

Otolith age validation and growth-rate variation in flyingfish (*Hirundichthys affinis*) from the eastern Caribbean

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Abstract. A study of otolith aging and growth-rate variation in the flyingfish *Hirundichthys affinis* (Günther) was conducted in the eastern Caribbean (10–16 °N; 58–62 °W) in 1987–1989. Daily otolith-increment formation was validated in laboratory-reared larvae, confirming the usefulness of otolith-increment counts for age determination of *H. affinis* juveniles (<150 mm fork length, FL). A mark-recapture programme to validate increment formation in wild adults was unsuccessful due to tetracycline-linked mortality and insufficient tetracycline uptake in slow-growing adult otoliths. A von Bertalanffy growth curve fitted to juvenile size-at-age data gave preliminary growth-curve parameters of $t_0 = 2.85$ d and $k = 0.00854$ on a daily basis, with an asymptotic length, L_∞ , of 245 mm FL, for eastern Caribbean flyingfish. Juvenile growth rate in *H. affinis* is sensitive to spatial and temporal variation in temperature. Growth rates were higher where sea-surface temperatures were higher, and were higher for juveniles hatched in warmer months (April–July) than in colder months (November–March). Growth rates were also higher near islands than at more oceanic locations. Variation in juvenile growth rates may influence the spatial and temporal variation in spawning frequency observed in *H. affinis*.

Introduction

Traditional age-determination techniques using annual growth increments in hard parts or length-frequency analyses based on the simultaneous presence of multiple cohorts are often unsuitable for tropical fish, which may be short-lived, show little seasonal variation in growth rates, and have protracted spawning and recruitment seasons. Age-determination techniques most commonly applied to tropical stocks include age determination through analy-

sis of modal progressions of length-frequency data over short periods of time (Pauly 1983), and direct age determination through enumeration of daily growth increments visible in otolith microstructure (Oxenford and Hunte 1983, Campana and Neilson 1985). Length-frequency analyses of a sequential series of samples require clear separation of modal size classes to examine their progression. This may be facilitated in tropical species by a short lifespan and fast growth rate, but can be complicated by a protracted recruitment period. Furthermore, their use requires assumptions that the length-frequency distribution of the sample truly represents that of the population, and that there is no size-specific immigration and/or emigration, or size-selective mortality. Examination of growth increments in hard parts requires validation of their periodicity to estimate true age (Beamish and McFarlane 1983). Typical validation techniques include laboratory rearing and/or marking otoliths of captive specimens with oxytetracycline (OTC) or alizarin complexone (Campana and Neilson 1985, Tsukamoto 1988).

Several studies examined monthly progression of size frequencies of flyingfish from the Philippines (*Oxyphorhampus micropterus*, Yacapin 1991; *Cheilopogon nigricans*, *Cypselurus opisthopus* and *O. convexus*, P. Dalzell, R. Dumlao, D. Pauly unpublished data), Indonesia (Watson 1990, cited in Gillet and Ianelli 1991), and the eastern Caribbean (*Hirundichthys affinis*, Lewis et al. 1962, Storey 1983, Khokiattiwong 1988, Lao 1989), and some of these attempted to estimate growth rates and longevity. The consensus from these studies is that flyingfish grow rapidly and have a maximum life expectancy of no more than 2 yr, with most fish being annual. Although Brothers (1979) confirmed that exocoetid otolith microstructure appeared suitable for age determination, no studies have attempted to age any flyingfish species using growth increments in hard parts. Given the limitations of length-frequency analyses for estimating age and growth, there are therefore no reliable age and growth data available for flyingfish, despite the importance of many species to commercial fisheries (see Mahon et al. 1986, Gillet and Ianelli 1991). The problems with length-frequency analyses are

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further compounded in *H. affinis* by a 9 mo spawning season with bimodal spawning peaks (Storey 1983, Khokiattiwong 1988, Lao 1989). The consequence is that the only attempt to model the stock dynamics of eastern Caribbean flyingfish (*H. affinis*) assumed that it was an annual species (Mahon 1989). Analytical stock-assessment modeling and variation in growth rates of early life-history stages of *H. affinis* have not been investigated.

The objectives of this study were to investigate the validity of using daily otolith growth increments for direct age determination of *Hirundichthys affinis*, to construct a growth curve for this species in the eastern Caribbean, and to investigate variability in growth rate of wild juveniles in the eastern Caribbean and thereby comment on possible seasonal and spatial variation in the success of early life stages.

