

## Settlement Dynamics of the Bicolor Damselfish, *Stegastes partitus*, in Chinchorro Bank, Mexican Caribbean

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### ABSTRACT

Settlement dynamics of the bicolor damselfish, *Stegastes partitus* (Pomacentridae), were determined by otolith shape and microstructure analysis and compared among different coral reef areas (Windward, reef Lagoon and Leeward) of Chinchorro Bank (northern Meso-American Barrier Reef System, eastern Yucatan Peninsula). Estimated age, settlement time, size at settlement, and larval otolith growth rates were compared. Significant differences in planktonic larval duration were found, with 28.8, 30.3 and 32.7 mean days spent at Windward, Lagoon and Leeward, respectively. Individuals with shorter larval durations (at Windward) showed faster otolith growth rates and settled at relatively smaller sizes than those with longer larval durations (at Lagoon and Leeward). However, there was no significant difference in otolith growth rates among reef areas, and there was no clear evidence for delay in metamorphosis. Based on both the planktonic larval duration and the prevalent current pattern in the area, it appears that strong northwesterly currents passively transport *S. partitus* larvae into Chinchorro Bank. Larvae may enter at Windward, passing through the reef Lagoon, and leave by the Leeward. Longer PLDs for *S. partitus* settling at Leeward are not due to differences in larval growth rates but more likely to a lack of access to suitable settlement habitat by the time the larvae is passing throughout the reef system. An otolith shape (Fourier) analysis also revealed a clear differentiation between otoliths from the three reef areas, suggesting that the environmental influence on otolith shape of *S. partitus* is relatively uniform, which means that this fish is affected by similar local environmental conditions within each reef area.

KEY WORDS: Chinchorro Bank, *Stegastes partitus*, Planktonic larval duration, Fourier shape analysis

### Dinámica del Asentamiento del Pez damisela *Stegastes partitus*, en Banco Chinchorro, México

La dinámica del asentamiento del pez damisela, (Pomacentridae) fue determinada mediante el análisis de la microestructura del otolito y comparada entre diferentes hábitat (barlovento, laguna y sotavento) del arrecife Banco Chinchorro (Porción Norte del Sistema Arrecifal Meso-Americano). Diferencias significativas en la duración larval fueron encontradas entre los hábitat arrecifales (ANOVA, F<sub>2</sub>, 123 = 24.15, p < 0.0000), con 28.81, 30.29, y 32.67 días pasados en el barlovento, la laguna y de sotavento, respectivamente. Los individuos con la duración larval más corta demostraron tasas de crecimiento más rápidas del otolito y se asentaron en tallas relativamente más pequeña que éstos con duración larval más largas. Sin embargo, no se encontraron diferencias significativas entre las tasas de crecimiento larval del otolito entre los hábitat arrecifales (ANOVA, F<sub>2</sub>, 87 = 2.50, p = 0.0884), y no se observaron evidencias claras de un retraso en la metamorfosis. Con base en el análisis de la duración larval y los patrones de corrientes actuales en el área, se sugiere que las corrientes fuertes provenientes del norte transportan pasivamente a las larvas hacia el banco de Chinchorro entrando por el de barlovento, pasando a través de la laguna del filón, y finalmente saliendo por el sotavento. La forma de Otolito (análisis de Fourier) reveló una diferenciación clara entre los hábitat arrecifales sugiriendo que la influencia de la factores ambientales sobre la forma del otolito es relativamente uniforme, y que condiciones ambientales locales similares tales como disponibilidad del hábitat y del alimento afectan a los individuos.

PALABRAS CLAVES: Banco Chinchorro, *Stegastes partitus*, Duración Larval Pelágica, Análisis de la Forma de Fourier

### INTRODUCTION

Early life history of nearly all coral reef fishes includes a dispersive, pelagic larval phase and a juvenile phase that undergoes a transition from a pelagic to a demersal existence (Leis 1991). In coral reefs, various environmental factors influence the dynamics of fish settlement not only over time in the same location but also simultaneously at different locations (Sponaugle and Cowen 1996). Several processes during the pelagic existence not only affect growth, survival and dispersion of fish larvae but also their dynamics of settlement. While fish larvae may continue growing, and simply dying if failing to encounter a reef to complete their development (Danilowicz 1997), few larvae are able to slow their development until

encountering an ideal juvenile habitat (Sponaugle and Cowen 1994). Various mechanisms and factors contribute to a successful transport of larvae to appropriate settlement habitats:

- i) Pelagic larval duration (Sponaugle and Cowen 1994),
- ii) Larval swimming behavior (Danilowicz 1997),
- iii) Rates in larval feeding, growth, and mortality rates (Leis 1991),
- iv) Presence of conspecifics (Booth 1992) and predators (Hixon and Beets 1993),
- v) Coral species they inhabit (Jones 1988), and
- vi) Physical processes, such as wind, tides and ocean currents (Cowen 1991).

