PART TWO: NEW INFORMATION BASIC TO FURTHER STUDY OF SICYDIUM SPP.

Life cycle, diadromy, larval types

Chapters 3-5

CHAPTER 3. LIFE HISTORY OF SICYDIUM PUNCTATUM PERUGIA: NESTING, BROODCARE AND LARVAL BEHAVIOUR

ABSTRACT

The sicydine goby *Sicydium punctatum* of the Caribbean is anadromous. *S. punctatum* spawns in rivers, where nests are excavated below the gravel bottom, and most parental care is provided by the male. Newly hatched larvae emerge from nests upon hatching and enter the river plankton. Larvae are denser than water but maintain position in the water column by cycles of upward swimming and passive downward sinking. This larval behaviour is important for drift to the sea, where the postlarval growth period is spent before return migrations to rivers.

Sicydine gobies are important because of the significant fisheries supported by migrating postlarvae. Yields are reported as declining where trends are mentioned, but the search for causes is hampered by the lack of life-history information. This paper presents the basic life history of one species for which neither nests nor larvae has been previously reported, in a group which has often been assumed to be catadromous but which is in fact anadromous.

The life history that clearly emerges from these observations is anadromy in the pre-1939 sense. Since this life history places both eggs and newly-hatched larvae in rivers and not the sea as has previously been suggested, riverine habitat conservation must be an integral part of management.

INTRODUCTION

The goals of this study were to establish the nature of the life cycle of sicydine gobies of Dominica, W.I., and obtain insight into population fluctuations which appear to cause variability, or declines, in fisheries there and elsewhere. This chapter assembles the general life-history information which is the essential underpinning of further work, some of which appears in subsequent chapters. An overview of world fisheries, etc., has been given in Chapter 1.

*Sicydium punctatum* Perugia (*sensu* Brockmann 1965) is the main focus of this thesis because it predominates in fishery yields in Dominica, W.I., and it is the species for which the most information was collected. Much of the life history of this species appears common to all Dominican river gobies (all of which appear to be river-spawned diadromous species), and is rarely consistent with the knowledge, however scant, of other sicydine gobies elsewhere. *S. punctatum* is abundant in rivers of coastal volcanic topography in Dominica (Atwood 1791), Puerto Rico (Erdman 1961), Jamaica (Aiken 1985; Aiken 1988) and elsewhere in the Caribbean. Note however that some authors synonymise, erroneously in my judgement, *S. punctatum* and other *Sicydium* spp. with *S. plumieri* (Chapter 1). A traditional fishery exists for postlarvae enterin rivers from the sea (Atwood 1791; Erdman 1961; Erdman 1984; Aiken 1985; Erdman 1986; Aiken 1988) in the Caribbean as it does for other sicydine oby (notably *Sicyopterus* spp.) postlarvae in the Philippines (Montilla 1931; Acosta 1952; Manacop 1953; Blanco 1956) and elsewhere in the Indo-Pacific (Jordan & Evermann 1905; Koumans 1953; Ego 1956; Aboussouan 1969; Titcomb 1977).

The literature on the life cycle of the group shows lack of agreement on the basic life cycle: while some authors provide evidence of anadromy, others assume catadromy. A part of this apparent disagreement may be due to different perceptions of categories of diadromy, their legitimacy, universality and definitions. For 'anadromy' in the sense of sicydine gobies, authors variously apply the terms: diadromy, amphidromy (coined by Myers (1949)), or freshwater amphidromy (modified terminology of McDowall (1992)). Manacop (1953) showed abundant evidence for an anadromous life cycle in *Sicyopterus extraneus*. Erdman (1961, 1986) looked for similarities in the life cycles of *Sicydium punctatum* and *Sicyopterus extraneus* and decided that "circumstantial evidence of upstream spawning is strong". The literature on Japanese species clearly supports anadromy (Dōtū & Mito 1955; Katsura & Hamada 1986). But several authors (Montilla 1931; Acosta 1952; Blanco 1956; Herre 1958; Johannes 1978) have asserted that adults of various genera (e.g.)
Chonophorus, Sicyopterus) descend to the sea to spawn. However, the only evidence for such downstream migrations is in Ego (1956) for Awaous guamensis, where both tagging and observation of eggs adhering to rocks at a sandbar near the river mouth supported the claim. Nevertheless, Ego does comment (p. 11) that this occurs during freshets, and may not occur otherwise.

Making what seems poetically complementary in the way of omissions, a recent paper (Penczak & Lasso 1991) neglects to acknowledge the existence of a marine period in the life history of riverine gobies (including Sicydium spp. which they list as S. plumieri) whose production was studied in Venezuela.

Together with the confusion on basic life history information, the apparently widespread decline of these fisheries, reported by numerous authors including Manacop (1953), and Erdman (1986) was a major motivation for this study. The main objectives were elucidation of the life cycle, and identification of factors critical to fishery- and conservation management.

