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Seasonal abundance and reproduction of the fourwing flyingfish, *Hirundichthys affinis*, off Barbados

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Synopsis

The seasonal abundance and reproductive cycle of the flyingfish *Hirundichthys affinis* was studied near Barbados. *H. affinis* shows large seasonal variation in abundance. They are common between December and June and scarce from July to November. The population size structure of *H. affinis* was determined by fishing with four different mesh sizes throughout one year. There appear to be two cohorts of *H. affinis* present in May and June, one of immature fish with a mean size of 19.8 cm FL, and one of mature fish with a mean size of 21.7 cm FL. From September to April there is only a single cohort of maturing fish with a mean size that increases from 20.4 cm FL in September to 22.0 cm FL in April. *H. affinis* spawns throughout the fishing-season (December–June) and shows a peak in spawning activity from March to June. Immature fish are present in Barbados waters from July to November but in very low abundance. Surface water temperature, wind speed and swell height are the only environmental factors with which catch rate of *H. affinis* showed significant correlation. Catch rate appears to be negatively correlated with temperature, whereas for wind speed and swell height there are optima. Three hypotheses for the seasonal variation in abundance of *H. affinis* were examined. The hypothesis that this species remains dispersed near Barbados during the off-season was rejected. The other hypotheses were refined. Both post-spawning mortality, resulting in an interval of low abundance between cohorts (non-overlapping generations), and migration of fish away from Barbados at the end of the fishing season, remain possible explanations for the observed seasonal variation in abundance of this species.

Introduction

The four-wing flyingfish, *Hirundichthys affinis*, is distributed throughout the western tropical Atlantic, and is reported from areas off western Africa (Breder 1938). In the western Atlantic, abundance is highest along the north coast of South America where the stocks supports fisheries off northeast Brazil, in the southern Lesser Antilles and around Curaçao (Barroso 1967, Mahon et al.[1], Zaneveld 1962). In the southeastern Caribbean the catch of the fishery for flyingfish consists almost entirely of *H. affinis*. Thus it is the most economically important species in the area (Oxenford et al. 1993). The fishery uses gillnets, and floating fish attracting devices (FADs) of dried sugar cane leaves or coconut boughs that are set for several hours. Ripe adults are attracted to spawn on the FADs.

Aspects of the biology of *H. affinis* that have been studied in the eastern Caribbean include age, growth, feeding and reproductive biology, distribution, migration and stock structure (Hall 1955, Lewis et al. 1962, Storey 1983, Hunte et al. 1995, Oxenford et al. 1995a,b, Campana et al. 1993, Oxenford et al. 1993, Oxenford 1994, Gomes et al. 1998, 1999). However, none of these

[1] Mahon, R., H.Oxenford & W. Hunte (ed.). 1986. Development strategies for flyingfish fisheries of the Eastern Caribbean. International Research Agency, Ottawa (IDRC-MR128e). 148 pp.

studies has focused on the most prominent feature of the fishery, which is its marked seasonality (Mahon et al. 1982). The flyingfish season extends from November to the following May. Within this period there are usually two peaks in abundance the timing of which may vary.

The hypotheses that have been proposed for this seasonality are: (1) that the fish migrate out of the range of the fleets; (2) that the fish go deeper in the water, where they are not available to the gear; (3) that fishable stock is absent during intervals between generations; and (4) that the fish are present year-round in the surface waters accessible by the fleet, but are only catchable in the spawning season when they aggregate to spawn on the drifting FADs (Mahon et al. 1982).

In this study visual surveys were carried out and gillnets of four mesh sizes were deployed year-round with the objective of assessing the availability of *H. affinis* of various sizes in the vicinity of Barbados. The reproductive state of the fish and the oceanographic conditions were monitored in order to evaluate factors that might be responsible for the seasonality of the fishery.

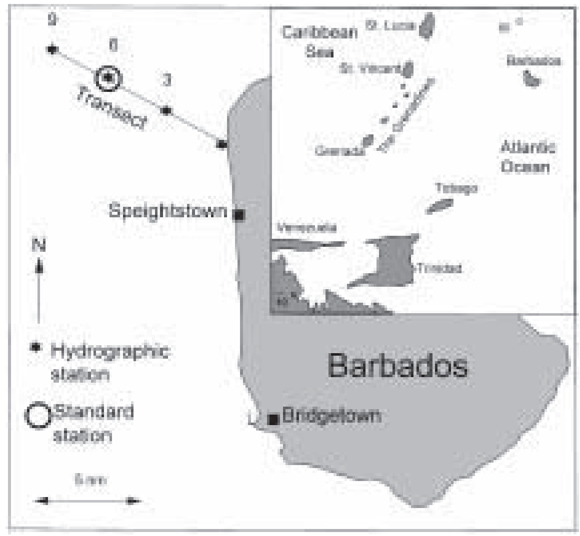

Figure 1. Locations of the standard fishing station and four water sampling stations for salinity and temperature (shore, 3, 6 and 9 nm) along a transect to the northwest of Barbados (inset is the location of Barbados in the southeastern Caribbean).

Materials and methods

Experimental fishing

The study was conducted off Barbados (13°10′ N, 59°30′ W), which is 140 km east of the Lesser Antilles island chain (Figure 1). Nets were set in the area commonly fished by the fishing fleet based in the northwest of the island (Speightstown and adjacent communities). This fleet fishes primarily off the west and northwest, and less frequently off the north of the island and has the highest catch-per-trip of flyingfish in the Barbados fishery[1].

We conducted two fishing trips per week during the flyingfish season (December 1987 to June 1988); one trip to a standard fishing station (Figure 1) and the other to fish with the commercial fleet to compare experimental and commercial fishing. During the off-season (July 1987 to November 1987 and July 1988), only the weekly trip to the standard fishing station was made. The standard station, which was six nautical-miles NW of a conspicuous landmark (Barbados Cement Co. plant) was located each trip using a compass and trailing log. This station was chosen as it was at the average distance from shore fished by the fleet, which ranges from 2 to 12 nautical miles (nm), and is a popular fishing area for the fleet.

At the beginning of the 1987/1988 fishing season the fleet was located by a light aircraft that radioed its position to the research boat. Due to problems with aircraft, pilot availability and weather conditions this approach was abandoned in December 1987, after which the fleet was located with the cooperation of the commercial fishermen using VHF radio and with the experience of the fishermen who crewed the research boat.

Gillnets have been the main fishing gear in the Barbados flyingfish fishery since the early 1940s (Brown 1942). The early gillnets were made from 12-ply cotton with a stretched mesh size of 17/8 inches. Hall (1955) suggested that the mesh size was critical; an increase or decrease of 0.125 inches produced a marked decrease in catch. The nets used today are similar except that the material has changed from cotton to monofilament nylon of stretched mesh size 41.3–44.5 mm (15/8–13/4 inches). Flyingfish gillnets in Barbados differ from those used in other fisheries. They are hung such that the lead-line opens the mesh rather than closes it, and the hanging coefficient (the ratio of the length of completed net to the stretched length of webbing used in it) is 1. A typical boat uses 2–3 nets of different mesh sizes (41.3–44.5 mm), 10–30 m long and 3 m deep.

The fishing methods used in this study were similar to those used by the commercial fishermen, with only those changes needed to ensure that the technique could be kept standard through the year. Four monofilament nylon gillnets (each 30 m long and 3 m deep) of different stretched mesh sizes, 25.4, 31.8, 38.1, and 44.5 mm (1.00, 1.25, 1.50 and 1.75 inches) were used. Since no commercial net company could supply nets of different mesh sizes hung as in the Barbados fishery, the experimental nets were hung in the conventional way, with a hanging coefficient of 0.5, which is the standard for gillnets. The mesh sizes used for experimental fishing were selected after trials in June and early July 1987, with stretched mesh sizes of 25.4, 31.8, 50.8, and 63.5 mm (1.00, 1.50, 2.00 and 2.50 inches). Meshes of 50.8 mm and 63.5 mm caught no flyingfish and were replaced by meshes of 31.8 mm and 44.5 mm.

The purpose of using a range of gillnet mesh sizes was to cover the full range of fish sizes available in the stock. The catch data from the four net sizes were used to evaluate gillnet selectivity and thus to estimate the actual size distribution of the flyingfish throughout the year (Mahon et al. 2000).

The nets were set concurrently in two gangs of two nets each (Figure 2). The nets in each gang were placed 10 m apart in order to minimise their competition for capture of the same fish, and the order of the nets was rotated with each sampling trip to reduce any possible bias due to their position (Clark & King 1986).

The nets were fished between 9:00 h and 13:00 h with a standard soak of 3 h. The experimental fishing used three FADs each made from two coconut boughs tied together, similar to those used by fishermen in Tobago (Jordan 1983) and fishermen in Barbados near the end of the fishing season. Dry sugarcane leaves, which are more popular with the commercial fishermen in Barbados, are not available year-round. The FADs were placed midway between nets and a punctured sardine can was hung near the first FAD in each gang of nets (Figure 2). The sardine cans were used instead of the traditional crushed flyingfish chum basket since fresh flyingfish are not available during summer. The fishing trip described above is referred to as the standard fishing trip and will be used as the unit of fishing effort for comparison of catch-per-unit-effort (CPUE) among months.

