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Life cycle, early life history, fisheries and recruitment dynamics of diadromous gobies of Dominica, W.I., emphasising *Sicydium punctatum* Perugia

by

© Kim Nigel Ian Bell

A thesis submitted to the School of Graduate Studies in partial fulfilment of the requirements for the degree of Doctor of Philosophy in the Faculty of Science

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Abstract

Fisheries for diadromous gobies occur widely in the coastal inter-tropics. Yields are rarely documented in detail, but there are many reports of and allusions to declines, which have not been satisfactorily explained. Basic life-history information has been at best sketchily known, or not at all, such that various sicydiine gobies have been incorrectly described as catadromous on the basis of assumptions alone. *Sicydium punctatum* Perugia is shown to be diadromous, spawning in rivers and spending 50 to 150 days at sea before migrating to fresh waters.

Larval behaviour is described and experiments show that larvae have the ability to select particular salinity layers in stratified systems. Implications for early life history transport, survival and vulnerability to terrigenous toxins are discussed.

Larval fish occurring in the rheoplankton are shown to be separable into five types, using pigment and other characteristics. The five types numerically correspond to the number of goby species known in Dominica, and one type is verified as *S. punctatum* through several captive spawnings and collected nests. Separation into types permitted an analysis of mortality in rivers, using stream drift data in a manner not previously applied. The theory of this manner of estimation is discussed, and field results for *S. punctatum* are compared with two types of analysis of mortality *in captivo*. Field data are also considered for several other taxa to demonstrate the method. The mortality rates found for *S. punctatum* are unprecedentedly high, but the agreement among multiple samples and with the captive observations suggests that stream mortalities may be extreme, and that larvae nearest the coast have a significant advantage. Coastal habitat is therefore the most important in sustaining the fishery. Implications and questions arise for the reproductive ecology, competition and upstream migration of *Sicydium* spp.

While age-at-recruitment (AAR) has thus far been treated as a constant (each species) plus error, the duration of the postlarval period of *S. punctatum* is shown on the basis of otolith analyses to vary systematically with time of year. There is contrary variation in size-at-recruitment, indicating strong seasonal variation in growth rate. The variation in age-at-recruitment suggests population dynamics not previously acknowledged in either fact or theory, and these are discussed in principle and the dynamics modelled by numerical simulation. The unavoidable conclusion is that, even where reproduction and daily risk of mortality remain constant in all seasons, observed levels of variation in AAR are sufficient to induce large variations in yield. The characteristics of the simulated yield patterns closely match the actual yield data. The amplitude of variation generated

depends on level of (constant in each simulation) mortality. The same principle applies not only where changes are seasonal, but to any temporal trends, and may have implications in other systems. Further variation in reproduction or mortality could increase or decrease these amplitudes, but since the variation in AAR generates variations over 10- to 30-fold at plausible field mortality rates, large variations in any other factor would be required to mask these effects.

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Five years is a substantial portion of a life; the volume of experiences fitted into this program make it seem almost a life on its own. This may help to account for the extent of these acknowledgements, each of which should be considered an understatement, each of which represents friendships remembered well.

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My final acknowledgement must be to the fish and other river life of Dominica, for their part in this study. What was found during this work exceeded all reasonable expectations and hopes.

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List of Abbreviations, Terms and Symbols

DOY day of year, numbered 1-365 from Jan. 1 to Dec. 31.

larva (in context of *Sicydium* spp.): newly hatched, 1.8mm, rheoplanktonic, non-feeding, with yolksac incompletely absorbed. Hatched from nests in rivers, and found in stream drift/river plankton.

postlarva (in context of *Sicydium* spp.): the period or developmental stanza(s) following yolk absorption (early postlarva) to approx. 20mm SL (late postlarva), entering fresh waters from sea, with incomplete pigmentation (barring pattern on body may be 0 to 100% present, but no pigmentation on dorsal fins). Mouth in process of transforming from terminal to inferior, dentition incomplete. Late postlarvae cannot yet be diagnosed beyond "*Sicydium* spp." without pigmentation. May also be referred to as incompletely settled, settling, recruiting, a recruit. When placed over sand, incompletely settled fish swim free of the bottom, while over stones they skip from stone to stone. See also JUVENILE.

juvenile: approx 20mm SL, recently entered fresh waters from the sea (as late postlarva), has completed development of characteristic juvenile pigmentation including somatic (permitting ready identification as *Sicydium punctatum* or *S. antillarum*) and dorsal fin pigmentation. Mouth completely transformed from terminal to inferior, dentition complete. May also be referred to as completely settled, recruited, metamorphosed.

tri-tri: late postlarvae of diadromous gobies migrating from sea into rivers. Tri-tri have been fished in Dominica since the 1700's or earlier. Term probably derived from the early settlers' phrase 'trez-trez'.

SL: Standard Length, from tip of snout to posteriormost fleshy part of caudal peduncle

FL: Fork Length, from tip of snout to termination of central caudal fin rays (or caudal membrane in larvae) (because of shape of caudal fin, *Sicydium* spp. FL=TL)

TL: Total Length, from tip of snout to termination of central caudal fin rays (because of shape of caudal fin, *Sicydium* spp. TL=FL). Note: Larval lengths are recorded as TL to avoid the suggestion that finrays are developed.

AAR: age-at-recruitment

S: survival. S_h = hourly survival.

M: mortality, $M = 1 - S$. M_h = hourly survival.

Early developmental stage names:

NE, EE, LUP, LEP, LP: Stages of development according to development of eye. No Eye (no trace of), Early Eye (trace of outer margin but no lens), Lens Un-Pigmented (lens present, retina unpigmented), Lens Early Pigment (lens present and pigment beginning to appear on retina but no part of retina less transparent than smoked glass), Lens Pigmented (retina no longer translucent). See also J<#>.

J<#>: Stage, numbered according to development of jaw. 0: no sign of jaw. J1: irregularities on snout indicating development of jaw structure. J2: posterior tip of mandible detectable as a bump or prominence, approximately below eye. J3: location of future opening of mouth is visible ("lips"). J4: ventral profile of mandible is clear. J5: intermediate. J6: mouth appears formed, but closed. J7: intermediate. J8: mouth open. J9: intermediate. J10: mandible seen to move at least once, presumed beginning of feeding capability. J11: mouth seen to be well formed, open and operating. See also NE, EE, LUP .... .

Fyg, Frb, Y, W, P: designations for larval goby types recognised in the river plankton (defined in Chapter 5).

Other symbols explained in text as they occur.

PART ONE: BACKGROUND INFORMATION ON GOBY FRY FISHERIES AND DOMINICA, W.I.

Chapters 1-2

Chapter 1. Overview of life-history and fisheries of *Sicydium* spp., *Sicyopterus* spp. and allied fishes

ABSTRACT

Sicydium spp., *Sicyopterus* spp. and allied fishes support fisheries based on return migrations of postlarvae to rivers. Among species, postlarvae range in length from 12 to 30 mm. Most fisheries are in areas with volcanic habitat with high rainfall, torrential streams and high rates of disturbance. Most are inter-tropical, although close relatives occur in Japan. Even though some fisheries have been large, almost no sources of historical yield time-series exist and, at present, data are not consistently collected in any location. This is a major obstacle in determining the verity of reports of declining yields, and quantifying them to relate trends to other variables for which records might exist. In addition, the life-history of this group has often been incorrectly described as catadromous. Postlarvae have often been mistakenly described as new species because adult characters are absent. Evidence gathered in this study supports diadromy, or anadromy in the sense of upriver spawning, early growth in saline, presumably nearshore, habitats. Several key features are common to most or all species in this group.

INTRODUCTION

Fisheries based on return migrations of postlarvae of sicydiine gobies exist in many locations and can be described as intertropically worldwide. Genera which support postlarval fisheries are represented virtually throughout the Indo-Pacific (references below) with the possible exception of Australia; in the Gulf of Guinea (Risch 1979); and in the Caribbean and Central America (references below).

Data on fisheries are difficult to find and are often unreported in the literature, for example, the fishery in Dominica that had not been documented since its first mention by Atwood (1791). This may be, as in other places, because the fishery is episodic and participants in it are therefore part-time and difficult to track, and because much of the product is consumed within the community or sold informally. It may also be that fisheries based on fish only 2 cm in length has been dismissed as a curiosity. Even in the Philippines, where the largest published yields have occurred, there is no available data on the long-term yield variations and the limited data that does exist is inadequate for serious analysis.

Because of the cryptic nature of the data, the geographic examples below cannot be considered exhaustive, and accounts cited are often less authoritative than similar accounts for other fisheries might be.

FISHERIES, BY LOCATION

Philippines

The most impressive documented yields occur in the Philippines. Montilla (1931) reports *ipon* (postlarval gobies) yields for the year 1928 by area within the La Union Province of Northern Luzon: Bangar 189,250 litres, worth 30,000 Philippine Pesos (₱); Bacoro R. 18,925L worth ₱6,000. For Caoayan and Santa (both near mouth of Abra R.) only values are given: Caoayan ₱18,000, Santa ₱15,000. Licence fees collected for *ipon* fishing were ₱2,200, ₱2,000 in the two towns, respectively. (Blanco (1956) equates one Peso to fifty cents U.S.).

Manacop's (1953) Figure 1 indicates average landings per fishing enterprise, based on 5 artisanal fishery groups ("5 *baling* [type of gear] outfits") of 1,000 gallons for the peak month, February, high yields in three months out of the year. He expresses regret that many fishermen understate or do not record landings, but estimates that "total annual landings in Cagayan River (Mindanao, not N. Luzon as above) alone is between 40 and 50 thousand cans [1 can = 15 kg]", therefore 600,000 to 750,000 kg. Manacop (1953) gives the value of this harvest as ₱20,000, indicating a price of about ₱0.29 per kg; he quotes Herre (1927) for a value of ₱500,000 for N. Luzon, allowing us to conservatively (i.e. neglecting inflation) estimate the annual N. Luzon harvest at approximately 16,875,000 kg.

Elsewhere in the Philippines, Blanco (1956) described the fishery methods, investment and return for the goby fry fisheries at Laoag, Ilocos Norte. The peak month is reported as December, during which 36,075 kg were harvested, with 84,750 kg harvested altogether during the September-February fishing period. The reports of FAO (e.g., Anonymous 1988) fail to indicate the species included under the designation 'freshwater gobies' (19,405 mt in 1983).

Montilla (1931) notes that the people of Aparri had considered a type of gear called *daclis* to be so destructive that its use was discouraged by an annual tax of 200 pesos per *daclis*, and as a result none were used in 1928. He goes on to say "That the supply of ipon has been endangered could not be definitely ascertained, for lack of statistical data. But it has been noted that the methods for capture have increased in number, effectiveness and destructiveness due to ingenuity of construction and operation. The catches are much more now than before and the demand has also become greater, incident to the increase in population." He suggests (p74d) simple regulatory measure, arguing "unless a regulation of this kind is made, this important industry is doomed to perish". Acosta (1952) states that "this [*ipon*] fishery is undergoing depletion. Effective regulatory measures appear necessary".

Manacop (1953) wrote that the fishery "has been observed by both fishermen and fish traders alike to be on a continuous decline". He also recommends a conservation plan which "was tried during the period of investigation of the fishery at Cagayan River, [and] has apparently resulted in a remarkable rehabilitation of the gradually declining fishery". The plan involved two measures: a closed season (Dec. 1 to Mar. 15) on the catching of adults as well as prohibition on catching migrating fry within the river (most of the catch being normally taken just outside the river mouth).

Blanco (1956) reported that "The..periodic appearance of *ipon* in northern and northwestern Luzon, commencing in September and lasting through February each year is always unstable. Intensive fishing done at the marine shores and river systems tends to deplete the *ipon* fisheries". The first part of the statement suggests a variability such that determination of long-term rate of change might be difficult; recognising this, one of his recommendations (#5, p. 69) is that "data on the *ipon* landings should be gathered from year to year..". He concludes that Fisheries Administrative Order No. 9 (signed into law by Benigno Aquino, Secretary of Agriculture and Commerce on July 28, 1939) pursuant to Act 4003 (Fisheries) require improved enforcement.

Hawaii

Titcomb (1977) cites informants on the local lore of fish usage in Hawaii. "*Hinana* (spawn)[sic] were especially popular as dainty food", and "the fish were plentiful as rubbish..when the *hinana* season came". Other informants are quoted referring to the "vast quantities [gathered] in certain areas", the use of weirs or nets to harvest *hinana*, and aquaculture practices using *hinana* to stock ponds. Jordan and Evermann (1905) describe poisons and torches used for harvesting adult gobies and weirs for harvesting postlarval gobies. The total harvest of 'o'opu, or gobies, for 1900 is listed as 4,193 pounds, with a value of $630. This reflects the commercial portion of the total catch, but the postlarvae are likely to be either excluded or underestimated because, as Jordan and Evermann note, the postlarvae are consumed principally by the fishermen and their families.

Ego (1956) reports a continuing commercial and sport fishery for adult *Awaous guamensis* in much of Hawaii. He describes illegal harvesting with weirs or chemicals (household bleach being among the most commonly used). Regarding postlarvae or *hinana* he reports "before the taking of fry was prohibited... considerable quantities of the larval fish were caught and sold in gallon lots".

Recent papers (e.g., Kinzie 1988, Radtke et al. 1988, Fitzsimons & Nishimoto 1990, Kinzie 1993) make no mention of harvests, and one of these authors confirmed that no fry fisheries currently existed to his knowledge (R. Radtke, SOEST, Univ. of Hawaii, Honolulu, Hawaii 96822; pers. comm.).

This, compared with earlier yields as documented above, suggests decline.

Caribbean

DOMINICA: Thomas Atwood (1791) gives what is probably the earliest account of the harvest of postlarval gobies, called *trez-trez*, a likely fore-runner of the terms (*tritri*, *titiwi*, *titi* etc.) heard today in the Caribbean. He reports that "vast quantities" are captured by a method employing cloth, baskets and stones, very similar to methods that can be seen in practice in Dominica to this day.

Tritri is now regarded as a delicacy and fetches a higher price than other fish, wholesaling at E.C.$100 per 80 L barrel and retailing at higher prices up to E.C.$2 per measure of about 300ml. Demand exceeds supply so that it is usually sold out before reaching the fish market. A retired forest ranger recalled the influx of *tritri* at Indian River, Portsmouth: "[*tritri*] used to be so plentiful it was almost disgusting because you would look at a river and not be able to see the stones" (J.D. Solway, Bells, Dominica, pers. comm.). This statement is in stark contrast to the virtual absence of a fishery in the same location now, and useful because it refers to times 10-30 y ago. Heavy recruitment does occur still in other rivers, but rarely, to justify the adjective "disgusting", as I witnessed at Taberi river on Oct. 31, 1989: such was my reaction to a continuous layer of *tritri* covering the entire river bottom, the stones not visible except when the fish moved to avoid being touched.

In Dominica, as elsewhere in the Caribbean (Erdman 1961, Erdman 1984, Aiken 1985, Erdman 1986, Silva Melo & Acero 1989-1990) the fisheries are heaviest in the late months of the year and the migrations are near the day of the last lunar quarter.

Natural poisons are sometimes referred to in Dominica in the context of capturing adult gobies, as is referred to for Hawaii by Jordan and Evermann (1905). Pesticides are also reported to have been used in the past to stupefy fishes to be caught for eating (Pat Rolle, Hillsborough Estate, pers. comm.). Reports exist of local fish kills associated with agrochemical spills while washing sprayers, etc. (pers. comm.: Lennox Honychurch, Turtle Point, Dominica; Keith Robinson, Goodwill, Dominica; Nigel Lawrence, Fisheries Division, Dominica).

Everybody in Dominica knows *tritri* as a delicacy, and its arrival is a matter of conversation, as the weather is in places where its variation affords material for discussion. Interviews with many people in Dominica were conducted taking care to avoid priming interviewees for a particular response; yet interviews uniformly tended to indicate a large decline in harvests of postlarval gobies (K. Bell unpub. data). Because of the diversity of sources (a factory/business manager, several fishermen/women, a poultry farmer, a local historian, a retired forester/ranger..) the agreement in details among responses is convincing that there must have been a decline. For example, Lennox Honychurch, a local historian, reported that 15-20 years previously the rivers in the northeast (and area now intensively farmed) were teeming but are now empty of fish; he blames agrochemicals associated with banana culture, and mentioned the nematocide known as MOCAP (L.H., Turtle Point, Dominica, pers. comm.). Many others commented that while once "tritri" was easy to get, it was now necessary to "know someone".

PUERTO RICO: Erdman (1984) reported a catch, during a single postlarval migration, of 1,360 kg. Wholesale values at the time in Puerto Rico ranged from U.S.$4.40 to $11.00/kg, clearly indicating its delicacy status. Erdman (1986) reported that populations of adult *Sicydium* spp. in rivers had declined considerably. He suggests that a rising human population and increasing development are implicated.

JAMAICA: Aiken (1988) reported that "brief but lucrative" fisheries still existed for postlarval *Sicydium* spp., but that migrations were "nowhere as impressive as in former years". The seasonality (Aiken 1985) is virtually identical with that found in Dominica (this work) and Puerto Rico (Erdman 1961, Erdman 1984, Erdman 1986). Aiken (1985) mentions stream dewatering as one agent of decline.

Indian Ocean

Fisheries are reported by Aboussouan (1969) for Réunion and Catala (1982) for Madagascar. According to Catala, the postlarval gobies play a smaller role in the diet and fishing of Madagascar than in Reunion, being restricted to the east coast. *Sicyopterus* or *Sicydium* spp. (genera sometimes considered synonymous) is reported in the Comores by (Fourmanoir 1954, Starmühlner 1976, Starmühlner 1979, Thys van den Audenaerde & Teugels 1984, Teugels et al. 1985), but fisheries for postlarvae are either small or unreported.

The role of postlarval gobies in diet is recorded in a comment attributed to Valenciennes: "Au point de vue culinaire...J'avoue, pour ma part, n'avoir jamais pu - et je ne suis pas seul - m'affranchir d'une certaine répulsion devant ces platées où l'on croirait voir des amas de gros asticots. Mais on me repondra avec raison: «Si vous n'aimez cela, n'en dégoutez pas les autres»" (Catala 1982).

The best, albeit short, time-series of catch data is that published for Réunion by Aboussouan (1969), who warns that the data are a conservative approximation because "les pêcheurs pour diverses rasions peuvent ne pas déclarer toutes leurs prises; de même, les produits de braconnage ne sont évidemment pas déclarés". Aboussouan gives Réunion's catch broken down by location for 1966, showing that the highest catches are on the windward, NE coast; he also gives the total harvest for the years 1954 to 1966: mean 39.933, lowest 12.8, highest 78 tonnes (Fig. 1.1). This data set is interesting for a number of reasons. (1) It shows the magnitude of harvest that a small island (<80 km) can experience. (2) Since Réunion is relatively isolated the harvest must be considered to be due to the resident adult population, which is difficult to say of any other area for which I have documentation of substantial yields; it shows that high yields need not be a result of asymmetrical exchange, among areas, of larvae and postlarvae, even though they may yet prove so to be in some places. (The ability to relate resident stock and local habitat to production, is an obvious concern for management). (3) The high variability in yields is highly important information, even though we lack collateral time-series data to make sense of it, because it establishes precedent not only for large decreases, but increases. This rules out an overall environmental deterioration as sole cause. In respect of the Réunion data, two immediately plausible high-level hypotheses (each can be further dissected) are prompted: i) variation in physical environment on a multi-year timescale affects recruitment and possibly also production of larvae; ii) variations in adult population, possibly due to earlier variations in recruitment or survival to adulthood, affect recruitment.

A PERSPECTIVE ON DECLINES INDICATED IN THE LITERATURE

The number of different sources commenting on declines is too large to be dismissed. Many sources (e.g., Ego 1956, Erdman 1986, Aiken 1988) invoke human alteration of natural habitat as a causal factor, while others invoke over-exploitation (e.g., Montilla 1931, Acosta 1952, Manacop 1953, Blanco 1956). Habitat destruction and over-exploitation have a long history in general, but the degree to which each of these, and any other causes not yet mentioned, is responsible has not been possible to address because no systematic yield data have been taken and too little has been known about the life history and ecology of sicydiines.

The Réunion data (Aboussouan 1969), brief as they are, advance the possibility that variation of a factor of 7 might be a natural feature of fisheries for goby postlarvae. Thus, even if we accept that all declines reported are real, they may not, in themselves, be meaningful. In other words, short-term trends may be poor indicators of long-term trends. Determining whether or not this is the case requires both long-term data and a thorough exploration of the life-history. This underscores the complaints of many of the authors from the Philippines who seem to have been repeatedly called upon at late hour to generate prognoses and remedial measures without being given the opportunity to obtain the necessary data for proper understanding and management.

At present, data are not consistently collected in any location that I know of. The absence of historic information is a major obstacle in determining the verity of reports of declining yields, and quantifying them to relate trends to other variables for which records might exist.

LIFE HISTORY - STATE OF KNOWLEDGE

In addition to the lack of fishery data amenable to analysis, the life-history of *Sicydium* spp. and allied genera has often been badly misunderstood. Dôtu and Mito (1955) provide a brief but clear account of the life history of *Sicydium japonicum*. Manacop (1953) provides the best account to date of the sicydiine life history in his consideration of *Sicyopterus extraneus* in the Philippines. Despite this, outright contradiction or simple omission of mention of these works from subsequent papers (e.g., Herre 1958) has allowed the embedded idea of catadromy as a default life-history structure for all freshwater gobies, reinforced even by a table notation in Johannes (1978). Erdman (1961, 1986) provides a useful summary of the literature and comments on circumstantial evidence in favour of upstream spawning of Caribbean *Sicydium* spp. but lamented the lack of more substantial evidence. Penczak and Lasso (1991) not only mis-cite Erdman with regard to reproduction of *Sicydium* spp. but attempt to discuss production of river gobies without acknowledgement that many or all may be diadromous. Erdman has been at least twice mis-cited about *Sicydium* spp. reproduction, and confirms to me (pers. comm., 20 July 1992) that he personally had not seen eggs but reported a remark by Beatty (1944). (Beatty's remark is itself suspect for a number of reasons).

The Hawaiian literature includes one claim of something similar to catadromy: Ego (1956) provides the only credible account of downstream movement of adult *Awaous guamensis* combined with spawning but remarks that there is no evidence for this occurring except after a freshet. He describes recapture near the river mouth during the spawning season of adults which were tagged four miles above the river mouth. However, Ego (1956) expresses some doubt as to whether the downstream spawning is a deliberate or accidental event; i.e., whether upstream spawning is the mode except when floods carry fish downstream.

A judicious reading of the literature for claims supported by evidence indicates the key features that are common to most or all species in this group. Available evidence supports diadromy, in the sense of upriver spawning, early growth in saline, presumably nearshore, habitats. Most fisheries are in areas with volcanic habitat with high rainfall, torrential streams and high rates of disturbance. Most are inter-tropical.

At the start of the present work, no newly-hatched larvae of river gobies from anywhere in the world had been found since Manacop reported eggs from river nests and larvae from river plankton. Aquarium spawnings had produced larvae of three species: *Sicydium punctatum* (K. Bell unpub. data), *Dormitator latifrons* (Todd 1975), and *Evorthodus lyricus* (Foster & Fuiman 1987). The larvae from these sources and the larvae reported by Manacop were morphologically and behaviourally similar.

The lack of resemblance of postlarvae to the adults, together with their very rapid metamorphosis which reduces the opportunities to witness intermediate forms, has confused ichthyologists who have described postlarvae as new species (for a summary in the Caribbean, see Erdman 1961). It has also meant that many residents have regarded postlarvae as a product of the sea alone. The most common question I was asked while conducting my fieldwork in Dominica was "where do the *tritri* come from?"; those who recognised a connection with adult river fish were a small minority.

TAXA INVOLVED

In Atlantic fisheries, the genus *Sicydium* is most important (Atwood 1791, Erdman 1960, Erdman 1961, Erdman 1984, Aiken 1985, Erdman 1986, Aiken 1988). In Dominican *tritri*, *Sicydium punctatum* accounts for nearly all of the bulk, followed by *S. antillarum* (<<5%) and *Eleotris pisonis* (<<5%). Postlarvae of *Awaous taiasica* and *Philypnus*

(Gobiomorus) dormitor are rare (about 3 and 0 collected respectively).

In Hawaii, *Stenogobius genivittatus*, *Awaous stamineus* (Radtke et al. 1988) and *Awaous guamensis* (Ego 1956) are important, although the lack of measured amounts of recruitment makes it difficult to say which account for most. Among the important species in the western Pacific and Indian Ocean are *Sicyopterus extraneus*, *S. lacrymosa*, *S. fuliag*, *Glossogobius giurus*, *G. celebius*, *Ophiocara aporos*, *Chonophorus melanocephalus* and *Eleotris melanosoma* (Annandale & Hora 1925, Acosta 1952, Koumans 1953, Manacop 1953, Aboussouan 1969).

An interesting feature of the Philippine fisheries in general is that there are many species, and a comparison of Manacop (1953) and Blanco (1956) suggests that while *Sicyopterus extraneus* dominates in Mindanao, *Chonophorus* spp. dominate in northern Luzon although there is no suggestion that either group has a limited range. A shift in the dominance of species in runs may be related to the makeup of the parental population; and indeed the Cagayan and other rivers of northern Luzon have extensive low-gradient areas and which are the preferred habitat of *Awaous* or *Chonophorus* spp., while the Cagayan de Oro and other rivers of Mindanao are higher-gradient and more likely to contain *Sicyopterus* spp.

As a fished item, postlarvae are small, ranging in length from 12 (e.g., *Eleotris pisonis*) to over 25 mm (e.g., *Sicydium antillarum*), and often lack adult characters (scales, pigmentation, mouth structure). Because of this, postlarvae have often been mistakenly described as new species (Erdman 1961).

TAXONOMY OF SICYDIUM SPP. IN THE CARIBBEAN

Much confusion exists as to the relationships and proper scientific names of many of the Gobiidae, partly due to the extreme ontogenetic variation in morphology, scalation and pigmentation, and the difficulty of counting scales even in adults. Lack of types (e.g. *Gobius plumieri* BLOCH, Ichth., 125, pl.178, fig. 3, 1786; based on a drawing by Père Charles Plumier in Martinique -- as cited in Jordan and Evermann, (1898) has also been a difficulty. Difficulty also arises due to several features which, in this group, show dramatic changes at recruitment: alignment of mouth (terminal, then inferior), pigment patterns (transparent, then pigmented), scalation (naked, then gradually scaled, beginning at caudal). These changes have sometimes resulted in postlarvae being erroneously described as separate species (Erdman 1961, Risch 1979).

The names *Sicydium punctatum* PERUGIA and *S. antillarum* OGILVIE-GRANT are here used following Brockmann (1965), who gives photographs and scale counts which are consistent with these species as collected in Dominica. In Dominica, both are known as 'Loche', and *S. antillarum* is differentiated as 'Loche Cabrece'. Adults are readily differentiable by the pigment patterns (Fig. 3.2), which show up at, or soon after, recruitment to fresh water. The postlarvae which are fished are collectively called 'tritri' (pronunciation varies) and include at least three gobiids (*Sicydium punctatum*, *S. antillarum* and *Eleotris pisonis*) common enough to count. The gobies *Awaous taiasica* and *Philypnus (Gobiomorus) dormitor* are present as adults in streams, and postlarvae may be present in very small numbers in *tritri*. Several non-goby species co-occur with *tritri*. Scale counts are of no diagnostic value in recruiting *Sicydium* spp., because the scalation is incomplete until some time after recruitment to fresh waters. Jordan and Evermann (1898) indicate a higher scale count for *S. plumieri* (84 in lateral series) than that given for *S. antillarum* (68 in lateral series); For Puerto Rico, Nichols (1930) listed 3 *Sicydium* species: *S. antillarum* ("apparently collected by him in mountain streams"), *S. caguitae* ("known only from type"), and *S. plumieri* ("recorded..by Poey"). Hildebrand (1935) held that only a single species was present in Puerto Rico, but that this was *S. plumieri*, not *S. antillarum* as per Nichols. Hildebrand argued that morphological variation such as existed was attributable to differences in sex and maturity in this single species. I disagree on this point, having found no such clear sexual dimorphism even in fish which I have videotaped while spawning in captivity; even the typical colourations diagnostic of males are condition- and situation-dependent, and therefore not continuously present in males of *Sicydium punctatum*. I believe that in *S. punctatum* the blue patterns are used by males only, while other patterns observed are ethological signals in the repertoire of both sexes. I have seen no significant variation in the pigment pattern of *S. antillarum*, neither have I any information on its spawning. Brockmann also disagreed with Hildebrand, and diagnosed 3 - 4 species in a sample from Puerto Rico.

Sicydium punctatum and *S. plumieri* are both names originating from specimens or descriptions of fish in Martinique. If Martinique's fauna proves to have only the same *Sicydium* spp. as Dominica's (they are neighbouring and similar islands), the identity of the species corresponding to Père Plumier's sketch might be obtained by elimination. Brockmann (1965) characterises Perugia's description as being the only *Sicydium* spp. with a lateral scale count in the low 50's. If the only other species in Martinique were *S. antillarum* then Bloch's *S. plumieri* could either be declared invalid, or if not, assigned to one of the species other than *S. punctatum*.

Because of the confusion in taxonomy, it is impossible to use a taxonomic system which is both informative and not liable to change in the future. Therefore, because 3 of Brockmann's (1965) excellent descriptions of the principal species in Panama also match 3 of the 5 species found in Dominica, I use, *sensu* Brockmann (1965), the names *Sicydium punctatum* Perugia, *Sicydium antillarum* Ogilvie-Grant and *Awaous taiasica* (Lichtenstein). The names *Eleotris pisonis* and *Philypnus (Gobiomorus) dormitor* are used following Jordan and Evermann (1898), and Nichols (1930). At least two *Sicydium* spp., *S. punctatum* and *S. antillarum* are present on Dominica, W.I., with specimens of the former being on deposit at the U.S. national museum (catalogued as USNM 314002). I believe *Sicydium plumieri* is absent from Dominica.

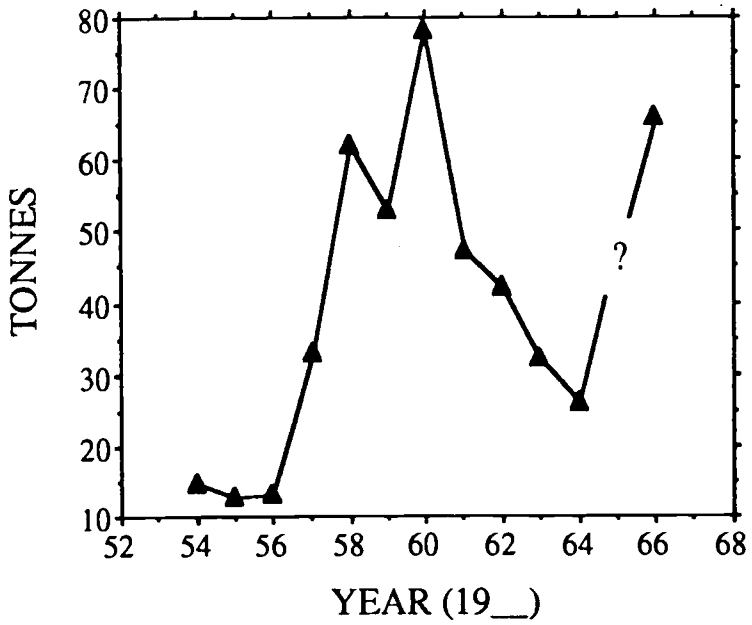


Figure 1.1. Yields in Réunion. Goby fry (postlarvae of *Sicyopterus* spp.) fishery. Data from Aboussouan (1969).

Chapter 2. Dominica, W.I.: physical setting and background

ABSTRACT

Dominica, W.I. is a volcanic island about 47 km long on its N-S axis, 25 km wide (E-W) in the Lesser Antilles. Centered about 15°30'N and 61°20'W, it lies between Guadeloupe (to the north) and Martinique (to the south). Persistent trade winds blow from the east. With two peaks rising to an altitude of 1400 m and interacting with the trade winds, much of Dominica experiences a high orogenic rainfall. This feeds numerous rivers, most of which are steep.

While Dominica has rainforests of international significance, their extent has diminished as increasing amounts of land are diverted to banana culture. Collaterally, increasing proportions of the coastline are being developed for industrial, residential and recreational (tourism) purposes. These have associated wastes which may deleteriously affect fish habitat.

LOCATION AND MAJOR FEATURES

Island arcs occur widely in the Pacific, but the Antilles (Fig. 2.1) are the sole island arc in the Atlantic ocean. The Antilles resulted from movement of the Caribbean plate against the Atlantic plate, which generates volcanic activity giving rise to islands like Dominica, Martinique, and Basse-

Terre of Guadeloupe. Dominica, W.I. (Fig. 2.2) is a volcanic island about 47 km long on its N-S axis, 25 km wide (E-W) in the Lesser Antilles. Centered about 15°30'N and 61°20'W, it lies between Guadeloupe (to the north) and Martinique (to the south).

Dominica, named for Sunday, was discovered by Columbus on the 3rd of November, 1493. It is said that Columbus, in order to describe Dominica's rugged terrain to Ferdinand and Isabella, demonstrated a crumpled piece of paper. Dominica was the last island holdout of the Caribs, and the last to be settled by Europeans.

The tectonic forces which created the Lesser Antilles are still evident in Dominica as numerous hot springs, a boiling lake, the frequent smell of sulphur, and the occasional earth tremor. A major eruption of Mt. Pelée on the neighbouring island of Martinique in 1902 destroyed the northern part of Martinique along with the city of St. Pierre, its residents (save one, a prisoner in a cell) and most of its politicians, and showered Dominica with ash. Other major eruptions have occurred in St. Vincent in 1902 and in the 1930's. The geological youth of the island is also evident in its sharp peaks and steep slopes. Much of it is extremely subject to erosion, particularly because of the high rainfall, and is sensitive to disturbance which removes the protective vegetative cover.

Persistent trade winds blow from the east. Dominica's two peaks rising to an altitude of 1400 m raise the airflow of the trade winds, and the condensation resulting from this pressure/temperature drop gives high rainfall over much of Dominica, feeding numerous rivers.

The coastal zone varies from cliff-like to steep. Most river mouths are steep, quick-flowing and stony. Few are gentle streams with mud or sand bottoms. The largest area of mud or sand bottom is the Layou river, of which the lowest portion, about 0.8 km, is sandy or silty, and the portion above that generally being a mixture of exposed outcroppings, bedrock, boulders, stones and gravel with little sand other than interstitially.

The high relief and high rainfall generally impede access because construction and maintenance of roads is difficult. These factors have somewhat protected natural aspects of Dominica by slowing its conversion by human activity, and at the same time have limited Dominica's economic success.

SAMPLE SITES

Sample sites for collection of river plankton or new recruits are indicated on map (Fig. 2.2) and listed in Table 2.1. The most frequently sampled sites are Layou (Coco Center, Hillsborough bridge, Layou mouth), Check Hall R. 10m from mouth, and Canefield R. at culvert bridge ~200m from mouth. The sites at Check Hall R. mouth and Canefield R. are similar and close (at opposite ends of Canefield airport's runway). The move to Canefield R. was made after the Check Hall R. site was found impossible for unattended gear, because of tampering and theft. For convenience and economy, plankton samples were routinely taken in the same location where the upmigration trap was installed. Check Hall R. is probably the most pristine available in that area, because of protection because it is the principal water supply for the capital. Canefield R. supported a large population of *Sicydium* spp., although below the sample site the river was heavily silted by the waste of a sand-and-gravel works.

WEATHER, RAINFALL, RIVER FLOW

Weather

The coastal zone of Dominica experiences only small daily or annual ranges of temperature. Between May 1 1989 and June 1 1991, the lowest recorded temperature at the Canefield airport was 20.6°C, and the highest was 33°C (Anonymous 1989-1991). Canefield airport data is useful because it is near most of the west coast sample sites used in this study. However, single-point weather data can suffer from local influences: rainfall was often seen to be localised, as when several patches of rainfall could be seen from a position still in sunlight. The temperature cycle (Fig. 2.3) shows a domed pattern in each year. Other than differences in their means, daily maximum and minimum temperature profiles seem very similar, with slightly more scatter apparent in daily minima. Pattern is not easily seen in the daily values for rainfall data alone (Fig. 2.4), but a superimposed smoothed mean (bi-directional 10-point running mean) shows high short-term variability, and shows that the 10-day expectancy of average rain varies five- to ten-fold seasonally. The maxima and minima of both temperature and rainfall coincide closely, but are slightly later for rainfall. Windspeeds (Fig. 2.5) vary from 0 to 12 knots, although the highest windspeeds, as occurred during hurricane Hugo, are probably mis-recorded as zeros due to limitations of equipment. Atmospheric pressure (Fig. 2.6) should be less subject to local influences, also shows seasonal structure, and is not well correlated with rainfall at Canefield ($r^2 = 0.01$, $p \leq 0.01$, $n = 749$). However, the correlation between ten-point running means of rainfall and atmospheric pressure was markedly better, although still poor, at $r^2 = 0.11$ ($p \leq 0.001$, $n=749$).

WATER-BORNE WASTE

One important feature of Dominica's rivers is that they handle virtually all liquid, and much solid, waste. This is important to recognise, because although such inputs are unavoidable in sampling, they may account for some of the variation in plankton data between sites and times. Therefore, although it was not the objective of this study to document such effects, the possibility of influence from these kinds of sources should be borne in mind as a possible factor in spatial or temporal differences found in, for example, larval abundances or mortality rates. The principal agricultural product of Dominica is the banana, and the influence of this industry can be readily detected by its refuse (blue plastic banana bunch covers in rivers). The quantities of herbicide, pesticide and nematocide imported by the Dominica Banana Marketing Corporation (DBMC) is summarised in (Towle 1991), and is reproduced in Table 2.2. The import data from DBMC underestimates total environmental loads because non-agricultural pesticides are also imported, and many toxic materials in waste may not be classified as pesticides. Since direct fish kills have been reported (Towle 1991, p62), some portion of the mortality risk is likely associated with the proximity of banana agriculture to streams, due to runoff, washing of sprayers and other equipment. Overspray from aerial spraying of cultivations could also enter streams directly; 600L of thiophanate methyl (Sigma™) was aerially sprayed in 1985 (Towle 1991). Farmers are generally unaware of hazards associated with agrochemicals, use of protective clothing is rare and equipment (backpack sprayers) is often leaky (pers. obs.).

Industrial wastes also find their way into rivers. Wastes of light industry in Roseau reach rivers or the sea via gutters or drains. On several occasions a film of diesel oil at Canefield R. was too thick to allow plankton sampling (a jam jar could be nearly filled without taking any water); the origin was difficult to determine, but may have been a paint factory, a repair shop, or a fuel station. On another occasion a large amount of sump oil from diesel generators at Fond Cole was seen to have been drained and dumped via a small stream into Woodbridge Bay (pers. obs.), resulting in a thick black layer over several ha. of the harbour area and fishing beach. Wastes in significant amounts drain, apparently on a chronic basis, from Dominica Coconut Products, depositing a white waxy sludge several cm thick over several hundred m^2 of Belfast River near its mouth (pers. obs.).

Silt from the P.H. Williams sand and cement works is deposited into Canefield river at approximately $4m^3$ per hour of operation. The silting is a pointless exercise in the first place since the gravel is made from crushed quarry stone and needs no washing because it contains no organics. The loss of the fine sediments actually impairs the utility of the sand for cement block making, and has to be compensated for by an increased ratio of cement, the most expensive component. I estimated the lost revenue over the past ten years of operation at US$800,000, using the most conservative values for the silt and neglecting the waste of electricity and amortization and depreciation of plant (K. Bell unpub. data). The siltation of the nearshore is claimed by locals to have eliminated the fishery, and at one point the accumulation of silt had impaired access to the P.H. Williams barge terminal. The lower portion of the river is heavily silted and appeared to be barren during 1989-1991.

These situations were brought to the attention of the Fisheries Division; however, they may be mere indicators of the increasing pressure on the local environment due to increasing industrialisation, construction and conversion of land to commercial and residential uses.

Table 2.1. List of sample sites where either river plankton or up-migrating postlarvae were captured. Sites can be located on map (Fig. 2.2). Number and abbreviation are as used in data.

#	Abbrev.	Location & Description
1	belfast	Belfast R. ~100m upstream from DCP & bridge
19	bouleau	Bouleau R. ~10m from sea, small stream, nearly dry when sampled: outflow at river mouth is sub-surface, percolates through beach gravel.
2	casbru	Castle Bruce R. close to mouth (10-20m). Banana cultivation dominates the valley upstream.
4	casbru.ff	Tributary to Castle Bruce river, where the main Castle Bruce road crosses above a deep pool to the right, above most cultivation. This is marked on some government maps as Fond Figues R.
5	chr	Check Hall R. close to mouth (below bridge on main coast road, near 'Warehouse Disco' and the north end of the runway of Canefield Airport)
5.1	chrh	Check Hall River near Springfield Guest House, at the bridge and nearby station lower at Dobrow's property. Altitude ~350m a.s.l.
17	clarkes	Clarke's river above Freshwater Lake, approx. midway between Roseau and Rosalie. Altitude ~800m a.s.l., cold, no adult gobies visible
6	laybells	Layou R. at Bells (5th stn. from mouth)
7	layco	Layou R. at Coco Center (about .5km above Hillsb'rough bridge, 3rd stn from mouth)
7.1	laymth	Layou R. river mouth
7.2	Layhbr	Layou R. Hillsb'rough bridge (bridge nearest coastline, second station from mouth)
8	laynven	Layou R. headwater/tributary, New Venture stream
9	layswbr	Layou R. at swing bridge (4th stn. from mouth)
10	melvhall	Melville Hall river (near airport), below bridge, ~0.5 km from coast
11	phw	Canefield river just above culvert bridge, PH Williams gravel works, ~200m from coast
11	phw aa	Canefield river, upstream ~150m from culvert bridge (above the ditch from the Texaco depot)
11	phwmth	Canefield river 5m from mouth
18	pmul	Pointe Mulatre river, near washed-out bridge, ~150 m from coast
12	rosalie	Rosalie river, just downstream from bridge, ~100 m from coast
13	roseau	Roseau river, either between 2 lower bridges (~250m from coast) or below lowest (0-200 m from coast)
14	rostraf	Roseau river at Trafalgar. Altitude ~800m a.s.l. Adult *Sicydium* spp. visible.
15	sansauv	river at San Sauveur, ~15 m from mouth
16	taberi	Taberi River, ~30m from mouth

Table 2.2. Dominica Agrochemical imports. A: Amounts of selected products for 1988 and 1989. B: Total herbicide and pesticide imports 1985-1989. (Source: Table 8.1(8) and p. 150 of Towle, 1991).