Materials and methods

Collection of flyingfish and surface-water samples

Juveniles of *Hirundichthys affinis* (Günther) were captured at night using attracting lights and handheld dipnets, from a single station 10 km off the northwest coast of Barbados (13°17'N; 59°40'W), weekly between October 1987 and September 1988 (present Fig. 1; see Lao 1989, for description of sampling protocol), and from 17 stations located throughout the eastern Caribbean (10–16°N; 58–62°W) between April and May 1988 (present Fig. 1; see Oxenford et al. 1993 b, for description of sampling protocol). For comparisons of spatial variation in growth rates, the stations were categorized as oceanic (open ocean, > 90 km from the nearest land), coastal windward (up wind, < 90 km from the nearest land) and coastal leeward (down wind, < 90 km from the nearest land). Surface-water samples were collected from each of the 17 stations and analysed for temperature, salinity, total reactive phosphorus (PO₄-P), oxidized nitrogen (NO₃-NO₂-N) and silicate (see Oxenford et al. 1993 a, for storage and analytical protocols). Adults were captured during daylight hours using surface gillnets of differing mesh size (25, 32, 38 and 44 mm), from an area between 4 and 22 km off the northwest coast of Barbados between July 1987 and July 1988 (see Khokiattiwong 1988, for full description of sampling protocol). The fork lengths (FL) of all fish were measured to the nearest mm, and stored frozen until extraction of otoliths.

Otolith preparation

All pairs of otoliths (sagittae, lapilli and asterisci) were removed initially from a wide size range of fish. Lapilli and asterisci were cleaned and mounted separately on glass microscope slides with cyanoacrylate glue. Sagittae were embedded in epoxy resin and thin-sectioned with a low-speed, diamond-tipped, double-bladed saw, before mounting on glass slides.

All otoliths (except for those of embryonic and larval fish) required grinding and polishing down to the otolith mid-plane with aluminium oxide lapping film of 30 and 3 µm grit size, for viewing with a transmitted light microscope. Polished sagittae, lapilli and asterisci all had growth increments clearly visible at 500× and 1250× magnification. Since sagittae were more difficult to prepare in juvenile and adult fish than other otoliths, and asterisci were absent from newly hatched larvae, lapilli were selected as the most suitable otolith for age determination in this species.

Growth increments in lapilli could be reliably counted in fish up to 150 mm FL (juveniles). In larger fish, the increments were difficult to interpret as they were frequently cracked and discontinuous, and not clearly discernible near the otolith margin. All increment

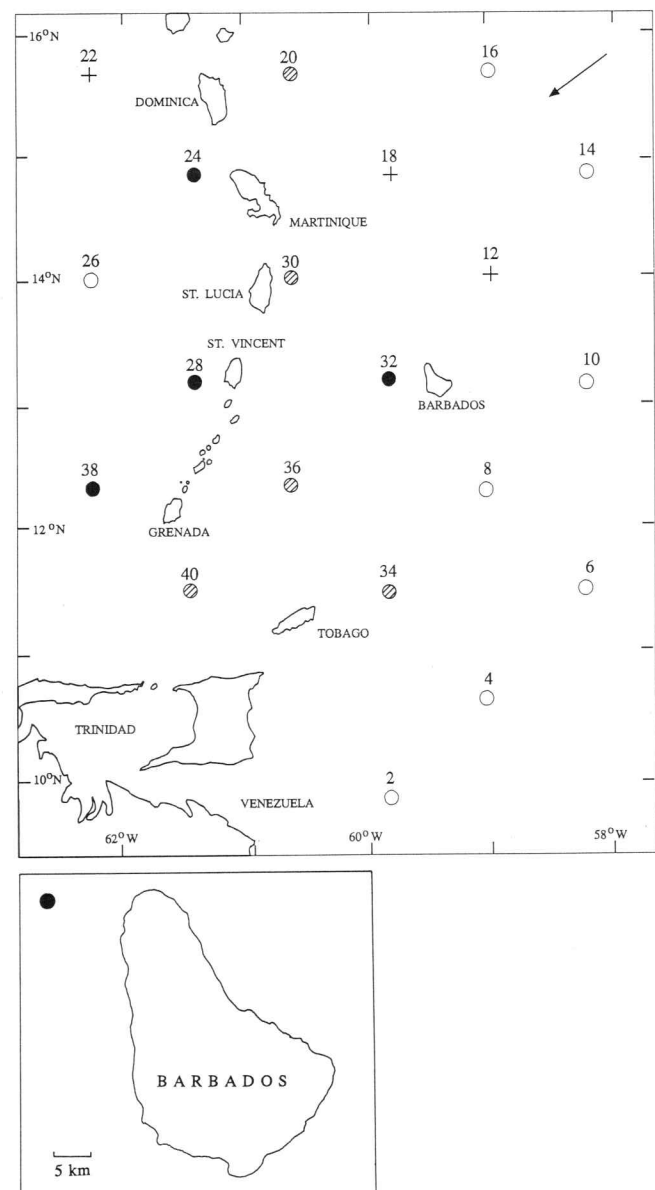


Fig. 1. Numbered dipnet sampling stations for juvenile *Hirundichthys affinis* over eastern Caribbean; sampling was conducted from April–May 1988. Small map shows single dipnet sampling station off Barbados used to collect juveniles weekly from October 1987–September 1988. ○: oceanic stations, ⊘: coastal windward stations, ●: coastal leeward stations, +: sampling stations where no juveniles were found; →: prevailing NE Trade Winds