Information from the catch

All species of flyingfish in the catch were identified each trip. The flyingfish samples from experimental fishing consisted primarily of two species, *H. affinis* and *Parexocoetus brachypterus*. In order to evaluate the hypothesis that flyingfish go deeper in the water in the off season, information on seasonal variation in vertical distribution of flyingfish was obtained by dividing the nets into upper (0–1 m), middle (1–2 m) and lower (2–3 m) zones, and recording the zone of capture of each specimen of *H. affinis*. If flyingfish do go deeper in the water in the off season, a greater proportion of fish would be expected in the lower zone of the net towards the end of the season.

Population size structure and reproductive parameters were studied in order to determine their

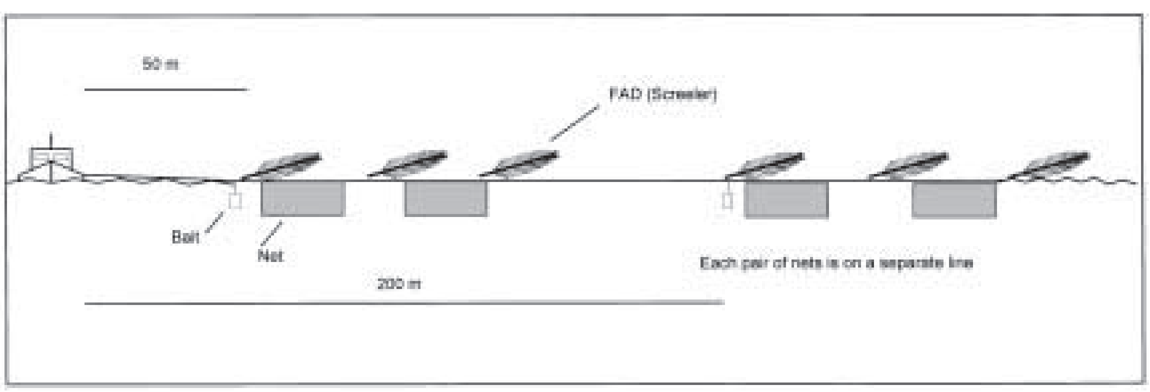

Figure 2. The method of setting the experimental gillnets of four different mesh sizes in two gangs. The position of the screelers and bait (sardine cans) are shown (not to scale).

Table 1. The maturity stages of gonads of *Hirundichthys affinis* (after Lewis et al. 1962).

Stage	Description of the gonads
1	Immature and virgin fish: gonads very small, string like, white. Ovaries translucent, testes opaque.
2	Maturing virgins and recovering spents: ovaries, rounded, pink, firm, ova just visible. Testes thickened but flat, white, creamy.
3	Maturing ripening fish: ovaries distended, orange or pink. Testes full, thick, convexly triangular, white or light gray.
4	Spawning fish: ovaries run on slight pressure. Eggs at least 1.4 mm in diameter, with investing tendrils. Testes run on firm pressure.
5	Spent fish: ovaries flaccid, shrunken, white, often with purple, some large eggs. Testes shrunken, prominent blood vessels.

relationship to the seasonal pattern of abundance. All specimens of *H. affinis* were measured to the nearest 1 mm fork length (FL). Up to 50 fish were retained from each set for measurement of body weight (g), gonad weight (g), sex, and stage of gonad development, according to Lewis et al. (1962; Table 1). A gonosomatic index (GSI) was calculated as: GSI = (gonad weight/body weight) $\times$ 100.

Fifty specimens of *H. affinis* were sampled from a single commercial gillnet (mesh size 40.6 mm) at Speightstown each week throughout the 1987/1988 fishing season, and treated in the same way as the fish caught in the experimental nets. In addition, monthly mean catch per trip for the Speightstown fleet was obtained from the Barbados Fisheries Division and compared to the catch per trip of the experimental nets.

Visual surveys

The distribution and size of flyingfish schools were investigated from September 1987 to July 1988 by visual observation on each fishing trip to the standard fishing location. This method of surveying flyingfish has been used in several studies and factors affecting these estimates were considered in detail by Freon (1992). The observations were made from the bow of the boat along a timed straight-line transect, 6 nautical miles in length, between the shore and the station. Flyingfish which flew as the fishing boat approached could be identified into three genera. Differences between the three genera of flyingfish in flight were clearly visible for adults. *H. affinis* is about 20 cm and has long, light colored pectoral fins. *Cypselurus* spp. are largest with long, almost black pectoral fins. *Parexocoetus brachypterus* is the smallest fish, even as adults (9–12 cm). The pectoral fins are light and the dorsal fin is large with a black spot. At certain times of the year there were also numerous small individuals that could not be identified by the above characteristics. Given the timing of their occurrence, they were probably young *H. affinis*. These were treated separately. The number of fish per school was estimated, and school position along the transect was recorded by time. The visual surveys always took place in the morning with the sun and wind behind the observer, giving the best viewing conditions.

Oceanographic and climatic parameters

Some environmental variables selected for measurement might affect flyingfish abundance directly, through flyingfish being associated with water having certain characteristics. Other variables might affect the index of abundance by affecting catchability or area fished. Surface salinity and water temperature were measured using Nansen bottles (500 ml) and reversing thermometers at 1 m and 3 m depths at 4 points along the transect to the standard fishing station: near shore, 3, 6 and 9 nautical miles offshore (Figure 1). Salinity was measured in the laboratory with a calibrated salinometer. Transparency and water-colour were measured at the fishing station each trip at midday using a Secchi disk and the Forel-Ule scale. As the Secchi disk was lowered into the water, the colour of the surface water was determined by comparing the colour of the Secchi disk, just as it disappeared, with a series of coloured solutions ranging from blue to green prepared according to the Forel-Ule scale (Borstad 1979, Royce 1984). Sea condition (swell height), wind speed and direction, rainfall and cloud coverage were all recorded for each trip at the fishing station every hour using the indices described in Table 2.

Since any pair of environmental variables that show seasonal variation will be significantly correlated at some lag period, no attempt was made to statistically explore the relationships among variables on a seasonal time-scale, although these are discussed in relation to known seasonal climatic variation in the eastern Caribbean region. The relations among environmental variables on a daily time-scale was examined by first removing the seasonal component of each variable. This was done by dividing each daily data point

Table 2. Indices for the oceanographic and climatic parameters recorded at the fishing station.

Index	Sea condition (swell height m)	Wind speed	Wind direction	Cloud cover	Rainfall
0				0	None
1	0.0–0.5	Calm	Northerly	1/8	Showers infrequent
2	1.0–1.0	Slight breeze	Northeasterly	1/4	Showers frequent
3	1.0–1.5	Wind	Easterly	3/8	Heavy rain infrequent
4	1.5–2.0	Strong wind	Southeasterly	1/2	Heavy rain frequent
5	2.0–2.5	V. strong wind	Southerly	5/8	
6	> 2.5			3/4	
7				7/8	
8				8/8	

by the monthly mean for that variable, thus removing differences between months. Spearman's rank correlation analysis was then used to examine the degree of association among variables. Relationships between the environmental variables and daily fish catches were examined in a similar fashion.

Results

Indices of abundance

Eleven species of flyingfish were caught by the experimental gillnets throughout the year (Table 3). *H. affinis* and *P. brachypterus* contributed 78% and 18% of the catch respectively.

Average monthly catch per unit effort (CPUE) of *H. affinis* increased substantially from November to December, and remained relatively high until June. The months of lowest catch rate were August to October (Table 4, Figure 3). The catch per trip from the Speightstown flyingfish fleet (available only in kg per trip) did not differ from the monthly variation in abundance as indicated by catch per trip of the experimental net ($X^2 = 3.51$, d.f. $= 6$, $p > 0.05$) (Table 5). Owing to the searching behaviour of the fleet, one would expect lower catch rates at the standard station, than when fishing with the fleet. Therefore, the comparison of experimental and commercial catch rates in Table 5 used only the experimental fishing trips in close proximity to the fleet. Despite this, the catch rate of the experimental net is significantly lower than that of the commercial nets (t-test, $t = 4.42$, $p < 0.05$).

The seasonal pattern for the Speightstown fleet was also similar to that of the experimental nets (Figure 3). However, the commercial catch rate differed from the average seasonal pattern for 1961–1986 in that an unusually high proportion of the catch was taken in December and January.

The possibility of an interaction between the CPUE of *H. affinis* and that *P. brachypterus* was examined. If there is an interaction, then the CPUE for *H. affinis* can not be interpreted without reference to the CPUE of *P. brachypterus*. The seasonal component of CPUE for both species was first removed by dividing catch in each trip by the mean catch per trip for that month. There was no correlation between the de-seasonalised daily catches of *H. affinis* and *P. brachypterus* (Spearman rank correlation, $R_s = -0.106$, $p > 0.05$). Nevertheless, there appeared to be very few instances of high catches of both species on the same day. The plot of detrended daily catch of *H. affinis* with that of *P. brachypterus* was divided into four quadrants by two lines corresponding to the median catch rate for each species, and chi-square was used to test whether the proportion of observations in each quadrant was significantly different from 0.25, the expected value if there was no relationship. The observed proportions did not differ significantly from 0.25. Therefore, the CPUE for *H. affinis* can be interpreted without reference to that for *P. brachypterus*.