METHODS

Sampling of river planktonic larvae

Larvae were obtained by sampling river plankton from several rivers in Dominica. About 120 samples were taken from July 1989 to May 1991, at varying intervals and times of day. River plankton was sampled with 80µm Nitex mesh long-aspect plankton nets. Samples were sorted while alive, usually within 1-6 hours of collection, but reported longer. The interval before sorting allowed sediment to settle, and because nearly all individuals of taxa of principal interest remained in the water column this portion could be decanted through a strainer and completely counted. Thus, subsampling errors were virtually eliminated. Sedimented matter in samples was routinely subsampled for live or dead larvae, and extrapolated counts of these were recorded. Dead larvae were separately recorded, but were usually few relative to live, although they remain detectable for 24-48 hours. Larvae of S. punctatum were differentiated from other larvae by a combination of features verified in the larvae from aquarium spawnings. (Virtually all larvae present in the river plankton are assignable to one of several distinct types, of which no two differ by less than two readily observable features; these will be the subject of a later chapter.)

Larvae were anaesthetised to facilitate counting and identification using 2-phenoxethanol, of which a few drops were mixed in approximately 20ml of fresh water and mixed to make a stock solution. One or two drops of this stock solution was sufficient to immobilise larvae in petri dishes containing approximately 20 ml of water. Anaesthesia resulted within seconds and recovery typically occurred within seconds after removal of larvae to fresh water.

Species identification of postlarvae

Postlarvae were captured and raised in aquaria to relate species identity and postlarval characters, and to verify that Sicydium punctatum is the major component of the tri-tri (returning postlarvae) fishery in Dominica.

Aquarium spawnings

Aquarium spawnings resulted from individuals captured as juveniles in the field and raised in aquaria either in Dominica or in Canada. Aquarium water was completely fresh. Temperatures were kept between 20° C and 30 °C (the natural range in Dominica), and were most often near 24-26 °C. In some cases shells were added to buffer pH. Aquaria ranged from about 30 L to 150 L, densities ranged from >natural (about 20 individuals in 30 L) to approximately natural (about 8 individuals in 150 L). Male:female ratios cannot be accurately determined because the sexes are not always distinguishable. Foods which were well accepted included spontaneous algal growth in aquaria, imported algal growth on stones, preparations of egg and vegetable matter baked together with gravel to achieve negative buoyancy, frozen cubes of blended vegetable matter, commercial flake food (TetraMin™ Staple food or Conditioning food), table scraps (cooked fish), live Daphnia, etc.; in short, a great variety of food sources were employed at different times and acceptance by the fish determined alterations in diet. Six aquarium spawnings had been detected up to May 1994 (Table 3.1). Due to nest siting and the type of equipment available, different observations were possible with different spawnings. Larvae from aquarium spawnings provided the material for comparison of characters with field-caught larvae. Data were obtained by observation, and by macro- and micro-photography using film or videotape.

Nests were searched for in rivers where S. punctatum was abundant by inverting and examining the surfaces of stones and boulders up to (estimated) 80 kg in weight; retrieved nests were transferred to buckets of water for transport to the field laboratory.

RESULTS AND DISCUSSION

Seasonal abundance of larvae in river plankton

Larvae were present virtually continuously, indicating that river gobies reproduce at all seasons. The presence of rheoplanktonic larvae is alone sufficient to confirm river spawning, or anadromy in the sense previous to Myers (1949). The overall mean abundance found was 56.8 larvae·m⁻³, however the inclusion of sites at high altitude, or in areas of
intensive cultivation where few or no adults were seen, may be misleading. At the four main (most frequently sampled) sites on the Caribbean coast (Layou R, at Coco Center, Layou R. at Hillsborough Bridge, Check Hall R., Canefield R.) abundances ranged from 0 to 1906 larvae m⁻³, with an arithmetic mean of 76 and a geometric mean of 19.6. Larval abundances were lognormally distributed. The abundance of larvae (m⁻³) varies considerably on a short timescale, and there are suggestions of longer scale temporal variations in sample-to-sample variance, and in levels of abundance (Fig. 3.1). Variation initially appeared to be aperiodic; for example, the high variance prevailing in the early samples (late 1989) followed Hurricane Hugo, and the low values in the (late 1990) do not match. But multiple timescales (time of day as well as time of year) or dimensions (different sample sites) which interact cannot be detected on a bivariate plot; multivariate analysis may explain the observations as periodic structures.

Multiple regression was used to analyse for seasonal and temporal variations, but using only the main west-coast sample sites (Chr. Layco, Layhbr, Phw; see Table 2.1), because these are comparable in altitude (<20m) and climate, and are within ~10km of each other.

