for Hawaiian *Chelonia*, where there is a preponderance of juveniles that grow at a relatively slow rate, and many of the adult females appear to be involved in only a single breeding season during the course of their lifetime.

4.2 Abundance and Density

Based on systematic tagging and monitoring during each breeding season since 1973, the approximate number of females nesting annually at French Frigate Shoals has been found to range from 94 in 1976 to 248 in 1978 (Figure 12). Mean annual number of females for this 7-yr period is 180. Not more than an estimated total of 20 females are thought to nest annually at Laysan and Lisianski Islands and Pearl and Hermes Reef.

Prior to 1973, the breeding colony at French Frigate Shoals was thought to be considerably larger due to inadequate data. Estimates for August of 1965 by personnel of the Pacific Ocean Biological Survey Program ranged from 650 to 1,300 adult females and males (Amerson 30). However, this was based on the short-term tagging of basking turtles, and the erroneous assumption that a large daily exchange of new turtles continuously takes place at each island throughout the breeding season. Using these values, Hendrickson (262), quoted by Amerson (30), incorrectly speculated that 650 to 1,300 different turtles would also be present in June, and twice as many would be present in July. The total breeding assemblage was therefore placed at between 2,600 and 5,200 turtles. Hendrickson (262) further qualified these values by indicating, "While it is very important to state flatly that this estimate has little basis and is *not* to be trusted, one can at least say that it does not appear to conflict violently with any other available quantitative information."

An estimation of the former size of the breeding colony can be obtained from an account in June of 1891 which states that at East Island, formerly known as Turtle Island, hundreds of turtles were found basking on the beach, and ten times as many were seen in the water (Walker 531).

The density of turtles nesting on each of the islands at French Frigate Shoals is presently at a level where the destruction of previously laid egg clutches is negligible (section 3.17). However, if larger breeding aggregations formerly existed under the same terrestrial conditions, density-dependent nest destruction may have naturally regulated the population size (see Hirth 265). This could be a significant factor in the future, in that density-dependent nest destruction can also result from reductions in the amount of available nesting habitat at a time when the population size is constant. At French Frigate Shoals, available habitat was reduced in 1942 with the extensive modification of Tern Island and establishment of permanent facilities. The reduction of nesting habitat due apparently to natural causes has also been documented by the author at East Island. At this location, the northeastern coastline has eroded at least 20 m into the vegetation zone since 1948, with a loss of 13% of the land area.

Counts of basking turtles in the NWHI made since 1950 (section 3.6) provide some indication of relative abundance at these resident foraging areas (Table 18). However, considerable variation can exist in both the numbers ashore at any one time, and the daily exchange of different turtles. Systematic tagging and observations over a defined period are therefore needed, particularly at Lisianski Island and Pearl and Hermes Reef, in order to adequately assess the present status of these aggregations. Reductions in the number of basking turtles have occurred within historical times at most of the NWHI, but particularly at Laysan (Ely and Clapp 211) and Lisianski (Clapp and Wirtz 171) Islands.

Underwater surveys with scuba along the Kau coastline resulted in the sighting of approximately three turtles during each hour of diving time. The use of a large mesh tangle net measuring 3.5 by 80 m resulted in the average capture of four turtles for each 14 h sample period (Balazs 64; Kam and Balazs 286).

4.3 Reproduction Rates

The basic reproductive data for Hawaiian *Chelonia* that have been determined at French Frigate Shoals (sections 3.15, 4.2) include 1) 104 eggs in each clutch, 2) 1.8 egg clutches laid within a season by each female, 3) 70.8% emergence of hatchlings from each nest, and 4) 180 females nesting annually. Using these values, a mean annual production of 23,857 hatchlings would occur at French Frigate Shoals. Since the number of nesting females over the 7-yr study period ranged from 94 to 248, the range in production would be 12,459 to 32,869 hatchlings. If the same egg clutch size, number of egg clutches, and percent emergence of hatchlings are assumed for the 20 females using Laysan and Lisianski Islands and Pearl and Hermes Reef, then 2,651 hatchlings would result from these locations. The mean annual production of green turtle hatchlings for all areas of the Hawaiian Archipelago would be 26,508.

4.4 Mortality

The known factors affecting the natural mortality of Hawaiian *Chelonia* have been presented in sections 2.22, 3.2, 3.33, and 3.34. Tiger sharks are almost certainly the principal cause of mortality following the transition from the pelagic environment to residency in a coastal area. Although the actual mortality rates resulting from this predator are unknown, differences in the levels of predation almost certainly exist between resident foraging areas. The precent of tiger sharks containing turtles has been found to vary considerably between some locations in the Hawaiian Archipelago, with the range extending from 6.7% to 75% (Table 19). Furthermore, at resident foraging areas in the NWHI where slower growth occurs, comparatively higher mortality rates would be expected for juveniles due to the greater length of time they are exposed to tiger sharks as small turtles. This is assuming, of course, that at least some increase in protection from predation is afforded as a turtle grows larger. Of the turtles recovered from tiger sharks at French Frigate Shoals, 44% were adults and 59% were juveniles (Balazs 70; Taylor and Naftel 482). This may indicate that larger turtles are less susceptible to attack, or it could simply reflect a greater abundance of juveniles.

The shorter reproductive cycles of males could serve to increase the mortality rate for this sex. By undertaking more frequent remigrations to French Frigate Shoals, males would be spending more time than females in an area where the risk of shark attack appears to be greater. In addition, the males that usually surround a copulating pair are undoubtedly more vulnerable to attack due to their erratic behavior and preoccupation with courtship activities. These accompanying males may also be inadvertently serving as a buffer against shark attack for the copulating pair. The long-distance remigration in itself may include certain hazards that increase mortality, such as disorientation in the open ocean and exposure to large predators not presently implicated with Hawaiian *Chelonia* (i.e. killer whales, *Orcinus orca*, and great white sharks, *Carcharodon carcharias*).

The minimum survival rate necessary to maintain the Hawaiian green turtle population at a stable level is one in which each female replaces herself with a female offspring that survives to lay fertile eggs during at least one breeding season. Assuming an equal sex ratio at the time of hatching, each adult female at French Frigate Shoals produces an average of 66 female hatchlings. If a female is only involved in one breeding season during her lifetime, then at least 1.5% of her female hatchlings would have to survive for the population to be stable. Some Hawaiian *Chelonia* are, however, involved in more than one breeding season. This would increase the number of female hatchlings produced, thereby lowering the percentage that must reach maturity. The survival rates and reproductive cycles of adult females after their first breeding season are only partially known at the present time (sections 3.16, 3.3). Due to the tagging effort thus far expended at French Frigate Shoals and other locations in the Hawaiian Archipelago, there is an excellent potential for acquiring this information within a 5-yr period.

It should be emphasized that it is unknown if the Hawaiian green turtle population is stable at the present time. The number of females nesting annually since 1973 has fluctuated substantially, and no trends can presently be detected (Figure 12).

4.5 Recruitment

The known factors affecting recruitment in the Hawaiian green turtle population are presented in sections 2.22, 3.12, 3.33, 3.34, 3.43, 3.51, 4.3, 4.4, and 5. The three principal levels of this recruitment are: 1) recruitment of hatchlings to the pelagic environment, 2) recruitment of juveniles to coastal foraging areas, and 3) recruitment of adult males and females to the breeding colony. The information acquired to date indicates that these processes are occurring in a closed system within the Hawaiian Archipelago and its surrounding pelagic waters. There is no indication that recruitment to resident areas within the Hawaiian Archipelago is occurring by juveniles that originated from other *Chelonia* populations in the Pacific. With the possible exception of Johnston Atoll and Wake, there is also no indication that green turtles of Hawaiian origin are utilizing any resident foraging area outside of the Hawaiian Archipelago. However, the possibility that such interactions may exist should not be entirely excluded at the present time. As in all marine turtle populations, basic data need to be acquired on the pelagic segment of juvenile development.

5. EXPLOITATION

5.1 Historical Overview

The exploitation of green turtles for food was found to be part of the native culture when Captain James Cook rediscovered the Hawaiian Islands in 1778 (Beaglehole 105; Anonymous 659). This traditional usage undoubtedly started as early as A.D. 600 with the initial occupation of Hawaii by Polynesians from other Pacific areas. Under the strictly enforced Hawaiian "kapu" system that remained in effect until 1819, turtles could only be eaten by men who were nobility or priests (Kalakaua 285). Turtles were captured principally by hand while diving underwater, with spears or harpoons from shore, and with nets made of cord from the bark of the olona plant, *Touchardia latifolia* (Cobb 176) and ahu'awa plant, *Cyperus javanicus* (Buck 145). The beveled edge of a pleural bone from a turtle's carapace was often used to scrape this bark and extract the durable fibers (Malo 341; Stokes 471; TenBruggencate 484). Another method of capture involved the use of two 7-cm hooks lashed to a flat stone that was attached to a long line (Cobb 176 with illustration). This was apparently used to hook turtles both from shore and while diving in areas where resting takes place.

Except for references to Nihoa in chants and legends, native Hawaiians were apparently not aware of the northwestern segment of the Hawaiian Archipelago at the time of Captain Cook's arrival (Emory 212). Exploitation of turtles was therefore confined to the main islands, although at a much earlier date some turtles were probably taken by the small groups of Hawaiians (or other Polynesians) that occupied Nihoa and Necker. An unresolved aspect of the exploitation of turtles by Hawaiians is the island which they called Ka Moku Papapa. This was described to Captain Cook and his officers on several occasions in both 1778 and 1779 as a low sandy island that was sometimes visited to catch turtles and seabirds. Ka Moku Papapa was said to be located to the west-southwest of Kaula (lat. 21°39'N, long. 160°33'W), which is a small rock island 35 km to the southwest of Niihau (Figure 1). From Kaula, where an overnight visit was usually made, the natives reported that they could "very easily paddle there in the course of the following day" (Beaglehole 105). On 16 and 17 March 1779, the *Discovery* searched for Ka Moku Papapa without success while departing from Hawaiian waters. Although no island has ever been found in this vicinity, a small shoal with a depth of 9 m is situated 6.5 km to the northwest of Kaula. In addition, an area of discolored water possibly representing a shoal was reported in 1955 at a site 35 km to the southwest of Kaula at lat. 21°28'N, long. 160°45'W. Nevertheless, for the short period of time involved and the absence of geological activity within this region of the Hawaiian Archipelago, it would not have been possible for an island to have settled into the ocean (G. A. MacDonald, personal communication).

The traditional controlled exploitation of turtles by Hawaiians gradually disappeared with the abolition of the kapu system, the influx of Caucasians and other racial groups, and the discovery of the unexploited and uninhabited northwestern segment of the Hawaiian Archipelago. Numerous commercial expeditions to the NWHI took place during the 1800's and early 1900's to exploit green turtles, seabirds, monk seals, sharks, and beche-de-mer (*Holothuria* spp.). Turtles were taken principally for meat, oil and, along with monk seals, for use as a superior shark bait. When the Japanese-chartered fishing vessel *Ada* visited these islands for 5 mo in 1882, at least 410 turtles were taken off the beaches and from the adjacent waters (Hornell 271). Other commercial expeditions to the NWHI that involved the exploitation of turtles during this early period are described by Amerson (30), Amerson *et al.* (32), Clapp and Ely (170), Ely and Clapp (211), Farrell (220), Galtsoff (231), Kemble (287), Munro (365-370), Walker (531), Woodward (556), and Anonymous (569). In June of 1923, the Tanager Expedition found evidence that turtles had been recently killed at French Frigate Shoals (Wetmore 541). It is also of interest to note that a newspaper article in June of 1867 described the rare presence of turtle eggs in the Honolulu market that had been imported from the NWHI (Anonymous 565).

Another factor in the exploitation of Hawaiian *Chelonia* was the occurrence of shipwrecks. The survivors of vessels that struck reefs in the NWHI often had to depend on turtles and other marine and terrestrial animals for food sources (Clapp and Wirtz 171; Lisiansky 335; Read 429; Ward 538; Anonymous 566). The 30 stranded crew members of a whaling vessel wrecked at French Frigate Shoals in March of 1859 killed in excess of 100 turtles before being rescued (Amerson 30; Walker 531).

In 1909 all of the NWHI except Midway were declared a United States of America preserve for native birds known as the Hawaiian Islands Reservation. In 1936 Kure was removed from this Reservation for military purposes and later, in 1952, transferred to the Territory of Hawaii. In 1940 the remaining areas of the Hawaiian Islands Reservation were redesignated as the Hawaiian Islands National Wildlife Refuge. However, until recent years this protected refuge status has not served as a significant deterrent to the exploitation of turtles. In 1946 a commercial fishing base was established by the Territory of Hawaii at French Frigate Shoals. Both turtles and fish were captured in the area and transported to Honolulu by small aircraft using the abandoned military landing strip on Tern Island. Turtle meat also became a main food source in the diets of the resident fishermen. One of the two fishing companies using this base estimated taking about 200 turtles from 1946 until they terminated operations in 1948 (L. K. Agard *in litt.* to Amerson 30). Over this period, the fishermen noted a decline in the numbers of turtles. Amerson (30) speculated that this was more the result of human disturbance than actual killing, however such an explanation seems unlikely. During the summer of 1959, turtles were again exploited on the islands at French Frigate Shoals by a commercial fishing company based in Honolulu (Pacific Ocean Fisheries Investigations 395; D. W. Strasburg, personal communication; J. J. Dirschel, personal communication).

Both the commercial and noncommercial exploitation of green turtles in the main islands proceeded with virtually no controls from the time of the 1819 abolition of the kapu system, until the adoption of a protective regulation by the

HDFG in May of 1974. During this period, the hunting techniques increased in both efficiency and sophistication, and the hunting range expanded to nearly all coastal areas. This was due principally to the availability of outboard motors, motor vehicles, firearms, spearguns, inexpensive machine-made nets and, at a later date, scuba equipment. In addition, the commercial demand for turtle meat and other Hawaiian seafoods increased considerably with the advent of large-scale tourism following statehood in 1959 (Balazs 48; Benson 115; Hendrickson 262; Smyser 448). Based on the available records, Hawaiian green turtles have apparently not been commercially exported since the turn of the century. However, such commerce with Japan was proposed as recently as 1973 (Borreca 128, Linder 332).

