

# GREEN TURTLE MIGRATIONS IN THE HAWAIIAN ARCHIPELAGO

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## ABSTRACT

*In order to understand better the natural history and conservation status of the unique land-basking Hawaiian green turtle population (*Chelonia* sp.), intensive tagging studies were conducted at French Frigate Shoals (24°N 160°W), a wildlife sanctuary comprising the only aggregate breeding site remaining in the 2600 km long Archipelago. Additionally, newly captured *Chelonia*, as well as individuals held for extended periods in display aquaria, were tagged and released around the large islands in the southeast. Tag recoveries of adults identified during the 1973 and 1974 nesting seasons documented migrations from French Frigate Shoals to the islands of Kauai, Oahu and Maui, distances of 713, 936 and 1069 km to the southeast, respectively, and to French Frigate Shoals from Lisianski Island and Pearl and Hermes Reef, distances of 834 and 1075 km to the northwest, respectively. A captive-held female released off Niihau travelled 658 km to French Frigate Shoals where nesting was recorded. Other animals released from captivity showed movement between the large islands, while those released shortly after capture remained in the same coastal area for up to 11 months. Combined results from the present study and previous intermittent taggings made since 1961 by Federal and State wildlife management personnel indicated that breeding colony members are derived from widely separated feeding areas within the archipelago and appear to be reproductively isolated from other Pacific *Chelonia*. Northwestern areas of the archipelago are thought to serve as important migratory stations for early life stage development.*

## INTRODUCTION

A complicating factor in the conservation of remaining populations of *Chelonia* is the periodic migrations which occur between feeding pastures and aggregate breeding grounds, locations which may be widely separated and not well known.

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Viewed in terms of navigational abilities and evolutionary adaptations, those long-distance travels that involve small oceanic islands present some of the most interesting unresolved aspects of marine turtle ecology. A green turtle population occurring in the Hawaiian Archipelago may serve as an ideal model to gain information on these problems.

Located in an isolated region of the north-central Pacific, the Hawaiian Archipelago ( $19^{\circ}$  to  $29^{\circ}$ N;  $155^{\circ}$  to  $179^{\circ}$ W) consists of large mountainous inhabited

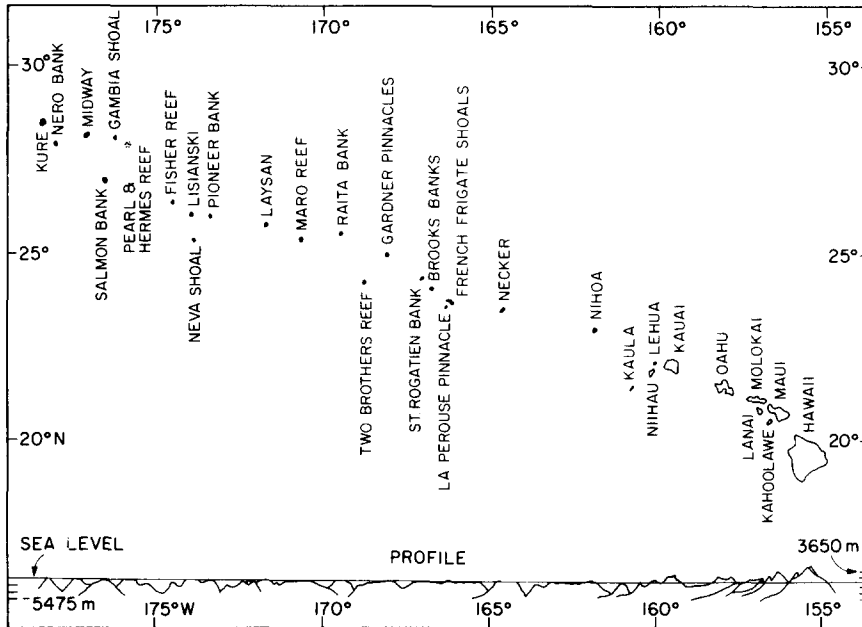


Fig. 1. Hawaiian Archipelago including submerged reefs and associated banks (after a figure made available by E. H. Bryan, Jr., of the Pacific Scientific Information Center, Bernice P. Bishop Museum, Honolulu). Hawaiian Islands National Wildlife Refuge includes Nihoa, Necker, French Frigate Shoals, La Perouse Pinnacle, Gardner Pinnacles, Laysan, Lisianski, and Pearl and Hermes Reef. Midway is a Naval Station and Kure is a Hawaii State Wildlife Refuge containing a Coast Guard Station.

