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Distribution and relative abundance of flyingfish (Exocoetidae) in the eastern Caribbean. I. Adults

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ABSTRACT: We investigated the distribution and relative abundance of adult flyingfish by transect visual survey across a 67 500 square nautical mile (nmi^2) area of the eastern Caribbean from April 10 to May 6, 1988, using a 26 m research vessel and a rotating team of 23 observers. Flyingfish abundance (no. of fish per 0.5 nmi) was significantly correlated between data sets from port and starboard viewing stations, and we detected no evidence of observer bias. Flyingfish abundance varied significantly across the survey area, but was not correlated with any of the surface water characteristics measured (temperature, salinity, NO_2-NO_3-N, PO_4-P, silicate). For the commercially harvested species *Hirundichthys affinis*, as well as for the smaller *Parexocoetus brachypterus*, abundance was high west (leeward) of the Lesser Antilles island chain and in an area between and to the east of Barbados and Tobago, and it was low between the Lesser Antilles chain and Barbados and Tobago. *Cypselurus cyanopterus* was less common than *H. affinis* and *P. brachypterus*, and was largely restricted to the northeast of the survey area. Flyingfish distribution was patchy in all geographical zones of the survey area, mean patch width being 3.9 nmi and mean inter-patch distance 2.0 nmi. Patch width and patch density (fish density in patch) were positively correlated with each other and with flyingfish abundance on a transect, and inter-patch distance was negatively correlated with fish abundance. Both within and outside of patches, flyingfish occurred in schools. Flyingfish fleets from eastern Caribbean islands presently fish across areas of both high and low *H. affinis* abundance. Moreover, *H. affinis* abundance did not appear to decrease towards the east or west boundaries of the survey area, suggesting that catch rates may be similar to current rates if fishing fleets expanded their present geographical range. The high abundance indices obtained for *P. brachypterus* indicate that the feasibility of developing a small-scale fishery for this species in the eastern Caribbean should be further explored.

KEY WORDS: Flyingfish · Adults · Visual survey · Eastern Caribbean

INTRODUCTION

Flyingfish (Exocoetidae) are common globally in tropical and subtropical waters. They are a significant component of the epipelagic food chain (Parin 1968), and an important fishery resource in Indonesia (Parin 1960, Zerner 1986), the Pacific Islands (Gillet & Ianelli 1991), Korea, China and the Sea of Japan (Parin 1960, Shiokawa 1969), southern California, USA (Herald 1969), West Africa (Gibbs 1981), South India (Pajot & Prabhakaradu 1993), northeastern Brazil (Cruz 1965, Barroso 1967, Ogawa & Alves 1971, Gibbs 1978), the Netherlands Antilles (Zaneveld 1961, Gibbs 1978), and the eastern Caribbean (Gibbs 1978, Mahon et al. 1986).

Twelve species of flyingfish have been reported from the eastern Caribbean (Gibbs 1978, Storey 1983, Khokiattiwong 1988, Lao 1989). Of these, *Hirundichthys affinis* (Günther) is the principal species taken by the commercial flyingfish fishery, and is important as prey and bait for species taken by other sport and commercial fisheries (Oxenford et al. 1993).

There have been several studies of the biology of *Hirundichthys affinis* near Barbados (e.g. Hall 1955, Lewis et al. 1962, Lewis 1964, Storey 1983, Khokiattiwong 1988, Lao 1989), a few studies of the smaller flyingfish *Parexocoetus brachypterus* (Gosse) (e.g. Lewis 1959, 1961, Khokiattiwong 1988, Lao 1989), and

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no studies of the larger flyingfish *Cypselurus cyanopterus* (Cuvier & Valenciennes). However, regional distribution and relative abundance have not been studied for any flyingfish species in the eastern Caribbean. It is therefore not known: (1) whether fishing fleets are presently targetting areas of higher relative abundance of *H. affinis* within the current fleet ranges; (2) whether a zone of comparable *H. affinis* abundance occurs outside of the current fleet ranges, and hence whether there is scope for geographical expansion of fishing effort; or (3) whether the distribution and abundance of *P. brachypterus* or *C. cyanopterus* make them suitable for exploitation in the eastern Caribbean.

This information is lacking because data on the quantitative distribution of oceanic pelagic species is difficult and expensive to collect. A cost-effective way of investigating quantitative distribution is by visual survey, as is feasible for marine mammals which are large enough to be counted from the air or from a moving vessel as they surface (e.g. Holt 1987, Barlow 1988), for large tuna schools, which can be viewed aerially in some regions (see Horwood & Cushing 1977), and for pilchards whose bioluminescent intensity can be assessed from aerial photography and used to estimate fish density (Cram & Hampton 1976). The habit of flyingfish of taking to the air and gliding when vessels approach makes visual survey feasible. Studies which have used this to assess flyingfish distribution include Beklemishev & Pasternak (1960), Shuntov (1973, cited in Zuyev & Nikol'skiy 1980), Parin (1975, cited in Storey 1983), Karaman (1980), Nesterov & Grudtsev (1980), and Zuyev & Nikol'skiy (1980). The methodology was reviewed by Parin (1983) and a modified technique was proposed by Freon (1988) for Caribbean flyingfish. A version of this was used by Khokiattiwong (1988) to investigate school size, distribution and relative abundance of flyingfish over a 1 yr period along a single onshore-offshore transect off the northwest coast of Barbados. He concluded that the 3 common genera of eastern Caribbean flyingfish (i.e. *Hirundicthys affinis*, *Cypselurus* spp., and *Parexocoetus brachypterus*) could be distinguished in flight, and that the technique was appropriate for detecting both seasonal and spatial variation in abundance of flyingfish, particularly over large spatial scales.

The objective of this study was to assess the distribution and relative abundance of adult flyingfish in the eastern Caribbean for the first time, using a visual survey technique. The data were also used to evaluate whether the current distribution of regional fishing effort for *Hirundichthys affinis* coincides with their regional distribution, and whether commercial exploitation of other flyingfish species is feasible based on their distribution and abundance.

METHODS

Data collection. *Hirundichthys affinis* is common throughout the eastern Caribbean between January and June, with peak abundance between April and May (Mahon et al. 1986). *Parexocoetus brachypterus* occurs year-round off Barbados (Lewis 1961, Khokiattiwong 1988), with peak abundance between March and June (Lewis 1961). We visually surveyed flyingfish adults during the period of peak abundance across a 67500 square nautical mile (nmi^2) area of the eastern Caribbean encompassing the known fishing range of the flyingfish fleets (Fig. 1), using a technique similar to that proposed by Freon (1988) and to that used by Khokiattiwong (1988). The survey was conducted from a 26 m research vessel, the RV 'Provider', from April 10 to May 6, 1988, during daylight hours (05:00 to 19:00 h) at vessel speeds of 5 to 8 knots. Two viewing stations were established above the bridge of the vessel, one looking to port, the other to starboard. Observers sat in a fixed location at each station, and viewing windows were framed by the railing uprights of the vessel. Each observer viewed for 1 h and rested for 30 min, such that observations were continuous and synchronised between port and starboard viewing stations along each transect. Each observer was ultimately used at both port and starboard viewing stations. A total of 23 observers were used, each joining the ship for 1 or more of the 4 cruise legs. All groups of airborne flyingfish observed through the viewing windows were considered as schools, and the number of fish in each school and the number of schools seen every 5 min were recorded. School sizes of more than 15 individuals were estimated to the nearest 5; those over 30 were estimated to the nearest 10.

