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Active salinity choice and enhanced swimming endurance in 0 to 8-d-old larvae of diadromous gobies, including *Sicydium punctatum* (Pisces), in Dominica, West Indies

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Abstract We studied the early life history of diadromous gobies in Dominica, West Indies, from May 1989 to May 1991, emphasising *Sicydium punctatum* Perugia. The transition of newly hatched larvae from upriver nest sites to the sea was studied in laboratory experiments. Newly hatched larvae are negatively buoyant but avoid settling to the bottom by active swimming during drift to the sea. Laboratory experiments evaluated salinity preferences and effects on swimming endurance. Larvae in haloclines actively selected low to intermediate salinities. Initially (0 to 5-d post-hatch), larvae minimized exposure to salinities >10 ppt, but later (5 to 8-d) occupied increasingly saline water. Larvae in no-choice freshwater or seawater treatments ceased activity at 4 to 5 d, but in haloclines larvae remained active up to 8 d post-hatch. Salinities < 10 ppt are important for early survival of sicydiine gobies. Implications for larval survival and transport are discussed.

Introduction

Larval behaviors affect larval distributions and transport and therefore can give insight into fisheries problems (Sulkin 1986). Horizontal transport of aquatic organisms is increasingly seen as a consequence of interactions of organismal behaviors or properties (e.g. density) with vertical structure of the water column (Leis and Miller 1976; Leis 1982; Williams et al. 1984; Lobel and Robinson 1986). The mechanisms by which fish eggs or larvae are associated with particular depths have so far been observed only as a passive process, based on relative densities of eggs or larvae and the surrounding water (Frank and McRuer 1989; Frank et al. 1989; Page et al. 1989). For whitefish (*Coregonus nasus*), de March (1989) reported that larvae "did not show the slightest tendency to choose certain salinity ranges" but instead distributed themselves according to the distribution of introduced food (*Artemia* sp.), although older fish (juveniles) avoided higher salinities.

Despite the importance for horizontal transport issues, there appears to be no report of active salinity choice in larval fish. However, active movement to particular water column positions is known in some juvenile or adult fishes (e.g. Jäger et al. 1981) and zooplankton (e.g. Arai 1976). Preferential occupation of particular depth layers could similarly be mediated by active responses of some larvae to sensory cues, so it is reasonable to evaluate this as a possibility for fish larvae.

The present study examined behavioral responses to salinity in larval gobies, with emphasis on *Sicydium punctatum*, in Dominica, W.I., and the consequences of differences in salinity exposure on swimming endurance.

The life cycle of *Sicydium punctatum* (Fig. 1) in Dominica, W.I. involves both freshwater (adults, eggs, larvae) and oceanic (larvae, postlarvae) habitats (K. Bell unpublished data). Adults live in rivers from the coastal zone to altitudes over 300 m and distances of 14 km inland. Spawning is pan-seasonal. Eggs are adhesive and deposited on the underside of stones, reached by tunnels excavated by males. Larvae are 1.8 mm (total length, TL) at hatch and are actively swimming within a minute or so of hatching. Larvae remain in the water column by alternately swimming upward and sinking, and are passively carried toward the sea by river currents. Feeding and visual function require ~5 d to develop, over which time there is little change in TL of larva. Developmental stages of larvae found within 0.2 km from the sea (124 river plankton samples, a total of 6950 larvae, from 23 September 1989 to 10 May 1991) indicate that most larvae reaching the sea are < 1 d post-hatch. Larvae are presumed to become pelagic postlarvae and remain in the sea until their return to river mouths at ~20 mm SL, whereupon they metamor-

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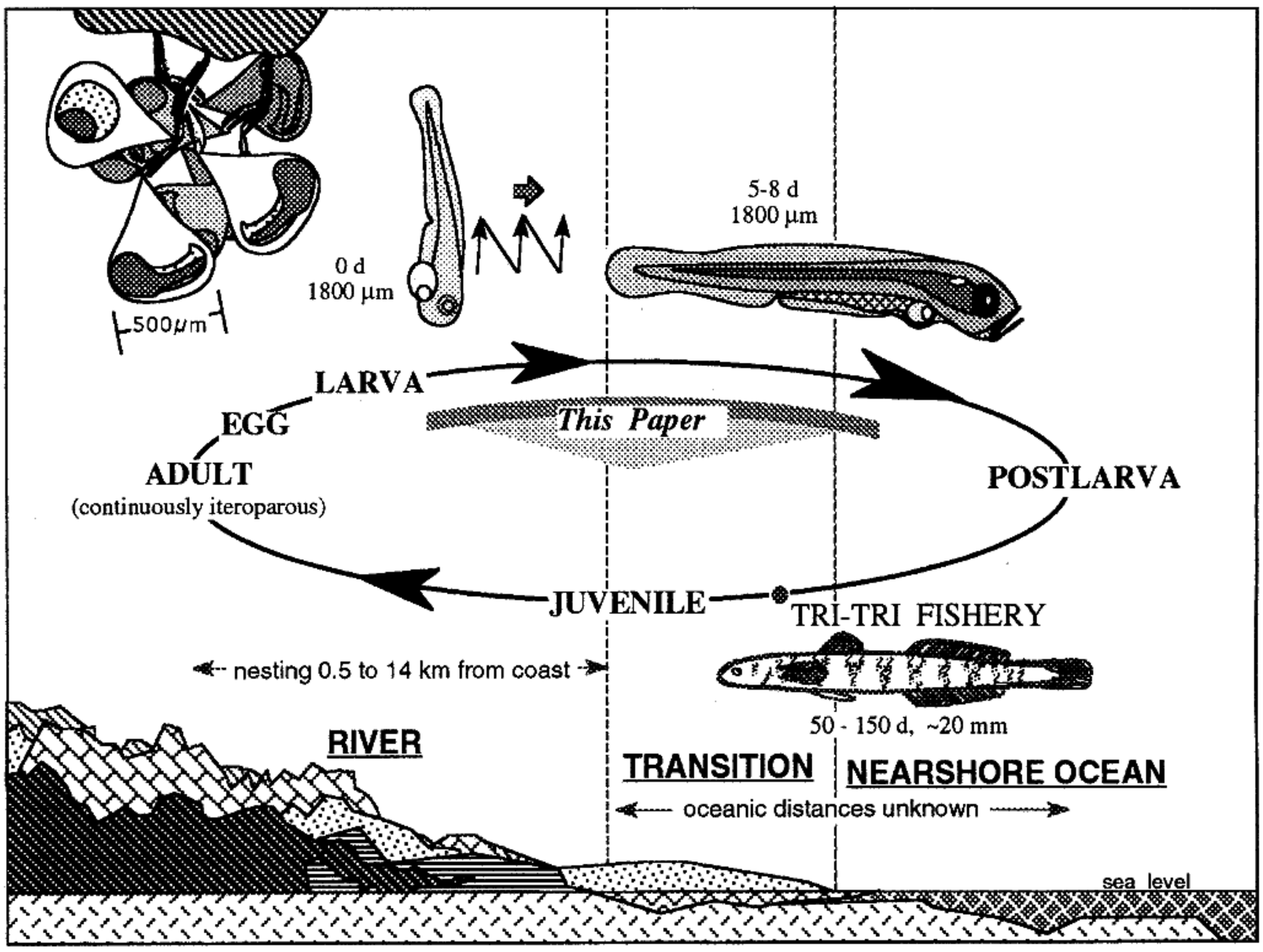