islands in the southeast and a series of small volcanic and low coral islands as well as submerged reefs and banks extending to the northwest (Fig. 1). All islands are under the jurisdiction of the United States and most of the northwestern islands are uninhabited wildlife sanctuaries which are extensively utilised by massive sea bird populations and the rare Hawaiian monk seal (*Monachus schauinslandi* (Matschie)). Green turtles are present throughout the entire Archipelago and are unique among marine turtles in that both adult males and females as well as sexually immature individuals come ashore for basking purposes at select un-

disturbed sites (Fig. 2). Although *Chelonia* in the Galapagos (and possibly at other locations) were formerly known to exhibit a true land-basking habit (Dampier, 1906), except in Hawaii such behaviour now appears to be absent (P. C. H. Pritchard, pers. comm.). Systematic relationships of the Hawaiian population have not as yet been adequately defined, however the steep-contoured carapace of most females and the predominantly black-pigmented dorsal (but not ventral) surfaces of most adults of both sexes suggest a close relationship to the eastern Pacific green turtle, *Chelonia mydas agassizi* (Bocourt). Benthic algae constitute the population's major food source and identified feeding pastures which host most size categories exist in coastal shelf areas of the large islands. Previous to 1974, commercial exploitation was permitted at these locations. Although most of the northwestern islands have been legally protected since 1909 as the Hawaiian



Fig. 2. Hawaiian green turtles land basking at Whale-Skate Island, French Frigate Shoals. Also shown are monk seals and black-footed albatross chicks. Photo by G. Balazs, July 1973.

Islands National Wildlife Refuge, green turtles have nevertheless been periodically exploited at these sites with the last known instance occurring in 1959 (Strasburg, 1959). The only colonial breeding site now remaining in the Archipelago is French Frigate Shoals (24°N 160°W); however select beaches on three of the large islands (Lanai, Oahu and Kauai) still hosted remnant aggregations as recently as 40 years ago. No green turtle reproduction at present takes place in the large islands but islands to the northwest of French Frigate Shoals may on occasion host a few separately nesting females.

Little published information exists on the ecology of *Chelonia* in Hawaii. Available data, most of which involve brief basking and nesting observations, have been historically summarised for the northwestern islands of French Frigate Shoals (Amerson, 1971), Kure (Woodward, 1972), Laysan (Ely & Clapp, 1973), Pearl and Hermes Reef (Amerson, 1974) and Lisianski (Clapp & Wirtz, 1975).

Hendrickson (1969), Hirth (1971) and Balazs (1973) have presented general status reports, while Carr (1964) has noted morphological differences between juveniles and adults.

In order to obtain comprehensive information on the ecological characteristics and survival outlook of Hawaiian *Chelonia*, intensive investigations were started by the author in 1973 with initial emphasis placed on the French Frigate Shoals' breeding colony. Previous to 1973 and dating as far back as 1961, Federal and State wildlife management personnel had tagged approximately 800 green turtles during intermittent short-term inspection visits to the northwestern islands. Most of these taggings involved baskers of an adult size and many were at locations other than the aggregate breeding site. This latter accomplishment has not been possible to any extent in other marine turtle populations due to the difficulties of capturing individuals directly from the sea. Hendrickson (1969) and Amerson (1971, 1974) have listed several long-distance tag recoveries resulting from this earlier work. The present paper discusses tag recoveries that have been made in relation to studies conducted at French Frigate Shoals since 1973. In addition, data are also presented on the movements of turtles that were tagged around the large islands. Other aspects of green turtle natural history in Hawaii will be the subject of future papers.

#### OBSERVATION AND TAGGING AREAS

##### *French Frigate Shoals*

French Frigate Shoals is a crescent-shaped 26 km atoll which contains ten small sand islands, six of which are used by green turtles for nesting purposes. Two of the islands, East (4.6 ha) shown in Fig. 3 and Whale-Skate (6.8 ha), account for nearly all egg deposition. During the greater portion of the 1973 and 1974 nesting seasons (mid-May to mid-August), activity on East Island was continuously monitored and as many individuals as possible were examined and tagged using techniques that imposed the least amount of disturbance to normal behaviour. Monel tags (size 49, National Band and Tag Co., Newport, Ky. USA) were attached at both a proximal and a distal site on the trailing edge of the front flipper. The distal site was utilised to permit tag identification on basking animals without disturbing them. Periodic daytime surveys of basking activity and the presence of nesting pits were made at the other five islands. Investigations were also periodically conducted at French Frigate Shoals during other times of the year in order to obtain information on turtles present during non-nesting periods.