counts were repeated three times without knowledge of fish length or previous counts, and only those with < 0.5% variation in counts were used. A sub-sample of each was repeated by a second reader to check observer reliability.

Validation of otolith growth-increment periodicity

Laboratory rearing of larvae

Validation of growth-increment periodicity was attempted for young fish by rearing larvae in the laboratory. Naturally fertilized eggs of *Hirundichthys affinis* were collected on two occasions (6 February and 24 April 1989) by dipnet from a fish-attracting device used by

commercial fishermen off the northwest coast of Barbados, and placed in aerated, flow-through aquaria in the laboratory where they hatched 3 to 6 d later. Newly hatched larvae were removed from the hatching aquaria every 24 h, and placed in separate aerated rearing tanks to ensure that the number of days after hatching was known for all fish. The larvae were raised at ambient water temperatures (mean = 26.7 °C, range = 24.4 to 28.6 °C) in natural seawater which was changed daily, and were fed laboratory-reared brine shrimp, *Artemia* sp. February fish were reared under natural day–night conditions. April fish were either reared under natural day–night conditions, or under continuous light to check the consistency of daily increment formation. A sub-sample of 2 to 4 known-age larvae was sacrificed every few days for examination of otolith increments.

Mark and recapture of wild adults

To validate growth-increment periodicity in older fish, otoliths of wild adults were chemically marked during a mark–recapture programme. Adults of *Hirundichthys affinis* were captured, tagged, injected with oxytetracycline hydrochloride (OTC), and released in the eastern Caribbean during a 1988/1989 tagging study (see Oxenford 1993 for details of tagging programme). A single-dose intraperitoneal (IP) injection (100 mg OTC kg⁻¹ fish body weight; i.e., 15 mg OTC dissolved in 0.1 ml water per fish) was administered to 961 of 3559 tagged fish in 1988, and a double-dose (30 mg OTC per fish) IP injection was administered to 186 of 3460 tagged fish in 1989. Otoliths from recaptured fish ($N = 21$) were prepared as described above and examined with a fluorescence microscope using transmitted ultra-violet light through a 270 to 380 nm excitation filter with 510 and 515 nm barrier filters.

Growth curve

Size-at-age data for a wide size range of wild *Hirundichthys affinis* juveniles ($N = 265$), and an asymptotic length (L_{∞}) estimated from the maximum observed length (L_{\max}) of adult *H. affinis* in the eastern Caribbean using the relationship $L_{\infty} = L_{\max}/0.95$ (Pauly 1979), were applied to a linearized von Bertalanffy growth model $-\ln(1-L/L_{\infty}) = -kt_0 + kt$ (see Sparre and Venema 1992). This was used to obtain a growth curve for *H. affinis* and approximate values for the standard growth parameters time at size zero (t_0) and rate of approach to asymptotic length (k).

Results

Otolith growth-increment periodicity

Laboratory-reared larvae

The inner ear was visible in embryonic *Hirundichthys affinis* 50 h after fertilization, and both saggittae and lapilli were clearly visible within the saccules 72 h after fertilization. Asterisci did not become apparent until 3 to 4 d after hatching. A single increment was visible in the otoliths of the majority of embryos and newly hatched (< 24 h old) larvae. This was therefore not included in subsequent increment counts. Increment counts were highly correlated with known age in all three rearing experiments (February rearing, normal day–night regime; April rearing, normal day–night regime; April rearing, continuous light; linear regression analyses; $r \geq 0.99$, $P < 0.001$ in all cases). Neither the slopes nor elevations of the regressions of otolith counts on age differed significantly between the

