Biology of Hawaiian Streams and Estuaries. Edited by N.L. Evenhuis & J.M. Fitzsimons. *Bishop Museum Bulletin in Cultural and Environmental Studies* 3: 35–61 (2007).

Opportunities in Stream Drift: Methods, Goby Larval Types, Temporal Cycles, *In situ* Mortality Estimation, and Conservation Implications

KIM N.I. BELL

Department of Ichthyology and Fisheries Science, Rhodes University, P.O. Box 94, Grahamstown 6140, South Africa; & Biology Department, Memorial University of Newfoundland, St. John's, NL, Canada, A1B 3X9; email: kbell@mun.ca

Abstract

Stream drift or rheoplankton study is relatively noninvasive. I describe methods and gear for quantitative stream drift sampling, partial self-sorting, goby larval identification, and analysis of cycles, and *in situ* mortality estimation. The rheoplankton of Dominica, W.I., includes abundant larvae of anadromous taxa (gobies, decapod crustaceans, and neritid gastropods), larval insects, acarines, calanoids, and nauplii. Other tropical volcanic coastal rivers tend to have similar assemblages. Goby larval types, of which one was confirmed as *Sicydium punctatum*, were distinguished by characters visible only in live larvae. This allowed separate analyses for each type. Abundances were analysed for temporal pattern on annual, lunar, and diurnal scales simultaneously. Twelve highly significant periodic regressions showed considerable diversity in temporal abundance patterns of different taxa or groups. Periodic regression can also enable rigorous inter-site, before/after, or impacted/unimpacted comparisons that are otherwise not reliable. A new approach to estimate *in situ* mortality was developed, and leads to important conservation and behavioural ecology implications.

Introduction

We still have much to learn about anadromous gobies, or, as some term them, amphidromous gobies. As fisheries, they are either nonexistent or by all the best accounts smaller than they used to be, and that is despite the fact that the value per kilo is likely higher per pound than any other fish locally available. Some species are listed as endangered. For fisheries and biodiversity conservation purposes, there is much we need to know. Why have the fisheries vanished or shrunk in so many places? Where are the oceanic habitats of larvae and postlarvae? How are the geographic groupings of sicydiines related; how did they disperse and where from? What larvae (free embryos) match what species? What are the main sources of mortality, or of recruitment variation? What reaches of a stream contribute the most to the larval pool? Do adult movements in-stream reflect this, as they should? Have growth rates changed? Why do the gobies in Hawai'i have much longer marine durations than those in Dominica? Are the abundances of adults in Dominican rivers typical, or are there fundamental reasons why some apparently suitable rivers have low abundances? For some of these, we have notions or even answers; but some questions lack even a background against which to pose them.

What do we know? Atwood (1791) is the first reference for sicydiine goby fisheries, and probably for sicydiine gobies. Manacop (1953) is the first reference, a milestone, for the anadromous life history, but the acceptance of his work may have suffered because it corrected a prevailing misunderstanding of the life history. The accepted knowledge that his work overturned was the following:

> "The Gobiidae are abundant in and about coral reefs, rivers, lakes, and mountain streams. A number of the small or minute kinds living in lakes or brooks are exclusively fresh-water fishes; but the vast majority, including all those of much economic importance, spawn in the sea, and the young ascend rivers and live in streams until mature. Indirect evidence is conclusive that those which survive the perilous journey to the sea return to their fresh-water haunts and continue to make the trips each way every year as long as they live" (Herre, 1927: 85c; elsewhere he lists *Sicyopterus lacrymosus* with others in the catadromous context).

Herre's (1927) assumption of catadromy was, of course, without evidence—nobody has ever reported adult sicydiines in the ocean, or re-entering rivers. His assumption of seasonally limited reproduction also could not have been supported by evidence, and I'm not sure whether it has yet been investigated; but in Dominica spawning is certainly pan-seasonal because larvae are obtainable in the stream drift year-round, and recruitment similarly is year-round (Bell & Brown, 1995; Bell *et al*., 1995; Bell, 1997). Erdman properly conceded to logic with appropriate reservations, writing (1961) "In spite of 5 yrs turning over rocks in Puerto Rico, [I have] not yet found eggs", and (1986) "while circumstantial evidence of upstream spawning is strong, I have not yet found attached eggs or nests under … rocks up to about 20 inches in diameter".

Despite Manacop's remarkable work, the idea of catadromy persisted amongst his colleagues (e.g., Montilla, 1931; Blanco, 1956) and even according to Herre (1958), who included under "List A – Marine fishes returning to sea or to brackish water to spawn" a number of Gobiidae including the genera *Sicyopterus*, *Sicyopus*, *Chonophorus*, and others. The giant can perhaps be forgiven, especially as he begins "Most people like to go fishing … I first went fishing in 1878…", but it is unaccountably surprising and also lamentable that Manacop's impressive work made no impression on an ichthyologist of such prodigious enthusiasm, even 20 years previously when Manacop was involved in his fieldwork and Herre must surely have been well aware of it. Perhaps even scientists sometimes develop an investment, which is by definition unscientific, in their ideas. (Respectful differences over the term "anadromy" as opposed to "amphidromy" are not that kind of debate about biological fact, they are about utility and communication; both terms, as defined by their users, usually apply.) Manacop's work was explicitly motivated by the need to conserve the Philippine ipon fisheries based on, like tritri in Dominica, postlarvae of anadromous gobies, but the work was not subsequently put to good use. We can only guess the time and opportunities lost because of a failure to distinguish knowledge from hypothesis and provisional assumption.

We have much too sparse information on past fisheries (Jordan & Evermann, 1905; Titcomb, 1977) in Hawai'i, and elsewhere (summarised in Bell, 1999). We have good information on methods and social patterns involved with the Philippine fisheries (Montilla, 1931) which seem all but gone, though there are evidences some products still for sale (e.g., C. Chong, pers. comm.).

We know a fair bit about biology and fisheries in the Philippines (Manacop, 1953), biology and genetics in Hawai'i (Ego, 1956; Nishimoto & Fitzsimons, 1986; Radtke *et al.*, 1988; Fitzsimons & Nishimoto, 1990; Fitzsimons *et al.*, 1990; Kinzie, 1993) and early life history, recruitment dynamics, and fisheries in Dominica (Bell & Brown, 1995; Bell *et al.*, 1995; Bell, 1997).

Manacop (1953) is also the first rheoplankton (or stream drift) reference for anadromous goby larvae in the rheoplankton. (A later work by people who knew his work claimed an inability to duplicate his results with plankton nets – this speaks again to the notion of an accepted dogma protecting itself.) Drift of other fish larvae or eggs has been acknowledged or sampled (e.g., Cambray, 1985; Copp & Cellot, 1988; Flecker *et al.*, 1991; Pavlov, 1994). Rheoplankton has been explored in anadromous goby work (Iguchi & Mizuno, 1990, 1991), and of course from 1989 in my study in Dominica in the West Indies (Bell & Brown, 1990; Bell, 1994). Kinzie (1993) commented "A more realistic measure of reproductive output of the entire stream would be to use drift sampling to catch newly hatched free embryos", underscoring the fact that despite the long but sparse history of stream drift work with anadromous gobies, unexploited opportunities remain for quantitative stream-drift work.

I have been surprised by the rheoplankton data I collected in Dominica. Before I knew how to analyse it, it seemed to say little, and that was how I reported it. Given as well the reputation of plankton data for being noisy, the uninformative bivariate plot of abundance over time seemed a confirmation until I applied periodic regression to it (as I do to almost everything). So analysis is one of the themes of this paper.

This paper gives an overview of the methods and opportunities in stream drift or rheoplankton sampling. The primary methods are quantitative sampling, live sorting and counting, and larval identification. The secondary methods involve analysis of temporal patterns, and – to be reported elsewhere – *in situ* mortality estimation. These have research and conservation implications.

Single quantitative samples can be analysed by periodic regression for estimation of temporal

patterns in abundances. Paired quantitative samples permit the *in situ* estimation of mortality in the stream drift; this does not seem to have been done before, except by Bell (1994).

Qualitative Sampling and Analysis

The previous literature has been criticised because "Virtually without exception, however, reports of drift lack statements of the precision of the estimate" (Allan & Russek, 1985). This is a clear reference to drift studies that are largely descriptive (with exceptions such as Kohler, 1985), and to data plotted as bars or line plots without objective analysis. Indeed, as this paper will show, it is very difficult to see temporal pattern on a bivariate basis, because pattern exists on multiple timescales that are superimposed. I hope here to provide a glimpse of the light at the end of the tunnel that will encourage a more adventurous application of stream drift study.

The desire for estimates of precision (e.g., Allan & Russek, 1985) can sometimes be satisfied not with replication at each time and place, but instead as the residual error of a regression. In fact I would suggest that effort is likely better spent on representation than replication, provided a regression is to result. I would go further than that, and say (supported by the results of this paper) that careful estimates of precision could be quite useless without establishing what the temporal and spatial patterns are. If replicated samples taken at two sites, one at 1045h on the third day after the new moon in September and the other at 0530h on the 12th day after the new moon in March, yield means that are "significantly" different, what does that mean? We know it is impossible to be in two places at once, therefore we cannot sample in two places at once. Can we say the difference is due to site? ... or due to before/after some environmental impact like hurricane or pollution? What if there is a pattern, and what if the difference found could be as well explained by the sample timing alone? We need some ways of characterising stream drift that take account of the pattern, or our work is nearly meaningless.

Rheoplankton, or stream drift, is rarely analysed for cycles in abundances. The expected natural cycles are the day, the tide, the lunar month, and the year (seasons). However, many studies are too brief to allow analysis of natural cycles longer than a day, and in many cases analyses that are possible are not attempted. This is possibly due to a lack of awareness of periodic regression (Bliss, 1958; Batschelet, 1981; Bell *et al.*, 1995; Bell, 2004) in biology.

Models like periodic regression bring many advantages. Obviously, they provide a description of patterns in abundance. Next, the mesor, which in the context of an ordinary regression is the intercept, gives a very robust estimate of central tendency that is effectively corrected for uneven sampling over the cycles—it is therefore much more meaningful than the simple mean of all data, and may be useful in comparing populations. Where periodic regressions explain a large amount of variation, they improve our ability to compare different populations because they reduce the amount of variation that is attributed to noise or error. When we have a temporal model of variation, observations can be put in the context of the pattern so that we avoid two possible errors: falsely attributing differences to situations or sites when they are really due to timing of samples; or falsely considering situations to be the same when this is only an accident of sample timing.

Sometimes more importantly, such models allow us to remove temporal trends and cycles from data so that we can analyse them with respect to other factors that are of interest, say, from the point of view of conservation. Conservation-related factors, such as the degree of development impact on sites, may not be capable of resolution with 'raw' data because the temporal/periodic signal overwhelms the factor signal.

Periodic regression is so readily manageable, and an understanding of cycles so important, that it should be a focal point for organising information in any studies where data can be affected by cycles.

Complex relationships cannot be fully represented on bivariate plots; indeed they can be quite difficult to visualize graphically. Any visualisation is therefore a crib, imperfect, but necessarily so, and a series of them can relate to a multiple regression. For these reasons, residuals become the chief avenue of diagnosis of the quality of an analysis that has more independent variables than can be graphically represented together.

Identification of larval goby larval types

Larvae of gobies can be distinguished using features that are visible when live. Identification from preserved larvae would have to rely on those features which reliably persist in the preserved state, and many of the features would not.

***In situ* mortality estimation**

Mortality rates in rheoplankton are often alluded to, but never have been estimated *in situ*. Only Bell (1994) provides a way to estimate drift mortality *in situ*. The approach and results will be briefly summarised here; the work has been extended and will be detailed elsewhere.

Why is it important? Considerable pressure is being exerted on natural systems by human systems (e.g., Brasher, 2003). Mortality estimated *in situ* is needed if we are to establish the losses that take place during the period of drift of hatchlings to the sea. Whatever the survival rate is, it is cumulative with time; this means that any increase in the drift distance that larvae must cover will result in an exponentially increased loss of larvae over that distance. Rates reported in Bell (1994) indicate survivals at or below 50% per hour (which is very close to per kilometer if the current speed is 0.3 m/s). At 50% mortality per hour only about 3% of larvae would survive a 5-hour drift. This is a very good reason for adults to select territories with the shortest drift times, i.e. nearest the sea. That in turn means the emphasis in conservation should be to preferentially preserve the habitats closer to the sea.