Fig. 1 *Sicydium punctatum.* Life history in Dominica, W.I. Adults spawn repeatedly and pan-seasonally, from < 40 mm standard length (*SL*). 20 mm SL postlarvae return after 50 to 140 d and sustain a traditional fishery

phose into benthic juveniles. Based on 153 otolith examinations, the duration of the oceanic postlarval phase of *S. punctatum* averages 83.4 d (range 54 to 136). Other Dominican gobies (*S. antillarum*, *Awaous taiasica*, *Eleotris pisonis*, and *Philypnus dormitor*) appear to have similar life cycles.

A similar life cycle was reported for the related Philippine goby, *Sicyopterus extraneus*, by Manacop (1953), although several authors (Montilla 1931; Acosta 1952; Blanco 1956; Herre 1958; Johannes 1978) erroneously describe various members of the group as catadromous. With the possible exception of *Awaous guamensis* (Ego 1956), there is no credible evidence of any adult goby going downstream in order to spawn.

Regulation of depth during the marine phase (beginning hours after hatch) would be expected to influence the rate and direction of transport and, hence, the success rate of return to riverine habitats at metamorphosis. Rates of successful return are of interest because return migrations of postlarvae of species in this group support significant fisheries. For example, *Sicyopterus extraneus* postlarvae recruiting into rivers once supported a fishery of 20 000 tonne yr^{-1} in northern Luzon, the Philippines (from data in Manacop 1953). Such fisheries occur widely in the Indo-Pacific and Caribbean (Atwood 1791; Jordan and Evermann 1905; Ego 1956; Aboussouan 1969; Erdman 1986; Aiken 1988).

The objective of the series of experiments reported here was to evaluate the salinity and depth preferences of larvae, and relationships of salinity of the larval environment to swimming endurance. Swimming endurance is defined here as maximum time (d) from hatch (or capture, as an estimator of hatch time) to cessation of swimming activity.

Methods

Source, age, size of larvae

Newly hatched *Sicydium punctatum* Perugia larvae (1.8 mm TL) used in experiments were obtained from collected nests (Expts 1, 2, 3), or mixed samples of goby larvae from river plankton (Expts 4, 5). Collection dates, from October 1989 to July 1990, and localities are given in Table 1 and Fig. 2. Nests were found on four occasions (three listed in Table 1, one other on 19 August 1990) under boulders and transported in water to the lab. Hatching was usually evident within minutes of collection. Hatched larvae were at stages within the range commonly seen in the river plankton, and aquarium-spawned eggs hatch in ~24 h (K. Bell unpublished data). Nests, when available, provided a source of same-age, same-species larvae in sufficient numbers to run several experimental treatments. On all occasions that nests were found, halocline experiments were set up if not already in progress. River plankton were the only alternative source of larvae; samples were taken with a 71-µm mesh conical net held in the current. When larvae were abundant, experiments could be initiated, but the small numbers typically collected in each sample meant that few were available for each treatment.

Post-hatch ages were 10 h in the case of larvae hatched in captivo from collected nests (total of five nests found 1989 to 1991 in the present study), which prior to our study had not been retrieved for Caribbean species (Erdman 1986). Larvae retrieved in plankton were at a similar developmental stage (incomplete eye development, no or little retinal pigmentation) to newly hatched larvae, indicating age generally < 24 h; while this was initially surprising, it proved consistent with later findings that larvae in rivers appear to suffer extremely high mortality (ca. 50% mortality h^{-1}, K. Bell unpublished data and manuscript in preparation).