##### *Large Islands*

On 14 and 15 May 1973, 15 sub-adult green turtles were captured by net and tagged in the North Kona district of the Island of Hawaii at a small mixohaline



Fig. 3. East Island, French Frigate Shoals viewed from the west at an altitude of 100 m. Tower at centre of island is a remaining portion of abandoned Coast Guard Station which existed from 1944–52. Since 1952, a similar facility has been situated on Tern Island, 10 km to the northwest. Photo by G. Balazs, July 1973.

pond (Kiholo) that connects to the sea. Animals were retained for several hours and then released 2 km from the site of capture.

On 29 January 1973, ten sub-adults from the Waikiki Aquarium were tagged and released at Queen's Surf Beach on the Island of Oahu. On 24 March 1973, seven adults and four sub-adults from the aquarium were tagged and released in a remote area off the north coast of the Island of Niihau. On 10 January 1975, eight sub-adults from a private oceanarium (Sea Life Park) were tagged and released at Makapuu, Oahu. All of these animals had been originally captured in waters around the large islands and held in captivity for unknown periods which may have ranged up to ten years.

#### RECOVERIES

##### *Long-distance migrations*

For the 1973 and 1974 nesting seasons, 67 and 108 females, respectively, were examined and tagged on East Island. Due to the island's small area and the thoroughness of surveillance, taggings accounted for nearly all nesters present at this location during each season. Nesting pit estimates indicated that fewer turtles utilised Whale-Skate Island during the same periods. Recovery data for turtles

that were either observed or originally tagged at French Frigate Shoals are presented in Table 1. Three long-distance recoveries have been made at sites in the large islands and five were made at French Frigate Shoals (Fig. 4). Migrations to the large islands included turtle No. 648 that was last observed nesting at East Island on 12 July 1973 and was captured by a fisherman 55 days later in Kailua Bay, Oahu, a minimum ocean distance of 936 km. Another turtle (No. 853) was last seen nesting at Whale-Skate Island on 15 July 1974 and was captured 31 days later off Princeville, Kauai, a minimum ocean distance of 713 km. Minimum rates of travel for these two relatively short-term recoveries equalled 17 and 23 km/day, respectively, speeds comparable to those reported by Pritchard (1973) for Surinam green turtles. Turtle No. 672, tagged at East Island on 9 July 1973, was recovered on 31 July 1974 close to shore at Maalaea Bay, Maui, a minimum ocean distance of 1069 km. The animal was found in a weakened condition with the left front flipper recently amputated, presumably by a shark.

Long-range recoveries of these three females help further to establish that turtles utilising feeding pastures in the large islands travel to French Frigate Shoals for reproduction. Two other turtles originally tagged at French Frigate Shoals by Federal wildlife management personnel have also been reported as being captured in the large islands (Hendrickson, 1969).

Long-distance recoveries made at French Frigate Shoals included female No. 216 which had been released from captivity on 24 March 1973 off Niihau, 658 km to the southeast. This animal was first noted at East Island on 3 June 1974 engaged in unsuccessful nesting activity. On 4 July 1974, she was observed basking on East Island at a site seldom used by turtles for this purpose. During the same evening, successful nesting occurred and, after allowing sufficient time for incubation and hatchling emergence, subsequent examination revealed that most of the eggs had been fertile. Fertilisation in *Chelonia* is believed to result from copulation which occurs during a previous season (Carr, 1965), therefore turtle No. 216 may have been inseminated while still in captivity. Mating activity as well as the infrequent release of eggs into the water has been known to take place at the Waikiki Aquarium (Mowbray, 1965). The documented movement of this animal from the feeding pasture to the breeding site supports the generally held concept of two-way migrations occurring in *Chelonia*, a pattern that is strongly indicated by circumstantial evidence which results from one-way tagging programmes.