Fish may not survive the dispersive larval stage without an appropriate transport to a given reef (Leis 1991). Currently, age-based studies have identified both temporal and spatial patterns in larval supply. From the otolith microstructure, valuable information (age, planktonic larval duration, origin, growth rates, and environmental history) on early life history phases can be obtained, while very useful information may also be obtained from the otolith shape analysis (in particular the Fourier analysis). While otolith shape is markedly species-specific (Pothin *et al.* 2006), the otolith nucleus and shape often vary geographically within a species (Campana and Jones 1992).

The present work was designed to improve the understanding of settlement dynamics in a reef fish (*Stegastes partitus*) from an atoll-like coral reef system (the Chinchorro Bank) in the Mexican Caribbean, eastern Yucatan Peninsula. From recently settled fish, based on otolith microstructure analysis we determined age, time and size at settlement, and growth rate. Additionally, by using otolith shape (through Fourier analysis) we inferred postsettlement spatial variations.

## MATERIALS AND METHODS

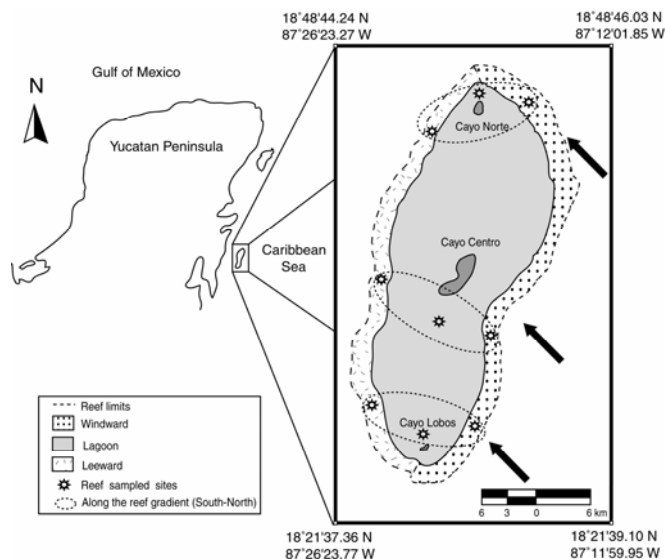
### Study Area

Chinchorro Bank (Figure 1), one of the largest atoll-like reefs in the Caribbean Sea (Jordan and Martin 1987), is an elliptical reef (40 km in length and 18 km wide) located to 30.8 km off the southeastern Yucatan Peninsula (Jordan and Martin 1987). Chinchorro has three sandy cays (Cayo Norte, Cayo Centro and Cayo Lobos) located on the North, Central and South sides, respectively. At least three sections (reef areas) are recognized (Jordan and Martin 1987) according to the degree of current and wave exposure:

- i) Windward, having a platform with 3-8 inclination degrees reaching 60 m in depth and comprising a well developed reef crest;
- ii) Reef Lagoon, having an open and shallow lagoon, varying from 7 to 9 m in depth at southern areas and 2 to 3 m in depth towards northern areas, with patch reefs and coral knolls gradually decreasing in number and size from South to North; and
- iii) Leeward, without a developed reef crest with reef structures less prominent than those in the windward.

A sampling design was established according to reef components, as follows: three sites for each reef area (Windward, Lagoon and Leeward) and three sites for each cay (Cayo Norte, Cayo Centro and Cayo Lobos) (Figure 1). Based on the proposed design, two gradients were investigated: (1) “across the reef gradient (East-West)”, comprising three sites for each reef area, and (2) “along the reef

gradient (South-North)”, compromising three sites for each Cay.



**Figure 1.** Location of the Chinchorro Bank, eastern Yucatan Peninsula. Based on the “across the reef gradient (East-West)”, three sampling sites were established for each reef area (Windward, Lagoon and Leeward). Based on the “along the reef gradient (South-North)”, three sampling sites were established for each Cay (Cayo Lobos, Cayo Centro and Cayo Norte). Arrows show most common current patterns.

### Study Species

The bicolor damselfish, *Stegastes partitus* (Poey 1868), is one of the nine species of Pomacentridae from the Caribbean Sea (Allen 1991). This species provided a useful model for the study as it shares similar life history traits with other reef fish species: planktonic larvae and strong site fidelity from settlement to adulthood (Chittaro *et al.* 2006). Females deposit a clutch of eggs (approximately 2,000 eggs) on benthic substrata where males fertilize the eggs externally (Robertson *et al.* 1988). Three days after egg deposition, larvae hatch, and begin a planktonic larval phase varying from 27 to 31 days (mean = 28.8 days) until settlement (Robertson *et al.* 1988, Wellington and Victor 1989). After settlement, individuals are relatively sedentary and occupy a relatively small territory (< 2m<sup>2</sup>) (Chittaro *et al.* 2006, Robertson *et al.* 1988).

