What Comes Down Must Go Up: The Migration Cycle of Juvenile-Return Anadromous Taxa

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Abstract.—The migration cycle of juvenile-return anadromous (a.k.a. amphidromous) taxa is overviewed using the goby *Sicydium punctatum* as representative. The first migration, a physiologically obligate drift to the sea, has a cost of extreme mortality, frequently exceeding 0.5/h, effectively a 1-h half-life. Stream drift may be the most hazardous known natural habitat. A nest sited 5 km upstream reduces larval drift survival to $0.5^5 = 0.0313$ or is 97% lower than a downstream nest. The conservation implication is strong: the lower reaches are disproportionately important for population maintenance. Mortality implies two new metrics for conservation and for understanding evolution of habitat choice: the mainstay habitat and point of expatriation. The second migration is oceanic, of which little is known beyond its duration until return to freshwater (recruitment), but salinity choice experiments demonstrated a requirement for intermediate salinities. Consistent with that and with others' stable isotope work, observations suggest that the combination of rain and onshore wind creates intermediate-salinity habitats on windward coasts of high islands. The third migration is the upstream migration of juveniles and adults. Drift (first migration) mortality, however, has strong implications for adult habitat choice: it challenges the notion that this goby can be successful by migrating far upstream because that entails a large reproductive penalty. The assumption that populations can be maintained through conservation of adults at high altitude or far from the sea is challenged.

Introduction

This paper will attempt to explore some new directions and place them in context of the juvenile-return anadromous migration cycle, using the goby *Sicydium punctatum* Perugia, 1896 (sensu Brockmann 1965) on the Caribbean island of Dominica as the main example. The migration cycle is the same as that for other coinhabitating juvenile-return anadromous taxa: gobies, neritid snails, and decapod shrimps. *Sicydium punctatum* is the ideal exemplar because we have more key information about it than for other taxa. The issues here are broadly relevant to most juvenile-return anadromous fishes and form a background against which differences among them will be more informative. The relationships between parts of the migration cycle are useful in visualizing evolutionary and conservation issues. I will overview and integrate previously published work with some newer work to improve the understanding of the life cycle, extract implications for conservation and management, and raise hypotheses that may help account for the worldwide declines documented for Sicydiine gobies.

A note is necessary regarding anadromy versus amphidromy. Despite that *Sicydium* was Myers's (1949) type genus for his definition of amphidromy, the ambiguous and teleological term was not justifiable as a term on the same level as anadromous and catadromous. Instead, there is good reason to treat it as a form of anadromy, from which it is distinguished solely (McDowall 2009, this volume) by a difference in the stage that migrates back to freshwaters. Other differences have been conscripted to support distinctness of amphidromy, but they are unavoidable correlates following on stage at return and therefore not independent, thus incapable of supporting distinctness. Amphidromy is for this

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and other reasons most logically and constructively considered a form of anadromy, here termed "juvenile-return anadromy." That makes anadromy the including term available to communicate with general audiences that may otherwise miss messages associated with the word amphidromous. The new term is synonymous with "amphidromy" but is unencumbered by its history.

Juvenile-return anadromous taxa are widespread: in the tropics gobies, eleotrids, gastropods, and decapod shrimps occur along virtually all volcanic coastlines and on islands. Many gobies support fisheries, which generally have declined (Bell 1999), such as the Philippines (Manacop 1953) where in the 1930s, the commercial fishery in northern Luzon alone approached 20,000 metric tons (mt)/year, or Reunion where landings of 65 mt were recorded in 1966 (Aboussouan 1969). In Dominica, the fishery at Layou, a principal fishing site, had, by 1990, declined to a few metric tons per year from yields credibly recalled to have been "two or three canoes [skiffs of about 5–7 m] full" and large enough to saturate the market, requiring it to be transported across the island to sell it all. By 1990, it was said that "tritri" (local name for postlarval gobies) used to be plentiful, but now to get any, "you have to know someone." Declines worldwide were not simultaneous, but plausibly followed land-use changes or development in each location.

The goby fry fishery in Dominica (15°30'N, 61°25'W) is dominated by *S. punctatum*, accounting for 95% or more of the catch (Bell 1994). There are two kinds of fishery for returning *Sicydium* postlarvae in Dominica: at a river mouth using a beach seine or in-river traps. The trap fishery is conducted by women and sometimes children, while the beach seine fishery at river mouths (only those with sandy substrates) is conducted by fishermen preferentially targeting the brief (1–2 d) but lucrative goby runs. The trap fishery begins a little later and diminishes over several days.

The beach seine is made of fine net material, commonly mosquito netting, about 8 × 3 m, with rope loops at the corners for holding with feet and hands. It is walked through the water and lifted to the surface, and the catch (which at Layou typically includes tritri, shrimps, and leaves) is coaxed into a mass at one end. The tritri are induced to self-sort by pulling the net in the direction away from the mass, stimulating a rheotactic response in the tritri,

which rush to the pulled end of the net. The net is then gathered around them for transfer to buckets while the undesired leaves, flotsam, and shrimps are discarded.

The in-river fishery uses a "bag-and-stones" trap to catch postlarvae after they have become benthic. It is reminiscent of the fishing baskets briefly mentioned by Atwood (1791), which may have been not ordinary baskets but basketwork traps, as are well known from the Philippines, and the Carib baskets may well have been similarly refined for fishing. The present trap is now a fertilizer or woven bag, slit up one side, placed with the open end facing downstream, and stabilized with stones (not mentioned by Atwood). The benthic postlarvae advance between the stones until they encounter the fabric and they remain trapped by their own rheotaxis; the bag is later lifted and the stones removed, leaving the tritri.

Life Cycle

In Dominica, the juvenile-anadromous life cycle (Figure 1) is seen in sicydiine gobies, some Eleotridae, some decapod shrimps, and Neritid gastropods. The *S. punctatum* life cycle (Figure 1) is rapid with immediate flush of hatched larvae to the sea (Bell 1994; Bell et al. 1995). After 50–150 d at sea, they return as transparent, pelagic, schooling, terminally mouthed postlarvae ~20 mm standard length (SL). When they reach hard substrates in rivers, they settle (with loss of a little SL) and become cryptically pigmented, benthic, inferior-mouthed, and nonschooling juveniles. They can mature (developing adult sexually dimorphic coloration) at ~30 mm SL and are iteroparous and long-lived. Spawning is typically in caves excavated in gravels below rocks. Reproduction is all year (as for all of Dominica's juvenile-return anadromous taxa) at the coast, but seasonally interrupted at higher altitudes.

Laboratory studies revealed spawning by temporary pairs, with males tending eggs. Females ~45 mm SL had clutch sizes of 20,000–30,000 eggs. Females could repeat spawn at intervals of about 14 d. Adult growth appears slow: a female collected in 1991 (likely hatched in December 1990) was, in 2006 and at 16.5 years old, only 67 mm SL (author's personal observation). If growth in rivers is comparable, then biologists should use restraint when sampling adults because they may well be
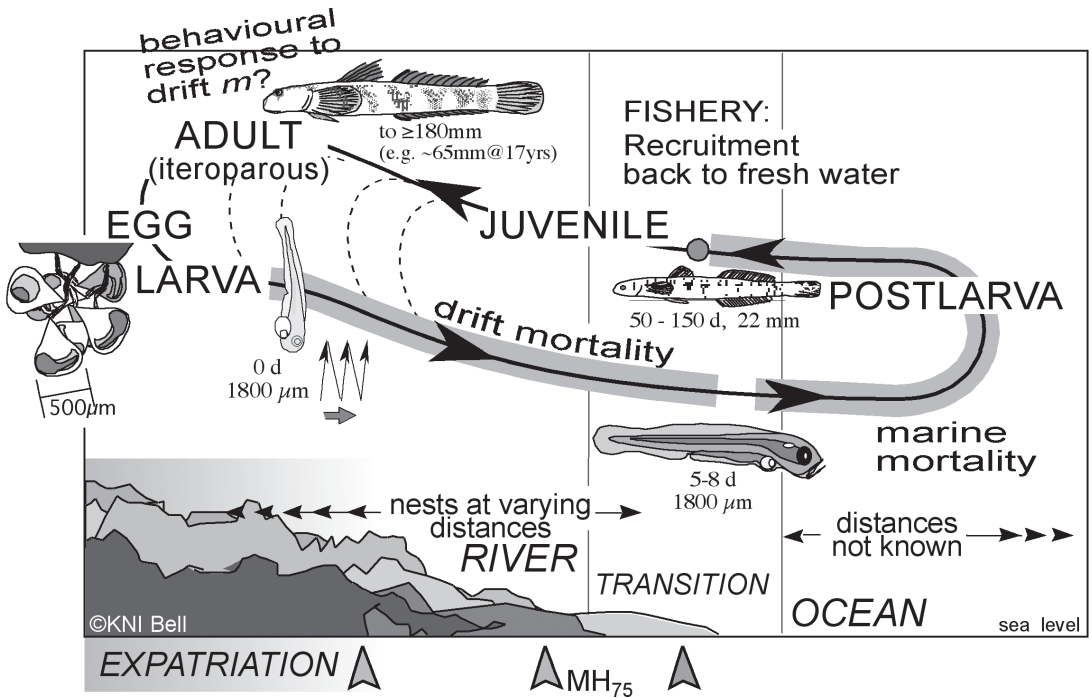
Figure 1.—Life cycle of *Sicydium punctatum* in Dominica, West Indies. MH_{75} = mainstay habitat below which (from point to river mouth) 75% of the river's drift survivors originate. PEX_x illustrates point of expatriation, above which drift survivorship falls below a critical level chosen (e.g., 5%); this metric is independent of spatial distribution of reproduction.

one to many decades old, and not quickly replaced. Laboratory studies also revealed one female using a "sneaky" strategy of intruding on a spawning in progress, displaying the female spawning motions without laying eggs, and resisting the male's effort to drive her away until the male in presumed confusion drove the actual spawning female away. The sneaker then ate the other female's eggs. Such behavior may permit the female sneaker to acquire extra nutrients to spawn more often or could result in better-provisioned larvae.