Table 1 *Sicydium punctatum* and goby larvae. Summary of results of halocline experiments. Larvae in Expts 1 and 2 confirmed as *S. punctatum* by diagnostic features, larvae in Expt 3 tentatively identified as *S. punctatum* (see "Methods"). Larvae from river plankton may include up to five goby species although *S. punctatum* is most abundant. Time until exhaustion (cessation of swimming) determined from time of last observation of activity. Seawater treatments were 30 to 35 ppt (mixed, stratification where indicated is spontaneous). Seawater and Halocline 1 (H1) treatments stocked with larvae hatched ≤10 h since hatch or capture. Halocline 2 larvae spent ~2 d in freshwater. Each halocline offered salinity ranges, as indicated. Expt 4 had two H1 treatments, for which data are separated by commas. (na not applicable)

	Expt				
	1	2	3	4	5
Container volume (l):	0.6	3–4	0.6 (sea), 3–4	3–4	3–4
Water depth (cm):	6	30–40	6 (sea), 30–40	30–40	30–40
Start/collection date:	31 Oct 1989	21 Aug 1990	16 July 1990	04 Apr 1990	01 Jul 1990
Larvae from:	Nest	Nest	Nest	Plankton	Plankton
Location of source:	Taberi R.	Springfield	Springfield	Roseau R.	Roseau R.
Species:	*S. punctatum*	*S. punctatum*	*? S. punctatum*	≤5 goby spp.	≤5 goby spp.
Treatment	Initial no. of larvae				
Freshwater	~250	~2–3000	~2000	110	48
Sea	~250	~350	~300	na	49
Halocline 1	~250	~350	~2000	112, 58	48
Halocline 2	~50	~300	na	na	na
	Salinities (ppt)				
Freshwater	0	0	0	0	0
Sea	~32	32–34	~33	na	35
Halocline 1	0–28	0–16	1–26	0–35, 0–35	1–35
Halocline 2	1.5–32	1.5–33	na	na	na
Results	Swimming endurance (d since hatch or capture)				
Freshwater	4.09	3.9	2.22	3.8	3.60
Sea	5.11	4.85	3.81	na	4.62
Halocline 1	6.7	7.0	4.97	6.32, 6.32	5.10
Halocline 2	8.19	8.29	na	na	na

Species identification

Taxonomy is incompletely resolved in this group. *Sicydium punctatum* and other *Sicydium* spp. have been treated by some authors (Hildebrand 1935; Aiken 1985; Erdman 1986; Aiken 1988) as synonymous with *S. plumieri*, but we followed the taxonomic conclusions of Brockmann (1965), whose diagnoses and figures of *S. antillarum* and *S. punctatum* correspond well with adult specimens we collected in Dominica. *Awaous taiasica*, *Eleotris pisonis* and *Philypnus dormitor* were identified according to various sources including Brockmann (1965) and Jordan and Evermann (1898).

Previous to our work, no rheoplanktonic goby larvae had been retrieved from the field in Caribbean or Atlantic watersheds. During the present study subtle differences were found which permitted separation of larvae in the plankton into five larval types, matching in number the species known as adults from Dominica: *Sicydium punctatum*, *S. antillarum*, *Awaous taiasica*, *Eleotris pisonis* and *Philypnus dormitor* (K. Bell unpublished data). Except for one pairing, each type differs from all others in 2 characters. Using descriptions of larvae from laboratory-spawned (known-parent) nests, we were ultimately able to assign one of these types to *S. punctatum*. This permitted us to determine after the fact that *S. punctatum* had been used in Expts 1 and 2; the nest collected for Expt 3 was from the same site (Springfield), where only *S. punctatum* was seen but is noted (Table 1) as ?*S. punctatum* to indicate that the diagnostic characters recorded could apply to either *S. punctatum* or the type most similar to it, which may be *S. antillarum*. Expts 4 and 5, using larvae obtained from river plankton, represented an assortment of up to five larval types. *S. punctatum* generally predominates among goby larvae in plankton samples (from 10 November 1990 to 10 May 1991: mean=83.5%, n=37).

Experiments

Experiments were designed to evaluate salinity preferences, depth preferences, and activity endurance of larvae exposed to freshwater, seawater, or a choice of salinity (halocline). Larval sources, container sizes, and treatments for each experiment are listed in Table 1.

Experiments were set up indoors in cylindrical glass jars (0.6 litres for Expt 1 and sea treatment for Expt 3) or (all others) rectangular silicone-jointed glass tanks 25 to 40 cm in depth and 10×10 cm in horizontal dimensions. Each experiment included up to four types of treatments: freshwater (F), seawater (S), primary halocline (H1), and secondary halocline (H2) treatments. The number of treatments possible at any time was limited by the initial supply of larvae, so some experiments contained all four, some did not (Table 1).

F, S and H1 treatments were stocked with newly hatched larvae (ca. 6 h after hatch or capture). H2 treatments were set up later and stocked with larvae from the freshwater treatments, using either (Expt 1) non-swimming larvae which had ceased swimming at 106.25 h, or (Expt 2) larvae taken from the water column at 69.6 h post-hatch.

Halocline treatments were established by slowly siphoning seawater to the bottom of a vessel partly filled with freshwater. This method does not produce identical haloclines each time, so we profiled salinity gradients separately for each. If the gradient was too sharp, slight stirring was done to make the discontinuity more gradual and the salinity profile was measured again. Haloclines proved to be surprisingly stable, remaining only slightly altered a month after set-up.

Natural water sources were used. Larvae were unfed, because feeding structures take several days to develop. Temperatures were 23 to 27°C, approximating river temperatures (annual range ob-