Visual observation of schools in flight indicated that for *H. affinis* school size ranged from 1 to 10 fish with one school of 27 individuals. For small unidentified flyingfish school size ranged from 1 to 18 fish (Figure 4). The total number of *H. affinis* observed and the number of schools observed per trip along the transect from shore to 6 nm was extremely variable but showed a similar seasonal pattern to that of the catches, particularly in regard to the peak in abundance in December (Figure 5). The similar pattern in number of fish and number of schools shown in Figure 5 reflects the fact that school size did not vary significantly throughout

Table 3. The relative abundance (% above) and numbers (below) of flyingfish species in the catch of the experimental gillnets in each month of the study (— = no catch).

Species	Aug/87	Sep/87	Oct/87	Nov/87	Dec/87	Jan/88	Feb/88	Mar/88	Apr/88	May/88	Jun/88	Jul/88	Total
Hirundichthys affinis	7.7	90.0	23.5	25.0	93.4	80.0	6.70	89.2	73.6	86.9	68.1	32.9	78.0
	(1)	(63)	(23)	(22)	(832)	(303)	(144)	(487)	(120)	(119)	(235)	(24)	(2481)
Hirundichthys speculiger	—	—	—	—	—	—	0.5	0.6	—	—	—	—	0.1
	—	—	—	—	—	—	(1)	(3)	—	—	—	—	(4)
Parexocoetus brachypterus	76.9	8.6	71.5	73.9	6.3	18.3	28.8	8.4	12.9	11.0	28.1	60.3	18.5
	(10)	(6)	(10)	(65)	(56)	(90)	(62)	(46)	(21)	(15)	(97)	(44)	(582)
Cypselurus comatus	15.4	1.4	—	—	—	0.6	1.4	0.4	11.0	—	—	—	0.9
	(2)	(1)	—	—	—	(3)	(3)	(2)	(18)	—	—	—	(29)
Cypselurus cyanopterus	—	—	2.0	—	—	—	0.5	0.2	1.2	0.7	0.3	—	0.2
	—	—	(2)	—	—	—	(1)	(1)	(2)	(1)	(1)	—	(7)
Cypselurus exsiliens	—	—	1.0	1.1	0.1	—	0.5	0.7	0.6	1.5	—	—	0.4
	—	—	(1)	(1)	(1)	—	(1)	(4)	(1)	(2)	—	—	(11)
Cypselurus heterurus	—	—	—	—	—	0.2	1.4	—	0.6	—	0.6	1.4	0.3
	—	—	—	—	—	(1)	(3)	—	(1)	—	(2)	(1)	(8)
Cypselurus melanurus	—	—	2.0	—	—	—	—	—	—	—	0.3	—	0.1
	—	—	(2)	—	—	—	—	—	—	—	(1)	—	(3)
Exocoetus obtusirostris	—	—	—	—	—	—	—	—	16.5	—	1.5	—	0.2
	—	—	—	—	—	—	—	—	(5)	—	(5)	—	(5)
Exocoetus volitans	—	—	—	—	—	0.2	—	—	—	—	—	—	0.0
	—	—	—	—	—	(1)	—	—	—	—	—	—	(1)
Prognichthys gibbifrons	—	—	—	—	0.2	0.4	—	0.6	—	—	0.9	5.5	0.5
	—	—	—	—	(2)	(2)	—		—	—	(3)	(4)	(14)
Unidentified (juveniles)	—	—	—	—	—	0.2	—	—	—	—	0.3	—	0.1
	—	—	—	—	—	(1)	—	—	—	—	(1)	—	(2)

Table 4. Number of trips per month, number of fish caught per month (N) and mean monthly CPUE (catch/trip) for *Hirundichthys affinis* caught by the four mesh sizes of experimental gillnets.

Month	# of trips	Mesh size in mm (inches)								Total fish per trip
		25.4 (1.00)		31.8 (1.25)		38.1 (1.50)		44.5 (1.75)		
		N	C/T	N	C/T	N	C/T	N	C/T	
Aug/87	6	—	—	—	—	1	0.2	—	—	0.2
Sep/87	5	—	–	40	20.0	20	6.7	3	1.5	12.5
Oct/87	5	1	0.2	7	1.4	15	3.0	—	—	4.6
Nov/87	4	—	—	11	2.8	8	2.0	3	0.8	5.5
Dec/87	7	35	5.0	499	71.3	239	34.1	59	8.4	118.8
Jan/88	6	12	2.0	112	18.7	226	37.7	43	7.2	65.5
Feb/88	8	8	1.0	55	6.9	69	8.6	12	1.5	18.0
Mar/88	9	53	5.9	184	20.4	224	24.9	26	2.9	54.1
Apr/88	9	8	0.9	46	5.1	56	6.2	10	1.1	13.3
May/88	8	1	0.1	47	5.9	64	8.0	7	0.9	14.9
Jun/88	9	8	0.9	74	8.2	144	16.0	9	1.0	26.1
Jul/88	5	—	—	11	2.2	11	2.2	2	0.4	4.8
Totals	83	126		1086		1092	172			

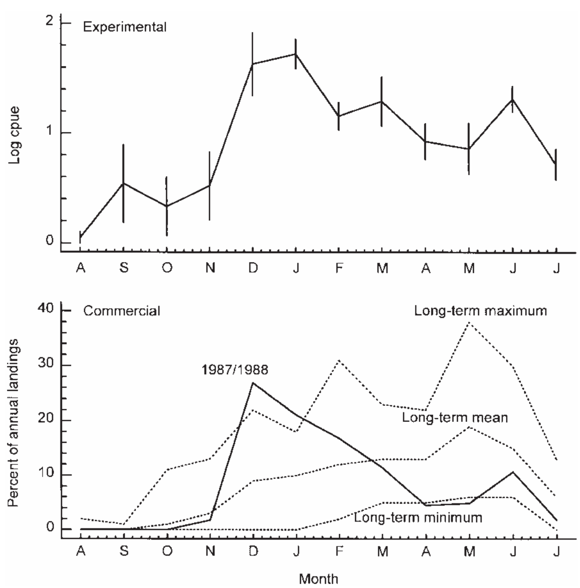

Figure 3. Seasonal abundance of flyingfish: a – Mean monthly Log CPUE in the experimental gillnets (all nets combined) of *H. affinis* ± 1 SE; b – the long-term (1962–1986) pattern of landings (monthly mean, maximum and minimum percentage of annual catch) through the fishing season by the Speightstown commercial fleet, and pattern for the 1987/1988 fishing season during which the study was carried out.

the season. Small unidentified flyingfish appeared for the first time in February and persisted through July, the end of the observations, and were most abundant from February to April.

Table 5. Adjusted monthly mean CPUE of commercial nets in the Speightstown fleet and of the 38.1 mm mesh experimental net.

Month	CPUE (kg)	
	Comm.	Exp.
Dec	41.6	7.3
Jan	32.2	5.5
Feb	26.0	1.3
Mar	23.2	4.0
Apr	9.1	0.9
May	8.3	2.4
Jun	25.1	2.1

Depth and horizontal distribution

The depth distribution of fish as indicated by the relative amounts caught in the three depth zones of the net differed significantly among months ($X^2 = 210.0$, d.f. $= 20$, $p < 0.01$)(Figure 6). Fish were most frequently caught at the surface from March to May, and to lesser extent in November.

The number of *H. affinis* schools per 0.5 nm interval along the transect increased with distance from shore to about 3.5 nm offshore, after which it leveled off; highest school densities occurred between 3.0–5.5 nm (Figure 7a). For small unidentified flyingfish the number of schools increased steadily to a peak at about 2.5 to 4.0 nm (Figure 7b). School size estimated by the visual survey was not correlated with distance

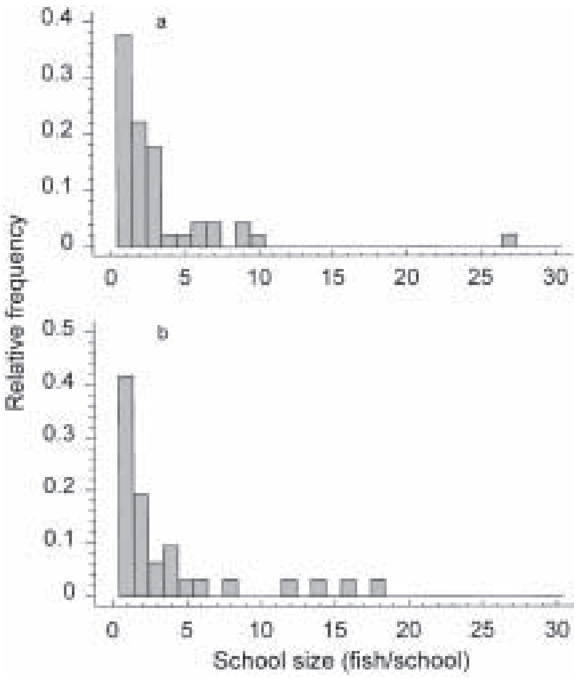

Figure 4. The frequency distribution of school size for a – adult *H. affinis* and b – small unidentified individuals, as determined by the visual survey.

