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## Movements of flyingfish (*Hirundichthys affinis*) in the eastern Caribbean

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## MOVEMENTS OF FLYINGFISH (*HIRUNDICHTHYS AFFINIS*) IN THE EASTERN CARIBBEAN

*H. A. Oxenford*

### ABSTRACT

A total of 3,559 flyingfish (*Hirundichthys affinis*) were tagged and released at three locations across the eastern Caribbean (Barbados, Dominica and Tobago) at the beginning of the 1988 fishing season (January and February) and at Tobago near the end of the season (May), to examine the extent and direction of their subsequent movements. A further 3,460 flyingfish were tagged and released at Tobago during the 1989 fishing season, between January and May, to examine seasonal variation in movements. Overall recapture rate was 4.5%. Post-tagging survival was not affected by sex or by the method of capture at tagging. However, recapture rates varied with both place and time of release. Total recapture rates were highest for fish released at Tobago and lowest for fish released at Dominica. Total recapture rates off Tobago were highest for fish released near the beginning (January/February) and at the peak (March/April) of the fishing season, and lowest for fish released near the end of the season (May). Some fish remained in the release location for several weeks. However, there was considerable mixing of adult flyingfish among eastern Caribbean islands, with 10% of all recaptures being from territorial waters other than those in which the fish were released. This suggests that *H. affinis* in the eastern Caribbean is probably not segregated into island-specific populations. Dispersion migrations were recorded in all directions, although north-westerly was most common. Dispersion rate was not affected by fish size or sex, but varied with maturity state and time of year at release. Fish at maturity Stages 2 (maturing) and 3 (mature) showed greater dispersion than fish in Stages 4 (running ripe) and 5 (spent). For flyingfish released at Tobago, dispersion was greatest in the early part of the year and decreased steadily through the season.

Despite the importance of flyingfish (*Hirundichthys affinis*) as a major fishery resource throughout most of the eastern Caribbean (Mahon et al., 1986) and the continued expansion of pelagic fishing fleets in the region, almost nothing is known about the movements of this species, and no attempt has been made to determine stock structure.

It is well known that there is considerable seasonal variation in availability of adult flyingfish to commercial fishing gear, resulting in a sharply seasonal (mid-November to mid-July) fishery for flyingfish throughout the eastern Caribbean islands (Mahon et al., 1986). Various hypotheses have been proposed to explain the seasonal variation (Brown, 1942; Hall, 1955; Mahon et al., 1981; Hunte and Mahon, 1982; Storey, 1983; Mahon et al., 1986; Khokiattiwong, 1988), but these have not been tested, and the pattern of movement remains unclear.

Tagging programs can be valuable in determining migration patterns and, in collaboration with other data, may allow determination of stock structure (Jones, 1977; White et al., 1982). For an open ocean species that has a short life-span and is commercially fished by several different fisheries, as is the case for flyingfish in the eastern Caribbean, such information is difficult to obtain by tagging. However, if tag returns can be obtained, they would provide valuable information on movements and mixing of individual fish, provide insights into determining stock structure, and assist in determining appropriate management options for the resource.

Previous attempts at tagging *H. affinis* (off Barbados: Mulloney, 1961; Lewis, 1964; off Brazil: Barroso, 1967) were successful but fairly small scale. Mulloney (1961) tagged and released 762 adult *H. affinis* off Barbados near the end of the

Table 1. Summary of release data for flyingfish (*Hirundichthys affinis*) in the eastern Caribbean showing release locations, dates and numbers of tagged fish (see Fig. 1).

Year	Location	Date	No. fish
1988	Barbados	17 Jan–24 Jan	859
	Tobago	30 Jan–02 Feb	806
	Dominica	08 Feb–11 Feb	979
	Tobago	16 May–20 May	915
1989	Tobago	17 Jan–20 Jan	500
	Tobago	13 Feb–17 Feb	230
	Tobago	13 Mar–17 Mar	1,100
	Tobago	24 Apr–28 Apr	1,520
	Tobago	27 May–30 May	110

1961 fishing season (May/June) and 18 (2.3%) were recaptured off Barbados after an average of 6 days at large (longest period 24 days). Lewis (1964) tagged and released 476 adult *H. affinis* off Barbados near the end the 1962 fishing season (May), of which 5 (1%) were recaptured off Barbados. Lewis (1964) also tagged and released 812 *H. affinis* off Barbados at the beginning of the 1963 season (January–March), of which 52 (6.4%) were recaptured off Barbados after an average of 8 days at large (longest period 50 days). Barroso (1967) tagged and released 552 *H. affinis* off the northeast coast of Brazil in 1965 during a period of peak abundance there (May–June). Fourteen (2.5%) of these were recaptured in the same area after an average of 3 days at large (longest period 15 days). These studies demonstrate that *H. affinis* can survive tagging and that at least some individuals remain in, or return to, the release location over a period of up to 50 days.

The objectives of this study were to investigate the direction and extent of movement of *H. affinis* in the eastern Caribbean on a larger scale than previously attempted, to examine seasonal variation in dispersion rates for the first time, and to provide information relevant to determining stock structure.