As a general index of potential exploitative pressures, it is of value to note that the resident human population of the main Hawaiian Islands was approximately 130,000 in 1831, 54,000 in 1876, and 770,000 in 1970. Since 1831 the distribution of the human population has changed from 23% on Oahu and 77% on the other main islands, to 82% on Oahu and 18% on the other main islands. In 1778 there were an estimated 200,000 to 300,000 Hawaiian inhabitants. In the NWHI, Midway was first colonized in 1902 by the Commercial Pacific Cable Company. As a U.S. territory, the atoll has been occupied continuously since that time under the jurisdiction of the Navy. In 1978 the resident population was reduced to approximately 400 from the former 2,200 where it had been maintained for a number of years. Kure has been continuously inhabited by approximately 20 personnel since the construction of a U.S. Coast Guard LORAN station in 1960. At Laysan Island, a small resident population existed from 1891 to 1910, primarily in conjunction with the mining of guano (Bryan 139-141; Ely and Clapp 211).

5.2 Commercial Catch Reports

Turtles captured in the Hawaiian Islands for commercial purposes have been periodically recorded under the category of "honu (turtle)" in conjunction with other fisheries statistics (see Subject Index). Except for the few rare cases where hawksbills and leatherbacks have been taken, these records are only known to involve green turtles.

Cobb (176) presents data showing that over a 4-yr period at the turn of the century, from 168 to 258 turtles were inspected and sold annually in the Honolulu fish market (Table 20). The total weight recorded for the 184 turtles sold in 1900 was 1,248 kg, which yields an average of 6.8 kg per turtle. This quantity therefore probably only represents the meat and other edible portions after butchering. Based on this reported weight, approximately 96% of the turtles were captured with spears and 4% with nets. Ice was not used in the Honolulu fish market or at markets on the other islands during this period due to the prohibitive cost. Spearing must therefore have been carried out in a manner that would allow the turtles to be kept alive until butchered and sold. For 1900, Cobb (176) also records the sale of 443 kg of turtle on Maui, 364 kg on Hawaii, and 68 kg on Molokai, all of which were taken with spears. It is also of interest to note that 192 1-lb cans of green turtle were among the large quantities of fisheries products imported to the Hawaiian Islands during the year 1900.

Since at least 1944, commercial fishermen in the Hawaiian Islands have been required to be licensed and to file catch reports on all species sold. From

1944 to 1947, the amount of turtle reported annually by live weight under this system was as follows: 1944 - 18,007 kg (no reports for January and February, report missing for April); 1945 - 8,954 kg (report missing for April); 1946 - 3,717 kg (no reports for June, July, and August); 1947 - 4,317 kg. Table 21 presents the amount of turtle reported annually by various methods of capture for the years 1948 to 1973. These data fluctuate considerably, with annual amounts ranging from 173 kg in 1963 to 11,628 kg in 1972. A total of 90,803 kg was reported during the 26-yr period. Due to the absence of a verification system, underreporting and nonreporting undoubtedly had a significant influence on these values (Hendrickson 262). On Kauai, no reports for turtles were filed from 1957 to 1969 (Table 17). In 1973 only 182 kg were reported for this island. However, information communicated to the author by a knowledgeable source indicated that approximately 4,500 kg of turtle were purchased from fishermen by a single tourist-oriented restaurant on Kauai during that year. There was also an absence of any turtle reports for Oahu during the years 1957, 1960, 1961, and 1968, as well as in 14 of the 26 yr for the island of Hawaii (Table 17).

The listing of the methods used in the capture operations was not well defined in the commercial reports. This resulted in a number of unclear categories that are subject to some interpretation (Table 21). In addition, prior to 1961 most of the reports did not specify the method of capture.

The most frequently reported capture method for all years was nets (49.5%). The categories of scuba (5.6%) and dive (0.5%) probably involved turtles that were captured solely by hand and therefore should be combined with the hand (2.3%) category to give a total of 8.4%. The first reported use of scuba for capturing turtles commercially was in 1958. The noose (0.3%) and handline (1.5%) methods are also probably synonymous. This involves placing a line around the flipper or neck of a turtle sleeping underwater. The turtle is then pulled to the surface by other fishermen waiting in a boat. The spear (3.4%) category, which was reported mostly after 1964, could include spearguns used while diving, as well as spears or harpoons thrown from a boat or from shore. The gaft (10.2%) category reported exclusively after 1968, along with the hook and line (0.3%) category, are believed to involve variations of the earlier Hawaiian practice of catching turtles with a line attached to a stone and two hooks (Cobb 176). One procedure incorporates a butcher's hook attached to a line that leads either to a boat where other fishermen are waiting, or to a free-floating buoy at the surface. The hook is then implanted into a large turtle found sleeping and subsequently either pulled to the surface or allowed to swim until exhausted from towing the buoy. Another gaft or hook and line technique is carried out from shore with barbed hooks cast into a lead weight that is attached to a pole and line. Working from coastal cliffs along foraging areas, turtles are then hooked in the flippers or neck when they swim within range. The single report listed under the category of trolling (0.1%) probably involved an accidental snagging while trolling for fish. No information is currently available on the category designated as trap (0.4%) which appeared in the records during 1962, 1963, and 1969. Possibly this involved the entry of turtles into large wire cages that are used by some fishermen to trap fish.

In addition to the methods presented in Table 21, the commercial capture of turtles is known to have included the illegal use of powerheads or underwater shark guns, as well as rifles used from shore in conjunction with a boat to retrieve the dead or wounded turtles.

Over the 26-yr period, the greatest amount of turtle was reported for March (11.6%), and the least amount reported for November (4.8%) (Table 22). Figure 13 shows that the greatest amount of turtle was reported from Maui (37.1%), followed by Oahu (34.1%), and Molokai (17.6%). However, the absence of reports from Kauai and Hawaii during a number of years undoubtedly biased these percentages.

Along with catch data, commercial fishermen occasionally included informative observational notes in their reports to the HDFG. A report filed for July 1968 recording the capture of 15 turtles in the area between Maui, Molokai, and Lanai stated "This area in 1948-1950 I used to catch at least 100 in 4 to 5 days fishing - for some reason there are no turtles there now."

Some of the turtles commercially captured in the NWHI were reported to the HDFG. These data are listed as follows. Pearl and Hermes Reef: 1953 - 161 kg, 1958 - 817 kg; Gardner Pinnacles: 1948 - 627 kg; Necker: 1951 - 690 kg; French Frigate Shoals: 1948 - 201 kg, 1950 - 531 kg, 1951 - 520 kg, 1953 - 730 kg, 1957 - 155 kg. Apparently no reports were filed for the 200 turtles taken commercially at French Frigate Shoals from 1946 to 1948, or the captures made in 1959 (section 5.1).

5.3 Noncommercial Catch

The noncommercial capture of green turtles in the Hawaiian Archipelago has resulted principally from sport and trophy hunting, and an esteem for turtles as food. The capture of turtles for true subsistence purposes has not been documented, but nevertheless may have occurred (and may still occur) in small numbers at some rural locations.

No records exist for the noncommercial capture of turtles prior to May of 1974. The annual amounts taken are therefore problematic but may have been substantial, particularly with the advent of scuba equipment. The Director of the HDFG, quoted in 1969 by Hendrickson (262), stated that "I have little doubt that the sport fishery take plus possible unlicensed commercial take far exceeds the legitimate commercial take." From May of 1974 to June of 1977, 48 adults and 1 juvenile (an illegal capture) were reported in compliance with the HDFG regulation that permitted only noncommercial exploitation.

The methods used for the noncommercial capture of turtles are the same as those employed for commercial purposes (section 5.2 and Subject Index). Some recreational fishermen have also successfully taken turtles using a surf rod and reel with a baited hook (Carter 158). Another novel technique involved the use of a hunting bow with a line attached to an arrow (Anonymous 583).

The capture of Hawaiian *Chelonia* for noncommercial purposes was stimulated in 1975 with the publication of a popular book that described how to prepare sunburn lotion from green turtles (McBride 348). The potential risks of attack by tiger sharks resulting from use of such ointments before entering the ocean have been pointed out (Balazs 65).

Prior to 1977, green turtles at Midway were at times exploited by resident personnel for trophies and food. Similar captures were sporadically made by military personnel stationed at Kure and French Frigate Shoals.

6. PROTECTION AND MANAGEMENT

6.1 Regulatory Measures

Regulatory controls on the capture of Hawaiian *Chelonia* prior to May of 1974 included a ban on the use of firearms and, since 1949, a prohibition on the sale of turtles taken with spears (Territory of Hawaii 486; State of Hawaii 457, 458). Both of these measures also covered crustaceans, mollusks, aquatic mammals, and fish (other than sharks). The prohibition on the sale of turtles taken with spears apparently was never enforced (Table 21).

In May of 1974, the adoption of Regulation 36 of the HDFG banned the commercial exploitation of green turtles and the use of tangle nets. Adults measuring 36 in. (91 cm) and larger in straight carapace length could be taken for "home consumption," but only from waters around the eight main islands. The eggs and progeny of captive Hawaiian *Chelonia* could be sold under permit, along with green turtle products imported from any area outside of the Hawaiian Islands (State of Hawaii 465). This regulatory measure also gave full protection at the State level to the hawksbill and leatherback, which were already listed in the Endangered category under the U.S. Endangered Species Act. The series of events surrounding the adoption of Regulation 36 are described in articles by Altonn (8, 9, 11, 12), Balazs (46-48), Benson (115, 116), Chiaviello (160), Ching and McCabe (161), Kido (289-298), Moake (358, 359), Smyser (448, 449), Standbury and Flattau (453), State of Hawaii (459-463), Stoffel (470), and Anonymous (594, 595, 597, 599, 600, 602-608, 610, 612, 618, 621, 622).

In September of 1978, Regulation 36 was superseded with the listing of Hawaiian *Chelonia* in the Threatened category under the U.S. Endangered Species Act (U.S. Department of Commerce 503, 504; Anonymous 668, 669). The population currently receives full protection through Federal regulations issued along with this listing. Under an agreement formalized in July of 1977, the jurisdiction over all marine turtles subject to Federal law is shared jointly by the National Marine Fisheries Service (NMFS) and the USFWS.

In the NWHI, full protection for green turtles in the Federally controlled Hawaiian Islands National Wildlife Refuge has at least theoretically been afforded since 1940. Although the exact refuge boundaries of each island-area have not always been clearly defined, as a minimum they encompassed all emergent land and the shoreline waters. It is relevant to note that in April of 1952 the Territory of Hawaii designated the Hawaiian Islands National Wildlife Refuge as a wildlife refuge under territorial law. However, according to this declaration (Resolution 7 of the Board of Commissioners of Agriculture and Forestry), this was only "...for management as a refuge for the mammal and bird wildlife found thereon...." Aspects of the disagreement between the State and Federal governments over the refuge boundaries and the involvement of Hawaiian *Chelonia* appear in articles by Benson (113, 121-123), Conant (180, 181), Kakesako (284), Miller (356), U.S. Department of the Interior (524), Zalburg (563), and Anonymous (650).

The first known regulatory measure on the capture of Hawaiian *Chelonia* at Midway was issued by the U.S. Navy station in 1969, and later formally incorporated into the area's wildlife management plan (U.S. Navy 528). Under this regulation, green turtles measuring 24 in. (61 cm) and larger in straight carapace length could be taken, but only by hand and not more than one per person each day. In 1975 this size restriction was increased to 36 in., and in 1977 the turtles were afforded full protection.

Between 1973 and 1976, a number of bills and resolutions relating to the protection and research of Hawaiian *Chelonia* were introduced into the Hawaii State Legislature (see Subject Index). The only measure to eventually receive legislative approval was the appropriation of funds that have been used to partially support the author's present research program (King 305; Anonymous 642).

6.2 Management Practices and Options

6.21 Artificial stocking

There are currently no proven techniques for replenishing marine turtle populations through stocking or other artificial manipulations. However, in a number of populations the high level of predation on eggs and hatchlings warrants the use of experimental measures. These include the transfer of eggs to protected areas for incubation and hatching, and the subsequent release of hatchlings under guarded conditions on the beach or a few kilometers offshore (Hirth 265; Parsons 400). Another experimental procedure is the "headstarting" or raising of hatchlings in captivity to a juvenile size where, presumably, less predation will occur when they are released into the wild.

The experimental stocking of Hawaiian *Chelonia* has thus far only been undertaken on a limited basis. In 1976, 295 of the 398 green turtle hatchlings that emerged from nests laid in captivity at Sea Life Park were released off Oahu as a stocking effort. The propagation of these turtles was made possible by the construction in 1974 of an 8 by 15 m pool and adjacent sand beach to serve as a display and experimental breeding facility (Bourke *et al.* 131; Anonymous 636, 643). All of the green turtles in this pool (9 females, 3 males, 6 subadults) had been captured in the main islands at various unrecorded times since 1964. On four occasions, eggs were recovered from the bottom of an earlier display pool in use at Sea Life Park, however, incubation attempts were not successful. Mating activity was occasionally observed after the turtles were moved to the new facility in 1974, but nesting did not commence until June of 1976. Only four of the nine females were believed to have been involved in the nestings. Although some mating activity has occurred since 1976, additional egg laying has not yet resulted. Mating activity, as well as the deposition of eggs in display tanks lacking a sand beach, have also been periodically recorded in Hawaiian *Chelonia* at the Waikiki Aquarium (De Luca 193; Mowbray 362) and the Kahala Hilton Hotel (Daacon 192).

Twenty-four of the hatchlings that originated from Sea Life Park were subsequently raised in captivity for 5 mo before being tagged and released off the western coast of Lanai (Bourke *et al.* 131). None of these turtles have thus far been recovered.

Between April of 1974 and August of 1977 a total of 54 juveniles, 20 to 60 mo of age, were released off Oahu after being raised in captivity from hatchlings that were obtained at French Frigate Shoals (Altonn 5). Fourteen of these turtles have been recovered under contrasting circumstances. One turtle was found resting under a coral ledge along the Kau coastline, a minimum movement of 380 km from the release site (section 3.43). Another turtle traveled 110 km and was speared by a fisherman off the north shore of Lanai 11 mo after being released. This was an interesting recovery since the turtle was observed with several other *Chelonia*. However, when the fisherman's presence was detected, all of the naturally occurring turtles rapidly left the area. Other recoveries included two turtles found swimming close to shore in an erratic manner 2 days after release; one turtle tangled in a crab net 2 days after release; one turtle found on shore inside an enclosure used for porpoise 6 wk after release; one turtle speared 2 wk after release; and eight turtles found within 200 m of the release site over periods ranging up to 4 mo after release.

In May of 1975, 26 other juveniles that had been raised in captivity from hatchlings were returned to French Frigate Shoals (Altonn 15). Five of these turtles have been recovered, with two individuals establishing a period of residency near Tern Island (section 3.43, Table 11). The other three recoveries were made 4 days after release, and included a turtle found crawling along the beach on Tern Island, a turtle found basking near an adult on Trig Island, and a turtle found swimming in shallow water adjacent to Whale-Skate Island.