Experienced observers could differentiate between 3 species of flyingfish, and recorded them separately. *Cypselurus cyanopterus* was recognised by its large size and dark brown 'wings'. *Parexocoetus brachypterus* was recognised by its small size, translucent wings and, under ideal viewing conditions, by its long, spotted dorsal fin. *Hirundichthys affinis* was recognised by its medium size and translucent wings. When fish flight times were very short, or viewing conditions were difficult (e.g. when looking into early morning or late evening sun), or when observers were inexperienced, no attempt was made to identify the species. Species that were seen infrequently (e.g. *Exocoetus* spp.) were recorded as unidentified flyingfish even when recognisable.

Additional parameters that may have affected viewing efficiency or the flight response of the fish were recorded hourly. These were sun position relative to observer, direction of vessel travel relative to waves, and time of day. Surface water samples were collected

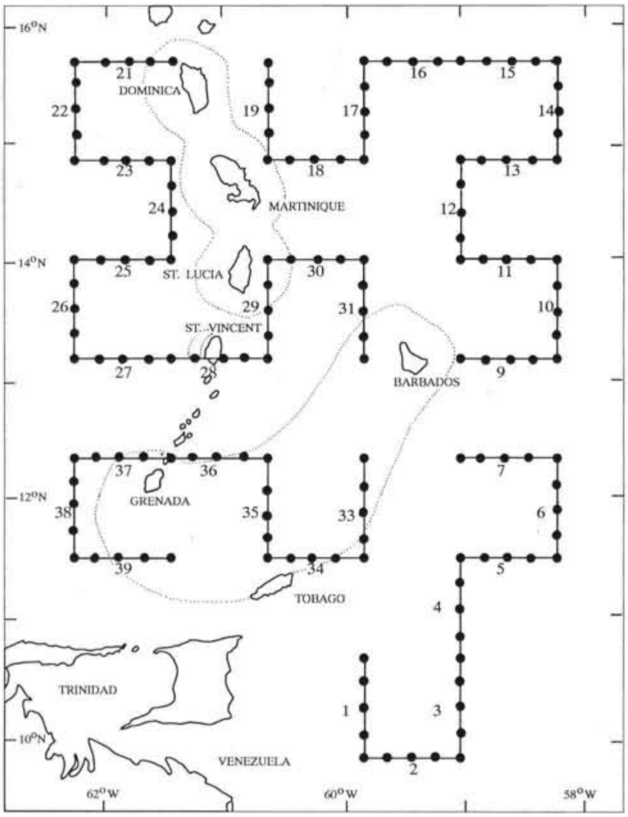

Fig. 1. Area surveyed for adult flyingfish in the eastern Caribbean, showing (——) cruise track, (●) surface water sampling stations, and (········) approximate area fished by regional flyingfish fishing fleets

along each transect at 4 stations spaced 12.5 nmi apart (Fig. 1). These were analysed immediately for temperature to the nearest 0.1°C using a bucket thermometer, and then stored in air-tight glass bottles or frozen in plastic bottles for later laboratory analyses of salinity (glass bottles), and total reactive phosphorus (PO_4-P), oxidised nitrogen (NO_3-NO_2-N) and silicate (plastic bottles), using standard titration methods (see Strickland & Parsons 1972). Qualitative information on water colour to distinguish blue and green water masses was also recorded.

Data handling. The number of fish recorded in each 5 min interval was standardised to a travel distance of 0.5 nmi (i.e. the distance travelled in 5 min at 6 knots), to give a standard index of flyingfish abundance. This was done by multiplying the number of fish recorded every 5 min by an adjustment factor (between 0.73 and 1.22) depending on the actual speed of the vessel. The mean number of fish per 0.5 nmi could then be calculated for each transect (transect mean), either for all fish or separately for fish viewed from port and starboard stations. Of a total of 1908 paired observations, there were 14 missing port observations and 18 missing starboard observations. Missing port observations were filled by multiplying the starboard observation by 0.81 (port mean / starboard mean), and missing starboard observations were filled by multiplying the port observation by 1.23 (starboard mean / port mean). Flyingfish abundance index data were non-normal and could not be normalised by standard transformations. Non-parametric statistical analyses have therefore been used throughout.

We termed flyingfish abundance within 0.75 nmi of water sampling stations 'localised abundance', and used this to examine local effects of water characteristics on abundance. Localised abundance is the mean of the 3 standard indices of abundance recorded over the 0.75 nmi either side of a sampling station (i.e. over a total distance of 1.5 nmi). Fine-scale distribution patterns of flyingfish were examined by investigating flyingfish patch width, patch density and inter-patch distance for smoothed (3 point running average) abundance data along visual transects. We defined a flyingfish patch as any area where the number of flyingfish observed in a 0.5 nmi interval exceeded the overall median abundance index for the entire survey area (i.e. 7.08 fish per 0.5 nmi). Patch dimensions and characteristics were not calculated for incomplete patches, i.e. those which were entered before the start of the day's observations or not exited by the finish of the day's observations. Patch width and inter-patch distance were estimated to the nearest 0.5 nmi, a limit set by the unit of sampling. Patch density (an index of flyingfish density in a patch) was taken as the mean number of fish per 0.5 nmi recorded in that patch, and patch size (an index of the number of fish in a patch) was taken as the total number of fish recorded in the patch. Two of the 4 patch characteristics (patch size, inter-patch distance) were non-normal and could not be normalised by standard transformations. Data on patch characteristics have therefore been analysed non-parametrically.

Flyingfish abundance indices and school sizes were examined separately by species for a subset of the data recorded by 'experienced' observers. Flyingfish abundance data by species were treated as described above for total flyingfish abundance data.

RESULTS

Flyingfish abundance and data reliability

A total of 31 264 flyingfish adults were recorded during the 159 h of simultaneous port and starboard observations along the 34 straight-line transects, covering 950 nmi of the eastern Caribbean (Fig. 1).

The overall mean flyingfish abundance index (i.e. no. of fish per 0.5 nmi) was 7.28 viewed from the port window (transect mean range: 0.15 to 22.49), and 8.97 from the starboard window (transect mean range: 0.43 to 25.14). The difference reflects the slightly larger size of the starboard window, but could also arise if there was a consistent port/starboard asymmetry in noise direction produced by the vessel. Port and starboard abundance data sets were significantly correlated at the level of each 0.5 nmi unit, as well as at the transect level (Spearman rank correlation: for transect means, $r_s = 0.759$, $n = 34$, $p < 0.0001$, Table 1; for 0.5 nmi intervals, $r_s = 0.369$, $n = 1908$, $p < 0.0001$; for 0.5 nmi intervals excluding zero pairs, $r_s = 0.162$, $n = 1594$, $p < 0.0001$). Port and starboard data have therefore been pooled for most subsequent analyses. The overall mean abundance for pooled data was 16.25 fish per 0.5 nmi travelled (transect mean range: 0.71 to 47.63; Table 1).