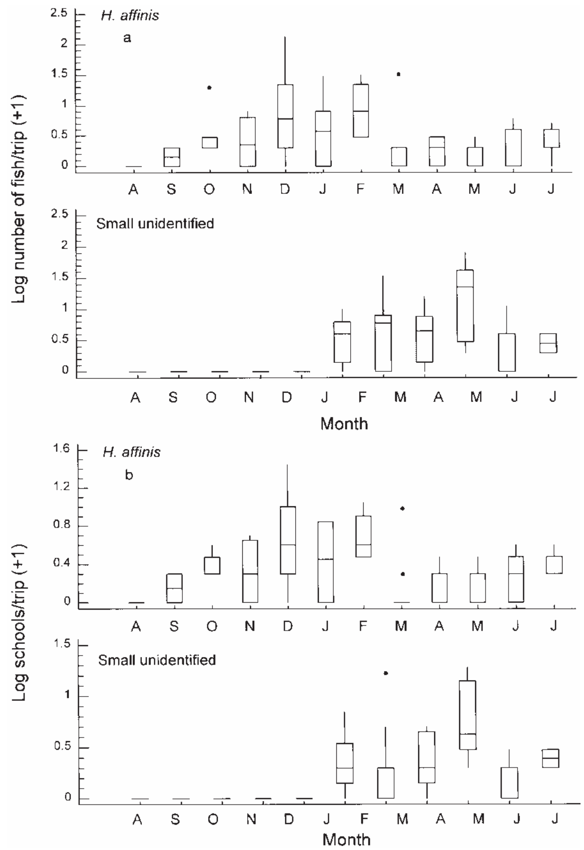

Figure 5. Results of the visual survey for *H. affinis* and small unidentified flyingfish: a – The seasonal pattern of the Log of the total number observed per trip, and b –the seasonal pattern of the Log of the number of schools observed per trip. In these box and whisker plots, the horizontal line shows the median, the boxes show the upper and lower quartiles, and the whiskers show the range of the data.

from shore, but was negatively correlated with distance between schools $R_s = -0.256$, $p < 0.001$.

The distribution of *H. affinis* schools along the transect on a given day, and the day to day variability in visual estimates along the transect and in catch rates at the standard station, suggest that *H. affinis* is patchily distributed. After removing the seasonal component of the data, daily visual estimates of abundance were significantly correlated with catch per trip at the standard station $R_s = 0.354$, $p < 0.05$. Evidence for the patchy distribution of this species was also obtained by comparing catch per trip of the 38.1 mm experimental net at the standard station with that of the same net fished in close proximity to the Speightstown fleet. Since catch per trip varies seasonally in both trip types, the seasonal component was removed before comparing catch per trip between trip types. This was done by dividing catch in each trip by the monthly mean catch per trip of the two trip types. Catch per trip (with seasonal component removed) for trips to the standard station was significantly lower than that for trips with the fishing fleet (Mann-Whitney-Wilcoxon test, $Z = 3.08$; $p < 0.05$).

Population size structure and growth

A gillnet selectivity study for *H. affinis* showed that the size structure of the combined catch of the 31.8 and 38.1 mm gillnets used in the present study does not differ from the size structure of the population adjusted for gillnet selectivity (Mahon et al. 2000). Therefore, the size structure of the catch of the two nets combined was used to evaluate seasonal patterns in population structure of *H. affinis*.

The length frequency distribution of the fish caught in each of five two-month periods is shown for males and females (Figure 8). The nets caught a narrow length range of *H. affinis*, 17.5–25.0 cm. The length frequency distributions were largely unimodal. However,

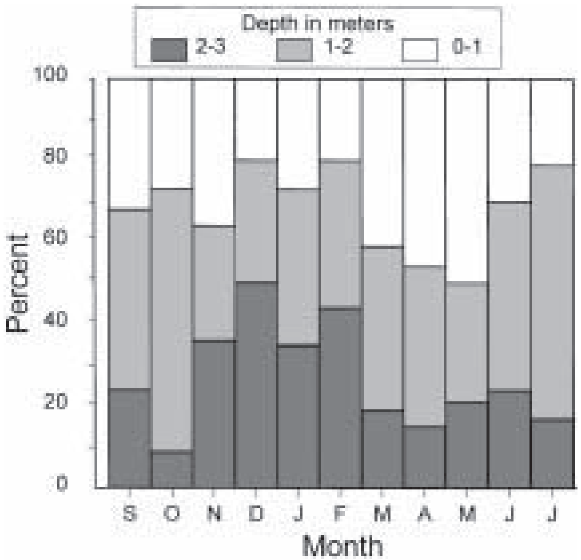

Figure 6. The percentage of *H. affinis* caught in each depth level of the experimental gill nets.

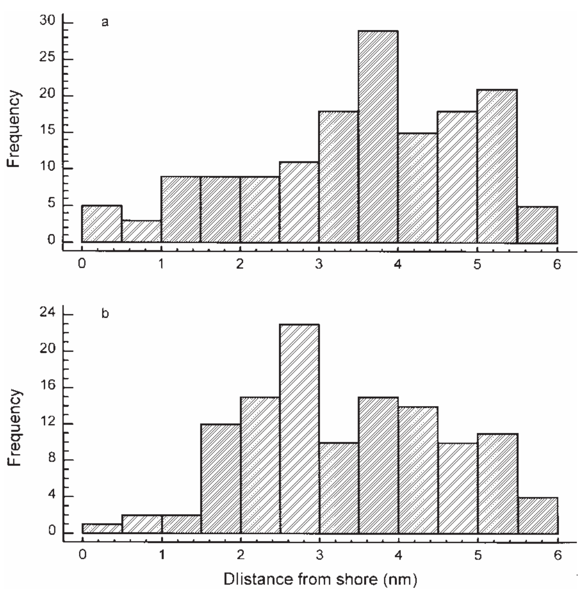

Figure 7. The number of schools of flyingfish in each 0.5 nm interval along the transect from shore to 6 nm offshore: a – *H. affinis*, b – small unidentified flyingfish.

for females there is possibly a small mode of large fish in the September/October sample, and a small mode of small fish in the January/February sample. For males there is an indication of a mode of small fish in the January/February period. For both sexes, mean length increased steadily through the season until March/April, and then decreases slightly in May/June (Figure 9). The data give a rough estimate of growth, although there are undoubtedly biases due to gear selectivity and to the availability to the gear of fish that are mainly mature.

The weight–length relationships for *H. affinis*, where weight is in g and length is fork length, were as follows: $W_{(male)} = 0.01241 \times L^{2.98}$ (n = 169), $W_{(female)} = 0.01094 \times L^{3.03}$ (n = 193), and $W_{(combined)} = 0.01160 \times L^{3.01}$ (n = 362).

Overall, the sex ratio of *H. affinis* in the experimental catch, was 49% male to 51% female, which does not differ significantly from 1 : 1 ($X^2 = 0.291$, d.f. = 1, $p > 0.05$). However, in both the experimental and commercial catch, the sex ratio varied significantly among months during the year. In the former, there were more males than females in November/December and April/May ($X^2 = 63.34$, d.f. = 10, $p < 0.01$). In the latter there were more males than females in December/February and May/June ($X^2 = 14.40$, d.f. = 7, $p < 0.05$).

The percentage of males and females in maturity stages 2–5 at various lengths is shown in Figure 10. In both sexes, mature individuals are found at ≥ 18 cm in length, but for males the percentage mature increases more rapidly with length than for females, such that the length at which 50% are mature is about 1 cm less than that for females.

In the experimental catch, immature individuals of both sexes were predominant in September and October (Figure 11). Thereafter, most fish were maturing or mature. The proportion of maturing and ripening fish of both sexes appeared to increase in July. Spawning fish of both sexes first appeared in November, and showed a generally increasing trend in proportion of the catch to a peak in April for females, and May for males. However, the percentage of males in spawning condition remained more constant over the season than did that of females. For both sexes, spent individuals were first recorded in December and the proportion of these remained relatively low and constant until July. A similar pattern was observed in the samples from the commercial catch but is not shown.