A potential exists for increasing the number of live hatchlings at French Frigate Shoals by excavating nests after natural emergence has occurred in order to retrieve those individuals that did not reach the surface. Although 76.7% of the eggs laid in each nest at French Frigate Shoals produce live hatchlings, only 70.8% result in live hatchlings reaching the surface (section 3.15, Table 7). The remaining 5.9%, or an annual average of 1,988 hatchlings, result in mortality. Many of these hatchlings can be salvaged in an apparently healthy condition if they are excavated within a 3- to 5-day period.

6.22 Predator control

No measures have thus far been taken to reduce the number of ghost crabs at French Frigate Shoals in order to enhance the survival of hatchlings when they leave the nest and cross through the intertidal zone. Although predation is not excessive compared to many other green turtle breeding areas, up to 1,200 hatchlings (5%) may be eliminated annually at French Frigate Shoals by these crustaceans (section 3.2). The small size of the islands would simplify the conduction of a limited experimental control program.

Shark fishing programs have been carried out on several occasions in the main islands for the purpose of decreasing the risk of attack on humans, promoting shark meat as a food source, and for biological research. These intensive fishing programs were undoubtedly beneficial to Hawaiian *Chelonia* in view of the large number of tiger sharks eliminated. In the NWHI, the capture of tiger sharks has taken place at a reduced level in conjunction with predator-prey research of the monk seal (Taylor and Naftel 482) and currently as part of the trophic analysis of fish communities (Parrish and Taylor 399). While an intensive control program at French Frigate Shoals would result in immediate survival enhancement for green turtles, the possible long-term implications of such action would have to be carefully assessed. One possible adverse impact might be an increase in the number of small sharks after the large predators have been removed (Taylor and Naftel 482; Tester 487). This, in turn, could conceivably result in greater predation on hatchlings.

6.23 Enforcement and education

The enforcement of Federal regulations protecting green turtles in the Hawaiian Archipelago is currently the responsibility of two agents with the USFWS and two agents with the NMFS. These personnel are based in Honolulu and are responsible for enforcing numerous other Federal wildlife and fisheries regulations (Benson 110; Vernon 530). Officers of the Department of Land and Natural Resources, State of Hawaii, continue to enforce the applicable provisions of Regulation 36. The Commanding Officer of the U.S. Navy station at Midway also has enforcement responsibilities for the protection of Hawaiian *Chelonia* under his jurisdiction (U.S. Navy 528). Unlike nearly all other green turtle populations, enforcement efforts with Hawaiian *Chelonia* are not complicated by international migrations. However, illegal exploitation is known to occur within the Hawaiian Archipelago and the magnitude of this catch needs to be determined.

Since 1973 a number of magazine and newspaper articles, as well as lectures, have served to provide information to the general public about Hawaiian *Chelonia* (Baldwin 94; Balazs 44, 48, 55, 60, 62; Chong 162, 165; Eliot 208; Hendricks 261; Kim 299; Lipman 333; Sekora 439; Whitten 547; Anonymous 580, 608, 649, 660, 661, 663). In addition, the display facilities and educational programs at Sea Life Park and the Wakiki Aquarium have helped to generate interest in the biology and conservation of this population (Engle 215; Taylor 477-479; Anonymous 636).

6.24 Aquaculture

The intensive culture and breeding of Hawaiian *Chelonia* for conservation purposes, such as artificial stocking of hatchlings and headstarting experimentation, offer some potential as a management technique (section 6.21). However, this is likely to be an expensive undertaking unless carried out in conjunction with existing display facilities.

Periodic interest has been expressed in the commercial aquaculture of Hawaiian *Chelonia* as a source of marketable meat, curios, and soup stock (Altonn 13; Benson 118; Borreca 129; Finnerty 221; Haugen 258; Mahikoa 340; Pryor 420-422; Anonymous 615). However, no operations were ever actually started. Investigations conducted by the author suggested that the commercial aquaculture of Hawaiian green turtles was neither biologically nor economically feasible under existing circumstances. Furthermore, such facilities were not considered to be in the conservation interests of naturally occurring marine turtle populations (Altonn 15; Balazs 52, 58-60; Benson 119; Ehrenfeld 206; Pfund 407). Under the present Federal regulations, commerce in green turtle products is not permitted, and turtles cannot be acquired from the wild for use in commercial aquaculture facilities.

The only aquaculture of *Chelonia* known to have been carried out by the early Hawaiians involved a 15 by 150 m coastal pond on Oahu named Pahonu that was used to maintain turtles until they were ready to be eaten (McAllister 345; Whitten 544).

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SUBJECT INDEX

Table 1. Number of *Chelonia* tagged throughout the Hawaiian Archipelago since 1973.

Location	Immature	Adult male	Adult female	Total
Kure Atoll	21			21
Midway Islands	65		1	66
Pearl and Hermes Reef		5	4	9
Lisianski	23	3	7	33
Laysan	1	1		2
Maro Reef				
Gardner Pinnacles				
French Frigate Shoals	130	122	483	735
Necker	7	4	6	17
Nihoa				
Kaula				
Niihau/Lehua	4	2	5	11
Kauai	2			2
Oahu	75	2	6	83
Molokai				
Lanai	28	1	1	30
Kahoolawe				
Maui	1			1
Hawaii	87	0	5	92
Total	444	140	518	1102

Table 2. Straight carapace length and width of adult female green turtles at French Frigate Shoals.

Year	Straight Length			Straight Width		
	Mean (cm)	Range	N	Mean (cm)	Range	N
1973	92.5	83.3–103.4	52	72.1	62.2–86.4	51
1974	92.7	85.0–106.2	91	72.1	63.5–85.6	93
1975	91.7	84.3–102.4	113	70.9	64.3–78.7	115
1976	93.0	87.6–99.8	7	70.9	68.6–74.4	6
1977	89.9	80.8–100.3	36	71.4	59.9–75.9	36
1978	92.2	82.0–101.6	46	70.9	70.4–81.5	46
1979	93.7	88.4–102.9	34	71.6	63.5–78.2	32
Overall	92.2	80.8–106.2	379	71.4	59.9–86.4	379

Table 3. Curved carapace length and width of adult female green turtles at French Frigate Shoals.

Year	Curved Length			Curved Width		
	Mean (cm)	Range	N	Mean (cm)	Range	N
1973	97.3	88.1–107.9	44	90.7	80.0–102.1	44
1974	97.8	90.2–113.0	108	91.1	82.6–105.4	108
1975	96.3	85.1–108.0	135	90.9	80.0–102.1	135
1976	97.5	93.2–109.7	18	89.9	81.3–102.1	18
1977	97.5	91.2–106.7	37	90.9	81.8–97.8	37
1978	97.3	89.7–107.2	46	91.2	81.3–106.7	44
1979	99.1	92.7–108.5	27	92.2	83.8–101.0	26
Overall	97.3	85.1–113.0	415	91.2	80.0–106.7	412

Table 4. Summary of growth rates and projected years to maturity for green turtles sampled at resident foraging areas in the Hawaiian Archipelago.

Location	Growth rates cm per month* Range	Mean	Years to maturity (35-92 cm) Range	Mean	No. of growth measurements	Range of intervals in months
Main Islands						
Kau, Hawaii No. captures--79 No. turtles---72	.38-.52	.44	9-12	10.8	4	7-17
Bellows, Oahu No. captures--24 No. turtles---21	.19-.21	.20	22-25	23.8	2	13-22
Northwestern Islands						
Necker No. captures---9 No. turtles----7		.14		33.9	1	20
French Frigate Shoals No. captures-214 No. turtles--130	.02-.13	.08	36-237	59.4	19	3-36
Lisianski No. captures--30 No. turtles---23		.13		36.5	3	2
Midway No. captures-293 No. turtles--250	.03-.21	.09	23-158	52.8	8	6-37
Kure No. captures--23 No. turtles---21	.04-.12	.08	40-119	59.4	2	13-24

* straight carapace length

Table 5. **Number of egg clutches laid by green turtles at East Island, French Frigate Shoals.**

No. of egg clutches	1974		1975		1974-1975	
	No. of turtles	%	No. of turtles	%	No. of turtles	%
0	13	12.1	7	7.0	20	9.6
1	31	28.7	53	53.0	84	40.4
2	20	18.5	34	34.0	54	26.0
3	26	24.1	6	6.0	32	15.4
4	12	11.1	0	0	12	5.7
5	5	4.6	0	0	5	2.4
6	1	0.9	0	0	1	0.5
Total	108	100.0	100	100.0	208	100.1
Mean	2.1		1.4		1.8	

Table 6. Internesting intervals of green turtles at East Island, French Frigate Shoals.

Interval in day	1974 No. of intervals	1974 %	1975 No. of intervals	1975 %	1974-1975 No. of intervals	1974-1975 %
11	6	8.0	1	6.7	7	7.9
12	17	23.0	4	26.7	21	23.6
13	26	35.1	2	13.3	28	31.5
14	13	17.6	5	33.3	18	20.2
15	8	10.8	2	13.3	10	11.2
16	2	2.7	1	6.7	3	3.4
17	1	1.4	0	0	1	1.1
18	1	1.4	0	0	1	1.1
Total	74	100.0	15	100.0	89	100.0
Mean	13.2 days		13.4 days		13.2 days	

Table 7. Results of 40 precounted egg clutches excavated and examined at East Island following the natural emergence of hatchlings.

	Mean	Standard deviation	Range
% of eggs hatched	76.7	24.2	0-100
% of hatchlings emerging at the surface	70.8	24.0	0-97.6
% dead hatchlings in the nest	5.9	9.4	0-52.1
% of eggs with partially developed but dead embryos	10.8	9.9	0-50.0
% of eggs with no apparent development (presumably infertile)	12.5	22.4	0-100

Table 8. Number of nesting green turtles tagged and subsequently recovered at East Island, French Frigate Shoals, 1973-1979.

Year	No. of tagging encounters	No. of tag recoveries No. of years since original tagging						% recovered with tags	No. and % of tags thus far removed
		1	2	3	4	5	6		
1973	42							-	3(7.1)
1974	100							0	2(2.0)
1975	103		1					1.0	3(2.9)
1976	26		1	1				7.7	2(7.7)
1977	44			1				2.3	11(25.0)
1978	79		1	3				5.1	
1979	62		11	1			1	21.0	
Total	456		14	6			1		21(4.6)

Table 9. Food sources recorded for green turtles in the Hawaiian Archipelago.

Location	Principal constituents	Other food sources
Hawaii	R* - *Pterocladia capillacea*	*Amansia glomerata*
Maui	R - *Pterocladia capillacea*	
Kahoolawe	?	R - *Gelidium* sp.
Lanai	R - *Amansia glomerata* *Acanthophora spicifera* B - *Sargassum polyphyllum*	R - *Hypnea cervicornis* *Champia parvula* *Leveillea jungermannioides* *Gracilaria* sp. G - *Codium phasmaticum* B - *Dictyota acuteloba* *Padina japonica* A - *Halophila hawaiiana*
Oahu	G - *Codium edule* *Codium arabicum* *Codium phasmaticum* *Ulva fasciata* *Ulva reticulata* R - *Pterocladia capillacea* *Amansia glomerata* *Ahnfeltia concinna*	R - *Gelidiella acerosa* *Gelidium pusillum* *Gracilaria coronopifolia* *Gracilaria bursapastoris* *Hypnea musciformis* *Hypnea chordacea* *Hypnea cernicornis* *Acanthophora spicifera* *Grateloupia filicina* G - *Caulerpa serrulata* *Caulerpa sertularioides* *Dictyosphaeria versluysii* *Enteromorpha* sp. *Cladophora fasicularis* B - *Dictyota acuteloba* *Padina japonica* BG - *Lyngbya majuscula* A - *Halophila hawaiiana* I - *Chondrosia chucalla* *Spongia oceania* *Brachidontes crebristriatus*
Kauai	R - *Pterocladia capillacea*	
Necker	G - *Caulerpa racemosa*	G - *Halimeda discoidea* R - *Amansia glomerata* *Hypnea* sp.

Table 9 (continued)

Location	Principal constituents	Other food sources
French Frigate Shoals	G - *Codium arabicum*	B - *Lobophora variegata*
	Codium phasmaticum	*Rosenvingea orientalis*
	Codium edule	*Sphacelaria tribuloides*
	Caulerpa racemosa	*Roschera* sp.
	Ulva fasciata	R - *Gracilaria* new species
	B - *Turbinaria ornata*	*Porolithon gardineri*
	R - *Spyridia filamentosa*	*Ceramium* sp.
		Polysiphonia sp.
		Liagora sp.
		G - *Microdictyon setchellianum*
		Chlorodesmis hildebrandtii
		Halimeda discoidea
		BG - *Microcoleus lyngbyaceus*
		I - *Physalia physalis*
		Cerithiidae
		Anthrozoa
		D - *Asterionella notata*
Laysan	?	R - *Spyridia filamentosa*
		Amansia glomerata
		G - *Microdictyon japonicum*
		Pseudobryopsis oahuensis
		Halimeda discoidea
		B - *Turbinaria ornata*
		Padina crassa
		Zonaria variegata
Lisianski	G - *Caulerpa racemosa*	R - *Gelidiopsis* sp.
	B - *Turbinaria ornata*	*Pterocladia capillacea*
		Jania capillacea
		Polysiphonia sp.
		G - *Halimeda discoidea*
		Chlorella sp.
		BG - *Lyngbya majuscula*
		Oscillatoria sp.
		I - *Velella velella*
		Janthina exigua
		D - *Melosira* sp.

Table 9 (continued)

Location	Principal constituents	Other food sources
Midway	G - *Codium edule* R - *Spyridia filamentosa*	G - *Codium coneatum* *Caulerpa serrulata* *Caulerpa sertuarioides* *Dictyosphaeria versluysii* R - *Amansia glomerata* *Ceramium* sp. *Falkenbergia* sp. B - *Sphacelaria tribuloides* *Padina* sp. BG - *Lyngbya majuscula* *Oscillatoria* sp. A - *Halophila hawaiiana* I - *Physalia physalis* *Velella velella* *Janthina exigua* Echinoidea
Kure	G - *Codium edule*	R - *Polysiphonia tsudana* I - *Physalia physalis* *Janthina exigua* Echinoidea

* R - red algae, Rhodophyta
B - brown algae, Phaeophyta
G - green algae, Chlorophyta
BG - blue-green algae, Cyanophyta
D - diatoms, Bacillarophyta
A - angiosperm (seagrass)
I - invertebrates

Algae identified by D. J. Russell and M. S. Doty; invertebrates identified by W. J. Cooke; seagrass identified by K. Bridges.