Table 1. Mean flyingfish abundance indices in the eastern Caribbean. The value for each transect is the mean of the numbers of fish along each 0.5 nmi of the transect. n: number of 0.5 nmi units surveyed per transect. Data by transect are presented separately for port and starboard observations, and for all observations combined. The locations of the transects are shown in Fig. 1

Transect no.	n	Mean flyingfish abundance index		
		Port	Starboard	Combined
1	78	2.90	3.10	6.00
2	48	4.35	4.00	8.35
3	73	7.76	11.94	19.70
4	41	14.49	14.89	29.38
5	72	22.49	25.14	47.63
6	16	5.27	6.33	11.60
7	98	5.48	10.91	16.39
9	82	5.40	10.72	16.12
10	3	9.09	7.18	16.27
11	72	17.22	14.37	31.59
12	24	4.81	1.53	6.34
13	96	3.60	4.22	7.82
14	17	6.11	6.19	12.30
15	79	4.63	6.29	10.92
16	24	4.37	2.96	7.33
18	60	3.31	8.35	11.66
19	54	0.97	3.02	3.99
21	84	7.85	8.33	16.18
22	30	8.48	18.48	26.96
23	79	13.23	11.98	25.21
24	79	10.54	7.96	18.50
25	24	16.39	24.30	40.69
26	26	9.60	5.24	14.84
27	60	11.43	22.51	33.94
28	40	0.97	0.82	1.79
29	60	1.19	3.58	4.77
30	6	0.28	0.43	0.71
31	87	3.94	2.68	6.62
33	86	16.24	18.51	34.75
34	36	7.36	4.55	11.91
35	66	1.74	6.18	7.92
37	93	1.85	3.02	4.87
38	19	0.15	9.90	10.05
39	92	5.43	4.97	10.40
Overall mean		7.23	8.97	16.25

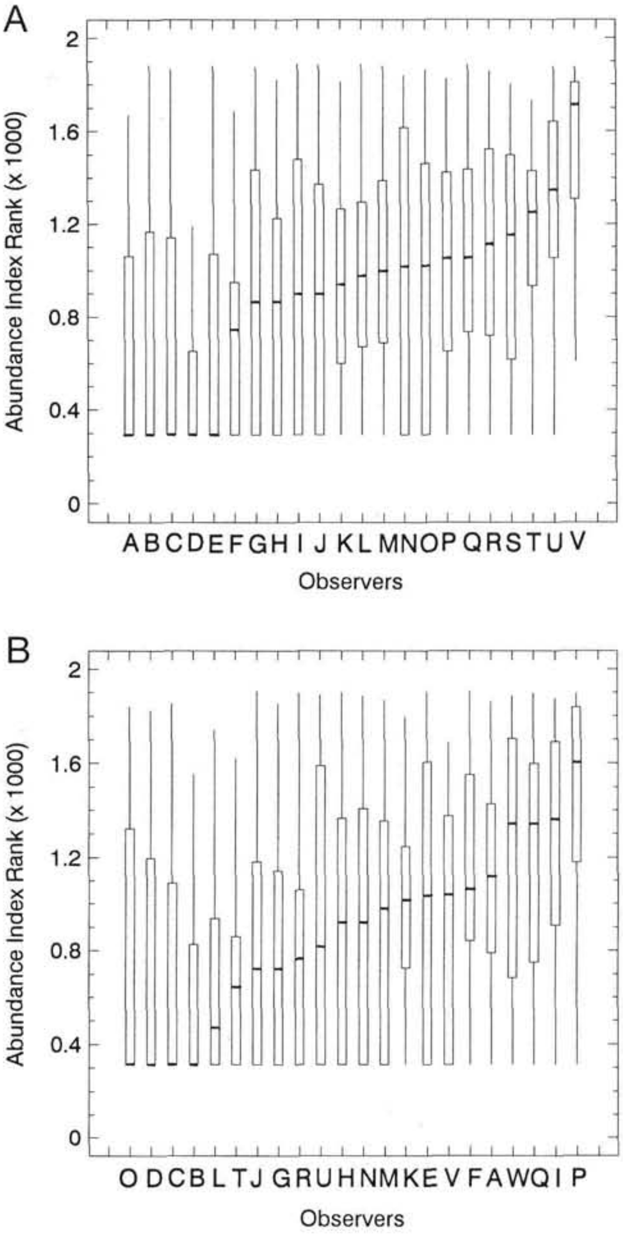

Fig. 2. Box and whisker plots of ranked records of (A) starboard and (B) port flyingfish abundance indices for different observers. Bars indicate the median, boxes indicate upper and lower quartiles, and whiskers indicate the range. Observers are ranked by order of increasing abundance index value

Mean flyingfish abundance indices differed significantly between observers for both the starboard and port data sets (Fig. 2A, B; Kruskal-Wallis tests: starboard, $H = 220.41$, n = 1890, $p < 0.001$; port, $H = 238.47$, n = 1907, $p < 0.001$). However, this is expected since the rotation of observers on different cruise legs resulted in their surveying different geographical areas. We defined an outlier as an observer with a median outside the upper and lower quartiles of any other observer. For the starboard data, the only outlier was observer V, who recorded consistently high flyingfish abundance (Fig. 2A). However, observer V recorded average abundances in the port data set (Fig. 2B). Moreover, comparison of the records of observer V from the starboard side with observers from the port side indicated no significant difference (Mann-Whitney test: $Z = 0.016$, n = 52, p = 0.987). This indicates that observer V's starboard observations were by chance during periods of high flyingfish abundance. As defined, no observers were outliers in the port data set (Fig. 2B). Observer P reported highest abundances. However, P reported average abundances in the starboard data set (Fig. 2A), and P's port records did not differ significantly from the simultaneous records of other observers on the starboard side (Mann Whitney test: $Z = -0.832$, n = 47, p = 0.405). Interestingly, observers B, C, and D reported low abundances in both data sets (Fig. 2A, B). However, in no case did their records differ significantly from simultaneous observers on the alternate viewing side (Mann Whitney tests: for B, $Z = 0.787$, n = 91, p = 0.431; for C, $Z = -1.660$, n = 158, p = 0.097; for D, $Z = -0.442$, n = 160, p = 0.659). We therefore conclude that observer bias was not significant during the survey.