## METHODS

*Tagging Locations.*—Specimens of *H. affinis* were tagged and released in the eastern Caribbean over two consecutive fishing seasons. In 1988, fish were tagged and released at three widely spaced locations, primarily to investigate the extent and direction of their movements over the eastern Caribbean region. These tagging locations were therefore chosen on the basis of their geographical position within the eastern Caribbean, i.e., Dominica was chosen for its northerly position, Barbados for its central position and Tobago for its southerly position (Fig. 1). Fish were tagged and released near the beginning of the fishing season (January/February) at all three locations to ensure maximum time for recapture by fishing fleets within the region. Fish were also tagged and released near the end of the season (May) at Tobago, to increase the chances of recapture in the following season, and the chance of recapture outside the region in the “offseason” (e.g., in Curaçao and Bonaire where peak flyingfish season is reported from May–September (Zaneveld, 1961)). In 1989, fish were tagged and released at a single location, Tobago, once a month for 5 months (January–May), primarily to examine seasonal variation in dispersal rates. Tobago was chosen as the tagging location, since recapture rates had been high for fish released at this location during 1988. Release locations, and dates and numbers of tagged fish, are given in Table 1 for both years.

*Tagging Procedure.*—A total of 7,019 adult fish was tagged and released in the 1988 (3,559 fish) and 1989 (3,460) fishing seasons (Table 1). A smaller tag than used in the studies by Mulloney (1961), Lewis (1964) and Barroso (1967) was chosen for this study to ensure minimal interference with the normal swimming and flight behavior of the flyingfish (size range: 190–270 mm FL). The tag (Floy Tag FTF-69) which was designed for use on 100mm fingerlings, was a 5 × 3 mm, brightly colored plastic disc bearing only an identification number. The lack of a return address necessitated that the tagging program be widely publicized throughout the region. Tag reward posters were therefore placed

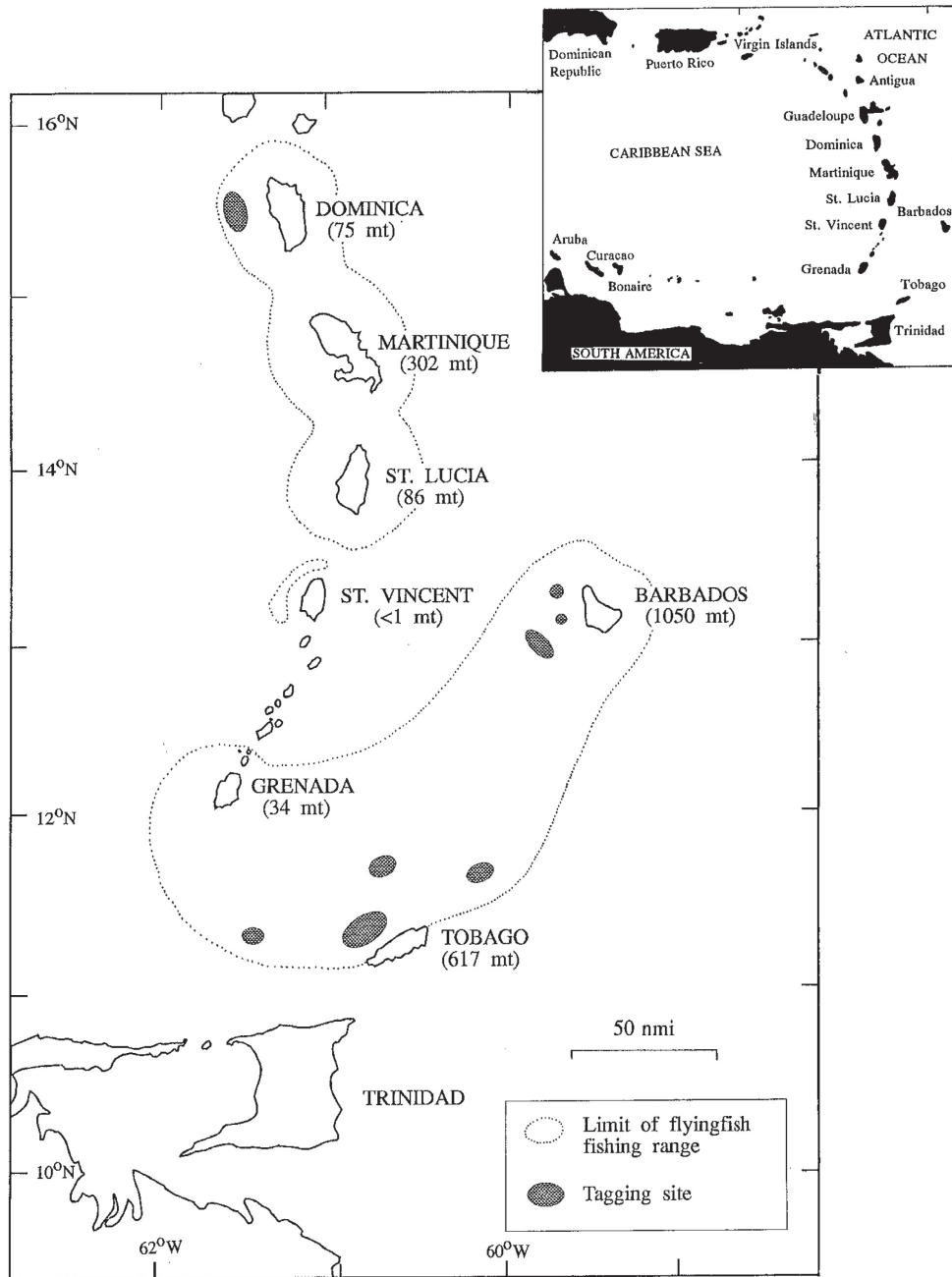


Figure 1. Map of study area showing eastern Caribbean islands, flyingfish fishing ranges and tagging sites. Numbers are estimated total landings of flyingfish (January–July 1988) from the waters around each island.

at all landing sites, markets, fishery offices and fish processing plants across the eastern Caribbean and also in the Netherlands Antilles at Curaçao and Bonaire. Local newspaper articles, local television, and local and regional radio interviews in English, French and Creole were also used to advertise the program.