A:

NAME	1988	1989	UNITS
Round-up	na	720	l
Reglone	na	48	l
Paraquat (Pillarxone)	40,000	119,825	l
Gramoxone	41,010	20,000	l
Benomyl	4,000	2,700	kg
Calixin	7,680	4,320	kg
Sigma	10,950	5,500	l
Primicid	6,157	26,300	l
Vydate	37,100	1,100	kg
Furadan	156,670	100,000	kg
Mocap	67,455	58,320	kg
Nemacur	na	1,250	kg
TOTAL	272,905	167,690	kg
PLUS	98,117	172,393	l

B:

YEAR	**AMOUNT**	
	(lbs)	**(kg)**
1985	140,000	63,636.4
1986	157,000	71,363.6
1987	1,000,000	454,545.5
1988	857,000	389,545.5
1989	650,000	295,454.5
total	*2,804,000*	*1,274,545.5*
average	560,800	254,909.1

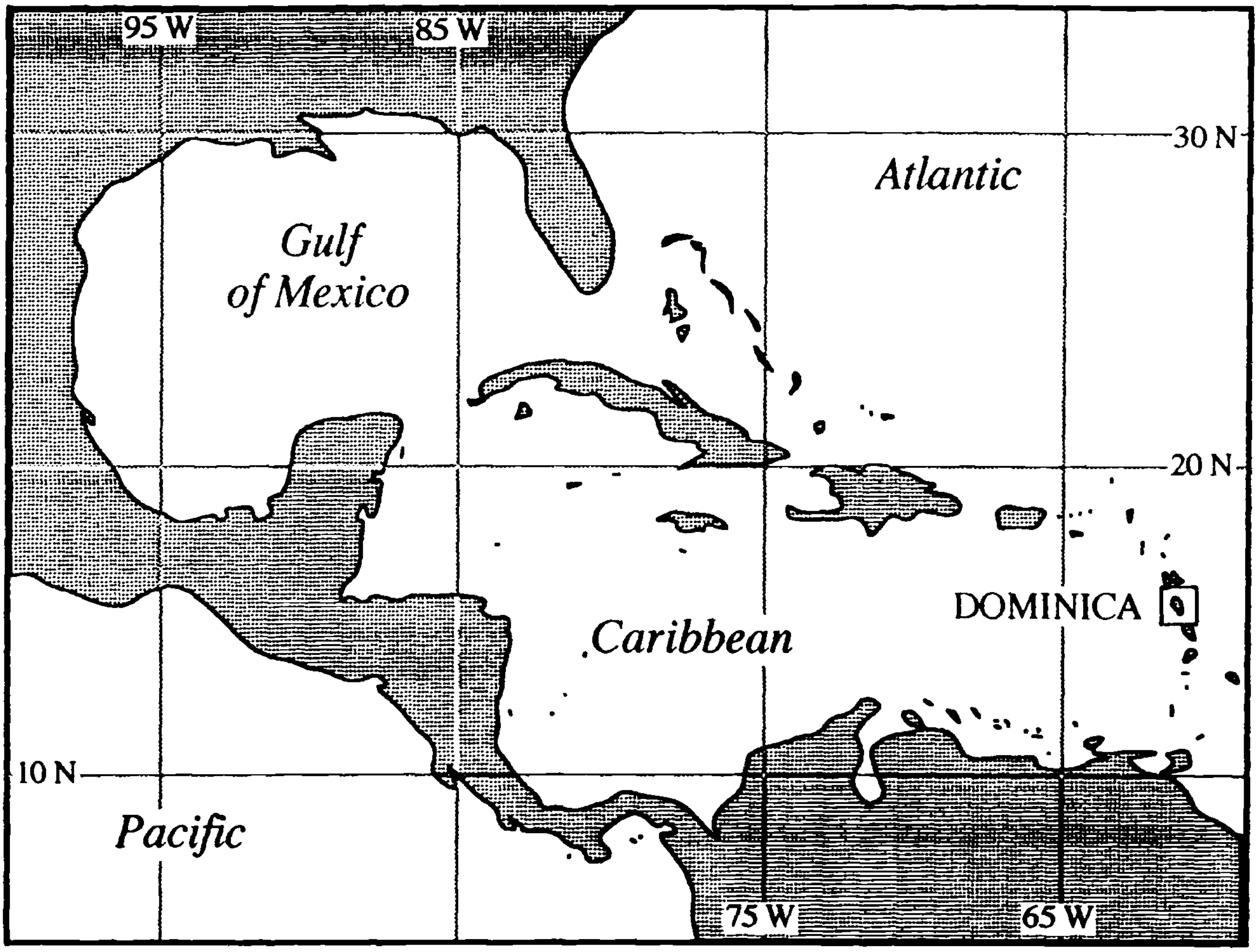


Figure 2.1. Map of the Caribbean.

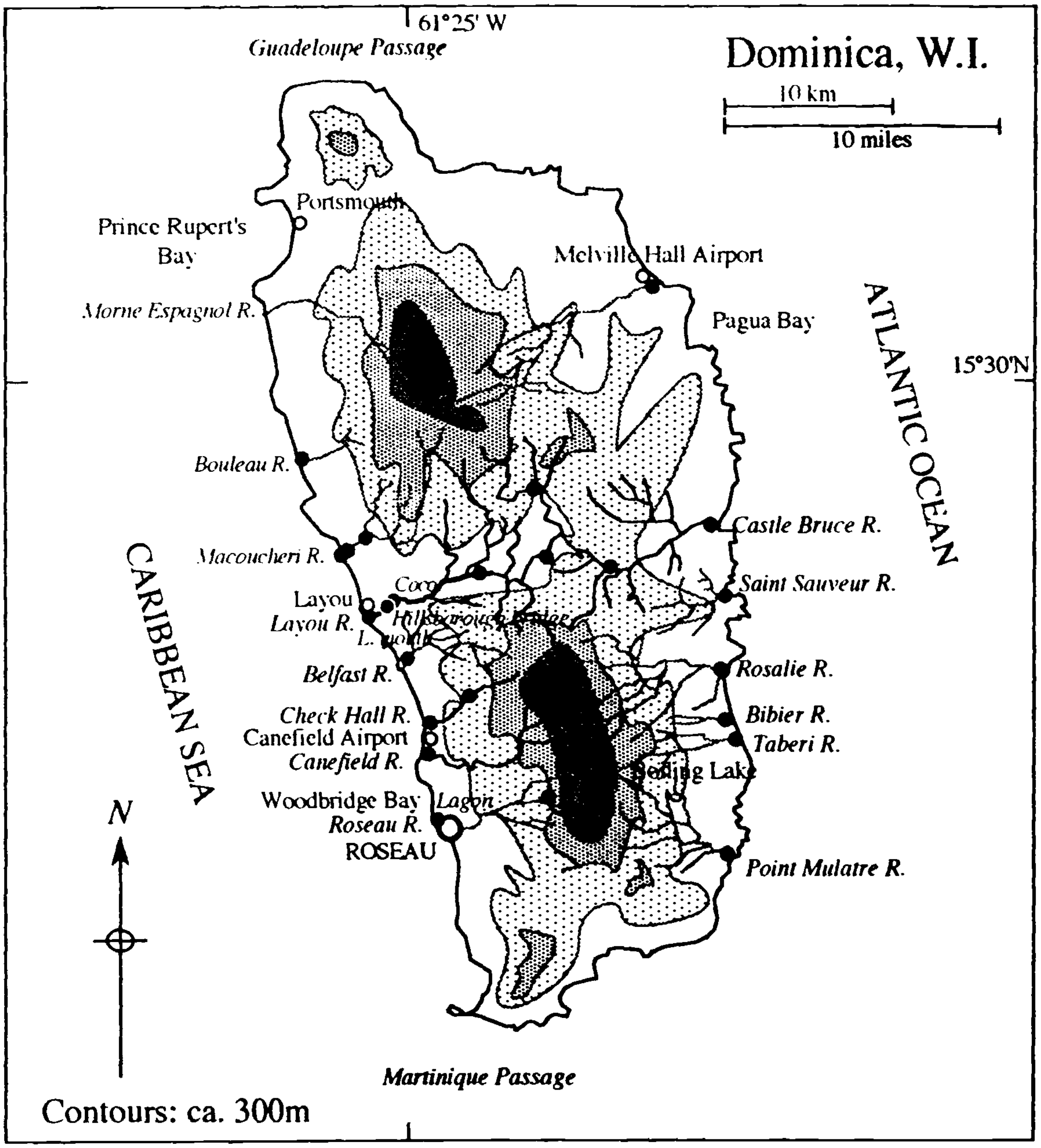


Figure 2.2. Map of Dominica, W.I., indicating sample sites (●) and towns (○).

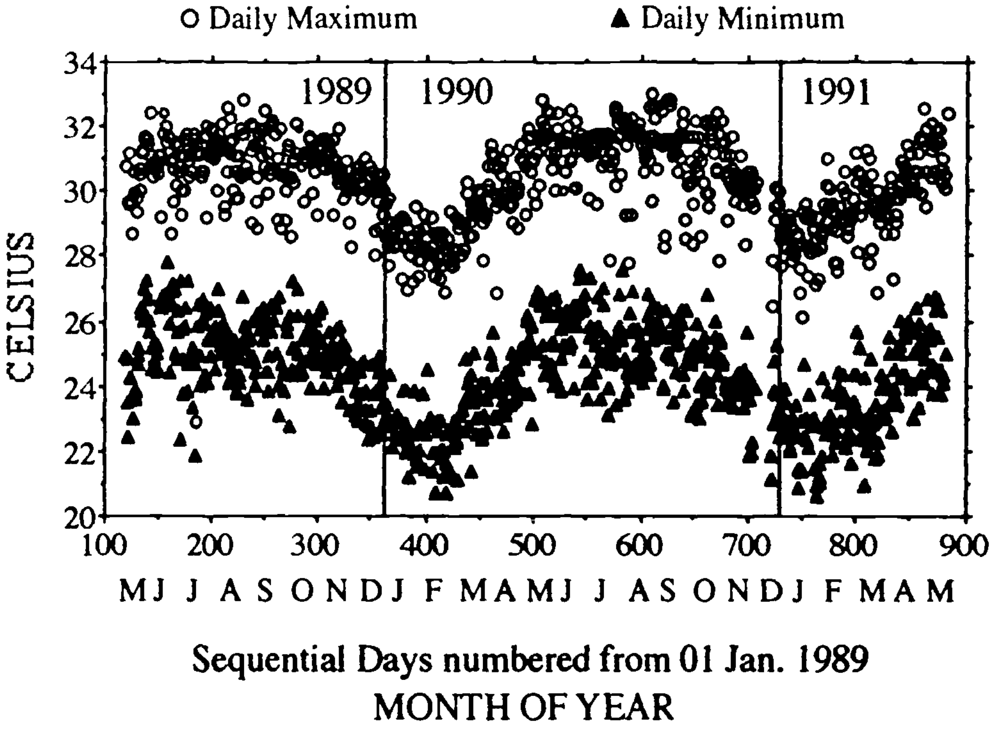


Figure 2.3. Air temperatures on Dominica's west coast. Compiled from daily weather reports from Canefield Airport.

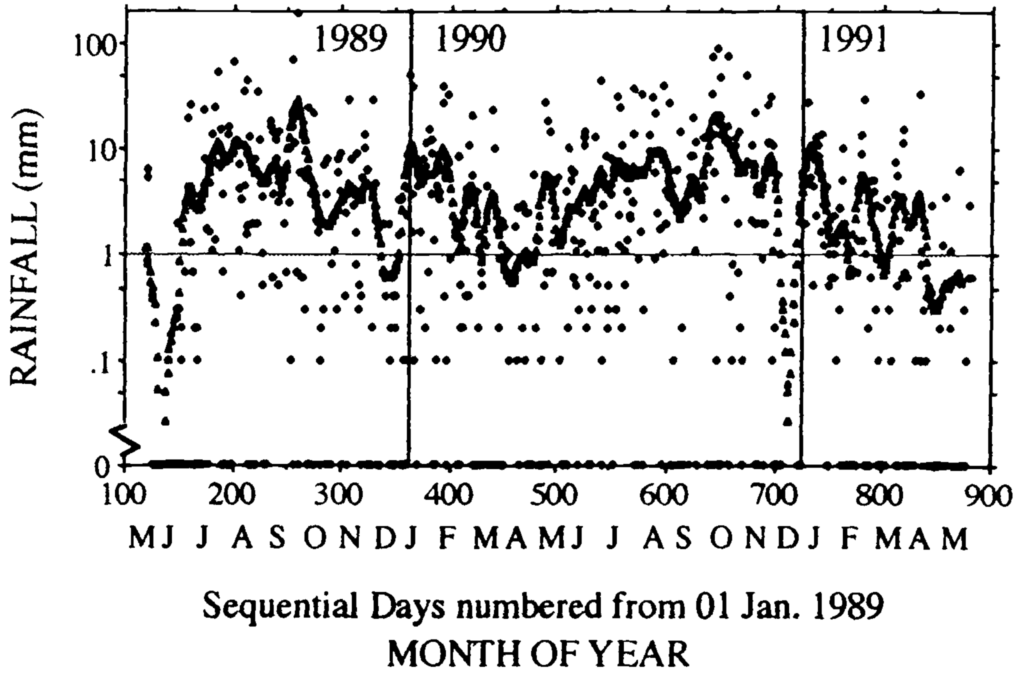


Figure 2.4. Rainfall on Dominica's west coast. Compiled from daily weather reports from Canefield Airport. Daily rainfall on log scale, with 10-point bi-directional smoothed mean (of 10 points in forward direction, then 10 backward).

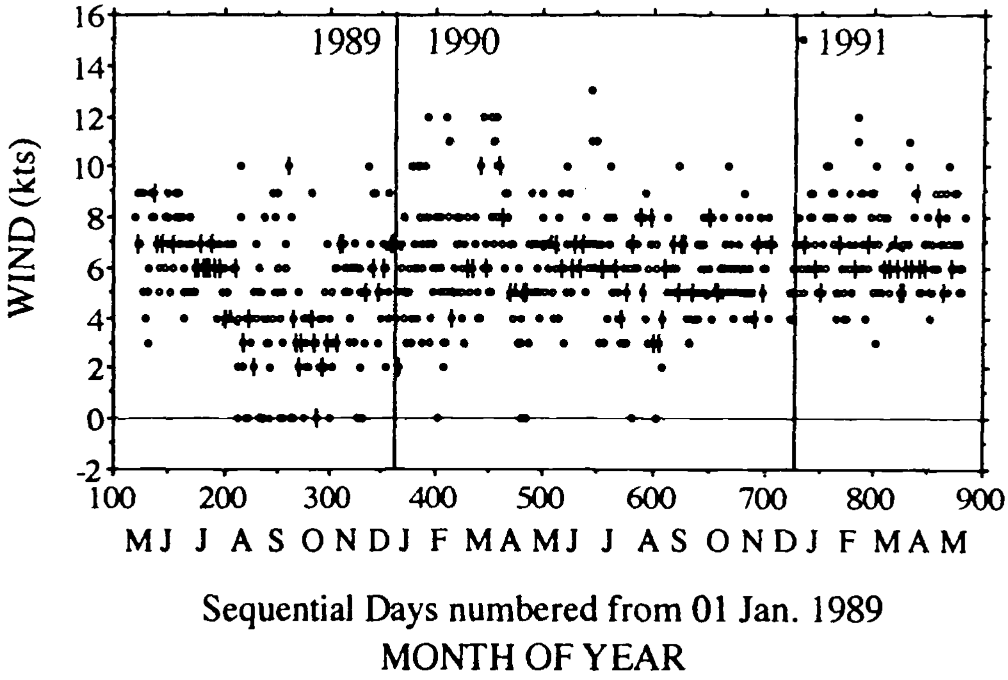


Figure 2.5. Wind speeds on Dominica's west coast. Compiled from daily weather reports from Canefield Airport.

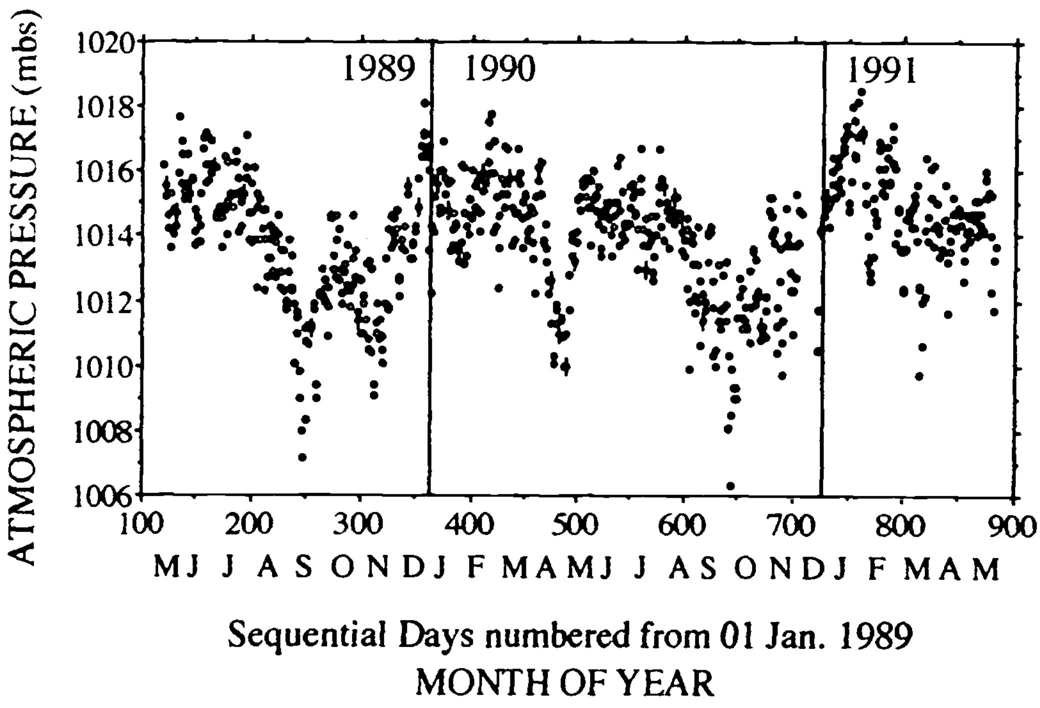


Figure 2.6. Atmospheric pressure, DominicaVariations in atmospheric pressure on Dominica's west coast. Compiled from daily weather reports from Canefield Airport.

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 sicydiine 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.

Sicydiine 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 sicydiine 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-spawning diadromous species), and is largely consistent with the knowledge, however scant, of other sicydiine 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 entering rivers from the sea (Atwood 1791, Erdman 1961, Erdman 1984, Aiken 1985, Erdman 1986, Aiken 1988) in the Caribbean as it does for other sicydiine goby (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 sicydiine gobies, authors variously apply the terms: diadromy, amphidromy (coined by Myers (1949b)), 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 (Dôtu & 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 occasionally 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-phenoxyethanol, 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 (1949b). The overall mean abundance found was 56.8 larvae$\cdot$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$\cdot$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 m^3 (lnGLM) was described as a function of the cosine of angular transforms (rDOY, rDECT) of day of year (DOY) and 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 (here in radians) was iteratively determined, for day and time separately, as that yielding the highest positive correlation with $\log_e$ concentration of larvae. The regression:

$$\ln GLM = 3.1 + 0.83\cos(rDOY+3.25) + 1.77\cos(rDECT+.5) \qquad \text{(eq. 1)}$$

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 the highest seasonal concentrations of larvae at mid-year, and the lowest daily concentrations are 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 cabrece'), 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 melanin), (2) a pale yellow cast to a (3) clear yolk (vs. clear 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-anaesthetised 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 flouresce 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 pale white. 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 riffles 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 riffle 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 grazer-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 on-going 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 (1987) for *Evorthodus lyricus* and by 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 (1987) for *Evorthodus lyricus* and by 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 barring patterns diagnostic of *S. punctatum* or loche cabrece), 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), 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.

	Captive Aquarium Spawnings						Field (1989-92)	
	1970	90	92a	92b	94a	94b	RPL	FNR
Gravel available?	y	y					y	y
Early Courting	y	y	y	y	y			
Late Courting			y	y	y			
"poaching^1 "					y			
egg predation			y	y	y	y		
Nest Siting.	y	y	n^2	n^2	n^2	n^2		y
Nest Constr.		y	n^2	n^2	n^2	n^2		y
Egg Deposition			y	y	y			
Broodcare	y				-	y		
--Fertile?--	y	y		y		y		
Hatching time	y^3			y^3	-	y^3		
Photo (Video,Film)				V	F	F		
Larval behaviour	y	y		y			y	y
Larv. pred'n mort.		y					y	
Larv. dev't				y		y	y	y
About larvae:								
stages	y				y		y	y
abundances					-		y	
types		y		y	y	y	y	y
development						y		y

Table 3.2. Summary of nests observed. SPRR=Springfield pool or riffle below pool (approx. 200m west of Springfield hotel, on Check Hall River).

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

SUMMARY OF NESTS OBSERVED:

DATE (YMD:H)	(N)	PLACE	SUBSTRATE	HATCHED AT STAGE
AQUARIUM SPAWNINGS				
70.12.03	(1)	Canada	in gravel[1]	no data
90.09.20	(1)	Dominica	in gravel[2]	fluor, lup
Aquarium spawnings in Canada 1991-1994 were in gravel-free aquaria, therefore supply no information on nests.				
FIELD NEST RETRIEVALS				
89.10.31:1645h	(1)	Taberi	no gravel[3]	~fluor, ne
Nest was only about 2m above sea level, almost within reach of wave influence.				
90.08.16:1710h	(2)	SPRR	in gravel	fluor, lep
90.08.19:1533h	(1)	SPRR	below gravel	fluor, ee
10 mins searching, then seeing blue male use tunnel.				
90.08.21:1720h	(1)	SPRR	in gravel	~fluor, ne/ee
	approx. 25 mins searching.			

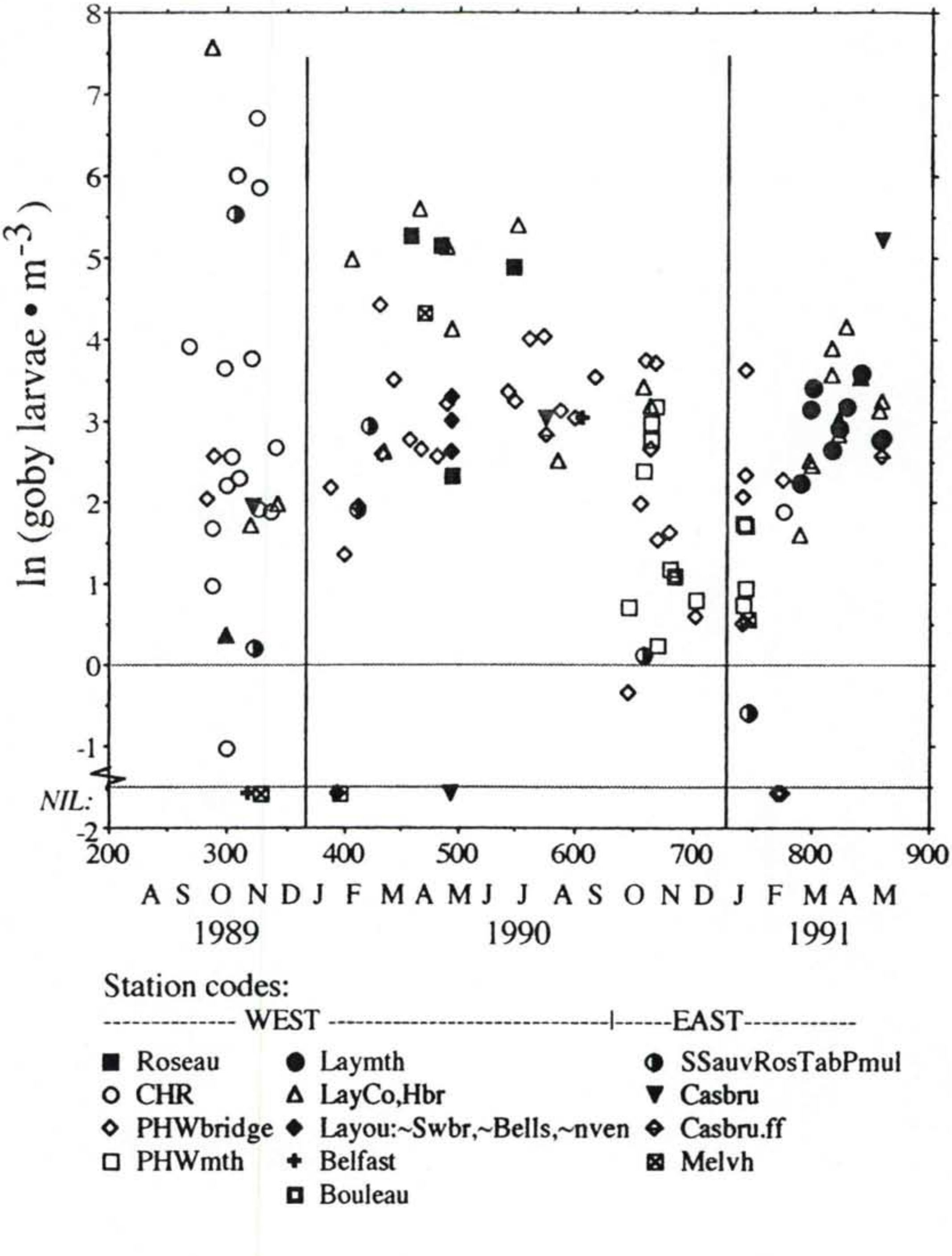


Figure 3.1. Abundance of goby larvae in river plankton from fall 1989 to spring 1991. Log_e numbers$\cdot$m^{-3}. Zeros (of goby larvae in samples) are indicated at bottom indicated by "NIL". Dates as sequential days from Jan. 01, 1989. Months indicated by first letters. Some stations near to each other are given the same symbol, as in SSauvRosTabPmul (sansauv, rosalie, taberi, point mulatre; as in Table 2.1).

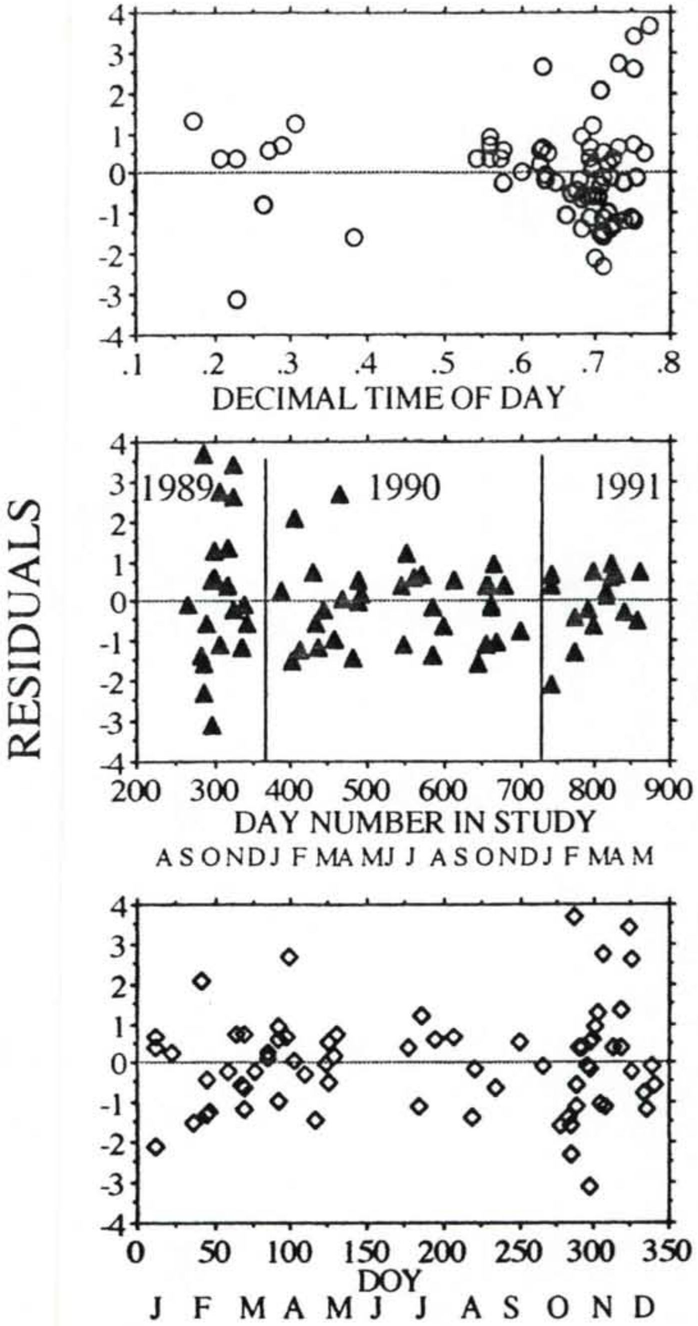
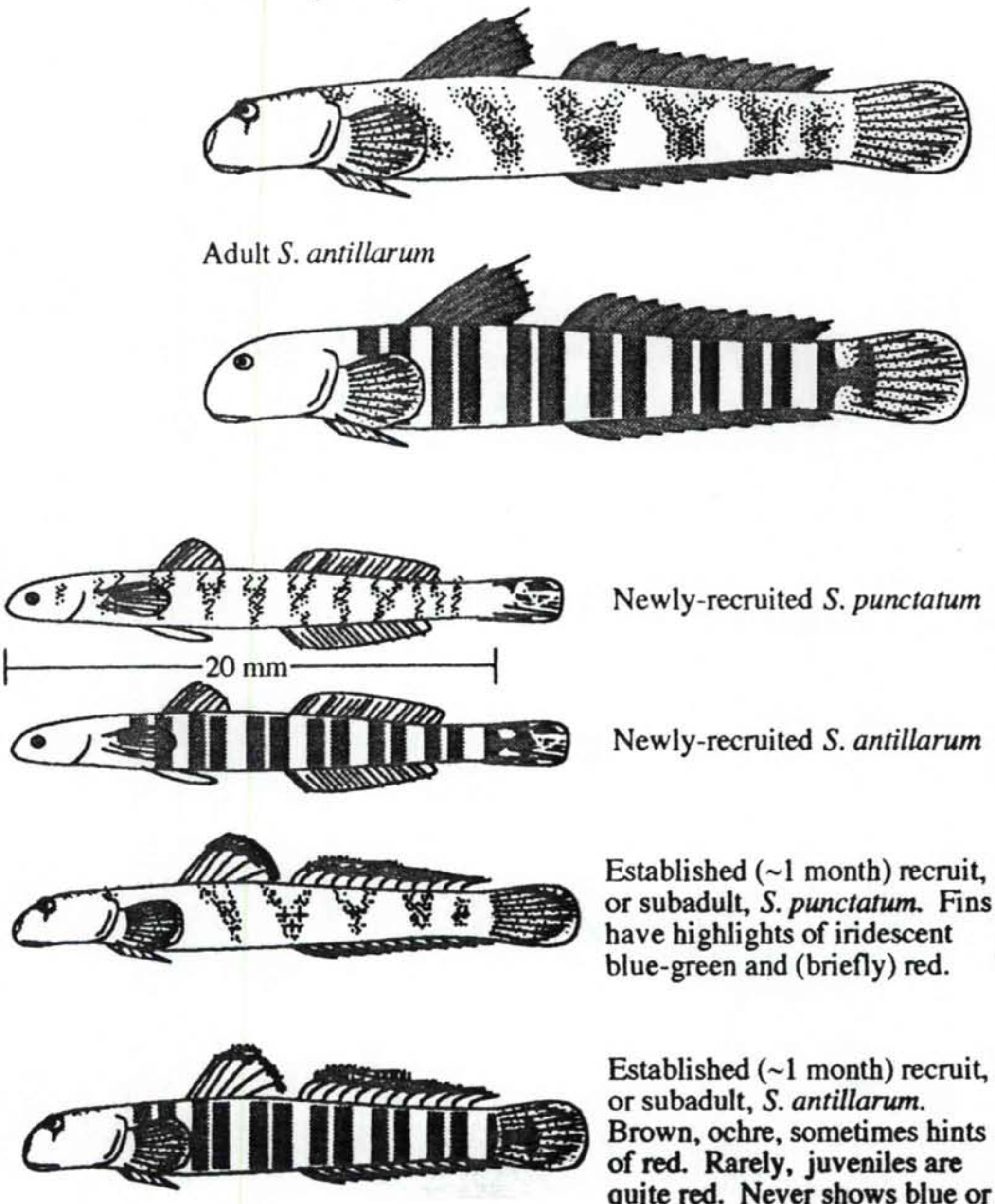


Figure 3.2. Residuals of regression (eq. 1) of $\log_e$ goby larvae$\cdot$m^{-3} Against (upper to lower) time of day, day number in study, and DOY (see text).



Adult *Sicydium punctatum*

Adult *S. antillarum*

Newly-recruited *S. punctatum*

Newly-recruited *S. antillarum*

Established (~1 month) recruit, or subadult, *S. punctatum*. Fins have highlights of iridescent blue-green and (briefly) red.

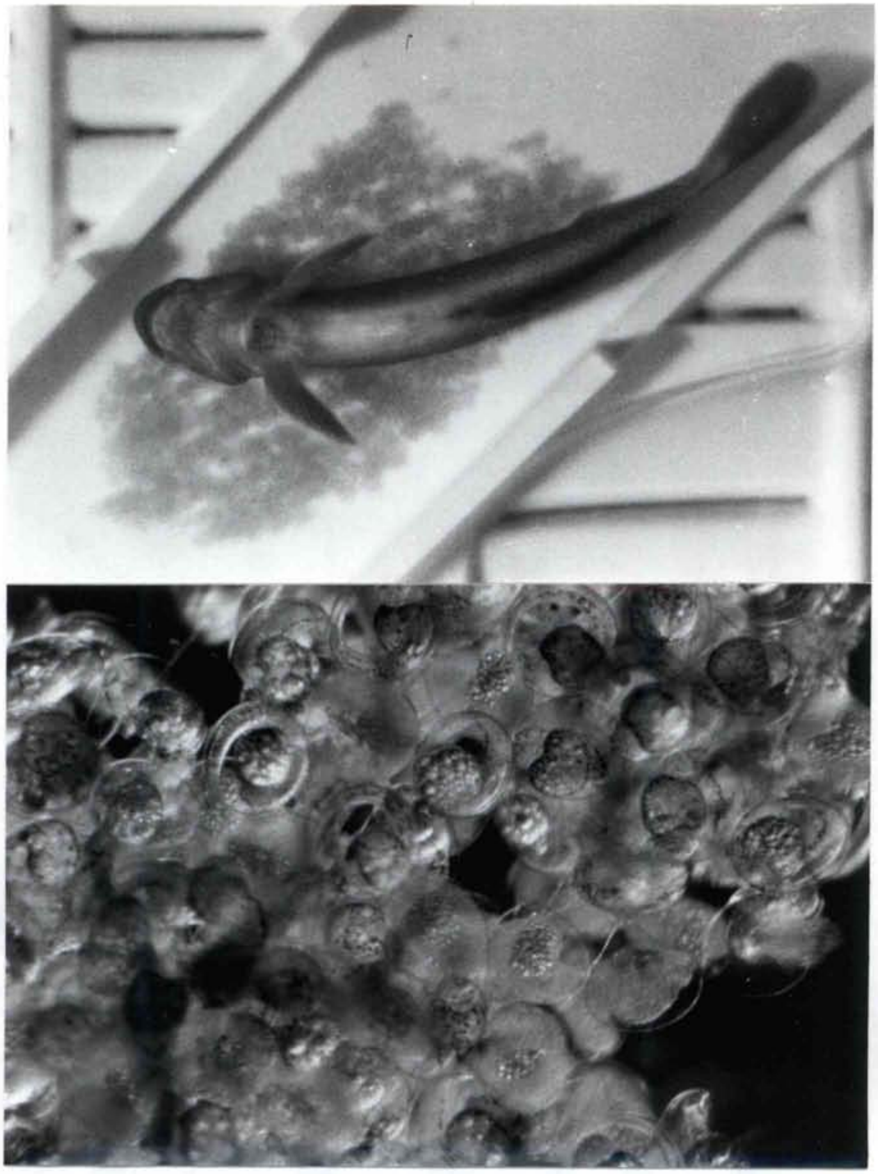
Established (~1 month) recruit, or subadult, *S. antillarum*. Brown, ochre, sometimes hints of red. Rarely, juveniles are quite red. Never shows blue or green. Generally slightly larger and heavier-bodied than *S. punctatum*.

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 3.5. 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 1533h, 19 Aug 1990, photographed at 1950 h. Diameter at large end of eggs is approx. 500µm.



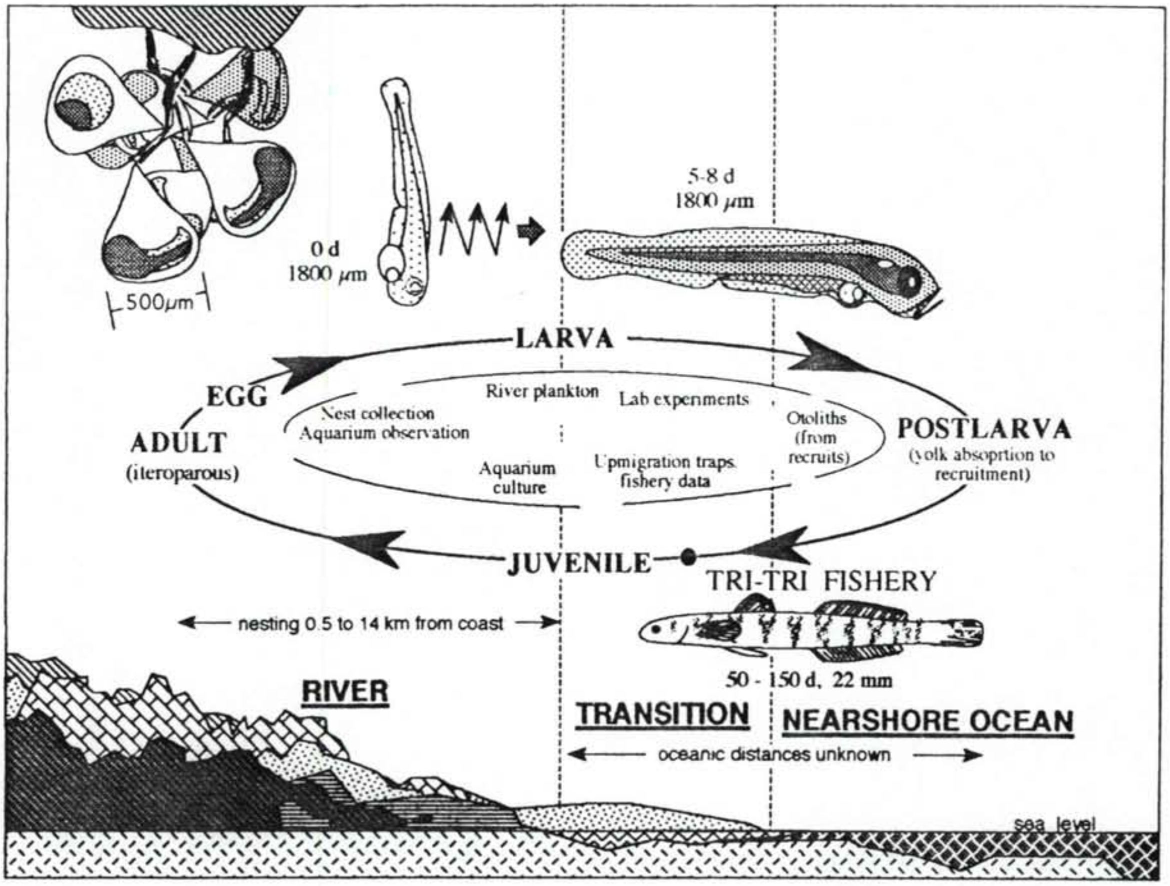


Figure 3.6. *Sicydium punctatum* life history in Dominica, W.I. Adults spawn repeatedly and pan-seasonally, from <40 mm SL. 20mm (SL) postlarvae return after 50-140 d and sustain a traditional fishery.

Chapter 4. A reconsideration of the usage of the terms Diadromous, Anadromous and Catadromous: terminology for aquatic species which migrate between fresh and salt water

ABSTRACT

Terms for migrations of fishes across salinity variations, and difficulties with the term 'amphidromy' are discussed. An alternative classification system is presented, relying largely on existing terms (diadromy, catadromy, anadromy) for which definitions consistent with common usage are accepted. The term 'amphidromy' is not recommended because its initial definition was ambiguous and has therefore generated confusion, and represents neither a process nor a monophyletic group.

Two new categories (obligate, facultative) of anadromy and catadromy are recognised; parallel terms (ontogenetic variability in salinity tolerance) are provided for non-diadromous classes, to facilitate comparisons between groups and thus test the biological significance of the established and new categories.

INTRODUCTION

The life-histories of aquatic species are qualitatively diverse. Categorization of various processes, such as feeding, reproduction, or dispersal, is a part of extending a vocabulary to include the concepts which we perceive to underlie variation.

Whether natural variables are continuous or discontinuous determines whether we describe them with words or numbers. If discontinuous, they may exist in one of two states (binary) or one of a large number of states. Binary classifications are particularly suited to hierarchical structures of terminology.

Myers (Myers 1949b) coined several new terms to describe migration styles in fishes which move between fresh and salt water. One of these terms, amphidromy, has generated more confusion than it eliminated and it is unlikely that all users of the term mean the same thing by it. McDowall (1992) points out “there seems to be some reluctance to use the term amphidromy...some even doubt that it denotes a distinct life-history”. His attempt to harmonize the use of the term is unlikely to succeed because, once established, ambiguity is almost impossible to erase. Furthermore, the philosophical basis of the term "amphidromy" is insufficiently apparent, or even present, to ensure a convergence in future semantics.