Disturbance (even by illumination) causes premature hatching of larvae of 1.3 mm total length (TL); even earlier hatching releases larvae that are for some time unable to uncurl or swim properly. In contrast, larvae of undisturbed nests hatch at 1.8 mm TL and larvae retain that length for several days (I suggest that the marker of proper hatching time is a stable TL, reported by many authors, in the first few days). Eggs hatch as quickly as a few hours to more than a day; however, the entire nest does not seem to hatch simultaneously but rather over a period of a day.

Drift is obligate since larvae cannot live long in freshwater (Bell and Brown 1995). Larvae begin drifting immediately following hatch, swimming vertically to keep suspended in the flow (Figure 2). Despite many experiments with larvae, no routine settling on the bottom was seen. The journey begins, however, with a shock: stream drift mortality is extreme and may be the most hazardous naturally occupied habitat we know of with survival only ~0.5/h or less. This has profound implications for conservation and habitat choice.

Methods

Otolith methods and protocols are given in previous papers (Bell 1994; Bell et al. 1995). The recruitment data available come from the Layou River fishery or from purpose-designed traps (Bell 1994; Figure 3) that face downstream and include a boul-
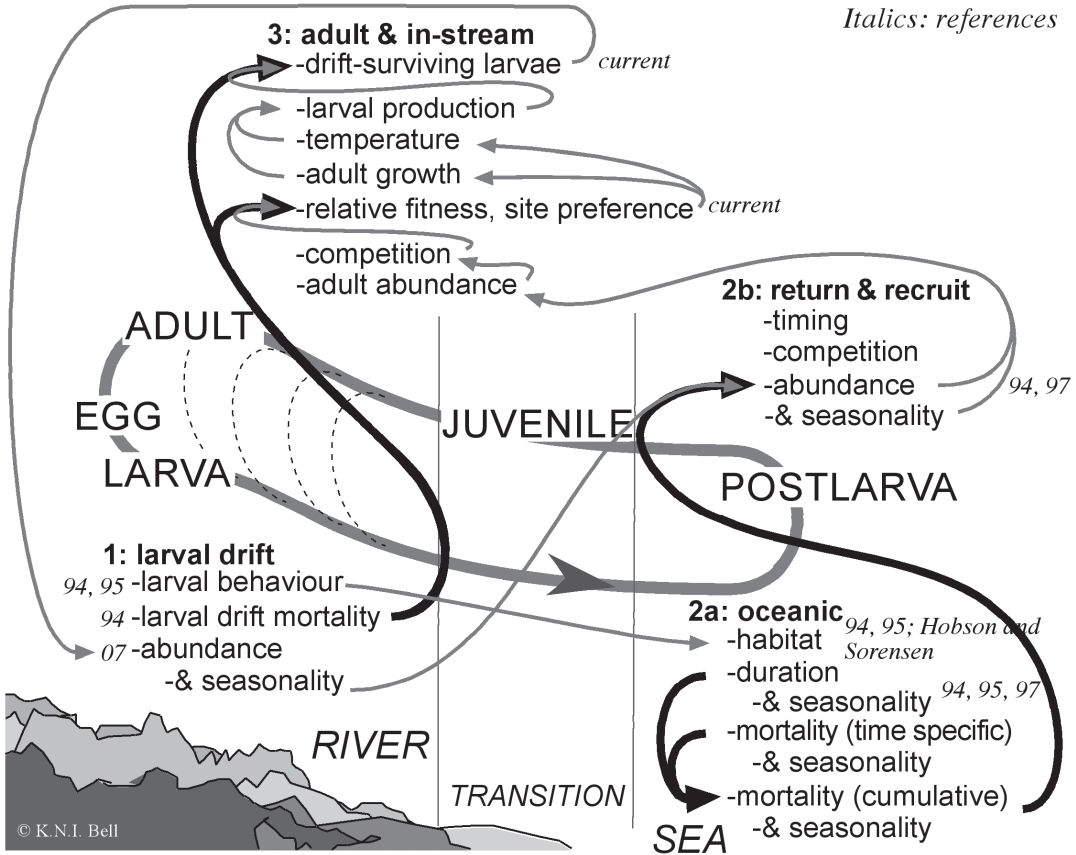
Figure 2.—Relationships among aspects associated with different of stages of the migration cycle. Heavier lines indicate key links. Italicized numbers (94, 95, 97, 07) refer to, respectively, Bell 1994, Bell and Brown 1995, Bell et al. 1995, Bell et al. 1997, and Bell 2007), and Sorensen and Hobson refer to Sorensen and Hobson (2005) and to Hobson et al. (2007). Larval drift mortality (first migration, downstream) interacts with upstream distance to directly determine larval survivorship and abundance. It has profound implications for adult habitat choice and, thence, adults' fitness through net production of drift survivors.

der-supported mesh (1 × 1 mm) fence that leads to a mesh cone, then to a removable accumulator. Methods for plankton sampling referred to here are given in Bell (1994) and Bell (2007).

Periodic regression (Bliss 1958, 1970; Batschelet 1981; Bell et al. 1995; Bell 2008) is a powerful and robust means of analyzing cycles. Significances are generally reported as exact P-values from parametric distributions (with exception of the novel D_{95}).

Remotely sensed oceanographic data maps were obtained from National Oceanic and Atmospheric Administration's CoastWatch Program and NASA's Goddard Space Flight Center, OceanColor Web (http://las.pfeg.noaa.gov/oceanWatch/oceanwatch_safari.php).

Comparing Cycles with Multiple Confidence Ellipses

Phasing can be compared by plotting as multiple confidence ellipses (MCEs), an extension of the single descriptive confidence ellipse (Bliss 1958). In this extension, if a straight line from the origin can intersect two ellipses, then they are not significantly different. If a centered circle can intersect two ellipses, their amplitudes (their effects on *Y*) are not significantly different.
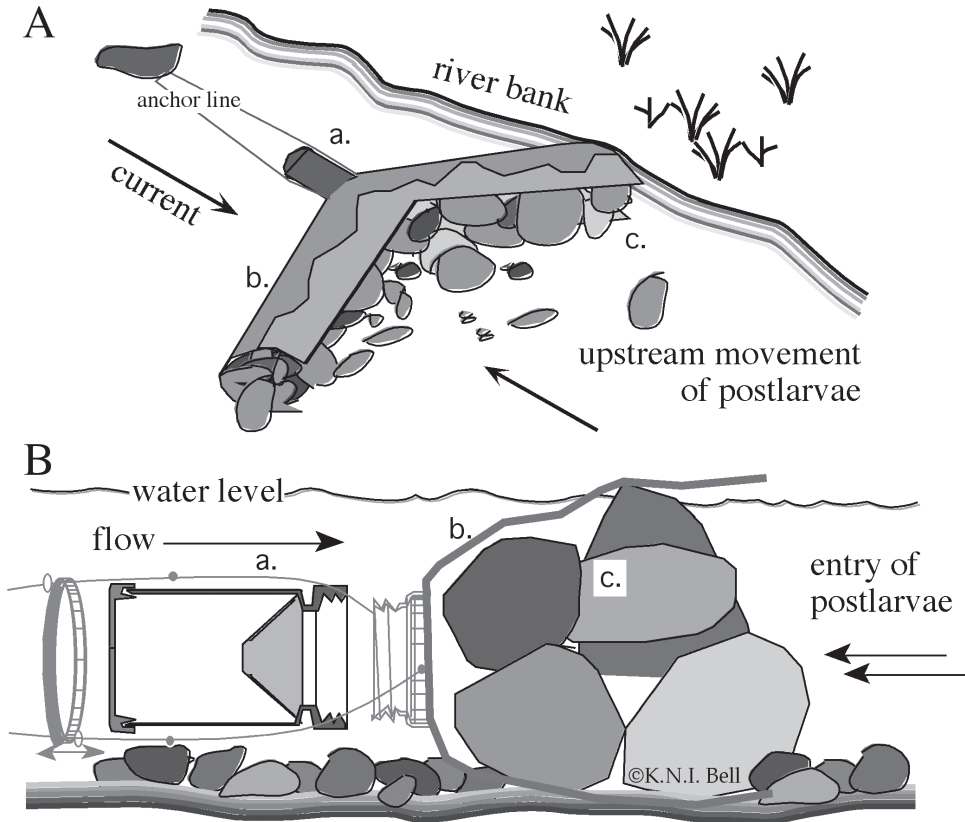
Figure 3.—Trap for upstream-migrating fauna, as installed (A) and in section (B). The trap includes a removable collector jar (a) having mesh windows to admit water flow, and a guide fence of ~1 mm mesh (b), which is supported by boulders (c).