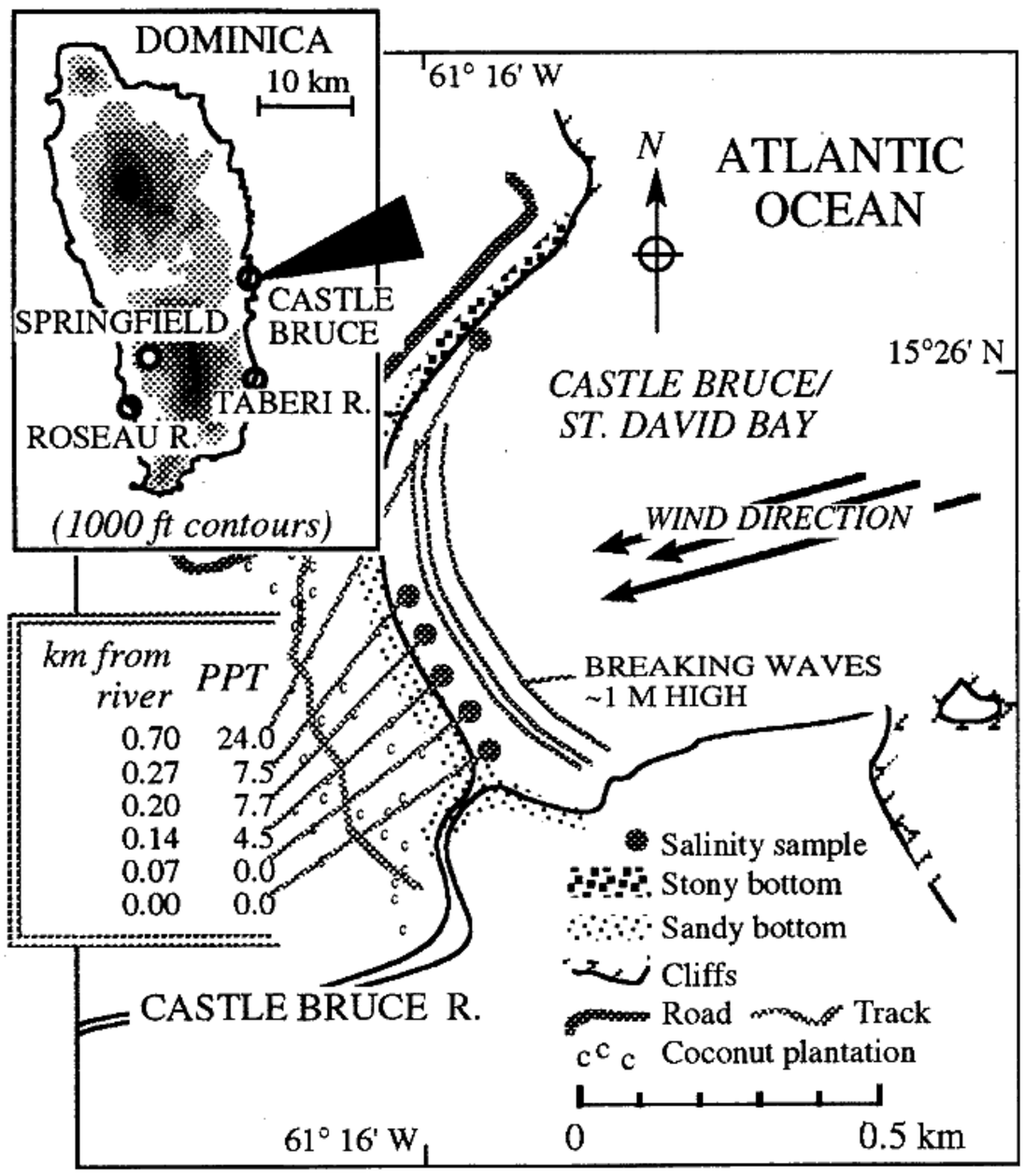

Fig. 2 Salinity observations at Castle Bruce beach in Dominica, W.I. on 17 November 1989, ca. 13:00 to 13:30 hrs. Data inset: distance (km) northward from river mouth, and salinity (ppt). Conditions: fair breeze from E-NE (landward), producing breaking waves >1 m trough to crest near the beach. Inset map: collection locations in Dominica mentioned in "Methods" and Table 1

served: 20 to 30°C). Logistics dictated that light regime was an extended day, natural dawn to cessation of laboratory work (at approximately 22:00 to 24:00 hrs). The remaining dark period was sometimes briefly illuminated by flashlight to record vertical distributions of larvae. Each vessel was stocked with up to ~3000 larvae by aliquots from a common container or (when few larvae were available) smaller numbers which were individually counted into each treatment. Given a rough estimate of 7.2×10^{-5} g wet weight per larva, adverse effects due to crowding were not expected to be important. Our checks on this were (quantitative test) the use of a range of numbers to permit statistical testing for an effect and (qualitative test) transfer of inactive larvae to new freshwater, seawater, or halocline treatments, noting whether this caused activity to be resumed.

The rectangular tanks were built of glass and silicone adhesive. To enable sampling at depth for salinity, Vacutainer needles were installed through the silicone joints and capped by impaled corks of solidified silicone rubber. Removal of a cork permitted water to flow (after discarding several drops to flush the needle) slowly onto the lens of a refractometer to measure salinities. Because of the gentle nature of sampling and the very small quantities (three to four drops) required for salinity determination with a refractometer, this avoided disruption of the halocline. The refractometer was frequently (every two to five readings) re-calibrated to zero according to manufacturer's instructions.

To obtain salinity profiles for haloclines, salinities were plotted for the depths sampled and interpolated as necessary from an eye-fitted curve joining points on a salinity-vs-depth plot. Interpolations over time were largely unnecessary because the haloclines changed very slowly.

Mean salinity exposures are not equivalent to salinity at mean depth because of nonlinear variation in salinity with depth. For each observation, where n represents the number of larvae, ppt represents salinity, and depth is indicated by subscript i, the mean salinity exposure of the population (MPPT) is calculated as:

$$\text{MPPT}=\sum_i^i n_i \text{ppt}_i / \sum_i^i n_i \,. \qquad \text{(Eq. 1)}$$

Sicydium spp. larvae are nearly transparent and about the thickness of a human hair. Because of this and the large volume of the containers relative to the size of larvae, numbers could not be recorded by either 35-mm or video-photography. Our only option was to evaluate larval depth distributions visually. The practical difficulty with this was that individual larvae moved rapidly and could not be precisely counted within depth bins unless very few were present. We dealt with this in the taller tanks by estimating either proportional numbers in each 5-cm depth interval (when total numbers were too high to count), or, if countable (low numbers), we recorded actual numbers and later converted these to proportions. In the 0.6-litre jars we noted modal, minimum (~5th percentile) and maximum (~95th percentile) depths.