The mean number of fish observed per 0.5 nmi did not differ significantly under different viewing conditions (Kruskal-Wallis test: for sun overhead, in front or behind; $H = -2.66$, n = 1856, p = 1.000), different sea conditions for flyingfish take-off (Kruskal-Wallis test: vessel travelling into, away from, or parallel to waves; $H = 0.09$, n = 1829, p = 0.957), or different times of day (Kruskal-Wallis test: for early morning 05:00 to 09:00 h, midday 10:00 to 14:00 h, or late afternoon 15:00 to 19:00 h; $H = 0.79$, n = 1908, p = 0.673), indicating that sun position, sea conditions, and time of day did not significantly affect the abundance index.

Surface water characteristics and flyingfish abundance

Mean salinity (35.3‰), temperature (27.3°C), PO_4-P (0.113 µg-at. l^{-1}) and NO_3-NO_2-N (0.358 µg-at. l^{-1}) of surface waters differed significantly between transects (Kruskal-Wallis tests: $p < 0.001$ in all cases), but mean silicate (1.453 µg-at. l^{-1}) did not (Kruskal-Wallis test: $H = 54.40$, n = 128, p = 0.053). Across all sampling stations, NO_3-NO_2-N was positively correlated with PO_4-P (Spearman rank correlation: $r_s = 0.230$, n = 136, p = 0.008) and negatively correlated with temperature ($r_s = -0.337$, n = 131, p = 0.001); but no other surface water characteristics were significantly inter-correlated (range in p is 0.31 to 0.85). Since few surface water characteristics were inter-correlated, a principal components analysis did not detect significant covariance among variables, indicating that distinct water masses could not be distinguished on the basis of simultaneous variation in the surface water characteristics measured.

Mean flyingfish abundance on a transect was not correlated with the transect mean of any of the surface water characteristics measured (Spearman rank correlation: range in p is 0.08 to 0.70). Moreover, mean flyingfish abundance indices did not differ significantly between areas of blue water and green water (Kruskal-Wallis test: $H = 1.44$, n = 64, p = 0.229). The lack of correlation between flyingfish abundance and the surface water characteristics may be because effects of the characteristics on abundance occur on a smaller spatial scale than can be detected at the transect level. We therefore investigated possible correlations between flyingfish abundance and surface water characteristics on a local scale, i.e. using flyingfish abundance data within 0.75 nmi on either side of the surface water sampling stations ('localised abundance', see 'Methods'). Localised abundance indices were not significantly correlated with any of the surface water characteristics measured at the adjacent sampling station (Spearman rank correlation: range in p is 0.12 to 0.61).

Spatial variation in flyingfish abundance

Geographical variation in flyingfish abundance was investigated by comparing flyingfish abundance indices between transects. Abundance indices differed significantly between transects (Kruskal-Wallis test: $H = 613.52$, n = 1908, $p < 0.001$; Table 1). Abundance appeared to be relatively high to the west (leeward and downcurrent) of the Lesser Antilles island chain, and in the Atlantic Ocean to the east (windward and upcurrent) of the area between Barbados and Tobago; abundance was relatively low in the area between the Lesser Antilles island chain and Barbados and Tobago (Fig. 3).

We investigated flyingfish distribution on a smaller spatial scale by examining variation in abundance indices along each transect. Flyingfish distribution along 2 randomly selected transects within each of 3 geographical zones (the high abundance areas west of the Lesser Antilles chain and east of Barbados and Tobago; the low abundance area between the Lesser

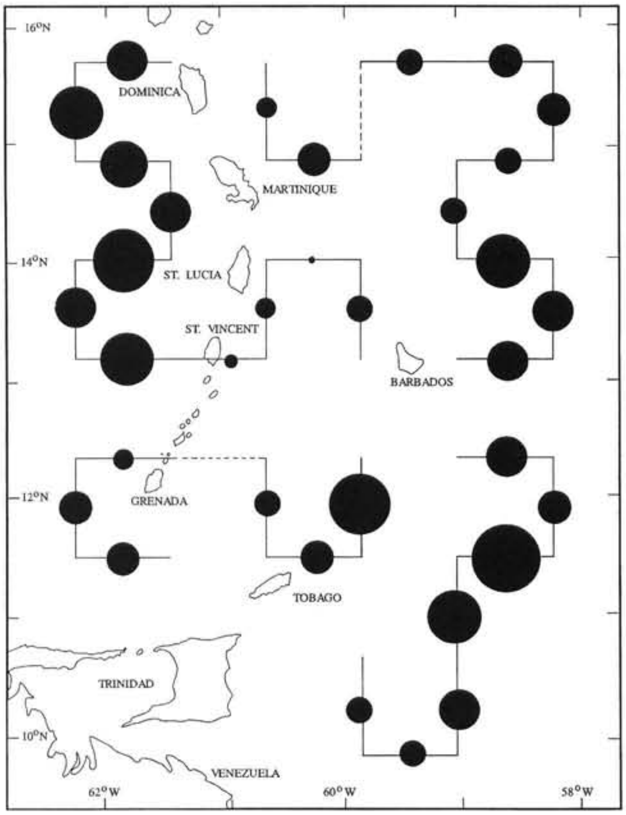

Fig. 3. Relative abundance of adult flyingfish across the survey area recorded by visual survey. Area of circle is proportional to the mean abundance index for the transect (range is 0.71 to 47.63 fish per 0.5 nmi of transect). (——) visual survey transect; (- - - -) cruise track with no visual survey

Antilles and Barbados and Tobago; see Fig. 3) is shown in Fig. 4. The data indicate that flyingfish distribution on this spatial scale is patchy in all geographical zones. As defined, 127 flyingfish patches were encountered during the survey, of which 109 were complete patches (see 'Methods'). Based on the complete patches, mean patch size was 121 fish, mean patch density 15.5 fish per 0.5 nmi, mean patch width 3.9 nmi and mean inter-patch distance 2.0 nmi. Patch size, patch density and patch width on a transect were all positively but weakly correlated with the mean fish abundance on that transect; and inter-patch distances were negatively but weakly correlated with transect fish abundance (Table 2, Fig. 5). This suggests that all patch characteristics contribute to the higher fish abundance in high abundance areas; i.e. patches are closer together, cover a larger area, contain more fish and have higher fish density. As might be expected, patch size was significantly correlated with patch width, i.e. more fish were present in larger patches (Table 2, Fig. 6). Interestingly, patch density was also significantly correlated with patch size and patch width, i.e. fish density was higher in larger patches (Table 2, Fig. 6). Correlations between inter-patch distance and other patch characteristics were not significant (Table 2).