Table 10. Major food sources of green turtles in the Hawaiian Archipelago.

Location	Benthic algae
Main Islands (sample size N=85)	R* - *Pterocladia capillacea* *Amansia glomerata*
Main Islands and Northwestern Hawaiian Islands	G - *Codium edule* *Codium arabicum* *Codium phasmaticum* *Ulva fasciata*
Northwestern Hawaiian Islands (sample size N=56)	G - *Caulepa racemosa* R - *Spyridia filamentosa* B - *Turbinaria ornata*

* R - red algae, Rhodophyta
G - green algae, Chlorophyta
B - brown algae, Phaeophyta

Table 11. Growth rates of Hawaiian green turtles released from captivity and raised in captivity.

Tag. no.	Site released	Site recovered	Straight carapace length, cm Initial	Straight carapace length, cm Recovery	Interval in months	Growth rate in cm per month
Returned to the wild after extended periods in captivity						
702	Oahu	FFS	67.9	73.0	28	.18
216FW	Niihau	FFS	97.8	97.8	14	0
Raised in captivity from hatchlings and released						
474	Oahu	Kau, Hawaii	42.5	42.5	11	0
1442*	FFS	FFS	45.7	51.4	8	.71
1414*	FFS	FFS	40.6	45.0	16	.28
Raised in captivity from hatchlings						
2056 (9/72)	at 19 months of age (1.82 cm/mo)		34.6	58.7	62	.39
2054 (8/72)	at 17 months of age (1.94 cm/mo)		33.0	48.9	63	.25
2053 (10/73)	at 17 months of age (1.94 cm/mo)		33.0	57.2	51	.47
2051 (9/74)	at 25 months of age (1.31 cm/mo)		32.7	47.3	32	.46

* regularly fed fish scraps by U. S. Coast Guard personnel on Tern Island

Table 12. Growth rates of adult green turtles recovered at French Frigate Shoals since June 1973.

Tag no.	Straight carapace length, cm Initial	Recovery	Interval in months	Growth rate in cm per month
Females				
699FW, 642	94.9	95.3	60	.01
372FW, 641	89.5	90.2	35	.02
362FW, 648	92.1	95.3	35	.09
391FW, 779	94.6	97.8	47	.07
T60FW, 723	88.3	91.4	25	.12
976FW, 763	94.6	96.5	37	.05
655FW, 828	90.2	92.7	75	.03
959FW	95.3	94.0	49	-
650, 1075	95.3	94.0	24	-
1029, 2605	94.0	95.6	36	.04
1047, 2729	100.6	101.6	36	.03
958FW, 2787	97.0	98.1	73	.02
2235, 3145	90.8	91.8	24	.04
2209, 2210	89.8	90.8	24	.04
842, 2270	94.6	95.6	24	.04
2253, 3228	92.7	92.7	24	0
2268, 3257	90.8	91.8	24	.04
2255, 3266	90.2	90.5	24	.01
5016, 5018	90.5	92.7	25	.09
651, 3264	87.0	87.9	72	.01
Male				
747FW, 2616	81.3	82.6	64	.02
Mean	91.8			.04
range	81.3-100.6		24-75	.01-.12 N=18

Table 13. Growth rates of Hawaiian green turtles captured from the wild and held for extended periods in captivity at Sea Life Park (diet—fresh frozen squid and fish).

Tag no.	Straight carapace lengths, cm			Interval in months		Growth rates in cm per month	
	1	2	3	1	2	1	2
Immature							
2057	69.2	70.8	80.0	9	13	.18	.71
2067	62.2	69.2	79.4	9	13	.78	.78
2014	63.5	68.6	79.1	9	37	.57	.28
2065	64.8	73.6		13		.68	
2071	76.8	84.8	89.2	13	24	.62	.18
2018	73.3	80.3	84.8	13	24	.54	.19
Adult Females							
2021	85.7	87.6		59		.03	
2013	86.4	86.7		59		.01	
684	94.6	95.6		35		.03	
2017	92.7	93.7		46		.02	
2062	85.1	86.0		46		.02	
Adult Males							
2015	78.1	78.7		59		.01	
2019	82.6	84.5		35		.05	
2069	78.7	79.7		46		.02	

Table 14. Movements of Hawaiian green turtles in the main islands after being held in captivity for extended periods.

Tag. no.	Straight carapace length, cm	Date released	Date recovered	Interval (months)	Location released	Location recovered	Ocean distance (km)	
Waikiki Aquarium *								
316	62.9	1-73	11-73	10	Waikiki, Oahu	Iloli, Molokai	80	killed by fisherman
308	67.9	1-73	1-74	13	Waikiki, Oahu	Hauula, Oahu	75	killed by fisherman
310	66.7	1-73	6-75	29	Waikiki, Oahu	Hana, Maui	175	killed by fisherman
218	91.4	3-73	12-73	8	Niihau	Palaoa, Lanai	360	released uninjured
Sea Life Park								
872	59.0	1-75	4-75	3	Makapuu, Oahu	Kailua, Oahu	15	moribund-cause unknown

* see Stafford 452, Anonymous 596, 598

Table 15. Locations and numbers of tag recoveries documenting long distance migrations by adult green turtles in the Hawaiian Archipelago (sources - Balazs 57 and unpublished data, Kridler 311-327, Olsen 380-385).

Tagging and recovery locations	Males	Females	Total
French Frigate Shoals to:			
Kauai	1	8	9
Oahu	2	9	11
Molokai	1	3	4
Maui	0	2	2
Hawaii	1	1	2
Lisianski	0	2	2
Pearl & Hermes Reef	1	3	4
Hawaii to:			
French Frigate Shoals	0	1	1
Oahu to:			
French Frigate Shoals	1	0	1
Niihau to:			
French Frigate Shoals	0	1	1
Lisianski to:			
French Frigate Shoals	0	4	4
Laysan to:			
French Frigate Shoals	0	1	1
Pearl & Hermes Reef to:			
French Frigate Shoals	3	7	10
Pearl & Hermes Reef to:			
Laysan	0	1	1
French Frigate Shoals to main islands	5	23	28
Main islands to French Frigate Shoals	1	2	3
Total	6	25	31
French Frigate Shoals to northwestern islands	1	5	6
Northwestern islands to French Frigate Shoals	3	12	15
Total	4	17	21

Table 16. Long distance migrations of adult Hawaiian green turtles recovered since June 1973.

Tag no.	Date tagged	Location tagged and status *	Location recovered and status *	Interval years/months	Date recovered
Females					
1048FG	13 March 1964	Pearl & Hermes-B	East, FFS-N	10-3	2 June 1974
440FW, 742	21 March 1967	Pearl & Hermes-B	Pearl & Hermes-B East, FFS-N	4-1 3-2	27 April 1971 30 June 1974
167FW, 794 795	26 September 1966	Pearl & Hermes-B	East, FFS-N	7-9	30 June 1974
883FW, 1291	April 1969	Pearl & Hermes-B	East, FFS-N	7-3	7 July 1976
132FW, 1303 1304	20 September 1966	Pearl & Hermes-B	Trig, FFS-B	5-3	10 July 1976
995FW	27 April 1971	Pearl & Hermes-B	Whale-Skate, FFS-B	5-3	10 July 1976
152FW, T209 1306	23 September 1966	Pearl & Hermes-B	Pearl & Hermes-B East, FFS-N	6-0 3-10	September 1972 10 July 1976
655FW, 758, 828	20 March 1968	Lisianski-B	East, FFS-N	6-3	4 June 1974
660FW, 1298 1299	20 March 1968	Lisianski-B	East, FFS East, FFS-N	3-2 5-2	16 May 1971 9 July 1976
362 FW, 648	10 July 1970	East, FFS-B	East, FFS-N Kailua Bay, Oahu-O	2-11 0-3	17 June 1973 12 September 1973
672	9 July 1973	East, FFS-N	Maalaea Bay, Maui-O	1-1	31 July 1974
853	15 July 1974	Whale-Skate, FFS-N	Princeville, Kauai-O	0-1	15 August 1974

Table 16. (continued)

Tag no.	Date tagged	Location tagged and status *	Location recovered and status *	Interval years/months	Date recovered
2229	27 June 1977	East, FFS-N	Hilo Bay, Hawaii-O	1-0	2 July 1978
T216FW, 816 818	24 March 1973	Niihau-RC	East, FFS-B,N	1-2	3 June 1974
702 (subadult)	6 December 1973	Makapuu, Oahu-RC	Whale-Skate, FFS-B Whale-Skate, FFS-B	2-1 0-3	16 January 1976 10 April 1976
5016, 5018	8 May 1977	Kau, Hawaii-O	East, FFS-N	2-1	28 June 1979
Males					
1060FG, 1272 2011	16 September 1964	Pearl & Hermes-B	East, FFS-B Pearl & Hermes-B	11-10 1-0	4 July 1976 July 1977
122FW, 2594	20 September 1966	Pearl & Hermes-B	East, FFS-B East, FFS-B	11-9 1-0	11 June 1978 18 June 1979
2411**	13 October 1977	Waikiki, Oahu-RC	East, FFS-B	0-8	11 June 1978

* FFS - French Frigate Shoals
B - basking
N - nesting
O - offshore
RC - release from captivity

** see Altonn 23, Taylor 477, 479

Table 17. Mean weights of turtles from the Hawaiian Islands reported as being commercially captured, 1948-1973.

Year	Hawaii				Maui			
	Mean weight, kg	SD	N	% kg with N	Mean weight, kg	SD	N	% kg with N
1948	none *	-	-	-	15.8	9.6	63	98.0
1949	none	-	-	-	31.3	23.1	113	96.9
1950	36.3	12.8	25	100	45.5	0	1	56.2
1951	40.8	19.9	3	100	none	-	-	-
1952	none	-	-	-	68.2	0	1	100
1953	90.9	0	1	100	90.9	0	1	100
1954	68.2	-	6	100	8.6	7.0	2	100
1955	none	-	-	-	21.7	2.4	7	100
1956	none	-	-	-	18.5	7.3	18	100
1957	none	-	-	-	16.1	2.7	10	100
1958	-	-	-	-	18.1	5.9	31	100
1959	16.8	-	5	100	45.5	-	2	40.0
1960	none	-	-	-	45.7	35.1	16	77.7
1961	none	-	-	-	92.3	21.4	3	100
1962	none	-	-	-	none	-	-	-
1963	none	-	-	-	-	-	-	-
1964	15	0	1	100	24.8	13.4	17	93.0
1965	none	-	-	-	27.3	-	2	100
1966	30.6	14.3	4	100	18.2	0	1	100
1967	none	-	-	-	34.7	20.3	7	94.9
1968	11.0	10.5	99	100	13.9	4.7	27	100
1969	48.4	25.5	16	100	55.1	23.6	63	99.5
1970	30.9	0	1	100	62.5	31.0	73	100
1971	37.5	1.7	23	90.3	65	31.4	87	87.9
1972	none	-	-	-	63.9	42.7	85	100
1973	none	-	-	-	56.7	25.8	42	-
			184			672		
Mean	38.8				40.9			
Range	11.0-90.9				8.6-92.3			

Table 17 (continued)

Year	Lanai				Molokai			
	Mean weight, kg	SD	N	% kg with N	Mean weight, kg	SD	N	% kg with N
1948	22.7	0	1	100	none	-	-	-
1949	none	-	-	-	none	-	-	-
1950	none	-	-	-	24.1	-	17	64.3
1951	none	-	-	-	-	-	-	-
1952	none	-	-	-	8.2	-	7	100
1953	none	-	-	-	30.2	4.0	22	47.8
1954	none	-	-	-	47.4	19.4	15	76.3
1955	none	-	-	-	66.4	22.5	56	89.1
1956	none	-	-	-	67.6	30.3	33	100
1957	none	-	-	-	none	-	-	-
1958	none	-	-	-	none	-	-	-
1959	none	-	-	-	none	-	-	-
1960	40.0	11.7	19	100	none	-	-	-
1961	45.5	0	1	100	none	-	-	-
1962	none	-	-	-	none	-	-	-
1963	none	-	-	-	none	-	-	-
1964	none	-	-	-	none	-	-	-
1965	none	-	-	-	44.5	18.3	11	100
1966	89.4	18.4	3	100	-	-	-	-
1967	48.9	3.3	20	100	none	-	-	-
1968	54.5	0	1	100	none	-	-	-
1969	22.7	4.0	3	100	68.2	0	1	-
1970	none	-	-	-	none	-	-	-
1971	43.2	35.4	2	100	95.5	-	8	-
1972	none	-	-	-	55.7	-	36	53.3
1973	none	-	-	-	42.1	20.4	33	-
			50				239	
Mean	45.9				50.0			
Range	22.7-89.4				8.2-95.5			

Table 17 (continued)

Year	Oahu Mean weight, kg	Oahu SD	Oahu N	Oahu % kg with N	Kauai Mean weight, kg	Kauai SD	Kauai N	Kauai % kg with N
1948	33.8	13.8	54	25.6	none	-	-	-
1949	37.2	8.0	43	44.9	-	-	-	-
1950	23.3	8.1	15	11.1	-	-	-	-
1951	61.4	9.9	3	24.3	none	-	-	-
1952	38.7	27.9	19	87.2	-	-	-	-
1953	-	-	-	-	none	-	-	-
1954	-	-	-	-	none	-	-	-
1955	45.7	19.4	4	54.5	22.5	7.0	9	100
1956	83.0	-	2	89.2	27	3.4	5	75.7
1957	none	-	-	-	none	-	-	-
1958	4.5	0	1	100	none	-	-	-
1959	-	-	-	-	none	-	-	-
1960	none	-	-	-	none	-	-	-
1961	none	-	-	-	none	-	-	-
1962	-	-	-	-	none	-	-	-
1963	-	-	-	-	none	-	-	-
1964	115.7	12.6	2	100	none	-	-	-
1965	104.5	0	1	74.2	none	-	-	-
1966	49.7	49.1	5	13.9	none	-	-	-
1967	-	-	-	-	none	-	-	-
1968	none	-	-	-	none	-	-	-
1969	22.7	-	3	30.1	none	-	-	-
1970	15.9	0	1	2.2	-	-	-	-
1971	44.9	38.9	8	100	40.4	13.3	4	41.5
1972	79.5	12.7	43	96.0	18.2	-	5	100
1973	39.8	33.7	96	-	90.9	-	2	-
			300				25	
Mean	50.0				39.8			
Range	4.5-115.7				18.2-90.9			

* no reports submitted for the year

Table 18. Maximum numbers of green turtles seen basking at one time during surveys in the Northwestern Hawaiian Islands since 1950.