History and difficulties

'Anadromy' and 'catadromy' are words with a long history. Figure 4.1 summarises the classifications from the early structure of broadly-defined terms (Fig. 4.1a), and those (Fig. 4.1b) of Myers, McDowall and Gross (Myers 1949a, Myers 1949b, Gross 1987, McDowall 1987, Gross et al. 1988, McDowall 1992). McDowall (1992) documents the usage of the terms anadromy and catadromy as long ago as 1753 where it appeared in that year's edition of Chambers Cyclopaedia. The terms are of such long standing, and in such wide circulation among laymen, fishermen and naturalists as well as scientists, that any attempt to restrict them would be unlikely to succeed, and perhaps for that reason such attempts should be discouraged. In usage, the words anadromous and catadromous imply migration on a systematic basis which involves either a change of salinity (coastal oceanic context) or of altitude (lacustrine/riverine context); the latter use has the potential to become confusing and I urge caution with its use. For anadromy, the eggs are expected at the upper or less saline migratory terminus, and for catadromy the opposite applies; the directions of the migrations and their relationship to life-history stage are also fairly reliably predicted from the an- or cat-adromy. Thus the words concisely convey meaningful information. Because the variation in meaning is generally context-sensitive, the usage is rarely ambiguous -- for example Whitehead (1959) on "the anadromous fishes of Lake Victoria".

George S. Myers (1937), in considering the zoogeography of fishes, recognised that major differences in their dispersal patterns were explained by differences in physiology: the ability to tolerate sea water. In the 1937 paper he asked the question "what are fresh water fishes?" and categorised fish occupying fresh waters as:

PRIMARY DIVISION ('strictly intolerant ... [e.g.] Dipnoi, Polypteridae, Cyprinidae, Characidae, most Siluroids, Centrarchidae, Percidae, etc.') and

SECONDARY DIVISION ('...relatively salt-tolerant, at least for short periods [e.g.] Cichlidae, Synbranchidae, Lepisosteidae, most Cyprinodontidae and Poeciliidae').

He later (Myers 1949a) added other divisions on a more ecological basis:

VICARIOUS ('presumably freshwater representatives of primarily marine groups [e.g.] *Labidesthes*, *Siniperca*, *Lota*, etc.'),

COMPLEMENTARY ('freshwater forms, often or usually diadromous, belonging to primarily marine groups, which become dominant in fresh waters only in the absence of [primary, secondary, and possibly vicarious fishes, e.g.] *Agonostomus*, *Sicydium*, certain New World *Gobiesox*'),

DIADROMOUS ('fishes which regularly migrate between fresh and salt water at a definite stage or stages of the life cycle [e.g.] *Entosphenus*, *Alosa*, *Oncorhynchus*, *Anguilla*, *Sicydium*'), and

SPORADIC ('fishes which live and breed indifferently in salt or fresh water or which enter fresh water only sporadically and not as a part of a true migration [no examples given]').

Most of these are useful terms, but they differ in their fundamental bases, which can be either physiological (*primary*, *secondary*), ecological (*vicarious*, *sporadic*), or both (*complementary*, *diadromous*). Because they differ in these ways, the categories are not mutually exclusive, e.g. sicydiine gobies are not only both complementary and diadromous, but are plausibly also secondary division fresh water fishes. These terms therefore are good adjectives, but bad categories.

Myers attempted to systematise a part of this into a binary system, (1949b) and implicitly recognised the long-standing system of categorisation of fishes as *anadromous* or *catadromous* (depending on whether reproduction of river-ocean migratory fishes occurred in fresh or sea water) and developed this by acknowledging that fishes could be *diadromous* (the global term he proposed to include both modes) or *not diadromous.* The result of this was a useful two-level hierarchical binary classification system. There is virtually no dispute on the utility of these terms, but there has been confusion resulting from the term *amphidromy* which he proposed as a third category of diadromy.

What justified the term *amphidromy*? Myers had read the 1941 M.A. thesis work of Porfirio Manacop, whose excellent work addressed the life history and fisheries of *Sicyopterus extraneus* (later published as Manacop 1953) in the Philippines, assigned to the genus *Sicydium* until that genus was split into *Sicydium* and *Sicyopterus* (see Akihito & Meguro 1979). Manacop's work showed that, instead of being catadromous, *Sicyopterus extraneus* was clearly a river spawner whose larvae and postlarvae spent a growth period in the sea before returning to rivers. *Sicydium* was the genus that Myers selected as the type for the kind of life cycle he wished to define as *amphidromous*; but unfortunately in his definition he failed to recognise the physiological ("*for the purpose*") and ecological ("*or vice versa*") basis of this type (sicydiine) of life cycle, and employed a definition that was too ambiguous to convey specific and useful meaning (italics are mine):

> "*Amphidromous*. Diadromous fishes whose migration from fresh water to the seas, or *vice versa*, is not *for the purpose* of breeding, but occurs regularly at some other stage of the life cycle. ...The prototype is the goby genus *Sicydium*. ...It should be noted that amphidromous migrations are not gametic migrations in the sense of Heape and [this is] one reason for recognizing them as a distinct type" (Myers 1949b).

The phrase "or vice versa" erodes the utility of the term, no less than inserting the same phrase into the generally understood meaning of anadromy could erode its utility. The phrase "for the purpose of breeding" is teleological and difficult to translate into a measurable criterion.

A recent modification (McDowall 1992) of Myers' third class of diadromy has introduced sub-categories of amphidromy which recognise the difficulty with Myers' (1949b) definition. The two new sub-terms proposed are *freshwater amphidromy* and *marine amphidromy*. The definitions amount to:

> *freshwater amphidromy*: egg hatching in fresh water, migration to sea, growth in seawater, return to freshwater, growth in freshwater and reproduction, but less growth in fresh water than *anadromous* fishes show.

> *marine amphidromy*: egg hatching in the sea, migration to fresh water, growth in fresh water, return to sea, growth in sea and reproduction, but less growth in sea than *catadromous* fishes show.

McDowall (1992) considers this a "fundamental" difference from other forms of diadromy. He describes the difference:

"The distinctive feature is that, whereas in anadromy and catadromy the return migration is of mature fishes that *typically* have ceased feeding and are *almost* ready to spawn, in amphidromy the return migration is of juveniles that then feed and carry out *most* of their growth in the water type in which spawning/hatching take place" (italics mine). To require a comparison of the relative amounts of growth in order to determine the classification is an unwieldy mix of continuous variable and categorical descriptor, and will continue to give trouble because of interpretations of the boundaries. For example, although *Sicydium* spp. recruit to fresh waters as a juvenile at 20-30 mm SL, they spawn as small as 37 mm (K. Bell unpub. data) and probably reach this size in about six months after recruitment. McDowall's definition forces us to weigh this continuous variable, and balance it with the words "typically" and "almost", to determine what class it falls into. Surely a salmonid life history is distinctly just that, recognisable despite the variations it exhibits, and a sicydiine life cycle is likewise distinct. Recognising the essence of patterns is necessary before applying terms.

Do binary properties of diadromy exist? Egg deposition in fresh water or the sea would seem so; but some species spawn in brackish water. Whether or not a migration takes place is another familiar dichotomy, but it is variable even within species: in some salmonid species many individuals forgo the oceanic excursion if favourable feeding conditions prevail in freshwater; landlocked salmon, trout, charr are well known. Several salmon (*Oncorhynchus gorbuscha, O. keta)* migrate seaward as fry, while others remain in fresh water for 1,2, or 3 years, or never go to the sea at all. But some life cycles lack such plasticity: newly-hatched larvae of *Sicydium punctatum* are intolerant of both purely fresh waters and purely sea waters for periods longer than a few days, requiring and selecting low to intermediate salinities. Unlike those salmonids which can be anadromous or complete their life cycle in fresh water, *S. punctatum* is obligately anadromous (Fig. 4.2). The same is probably true of american shad, which are not known to exist as landlocked populations; similarly, anguillids are probably obligately catadromous.

How do we map these variations? The most accurate map of a town is the town itself. A map cannot contain all of the information, but distils particular information for which a requirement and use is anticipated. The purpose of the map therefore has to be anticipated, and it may be physiographic, political, climatic, etc. A map is a paraphrase addressing a purpose.

The classification of fish life cycles has played a part in the investigation of life history. Renaissance naturalists distinguished anadromous from other fishes. Myers' interest appears to have been zoogeographic at the outset (Myers 1937, Myers 1949a), but his terminology (Myers

1949b) has conditioned studies (Gross 1987, Gross et al. 1988) directed at the evolution of diadromy and at (McDowall 1987) the geographic/latitudinal incidence of forms of anadromy and catadromy. The validity of such studies depends on the assumption that the definitions of groups considered are objective and not arbitrary. A term such as *amphidromous* can constrain the analysis if it permits truncation of what would otherwise be 'real' groupings. The absence of perceived reality pertaining to the term *amphidromous* may account for McDowall's (1992) observation that "there seems to be some reluctance to use the term *amphidromy*".

The avoidance of constraint of hypotheses raised by future workers requires that the system be as objective as possible, and that investigators carefully evaluate the classification system's appropriateness for their questions. Myers never claimed that states of diadromy were monophyletic, or that they arose through the same mechanisms.

A term for all seasons? The *Schtick* in evolutionary ecology?

Although no single classification satisfies all requirements for description, certain classification properties are desirable, and others not:

1. A good classification should give insight into real processes and properties pertaining to the system (or the question);
2. Categories should be mutually exclusive;

3. Categorical groupings should be used only where there are well-established discontinuities within the variation, and not for continuously variable characters;
4. Classification systems should be hierarchical wherever possible;
5. Levels within the hierarchy should correspond to increasing (going up) and decreasing (going down) degree of difference;
6. Category names should be self explanatory wherever possible (whether in Latin, Greek or any other language);
7. Definitions should not be arbitrary;
8. As the classification evolves, terms which have become confusing should be discarded rather than resuscitated (since the latter leads to excessive use of the phrase "*sensu* Jones, Jones & Jones").

These largely are attributes of the system of biological nomenclature, with the greatest differences being observed at the highest level, and the most minor at the lowest. In devising schemes to classify life-history patterns, it may be impossible to objectively determine which differences should occupy the highest rank in the classification: the relative rankings may change according to the purpose of the classification. On the basis of the criteria above, McDowall's revision and subdivision of *amphidromy* into subgroups fails because it implies that any freshwater-amphidromous fish is more like any marine-amphidromous fish than it is like any occupants of the categories anadromous and catadromous.

Myers' term *diadromy* has stood the test of time and proven useful; *amphidromy* has not and it should now be discarded. Within *diadromy*, I suggest continuation of the broad egg-location-based definitions of anadromy and catadromy, as in (Fig. 4.3).

Since we can at present only speculate on the nature of the forces driving the evolution of anadromy and catadromy we must accept that classifications will be to a greater or lesser extent arbitrary. Arbitrary classifications cannot function as independent variables (e.g. Gross et al.1988) to exclude groups from analyses aimed at evaluating limited hypotheses, especially hypotheses on the evolution of a group constrained by the definition.

Extant organisms, by definition, do things that have kept them from extinction. What they do is indescribably varied and complex. Many of the subtleties which escape our explicit recognition can be implicitly acknowledged as a part of their *schtick*, their routine with all its tricks. A *schtick* denotes a sequence of actions, like a vaudeville act; complex, categorisable only in the broadest sense, honed toward a special result. An evolved complex life-history in which many features are co-evolved is in many ways similarly difficult to categorise. Comedy cannot be classified to the point where it can be predicted by its classification.

Similarly, only a few aspects of species' *schticks* are explainable, and the rules that constrain them only inferred as yet. This is primarily because of the multi-dimensionality generated by many types of variable operating at different levels and strengths. Thus there are many *schticks* in anadromy, many in catadromy; the idea supported by our use of these words for two hundred years is that they describe categories which differ in (this) one of these dimensions, but the variation within each has not been contested. *Amphidromy* as a term has provided a route by which some anadromous and catadromous species could be removed to make a third category, but the reluctance (McDowall, 1992) of the community to use the word is evidence that it does not improve the categorisation.

The most direct and useful revision (Fig. 4.3) would accept the older (broad) definitions of *anadromy* and *catadromy*, omitting the concept of *amphidromy* but including Myers' (1949b) term *diadromy* in an hierarchical dichotomously branching system. The obligate/facultative dichotomy in categories of diadromy can be recognised at the lowest level, and link this classification to some ideas presented by Myers (1949a). The amended system provides dichotomies more readily seen to be mutually-exclusive, in which the subsidiary categories span all variation expected in fishes according to whether and how they migrate across salinity boundaries. The criteria of ontogenetic variability in salinity tolerance is suggested for the euryhaline and stenohaline categories in order to provide a basis of inquiry into relationships of conditions of diadromy. Further possible dichotomies exist which apply equally to anadromy and catadromy, but I urge that these be used descriptively but not diagnostically: they should not be ranked into the hierarchy until they are better understood.

The amended system deals with salinity variations in the life histories of species, and the major categories substantially follow Myers (Myers 1949b) except that the category 'amphidromy' has been subsumed into anadromy and catadromy based on the criteria below:

Stenohaline: species which cannot tolerate (or navigate) a wide range of salinities during their life histories.

- Freshwater
- Marine
- Other (salt lakes, etc.)

Euryhaline: species which may move through differing salinities, whether at all stages or only one, and whether movement is or is not life-history structured.

- Non-diadromous: species without movements across a wide range of salinity, or in which such movements are not life-history structured.
- Diadromous: species which evidence a structured life-history migration through differing salinities.
    - Anadromous: diadromous species whose eggs or reproduction occur at or near the low-salinity terminus of their life-history experience (e.g. *Salmo, Oncorhynchus, Alosa, Sicydium, Sicyopterus*).
        - Obligate (defined below*)
        - Facultative (defined below*)
    - Catadromous: diadromous species whose eggs or reproduction occur at or near the high-salinity terminus of their life-history experience (e.g. *Anguilla*).

Obligate (defined below*)

Facultative (defined below*)

*Obligate (anadromy or catadromy): diadromous fishes whose life-history trajectory of salinity tolerance reveals at some point an intolerance for the conditions in which eggs are produced (e.g. *Sicydium punctatum*).

*Facultative (anadromy or catadromy): diadromous fishes which at all life history stages are able to tolerate the salinity in which the eggs are produced (e.g. many salmonids).

This is one possible plan out of several. It would be possible, for example, to consider eury- and steno-halinity at the lowest level of classification, and then to include under non-diadromous fishes freshwater, marine and other fishes which make no life-history structured movements across wide ranges of salinity.

Myers' other useful migration descriptors

Myers' zoogeographic terms (*primary*, *secondary*, *vicarious*, *complementary*, *sporadic*) apply to the fresh-water occurrence of fish, whether as a complete life cycle or particular stages. They have ecological utility, and can also be combined with the diadromy-system terms.

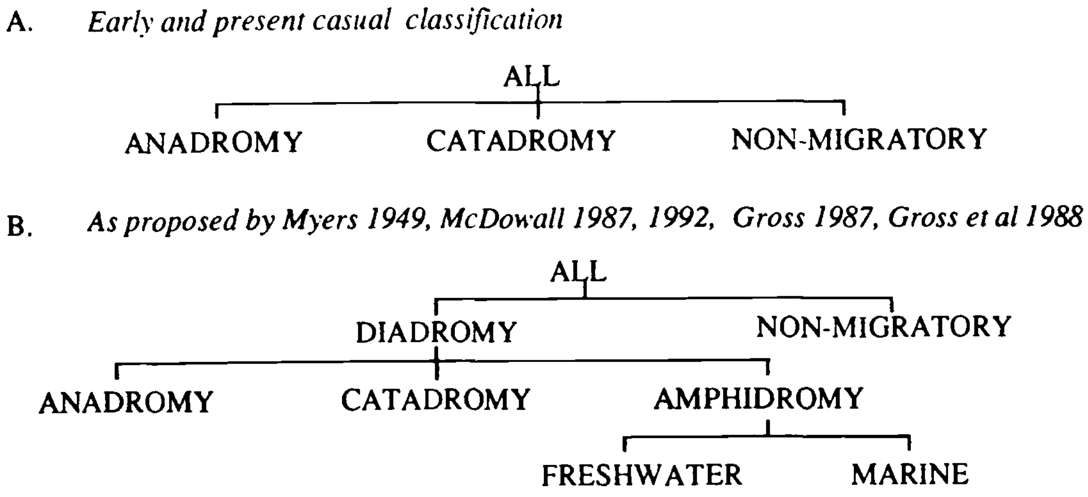
Obligate vs. Facultative Diadromy

The aspect of obligate/facultative diadromy has not previously been explored in terms of the ability of the individual to remain in the same osmotic environment as experienced by the deposited egg or hatched larva. This is surprising, since there exist species which are diadromous and yet do not form landlocked/sealocked populations, e.g. anguillids, American shad, many salmonids, and also crustacea (e.g., some Penaeid shrimps). The principle is that (Fig. 4.2) if some stage of the species is intolerant of the osmotic conditions prevailing at the spawning site, the species has no possibility of becoming non-diadromous. Only in species which retain throughout life their competence in the osmotic conditions at spawning or hatching can migration be dispensed with. Thus, salmonids which are able to complete their lives in fresh water but still do migrate are (under the scheme in Fig. 4.3) facultatively anadromous. Anguillids clearly have a restricted requirement for the egg and larval stages; if later stages become intolerant of the hatching condition and require fresh water they are obligately catadromous - but if not then catadromy in anguillids would be facultative. As described above, *Sicydium punctatum* is obligately anadromous because larvae cease activity after 3-4 d in the hatching environment while they continue up to 8 d in salinities of 5-10 ppt.

There are few reports of investigations into ontogenetic variations in sensitivity or tolerance to salinity. de March (1989) showed that larval *Coregonus nasus* ignored salinity changes, while juveniles did not although survival time of larvae and juveniles was about four days in salinities of 12-15 ppt -- since this is not the hatching environment it is suggestive of obligate anadromy. *Sicydium punctatum* (Fig.

4.2, Chapter 6) larvae are intolerant of both the fresh waters where they naturally occur (on a passive migration) and of sea water (the general direction of the migration); when presented with variation in salinity they actively choose low salinities and live significantly longer when given this choice. *S. punctatum* is therefore obligately anadromous.

Thus, between obligate and facultative diadromies, there is a real difference which is of interest from a life history viewpoint. In this thesis the term "amphidromous" will not be used to describe the life cycle of *Sicydium punctatum*; instead, the will be described as diadromous, anadromous or obligately anadromous.



A. *Early and present casual classification*

B. *As proposed by Myers 1949, McDowall 1987, 1992, Gross 1987, Gross et al 1988*

Figure 4.1. Extant life-history classification Two systems for aquatic species with regard to migration patterns across salinity variations. A: early and present casual classification. B: as revised by Myers 1949, McDowall 1987, 1992, Gross 1987, and Gross et al. 1988 and McDowall 1992.

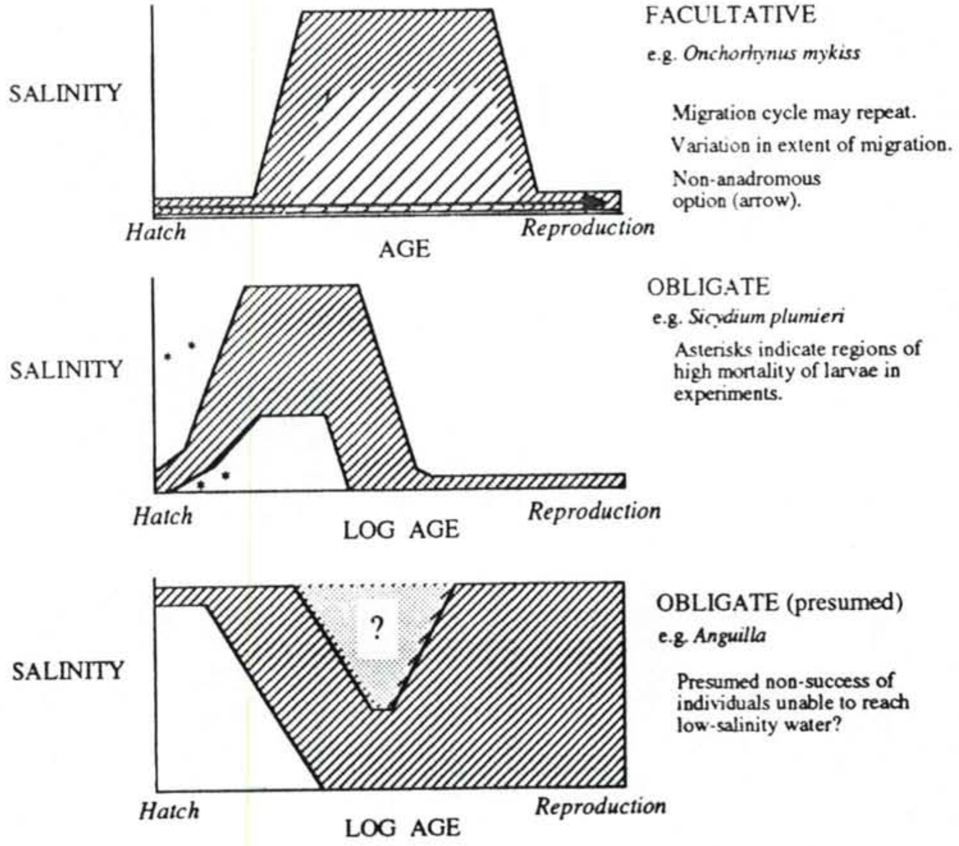
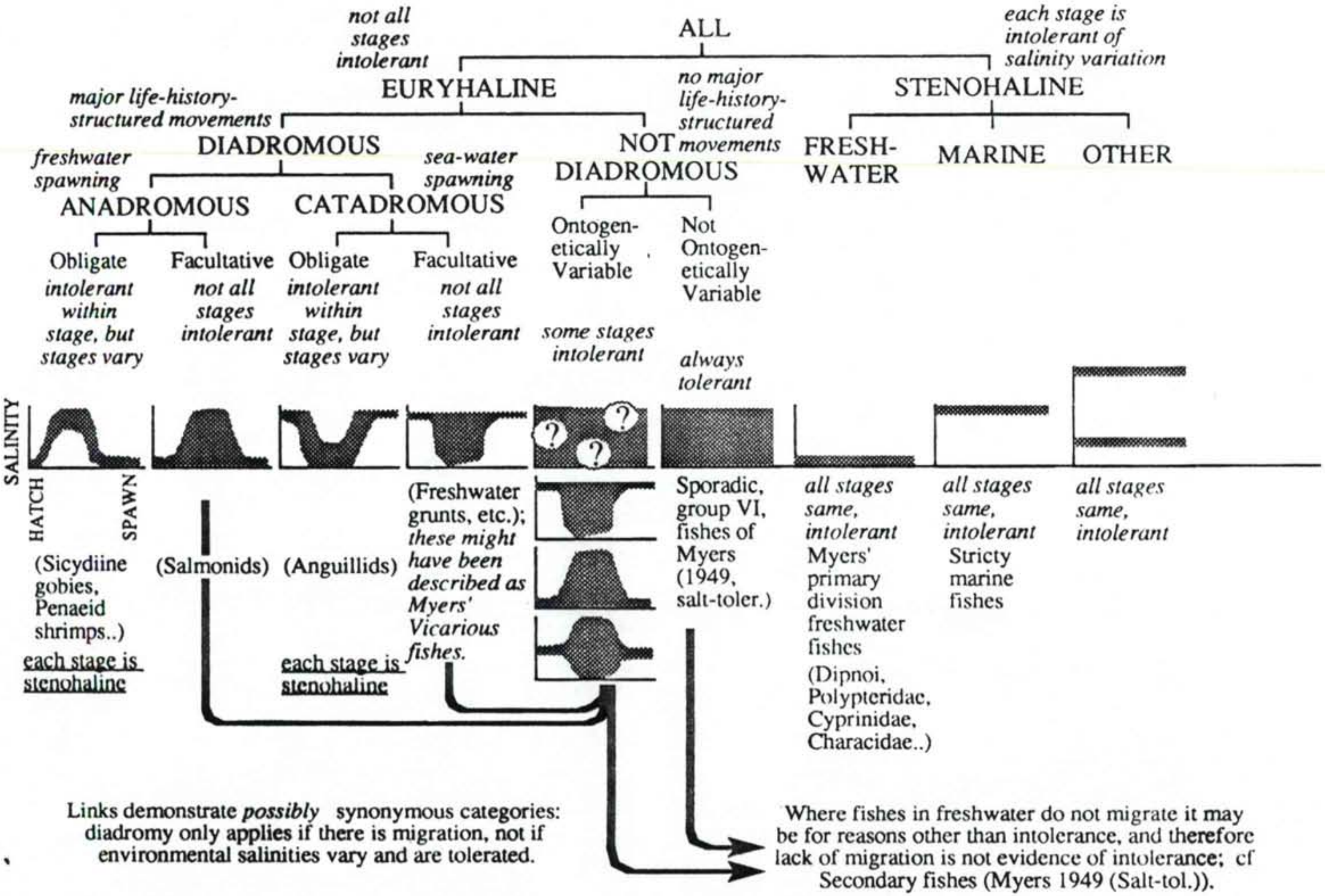


Figure 4.2. Life history salinity tolerance, pattern throughout life history, examples: *Oncorhynchus mykiss* (facultatively diadromous), *Sicydium punctatum* (obligately anadromous), *Anguilla* (presumably obligately catadromous). The existence of a salinity tolerated by all stages is indicative of potential non-diadromy; thus a criterion of facultative diadromy. If the life history of physiological competence requires a salinity different from the hatching environment during ontogeny, then diadromy is obligate.



Links demonstrate *possibly* synonymous categories: diadromy only applies if there is migration, not if environmental salinities vary and are tolerated.

Where fishes in freshwater do not migrate it may be for reasons other than intolerance, and therefore lack of migration is not evidence of intolerance; cf Secondary fishes (Myers 1949 (Salt-tol.)).

Chapter 5. Rheoplanktonic fish larval types in Dominica, W.I., with identification features for larvae of *Sicydium punctatum*

ABSTRACT

The gobiid larvae in the rheoplankton of Dominica, W.I. can be differentiated into five types. Except for one pairing of types, each differs by two or more characters. Species present are: *Sicydium punctatum*, *S. antillarum*, *Awaous taiasica*, *Eleotris pisonis*, *Philypnus dormitor* (=*Gobiomorus dormitor*). The number of larval types thus corresponds numerically to the goby species present. Five types (Fyg, Frb, W, Y, P) are described here. One type (Fyg) is conclusively identified as *S. punctatum* through captive spawning and nest collections.

The ability to separate species at the larval stage enables the study of larvae of the (economically) most important species, *Sicydium punctatum*, alone rather than as a complex of goby species. It also presents the possibility of conducting separate but simultaneous recruitment studies on sympatric populations of these five species.

INTRODUCTION

Larval biology and ecology can yield information important to recruitment studies (Sulkin 1986). Identification of larvae is necessary if larval ecology is to be related to ecology at other stages.

Prior to this study no larvae of Caribbean river-spawning gobies had been retrieved, nor had nests been found. Limited information on aquarium spawnings (Todd 1975, Foster & Fuiman 1987), information on estuarine/shore goby larvae from nearshore plankton tows (Hildebrand & Cable 1938) and from eggs collected in the Philippines (Manacop 1953) indicated that in terms of gross morphology even these widely separated (6 genera, 3 separated regions) larvae might be easily confused.

It was therefore not reasonable to expect the river-planktonic goby larvae of Dominica to be distinguishable, and I initially regarded the evident variation as being continuous and independent variation in a number of characters, and for the early part of the study did not believe larvae could be differentiated to species.

The observation, that larvae from nests found at Springfield showed virtually no variation comparable to that found in any given sample of river-planktonic larvae, prompted investigation of whether the variations seen in river larvae were indeed continuous and independent. The states of different characters turned out to be associated, and enabled the recognition of five types of larvae.

The utility of knowing individual larval types, even though not all can yet be assigned to parent species, is that the types can be treated differently, for example in analyses of temporal or spatial variations in abundance.

This chapter describes larval types, and the characters required to identify them. I assign one type to *Sicydium punctatum* based on captive spawning information. To encourage work toward definitive species-identity for the other types, I provide a tentative type-to-species association based on circumstantial evidence.

MATERIALS AND METHODS

Taxonomy

The names *Sicydium punctatum* and *S. antillarum* are used here (*sensu* Brockmann 1965), who gives photographs and scale counts which are readily matched with these species in Dominica (Chapter 1). Other species present in Dominica are *Awaous taiasica*, *Eleotris pisonis*, and *Philypnus dormitor* (a.k.a. *Gobiomorus dormitor*), which were identified using (Brockmann 1965) and (Jordan & Evermann 1898).

Rheoplankton Samples

Collections of river plankton were made at over 15 locations in Dominica (Fig. 2.2). The sites most important to this study are on the central west coast: Layou River about 1100m from the ocean and slightly lower, 800m, coastal road bridge on the same river; the Check Hall River about 20m from the ocean; and the Canefield River about 300m from the ocean. These sites were selected on the basis of accessibility and proximity to the coastline, to meet the objective of assessing production of larvae.

Sicydium spp. larvae in river plankton were sampled with conical nets made of 80µm Nitex™ mesh; nets were constructed so as to have a high ratio (30:1) of filtering area/mouth area to reduce damage to captured organisms, and were made small in diameter (46 mm mouth diam. in a triple configuration, and 105 to 115 mm mouth diam. in both single or triple configurations) to facilitate use in shallow streams; the triple configurations were made to rotate while sampling so that the mean position did not differ between nets.

Mean volume sampled was about 1.5 m^3, typically obtained in 5 to 8 minutes. Volumes were calculated using calibrated mechanical current meters which estimated the "distance towed" or linear passage of water during the sample. This distance was multiplied by the mouth area of the net for an estimate of volume sampled. Filtering efficiencies were assumed to be unity, which means that the volumes may be overestimated and the larval densities therefore underestimated.

Nets were deployed from shore using a system of pole, floats and weights to maintain sampling depth at 20-25 cm about 2 m from shore. The plankton net was visually monitored during the set and time in water was kept short to reduce occlusion of mesh pores by detritus.

Samples cover all river flow conditions except heavy flood. A single attempt to sample in flood conditions resulted in the loss of a current meter, and was not repeated.

Characters for larval types

The characters found useful for differentiation of larval types were yolk sac shape, yolk colour, yolk sac texture, yolk sac size, presence of abundant brilliant yellow-green pigment in ventral mid-body, and size of larva. These characters yield five types which I operationally term Fyg, Frb, Y, W, and P.

Sicydium larvae are small (1800µm TL) and preserve poorly, and only in live material can the identified (this study) types of goby larvae be differentiated. Therefore, counts were done with live material. Samples were counted after allowing detritus to settle and decanting the clear (upper) portion, which was then concentrated through a sieve of 80µm Nitex™ and transferred to a petri dish for counting and sorting. Goby larvae were virtually all in the decanted clear portion, usually absent in the settled portion. The process was usually repeated and a sub-sample (15 to 50%) of the settled portion was routinely examined for the taxa of interest, with that sub-count being extrapolated to the entire settled volume and added to the count obtained in the decanted portion.

Nest collections and aquarium spawnings which furnished data for these determinations are described in Chapter 3.

RESULTS AND DISCUSSION

The larvae retrieved are all extremely similar in developmental stage and general structure. Differentiation of larval types on the basis of pigmentation, yolk sac shape and size became possible in the second year of the field study.

The types recognised are Fyg, Frb, W, Y, and P (Table 5.1). Types Fyg and Frb both have a bright pigment abundantly scattered throughout the trunk or midbody of the larva, from near the pectorals to a point posterior to the anus about 1/3 of the distance to the caudal fin. While all types can possess traces of yellow-green pigment near nervous tissues and the yolk sac, there is no intermediate level between this and the abundance, especially in the trunk region, in types Fyg and Frb. This pigment shows well against a dark field, but poorly by transmitted light (Fig. 3.4). Oblique illumination against a dark field is essential to detect this feature. In type Fyg this pigment is a yellowish-green, but in Frb it has a reddish-brown colour. The difference may be due either to the nature of the pigment or to the presence of an additional pigment. *S. punctatum* was confirmed by several collected nests and aquarium spawnings to produce type Fyg larvae only. Larvae from all collected nests and spawnings represent several different parental sets, yet virtually no variability in any of the diagnostic characters has been seen. The captive spawnings occurred in aquaria in Dominica and in Newfoundland, and the nests were field-collected in two locations in Dominica. Type Fyg is therefore shown to be *S. punctatum*. No such definitive evidence for species-identity exists as yet for the other types.

The most salient type characteristics are diagrammed in Figure 5.1. The Fyg and Frb type larvae in the rheoplankton are usually at the unpigmented optic lens stage, or later, indicating that hatching usually occurs at that stage. In contrast, the W type larvae frequently occur at the no-eye stage (i.e. not even an outline of the future eye). The Y type larvae also appear from the unpigmented eye stage. The P type is probably too rare for generalisation, but has occurred at stages with lens formed and retinal pigment either absent to early (i.e. only slightly pigmented retina).

Except for the pair Fyg and Frb, each type differs in at least two characters from any other. Arbitrarily modifying any single character in a description results in a type never encountered; therefore the variation is discontinuous among the types W, Y, P, and {Fyg or Frb}.

Types Frb, W, Y, and P cannot be definitively ascribed to particular species. However, the number of species of goby otherwise encountered during the field study was five, numerically matching the number of types found. Because of the discontinuous variation among most types and the numerical match to the number of known species in Dominica, the types convincingly represent species.

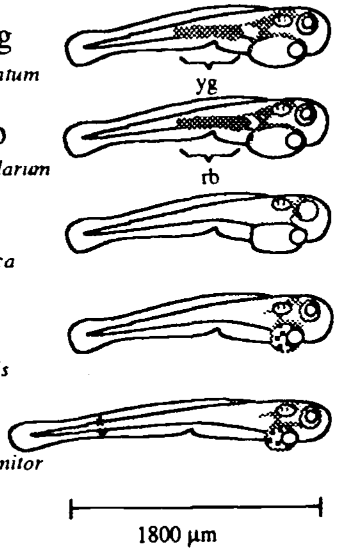
Type Fyg is identified with *Sicydium punctatum* by captive spawning and nest recovery. If type Frb is not another variant produced by *S. punctatum*, then it would most conservatively be *S. antillarum*, assuming that differences (in all features except the red-brown pigment) would be least within a genus. On the basis of pigment and yolk characters, Y and P should be more closely related to each other than either should be to F or W, and since there are two eleotrids (*Eleotris pisonis* and *Philypnus dormitor*), one of which (*P. dormitor*) is exceedingly rare as an adult (3 seen over two years) just as type P is as a larva (ca. 20 seen in two years), tentative assignment of types Y and P to *E. pisonis* and *P. dormitor* would be reasonable. *Awaous taiasica* is a united-pelvic-fin goby as are *Sicydium* spp., and (by similarity of yolk texture and by elimination) it seems best associated with type W. Other matchings are possible, but on the basis of present evidence are less supportable; these matchings (other than Fyg = *S. punctatum*) are of course tentative until tested by captive spawnings or other definitive methods.

Table 5.1. Larval types. Summary of larval features, with confirmed (*Sicydium punctatum*) and tentative (other spp., indicated by '?') identifications. *Sicydium punctatum* larval assignment to species confirmed by captive spawning observations both in Dominica and in Canada. Other species associations are based on various factors discussed in text, and are circumstantial, tentative, and subject to revision.

TYPE	Y-G PGMT. present?	YOLK PROPERTIES shape, colour, texture.	*SPECIES*
Fyg:	*yes*	Oval, pale yellow-green, clear. Most abundant type, usually stage LUP.	*Sicydium punctatum*.
Frb:	*yes+r*	Oval, pale yellow-green, clear. usually stage LUP	*S. antillarum*?
W:	*no*	Elongate/cylindrical, no colour, clear. Usually at stage NE or EE.	*Awaous taiasica*?
Y:	*no*	Round, yellow, crusty. Yolk smaller than in 'F'.	*Eleotris pisonis*?
P:	*no*	Round, yellow/no colour, crusty Longer larvae, 2 large melanin patches halfway from anus to caudal, with post-anal area showing trace of yellowish pigment, easily missed; extremely rare.	*Philypnus dormitor*?

Figure 5.1. Larval types in the rheoplankton of Dominica. Eye stages refer to development of lens and of retinal pigment: ne = no eye (outline of future optic capsule cannot be seen), ee = early eye (trace can be seen), el = early lens (lens outline present but has no or minimal difference in refractive index), lup = lens/unpigmented (lens is refractive, retina is not pigmented), lep = lens/early pigment (lens refractive, pigmentation beginning to appear on retina), lp = lens/pigmented (lens refractive, retina pigmented to the point of opaqueness). These stages are suitable for examination with lighting from below, while sorting plankton. Lighting from above will show similar results but the silver membranous covering of the optic capsule will be more apparent and the later-stage eye will appear as a silver orbit with a black iris - reverse of the last stages shown.

Type Fyg is conclusively identified with *Sicydium punctatum* by captive spawning and nest recovery. Assuming type Frb is not a variant produced by *S. punctatum*, *S. antillarum* is its most plausible match because of the similarity in all features except the red-brown pigment. On the basis of pigment and yolk characters, Y and P should be more closely related to each other than to either Fxx or W, and since there are two eleotrids, one of which (*Philypnus/Gobiomorus dormitor* = Dormé palain) is exceedingly rare as an adult (3 seen in two years) just as type P is as a larva (ca. 6 seen in two years), tentative assignment of types Y and P to Dormé and Dormé palain would be reasonable. *Awaous taiasica* is a united-pelvic-fin goby as are *Sicydium* spp., and (by elimination and similarity of yolk texture) it it seems best associated with type W. Other matchings are possible, but on the basis of present evidence are less supportable; these matchings (other than F/yg = *S. punctatum*) are of course tentative until tested by captive spawnings or other definitive methods.



Type	Subtype	Eye*	Yolk Shape	Yolk Colour	Yolk Texture	Yolk Size
F	F/yg *Sicydium punctatum*	lup	oval	pale yellow	clear	med
		yellow-green trunk pigment				
	F/rb *?Sicydium antillarum*	lup	oval	pale yellow	clear	med
		reddish-brown trunk pigment as well as yg *rb pigment disperses only under higher doses of 2-phenox.*				
W *?Awaous taiasica*		ne/ee	oblong	clear	clear	small
		non-melanic pigments absent or nearly so				
Y *?Eleotric pisonis*		el?	spherical	yellow orange	crusty	large
		non-melanic pigments absent or nearly so				
Ppdbs *?Philypnus dormitor*		el/lup	spherical	yellow orange	crusty	small
		non-melanic pigments absent or nearly so *dorsal and ventral post-pelvic spots*				

Eye stages:

ne ee el lup lep lp .... aimed

*: modal stage in plankton

PART THREE: ECOLOGICAL INFORMATION RELEVANT TO FISHERIES AND CONSERVATION

Chapters 6 to 9

Chapter 6. Active Salinity Choice and Enhanced Swimming Endurance in 0-8 Day-Old Larvae of Diadromous Gobies, including *Sicydium punctatum* (Pisces), in Dominica, W.I.

ABSTRACT

I 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 (0-5 d post-hatch), larvae minimized exposure to salinities >10 ppt, but later (5-8 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.

Implications are: (1) sensitivity of early survival to wind mixing; (2) wind may influence transport of early larvae; (3) exposure to terrigenous pollutants in runoff would be prolonged by larval behavior.

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 & Miller 1976, Leis 1982, Williams et al. 1984, Lobel & 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 & 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 appear to be no reports 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. 3.5) in Dominica, W.I. involves both freshwater (adults, eggs, larvae) and oceanic (larvae, postlarvae) habitats (K.Bell, unpub. data). Adults live in rivers from the coastal zone to altitudes over 300m 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 (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 6,950 larvae, from Sept. 23, 1989 to May 10, 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 metamorphose 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 (*Sicydium 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 $\text{tonne}\cdot\text{yr}^{-1}$ in northern Luzon, the Philippines (from data in Manacop 1953). Such fisheries occur widely in the Indo-Pacific (Atwood 1791, Jordan & 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 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 6.1 and Figure 6.1. Nests were found on 4 occasions (3 listed in Table 6.1, 1 other on August 19, 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 (Chapter 3). 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 5 nests found 1989-

1991 in this study), which prior to this 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 (Chapter 7).

Species identification

Adults: Taxonomy is incompletely resolved in this group and is discussed in Chapter 1. *Sicydium punctatum* and other *Sicydium* spp. have been treated by some authors (Hildebrand 1935, Aiken 1985, Erdman 1986, Aiken 1988) as synonymous with *Sicydium plumieri*; but I followed the taxonomic conclusions of Brockmann (1965), whose diagnoses and figures of *Sicydium antillarum* and *S. punctatum* correspond well with adult specimens I collected in Dominica. *Awaous taiasica*, *Eleotris pisonis* and *Philypnus dormitor* were identified according to various sources including Brockmann (1965), and Jordan and Evermann (1898).

Larvae: Previous to this study, no rheoplanktonic goby larvae had been retrieved from the field in Caribbean or Atlantic watersheds. During this study subtle differences were found which permitted separation of larvae in the plankton into 5 larval types (Chapter 5), matching in number the species known as adults from Dominica: *S. punctatum*, *S. antillarum*, *Awaous taiasica*, *Eleotris pisonis* and *Philypnus dormitor* (K. Bell unpub. data). Using descriptions of larvae from laboratory-spawned (known-parent) nests, I was ultimately able to assign one of these types to *S. punctatum*. This permitted me to determine after the fact that *S. punctatum* had been used in experiments 1 and 2; the nest collected for experiment 3 was from the same site (Springfield), where only *S. punctatum* was seen, but is noted (Table 6.1) 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 *Sicydium antillarum*. Experiments 4 and 5, using larvae obtained from river plankton, represented an assortment of up to 5 larval types. *S. punctatum* generally predominates among goby larvae in plankton samples (from Nov. 10, 1990 to May 10, 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 6.1.