For 4 main (similar) stations on the West coast of Dominica 1989-1991, the variation in (natural log of) numbers of goby larvae per m³ was described as a function of the cosine of an angular transform of DOY and the cosine of an angular transform of time of day (DECT). Although there is little a priori reason for any particular model, a cosine function provides a symmetrical and repeating function over multiple cycles. The appropriate lag was iteratively determined, for day and time separately, as that yielding the highest positive correlation with logE concentration of larvae. The regression:

\[ \ln \text{GLM} = 3.1 + 0.83 \cos (r \text{DOY} + 3.25) + 1.77 \cos (r \text{DECT} + 0.5) \]

is significant overall and in both parameters \((n=71, r^2=0.286, p=0.0001)\). The residuals from this regression are without trend when plotted against DOY, time of day, or sequential day number in the study (Fig. 3.2). The regression indicates that the highest seasonal concentrations of larvae are at mid-year, and the lowest daily concentrations are at mid-day.

Identification of juveniles and adults

The taxonomy used for Sicydium spp. follows Brockmann (1965), as discussed in Chapter 1. No taxonomic guides are available in the literature for sub-adults, and the usefulness of scale counts is nil for stages which have not yet fully developed scale complements. I therefore cultured live recruits until they could be identified with adult characters, in order to relate juvenile features to species. What follows is a generalisation of those results.

Postlarvae that completely lack pigment cannot be identified beyond genus level, because morphology is too similar (see taxonomy section in Chapter 1). However, most recruits possess sufficient pigment to identify patterns under the microscope. Sicydium punctatum shows, from earliest pigmentation following recruitment to fresh waters, a pattern of vertical 'bars' whose arrangement roughly forms the letters I, V and X from posterior, giving way to nearly vertical bars anteriorly (Fig. 3.3). This pattern readily distinguishes S. punctatum from the other species present in Dominica (S. antillarum, locally called 'Loche cabrée'), which has vertical pairs of brown bars on a yellowish background, does not show reticulation (due to arrangement of chromatophores, where present, on scales); this pattern is the same in all stages seen. The species difference is therefore very obvious in specimens more than a few days post-recruitment to fresh waters. Although S. antillarum tends to be larger at recruitment, there is too much overlap with S. punctatum for this to be an unambiguous species character.

Verification of species identity of newly-hatched larvae of Sicydium punctatum was established by comparison of characters of larvae from aquarium spawnings with larvae obtained from river plankton. Although this will be dealt with more fully in a later chapter, S. punctatum larvae were congruent with one of five major types of goby larvae identified in the river plankton. This type is referred to as "Fyg" (Fig. 3.4) and is distinguished by: (1) the presence of yellow-green trunk pigment visible with lateral illumination against a dark field (vs. no trunk pigment other than melanic), (2) a pale yellow cast to a (3) clear yolk (vs. colourless or semi-opaque yellow), a (4) smooth yolk membrane (vs. wrinkled, granular or crusty looking), and, in side view, an (5) ovate (becoming round as development proceeds) yolk sac (vs. oblong or spherical). The yellow-green trunk pigment is best seen with oblique illumination against a dark background; lighting from below will not show the pigment well, if at all. It exists as an irregular scatter of ovate concentrations on the ventral trunk in un-anesthetised specimens, but the pigment diffuses in numerous strands running posteriorly and anteriorly under varying degrees of 2-phenoxyethanol anaesthesia. The pigment looks fluorescent (hence the "Fyg" designation), although it failed to fluoresce under either short- or long-wavelength UV. The abundant yellow-green pigment is the most reliable character, the others are supplementary; none are reliable after preservation, so this work must be done with live larvae. The nearest type shows a similar appearance in all characters except that the pigment has a
pronounced reddish tint. Since no variation was seen among larvae from the nests collected at Springfield, and larvae from captive spawnings in Dominica and in Newfoundland, the contribution of environmental factors to these characters is obviously very small and they therefore appear to be reliable species-diagnostic features.

ASPECTS OF REPRODUCTION

Courting colours

The male courting colours of *Sicydium punctatum*, observed in aquaria and in the field, are a brilliant blue background with the bars becoming a deep black, with the caudal peduncle often a white pale. The pectorals tend to be clear except in courting and territorial males, in which they may be a dusky blue and may show a white border. Females and juvenile or subordinate males show a similar pattern of reticulated barring on brown background, and often cannot be separated by external appearance. Since patterns can change (or fade) within seconds, as in response to disturbance, courting or agonistic behaviour, pattern would appear to have ethological functions.

No variation in pattern or structure was noted in *Sicydium antillarum* in the field, and no reproduction or associated behaviours were observed either in the field or in aquaria. *S. antillarum* was kept for extended periods, and the pigment patterning appeared to be constant, with no suggestion of ethological function. I cannot claim that sexual variations are absent, but they would appear to be subtle at best.

Some minor details of pattern and colour of *S. punctatum* vary slightly from those described by Erdman (1961; 1986) for the same species, which suggests either regional or observer components to the observation, or that other species have been included in previous observations.