The distribution of stages of gonad development of males and females in the catches of the 38.1 mm experimental nets and the commercial catches do not differ significantly (Table 6). The median gonosomatic index (GSI) had two peaks during the year in both males (December and June) and females (January and April)

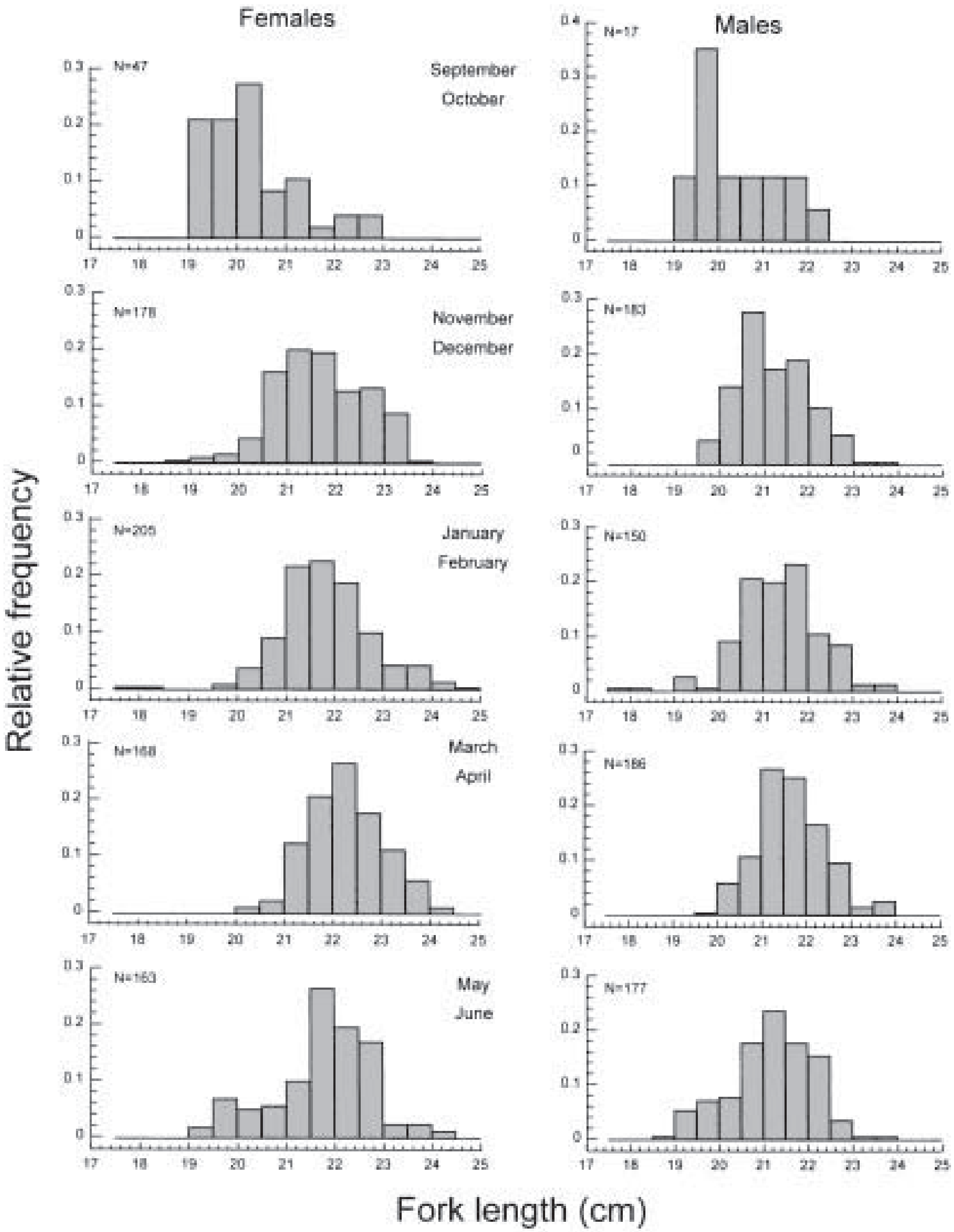

Figure 8. The frequency distributions of length for fish caught by the 31.8 mm and 38.1 mm nets in each of five two-month periods.

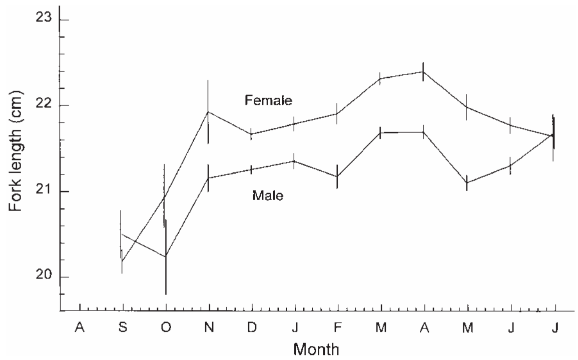

Figure 9. Monthly mean lengths (FL) of males and females of *H. affinis* ± 1 SE.

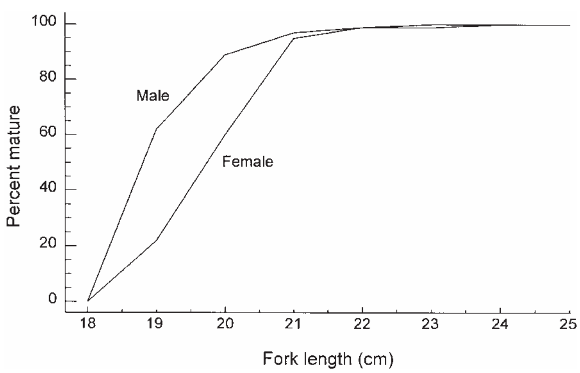

Figure 10. The percentage of individuals mature at length for males and females of *H. affinis*.

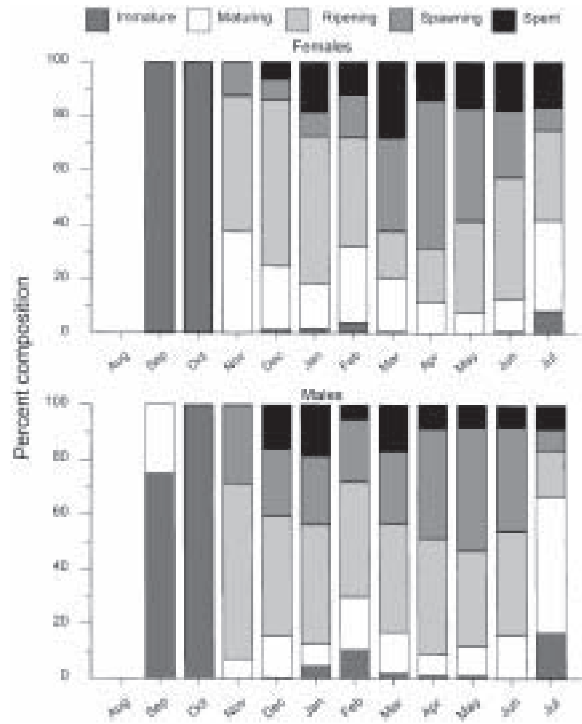

Figure 11. The monthly percentage of fish in each maturity stage for *H. affinis* in the commercial catch: a – males and b – females.

(Figure 12). This indicates that there are two spawning periods and is consistent with the observation that there are two peaks in catch each year.

The difference in timing of the peaks between the sexes indicates males reach breeding condition sooner and remain in that condition longer than females. If fish are more vulnerable to the gear when spawning, this observation is consistent with the fact that sex ratio of the catch is biased towards males near the beginning and near the end of the fishing season. For both sexes fish increase very little in length after maturity stage 2, then show slight decrease in median length at maturity stage 5 (Figure 13).

Table 6. The percentage of fish in each maturity stage caught by the experimental and commercial (38.1 mm) nets.

		Maturity stage				
		I	II	III	IV	V
Male	Comm.	0.7	11.9	40.3	35.6	11.5
	Exp.	2.4	13.7	40.9	29.7	13.3
Female	Comm.	0.4	12.5	50.9	17.0	19.2
	Exp.	1.4	18.7	42.5	20.6	16.8
Both	Comm.	—	12.1	45.4	27.1	15.1
	Exp.	1.9	16.2	41.7	25.2	15.1
Both	Comm.	—	12.1	45.4	27.1	15.1
	Exp.	—	14.6	43.6	26.0	15.3

Seasonal variation in environmental factors

Most of the abiotic environmental factors that could be expected to affect flyingfish abundance, distribution and/or vulnerability to the fishing gear showed some degree of seasonal variation (Figure 14). Sea temperature and salinity showed the most marked seasonal pattern (Figure 14a,b). The range of temperature was 26.75–28.95 °C with a maximum in September/October and a minimum in February/March. The range in salinity was 32.4–36.2 $^{o}/_{oo}$ with a maximum in April and a minimum in July. In contrast, water color changed little during the year. It was usually blue or blue-green, except in July when it was often green. Transparency (as measured by Secchi disk) ranged from 18 m in

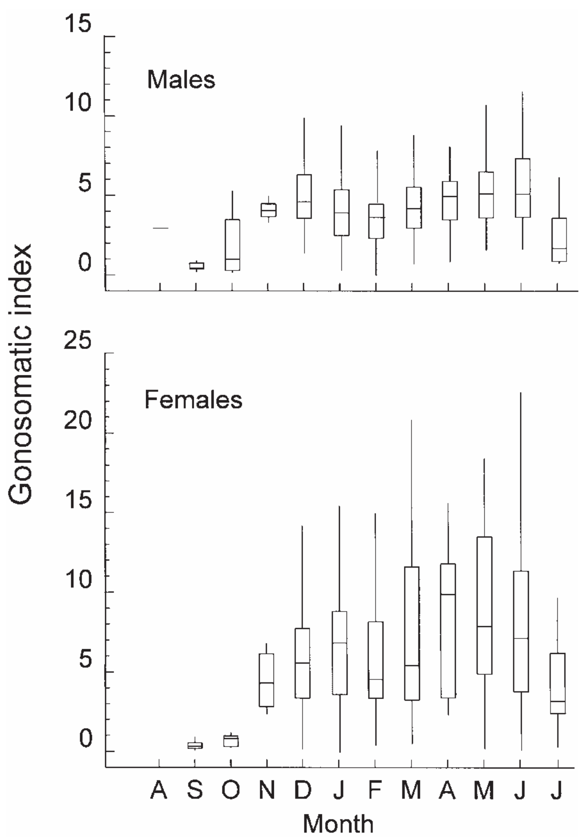

Figure 12. Monthly mean gonosomatic index of *H. affinis*. See figure 5 legend for interpretation of the box and whisker plots.