Experiments were set up indoors in cylindrical glass jars (0.6 l, expt. 1 and sea treatment for expt. 3) or (all others) rectangular silicone-jointed glass tanks 25 to 40 cm in depth and 10 cm x 10 cm in horizontal dimensions. Each experiment included up to four types of treatments: freshwater (F), seawater (S), 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 6.1).

F, S and H1 treatments were stocked with newly-hatched larvae (about 6h 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 fresh water. This method does not produce identical haloclines each time, so I 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 23-27° C, approximating river temperatures (annual range observed: 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). 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. My 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 (3-4 drops) required for salinity determination with a refractometer, this avoided disruption of the halocline. The refractometer was frequently (every 2-5 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:

$$\mathrm{MPPT} = \sum^{i} n_i ppt_i / \sum^{i} n_i \qquad \text{(eqn. 1).}$$

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 35mm or video-photography. My 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. I 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), I recorded actual numbers and later converted these to proportions. In the 0.6 l jars I noted modal, minimum (~5th percentile) and maximum (~95th percentile) depths.

I 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. I 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 fresh water (-0.0035) from all values. Conversion to approximate salinity in parts per thousand (ppt) was then calculated as:

Salinity =1000*((corrected spec. grav.)-1). (eqn. 2)

RESULTS

Qualitative description of behavior in fresh water

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 sec, 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 6.1), I obtained replication for the purposes of analysis (Steel & Torrie 1980) of variations in time to exhaustion. I used ANCOVA to test for effects of the factors: larval source (2 levels: nest, plankton) and treatment type (4 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 6.1) is shortest in freshwater (2-4 d), about one day longer in seawater, nearly three days longer in a primary halocline (H1 = occupied from hours after hatch), and four days longer for a total of >8 d in a secondary halocline (H2 = occupied after initial 3-4 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. 6.2) 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.

FRESHWATER (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 (yolk-sacs ~280 µm diam. in newly-hatched larvae; ~200 µm in 2.9d larvae; ~140 µm diam. in ~4d 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.

SEAWATER (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 about 100 h, larvae distributed themselves at all depths, and at about 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 (approx. 5 ppt) failed to resume activity.

PRIMARY HALOCLINE (H1) TREATMENTS: larvae showed modal abundances at intermediate salinities (5-15 ppt), which in expt. 2 (Fig. 6.2) existed in the upper 10 cm (about 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 fresh water or sea water. Larvae at the end of halocline treatments had forward-directed, well-developed eyes, lower sinking rates (no swim bladder, but 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. sagittal plane vertical). Yolk sacs were completely or nearly exhausted, a small oil droplet sometimes remaining. I consider larvae to have been capable of feeding during the last 2-3 d of the halocline treatments.

The progression of active larvae into higher salinities over time was consistent among halocline treatments from different experiments (Fig. 6.3). Second-order polynomial regressions for these four curves are all highly significant

($p \leq .0001$) and explain from 67% to 89% of the variation in larval distribution over time within each treatment (Table 6.2). Note that treatments having no variation in salinity over depth cannot be expressed on the same graph.

SECONDARY HALOCLINE (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 haloclines, 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. 6.2 and 6.3).

Swimming activity in larvae in H2 treatments persisted until 8 d post-hatch (Table 6.1). This was 31 h (experiment 3) to 35 h (experiment 1) longer than seen in the first halocline (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. 6.3). 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 fresh water 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, I therefore also tried transferring inactive seawater larvae to low salinity (5-10 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 larvae suspended in river flow. The superior swimming endurance of larvae in primary and secondary halocline treatments (H1, H2) 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* (1956), *Dormitator latifrons* (1975), and *Evorthodus lyricus* (Foster & 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 6.1). This suggests that 0 ppt and >30 ppt are salinity extremes outside the range required for 0-5 day-old larvae. The preference shown by larvae in haloclines (Figs. 6.2, 6.3) 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 sea water (34 ppt) lived 8 d, while larvae in fresh water 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% sea water lived >30 d while those in fresh water lived <7 d (Katsura & 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 my results for larvae in fresh water. 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. I 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 mean salinity exposure (MPPT) observed in haloclines (Fig. 6.3) was accompanied in my 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 freshwater (F) to the secondary halocline treatments (H2). This suggests that some period spent in fresh water 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 treatments (F) 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. I 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 layered water masses for which these treatments are analogues. Because of density differences, fresh water 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 5-12 ppt should therefore swim upward if experiencing high salinities, and permit themselves to drift downward if experiencing lower salinities. This is consistent with my results. In fresh water, 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 fresh water into more saline water, activity could be resumed. Larvae in haloclines demonstrate preference for intermediate salinities. Larvae in sea water 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 *S. punctatum* larvae was clearly not determined by relative density. Since previous work (de March 1989, Frank & 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 5-8 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 land-mass 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 $m \cdot yr^{-1}$ (Towle 1991), and creates a wind-shelter on the leeward coasts.

Because of disruption by the constant wind, the east (windward) coast is where I would least expect to find low-salinity systems. However, on Nov. 21, 1989, in typical conditions on the eastern coast (breaking 1-m waves and a steady wind), I 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. 6.1). These salinity measurements reflect a substantial mass of low-salinity water corresponding to the range selected by larvae in my 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 I would expect more extensive low-salinity areas. On numerous occasions, on both coasts, I 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 0-8 day 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 & 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 (Chapter 1, 8). Recruitment of the similar fish, *Sicyopterus* sp., in Réunion shows substantial seasonal and inter-annual variation (Aboussouan 1969). The results presented here suggest that future work on the nearshore oceanography may lead to a better accounting of recruitment variation. I recommend such work and encourage managers to collect the collaterally important sicydiine fishery data.

Table 6.1. Summary of results of halocline experiments. Larvae in expt. 1 and 2 are confirmed as *Sicydium punctatum* by diagnostic features, larvae in expt. 3 are tentatively identified as *S. punctatum* (see text). Expts. 4 and 5 use larvae from river plankton and may include up to 5 goby species although *S. punctatum* is most abundant. Time until exhaustion (cessation of swimming) determined from the time of the last observation of activity. Seawater treatments were 30 to 35 ppt (mixed, stratification where indicated is spontaneous). Seawater and Halocline 1 treatments stocked with larvae hatched ≤10h since hatch or capture. Halocline 2 larvae spent first ~2 d in fresh water. Each halocline offered salinity ranges, as indicated. Expt. 4 had two H1 treatments, for which data are separated by commas. "n.a." = not applicable.

Experiment:	**1**	**2**	**3**	**4**	**5**
Container volume:	0.6 l	3-4 l	0.6(sea), 3-4 l	3-4 l	3-4 l
Water depth (cm)	6	30-40	6(sea),30-40	30-40	30-40
Start/collection date	31 Oct '89	21 Aug '90	16 Jul '90	04 Apr '90	01 Jul '90
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 NUMBERS OF LARVAE				
Freshwater	~250	~2-3000	~2000	110	48
Sea	~250	~350	~300	n.a.	49
Halocline 1	~250	~350	~2000	112, 58	48
Halocline 2	~50	~300	n.a.	n.a.	n.a.
	SALINITIES (ppt)				
Freshwater	0	0	0	0	0
Sea	~32	32-34	~33	n.a.	35
Halocline 1	0-28	0-16	1-26	0-35,0-35	1-35
Halocline 2	1.5-32	1.5-33	n.a.	n.a.	n.a.
RESULTS:	SWIMMING ENDURANCE (DAYS, since hatch or capture):				
Freshwater	4.09	3.9	2.22	3.8	3.60
Sea	5.11	4.85	3.811	n.a.	4.62
Halocline 1	6.7	7.0	4.973	6.32, 6.32	5.10
Halocline 2	8.19	8.29	n.a.	n.a.	n.a.

Table 6.2. Depth/time regressions for *Sicydium punctatum* and goby larvae from river plankton (≤5 spp.). Regressions for curves in Fig. 6.3, mean population salinity exposure in halocline treatments. Regressions are MPPT = $\beta_0 + \beta_1 T + \beta_2 T^2$, where T = time (days). Response of mean salinity (MPPT) to time (d) since capture or hatching for 4 halocline treatments. H1a and H1b have sharp, and gradual (respectively) haloclines. H1 (Expt. 2) had a maximum salinity of ~16 ppt.

	MPPT=					
TRMT	β_0	$\beta_1 T$	$\beta_2 T^2$	AdjR^2	p	N
(Expt. 4, ≤5 spp., larvae from river plankton)						
H1aJ2	14.35	-6.43T	+1.24T^2	.8	.0001	16
H1bJ3	7.82	-1.04T	+0.49T^2	.86	.0001	16
(Expt. 2, *S. punctatum* larvae hatched *in captivo*)						
H1	5.34	-0.54T	+0.27T^2	.67	.0001	22
H2	27.74	-11.62T	+1.38T^2	.89	.0001	16

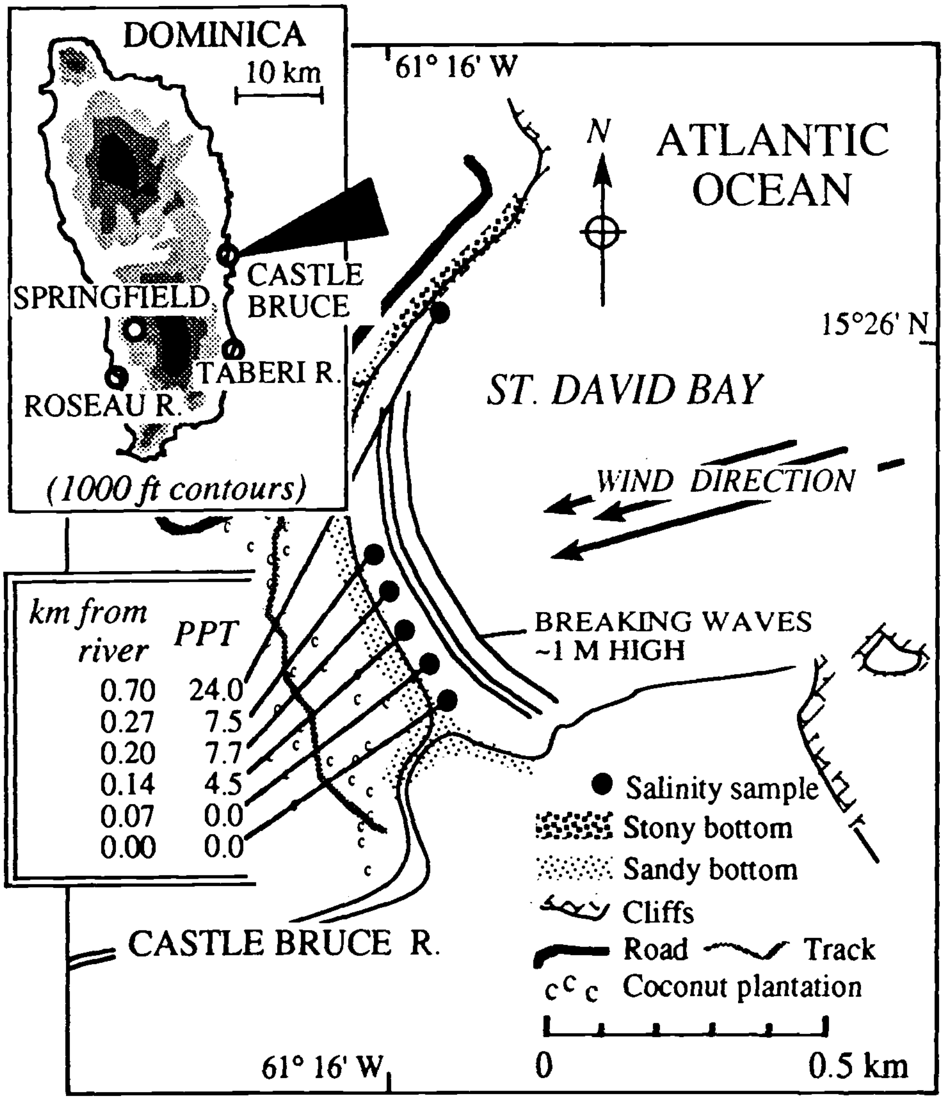
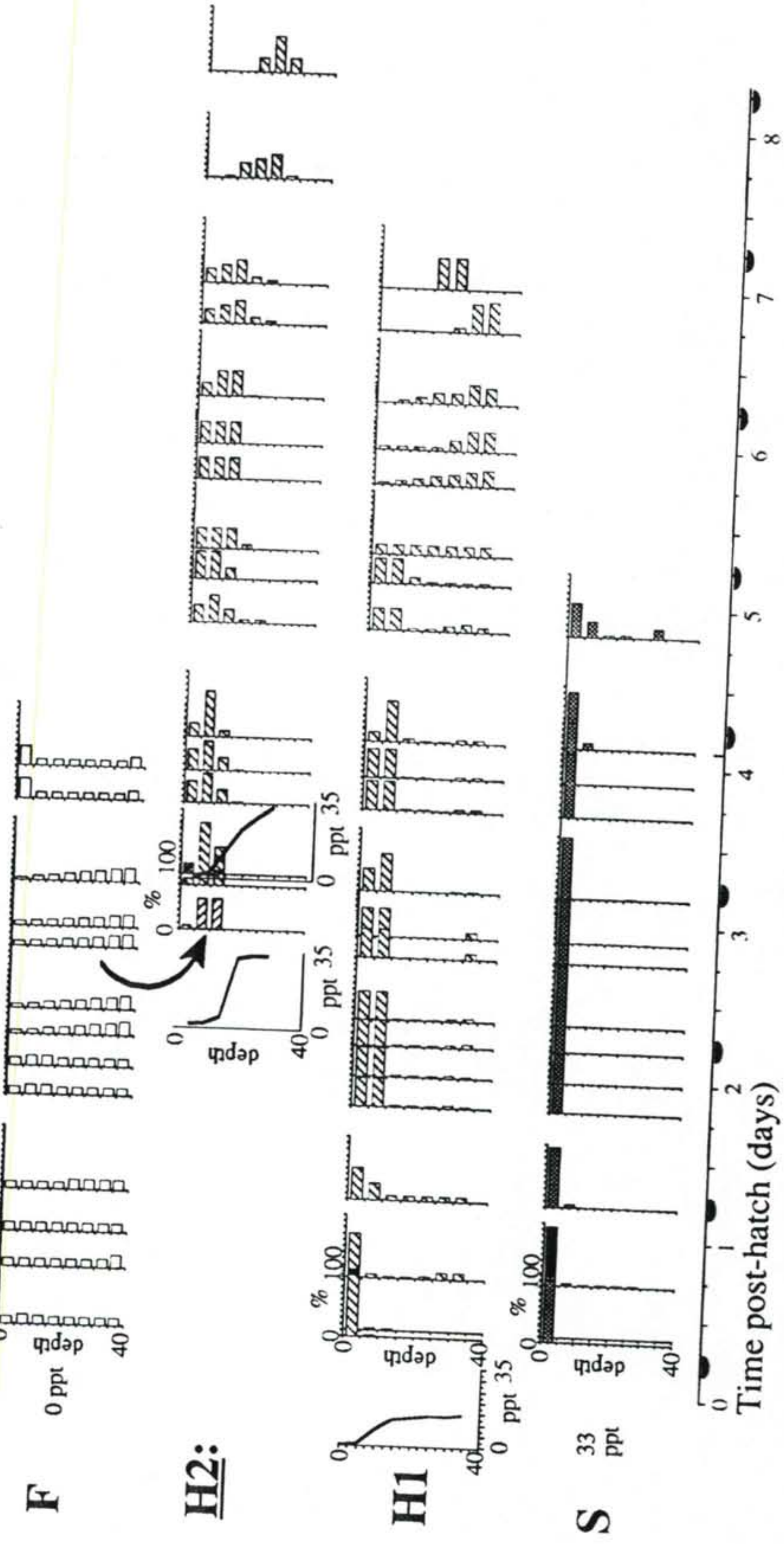


Figure 6.1. Collection locations and salinity observations at Castle Bruce beach in Dominica, W.I. on 17 Nov. 1989, approx. 1300-1330h. Inset map: collection locations in Dominica mentioned in text. Data inset: distance (km) northward from river mouth, and salinity (ppt). Conditions: fair breeze from ENE (landward), producing breaking waves >1m trough to crest near the beach.

Figure 6.2. *Sicydium punctatum*: Depth distributions over time (experiment 2, using newly-hatched larvae) in treatments Freshwater (F), Seawater (S), 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 (0-40 cm). Time (d) since hatch shown on the long horizontal axis below; filled semicircles indicate midnight of calendar day. Last panel in each series is the last observation in which active larvae were seen. Salinity curves are superimposed with left axis placed to indicate measurement time.


F
0 ppt
H2:
H1
S
33 ppt
depth
%
0
100
40
0
ppt 35
Time post-hatch (days)
0
1
2
3
4
5
6
7
8

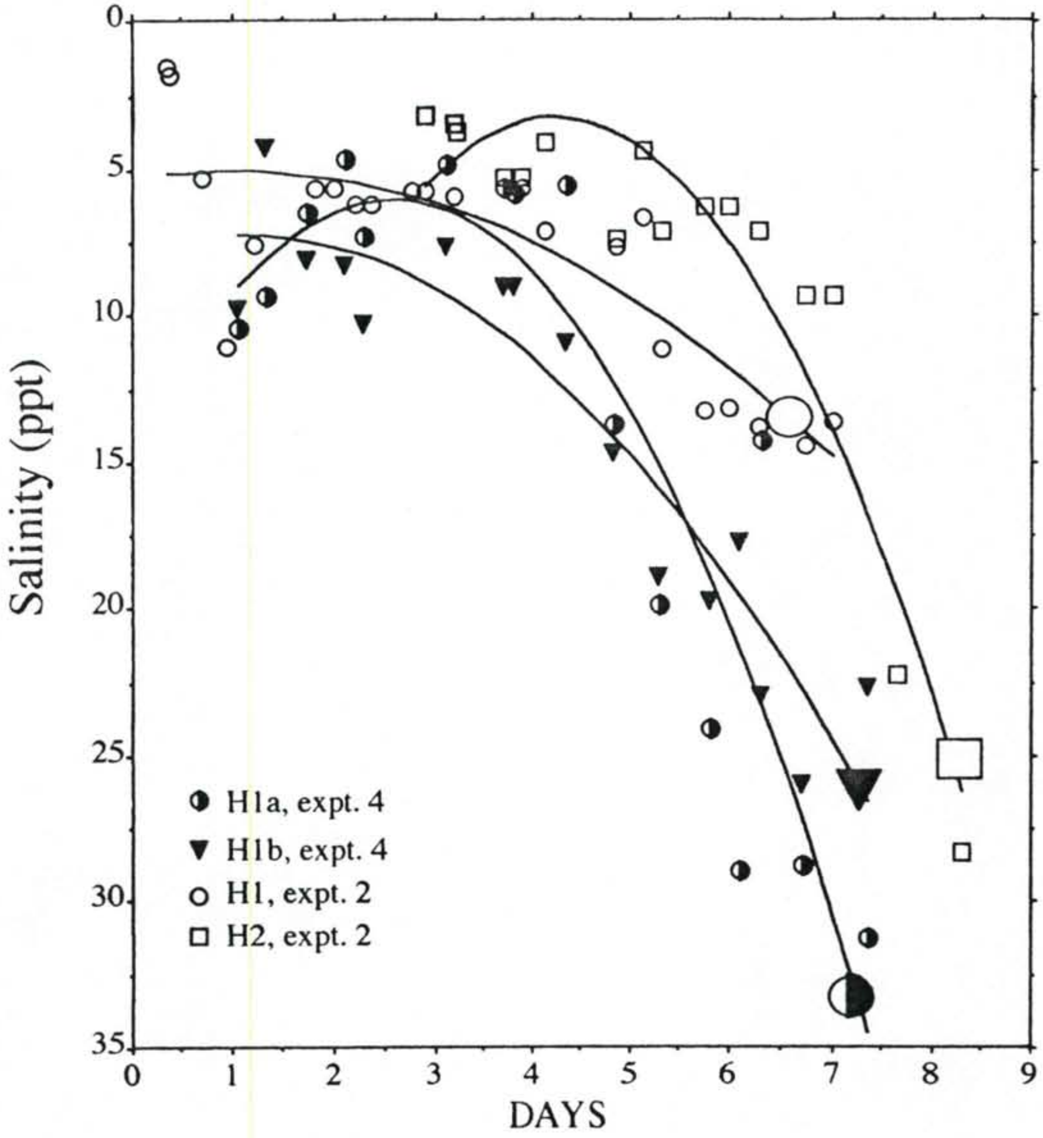


Figure 6.3. *Sicydium* spp. larvae Mean salinity exposure in each of four halocline (three H1 and one H2) treatments over time. Note inverted y axis scale. Lowercase a or b distinguish similar treatments in same experiment. Ages are days since either hatch (expt. 2) or capture (expt. 4). Large symbols identify curves. Maximum salinity available in H1 of expt. 3 was approximately 16 ppt. Adjusted r^2 range 0.67 to 0.89; $p \leq 0.0001$ for all.

Chapter 7. Using Stream-Drift Data to Estimate Mortality Rates: *In Situ* Mortality of Recently Hatched Larvae of Diadromous Gobies at Layou River, Dominica, W.I.

ABSTRACT

Stream-drift data properly collected can be suitable for estimation of mortality or production rates for many taxa. Suitability and assumptions of the method can be determined from knowledge of organismal behaviour. *Sicydium punctatum* and other rheoplanktonic organisms in Dominica, W.I. were sampled to assess mortality and test the method. Results show high mortalities of recently hatched *S. punctatum* larvae. These mortality rates are consistent with rates attributed to conspecific predation in aquaria. Indicated population half-lives are less than one hour. This suggests that the most important segment of the population for conservation is that nearest the coast, and that larvae originating far upriver suffer mortality that may increase exponentially with the distance upstream. In this chapter the utility of the paired-sample method for estimation of mortality in stream drift populations is demonstrated, assumptions are systematised, and the method's utility for various taxa is discussed in the context of these results.

INTRODUCTION

Mortality rates of larval fishes tend to be high relative to later stages and thus may contribute to variations in year-class strength (Victor 1986c, Pepin 1989, Pepin 1991, Pepin & Myers 1991). Mortality rates in field studies are usually based on sequential estimates of abundance. For use in mortality estimation, samples must be assumed to belong to the same population but this is subject to errors arising from variations in spatial distribution of fish and mixing of differing age-groups. Further uncertainty exists where elapsed time is estimated from age or stage groups, because of differing growth rates contributing to errors in age determination and the rounding errors associated with placement of continuous variables (time) into categories (stages).

There is a need for highly tractable natural systems, to supplement and bridge existing lab and field mortality determinations. An ideal unexploited opportunity exists in the case of some categories of stream-drifting biota. This study introduces this opportunity, a suitable method, its assumptions, and data on 11 taxa as a demonstration of the method. The direct findings in the case of one species (*Sicydium punctatum* larvae) are considered in light of mortality data acquired in a laboratory setting, and implications for *S. punctatum* ecology are discussed.

Riverine populations of many planktonic larval fish and other taxa are spatially confined and, because of unidirectional flow can be assumed to be spatially ordered by residence time; they therefore offer unique opportunities for studies on mortality using two-site sampling. The conditions in which spatial ordering corresponds to residence time are: (1) larvae move in one direction only; (2) contributions of new larvae are assumed not to occur between the two sites; (3) contributions of water masses with differing larval abundances are assumed not to occur. These assumptions usually can be confirmed or rejected by existing knowledge and a simple visual assessment of the system.

Despite the utility of this approach, it appears not to have been used in stream drift (organisms suspended in flowing water) studies. In 23 stream-drift papers (Suter & Williams 1977, Allan 1978, Stoneburner 1978, Peckarsky 1980, Zale & Neves 1982, Haney et al. 1983, Kohler 1983, Krueger & Cook 1984a, Krueger & Cook 1984b, Allan & Russek 1985, Bruce 1985, Kohler 1985, Larkin & McKone 1985, Malmqvist & Sjoestroem 1987, Petranka et al. 1987, Neves & Widlak 1988, Layzer et al. 1989, Martin & Knight 1989, Wilzbach 1990, Boothroyd & Dickie 1991, LeRoy et al. 1991, Weaver et al. 1991, Werner & Hilgert 1992) none dealt with paired-sample mortality estimation. This may be because, of the taxa studied, many or most are only temporarily in the stream drift; since settlement for such taxa cannot be equated with mortality, mortality estimation is difficult. However, in cases where disappearance from the stream drift is plausibly associated with mortality, for example Layzer et al. (1989) who include threadfin shad in the drift fauna, it may be possible to estimate mortality rates realistically.

Assessment of mortality from stream drift data

Whether or not mortality can be estimated from stream drift depends first on whether mortality, or other factors, dominates in the disappearance of organisms from the drift, and whether the contribution of the other factors is measurable. The factors to be considered depend on the life history and behaviour of the organisms. Figure 7.1 shows the origins and fates of organisms in the stream drift. A very general model could state that the rheoplankton or drift exiting (RHP_{final}) a given segment of river is composed of numbers arriving (RHP_{init}) from upstream, plus numbers emerging (E_s) or hatching (E_h) from local substrate, minus deaths in the plankton (D_p), minus settlement (SET), plus local re-emergence (E_r) of temporarily settled organisms, minus deaths on the bottom (D_b) of temporarily settled organisms, minus emergence from river due to metamorphosis (AT). (We are concerned here with aquatic fauna, not atmospheric or terrigenous accidental inputs, which we assume are recognisable as such.) We have, therefore:

$$RHP_{final} = RHP_{init} + E_s + E_h - D_p - SET + E_r - D_b - AT, \qquad \text{(eq. 1)}$$

which we can simplify for any particular taxon by removing terms presumed to be near zero.

For stages of insect larvae which settle and occasionally erupt from the bottom until re-settling, most of these terms apply, which makes it difficult to solve for the mortality terms; I identify such taxa as GROUP A. However, some species' occupation of the benthic and planktonic realms is more structured (and therefore more predictable), such as for threadfin shad (Layzer et al. 1989) or diadromous gobies (Bell et al. 1994 MS, Chapters 3,6,8), and some terms can be treated as zeros. As a result there remains a more manageable number of terms, and mortality estimation is possible in many situations; I identify such taxa as GROUP B. For example, diadromous gobies such as *Sicydium punctatum* nest in rivers, and hatchlings immediately become planktonic and remain so for up to several days during their drift toward the sea (where they spend approximately two months before re-entering rivers as postlarvae and settling as juveniles). Thus, using newly-hatched *S. punctatum* as an example, many terms can be taken as zeros, so that:

$$RHP_{final} - RHP_{init} = E_h - D_p. \qquad \text{(eq. 2)}$$

Since *S. punctatum* requires stone and gravel bottoms for nesting, silted areas can be assumed to have no nesting, and hence no hatching, thus allowing us to eliminate one more term, leaving:

$D_p = -(RHP_{final} - RHP_{init})$. (eq. 3)

The reverse would also hold, i.e. if we could assume zero mortality, we would be able to estimate hatching inputs.

$E_h = RHP_{final} - RHP_{init}$. (eq. 4)

Since (E_h - D_p) is *net change*, a *negative net change* is a conservative estimate of D_p, while a *positive net change* is a conservative estimate of E_h. Violating assumptions (wrongly assuming "no-deaths" or "no-hatches") would bias solutions for either D_p or E_h toward zero (i.e. $D_p < D_p + E_h$, and $E_h > E_h - D_p$). The method is therefore conservative, whether the quantity estimated is hatching or mortality.

While hatching can only be thought of as an input independent of the abundance of larvae in the plankton, D_p is better represented as a per-capita mortality rate (M, such that $0 \leq M \leq 1.0$), so that (3) can be rewritten, if

$D_p = M(RHP_{init})$, as (eq. 5)

$RHP_{final} = RHP_{init} - M(RHP_{init})$, and (eq. 6)

$RHP_{final}/RHP_{init} = 1 - M = S$, (eq. 7)

where S is survival, $0 \leq S \leq 1.0$, and $M + S = 1.0$ by definition. In this chapter, M, S (etc.) most often have subscript $_h$ indicating that they are one-hour rates.

Note that although negative mortalities or $S>1.0$ *indicate* production (increase), production will often (because larvae are non-reproductive) be more reasonably expressed as absolute numbers. Since ratios and absolute numbers do not share common units they cannot be grouped together on a single axis, in a single average, or in a single confidence interval. An essential feature of field sampling is that error is constantly present, and generally the smaller the number the more susceptible it is to error. Thus, where negative mortalities are plausibly attributable to sampling error, they should be included in confidence interval (etc.) calculation. Likewise, where production dominates, small negative values ($RHP_{downstream}<RHP_{upstream}$) may occur due either to mortality exceeding production, or to sampling error; all cases should be included to avoid biasing the calculations by removing only low values. Where a set of data includes high production values intermixed with low survival values, it may be unreasonable to assume that the range of values results from large errors, and the set may be separated into two groups: production (to be estimated as absolute numbers), and survival (to be estimated as ratios). This situation may often arise where temporal variability in production or predation is large.

The class of organisms for which the use of equations 2 - 7 are valid is identified in Fig. 7.1 as group B. Group A are the comparatively intractable taxa on account of their unstructured settling/erupting behaviour, or because of the potential to metamorphose and leave the river as (e.g.)

winged adults which have near-zero probability of showing up in the downstream plankton samples.

To apply these equations paired samples are required, one upstream and one downstream. Ideally, the downstream sample should be taken later such that the time delay = distance/flow rate to maximise the likelihood of encountering the same drifting population sampled upstream. Failure to observe this condition would result in high variances if either (1) the populations are in patches drifting downstream, or (2) if mortality is *temporally* structured such that different groups of similar density experience differing mortality. If distances (between upstream and downstream sample sites) are short, the ideal time lags will be also, and as these become small the temporal variability in drift density will have a smaller role. Therefore, failure to sample with exact lags is unlikely to generate consistent, but erroneous, results. Consistent results cannot be attributed to timing errors.

The effect of time (on processes like mortality) is exponential. We can recognise that by rewriting 7 as

$$RHP_{final} = RHP_{init} * S^{WMT} , \qquad \text{(eq. 8)}$$

where the exponent WMT (Water-Mass-Transit time), is the time, in the same units as the subscript of S, required for the water mass to move from the upstream to the downstream site (*NOT* always equal to the time between samplings). Survival can be calculated for a single time unit as

$$S = (RHP_{final}/RHP_{init})^{1/WMT} . \qquad \text{(eq. 9)}$$

The water-mass transit time (WMT) can be estimated using measured velocity ($m \cdot min^{-1}$) and distance (m) along the river's path. Changes in river cross-sectional area affect WMT, so that in complex river topology WMT is best directly measured by timing transit of drogues, passive particles, etc, or by multiple velocity measurements along the river reach. In river stretches with fairly uniform cross-section, single-point measurements of current speed may be sufficient.

Logistics of plankton sampling dictate that the volume filtered is rarely the same for all samples. It therefore is more convenient to deal with plankton concentrations, which take into account the varying volumes filtered. Equations 1-9 apply as well to concentrations as they do to counts, so that (8) can be rewritten as

$$C_d = C_u * S^{WMT} \qquad \text{(eq. 10)}$$

where C_d and C_u are, respectively, the downstream and upstream concentrations (as numbers$\cdot m^{-3}$ of water).

The mortality rates developed here can provide a basis for the considerations of the constraints influencing the choices of residence and nest sites by *S. punctatum* and similar species, and illustrate at least one mechanism by which land-use alteration can reduce the recruitment of *S. punctatum* to the fishery.

MATERIALS AND METHODS

Field data

I chose for the *in situ* work a section of the Layou river where adult *Sicydium punctatum* were virtually absent, so that "$E_h = 0$" would be a reasonable assumption. Note that violations of this assumption result in reduced (i.e. conservative, closer to no change), not elevated, estimates of mortality. The assumption is reasonable for some, but not all, of the remaining taxa counted: the other gobiid and eleotrid species inhabiting the reach between stations may produce new larvae, and production of invertebrate larvae is also a likelihood.

Larval abundances were assessed at an upstream (Hillsborough bridge) and a downstream (river mouth) site, which are approximately 0.8 km apart, on the Layou river on the west coast of Dominica, W.I. (Fig. 7.2) This pair of sites was chosen because I never detected *Sicydium punctatum* adults in the intervening reach, so the estimates would be less affected by hatching between sample sites at this location than they would at other locations where nesting is more or less continuous and hatching cannot be assessed directly. Any hatching that occurs within the river stretch will decrease the estimate of mortality (increase survival), so the mortality estimates are therefore conservative in this respect.

Water mass transit time (WMT) was estimated using the current speed and the distance between the two sample points. The current speed was estimated from a current meter reading and time elapsed. The current speed thus determined at the upper station (Hillsborough bridge) was used to represent average current speed between the two stations, because the cross section of Layou River is fairly uniform for most of the length of this reach (Hillsborough bridge to river mouth). Readings were independently taken with each sample by a current meter attached to the net, so assessments of volume sampled were not affected by local variations in flow.

Plankton samples were taken using a small conical plankton net deployed using a system of floats and weights to maintain sampling depth at 20-25 cm below the surface (Fig. 7.3). The net used was the same for all mortality sampling, and was approximately 10.7 cm mouth diameter, 101 cm long (filtering portion) and used Nitex™ 71 µm (opening size) mesh, and the ratio of filtering area to mouth area was high, approximately 34:1; the fine mesh and high filtering ratio were chosen to minimise damage to captured specimens. Seams were all sealed with thermoplastic glue and smoothed to eliminate pockets and seam features that could retain larvae. A mechanical flowmeter was attached to the outside of the net collar, and vanes also attached to the collar caused the assembly (net and flowmeter) to rotate slowly (~0.05 - 0.3 Hz) so that their average positions would be similar.

Buoyancy compensators on the collar kept the net trailing horizontally. (Rotation would be less important in larger systems where sampling could be done well away from boundary and edge effects.)

Mean volume sampled was about 1.5 m^3. The plankton net was visually monitored during the set and time in water was kept short (5 to 10 mins) to reduce occlusion of mesh pores by detritus. Volumes were calculated using mechanical current meter readings to estimate the "distance towed" or linear passage of water during the sample, which was multiplied by the mouth area of the net for an estimate of volume sampled. Filtering efficiencies were assumed to be unity, which means that the volumes may be overestimated and the larval densities therefore underestimated. The sample was timed to allow calculation of water speed, to in turn allow calculation of transit times of the sampled population between the two sampling sites.

The paired samples were taken within ca. 0.5 hr of each other. Sampling avoided periods where the tide was rising. Although I preferred to take the upstream sample first, the downstream sample was sometimes taken first (reverse order) to eliminate the waste associated with taking the upstream sample only to find that the downstream sample could not be taken because of the tide. Reverse-order sampling is vulnerable to short-term changes in mortality and larval flux into the samples section, both of which would add noise to the data; if short-term changes in these are small and samples are sufficiently large then the noise added by reversing sample order will be small. Sampling was done in daylight for practical reasons. Temporal variation of larval abundance in the presence of zero mortality would yield varying estimates of apparent mortality, with a mean close to zero; temporal variation in the presence of real mortality will reduce the precision with which mortality is estimated but should not bias the estimate.

I assumed that larvae were randomly distributed across the river's width, because the river is shallow (generally ≤1m deep) and of uniform bottom type across its width. The lower portion of the river has corners which could generate flow asymmetries which could cause a non-random distribution of larvae, or variation in WMT for different patches or streamlines, but these were not apparent in different motions or velocities of drifting particles (wood, leaves), of which several passed the net in most sets. In taking samples care was exercised to ensure that the net sampled at least 2m from the shore. Sampling was done only on out-flowing tides. In retrospect, although the pair of sites chosen to span the entire stretch where *S. punctatum* was rare/absent, the lower site would better have been replaced by a site at the bottom of the straight section of the river.

Larval types

Because several gobiids inhabit rivers in Dominica, W.I., this work could not be done without the ability to distinguish *Sicydium punctatum* larvae from larvae of other gobiids. This only became possible as a result of previous work in this study (Ch. 5).

The purpose of type identification during mortality sampling is the differentiation of types not representing *Sicydium* spp. and which may be produced between sampling points. *A. taiasica* (at least) inhabits the river stretch between samples and production of *A. taiasica* larvae could therefore confound the results if larvae could not be differentiated. The species identity of *S. punctatum* larvae alone is sufficient to accomplish this. For this part of the study we treat the types Fyg (confirmed *S. punctatum*) and Frb (suspected *S. antillarum*) together as 'type F' because they are extremely similar larvae and are both believed rare or absent as adults in the river reach sampled.

Sicydium larvae are small (1800µm) and preserve poorly, and only in live material can the various types of goby larvae be differentiated; therefore, counts and identification were done with live material. Samples were counted after allowing detritus to settle and decanting the clear (upper) portion, which was then concentrated through a sieve of 80µm Nitex™ and transferred to a petri dish for counting and sorting. Goby larvae were virtually all in the decanted clear portion, and were rarely present and never abundant in the settled portion. The process was usually repeated and a sub-sample (15 to 50%) of the settled portion was examined for the taxa of interest, with that sub-count being extrapolated to the entire settled volume and added to the count obtained in the decanted portion. Each larva was counted and pipetted to another dish, because mobility of larvae impeded counting in the same dish. Repeat counts were highly consistent, rarely differing by more than one or two. Counting of larvae by type required immobilisation so the diagnostic features could be seen clearly. I used 2-phenoxyethanol (Bell 1967) to immobilise larvae in a petri dish, adding one drop at a time of a stock solution (5-10 drops 2-Phenoxyethanol in 20 ml H_2O), ceasing addition when larvae became inactive. Anaesthesia occurred within seconds once the critical level was reached, and larvae recovered within seconds after a change of water, even after several minutes of anaesthesia.

For comparison, invertebrate taxa (broadly categorised as decapod larvae, nauplii, gastropod larvae, caddisfly larvae, mayfly larvae, calanoids, and mites/ticks) in the stream drift were also sufficiently abundant for mortalities to be calculated. All these taxa occur up to the higher reaches of rivers, 30 to 300 m above sea level, and do not seem particularly associated with any altitude. Decapod larvae were counted using the same method as for *S. punctatum* larvae. Caddis and mayfly larvae were countable without requiring pipetting out of petri dishes unless unusually abundant. Nauplii and mollusc larvae were small, often difficult to detect, and not central to the objectives of the study, and therefore were not individually counted when numerous (100s to 1000s); instead numbers were one-look estimated with an intended precision of ≤20% of the estimate, i.e. to the nearest 50, 100 or 1000. When compared with estimates made from counts in a number of fields of the sample dish, the one-look estimates were generally conservative. Mites/ticks and calanoid copepods were counted as ≥n. Mites/ticks, caddisfly larvae and mayfly larvae were less efficiently separated from the sediments by the settling method and are therefore less accurately estimated. Use of data obtained with greater expected errors in calculating mortalities requires the assumption that errors are similarly distributed at both stations of a pair.

Concentrations (C, number$\cdot m^{-3}$) for all taxa were calculated by dividing counts by volume filtered. Survival over time WMT was estimated by the ratio $C_{downstream}/C_{upstream}$. Explicit hourly survivals (S_h) and mortalities (M_h) were calculated as

$$S_h = (C_{downstream}/C_{upstream})^{1/t}, \text{ and} \qquad \text{(eq. 11)}$$

$$M_h = 1-S_h. \qquad \text{(eq. 12)}$$

Data with zeroes in the lower sample all converge as zero survival, regardless of the value in the upper sample. For F-type larvae no zeroes appeared in the upper sample, so there is no bias arising from undefined expressions (i.e. $n \div 0$); undefined quotients do however appear in some of the other taxa and these are left as missing mortality data.

Captive observation of predation and mortality

Sicydium punctatum were kept in an aquarium which was furnished with gravel and stones from a stream supporting this species. Six or eight *Sicydium punctatum* 30-50 mm SL were present on an area of approximately 0.9 m by 0.4 m; this was judged to be within the range of adult densities observed, and well below the highest observed natural densities. When a spawning was discovered, an estimate was made of the number of larvae present by extrapolation from a count of larvae removed in a known volume of water.

Larvae were observed periodically, and the time when larvae were difficult to find was noted along with the best estimate (visual inspection lasting ≥ 1 minute) of the number remaining, and time elapsed noted with the number of larvae that could be located. Fitted to an exponential decay (eq. 9, with time elapsed replacing WMT), an estimate of hourly mortality was made.

Observation of conspecific adults showed predation occurring, and an approximation of the search and handling time was used to assess the possible contribution of conspecific predation to the observed decline.

RESULTS

Field results

Abundances of most taxa showed marked declines *in situ*. Between the upper and lower stations on Layou River, mortality is high (Fig. 7.4) for all taxa except nauplii, which increased in 4 out of 5 cases. In the table of calculated survival ($C_d/C_u{}^{1/t}$, hourly rate of relative change in standing crop) rates (Table 2) for all taxa, there are 66 independent cells. Of these, 13 values could not be calculated, 12 indicate $S_h=0$ (complete mortality), 28 indicate $0<S_h<1.0$, 1 indicates $S_h=1$ (no change), and in 12 cases $S_h\geq1$. Mortality for *Sicydium* spp (F type larvae) is extremely high ($0.216\leq S_h\leq0.861$), as it is for W type larvae.

Aquarium result

The aquarium mortality of larvae was approached in two ways, (1) simple calculation of total mortality rate, and (2) estimation of potential losses from observations of predation of the portion of total mortality accountable for by predation.

The larvae declined in numbers from an estimated 2890 (remaining in the aquarium after sample removal at 1055h) to approximately 2 in 7.67hr, yielding an S_h of 0.39. In contrast, the maintenance of large numbers of larvae for several days in otherwise empty (no gravel, no predators) containers was routine (Bell & Brown 1994 in press, Ch. 6), with losses for the first few days being negligible.

Mortality was at least partly a result of predation by some of the adult *S. punctatum* present (the parent male did not prey on larvae, but took no action to defend larvae). The adult most active in predation was approximately 45mm, the mass of the larva being <0.0001 of the mass ($1.8^3 \div 45^3$) of the predatory adult.