Bliss (1970) used a superior method of calculating the ellipse; the approximation here is a computational economy more simply based on the 95% confidence bounds for a cycle's (sin, cos) coefficents in the periodic regression, which are plotted as rectangles in (sin,cos) space and the ellipse inscribed. I believe this computational economy results in fractionally larger ellipses than Bliss's method and they would therefore be conservative for purposes of declaring significance of cycles and significance of difference between them.

Drift Mortality: Estimation Method

Mortality is a key demographic parameter in the stream drift. Drift mortality estimation contains some traps and subtleties, and there is limited space to present it all here. The basic method (Bell 1994) uses paired samples (Figure 4) in the before/after sense, as has been applied to marine larvae. It had never been applied to stream drift, perhaps because the adjacency of adults and the drifting stages being sampled leads to ambiguities that can be quite daunting. Nevertheless, the stream situation virtually invites the challenge because, unlike the marine situation, the population is confined by stream banks.

Principles

Estimation can be complex and problematic, but for larvae that drift without settling and in a location where reproduction is rare, it becomes tractable. Survival (S) and mortality (M) sum to 1, and it is necessary to calculate S first. Survival is calculated from paired abundances (A, units/m³) upstream
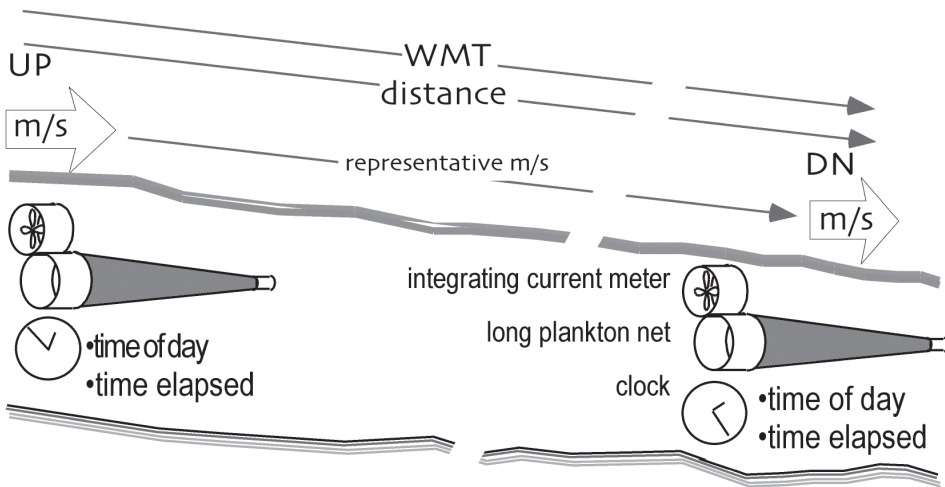
Figure 4.—Paired-net estimation of drift mortality. WMT = time for water mass to transit the sample reach, calculated from current speed and intersample distance.

(A_0) and downstream (A_t) and from exposure time t (here in hours, from water mass to transit (Figure 4) or distance (kilometers, which in calculation functions like t). S is expressed per hour or per kilometer, as S_h or S_{km}. S, A, and t are related as

$$A_t = A_0 S^t \text{ or } S = (A_t/A_0)^{1/t}, \qquad (1)$$

which assumes that S dominates over settling and inputs of larvae (the no-reproduction assumption). For juvenile-return anadromous species like *Sicydium* that remain in the water column during drift, the key ambiguity of reproduction can be eliminated in reaches unsuitable for reproduction. Once eliminated, or tolerably reduced, in situ mortality can be estimated.

Generally, there is a nonsensicality to $S > 1.0$, so it is preferable to express a difference rather than a ratio like S because larvae do not reproduce (i.e., larvae cannot come from larvae, which are counted, but they can come from adults, which are not counted and are therefore an externality). The exception is where $S > 1.0$ is believed to result from sample error—instead of from hatching in the sample reach—and expressing the data point as S lets it be used with other estimates to generate fair means or medians. Objective disambiguation of error from spawning is possible using the criterion D_{95} below.

Drift survivorship, S_{drift}, is the drift survival probability or the proportion of larvae, from a given

distance d upstream, that survives drift and reach the sea:

$$S_{drift} = S_{km}{}^d. \qquad (2)$$

Sites and Sampling

In the Canefield and Layou rivers, Dominica, I sampled reaches within 1 km of the mouth. The upper and lower stations were separated by about 400 m in Layou River and 150 m at Canefield River. There were no tributaries to these reaches. The key to reducing ambiguities is to choose a reach with poor nesting conditions in order to reduce role of reproduction on the data and to assume that reproduction = 0.

The following are axiomatic but easily missed:

1. Where $S < 1.0$, S is a conservative estimate of mortality.
2. Where $S > 1.0$, $A_t - A_0$ is a conservative estimate of production.

Even in a reach generally unsuitable for reproduction, there may be some rock or object that provides a little grazing and nesting habitat, and one hatching of 30,000 larvae (within the capability of a 45-mm adult as frequently as every 10 d) can occasionally elevate local abundance and generate negative mortalities. Negative mortalities are a key issue in any mortality estimation and must be handled

in a fair way. It is not justifiable to simply delete instances of $S \geq 1.0$ as nonsensical—even though in a limited sense they are—because they represent either sampling error (in which case they are a valid part of the survival data and must be included in aggregate statistics) or violation of the no-reproduction assumption (in which case they are not part of the mortality data). Only when mortality is dominated by reproduction are negative mortalities not part of the survival data. We need a way of deciding which.

To objectively disambiguate sample error from violation of the assumption that reproduction = 0, for each taxon, I obtained the D_{95} criterion, representing the 95th percentile of differences expected under the null hypothesis, using a resampling approach with a larger body of real plankton data from the same locations. Abundances A_i from the same locations were detrended for effects of time (seasonal, lunar, and daily cycles) by periodic regression (like equation 3, except that Y is rheoplanktonic larvae not recruits). Temporal detrending was required because mortality samples pairs are near-simultaneous, while the A_i used for D_{95} were not. The residuals were used to generate all possible differences (simulating $[A_t – A_0]$ in the null situation), comprising the null distribution from which D_{95} is identified for the taxon. D_{95} is applied to each case i of the downstream-minus-upstream difference x_i, and if $x_i = (A_t – A_0)_i > D_{95}$, then we say x_i is significantly different from the null and inconsistent with the no-reproduction assumption, and we treat it as production and not mortality. It is then possible to estimate S without contamination from reproduction.

Estimating Mainstay Habitat and Point of Expatriation

Mainstay habitat (MH_c; Figure 1), the most productive habitats accounting for a chosen $c\%$ of drift survivors, is calculated by integrating S_{km}^{x} over a downriver range 0 (min) to x km (using the definite integral $[S_{km}\hat{\ }x]/\ln[S_{km}] – [S_{km}\hat{\ }min]/\ln[S_{km}]$), and over an upriver range x km to 40 (max) km ($[S_{km}\hat{\ }max]/\ln[S_{km}] – [S_{km}\hat{\ }x]/\ln[S_{km}]$), and then iteratively solving for the value of x giving downriver integral equal to $c\%$ of the total. The truncation of river length to 40 km is an economy justified by the fact that at survival values in the range of the pres-

ent results, 40 km is well past the point where drift survivorship is nearly nil: about one drift survivor per thousand larvae at $S_{km} = 0.8$ and about one in a million at $S_{km} = 0.5$.

Point of expatriation (PEX; Figure 1) is the point above which the population cannot be self-sustaining. Conceptually simple, it requires either knowledge of all survivals through the life cycle to identify the point where one adult's entire reproduction results in one replacement adult or an assumption about the minimum drift survivorship required for that to pertain. As drift survivorship $S_{drift} = S_{km}^{d}$, where d is a distance in kilometers, an assumed minimal necessary S_{drift} allows d_{PEX} to be calculated as $\ln(S_{drift\_minimal})/\ln(S_{km})$.

Results and Discussion

In this overview, I will discuss the first migration (drift to the sea and mortality and implications), the time at sea, and the return to freshwaters (age at return, synchrony within and among taxa and its implications).