Other long-distance recoveries at French Frigate Shoals included three females from Pearl and Hermes Reef and one from Lisianski Island, 1075 km and 834 km, respectively, to the northwest. All of these animals had been tagged during previous years as basking adults. Although details were not given, Amerson (1974) indicated that Federal wildlife management personnel have also recorded a migration from Pearl and Hermes Reef to French Frigate Shoals, as well as the movement of two turtles in the opposite direction and one from Laysan Island to French Frigate Shoals. Additionally, no tag recoveries have ever been made from areas outside

TABLE 1  
RECOVERY DATA FOR GREEN TURTLES OBSERVED OR ORIGINALLY TAGGED AT FRENCH FRIGATE SHOALS

Tag No.	Date tagged	Location tagged/status*	Location recovered/status*	Interval (years-months)	Date recovered or first observed
699	11 June 1968	Whale-Skate, FFS-BF	1973 Nesting season	5-0	10 June 1973
372	10 July 1970	East, FFS-BF	East, FFS-N	2-11	10 June 1973
648	10 July 1970	East, FFS-BF	East, FFS-N	2-11	17 June 1973
648			Kailua Bay, Oahu-O	—	12 September 1973
391	13 July 1970	East, FFS-BF	1974 Nesting season	3-11	2 June 1974
370	10 July 1970	East, FFS-N	East, FFS-N	4-0	5 July 1974
60	7 May 1972	East, FFS-BF	East, FFS-N	2-1	3 June 1974
976	18 May 1971	Ein, FFS-BF	East, FFS-N	3-1	11 June 1974
655	20 March 1968	Lisianski-BF	East, FFS-N	6-3	4 June 1974
1048	13 March 1964	Pearl and Hermes-BF	East, FFS-N	10-3	2 June 1974
167	26 September 1966	Pearl and Hermes-BF	East, FFS-N	7-9	30 June 1974
440	21 March 1967	Pearl and Hermes-BF	Pearl and Hermes-B	4-1	27 April 1971
440			East, FFS-N	3-2	3 June 1974
216	24 March 1973	Niihau-RC	East, FFS-N	1-2	3 June 1974
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	—	15 August 1974
747	14 June 1968	East, FFS-BM	Non-nesting periods	5-4	15 October 1974
747			Trig, FFS-B	1-4	14 February 1975
464	16 March 1967	Trig, FFS-BF	Whale-Skate, FFS-B	6-7	16 October 1973
74	29 August 1965	Trig, FFS-BM	Trig, FFS-B	9-6	14 February 1975
473	14 March 1967	Trig, FFS-BF	Trig, FFS-B	7-11	19 February 1975
22	5 May 1972	Trig, FFS-BF	Trig, FFS-B	2-9	19 February 1975