Five and one-half hours after the first observation and assessment of the number of larvae, they had declined to somewhere near 30 (in about 10 seconds of observation 2 or 3 larvae could be sighted), which is within the range of abundance in field plankton samples (124 samples log-normally distributed, range 0 to 1900 $\text{ind}\cdot\text{m}^{-3}$, arithmetic mean $57\cdot\text{m}^{-3}$, geometric mean $12.8\cdot\text{m}^{-3}$; K. Bell unpub. data). At this low level of prey abundance, the capture cycle of one predatory conspecific was observed and is summarised: departure from resting place, followed by hovering in the water for a few seconds; after which larvae were apparently sighted, then captured by gulping, usually on the first or second attempt; the predator adult, after capturing a larva, settled again on a resting place, and made mandibular movements interpreted as handling the small item in the buccal cavity; handling movements took on the order of two seconds, and after a small pause the cycle repeated. The entire cycle was about ten to fifteen seconds. Predation was not seen during the last observation, when several minutes were required to verify the presence of two larvae.

Using fifteen seconds as the time for an adult to catch a single larva, and without allowing for likely positive effects of density on predation efficiency, simple arithmetic indicates that a single fish could have consumed 1,840 larvae. Since several fish were engaged in this activity, their predation appears adequate to account for the observed mortality.

DISCUSSION

The majority of all taxa counted show reduction in abundance between Hillsborough bridge and the river mouth (Fig. 7.4, Table 2). Only nauplii consistently showed increases, with calanoids being ambiguous. Given the assumptions discussed above, the presence of mixed results (C_t/C_o both above and below 1.0) in any species suggests a temporally shifting balance between mortality and production, with high values conservatively indicating production and low values conservatively indicating mortality.

Sicydium punctatum larvae are diadromous (Bell & Brown 1994 in press), which also appears to be the case for other Dominican riverine gobies (K. Bell unpub. data). Settlement by larvae in culture jars was rare or nonexistent (Bell & Brown 1994 in press). The same probably holds for mollusc larvae and the clearly diadromous decapod (Atyidae and Penaeidae) larvae which enter rivers from the sea at the same times as, and in company with, *S. punctatum*. These taxa are therefore categorised as group B, and $C_{downstream}/C_{upstream}$ ratios >1.0 would indicate the presence of reproductive adults in the between-sample river reach. Reductions in abundance are most parsimoniously attributed to mortality, and increases attributed to new production: *Sicydium punctatum* larvae (the numerically dominant goby larval type) consistently show mortality; W-type larvae show no cases of increase (out of four values, three indicate decrease and one is no-change). Mollusc larvae, probably larvae of *Neritina punctulata* (Starmuehlner & Therezien 1982), show consistent decrease; decapod larvae show 5 decreases and one increase.

For taxa which are clearly *not* diadromous (insect larvae) intermittent and alternating occupation of the benthos and the stream drift is expected (Krueger & Cook 1984b, Malmqvist & Sjoestroem 1987, Layzer et al. 1989, Wilzbach 1990, LeRoy et al. 1991), and disappearance can also occur via metamorphosis into winged adults. These are categorised as group A, for which more data are required to attribute changes in abundance to any in particular of the sources indicated in figure 7.1 or equation (1).

Abundance changes in calanoid copepods and nauplii (presumably but not certainly of the same species) may reflect the balance between production and mortality, because settlement is not an expected behaviour and escape by metamorphosis is not a consideration. However, the existence of dynamic retention properties based on the interaction of the riverine hydrography and species' behaviour is likely; the assumption potentially violated is that of directionality of movement. The life history of the riverine calanoid copepods sampled is not clear, so they cannot be assigned to a group which permits interpretation of results in light of possible biases. The mites/ticks are unlikely to be marine at any stage, so the movement of stages caught cannot be assumed to be one-directional and reductions in abundance cannot be attributed to mortality. Their association with sediment portions of samples suggests that a greater part of the population is to be found on the bottom, so that estimation of transit rates from river flow is unlikely to be reliable.

Estimates for *Sicydium punctatum* larvae (i.e. F-type larvae) consistently indicate mortality, supporting an absence of nests in the intervening area between sample points. Since the presence of undetected production would reduce apparent mortality, the mortality estimates here are conservative. The hourly survival estimates are low (i.e. high mortality) and suggest a large cost to upstream positioning of nests: the geometric mean hourly survival (S_h) was 0.45, which, assuming a current velocity of 0.3m sec^{-1} corresponds to a distance-based survival S_{km} =

0.422. Although the predator cannot be identified for the *in situ* mortalities, and bearing in mind that the river stretch was deliberately chosen on the basis of virtually absent *S. punctatum* adults, the numerous estuarine fishes which are visibly abundant in that stretch, including mountain mullet (*Agonostomus* sp.) and the goby *Awaous taiasica*, may be implicated. *Philypnus dormitor* and *Eleotris pisonis* may also be present in this area. The observations of aquarium predation by *Sicydium punctatum* suggest that the predation by fishes in the 20-50mm size range have the potential to cause high mortality of planktonic larval gobies, so that predation by other species is a plausible cause for the mortalities observed here, and similar mortalities may be expected where adult *S. punctatum* are abundant, although the production of new larvae from nests might mask this.

The aquarium results, both from actual disappearance of larvae and from observation of predation rates, show that conspecific adult predation is capable of inflicting high mortalities on larvae. Since the density of *S. punctatum* in the aquarium was similar to that in many field locations, if this predation accounted for even half of the total mortality, then the population of larvae might have a half-life of under two hours due to conspecific adult predation alone. Species other than *S. punctatum* are also potential predators; indeed, it would be reasonable to assume a greater predatory success for the terminally-mouthed predatory eleotrids, mountain mullet and other fish in the silt-bottomed estuarine areas. Although there may be factors which reduce predatory activity of fish in the field (e.g. occupation with other feeding activities), other factors (e.g. available light) may increase effectiveness of predation.

Larvae of types Y and P each show one case of increase and three cases of decrease, indicating that mortality is sometimes balanced by new production of larvae in this river section. This presumably is because adults of these species are not excluded by the silty substrate; indeed, *Awaous taiasica* (a possible match for larval types W,Y,P) is common in this section of Layou River. However the W, Y, and P type larvae are not as common as type F (*S. punctatum*), so the upstream count tends to be lower and because of zeros in the upper sample there are missing (undefined) ratio data. However, there are virtually no cases where zeros in the upper sample are paired with significant numbers in the lower sample (Table 1), so significant production is not masked by undefined numbers (0/n) in these data.

Given a rate of transport approximating a fairly typical river flow of $0.3\text{m}\cdot\text{sec}^{-1}$, and with an $S_h = 0.5$ (better than observed survival for *S. punctatum*), a population of larvae would be halved during each kilometer of downstream drift. A reproducing fish at a distance *d* (Km) upriver from a reference equivalent fish has reduced relative reproductive success which is 1-S, where S = 1 x Sh^{d}. Using *d* as the distance upstream of the coast and with kilometer survival = 0.5, the penalties are 50% for 1 km, 75% for 2 km, to 96.8% for 5 km upstream. Larvae can be found in the stream drift of headwaters approximately 14 km from the river mouth (K. Bell unpub. data), and of these the expected survival (at S_h = 0.5) to the coast would be 6.1 x 10^{-5} per larva hatched.

Implications of results for *Sicydium punctatum*

The conclusion is consistent from both *in situ* and aquarium sources that mortality of *Sicydium punctatum* is high during river transport, and the mortality observed seems attributable to predation because longevity of larvae in a variety of containers without predators or special treatment is typically 2 to 9 days, with near-zero mortality during the first two days post-hatch (Ch. 6, K. Bell unpub. data).

Mortality could differ spatially according to either the habitat, light, current speed, or species and abundance of predators present. However the close correspondence of the aquarium survival rate and the mortality calculated on the basis of adult *S. punctatum* predation observation in the aquarium (where light, current, species etc. all differed from the Layou site), and the *in situ* mortalities of *S. punctatum* larvae are very much in accord.

While the field results show mortality in the absence of *Sicydium punctatum* adults (presence of other species), the aquarium result shows that predation by conspecifics does occur, and suggests that it can inflict high mortalities. The *in situ* mortalities, in a river section chosen for its absence of *Sicydium* spp., likely stem from predation by mountain mullet (*Agonostomus* sp.), *Awaous taiasica*, and *Eleotris pisonis*, as well as various occasional marine species entering the river mouth. Toxins in runoff pulses are in general also a possible cause of mortality. While the dominant agricultural crop in the area immediately upstream has changed from coconut (Anon. 1978) to banana (pers. obs.) with its greater use of agrochemicals (Towle 1991), the present results are relevant to a shorter-term situation than is appropriate to measure low-level toxic mortality, and there were no overt indications of high-level toxicity.

The hourly survivals estimated *in situ* (mean $S_h = 0.45$) are impressively close to the estimate for survival in the populated aquarium ($S_h = 0.39$), and suggest that mortality may be similar in zones with and without adult *Sicydium* spp. This would imply a high reproductive cost associated with upstream nest placement. With increasing distance upstream, a larva would have a steeply diminishing probability of reaching the sea because time for transit to the river mouth increases with distance. At a stream velocity of 0.3 m s^{-1}, transit of drifting particles is about 1.08 km h^{-1}, so 1 km equates to a time of 0.93 h. Survival over 1 km equals survival over 0.93 h, so $S_{km} = S_h{}^t = 0.45^{0.93} = 0.477$. We can then describe gross survival as $S = S_{km}^{dist}$, where *dist* is distance in km that must be drifted by the larva to a reference point. We can relate survivals of cohorts originating in different positions, say 3 km and 1 km from the coast, by

$$S_{3km}/S_{1km} = S_{km}^3/S_{km}^1 = 0.47^3/0.47^1 = 0.228 \quad \text{(eq. 13)}$$

meaning that survival of larvae hatched 3 km from the sea is worse by a factor of 0.228 than for the 1-km position, and that the number of larvae required to reach the same contribution to the population at the reference point is nearly five times as great. Only where conditions permit production of >1/0.228 times as many larvae, would the upstream site be preferable. Substantial changes in life expectancy, generation time, etc. could affect the net fitness loss or gain, but are beyond the scope of this analysis.

The clearance of land and consequent increased siltation rates are expected to reduce the suitability for *Sicydium punctatum* of low-gradient areas near the coast, and there is considerable anecdotal data (obtained from interviews -- there are virtually no formal records) that presence of adult *S. punctatum* in river reaches near the coastline has diminished over the past two decades, as has been reported by Erdman (1986) for *S. punctatum* in Puerto Rico, and observed by myself for some sites in Dominica, W.I. (pers. obs.).

Siltation would affect both nesting, because the species is a gravel-excavating subterranean nester (K. Bell unpub. data), and feeding, because *Sicydium* spp. are predominantly lithophyton/aufwuchs grazers. With the deterioration of sites nearest the coast and the mortality cost clearly associated upstream nesting, the potential for a fishery decline following low-elevation habitat degradation becomes evident: the burden of population maintenance falls to those reproducers whose output is exponentially reduced with upriver distance.

Considering the added larval mortality, the abundance of *Sicydium punctatum* in headwater habitats 10 km or more inland is difficult to explain unless on the basis of displacement from downstream habitats. There is an indication of a small increase in swimming endurance of larvae exiting the river mouth, associated with a short initial period spent in fresh water (Bell & Brown 1994 in press), but benefits, in this respect, of upstream nest placement may be minimal. There is likely reduced predation on adults, and possibly better feeding and growth upstream, but attributing upstream migration to this implies perception (through olfactory cues perhaps) or a general tendency reinforced by selection. There appear two possibilities: either (1) beyond some distance from the sea, perhaps 0.5 km or so, upstream migration is disadvantageous and carried out by the less competitive individuals, or (2) better growth and lower predation compensate for the multiple (temperature and larval survival) penalties associated with higher elevations and greater distance from the sea. These areas merit further study.

From the point of view of larval supply to the ocean (the habitat for postlarval stages), the segment of the reproductive population most important to maintaining the fishery appears to be that nearest the coastline. In smaller rivers which are riffle nearly to the sea reproduction may take place within meters of the sea, while in larger rivers with naturally sandy transitional zones or estuaries the important segment of the *Sicydium punctatum* population would be located slightly upstream in stony/gravelly areas of river bottom. Conservation efforts aimed at preserving the fishery should therefore concentrate on maintaining habitat suitability in the near-coastal zone.

Table 7.1. Abundance data from which survivals were calculated. Abundances truncated to single decimal point. Multiplying abundance by m^3 filtered will approximately restore absolute number retrieved.

# of set	1		2		3		4		5		6	
(1991)MMDD	0327	0327	0402	0402	0408	0408	0420	0420	0506	0506	0510	0510
hhhh	1644	1624	1325	1250	1634	1605	1656	1727	1600	1635	0656	0725
kind of sample	UP	DN	UP	DN	UP	DN	UP	DN	UP	DN	UP	DN
m^3 filtered	1.76	1.33	2.10	1.37	1.83	1.19	1.80	1.91	1.36	1.56	1.48	1.67
Celsius	27°	27°	25°	25°	27°	27.8°	26°	26°	27.8°	27.8°	24°	24
ABUNDANCE, m^{-3}, of:												
G (all)	35.1	14.2	19.9	18.2	63.6	24.3	34.3	36.5	22.7	15.9	25.5	16.1
F (*S.punctatum*)	31.1	13.5	19.4	18.2	53.9	21.8	25.2	13.6	18.3	14.5	24.8	14.7
Y (sp.?)	1.6	0	0	0	9.2	2.5	4.0	13.6	2.9	0	0	0.6
W (sp.?)	1.1	0.7	0.4	0	3.8	0	0	0	0.7	0.7	0	0
P (rare, sp.?)	1.1	0	0	0	0	0	5.1	7.8	0	0.7	0.7	0.6
decapod larvae	0.5	0	0.4	0	2.7	0	4.9	3.1	5.8	11.4	2.0	0.5
nauplii	5.6	9	5.2	3.6	21.7	·	2.7	15.6	4.3	95.7	2.0	14.9
gastropod larv	169.8	37.5	140	72.9	16.3	·	83	78.2	91.5	51	168.2	104
caddisfly larv	7.3	3.7	3.3	1.4	4.9	8.3	4.4	2.6	3.6	1.9	6.7	0.5
mayfly larvae	2.8	0	1.4	1.4	1.1	0.8	0.5	0	0.7	1.2	2.0	1.7
calanoids	1.1	2.2	0	0	1.1	·	1.1	0	·	1.2	0	1.2
mites/ticks?	0.5	0	1.4	0.7	2.7	2.5	1.1	0.52	0.7	1.9	4.0	1.7

Table 7.2. Hourly survival (S_h) rates for 12 taxa at Layou, calculated from data in Table 7.1. Dates given in format YYMMDD, times (rounded average of pair of samples) of day are given in 24-hr format. Goby larvae are types F, Y, W and P; F is *Sicydium punctatum*, and Y, W and P are recognised types tentatively associated with particular species (Chapter 5). G is all goby larval types treated together. SHR = decapod larvae, MOLL = mollusc larvae, CADD = caddisfly larvae, MAYF = mayfly larvae, CALAN = calanoid copepods, TICK = either ticks or tick-like water mites. Larval type P is extremely rare.

DATES:	910327	910402	910408	910420	910506	910510	
Times:	1630h	1310h	1615h	1715h	1615h	0715h	GROUP
COUNTED TAXA							
GOBY LARVAL TYPES:							
G (all goby)	0.346	0.796	0.198	1.119	0.727	0.545	B
F (*Sicydium* spp.)	0.376	0.861	0.216	0.304	0.81	0.511	B
Y	0	•	0.112	10.788	0	•	B
W	0.618	0	0	•	1	•	B
P	0	•	•	2.248	•	0.858	B
INVERTEBRATES							
decapod larvae	0	0	0	0.409	1.824	0.206	B
nauplii	1.736	0.407	•	28.487	15.656	13.85	?
mollusc larvae	0.173	0.205	•	0.887	0.596	0.534	B
caddisfly larvae	0.448	0.137	2.453	0.36	0.558	0.042	A
mayfly larvae	0	1.049	0.632	0	1.631	0.858	A
calanoids	2.168	•	•	0	•	•	?
mites/ticks?	0	0.196	0.87	0.232	2.363	0.34	?

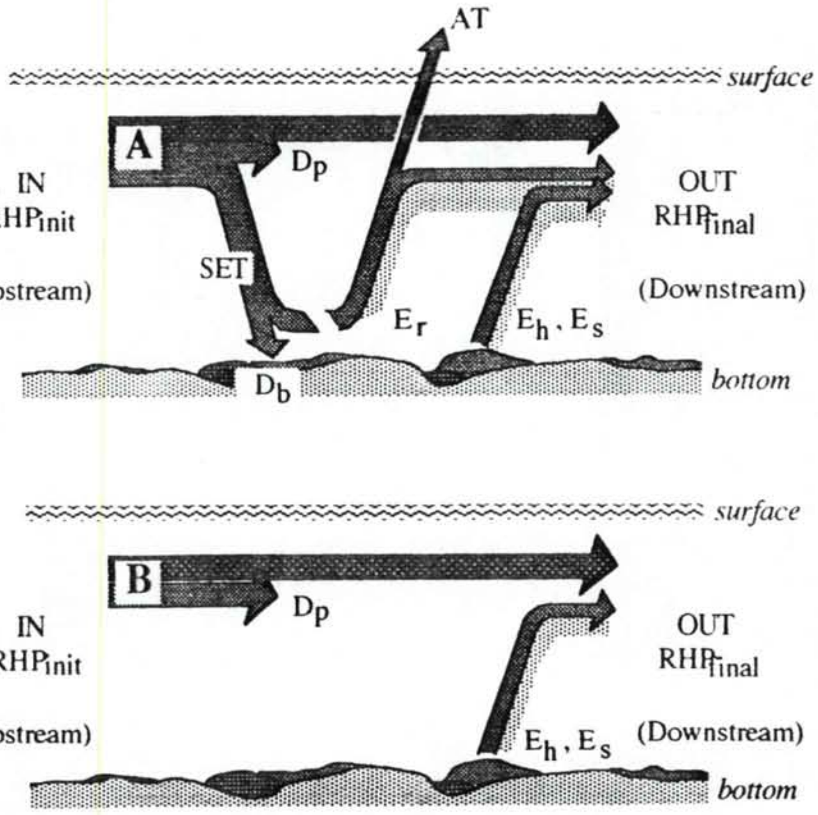


Figure 7.1. Fate of drift. Main confounding factors in the simple estimation of mortality from paired river plankton (stream drift) samples. Taxa which may settle out of, or re-enter, stream drift is indicated as group A; Taxa which are non-settling in the inter-sample river reach are indicated as group B; some subset of this group B is also vulnerable to benthic and pelagic mortality. All movement is assumed to be downstream. Light dotted shading stresses the possibility of 'negative mortalities' when assumptions are violated. D_p = pelagic mortality, D_b = benthic mortality, SET = settlement, E_r = re-entry of stream drift by settled individuals which were vulnerable to sampling at upstream site (variable time lag indicated by break), E_h = hatching, E_s = emergence from benthos into drift, AT = metamorphosis into aerial or terrestrial (e.g., winged adult) forms.

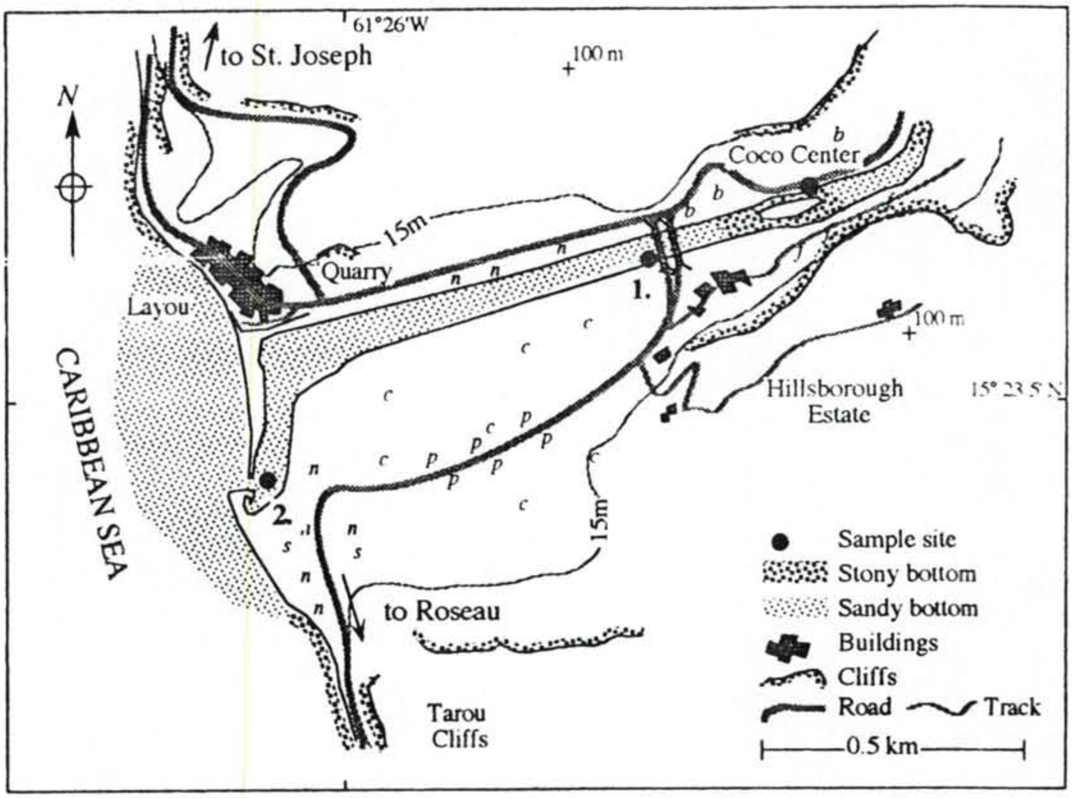
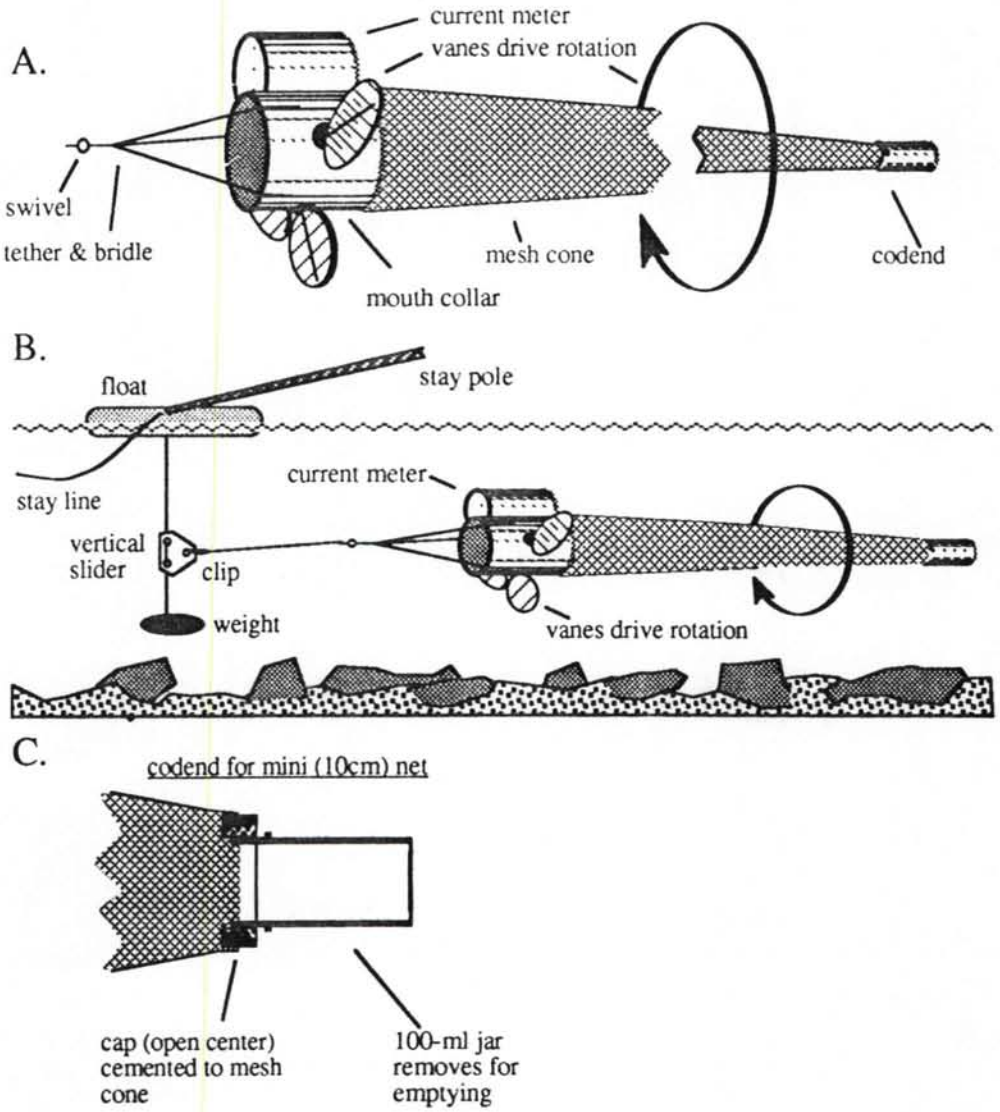


Figure 7.2. Sample sites for mortality sampling at Layou River, Dominica, W.I. Sample sites marked by dot (●) are 'UP' (1), 'DN' (2) and Layou-Coco-center (no number). Small italic letters indicate vegetation: n = coconut, b = banana plantation, c = cocoa, f = forest, p = royal palms (a landmark), s = scrub.

Figure 7.3. River plankton sampling for small streams. Net and current meter version N4P3. A: net is 10.7 cm mouth diam., mesh cone length 1.01 m, pore size 71μm square Nitex™. Seams are sealed with hot-melt glue to eliminate pockets and traps, resulting in a net that washes down cleanly. Rotation is driven by adjustable vanes and equalises average position of net and meter, thus improving accuracy in non-uniform currents. Vane mounts double as ballast adjustments to obtain neutral buoyancy and prevent sinking or floating in slow currents. B: float with stay pole and stay line enable positioning from bank of stream. Vertical slider on weight line enables depth setting. Clip enables quick attachment and detachment of net to and from vertical slider. C: cod-end is removable 100-ml jar.


A.
current meter
vanes drive rotation
swivel
tether & bridle
mesh cone
codend
mouth collar
B.
float
stay pole
stay line
current meter
vertical slider
clip
weight
vanes drive rotation
C.
codend for mini (10cm) net
cap (open center) cemented to mesh cone
100-ml jar removes for emptying

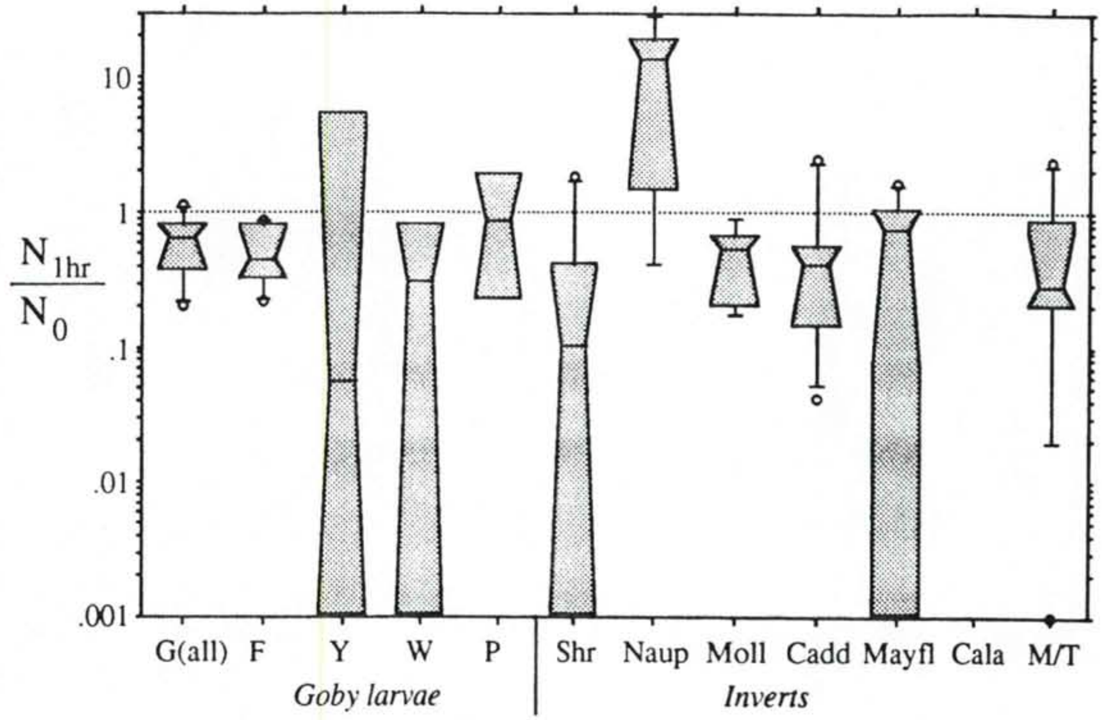


Figure 7.4. Hourly survival in drift at Layou R. Notched box plot of ratios N_t/N_0, or one-hour survival rates (S_h) for 11 taxa. Center bar indicates median, notch is 95% C.I. for median, box includes 50% of data, range bars include further 30%, endpoints are shown individually (circles) if outside the C.I. Taxa are abbreviated as: G (all goby larvae), F (*Sicydium* spp. larvae, including Fyg, *Sicydium punctatum* and Frb, presumed *S. antillarum*), Y, W, P (3 types not yet matched to species but possibly *Eleotris pisonis*, *Awaous taiasica*, and *Philypnus (Gobiomorus) dormitor*), Shr (decapod crustacean larvae), Naup (nauplii), Moll (mollusc larvae), Cadd (caddisfly larvae), Mayfl (mayfly larvae), Cala (calanoid copepods), M/T (aquatic mites or ticks).

Chapter 8. Seasonally structured variation in age-at-recruitment, size-at-recruitment, and pre-recruitment growth history of the diadromous gobies *Sicydium punctatum* and *Sicydium antillarum* (Pisces) in Dominica, W.I.

ABSTRACT

The diadromous hill-stream gobies *Sicydium punctatum* Perugia and *Sicydium antillarum* Ogilvie-Grant are panseasonal spawners in Dominica, W.I. Recruitment to fresh water is also panseasonal and supports a directed fishery. Size and age, although poorly related overall, are strongly related within recruiting cohorts, and each shows a systematic seasonal component. There is seasonal variation in recruitment and fishery yield. Peak fishery yields coincide with the youngest, but largest, recruits, and low yields with the reverse, suggesting that growth rate variations are implicated in fishery yield. This is the first documentation of systematic seasonal variation in age-at-recruitment. Given these findings, age-at-recruitment cannot be thought of as a constant, even for tropical fishes.

INTRODUCTION

Age at recruitment (AAR, here equivalent to planktonic larval duration, settlement age, postlarval duration, etc.) in tropical fishes is often expressed as a single value surrounded by some error (Victor 1986b, Radtke et al. 1988, Wellington & Victor 1989, Cowen 1991). However, there are indications, even within these studies, that this may not always be the case. Both Victor (1986b) and Wellington and Victor (1989), while emphasising differences between species, report cases of significant within-species geographic difference in planktonic larval duration and caution that temporal and spatial variations are not addressed by their data beyond this. Beckman et al (1984) report differing growth rates of spot (*Leiostomus xanthurus*) between February/March and April/May. There remains, however, some dispute as to the reality of such differences: McCormick (1994) found high (but unstructured) daily variation in age of settling goatfish *Upeneus tragula*, and suggested that the (significant) differences reported by Victor (1986b) and Wellington and Victor (1989), "may simply be the product of small-scale temporal variation at a single site".

As suggested by Cowen (1991), the variation evident in a single sample can reflect a flexibility which permits recruitment to occur over a range of environmental conditions encountered by individuals within a cohort. But if variation exists in single samples, it is also likely to exist over the temporal range of recruitment (or any other process). Since variation has been found within samples, it is reasonable to think that seasonal environmental variation could add structure to variation in age-at-recruitment.

If seasonal variation in age-at-recruitment exists, it may affect recruitment because, where N is numbers at times 0 and t, and I use r (equivalent to -Z *sensu* Ricker 1975) as rate of change in numbers,

$$N_t = N_0e^{rt}. \qquad \text{(eqn. 1)}$$

Cumulative survival (and therefore recruitment) should be negatively related to t, because it is the compounding factor for survival. This paper represents the first step of probing for temporal patterns in age-at-recruitment.

Understanding effects of environmental variation on cohort strength is a critical objective of recruitment studies. In species with protracted spawning and recruitment, observation of success rates in these processes can span a range of environmental variation within each seasonal cycle. Resulting relationships of environmental variation to biology can improve predictive ability (e.g., Leggett et al 1984). However, when life-history events are restricted to narrow environmental or time windows, success rates tend to be zeroes or ones with few of the intermediate values. In such non-linear or binary situations it is difficult to link environmental conditions and cohort strength. This is usually the situation in high latitudes. Furthermore, environmental variables in strongly seasonal systems may be changing abruptly or quickly (e.g., stratification, turnover, etc. of aquatic systems), which limits confidence in accuracy even if measurements are precise. However, in weakly seasonal (e.g., tropical) habitats major life-history events occur over wider temporal windows and can be pan-seasonal; this increases the opportunity to relate conditions to variation in recruitment processes.

The structure of the life cycle affects the accessibility of species and populations to sampling effort and data interpretation. For fish recruitment studies, the ideal species would have year-round availability of all stages, would be amenable to ready quantification of parental stock, reproductive output, recruitment success, and growth rates. Completion of the life cycle in a small geographic area would imply good accessibility, and a temporally compressed life cycle would imply that more cycles could be observed in a given time. A parental population stable in size could eliminate an important potential cause of variation. The ability to define recruitment to coincide with a natural transition can be an asset to both sampling and interpretation (e.g., Roughgarden et al 1988).

These features are exhibited by sicydiine gobies (*Sicydium* spp.) on the island of Dominica, West Indies (15°30'N, 61°25'W). Adults are long-lived (>5 yr) and iteroparous. Both spawning and recruitment occur panseasonally. Times from egg to recruitment are short (50-150 days), as are times from recruitment to first reproduction (<12 months). They are diadromous and have a clearly defined settlement which coincides with recruitment to an artisanal fishery. Since artisanal fisheries for fry of sicydiine gobies and related groups (e.g., the genera *Sicydium*, *Sicyopterus*, *Lentipes*, *Chaenogobius*, *Awaous*, *Chonophorus*, *Stenogobius*, *Glossogobius*) are widespread and often substantial (Jordan & Evermann 1905, Montilla 1931, Koumans 1953, Manacop 1953, Ego 1956, Aboussouan 1969, Titcomb 1977) there is the possibility of geographic comparisons. There are direct management motivations because fishery declines have been reported (Manacop 1953, Blanco 1956, Ego 1956, Erdman 1961, Erdman 1986, Aiken 1988), but rigorous investigation of possible causes has been limited by the insufficiency of life-history information on these species.

In this study, I investigate seasonal variation in age-at-recruitment, size-at-recruitment and growth history of *Sicydium punctatum* and *Sicydium antillarum* (*sensu* Brockmann 1965), using data acquired over a two-year period in Dominica (Fig. 8.1). For purely comparative purposes I include data on *Eleotris pisonis* (Gmelin) in Dominica, an eleotrid goby with a similar (K.N.I.Bell, unpub. data) life history. *Sicydium* species are abundant in rivers of coastal volcanic topography in the Caribbean and some areas of south and central America (Atwood 1791, Jordan & Evermann 1898, Hildebrand 1935, Erdman 1961, Brockmann 1965, Aiken 1985, Erdman 1986, Aiken 1988). In the Caribbean a traditional but declining fishery exists for postlarvae, locally called

tritri, entering rivers from the sea (Atwood 1791, Erdman 1984, Aiken 1988).

Sicydium punctatum (Fig. 3.5) is diadromous, with larvae hatching from nests in rivers and immediately becoming planktonic and drifting to the sea (Chapter 3). The marine postlarval period is followed by recruitment to fresh waters, at which point fisheries are concentrated. Following recruitment adults remain in fresh water, spawning frequently. This is consistent with observations of Manacop (1953) for *Sicyopterus extraneus* in the Philippines, and with circumstantial evidence put forth by Erdman (1986) for *Sicydium* spp. in Puerto Rico.

METHODS

Source of samples

Samples were collected over a 19-month period, from October 1989 to April 1991. All samples were obtained as newly-recruiting fish, with some pigment and partial scalation. Unpigmented pelagic postlarvae (beginning recruitment) kept in culture become benthic almost immediately and well pigmented in under three days, so that these features are usefully precise indicators of the stage of recruitment/settlement. Most of the samples were taken at a permanently maintained, specially designed upstream-migration trap at Canefield River (Fig. 8.1). The upstream-migration trap is a mesh cone whose large end faces downstream; it is kept open by a filling of loose stones. The cone leads up-river moving fish to a removable collector which is a modified funnel trap. The trap was designed to maintain larvae alive for several days, and was checked daily during the recruitment part of the lunar month (4th to 10 day following the last lunar quarter) and less frequently outside that period depending on the intensity of recruitment. A few samples of newly-recruited fish were also taken from the fishery at Layou or from other sites within 10 km on the same (west) coast, or from 3 sites within a 10 km portion of the east coast. All sampling sites are within a 12 km radius. Another reason the upstream-migration trap samples were needed was that in some months the recruitment was too low to be detected by the fishery.

Samples were preserved in weak alcohol buffered with $NaHCO_3$ to saturation. Because lab grade ETOH was unobtainable on the island, I substituted white rum, approx. 40% ETOH. To compensate for the low ETOH concentration and the dilution due to water content in the larger samples, the preservative in these was replaced 1-2 days afterwards for most samples.

Total length (TL), standard length (SL) and body depth at the anterior base of the anal fin (BDA) were taken on approximately 500 specimens after preservation and before dissecting otoliths. Large measurements (>5mm) were taken using calipers for the first few specimens, but later using a petri dish onto which a scale was engraved. Small measurements (<5mm) were made using an ocular micrometer on a stereoscope.

Adult *Sicydium punctatum* Perugia and *S. antillarum* Ogilvie-Grant were identified according to Brockmann (1965). I identified recruiting postlarvae using morphology to identify genus and pigment patterns (Fig. 3.2) to separate species. I verified this by rearing recruits until they acquired the adult characters (K. Bell unpub. data). A sample containing *S. punctatum* (identified as above) is on deposit at the Smithsonian (cat. no. USNM 314002). Totally unpigmented recruits of these two species cannot be reliably differentiated, and were therefore avoided in this analysis. I caution that some workers (e.g., Aiken 1985; Erdman 1986; Penczak & Lasso 1991) may assume synonymy and include these or other species under the nomen *Sicydium plumieri* (Bloch), *sensu* Erdman (1961). *Eleotris pisonis* (Gmelin) were identified using adults and following Jordan and Evermann (1898).

Fishery data are those reported to me by fishers at Layou River, where return-migrant postlarvae, called "tri-tri", are caught. The fishery is a reliable source of recruitment data because fishing for tri-tri, when they are present, takes precedence over other activities. I coded information as poor, moderate or good quality depending on how well I knew the source, how many independent reports were in agreement, etc., and used only data coded moderate or good. Unfortunately this is the only available approach because there has never been a systematic collection of data for this fishery in any location, the best but nevertheless limited information coming from Manacop (1953), Aboussouan (1969), and Erdman (1984).

Weather data used are those reported at Canefield Airport, Dominica (Mr. Mark Blanc, Meteorological Records Officer, Botanical Gardens, Roseau, Commonwealth of Dominica, W.I.; personal communication).

Otolith-age evaluation

Age evaluation on approximately 200 specimens was by examination of dextral sagittal otoliths. Sagittae were the largest otoliths and had the clearest increments, and I found no difference between right and left otoliths. The interpretation of otolith increments in young fish as daily is supported by previous work: '..deposition of daily increments appears to be a universal phenomenon under all but the most severe conditions' (Jones 1992). In this paper, I treat increments as linear indicators of age which are deposited daily in *Sicydium punctatum* and *S. antillarum*.

Otoliths (~500 µm in diameter) were extracted (after measuring specimens) with minimal damage to the specimens by surgery using glass microscalpels. Otoliths were then soaked in 60% H_2O_2 for several minutes and then mounted, with the flat or concave side up, in Crystalbond™ adhesive on glass slides. Sinistral otoliths were left in the specimens, which were placed in individually labelled vials for future reference. Grinding, polishing or further cleaning were rarely necessary when otoliths were soaked for several minutes in H_2O_2.

Eroded otoliths were rejected if the erosion had removed the entire outer edge, and used if the final increments could still be counted. Erosion of otoliths during storage is readily detected because a rough erosional profile replaces the smooth depositional profile.

Increment counts were obtained from sequences of individual increment widths. Increment widths were obtained using the 50x objective of an Olympus BHC compound microscope (trans-illumination) fitted with a videocamera, and a frame-grabber board and video display. A polarising filter on the light source improved the readability of many otoliths. The sagittal otoliths (Fig. 8.2) of pre-recruiting *Sicydium punctatum* and *S. antillarum* postlarvae are roughly the shape of a handprint, and the growth emphasis is in the direction of the fingers (toward top, or 12-0'clock in Fig. 8.2). The transect used for increment measurement and counting was chosen to cross increments at their greatest widths.

The features recognised in otoliths were center crystal (or primordium), core (presumed hatch) increment, recruitment feature, and daily increments. The center crystal usually appears as rectangular and often slightly red in colour. The core increment is usually circular, symmetrical about the center crystal, and marks a change in texture of the otolith.

Increment counts were done blind, with reference only to the otolith reference number, to minimise intrusion of known data into the counts. *Sicydium punctatum* and *S. antillarum* otoliths are indistinguishable, so species identity could not condition otolith evaluation either. Repeated blind readings were often exact and rarely departed by more than 3 increments. Increment counts were made beginning at the center of the crystal (primordium) at the origin, and the distances to the end of the crystal, a pre-core increment if present, and the core were taken. The center crystal and pre-core increment were the most variable in visibility or presence. Where the center crystal could not be explicitly recognised, its position was estimated, and the next visible increment digitised. If the next visible increments were visible only in a transect other than the 12-o'clock, they were counted and the count digitised on the 12-o'clock transect with a coding to indicate that those widths were not usable, but that the cumulative width indicated to the next on-transect visible increment remained accurate. Subsequent increments up to the edge of the otolith were then taken.