The tagging technique is described briefly below (see Oxenford, 1988 for details). The tag wound was minimized by using a new fine sewing needle to apply each tag. An interperitoneal antibiotic injection of oxytetracycline (single dose:  $100 \text{ mg} \cdot \text{kg}^{-1}$  body weight) was also administered to approximately one third of the tagged fish in 1988 and a double dose was given to approximately 5% of the fish in 1989, as part of an aging validation study. The tagging procedure took approximately 30 s per fish and tagged fish were released immediately. Release positions were determined by dead-reckoning, radio direction finder or satellite navigator, depending on the distance from shore and the equipment available on the tagging vessel. The method of capture, tag number, place and date of release, and whether the fish received an antibiotic injection was recorded for each tagged fish. To minimize handling time and stress to the fish, size was not measured at tagging, although the sex was noted for all running ripe (Stage 4) individuals in 1989.

*Recapture Data Collection.*—The tag number was recorded for all recaptures. The amount of additional information that could be collected varied according to the stage at which the tag was detected, and whether the whole fish, or just the tag was returned. For the 46% of recaptures which were detected by fishermen at the time of capture, precise information on the date and place of capture were recorded. For the 15% which were detected by vendors, information on the date and often the approximate area of recapture were recorded. Less information was obtained from the 1% that were not detected until consumer purchase and the 39% which were detected by commercial processors. With the latter, time-at-large could only be estimated as being less than the number of days between tagging and detection, since up to 2 weeks could have elapsed between capture and tag detection. In most cases in 1988, processors had bought the flyingfish directly from 'ice-boats' known to be fishing in the area between Barbados, Grenada and Tobago. However, since the place of capture could not be defined any more accurately than this, it was recorded as unknown. In many cases in 1989, processors had contracted ice-boats to buy flyingfish directly from commercial fishermen in Tobago and the approximate area of capture, although not the date of capture, was therefore known for these boats.

All returned recaptured fish ( $N = 220$ ) were measured for fork length, and the sex and reproductive stage of the gonads (Lewis et al., 1962) were recorded.

*Data Analysis.*—Travel distance for all recaptures was measured as the shortest straight-line distance between the release and recapture position. Where recapture position was given only by country and coastline (e.g., off west coast of Grenada) the recapture position was taken as 10 nmi off the midpoint of the given coastline. Fish whose recapture positions were only given by country were not included in the "distance travelled" data set.

Total recapture rates were taken as the percentage of all releases which were recaptured. Recaptures were further categorized as "local" (for fish recaptured in the same territorial waters as they were released), or "dispersed" (for fish recaptured in territorial waters other than those in which they were released).

A comparison of local recapture rates between different release locations in 1988 was attempted to examine differences in retention of tagged fish between release locations. The assumption was that if fish were not recaptured in local waters (indicating retention), then they had presumably dispersed to distant waters outside the fishing range of commercial fishing fleets, or into other territorial fishing ranges. This analysis required information on the relative abundance of untagged *H. affinis* at the three release locations in 1988 (to assess the "dilution factor" when releasing tagged individuals), and information on the size of flyingfish catches at the three locations in 1988 (to assess the probability of local recapture).

Flyingfish catch data from local waters (defined as within 50 nmi of the coast) were obtained for each release location, for the period January–July 1988. Catch data for Dominica and Tobago were obtained from the respective Government Fisheries Divisions both of which had, in late 1987, implemented a flyingfish catch data collection system. Those for Tobago were subsequently corrected to reflect additional catches from local Tobago waters by Barbados ice-boats. Catch data for Barbados were obtained from the Government Fisheries Division which has been collecting reliable catch data for flyingfish since 1958. These data were subsequently corrected to remove ice-boat catches from areas outside local waters.

Although catch data were available from Government Fisheries Divisions, fishing effort data have not been recorded for all locations, and units of fishing effort have not yet been standardized between islands in the eastern Caribbean. Indices of flyingfish abundance could not therefore be generated using commercial CPUE data. However, visual survey data for adult *H. affinis* (number of flyingfish observed per 0.5 nmi transect survey) were available from the April/May 1988 Eastern Caribbean Flyingfish Abundance Survey Cruise. Details of visual survey data collection are given in Oxenford et al. (1989). All visual survey data collected within 50 nmi of Dominica, Barbados and Tobago were used to generate a mean *H. affinis* abundance index for each location for the 1988 fishing season. An index of tagged flyingfish abundance (number of tagged releases/*H. affinis* abundance index) was then calculated. This index, together with total *H. affinis* catch data, was used to generate an index of

expected local recapture (total catch/tagged fish abundance index), which could be compared with actual recapture numbers.

## RESULTS

*Total Recaptures.*—Recapture data for both years are summarized in Table 2. The total tag returns for 1988 releases was 103 (total recapture rate of 2.9%) and for 1989 was 206 (total recapture rate of 6.3%), giving an overall total recapture rate for the 2-year period of 4.5%. Infection resulting from tagging is believed to have been minimal since all but one of the returned fish were in excellent condition.