Pairing, Nesting, Broodcare

PAIRING: Outside spawning, individual relationships other than territoriality were not evident in >5 years of observing groups of *Sicydium punctatum* in aquaria. The rapid (~24 h to hatch) development of eggs suggests that territorial males could sequentially reproduce with different females, but whether they do this is not clear. While one pair spawned twice, approximately a month apart, another pair went through incomplete courting behaviours at those same times, and did later spawn successfully. Because this occurred within a small group (three males and three females), it might represent random pairing. Thus the logistics (short duration of male broodcare duty, contrasted with longer time for a female to generate eggs, suggesting different inter-spawning times for males and females) and limited aquarium observations appear to conflict.

NESTING: Nests retrieved (Table 3.2) were (one exception, see below) about 10 cm below gravel level, with eggs being deposited on the underside of a single stone (Fig. 3.5). Access to the nest appeared to be via a single tunnel in such nests. Males vigorously defend the territory surrounding the entrance to the nest against other males despite large disparities in size in favour of the transgressor; females did not often elicit the territorial response. All nests found in the field (n=5) were found in loose gravel in ripples with the exception of one which was under a stone wholly above the gravel layer; this last is thought to have been a nest already disturbed by fishing activity in the river at that time.

Despite searches in >20 places where plankton was sampled or other observations were being made, nests were found in two places only, and in only one of these was more than one nest found. No nests were found in fine substrate or silted areas. The only place in which nests were found more than once was in the ripple below Springfield pool in the Check Hall river at ca. 350m elevation (four nests found in three occasions representing <30 minutes total searching time). In silty areas adult *S. punctatum* are rare or absent (other species predominate), whereas in stony-substrate streams (e.g. Point Ronde R., Belfast R., Canefield R., lower Check Hall R., Fond Figues pool of the Castle Bruce river) they are usually abundant, yet nests were not found despite searching in apparently likely locations. One possible explanation for the failure to find nests in some apparently suitable locations is that the sediment size distribution may permit nests to be deeper and more difficult to retrieve. For example, in the Fond Figues pool of the Castle Bruce River a thousand or more adults were present, with many in brilliant courting colours so all indications were that reproduction was in progress. Yet, despite clear water, with mask and snorkel no nests were found (in May of 1989) in about 30 minutes of effort, even though gobies were seen to disappear into tunnels and spaces which were excavated as far as possible (down to 30 cm in loose gravels).

Nest construction was witnessed in only one (1990) of the aquarium spawnings; other spawnings either used an existing structure (Fig. 3.5), or occurred on the glass where the aquarium had been deliberately set up without gravel. This (1990) aquarium nest was accessed by a tunnel which traced the surface of a large stone partially buried. In tunneling, the male (no female was seen to engage in excavation of nests) cleared debris by entering the tunnel headfirst and thrashing, creating a current that carried fine debris out of the entrance. This male also entered headfirst and emerged headfirst either pushing pebbles, or carrying in its jaws pebbles approximately its own head diameter, depositing them outside the access tunnel. The tunnel was barely large enough for the fish (~40 mm TL)
digging it. In the first (1970) observed spawning which was on the underside of the plate of an undergravel filter, access was via the 7mm diameter clear plastic airlift tube. The male filled the tube almost completely, such that bubbles (from airlift) were prevented from rising while the fish was in the tube: the fish was not only confined but had to make its way down against an accumulating buoyant column of air. Tunnel size would limit the size of the female: therefore pairs are either size-symmetric, or asymmetric in favour of the male, or males dig larger tunnels to suit larger females.

Several other gobies employ inverted positioning of eggs on the underside of objects in fresh waters: Chaenogobius urotaenia (Katsura & Hamada 1986), Evorthodus lyricus (Foster & Fuiman 1987), Sicyopterus extraneus (Manacop 1953), and Eleotris pisonis (Todd 1975).

In two aquarium spawnings the process of egg deposition was witnessed, and once videotaped. Deposition of the eggs in the latter case took 1 to 1.5 hours; this was an inexperienced pair (their spawning 36 days previously had been infertile) so this may be an overestimate of the typical time. Fertilisation was evident by actions of the male (development and hatching of normal larvae was subsequently observed) but no milt could be seen. The small size of this pair, their inexperience, and the lack of natural nesting materials/sites likely contributed to their failure to defend the eggs against other conspecifics, which succeeded in consuming fragments of the egg mass.

The egg masses are light brown to greenish, and eggs can be seen to swing about in clusters. Threads cannot be resolved with the unaided eye but are visible microscopically. An egg patch about the size of a thumbprint (the approximate size of all nests recovered or seen) was conservatively estimated (from a photograph) to contain on the order of 5,000 eggs (this patch was spawned by parents <40mm). A dilution count (which was conservative because some mortality may have occurred between hatching and counting) of hatched larvae in the 1990 aquarium spawning by a male yielded an estimate of 3,300 larvae present at that time. For comparison, the number of maturing eggs in a single 66 mm female Sicyopterus extraneus was estimated by Manacop (1953) to be 46,000.