### Fieldwork

Fish collection was conducted in August 2005, since *Stegastes partitus* has its highest recruitment point during summer (Almada-Villela *et al.* 2003). Previous to collection, fish were anesthetized (75% ethylic alcohol and 25% clove oil; Ackerman and Bellwood 2002) and then taken with a hand net. Individuals less than 3 cm were only considered for collection since newly recruits are 2.5

cm in maximum total length (Almada-Villela *et al.* 2003). Specimens were stored in 97% ethanol until they could be dissected in the laboratory. Morphometrics (to the nearest  $10^{-1}$  mm) for each fish taken using calipers, included: total length (TL), standard length (SL) and head length (HL). Out of the 135 specimens collected (15 per site, with a size range of 1.22 to 2.81 cm, mean = 1.56 cm), we only included in the analyses those in the range of 1.22 to 2.5 cm; consequently, there were 126 specimens (14 per sampling site and 42 per reef area).

### Otolith Preparation and Age Determination

Under the stereomicroscope, sagittal otoliths were removed from each fish using the 'open-the-hatch-method', then otoliths were cleaned and stored dry in vials (Secor *et al.* 1992). Sagittal otoliths were chosen from other otolith types because of their larger size, degree of interspecific variation, and relative ease the microstructures can be assessed (Secor *et al.* 1992). Using a transmitted light and a photographic camera, high contrast images were taken from each otolith placed on a microscope slide (for minimizing distortion errors in the normalization process, the sulcus always faced downwards and the rostrum pointing in the same direction).

The age (in days) and the pelagic larval duration (in days) were determined following standard protocols of microstructure examination (Wilson and McCormick 1997). Mounted otoliths (with thermolabile resin Cristal Bond 590™ in glass slides) were polished by hand, using wet lapping films (1000 - 0.3  $\mu\text{m}$ ), successively until the core and the micro-increments could be observed clearly. Thin, transverse sections through the nucleus of each otolith were obtained and examined with transmitted light at 400 - 1000x magnification. Images were captured using a digital still camera and measurements taken on a computer screen using the OPTIMAS image-analysis system (Version 6.1: OPTIMAS 1996). In order to determine otolith growth rates during larval periods, the width ( $\mu\text{m}$ ) of each successive otolith increment was measured as the distance between two consecutive opaque zones. Otoliths displayed a prominent growth increment surrounding the primordium; this latter was used as the starting point in counting increments. Daily increments were counted twice by the same reader (counts differing no greater than 5% were averaged, those differing more than 5% were counted a third time; if differing more than 5% of the previous counts the otolith was rejected). In *Stegastes partitus*, otolith increments are deposited on a daily basis (Robertson *et al.* 1993, Wellington and Victor 1989). The age of each specimen was determined considering an increment correction of three days to the total number counted, on the assumption that the first increment was not formed until the first feeding (i.e. approximately three days after fertilization) (Campana and Jones 1992). This corrected increment count was subtracted from the capture date to determine the hatch date or back-calculated birth

dates. Presumed settlement marks were identified by a sharper contrast than preceding marks (where the pattern in increment widths changes markedly and the postsettlement widths are consistently narrower than those laid down before settlement (Wellington and Victor 1989). Increments were counted from the primordium (core) to the settlement mark, and a correction of three increments was added for estimating the number of days before settlement mark (or planktonic larval duration). Settlement dates were backcalculated by subtracting the number of post-settlement increments from the date of capture.

Individual fish sizes (standard length) at settlement by reef area were backcalculated using the biological intercept procedure (Campana and Jones 1992), given by  $L_a = L_c + (O_a - O_c) (L_c - L_0) (O_c - O_0)^{-1}$ , where  $L_a$  is the estimated fish length at age  $a$ ,  $L_c$  is fish length (standard length) at capture,  $O_c$  is otolith radius at capture,  $L_0$  and  $O_0$  are the size of the fish and otolith at the biological intercept, respectively. The biological intercepts of  $L_0$  and  $O_0$  were fixed at 2.2 mm fish length and 0.10 mm otolith radius, respectively.

### Otolith Shape (Fourier) Analysis

The method of elliptic Fourier shape analysis (Kuhl and Giardina 1982) fits an arbitrary closed curve to an ordered set of data points in a two-dimensional plane, with any desired degree of precision, and generates a set of shape-representative variables to be used in statistical comparisons. Using this analysis any outline is reduced to its  $x$ - and  $y$ - projection, and expressed by Fourier expansions as an infinite sum of successive waves of cosines with an amplitude and angle. The amplitude of the wave is the elliptic Fourier shape descriptor, also named harmonic (Kuhl and Giardina 1982, González-Salas and Lenfant 2007). The contribution of each harmonic, with both  $x$ - and  $y$ - variations, is an ellipse. The harmonics for the  $x$  and  $y$ -coordinates are computed by using the incremental changes in the  $x$  and  $y$  direction.