Drift Mortality

Mortality in the stream drift is important to trophic relationships, demographics, and dispersal; yet, despite many mentions in the literature (Elliott 1970; McLay 1970; Allan 1978; Allan and Russek 1985), the first direct estimate was by Bell (1994). There is not space here to treat this issue fully, so this brief overview uses data of Bell (1994), augmented in 1997 from Dominica.

Drift mortalities are extreme (Figure 5). While there are complexities in mortality analysis, including how to handle so-called negative mortalities, the data simply do not allow room to think that mortalities are trivial: stream drift mortalities far exceed any known mortalities for fish larvae and may reflect the most hazardous naturally occupied habitat yet found. Published data (Pepin et al. 1987), available only for marine fish larvae, show survivals generally higher than 0.97/d. In contrast, the present data show such extreme mortality that survival (S) has to be expressed on an hourly basis (it is near zero on a per-day basis). I use in discussion, conservatively and for simplicity, a value of S = 0.5/h, noting that the implications are more severe with higher mortalities.
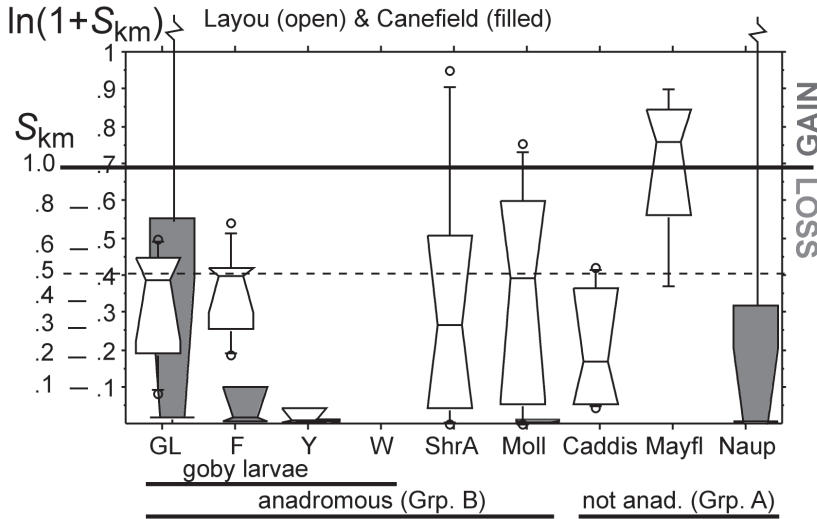
Figure 5.—Per-kilometer survival rates (S_{km}) in lower Layou (open symbols), lower Canefield (filled), filtered by D_{95} criterion, which identifies whether high outliers can be considered part of the mortality data population or not. Plots of survival for four juvenile-return anadromous taxa and three others for comparison: two insect (nonanadromous) taxa and nauplii (unknown life cycle, not expected to be anadromous). GL = all goby larvae; F = *Sicydium punctatum*; Y and W are unknown goby larvae (W data all were above the D_{95} critical level, indicating net production rather than sample error). ShrA is a complex of decapod shrimps; Moll is Neritid gastropods; Caddis are caddis-like larvae; Mayfl are mayfly-like larvae; Naup are nauplii. Box plots show median, 95% confidence interval for median (notches), the 25th and 75th percentile estimates (boxes), 10th and 90th percentiles (T-bars), and outer data (circles).

Mortality rates were far more severe in Canefield River than in Layou River. Although Canefield is visibly impacted by siltation from light industry (gravel works), the difference is not usefully amenable to statistical generalization (i.e., we could distinguish Canefield from Layou, but that is trite because we do not have the degrees of freedom for river condition to associate that difference with the impacts).

The high rate of mortality is supported by the stage distribution of larvae retrieved in drift plankton samples, which are predominantly at very early stages of development (eye at outline stage, no lens function, no eye pigmentation). Though we cannot identify sources of mortality; I suggest that predation by fish dominates. I have seen an adult *Sicydium* (SL ≈ 70 mm) in aquaria picking off larvae continuously, at the rate of one every few seconds for 8 h, despite that the mouth of an adult *Sicydium* is subterminal and adapted for grazing aufwuchs and despite that mouth–eye coordination was clearly a little clumsy for capturing swimming prey. Also likely as predators are mountain mullet *Agonostomus*

monticola, abundant in the lower reaches of Dominican rivers.

If drift takes a day, then survival to the sea would be $S_{24\,h} = 0.5^{24} = 5.96E - 08$, and at that level, a lifetime of spawning would likely yield zero drift survivors. That would certainly imply expatriation. That S_h^{24} is nearly zero does not mean an error in calculation or judgment; it simply means that average drift time cannot possibly be that long. Plausible drift time is a few hours at most. It is useful to consider the rates on a per-kilometer as well as a per-hour basis. Per-hour rates allow comparison with the literature; per-kilometer rates allow us to develop the implications. Rates/h approximates rates of per kilometer because typical river flow at my study sites approximated 1 km/h.

Conservation Implications

Conservation implications are profound. Distance-specific survival data let us, in principle, calculate the extent of (1) the most productive nesting habitats

(those accounting for most of the larvae reaching the sea), and (2) the point above which reproduction is insufficient to sustain the local adult population. We can name these two useful concepts: (a) mainstay habitat (MH_x), and (b) PEX.

Drift mortality implies mainstay habitat.—Let MH_x denote the habitat accounting for x% of the larvae reaching the sea. MH_x integrates production and drift survivorship beginning at the lowest-altitude reproductive habitat, extending upstream to include the habitat accounting for x% of the river's drift survivors. MH can accommodate spatial variations in production, but we rarely have that information, so we assume uniform reproductive output (eggs/t/m, eggs per unit time per unit river length [and across all tributaries]) along a river. Reproduction, however, is likely greater downstream, so MH_{75} would be even smaller than estimated under the simplifying assumption. With reasonable assumptions or historic data on substrate, stream cover, and so forth, the approach can be used to estimate production already lost due to previous land-use changes. Higher S (lower mortality) extends MH_x over a greater area, while lower S reduces MH_x. We can choose x, and here $MH_x = MH_{75}$. $S \approx 0.5$/km implies that 75% of drift-surviving larvae originate in the first 2 km of river, so the 75% mainstay habitat or MH_{75} is 2 km (Figure 1).

Unavoidably, and consistently with the findings of Iguchi and Mizuno (1999), lower reaches are disproportionately responsible for population maintenance and therefore critical for conservation. We waste our time if we think a few adults 10 km upstream constitute conservation (yes, those habitats are important but mostly as water source). Thus, conservation of the coastal zone, the most contended for by development, is a critical conservation target.

Selection and behavior implications also generate interesting and testable hypotheses about adult choices and behaviors. The mathematically unavoidable decline in drift survivorship (the portion of larvae that survive to reach the sea) with upstream distance implies that adults should compete for downstream habitats and that the upstream adults are those that earlier in life were subordinate and excluded and that their upstream journey was not a desire for altitude as some (including I) have sometimes supposed, but instead a forced exile.

Drift mortality implies a point of expatriation.—Any mortality ($M_{km} = 1 - S_{km}$) implies a point (the PEX) upstream of which adults are ecologically

nonreproductive (i.e., do not replace themselves). The very word "reproduction" implies success. In contrast, unsuccessful reproduction is typical of expatriate populations whose adults may be healthy and reproductive but whose larvae cannot access the nursery grounds from which they can recruit back to the parental population. Expatriate populations (Haedrich and Judkins 1979) are those sustained by exogenous reproduction but may not look any different. The challenge in the context of conservation of stream gobies is that there are often healthy looking populations far upstream; yet, even at 5 km, the drift survivorship (S_{drift}) is only 0.03%.

We cannot easily know life cycle's survival values well enough to precisely identify the point at which the population replacement rate falls below two recruits per parent lifetime, so we must assume a drift survivorship level, for instance $S_{drift} \leq 0.01$, below which we should assume expatriation. Then, at $S_{km} \approx 0.5$, $S_{drift} \leq 0.01$ occurs just 6.64 km upstream ($0.5[6.64] = 0.01$).

Upstream adults may be expatriate or ecologically sterile because of low drift survivorship of their larvae. Upstream fish are often noted to be larger than the downstream adults, but the low drift survivorship of their larvae makes us wonder why they are there at all. The answer may be that they were out-competed for superior space downstream once those habitats became saturated. Do they have some remaining possibilities; for instance, do their larvae hatch during a flood so that higher current speeds will shorten drift time? We know nothing of drift mortality during those conditions however, so we have no basis to deny that floods leave drift survivorship unimproved. Reliance on floods also means relying on a state that is both unpredictable and brief, thereby reducing the effective spawning season.

Do upstream adults know where they are?—Adult Sicydiines have been reported to be faithful to home ranges or sites for long periods (Nishimoto and Fitzsimons 1986; Fitzsimons and Nishimoto 1990). This is appealing, logical, and plausible for a dominant individual in the best habitat it has access to, but what about nondominant individuals? We need to know more about competition for habitats, about which habitats are "choice'" from the goby point of view on spatial scales both small (within-pool) and large (along-stream) and about male–female differences in territoriality and habitat choice.