Materials and Methods

Primary Methods

Sampling

Sampling gear

Quantitative samples were taken using specially made small conical nets suspended at a settable depth below the water surface and with a mechanical integrating current meter outside of the net (Fig. 1). A variety of configurations were experimented with, including triple nets that produced three replicates at each set, but the preferred design is the one presented here.

The nets used were made from 81-µm Nitex™ mesh. The net sizes varied from 46 mm diameter at the mouth (a truly micro net), to 112 mm diameter at the mouth, used as a single net (tested also as a group of three but was not workable). The 112 mm diameter nets were ~1.0 m long (mesh portion of the cone). This made for a very high mesh/mouth area ratio, and therefore for a high filtering efficiency (FE). FE appeared to be close to 1.0, because particles drifting inside the net could not be seen to slow down, compared to particles outside the net, until they actually hit the mesh. Two practical considerations are: (1) overestimating FE reduces (does not increase) the calculated abundances; and (2) any constant error in FE has no effect on ratios of abundances. Calculations treated FE as equal to unity.

Nets had: [1] ballast chambers, made by gluing lids of film canisters onto the net collar, so that the canister could be snapped on with any desired air/water balance, to adjust buoyancy to near zero; [2] vanes (built onto the canisters) to induce rotation, and because of the attachment means the vane pitch could easily be adjusted; [3] an attachment for the current meter to be mounted on the side; and [4] a bridle with a swivel and clip for attachment to the deployment system. Rotation was in order to have the average position of the current meter equal to the center of the net mouth. There were other configurations but they were analogous.

Nets typically were attached to a bridle that clipped to a slidable element on a vertical cable between a float and a weight suspended from it. This allowed depth to be set (the target was usually about 1/3 of the water depth from the surface). A stayline and staypole was attached to the float. The gear was supportable either by a stayline alone (for sampling from bridges) or, for sampling from shore, the operator would hold the stayline taut on the upstream side and push out with the staypole on the downstream side to keep the gear in the desired position. All nets were made to be easily handled, rinsed, and emptied. A mechanical integrating current meter attached to the outside of the net provided an index of the amount total flow past the net (which, at FE = 1.0 is the same as

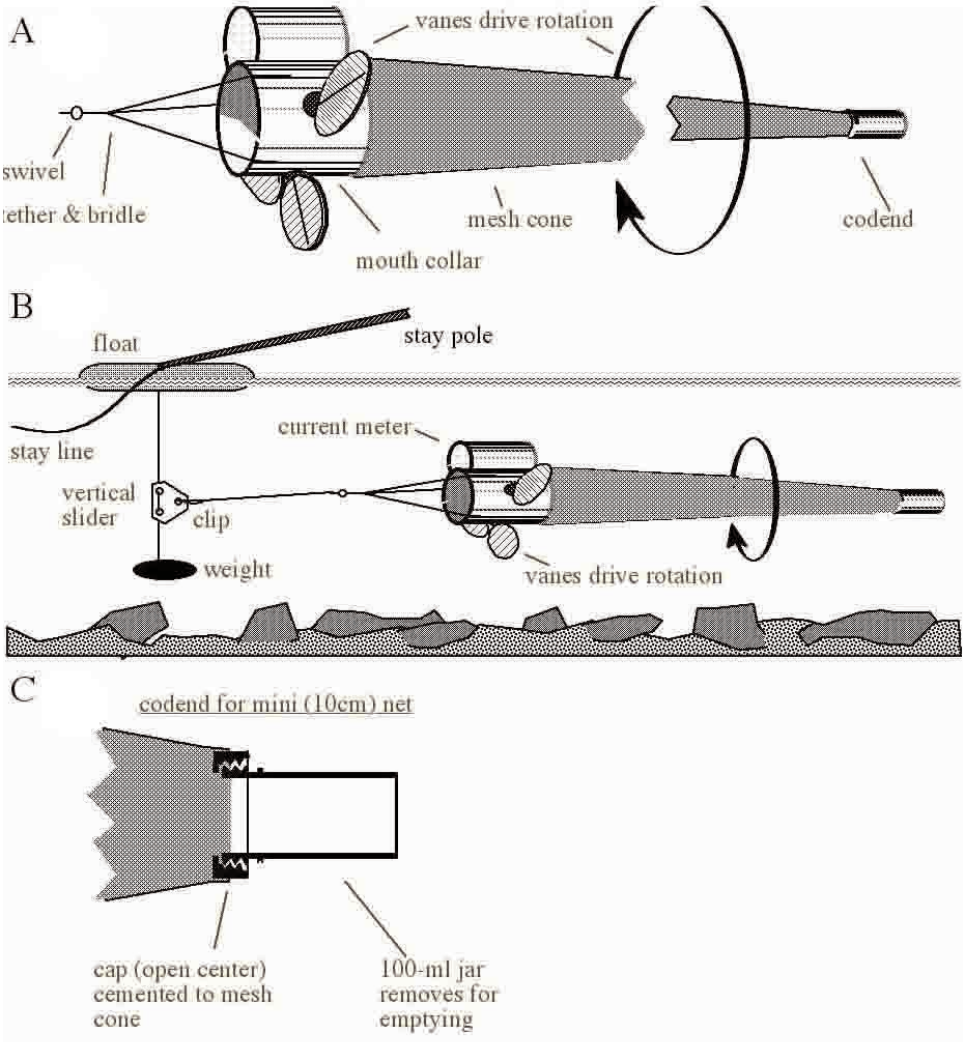

Figure 1. Plankton gear, semi-miniature for quantitative rheoplankton sampling in small rivers. **A**: Net, buoyancy chambers, vanes, attached current meter, and bridle and swivel attachment. Mouth diameter of net is ~11 cm diam. and the mesh cone is ~1 m long. Rotation caused by vanes allow the average position of the attached current meter to be the same as the position of the net. **B**: Deployment: float and weight system allows sample depth to be easily set; clip allows quick detachment. **C**: Threaded cod end for quick emptying.

flow inside the net). Calibration of the meter allowed this index to be converted to distance, which, multiplied by the mouth area of the net, estimated volume sampled and made the sample quantitative. A subtle point is that even after calibration (of virtually any meter), we have no estimate of what actually flows through the meter itself, we merely correlate a reading with a distance. That means we must avoid the a temptation to put the meter inside the net itself, even though it seems a neat thing to do, because that configuration cannot be calibrated by pulling the gear through a known distance.

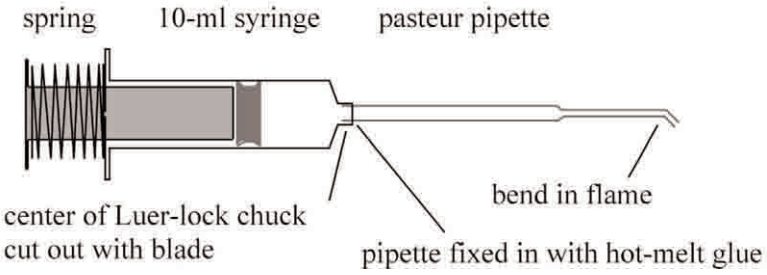

Figure 2. Spring-loaded suction pipette for counting live plankton out of a dish. Spring can be made by winding tempered wire around the syringe barrel; it will expand slightly when released. The plunger is pulled out, put through the spring, and replaced. Spring can be tensioned as needed. Needle end of syringe, inside the collar, is cut out with a blade. The Pasteur pipette is cut, bent as desired, and the end fire-polished (a butane lighter is hot enough); then it is glued with hot-melt glue into the collar. In use, syringe is gripped so that the thumb depresses the plunger at the start, and releases it in small jumps as plankton organisms are suctioned. This gives effective and easy control.

Sampling procedure

Each sample was accompanied by data for: location, date, time, water temperature, current meter reading, and elapsed time (typically 5–10 minutes, a sampled volume of about 1 m^3, which typically would yield several dozen larvae). Samples were rinsed from the net within a minute or two of ending the sample, into labeled carrying jars. Sufficient water was kept in order that the sample remained alive. Samples could remain alive for at least 24 hours, although counting was usually done before that. A check on this is the count of dead larvae; these were typically nil to < 5%, even after 24 hours.

Live counting of samples

Preservation can reduce a sample to a grey sludge of barely recognizable items stuck together, such that within normal limits of human patience they cannot be accurately counted. Live counting gives better results because live organisms are more readily detectable and identifiable. Live counting is necessary to identify larvae as types or species, because while black pigments may persist in preserved specimens, the green pigments certainly do not, and the yolk colours and textures would probably also be lost; there may also be distortion of larvae. Counting dishes used were small, ~20 mm diameter, so as to fit within the low-power field of the microscope.

Before counting, 'self-sorting' takes advantage of larval behaviour. Firstly, as the sample is allowed to stand for an hour in the collecting jar, debris and detritus settles to the bottom. The sample is then carefully decanted through a sieve (70 to 80 µm mesh) and the sample transferred to a counting dish while the water is returned to the sample. This allows the decanting procedure to be repeated as needed. Goby larvae and decapod larvae, for instance, are virtually all recovered alive in the first decant, few in the second, and rarely any in the third. Mollusc (Neritidae) larvae show abundantly in the decanted portion, but often a considerable number remain in the sediment. Caddis- and to a lesser extent mayfly larvae favour the sediment. The settled sediment can be easily subsampled using a suction tube and estimating the portion sampled (easily done on an area basis because the removed sediment leaves an empty area that is easy to estimate as a fraction of the total).

Once in the counting dish, the most reliable way of counting is to suction out individuals, one by one, for all OTUs (Operational Taxonomic Units) of principal interest. Other OTUs of peripheral interest to the study, such as mollusc larvae that often numbered in the hundreds or thousands, can be estimated, and the estimates can occasionally be checked against counts. If the estimates are terrible, the analyses will not likely show significance.

Counting pipette and anaesthetic

Key to live counting is a spring-loaded pipette (Fig. 2) made for the purpose. Several pipetting approaches were tried but the suction from rubber bulbs and standard lab devices is too slow, the effort makes the pipette hard to aim, and the plankton escape; and if too much is suctioned at once the operator cannot count the items. A quick-acting suctioning device that could decisively suction up a wary larva was made from a pasteur pipette fixed to a 10-ml syringe that in turn was modified to be spring-loaded. Pushing on the plunger compressed the spring and emptied the syringe, and releasing pressure allowed the syringe to suction up water. Releasing thumb pressure in controlled amounts is much more amenable to human control than applying it in controlled amounts. The plankton ejects easily, almost never did anything get stuck in the syringe, and the device stays clean for a long time. A quick rinse is easy by suctioning clean water, shaking, and expelling; but to allow use of a squirt bottle to occasionally rinse the syringe without having to remove the plunger, a 6 mm 'rinse hole' was punched in the syringe body just below where the plunger would stop when pulled all the way back.

Suctioning out goby larvae is much easier if the larvae are anaesthetised. I used 2-phenoxyethanol, from which I would make a stock dilution of about 0.1 to 1.0%, or a few drops of 2-phenoxyethanol in about 50 ml of water. It is important to make the stock dilution beforehand because 2-phenoxyethanol is an oily alcohol and takes a long time to mix. The stock dilution keeps, for practical purposes, indefinitely, and a couple of drops of this in the counting dish will anaesthetise goby larvae in a few seconds to a minute. Recovery occurs quickly after a water change. Identification much less reliable (and impossible if it requires reference to features that don't preserve) with preserved larvae, and anaesthetic is very helpful in keeping the live ones still. An emergency alternative anaesthetic might be ice water, but condensation on the bottom of the dish might interfere with the oblique/below illumination needed to see the larval features.

Goby larvae are best counted out in groups of any single type, which means one first needs to see the group that one will next count out; but the decapod larvae are very active and create problems by moving the goby larvae, interfering with the process of identification and counting. It is therefore best to remove decapod larvae first, but they do not succumb to 2-phenoxyethanol at the concentrations used. However a little practise seems sufficient to cope with them, and swirling the counting dish causes the inactive particles to move to the center, simplifying the process of suctioning out the decapod larvae from the edges.