In this study, the otolith (shape) contour of *S. partitus* was used to calculate the elliptic Fourier descriptors using the Shape 1.2 software (Iwata and Ukai 2002); this software provides a normalization process of the Elliptic Fourier Descriptors (EFDs) (Kuhl and Giardina 1982). The number of harmonics required can be estimated from the average Fourier Power spectrum (FP) which provides a measure of the amount of shape information (Renaud *et al.* 1996). The amplitudes of a harmonic are calculated for  $A^2 + B^2 + C^2 + D^2$ . For the  $n^{\text{th}}$  harmonic, the Fourier Power ( $FP_n$ ) is given by the expression:  $FP_n = (A_n^2 + B_n^2 + C_n^2 + D_n^2) / 2$ , where  $A_n$ ,  $B_n$ ,  $C_n$  and  $D_n$  are the Fourier coefficients of the  $n^{\text{th}}$  harmonic. Then, the cumulated power percentage ( $FP_c$ ), defined by  $FP_c = \sum_1^n FP_n$ , is calculated (Pothin *et al.* 2006). The number of harmonics that reach more than 99% of the total variation from  $FP$  is the total of harmonics required to further analysis (Pothin *et al.* 2006). In Chinchorro Bank, 15 harmonics were

required for describing the complex morphology of the sagittae otolith of *S. partitus*. The first harmonic represents the initial point or mean radius of the shape, thus it is not relevant to the analysis (Renaud *et al.* 1996); consequently, the coefficients corresponding to this harmonic were eliminated from the analysis.

### Statistical Analysis

A one-way ANOVA was performed to investigate whether the age, the planktonic larval duration (PLD), the larval otolith growth rates and the backcalculated size (standard length) of *S. partitus* at settlement differed among reef areas or among cays. Where applicable, a *post-hoc* Tukey's HSD multiple comparison test was used to determine the nature of significant differences (Zar 1996). Previously, data were examined for normality and homogeneity of variances, and subsequently  $\text{Log}_e$  transformed if these criteria were not satisfied (Zar 1996).

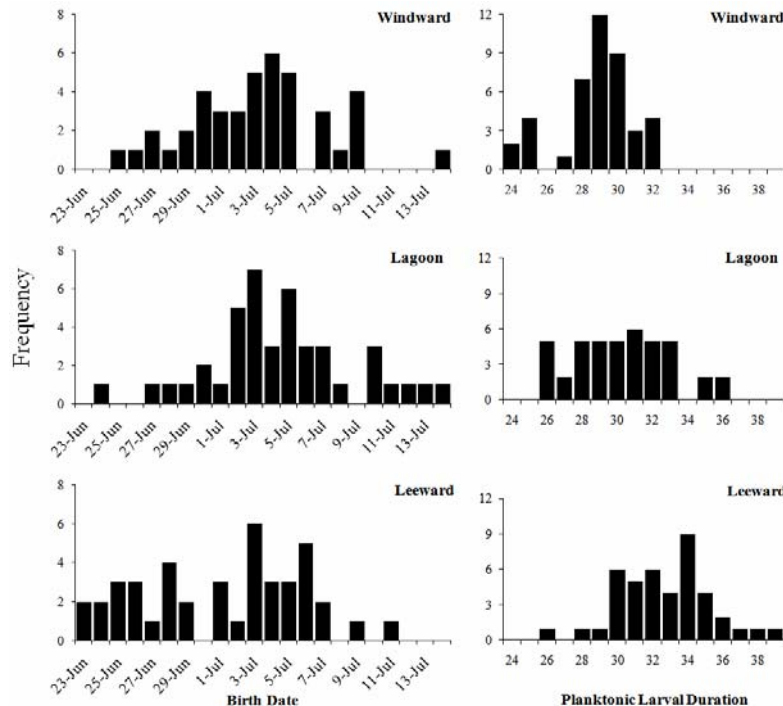
Otolith data shape descriptors (amplitudes) were also used to determine differences among reef areas or among cays. All comparisons were conducted using a permutational multivariate analysis of variance (PERMANOVA; Anderson 2005) which allows testing the simultaneous response of one or more variables to one or more factors in the ANOVA experimental design. PERMANOVA was based on the Bray-Curtis dissimilarity measure (4999 random permutations and 95% confidence). When PERMANOVA was significant at 95% confidence, the levels of each factor were investigated through a *posteriori*

pair-wise comparisons using 4,999 random permutations to obtain *P*-values.