The sex ratio of tagged fish recorded in 1989 from running ripe individuals did not differ from the sex ratio of recaptures in that year (Tagged fish sex ratio = 565 (56%) female to 444 (44%) male; recaptured fish sex ratio = 90 (54%) female to 78 (46%) male; Chi squared  $2 \times 2$  contingency test:  $\chi^2 = 0.343$ ,  $v = 1$ ,  $P = 0.558$ ), suggesting no difference in post-tagging survival of males and females. Moreover, there was no apparent difference in post-tagging survival of fish which were captured at the time of tagging by barbless hook and those captured by dipnet (Chi squared  $2 \times 2$  contingency test:  $\chi^2 = 0.250$ ,  $v = 1$ ,  $P = 0.619$ ), nor between fish receiving a single dose of antibiotic and those which did not (Chi squared  $2 \times 2$  contingency test:  $\chi^2 = 1.525$ ,  $v = 1$ ,  $P = 0.217$ ). However return rates for fish receiving a double antibiotic dose were lower than those which did not (Chi squared  $2 \times 2$  contingency test:  $\chi^2 = 10.290$ ,  $v = 1$ ,  $P < 0.005$ ). Therefore all injected fish receiving a double dose (185 released fish and 1 returned) were omitted from the analyses.

Total recapture rates varied with place and time of release. For fish released early in the season (January/February), total recapture rates varied between fish released at Dominica (0.5% of releases), Barbados (4.3%) and Tobago (6.0%) (Chi squared  $3 \times 2$  contingency test:  $\chi^2 = 43.083$ ,  $v = 2$ ,  $P < 0.001$ ). For fish released at Tobago over the 2-year period, total recapture rates varied between fish released early in the season (January/February: 6.2% of releases), in mid-season (March/April: 6.5%) and late in the season (May: 1.3%) (Chi squared  $3 \times 2$  contingency test:  $\chi^2 = 42.194$ ,  $v = 2$ ,  $P < 0.001$ ). This trend of highest recaptures for fish released in mid-season and lowest recaptures for fish released late in the season, is even more marked when only fish which were known to be recaptured within 30 days of their release are considered (Table 3).

The reproductive stages of gonads for all returned fish are given separately by sex and season of recapture in Table 4. The majority of males (57%) were in running ripe (Stage 4) condition, whereas the majority of females (60%) were fully spent (Stage 5) at recapture. The proportion of fish at each reproductive stage did not vary significantly with season for males (Chi squared  $4 \times 3$  contingency test:  $\chi^2 = 11.587$ ,  $v = 6$ ,  $P = 0.072$ ). For females, a significantly higher proportion of mature (Stage 3) fish were recaptured early in the season ( $\chi^2 = 13.612$ ,  $v = 6$ ,  $P = 0.034$ ; Table 4). The proportion of fish at each reproductive stage did vary between the main recapture locations (St. Lucia, Barbados and Tobago) for both males (Chi squared  $4 \times 3$  contingency test:  $\chi^2 = 24.751$ ,  $v = 6$ ,  $P < 0.001$ ) and females ( $\chi^2 = 26.246$ ,  $v = 6$ ,  $P < 0.001$ ; Table 5). Relatively more running ripe (Stage 4) and spent (Stage 5) fish were recaptured at Tobago than at the other locations.

The exact date of recapture was reported for 129 tagged fish. Of these 13% were not recaptured until more than 1 month after their release. The longest period at large before recapture was 121 days (recorded for 2 fish) and the mean time-at-large was 20 days. The greatest recorded displacement of a tagged fish was 200

Table 2. Summary of recapture records for tagged flyingfish (*Hirundichthys affinis*) released in the eastern Caribbean, showing total recaptures, local recaptures and dispersed recaptures separately by place and time of release

Year	Release location	Release month	Total tagged	Total recaptures			Local recaptures (recaptures in tagging area)			Dispersed recaptures (recaptures away from tagging area)			Recaptures from unknown area	
				No.	% Total releases	Mean days at large	No.	% Total recaptures	Mean days at large	No.	% Total recaptures	Mean days at large	No.	% Total recaptures
1988	Barbados	Jan	859	37	4.3	20.2	25	67.5	18.1	11	29.7	24.8	1	2.7
	Tobago	Jan/Feb	806	48	6.0	21.8	17	35.4	33.2	8	16.7	12.3	23	47.9
	Dominica	Feb	979	5	0.5	29.7	1	20.0	7.0	4	80.0	41.0	0	—
	Tobago	May	915	12	1.3	11.3	12	100	11.3	0	—	—	0	—
Totals			3,559	103*	2.9	20.4	55	53.4	19.3	23	22.3	22.4	25*	23.3
1989	Tobago	Jan	314	31	9.9	20.5	13	41.9	16.0	4	12.9	28.0	14	45.2
	Tobago	Feb	230	5	2.2	28.0	4	80.0	30.0	1	20.0	26.0	0	—
	Tobago	March	1,100	97	8.8	20.4	94	86.9	18.9	2	2.1	58.5	1	1.0
	Tobago	April	1,520	72	4.7	18.6	67	93.1	18.6	0	0	—	5	6.9
	Tobago	May	110	1	0.9	—	1	100	—	0	0	—	0	—
Totals			3,274	206	6.3	20.2	179	86.9	18.8	7	3.4	37.8	20	9.7
Overall			6,833	309*	4.5	20.3	234	75.7	18.9	30	9.7	26.3	45*	14.6

\* Total includes a recaptured fish whose tag # was lost.

Table 3. All flyingfish (*Hirundichthys affinis*) recaptured within 30 days of release off Tobago, shown separately by time of season at release

Time of season at release	Releases (No.)	Recaptures (within 30 days) (No.)	Releases (%)
Early (Jan/Feb)	1,350	17	1.3
Mid (Mar/Apr)	2,620	57	2.2
Late (May)	1,025	4	0.4

nmi and the fastest estimated speed of travel was greater than 16 nmi per day (from Barbados to Martinique in <7 days).