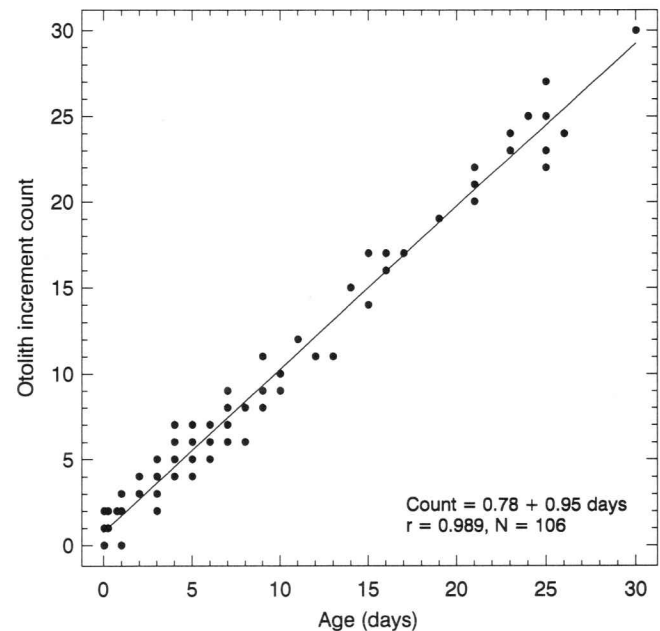


Fig. 2. *Hirundichthys affinis*. Relationship between known age and otolith-increment count for laboratory-reared larvae

three experiments, indicating that the periodicity of increment formation was not affected by collection month or photoperiod (ANCOVA; for slopes, $F = 0.76$, $P > 0.25$; for elevations, $F = 0.56$, $P > 0.25$). The data from the three experiments were therefore pooled. For the pooled data, increment counts were highly correlated with known age (linear regression analysis; $P < 0.001$; Fig. 2), and the slope did not differ significantly from 1 (Student's t -test; $t = 1.87$, $P > 0.05$), confirming a daily periodicity for increment formation.

Marked and recaptured adults

Thirty-three (3.4%) of the 961 single-dose OTC, tagged, adult fish injected in 1988 were recaptured. Twenty-one of these were returned as whole fish, allowing otoliths to be extracted. The mean size of the 21 fish was 222 mm FL (range = 204 to 233 mm FL). The date of recapture was recorded for 13 of the fish, the mean time-at-large being 15 d (range = 5 to 29 d). Recapture rates did not differ significantly between these tagged, single-dose OTC injected fish and the 2598 tagged fish that were not injected, indicating no additional mortality from the IP injections of OTC (chi-squared 2×2 contingency test; $\chi^2 = 1.525$, $P = 0.217$). Examination of the marked otoliths revealed either no OTC fluorescence or a faint fluorescence which could not be clearly distinguished from the edge autofluorescence. For this reason, double-dose OTC injections were used in 1989. However, only 1 (0.5%) of the 186 double-dose OTC injected, tagged fish (233 mm FL) was recaptured, with time-at-large being less than 16 d. This recapture rate was significantly lower than that for the 3274 tagged fish receiving no injection (chi-squared 2×2 contingency test; $\chi^2 = 10.290$, $P < 0.005$), indicating that the double-dose of OTC may have induced significant addi-

tional mortality. The OTC fluorescence in the only returned double-dose fish was no stronger than that detected in single-dose fish, and also could not be separated from the otolith edge.

Larval and juvenile growth rates

Size was significantly correlated with age in laboratory-reared larvae (mean size = 8 mm; range = 3 to 24 mm FL) in all three rearing experiments (February rearing, normal day–night regime; April rearing, normal day–night regime; April rearing, continuous light; linear regression analyses; $r > 0.91$, $P < 0.001$ in all cases). Neither the slopes nor the elevations of the regressions of size-on-age differed significantly between the three experiments, indicating that the growth rate of laboratory-reared larvae did not differ with month of egg collection nor with variation in photoperiod (ANCOVA; for slopes, $F = 1.84$, $P > 0.10$; for elevations, $F = 1.50$, $P > 0.10$). Data were therefore pooled for all laboratory-reared larvae. For pooled data, size was significantly correlated with age (linear regression analysis; $P < 0.001$; Fig. 3), and the overall growth rate for laboratory reared larvae was 0.47 mm d^{-1} .

A total of 265 wild juveniles (mean size = 67 mm FL; range = 20 to 140 mm FL) collected off Barbados and across the eastern Caribbean were aged by counting the daily otolith increments. Size was linearly correlated with age (linear regression analysis; $P < 0.001$; Fig. 4), indicating a growth rate of 1.41 mm d^{-1} for wild eastern Caribbean flyingfish juveniles.