Abundance by species

A total of 15346 flyingfish was recorded separately by species over 27 survey transects. Of these, 7957 (52%) were *Parexocoetus brachypterus*, 7209 (47%) were *Hirundichthys affinis*, and 180 (1%) were *Cypselurus cyanopterus*. Mean transect abundances from port and starboard data sets were significantly correlated for each species (Spearman rank correlation: *P. brachypterus*, $r_s = 0.614$, $p = 0.002$; *H. affinis*, $r_s = 0.482$, $p = 0.016$; *C. cyanopterus*, $r_s = 0.516$, $p = 0.010$; $n = 27$ in each case). Port and starboard data sets have therefore been pooled for subsequent analyses. The overall mean abundance for pooled data was 6.91 fish per 0.5 nmi for *P. brachypterus*, 5.89 for *H. affinis*, and 0.17 for *C. cyanopterus* (Table 3). *P. brachypterus* and *H. affinis* showed a similar distribution, being most abundant east of Tobago and Barbados and west of the Lesser Antilles island chain, and less abundant between the Lesser Antilles island chain and Barbados and Tobago (Figs. 7 & 8 for *P. brachypterus* and *H. affi-*

Table 2. Spearman rank correlation coefficients for flyingfish patch characteristics, and for patch characteristics with transect mean flyingfish abundance. Transect mean flyingfish abundance: mean of the number of fish observed per 0.5 nmi along the transect; patch size: number of fish in the patch; patch density: mean number of fish per 0.5 nmi of transect in the patch

Patch characteristic		Flying fish abundance	Patch density	Patch size	Patch width
Patch density	r_s	0.410	–	–	–
	n	109			
	p	<0.0001			
Patch size	r_s	0.381	0.873	–	–
	n	109	108		
	p	0.0001	<0.0001		
Patch width	r_s	0.346	0.757	0.950	–
	n	109	108	109	
	p	0.0003	<0.0001	<0.0001	
Inter-patch distance	r_s	−0.368	0.033	−0.001	−0.027
	n	93	92	92	92
	p	0.0004	0.753	0.993	0.799

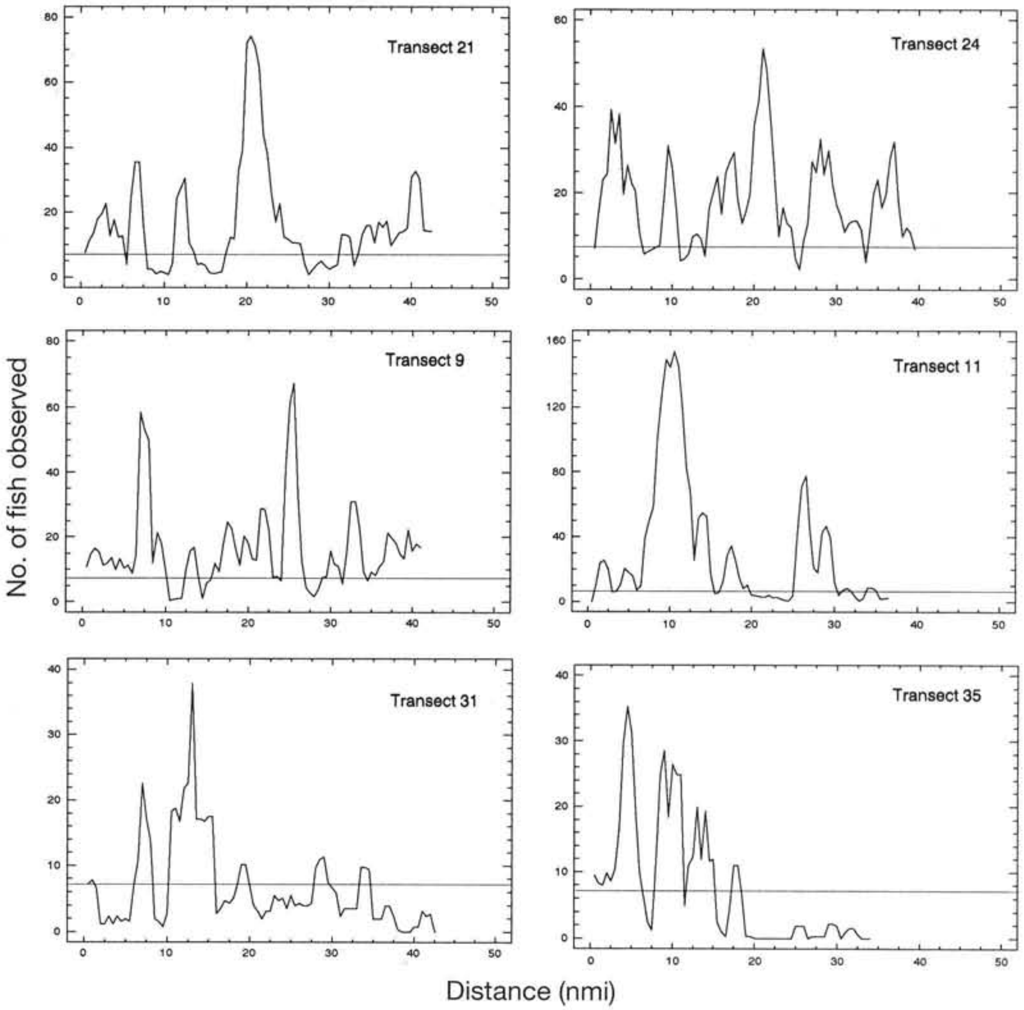

Fig. 4. Flyingfish distribution (number of fish observed per 0.5 nmi of transect) along 6 survey transects. Transects 21 and 24 are from the high abundance area west of the Lesser Antilles; 9 and 11 from the high abundance area east of Barbados and Tobago; and 31 and 35 from the low abundance area between the Lesser Antilles and Barbados and Tobago (see Figs. 1 & 3). Lines are smoothed by 3-point averaging. Fish densities >7.08 fish per 0.5 nmi of transect (i.e. the median value for all transects) indicate a flyingfish patch. The median is shown on each graph

nis respectively). *C. cyanopterus* was most abundant in the northeast of the survey area, and scarce in the southwest, e.g. in the area southwest of Grenada (Fig. 9). The species composition of flyingfish by transect is shown in Fig. 10. Species composition is not presented for Transects 1 to 7 (Figs. 1 & 10) since observers were not experienced in species identification in this initial portion of the cruise. The data confirm the tendency of *C. cyanopterus* to occur primarily in the northeast of the sur-

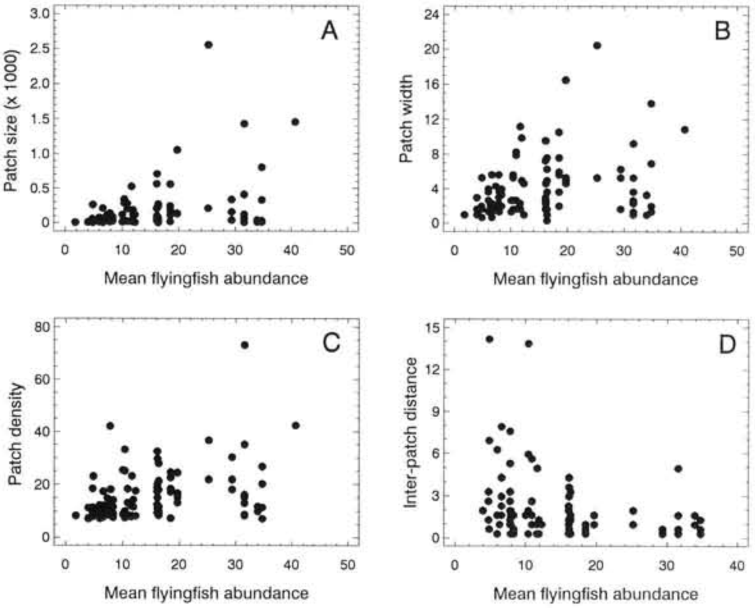

Fig. 5. Relationships between the mean flyingfish abundance per transect and (A) patch size, (B) patch density, (C) patch width (nmi), and (D) inter-patch distance (nmi). Patch size is the number of fish in a patch. Patch density is the mean number of fish per 0.5 nmi of transect within the patch. Correlation coefficients are presented in Table 2