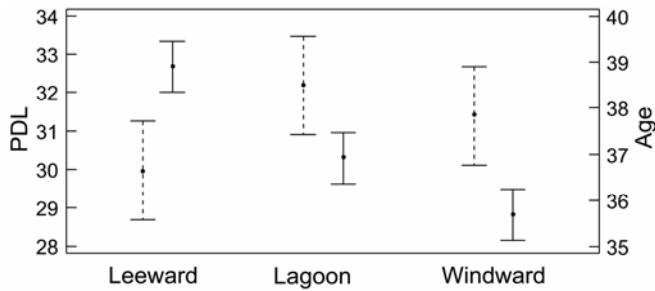
Linear discriminant function analysis (Blackith and Reyment 1971) was also used for supporting the PERMANOVA in determining differences among reef areas. We used a data array of the harmonic coefficients; each of the fourteen harmonics considered is defined by four coefficients (14 harmonics x 4 coefficients). Therefore, each otolith was described by 56 variables. We used Mahalanobis' generalized distance ( $D^2$ ) (Mahalanobis 1936) to characterize the differences in the otolith shape among reef areas.

### Early Life History Traits

Based on backcalculated birth dates, newly *S. partitus* settlers hatched simultaneously from late June to mid July, peaking between July 3<sup>rd</sup> and 5<sup>th</sup> in all three reef areas (Figure 2). Statistical analyses revealed that fish were not significantly different in age among reef areas (ANOVA,  $F_{2,123} = 2.94$ ,  $p = 0.0567$ ). Planktonic larval durations (PLDs) ranged from 24 to 32 days at Windward (mean = 28.8 d), 26 to 36 days at Lagoon (mean = 30.3 d), and 26 to 39 days at Leeward (mean = 32.7 d) (Figures 2 and 3), and differed significantly from each other (ANOVA,  $F_{2,123} = 24.15$ ,  $p < 0.0000$ ). Tukey's HSD *post-hoc* test showed significant differences in PLDs for all pair comparisons (Figure 3). Fish at Windward had significantly shorter PLDs than fish at Lagoon and Leeward, while fish at Lagoon had significantly shorter PLDs than fish at Leeward.



**Figure 2.** *Stegastes partitus*. Frequency distributions of (a) planktonic larval durations and (b) birth dates of newly settled fish collected at Windward ( $n = 42$ ), Lagoon ( $n = 42$ ) and Leeward ( $n = 42$ ).



**Figure 3.** *Stegastes partitus*. Mean and 95% Tukey's HSD intervals for age (dashed line) and planktonic larval duration (PLD) (solid line) at Windward, Lagoon and Leeward. Means whose intervals do not overlap are significantly different.

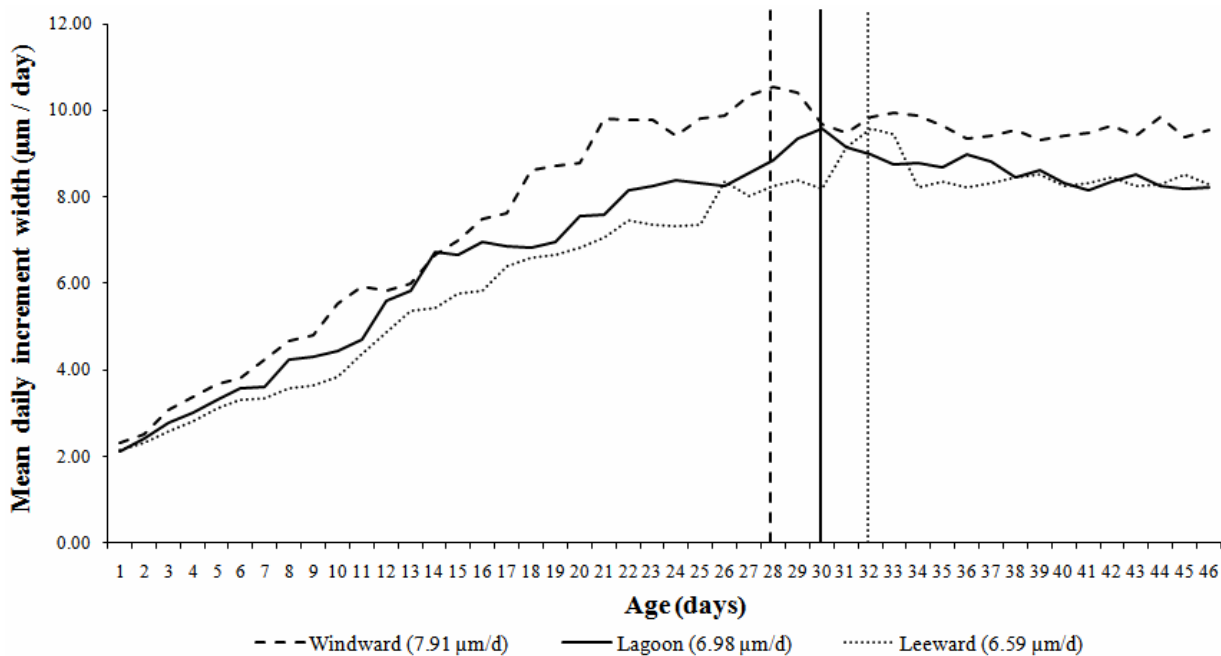
Estimated larval otolith growth rates ranged between 1.32 and 12.23  $\mu\text{m}/\text{day}$ , with growth being generally faster at Windward (mean = 7.91  $\mu\text{m}/\text{day}$ ), intermediate at Lagoon (mean = 6.98  $\mu\text{m}/\text{day}$ ) and slower at Leeward (mean = 6.59  $\mu\text{m}/\text{day}$ ) (Figure 4). However, larval otolith growth trajectories were not significantly different among reef areas (ANOVA,  $F_{2,111} = 2.66$ ,  $p = 0.0743$ ). The relationship of standard length (SL) and otolith length (OL) of newly settlers was well described by a simple linear regression suggesting a proportionality between otolith growth and fish somatic growth in all three reef areas:

Windward ( $r^2 = 0.8357$ ,  $p < 0.000$ ,  $n = 42$ ), Lagoon ( $r^2 = 0.8891$ ,  $p < 0.000$ ,  $n = 42$ ) and Leeward ( $r^2 = 0.8426$ ,  $p < 0.000$ ,  $n = 42$ ) (Figure 5). Using the biological intercept method, size (standard length) at settlement was backcalculated in all three reef areas: Windward ( $r^2 = 0.8432$ ,  $p < 0.000$ ,  $n = 42$ ), Lagoon ( $r^2 = 0.9064$ ,  $p < 0.000$ ,  $n = 42$ ) and Leeward ( $r^2 = 0.9485$ ,  $p < 0.000$ ,  $n = 42$ ) (Figure 6). There were differences in size at settlement among reef areas (ANOVA,  $F_{2,123} = 5.87$ ,  $p = 0.0037$ ). Fish were settling at smaller sizes at Windward (mean SL = 1.05 cm), intermediate sizes at Lagoon (mean SL = 1.11 cm) and larger sizes at Leeward (mean SL = 1.21 cm) (Figure 7).

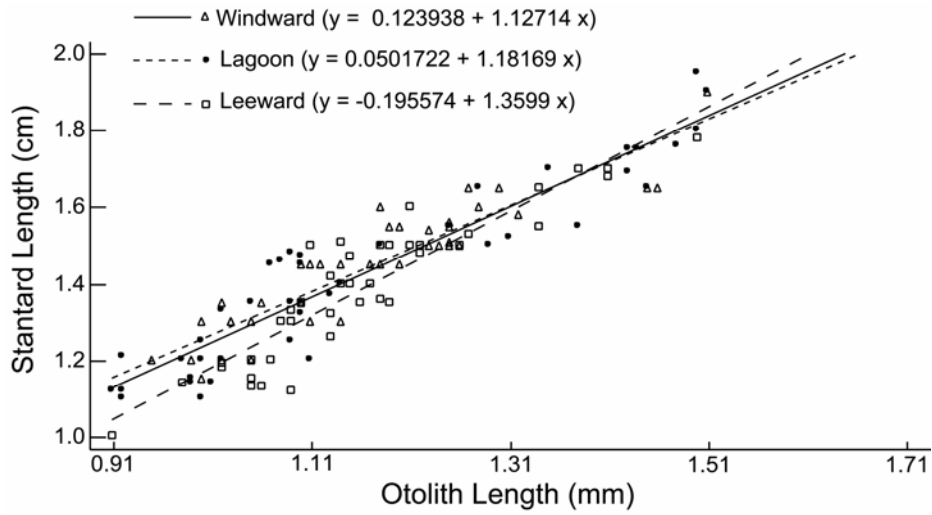
None of the statistical analyses on age, PDLs, larval otolith growth rates and size at settlement were found to be significant different in the "along the reef gradient (South-North)".