Questions are raised by the very fact of any nonnegligible drift mortality rate. Do upstream adults recognize that their larvae face a very low drift survivorship? Cues could be temperature (usually the upstream reaches are cooler) and the fish's own travel history. Are there circumstances in which drift survival increases (e.g., during floods?), and if so, do they take advantage of these?

Could large upstream adults drop down waterfalls to return to the more desirable lower reaches after they attain competitive size? The goboid sucker has a trailing form, suggesting it would be more difficult for the fish to establish a seal when moving backwards, and the sucker is situated well anterior of the center of mass and drag, so a headfirst controlled descent seems implausible because it would be opposed by forces that would tend to rotate the fish back to a head-upstream position. Those factors have tended, until recently, to make me regard upstream migration as a one-way trip. But if the lower reaches afford sufficiently greater larval drift survivorship, and if the larger sizes acquired by adults having grown in cooler and less desirable habitats would give them advantage in lower reaches, the question becomes not whether but when the risk of a relatively uncontrolled descent would be balanced by the rewards (Figure 1). A large adult may profitably accept a substantial risk of injury or death in descending downstream for a chance to be the bigger fish in a better pool and realize the advantage of higher drift survivorship.

The possibility for an adult downstream journey, even if risky, invites questions about the partitioning of energy to growth and reproduction and whether partitioning is contingent on location so as to support a strategy of exile to upper reaches followed by return at advantageous size. The choices faced by males and females may be qualitatively different because it seems that males are territorial and females are not (author's personal observation), so it is possible that the sex distribution of upper-reaches gobies would be biased toward males. Microchemical composition of otoliths might help show whether some downstream adults have an upstream history.

Marine Stage of Migration Cycle

We know very little about the marine journeys undertaken by sicydiine gobies or other juvenile-return anadromous taxa. We have some information on the time spent in the marine environment by juvenile-return anadromous taxa: some gobies (Iida et al. 2009, this volume) and Galaxiids (Rowe and Kelly 2009, this volume), but not for neritid gastropods (Hau 2007) or decapod shrimps (Hunte and Mahon 1983). We have some strong indications (for sicydiine gobies) of the required habitat for the first week of life and, beyond that, indications that the journeys might be small in extent (Sorensen and Hobson 2005) and some indications to the contrary (Maeda et al. 2007; Iida et al. 2009) but not necessarily for the same situations, so both may prevail.

The time spent at sea, from soon after hatch to recruitment, was first examined for diadromous gobies in Hawaii (Radtke et al. 1988). This period is referred to in the literature variously as PLD for postlarval duration or AAR for age at recruitment or OLD/MLD for oceanic/marine larval duration (Iida et al. 2009; Rowe and Kelley 2009). Because the freshwater period for juvenile-return-anadromous gobies before entry to the ocean is almost certainly mere hours, there is little scope for any of these terms to be much different.

Until the work in Dominica, variation in OLD had been ignored as error, but Bell et al. (1995) showed that this was incorrect: temporal structure was instead apparent as a highly significant seasonal cycle in OLD shown by periodic regression (Bliss 1958, 1970; Batschelet 1981; Bell et al. 1995; Bell 2008) for *S. punctatum* ($r^2 = 0.28$, $p \le 0.0001$). The regression equation was

$$OLD = 83.835 + 10.1 \sin`DOY - 0.213 \cos`DOY,$$

where the grave accent mark (`) indicates a proper transform of a variable (here, day of year [DOY]) to the correct units for taking sine and cosine. The intercept—or periodic mean, called a "mesor" in the periodic regression context to show its special utility as the expected mean value (correcting for or detrending with respect to) through the cycle(s)—is 83 d. The amplitude (A, contribution of the cycle to the value of OLD through the cycle), calculated by Pythagoras' theorem from the sine and cosine coefficients ($10.1^2 + (-0.213)^2 \cdot 0.5 = 102.055^0.5$) = 10.102, meaning a seasonally associated fluctuation of ± 10.1 d around the mesor; the regression indicates a seasonal acrophase (timing of peak or maximum contribution of the cycle to Y) near April 2 each year. The "error" contained temporal structure: a cycle that was informative for a new source

of recruitment variation (Bell 1997), which was a plausible cause of the observed fishery seasonality. Regrettably, however, temporal structure remains largely ignored in otolith aging studies.

The cycle held a key to explaining seasonal structure in recruitment via two routes. One was as an exponent of time-specific survival. The second was a variation in the lag from hatch to recruitment, which forms the first application of the Doppler effect (Doppler 1842, cited by Hujer 1955) outside sound or electromagnetic radiation. Both routes were combined in Bell-Doppler theory (Bell 1997), which can be numerically simulated or explicitly estimated via an equation. It can mimic (potentially explain) a fairly complex recruitment pattern, so it is no longer justified to assume that a recruitment pattern is a lagged copy of the reproduction pattern; that is shown in the case of *S. punctatum* where the spawning pattern is not a tidy preview of the recruitment pattern, but recruitment well matched by a model using the observed OLD cycle and constant reproduction over the year.

Recruitment to Freshwater: The Journey Home—Synchrony within and among Taxa

Many juvenile-return anadromous taxa are reported to recruit at some stage of the lunar cycle (Bell 1999). In Dominica, recruitment (several taxa) is phased to the fourth day following the last quarter moon (Bell 1994).

Periodic regression (Bliss 1958; Batschelet 1981; Bell et al. 1995; Bell 2008) can, by definition, confirm (according to significance of a given cycle) synchrony within a (statistical) population. For example, for temporal recruitment of *S. punctatum*, the periodic regression equation found for the instream trap data (ln[CPUE]) was equation (3)

$Y = \ln(1 + CPUE) = $ mesor $+ f$(day cycle, second harmonic of day cycle, seasonal cycle, second harmonic of seasonal cycle, lunar cycle, second harmonic of lunar cycle, linear trend)

$Y = \ln(1 + CPUE) = 6.985 - 0.64*\sin`DOY$
$+ 0.97*\cos`DOY + 0.669*\sin2DOY$
$+ 0.602*\cos`2DOY + 1.008*\sin`L$
$- 0.858*\cos`L - 0.363*\sin`2L - 1.125*\cos`2L$
$- 0.011*d,$ (3)

where the grave symbol (`) functions as above. This regression was significant at $p \leq 0.0001$ (and highly significant in first and/or second harmonics of the day, lunar, and seasonal cycles), $R^2 = 0.625$, $n = 186$ (Bell et al. 1995).

Regressions for all other juvenile-return anadromous taxa in Dominica were also significant ($p \leq 0.0084$). All showed significance in either primary or secondary lunar cycles or both. None showed a significant tendency to depart from the same phasing.

Synchrony among Taxa

Lunar phasing does not significantly differ among juvenile-return anadromous taxa in Dominica, either with regard to the first harmonic (29-d cycle) or the second harmonic (≈14.5-d cycle). Phasing was compared by plotting as MCEs (Figures 6 and 7). Note that because the second harmonic completes its full cycle in one-half of the full cycle, it "begins twice" in the full cycle. There are peaks about 8 d after the first quarter and the last quarter. The second peak is within ˜3 d of the main or first harmonic; the recruitment we see at that time is the sum of the first and second harmonic peaks, whereas the first peak of the second harmonic acts alone about two weeks later at ˜8 d after the first (not last) lunar quarter.

Hypothesis: Passive Tidal Transport (Eliminated)

Tidal transport leaps to mind because of significance of response of recruitment to second lunar component. However, (1) tides in the region are small, partly due to the presence of an amphidromic point south of Puerto Rico, (2) tidal currents are diminished by the great water depth, and (3) use of reversing currents in open water requires vertical migration through most of the depth, so it is not advantageous in deep water. These reasons appear sufficient to eliminate passive tidal transport.