\* F/M—Female/Male

B—Basking

N—Nesting

O—Offshore

RC—Release from captivity

FFS—French Frigate Shoals

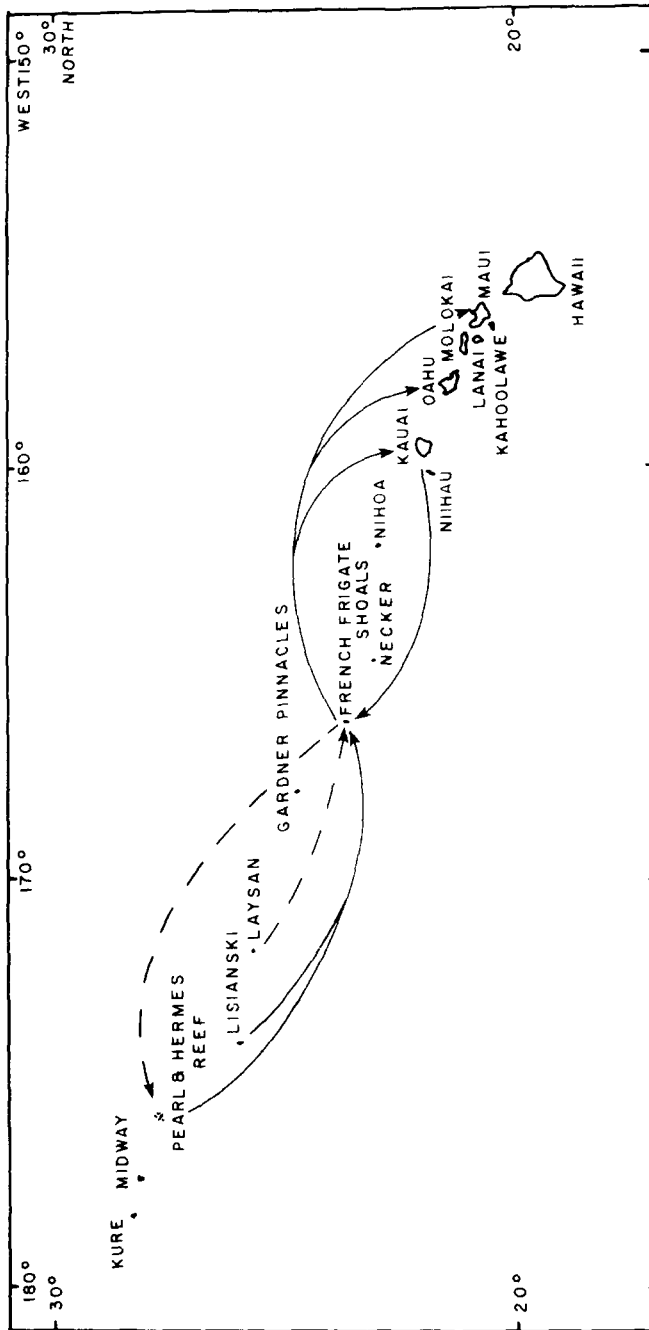


Fig. 4. Green turtle migrations recorded in the Hawaiian Archipelago that involve French Frigate Shoals. Broken lines represent migrations previously recorded by Federal wildlife management personnel other than found during the present study. Lines do not necessarily represent actual routes taken.



the Archipelago (US Fish & Wildlife Service, pers. comm.). Based on these combined findings, it would appear that animals from two widely separated locations within the Archipelago converge at the central site of French Frigate Shoals for reproduction, with subsequent return to resident pastures. Hendrickson (1969) has previously suggested the presence of such a double nesting population for Hawaii. Seasonal nesting aggregations of *Chelonia* at Costa Rica and Ascension Island (Carr, 1967), Southern Yemen (Hirth & Carr, 1970) and Heron Island (Bustard, 1974) are also derived from geographically separated areas; however, due to the Archipelago's linear configuration, the Hawaiian pattern represents an extreme case.

Seafloor spreading theory has recently been offered to explain open-sea migratory adaptations in the *Chelonia* population nesting at mid-Atlantic Ascension Island (Carr & Coleman, 1974). Similar geophysical mechanisms may also help to account for evolution of the Hawaiian pattern, particularly those portions occurring between the geologically older northwestern areas and the more recently formed French Frigate Shoals' breeding site. This migratory segment appears to be comparable to the Ascension pattern; as new islands progressively appeared and disappeared, ancestors of Hawaiian *Chelonia* may also have gradually extended their travelling distance between resident pastures and acceptable breeding grounds. This theory does not, however, seem to offer a reasonable explanation for reproductive migrations occurring from the large islands in the southeast, areas that are thought to be more recent than French Frigate Shoals.

No information exists on the distribution and carrying capacity of resident algal feeding pastures in the northwestern portion of the Archipelago. Although types of benthic algae utilised by *Chelonia* occur around the northwestern islands (Buggeln, 1965; Tsuda, 1966), standing crop densities are known for only a few sites in the large islands (Soegiarto, 1973; Doty, 1975). The ecological importance of areas to the northwest of French Frigate Shoals in comparison to areas in the southeast should not, however, be viewed strictly in terms of population numbers when such data become available. Surface drift trajectories compiled from average current measurements (US Naval Hydrographic Office, 1950) in Fig. 5 show the theoretical movements of hatchlings entering the sea at French Frigate Shoals for the months of July to October. Prevailing currents would tend to transport these turtles in a westerly direction, with some initial northerly variations for August (peak hatching month) and October. Because of the widespread absence of human contact with hatchlings after leaving the natal beach, it is unknown at what age swimming and motivation become strong enough for the animals to move independently of such environmental factors. However, juveniles as small as 6 kg have been regularly found around Laysan, Lisianski, Midway and Kure. Additionally, a substantial number in this size category have been sighted throughout the year at French Frigate Shoals, with a basker estimated to weigh not more than 2 kg observed during June 1974. Both sub-adults and adults are