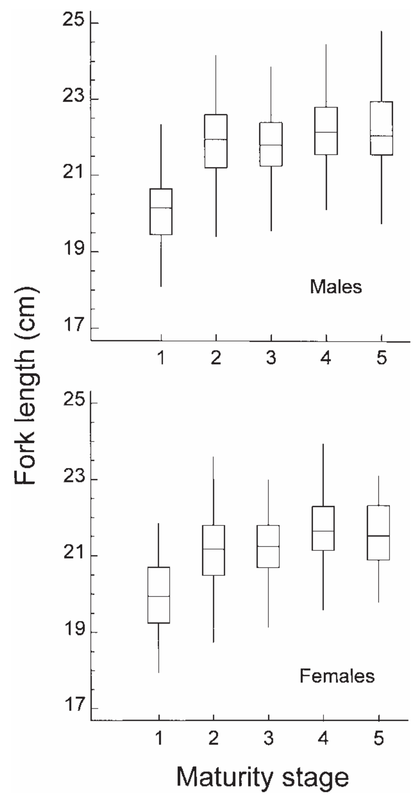

Figure 13. The distribution of size of *H. affinis* in each maturity stage. See figure 5 legend for interpretation of the box and whisker plots.

August to 25 m in October. Transparency was highest from October to December (Figure 14d). Wind condition varied from slight to strong (index numbers 2–3). The strongest wind occurred in January and February (Figure 14e) in the period when winds tended to be from the northeast (Figure 14f). Swell height was usually between 1–2 m (index numbers 3–4). Swells higher than 2 m occurred in some months; i.e. October–November and January–February (Figure 14g). Cloud cover was highest from September to November, and lowest from April to June.

Temperature and salinity trends from the surface (1 m) to a depth of 3 m along the transect from shore to offshore (9 nm offshore) were considered to be oceanographic conditions that might affect the distribution of juvenile and adult flyingfish. Temperature and salinity did not differ along the transect from shore to 9 nm offshore and did not differ between 1 m and 3 m depth in any month of the year.

The effects of environment on catch rate

The effects of environmental/climatic variables on catch rates were examined after removing the seasonal component by dividing the individual values by the mean for the month in which they occurred. Spearman Rank correlation analysis was then used to investigate the association between environmental variables (including distance of net drift) and catch rate. The only significant correlation between *H. affinis* and an environmental variable was the negative relationship with temperature ($R_s = -0.260$, $p < 0.05$).

Significant correlation between environmental variables and relative daily catch rate may not be evident because the relationships between catch rates and environmental variables are not linear. Thus the relationships between daily catch rate and environmental factors were investigated using second order polynomial multiple regression of catch rate on the environmental variables. This was considered to be

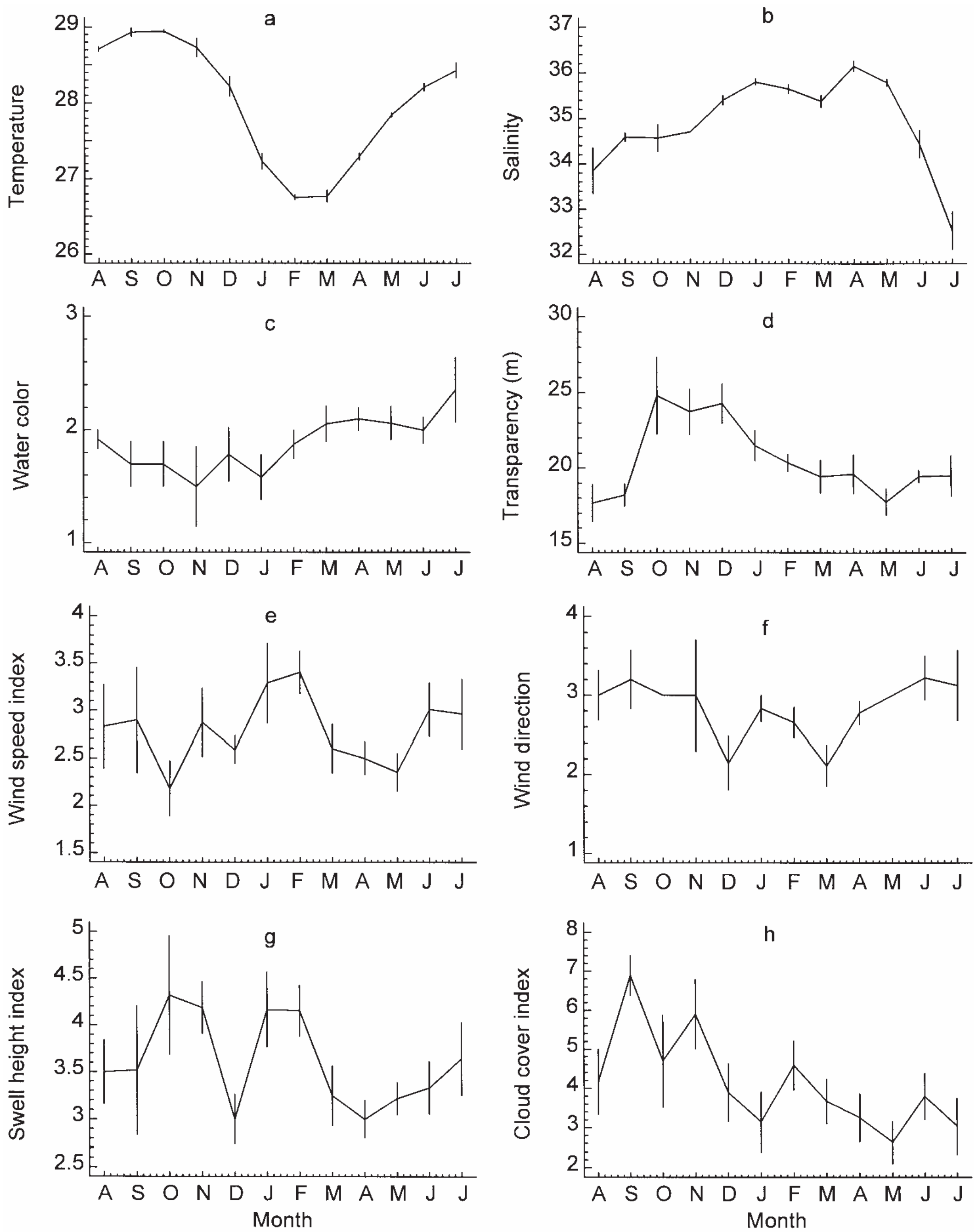

Figure 14. The seasonal patterns for the environmental/climatic variables.

an appropriate way of detecting environmental optima, which should occur if the full environmental range of the organism has been sampled. A significant fit was obtained for both wind speed and swell height (wind speed, $F = 4.19$, $R^2 = 0.096$, $p < 0.05$; swell height; $F = 5.572$, $R^2 = 0.122$, $p < 0.01$). This suggests that relative daily catch rate of *H. affinis* is low when wind speed is low and swells are small, increases to a maximum at medium values of the two parameters, and then decreases when wind speed is high and swells are large.

Discussion

Seasonal abundance of Hirundichthys affinis

The main purpose of fishing the experimental gill nets throughout the year was to determine the relative availability of flyingfish in the vicinity of Barbados, particularly during the off-season when fishing effort by the commercial fleet is minimal. The experimental fishing showed that *H. affinis* was most abundant in the period from December to June. This is consistent with the average seasonal abundance as indicated by the commercial catch and the visual survey. The catch rates in the present study were particularly high early in the season, rather than in March to May as is usually the case in the commercial fishery. However, data on flyingfish catches over the past three decades suggest that this type of variability about the average seasonal pattern is not uncommon[2].