That suggests that the lunar response is merely a cue to enable synchrony. Consistent with that, lunar phasing varies worldwide (Figure 8): the data are incomplete but show clearly that there is a considerable variation in lunar phasing, which is not what we would expect if tidal transport was generally important. Predator swamping may be the sole
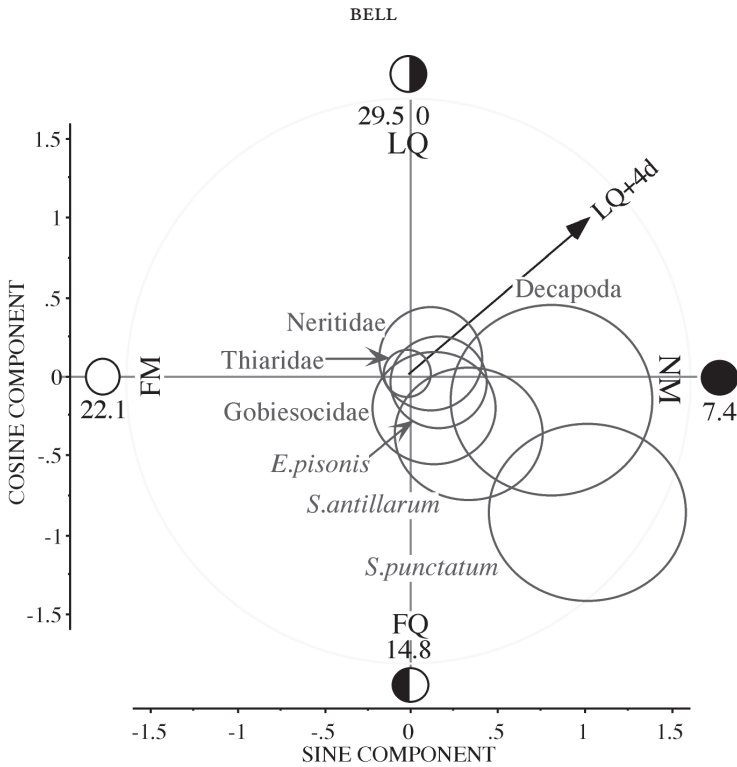
Figure 6.—Lunar recruitment and synchrony across taxa in Dominica: multiple confidence ellipses for the amplitude (distance from origin) and phase (angle from the origin) on the first harmonic cycle. The Layou beach seine fishery occurs on the fourth to fifth day after the last quarter, but the in-river traps catch slightly later and longer, hence the later in-river peak for *Sicydium punctatum* indicated at about 8–12 d.

plausible advantage to account for similar lunar phasing among taxa.

Where Are Early Growth Habitats?

The obvious constraint on early growth habitats is that larvae must be able to reach them and return. Recent work (Leis and Carson-Ewart 1997; Bellwood and Fisher 2001; Leis 2006) frees us from the constraint that larval fish are helpless against the currents. Larvae can sustain speeds of 10–50 body lengths (bl) per second, which means that larvae of 5–10 mm can generally counter the currents typical of the eastern Caribbean (rarely exceeding 0.07 m/s except in the channels between the Windward Islands). Leis and his colleagues (1997) and Leis (2006) have not denied that larvae can be plankton, nor claimed to be first to say they can be nekton, but what is of great value is that they have dissociated swimming incompetence with the word "larva." Next we can acknowledge—and this harkens back

to the classic migration triangle—that whether a fish is plankton or nekton depends both on the fish (size or age) and the currents it is in (i.e. that it is conditional and that there is a transition of which the timing is also conditional). It remains reasonable for us to think of transport of newly hatched larvae as being mainly due to currents, but with the contribution or constraint of currents diminishing as the larva grows. That also would not be a knife-edged transition, but certainly if, for the later half of its pelagic larval period, a fish could sustain speeds of more than double the current speed, then wherever it drifted during the first-half of the pelagic period would be within range of return. Excess sustained swimming capacity could be allocated to foraging; indeed, what we see as sustained swimming ability probably has its origins in foraging and the need for it.

We can use swimming speeds and current speeds to make an order-of-magnitude estimate of the ability of a postlarva to move from an early
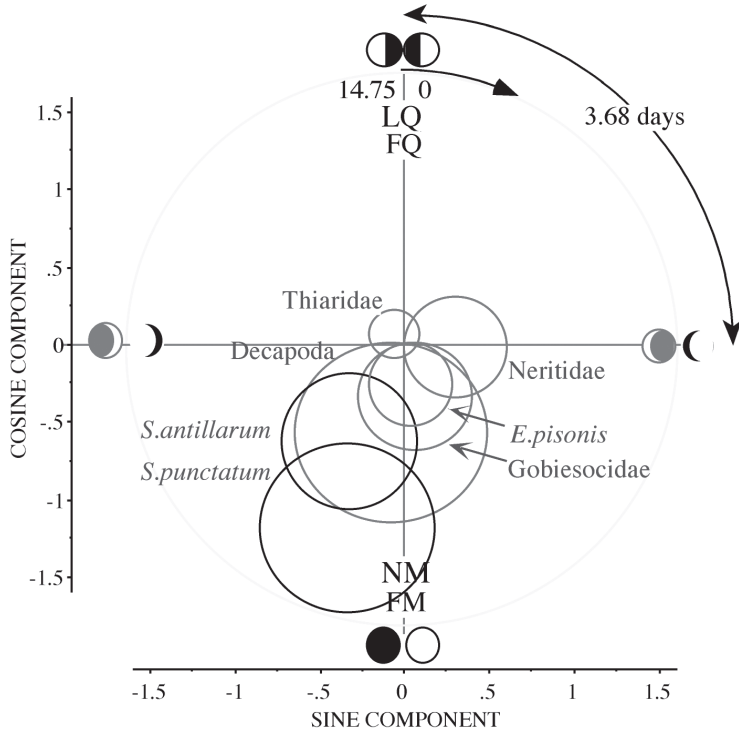
Figure 7.—Lunar recruitment and synchrony across taxa in Dominica: multiple confidence ellipses for amplitude (distance from origin) and phase (angle from the origin) on the second harmonic cycle. The second harmonic peak strikes twice in the first harmonic cycle, and one of those peaks occurs at 7–9 d following the last quarter. In other words, a portion of the recruitment seen 8 (traps) or 4 (seine fishery at Layou) d after the LQ is due to the second harmonic.
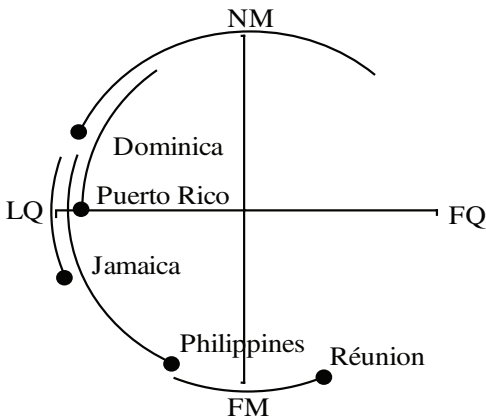

Figure 8.—Recruitment timing on the lunar scale, worldwide.

growth habitat back to the Windward Islands. This will give us some idea of the (maximum) distances it might travel during its marine stage. Consider an average of in situ estimates of sustained swimming speeds published for larvae of a range of fish taxa; sicydiine gobies are not included in the taxa reported, but let us suppose that as a fusiform larva, it would have a capability of at least average. Assume a larva of length 15 mm and a sustained swimming speed of 10 bl/s (Leis and Miller 1976) or 15 cm/s, less say 5 cm/s for opposing currents, for a net sustained progress of 10 cm/s, which equates to 8.64 km/d. Assume that the larva is three-fourths of the way through its marine period and has 20 d to reach its destination river or island: during that time, it can cover a distance (net, after allowing for opposing currents) of about 170 km. If, however, favorable currents exist and behaviors enable larvae to use them, then the potential travel distance could

be twice as far (i.e., [15 + 5]/[15 − 5] = 2). Other considerations would include productivity, the ability of a larva to continue feeding and growing on its way home, the best path through the currents, the availability of suitable cues to prompt appropriate behavioral responses, and so forth. At the low precision of data we have, we should not take this as anything more than a reasonable indication that an early growth habitat for postlarvae could be, or could extend, hundreds of kilometers away from recruitment sites.

Population independence—often a key conservation question—is related to whether EGHs are one or many for a region or are isolated or contiguous. Lack of genetic/molecular difference between sites may imply a single population, but certainty with negatives is notoriously difficult and we rely on exhaustiveness for confirmation: differences may exist, but outside the molecular markers investigated. It is also possible for populations to be functionally independent (and subject to local extirpation), even without genetic distinctiveness.

Larval Active Salinity Choice Shows Early Growth Habitat Intermediate Salinity Requirement

Sicydium punctatum larvae actively chose intermediate salinities for the first 10 d of life (Bell and Brown 1995). The experiments involved setting up haloclines in experimental containers and placing larvae in them. In a halocline, larvae show an impressively uniform response, such that although one cannot see a halocline unless it is sharp enough to generate an optical discontinuity, the point where sinking larvae turn and swim upward is so uniform that they appear to be bouncing off a flat surface. Drift mortality rates do not permit larvae to spend more than a few hours in rivers, so those 10 d must reflect EGH, which therefore must have intermediate salinities.

Oceanography and Likely Intermediate-Salinity Regions

Visible photography from space shows the island wakes of the Windward Islands (Figure 9). The photo is useful for showing the extent of influence of the islands, but these visible components are atmospheric and may not correlate with oceanic wake components. The problem is that visible photography has a far higher resolution than present remotely sensed current or chlorophyll data, and such oceanic properties do not show well in visible photography. To visualize wakes, eddies, and fronts, a resolution of about 1 km is necessary, but only 27-km resolution data are available (Anonymous 2007) so inferences will have to be limited.

From first principles, a sheltered lee zone is not doubtable. Freshwater outflows would then be slower to mix on the leeward side because of reduced wind velocity, so suitable halocline conditions are plausible here. However, these low-salinity lenses might not be stable if subject to intermittent mixing and dissipation by anomalous winds or atmospheric systems passing through, and the lack of mixing in calm times may mean limited productivity. They could also be subject to runoff, and runoff regimes can be affected (made less moderated, more noisy) by deforestation and land-use changes (including area draining systems) that reduce soil water storage. If freshwater lenses in the island lee are important as EGHs, then such locally anthropogenic hydrographic change would affect population dynamics and recruitment.

