

Seasonal, inverse cycling of length- and age-at-recruitment in the diadromous gobies *Sicydium punctatum* and *Sicydium antillarum* in Dominica, West Indies

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Abstract: We report on an 18-month field study of temporal pattern and interrelationships of size- and age-at-recruitment (to fresh waters) for two diadromous hill-stream gobies in Dominica, West Indies (15°30'N, 61°25'W). Recruitment is panseasonal in *Sicydium punctatum* and *Sicydium antillarum* and supports a directed fishery similar to other goby fry fisheries. We found both size and age of recruits to vary seasonally, but the relationship of size to age is complex. Although positively related within lunar-monthly recruiting cohorts, the overall relationship of size and age was poor because seasonal variation in size is out of phase with age. Among recruiting cohorts, mean (or predicted) size and age are negatively correlated. Recruitment (fishery yield) also varies seasonally, in phase with size and out of phase with age. Peak fishery yields coincide with the youngest, but largest, recruits; low yields coincide with the reverse, implicating growth rate variations in fishery yield. This is the first such report of systematic seasonal variation in age-at-recruitment. Given these findings, size- and age-at-recruitment (here similar to settlement or metamorphosis) should not be assumed invariant, even for tropical fishes.

Résumé : Nous avons réalisé pendant 18 mois une étude sur le terrain du profil temporel et des relations entre la taille et l'âge au recrutement (dans les eaux douces) chez deux gobies diadromes des ruisseaux de montagne, en Dominique, aux Antilles (15°30'N, 61°25'W). Chez *Sicydium punctatum* et *Sicydium antillarum*, le recrutement est pansaisonnier et fait l'objet d'une pêche dirigée similaire à d'autres pêches de gobies pour les jeunes poissons. Nous avons observé que la taille et l'âge des recrues varient de façon saisonnière, mais que la relation entre la taille et l'âge est complexe. Bien que la relation taille-âge soit positive à l'intérieur de la cohorte de chaque mois lunaire, elle est peu marquée pour l'ensemble des cohortes, du fait que la variation saisonnière de la taille est déphasée par rapport à l'âge. Entre les cohortes de recrues, la taille et l'âge (moyens ou prédits) présentent une corrélation négative. Le recrutement (production de la pêche) varie aussi de façon saisonnière, en phase avec la taille et déphasé par rapport à l'âge. Les productions les plus élevées coïncident avec la présence des recrues les plus jeunes, mais les plus grandes; les faibles productions coïncident avec l'inverse, ce qui indique qu'il y a des variations de la production de la pêche liées au taux de croissance. C'est la première fois que l'on établit une telle variation saisonnière systématique de l'âge au recrutement. Étant donné nos résultats, il ne faut plus considérer comme invariables la taille et l'âge au recrutement (qu'on peut assimiler à l'installation sur le fond ou à la métamorphose), même chez les poissons tropicaux.

Introduction

Age-at-recruitment (here equivalent to planktonic larval duration, age-at-settlement, postlarval duration, etc.) in tropical fishes is often expressed for each location as

a single value surrounded by some individual variation (e.g., Victor 1986; Radtke et al. 1988; Wellington and Victor 1989; Cowen 1991). Geographic variations have been the subject of increasing interest, but seasonal variations have not been found. Both Victor (1986) and Wellington and Victor (1989), while emphasising differences among species, report significant within-species geographic differences in planktonic larval duration, but they caution that temporal variations are not addressed by their data. Beckman et al. (1984) report differing growth rates of spot (*Leiostomus xanthurus*) between February–March and April–May. McCormick (1994) found short-term (days)

Received April 21, 1994. Accepted February 22, 1995.
J12358

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variation in age of settling goatfish (*Upeneus tragula*) to be high but unstructured.

Variation of age within samples of recruiting, settling, or metamorphosing fish have been reported for several taxa (Victor 1986; Chambers and Leggett 1987; Radtke et al. 1988; Wellington and Victor 1989; Cowen 1991). The variation evident within a sample indicates a "window" of possible settlement ages, with a wider window permitting more sampling of settlement cues. Given that variation exists in single samples, it may exist over the temporal range of recruitment; this would be easiest to detect in panseasonally recruiting species.

Variation in age-at-recruitment is important because of its effect on cumulative survival. Cumulative survival (and therefore recruitment) is negatively related to time t , because it is the compounding factor for survival:

$$[1] \quad N_t = N_0 e^{-Zt},$$

where N is numbers at times 0 and t , and $-Z$ is the natural log of survival (Ricker 1975).

This paper represents the first step of probing for temporal patterns in age-at-recruitment, using *Sicydium* species.

Features of the life cycle of *Sicydium* species make them particularly suited to recruitment studies. Previous work (Bell 1994; Bell and Brown 1995) in Dominica, West Indies (15°30'N, 61°25'W) (Fig. 1) established the life cycle (Fig. 2). *Sicydium punctatum* is diadromous, with yolk-sac larvae hatching from nests in rivers and immediately becoming planktonic and drifting to the sea. The marine postlarval (after yolk absorption) period is followed by recruitment to fresh waters; during these return migrations, recruits are fished near river mouths. Following recruitment, adults remain in fresh water, spawning repeatedly. Adults are long lived (>5 yr) and iteroparous. Because spawning and recruitment occur panseasonally, all stages can be sampled year round. Parental stock, reproductive output, recruitment success, and growth rates can all be readily estimated. Times from egg to recruitment to the fishery (50–150 days) are short compared with temperate fishes, as are times from then to first reproduction (<12 months). An asset to both sampling and interpretation is that (e.g., Roughgarden et al. 1988) a biological transition coincides with recruitment to the artisanal fishery.

Such artisanal fisheries, for so-called goby fry (post-larvae ~12 to 25 mm SL) of sicydiine and other gobies are widespread and often substantial (Jordan and Evermann 1905; Montilla 1931; Koumans 1953; Manacop 1953; Ego 1956; Aboussouan 1969; Titcomb 1977). Fishery declines have been reported in the Philippines and the Caribbean (Manacop 1953; Blanco 1956; Ego 1956; Erdman 1961, 1986; Aiken 1988), but investigation of causes has been hampered by the lack of life-history information on these species.