Sampling protocol

Many cycles act together to influence the systems we study. It is common that people are advised to constrain sampling to, say a particular time of day or time of tide in order to eliminate variation from that source. But there are some major problems with that approach. First, the same time of day and tide do not recur often, and this reduces sampling opportunities. Second, how useful, really, is the sample set going to be if it cannot be related to the values (whether CPUE or temperature) outside a narrow range of times of day or other cycle? Third, taking the 'same time of day' approach can impose an artificial periodicity on the data and may limit the ability to resolve other cycles. The best approach is random sampling in time, but a close approximation is to use the world as your random number generator, and sample whenever manageable. (Logistical factors like vehicle availability, gear failures, time demands of other work, holidays, staff availability, etc., cannot be expected to correlate with the independent variable (number of larvae) being sampled, so there is no basis to declare a bias). Sampling times were therefore chosen haphazardly or opportunistically, within the conditions that permitted sampling.

The general difficulties of fieldwork at night hardly need explanation. A few remarks may help put into perspective any concern about the lower density of samples in the night and the inferences for night time. The analysis decomposes temporal pattern into a series of sinusoidal patterns; sinusoidality is the most parsimonious assumption for a cycle because a sinusoidal curve results from the intersection of a flat plane and a cylinder, so it is equivalent to the straight-line assumption for regression, and the regression can indeed be represented in such a form. Concern over a sparsely-sampled region of a sinusoidal curve is therefore exactly—no more, no less—the same as for a

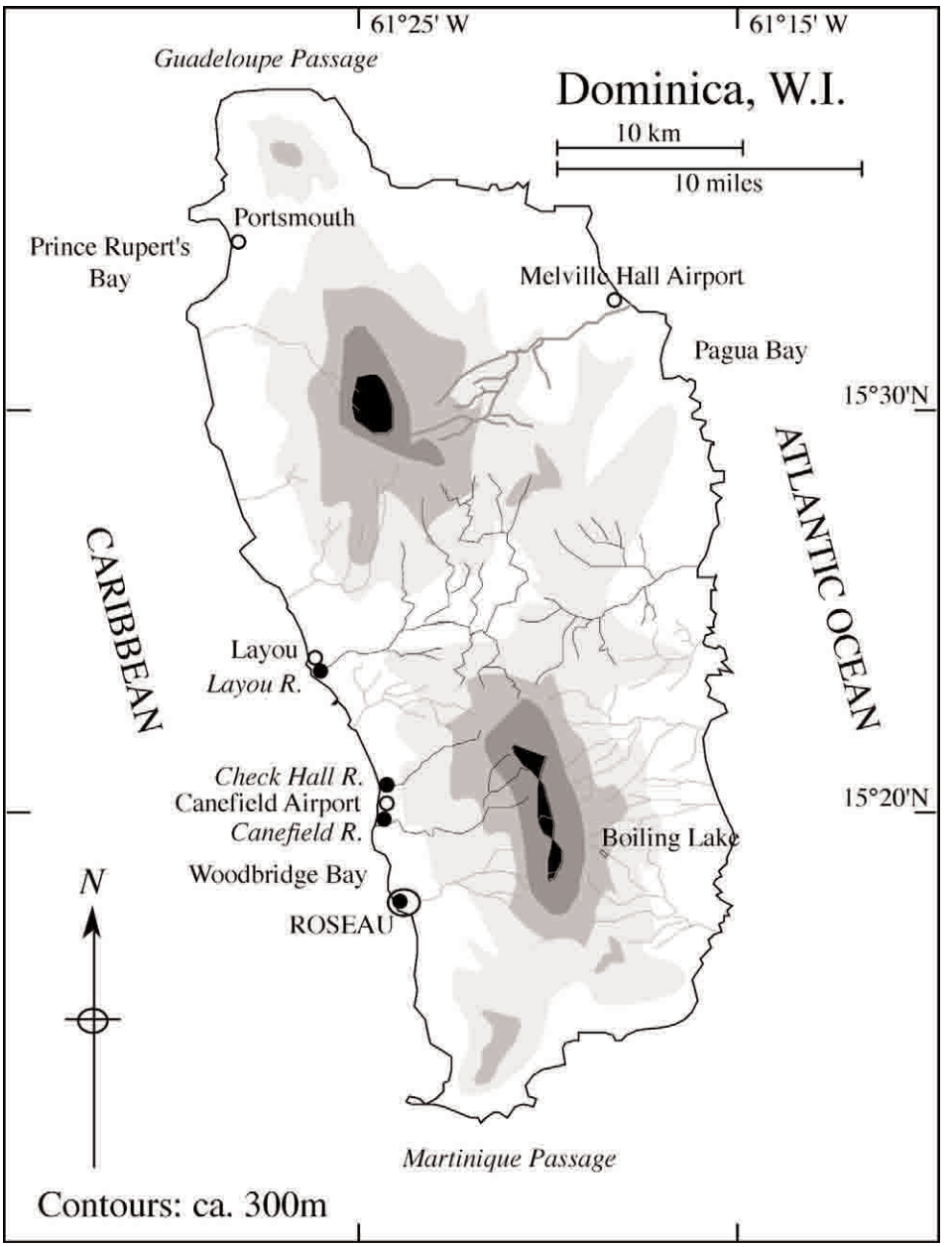

Figure 3. Sample sites for this study: Layou, Check Hall, Canefield, and Roseau Rivers. Only selected watersheds are shown. By volume, Layou and Roseau Rivers are similar and about twice either Check Hall or Canefield Rivers.

sparsely-sampled region of a straight-line regression. Residuals are the prime diagnostic test for this kind of issue. Concern over the lower representation of night-time samples would relate only to the diurnal cycle, first harmonic only. The peaks, it should be remembered, are the counterparts of the troughs, 180° out of phase. Peaks in pattern are not estimated individually or simply from peaks in

observed abundance, instead it is a pattern that is estimated from all the data. The sine curve has parameters amplitude and phase, and nothing more. A reasonably dense sampling of half of a sinusoidal cycle is more than adequate to estimate the entire cycle. The sole issue is that of the assumption of sinusoidality, but as explained this is the simplest, most parsimonious cycle that can be proposed.

Sample locations
The work reported here was carried out in four rivers on the west coast Dominica, West Indies (Fig. 3). The *in situ* drift mortality study was carried out in lower reaches of Layou and Canefield Rivers.

Identification (species). Goby adults were identified according to Brockmann (1965) and Jordan & Evermann (1898). Brockmann (1965) supplies photographs as well as scale counts, leading to the identification of *Sicydium punctatum* Perugia, *S. antillarum* Ogilvie-Grant, and *Awaous taiasica* (Lichtenstein). *Sicydium punctatum* is often called *S. plumieri* (e.g., Erdman, 1986) and probably in error because the latter was described on the basis of a drawing, and there are no type specimens. Voucher specimens of *S. punctatum* recruits from Dominica are in the U.S. National Museum (catalogued as USNM 314002).

Identification (goby larval types). Larval type identification allowed analysing of individual types contained within the mix of "goby larvae". Features or characters used in larval typing are the location and pattern of each kind (black and yellow-green) of pigment, and the yolk size, colour, surface texture, and shape. These need to be seen with oblique lighting, so that larvae are seen against a dark field. Larval size is similar for most types (~1800 µm) but one type seems markedly larger (~2000 µm). Because the most important larval typing features do not preserve (at all), [1] all work had to be done with live samples; and [2] there had to be reliance on sketching and notes from live specimens. Few good photographs were taken, and the features rarely show as well in photographs as in life, but the future for this kind of work looks brighter, with advances in digital photography making it possible to confirm immediately that a good photograph has been taken. The best photographs are taken with lighting from the side against a dark field; transmitted light tends to hide differences. Good photographs can be taken under stereo/dissecting microscopes, or with compound microscopes and a depression slide.

OTUs—operational taxonomic units
Operational taxonomic units were employed as in Table 1, to accommodate identification to a level that was reasonable in terms of the central objective of the study, which was to determine features of sicydiine goby life-history that would be relevant to management and conservation.

Secondary Methods 1: **Temporal Cycles**
Periodic regression is described in previous works (Bliss, 1958; Batschelet, 1981; Bell *et al.*, 1995; Bell, 1997; Bell, 2004). The kind of situation with a periodic or circular x and a linear y is often termed "cylindrical" because the periodic x is transformed into the coordinates of the unit circle forming the base of the cylinder, and the linear y is visualised as marked as the height of the cylinder. If you like, imagine the dial of a 24-hour clock, with some values (e.g., air temperature) represented as columns of height y positioned on the rim of the clock according to the time of the observation. Visualising periodic regression is helped by remembering that a sine curve results, around the cylinder, if the cylinder is cut on a flat plane. That plane can be described by the coefficients of the sine and cosine components of a cycle.

Temporal variables (three periodic and one aperiodic) derived from the date observed with each sample are:

- DOY = day-of-year (0 to 364.999);
- TOD = time of day;
- LQ = phase in lunar cycle (with zero set at Last Quarter). For each lunar month, lunar phase is trued to the U.S. Naval Office (USNO) lunar phase tables because lunar months vary in length;

- NDOY = a sequential index of days past since the beginning of the study. The periodic variables were converted to a standard angular system (degrees or rads) so that sine and cosine could be taken for use in the regression analysis. The regression equation used for all taxa was:

Equation 1:

$$\ln(1+OTU/m^3) = B0 + B1NDOY + B2sin`DOY + B3cos`DOY + B4sin`2DOY + B5cos`2DOY + B6sin`TOD + B7cos`TOD + B8sin`2TOD + B9cos`2TOD + B10sin`LQ + B11cos`LQ + B12sin`2LQ + B13cos`2LQ + e$$

where the Bs are coefficients with numbered subscripts, sin` and cos` mean "proper" sine and cosine (i.e., taken after conversion of the natural periodic variable to a conventional angular system), and the numeral 2 (e.g., sin`2DOY) indicates a doubling of the index in order to obtain the second harmonic, and *e* is a normally-distributed error.

Second harmonics are commonly significant in climatic (etc.) data, and improve the fit. I prefer to have the same model for all groupings, and so I have kept the harmonics, whether significant or not. (And regarding dropping non-significant parts of a sine and cosine pair, and despite published bad advice to the contrary, dropping the non-significant part of a (sin, cos) pair is improper because where the peak is aligned with 0°, 90°, 180° or 270°, one will inevitably be non-significant; removing it illegitimately inflates the mean square because you used it to discover where the peak was. This all goes to the point that a cycle cannot be expressed in less than 2 dimensions.)

Residuals were used to help determine the suitability of the analysis and transformation used.

Secondary Methods 2: ***In Situ*** **Mortality**

Methods are as described in Bell (1994). In summary, the method is based on paired (one upstream and one downstream) quantitative stream drift samples with known distance and drift time between them, so that survival can be solved for each pair. The method estimates net disappearance rate from the plankton. That equates to mortality in taxa and stages that drift until they either die or reach the sea (or at least pass the lower sample station); that description fits drifting larvae of the anadromous taxa discussed here. Goby larvae in Dominica kept in aquaria were never seen to settle until death was imminent. The reach chosen should be one where reproduction can be assumed to be zero; but if that is violated, it only makes estimates of survival larger, therefore they are conservative. Production is indicated where S exceeds unity, and that again will be conservative to the extent of the actual mortality.

Results and Discussion

Larval types

Types can in principle be nominated on the basis of actually arising from a species (in which case the differences, however slight, are accepted), or on the basis of evident distinctiveness. The latter is used here because we do not have, from all known species, samples of their larvae matched to them.

Five credible types were defined from field samples: F, Y, W, PADBS, and PAF (Table 1, Fig. 4). These types are credible because they differ from each other by at least two characters. If these characters are taken separately for all the types, and randomly recombined, most combinations have no larvae to match them. Therefore the observed character combinationss cannot freflect independent random variation. Furthermore, amongst the many thousands of verified (captive spawning) *S. punctatum* larvae, all of type F. Field-collected nests from reaches inhabited by *S. punctatum* also showed virtually no within-nest variation, and the consistency of larvae from nests and captivity also tends to eliminate the possibility that larval types are determined by local conditions, or diet, etc. And, finally, the regressions show that types have differing temporal characteristics. This constancy suggests that the characters used (yolk colour, texture, size; pigment types, patterns and somatic distribution) are determined by the species, and therefore that the unique combinations of characters are

Table 1. List of Operational Taxonomic Units [OTUs]

Goby larval types

gl — all goby larvae

F — verified to correspond to *Sicydium punctatum*. Clear greenish smooth yolk, "fluor" (a bright yellow-green pigment that looks fluorescent, like fluorescein, although it isn't) in trunk (dorsal of midline). Subsumes possible but uncertain variation noted as subtypes **Fyg** (common) and **Frb** (rare),

Y — yellow spherical crusty yolk

W — clear yolk, no fluor

PADBS — postpelvic double brown spot. Rare.