Wake eddies are known in the literature (Coutis and Middleton 2002; Hasegawa et al. 2004). Eddies seem probable in the oceanic island wake of Dominica: the island's calculated Reynolds number Re ≈ 3E10 is vastly greater than turbulence-threshold Re of 500 (Chen and Jirka 1995) and therefore implies a turbulent oceanic wake. It is not clear to what extent eddies might successfully transport nutrients to the photic zone, but there are cases where enrichment is known or argued (Hasegawa et al. 2004). We do not know to what extent eddies are consistent with moderately stable intermediate salinity conditions and with production that would be needed to sustain larvae.

So at present, we still have questions about eddies. If there are eddies in a turbulent oceanic wake, they may exist perennially or seasonally. Von Karman vortex streets are a possibility and intriguing for transport because given appropriate behaviors by larvae, they could supply currents that could help transport larvae both down and up the wake.

As Leis (2006) said, fish larvae are "nekton, not plankton" because their sustained swimming speeds can be several tens of bl/s, while the oceanic current speeds in the Caribbean west of Dominica are generally of the order of 5 cm/s (Anonymous 2007). Island
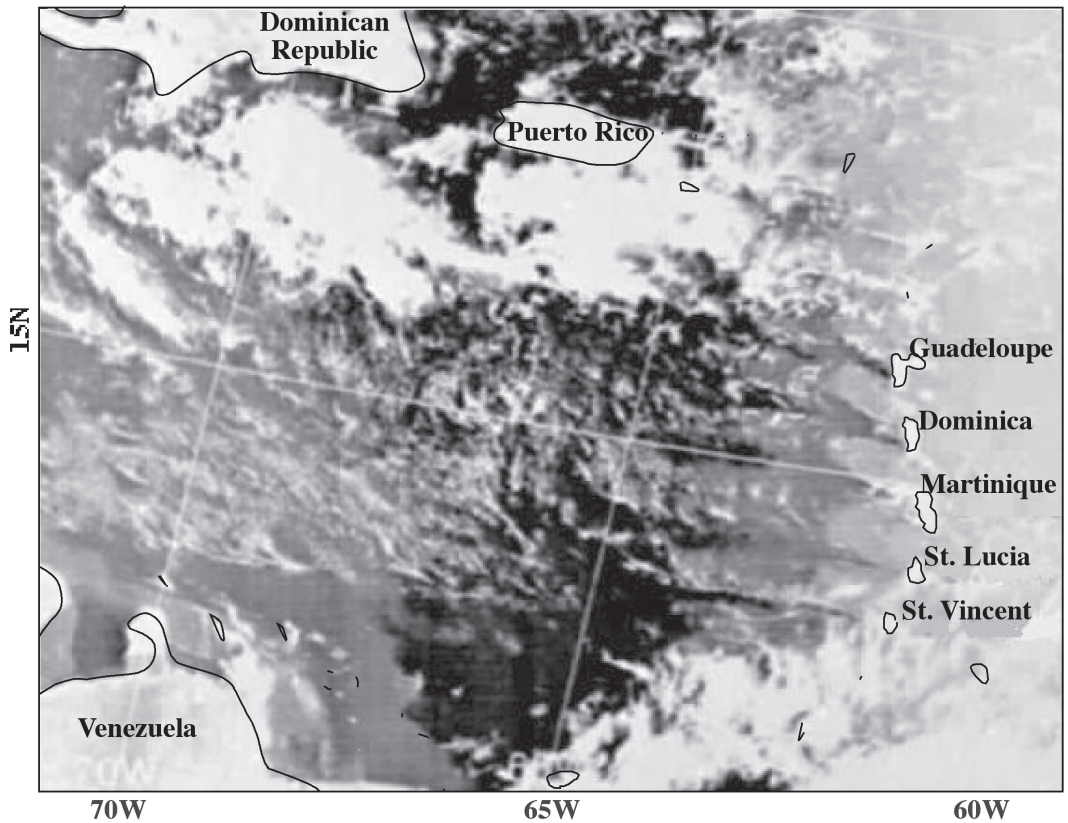
Figure 9.—Island wakes (atmospheric) of the Windward Islands, May 10 1979, photographed from space (Defense Meterological Satellite Program). Note that the low islands north of Guadeloupe have qualitatively different wakes.

wakes would be weaker currents than the surrounding waters. If larvae use wakes, they should not have trouble moving up the wakes to regain the islands. The strongest currents are those in the channels between the Windward Islands, reportedly averaging about 50 km/d or slightly more than 0.5 m/s. Those currents would likely challenge most larvae swimming against them, but the boundary and turbulent layers near the coasts might well allow fish to move from the lee to the windward coasts. The textbook image of the islands situated in a steady westward current is of course simpler than reality, but just how much so becomes apparent from detailed information (Figure 10). Available satellite data (Anonymous 2007) on currents is too coarse to detect oceanic wake eddies. Over time, however, there may be variation in the channel currents, just as there is temporal variation in the current field surrounding the islands.

Currents to the west of the Windward Islands show considerable temporal variations. Using the data (27-km resolution, 14-d averages) from January 2007 to June 2007 (all that is available from this source), the earlier months show currents tending to be more directed to the west or southwest, while by May, more meandering and features that could be interpreted as vortices appear. Unfortunately a full year cycle is not available from this source, but when it becomes available, it will be interesting to compare the current fields associated with low and high recruitment to the fishery.

Lee and Windward Systems of Island Arcs (e.g., Eastern Caribbean)

Chlorophyll-*a* distributions from imagery described in this paper are difficult to relate to currents in the
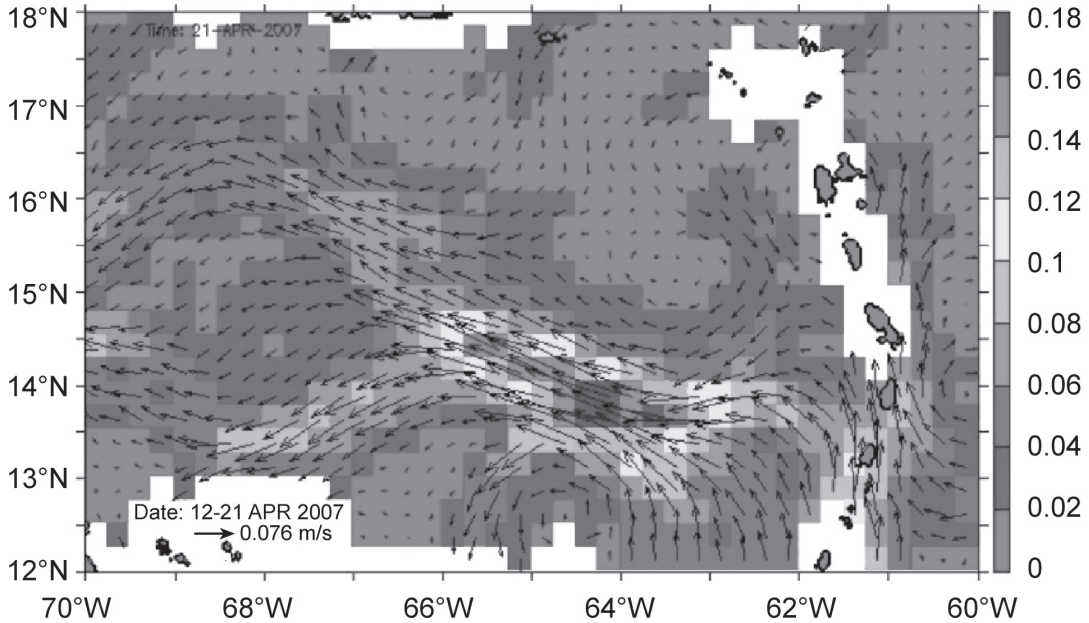
Figure 10.—Currents (geostrophic) on April 21, 2007, 27-km resolution, 14-d averages. The current structures are complex and are highly variable over time. Note that the current vectors are symbolic and not to map scale, and most of the currents are of the order of 5 cm/s or less, so that if sustained swimming speeds are only 10× body length, a larva as small as 5 mm could overcome most of the currents on this map.

remotely sensed data maps, except that the southeast Caribbean often shows higher productivity than surrounding areas and that seems to be related to flow from the southeast. I discussed above the ability of larvae to cover significant distances. Larvae may not, however, need to venture far to find high-productivity regions. Remotely sensed data (Anonymous 2007) suggests (persistently) higher chlorophyll *a* off windward coasts of the high islands (Figure 11). The high Hawaiian Islands also tend to show windward enhancement. There is little indication of high leeward productivity except in the low islands, (e.g., Antigua, St. Croix), suggesting a qualitatively different behavior in high and low islands. High islands tend to have higher rainfall (Dominica has up to 900 cm of rain per year) and a more sheltered (less well mixed, probably less upwelling) zone to the leeward. These could account for the difference by island type. Why should the productivity be highest off the windward coasts of high islands? Terrigenous nutrient outwash is likely highest on the windward coasts, but by no means absent from the leeward coast. In a well-mixed sea at low latitudes (where the

Coriolis force is weak), an onshore wind will cause shoreward surface currents and downwelling at the shore—so far is not promising for productivity—but the high rainfall and freshwater input could add complexity to that circulation pattern.