Here, we investigate seasonal variation in age- and size-at-recruitment *S. punctatum* and *Sicydium antillarum* (both sensu Brockmann 1965), using data acquired over a 2-year period in Dominica (Fig. 1). *Sicydium antillarum* is morphologically quite similar to, but rarer than, *S. punctatum*. For comparison, we include some data on Dominican *Eleotris pisonis* (Gmelin), an eleotrid goby with a similar (Bell 1994) life history.

Methods

Source of samples

All fish samples were collected over a 19-month period, from October 1989 to April 1991 as newly recruiting fish, with some pigment and partial scalation. These features are good indicators of the stage of recruitment/settlement. Most samples were taken at a permanent upstream-migration trap at Canefield River (Fig. 1); a few samples were taken at other sites (Fig. 1) within a 15-km radius. This trap is a mesh cone whose large end faces downstream and leads upriver migrating fish (recruits) to a removable collection chamber, which is a modified funnel trap. The trap was designed to collect and maintain fish alive for several days and was checked daily during the recruitment part of the lunar month (4–10 days following the last lunar quarter) and less frequently at other times.

Samples were preserved in weak alcohol buffered with NaHCO_3 to saturation. Because laboratory grade ethanol was unobtainable on the island, we substituted white rum, approximately 40% ethanol. To compensate for its low ethanol content, the preservative in samples was replaced 1–2 days after initial preservation for most samples. Standard lengths reported are those taken on approximately 500 preserved specimens.

Identification

Adult *S. punctatum* and *S. antillarum* were identified according to Brockmann (1965) using morphology (dentition, lateral scale counts). Published keys at the species level do not cover prerecruit and early recruit stages, because pigment, dentition, and scalation all change during recruitment. Dentition, mouth, and body structure are sufficient to identify recruits as *Sicydium* spp. (Jordan and Evermann 1898) but not to the species level. To separate species, we identified recruiting postlarvae using pigment patterns that we had previously verified by rearing recruits until they acquired the adult characters (Bell 1994). These patterns (Fig. 3) are the most useful identifying features. Both species contain bars, those of *S. antillarum* are vertical, parallel pairs of brown bars on a lighter yellow brown background, while *S. punctatum* has oppositely angled or crossed black bars in pairs (resembling the letters X, V, Y, I). Very early recruits completely lacking in pigmentation can be identified if kept for 1–3 days in freshwater aquaria to allow development of sufficient pigmentation to show patterns. A sample containing *S. punctatum* collected by us in Dominica is on deposit at the Smithsonian Institute, Washington, D.C. (catalogue No. USNM 314002). We caution that, following Hildebrand (1935), some workers (e.g., Aiken 1985; Erdman 1986; Penczak and Lasso 1991), synonymize (incorrectly, according to Brockmann 1965) several *Sicydium* spp. and call them *Sicydium plumieri*, sensu Erdman (1961). *Eleotris pisonis* were identified from adults following Jordan and Evermann (1898).

Amounts of postlarvae harvested during lunar-monthly recruitment episodes are those reported to us by fishers at Layou River, where return-migrant postlarvae are caught, and which we consider reliable. The fishery is a convenient indicator of recruitment intensity because it is

preferentially targeted toward tritri (goby postlarvae) when they are present. Unfortunately, there has never been a systematic collection of data for this or any similar fishery, the best (a 10-year series) information coming from Aboussouan (1969) in Réunion.

Otolith-age evaluation

Age was estimated for about 200 specimens, using dextral sagittal otoliths. Sagittae were the largest otoliths and had the clearest increments. We were not able to obtain or culture fish at marine stages preceding recruitment and were, therefore, not able to validate otolith increment periodicity for that stage. We assumed daily periodicity, since this is virtually the only periodicity that has been shown for larval fish under normal conditions (Jones 1992).

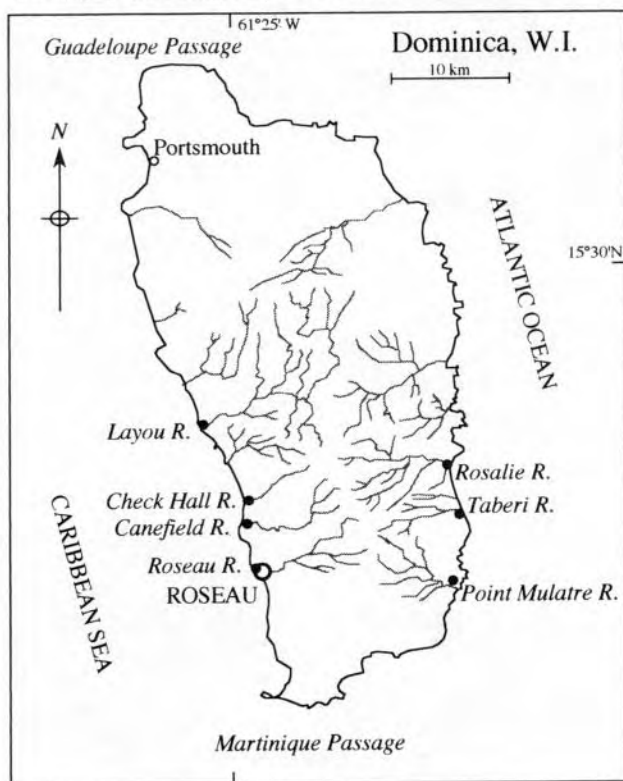
Otoliths (~500 μm in diameter) were extracted using glass microscalpels, then soaked in 60% H_2O_2 for at least several minutes to remove tissue residues, and then mounted with the convex side down in Crystalbond™ 509 clear thermoplastic adhesive (AREMCO Products Inc., Ossining, NY 10562-0429, USA.) on numbered glass slides. Grinding, polishing, or further cleaning were rarely needed.