Growth curve

A von Bertalanffy growth curve was fitted by a least-squares method to the wild juvenile size-at-age data, using a value of $L_{\infty} = 245 \text{ mm FL}$ (i.e., the largest flyingfish observed, $L_{\infty} = 233 \text{ mm FL}/0.95$). The fit was significant ($r = 0.940$, $P < 0.001$), and extension of the growth curve to adult size-classes produced a close fit to previous indirect estimates of adult size-at-age by Storey (1983) and by Khokiattiwong (1988) (Fig. 5). The model gave growth parameters for eastern Caribbean flyingfish of $t_0 = 2.85 \text{ d}$ ($t_0 = 0.008 \text{ yr}$) and $k = 0.00854$ on a daily basis ($k = 3.12$ on a yearly basis). It also suggests that age at sexual maturity for *Hirundichthys affinis* in the eastern Caribbean is reached at ~ 7 to 8 mo of age, since size at sexual maturity has been reported as 200 to 217 mm FL (Storey 1983, Khokiattiwong 1988).

Spatial variation in juvenile growth rates

A total of 84 juveniles of *Hirundichthys affinis* were captured from 17 stations across the eastern Caribbean in April/May 1988 (Fig. 1). The mean size of juveniles sampled was 69 mm FL (range = 29 to 141 mm FL) and the mean age was 42 d (range = 17 to 111 d). Mean age did not differ between stations (Kruskal-Wallis test; $H = 14.031$, $P = 0.447$).

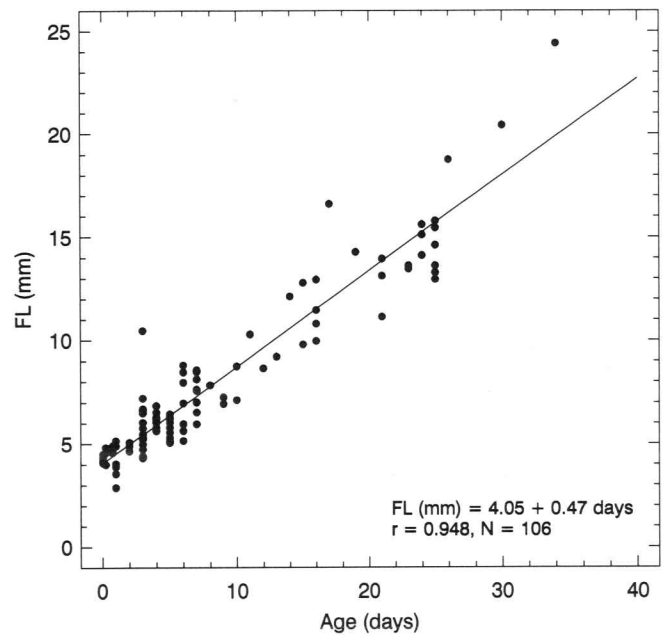


Fig. 3. *Hirundichthys affinis*. Relationship between size (FL; fork length) and age for laboratory-reared larvae

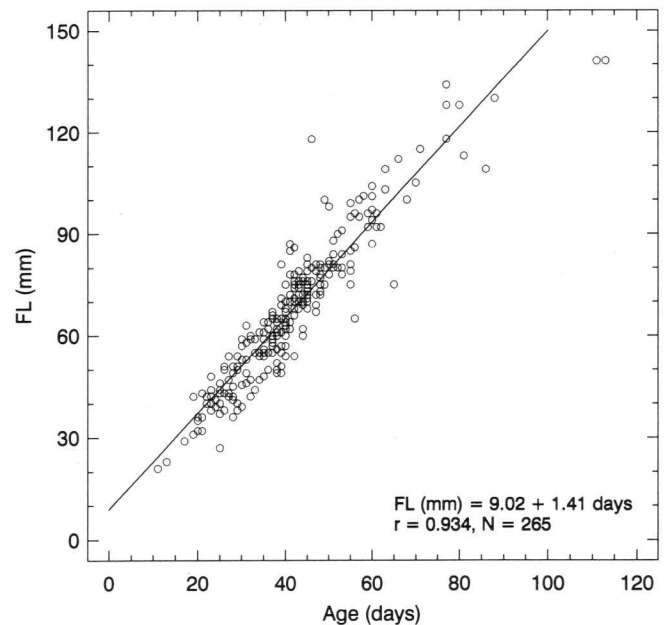


Fig. 4. *Hirundichthys affinis*. Relationship between size and age for wild juveniles collected off Barbados and across eastern Caribbean

The mean growth rate of juveniles sampled was 1.66 mm d^{-1} (range = 1.15 to 2.12 mm d^{-1}). Growth rates differed significantly between stations (ANOVA; $F = 2.188$, $N = 15$, $P = 0.02$; Table 1), increasing with increasing proximity to the nearest land (linear regression analysis; $r = -0.724$, slope = -0.001 , $P = 0.001$). Mean distance from the nearest land for oceanic, coastal windward and coastal leeward stations was 172, 50, and 46 km, respectively. Mean growth rate was significantly lower at oceanic stations than at either coastal windward or coastal leeward