Consistent with the observations of regionally elevated chlorophyll *a* on windward coasts of the high islands, first principles and simple shore-based observations suggest a windward circulation system that could provide the required intermediate salinities and the mixing that could support high productivity for growth. Bell and Brown (1995) reported low salinities all along the beach of Castle Bruce despite constant onshore wind and breaking waves. After heavy rain, I photographed a visible front on the order of 1 km out from Rosalie beach, with the inshore water made visible by the mud carried in a brief flash flood (Figure 12). In fair weather a characteristic lighter color of inshore water can also be seen, as photographed near Bibier on the windward coast (Figure 13). These indicate a circulation more complex than that expected in a well-mixed sea. The key is that mixing takes energy and time: there must
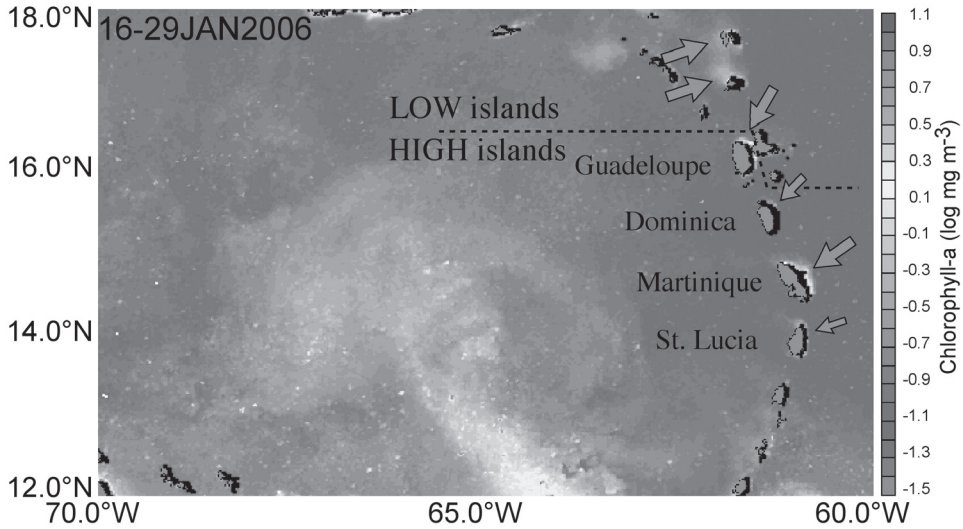
Figure 11.—Chlorophyll-*a* distribution on January 29, 2006 in the eastern Caribbean (NASA: MODIS on Aqua 2.5 km). Resolution is coarse, and high productivity (light gray) could be hidden by land-mask pixels (black). Arrows show high-productivity areas. High islands show enhanced productivity only on windward coasts. High islands generate orogenic rainfall, most heavily on windward coasts where enhanced productivity is apparent (clearest in Martinique), and have a sheltered lee with low productivity; the low islands generate little orogenic rainfall, lack a sheltered lee, and seem to show higher neritic productivity to the leeward.

Figure 12.—Rosalie beach, windward coast of Dominica, November 24, 1989. Turbid flash flood waters mixed through most of the bay in less than an hour. The demarcation at the outer edge (highlighted with four short lines) is interpreted as the outer edge of the circulation cell that comprises a nearshore system featuring intermediate-salinity water.

Figure 13.—Bibier (a few kilometers south of Rosalie), windward coast of Dominica, February 4, 1990. The different color of nearshore water (pointed to by two short lines) suggests an inshore system that is different from oceanic water.

always be, from fresh to salt, a gradient; its extent determined by freshwater input balanced against the energy available to mix it.

I propose that we can envision the windward circulation system of high-rainfall coasts being first a lower-salinity water mass (Figure 14), which develops its own circulation due to wind stress, with the upper layer moving landward, then downwelling along the bottom to some depth, then rising again at a front edge where oceanic water also moving landward under wind stress dips below it, creating a mixing zone with opposed upwelling (low salinity) and downwelling (oceanic salinity). The freshwater is typically several degrees cooler than seawater in Dominica, which adds an interesting feature. This circulation pattern explains the salinity and color observations and is consistent with the high chlorophyll *a* seen to the windward in the tall islands of the Lesser Antilles.

Such a circulation system must be dependent on a density difference sustained by high freshwater runoff. The system would be charged by runoff while being eroded by mixing at the frontal zone. Its extent could be seasonally variable (with rainfall and wind) in some locations or subject to breakdown if rainfall anomalously diminishes or if climate change reduces runoff or increases variance in it. Likewise, as commented in the context of leeward low-salinity lenses formed by runoff, development and land-use changes can make runoff noisy and river flows more variable (lower on average with excess water flushing in flash floods). If my hypothesized "windward system" circulation exists, and if it is important as an EGH for juvenile-return anadromous gobies, then disruptions could affect the population dynamics and recruitment dynamics of these species. It would also mean a longer exposure of larvae to terrigenous pollutants that persist in the windward system circulation than might be the case if larvae merely transited this system and went elsewhere.

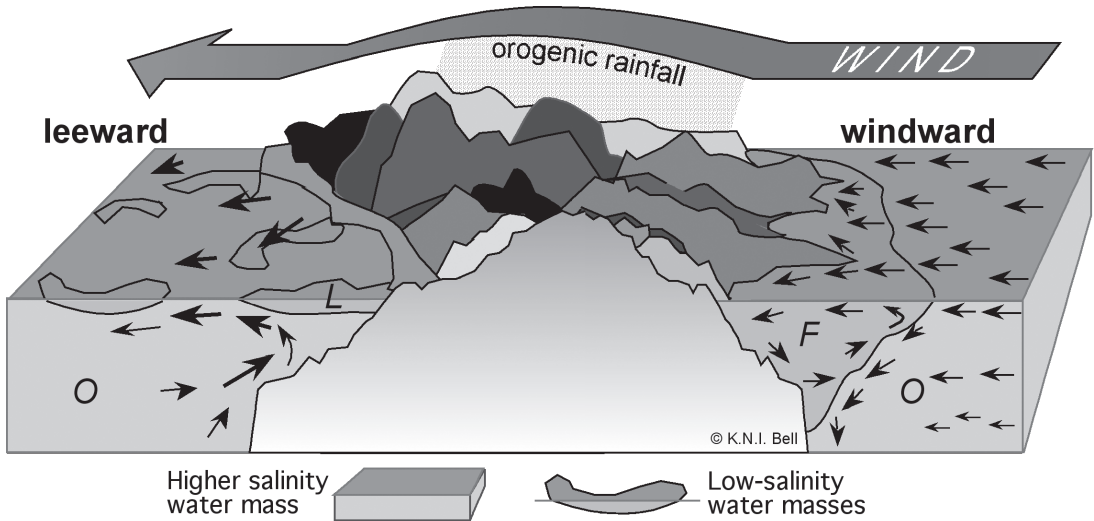The role of high freshwater runoff in early growth habitats is consistent with larval behavior

Figure 14.—An illustration of the proposed circulation model for the nearshore of an island like Dominica. Leeward freshwater lenses (L) sheltered from prevailing winds may persist and mix slowly. The model has a low-salinity water mass (F) kept to the shore by prevailing winds and has a shoreward current at the surface, a down-welling at the shore, and an upwelling at the oceanic front, where oceanic water (O) must downwell and mix.

(Bell and Brown 1995) and the implications of stable isotope analyses for Hawaiian gobies (Sorensen and Hobson 2005; Hobson et al. 2007), which help answer the question for these fishes of whether the life history period that we have generally been referring to as marine is not fully marine but considerably influenced by freshwater. The authors comment on interannual variability and on future extensions of the work (including different isotopes) that we all hope takes place, and I would suggest that to include samples randomized over seasons could also add even more interest to the results.

Conclusions

A core motivation of this work has been to supply information and ideas relevant to conservation of juvenile-return anadromous gobies and other juvenile-return anadromous fauna. There have been considerable declines in juvenile-return anadromous goby fisheries (Bell 1999). The declines did not all occur simultaneously. This paper provides at least two new routes by which anthropogenic changes could have played a role in the decline: (1) stream drift mortality implies a disproportionate reliance on downstream mainstay habitats, and degradation of mainstay habitats has certainly occurred due to deforestation, canal-ization, and coastal zone development; (2) reduced or more noisy runoff pattern, which could affect the stability and persistence of two candidate EGHs. Both of these could have occurred due to local effects in the regions where we have reports of fishery declines, and the hypothesis does not require them to have occurred at the same time worldwide.

Acknowledgments

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