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

Ages (total) were obtained from counted sequences of individually measured increment widths. Increment widths were obtained under 50 \times (usually) or 100 \times (rarely) objectives of an Olympus BHC compound microscope (transillumination) fitted with a 10 \times intermediate lens and video-camera, and a frame-grabber board and video display. A rotatable polarizing filter on the light source often improved otolith readability. Sagittal otoliths (Fig. 4) of prerecruiting *S. punctatum* and *S. antillarum* postlarvae are nonsymmetrical as viewed, like the shape of a wide hand print, and the growth emphasis is in the direction of the fingers. The transect used for increment measurement and counting was chosen to cross increments at their greatest widths (near the 12 o'clock position in Fig. 4).

Increment counts were done blind (with reference only to the otolith reference number), beginning at the center of the crystal (primordium; rodlike feature) at the origin, taking the distances to the end of the crystal, to precore increments if visible, to the core (circular feature), and to subsequent increments (not circular) until recruitment. Because the center of the otolith is the most difficult to read, we assumed that all possessed the features seen in those that were clear in that region: there is usually only one increment within the core, so the core is the third feature digitized. Because hatching is usually 24–48 h (Bell 1994) after fertilization, the core is probably a hatch check, but we have not yet confirmed this and have not adjusted ages to reflect this. No otoliths requiring adjustment after the core feature were used in these analyses, but similar analyses (Bell 1994), which included adjusted otoliths, gave virtually identical results. Increments visible only in a transect outside the growth-emphasis sector near the 12 o'clock position were counted and digitized on the 12 o'clock transect with a coding to indicate that those widths were not

Fig. 1. Collection sites for recruiting gobies (●) and towns (○) in Dominica, West Indies.



usable, but that the cumulative width indicated to the next on-transect visible increment remained accurate. Subsequent increments up to the edge of the otolith were then taken. Repeated blind readings (in the same or later sessions) showed good matches of increment width sequences, and were usually exact or within 1, rarely ≥ 3 , increment.

Various workers (e.g., Victor 1986; Wellington and Victor 1989; Campana 1992) have discussed “subdaily” increments, but not all agree that these are real. We counted only those features we could confidently describe as increments, avoiding those which could be explained as optical artefacts. Features that could be focused to near-invisibility while keeping both adjacent increments in focus were not counted as increments.

The recruitment feature was by definition the outer edge of the otolith (as in Fig. 4) where the fish was captured at entry to fresh water. In cultured fish, or fish captured postrecruitment, it was identified by an altered growth direction in the otolith. This feature is comparable with reported settlement marks (e.g., Wellington and Victor 1989), but clearer than that reported by Victor (1982) for *Thalassoma bivittatum*. The stage in recruitment was also evident from the external pigmentation, mouth structure, behaviour of fish and their location: early recruits (no pigment, terminal mouth) and late recruits (pigmented, sub-terminal mouth) are separated by only 1–5 days yet are very easily distinguished.

The analyses of age use information from 143 newly recruited fish: 117 *S. punctatum*, and 25 *S. antillarum*

Fig. 2. Life cycle (above appropriate habitat) of sicydiine gobies in Dominica (Pyriform stalked eggs under stones, vertically swimming and drifting larva absorbing yolk over 5–8 d, recruiting at 50–150 d to fresh waters and to fishery.)

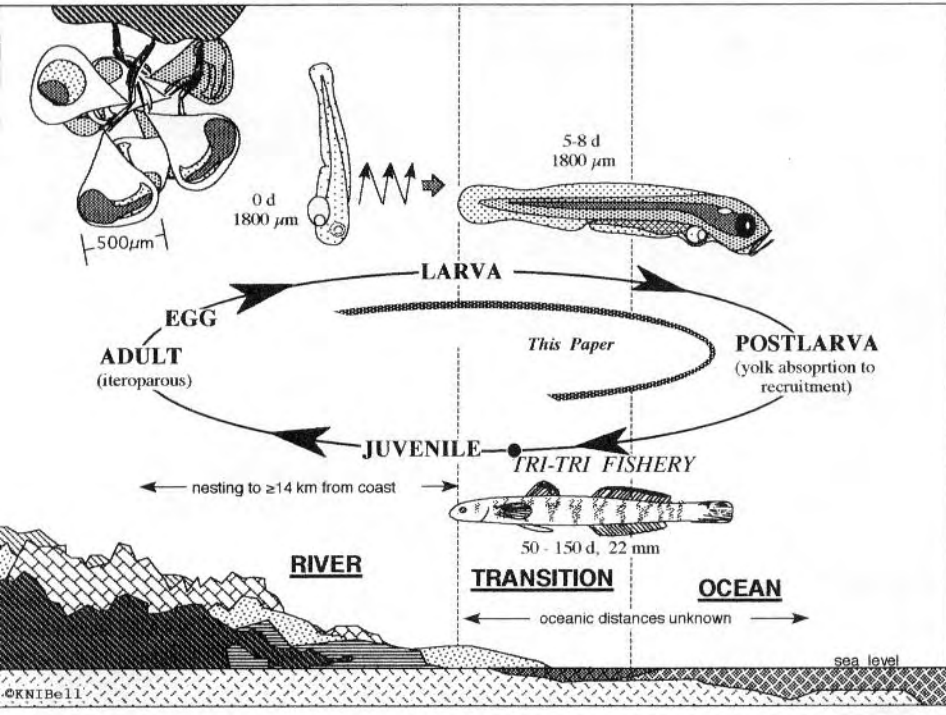
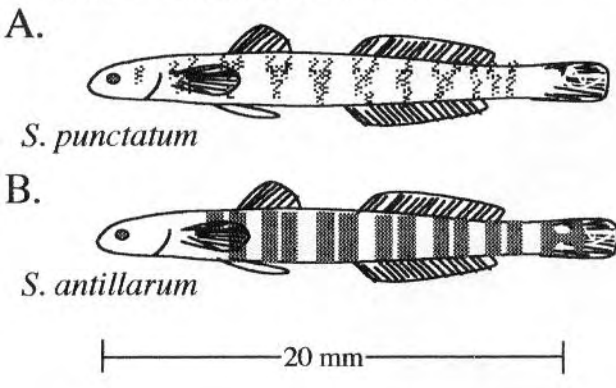


Fig. 3. Diagnostic features of recruiting *Sicydium punctatum* and *S. antillarum* (sensu Brockmann 1965) in Dominica, W.I. See Introduction for details.



otoliths that could be read from the core to the recruitment feature (or edge) and did not require adjustment.