PAF — post-anal fluor that is both dorsal and ventral to notochord (unlike F where fluor is centered on pelvic region and is only ventral to notochord). Rare (not found prior to 1997).

Other anadromous OTUs

shrABC ("shr" may be written "shrimp" for readability) or **SHRall** — candidates: all decapod larvae. Many species (Atyidae, Palaemonidae, and crabs) are in Dominica's rivers (Chace & Hobbs, 1969).

shrA or ShrimpA — Decapodan larva 2mm long, body depth through cephalothorax not more than 2x depth through anterior abdominal segments. This is the most abundant type.

shrB — decapodan larva > 2 mm, cephalothorax depth > 2 x depth of anterior abdominal segments. Second most abundant type but insufficient data for analysis.

shrC — like shrB except curled and with a cephalothoracic spike like a cypris larva, may be a later moult of B. Insufficient data for analysis.

moll — mollusc larvae, Neritidae; there seem to be at least two Dominican Neritids (Noblet & Damian, 1991), with possibly similar larvae, but one, possibly a smaller kind (lived ~7 yr in aquarium, stayed small but continuously produced larvae) liberates swimming larvae directly into the water and another species may lay eggs in capsules as is referred to elsewhere.

Nonanadromous or uncertain OTUs

mayfl — mayfly larvae

cadd — caddisfly larvae

cala — calanoid copepodites (diadromous? opportunistic?)

naup — nauplii

tick — acarines (likely ticks)

a sound way to differentiate and identify larvae. Time and growth will reduce the size of the yolk and there will be development of eyes and the jaw structure, but the key features distinguishing the five credible types remain clear during the short time spent in fresh water. We thus have ample reason to accept that the larval types are different species, even though we have not trued them all.

In addition to the five credible types based on two or more clear differences, one questionable sub-type distinction exists based on a single difference that is extremely subtle. Within Type F is a subtle difference between sub-types designated Fyg (most of F) and Frb. The difference is a brownish reddish tint to the otherwise yellow-green pigment, and a possibly slower reaction to the anaesthetic 2-phenoxyethanol. Frb is either a type, or a subtype, or a developmental error, or an artefact of lighting conditions, etc.; we cannot yet be sure which. The subtleness of the difference makes it very difficult to quickly and reliably distinguish Frb from Fyg, which is why the data are not good enough to analyse it separately.

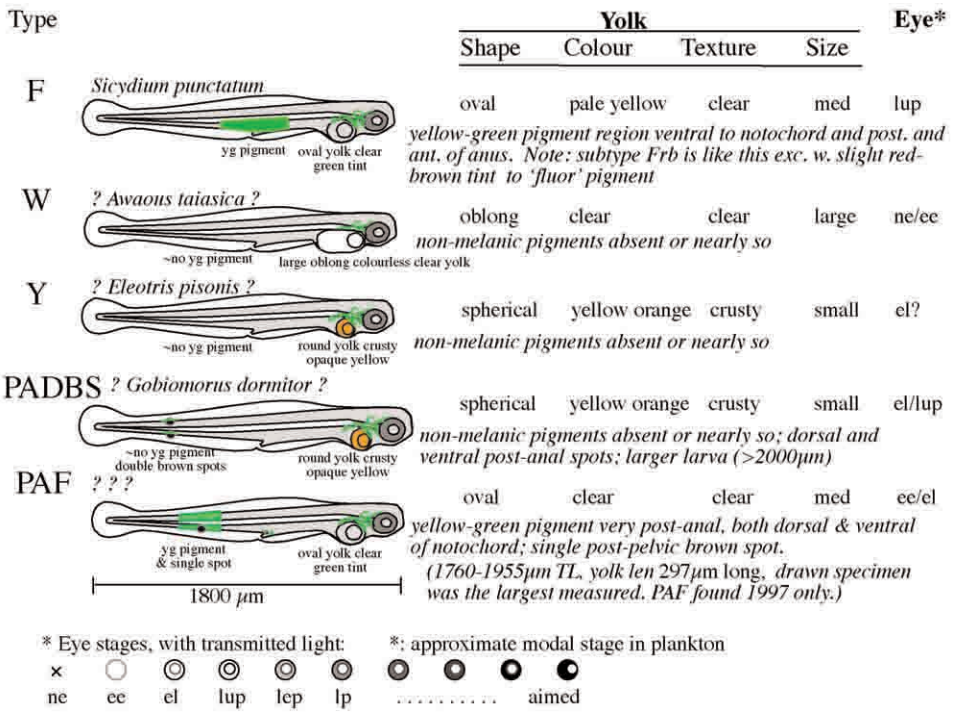

Figure 4. Characteristics of larval types recognised from Dominica, W.I. Type F corresponds to *Sicydium punctatum.* Circumstantial evidence prompts tentative linking of other types with species named between question marks. The yellow green pigment is sometimes referred to in notes as 'fluor' because its colour is like flourescein, although it does not fluoresce. PAF has a single brown spot, instead of the 2 in Ppdbs, and a very different pattern of 'fluor' pigment compared to F.

If the Frb sub-type were a good type, i.e. the sole match to a single species, the most plausible candidate would be a species in the same genus, which would be *Sicydium antillarum*; if not, the next most similar type seems to be PAF, but the low incidence of PAF (not seen prior to 1997 and even then uncommon) would be inconsistent with the presence of *Sicydium antillarum* at 1% to 5% of returning recruits (entering freshwater as postlarvae). Here I treat the Fyg/Frb distinction as insufficient to support a type, but the issue remains until the types are all accounted for by species.

The known numbers of credible larval types and of goby species match identically (unless subtype Frb is a good type).

The number of species recognised as adults may not be complete; it could be that a very rare larval type could represent a species that only occasionally occurs in Dominica, or that is rare enough to appear as larvae only once in a few hundred samples. Alternatively, there have been seen some adult morphs which look like *S. punctatum* but with a completely different, disorganized, colour pattern; they show a blotchy pattern of yellow/orange and brown/black, which interestingly are close to the colours of *Lentipes concolor*. These are very rare, and have been seen as postlarvae and as adults, in more than one river, and spanning decades; we do not know whether they are variants or hybrids. Species hybrids could generate unique larvae as rare as the hybrids. Or, if rare genetic colour morphs exist within a species, then it is possible that they might contribute larvae that show subtle variation from the normal species type.

Candidate species to match the types (see Fig. 4) are *Sicydium punctatum*, *S. antillarum*, *Eleotris pisonis*, *Awaous taiasica* [sensu Brockmann (1965) but disputed by Helen Larson (pers. comm.)], and *Gobiomorus dormitor* (very rare, only ~5 adults seen).

The present work was done 1989–1991 and 1997. Genetic matching of larvae and adults could match larvae with species, and Lindstrom (1999) has since done that nicely for several Hawaiian species. Captive spawnings of the other species present could also definitively resolve this issue. The credible types already permit a more interesting analysis of the goby larvae in the stream drift.

Temporal cycles of abundance

All but three taxonomic groupings show higher adjusted multiple R^2 when analysed as $\ln(1+N/m^3)$ as opposed to N/m^3, or concentration. Even those three exceptions were not markedly better as number/m^3, and therefore for consistency all taxonomic groupings are analysed as $\ln(1+N/m^3)$.

Many of us feel somewhat uneasy about transformations, and about interpreting the results, and would intuitively prefer to use un-transformed data, even at the cost of a slightly lower R^2 and reduced significance. However, there are hazards to not using the transformation, because certain aspects of the pattern may be exaggerated due to the distribution (i.e. non-normal distribution) of the data and consequently (and this rather than the distribution of data is what matters) the distribution of the residuals. Plankton data tend to be somewhat log-normally distributed, and these are no exception. Least-squares regression assumes normally-distributed residuals, and if data are not normal a few high values can distort a regression. For example, the mesor in a periodic regression establishes the central value to which all cyclic effects add variation (the net effect of a cycle over an entire period is zero). Mesors from a log regression are obviously in log scale, so, comparing log and untransformed regressions, the mesor of the regression of all goby larvae using $\ln(1+N/m^3)$ vs. the first and second harmonics of seasonal, lunar, and diurnal cycles yields a mesor of 3.903, which (exp(y)–1) is 48 larvae per cubic meter, whereas if we use the untransformed variable (N/m^3), the mesor is 298 larvae per cubic meter. But is 298 larvae the median, or modal number of larvae/m^3 found in the samples? No. The median is about 13, even the 75th percentile is still only 40, the arithmetic mean is 94, and the mode is whatever interval includes zero. A median value of 298 larvae/m^3 is simply inconsistent with the data. Therefore the 'untransformed' model does not fit, and we are compelled to use the transformation.

Some of the cycles in Figs. 5, 6, and 7 dip into negative values. (This happens, by the way, in the un-transformed regressions as well.) There is no such thing as a negative larva, so how do we interpret these? Negative values simply reflect the fact that periodic regression decomposes temporal trends into a number of specified cycles that are symmetrical, so, just as a straight-line function can dip into negative values if extended into a region of x where the expected values of y are zero (if actual values are not zero, this is either a result of a limitation of the model or the result of scatter around the expected value), a periodic regression is no different. We could ask the regression to replace those negative values with zeroes, but that is cumbersome and we can do it by eye just as well. Remember that, just as a straight line is the most parsimonious non-cyclic regression, a sine wave is the most parsimonious repeating pattern, because it is analogous to the intersection of a cylinder by a flat plane. Elimination those negative values would require defining a non-flat plane to intersect the cylinder, and the model would quickly gain extra terms (at least one per cycle, and probably more).

Periodic regression results are summarised in Tables 2 and 3. Residuals (Fig. 8) are acceptably close to normally distributed for all the regressions, with a few outliers that were not deleted from the analysis (other than their values, there was no justification to delete them). The model cycles indicated by the regressions are presented in Figs. 5, 6, and 7 (they are calculated from the mesor, the linear time term, and the coefficients for the first and second harmonics of the cycle being presented, and omitting all other cycles).

One has to be impressed by the degree to which variation can be explained by variables that we typically do not use. In the case of F, the larval type that is confirmed to be produced by *Sicydium punctatum*, the variation explained by time (periodic and linear terms) is 72%. Given the well-known variability of plankton data, this is little short of phenomenal.

All of the OTUs produce periodic regressions that are highly significant (2 at $p < 0.01$, the rest at $p < 0.001$). With random data, $p < 0.001$ would occur only in 1 out of 1,000 regressions. Many of the cycles represented in the regressions are also significant. Clearly, these regressions are not due to chance.

Table 2. Summary of regressions: abundance (as $\ln(1+N/m^3)$) of each OTU in terms of 3 cycles (seasonal, lunar, and diurnal) including their first and second harmonics, as well as a linear term, B(ndoy) to account for any long-term trend that might appear monotonic over this time scale. Each column represents one taxon and one regression. The table sections are: *Adjusted Multiple R-squared* which is a conservative estimate of the variation explained by the regression; *Probabilities*, for which the first row is the *p*-value for the overall regression and the next six rows refer to periodic components (under "*cycle*" and harmonic "***H***", 1st or 2nd) as noted; *Peak locations* give for each cycle the times of the peak ("peak") for each first harmonic, and the first peak ("peak1") for the second harmonic (the second peak of the second harmonic will be later by half a period of the main cycle); *Amplitudes*, which indicate the size of the effect of each cycle and harmonic; *Mesor* which is the mean value around which each cycle adds variation; and finally *B(ndoy)* which estimates the monotonic trend explained by a linear time term. Probabilities italicised are those that are significant at $p < 0.05$ or better; corresponding amplitudes are also italicised.