**Statistical Fourier Shape Analysis**

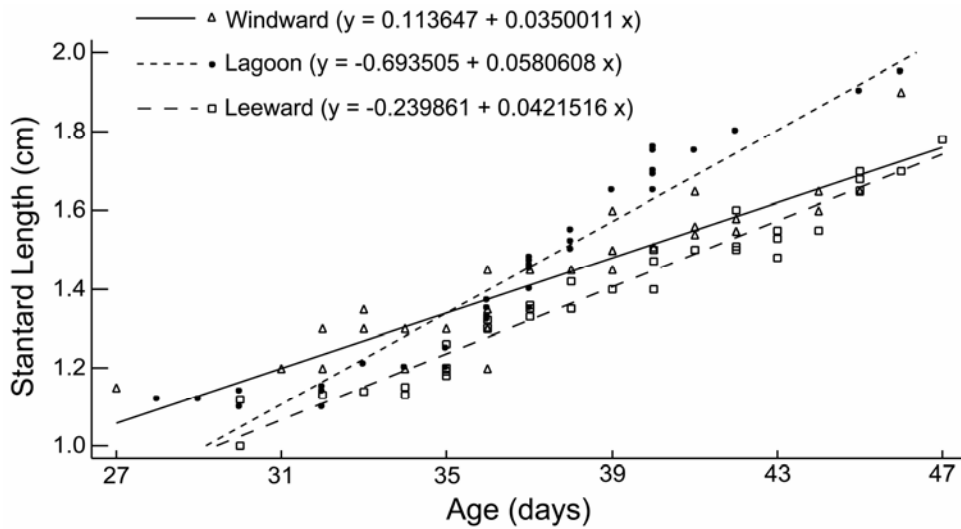
There were significant differences among reef areas (PERMANOVA,  $F_{2,123} = 15.459$ ,  $p = 0.0002$ ) (Table 1). Pairwise comparisons showed that reef areas (Windward, Lagoon and Leeward) were significantly different from each other (Table 1). However, there was no evidence of significant difference among cays (Cayo Norte, Cayo Centro, Cayo Lobos) (PERMANOVA,  $F_{2,123} = 1.771$ ,  $p = 0.1294$ ) (Table 1).



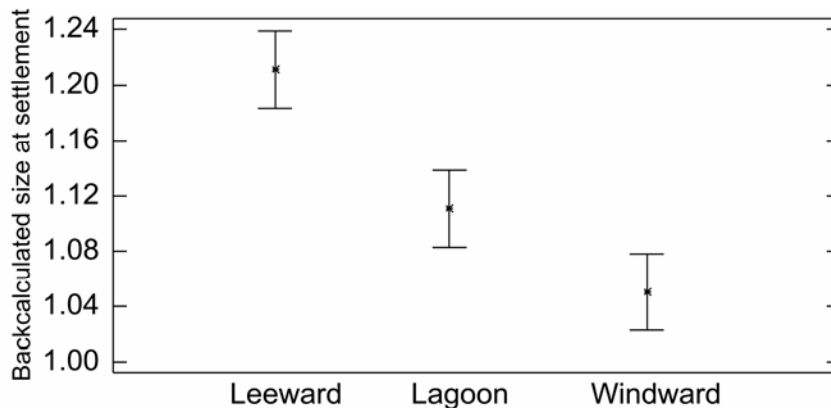
**Figure 4.** *Stegastes partitus*. Mean daily increment widths from cross sections of sagitta from 15 newly settled fish per reef area (Windward, Lagoon and Leeward) plotted to the capture date. Mean otolith growth rate ( $\mu\text{m}/\text{day}$ ) for the 15 individuals used from each reef area are given. Vertical straight lines represent the mean settlement day for each reef area.



**Figure 5.** *Stegastes partitus*. Simple linear regression of otolith length (OL) and standard length (SL) for newly settled bicolor damselfish at Windward ( $r^2 = 0.8357$ ,  $p < 0.000$ ,  $n = 42$ ), Lagoon ( $r^2 = 0.8891$ ,  $p < 0.000$ ,  $n = 42$ ) and Leeward ( $r^2 = 0.8426$ ,  $p < 0.000$ ,  $n = 42$ ).



**Figure 6.** *Stegastes partitus*. Simple linear regression of standard length (SL; cm) on age (days) for newly settled bicolor damselfish captured at Windward ( $r^2 = 0.8432$ ,  $p < 0.000$ ,  $n = 42$ ), Lagoon ( $r^2 = 0.9064$ ,  $p < 0.000$ ,  $n = 42$ ) and Leeward ( $r^2 = 0.9485$ ,  $p < 0.000$ ,  $n = 42$ ).



**Figure 7.** *Stegastes partitus*. Mean and 95% Tukey's HSD intervals for backcalculated size (standard length; cm) at settlement at Windward (mean = 1.05 cm), Lagoon (mean = 1.11 cm) and Leeward (mean = 1.21 cm). Means whose intervals do not overlap are significantly different.

**Table 1.** PERMANOVA and associated pairwise *a posteriori* comparisons using Fourier descriptors (amplitudes) as variables, and 4999 random permutations with a 95% confidence. Two grouping sources were analyzed: 1) Across the reef gradient (East-West) with 3 levels (reef areas): Windward, Lagoon, and Leeward, and 2) Along the reef gradient (South-North) with 3 levels (cays): Cayo Norte, Cayo Centro, and Cayo Lobos. Significant *p* values are shown in bold. *F*: F-test; *t*: t-test statistic.