Analysis of seasonal variations

Recruitment is panseasonal and periodic for *Sicydium* species in Dominica, and elsewhere in the Caribbean (Erdman 1986), as for *Sicyopterus extraneus* in the Philippines (Manacop 1953). As indicated by the commercial fishery and catches in our upstream-migration traps (Bell 1994), recruitment episodes tend to begin on the fourth day following the last lunar quarter (Fig. 5) and continue with diminishing intensity for several days. Such lunar-phased recruitment episodes are a useful way of

defining recruiting cohorts. We consider each episode to begin on the day of the last lunar quarter (LLQ) and end on the day preceding the next. Thus, "LLQ n " (in text or figures) denotes the n th sequential last-lunar-quarter recruitment episode observed during this study, with LLQ 1 beginning May 27, 1989; LLQ 2 beginning June 26, 1989; and so on.

To evaluate whether periodic functions of time could explain variations in the dependent variables length-at-recruitment, age-at-recruitment, and numbers recruiting, we applied techniques similar to those of Batschelet (1981) and Zar (1984). ANOVA is a legitimate technique with periodic (or circular) data, provided residuals are independently and normally distributed, and least squares provides an unbiased fit even if these assumptions are not met (Batschelet 1981, p. 160). Sinusoidal variation (with a frequency of 1) in a Y variable over a cycle can be expressed as

$$[2] \quad Y = b + m(\cos(RX + \delta)),$$

where RX is the angular transformed independent X variable (day of year (DOY), time of day, etc.), and b is an intercept, m is the slope, and δ is the phase lag.

While Eq. 2 can be fitted iteratively by varying δ , it is equivalent (Batschelet 1981) to

$$[3] \quad Y = \beta_0 + \beta_1 \sin(RX) + \beta_2 \cos(RX)$$

where β_1 and β_2 are coefficients, and β_0 is a mean level, equivalent to an intercept in a nonperiodic regression. (Here we use the azimuthal system, in which an angle α is measured in a clockwise direction from the positive Y axis,

as on a compass.) Equation 3 can be solved directly using $\sin(RX)$ and $\cos(RX)$ as new variables. Batschelet (1981, p. 164) states "... to obtain meaningful results ... a minimum of $n = 6$ equally spaced [data points] will suffice... however, if the intervals are not equal, at least $n = 8$ data points are required." He also points out that reliability of estimation of the parameters will suffer if all the points are clustered in a single narrow section or phase of the cycle.

Location of peaks (P) can be determined by visual inspection of plots, or by algebra provided by Batschelet (1981, sec. 8.2). Where the position of the peak (P_p) is ∂ units (here in degrees) after the nominal zero of the cycle (t_0),

$$[4] \quad P_p = t_0 + \partial$$

$$[5] \quad \partial' = \arctan(\beta_1/\beta_2)$$

$$[6] \quad \partial = \partial' + QC$$

where QC is a quadrant correction to be added to ∂' : $QC = 0^\circ$ if (β_1, β_2) are $(+, +)$; $QC = 180^\circ$ if $(+, -)$ or $(-, -)$, and $QC = 360^\circ$ if $(-, +)$.

Dates (independent variables) were first transformed into circular variables (RDOY) by multiplying DOY (0–365) by $2\pi/365$ to obtain an equivalent radian measure, or by $360/365$ for degrees. For solution as (3) the proxy X -variables become $\sin(RDOY)$ and $\cos(RDOY)$.

Residuals were examined for trends with respect to the untransformed time variable (DOY). The curves represented by the regressions were then expressed on DOY axes by tracing fitted values.

Growth indices

A linear length-based average growth index (G_L , millimetres per day) was calculated as

$$[7] \quad G_L = (SL - 1.8)/age_{\text{hatch}}$$

where SL is the standard length in millimetres, 1.8 is the size in millimetres of a newly hatched larva (Bell 1994), and age_{hatch} is total age (days) less three.

Results

The mean age at recruitment of *S. punctatum* was 83.4 ± 1.3 (mean \pm SE) days (range 54–136, $n = 117$), and for *S. antillarum* was 86.7 ± 3.4 d (range 63–139, $n = 25$). The mean SL for *S. punctatum* was 19.5 ± 0.1 mm (range 16–25, $n = 324$), and for *S. antillarum* was 21.8 ± 0.8 mm (range 18.8–25.5, $n = 78$). Although the overall (all seasons pooled) correlations of age and size for *S. punctatum* and *S. antillarum* are not significant (Fig. 6b), within most lunar-monthly recruitment episodes (LLQs) the relationships are all positive and often significant (Fig. 6c, Table 1). All correlations thus obtained ($0.25 \leq r_{LLQ}^2 \leq 0.89$; Table 1) far exceed those obtained by pooling all samples ($r^2 \leq 0.02$), clearly indicating temporal variation in this relationship. For *S. punctatum* there are 11 LLQs with >2 points; of these, six are significant ($0.0001 \leq p \leq 0.05$) and two are marginally so ($0.05 \leq p \leq 0.1$). For *S. antillarum* there are four LLQs with

Fig. 4. Sagittal otolith of newly recruited *Sicydium punctatum*. Nucleus is visible below centre.