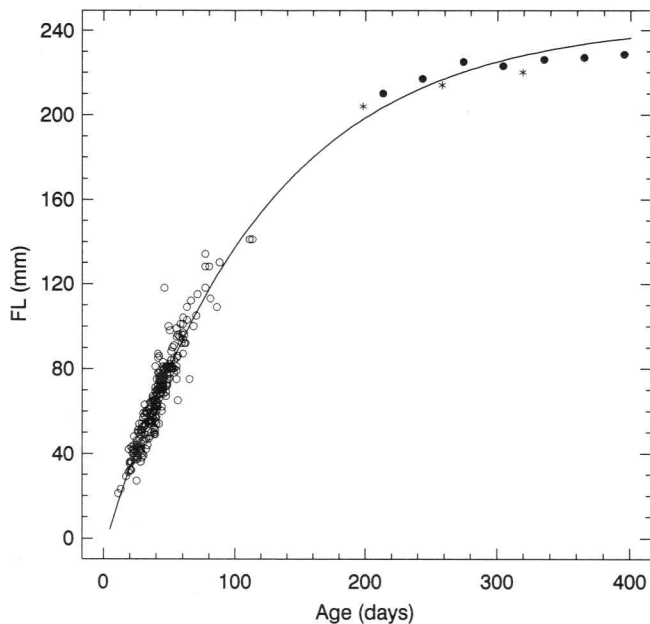


Fig. 5. *Hirundichthys affinis*. Von Bertalanffy growth curve fitted to size-at-age data for wild juveniles (○). Indirect estimates of size at age for adults from Storey (1983) (●) and from Khokiattiwong (1988) (*) are shown, but were not used to calculate growth curve

stations (Tukey's multiple-range test; $P < 0.05$ in both cases), but did not differ between coastal windward and coastal leeward stations ($P > 0.05$). The highest mean growth rates occurred at Station 40 (54 km windward of Grenada, 1.78 mm d^{-1}) and at Station 24 (39 km leeward of Martinique, 1.93 mm d^{-1}) (Fig. 1, Table 1).

Mean juvenile growth rates at stations were not correlated with salinity, nor with phosphate, nitrate or silicate concentrations in surface waters at the same stations on the same collection days (linear regression analyses; $P > 0.05$ in all cases), but were positively and significantly correlated with sea-surface temperature (linear regression analysis; $r = 0.522$, slope = 0.147 , $P = 0.032$; Table 2). The slope indicates an increase in juvenile daily growth rate of 0.07 mm (i.e., 5.2% of mean daily growth rate as predicted by the linear model, see Fig. 4) for every 0.5°C increase in temperature. Sea-surface temperatures were not significantly correlated with distance from land (linear regression analysis; $r = -0.375$, $P = 0.138$).

Seasonal variation in juvenile growth rates

A total of 181 juveniles of *Hirundichthys affinis* were captured from a single station northwest of Barbados between October 1987 and September 1988. The mean size of juveniles sampled was 66 mm FL (range = 21 to 141 mm FL) and the mean age was 41 d (range = 11 to 113 d). Mean age differed significantly between months (Kruskal-Wallis test; $H = 67.58$, $P < 0.001$), which is expected given the reported bimodality of the spawning season (minor peak November–January, major peak May–July; Storey 1983, Khokiattiwong 1988). The bimodality of spawning was indicated in this study by hatch-date distribution of juveniles

Table 1. *Hirundichthys affinis*. Mean growth rates of juveniles collected over eastern Caribbean, presented for each station and station type. Station locations numbered as on Fig. 1. (N): number of individuals

Station type and No.	(N)	Mean growth rate (mm d^{-1})
Oceanic		
2	(2)	1.52
4	(1)	1.46
6	(3)	1.29
8	(4)	1.56
10	(4)	1.58
14	(2)	1.37
16	(4)	1.60
26	(1)	1.73
	(21)	1.52
Coastal windward		
20	(2)	1.68
30	(2)	1.73
34	(3)	1.66
36	(18)	1.68
40	(16)	1.78
	(41)	1.72
Coastal leeward		
24	(2)	1.93
28	(3)	1.66
32	(2)	1.57
38	(5)	1.66
	(12)	1.69
Overall	(74)	1.66

Table 2. *Hirundichthys affinis*. Results of linear correlation analyses between mean growth rates of juveniles and surface-water characteristics at sampling stations across eastern Caribbean

	Salinity	PO ₄ -P	NO ₃ -NO ₂ -N	Silicate	Temperature
r	0.055	0.157	-0.159	-0.187	0.522
(N)	(12)	(17)	(17)	(15)	(17)
P	0.864	0.547	0.541	0.504	0.032

collected over the year. Most fish were hatched either in late November 1987 or between late May and early July 1988 (Fig. 6).