No tagged fish were recaptured in the following season for either 1988 or 1989 releases, and no tagged fish were recaptured at either Curaçao or Bonaire.

*Local Recaptures.*—Many tagged fish (76% of all recaptures) were recaptured in the vicinity of their release location. Local recaptures indicate that some fish remain in, or return to, the vicinity of tagging over a period of up to 4 months. The mean time-at-large for local recaptures was 19 days (Table 2).

As with total recaptures, local recapture rates also varied with place and time of release. For fish released early in the season (January/February), local recapture rates varied between Dominica (0.1% of releases), Barbados (2.91%) and Tobago (2.11%) (Chi squared  $3 \times 2$  contingency test:  $\chi^2 = 24.243$ ,  $v = 2$ ,  $P < 0.001$ ). For fish released at Tobago over the 2-year period, local recapture rates varied between fish released early in the season (January/February: 2.54% of releases), in mid-season (March/April: 6.15%), and late in the season (May: 1.27%) (Chi squared  $3 \times 2$  contingency test:  $\chi^2 = 59.964$ ,  $v = 2$ ,  $P < 0.001$ ).

A more critical comparison of local recapture rates between tagging locations was conducted by comparing observed and expected local recaptures at each location. Mean abundance indices calculated for adult *H. affinis* using visual survey data showed significant differences in abundance of untagged fish between the three tagging locations (Kruskal Wallis analysis of variance:  $H_c = 10.205$ ,  $N_1 = 201$ ,  $N_2 = 127$ ,  $N_3 = 119$ ,  $P = 0.006$ ; Table 6). An index of tagged flyingfish abundance was thus calculated separately for each location (Table 6). These in-

Table 4. Gonad reproductive stages of recaptured flyingfish (*Hirundichthys affinis*) in the eastern Caribbean, shown separately by sex and time of season at recapture

Sex	Reproductive stage	Time of season at recapture				Total
		Early (Jan/Feb)	Mid (Mar/Apr)	Late (May/June)	Unknown	
Female	1 immature	0	0	0	0	0
	2 maturing	0	1	0	0	1
	3 mature	5	0	1	1	7
	4 running ripe	3	5	8	18	34
	5 spent	9	12	5	36	62
Total females		17	18	14	55	104
Male	1 immature	0	0	0	0	0
	2 maturing	3	0	0	1	4
	3 mature	12	2	4	6	24
	4 running ripe	8	22	5	26	71
	5 spent	7	5	3	10	25
Total males		40	29	16	43	124

Table 5. Gonad reproductive stages of recaptured flyingfish (*Hirundichthys affinis*) in the eastern Caribbean, shown separately by sex and place of recapture

Sex	Reproductive stage	Recapture location					Total
		Martinique	St. Lucia	Barbados	Tobago	Unknown	
Female	1 immature	0	0	0	0	0	0
	2 maturing	0	0	1	0	0	1
	3 mature	0	1	3	3	0	7
	4 running ripe	0	2	0	25	7	34
	5 spent	0	1	4	49	8	62
Total females		0	4	8	77	15	104
Male	1 immature	0	0	0	0	0	0
	2 maturing	0	2	0	2	0	4
	3 mature	0	3	4	12	5	24
	4 running ripe	1	1	5	54	10	71
	5 spent	0	0	2	20	3	25
Total males		1	6	11	88	18	124

dices, together with total *H. affinis* catches from Dominica, Barbados and Tobago waters in 1988 (January–July) were used to calculate indices of expected recaptures for each location (Table 6). The ratio of expected local recaptures was 1:7.6:7.4, and the ratio of observed local recaptures was 1:25:17 for Dominica, Barbados and Tobago respectively (Table 6). Although the observed number of recaptures was lowest for Dominica and highest for Barbados as the model predicts, the ratio was not the same as predicted. Compared with Dominica, local recaptures at Barbados and Tobago were higher than expected, and recaptures at Barbados were slightly higher than expected compared with Tobago.

*Dispersed Recaptures.*—There was dispersal and mixing of tagged fish among islands, particularly near the beginning of the fishing season, with 10% of recaptures dispersing to territorial waters other than where they were released (Table 2). Dispersion migrations for 1988 and 1989 releases are shown in Figure 2. The greatest mixing was recorded at Grenada and St. Lucia. Fish recaptured at Grenada had travelled from three different release sites at the southerly tagging location (Tobago), from the central tagging location (Barbados) and from the northerly tagging location (Dominica). Fish recaptured at St. Lucia had also travelled from all tagging locations, Dominica, Barbados and Tobago (Fig. 2). The widest range of dispersal migrations was recorded from the central tagging location, Barbados. Fish dispersing from Barbados were recaptured at Tobago (SSW), Grenada (SW), St. Lucia (WNW), Martinique (NW) and Dominica (NW) (Fig. 2). Fish dispersing from the southerly tagging location (Tobago) were recaptured at Grenada (NW),

Table 6. Indices of abundance, total catch, expected ratio of local recaptures (calculated) and actual numbers of local recaptures for flyingfish (*Hirundichthys affinis*) in the eastern Caribbean, shown separately by the three release locations

Release location	No. tagged releases	<i>H. affinis</i> abundance index (fish/0.5 nmi)	Tagged fish abundance index (releases/ <i>H. affinis</i> abundance index)	Total catch (Jan–Jun 1988) (kg)	Expected recapture index (catch/tagged abundance index)	Expected recapture ratio	Actual No. local recaptures
Dominica	979	7.39	132.48	74,934	565.63	1	1
Barbados	859	3.82	224.87	1,050,233	4,323.21	7.6	25
Tobago	806	5.46	147.61	616,978	4,179.78	7.4	17