Location	Number of basking turtles	Month-Year	Reference
Nihoa (23°06'N, 161°58'W)	2	September 1971	Kridler (326)
Necker (23°35'N, 164°42'W)	7	November 1977	Balazs, unpublished data
French Frigate Shoals (23°45'N, 166°10'W) (nonbreeding months)	22	February 1975	Balazs, unpublished data
Laysan (25°43'N, 171°44'W)	6	September 1966	Kridler (316)
Lisianski (26°02'N, 174°00'W)	13	March 1964	Clapp & Wirtz (171)
Pearl and Hermes Reef (27°55'N, 175°45'W)			
Southeast Island	50	September 1966	Kridler (316)
North Island	10-20	1957-58	Kenyon & Rice (288) personal communication to Parsons (400)
Little North Island	10-20	1957-58	"
Bird and Sand Islands	8	January 1962	A. F. Carr, personal communication to Amerson *et al.* (32)
Midway (28°13'N, 177°21'W)	1	May 1975 (only record)	J. Bradley, personal communication
Kure (28°25'N, 178°10'W)	1	January 1979	J. Stark, personal communication

Table 19. Tiger sharks, *Galeocerdo cuvier*, captured at locations in the Hawaiian Archipelago where turtles were found to be prey items. (Sources - A. Tester 487 and unpublished data; Taylor and Naftel 482).

Location: Island	Location: Coastline	No. tiger sharks containing food	No. tiger sharks containing turtles	Percent tiger sharks containing turtles
*Main Islands**				
Hawaii	southwest	9	1	11.1
	northwest	14	2	14.3
Maui	southwest	9	1	11.1
	west	5	1	20.0
Oahu	northeast	24	3	12.5
	southeast	6	1	16.7
	south	32	5	15.6
Kauai	northeast	4	3	75.0
	southwest	18	2	11.1
Niihau	east	13	2	15.4
	west	15	1	6.7
Northwestern Hawaiian Islands				
French Frigate Shoals		16	5	31.2
Pearl and Hermes Reef		11	4	36.3

* 25 tiger sharks that contained food but not turtles were captured by Tester (487) at other locations in the main islands

Table 20. Monthly number of turtles sold in the Honolulu Fish Market, 1900, 1902-1904. (source - Cobb 176).

Month	1900		1902		1903		1904	
	Number	Percent	Number	Percent	Number	Percent	Number	Percent
January	-	-	6	3.1	6	3.6	9	3.5
February	6	3.2	7	3.6	9	5.4	-	-
March	4	2.2	19	9.8	10	6.0	9	3.5
April	12	6.5	24	12.4	18	10.7	14	5.4
May	11	6.0	13	6.7	26	15.5	24	9.3
June	23	12.5	15	7.7	29	17.3	11	4.3
July	71	38.6	14	7.2	19	11.3	8	3.1
August	16	8.7	34	17.5	11	6.5	4	1.5
September	14	7.6	23	11.9	10	5.9	82	31.8
October	2	1.1	22	11.3	13	7.7	24	9.3
November	19	10.3	11	5.7	7	4.2	35	13.6
December	6	3.3	6	3.1	10	5.9	38	14.7
Total	184	100	194	100	168	100	258	100

Table 21. Kilograms and percent of turtle from the Hawaiian Islands reported as being commercially captured by various fishing methods, 1948-1973 (compiled by G. H. Balazs, R. Chau and E. Corbin from data on file at the Hawaii State Division of Fish and Game).

Year	Net	Gaff	Scuba	Spear	Hand	Dive
1948	1,821 (20.1%)			4 (.1%)		
1949	4,509 (63.2%)			27 (.4%)		
1950	4,462 (82.9%)					181 (3.3%)
1951	599 (25.6%)					
1952	689 (55.5%)					
1953	1,814 (42.2%)					
1954	445 (32.2%)					
1955	3,296 (65.2%)					
1956	1,226 (38.9%)					
1957	120 (38.1%)					
1958	59 (4.1%)		164 (11.2%)		130 (8.9%)	208 (14.3%)
1959	97 (30%)					
1960					59 (3.5%)	
1961					322 (100%)	

Table 21 (continued)

Year	Noose	Trap	Hook and Line	Trolling	Handline	Unknown	Yearly Total, kg.
1948			175 (1.9%)		1,362 (15%)	5,699 (62.9%)	9,060
1949						2,601 (36.4%)	7,137
1950						741 (13.8%)	5,384
1951						1,740 (74.4%)	2,339
1952						552 (44.5%)	1,241
1953						2,489 (57.8%)	4,303
1954						937 (67.8%)	1,382
1955						1,760 (34.8%)	5,056
1956						1,923 (61.1%)	3,148
1957						196 (61.9%)	316
1958				76 (5.2%)		821 (56.3%)	1,458
1959						227 (70%)	324
1960						1,641 (96.5%)	1,699
1961							322

Table 21 (continued)

Year	Net	Gaff	Scuba	Spear	Hand	Dive
1962						
1963	102 (58.9%)					
1964	32 (4.3%)				332 (45.4%)	
1965	36 (5.3%)			545 (79.5%)		
1966	1,960 (83.4%)			268 (11.4%)		
1967	1,104 (48.4%)			1,175 (51.6%)		
1968	1,355 (88.9%)			54 (3.6%)		
1969	3,089 (66.8%)	227 (4.9%)	550 (11.9%)		662 (14.3%)	
1970	4,599 (80.9%)	423 (7.4%)		245 (4.3%)	190 (3.4%)	
1971	2,776 (30.7%)	4,605 (50.9%)	341 (3.8%)	620 (6.9%)	339 (3.7%)	52 (.6%)
1972	5,249 (45.1%)	3,181 (27.4%)	1,954 (16.8%)	115 (1%)	16 (.1%)	
1973	5,516 (63.4%)	866 (10%)	2,085 (24%)		27 (.3%)	
1948-1973	44,955 (49.5%)	9,302 (10.2%)	5,094 (5.6%)	3,053 (3.4%)	2,077 (2.3%)	441 (.5%)

Table 21 (continued)

Year	Noose	Trap	Hook and Line	Trolling	Handline	Unknown	Yearly Total, kg
1962		217 (100%)					217
1963		71 (41.1%)					173
1964			45 (6.2%)			322 (44.1%)	731
1965						104 (15.2%)	685
1966			9 (.4%)			114 (4.8%)	2,351
1967							2,279
1968						114 (7.5%)	1,522
1969		97 (2.1%)					4,625
1970						227 (4%)	5,684
1971	161 (1.8%)					145 (1.6%)	9,037
1972						1,114 (9.6%)	11,628
1973	182 (2.1%)					19 (.2%)	8,695
1948–1973	343 (.3%)	385 (.4%)	229 (.3%)	76 (.1%)	1,362 (1.5%)	23,486 (25.9%)	90,803

Table 22. Kilograms and percent of turtle from the Hawaiian Islands reported as being commercially captured by month, 1948-1973.

Month	Kilograms	Percent of total
January	8,950	9.9
February	7,729	8.5
March	10,524	11.6
April	8,977	9.9
May	6,900	7.6
June	8,477	9.3
July	7,680	8.5
August	7,682	8.5
September	7,298	8.0
October	6,073	6.7
November	4,312	4.8
December	6,201	6.8
Total	90,803	100.0

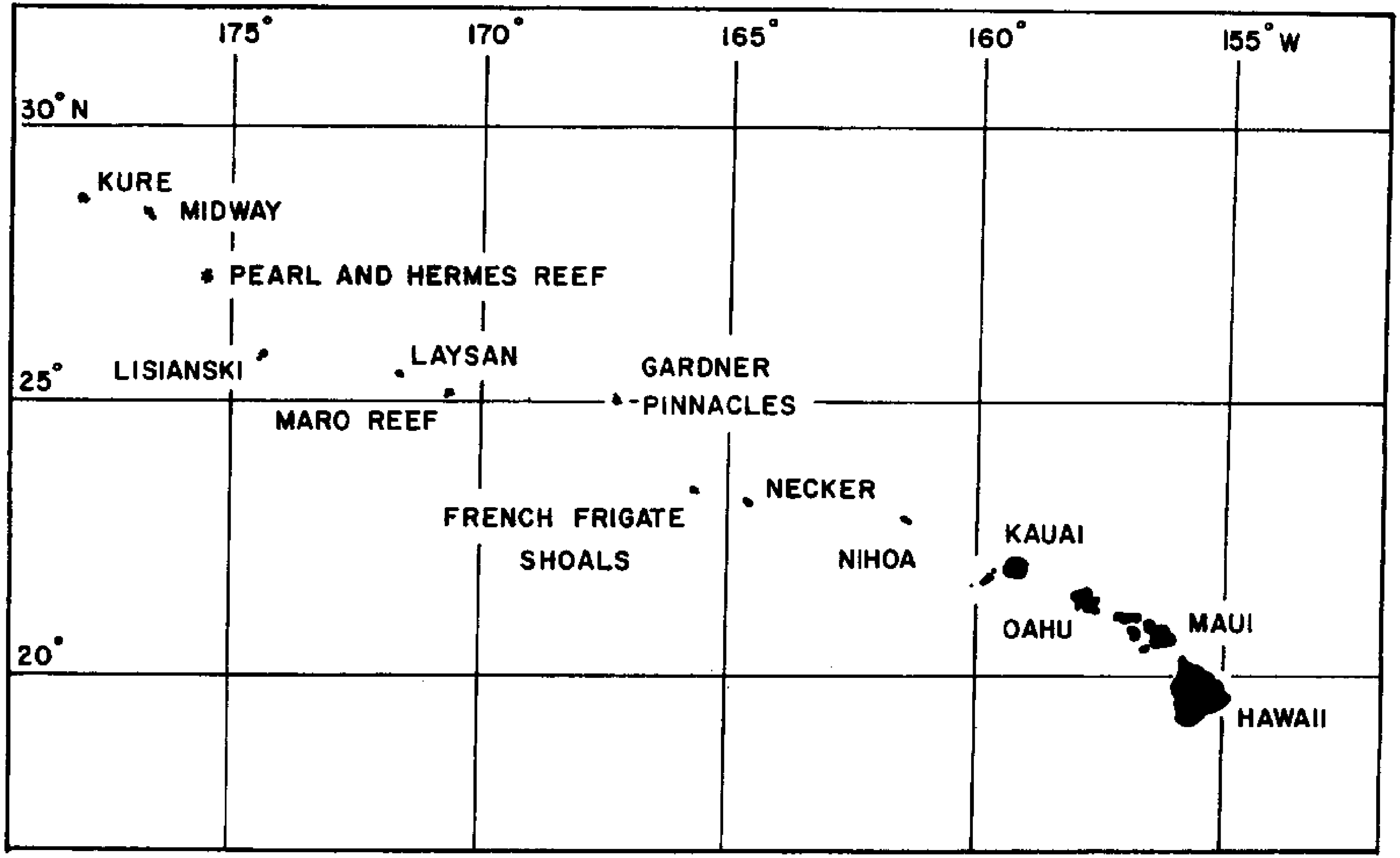

Figure 1. Hawaiian Archipelago, North Pacific Ocean.

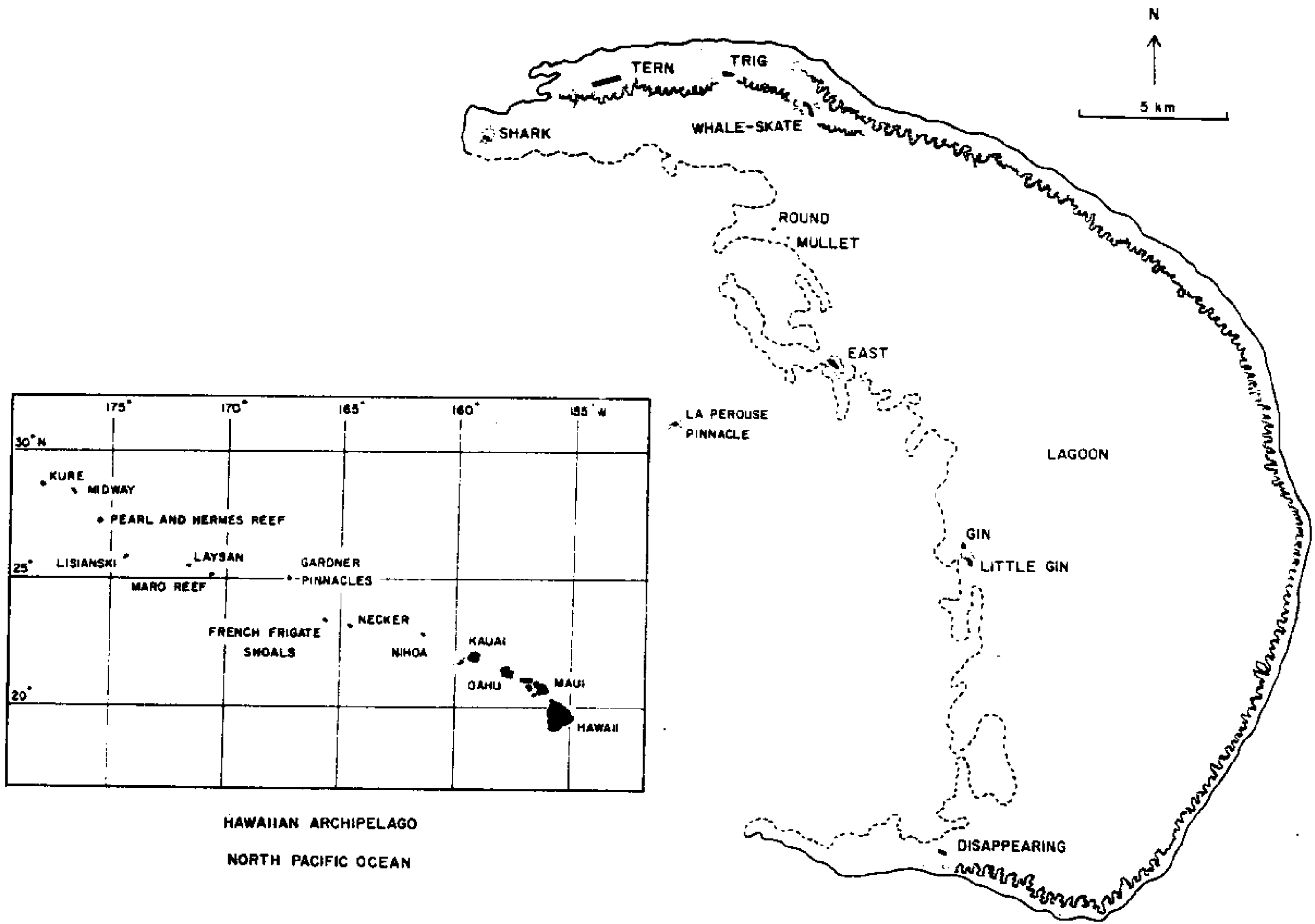

Figure 2. French Frigate Shoals, 23°45'N, 166°10'W.