We used analysis of covariance (ANCOVA) to quantify significance of differences in larval swimming endurances (time from hatch/capture to inactivity or death) according to treatment type, source of larvae, and larval stocking density. We describe the qualitative variation by comparing depth-frequency histograms among treatments. The change in distribution over time in halocline treatments was characterized by second-order polynomial regression of mean salinity exposure against time.

Field salinities were measured using an analytical hydrometer. Specific gravity readings were corrected for temperature (28°C) in excess of calibration temp (20°C) by subtracting error observed with freshwater (–0.0035) from all values. Conversion to approximate salinity in parts per thousand (ppt) was then calculated as:

$$\text{Salinity}=1000\ (\text{corrected specific gravity}-1). \qquad \text{(Eq. 2)}$$

Results

Qualitative description of behavior in freshwater

Larval behavior for the first several days following hatch (the time span of these experiments) involves a continuous series of ascents and descents, with upward excursions (quick swimming) rarely exceeding 1 s, and downward excursions (slow, passive sinking) rarely exceeding 1 min. Larvae rarely (freshwater) or never (seawater and haloclines) rested on the bottom of containers.

Experimental results

By repeating experimental treatments over time (Table 1), we obtained replication for the purposes of analysis (Steel and Torrie 1980) of variations in time to exhaustion. We used ANCOVA to test for effects of the factors: larval source (two levels: nest, plankton) and treatment type (four levels: F, S, H1, H2), and the covariate: numerical density of larvae in containers (continuous variable). Swimming endurance was significantly affected by treatment type ($F_{3,11}=13.9$, $p<0.001$), but not by either larval source ($F_{1,11}=2.0$, $p>0.05$) or numerical density of larvae in containers ($F_{1,11}=2.9$, $p>0.05$). Examination of residuals revealed no pattern with respect to either factors or covariate. Time to exhaustion (Table 1) is shortest in freshwater (2 to 4 d), ca. 1 d longer in seawater, nearly 3 d longer in a H1 (occupied from hours after hatch), and 4 d longer for

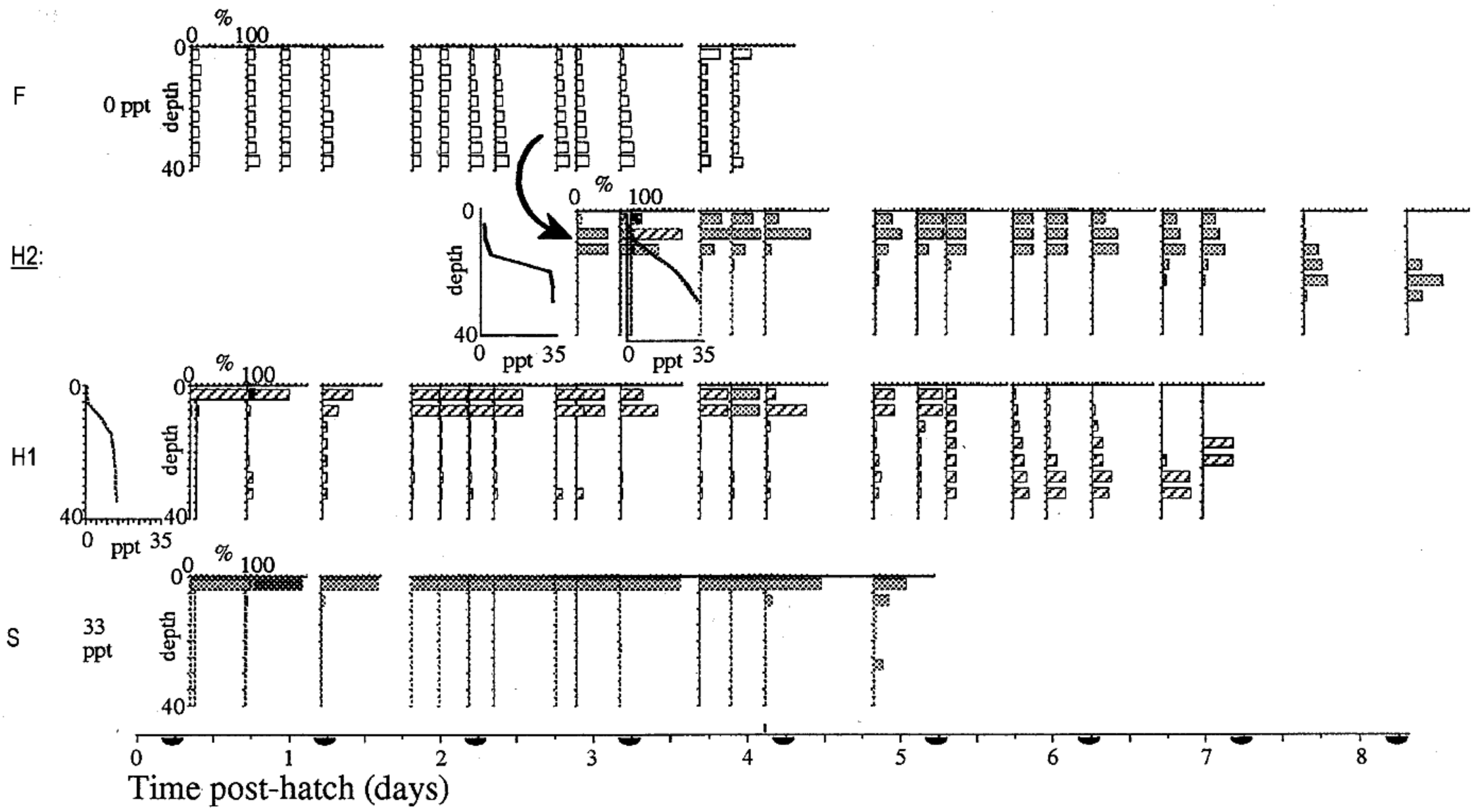

Fig. 3 *Sicydium punctatum* (Expt 2, using newly hatched larvae). Depth distributions over time in treatments Freshwater (*F*), Seawater (*S*), Primary Halocline (*H1*), Secondary Halocline (*H2*, set up with ~300 larvae from *F* at 2.7 d, indicated by curved arrow). Horizontal axes at top (each panel) indicate percentage of larvae in each 5-cm depth interval shown on vertical axes (0 to 40 cm). Time (d) since hatch shown on long horizontal axis below; filled semicircles indicate midnight of calendar day. Last panel in each series is last observation in which active larvae were seen. Salinity curves superimposed with left axis placed to indicate measurement time

a total of >8 d in a H2 (occupied after initial 3 to 4 d in freshwater).