TABLE of p, amplitude, peaks

	OTU		anad. GL	anad. F	anad. Y	anad. W	anad. SHRall	anad. SHRA	anad. MOLL	non- CADD	non- MAYFL	non- CALA	non- NAUP	non- ACAR
Adj.Mult.Rsq:			0.382	0.722	0.403	0.53	0.432	0.288	0.375	0.37	0.223	0.142	0.295	0.147
Probabilities:			*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*0.006*	*<0.001*	*0.004*
	cycle	***H***												
p	annual	**1**	*<0.001*	*<0.001*	0.588	0.069	*0.001*	*0.002*	*<0.001*	*0.036*	*0.006*	0.329	0.641	*0.015*
p		**2**	*0.002*	*0.021*	0.206	0.417	0.151	0.561	*0.016*	*0.003*	*0.032*	0.227	*0.005*	0.939
p	diurnal	**1**	*<0.001*	*<0.001*	*0.004*	*<0.001*	*<0.001*	*<0.001*	0.541	*0.028*	0.367	0.079	0.152	0.234
p		**2**	*0.006*	*0.018*	0.115	*0.011*	*<0.001*	*0.025*	0.314	*0.024*	0.502	*0.015*	*0.047*	0.179
p	lunar	**1**	*<0.001*	0.06	0.554	0.301	*0.001*	0.654	0.077	0.231	0.075	*0.041*	0.191	0.205
p		**2**	0.34	0.344	0.557	0.608	0.177	0.608	*0.005*	*0.007*	*0.023*	0.575	0.394	0.417
Peak locations														
peak	annual	**1**	jun06	feb24	jan17	aug30	jul09	jul10	jun18	feb18	apr07	sep09	sep04	may28
peak1	*365d*	**2**	may26	apr25	apr23	mar03	jun17	may22	jan25	may21	may31	jan10	feb13	mar08
peak	diurnal	**1**	0.90	1.0	0.82	0.78	0.91	0.94	0.04	0.84	0.79	0.12	0.08	0.69
peak1	*0-1*	**2**	0.40	0.44	0.24	0.32	0.43	0.49	0.29	0.37	0.36	0.14	0.09	0.27
peak	lunLQ	**1**	0.54	4.86	6.55	26.3	29.1	27.6	21.7	26.6	25.2	23.6	23.7	26.5
peak1	*29.5d*	**2**	9.4	14.2	1.7	11.3	3.6	6.1	8.2	11.1	8.0	13.7	5.5	8.9
Amplitudes														
	annual	**1**	*1.09*	*2.60*	0.80	1.01	*0.64*	*0.58*	*1.57*	*0.43*	*0.29*	0.29	0.15	*0.37*
		2	*0.60*	*1.41*	1.03	0.54	0.27	0.10	*0.84*	*0.47*	*0.26*	0.41	*0.95*	0.01
	diurnal	**1**	*2.04*	*1.72*	*0.85*	*0.67*	*2.23*	*1.59*	0.48	*0.48*	0.11	1.09	1.18	0.16
		2	*0.99*	*0.70*	0.51	*0.78*	*1.28*	*0.51*	0.45	*0.64*	0.13	*1.45*	*1.25*	0.21
	lunar	**1**	*0.62*	0.48	0.18	0.28	*0.46*	0.07	0.43	0.20	0.20	*0.56*	0.36	0.15
		2	0.2	0.17	0.19	0.08	0.18	0.08	*0.74*	*0.36*	*0.22*	0.17	0.31	0.10
Adj.Mult.Rsq:			0.38	0.72	0.40	0.53	0.43	0.29	0.38	0.37	0.22	0.14	0.30	0.15
Mesor			3.90	2.01	-0.75	0.58	2.21	1.59	3.64	1.30	0.53	2.11	4.43	0.60
B(ndoy)			-0	0	0	0	0	0	0.001	0.001	0	0	-0	0

The fact that these results are so significant may have implications for methodology. Plankton data are notorious for being very variable, so high R-squareds were unexpected (I had expected that 'good' results might have been R-squareds in the region of 0.2–0.3). In part the good fits found for several OTUs here may be an indication that some portion of the unexplainable variation we expect in plankton samples is not intrinsic. Instead, the notorious variability of plankton data may be a result of the normal pattern of plankton work: sample, preserve (with all the attendant loss of salience and identifiability in the sample), count later. Alternatively or as well, the periodic signals in data are perhaps, when ignored, large enough to swamp most other signals. Whereas the live-counting procedure results in data that are evidently very good, and periodic regression readily extracts that signal.

The results also have implications for how we approach something as simple as comparing two species' abundances at one site. If we sample, even with replicates, and find that species 2 is twice as abundant as species 1, that simple conclusion could mislead us because the abundance trends of different species can cross each other as the cycle progresses. For example, if we sampled around day 250, we would tend to find many more type W larvae than type F; but at day 100 the situation is very much reversed. We must accustom ourselves to think of abundance as not a number, but a pattern, just as was found for age-at-recruitment (Bell *et al.*, 1995). This also means we cannot compare abundances between sites without taking temporal pattern into account: even good replicated samples cannot suffice for comparison, unless either taken simultaneously amongst sites or corrected for a known pattern.

Responses of OTUs to annual, lunar and diurnal cycles

Operational taxonomic units (OTUs) are identified in Table 1, and goby larval types are further described in Fig. 4.

Curves (in Figs. 5, 6, and 7) incorporate both the first and second harmonics from the regressions, and can be perceived by inspecting the plots. For example, in Fig. 5: a curve showing a single peak (e.g., SHRA) indicate a dominance by the first harmonic, and curves showing two near-equal peaks (e.g., Naup) indicate dominance by the second harmonic, while curves showing two unequal peaks or a moderated peak (e.g., Moll) can result from an equal role of both.

Bear in mind that significance is harder to achieve with small amounts of data, as for the rarer OTUs, and the significance is not due to amplitude of the curve but the extent to which data are scattered about it. Also, although I usually disdain even talking about results that are not statistically significant, I may be slightly Bayesian and treat the curves/regressions as the best information available, and the presence of the exact information in the Tables should prevent me from misleading you. Note also that statistical significance I report for each cycle or harmonic is conservative: it is the lesser of the two p-values of the cycle's two components (sine and cosine), whereas the true probability for the cycle should be even smaller than that, but as yet I have no convenient way to combine them into a single, accurate, joint probability.

Discussion will follow Figs. 5, 6, 7, and Table 2. Residual plots are shown in Fig. 8. Responses to cycles vary, and indicate considerable diversity amongst OTUs—even amongst goby larvae.

Considering the anadromous taxa (fish, decapod shrimps, neritid molluscs), all but goby larval types Y and W (which hint at a response) show a significant response to the seasonal cycle, and all but neritid molluscs respond to the diurnal cycle. Regarding Y and W, W shows a marginal ($p = 0.07$) response on the first seasonal harmonic and the first peak of its (n.s.) second harmonic is close to; but Y, which shows neither harmonic as significant, produces a curve that is qualitatively similar to, but at a lower level than, Type F.

All goby larval types show a significant response to the primary diurnal cycle, but only type F responds significantly to the seasonal cycle and none to the lunar cycle. The lack of lunar response is interesting given that as postlarvae these species are such an example of lunar response: recruitment (of virtually all the anadromous taxa here) is timed to the 4th day following the last lunar quarter day. The aggregate of all goby larval types shows a response to the lunar cycle; but given that they individually decline to respond, this is more of an illustration of the hazard inherent in combining groups together.

Type F shows its strongest response to the annual and diurnal cycles (first harmonics of both); there is peak near day 90 of the year, a peak late at night, and very little variation on the lunar cycle.

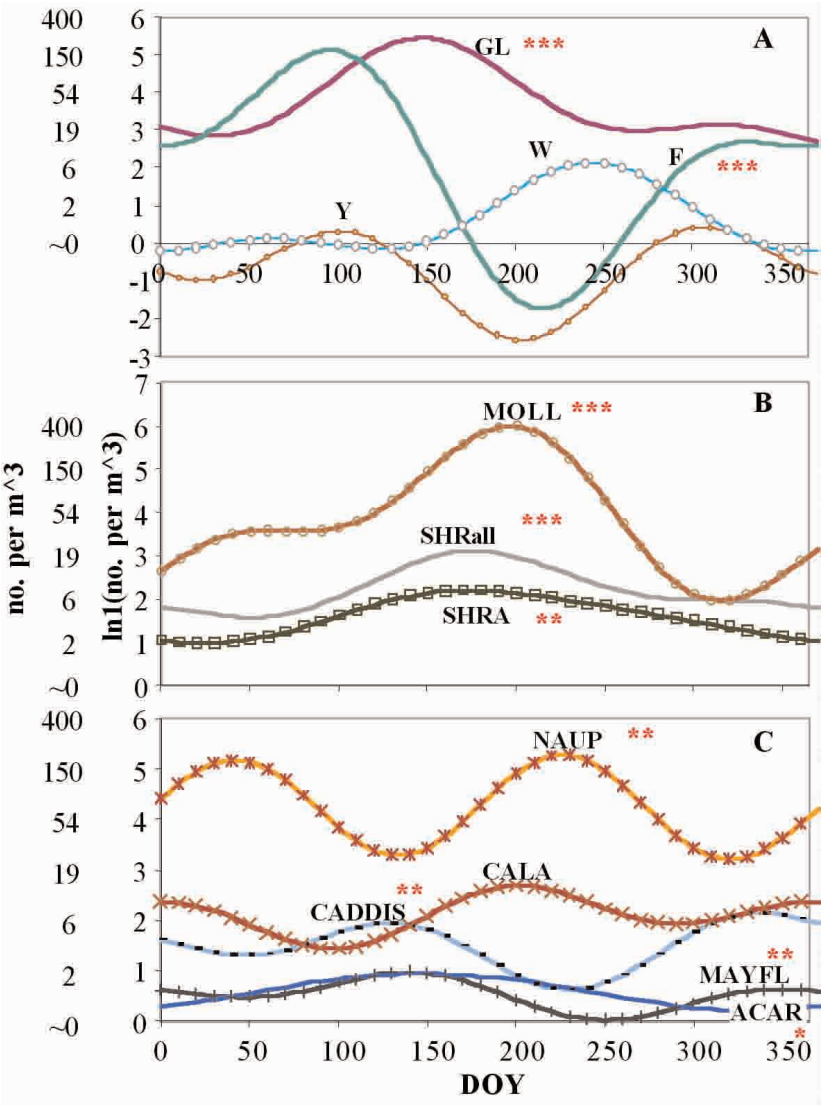

Figure 5. Seasonal cycles, based on regression using ln(1+N/m3). Each curve combines both first and second harmonics, and includes the mesor and the linear time term. A: anadromous gobies, by larval type; **B**: anadromous decapod crustaceans and neritid molluscs; **C**: nonanadromous taxa. Significance of each cycle (the more significant harmonic is given) indicated by *, **, and *** for p<0.05, 0.01, 0.001 respectively (applies to following figures also). Points are fitted values, i.e., x-values at which y is evaluated using the regression function.

Type Y and type W show a significant response only to the diurnal cycle, not to the lunar or seasonal (marginal for W) cycles.