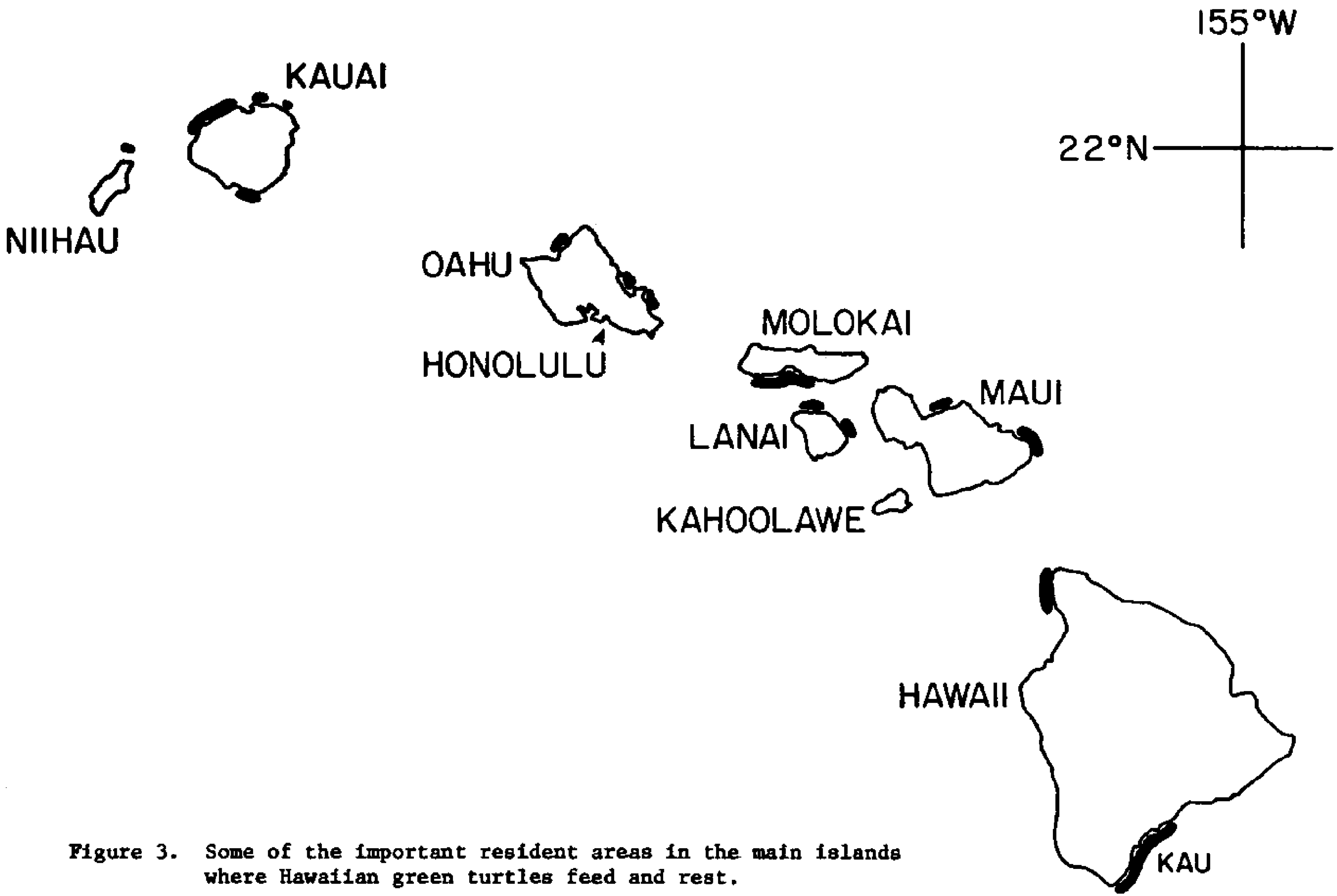

Figure 3. Some of the important resident areas in the main islands where Hawaiian green turtles feed and rest.

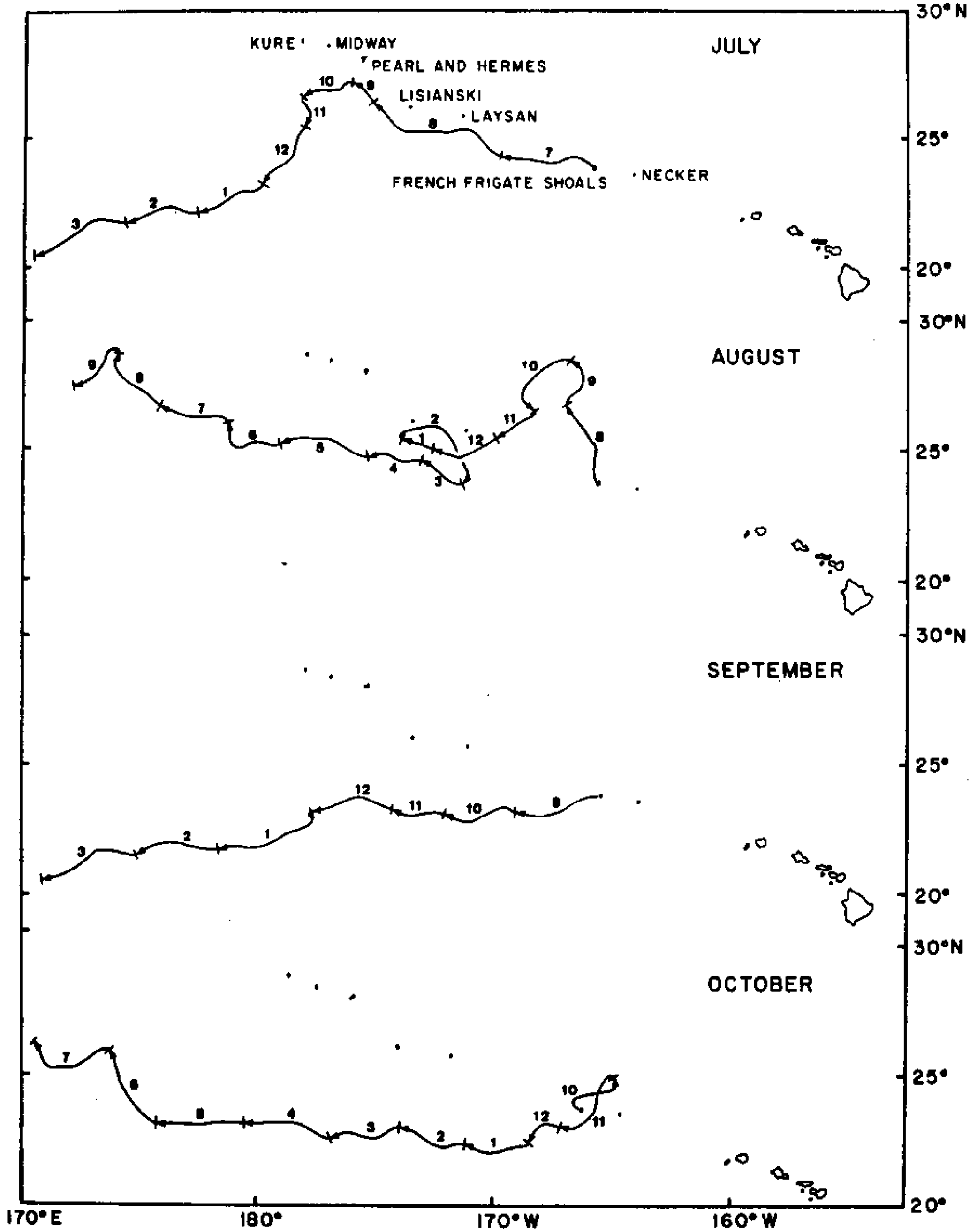

Figure 4. Surface drift trajectories representing the theoretical movement of hatchling and posthatchling *Chelonia* leaving French Frigate Shoals. Segments of paths represent estimated distances covered during subsequent months. Most hatchlings emerge during August. (From Balazs 57, courtesy of R. H. Barkley, Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, Hawaii 96812.)

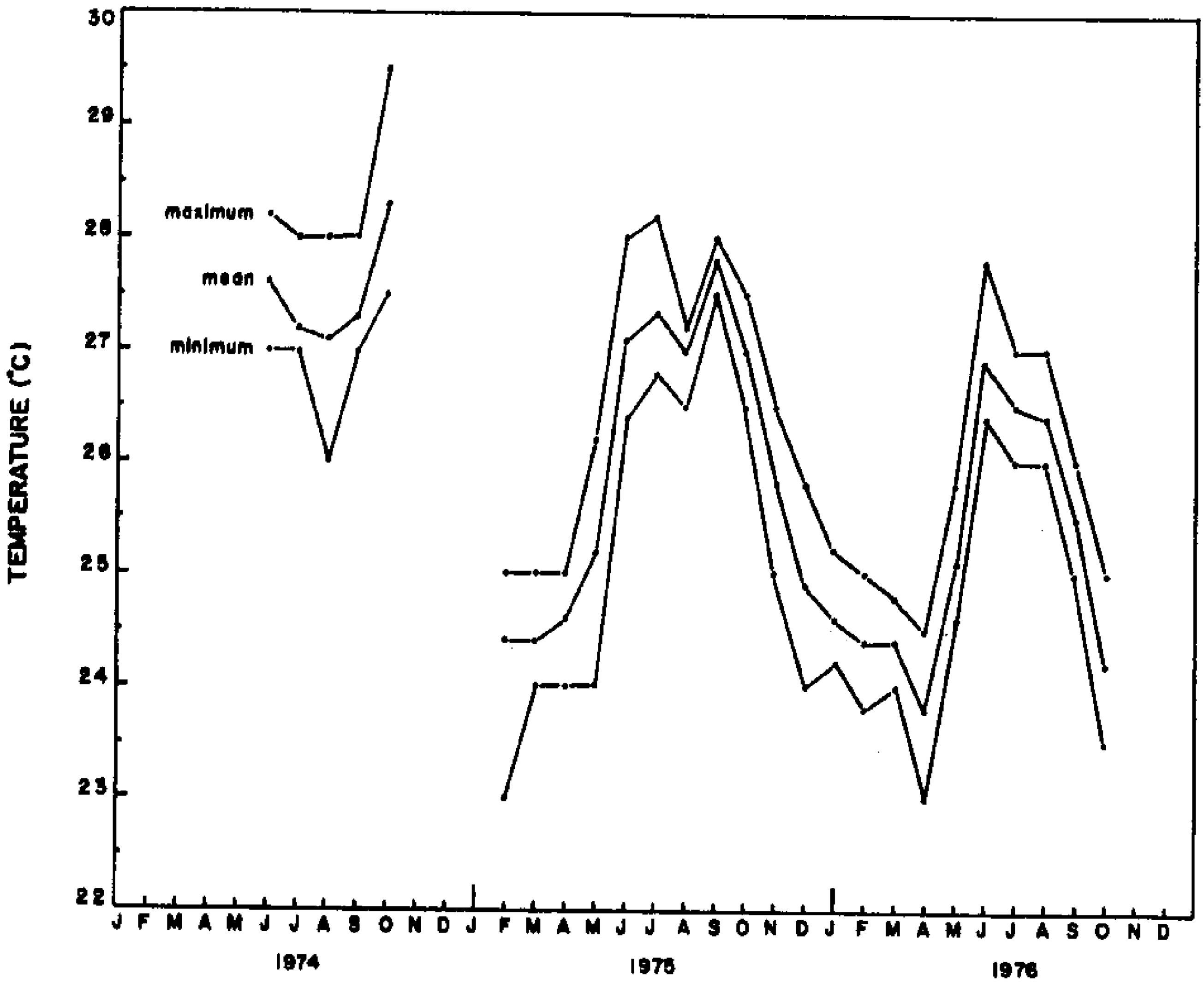

Figure 5. Sea surface temperatures at French Frigate Shoals. Data presented for each month represent an average of seven recordings. (Source: G. H. Balazs and U.S. Coast Guard personnel.)

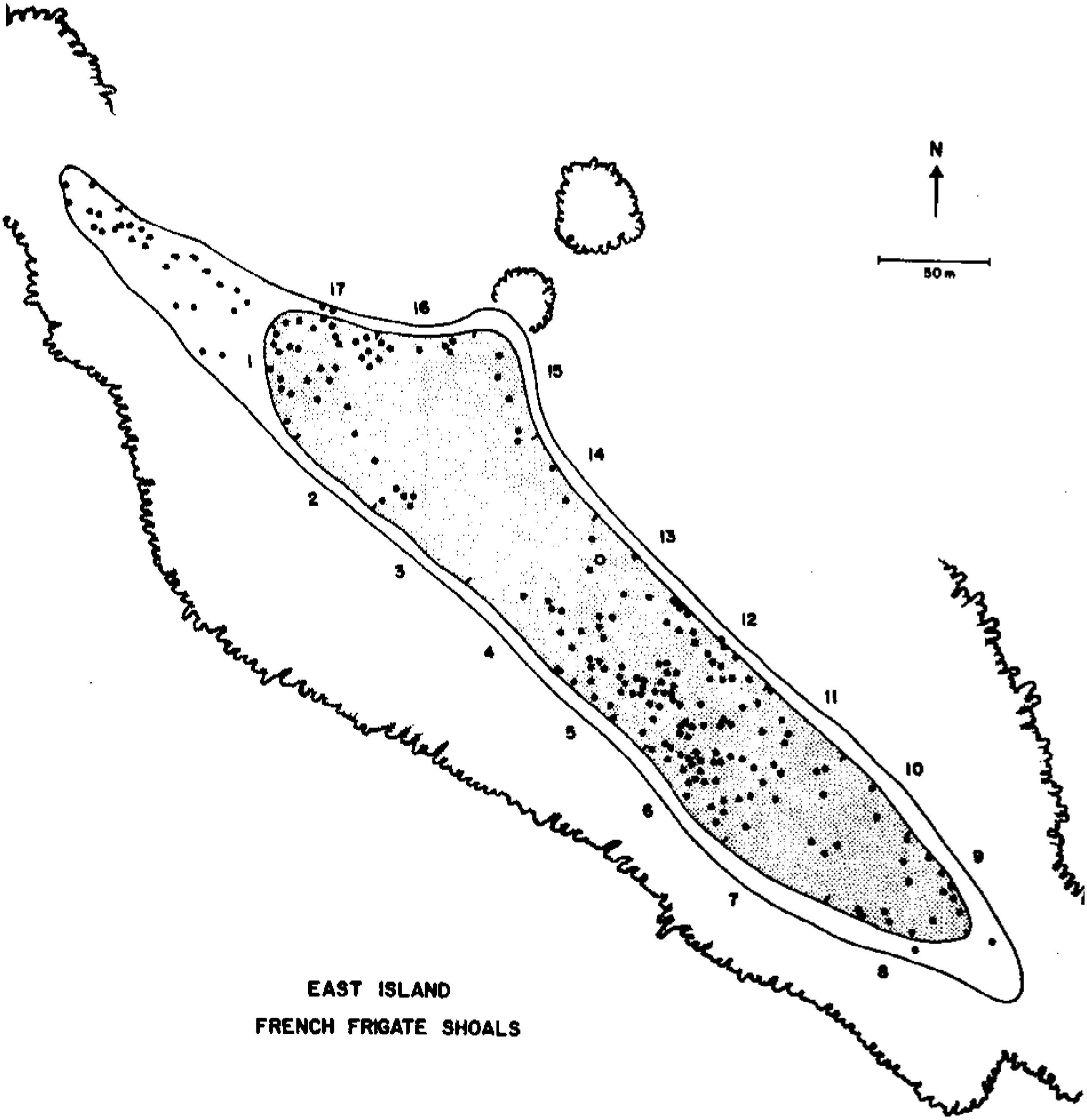

Figure 6. Locations of 220 nests recorded on East Island from June to August of 1974. The numbers on the island's perimeter identify the 17, 50-m long nesting areas that have been established for reference purposes.