Depth distributions over time were markedly different between different treatments, and this was consistently observed in all experiments. The depth distributions (percent occupancy of each depth by larvae still active) are graphed in detail (Fig. 3) for Expt 2 only, as typical for all. The salinity profiles for this experiment are roughly represented in small graphs on the same figure. Similar treatments (F, S, H1, H2) showed similar time/depth sequences in all experiments.

F treatments

Larvae distributed themselves fairly uniformly with depth, but at about 96 h post-hatch abruptly ceased swimming and sank to the bottom. Microscopic examination of larvae retrieved from the bottom at that time showed that many larvae were still alive and yolk reserves still remained (yolksacs ~280 µm in diameter in newly hatched larvae; ~200 µm in 2.9 d larvae; ~140 µm in diameter in ~4 d larvae after cessation of swimming). Jaw structures were incompletely developed. Such larvae resumed activity when transferred to a halocline (H2), but did not do so when placed in jars or petri dishes with new, fresh, water.

S treatments

Larvae aggregated within a few body lengths of the surface and occupied the upper 1 to 2 cm for most of the experiment. After ca. 100 h, larvae distributed themselves at all depths, and at ca. 120 h sank to the bottom. Microscopic examination showed that a few larvae were still alive but with little or no yolk remaining. Larvae transferred to a halocline or to low-salinity water (ca. 5 ppt) failed to resume activity.

H1 treatments

Larvae showed modal abundances at intermediate salinities (5 to 15 ppt), which in Expt 2 (Fig. 3) existed in the upper 10 cm (ca. 50 body lengths) from the surface. The modal depth increased (and occurred in higher salinities) with time, with some smooth and some abrupt transitions. At about 120 to 160 h post-hatch (130 h in Expt 2), larvae became fairly evenly distributed at all depths and then ceased activity altogether.

The interval from the time when the larvae first noticeably reduced depth preference and began to sink to the bottom, to the time when there were virtually no swimming larvae remaining, typically was short, i.e., a matter of 6 h or less. Larvae in the halocline treatments – the only treatments in which there was scope for salinity choice – remained swimming much longer than larvae in freshwater

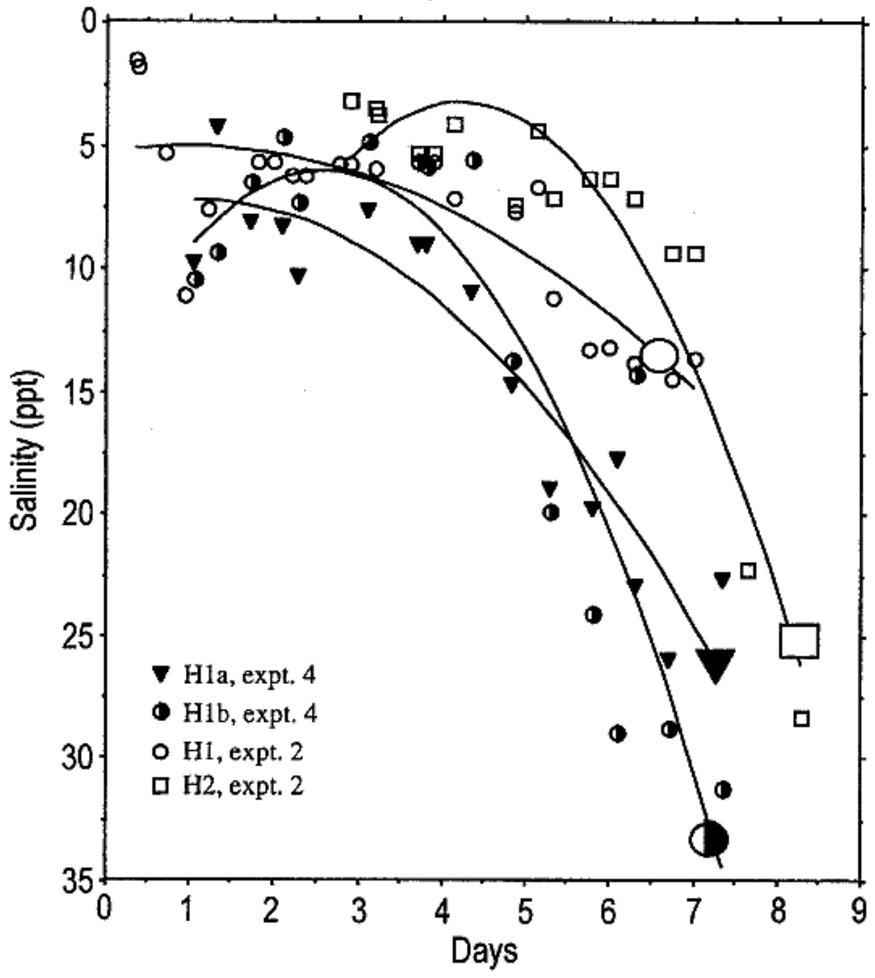

Fig. 4 *Sicydium* spp. larvae. Mean salinity exposure in each of four halocline [three primary (H1) and one secondary (H2)] treatments over time. *a* and *b* distinguish similar treatments in same experiment. Ages are d since either hatch (Expt 2) or capture (Expt 4). Large symbols identify curves. Maximum salinity available in H1 of Expt 2 was ca. 16 ppt. Adjusted r^2 range 0.67 to 0.89; $p \leq 0.0001$ for all