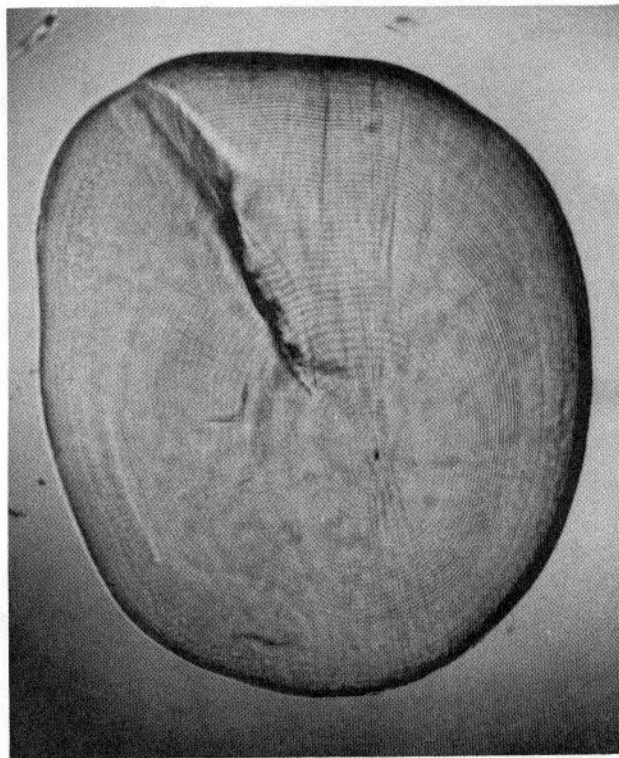
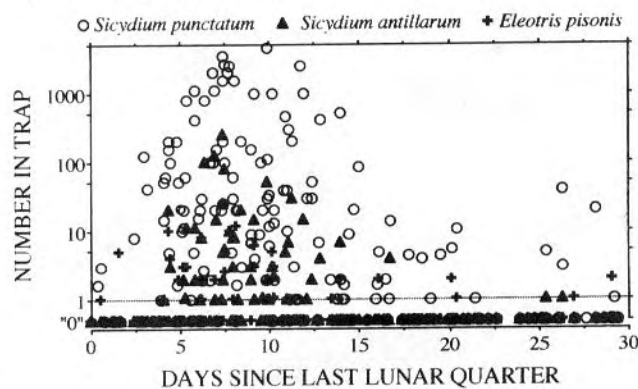


Fig. 5. Lunar-monthly recruitment pattern (numbers caught in upstream-migration trap). Because zeros cannot occur on a logarithmic axis, an artificial zero is marked "0" to show zero catches.

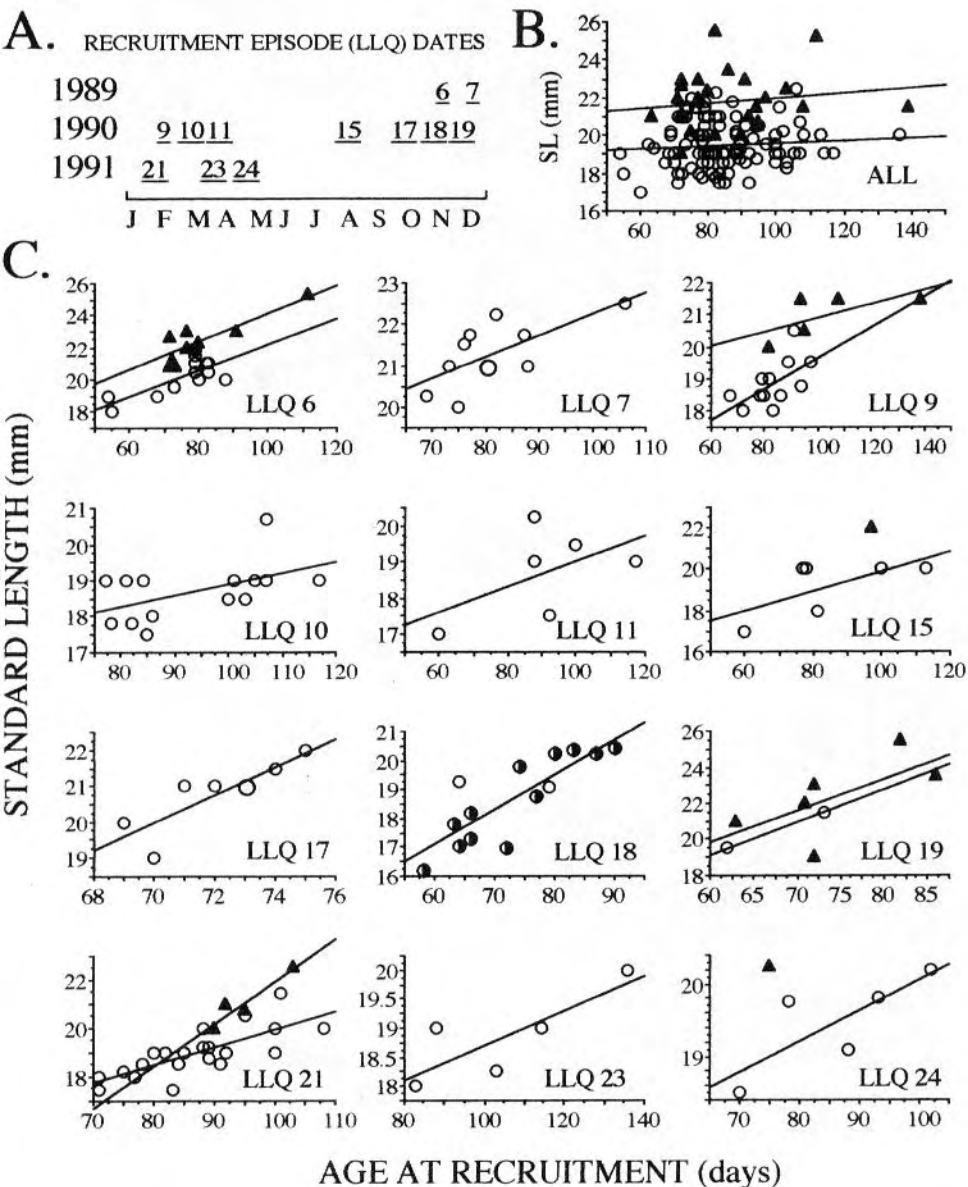


>2 points; of these, one is highly significant, one is marginal, and two are not significant.

Contrasting with the positive relationship of (individual) size and age found within LLQs, the relation of (mean) size and age is negative across LLQs (Fig. 7). Samples from similar months of different years are also similar on this plot. The negative trend is significant ($p < 0.05$) for *S. punctatum* but marginal ($0.05 < p < 0.1$) for *S. antillarum*, which shows a similar trend but for which there are fewer observations.