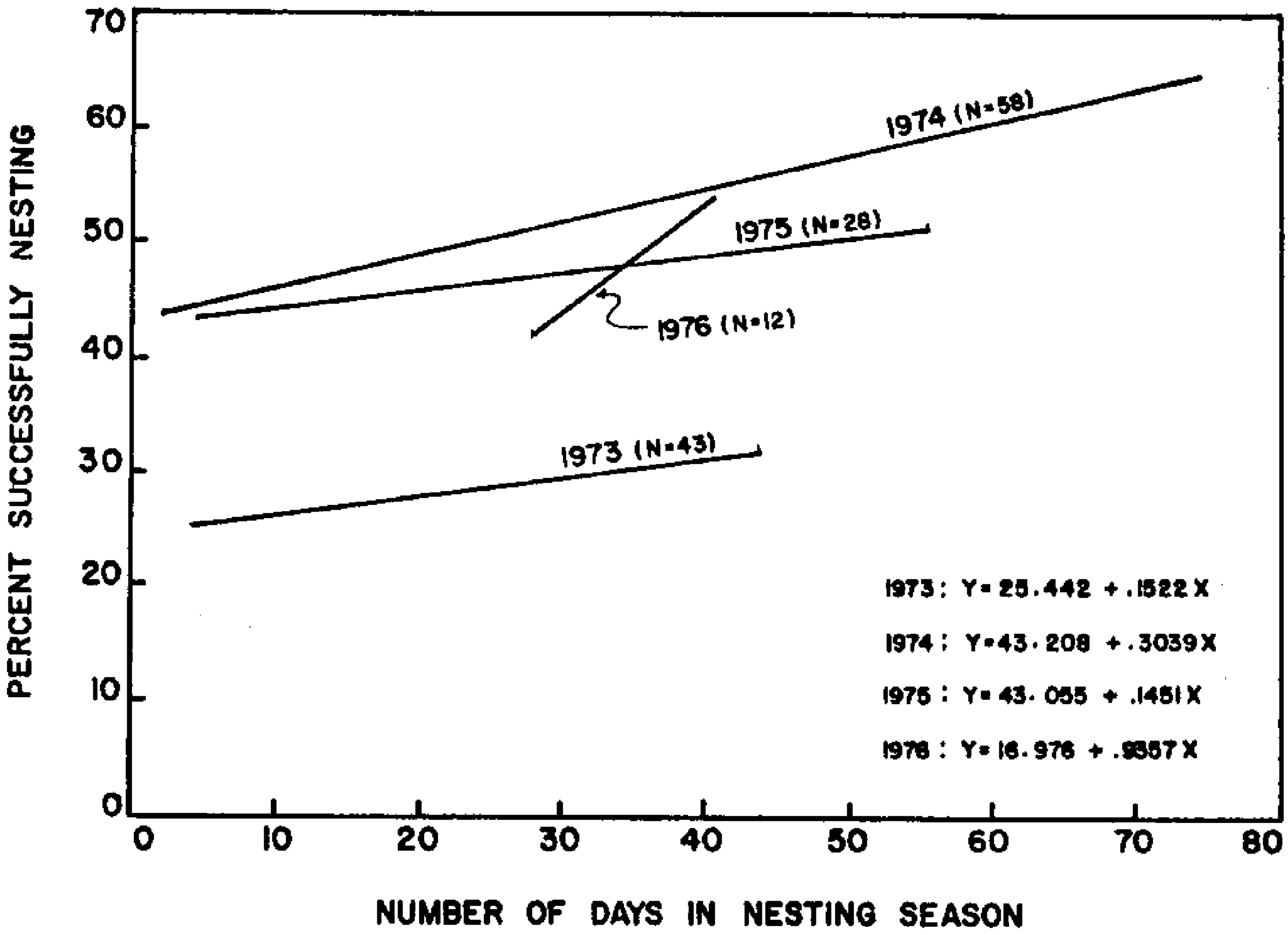

Figure 7. Percent of green turtles successfully nesting each night at East Island, French Frigate Shoals (day 1 = 1 June).

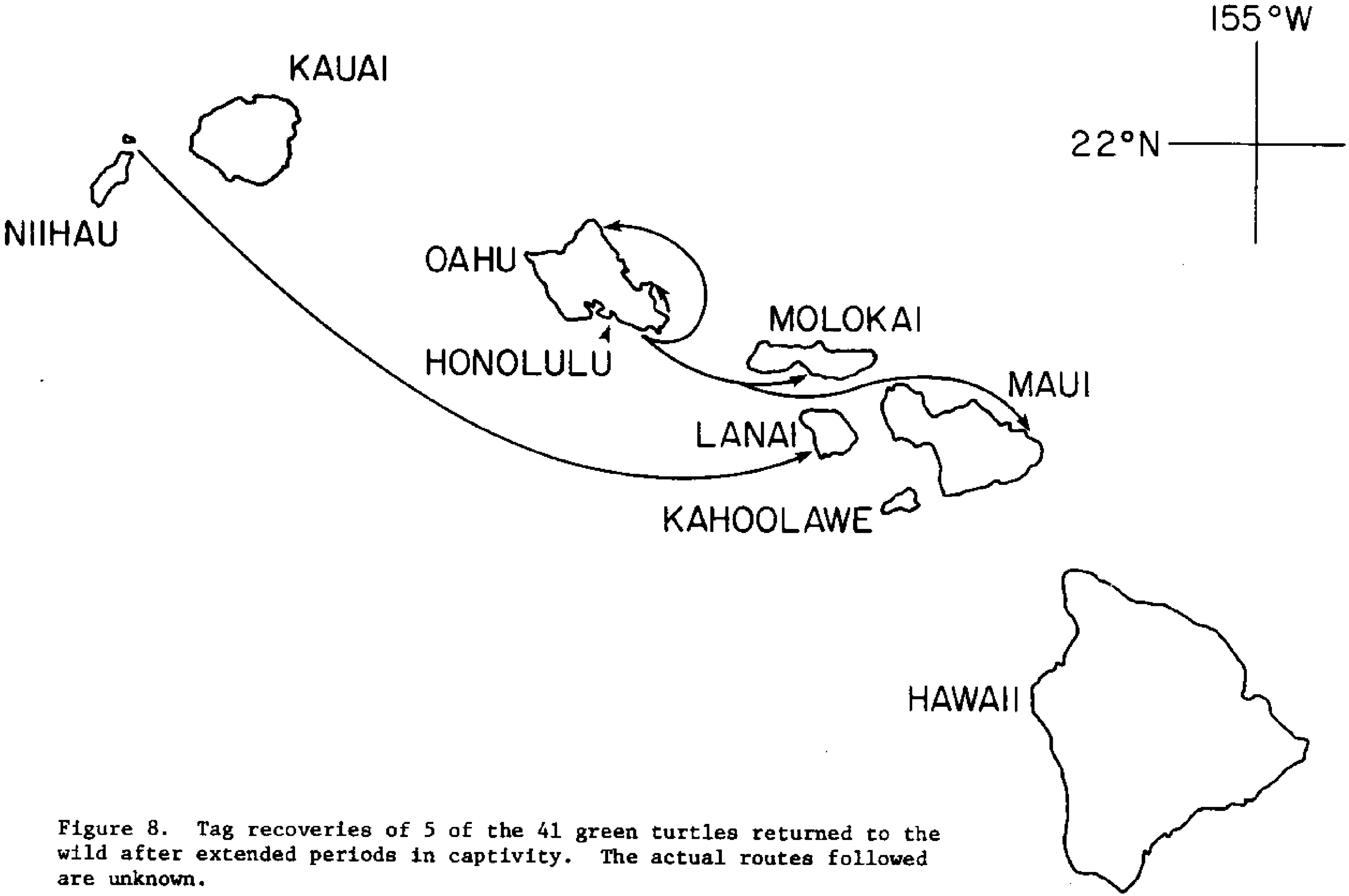

Figure 8. Tag recoveries of 5 of the 41 green turtles returned to the wild after extended periods in captivity. The actual routes followed are unknown.

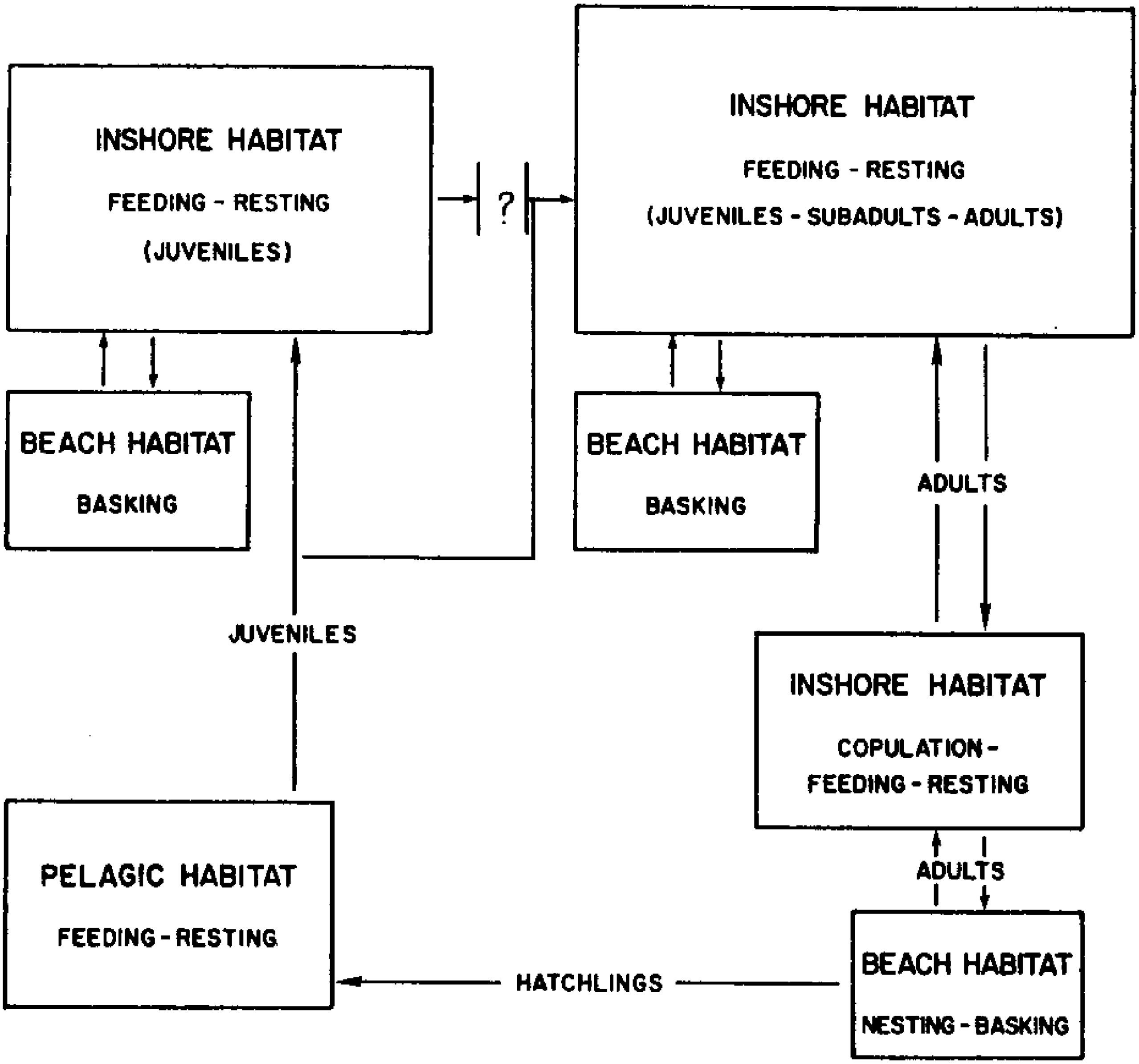

Figure 9. Life history and habitat model for Hawaiian *Chelonia* (adapted from Carr *et al.* 153).