The faint marks sometimes referred to as sub-daily increments were rarely present. While other workers (Victor 1986b, Wellington & Victor 1989, Campana 1992) speak of these as real structures, I interpreted them as resulting from increments whose 3-dimensional shape gives multiple optical opportunities to appear in focus, and my arbitration procedure reflected this. Since lines similar to sub-dailies can be easily induced by parallel lines, (e.g., graduations on slide micrometers), I rejected them as optical artifacts if they could be focused to near-invisibility while keeping adjacent increments in focus.

The recruitment feature was either by definition the outer edge of the otolith where the fish was captured at recruitment (i.e. entry to fresh water), or (e.g., in cultured fish or fish captured post-recruitment) identified by an alteration in the direction of greatest growth (greatest increment widths) in the otolith. This is comparable to the use of settlement marks (Wellington & Victor 1989), but this feature is clearer than the settlement mark reported by Victor (1982) for *Thalassoma bivittatum*. The stage in recruitment is also evident from the external pigmentation, mouth structure, behaviour of fish and their location: early recruits (no pigment, terminal mouth) and late recruits (pigmented, sub-terminal mouth) are separated by only 1-5 days yet are very easily distinguished. It is thus easy to ensure that ages of post-recruitment fish are not used as ages at recruitment.

Of 197 *Sicydium* spp. otoliths processed (159 *S. punctatum* and 38 *S. antillarum*), 75% were completely countable from the core outward. A subset of these (i.e. 104 *S. punctatum* and 15 *S. antillarum*) otoliths were clear in all details including the nucleus and the core, such that all details could be measured on the same transect as well as counted. Data from these ("reference", $_{ref}$) otoliths were used as a guide for adjustments (by species) to those otoliths *not* completely readable in the post-core region (38 *S. punctatum* and 12 *S. antillarum*) due to low-contrast zones between the nucleus and increment #11. The adjustment uses width information to replace a featureless zone with known position and length on the counting transect with the number of increments that would account for that distance at that position in the average (all dates) near-perfect otolith of that species. Where counts could be obtained on other transects this procedure was unnecessary. To adjust for a featureless zone in otolith a ending a known distance from the nucleus (D_a), I located its closest match D_{ref} in the sequential list of cumulative widths representing the average of the "reference" otoliths. The increment number of the matching D_{ref} was then taken as an objective estimate of the increment number corresponding to the position of the first readable increment after the featureless zone, and the subsequent portion of the list of $widths_a$ was then modified to reflect the adjusted increment numbers. A specimen thus adjusted never contributed to the adjustment of any other. The distances requiring interpretation in this way were all smaller (mean = 20.4 µm, 90% ≤32.8 µm) than the typical 0th to 20th increment distance (88.35 µm for *S. punctatum*, n=104; 90.55 µm for *S. antillarum*, n=15). In this group I found no variation in the number of features found in the core. Therefore, only adjustments in the post-core portion of the otolith affect the age assignment, and all such adjustments are ≤9 increments (Fig. 8.3). This procedure amounts to an interpretation of missing increments by using both the position of the missing portion and its magnitude; I prefer this protocol to an on-the-spot guess, which might suffer from undue influence of the previous otolith, operator fatigue, etc. It is comparable to those described by Victor (1986b). Because the procedure brings adjusted counts toward the mean of all samples, it is a conservative bias when seeking differences across season, location, etc.

Otoliths processed but identified as having been from fish post-recruitment at capture (body >60% scaled, n=6) are excluded from most analyses (because the post-recruitment otolith is generally difficult to read precisely, which means the recruitment date also cannot be reliably calculated); this leaves 191 specimens available. Specimens cultured (e.g., to permit identification) in excess of 4 days are not used in analyses involving length, leaving 407 specimens. Analyses involving length- and age-at-recruitment together are restricted for both these reasons, and generally use data from 176 specimens (the single exception is in Figure 7, where some points in LLQ 18 represent recruits which were cultured 29 d post-capture).

Analysis of seasonal variations

Recruitment is panseasonal and episodic for *Sicydium* spp. in Dominica, and elsewhere in the Caribbean (Erdman 1986), as for *Sicyopterus extraneus* in the Philippines (Manacop 1953). As indicated by catches in my up-migration traps, recruitment episodes tend to begin on the fourth day following the last lunar quarter (Fig. 8.4) and continue with diminishing intensity for several days. Such lunar-phased recruitment episodes are a useful way of defining recruiting cohorts. I consider each episode to begin on the day of the last lunar quarter and end on the day preceding the next. Thus, "LLQ *n*" denotes the *n*th sequential last-lunar-quarter recruitment episode after Jan. 1, 1989.

To evaluate whether cyclic functions were applicable, dates were first transformed into circular variables (RJD) by multiplying Julian dates (JD, 0-365) by $2\pi/365$ to obtain an equivalent radian measure. Then, least-squares regression was used to describe (Y) size-, age-at-recruitment, etc. in terms of cos(RJD) plus a lag. The lag or rotation was determined by iterative fitting. Scaling parameters of the cosine function

$$Y = b + m(\cos(RJD + \partial)) \qquad \text{(eqn. 2)}$$

(where b is an intercept, m is a slope and ∂ is a lag) were accepted from the best regression. The curves represented by these functions are then expressed on Julian date axes by plotting fitted values.

growth indices

A linear length-based average growth index (G_L, $mm \cdot d^{-1}$) was calculated as

$$G_L = (SL - 1.8)/age \quad , \qquad \text{(eqn. 3)}$$

where SL is the standard length in mm, 1.8 is the size in mm of a newly hatched larva, and age in days is estimated by the number of pre-recruitment increments. I prefer the term 'index' to 'rate' because random temporal variation and structural nonlinearities would be expected which are not accounted for by an arithmetic mean.

RESULTS

The mean age at recruitment of *Sicydium* spp. was 84.1 days (S.E. = 1.03, n = 191) and the mean SL is 19.9 mm (S.E. = 0.08, n = 405). Although the overall (all samples pooled) correlation of age and size for *Sicydium punctatum* and *Sicydium antillarum* together is very weak (Fig. 8.5b), the correlations within each recruitment episode (LLQ, last lunar quarter) are generally strong and significant (Fig. 8.5c). The lowest r-squared obtained (0.22 for LLQ# 19) far exceeds the correlation obtained pooling all samples ($r^2 = 0.046$) -- a clear indication of seasonal growth rate variation.

When broken down by lunar monthly recruitment episode (LLQ), all regression slopes are positive, 9 of the 12 are significant at $p<0.05$ (Fig. 8.5c), and the remaining 3 are marginally significant ($0.1>p>0.05$). *S. antillarum* is rarer than *S. punctatum* and therefore insufficiently represented in the data to permit separate regressions for each species in each recruitment episode. However, in each recruitment episode the two species appear to lie close to the same regression line, indicating similar growth rates, with *S. antillarum* recruiting at a slightly greater age and size than *S. punctatum*. This is supported by an ANCOVA of growth rate by species and season (a modification of eq. 2 to include a classification variable for species) which showed the difference in growth rates between these species to be small ($0.004\ \mathrm{mm \cdot d^{-1}}$) and not significant ($F_{1,170} = 1.7$, $p>0.1$) while the effect of recruitment date (transformed) was highly significant ($F_{1,170} = 110$, $p < 0.001$).

Age-at-recruitment (Fig. 8.6a) shows a highly significant seasonal variation ($r^2 = 0.21$, $n=193$, $p<0.001$). This function is about 180° out of phase with the seasonal length-at-recruitment (Fig. 8.6b) variation ($r^2 = 0.22$, $n=407$, $p<0.001$).

Because size at recruitment varies seasonally, growth rate cannot be inferred from age-at-recruitment alone. For these data, variation in age-at-recruitment underestimates variation in growth rate. The linear growth rate index (G_L, eq. 3) is strongly seasonal ($r^2=0.45$, $n=176$, $p<0.001$), peaking at recruitment dates in Sept.-Oct., and lowest for Mar.-Apr. recruits (Fig. 8.6c).

The directed fishery (Fig. 8.6d) for return-migrant postlarvae at Layou River is a useful source of recruitment information. Although the highest fishery yields occur in the fall, even in that season there is much short-term variability such that yields can be either large or nonexistent. Yields in the spring are reported to typically vary from nil to one barrel (80 L), which is consistent with my data. Thus, both magnitude and month-to-month variability appear to vary with season, with yields being reliably low February to April, and possibly moderate to high in other months.

The fishery yield (in barrels, BBL) is reasonably described ($r^2 = 0.46$, $p < 0.001$) as $BBL = 4.12 + 5.2\cos(RJD_{rec} + 1.2)$. Despite the acceptable correlation however, the cosine curve appears excessively symmetrical for the fishery profile, which has a narrow peak of high yields and a wide trough where the yields are low. Highs and lows in the fishery variation curve coincide with extremes in the age- and size-at recruitment curves; in phase with the size and growth curves, and ~180° out of phase with the age curve. The youngest recruits are generally the largest, indicating marked variation in growth rates between seasons.

Because of the seasonal variation of age-at-recruitment, plotting against hatch dates (Fig. 8.7) is a non-trivial extension of plotting against recruitment dates (the strengths of relationships are not the same for both). Estimated hatching dates result from the subtraction of age from date, so the inclination of rows of age-at-recruitment points has no meaning in itself; it merely results from the fact that for each point, $X_i + Y_i$ = collection date.

Age-at-recruitment has a lower correlation with hatch date ($r^2 = 0.09$, instead of 0.199 against recruitment date). Similarly, G_L has $r^2 = 0.33$ against hatch date, instead of 0.45 against recruitment date. Age-at-recruitment is at a minimum in the summer (Jun.-Jul.-Aug.) and a maximum in the winter (Dec.-Jan.). G_L 'expected' at hatch is about 0.2 $mm \cdot d^{-1}$ in the late fall of either year, and rising by about 30% to peak (0.26 $mm \cdot d^{-1}$) in the late summer. The mid to late summer thus appears to be the best times for a larva to hatch if rapid growth and quick recruitment is desirable.

DISCUSSION

Seasonal variation is evident in recruitment age, length at recruitment, and recruit quantity for *Sicydium punctatum* and *Sicydium antillarum* (Fig. 8.6). The variations shown in data covering nearly two years clearly support recurring annual cycles, however the phase of the seasonal variation differs among variables. Maximum recruitment is associated with greatest size and smallest ages. The maximum growth rate occurs in larvae hatched at mid-summer, while the maximum recruitment occurs in the Fall. The minima are similarly associated. The time lags (mid-summer to Fall, midwinter to spring) closely approximate age-at-recruitment, strongly implicating growth rates in recruitment variation. The association of growth rate (with its implication of a more rapidly reached recruitable size) and fishery yield is consistent with theory. While much effort has in the past been directed at variations in daily mortality rates, I suggest that the increasing availability of precise age data from otoliths justifies an increased emphasis on temporal variation in age-at-recruitment and growth rates.

Age-at-recruitment is clearly not a constant as may be inferred from reports based on single samples (Victor 1986b, Radtke et al. 1988, Wellington & Victor 1989), but a function to which individual variation is added. The existence of seasonality in time to recruitment, size at recruitment, and in growth rates shows that causes other than variation in reproductive output should be considered when seeking to explain variation in fishery yields. When relations between recruitment and spawning are sought (e.g., Robertson 1990), the possible existence of seasonal variation in the lag time from spawning to recruitment should be taken into account, or the assumption of invariant age-at-recruitment should be acknowledged as a source of uncertainty tending to obscure the relationship.

As well as the clearly cyclic seasonal variations in expectation of certain times to recruitment (etc.) at any hatchdate, there is considerable individual variation at all seasons. Age variation in single samples was examined by Cowen (1991), and attributed to the time between attainment of a stage of development where settlement could occur, and reaching a location where settlement occurred. The length of this period, termed 'postcompetent', is presumably a waiting-time, dominated by the chance arrival at a suitable settlement site. Cowen identifies the postcompetent period in the otolith as a period of very slow otolith growth; I see this in many of my specimens as well. The maximum postcompetent period is the upper limit of ability to survive in the plankton while being competent to settle should a suitable settlement substrate be encountered. Since the incidence of suitable settlement sites along the horizontal trajectory of a pelagic larva is essentially unpredictable, the ability of postcompetent larvae to sample many environments during a long planktonic period increases the likelihood of successful settlement, but may also result in higher cumulative risk of mortality. This undoubtedly is a major selection factor in fishes with isolated adult habitats, e.g., reef fishes. Similarly, in *Sicydium* spp. a potentially long postcompetent planktonic period may be selected for by the imperative to colonise new habitat as previous habitat undergoes the frequent changes associated with volcanic terrain, the habitat with which this group of fish is strongly associated. The ability to colonise new habitats increases with the upper limit of the duration of the dispersal phase, the pelagic larva. Victor (1986b) reported on planktonic larval durations of wrasses in the Caribbean, the western Pacific, and Hawaii, finding that longer larval durations tended to prevail in more isolated areas; he remarked that larval duration did "not appear to respond inversely to the degree of isolation...as might be expected if planktonic larvae were at risk of being washed away" and that geographic variation is "a product of physical factors operating in the plankton". This is plausible but offers no explanation for the tendency of larval durations to be longer in remote locations. However an alternative view could be that the isolation of some habitats permits colonisation only by larvae with long planktonic durations, although this might suggest substantial heritability of growth rates. This would be consistent with the greater ages at recruitment found for Hawaiian diadromous gobies (Radtke et al. 1988) compared with *Sicydium* spp. in Dominica. Considering fish having attained a remote habitat, the next generation would benefit from either having (if variation has not been selected out) or developing (if variation suppressed by selection of remote site) the potential of recruiting after a shorter time.

I know of no previous similar report of systematic cyclic seasonal variation in age at recruitment. This variation is qualitatively different from that reported within single samples (e.g., Victor 1982, Victor 1986b, Radtke et al. 1988, Wellington & Victor 1989, Cowen 1991, McBride & Conover 1991, McCormick 1994). Because the seasonal variation I find in age at recruitment of *Sicydium* spp. is accompanied by nearly as much variation in size at recruitment, it cannot be attributed solely to variation in the postcompetent period (Victor 1986a, Cowen 1991). Many systems may contain such variation, although it may be more difficult to demonstrate in systems with short recruitment seasons, or in systems where life-history transitions are more difficult to identify (e.g., McBride & Conover 1991, McCormick 1994).

Over longer terms, such as over years in temperate and northern fisheries, variations in growth rate are acknowledged by the use of regularly repeated age/length relationships. However this has been directed at the accounting process of estimating numbers in each year-class. Treating the well-known growth equation ($N_t=N_0e^{rt}$) as a survival equation where $e^r<1.0$ (equivalent to saying $N_t=N_oe^{-Zt}$), the role of t in determining the ratio N_t/N_0 (= gross survival) may have been unduly subordinated to questions centering on the role of r (or M, Z, etc.). Whether mortality is higher or lower for younger or older, larger or smaller, fast-growing or slow-growing larvae, the compounding effect of t (age-at-recruitment) on cumulative mortality can readily supersede the effect of all but the most extreme short-term variations in daily mortality.

Hawaiian diadromous gobies (Radtke et al. 1988) have significantly longer planktonic durations than do Dominican diadromous gobies reported on here (144 d vs. 85.9 d overall, $F_{1,231} = 291.2$, $p<0.001$). In Dominica the recruitment of *Sicydium* spp. occurs sooner ($F_{1,212} = 362.5$, $p<0.001$) than it does for Hawaiian *Awaous stamineus* and *Stenogobius genivittatus* (Fig. 8.8), and despite quicker recruitment *Sicydium* spp. recruit at a larger size, indicating more rapid growth. *Eleotris pisonis*, with the highest age-at-recruitment in Dominica so far, also has significantly lower age-at-recruitment ($F_{1,43} = 71.7$, $p<0.001$) than the Hawaiian species. The data for *S. punctatum* and *S. antillarum* show more scatter than the Hawaiian gobies; however that is substantially because the Dominican data cover a greater temporal range (all seasons, 2 years) than the Hawaiian data (a single sample from Oahu, early June 1986). To provide perspective on the differences, data from *Eleotris pisonis* in Dominica and the Hawaiian data from Radtke et al (1988) are shown on the same plot. While some part of the difference may be due to differences in otolith examination methods, the difference in size (length) is clearly too large to be method-related. Since the data from *Eleotris pisonis* and *Sicydium* spp. were obtained and processed similarly, the role of operator or methodological biases can be dismissed in the difference within the Dominican data, and therefore must be species-related in origin. Given that there is species-based variation in growth rates in Dominica, the difference between Dominican and Hawaiian data is plausible as the result of species and/or habitat differences. If more data is obtained on other species in Dominica and Hawaii and a better control of species-related differences is obtained, insights into habitat differences may follow. The difference between Hawaii and the Caribbean appears in other families as well: I used one-way ANOVA to compare within-family planktonic larval durations in the Caribbean and Hawaii, using the species means for Labrids and Pomacentrids from Victor (Victor 1986b) and Wellington and Victor (Wellington & Victor 1989). Because use of species means entails a loss of degrees of freedom, this method should be conservative. Labrids have significantly longer planktonic durations in Hawaii (55 days vs. 40 days, $F_{1,37} = 4.955$, $p<0.05$), while Pomacentrids have non-significantly longer planktonic durations in Hawaii (26 days vs. 23 days, $F_{1,21} = 2.99$, $p>0.05$, n.s.).

One of the prime motivations for this study was an elucidation of factors which could contribute to fishery variations, especially the apparent declines (Manacop 1953, Blanco 1956, Ego 1956, Erdman 1961, Erdman 1986, Aiken 1988) reported in such fisheries. The results discussed here strongly implicate variations in age-at-recruitment (associated with variation in growth rate) in fishery variation on seasonal timescales. If systematic variation can exist on these timescales in a single location, I might expect it over longer (e.g., decadal) timescales as well. Spatial variations (as shown by Victor 1986b, Wellington & Victor 1989, for damselfishes and wrasses) appear to apply also for gobiids in general. Thus, the lower growth rates in Hawaii would be consistent with the lower (Jordan & Evermann 1905) or nonexistent (R. Radtke, SOEST, Biological Oceanography, Hawaii Inst. of Geophysics, Univ. of Hawaii, Honolulu, Hawaii 96822, pers. comm.) fishery yields in Hawaii compared to Dominica. Unfortunately, there exist no specimens from the West Indies suitably preserved to permit comparison of age-at-recruitment previous to this study.

I have demonstrated clear variation over seasons in recruit age, growth history and size; this is directly relevant to the recruitment of these tropical species. Further, these species may represent over short periods and in a more structured way (seasons) what happens in temperate situations over years instead of months; if so, these species may be ideal systems in which to study recruitment processes. I believe age and growth are the major factors determining recruitment in *Sicydium* spp. in Dominica, but caution that variations in reproduction could affect the conclusions. Because of the complexity of modelling recruitment with variable time lags, I defer further exploration of this question to the next chapter.

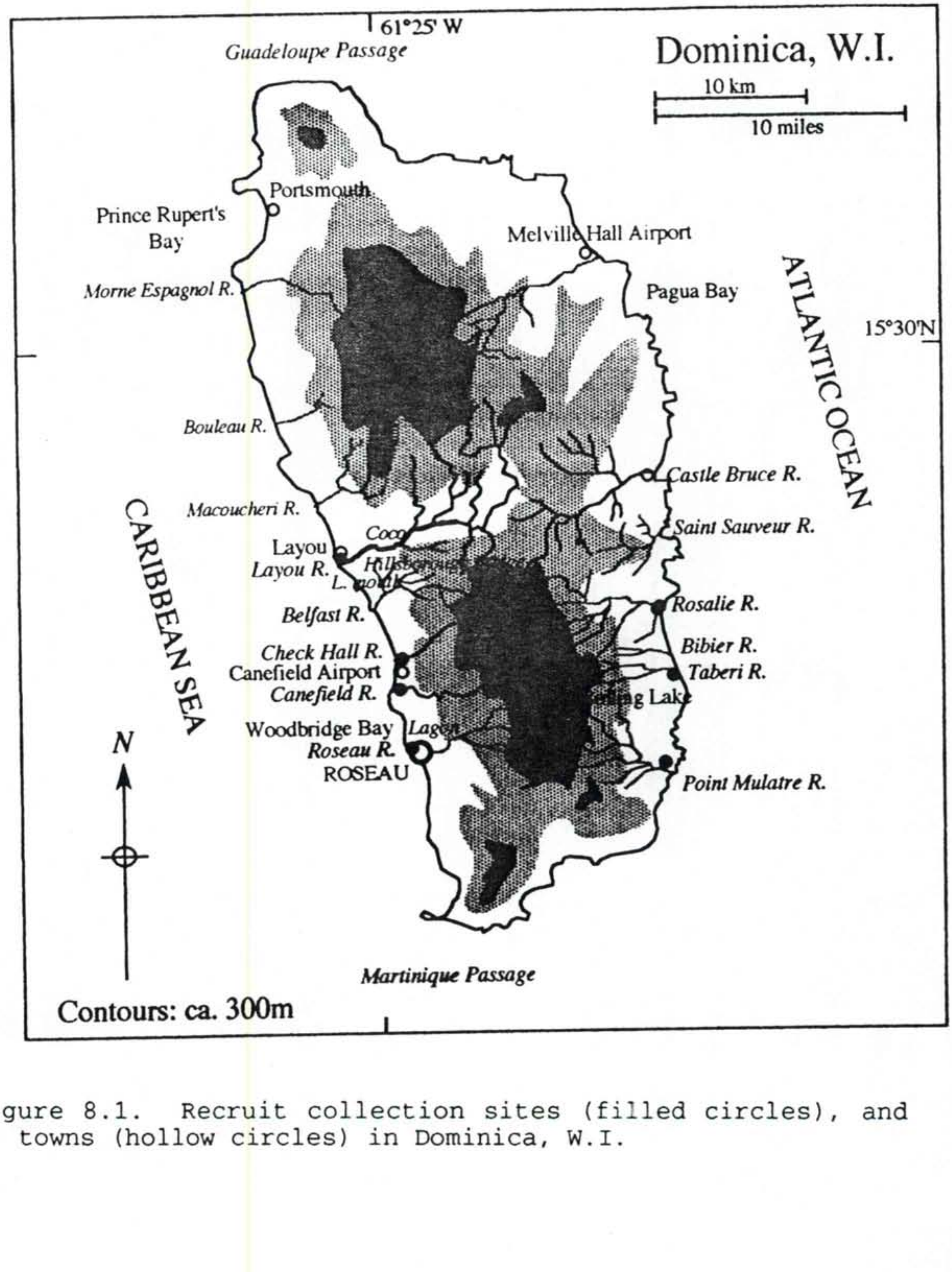


Figure 8.1. Recruit collection sites (filled circles), and towns (hollow circles) in Dominica, W.I.

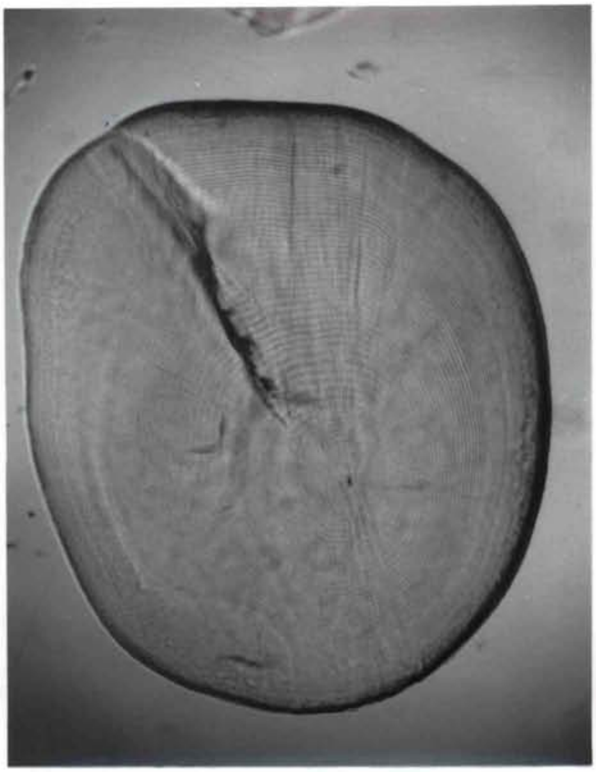


Figure 8.2. Sagittal otolith of newly-recruited *Sicydium punctatum*. Nucleus is visible below centre. Increment measurements and counts were taken on a 12-o'clock transect from the nucleus.

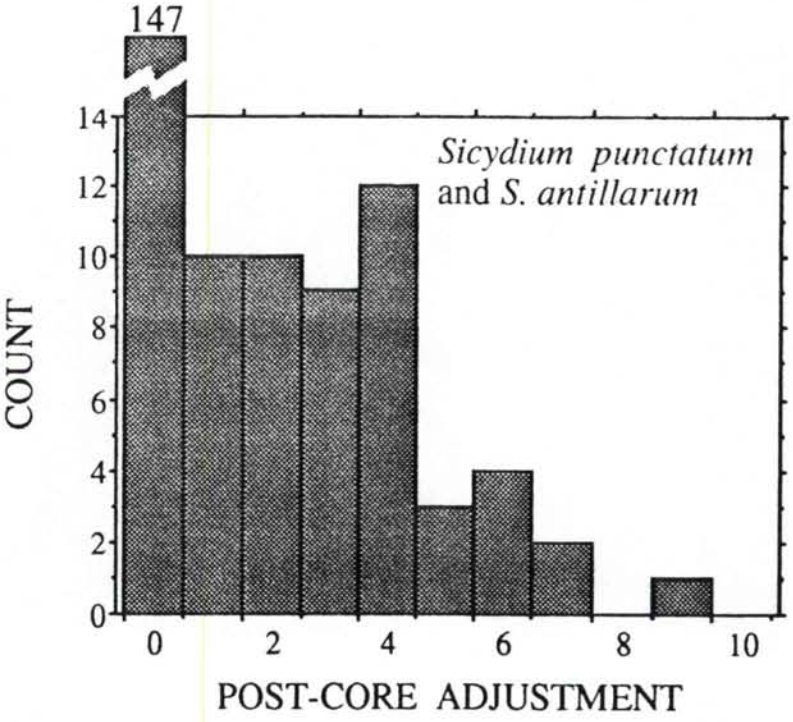


Figure 8.3. Adjustment of increment counts. Amount of adjustment (on the basis of width of post-core unreadable parts of sagittal otoliths) in age determination of 198 *Sicydium punctatum* and *S. antillarum*. 147 otoliths or 74% required no adjustment. See text for details.

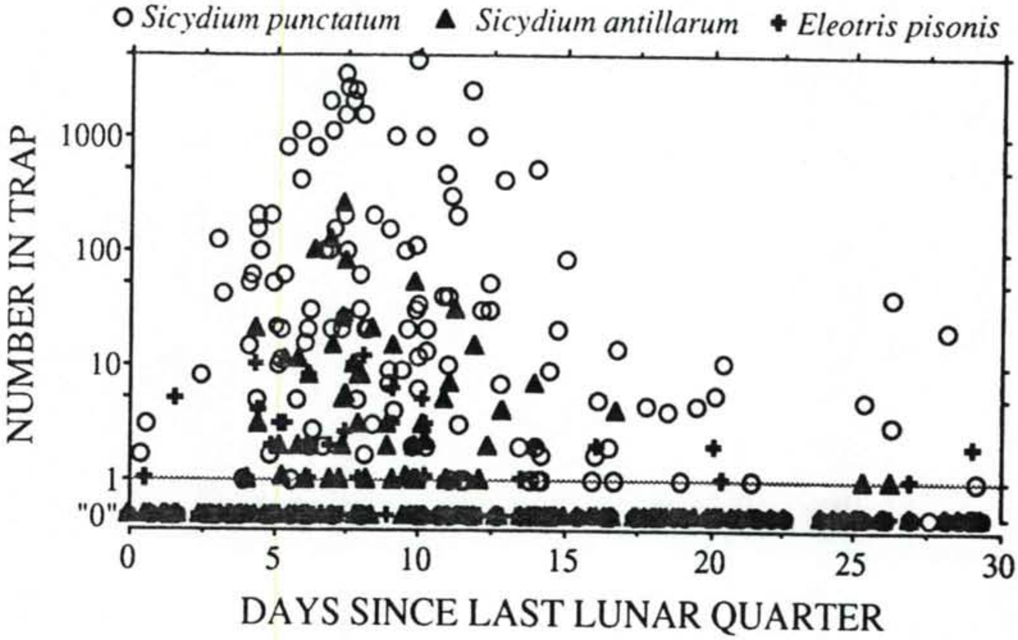


Figure 8.4. Lunar recruitment pattern (numbers caught in upstream-migration trap) for *Sicydium punctatum* (open circles), *Sicydium antillarum* (filled triangles), and *Eleotris pisonis* (plus signs).

Figure 8.5. Recruit length-at-age within each recruiting cohort for *Sicydium punctatum* (○); *S. antillarum* (▲). "LLQ ##" refers to sequential number of last-lunar-quarter recruitment episode. A: Dates of last lunar quarters. B. Overall length-at-age of recruiting fish (all LLQs). C: Same within each recruitment episode (LLQ#).

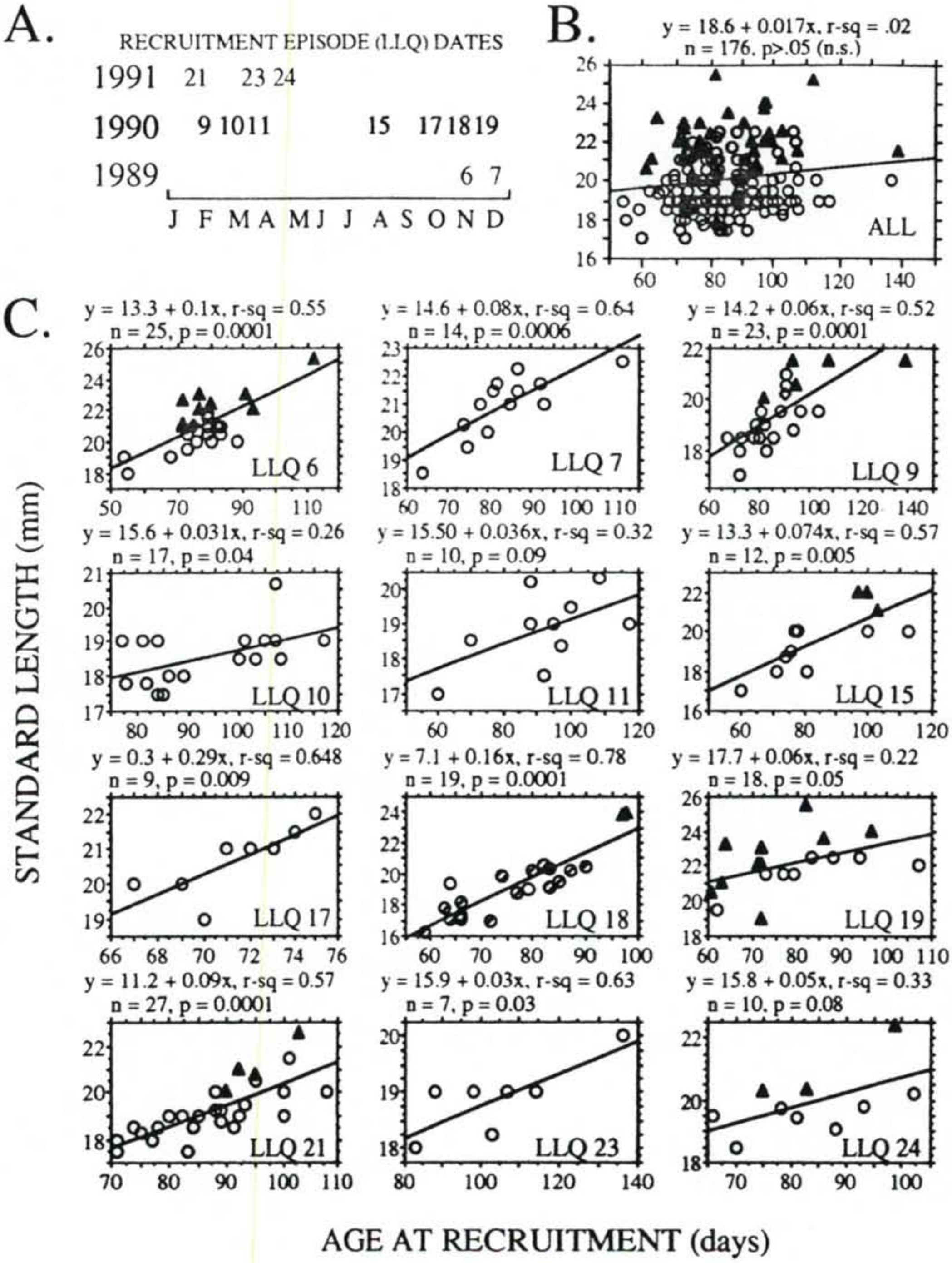

A.
RECRUITMENT EPISODE (LLQ) DATES
1991 21 23 24
1990 9 10 11 15 17 18 19
1989 6 7
J F M A M J J A S O N D
B.
y = 18.6 + 0.017x, r-sq = .02
n = 176, p>.05 (n.s.)
ALL
C.
y = 13.3 + 0.1x, r-sq = 0.55
n = 25, p = 0.0001
LLQ 6
y = 14.6 + 0.08x, r-sq = 0.64
n = 14, p = 0.0006
LLQ 7
y = 14.2 + 0.06x, r-sq = 0.52
n = 23, p = 0.0001
LLQ 9
y = 15.6 + 0.031x, r-sq = 0.26
n = 17, p = 0.04
LLQ 10
y = 15.50 + 0.036x, r-sq = 0.32
n = 10, p = 0.09
LLQ 11
y = 13.3 + 0.074x, r-sq = 0.57
n = 12, p = 0.005
LLQ 15
y = 0.3 + 0.29x, r-sq = 0.648
n = 9, p = 0.009
LLQ 17
y = 7.1 + 0.16x, r-sq = 0.78
n = 19, p = 0.0001
LLQ 18
y = 17.7 + 0.06x, r-sq = 0.22
n = 18, p = 0.05
LLQ 19
y = 11.2 + 0.09x, r-sq = 0.57
n = 27, p = 0.0001
LLQ 21
y = 15.9 + 0.03x, r-sq = 0.63
n = 7, p = 0.03
LLQ 23
y = 15.8 + 0.05x, r-sq = 0.33
n = 10, p = 0.08
LLQ 24
STANDARD LENGTH (mm)
AGE AT RECRUITMENT (days)

Figure 8.6. Seasonal cyclic trends with respect to date of recruitment, indicated by calendar month and sequential day number from Jan. 1, 1989. Open circles are for *Sicydium punctatum*, solid triangles are *S. antillarum*. Length data are more numerous than age data. Cosine regression lags (of date) are iteratively fitted using least-squares regression. A: recruit ages (d), y = 84.758+8.728*cos(RJc-1.5R), where RJc = recruitment date transformed to radians, and -1.5R indicates lagging in radians; r^2 = 0.199, n=193, p=0.0001. B: Length (mm) at recruitment, y = 19.99+1.096*cos(RJc+1.15R); r^2 = 0.22, n=407, p = 0.0001. C: Linear growth index G_L (mm/d), G_L=0.252+ 0.041(cosRJc+1.6R), r^2 = 0.45, n=176, p=0.0001. D: Lunar-monthly fishery yields (barrels) at Layou River, Dominica (missing data indicated by question marks), yield = 4.121 + 5.194ç(RJc+1.2), r^2 = 0.462, n=19, p=0.0014. The fishery is pursued in preference to other activities when recruits are present in harvestable quantities, and both magnitude and month-to-month variability appear to vary with season.

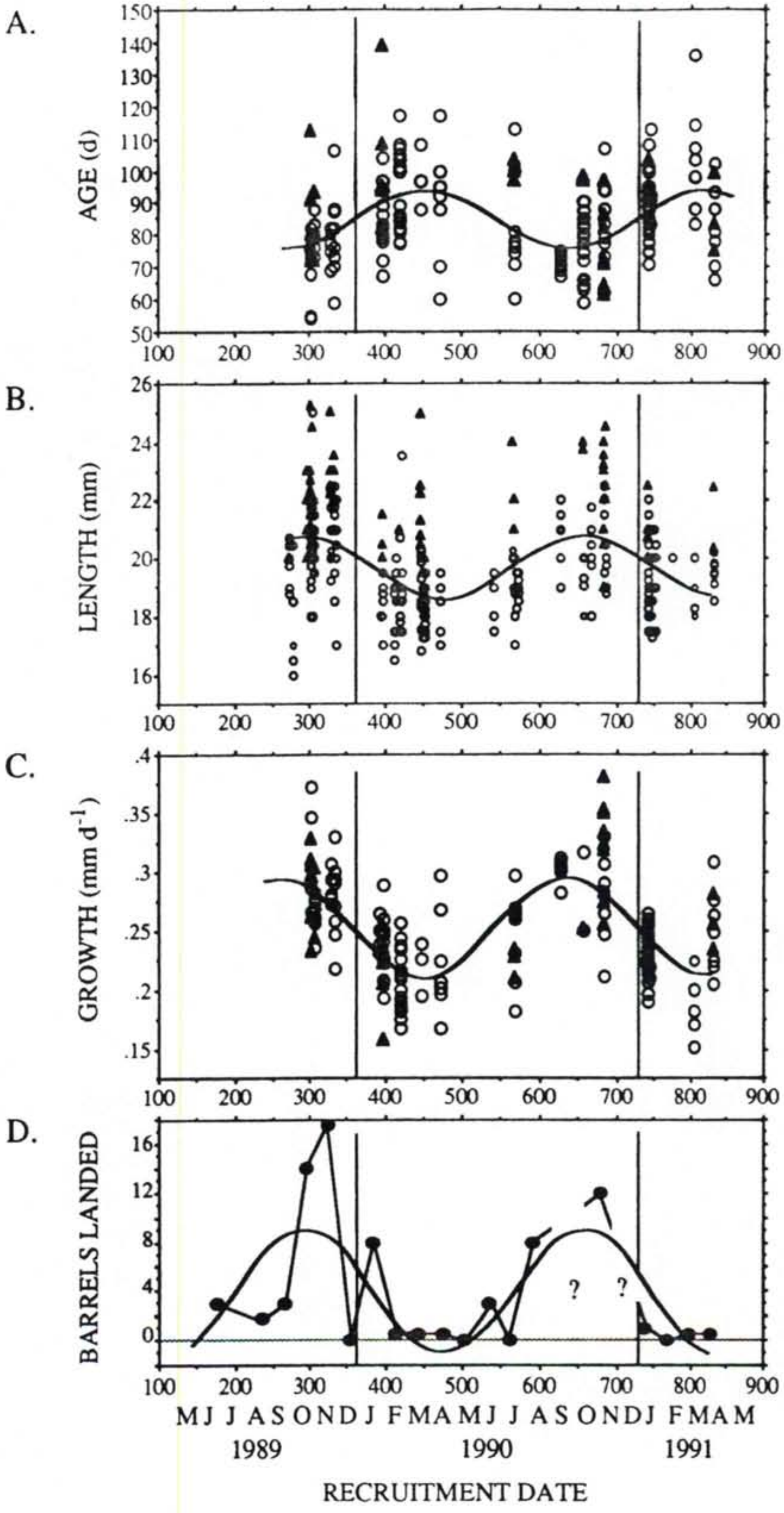

A.
AGE (d)
150
140
130
120
110
100
90
80
70
60
50
100 200 300 400 500 600 700 800 900
B.
LENGTH (mm)
26
24
22
20
18
16
100 200 300 400 500 600 700 800 900
C.
GROWTH (mm d^{-1})
.4
.35
.3
.25
.2
.15
100 200 300 400 500 600 700 800 900
D.
BARRELS LANDED
16
12
8
4
0
?
?
100 200 300 400 500 600 700 800 900
M J J A S O N D J F M A M J J A S O N D J F M A M
1989
1990
1991
RECRUITMENT DATE

Figure 8.7. Days-to-recruitment, and growth vs. hatch date, with fitted cosine functions, for *Sicydium punctatum* (open circles) or *S. antillarum* (filled triangles). Hatch dates are indicated for 1989, 1990 and 1991, as day numbers beginning with January 1, 1989; letters below x-axis indicate months. A: Days-to-recruitment = y = 81.346 + 6.447*cos(RJ_{hatch}+0), r^2 = 0.094, p = 0.0001, n = 193. Inclination of groups of points is because samples were collected at recruitment, not hatch, and $X_i + Y_i$ = collection date; this is illustrated by the arrow which graphically locates recruitment date for one sample. B: Linear growth index (G_L, see text) against hatch day, compared with cosine function of day of year (curve). The least-squares fitted equation y = 0.229 + 0.035*cos(RJ_{hatch}-3.3), with r^2 = 0.33, n = 176, p = 0.0001.