Age-at-recruitment varies seasonally (Fig. 8a, Tables 1 and 2) and is nearly 180° out of phase with, or is inverse

Fig. 6. Temporal variation of age-at-recruitment in relation to standard length. "LLQ" refers to sequential number of last-lunar-quarter recruitment episode. (A) Dates of last lunar quarters. (B) Overall length–age relationship. (C) Length–age relationship within each recruitment episode (regressions summarised in Table 1). (○) *S. punctatum*; (▲) *S. antillarum*. With the exception of LLQ 18, in which 12 *S. punctatum* were cultured ~29 d (●) following recruitment, all length measurements are taken on fish cultured ≤4 d after capture. Coincident points are indicated by larger symbols. See also Table 1.



to, the seasonal variation in length-at-recruitment (Fig. 8b, Table 2). Both variations are significant ($p < 0.05$), for either species or in combination, and species are in phase with each other.

Where seasonal variation in size- and age-at-recruitment is not concordant, growth rate cannot be inferred from age-at-recruitment alone. For these data, variation in age-at-recruitment underestimates variation in growth rate because age and size variations are nearly 180° out of phase. The linear growth rate index (G_L ; Eq. 7) is strongly

seasonal for both *S. punctatum* and *S. antillarum*, peaking at recruitment dates in September–October, and lowest for March–April recruits (Fig. 8c).

The directed fishery (Fig. 8d) for return-migrant post-larvae at Layou River has its highest yields in the fall. However, even in that season there is much short-term variability such that yields can be either large or nonexistent. Yields in the spring are reported to typically vary from nil to one barrel (80 L), which is consistent with our data. Thus, both magnitude and month-to-month variability

Table 1. Regressions of length against age-at-recruitment by species and recruitment episode (LLQ) as $SL = \beta_0 + \beta_1 AGE$. See also Fig. 6.

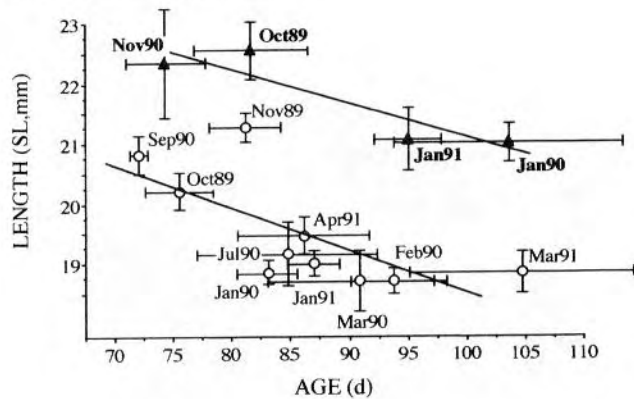
	<i>N</i>	r^2	<i>p</i>	β_0	β_1
All LLQs					
<i>S. punctatum</i>	105	0.006	0.4306	25.35	0.008
<i>S. antillarum</i>	25	0.006	0.7111	25.258	0.008
LLQ 6					
<i>S. punctatum</i>	13	0.576	0.0026	14.191	0.08
<i>S. antillarum</i>	8	0.789	0.0032	15.511	0.086
LLQ 7					
<i>S. punctatum</i>	11	0.461	0.0217	17.025	0.052
LLQ 9					
<i>S. punctatum</i>	12	0.355	0.0409	14.856	0.048
<i>S. antillarum</i>	5	0.441	0.2214	18.771	0.022
LLQ 10					
<i>S. punctatum</i>	14	0.254	0.0661	15.84	0.03
LLQ 11					
<i>S. punctatum</i>	6	0.283	0.277	15.52	0.035
LLQ 15					
<i>S. punctatum</i>	6	0.434	0.1551	15.213	0.047
LLQ 17					
<i>S. punctatum</i>	8	0.726	0.0072	-7.132	0.387
LLQ 18					
<i>S. punctatum</i>	14	0.674	0.0003	9.911	0.12
LLQ 19					
<i>S. antillarum</i>	6	0.424	0.161	9.347	0.175
LLQ 21					
<i>S. punctatum</i>	21	0.578	0.0001	12.518	0.075
<i>S. antillarum</i>	4	0.894	0.0542	4.583	0.173
LLQ 23					
<i>S. punctatum</i>	5	0.663	0.0934	15.718	0.03
LLQ 24					
<i>S. punctatum</i>	5	0.623	0.1126	15.833	0.042

Note: Regressions included only otoliths from fish cultured ≤ 4 days following capture, except in LLQ 18 (12 specimens cultured ≤ 29 days, identified by symbols in Fig. 7).

appear to vary seasonally. Much of the variation in fishery yield (in barrels, BBL) is accounted for by a periodic regression (Table 2). The calculated peak yield (Eqs. 4–6) is on DOY = 296, or October 23. Despite the acceptable correlation however, the cosine curve (Fig. 8d) appears excessively symmetrical for the fishery profile, which has a narrow peak of high yields and a wide trough with low yields. Highs and lows in the landings coincide with extremes in the age- and size-at-recruitment curves, and are in phase with the size and growth curves and $\sim 180^\circ$ out of phase with the age curve.

Relationships of age-at-recruitment and growth with hatch (Fig. 9) date are less strong (Table 2) than relationships with recruitment date (Fig. 8), for both *Sicydium* species (10–20% less variation explained by hatch date). Age-at-recruitment is at a minimum for larvae hatching in the summer (June–August) and a maximum for larvae hatching in the winter (December–January). Growth (G_L) expected as a function of hatch date is about $0.21 \text{ mm}\cdot\text{d}^{-1}$

Fig. 7. Correlation of mean length (SL) and mean age of *S. punctatum* and *S. antillarum* among LLQs. The relationship is opposite to that within LLQs. Mean values for each LLQ ($\pm 1\text{SE}$) are plotted. (\circ) *S. punctatum*; (\blacktriangle) *S. antillarum*. Regression for *S. punctatum* is $SL = 25.597 - 0.071(\text{age})$, $r^2 = 0.495$, $n = 10$, $p = 0.0232$; *S. antillarum*: $SL = 26.782 - 0.057(\text{age})$, $r^2 = 0.838$, $n = 4$, $p = 0.08$. Month of recruitment for each sample is indicated in plain and bold type for *S. punctatum* and *S. antillarum* respectively.



in the winter, and rising by about 30% to peak ($0.29 \text{ mm}\cdot\text{d}^{-1}$) in the summer. The middle to late summer, thus, appears to be the optimal hatch period for rapid growth.