For spawnings in aquaria with gravel, eggs were attended by the male until most had hatched. Two active egg-care behaviours were observed, which I term fanning and scrubbing. Fanning consisted of adhering to the surface, on which the eggs were deposited, with ventral sucker (united ventral fins typical of Gobiidae), stabilising with the pectorals, and using the body posterior to the pectorals to sweep the egg patch with a sinuous motion. Scrubbing consisted of a repeated cycle of sucker adhesion and vigorous pectoral strokes (left and right beating in phase) over the eggs to either side, in a series of advancing steps across the egg patch. Despite the apparent roughness of this action, neither egg detachment nor damage could be seen to immediately result from this activity. The behaviours resemble the locomotory patterns seen in strong swimming (fanning) and climbing (scrubbing).

There was no evidence of visually-directed cleaning behaviours (removal of defective or unfertilised eggs) such as seen in some cichlids; this may be accounted for by both the low light levels that must prevail in natural (subterranean) nests and the smallness of the eggs together with their arrangement in bunches. Although I videotaped some fanning by a female after one spawning, she was not seen more than an hour after spawning; in no other case have I seen the female remaining near the eggs after spawning.

**Eggs**

Eggs (Fig. 3.5) are clear pyriform capsules 500 μm in length (apex to base) and diameter (of round end), with attaching apical filaments as typical for gobies (Breder & Rosen 1966). The filaments attach eggs to the substrate or to other filaments, so that clusters of eggs are suspended from single substrate points. The motion of clusters in moving water is useful in distinguishing them from other matter adhering to stones. The clusters of empty capsules remained for a week or more (in grazing-absent conditions) after hatching in the field-collected nests, but were never otherwise seen in the rivers. The embryo develops, coiled, in the round end of the capsule. Hatching is by wriggling of the embryo, and usually took only minutes until the egg membrane ruptures, and seconds afterward the larva escapes and almost immediately swims upward. Todd (1975) stated that larvae of Dormitator latifrons hatch tail-first, but I have seen both in Sicydium punctatum; however, when both can occur, a tail-first larva is apt to remain partially in the egg for longer than a head-first larva. This would make tail-first larvae appear to predominate in a scan of partially-hatched larvae, and may explain Todd's conclusion.

**Hatching time**

Position within a nest, and the amount of illumination, agitation, aeration and other factors may affect incubation time. I have insufficient data to comment on the role of temperature; all hatch-time data from Dominica applied to nests with temperatures near 24°C (±2), and stream temperatures where larvae were found from 1989-1991 were between 20° and 30°C. Illumination of eggs under the microscope was found to stimulate (within seconds) activity and hatching of larvae, even several hours before any indication of an eye structure was detectable. In 4 of the 5 field-collected nests, hatching was in progress within minutes of
removal. This suggests either a short incubation time, or a wide range of hatching time, during the latter part of which larvae remain unhatched but ready to hatch if disturbed. The appearance of larvae in the 1990 aquarium spawning was preceded by the disappearance of the male (TL approximately 40mm) for several days, which might suggest a rather long incubation in this case. The hatching times seen in the Oct. 1992 aquarium spawning varied from 21 to 36 h after the commencement of spawning; the times are reliable because most of the process was videotaped, but the circumstances (fish were deliberately deprived of suitable nest sites so the spawning could be recorded with greater detail) and handling (removal of eggs from spawning site) may have accelerated hatching.

Hatching in the first (1970) aquarium spawning began about 20 hours, and continued until about 36 hours after the estimated time of deposition. This is almost identical to the 1992 spawning; both egg masses were exposed to higher light levels than would be expected in an subterranean nest. Position within the egg mass seems to affect time to hatching because partway through hatching a greater proportion of those in the center had hatched than had those on the edge of the patch; this could result from variation in brood care effects (e.g., aeration, agitation, distortion). In the 1990 spawning the eggs were not visible so the hatching time could not be estimated, but hatching seemed not to have been extended as it was in the 1970 captive spawning even though the upper limit (duration of occupation of the nest by the male) of plausible incubation times is large. The 1990 spawning occurred in an aquarium with natural conditions insofar as the gravel and stones (obtained from the river), which may account for the less protracted hatching period.

When nests were recovered in the field, hatching in 3 nests from the Springfield pool and the nest from Taberi R. mouth appeared to be ongoing or perhaps stimulated by the disturbance, since within minutes hundreds of larvae were evident in the buckets into which the nests were placed. In one nest from Springfield pool, few larvae hatched and the eggs fungused quickly. The high proportion of nests showing hatching almost immediately after retrieval suggests that hatching occurs in a developmental window during which the threshold level of stimulus required to initiate larval wriggling diminishes over time.