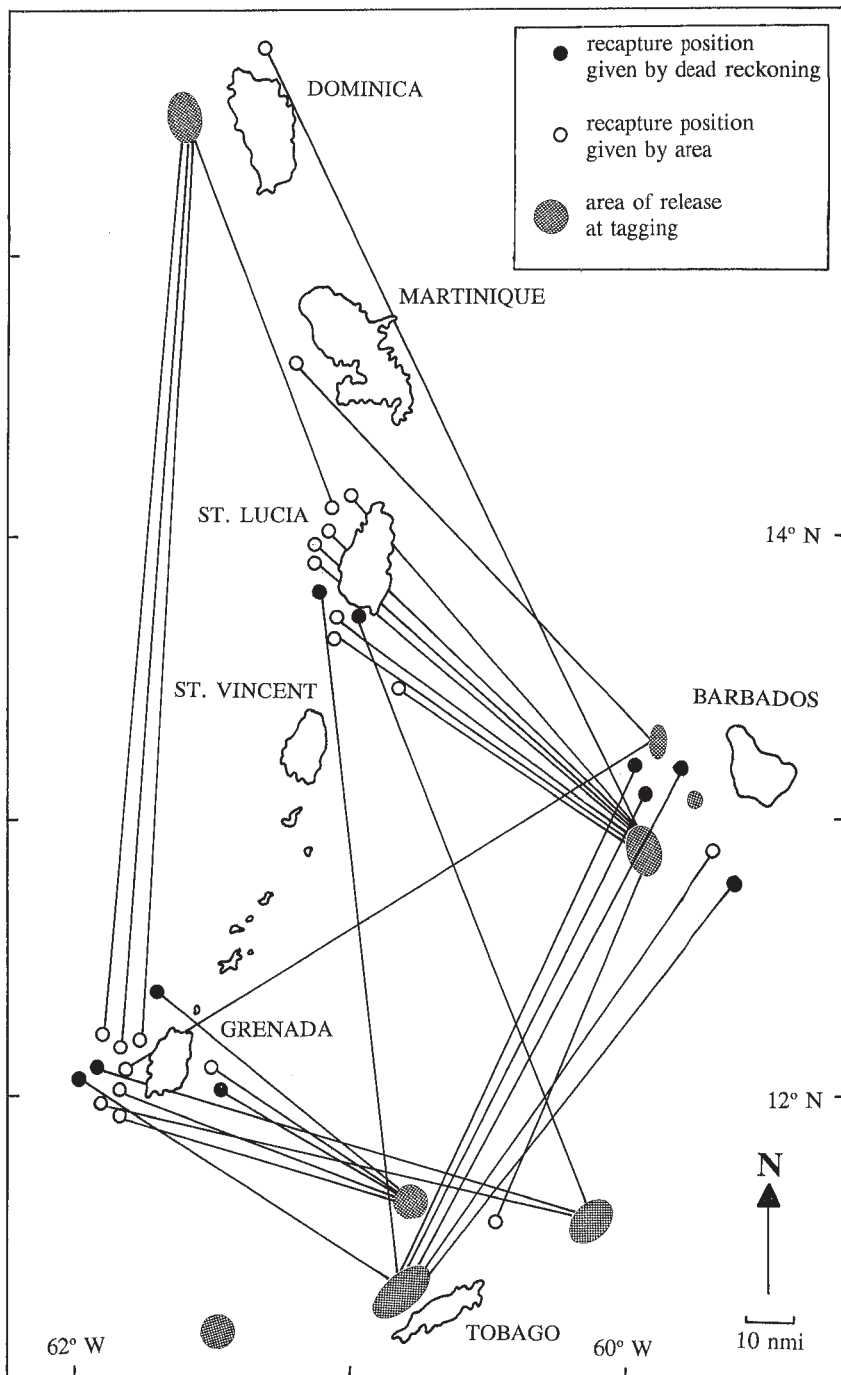


Figure 2. Dispersal migrations for tagged flyingfish (*H. affinis*) released in 1988 and 1989 in the eastern Caribbean.