Discussion

Seasonal variation is evident (Fig. 8) in age and length at recruitment for *S. punctatum* and *S. antillarum*, and in fishery landings (an indicator of recruiting numbers) for a mixture of species in which *S. punctatum* predominates ($\sim 95\%$). The variations repeat in data covering nearly 2 years, supporting interpretation as recurring annual cycles. The seasonal variations in age, size, and growth have virtually identical phases with respect to time of year in *S. punctatum* and *S. antillarum*. The opposite phasing of the size- and age-at-recruitment curves restates what is shown in Fig. 7: among cohorts, the predicted age-at-recruitment is negatively related to predicted SL, and contrasts with the positive individual age-size relationship within cohorts.

The phase of the seasonal variation differs among variables. Maximum recruitment is associated with cohorts having the greatest mean size and the lowest mean ages. Recruitment (with migration to fresh waters) is therefore not determined by either size or age alone, but by both in combination: the “decision line” for each species is approximated by the regressions in Fig. 7; individual growth trajectories would cross them near recruitment. The regressions should perhaps be curvilinear, but the point is moot with these data. The contrary variation of size versus age within and among LLQs (recruiting cohorts) is a strong caution against the application of a single age-length key across seasons. It is also a generally useful pointer to temporal variation in growth rates.

Table 2. Relation of age-at-recruitment, length-at-recruitment, average growth-to-recruitment, and fishery landings to recruitment date, and of age and growth to hatch date, for *S. punctatum* and *S. antillarum*. See also Figs. 8 and 9.

Parameter	Equation	Peak	r^2	n	p
Relationships with recruitment date					
Age-at-recruitment ^a (days)					
Age	= Int + $\beta_1\sin(\text{RDOY}) + \beta_2\cos(\text{RDOY})$				
<i>S. punctatum</i>	= 83.835 + 10.1sin(RDOY) - 0.213cos(RDOY) $p = 0.0001$ $p = 0.9243$	April 02	0.28	117	0.0001
<i>S. antillarum</i>	= 89.077 + 12.42sin(RDOY) - 2.12cos(RDOY) $p = 0.0203$ $p = 0.7878$	April 11	0.238	25	0.0503
Length-at-recruitment ^b (SL, mm)					
SL	= Int + $\beta_1\sin(\text{RDOY}) + \beta_2\cos(\text{RDOY})$				
<i>S. punctatum</i>	= 19.3 - 0.87sin(RDOY) + 0.411cos(RDOY) $p = 0.0001$ $p = 0.0004$	October 26	0.249	324	0.0001
<i>S. antillarum</i>	= 21.62 - 0.6sin(RDOY) - 0.017cos(RDOY) $p = 0.0148$ $p = 0.9665$	September 28	0.079	78	0.0462
Growth ^b (mm·d ⁻¹)					
Growth	= Int + $\beta_1\sin(\text{RDOY}) + \beta_2\cos(\text{RDOY})$				
<i>S. punctatum</i>	= 0.25 - 0.042sin(RDOY) - 0.002cos(RDOY) $p = 0.0001$ $p = 0.7196$	September 27	0.496	105	0.0001
<i>S. antillarum</i>	= 0.26 - 0.051sin(RDOY) - 0.004cos(RDOY) $p = 0.0003$ $p = 0.8466$	September 26	0.469	25	0.0009
Fishery yield (at Layou, barrels, all species, ~99% <i>Sicydium</i>)					
Barrels	= Int + $\beta_1\sin(\text{RDOY}) + \beta_2\cos(\text{RDOY})$				
Barrels	= 4.112 - 4.807sin(RDOY) + 1.979cos(RDOY) $p = 0.003$ $p = 0.163$	October 23	0.46	19	0.007
Relationships with hatch date					
Age-at-recruitment ^a					
Age (d)	= Int + $\beta_1\sin(\text{RHDOY}) + \beta_2\cos(\text{RHDOY})$				
<i>S. punctatum</i>	= 79.513 - 0.794sin(RHDOY) + 8.593cos(RHDOY) $p = 0.7462$ $p = 0.0001$	December 25	0.179	117	0.0001
<i>S. antillarum</i>	= 85.636 + 1.038sin(RHDOY) + 5.486cos(RHDOY) $p = 0.8917$ $p = 0.4159$	January 10	0.031	25	0.7056
Growth ^b					
Growth	= Int + $\beta_1\sin(\text{RHDOY}) + \beta_2\cos(\text{RHDOY})$				
<i>S. punctatum</i>	= 0.252 + 0.001sin(RHDOY) - 0.039cos(RHDOY) $p = 0.94$ $p = 0.0001$	May 30	0.375	105	0.0001
<i>S. antillarum</i>	= 0.257 - 0.005sin(RHDOY) - 0.04cos(RHDOY) $p = 0.8$ $p = 0.0288$	June 08	0.201	25	0.0845

Note: RDOY = DOY(2 π /365) (i.e., DOY transformed to radians of year), RHDOY is same but for hatch date (= DOY_{rec} - Age + 3). Regressions are of the form $Y = C + \beta_1\sin(\text{RDOY}) + \beta_2\cos(\text{RDOY})$ (see Methods), with parameter significance and calculated peak date on following line. For growth calculation and relationships with hatch date, age is adjusted by -3 to exclude features within the core, assumed to be deposited at hatch when the length is ~1.8 mm.

^aUsing fish cultured 0–30 d.

^bUsing fish cultured 0–4 d.

(age-at-recruitment in Hawaii is greater than in Dominica). If more data are acquired on other species in Dominica and Hawaii to obtain a better control of species-related differences, insights into habitat differences may follow.