Manacop (1953) reports hatching of Sicyopterus extraneus after 20 to 50 hours. Foster and Fuiman (1987) report that Evorthodus lyricus hatched in 16 to 20 hours, and Todd (1975) reports that "normal prolarvae [of Dormitator latifrons] can hatch within seven hours of fertilisation". I differ with Todd on his un-defined use of the adjective 'normal' and suspect that what he describes is, as I have described above, the premature (earlier than typically occurs) hatching of S. punctatum that can occur when larvae are unusually handled. Normal hatching might be 50% longer, although even this is shorter than I believe can be accomplished by S. punctatum. Overall however, these four river-spawning tropical gobies show hatching rates of a similar order.

**Stage at Hatching**

Larvae hatched successfully from ≥3 of the 4 nests found in the Springfield pool, at stages varying from no-eye/early eye. The eggs from the nest collected at the Taberi R. mouth hatched at the no-eye stage.

**Developmental Stage at Hatch Estimated from Plankton Composition**

In the plankton samples S. punctatum larvae usually are at or beyond the stage of having a clearly evident lens in an unpigmented or scarcely-pigmented eye. The developmental stage at hatch should be reflected in the stage distribution, with the least developed stages indicating the earliest hatch and the developmental mode indicating the modal hatch stage (mortality, unless highly structured, cannot create a later mode). The presence of small numbers of larvae bearing the S. punctatum characters (pale yellow transparent yolk, patches of pigment appearing brownish to reddish under transmitted light but greenish-yellow fluorescing under reflected light with dark field) but at earlier developmental stages is attributed to premature hatching due to nest disturbances which may be natural (e.g., floods, predation, etc.).

**Larval Morphology**

Recently hatched larvae of Sicydium punctatum were approximately 1800µm in total length, and at stages from no eye structure visible (NE) to eye with lens and some retinal pigment (LEP). Since Sicydium punctatum larval stages earlier than LEP were rare in the river plankton, I conclude that earlier stages only hatch rarely or under unusual conditions.

The otolith sac is evident and appears to contain two otoliths. The mouth is incompletely developed until about 3 days. Some melanophores and small amounts of yellow-green pigment surround the anterior part of the yolk sac and parts of the nervous system, especially in the cephalic region. With lateral illumination against a dark background, greenish-yellow pigment can be seen as small bright spots in the trunk and around the yolk sac (described above under identification of larvae). This pigment seems fluorescent because of its chromatic purity and intensity, but it does not in fact fluoresce under UV light. Under anaesthesia with 2-phenoxyethanol the yellow-green pigment disperses temporarily. Dispersion is not a diagnostic character, but can lead to confusion because it does not occur in all larvae at the same anaesthetic levels. No larva was found in which such pigments did not disperse with slightly increased anaesthetic concentrations. The yolk sac is a clear pale yellow.
Overall morphology and size are similar to those reported by Foster & Fuiman (Foster & Fuiman 1987) for Evorthodus lyricus and by Todd (Todd 1975) for Eleotris pisonis. Morphology for all goby larvae in the Dominica rheoplankton is similar, with differentiation possible on characters of pigment and texture (Chapter 4).

**LARVAL BEHAVIOUR**

Larval behaviour of Sicydium punctatum in fresh water was invariant for all larvae observed, whether aquarium-spawned, hatched from field-collected nests, or retrieved from river plankton. Behaviour is similar for river-planktonic larvae of all goby species. Larvae are denser than water and sink headfirst, then turn and swim upward. This behaviour continues almost as long as it has been possible to keep larvae alive (approximately 4 days in freshwater, 8 in partially-saline treatments). This larval behaviour in a fluvial situation is consistent with a downstream passage to the sea, and with the observed subsequent migration of postlarvae of Sicydium punctatum from the sea into rivers. The larval behaviour is similar to that noted by Foster & Fuiman (Foster & Fuiman 1987) for Evorthodus lyricus and by Todd (Todd 1975) for Dormitator latifrons.

A more complex behaviour by larvae in varying salinities (Ch. 6; Bell & Brown 1994 in press) is shown by larvae in laboratory tanks: those in fresh water tended to distribute uniformly to the depth of the containers (~0.4m), those in sea water stayed within a few millimeters of the surface, and those in a salinity gradient showed highest numbers in the range of approximately 8 to 18 ppt. Larvae in halocline treatments consistently survived longer than larvae in either fresh or sea water.

**Recruitment**

The recruitment (arrival at river mouths) of marine postlarvae of Sicydium punctatum in Dominica is panseasonal but shows cyclic variation on both a seasonal and lunar scale. In Dominica the recruitment is episodic (Ch. 8), occurring reliably on the fourth day after the last lunar quarter (Fig. 8.4).

According to a combination of local lore and limited data, the heaviest yields to the fishery are in the fall, especially November, when the yield recorded was as much as 17-fold greater than an estimate of the lowest month's catch (Fig. 8.6d). Atwood (1791, pp.35-40) reported "the rivers are filled [with 'Tréz-tréz'] twice or thrice every year", which accords reasonably well with the frequency of tritri runs large enough to attract fishing effort.