Amongst goby larvae, types F and Y both have annual peaks near day 100, but all have or hint at a response on the second harmonic and therefore two peaks per year, the first being near Feb–Mar (Tables 2 and 3) and the second peak near day 300 (the second peak if calculated from the second harmonic alone, would always be 0.5 cycle later than the first, but that does not apply when the peaks result from two interacting cycles). Type W has a major peak nearly 150 days out of phase from the

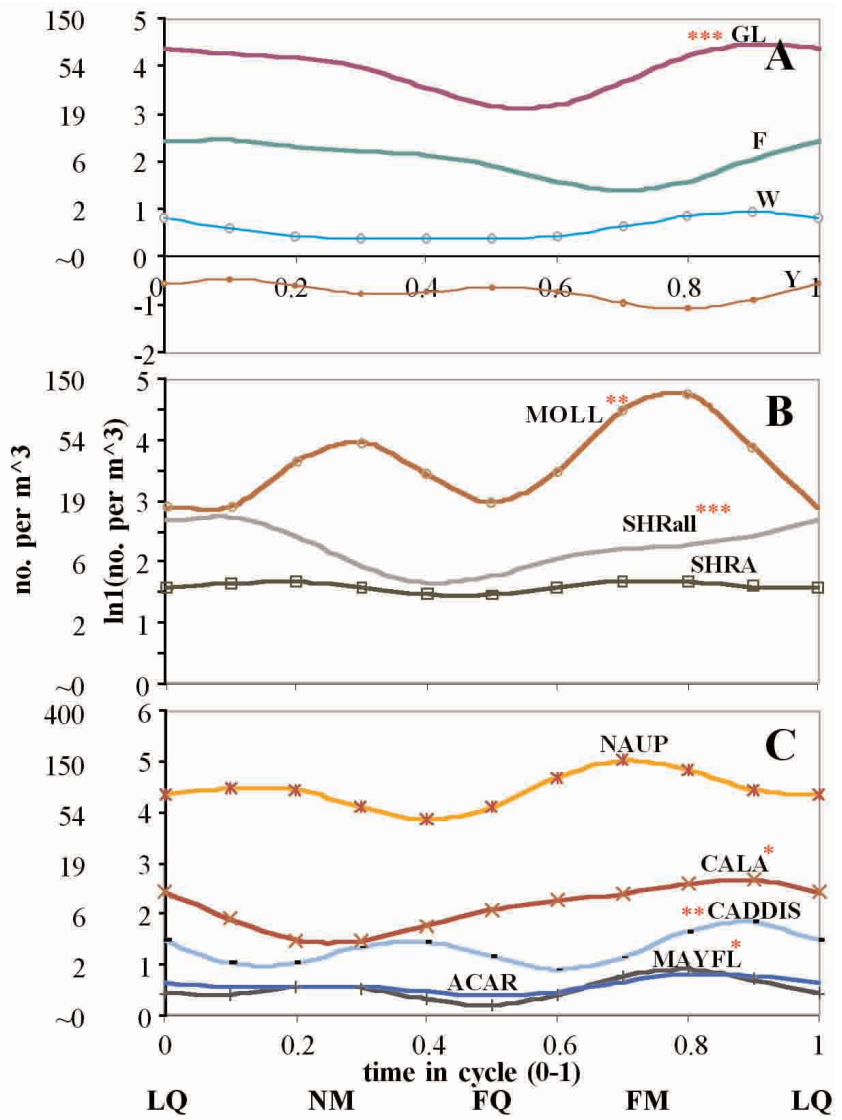

Figure 6. Lunar cycles, based on regression using ln(1+N/m3). Each curve combines both first and second harmonics. A: anadromous gobies, by larval type; **B**: anadromous decapod crustaceans and neritid molluscs; **C**: nonanadromous taxa.

day-100 peaks of F and Y, and a barely perceptible peak near day 70. These are descriptions a long way from being explained, however we can notice that although the second harmonic is not significant in all, it results in a first peak about the same time that water temperature (Fig. 9) shows its first peak. In regard to a possible temperature relationship, *Sicydium punctatum* from Dominica seem intolerant of temperatures as low as about 18 °C (pers. observ.); this was shown in an aquarium in Newfoundland that cooled during a power failure. At about 18 °C temperature they became torpid and unreactive, but when the temperature was brought back to 20 °C they resumed normal activity.

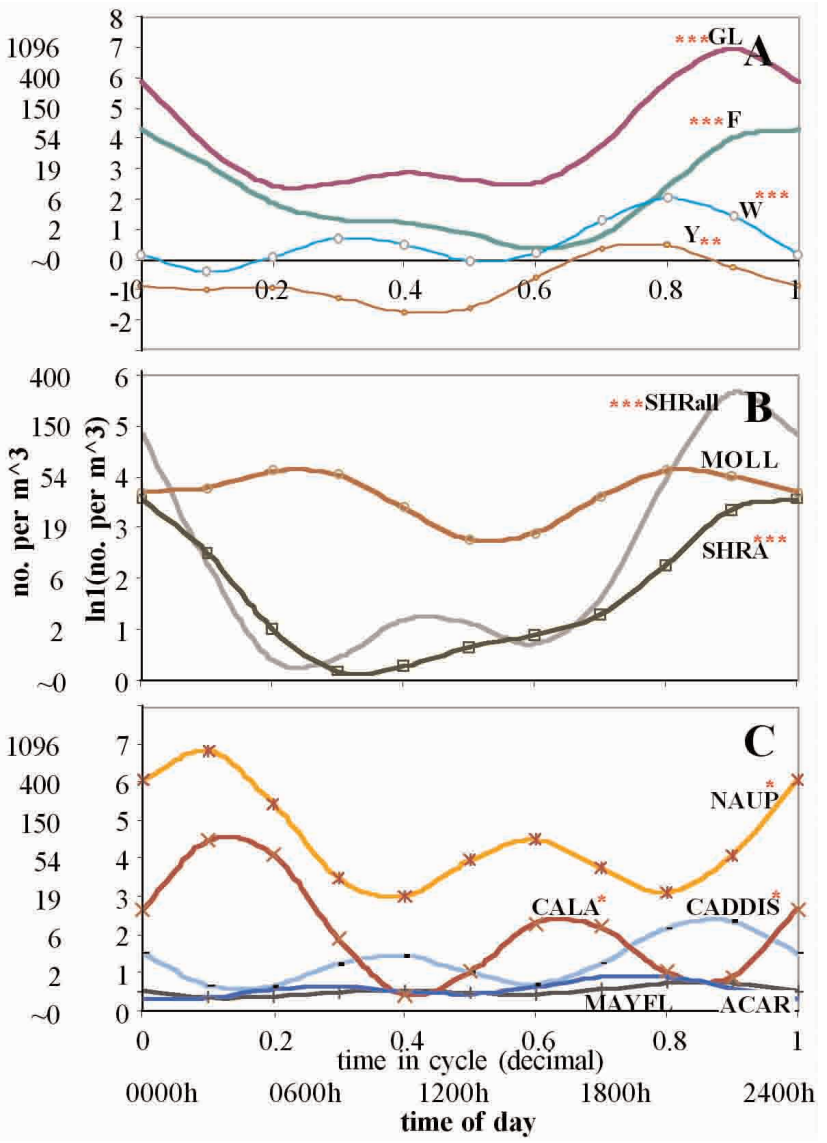

Figure 7. Diurnal cycles, based on regression using ln(1+N/m3). Each curve combines both first and second harmonics. **A**: anadromous gobies, by larval type; **B**: anadromous decapod crustaceans and neritid molluscs; **C**: nonanadromous taxa.

The temperatures I observed in Dominica during my study ranged from extremes of 20 °C to 30 °C, virtually exactly. Thus it is plausible that goby reproduction could respond to temperature.

In the non-goby OTUs I cannot see a similar response. Seasonally, calanoids and nauplii have similar patterns slightly out of phase, but they are nearly inverse to the patterns of caddis- and mayflies (similar to each other). Acarines show a weakly significant seasonal response on the first harmonic (only one peak).

Lunar cycles are not shown by individual goby OTUs; but are shown by mollusc (larvae of neritid snails) and decapod shrimps. Nauplii show a strong response to the second harmonic of year, with peaks near days 40 and 230 (Fig. 5), but only a small response to the first harmonic. A strong

Table 3. Summary and interpretation of periodic regressions for 13 operational taxonomic units (OTUs) or groupings. Data are from samples taken at lower reaches of the Layou, Check Hall, Canefield and Roseau rivers in Dominica, W.I. 1989–1991 and 1997. To fit the table, "sine" and "cosine" are sometimes abbreviated "s" and "c", and the meaning is the proper sine or cosine, i.e. after conversion to conventional angular units. B0, the intercept of common parlance, is called the mesor to reflect its properties in a periodic regression. Each regression has the form Y = B0 + B1*X1 + B2*X2 + ... B(n)*X(n), where Y is the ln(1+x) transform of counts/m^3 of each OTU, the Bs are the regression coefficients and the Xs represent the independent variables. The variables are named in the table header and their relation to a natural cycle is given. Peaks are calculated for each cycle, and in the case of the annual cycle are given as dates. For second harmonics, because they peak twice in their 'parent' cycles, the second peak is given in a second row. Adjusted Multiple R^2 (AMRsq) is a more conservative indicator of fit than R^2.

	B0	B1	B2	B3	B4	B5	B6	B7	B8	B9	B10	B11	B12	B13
CYCLE NAME:		na	**ANNUAL**		**SEMI-ANNUAL**		**DAILY**		**SEMI-DAILY**		**LUNAR**		**SEMI-LUNAR**	
Variables:	B0	NDOY	sDOY	cDOY	s2DOY	c2DOY	sTOD	cTOD	s2TOD	c2TOD	sLQ	cLQ	s2LQ	c2LQ
transform:	B0	NDOY	sin	cos	sin	cos	sin	cos	sin	cos	sin	cos	sin	cos
harmonic:			first		second		first		second		first		second	
period:			365	days	182.5	days	24	hours	12	hours	29.5	days	14.75	days
			for each OTU N, AMRsq and p are given; then Amplitude, Peak(s) follow under cycle headings above, then coefficients and p under variable headings above.											
ANADROMOUS: FISH														
OTU:		N	AMRsq	p										
GL		165	0.382	<0.001			**All goby larvae**							
amplitude (in units of Y)			1.0931		0.6028		2.0374		0.991		0.616		0.199	
Peak in cycle units			156.45	jun06	145.23	may26	21.545		9.6566		0.5347		9.368	
If 2nd harmonic, second peak:					327.73	nov24			21.657				24.12	
coeffs:	3.903	-0.001	0.474	-0.985	-0.578	0.171	-1.221	1.631	-0.933	0.334	0.07	0.612	-0.15	-0.132
p	<0.001	0.001	0.01	<0.001	0.002	0.364	<0.001	0.003	0.006	0.261	0.676	<0.001	0.34	0.429
OTU:		N	AMRsq	p										
F		62	0.722	<0.001			**Goby larvae of type F (*S. punctatum*)**							
amplitude (in units of Y)			2.605		1.4135		1.721		0.7027		0.4785		0.165	
Peak in cycle units			54.203	feb24	114.02	apr25	23.993		10.665		4.8512		14.15	
If 2nd harmonic, second peak:					296.52	oct24			22.665				28.90	
coeffs:	2.007	0	2.093	1.551	-0.998	-1.001	-0.003	1.721	-0.452	0.538	0.411	0.245	-0.042	0.16
p	0.009	0.005	<0.001	0.121	0.109	0.021	0.988	<0.001	0.162	0.018	0.06	0.289	0.804	0.344

Table 3 (continued) ...

	B0	B1	B2	B3	B4	B5	B6	B7	B8	B9	B10	B11	B12	B13
CYCLE NAME:		na	**ANNUAL**		**SEMI-ANNUAL**		**DAILY**		**SEMI-DAILY**		**LUNAR**		**SEMI-LUNAR**	
Variables:	B0	NDOY	sDOY	cDOY	s2DOY	c2DOY	sTOD	cTOD	s2TOD	c2TOD	sLQ	cLQ	s2LQ	c2LQ
transform:	B0	NDOY	sin	cos	sin	cos	sin	cos	sin	cos	sin	cos	sin	cos
harmonic:			first		second		first		second		first		second	
period:			365	days	182.5	days	24	hours	12	hours	29.5	days	14.75	days
			for each OTU N, AMRsq and p are given; then Amplitude, Peak(s) follow under cycle headings above, then coefficients and p under variable headings above.											
ANADROMOUS: FISH														
OTU:		N	AMRsq	p										
Y		62	0.403	<0.001			**Goby larvae of type Y**							
amplitude (in units of Y)			0.7962		1.033		0.8552		0.5085		0.1828		0.185	
Peak in cycle units			17.33	jan17	112.61	apr23	19.581		5.6296		6.549		1.673	
If 2nd harmonic, second peak:					295.11	oct23			17.63				16.42	
coeffs:	-0.747	0	0.234	0.761	-0.693	-0.766	-0.783	0.344	0.098	-0.499	0.18	0.032	0.121	0.14
p	0.477	0.076	0.746	0.588	0.427	0.206	0.004	0.51	0.83	0.115	0.554	0.921	0.611	0.557
OTU:		N	AMRsq	p										
W		62	0.530	<0.001			**Goby larvae of type W**							
amplitude (in units of Y)			1.0129		0.5363		0.6648		0.7775		0.2822		0.08	
Peak in cycle units			241.96	aug30	61.517	mar03	18.623		7.5608		26.296		11.33	
If 2nd harmonic, second peak:					244.02	sep02			19.561				26.08	
coeffs:	0.583	0	-0.865	-0.527	0.458	-0.279	-0.656	0.108	-0.567	-0.532	-0.178	0.219	-0.079	0.009
p	0.391	0.223	0.069	0.562	0.417	0.473	<0.001	0.749	0.058	0.011	0.368	0.301	0.608	0.951
ANADROMOUS: NON-FISH														
OTU:		N	AMRsq	p										
ShrimpALL		162	0.432	<0.001			**Decapod shrimp larvae (all 3 recognised groupings: A,B,C)**							
amplitude (in units of Y)			0.6429		0.2701		2.2319		1.2751		0.4547		0.182	
Peak in cycle units			189.66	jul09	167.3	jun17	21.773		10.251		29.097		3.597	
If 2nd harmonic, second peak:					349.8	dec16			22.251				18.35	
coeffs:	2.213	0	-0.079	-0.638	-0.135	0.234	-1.229	1.863	-1.011	0.777	-0.039	0.453	0.182	0.007
p	<0.001	0.836	0.609	0.001	0.399	0.151	<0.001	<0.001	<0.001	0.003	0.784	0.001	0.177	0.964

Table 3 (continued) ...