The mean growth rate of juveniles sampled was 1.63 mm d^{-1} (range = 1.08 to 2.21 mm d^{-1}). Growth rates differed significantly between juveniles hatched in different months (ANOVA; $F = 13.93$, $N = 7$, $P < 0.001$). Fish hatched in colder months (November–March; i.e., primarily the first spawning peak) grew significantly slower (mean growth rate = 1.41 mm d^{-1}) than fish hatched in warmer months (April–July; i.e., the second spawning peak, Fig. 6; mean growth rate = 1.66 mm d^{-1}) (Student's t -test; $t = 8.08$, $P < 0.001$; Table 3). Surface-water sampling confirmed that the mean sea-surface temperature was significantly lower in the earlier months (November–

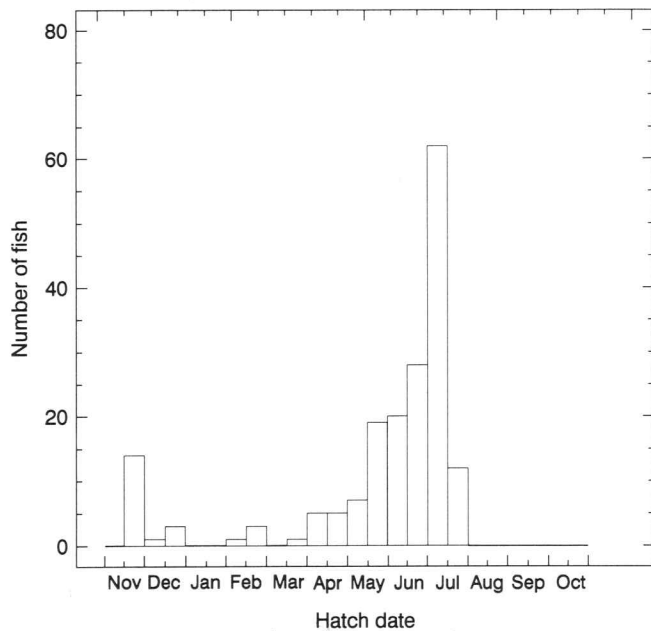


Fig. 6. *Hirundichthys affinis*. Hatch-date distribution for juveniles collected monthly at a single station off Barbados from October 1987–September 1988

Table 3. *Hirundichthys affinis*. Mean growth rates of juveniles collected at a single station, northwest of Barbados. Data presented by month of capture and by month of hatching, and separately for cool (mean 27.5°C) and warm (mean 28.2°C) months. (N): number of juveniles

Month of capture	(N)	Mean growth rate (mm d ⁻¹)	Month of hatching	(N)	Mean growth rate (mm d ⁻¹)
Cool					
December	(13)	1.36	November	(14)	1.35
January	(1)	1.43	December	(4)	1.59
February	(1)	1.59	February	(4)	1.40
March	(6)	1.36	March	(1)	1.50
	(21)	1.38		(23)	1.41
Warm					
May	(8)	1.59	April	(10)	1.66
June	(32)	1.71	May	(33)	1.68
July	(13)	1.78	June	(43)	1.70
August	(107)	1.64	July	(72)	1.64
	(160)	1.66		(158)	1.66
Overall	(181)	1.63		(181)	1.63

March; mean temperature = 27.5°C) than in later months (April–August; mean temperature = 28.2°C) (Student's *t*-test; $t = 8.959$, $P < 0.001$).

Discussion

Daily growth increments were clearly visible from the centre to the margin in all otoliths of larvae and juveniles of

Hirundichthys affinis after appropriate preparation. The daily periodicity of the increments was confirmed in slow-growing, laboratory-reared larvae. Since unresolvable increments associated with low larval growth rates are the primary source of non-daily increment formation (Campana et al. 1987), our results validate the use of daily increment counts for age determination of faster-growing, wild fish.

The use of chemical markers such as OTC is a common procedure for validating daily increment formation in the otoliths of captive fish (Campana and Neilson 1982, Hettler 1984), and has also been used for tagged wild fish (e.g. Wild and Foreman 1980, Secor et al. 1991). In the present study, fluorescence in recaptured, OTC-injected and tagged, adult wild fish was either too faint to be seen or too close to the otolith margin to detect subsequently-formed daily increments with the light microscope. The results suggest that otolith growth in mature flyingfish is too slow to incorporate sufficient chemical marker with a single injection and/or to allow discrimination of daily increments formed subsequent to fish injection and release. Double-dose OTC-injected fish had high mortality rates, as was observed by McFarlane and Beamish (1987). Our results emphasize the importance of using immature fish, or fish which are still growing rapidly, for validation of otolith-increment periodicity through chemical markers.