Implications

Over longer terms (than seasons), such as years in temperate and northern fisheries, variations in growth rate are acknowledged by the frequent reevaluation of age-length relationships. However, this has been directed at estimating numbers in each year-class. Terms of the equation $N_t = N_0e^{-Zt}$

include most acknowledged contributors to cohort strength. We feel the effect of t on gross survival has been unduly subordinated to questions centering on the role of mortality rates or larval production. We observe that, whether mortality is higher or lower for younger or older, larger or smaller, fast-growing or slow-growing larvae, the compounding effect of t (age-at-recruitment) on cumulative mortality can readily supersede the effect of all but the most extreme short-term variations in daily mortality.

An initial motivation for this study was an elucidation of factors which could contribute to fishery variations,

Fig. 9. Seasonal cycles with respect to hatch date, for *S. punctatum* (○) or *S. antillarum* (▲). Hatch dates are indicated as day numbers beginning with January 1, 1989; letters below x-axis indicate months. (A) Days hatch-to-recruitment (= AAR - 3). (The angled alignment of age-at-recruitment points in each sample has no meaning here; it merely results from the fact that, for each point i , $X_i + Y_i =$ collection date). (B) Growth index (millimetres per day) against hatch date. Regression equations are given in Table 2.

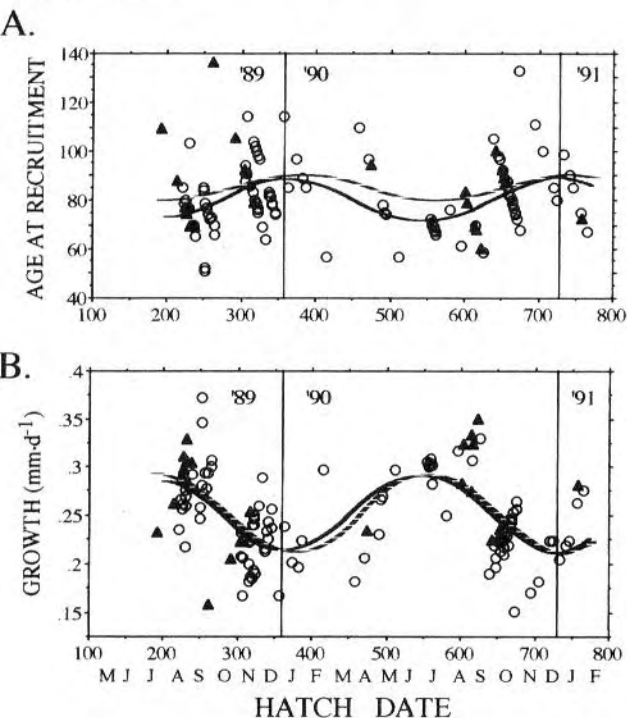
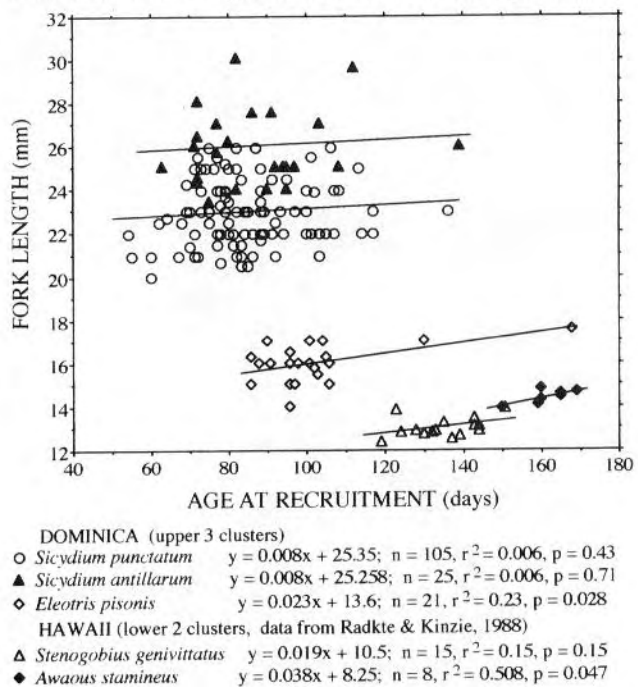


Fig 10. Comparison of recruit length-at-age for diadromous gobies in Dominica (three species) and from Hawaii (two species; Radtke et al. 1988), with regression lines. (Fork lengths are used to enable comparison with published data.) Hawaiian data are from single collections, *Eleotris pisonis* are mostly from a single collection, while *Sicydium* data are from multiple seasons.



recruitment with variable time lags, we defer further exploration of this question to subsequent papers.

Acknowledgments

We acknowledge the Young Canadian Researchers Award (IDRC) for support of field work by K.N.I.B.; the Fisheries Division of the Commonwealth of Dominica, W.I.; support from a Natural Sciences and Engineering Research Council grant to J.A.B.; and a fellowship (K.N.I.B.) from Memorial University; discussion with Ian McLaren, Robin Mahon, Iain Suthers, Michel Kreiber, Don Erdman, Roger Doyle, Nigel Lawrence, and John Archbold; Katherine Bridger's conscientious work; useful comments from two anonymous reviewers; and statistical advice from W.G. Warren. We thank Peter, Lieda, and Jane Robin Bell for much help and many others for encouragement. This work is in partial fulfilment of the requirements for the degree of Doctor of Philosophy at Memorial University of Newfoundland.

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especially the apparent declines (Manacop 1953; Blanco 1956; Ego 1956; Erdman 1961; Erdman 1986; Aiken 1988) reported in goby fry fisheries. The results discussed here identify variations in age-at-recruitment (associated with variation in growth rate) as potential contributors to fishery variation among seasons. Such variation may exist as well over longer (e.g., annual, decadal, etc.) timescales responding to, for example, environmental and climatic changes. Spatial variations as shown by Victor (1986) and Wellington and Victor (1989) for damselfishes and wrasses appear to apply also for gobiids in general.

We have demonstrated significant variation over seasons in recruit age, growth history and size; these are relevant to the recruitment of these tropical species. Furthermore, these species may represent over short periods and in a more structured way (seasons) what happens in temperate situations over years instead of months; if so, these species may be ideal systems in which to study recruitment processes. We believe age and growth are the major factors determining recruitment in *Sicydium* species in Dominica, but we caution that variations in reproduction could occur and also contribute to recruitment variation (Bell 1994). Because of the complexity of modelling

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