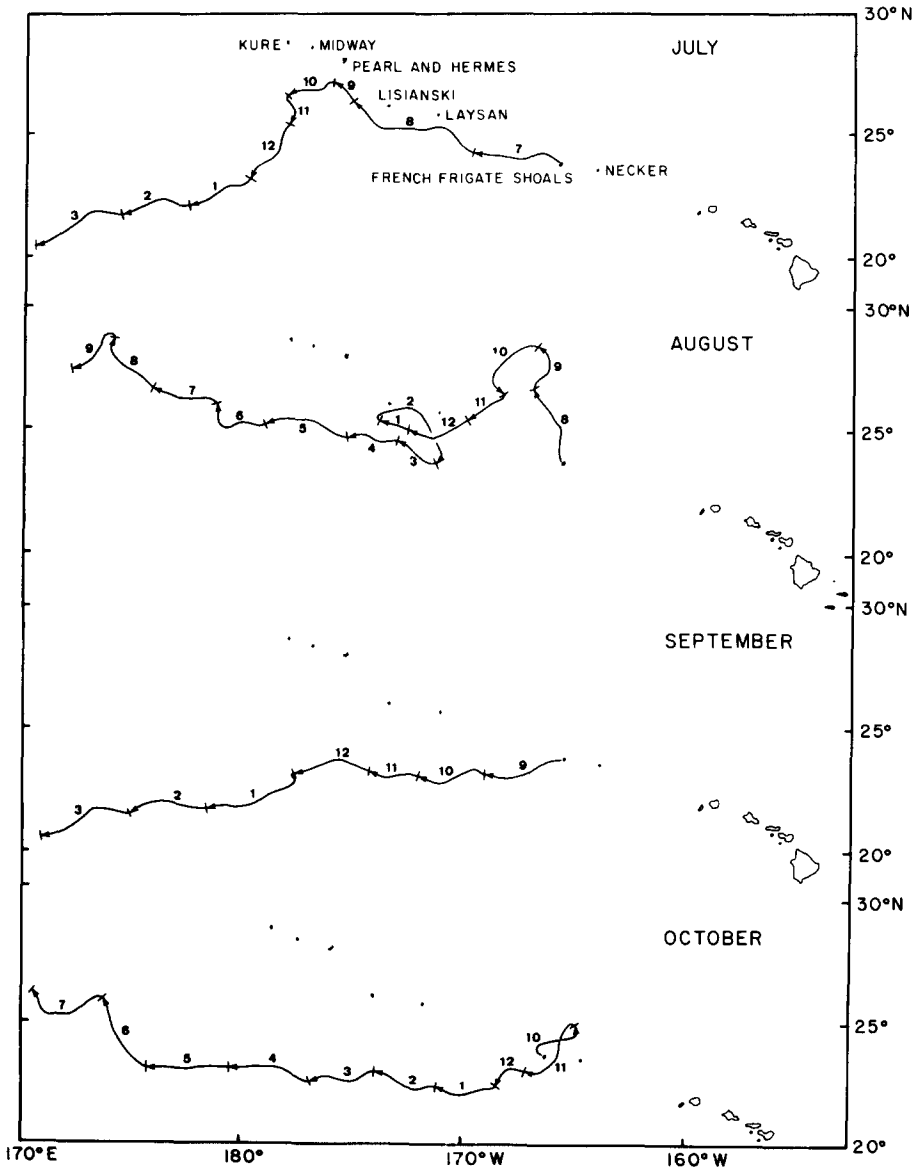


Fig. 5. Surface drift trajectories representing the theoretical movement of hatchling green turtles leaving French Frigate Shoals. Segments of paths represent estimated distance covered during each subsequent month.

also periodically found at these same locations as well as at Nihoa, Necker and Pearl and Hermes Reef. Around the large islands turtles smaller than 12 kg are less frequently reported, with the most common sizes ranging between 20–100 kg. These observations strongly suggest that northwestern areas of the Archipelago serve as stations for developmental migrations occurring in the animal's life cycle. Detailed information on such aspects of any *Chelonia* population is virtually non-existent. The role of the little-studied submerged reefs and banks (Fig. 1) in the Hawaiian pattern is a particularly important unanswered question at the present time. Such areas are not clearly defined as sanctuaries and interest exists in various forms of resource exploitation including commercial fishing and the removal of minerals and precious coral.