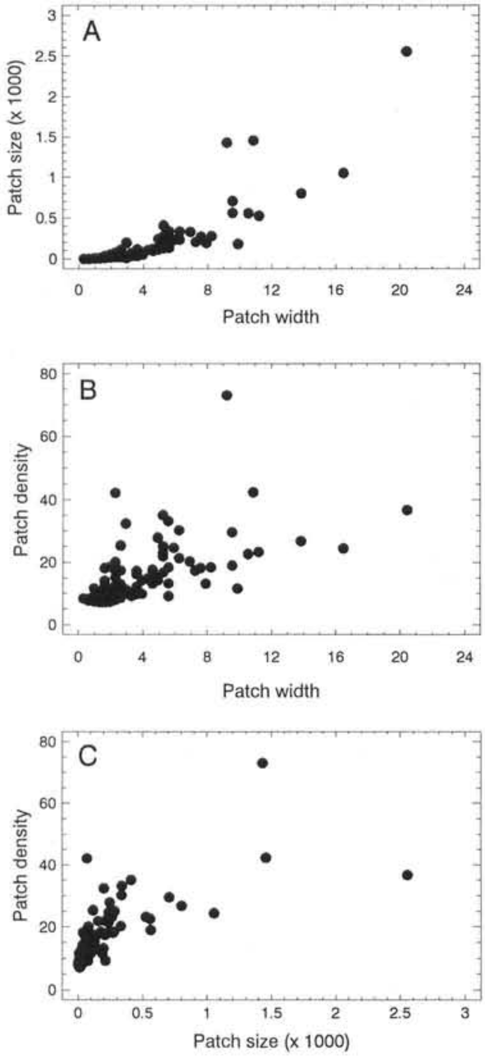

Fig. 6. Relationships between (A) patch size and patch width, (B) patch density and patch width, and (C) patch density and patch size. Patch size: number of fish in a patch; patch density: mean number of fish per 0.5 nmi of transect within the patch. Correlation coefficients are presented in Table 2

vey area, and suggests that the proportion of *P. brachypterus* to *H. affinis* is higher in the low flyingfish abundance area east of the Lesser Antilles than in the high flyingfish abundance area west of the Lesser Antilles.

Airborne flyingfish schools were typically single-species. Based on a subsample of 740 single-species schools, airborne school size varied significantly between species (Kruskal-Wallis test: $H = 53.96$, $n = 740$, $p < 0.001$), with the mean school size being 4.1, 2.6 and 1.1 for *Parexocoetus brachypterus*, *Hirundichthys affinis*, and *Cypselurus cyanopterus* respectively. Although airborne school size was larger for *P. brachypterus* than *H. affinis*, schools of the latter were more numerous, occurring in a ratio of approximately 4:10:1 for *P. brachypterus*, *H. affinis* and *C. cyanopterus* respectively.

DISCUSSION

Using the number of airborne flyingfish observed as an index of flyingfish abundance assumes that the proportion of fish that takes to the air at the approach of a survey vessel is constant for that vessel. This was assumed in all previous visual surveys of flyingfish abundance (Shuntov 1973, cited in Zuyev & Nikol'skiy 1980; Nesterov & Grudtsev 1980, Zuyev & Nikol'skiy 1980, Khokiattiwong 1988). The proportion taking to the air is likely to vary with vessel size, type, speed and engine revolutions (Freon 1988), with distance from the vessel (Zuyev & Nikolsk'skiy 1980), and perhaps with direction of vessel travel in relation to wave and wind direction (see Breder 1929, Hubbs 1933, 1937 for conflicting observations on effects of wind direction).

Table 3. Mean flyingfish abundance indices in the eastern Caribbean shown separately by species. The value for each transect is the mean of the numbers of fish along each 0.5 nmi of the transect. n: number of 0.5 nmi units surveyed per transect. Locations of transects are shown in Fig. 1

Transect no.	n	*Hirundichthys affinis*	*Parexocoetus brachypterus*	*Cypselurus cyanopterus*
9	64	8.67	4.16	0.32
10	3	13.97	4.89	1.40
11	72	3.85	21.67	0.32
12	24	2.21	3.26	0.19
13	73	3.67	2.14	0.10
14	17	2.91	10.02	2.44
15	66	5.50	2.97	0.45
16	24	2.53	2.73	0.10
18	60	3.05	3.36	0.30
19	42	1.60	0.73	0.25
21	84	8.82	5.50	0.10
22	30	9.70	14.49	0.17
23	79	14.81	8.68	0
24	79	2.06	15.71	0.08
25	24	28.47	11.25	0.03
26	26	8.04	4.80	0.06
27	60	24.11	7.03	0.09
28	40	0.39	0.85	0.03
29	60	0.83	2.91	0.01
30	6	0.43	0.57	0
31	87	1.37	5.29	0.01
33	80	9.02	21.02	0.24
34	36	3.11	3.55	0.29
35	66	1.34	5.69	0.17
37	93	1.47	0.05	0.03
38	19	5.36	0	0
39	92	3.37	5.18	0
Overall mean		5.89	6.91	0.17

However, in this study, the same vessel was used throughout the survey at similar engine revolutions and vessel speeds, and the distance over which fish were counted was standardised by use of specific viewing windows of fixed size. Moreover, the direction of vessel travel in relation to wave direction did not significantly affect the abundance indices obtained. Observations conducted prior to and during the survey indicated that the direction of flight away from the vessel was not affected by wind direction. Other factors which might affect the reliability of the abundance indices are observer bias and observer accuracy, the latter with particular respect to time of day and hence position of the sun in relation to the field of view. We detected no evidence of observer bias in this study, and the abundance indices obtained did not differ with time of day. We therefore conclude that the values obtained are an appropriate index of flyingfish abundance. This is supported by the observation that fish abundance along transects was significantly correlated in port and starboard data sets.