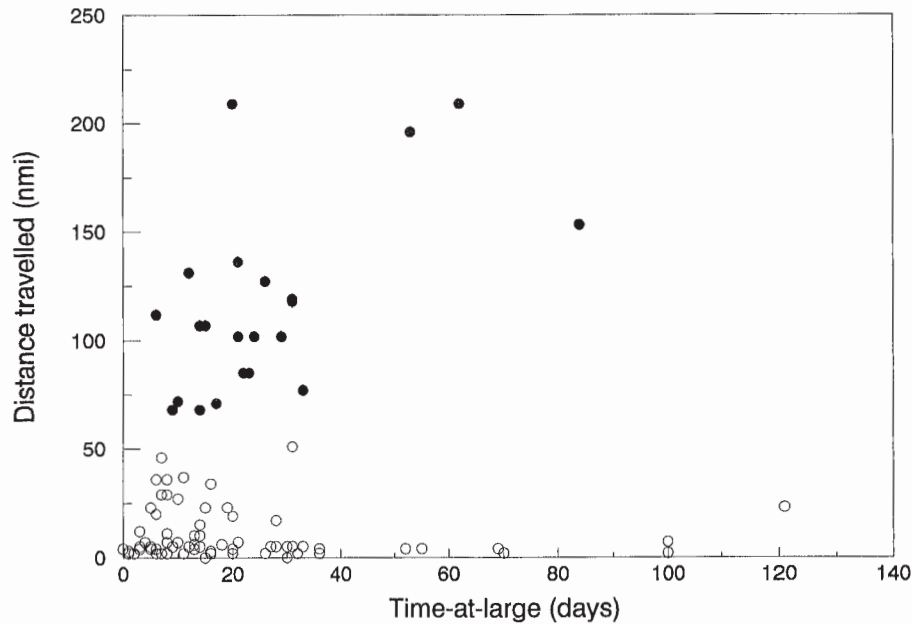


Figure 3. Relationship between distance travelled and time-at-large for tagged flyingfish (*Hirundichthys affinis*) in the eastern Caribbean. Clear circles indicate fish recaptured in the same territorial waters as released (local recaptures); solid circles indicate fish recaptured in territorial waters other than where released (dispersed recaptures).

Barbados (NE) and St. Lucia (N). Fish dispersing from the northerly tagging location were recaptured at St. Lucia (S) and Grenada (S).

The relationship between distance travelled and time-at-large is shown in Figure 3 and indicates that dispersion from tagging sites was rapid. More than half (54%) of the dispersion migrations (for which exact time-at-large was known) occurred within 21 days of release (Fig. 3). The mean time-at-large for dispersed recaptures was 26 days (Table 2).

As with total and local recapture rates, dispersal rates also varied with both place and time of release. For fish released early in the season (January/February), dispersal rates varied between fish released at Dominica (80% of recaptures), Barbados (29.7%) and Tobago (15.5%) (Chi squared  $3 \times 2$  contingency test:  $\chi^2 = 6.222$ ,  $v = 2$ ,  $P = 0.045$ ). For fish released at Tobago over the 2-year period, dispersal rates varied between fish released early in the season (January/February: 15.5% of recaptures), in mid-season (March/April: 1.2%) and late in the season (May: 0%) (Chi squared  $3 \times 2$  contingency test:  $\chi^2 = 13.966$ ,  $v = 2$ ,  $P < 0.001$ ).

Dispersion did not appear to be affected by fish length, since no significant difference was found in the mean size of dispersed (221.3 mm FL) and non-dispersed (224.8 mm FL) fish (Two sample  $t$ -test:  $t = -1.270$ ,  $v = 178$ ,  $P = 0.206$ ). Dispersion was not affected by sex, since there was no difference in the sex ratio between dispersed (11 males: 6 females) and non-dispersed (97 males: 85 females) fish (Chi squared  $2 \times 2$  contingency test:  $\chi^2 = 0.815$ ,  $v = 1$ ,  $P = 0.367$ ). However, maturity state did appear to affect dispersion in both males and females, with comparatively greater dispersion occurring in maturing and mature (Stages 2 and 3) fish, than in running ripe and spent (Stages 4 and 5) fish (Chi square  $4 \times 2$  contingency tests: for males:  $\chi^2 = 17.790$ ,  $v = 3$ ,  $P = 0.0005$ ; for females:  $\chi^2 = 21.212$ ,  $v = 3$ ,  $P < 0.0001$ ; Table 7).

Table 7. Gonad reproductive stages of recaptured flyingfish (*Hirundichthys affinis*) in the eastern Caribbean, shown separately by sex for those recaptured in territorial waters other than where they were released (dispersed) and those recaptured from the release location (not dispersed)

Reproductive stage	Male		Female	
	Dispersed	Not dispersed	Dispersed	Not dispersed
1 immature	—	—	—	—
2 maturing	2	2	1	0
3 mature	5	14	2	5
4 running ripe	3	58	2	25
5 spent	0	22	1	53
Total	10	96	6	83

## DISCUSSION

The overall recapture rate of 4.5% obtained in this study was high compared with other studies of oceanic pelagics in the Caribbean (Mather et al., 1972; Beardsley et al., 1972; Bertolino, 1985), especially given that *H. affinis* is a small, short-lived species with a maximum life expectancy of no more than 2 years (Lewis et al., 1962; Storey, 1983). The artisanal nature of most of the flyingfish fleets in the eastern Caribbean, combined with the high profile advertising campaign for the tagging program and instant high tag return rewards (U.S. \$10 per tag), ensured high tag detection and reporting rates. Most flyingfish are individually handled by fishermen at capture (hand picked from gillnets) and again during wholesale (individually counted), thus giving ample opportunity for tag detection by fishermen. Furthermore, flyingfish are usually retailed by number, either whole or hand filleted so that even if fishermen failed to detect tags, they were likely to be found by retailers. Even with the larger-scale fishing operations involving ice-boats and direct wholesale of fish to processors, the probability of tag detection was high, since each fish is individually hand-processed (descaled and filleted) before packaging.

A high recapture rate, low rate of observed tag wound infection and no difference in post-tagging survival between hooked and dipnetted individuals and between fish treated with a single dose antibiotic and those not treated, indicate that the tagging procedure resulted in minimal stress to the fish.

Assessing differences in total recapture rates between tagging locations is complex and also assumes that detection and reporting rates are the same for all locations. This assumption is reasonable given the high profile advertising program, the high incentive rewards offered and the high level of interest in the program shown by all sectors of the fishing industry over the region. The probability of recapture will depend on i) the number of tagged fish relative to untagged fish, and ii) the total number of fish caught. Therefore recapture rates can be expected to be lower when tagged fish are released into, or travel into, areas of higher fish abundance. Similarly, recapture rates can be expected to be lower where catches are lower. The observed differences in total recapture rates between different release locations is particularly problematic to interpret given that adult *H. affinis* abundance over the eastern Caribbean is highly variable geographically (Oxenford et al., 1989), and that flyingfish catches varied over the eastern Caribbean in the 1988 fishing season from zero outside the limited fishing ranges of commercial fleets (no chance of recapture) to between 1 and 1,000 mt inside the fishing ranges of different eastern Caribbean islands (variable chance of recapture) (Fig. 1).