Juvenile size-at-age data for *Hirundichthys affinis* was well described by a linear model, but also closely fitted a standard von Bertalanffy growth model. Extrapolation of a model based on juvenile growth to estimate adult growth should be done with caution. In this study however, independent, indirect size-at-age estimates for adult *H. affinis* (Storey 1983, Khokiattiwong 1988), as well as a recent direct estimate of adult size-at-age using radiochemical dating (Campana et al. 1993), were very close to those based on the extrapolated growth curve, suggesting that the extrapolated juvenile growth curve is a good predictor of adult growth in *H. affinis*. The growth model gave a k value of 3.12 on a yearly basis, which indicates a fast approach to asymptotic length, and suggests a high metabolic rate, typical of oceanic pelagic species (Lipskaya 1974).

The growth rate of juvenile fish is typically variable, and often influenced by temperature and competition for food (Ricker 1979, Weatherley and Gill 1987, Campana and Hurley 1989). In the present study, growth rates of juvenile flyingfish were positively correlated with sea-surface temperatures. This may be a simple consequence of the effects of temperature on metabolic rate, and it would indicate that larvae and juveniles of *Hirundichthys affinis* remain associated with particular water masses long enough to be affected by the water-mass characteristics. Juvenile growth rates were also higher nearer to islands than at oceanic locations, although there was no correlation between temperature and distance from land. The faster growth near to islands may result from the higher productivity, and therefore greater food abundance, which is typically associated with island masses (Doty and Oguri 1956). Furthermore, eddies and gyres which form to leeward of islands can cause upwellings resulting in increased productivity, as well as retain and therefore aggregate potential prey items (Lao 1989, Hunt von Herbing and Hunte

1991). In the present study, the faster growth rates observed close to islands may result primarily from retention of prey items, rather than higher productivity, since juvenile growth rates were not correlated with salinity nor with phosphate, nitrate or silicate concentrations in this study. Lao (1989) found that the abundance and mean size of larval and juvenile fish, including flyingfish, leeward of Barbados were greater at his most offshore station (17 km from land), than at stations closer to land. He suggested that the higher abundance was the consequence of eddies and gyres retaining larvae and juveniles some distance to the lee of Barbados. Our results suggest that the larger mean sizes observed by Lao could have resulted from a faster growth rate at such locations.

Oxenford et al. (1993 a) found that during the spawning season, adults of *Hirundichthys affinis* in the eastern Caribbean were more abundant close to islands, particularly leeward of islands, than at more oceanic locations. Given the distribution of growth rates observed in this study, this may suggest that flyingfish preferentially spawn at locations where larval and juvenile growth will be highest. Oxenford (1993) provided indirect evidence indicating that the area between Tobago and Grenada may be a preferred spawning location of eastern Caribbean flyingfish, and growth rates at this location were among the highest observed in the present study.

Juveniles hatched in warmer months (i.e., April–July, towards the end of the spawning season) grew significantly faster than those hatched in colder months (i.e., November–March, towards the beginning of the spawning season). This may again be the consequence of temperature effects on metabolic rate. However, Lewis et al. (1962), Kidd and Sander (1979) and Borstad (1982) showed that total plankton abundance off Barbados is higher in summer than winter months, suggesting that the faster growth in summer could also be the consequence of greater food availability for *Hirundichthys affinis* juveniles. The present results support previous studies indicating that the spawning season of *H. affinis* extends from November through July, with a minor peak early in the season (November–January) and the major peak late in the season (May–July) (Storey 1983, Khokiattiwong 1988). This indicates that most flyingfish therefore hatch in the months of the spawning season when juvenile growth is fastest.

In conclusion, our results suggest that flyingfish may spawn at times of year, and perhaps at locations, where juvenile growth rates are fastest, and that sea-surface temperature and possibly food availability may influence growth rates. Rapid juvenile growth may increase juvenile survivorship by decreasing the length of time juveniles are exposed to predators (Houde 1987). Inter-annual variation in juvenile growth rates may therefore influence inter-annual variation in juvenile survivorship, and could be a major component of the considerable inter-annual variation in flyingfish catch rates observed in the eastern Caribbean (Mahon 1989). Attempts to identify correlations between inter-annual variation in catch rates and environmental factors, and to thereby allow predictions of recruitment success and availability of harvestable stock, should pay particular attention to temperature and other environmental factors which may influence juvenile growth rates.

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