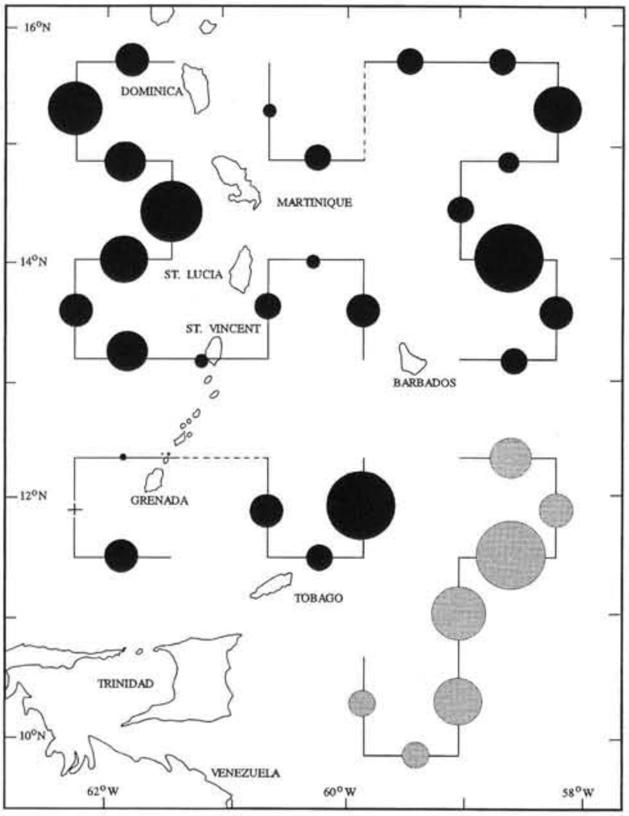

Fig. 7. *Parexocoetus brachypterus*. Relative abundance of adults recorded by visual survey. Area of circle is proportional to the mean abundance index (range is 0 to 21.67 fish per 0.5 nmi of transect). Grey shaded circles indicate transects where *P. brachypterus* abundance is estimated from the total flyingfish abundance along the transect and the proportion of flyingfish that was *P. brachypterus* regionally. (+) transect with no *P. brachypterus*; (——) visual survey transect; (----) cruise track with no visual survey

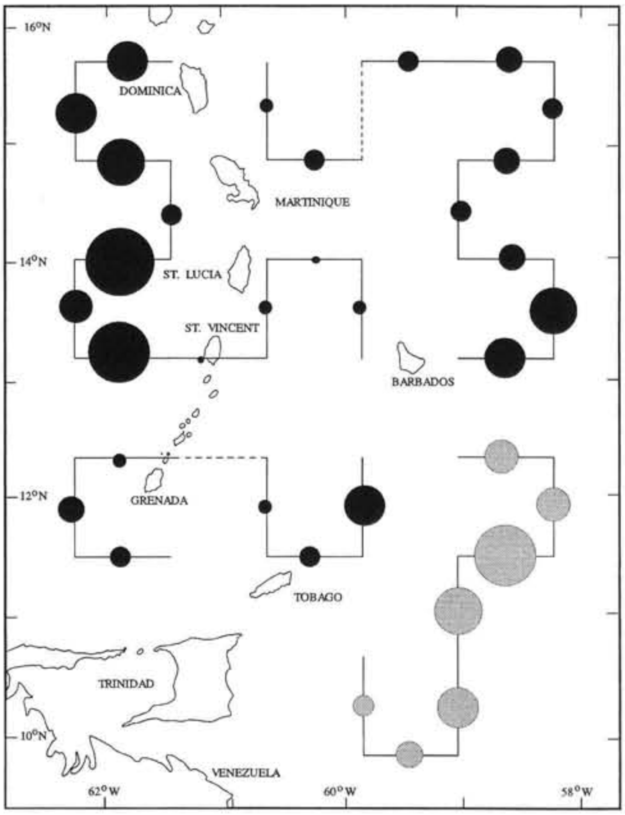

Fig. 8. *Hirundichthys affinis*. Relative abundance of adults recorded by visual survey. Area of circle is proportional to the mean abundance index (range is 0.39 to 28.47 fish per 0.5 nmi of transect). Grey shaded circles indicate transects where *H. affinis* abundance is estimated from the total flyingfish abundance along the transect and the proportion of flyingfish that was *H. affinis* regionally. (——) visual survey transect; (----) cruise track with no visual survey

Some studies have attempted to estimate absolute abundance of flyingfish from visual surveys by either assuming a value for the proportion of fish taking to the air (e.g. Shuntov 1973, cited in Zuyev & Nikol'skiy 1980; Nesterov & Grudtsev 1980) or attempting to estimate it (Zuyev & Nikol'skiy 1980). Working under ideal viewing conditions that allowed fish above and below the water to be seen simultaneously, Zuyev & Nikol'skiy (1980) estimated the percentage of flyingfish (primarily *Exocoetus* sp.) taking to the air to be about 20% in an area extending 25 m from the vessel. The proportion of *Hirundichthys affinis* becoming airborne in the present study may be lower than this since *H. affinis* is distributed deeper than other species of flyingfish, including *Exocoetus* sp. and *Parexocoetus brachypterus* (Shiokawa 1969, Gorelova 1980, Nesterov & Bazanov 1986) and since the vessel used by Zuyev & Nikol'skiy (1980) was larger and surveyed at twice the speed as that used in this study. For the latter reasons, the estimate of 20% may also be high for *P. brachypterus* in this study.

Flyingfish abundance varied significantly across the survey area, but did not differ between areas of blue water and green water, and was not correlated with any of the surface water characteristics measured. For both *Hirundichthys affinis* and *Parexocoetus brachypterus*, abundance was high west of the Lesser Antilles island chain and in an area between and to the east of Barbados and Tobago, and low in the area between the Lesser Antilles chain and Barbados and Tobago. Catch rate data from the flyingfish fishery are consistent with the high abundance between and to the east of Barbados and Tobago (Oxenford 1994). The high abundance west of the island chain may be the consequence of eddies and turbulence that typically occur downcurrent of islands (Doty & Oguri 1956, Sander 1971, Emery 1972 and Powles 1975 for Barbados). These have also been reported on the leeward (west) sides of both St. Vincent and St. Lucia (Leming 1971, Febres-Ortega & Herrera 1976). The high abundance between and to the east of Barbados and Tobago may be similarly caused since large eddies have been reported between Barbados and Tobago by Mazeika et al. (1980), and east of Tobago by Febres-Ortega & Herrera (1976). Turbulence may result in transport of nutrients from deeper water, increased plankton productivity, and hence increased abundance of zooplankton on which flyingfish feed. Eddies may retain and thereby concentrate zooplankton, further increasing food availability in such areas. Eddies could also retain and concentrate floating material on which flyingfish may spawn, but spawning substratum was rare throughout the survey area (Hunte et al. 1995, this issue), as well as in a more intensively surveyed area northwest of Barbados (Lao 1989).