The fishing period at Layou is rarely more than two days in duration, because fishing is conducted by seining at the river mouth, while a trap-type fishery above the river mouths on other rivers continues several days longer. Recruitment appeared to be, and is said to be, more reliable on the west coast (notably Layou river) than the east (notably Taberi river and nearby rivers). Erdman (1961) reports that Sicydium punctatum postlarval recruitment episodes in Puerto Rico begin "one to two days after the third or last quarter phase of the moon" and last about two days. In the Ilocos provinces of the Philippines however, the runs are reported (Acosta 1952) as occurring “nine days following the full moon each month from November to March”, and Manacop (1953, p. 42) reports that further south in the Cagayan river the run lasts one to nine days, commencing on “the second to the fifth day after the full moon, or shortly after the highest tide of the series”.

Sicydium punctatum postlarvae upon returning in Dominica were 16 mm to 22 mm SL, and had 50 to 140 sagittal otolith increments (mode at 65-75), interpreted as days, suggesting a shorter duration than for the related species reported on by Radtke et. al. (1988). The returning postlarvae are pelagic, transparent and schooling fish with a terminal mouth; upon entering freshwater they become pigmented (larvae captured in fresh water almost always have enough pigmentation to show one of the barrin patterns diagnostic of S. punctatum or loche cabree), benthic fish and the mouth metamorphoses to become inferior, and the fish begin to graze periphyton.

**CONCLUSIONS**

The results of this work, together with the established (fishery observations of Erdman 1961, etc.) postlarval immigration to rivers, support a diadromous life cycle as depicted in Figure 3.6, corresponding to the traditional understanding of anadromy, and do not support catadromy as claimed by some authors.

While Manacop (1953) did not report the vertical swim/sink cycle of Sicyopterus extraneus larvae, this is easily accounted for by the limitation of height in the finger-bowls and petri-dishes he used; otherwise, his observations are virtually all congruent with what I have found for Sicydium punctatum. Todd (1975) reports that Eleotris pisonis larvae perform vertical swimming from “immediately after they hatched”. I document elsewhere the ontogenetic changes in salinity selection by S. punctatum (Bell & Brown 1994 in press and Chapter 6) and their implications for larval transport and vulnerability to terrigenous toxins.

Manacop (1953, p.22) (p. 22), in discussing six published assertions of catadromy for other Sicyopterus spp., observed “it is very doubtful that these closely related species, under practically the same tropical conditions, would exhibit different spawning habits”, and that those authors “cannot fully substantiate their claim that these fishes are
catadromous”. The high degree of congruence of the life cycle of *Sicydium punctatum* and *Sicyopterus extraneus* and the absence of major differences among the sicydiines suggests generality. Where contrary data are absent, similarity in life history features within the group is the more conservative assumption: river-spawning diadromy is the proper null assumption.

Table 3.1. Principal sources of data for this study. A ‘y’ = source of data, an ‘n’ indicates no such data collected from this source, a missing entry indicates no data. ‘RPL’ = river plankton sampling, ‘FNR’ = field nest retrieval. 1: poaching into other pair’s courting arena by female deserted by male. 2: no gravel substrates provided. 3: egg masses exposed to more than expected natural subterranean light levels.

<table>
<thead>
<tr>
<th>Captive</th>
<th>Aquarium Spawnings</th>
<th>Field (1989-92)</th>
</tr>
</thead>
<tbody>
<tr>
<td>19xx:</td>
<td>70</td>
<td>90</td>
</tr>
<tr>
<td>Gravel available?</td>
<td>y</td>
<td>y</td>
</tr>
<tr>
<td>Early Courting</td>
<td>y</td>
<td>y</td>
</tr>
<tr>
<td>Late Courting</td>
<td>n</td>
<td>n</td>
</tr>
<tr>
<td>&quot;poaching1&quot;</td>
<td>y</td>
<td>y</td>
</tr>
<tr>
<td>egg predation</td>
<td>y</td>
<td>y</td>
</tr>
<tr>
<td>Nest Siting.</td>
<td>y</td>
<td>y</td>
</tr>
<tr>
<td>Nest Constr.</td>
<td>n</td>
<td>n</td>
</tr>
<tr>
<td>Egg Deposition</td>
<td>n</td>
<td>n</td>
</tr>
<tr>
<td>Broodcare</td>
<td>y</td>
<td>n</td>
</tr>
<tr>
<td>--Fertile?--</td>
<td>y</td>
<td>y</td>
</tr>
<tr>
<td>Hatching time</td>
<td>y³</td>
<td>n</td>
</tr>
<tr>
<td>Photo (Video,Film)</td>
<td>n</td>
<td>n</td>
</tr>
<tr>
<td>Larval behaviour</td>
<td>y</td>
<td>y</td>
</tr>
<tr>
<td>Larv. pred'n mort.</td>
<td>n</td>
<td>y</td>
</tr>
<tr>
<td>Larv. dev't</td>
<td>n</td>
<td>n</td>
</tr>
<tr>
<td>About larvae:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>stages</td>
<td>y</td>
<td>y</td>
</tr>
<tr>
<td>abundances</td>
<td>y</td>
<td>y</td>
</tr>
<tr>
<td>types</td>
<td>y</td>
<td>y</td>
</tr>
<tr>
<td>development</td>
<td>y</td>
<td>y</td>
</tr>
</tbody>
</table>
Table 3.2. Summary of nests observed. SPRR=Springfield pool or riffle below pool (approx. 200m west of Springfield hotel, on Check Hall River). Stages abbreviated as (see also Ch. 5 and Fig. 5.1): ne (no trace of eye); ee (early eye outline); lup (lens refractive, retina unpigmented); lep (lup-retina partially pigmented); lp (retina pigmented, blocks transmitted light). Fyg = larval type characters confirm *S. punctatum*; ~Fyg = most characters positively recorded, no non-matching characters observed.