A comparison of local recaptures between tagging locations was possible by calculating indices of expected local recapture at each location (based on indices of local *H. affinis* abundance and on local catches) and comparing these with observed numbers of local recaptures. Results indicate that local recaptures were considerably higher than expected at the central (Barbados) and southern (Tobago) locations, compared with the northerly location (Dominica). This suggests either that a greater proportion of tagged *H. affinis* stayed around the central and southern islands than around Dominica in the north (i.e., dispersion rate from Dominica was higher), or that post-tagging mortality for Dominica releases was higher.

That total recapture rates (as % of releases) for fish released off Tobago varied with time of release is not surprising given that fishing effort in the region is highly seasonal. Total recapture rates can be expected to be highest for fish released early in the season, since tagged fish will be available for recapture over an extended period, and lowest for those released late in the season when fishing effort will soon decline and therefore the time available for recapture will be much shorter. However, if time available for recapture is standardized by only considering fish which were recaptured within 30 days of release, differences in total recapture rate with season are expected to be minimal, since fishing effort is relatively steady from January through June and only declines significantly from mid-July onwards. Interestingly, the observed trend in total recapture rates became even more marked when time available for recapture was standardized. This suggests that fish are most susceptible to recapture in mid-season (March/April), less so near the beginning of the season (January/February) and have a low probability of recapture near the end of the season (May). Since a bimodal pattern of spawning with a minor spawning peak in December and the major spawning peak in May is well known for *H. affinis* in the eastern Caribbean (Storey, 1983; Khokiattiwong, 1988), this pattern of recapture rates supports the suggestion that flyingfish suffer high post-spawning mortality which is particularly severe after peak-spawning in May (Khokiattiwong, 1988; Lao, 1989). This is further supported by the fact that there were no tag returns from the following fishing season for either 1988 or 1989 tags, indicating that flyingfish have non-overlapping generations.

The maximum and mean times-at-large recorded in this study were considerably longer than reported by other tagging studies of flyingfish (Mulloney, 1961; Lewis, 1964; Barroso, 1967) even when considering only data for local recaptures. Tag induced mortality caused by the larger tags used in previous studies could explain these differences.

Dispersed recaptures show that adults of *H. affinis* move between islands of the eastern Caribbean and mix freely, indicating that an island-discrete stock structure for *H. affinis* in the eastern Caribbean is unlikely. Throughout this study, the migration passage taken by individuals is assumed to be represented by a straight line drawn between the points of release and recapture. In practice this is very unlikely, but a straight line does indicate the net movement by any individual fish over the given time period. The dispersal pattern indicated by all dispersed recaptures (Fig. 2), is not necessarily indicative of the general movement of adult flyingfish in the eastern Caribbean, since no attempt was made to recapture fish outside the limited range of commercial fishing fleets. As such, any fish migrating to locations outside these fishing ranges would not have been detected. It is therefore not surprising that the widest range of dispersal migrations was recorded from the central tagging location, with commercial flyingfish fisheries in several islands to the NW and SW. Only a limited range of dispersal migrations could be detected from the northerly and southerly tagging locations, since there are no commercial flyingfish fisheries in islands north of Dominica or south of Tobago.

The direction and extent of dispersal migrations showed no seasonal pattern, but a difference in dispersal rates with season was detected for fish released at Tobago, indicating that flyingfish move between islands more frequently in the early part of the season (January/February), less frequently in mid-season (March/April) and very little near the end of the season (May). This information, together with a difference in dispersal rates between maturity stages (decreasing dispersion with increasing maturity), suggests that flyingfish mix freely among islands prior to the May peak spawning, but remain in the same location when spawning condition is reached. Further study is needed to examine dispersal rates prior to the earlier but smaller spawning peak in December. It is predicted on the basis of these results that dispersal rates would be high in November and decline in December for a relatively brief period.

That dispersal rates appear to be the same for males and females suggests a similar migration behavior between the sexes. The fact that the majority of recaptured males were in running ripe condition, whilst the majority of females were fully spent, suggests that the intervals between spawning episodes for individual fish may be shorter for males. The higher proportion of spawning and spent fish recaptured at Tobago compared with St. Lucia and Barbados suggests that this may be a favored spawning area for *H. affinis*.

In conclusion, the dispersion results demonstrate that there is considerable mixing of adults of *H. affinis* over the eastern Caribbean prior to peak spawning, indicating a common stock for the region. Furthermore, the stock may not extend into the southern Caribbean (e.g., to Curaçao and Bonaire). The sharp decrease in total recapture rate following the month of peak spawning, and the absence of any tag returns in the subsequent season, support the hypothesis put forward by Khokiattiwong (1988) and Lao (1989), of high post-spawning mortality and non-overlapping generations, to explain the intra-annual variation in availability of flyingfish in the eastern Caribbean. Finally, the high retention rates indicated for adult flyingfish around central and southern locations (higher than expected local recapture rates), particularly around Tobago (lower dispersal rate compared with other locations), suggests that flyingfish tend to aggregate towards the south. Aggregation and a high proportion of spawning and spent recaptures at Tobago supports the idea that Tobago may be an important spawning area for *H. affinis* in the eastern Caribbean.

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