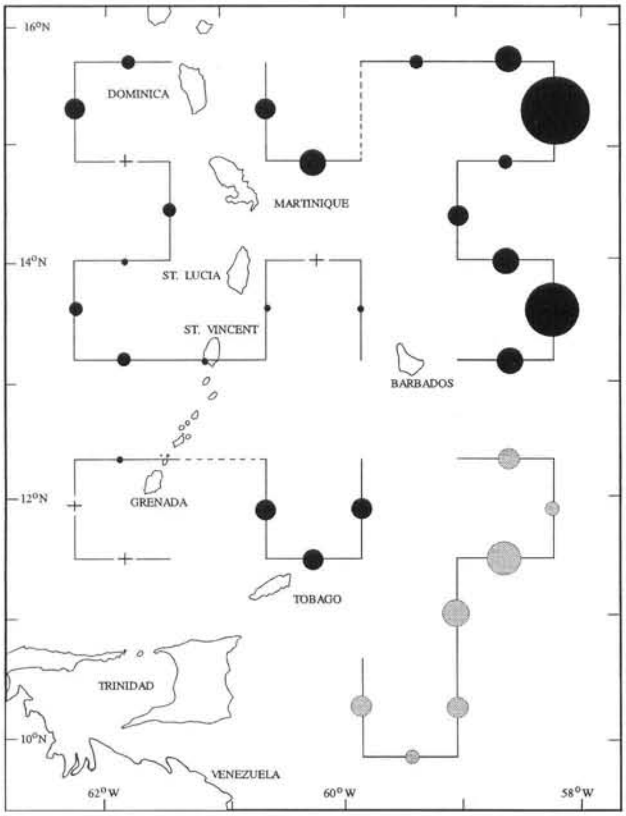

Fig. 9. *Cypselurus cyanopterus*. Relative abundance of adults recorded by visual survey. Area of circle is proportional to the mean abundance index (range is 0 to 2.44 fish per 0.5 nmi of transect). Grey shaded circles indicate transects where *C. cyanopterus* abundance is estimated from the total flyingfish abundance along the transect and the proportion of flyingfish that was *C. cyanopterus* regionally. (+) transects with no *P. brachypterus*; (——) visual survey transect; (----) cruise track with no visual survey

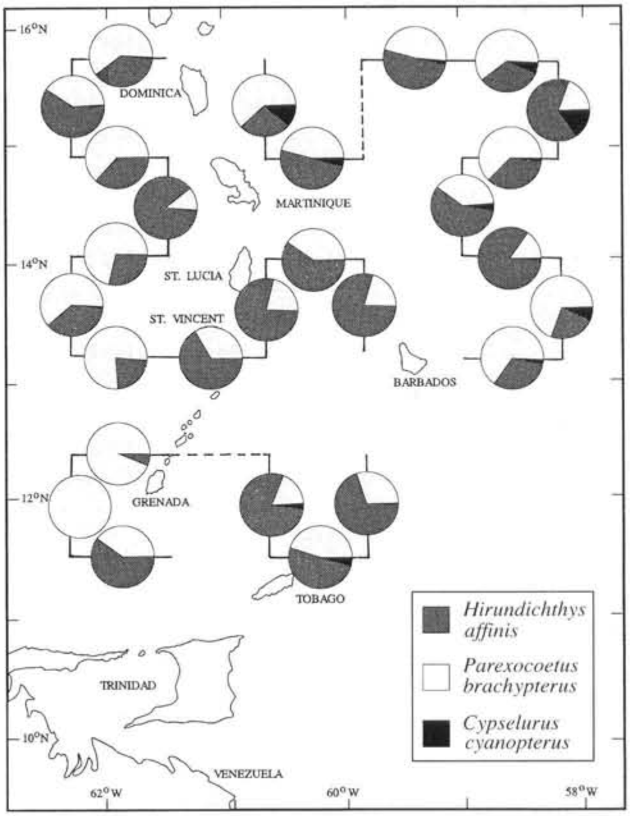

Fig. 10. Species composition of adult flyingfish recorded by visual survey across the eastern Caribbean

Flyingfish distribution was also patchy on a smaller spatial scale (mean patch width: 3.9 nmi; mean inter-patch distance: 2.0 nmi). Moreover, flyingfish were patchily distributed on an even smaller scale, i.e. both within and outside of patches, they appear to occur in schools. The patchy distribution of flyingfish on these smaller spatial scales again may result from aggregation in areas of high zooplankton abundance, and/or for spawning. The distribution of oceanic zooplankton is typically patchy, although the processes underlying this are often inadequately understood (Steele 1977, Cowen & Castro 1994). Moreover, many pelagic fish are now known to be non-randomly distributed, possibly reflecting their prey distribution (Horwood & Cushing 1977). Patchy local distribution may bias geographical estimates of abundance (Simmonds et al. 1992). The information on patchiness observed in this study should be used in designing future abundance surveys.

The flyingfish fleets of eastern Caribbean islands presently fish across areas of both higher and lower *Hirundichthys affinis* abundance (Figs. 1 & 8). This suggests that, even in poorer areas, *H. affinis* abundance is enough to maintain viable catch rates. Alternatively, there could be seasonal movement/migration of geographical centres of higher abundance (see Simmonds et al. 1992 for effects of migration on relative abundance during surveys). However, centres of abundance move little seasonally, as indicated by a common seasonality of *H. affinis* catch rates throughout the region (Oxenford 1986, Hunte 1987) and by tagging results for *H. affinis* conducted at different times of the year (Oxenford 1994). Movement of centres of abundance may be more likely on the patch rather than the geographical scale. The tendency of fishermen to change fishing locations within the fleet range, both within and between fishing days, may be an attempt to locate flyingfish patches. Data from Khokiattiwong (1988) suggest that they may often be successful in doing so. This is important in a commercial context, since catch rates are likely to differ considerably when fishing outside of patches, within small patches and within large patches, given the positive correlation between patch size and fish density in the patch.

Flyingfish abundance does not appear to decrease towards either the east or west boundaries of the survey area, suggesting that the resource extends beyond 100 nmi west of the Lesser Antilles chain, 100 nmi east of Barbados, and 150 nmi east of Tobago. This suggests that flyingfish fleets could probably expand their current geographical range and still maintain similar catch rates. The viability of this would be determined largely by net economic returns, given the greater cost of fishing farther offshore. The economic constraint could be lessened by increasing the duration of fishing trips, thereby increasing the number of fishing days per unit of travel time to fishing grounds. Constraints to geographical fleet expansion imposed by social costs to fishermen of remaining longer at sea would require examination.

Cypselurus cyanopterus was considerably less abundant than either *Parexocoetus brachypterus* or *Hirundichthys affinis*, and was largely restricted to the northeast sector of the survey area. The mean abundance index for *P. brachypterus* (6.91 fish per 0.5 nmi) was higher than for *H. affinis* (5.89 fish per 0.5 nmi). The 2 species had a similar geographical distribution, although the proportion of *H. affinis* to *P. brachypterus* was higher in the high abundance area west of the Lesser Antilles than it was in the low abundance area between the Lesser Antilles and Barbados and Tobago. Since the proportion of fish that take to the air when a vessel approaches is likely to be species-specific, and may be higher for *P. brachypterus* than *H. affinis* as the former lives closer to the surface (Khokiattiwong 1988), we cannot conclude that the absolute abundance of *P. brachypterus* is greater than that of *H. affinis*. Nevertheless, the high abundance indices obtained for *P. brachypterus* indicate that the feasibility of developing a small-scale fishery for this species in the eastern Caribbean should be further explored.

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