Table 2 *Sicydium punctatum* and goby larvae from river plankton (≤5 spp.). Regressions for curves in Fig. 4, mean population salinity exposure in halocline (H1, H2) treatments. Regressions are mean salinity ($MPPT$)=$\beta_0+\beta_1 T+\beta_2 T^2$, where T=time (d). Response of $MPPT$ to time (d) since capture or hatching for four halocline treatments. H1a and H1b have gradual, and sharp (respectively) haloclines. H1 (Expt 2) had a maximum salinity of ~16 ppt. ($Adjr^2$ adjusted r^2)

Treatment	β_0	$\beta_1 T$	$\beta_2 T^2$	Adjr^2	p	N
Expt 4 (≤5 spp., larvae from river plankton)						
H1b	14.35	–6.43 T	+1.24 T^2	0.8	0.0001	16
H1a	7.82	–1.04 T	+0.49 T^2	0.86	0.0001	16
Expt 2 (*S. punctatum* larvae hatched in captivo)						
H1	5.34	–0.54 T	+0.27 T^2	0.67	0.0001	22
H2	27.74	–11.62 T	+1.38 T^2	0.89	0.0001	16

or seawater. Larvae at the end of halocline treatments had forward-directed, well-developed eyes, lower sinking rates (a larger volume due to filling out of fin-folds), and an operable mandible. Their swimming was less vertical and more horizontal, and orientation was consistent and conventional (i.e., dorsal up). Yolk-sacs were completely or nearly exhausted, a small oil droplet sometimes remaining. We consider larvae to have been capable of feeding during the last 2 to 3 d of the halocline treatments.

The progression of active larvae into higher salinities over time was consistent among halocline treatments from different experiments (Fig. 4). Second-order polynomial regressions for these four curves are all highly significant ($p \leq 0.0001$) and explain from 67 to 89% of the variation in larval distribution over time within each treatment (Table 2). Note that treatments having no variation in salinity over depth cannot be expressed on the same graph.

H2 treatment

These treatments employed larvae transferred from the freshwater treatment to a newly prepared halocline (F → H2) but could not be meaningfully run in experiments which began with small numbers of larvae such as were available from river plankton. Thus, in experiments with enough larvae, H2 treatments involved removal, and transfer to new halcolines, of either (Expt 1) non-swimming larvae from the bottom after 4.5 d or (Expt 2) larvae still active in the water column at 2.9 d. Larvae behaved similarly in both: larvae soon resumed swimming in the new halocline treatments and again displayed distributions that favored the lower salinities available (e.g. curve H2 in Figs. 3 and 4).

Swimming activity in larvae in H2 treatments persisted until 8 d post-hatch (Table 1). This was 31 (Expt 3) to 35 h (Expt 1) longer than seen in the H1 treatments, which in turn had sustained larvae for markedly longer than had the no-choice freshwater or seawater treatments.

Similar progressions of depth selection by larvae were seen in all haloclines (Fig. 4). The progression in H2 treatments was similar to that in H1 but occurred later, by roughly the amount of time spent in freshwater previous to transfer to a halocline.

Other secondary treatments

Of all the possible transfers of larvae to similar or different treatments, the only pattern of transfer to result in markedly prolonged activity was the transfer of larvae from freshwater to a halocline (F → H, called H2). Transfer of inactive larvae from any treatments to new but similar treatments (e.g. F → F, S → S, S → H) did not result in resumption of activity, thus eliminating deteriorating water quality as a factor.

Transfer of inactive larvae from seawater treatments to a halocline (S → H) did not prolong survival. Thinking this may have been because larvae sank too quickly through the upper low salinity layers to trigger a response and that they had, in effect, experienced a S → S transfer, we therefore also tried transferring inactive seawater larvae to low salinity (5 to 10 ppt). No significant resumption of activity was detected, and most died within 12 h.

Discussion

Swimming behavior functions

Two consequences of the continuous vertical swim/sink behavior can be suggested. Passive seaward transport to coastal nursery areas would be promoted by keeping lar-

vae suspended in river flow. The superior swimming endurance of larvae in H1 and H2 treatments during their first week suggests that after they exit their natal rivers avoidance of very low or high salinities has survival value.

The swim-up/sink-down behavior has also been observed in several related gobies: *Awaous guamensis* (Ego 1956), *Dormitator latifrons* (Todd 1975), and *Evorthodus lyricus* (Foster and Fuiman 1987). Observations on *Sicyopterus extraneus* (Manacop 1953) are also consistent, given the circumstances under which they were observed.

Salinity and swimming endurance

Swimming endurance was marginally longer in seawater than in freshwater, and the greatest swimming endurances were in haloclines (Table 1). This suggests that 0 and >30 ppt are salinity extremes outside the range required for 0 to 5-d-old larvae. The preference shown by larvae in haloclines (Figs. 3, 4) for low salinities is consistent with their superior swimming endurance compared to larvae in freshwater or seawater treatments and, therefore, suggests an adapted response.

Ego (1956) reported that larvae of *Awaous guamensis* placed in seawater (34 ppt) lived 8 d, while larvae in freshwater lived only 4 d. *Chaenogobius urotaenia*, with large larvae (5.3 mm TL at hatch), is reported to possess chloride cells soon after hatching, and larvae kept in 50% seawater lived >30 d while those in freshwater lived < 7 d (Katsura and Hamada 1986).