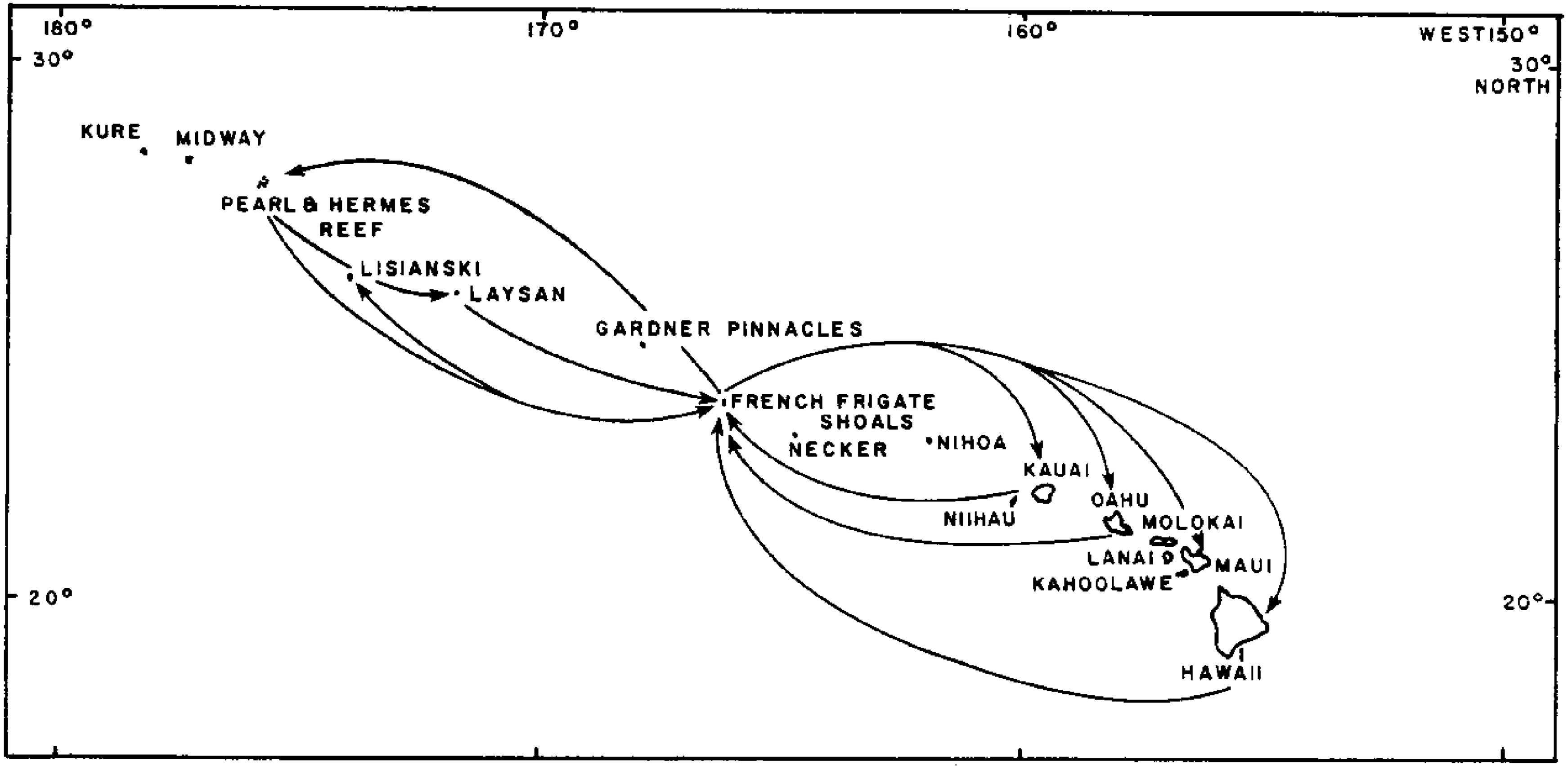

Figure 10. Long distance movements of adult green turtles in the Hawaiian Archipelago. The actual routes traveled are unknown.

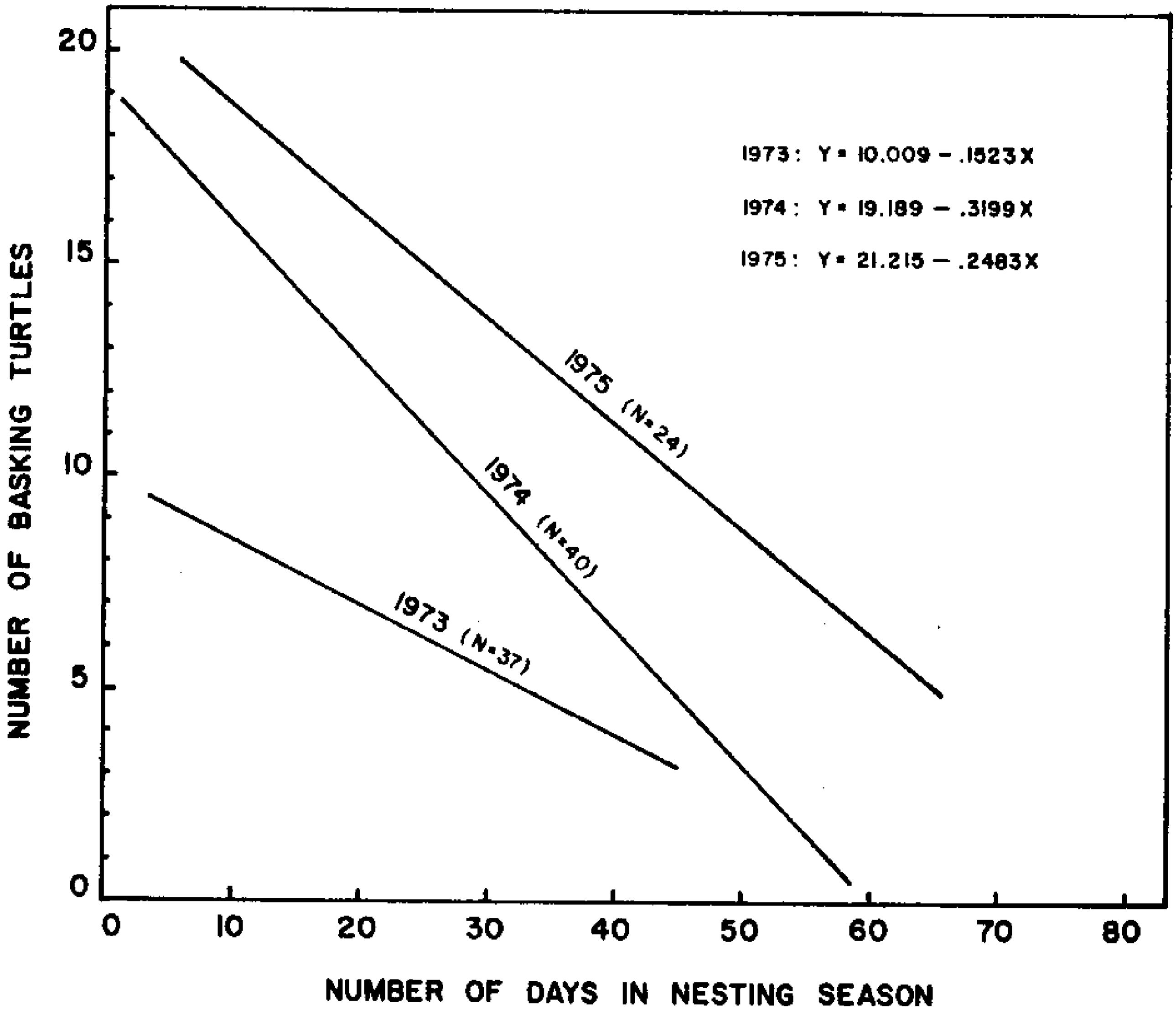

Figure 11. Incidence of daily basking at East Island, French Frigate Shoals (day 1 = 1 June).

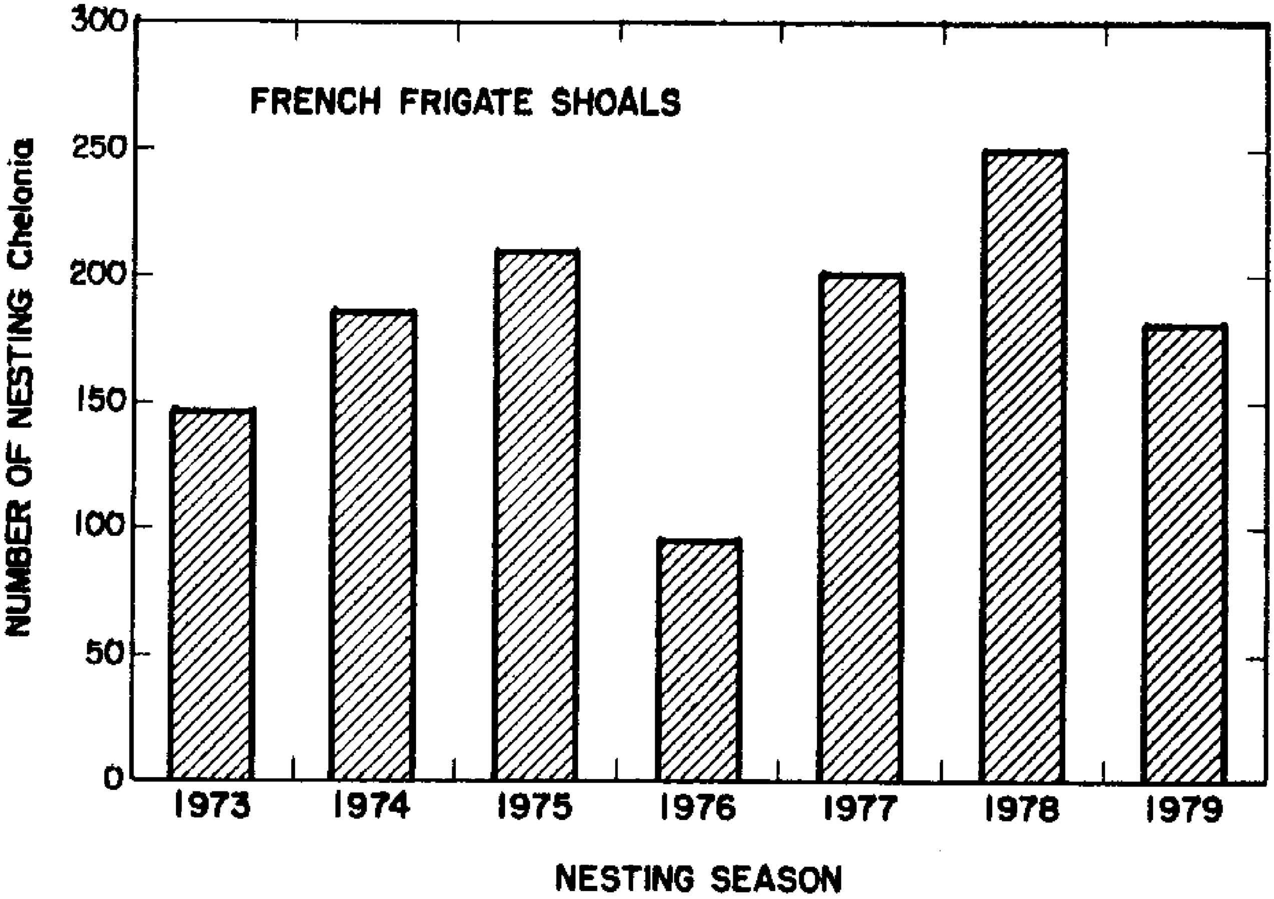

Figure 12. Number of females nesting annually at French Frigate Shoals.

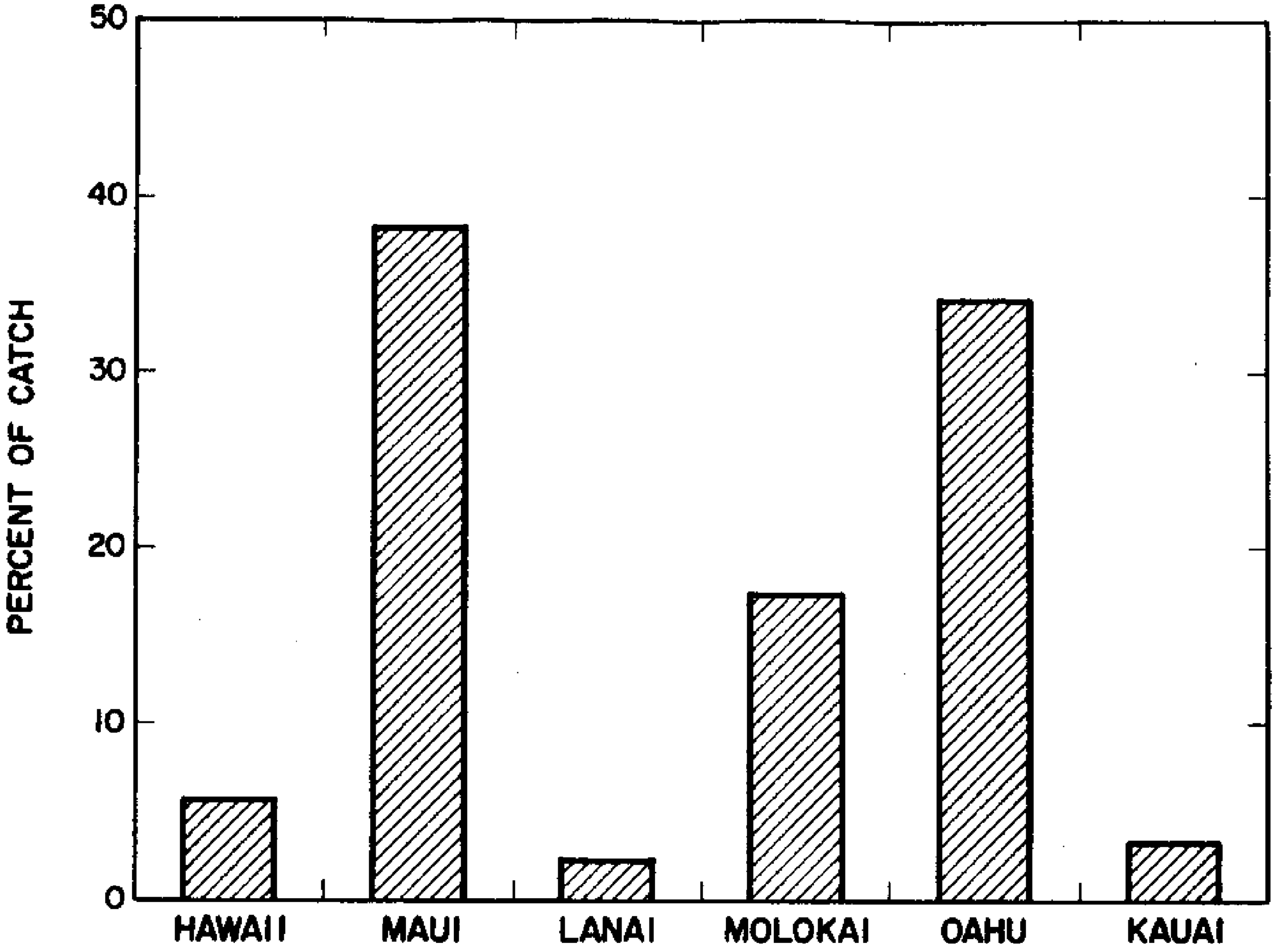

Figure 13. Percent turtle reported as being commercially captured for each of the main islands, 1948-1973.