During the off-season (mid-July to mid-November), the catch was almost zero in August, and very few fish were caught from September to November. The indices of abundance from the experimental fishing were similar to those from the Speightstown fleet, where catch rates in the fishing season were also relatively low in April–May and catch was zero in August–October as fishing had ceased. Thus the experimental fishing suggests that there were no fish of catchable size in the vicinity of Barbados in August and very few in September through to November.

Estimates of relative abundance of *H. affinis* by visual observation were very variable from day to day. However, the seasonal pattern was similar to that indicated by the experimental and commercial fishing. The visual method should probably be considered as only appropriate for rough, large-scale estimates of relative abundance of *H. affinis*.

The relatively low numbers of flyingfish observed would have contributed to the variability in visual estimates. Zuyev & Nikol'skiy (1981) have conducted visual estimates of the abundance of flyingfish, primarily *Exocoetus* spp. They estimated that about 25% of fish in the observation zone flew as the boat approached. The proportion of *H. affinis* becoming airborne in this study is probably lower than 25% for two reasons. First, the data from the experimental fishing show that many individuals of this species are distributed deeper than is reported to be the case for other species of flyingfish (Shiokawa 1969, Gorelova 1980, Zuyev & Nikol'skiy 1981, Nesterov & Bazanov 1986). The second reason is that the research boat, a 10 m fishing boat, is much smaller than the research vessels used in the studies cited above, and probably does not scare as high a proportion of individuals from deeper water (1–3 m). This suggested that the use of a larger research vessel might result in less variable visual estimates for this species, as was subsequently found to be the case (Oxenford et al. 1995a,b, Hunte et al. 1995).

Distribution of Hirundichthys affinis

Over the entire year, the proportions of individuals caught in each of the three depth ranges (0–1, 1–2, 2–3 m) were almost equal. This suggests that the vertical distribution of *H. affinis* differs from other exocoetids, which are most abundant at the surface with very low abundance or only occasional individuals below 1 m (Shiokawa 1969, Gorelova 1980, Zuyev & Nikol'skiy 1981, Nesterov & Bazanov 1986). Abundance at the surface was highest in March–May, which corresponds to the peak spawning period. Therefore shifts in depth distribution appear to be related to spawning activity, which is expected since spawning is reportedly at the surface, on floating material.

Visual observations show the highest frequency of fish schools between 3 and 5.5 nm from shore (Figure 2) which corresponds with the distance offshore usually fished by the Speightstown fleet. Temperature and salinity did not differ along the transect and thus cannot explain the differences in flyingfish distribution along the transect.

The high daily variability in both the visual and experimental fishing indices of abundance may suggest that flyingfish are patchily distributed. If the patchiness were on a spatial scale of about 1 nm or less, summing observations over the entire 6 nm transect should have reduced the effect of patchiness. That it did not, suggests a spatial scale of patchiness that is greater than 1 nm. Moreover, daily visual estimates of abundance

[2] Mahon, R., F. Murphy, P. Murray, J. Rennie & S. Willoughby. 1990. Temporal variability of catch and effort in pelagic fisheries in Barbados, Grenada, St. Lucia and St. Vincent: with particular reference to the problem of low catches in 1989. FAO FI: TCP/RLA/8963 Field Document 2. 74 pp.

and the catches from experimental fishing on the same day were correlated. This indicates that the patches of flyingfish were large enough to encompass the entire transect and fishing station, and thus that the spatial scale of patchiness in the study area is in the order of, or larger than 6 nm. This is larger than the mean patch width of 3.9 nm reported for flyingfish in the eastern Caribbean (Oxenford et al. 1995a). The fact that catch rate of the experimental nets at the standard station differed from that when the nets were fished in the vicinity of the commercial fleet also suggests a patchy distribution of *H. affinis*, and that fishermen are able to locate patches.

The annual pattern of size and reproduction

The four mesh sizes of experimental nets fished throughout the year caught very few fish smaller than 19 cm or larger than 24.5 cm. Considering that the optimal selectivities of the 1.0" and 1.75" experimental nets should be about 14 cm and 25 cm respectively (Mahon et al. 2000), the absence of fish of these sizes from the catch suggests that they are absent from the waters around Barbados, or at least are unavailable to the gear.

Although the fishery is largely based on attracting mature spawning fish to the screelers, the bait would also serve to attract immature fish, and if small individuals were present, at least some of these individuals should be caught by the smallest mesh nets.

The annual pattern of size and reproduction can be summarized in five two-month time periods. In September–October, males and females showed a single mode in the size range 19–21 cm, and were immature and virgin. The growth curve presented by Oxenford et al. (1994) indicates that these fish would have resulted from spawning about 7 months before in February–March. There was also a small mode of larger females in the 22–23 cm size range, that according to the growth curve, would have resulted from spawning towards the end of the previous year. However, very few fish were caught in this period.

In November–December, males and females had increased in size. Very few flyingfish were smaller than 20 cm or bigger than 23 cm (Figure 8). By this time, the average length of females was about 0.5 cm greater than that of males, and most fish were in the ripening stage (Figures 9, 13). In January–February, the range in fish length was the same as in the previous period although they were slightly larger on average (Figure 9), with females continuing to be larger than males. In this period the proportion of ripening fish was about the same as in the previous period (Figures 11, 13). In March–April, growth continued and females remained about 0.5 cm larger than males. In this period the proportion of spawning fish increased considerably, particularly females, which showed a distinct peak in April.

In the final period, May–June, a small mode of small fish about 20 cm in length appeared. This individuals would have resulted from spawning in October–November, the earliest spawning activity of the season. By May–June, the mean size of larger fish was less than in the previous period. During this period, the proportion of spawning fish decreased, indicating the end of the spawning season. However, note that throughout the fishing season, most fish were mature (Figure 11a,b), as also observed by Lewis et al. (1962) and Storey (1983). Too few fish were caught in July–August to include this period in the above time sequence. The few fish caught in the off-season (July–October) were mostly immature, about 20 cm in length.

Storey (1983) investigated seasonal changes in maturity stages and GSI values for *H. affinis* near Barbados, as well as changes in mean size of *H. affinis* caught by the commercial gear and recovered from the stomach of the dolphinfish, *Coryphaena hippurus*. He suggested the same explanation for the seasonal changes in reproduction and body size as described above. The sex ratio also varied through the year, with a different pattern for fish caught in the experimental and commercial nets. This difference might have resulted from the gears being fished on different days, or from differences in the response of spawning fish to the fishing methods. However, the overall sex ratio throughout the year in both experimental and commercial nets was 1 : 1. Hall (1955) found a ratio of 44% to 56%, which is close to 1 : 1, but did not give actual numbers of fish examined.

The mean length of females and males was not different early in the fishing season, at which time most fish were immature, but during the year female length increased more quickly than that of males (Figure 9). The weight–length relationships show that males are heavier than females at any given length. This result is unusual, as females are usually relatively heavier than males due to their gonads, and female GSI was greater than male GSI in this study. Storey (1983) also found that males are heavier than females at a given length, and that the GSI of females is greater than that of males.

Precise interpretation of the size frequency data in the present study is difficult because of the extended spawning period of *H. affinis*. Moreover, the sampling method is largely dependent on fish becoming mature before they are available to the gear. Therefore the size structure of the sample at any time will be determined by the relative rates of growth and maturation, that determine the rate of recruitment to the sampled population, and of mortality and/or emigration, that remove fish from the sampled population. Since these rates are contemporaneous, it is not possible to separate them using the data from this study.

Environmental effects on flyingfish abundance

The correlation analysis of flyingfish catch rate and the environmental variables using residuals around the seasonal patterns yielded little insight into the effects of environment on flyingfish abundance. The environmental variables measured in this study show that there is strong seasonal signal. The signal is consistent with the known climatic cycle that is dominated by the annual displacement of the Intertropical Convergence Zone (ITCZ) northward, beginning in April–May, to its northernmost location at about 10 °N in August–September, and its return to its southernmost location just south of the equator in January–March (Hastenrath 1988). This seasonal cycle can be summarised as follows[3]:

ITCZ North (June–November)	ITCZ South (December–April)
High rainfall	Low rainfall
Increased cloud cover	Clear sky
Low wind speed	Strong NE trade winds
Warmest temperatures	Coolest temperatures
Low atmospheric pressure	High pressure

The seasonal pattern of flyingfish reproduction and abundance described in this paper may be linked to the seasonality in climate and oceanography. The period of highest abundance and spawning takes place in the period when the ITCZ is in a southern position. Correlation analysis between the pattern for flyingfish and the environmental parameters on a seasonal scale would indicate the environmental conditions during which spawning takes place. However, cause and effect cannot be established with the data from this study. That question will have to be addressed using time series of data on environment and abundance over many years[3], or through process oriented field studies.