Todd (1975) reported that larvae of *Dormitator latifrons* ceased to swim at 68 h in nearly fresh (3 ppt) water. This accords fairly well with our results for larvae in freshwater. Todd interpreted swimming cessation as a transition to a benthic phase, but this interpretation may have been conditioned by an assumption that *D. latifrons* was capable of completing its life cycle in a single habitat. Settlement at 3 d in an initially pelagic larva is unprecedented. We suspect more similarity among life histories of riverine/estuarine gobies than is currently acknowledged and suggest instead that Todd's larvae may have reached the limit of their freshwater endurance, as might be expected if *D. latifrons* were diadromous, as is *Sicydium punctatum*.

The gradual increase in MPPT observed in haloclines (Fig. 4) was accompanied in our experiments by increasing depth choice by larvae. The similarity in changes in MPPT among H1 treatments, despite the presence of sharper haloclines in some treatments, suggests salinity choice by active larvae whose salinity tolerance shows an ontogenetic progression.

The longest swimming endurance was seen in larvae transferred from the F to the H2 treatments. This suggests that some period spent in freshwater is advantageous at least in physiological terms (i.e., neglecting any considerations of predation mortality in the freshwater environment).

Only in saline treatments (S, H1, H2) were larval yolks nearly or completely exhausted, and only in these treatments had larvae developed to the stage where they appeared able to feed, having well-developed eyes directed slightly forward, and a mouth capable of opening and closing. After cessation of swimming activity in non-saline (F) treatments, yolk reserves were visible and mouth development was incomplete. Mortality in the F treatments cannot be due to lack of available food and must be a result of the inability of the larvae to develop beyond an early stage in those environments before becoming inactive. On the other hand, in the saline treatments (S, H1, H2), yolk exhaustion coupled with more complete development of larvae suggests that mortality of larvae may have resulted from starvation. We have not yet been able to successfully feed larvae.

The behaviors of the larvae in all treatments are consistent when considered in light of the layering of the water masses of which these treatments are analogues. Because of density differences, freshwater would overlie a water mass of intermediate salinity, which would in turn overlie a water mass of high salinity. Larvae seeking salinities in the range of 5 to 12 ppt should, therefore, swim upward if experiencing high salinities and permit themselves to drift downward if experiencing lower salinities. This is consistent with our results. In freshwater, for the first few days, larvae sought no particular depth but avoided contact with the bottom; when this response disappeared and larvae became inactive, they were still viable if transferred to a halocline (H2), whereupon they adopted a vertical distribution favoring intermediate salinities, as in H1. This showed that if inactive larvae sank out of freshwater into more saline water, activity could be resumed. Larvae in haloclines demonstrate preference for intermediate salinities. Larvae in seawater remained at, or within a few body lengths of, the surface until the limit of swimming endurance was reached. At no depth in any treatment was the density (specific gravity) of the medium equal to that of the larvae. Active upward swimming is required to compensate for the sinking of the inactive larva even at the highest salinities used (~30 ppt), so the mean depth of *Sicydium punctatum* larvae was clearly not determined by relative density. Since previous work (de March 1989; Frank and McRuer 1989; Frank et al. 1989; Page et al. 1989) has not shown depth or salinity choice based on means other than density relative to the medium, this is the first report of active salinity choice by larval fishes.

Are there in fact low salinity habitats as suggested by this larval behavior? Near-shore oceanographic information for Dominica or neighboring islands is virtually nonexistent at the fine scale needed to describe the systems anticipated. Low-salinity habitats have not previously been described. However, it is axiomatic that since *Sicydium* spp. are abundant in the Caribbean, the conditions for them to persist must also exist, and since these results indicate a strong requirement for intermediate salinities during at least their first 5 to 8 d, these conditions must therefore exist. Since early larvae are non-feeding and gradually accept higher salinities over this time, even small low-salinity areas may be sufficient.

Dominica is a recent volcanic landmass situated in persistent atmospheric and oceanic flows: the trade winds and

a prevailing westward current. The height of such volcanic islands generates persistent high orogenic rainfall, with >90% of Dominica receiving 2.54 to >7.62 m yr^{-1} (Towle 1991), and creates a wind-shelter on the leeward coasts.

Because of disruption by the constant wind, the east (windward) coast is where we would least expect to find low-salinity systems. However, on 21 November 1989, in typical conditions on the eastern coast (breaking 1-m waves and a steady wind), we found Castle Bruce beach dominated by surface salinities in the surf zone of 0 to 8 ppt, with the highest salinity found (24 ppt) near the northern end of the bay (Fig. 2). These salinity measurements reflect a substantial mass of low-salinity water corresponding to the range selected by larvae in our experiments, and this is remarkable considering the wind and wave activity prevailing at the site. Mixing would be slower on the sheltered side of the island; so, with similar runoff we would expect more extensive low-salinity areas. On numerous occasions, on both coasts, we observed or photographed overt (heavily colored by river-borne sediments) or putative (suggested by texture) extensive plumes of river water in the sea.

These observations show that the influence of river water can be large in the nearshore, even in high-energy conditions, and that low-salinity habitats do exist which conform to preferences shown by 0 to 8-d-old larvae in experiments. There are important implications for early survival: (1) seasonal and irregular variation in weather (wind, rain, currents) could affect survival by altering the availability of the preferred salinities, and (2) affect larval advection and dispersal since the low-salinity layers are at the surface; (3) in low-salinity habitats maintained by river outflow larvae may experience longer exposure to terrigenous pollutants than would be expected in higher-salinity habitats in which the terrigenous component is more dilute (McFadzen and Cleary 1994). Working hypotheses to explain long-term fishery declines may be developed from these implications.

Sicydium punctatum in Dominica shows high seasonal variation in the fishery for larval recruits (K.Bell unpublished data). Recruitment of the similar fish, *Sicyopterus* sp., in Réunion shows substantial seasonal and interannual variation (Aboussouan 1969). The results presented here suggest that future work on the nearshore oceanography may lead to a better accounting of recruitment variation. We recommend such work and encourage managers to collect the collaterally important sicydiine fishery data.

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