	B0	B1	B2	B3	B4	B5	B6	B7	B8	B9	B10	B11	B12	B13
CYCLE NAME:		na	**ANNUAL**		**SEMI-ANNUAL**		**DAILY**		**SEMI-DAILY**		**LUNAR**		**SEMI-LUNAR**	
Variables:	B0	NDOY	sDOY	cDOY	s2DOY	c2DOY	sTOD	cTOD	s2TOD	c2TOD	sLQ	cLQ	s2LQ	c2LQ
transform:	B0	NDOY	sin	cos	sin	cos	sin	cos	sin	cos	sin	cos	sin	cos
harmonic:			first		second		first		second		first		second	
period:			365	days	182.5	days	24	hours	12	hours	29.5	days	14.75	days
			for each OTU N, AMRsq and p are given; then Amplitude, Peak(s) follow under cycle headings above, then coefficients and p under variable headings above.											
ANADROMOUS: NON-FISH														
OTU:		N	AMRsq	p										
ShrimpA		138	0.288	<0.001			**Decapod shrimp larvae type A only**							
amplitude (in units of Y)			0.5832		0.0952		1.5868		0.5125		0.0654		0.083	
Peak in cycle units			191	jul10	141.47	may22	22.456		11.776		27.58		6.097	
If 2nd harmonic, second peak:					323.97	nov20			23.776				20.85	
coeffs:	1.593	0	-0.085	-0.577	-0.094	0.015	-0.624	1.459	-0.06	0.509	-0.026	0.06	0.043	-0.071
p	<0.001	0.281	0.579	0.002	0.561	0.924	<0.001	0.001	0.823	0.025	0.843	0.654	0.743	0.608
OTU:		N	AMRsq	p										
MOLL		133	0.375	<0.001			**Neritid mollusc larvae (could be 2 indistinguishable spp.)**							
amplitude (in units of Y)			1.5668		0.8388		0.4786		0.4478		0.432		0.745	
Peak in cycle units			168.42	jun18	25.805	jan25	0.8777		6.8321		21.679		8.162	
If 2nd harmonic, second peak:					208.3	jul28			18.832				22.91	
coeffs:	3.641	0.001	0.376	-1.521	0.651	0.529	0.109	0.466	-0.189	-0.406	-0.43	-0.041	-0.245	-0.703
p	<0.001	0.048	0.155	<0.001	0.016	0.055	0.737	0.541	0.697	0.314	0.077	0.864	0.297	0.005
Arthopoda (non-anadromous)														
OTU:		N	AMRsq	p										
CADD		155	0.370	<0.001			**Caddisfly larvae**							
amplitude (in units of Y)			0.4264		0.4728		0.4837		0.6403		0.1962		0.356	
Peak in cycle units			48.902	feb18	140.01	may21	20.253		8.8776		26.56		11.12	
If 2nd harmonic, second peak:					322.51	nov19			20.878				25.87	
coeffs:	1.302	0.001	0.318	0.284	-0.47	0.051	-0.402	0.269	-0.639	-0.041	-0.115	0.159	-0.356	0.009
p	<0.001	<0.001	0.036	0.128	0.003	0.74	0.028	0.548	0.024	0.866	0.403	0.231	0.007	0.947

Table 3 (continued) ...

	B0	B1	B2	B3	B4	B5	B6	B7	B8	B9	B10	B11	B12	B13
CYCLE NAME:		na	**ANNUAL**		**SEMI-ANNUAL**		**DAILY**		**SEMI-DAILY**		**LUNAR**		**SEMI-LUNAR**	
Variables:	B0	NDOY	sDOY	cDOY	s2DOY	c2DOY	sTOD	cTOD	s2TOD	c2TOD	sLQ	cLQ	s2LQ	c2LQ
transform:	B0	NDOY	sin	cos	sin	cos	sin	cos	sin	cos	sin	cos	sin	cos
harmonic:			first		second		first		second		first		second	
period:			365	days	182.5	days	24	hours	12	hours	29.5	days	14.75	days
			for each OTU N, AMRsq and p are given; then Amplitude, Peak(s) follow under cycle headings above, then coefficients and p under variable headings above.											
Arthopoda (non-anadromous)														
OTU:		N	AMRsq	p										
MAYF		130	0.223	<0.001			**Mayfly larvae**							
amplitude (in units of Y)			0.2854		0.2554		0.114		0.1255		0.1946		0.215	
Peak in cycle units			96.959	apr07	150.95	may31	18.879		8.617		25.214		7.982	
If 2nd harmonic, second peak:					333.45	nov30			20.617				22.73	
coeffs:	0.525	0	0.284	-0.028	-0.226	0.119	-0.111	0.026	-0.123	-0.025	-0.154	0.119	-0.055	-0.208
p	0.012	0.067	0.006	0.809	0.032	0.246	0.367	0.925	0.502	0.861	0.075	0.184	0.52	0.023
OTU:		N	AMRsq	p										
ACAR118		0.147	0.004				**Acarines: ticks (or mites)**							
amplitude (in units of Y)			0.3664		0.012		0.1627		0.2093		0.151		0.101	
Peak in cycle units			147.81	may28	66.731	mar08	16.481		6.3859		26.541		8.923	
If 2nd harmonic, second peak:					249.23	sep07			18.386				23.67	
coeffs:	0.59	0	0.206	-0.303	0.009	-0.008	-0.15	-0.063	-0.042	-0.205	-0.089	0.122	-0.062	-0.08
p	0.006	0.002	0.042	0.015	0.939	0.944	0.234	0.825	0.826	0.179	0.33	0.205	0.51	0.417
Possible marine association														
OTU:		N	AMRsq	p										
CALA		115	0.142	0.006			**Calanoid copepods**							
amplitude (in units of Y)			0.2919		0.4114		1.0945		1.4546		0.5608		0.168	
Peak in cycle units			251.09	sep09	10.462	jan10	2.7704		3.3299		23.554		13.68	
If 2nd harmonic, second peak:					192.96	jul12			15.33				28.43	
coeffs:	2.105	0	-0.27	-0.111	0.145	0.385	0.726	0.819	1.433	-0.25	-0.535	0.168	-0.074	0.151
p	0.001	0.156	0.329	0.75	0.676	0.227	0.079	0.329	0.015	0.561	0.041	0.555	0.776	0.575
OTU:		N	AMRsq	p										
NAUP		140	0.295	<0.001			**Nauplii (could be of many families)**							
amplitude (in units of Y)			0.1529		0.9445		1.1789		1.2543		0.3618		0.309	
Peak in cycle units			246.99	sep04	43.501	feb13	1.8101		2.0716		23.685		5.451	
If 2nd harmonic, second peak:					226	aug15			14.072				20.20	
coeffs:	4.427	-0.001	-0.137	-0.068	0.942	0.069	0.538	1.049	1.109	0.586	-0.342	0.118	0.226	-0.211
p	<0.001	0.001	0.641	0.848	0.005	0.824	0.152	0.225	0.047	0.203	0.191	0.66	0.394	0.436

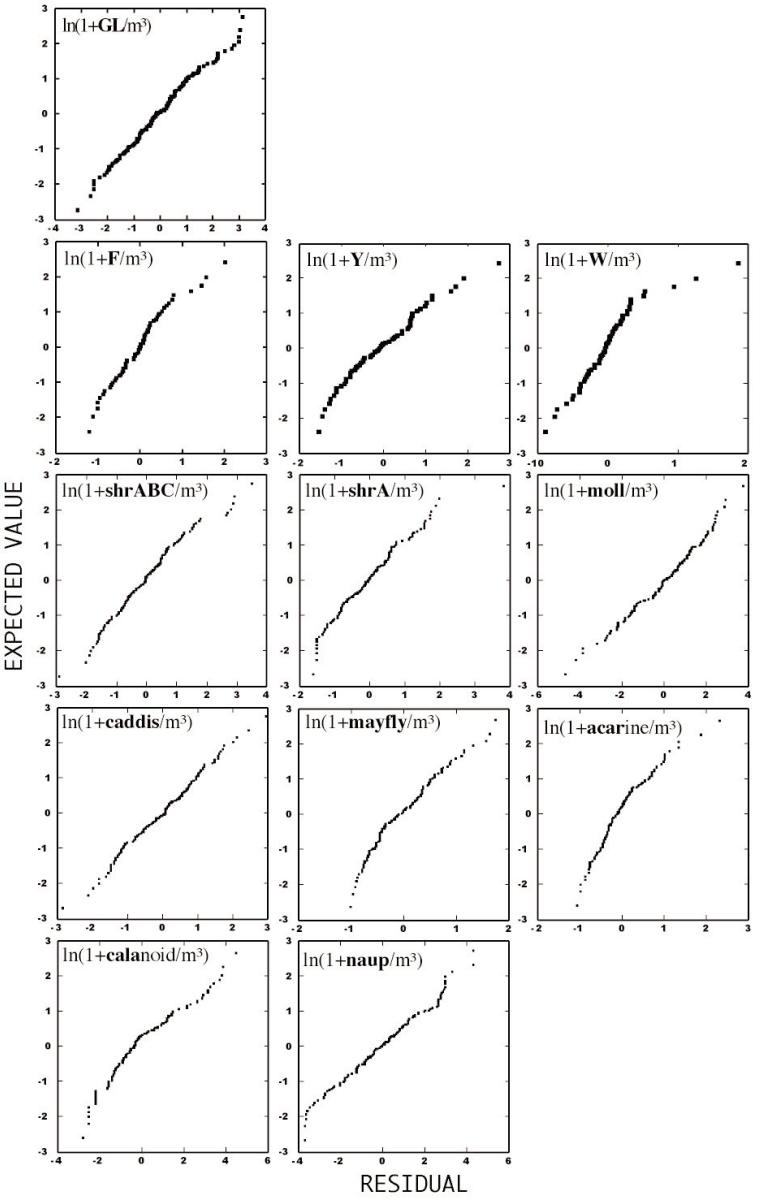

Figure 8. Residuals from regressions of ln(1+N/m3), according to Eq. 1 for each Operational Taxonomic Unit. The upper plot (GL) is an aggregate of all goby larvae including types having insufficient data for separate analysis; the second row are three goby larval types (F, Y, W); the third row are non-fish anadromous taxa (ShrimpABC subsumes three decapod larval types; ShrimpA is about 2mm long with cephalothorax not markedly larger than the set of abdominal segments, Shrimps B and C have insufficient data to analyse separately); the fourth row are insect larvae (caddis and mayfly) and acarines (which look more like ticks than mites); the fifth row is calanoid copepods and nauplii (which may be associated, or not).

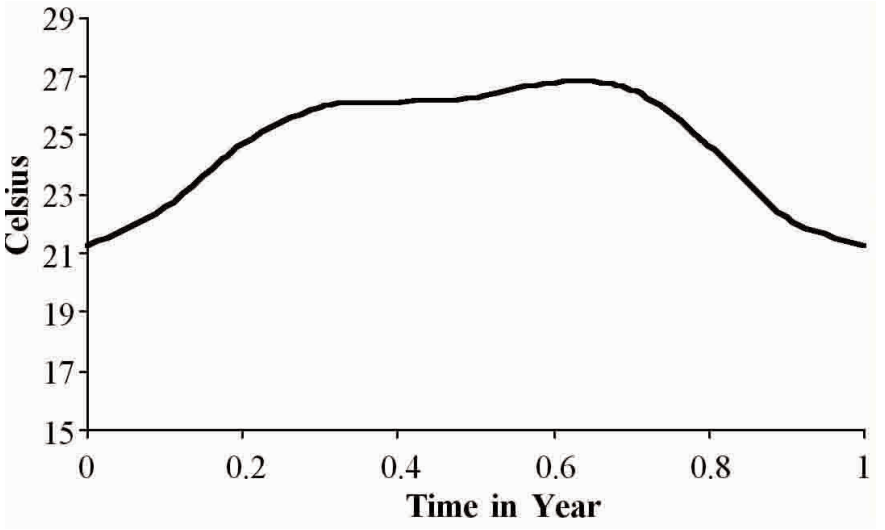

Figure 9. Seasonal water temperature pattern for same group of stations [on the lower Layou, Check Hall (CHR), Canefield (PHW), Roseau Rivers] as used for rheoplankton data in this paper.

semilunar response (Fig. 6) that hints at a response linked to tides; although in Dominica for a number of reasons the tides are very small, so the result raises the interesting question about what mechanism could be behind that association, and how many species of nauplii are subsumed here. The tidal cycle precesses against days, so it would be a mistake to think the strong response to time of day (Fig. 7) is related to tides.