Synthesis of seasonality of Hirundichthys affinis

This study allow further evaluation and refinement of the hypotheses for the seasonality of *H. affinis*. The findings do not support the hypothesis that fish are present year round in surface waters in the vicinity of Barbados and are aggregated during the spawning season and dispersed in the off-season. If this were true, the visual observation data should show a pattern of increased school size and decreased number of schools in mid-fishing season, with smaller and more numerous schools at the beginning and end of the season, and in the off season. These patterns were not evident, as both school size and frequency of schools sighted increased in the fishing season. This suggests that the actual abundance of fish in the vicinity of Barbados increases in the fishing season. This is supported by the low, almost zero catches of fish by the experimental nets in the off-season. If the fish were dispersed in the vicinity of Barbados, at least a few should have been taken by chance in August.

Whereas, the findings of this study do indicate a shift in depth distribution through the year, they do not show a distinct tendency for fish to be caught in the deeper parts of the net in the off season. However, we cannot reject the hypothesis that the fish are present year round in the vicinity of Barbados, but move to greater depths than those fished by the experimental gear.

A second hypothesis was that the period of low abundance in August–October is an interval between adult cohorts. During this period, the incoming cohort would be too small and immature to be exploited by the fishery. Population size structure through the fishing season showed only one length mode, and the average fish size increased through to the fourth period (March–April) then decreased in the fifth period (May–June). Since it appears that the fish recruiting to the fishery at the beginning of the fishing season belong to a single cohort, average size would be expected to increase steadily through the fishing season. The fourth (March–April) period was the peak spawning period as indicated by the high percentage of spawning fish. Therefore, the decrease in mean size in the fifth period (May–June) indicates either an increase in mortality or emigration of the larger members of the stock following spawning.

[3] Mahon, R. 1990. Seasonal and interseasonal variability of the oceanic environment in the eastern Caribbean: with reference to possible effects on fisheries. FAO FI: TCP/RLA/8963 Field Document 5. 45 pp.

Stress due to spawning can be a cause of senescence and mortality (Andersen & Ursin 1977, Laevastu & Larkins 1981). Group spawning, as observed for flyingfish around floating objects, may also result in increased mortality due to predation (Johannes 1978). Hall (1955) and Storey (1983) have suggested that *H. affinis* might spawn three to four times in its lifetime. The length distributions of the maturity stages show that this species begins spawning at a size of about 20.5–21.0 cm.

This study supports the hypothesis that the low availability of fish around Barbados during the off-season may be an interval between cohorts. However, this can not be the only explanation, since in the fifth period there is still a relatively high proportion of young fish in the population, and evidence of an incoming cohort of fish resulting from eggs deposited at the beginning of the season. Therefore, either seasonal changes in oceanographic conditions result in arrested development and cessation of spawning, or these fish should ripen and spawn through the off-season. The fact that none were caught or seen suggests that they migrate away from the vicinity of Barbados, or perhaps into deeper water. Therefore, we conclude that the observed seasonality has two components: the main one being an interval of low abundance between cohorts, and the minor one being emigration of fish in the off-season. Whether these fish return to Barbados in the next season is unknown.

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References cited

Andersen, K.P. & E. Ursin. 1977. A multispecies extension to the Beverton and Holt theory of fishing, with accounts of phosphorus circulation and primary production. Medd. Danm., Fish. Havunder. (Ny Ser) 7: 319–435.

Barroso, L.M. 1967. Biologia e pesca do peixe-voador (*Hirundichthys affinis* Gunther) no estado Rio Grande do Norte. Bull Est. Pesca 7: 9–37.

Borstad, G. 1979. ASTP at Barbados: mesoscale pools of Amazon River water in the western tropical Atlantic. pp. 18–32. *In*: F. El Baz & D.M. Warner (ed.) Appollo-Soyuz Test Project Summary Science Report Vol. II, NASA SP 412, Washington, D.C.

Breder, C.M. 1938. A contribution to the life histories of Atlantic Ocean flyingfish. Bull. Bingham Oceannogr. Coll. 6: 1–126.

Brown, H.H. 1942. The sea fisheries of Barbados. Bull. Develop. Welf. W.I. 1: 1–42.

Campana, S.E., H.A. Oxenford & J.N. Smith. 1993. Radiochemical determination of longevity in flyingfish *Hirundichthys affinis* using Th-228/Ra-228. Mar. Ecol. Prog. Ser. 100: 21–219.

Clark, D.R. & P.E. King. 1986. The estimation of gillnet selection curves for Atlantic herring (*Clupea harengus* L.) using length/girth relations. J. Cons. int. Explor. Mer. 43: 77–82.

Freon, P. 1992. A methodology for visual estimation of abundance applied to flyingfish stocks. Proc. Gulf. Caribb. Fish. Instit. 41: 11–35.

Gomes, C., R.B. Dales & H.A. Oxenford. 1998. The application of RAPD markers in stock discrimination of the four-wing flyingfish, *Hirundichthys affinis* in the central western Atlantic. Molecular Ecology 7: 1029–1039.

Gomes, C., H.A. Oxenford & R.B. Dales. 1999. Mitochondrial DNA D-loop variation and implications for stock structure of the four-wing flyingfish, *Hirundichthys affinis* in the central western Atlantic. Bull. Mar. Sci. 64: 485–500.

Gorelova, T.A. 1980. The feeding of young flyingfishes of the family Exocoetidae and of the smallwing flyingfish, *Oxyporhamphus micropterus*, of the family Hemirhamphidae. J. Ichthyol. 20(4): 60–71.

Hall, D.N.F. 1955. Recent developments in the Barbadian flyingfish fishery and contributions to the biology of the flyingfish, *H. affinis* (Günther 1866). Eng. Colonial Office, Fish. Publ. No. 7. 41 pp.

Hastenrath, S. 1988. Climate and circulation in the tropics. D. Reidel Publishers, Dordrecht. 455 pp.

Hunte, W., H.A. Oxenford & R. Mahon. 1995. Distribution and relative abundance of flyingfish (Exocoetidae) in the eastern Caribbean. II. Spawning substrata, eggs and larvae. Mar. Ecol. Prog. Ser. 117: 25–37.

Johannes, R.E. 1978. Reproductive strategies of coastal marine fishes in the tropics. Env. Biol. Fish. 3: 65–84.

Jordan, C.M. 1983. The flyingfish industry (Tobago): a continuing case study. Proc. Gulf Caribb. Fish. Instit. 36: 1–11.

Laevastu, T. & H.A. Larkins. 1981. Marine fisheries ecosystem, its quantitative evaluation and management. Fishing News Books, London. 170 pp.

Lewis, J.B., J.K. Brundritt & A.G. Fish. 1962. The biology of the flyingfish, *Hirundichthys affinis* (Gunther). Bull. Mar. Sci. Carib. 12: 73–94.

Mahon, R., S. Khokiattiwong & H.A. Oxenford. 2000. Selectivity of experimental gillnets for fourwing flyingfish, *Hirundichthys affinis*. Env. Biol. Fish. (in press).

Mahon, R., W. Hunte, H. Oxenford, K. Storey & R.E. Hastings. 1982. Seasonality in the commercial marine fisheries of Barbados. Proc. Gulf. Caribb. Fish. Instit. 34: 28–37.

Nesterov, A.A. & M. Ye. Grudtsev. 1981. The quantitative distribution of flyingfish of the family Exocoetidae (Beloniformes) in the tropical Atlantic. J. Ichthyol. 20: 137–140.

Nesterov, A.A. & S.I. Bazanov. 1986. Vertical distribution and behavior of flyingfish (*Exocoetidae*). J. Ichthyol. 26(5): 159–162.

Oxenford, H.A. 1994. Movements of flyingfish (*Hirundichthys affinis*) in the eastern Caribbean. Bull. Mar. Sci. 54: 49–62.

Oxenford, H.A., R. Mahon & W. Hunte. 1993. The eastern Caribbean flyingfish project. OECS Fishery Report No. 9. 171 pp.

Oxenford, H. A., R. Mahon & W. Hunte. 1995a. Distribution and relative abundance of flyingfish (Exocoetidae) in the eastern Caribbean. I. Adults. Mar. Ecol. Prog. Ser. 117: 11–23.

Oxenford, H.A., R. Mahon & W. Hunte. 1995b. Distribution and relative abundance of flyingfish (Exocoetidae) in the eastern Caribbean. III. Juveniles. Mar. Ecol. Prog. Ser. 117: 39–47.

Royce, W.F. 1984. Introduction to the practice of fishery science. Academic Press, New York. 428 pp.

Shiokawa, T. 1969. Study of the swimming habits of flyingfish in the spawning season. Proc. FAO Conf. on Fish Behaviour in Relation to Fishing Technique and Tactics, Bergen, Norway, 19–27 Oct. 1967, Vol. 3, FAO Fish. Rep. 62: 579–589.

Storey, K.W. 1983. Aspects of the biology and fishery of the flyingfish, *Hirundichthys affinis*, at Barbados. M. Ph. Thesis, University of West Indies, Barbados. 161 pp.

Zaneveld, J.S. 1962. The fishery resources and fisheries industries of the Netherlands Antilles. Proc. Gulf Caribb. Fish. Instit. 14: 137–170.

Zuyev, G.V. & V.N. Nikol'skiy. 1981. Procedure for the quantitative recording of flyingfish (Exocoetidae). J. Ichthyol. 20(6): 147–149.