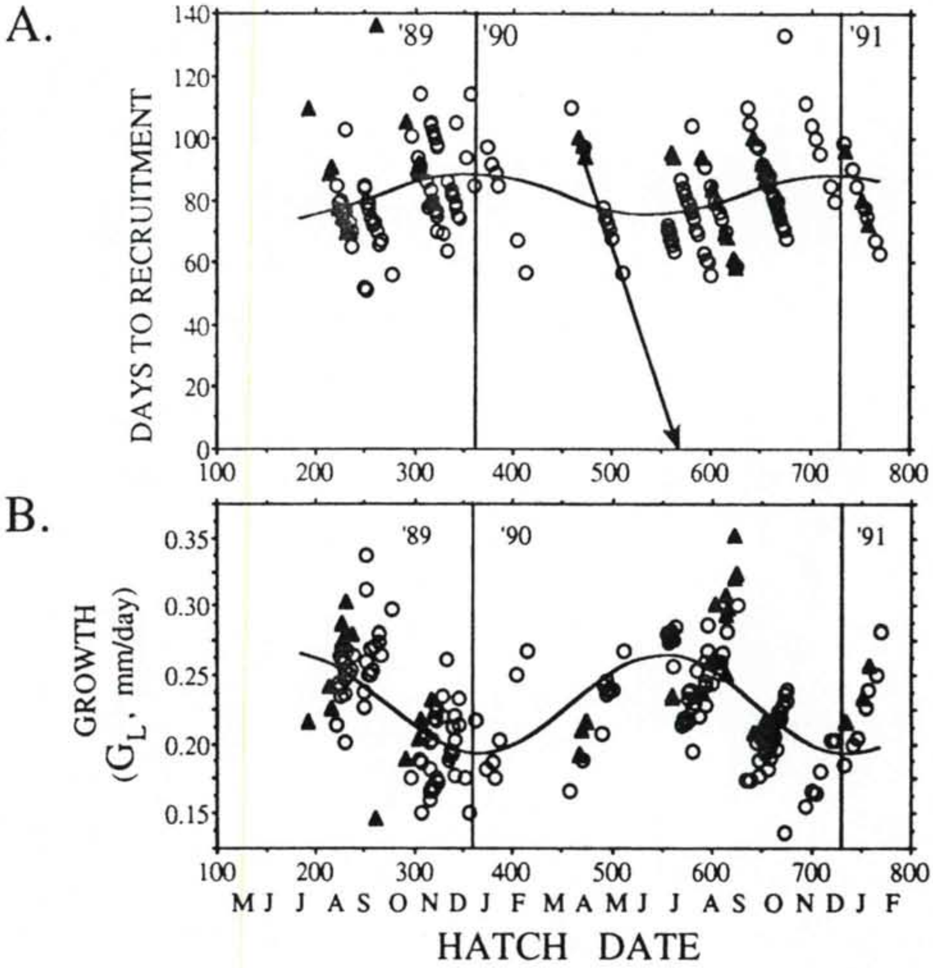
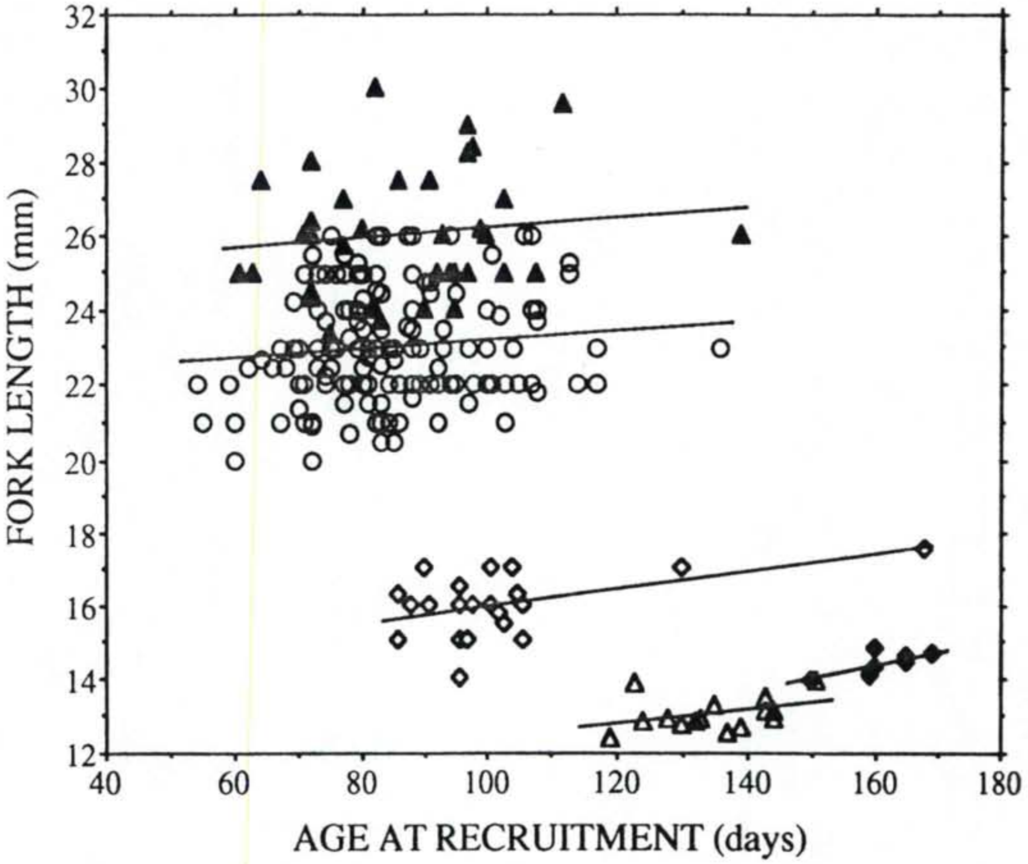

A.
DAYS TO RECRUITMENT
0
20
40
60
80
100
120
140
'89
'90
'91
100
200
300
400
500
600
700
800
B.
GROWTH
(G_L, mm/day)
0.15
0.20
0.25
0.30
0.35
'89
'90
'91
100
200
300
400
500
600
700
800
M J J A S O N D J F M A M J J A S O N D J F
HATCH DATE

Figure 8.8. Length-at-age, with least-square linear regressions, for recruiting fish (3 spp.) in Dominica with published data from Hawaii (2 spp., Radtke and Kinzie, 1988). Fork lengths are used (instead of standard length as elsewhere in this paper) to enable comparison with published data. Radtke and Kinzie (1988) data are from a single collection while Dominica data are from multiple collections. *Eleotris pisonis* is a preferentially carnivorous fish which shows slow pre-recruitment growth but rapid post-recruitment growth, as reported by Radtke and Kinzie (1988) for *Stenogobius genivittatus* and *Awaous stamineus*.



DOMINICA (upper 3 clusters)

○ *Sicydium punctatum* y = 0.013x + 22.0; n = 139, r-sq = 0.014, p = 0.16

▲ *Sicydium antillarum* y = 0.013x + 25.0; n = 36, r-sq = 0.015, p = 0.47

◇ *Eleotris pisonis* y = 0.023x + 13.6; n = 21, r-sq = 0.23, p = 0.028

HAWAII (lower 2 clusters, data from Radkte & Kinzie, 1988)

△ *Stenogobius genivittatus* y = 0.019x + 10.5; n = 15, r-sq = 0.15, p = 0.15

◆ *Awaous stamineus* y = 0.038x + 8.25; n = 8, r-sq = 0.508, p = 0.047

Chapter 9. Doppler- and Mortality-Effects in Recruitment Series: Consequences of Temporal Variation in Age-At-Recruitment

ABSTRACT

Systematic variation, beyond individual variation within samples, in age-at-recruitment can lead to profound alterations in episode-to-episode recruitment. These effects have not previously been discussed because systematic variation in age-at-recruitment had also not been shown. However, recent work demonstrated cyclic seasonal variation over two years for *Sicydium punctatum* and *S. antillarum* in Dominica, W.I. Simulation models employing natural levels of temporal variation show the consequence of this variation on recruitment.

I examine both seasonal and one-time variations. Recruitment profiles resulting from these under situations of constant larval output show that recruitment can incorporate Doppler-like effects which could be mistaken for variations in either larval output or mortality. The most profound effects of variation in age-at-recruitment arise when it is coupled with survival rates <1.0.

Similar or analogous dynamics are possible in tropical recruitment series based on pan-seasonal recruitments in the tropics, and multi-year series of temperate and other fisheries which may experience long-term variation such as El Niño events and incorporate the signal as variation in age-at-recruitment and recruitment fluctuations.

These results indicate a source of caution for length-based assessments, and also provide a new avenue for exploration of recruitment variation.

INTRODUCTION

In a discussion of recruitment in complex life cycles, Roughgarden et al. (1988) recognised not only the complexities of two-phase life cycles, but also, implicitly, the value of using a natural change in niche and habitat as a recruitment definition in investigation of recruitment processes. The existence of a change in niche, i.e. from planktonic to benthic, is a reference point which has biological meaning, as opposed to an arbitrarily size-based recruitment threshold which often does not. While Roughgarden et al. (1988) comment that erratic fluctuations in abundance of exploited species has long standing as a topic of human interest, it is equally true that regular variations and their anticipation have been as well. At each step in developing comprehension there remain some unexplainable observations, some residuals. It is the residuals which focus further interest, the unexplained which can lead to insight (as often remarked by Ian A. McLaren, Dalhousie).

The relationship of recruitment variations to changes in larval production, mortality, etc. has been of long-standing interest. Recently while seeking factors which might be associated with variations in the recruitment of

Sicydium spp. in Dominica, W.I., I found approximately 20% of variation in age-at-recruitment explained by recruitment date (Bell et al. in press, Ch. 8). While this was the first evidence for seasonal variation in age-at-recruitment, occasional geographic variation within species has been noted for *Stegastes partitus* and *S. flavilatus* (Wellington & Victor 1989) which suggested a mean difference between locations of 8 and 7 days. A significant ($p<0.0001$) geographic difference in larval durations of 6 species of wrasses was shown by Victor (1986b), with postlarval durations in Hawaii exceeding those in Palau. However, since the wrasse samples were not collected in the same season, differences could have been increased or reduced by seasonal effects. The finding of systematic seasonal variation (Bell et al. in press, Ch. 8) challenges the practice of reporting of age-at-recruitment (AAR) simply as a single number plus error or individual variation. Geographic differences cannot be assumed from differences in sample means unless they are taken at similar times. Because AAR at a single location may be a function of time, curve shape, phase, as well as mean value are important.

Variation in AAR is important to recruitment because it can disrupt the synchrony of hatch cohorts so that their temporal spacing at recruitment (observed frequency) differs from their original spacing at hatch (source frequency), or so that recruitment is not in order of hatching. This is analogous to the well-known Doppler effect of alteration of perceived signal frequencies due to displacement of either source or observer during the transmission of the signal. A similar effect occurs if speed of transmission changes (for sound, this would occur if air density changed), or if the signal takes a longer route. A changing AAR is analogous in this sense because it, by definition, determines the time until recruitment. (If size-at-recruitment also varies, growth rate variation may or not be concordant with AAR variation). Like a Doppler effect, the perceived (recruitment) change in frequency only persists while the speed of transmission (AAR) is changing.

The theoretical basis for a relationship of variable AAR to variable recruitment is twofold, arising out of (a) Doppler-like effects just described, and (b) variable accumulation of mortality even where daily rates are constant. Part (b) arises from the familiar equation

$N_t = N_o e^{rt}$, equivalent to (eq. 1)

$N_t = N_o e^{-Zt}$, (eq. 2)

where r is the natural logarithm of survival over one time unit and t is the number of time units (equivalent to AAR), and Z is the natural logarithm of survival with the sign changed (Ricker 1975).

The resulting temporal patterns in recruitment are not intuitively obvious, and so the purpose here is to explore these two issues. I do not aim in this chapter to address other factors possibly contributing to the seasonal recruitment (fishery) variation seen for *Sicydium* spp. in Dominica, W.I., but defer that to subsequent work.

Definitions, data and generalities

The word "recruitment" is used both in an aggregate sense and an individual sense. It is often used to indicate the attainment by individuals of some specified stage of development, or size, or vulnerability of a cohort (group) to a fishery (Ricker 1975). Completion of a life-history structured transition to new habit/habitat is often called either recruitment (Radtke et al. 1988) or settlement (Victor 1982, Victor 1986c, Victor 1986b, Breitburg 1989, Breitburg 1991, Cowen 1991, Robertson 1992). Collateral with these usages, the word "recruitment" is also used to indicate the quantity of recruits, the rate of recruitment or settlement. I use the phrase "age-at-recruitment" (AAR) to indicate the time from egg to recruiting or settling stages, as for settlement of reef fishes (Victor 1982, Victor 1984, Victor 1986c, Victor 1986a, Wellington & Victor 1989, Robertson 1992) or settlement/recruitment of sicydiine gobies (Radtke et al. 1988, Bell et al. in press).

The emphasis of this chapter is the effects of early life history on recruitment both by individuals and cohorts. For both, recruitment follows a period of growth, and size has historically been the main recognised indicator or correlate of recruitment (Ricker 1975). Identifying variations in age-at-recruitment (AAR) has become possible only recently because of the advent of techniques for obtaining fairly precise age estimates from otoliths (e.g. Victor 1982; Victor 1986b; Radtke et al. 1988; Wellington & Victor 1989). Until recently there has been no evidence of systematic temporal variation in age-at-recruitment. There has therefore been no reason until now to address the effects of such variations on recruitment patterns.

The variation in age-at-recruitment found in *Sicydium* spp. in Dominica, W.I. (Bell et al. in press, Ch. 8) is seasonally structured (Fig. 8.7). A fitted least-squares cosine regression against hatch date yielded the relationship:

$$AAR = 81.3 + 6.4*\cos((RJD_{hatch})+0), \qquad \text{(eq. 3)}$$

where JD is day of year and RJD is the same transformed to a cyclic variable in units of radians ($RJD = JD*2\pi/365$), the subscript ($_{hatch}$) is a qualitative identifier, and "+0" indicates (in this example) a nil phase lag with the calendar year (year viewed as a circular variable). The low correlation ($r^2 = 0.094$) reflects the variation among individuals at each date, but the relationship is highly significant ($p = 0.0001$, $n = 193$). Although the correlation is lower than that using recruit date, I preferred simulation based on hatch date over one based on recruitment because the steps flow with time instead of counter to it (which creates logical complications). Restricting the hatchdate analysis to *Sicydium punctatum* alone explained slightly more of the variance (15%) but I chose to include *S. antillarum* since it does form a part of the harvest, albeit a minor one. This choice results in a more moderate amplitude of variation than do the others, and is therefore a conservative choice for the simulations.

Seasonal variation (SVAR), as seen in *Sicydium* spp. in Dominica, is a special case of many possible patterns of dynamically varying age-at-recruitment. Reproduction and recruitment of *Sicydium* spp. in Dominica, W.I. are pan-seasonal, the former continuous and the latter episodic in synchrony with the last lunar quarter (Bell et al. in press, Ch. 8); the highest yields occurring in the fall. In exploring the origins of the seasonally skewed fishery profile for *Sicydium* spp., the peculiar and interesting effects of age-at-recruitment as a dynamic variable emerged.

THEORY

Systems with dynamic age-at-recruitment results show convergence of hatchdate-cohorts on single recruitment dates at some seasons, and divergence of adjacent hatchdate-cohorts to more separate recruitment dates in other seasons.

To model this process we need to make an assumption about when in the life-history AAR is determined (anywhere from hatch to recruitment). If we assume that AAR is substantially determined by the date of hatch, as would be so if events and conditions experienced in early life history have the greatest influence on later success, we can graphically model the process easily.

The main components of the graphic models are HATCH surfaces and RECRUITMENT surfaces. Larvae originate on the hatch surfaces and, with accumulation of age, progress on a 1:1 line (negative in the hatch-date-referenced model, positive in the recruitment-date-referenced model) toward the recruitment surface, and any intersection of a larval trajectory with a recruitment surface indicates by definition a recruitment event. Three basic graphic models are presented to illustrate the range of possibilities which have qualitative differences: they show the consequences of selected combinations of (a) AAR curves with slope >1.0 or <-1.0, and of (b) the larval age/stage when AAR is determined.

HATCH-DATE referenced AAR

If (Fig. 9.1) an individual's hatchdate is represented by X and the ordained AAR by Y, the line passing through that point with slope -1 will intersect with the X-axis at the recruitment date. The intersections of such lines with the curve of expected AAR vs. hatchdate can be used to graphically relate the hatching interval corresponding with any recruitment interval. Figure 9.1 shows the simplest situation: for an AAR-at-hatch curve which has no slope of absolute magnitude >1. (For a cosine curve, I expect slopes approaching 1 would be rare, so most situations should fit this model.) An arbitrarily chosen recruitment window is represented by the segment AB of the X-axis. This is graphically related to the segment GH, identified by the X-coordinates of the intersections C and D of the AAR-at-hatch curve and the -1:1 lines to A and B. The straight lines having slope -1 ($Y=b-X$) simply illustrate the trajectory of time remaining to recruitment: each day is one day closer.

Hatch-Date referenced AAR with RAPID CHANGE (steep slope)

A complication arises if the maximum negative slope of the AAR-at-hatch curve is lower than -1, when it is possible to have recruitment corresponding to two non-adjacent hatch intervals (Fig. 9.2). The horizontally pointing triangles bracket the two hatch intervals and also point to the intersections which define them. The consequence of this type of situation could be a discontinuous age distribution in the recruits (mortality would affect the older cohort for a longer time, and exponentially reduce its proportion).

RECRUITMENT-DATE referenced AAR with rapid change (steep slope)

A cautionary note: AAR could be treated other than as a function of hatch date, and this could affect prediction if AAR curves have slopes exceeding ±1. For example, I could view AAR as being determined at and therefore related to recruitment date instead of hatch date. Then, in the diagram (Fig. 9.3) the vertical lines would relate instead to the recruitment event and *positive* 1:1 lines would lead from hatch dates (x,0) until recruitment, indicated by the intersection of these with the AAR curve. Each larva starts on the x-axis, and rises at 45° UNTIL it hits the AAR curve. The value of the recruitment curve in this model is (by def.) equal to the larva's age so far. The larva recruits, and therefore does not reach other further-back parts of the AAR curve. Therefore, recruitment shadows can be formed. The x-values of the intersections would indicate the recruitment dates. However, this change of reference for AAR can produce qualitatively different behaviour, with segments of the curve following transition to slope in excess of 1 day/day being associated with recruitment shadows, as shown by Figure 9.2. Thus (with AAR curve maximum slopes exceeding ±1), while a Hatchdate-referenced AAR gives bimodal age distributions because of accumulation, a Recruit-date-referenced AAR generates at some places a recruitment shadow. This is because, in both models, the recruitment surface is 'opaque' to larvae, i.e. they must recruit when they encounter it; so while in the hatch-date referenced model the recruitment surface is the X-axis (which is flat and cannot have 'shadows') and the AAR curve is 'transparent' so that larvae are uninfluenced by encountering the curve at x-values not equal to their own hatch dates (i.e. except on first encounter), in the recruit-date referenced model the recruitment surface is the AAR curve which can have shadows because it is opaque. Other geometric models could describe systems where AAR is determined at any intermediate points partway through the postlarval period; these models would necessarily be more cumbersome and at this point not significantly more plausible. This digression completed, I now continue with Hatchdate-referenced systems.

CONTINUING WITH HATCHDATE-REFERENCED AAR WITH MODERATE SLOPES

While it is a simple task, given an AAR-at-hatch curve, to identify the production interval(s) corresponding to any chosen recruitment interval, estimating recruitment-vs-season profiles using this method would be extremely tedious. Therefore, because these systems are difficult to deal with algebraically, I chose to use simulation models, both deterministic and stochastic, which could also incorporate the compounding effects of mortality over time on cohorts.

SIMULATION OF POPULATION-LEVEL RECRUITMENT EFFECTS OF VARIABLE **AAR**, USING A HATCH-DATE REFERENCED MODEL

I aim to show the properties of the type of recruitment variation which can result from a simple situation where the following prevail: (1) constant larval output; (2) constant daily survival rates; (3) age-at-recruitment varies as a function of the hatch date. I then briefly introduce individual stochastic variation into this system to check whether the effects vary qualitatively between deterministic and stochastic situations.

The model

The system envisioned is one such that each larva has an expected recruitment date, and the total number of recruits on a particular day is the sum of all larvae having that expected recruitment date. Cumulative mortality (M_{cum}), daily mortality (M_d), daily survival (S_d), cumulative survival (S_{cum}) are related to each other and time (days) as follows:

$$M_d + S_d = 1, \qquad \text{(eq. 4)}$$

$$S_{cum} = S_d^{days}, \qquad \text{(eq. 5)}$$

$$M_{cum} + S_{cum} = 1. \qquad \text{(eq. 6)}$$

Since cumulative mortalities must be calculated from survival (i.e. cannot be calculated from daily mortality directly), survival (defined as N_t/N_0 where $t=date_0 + days$) is a convenient, meaningful and mathematically accessible term. Cohort size at some time t is given by:

$$N_t = N_0 * S_d^{days}, \qquad \text{(eq. 7)}$$

or

$$N_t = N_0 * e^{\ln(S)days}, \qquad \text{(eq. 8)}$$

which can be rewritten as

$$N_t = N_0 * e^{-Zt}, \qquad \text{(eq. 9)}$$

as often used in the fisheries literature.

The simulation model (Fig. 9.4) used expected AAR calculated as a cosine function of the day of the year, and calculated both the date of recruitment and the resulting overall survival and numbers remaining at the date of recruitment. The parameters of the cosine function were chosen to be close to those determined from otolith data for *Sicydium* spp. The model employed constant daily probabilities of survival in each run of the program (i.e. constant S_d over all seasons), and could be run with any chosen constant daily survival rate. Recruits were accumulated for each recruit date while the program cycled through an entire year of hatch-dates.

For these model runs I held daily survival (S_d) constant at all seasons and for all ages. This simplified the task, and avoided relying on contentious assumptions, discussion of which is beyond the scope of this paper. Cumulative survival (S_{cum}) is a function of S_d and time, and so may vary as a consequence of variation in AAR.

Where individual variation was incorporated into the model, it was as a scaled random number added to the age-at-recruitment for that day's hatch. It approximates the within-date variation found in *Sicydium* spp. in Dominica, W.I. Each day, ages-at-recruitment, date of recruitment and cumulative survival were calculated for a number of such pseudo-individuals. Fractional individuals were permitted in the model because the (real) population of postlarval gobies is large enough to make integer effects unimportant. Mean values for age-at-recruitment (where recruits per day >1) and survival were calculated within the model. Smoothing of plots was done by taking 28-day running means, because recruitment of *Sicydium punctatum* is episodic at approximately that interval. Finally, the simulation program wrote results to a file that could be imported by statistics software.

Effects of variation in age-at-recruitment

The simplest variations are step or spike functions. I use the case of daily survival = 1.0, i.e. all larvae have the same cumulative survival (i.e. to recruitment), because at $S_d = 1.0$ a cohort retains its number over time. For an abrupt and step-like change in AAR, increases in AAR are followed by abrupt decreases in recruitment; the decrease is of duration approximately equal to the difference between the new and previous AAR (Fig. 9.5a,b). A positive difference of ten days results in a decrease which lasts about ten days. Restoration of previous AAR is just a change in the other direction -- in this case a decrease, which in this case (Fig. 9.5a,b) is also ten days, causing an increase in recruitment which lasts about ten days. If we then add mortality effects ($S_d < 1.0$), cumulative survival will vary inversely and exponentially with AAR.

Triangular spikes in an otherwise stable AAR sequence generate subsequent oscillations in recruitment. Oscillations caused by upward spikes show decreases followed by increases; those caused by downward spikes show the reverse -- increases followed by decreases (Fig. 9.5 a,b).

Using values from *Sicydium punctatum*

If we use a seasonally varying AAR as is found in *Sicydium* spp. in Dominica, W.I., we can estimate the seasonal recruitment profile that should prevail at various chosen S_d (daily survival). In all of the simulations in this chapter, production of larvae is held constant over time, so that it plays absolutely no role in the temporal variation in recruitment.

A range of daily survivals produces a range of recruitment profiles (Fig. 9.6). At $S_d = 1.0$ the variation is over 25% (of the maximum). The recruitment curve is a symmetrical hill with a maximum nearly coincident with the quickest AAR (this will not turn out to be a generality!). At $S_d = 0.99$ the variation is a factor of 40% and the curve is losing its left-right symmetry as a trough of low recruitment begins to show on the left side. As daily survivals are reduced, the trough becomes a flat minimum which becomes lower and wider, and the peak relatively higher and much narrower. Even by $S_d = 0.90$ the variation is a factor of 4, so recruitment can only marginally be described as pan-seasonal. At $S_d = .7$ recruitment is virtually zero during the winter and spring. (But beware, because in field observations minimum values may be low and erroneously interpreted as zeroes, while the higher values are less difficult to measure with the same confidence; wrong zeroes would inflate the estimated geometric variation. For these graphs the minima are output of simulations and are not subject to the same observational error.) The temporal locations of maximum and minimum recruitment vary with S_d. Initially ($S_d = 1.0$) the peak is near day 180, the trough near day 0/365. Progression of both of these is rapidly to the right as S_d decreases even minutely from 1.0; but then a stable position appears to be achieved near $S_d = 0.90$, with little change down to $S_d = 0.60$. However, although the timing of the peak and valley tend to stabilise quickly, with decreasing S_d the peak of maximum seasonal recruitment becomes increasingly narrow, and (complementarily) the valley of minimum recruitment keeps flattening and widening.

How realistic is the scenario so far? There is good correspondence with the recruitment profile obtained from the fishery (Fig. 9.7) for *Sicydium* spp. in Dominica, W.I. and that obtained for $0.80 \leq S_d \leq 0.90$. Seasonal variation in AAR is therefore plausible as an origin for the seasonal fishery profile.

Before considering why the recruitment maxima/minima behave as they do, let us observe what happens when AAR is scaled. I ran simulations using the AAR function found for *Sicydium* spp. multiplied by constants 2, 0.5, 0.25 (Figs. 8,9,10). This preserved the same variation relative to the mean. Since we saw that temporal locations of peaks/troughs changed little below $S_d = 0.90$, I plot only $S_d = 1.0$ and $S_d = 0.70$ to show the recruitment patterns resulting under conditions of zero and substantial mortality.

The results show that even though the multipliers do not affect the seasonal phase of the AAR functions, the timing of maxima/minima of recruitment is profoundly shifted. With doubled AARs (150 to 175 days-to-recruitment) curves are shifted to the right for both S_d values. With halved values the peak at $S_d = 1.0$ precedes the AAR minimum, and the $S_d = 0.70$ peak is about 40 days after the AAR minimum. With quartered AARs, the $S_d = 1.0$ peak is further still to the left, and the $S_d = 0.70$ peak is only slightly later than the AAR minimum.

Why are the peaks where they are?

If our expectation was that timing of peaks/valleys should relate to the AAR minimum and maximum, these results will appear counterintuitive. The important distinction between $S_d = 1.0$ and $S_d = 0.70$ is that mortality plays no role in the former and a significant role in the latter. Since

$$S_{cumulative} = S_d^{AAR} \quad \text{(eq. 10)}$$

fewer recruits result from a slow-growing cohort than from a faster-growing cohort, where a certain size (which may be a constant or nearly so for some species) must be reached in order to recruit. (This is nothing to do with size- or age-dependent mortality, but simply the result of cumulative mortality.) At $S_d = 1.0$ there is no difference in $S_{cumulative}$ with varying AAR, so the timing of recruitment peaks is purely determined by a Doppler-like effect which, when AAR is decreasing, causes convergence of multiple day-hatch-cohorts on fewer recruitment-days; at lower S_d mortality plays a greater role, until at $S_d = 0.70$ the Doppler-like effect is swamped by variable survival. The seasonal recruitment profile thus shifts (as mortality increases from zero) from being Doppler-dominated to being mortality-dominated.

The phase relationships are visualised graphically in Fig. 9.11. The pairs of horizontal bars show the minimum and maximum AAR as it would appear on the X-axis. At very low mortality rates (S_d near 1.0) the recruitment peak will be approximately one AAR after the point of greatest **negative** rate of change in AAR (**max. negative** dAAR/dt) The recruitment minima, similarly, are lagged approximately one AAR after the point of greatest **positive** rate of change in AAR (**max. positive** dAAR/dt). At higher mortalities (e.g. $S_d = 0.70$) the recruitment peak will be approximately one AAR after the AAR **minimum value**, and the recruitment minimum will be approximately one AAR after the AAR **maximum value**. Thus under low mortality the timing of peak recruitment is dominantly influenced by derivatives of the AAR curve, while under considerable mortality it is influenced by extreme values of the AAR curve. The transition from $S_d = 1.0$ to $S_d = 0.7$ shows joint influence. This pattern can be seen in all levels of AAR simulated here.

Note that where the minima are wide troughs, the graphic calculation generally finds the center. This makes sense if the recruitment curves are plotted on a log scale, which shows the troughs to approximate part of a negative sine-wave (just as the recruitment profile at $S_d = 1.0$ is a sinusoidal curve). The calculated temporal occurrence of minima accurately locates the real minima. Relative variation -- range/minimum -- increases with higher mortalities/lower survival. This makes the lower values occupy large ranges on logarithmic scales although they are (arithmetically) extremely close.

Adding individual random variation in AAR to the model

So far I have used only models which are entirely deterministic. However, empirical data show individual variation in AAR at each hatchdate (Victor 1982, Victor 1986b, Wellington & Victor 1989, Cowen 1991, Bell et al. in press) (Fig. 8.7) so it is reasonable to ask how such variation would affect recruitment dynamics. I modified the simulation program to 'sample' 20 randomised AARs on each day of the year (Fig. 9.4). The randomised AARs were first calculated according to the cosine-regression formula found for *Sicydium* spp., then modified by adding a normally distributed randomly chosen number scaled to range from -40 to +40 days (Fig. 9.12a). (The random numbers were read randomly from a list of 5000 normally-distributed pseudo-random numbers). AARs were further constrained by rejecting any AARs below 50 to preserve the similarity with data for *Sicydium* spp. Finally, the program wrote a file containing the number of surviving recruits, the geometric mean AAR, and the variance in AAR for each recruitment date.

With substantial individual random variation added at each hatchdate the recruitment seasonality remains (Fig. 9.12c,d,e). The Sd=1.0 recruitment pattern appears to have been substantially damped, as expected, by the added randomness. Although randomness would be expected to reduce relative seasonal differences, and the peak is less distinct, it still occurs approximately when predicted by the graphical method. For the Sd=0.75 recruitment pattern, the maximum occurs nearly where predicted by the graphical method, and the running mean indicates a seasonal difference of nearly two orders of magnitude. There is much day-to-day variation, resulting from the influence of early (expected) AARs produced at each hatchdate by the randomness added to AAR in the model.

IMPLICATIONS

Where there are peaks in recruitment it is natural to assume that they are generated by corresponding peaks in spawning, or pulses of good conditions which increase survival. However, as these results demonstrate, there can be situations where recruitment variation is spectacularly decoupled from spawning intensity. The close match of the observed seasonal recruitment of *Sicydium* spp. to a simulation suggests that not only is this a theoretical possibility, it is a real phenomenon. There is no reason to expect that this phenomenon is peculiar to a single species, but some species provide better opportunities to observe recruitment phenomena. (The features of *Sicydium* spp. are rapid and pulsed recruitment, spatial restriction and migration (diadromy) which increases accessibility, and pan-seasonal reproduction and recruitment.)

Several dimensions of structural complexity can be added to the AAR pattern and mortality rate, life-history structured and seasonally structured mortality and growth rates foremost among them. The model portrayed here is believed to show one, but not the only, source of recruitment variation; various sources would have combined effects which might be evident as departures from model expectations.

A conventional view of the components of recruitment is

$$\text{Recruits} = \text{Natality} * S_d^{t} - E + I \,, \qquad \text{(eq. 11)}$$

where natality is the production of larvae, S_d is daily survival ($S_d + M_d = 1$), t is time in days (AAR in days), E is emigration and I is immigration.

In this representation, Doppler-like effects at high survival (low mortality) could only be subsumed under E and I, and effects at lower survivals accounted for within the exponent t. Alternatively, the equation (eq. 11 above) can be modified as

$$\text{Recruits}_i = \sum(\text{Natality} * S_d^{t})_i - E + I \,, \qquad \text{(eq. 12)}$$

where the subscript i denotes the cohort(s) with recruitment in time interval i.

Possible effects can be categorised as population-dynamic (the shorter term), and selection (over the longer term). Population-dynamic effects could influence selection if they persist.

What population-dynamic effects could result from recruitment peaks with origins in seasonally variable AAR? A recruitment cycle is the first result, through which further effects if present should be generated. *Sicydium* spp. are long-lived, continuously iteroparous fish, and this makes it unlikely that there would be entrainment of recruitment cycles into subsequent life-history events. Because recruits are joining an established population which is pan-seasonally reproductive, and delay until first reproduction is probably three to six months -- during which time they would be subject to mortality which is probably density-dependent and negatively size-dependent since adults are territorial (Nishimoto & Fitzsimons 1986, Fitzsimons & Nishimoto 1990) -- peak recruitments probably do not result in subsequent and significant peaks of spawning. The minimal seasonality of spawning in *Sicydium* spp. in Dominica (Ch. 3) also does not support the existence of effects on subsequent maturity. (However, in species like temperate fish, insects, or plants, which are semelparous or seasonal, a seasonal signal generating the Doppler-like effects here described could affect later stages, including condition factors at time of reproduction, and could then have more profound and long-term effects than would be expected in *Sicydium* spp.)

Under conditions of density dependence at particular stages, stable seasonal recruitment of *Sicydium* spp. could partially balance selection for arrival at the recruitment peak (balance occurring according to the marginal increase in mortality with increasing recruit density, against the marginal increase in mortality due to postponement of recruitment). Negative density-dependences are also likely at some stages, for example stages which are schooling and may benefit from predator swamping and/or information exchange (Pitcher et al. 1986). Thus, at various life-history points there are plausible opportunities for both positive and negative frequency-dependent selection for AARs which either are shorter, or which are out of phase, or possibly longer as well. Presumably, AARs are the result of selection. The AARs of three species of goby in Dominica are different to very different (Bell et al. in press), indicating that the same AAR is not always selected for even with closely related and sympatric fishes. Some of the difference may be due to selection averaging over a wide geographic range within which gene exchange is sufficient to prevent adaptations to all local conditions, where each of the three goby species has a particular range and thus a potentially different geographic base for inputs to selection. Entrained recruitment cycles might influence the development and maintenance of spawning seasonality (e.g. in spring- or fall- spawning salmonids, in early- or late-spawning clupeoids). Irregular effects would less likely be accommodated within an inherited behavioural framework, and intermittent drastic declines in population would be seen in species not so adapted; the phenomenon which comes to mind in this context is El Niño. This suggests that survival through the larval stage is not the only potentially important variable that could be addressed under tests of match-mismatch hypotheses.

Within-sample variation in AAR (or settlement time) has been discussed in terms of the benefit associated with greater flexibility in settlement and greater opportunity to select superior habitats. Cowen (1991) has visualised postlarval growth as falling into two categories: pre- and post-competent, depending on whether the postlarva was insufficiently developed to settle, or was of settlement capability but had not settled. He associates the later period with reduced otolith (and presumably somatic) growth. Such flexibility may provide some scope for damping of entrained patterns generated by seasonally variable AAR.

As cautioned above, it has been beyond the aims of this chapter to eliminate competing mechanisms which may contribute to the yield variation in *Sicydium* spp. in Dominica, W.I. However, structured seasonal variation in age-at-recruitment (AAR) is clearly capable of generating such variation, and the phase relationships (e.g., temporal locations of minima, maxima in AAR and in yield) support a strong connection. It remains to be seen to what extent other factors moderate or accentuate the portion of variation that is due to the Doppler-like and compounded mortality effects which have been described here.

Figure 9.1. Recruitment dynamics, hatch-date referenced. (See text). Relationship (neglecting mortality) of arbitrarily defined hatch window to recruitment window with variable AAR. For generality the lower axis, representing time, is expressed as degrees of a cycle, but could be days of a year. Recruitment over the period AB results from larval production over period GH. By definition, angle ECF=45°, because the number of days to recruitment declines by one each day of an individual's life. Similarly, CEF=90°, and CFD=135°. FD=AB, and ED=GH. In this example, recruitment rate is more intense than hatching; but the converse occurs with equal frequency. X,Y coordinates of points C and D are (respectively) the intersections of equations 1 and 2, and 1 and 3. The X-coordinates of G and H are those of C and D; the size of the hatch or production window GH is the difference between these.

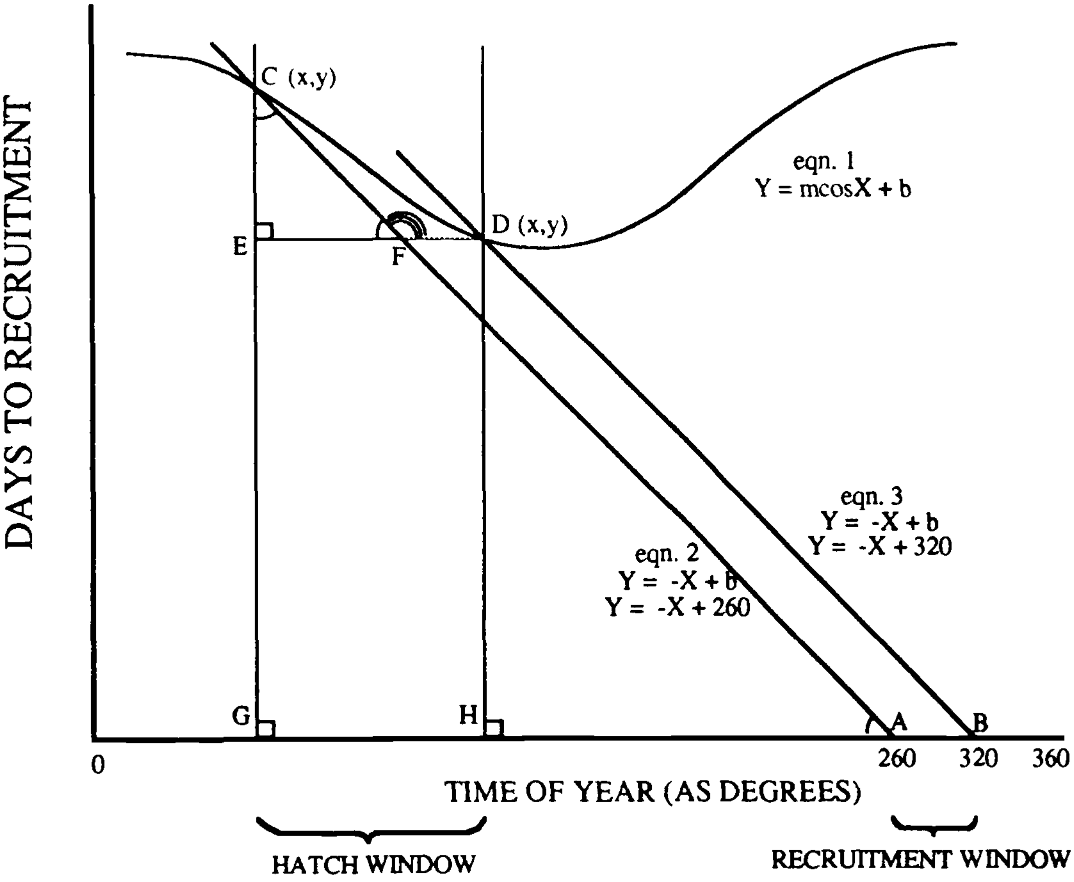

DAYS TO RECRUITMENT
C (x,y)
D (x,y)
E
F
G
H
A
B
eqn. 1
Y = mcosX + b
eqn. 2
Y = -X + b
Y = -X + 260
eqn. 3
Y = -X + b
Y = -X + 320
0
260
320
360
TIME OF YEAR (AS DEGREES)
HATCH WINDOW
RECRUITMENT WINDOW

Figure 9.2. Recruitment dynamics, hatch-date referenced, with high dAAR/dt. (see text, and previous figure legend). Where dAAR/dt <-1, recruits show bimodal age distribution at some times. The mechanics are similar to the previous example, except that because of the high negative slope (i.e. <-1) it is possible to have multiple intersections with eqn. 1 and eqn. 2,3,...etc., and as a consequence the hatch window corresponding to the recruitment window AB is split because larvae hatching in the interval IJ recruit prior to time A. Neglecting mortality effects, fish recruiting during interval AB will have a discontinuous age distribution. Recruitment over the period AB results from larval production over period GH. By definition, angle ECF=45°, because the number of days to recruitment declines by one each day of an individual's life. Similarly, CEF=90°, and CFD=135°. FD=AB, and ED=GH. X,Y coordinates of points C and D are (respectively) the intersections of equations 1 and 2, and 1 and 3. The X-coordinates of G and H are those of C and D; the size of the hatch or production window GH is the difference between these. Note that vertically moving the AAR curve (eq. 3) changes only the interval between hatch and recruit times, but does not affect the convergence or divergence that is possible at different seasons.