***In situ* mortality**

The mortalities reported by Bell (1994) for *S. punctatum* (identified as Type F in Tables and Figures) in Dominica (West Indies) exceed 50% per hour in the drift. Typical drift speeds are 0.3 m/s, or about 1 km/h, so the mortalities are on the order of 50% per kilometer as well. Goby larval types Y and W show even lower survival.

Conclusions

Stream drift study offers many advantages as a standard monitoring and investigative tool. The interesting general conclusion about cycles is that there is no standard response shown by all taxa. That the cycle is not stereotyped means they have to be characterised for each taxon. There are two main conservation-relevant reasons for investigating and analysing cycles. Firstly, cycles are much more likely to be present than absent. Any single sample, or group of samples that do not permit a cycle to be estimated, is by definition incapable of being reliably used to estimate total production over a cycle. Cycles therefore need to be characterised in order to make the best use of the sample data. Secondly, analysis of cycles can help identify anomalies. Anomalies are the indicators of the effect of unacknowledged factors, and can reveal short-term or spatially-limited conditions that affect production of larvae.

Stream drift study provides superior production data on in a much less invasive way than other methods and can be paired to develop *in-situ* mortality estimates. I raise also the possibility that by knowing the development rates of certain larval features (e.g. eye pigmentation, jaw development, reduction in oil/yolk) in fresh water, each larva can be given an approximate age (in hours); with sufficient data, mortality can be estimated from the descending limb of a histogram of abundances.

The high mortality rates found in Dominica (Bell, 1994, unpubl. data) are at present the only direct mortality estimates we have for drifting goby larvae anywhere. Whatever the mortality rate, it is cumulative, and, unless much lower than that found in Dominica, the strong implication is that fish at a distance from the sea are, egg for egg, at a substantial disadvantage. That raises the question of why large fish are found inland at all. Are they there because they were excluded from lower elevations? If there seem to be fewer fish at lower elevations, is it [a] because adults preferentially moved upstream and were not replaced, or [b] because they were lost (adults appear to be slow-growing and populations may take some time to recover) to the effects of anthropogenic disturbance? A drive to move ever further inland would need further explanation as an evolved behaviour if the consequence is exponentially reduced larval survival. The unavoidable conservation implication of mortality, because it is cumulative, is that, unless compensated for by greater egg production, the nesting habitats with the shortest drift times are the most important for the population.

Acknowledgements

I thank the fishes of Dominica that treated me well, the IDRC for the Young Canadian Researchers Award that funded the work in Dominica, Nigel Lawrence and the Fisheries Division of Dominica for their hospitality, J.A. Brown, and fellowships at Memorial University of Newfoundland. I also thank many friends and colleagues for support and challenge, amongst whom are: Pierre Pepin, W.G. Warren, Don Erdman, John D. Archbold, Martina Kelly, the Deorksen Institute, Horst Kaiser, Tony Booth, David Schneider, and the helpful comments of an anonymous reviewer.

Literature Cited

Allan, **J**.**D**. **& E**. **Russek**. 1985. The quantification of stream drift. *Canadian Journal of Fisheries & Aquatic Sciences* **42**: 210–215.

Atwood, **T**. 1791. *The history of the island of Dominica. Containing a description of its situation, extent, climate, mountains, rivers, natural productions, &c. &c. Together with an account of the civil government, trade, laws, customs, and manners, of the different inhabitants of that island. Its conquest by the French, and restoration to the British dominions.* J. Johnson, London. vii + 285 p.

Batschelet, **E**. 1981. *Circular statistics in biology*. Academic Press, London. xvi + 371 p.

Bell, **K**.**N**.**I**. 1994. Life cycle, early life history, fisheries, and recruitment dynamics of diadromous gobies of Dominica, W.I., emphasising *Sicydium punctatum* Perugia. Ph.D. Thesis, Memorial University of Newfoundland, St. John's. xviii + 275 p.

———. 1997. Complex recruitment dynamics with Doppler-like effects caused by shifts and cycles in age-at-recruitment. *Canadian Journal of Fisheries and Aquatic Sciences* **54**: 1668–1681.

———. 1999. An overview of goby-fry fisheries. *NAGA* **22**: 30–36.

———. 2004. *Introduction to circular variables & periodic regression in biology*. Razorbill Press, St. John's. ca. 50 p. (electronic book in PDF format).

———. & **J**.**A**. **Brown**. 1990. Aspects of the early life history of an anadromous goby in Dominica, W.I. Unpublished poster presented at conference: Ecological and Evolutionary Ethology of Fishes, Northern Arizona University, May 19–23, 1990.

———. & **J**.**A**. **Brown**. 1995. Active salinity choice and enhanced swimming endurance in 0 to 8-d-old larvae of diadromous gobies, with emphasis on *Sicydium punctatum* (Pisces), in Dominica, West Indies. *Marine Biology* **121**: 409–417.

———., **P**. **Pepin & J**.**A**. **Brown**. 1995. Seasonal, inverse cycling of length- and age-at-recruitment in the diadromous gobies *Sicydium punctatum* and *Sicydium antillarum* (Pisces) in Dominica, West Indies. *Canadian Journal of Fisheries and Aquatic Sciences* **52**: 1535–1545.

Blanco, **G**.**J**. 1956. Assay of the goby fry (ipon) fisheries of the Laoag River and its adjacent marine shores, Ilocos Norte Province. *Philippine Journal of Fisheries* **4**: 31–80.

Bliss, **C**.**I**. 1958. Periodic regression in biology and climatology. *Bulletin of the Connecticut Agricultural Experiment Station, New Ha*ven **615**: 1–55.

Brasher, **A**.**M**. 2003. Impacts of human disturbances on biotic communities in Hawaiian streams. *BioScience* **53**: 1052–1060.

Brockmann, **F**.**W**. 1965. *A taxonomic study of the Panamanian freshwater gobies of the genera Awaous and Sicydium.* M.S. Thesis, Florida State University, Tallahassee. v + 73 p.

Cambray, **J**.**A**. 1985. Early ontogeny of *Labeo capensis* (Pisces:Cyprinidae). *South African Journal of Zoology* **20**: 190–196.

Chace, **F**.**A**. **& H**.**H**.**J**. **Hobbs**. 1969. The freshwater and terrestrial decapod crustaceans of the West Indies with special reference to Dominica. *Bulletin of the United States National Museum* **292**, 258 p.

Copp, **G**.**H**. **& B**. **Cellot**. 1998. Drift of embryonic and larval fishes, especially *Lepomis gibbosus* (L.), in the upper Rhone River. *Journal of Freshwater Ecology* **4**: 419–424.

Ego, **K**. 1956. Life history of freshwater gobies. Project No. 4-4-R. Freshwater Game and Fisheries Management Research, Department of Lands and Natural Resources, Honolulu. 23 p.

Erdman, **D**.**S**. 1961. Notes on the biology of the gobiid fish *Sicydium plumieri* in Puerto Rico. *Bulletin Marine Sciences of the Gulf and Caribbean* **11**: 448–456.

———. 1986. The green stream goby, *Sicydium plumieri*, in Puerto Rico. *Tropical Fish Hobbyist* **1986** (February): 70–74.

Fitzsimons, **J**.**M**. **& R**.**T**. **Nishimoto**. 1990. Territories and site tenacity in males of the Hawaiian stream goby *Lentipes concolor* (Pisces: Gobiidae). *Ichthyological Exploration of Freshwaters* **1**: 185–189.

———., **R**.**M**. **Zink & R**.**T**. **Nishimoto**. 1990. Genetic variation in the Hawaiian stream goby, *Lentipes concolor*. *Biochemical Systematics and Ecology* **18**: 81–83.

Flecker, **A**.**S**., **D**.**C**. **Taphorn**, **J**.**A**. **Lovell & B**.**P**. **Feifarek**. 1991. Drift of characin larvae, *Bryconamericus deuterodonoides*, during the dry season from Andean piedmont streams. *Environmental Biology of Fishes* **31**: 197–202.

Herre, **A**.**W**. 1927. *Gobies of the Philippines and the China Sea*. Monographs of the Bureau of Science 23. Philippine Bureau of Science, Manila. 352 p.

———. 1958. Marine fishes in Philippine rivers and lakes. *Philippine Journal of Science* **87**: 65–88.

Iguchi, **K**. **& N**. **Mizuno**. 1990. Diel changes in larval drift among amphidromous gobies in Japan, especially *Rhinogobius brunneus*. *Journal of Fish Biology* **37**: 255–264.

———. **& N**. **Mizuno**. 1991. Mechanisms of embryonic drift in the amphidromous goby *Rhinogobius brunneus*. *Environmental Biology of Fishes* **31**: 295–300.

Jordan, **D**.**S**. **& B**.**W**. **Evermann**. 1898. *The fishes of north and middle America*. Bulletin of the United States Natural Museum. No. 47, Part III xxiv + p. 2183–2860. United States National Museum, Washington (reprinted 1963 for the Smithsonian Inst. by T.F.H. Publications Inc., Jersey City, New Jersey).

———. **& B**. **W**. **Evermann**. 1905. *The aquatic resources of the Hawaiian Islands*. Bulletin of the United States Fish Commission for 1903, Part I, *The shore fishes* Vol. XXIII. 392 p. United States Fish Commission, Washington.

Kinzie, **R**.**A**. 1993. Reproductive biology of an endemic, amphidromous goby *Lentipes concolor* in Hawaiian streams. *Environmental Biology of Fishes* **37**: 257–268.

Kohler, **S**.**L**. 1985. Identification of stream drift mechanisms: An experimental and observational approach. *Ecology* **66**: 1749–1761.

Lindstrom, **D**.**P**. 1999. Molecular species identification of newly hatched Hawaiian amphidromous gobioid larvae. *Marine Biotechnology* **1**: 167–174.

Manacop, **P**.**R**. 1953. The life history and habits of the goby, *Sicyopterus extraneus* Herre (Gobiidae) with an account of the goby-fry fishery of Cagayan River, Oriental Misamis [Province, Mindanao, Philippines]. *Philippine Journal of Fisheries* **2**: 1–60.

Montilla, **J**. 1931. The ipon fisheries of northern Luzon. *Philippine Journal of Science* **45**: 61–75.

Nishimoto, **R**.**T**. **& J**.**M**. **Fitzsimons**. 1986. Courtship, territoriality, and coloration in the endemic Hawaiian freshwater goby, *Lentipes concolor*, p. 811–817. *In*: Uyeno, T., R. Arai, T. Taniuchi & K. Matsuura (eds.*), Indo-Pacific fish biology.* Proceedings of the Second International Conference on Indo-Pacific fishes. Ichthyological Society of Japan, Tokyo.

Noblet, **G**.**P**. **& R**.**T**. **Damian**. 1991. On the status of *Biomphalaria* and *Thiara* snails and the threat of schistosomiasis and paragonimiasis on Dominica, West Indies. *Journal of Medical & Applied Malacology* **3**: 1–6.

Pavlov, **D**.**S**. **1994**. The downstream migration of young fishes in rivers—mechanisms and distribution [English review]. *Folia Zoologica* **43**: 193–208.

Radtke, **R**.**L**., **R**.**A**. **Kinzie & S**.**D**. **Folsom**. 1988. Age at recruitment of Hawaiian freshwater gobies. *Environmental Biology of Fishes* **23**: 205–213.

Titcomb, **M**. 1977. *Native use of fish in Hawaii*. 2nd edition. University Press of Hawaii, Honolulu.