Limitations in the amount of food available to the newly herbivorous juvenile green turtles when they arrive at areas to the northwest of French Frigate Shoals may provide an explanation for reproductive migrations occurring from the southeast. If insufficient quantities of algae exist in northwestern pastures, resulting competition could force a percentage of the immature population to travel southeast in search of food. Such movement is to some extent supported by the author's observations of groups of juvenile turtles periodically occurring at French Frigate Shoals, thereby suggesting that arrivals and departures are taking place. Those animals reaching algal pastures around the large islands would probably establish residency, with subsequent growth and development taking place. After achieving sexual maturity, reproductive migrations to French Frigate Shoals could result, while individuals maturing in the northwestern areas would also be expected to travel to the same natal site. Aggregate breeding sites that formerly existed in the large islands may have resulted from individuals who either did not possess the ability or did not feel compelled to make an extensive migration back to French Frigate Shoals. The proposal that some young *Chelonia* can be motivated by environmental pressures to migrate as far as 2600 km against prevailing currents, while others remain to inhabit successfully more localised areas where they were transported as hatchlings, is an interesting concept that deserves further investigation. Additional supporting data in this matter would result from the recovery around the large islands of an immature turtle tagged at French Frigate Shoals or one of the other northwestern areas.

It is interesting to note that no apparent morphological differences exist between adults identified as originating from opposite ends of the Archipelago. It therefore seems unlikely that a genetic basis accounts for the geographical separation. Additionally, in order for such a trait to be inherited, selective mating would have to occur at the aggregate breeding site. This is an unlikely event in view of the apparent polygamous behaviour observed.

Because none of the adults tagged to the northwest of French Frigate Shoals have been recovered in the southeast, indirect evidence suggests that breeding colony members from different ends of the Archipelago return to their same

respective feeding pastures after each season. Such orientation would imply a degree of fixation for the feeding site. Although it is generally believed that some form of imprinting for the natal site takes place in hatchlings, little consideration has been given for a similar procedure occurring later in life for the resident feeding pasture.

Another interesting aspect of the Hawaiian pattern is that, unlike counterparts in the northwest and the *Chelonia* population using Ascension Island, animals migrating from the southeast to French Frigate Shoals are moving with prevailing currents. This would prohibit the direct use of any chemical cues originating from the breeding site for possible navigational purposes, as suggested by Koch *et al.* (1969) for Ascension Island. Indirect use could result, however, if the island goal was first bypassed with subsequent back-tracking taking place against the currents. Animals from the northwest would also be presented with the same circumstances during their return trip from French Frigate Shoals.

### *Remigrations*

Recoveries at French Frigate Shoals of turtles tagged at this location during previous years probably represent remigrations (Table 1). Nesting activity gradually ends during early August and few adults are subsequently present, indicating an almost complete departure from the atoll. Although numbers of adults begin to increase in January, the large seasonal influx accompanied by mating activity occurs during mid-April.

Reproductive cycles of green turtles nesting in Costa Rica have been well documented, with three-year intervals being most common and two- and four-year intervals occurring less frequently (Carr & Carr, 1970). Only in Surinam are turtles sometimes known to nest in successive years (J. P. Schulz, pers. comm. cited by Pritchard, 1973). Because only two nesting seasons at East Island have thus far been comprehensively studied, most of the remigration intervals shown in Table 1 cannot be considered as true reproductive cycles. Intervals believed to be accurate representations include one return after two years (No. 60) and four returns after three years (Nos. 372, 648, 976 and 440). None of the nesting turtles tagged during the 1973 season were observed during the 1974 season, so that it is unlikely that the three-year returns were combinations of smaller intervals. Intervals of four years and longer could, however, represent two or more previously unrecorded cycles. Four turtles, all originally tagged in July 1970, were recovered after apparent absences of differing intervals (3 years; and either 2 or 4 years). Carr & Carr (1970) have suggested that the length of time needed to gain reproductive readiness may be a reflection of variable ecological conditions at the feeding pasture, thereby resulting in occasional modulation. At French Frigate Shoals, different intervals may also be the result of consistently different ecological conditions existing at the widely separated feeding areas.

Two of the seven East Island remigrations were animals originally tagged at other locations in the atoll, suggesting a lesser degree of island tenacity between

seasons than reported for the Capricorn Cays on the Great Barrier Reef (Bustard, 1974). At this latter location all *Chelonia* under observation were found to return to the same island during subsequent seasons.

The exact status of previously tagged adults recovered during non-nesting periods (Table 1) is at present unknown. However, such individuals could represent late departures, early arrivals and a few permanent residents. Because virtually nothing is known about the reproductive cycles of males, it is relevant to note that adult male basker No. 747 was observed after an interval of only 1 year and 4 months.