Notes: ¹thus categorised because eggs were deposited on a structure which extended above the gravel; ²precise nest site inferred from observation of access tunnel; ³nest likely to have been disturbed prior to discovery

**SUMMARY OF NESTS OBSERVED:**

<table>
<thead>
<tr>
<th>DATE (YMD)</th>
<th>PLACE, SUBSTRATE</th>
<th>HATCHED @ STAGE</th>
</tr>
</thead>
<tbody>
<tr>
<td>70.12.03</td>
<td>Canada, in gravel¹</td>
<td>no data</td>
</tr>
<tr>
<td>90.09.20</td>
<td>Dominica, in gravel²</td>
<td>Fyg, lup</td>
</tr>
<tr>
<td>90.08.16</td>
<td>SPRR, in gravel</td>
<td>Fyg, lep</td>
</tr>
<tr>
<td>90.08.19</td>
<td>SPRR, below gravel</td>
<td>Fyg, ee, no membrane; most hatching occurred following day. Good photos of eggs, nest on stone.</td>
</tr>
<tr>
<td>90.08.21</td>
<td>SPRR, in gravel</td>
<td>~Fyg, ne/ee approx. 25 mins searching.</td>
</tr>
</tbody>
</table>

**FIELD NEST RETRIEVALS**

89.10.31:1645h (1) Taberi, no gravel³ ~Fyg, ne

Nest was only about 2m above sea level, almost within reach of wave influence.

90.08.16:1710h (2) SPRR, in gravel Fyg, lep
90.08.19:1533h (1) SPRR, below gravel Fyg, ee, no membrane; most hatching occurred following day. Good photos of eggs, nest on stone.

10 mins searching, then seeing blue male use tunnel.
90.08.21:1720h (1) SPRR, in gravel ~Fyg, ne/ee approx. 25 mins searching.

Figure 3.1. Abundance of goby larvae in river plankton from fall 1989 to spring 1991. Logₑ numbers m⁻³. Zeros (of goby larvae in samples) are indicated at bottom indicated by "NIL". Dates as sequential days from Jan. 01, 1989. Months indicated by first letters. Some stations near to each other are given the same symbol, as in SSauvRosTabPmul (sansauv, rosalie, taberi, point mulatre; as in Table 2.1).
Figure 3.2. Residuals of regression (eq. 1) of loge goby larvae m⁻³
Against (upper to lower) time of day, day number in study, and DOY
(see text).

Figure 3.3. Diagram of pigment patterns of recruited *Sicydium punctatum*
and *S. antillarum*. Both species are morphometrically very similar,
but pigment patterns are distinct and can be used to differentiate these
two species. See text for further details.
Figure 3.4. Larva (about 8.4 d post-hatch, 1800 to 2000 µm TL) from spawning of 7 April 1994 of *Sicydium punctatum*. Above: fluorescent-like yellow-greenish pigment in trunk area, diagnostic for *S. punctatum* among other Dominican river goby larvae, is distinctive and visible with oblique illumination against dark field. Below: same larva, this pigment not clearly showing under transmitted light.

Figure 3.5. Nest and eggs of *Sicydium punctatum*.  
Top: Eggs deposited on underside of undergravel filter (1970), with male. For scale, filter slots are spaced about 7mm.  
Bottom: Eggs with embryos subsampled from nest retrieved [Check Hall river, mid reaches in Springfield Estate, Dominica] 1533h, 19 Aug 1990, photographed at 1950 h. Diameter at large end of eggs is approx. 500µm. [Photograph is less than one-quarter of a subsample of <10 mm² of nest.]
Figure 3.6. *Sicydium punctatum* life history in Dominica, W.I. Adults spawn repeatedly and pan-seasonally, from <40 mm SL. 20mm (SL) postlarvae return after 50-140 d and sustain a traditional fishery.

**LITERATURE CITED** [originally no by-chapter lit.]