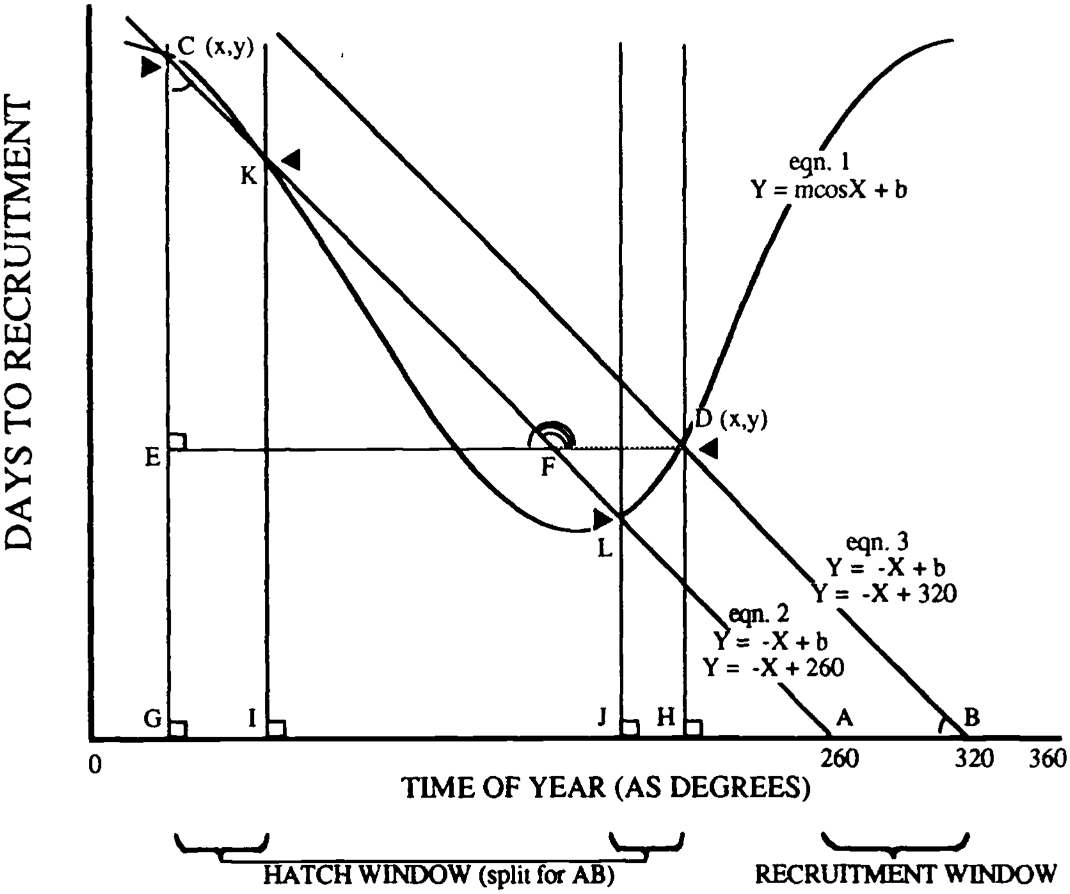
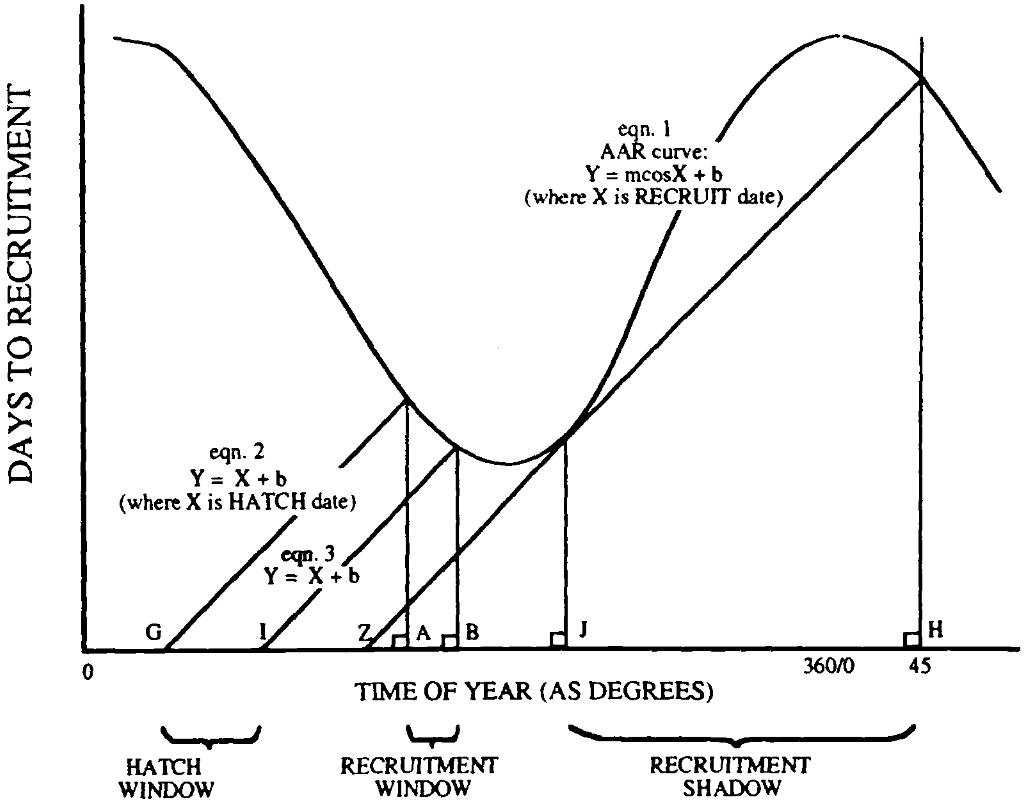

DAYS TO RECRUITMENT
TIME OF YEAR (AS DEGREES)
0
260
320
360
C (x,y)
K
D (x,y)
E
F
L
G
I
J
H
A
B
eqn. 1
Y = mcosX + b
eqn. 2
Y = -X + b
Y = -X + 260
eqn. 3
Y = -X + b
Y = -X + 320
HATCH WINDOW (split for AB)
RECRUITMENT WINDOW

Figure 9.3. Recruitment dynamics, recruitment-date referenced, with high dAAR/dt. If AAR is thought of as being determined at recruitment date instead of hatchdate, qualitatively different dynamics are generated where maximum slope of the AAR curve exceeds 1. Larvae hatched in interval GI gain age at one day per day, until intersection with the AAR curve, which now acts as a recruitment surface; they recruit in interval AB. However, recruitment under segments of the AAR curve is zero from any point where maximum slope first exceeds 1 to the next intersection of that (45°) tangent and the AAR curve. Thus, while production during GI is concentrated over the shorter interval AB, Z marks the date where time to intersection with the AAR curve becomes very long. Larvae hatched immediately before Z recruit before J; however larvae hatched after Z cannot recruit until H, so there is no recruitment between J and H.

Thus (with AAR curve maximum slopes exceeding ±1), a Hatchdate referenced AAR gives bimodal age distributions because of accumulation, and a Recruit-date referenced AAR generates at some places a recruitment shadow. This is because, in both models, the recruitment surface is 'opaque' to larvae, i.e. they must recruit when they encounter it; but in the Hatchdate referenced model the recruitment surface is the X-axis (which is flat and cannot have 'shadows') and the AAR curve is 'transparent' so that larvae are uninfluenced by encountering the curve at x-values not equal to their own hatch dates, while in the Recruit-date referenced model the recruitment surface is the AAR curve (recruitment surfaces are opaque by def.) which can have shadows.


DAYS TO RECRUITMENT
eqn. 1
AAR curve:
Y = mcosX + b
(where X is RECRUIT date)
eqn. 2
Y = X + b
(where X is HATCH date)
eqn. 3
Y = X + b
G
I
Z
A
B
J
H
0
360/0
45
TIME OF YEAR (AS DEGREES)
HATCH WINDOW
RECRUITMENT WINDOW
RECRUITMENT SHADOW

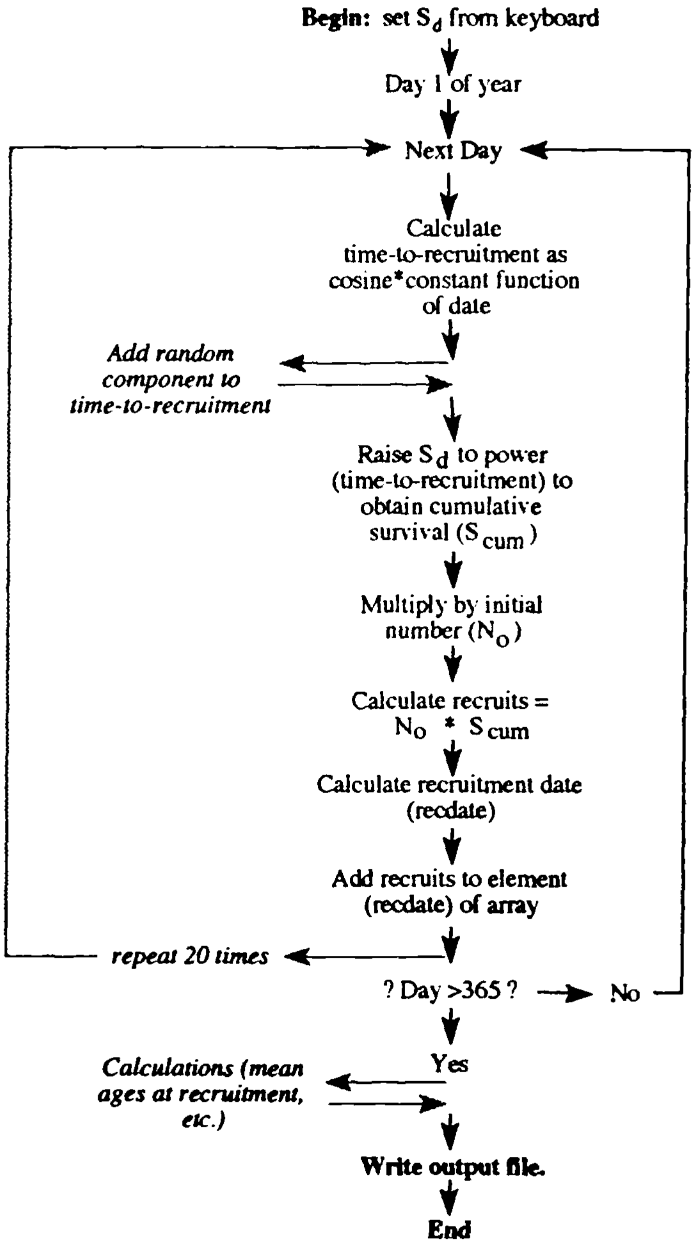


Figure 9.4. Flowchart for simulation, showing steps taken by the simulation program. Greyed arrows and italicised text on the left indicate additional steps which can incorporate individual variation into the model.

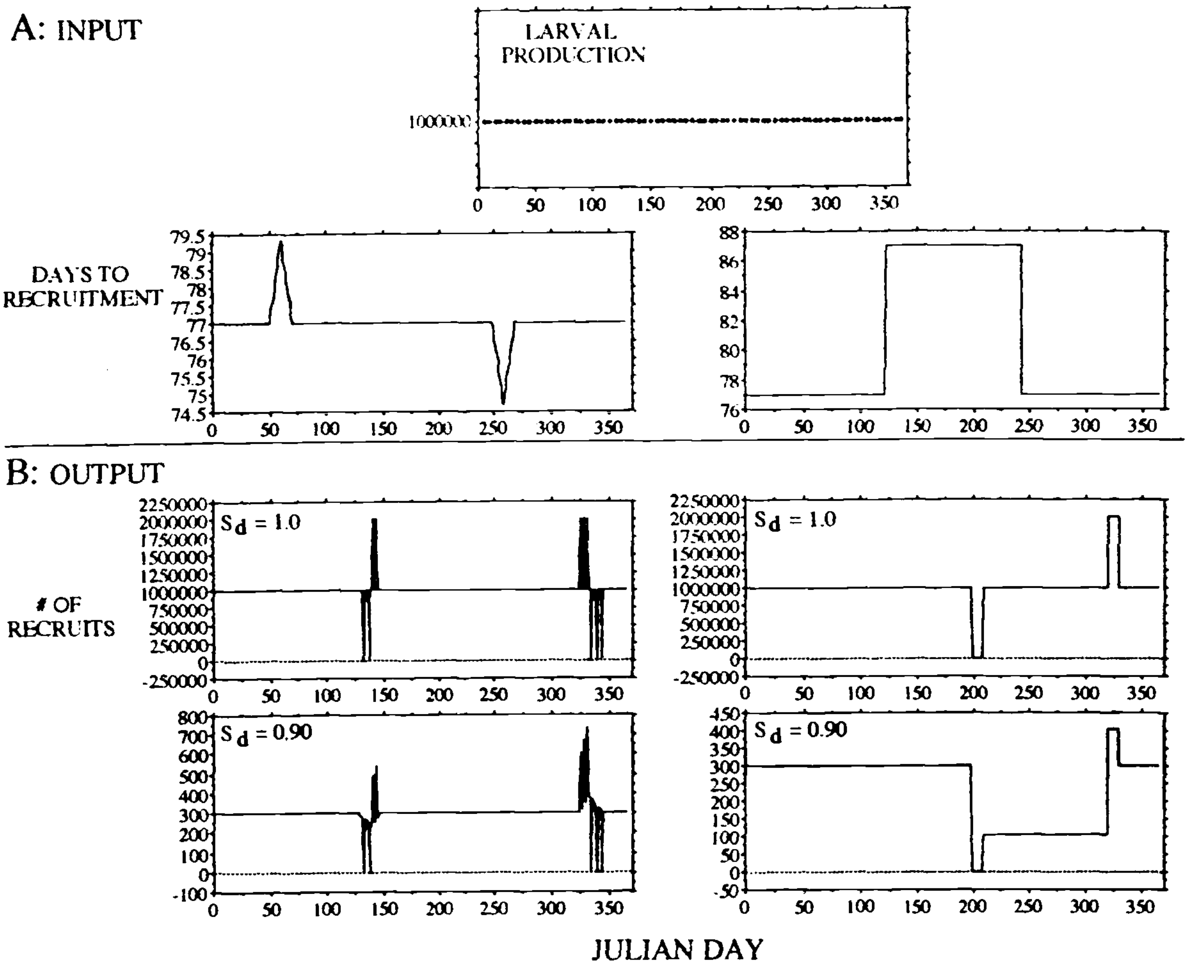
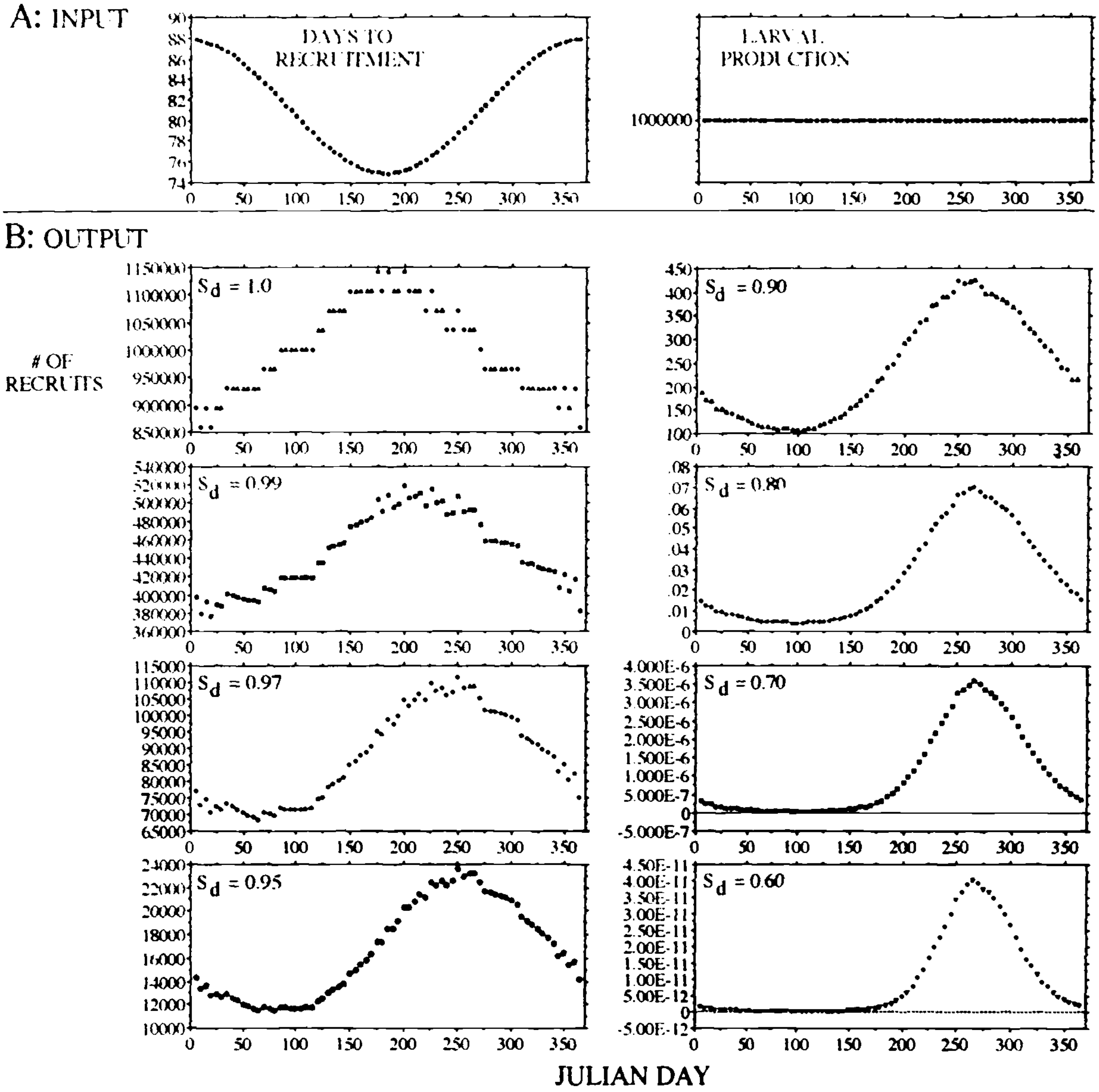


Figure 9.5. Effects of abrupt changes in AAR. Doppler-like effect in recruitment for two simplistic seasonal patterns of AAR (not natural data). Reproduction is seasonally constant (1,000,000/day) for these simulations. Upper graphs (A) show inputs to model: time to recruitment and larval production at each hatch date. Subsequent graphs (B) show simulated recruitment patterns obtained with daily survival rates as noted on each graph.

Figure 9.6. Simulation (deterministic) results showing Doppler effect and effect of AAR on cumulative survival. Inputs are using parameters of seasonal variation of age-at-recruitment vs. hatch date of *Sicydium* spp. in Dominica, W.I and constant larval production (1,000,000/day). Upper graphs (A) show inputs to model: time to recruitment and larval production at each hatch date. Subsequent graphs (B) show simulated recruitment patterns (28-day moving averages contribute a constant additional recruitment lag of 14 days) obtained with a range of daily survival rates as noted on each graph. At $S_d = 1.0$ all variation is due to Doppler-like effects giving a recruitment peak near day 180, but increasing role of mortality shifts the recruitment peak to the right, stabilising near day 265.


A: INPUT
DAYS TO RECRUITMENT
90
88
86
84
82
80
78
76
74
0
50
100
150
200
250
300
350
LARVAL PRODUCTION
1000000
B: OUTPUT
OF RECRUITS
S_d = 1.0
1150000
1100000
1050000
1000000
950000
900000
850000
S_d = 0.99
540000
520000
500000
480000
460000
440000
420000
400000
380000
360000
S_d = 0.97
115000
110000
105000
100000
95000
90000
85000
80000
75000
70000
65000
S_d = 0.95
24000
22000
20000
18000
16000
14000
12000
10000
S_d = 0.90
450
400
350
300
250
200
150
100
S_d = 0.80
.08
.07
.06
.05
.04
.03
.02
.01
0
S_d = 0.70
4.000E-6
3.500E-6
3.000E-6
2.500E-6
2.000E-6
1.500E-6
1.000E-6
5.000E-7
0
-5.000E-7
S_d = 0.60
4.50E-11
4.00E-11
3.50E-11
3.00E-11
2.50E-11
2.00E-11
1.50E-11
1.00E-11
5.00E-12
0
-5.00E-12
JULIAN DAY

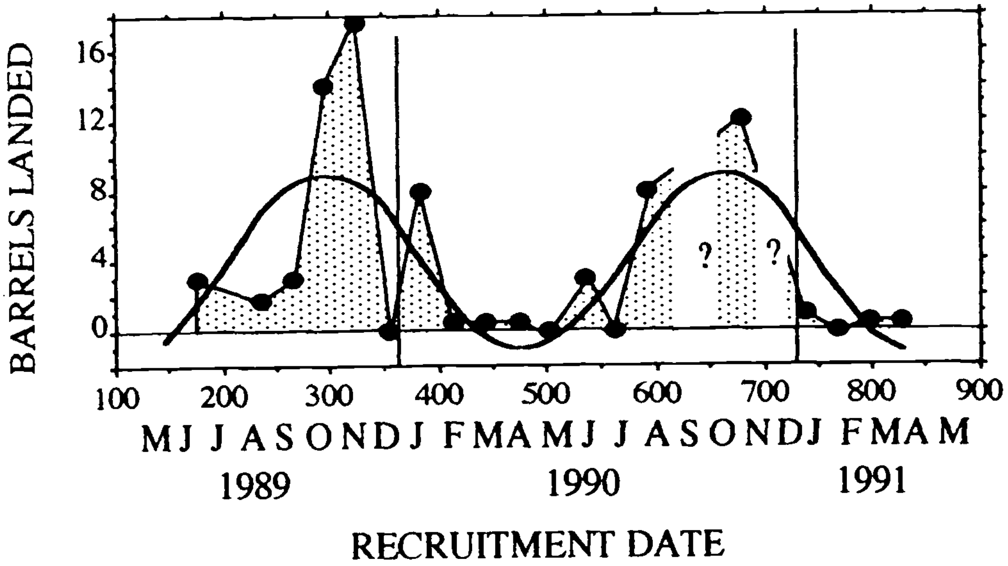


Figure 9.7. Yield of *Sicydium* spp. in Dominica, W.I. Postlarval recruits at Layou. Migrations are typically on the fourth day following the last lunar quarter and sustain a traditional fishery. The shape of the seasonal profile is quite similar to that produced by the simulation at $S_d \cong 0.9$ using as input *Sicydium* spp. data with constant daily larval production.

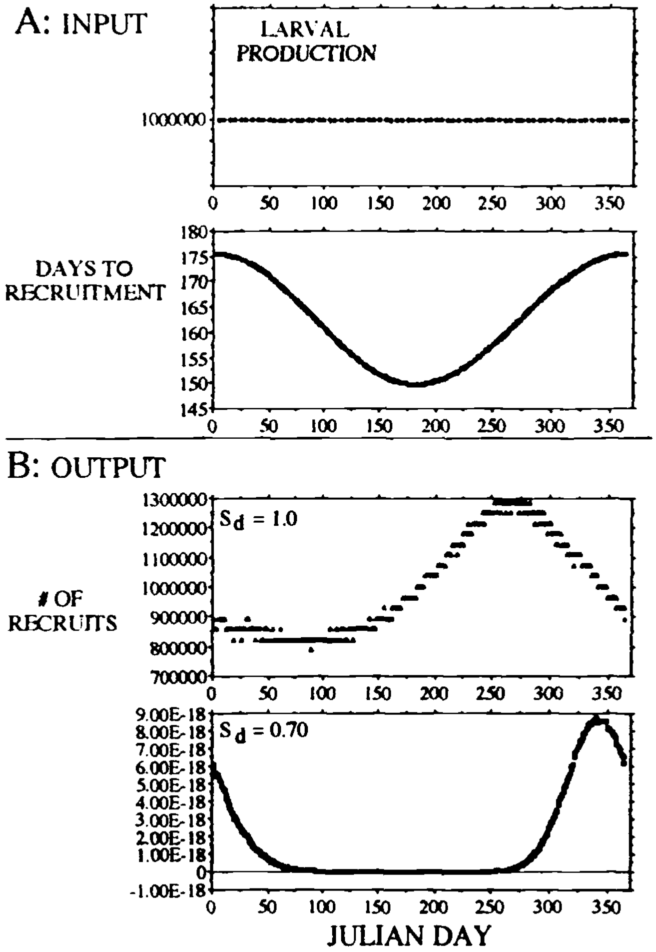


Figure 9.8. Simulation with doubled AAR amplitude. Simulation results: Doppler effect and effect of AAR on cumulative survival. Inputs are using parameters of 2*seasonal variation of age-at-recruitment vs. hatch date of *Sicydium* spp. in Dominica, W.I., and constant larval production as before.

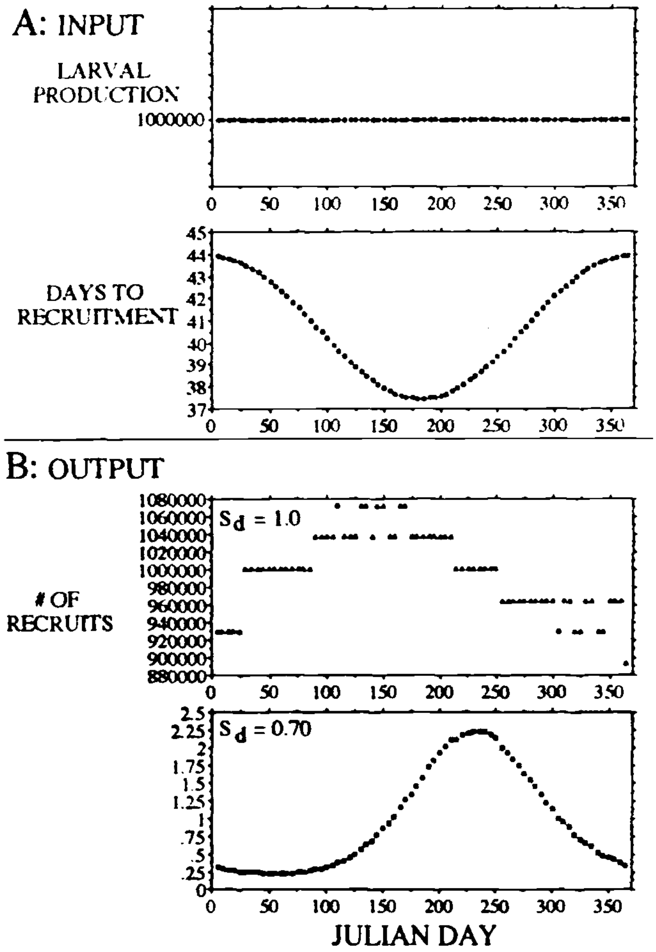


Figure 9.9. Simulation with halved AAR amplitude. Simulation results: Doppler effect and effect of AAR on cumulative survival. Inputs are using parameters of 0.5*seasonal variation of age-at-recruitment vs. hatch date of *Sicydium* spp. in Dominica, W.I and constant larval production as before.

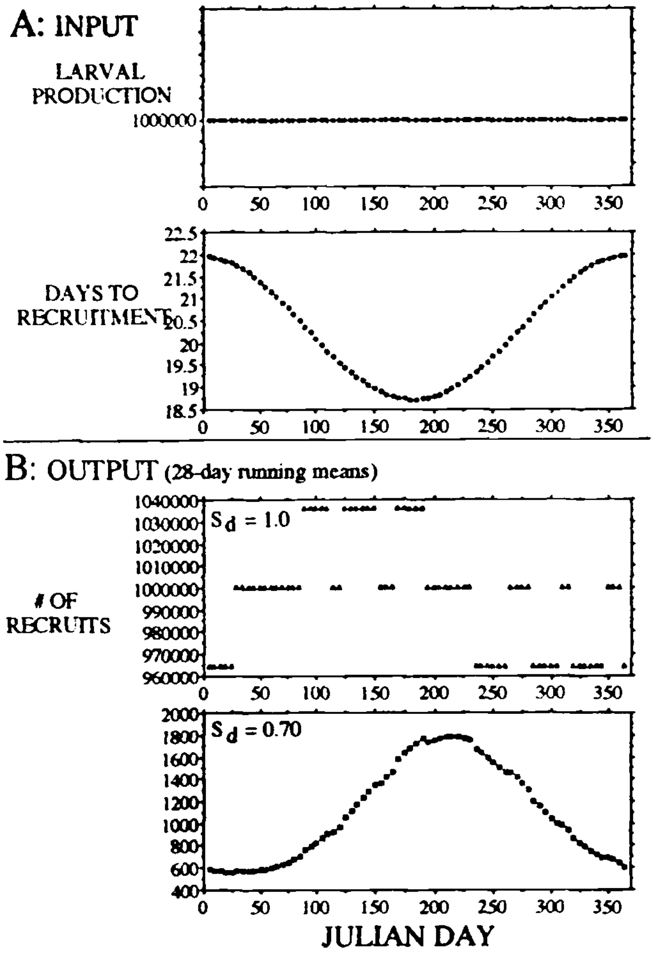


Figure 9.10. Simulation with one-quarter AAR amplitude. Doppler effect and effect of AAR on cumulative survival - AAR is 1/4 that of Sicydium spp. in Dominica, W.I. Reproduction is seasonally constant (1,000,000/day) for these simulations; all recruitment variation is due to Doppler-like effects. Upper graphs (A) show inputs to model: time to recruitment and larval production at each hatch date. Subsequent graphs (B) show simulated recruitment patterns (28-day moving averages) obtained with a range of daily survival rates as noted on each graph.

Figure 9.11. Predicting high and low recruitment from AAR profile. FROM LEFT TO RIGHT: graphs of AAR functions equal to 2x, 1x, 0.5x and 0.25x the fitted values for *Sicydium* spp. in Dominica. FROM TOP DOWN: graphs of larval production (only one graph shown for all), AAR in days, recruitment assuming zero mortality, and recruitment assuming 30% mortality per day.

Prediction of location of recruitment peaks uses (i) max and min AAR (circles); (ii) max and min dAAR/dt (triangles). The prediction method differs for situations high S_{cum} (negligible mortality) and situations with considerable mortality ($S_{cum}=Sd^{AAR}$ = (e.g.,) 0.7^{AAR}). The nodes (triangles) are useful in predicting timing of maximum and minimum recruitment at Sd=1.0, while the extremes (circles) are useful in predicting timing of maximum and minimum recruitment at Sd<<1.0. This reflects that different components can dominate in the formation of peaks, depending on mortality rates and time over which they affect growing cohorts.

Graphical relationships are overlaid on previous figures. Graphical relationships between AAR and pairs of recruitment maxima and minima at Sd=1.0 and Sd<<1.0 are demonstrated by arrows and bars (for high and low AAR). To visualise predictive relationships, trace the bars (horizontal) and arrows (vertical) which connect each peak or trough on either curve with points on the AAR curve.

If yields (recruitments) are plotted on a logarithmic axis, values take the shape of a sinusoidal curve.

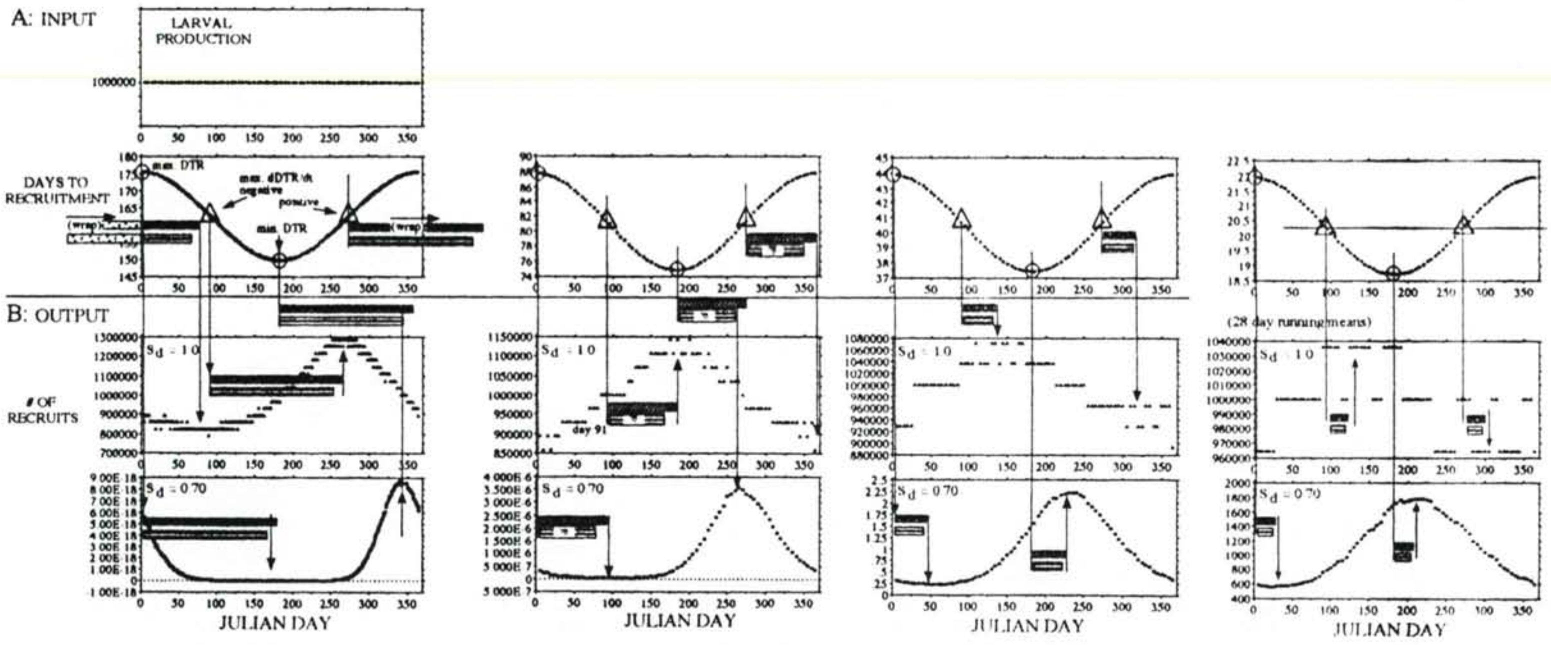
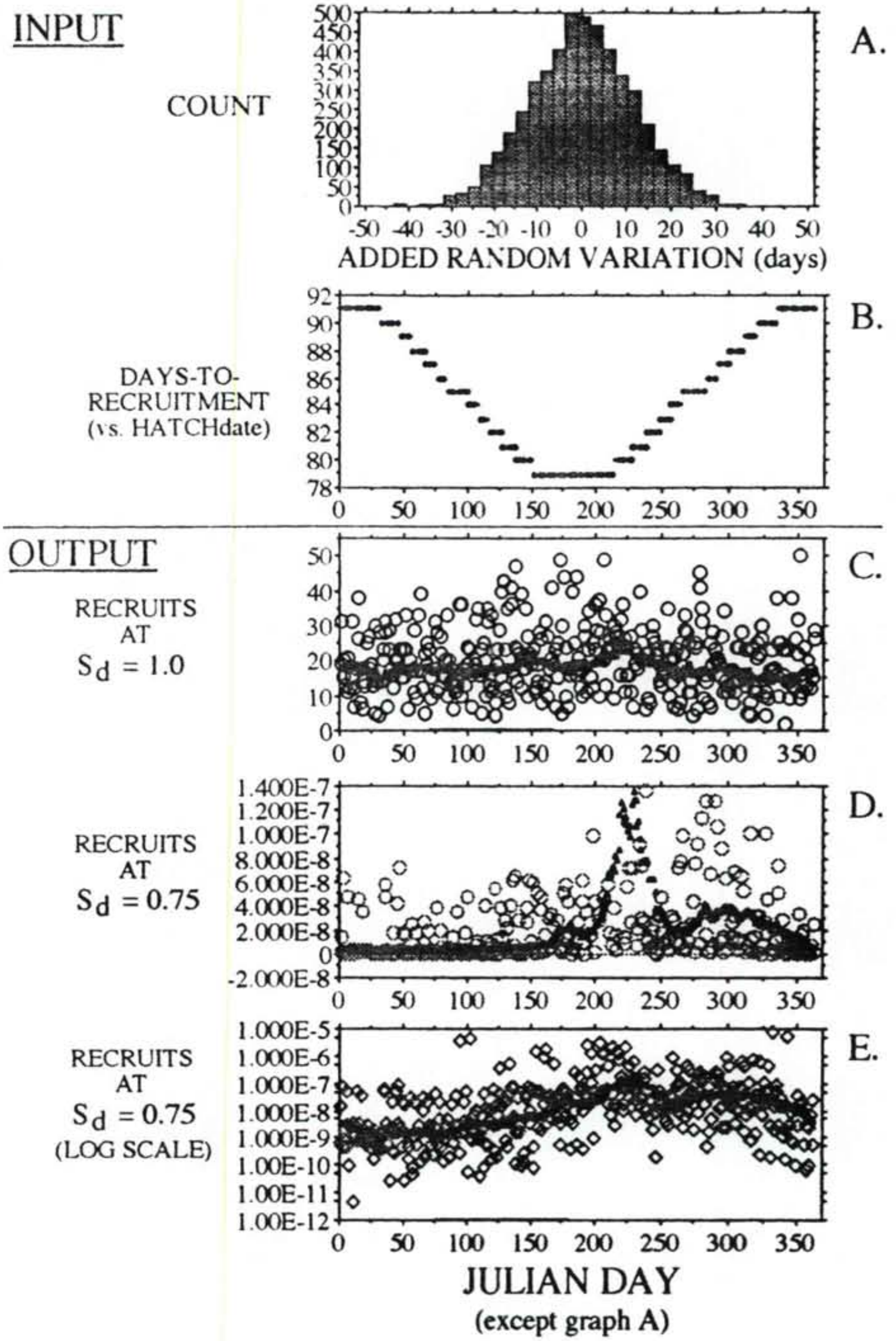

A: INPUT
LARVAL PRODUCTION
1000000
DAYS TO RECRUITMENT
max. DTR
max. dDTR/dt negative
positive
min. DTR
(wrap)
B: OUTPUT
OF RECRUITS
$S_d = 1.0$
$S_d = 0.70$
day 91
(28 day running means)
JULIAN DAY
JULIAN DAY
JULIAN DAY
JULIAN DAY

Figure 9.12. Effect of individual variation.; Recruitment pattern with individual variation added (sampled from distribution in A) to seasonally variable AAR (graph B). C, D: recruitment profiles under conditions of daily survival (Sd) = 1.0 and 0.75. The range of recruitment is too high to fit on the linear plot for Sd = 0.75 (graph D), so high-value outliers are omitted and a 28-day geometric-running-mean is overlaid (smaller points). E: Log-scale plot of D, recruitment @Sd = 0.75, to show location of outliers.

The Sd=1.0 recruitment pattern appears to have been damped, as expected, by the added randomness which would reduce relative seasonal differences. However, although the peak is less distinct, it occurs approximately when predicted by the graphical method. For the Sd=0.75 recruitment pattern, the maximum occurs sooner than would be predicted by the graphical method, by about AAR*0.5. This would appear to result from dominance of the profile by the early recruiters resulting from the high degree of randomness added to the model.


INPUT
A.
COUNT
500
450
400
350
300
250
200
150
100
50
0
-50 -40 -30 -20 -10 0 10 20 30 40 50
ADDED RANDOM VARIATION (days)
B.
DAYS-TO-RECRUITMENT (vs. HATCHdate)
92
90
88
86
84
82
80
78
0 50 100 150 200 250 300 350
OUTPUT
C.
RECRUITS AT Sd = 1.0
50
40
30
20
10
0
0 50 100 150 200 250 300 350
D.
RECRUITS AT Sd = 0.75
1.400E-7
1.200E-7
1.000E-7
8.000E-8
6.000E-8
4.000E-8
2.000E-8
0
-2.000E-8
0 50 100 150 200 250 300 350
E.
RECRUITS AT Sd = 0.75 (LOG SCALE)
1.000E-5
1.000E-6
1.000E-7
1.000E-8
1.000E-9
1.00E-10
1.00E-11
1.00E-12
0 50 100 150 200 250 300 350
JULIAN DAY
(except graph A)

SUMMARY
of major findings and implications

MAIN POINTS LISTED

This thesis described work which developed, from a state of virtually no prior knowledge, the basic life cycle of *Sicydium punctatum* in Dominica, W.I. The thesis documents production of larvae, behaviour of larvae, mortality during drift, patterned length- and age-at-recruitment, seasonality in the goby fry fishery of Dominica, W.I., and the species most important in the fishery.

For the first time in any fish, the work has shown: (1) active salinity choice by a fish larva; and (2) Seasonal, inverse cycling of length- and age-at-recruitment in *Sicydium punctatum* and *Sicydium antillarum*.

Methodological/theoretical sections contribute a (1) new field method for estimating mortality in stream drift, and (2) a new theoretical/modelling treatment of recruitment variation arising from varying age-at-recruitment.

Life history of *Sicydium punctatum*

Sicydium punctatum is anadromous (diadromous with river spawning), and related gobies (*S. antillarum*, *Awaous taiasica*, *Eleotris pisonis*) in Dominica W.I. appear to share this life history as recruits have been found entering rivers from the sea either in company with or in similar manner to *S. punctatum*.

The presence of goby larvae in low-altitude river plankton at all times of the year indicates pan-seasonal reproduction.

There is corresponding panseasonality, with a lunar-phased peak in the last quarter, in recruitment or settlement of marine late-postlarval gobies to rivers.

Sicydium punctatum larvae appear unable to survive to mouth development in either 0 (fresh) or 30 ppt (sea) water, but behaviourally select intermediate salinities and this behaviour is associated with longer swimming endurance and development of a functional mouth and apparently complete eye structure.

Types of goby larvae can be separated, and numerically match the number of gobies (*Sicydium punctatum*, *S. antillarum*, *Awaous taiasica*, *Eleotris pisonis*, *Philypnus dormitor*) present in Dominica, W.I. The ability to distinguish larvae of *Sicydium punctatum* and other larval types enables separate consideration of production and mortality in future studies.

Larvae of *S. punctatum* drifting downstream appear to suffer very high mortalities (see below), which implies a disproportionate success of and contribution to fisheries by goby populations nearest the sea.

Methodological/theoretical

A new approach was devised (not previously documented or used) for estimating mortalities during stream drift. This approach was used to show, consistent with aquarium mortality observations, that *S. punctatum* larvae suffer very high mortalities during their downstream drift. Since there are important implications for the cost of upstream (vs. downstream) nest placement, it would be worthwhile extending these results by further fieldwork. This method could be applied to assessment of drift mortality elsewhere.

A theoretical development of the consequences of varying age-at-recruitment (AAR) on subsequent recruitment variation showed that, notwithstanding that other factors may contribute as well, varying AAR contributes to seasonal fluctuations of 40% to several hundred percent in recruitment. Although the variation explored is on a scale of seasons, it is possible that longer-term (climatic) variations do occur and if so they should also produce variations in recruitment.

SUGGESTIONS FOR MANAGEMENT/CONSERVATION

Insufficient background data was a serious impediment to management decisions/philosophy at the outset of this work, and became an intermediate objective of this work for that reason. Data on reproduction is relatively easy to collect, and data on recruitment can be obtained from fishery yields with little trouble. Without a history, diagnosis or even confirmation of the existence of a problem, such as a variable or declining fishery, can be impossible.

Collateral information from adjacent areas (the adjacent islands in the Antilles) would over time give some idea about whether fluctuations were related or not. I was unfortunately not successful in arranging either a long-term collection of data on recruitment (the tritri fishery at Layou, for example, is accessible for observation and easy to assess by interviews), or in obtaining samples from adjacent islands for later comparisons of age-at-recruitment.

A further reason for tropical fisheries management organisations to include goby fry fisheries and diadromous goby biology in their activities is the teaching/training opportunities presented by river gobies. These derive from the small time (demonstrated in this thesis) and space (assumed) within which eggs hatch and grow to recruitment, and the accessibility of the population to assessment of adult abundance, larval production and mortality, and (through the fishery itself) recruit abundance. Experience with an easily-visualised system like this one could help to build, in students and trainees, better skills which can be applied to systems not so easy to visualise.

If systems of data collection as described can be installed, there can be the beginning of a basis on which to pose questions about the transfer of larvae among sites, or the degree of independence of island stocks from one another.

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