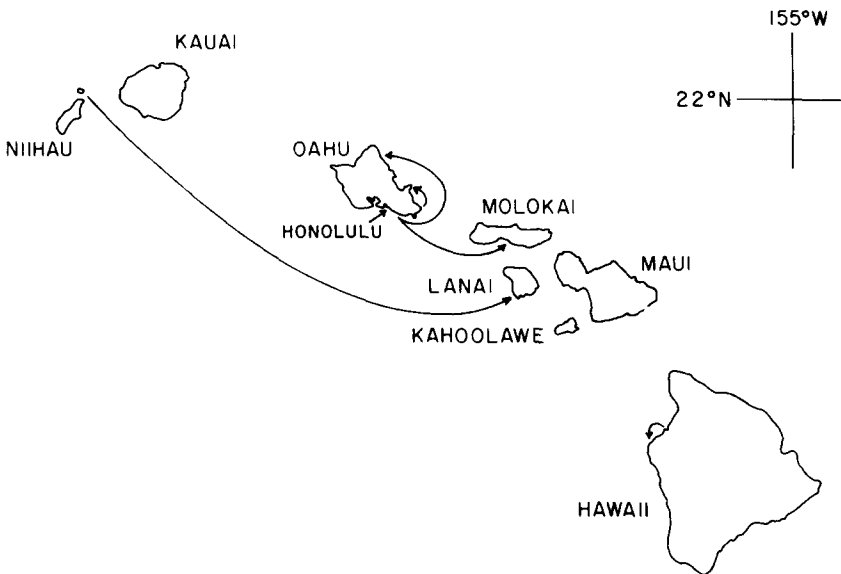


Fig. 6. Movements of green turtles recorded around the large islands of the Hawaiian Archipelago.

#### *Movements around the large islands*

Recovery data for turtles that were tagged and recaptured around the large islands are presented in Table 2. Two of these animals travelled inter-island while five were recovered near the original island of tagging (Fig. 6). Two of the sub-adults originally captured at North Kona (Kiholo) were recaptured at this same location after periods of 1 day and 4 months. A third member of this group was taken 11 months later only 9 km to the south, suggesting an extended period of residency in the general coastal area.

All other recoveries shown in Table 2 involved turtles that had been held in captivity before release and it is unknown how this may have affected the orienta-

TABLE 2  
RECOVERY DATA FOR GREEN TURTLES TAGGED AND CAPTURED AROUND THE LARGE ISLANDS OF THE HAWAIIAN ARCHIPELAGO

<i>Tag No.</i>	<i>Date tagged</i>	<i>Location tagged/status*</i>	<i>Location recovered status*</i>	<i>Interval (years-months)</i>	<i>Distance (km)</i>	<i>Date recovered</i>
604	14 May 1973	Kiholo, Hawaii-O	Kiholo, Hawaii-O	—	0	15 May 1973
605	14 May 1973	Kiholo, Hawaii-O	Kiholo, Hawaii-O	0-4	0	9 September 1973
616	15 May 1973	Kiholo, Hawaii-O	N. Kona, Hawaii-O	0-11	9	14 April 1974
316	29 January 1973	Queen's Surf, Oahu-RC	Iloli Pt., Molokai-O	0-10	81	28 November 1973
308	29 January 1973	Queen's Surf, Oahu-RC	Hauula, Oahu-O	1-0	74	20 January 1974
218	24 March 1973	Niihau-RC	Palaoa Pt., Lanai	0-8	358	9 December 1973
872	10 January 1975	Makapuu, Oahu-RC	Kailua Bay, Oahu-O	0-3	15	13 April 1975

\* O—Offshore.

RC—Release from captivity.

tion and survival abilities. Both adult female No. 218 and sub-adult No. 308 were reported as being captured at a depth of approximately 18 m, with the latter individual found sleeping in a cave in a normal manner. In contrast, sub-adult No. 872 was captured in an extremely weakened condition but with no apparent external injuries.

Several sites in the large islands seem to be well suited for the relatively efficient netting of turtles for tagging and release. The establishment of a regular sampling programme in these feeding pastures offers considerable potential for a better understanding of the life cycle of *Chelonia*, particularly when viewed in combination with continued intensive studies at French Frigate Shoals and periodic surveys of the other northwestern islands.

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