Grouping source	Factor	<i>F</i> statistic and degrees of freedom	Significance	Pairwise comparisons	
Across the reef gradient	Reef areas	$F_{2, 123} = 15.4599$	<b>0.0002</b>	Windward vs. Lagoon	$t = 2.846; p = \mathbf{0.002}$
				Windward vs. Leeward	$t = 5.058; p < \mathbf{0.000}$
				Lagoon vs. Leeward	$t = 3.073; p = \mathbf{0.002}$
Along the reef gradient	Cays	$F_{2, 123} = 1.7711$	0.1294	Cayo Norte vs. Cayo Centro	$t = 0.511; p = 0.831$
				Cayo Norte vs. Cayo Lobos	$t = 1.636; p = 0.061$
				Cayo Centro vs. Cayo Lobos	$t = 1.540; p = 0.087$

The linear discriminant analysis showed differences among reef areas (Figure 8). The first two canonical discriminant functions accounted for more than 80% of the total variation among groups. The classification success of the discriminant analysis (Table 2) indicated a strong separation among reef areas, with the *F* test associated to Wilks' lambda being highly significant ( $\lambda = 0.1809$ ,  $F_{120, 128} = 1.4414$ ,  $p = 0.0211$ ). In the classification matrix, each case is placed in the group where its classification function value is largest. The Windward, Lagoon and Leeward areas (37, 36, and 36 individuals respectively) were correctly classified. In total, 87% of individuals were correctly classified. Mahalanobis squared distance test ( $D^2$ ) showed that the less distant centroids were between the Lagoon and the Windward ( $D^2 = 4.7$ ), while the more distant centroids were observed between the Windward and the Leeward ( $D^2 = 8.1$ ) (Figure 8).

## DISCUSSION

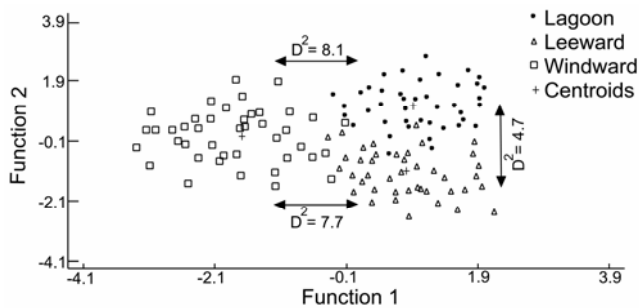
### Planktonic Larval Duration

While otolith growth trajectories revealed no clear evidence for changes in the reduction of otolith growth in the late-larval stages (Fig. 4), which often indicates a delay of metamorphosis (Cowen 1991, Wellington and Victor 1989), no difference in otolith growth rate among reef areas was evident. This suggests that *Stegastes partitus* larvae occupied similar water masses when hatching. Despite similar larval otolith growth trajectories, PLDs showed a significant degree of variation among reef areas (Windward =  $28.8 \pm 2.1$  days, Lagoon =  $30.3 \pm 2.8$  days, and Leeward =  $32.7 \pm 2.8$  days). Fish with significantly shorter larval durations (at Windward) showed faster otolith growth rates and settled at relatively smaller sizes than those larvae with longer larval durations (at Lagoon

**Table 2.** Linear discriminant analysis using the Fourier's harmonics as variables in shape analysis. Classification matrix for the reef areas (Windward, Lagoon, and Leeward).

Reef area	N	Windward	Lagoon	Leeward	% Correct classification
Windward	42	37	3	2	88
Lagoon	42	2	36	4	86
Leeward	42	1	5	36	86
Total	126	40	44	42	87

and Leeward) (Figures 2, 3, and 7). Typically, faster growing larvae are thought to be smaller at settlement because they spend a shorter period in the plankton (Searcy and Sponaugle 2000). Therefore, this trend of *S. partitus* in Chinchorro Bank (shorter sizes at settlement) and the significant differences in age at settlement for Windward, compared to the Lagoon and Leeward, suggest that food and habitat availability, rather than growth, determined the timing at settlement. Similar findings (Denit and Sponaugle 2004, Searcy and Sponaugle 2000) support the idea that the PLD is related to larval growth since faster-growing larvae often settle earlier and at shorter sizes. Denit and Sponaugle (2004) found that larval otolith growth trajectories were generally similar for larvae of gray snapper (*Lutjanus griseus*) from different sites and years (2000 and 2001); however, the mean PLD was one day longer for fish from North Carolina than those from southern sites (South Florida) in both years. They suggested that patterns of larval and juvenile growth, coupled with recruitment dynamics across the latitudinal gradient, are consistent with the northward Gulf Stream transport of larvae from southern spawning sites.



**Figure 8.** *Stegastes partitus*. Canonical discriminant analysis based on the Fourier coefficients describing an otolith. The correct classification percentage of Windward, Lagoon and Leeward, was 88 %, 86 % and 86 %, respectively. The Mahalanobis distances ( $D^2$ ) between centroids are indicated.

Oceanographic features also explain differences in PLDs at different reef areas. For example, if *S. partitus* were transported northwest by the Caribbean current, a small time lag may have been associated with finding a suitable settlement habitat. There is a slightly longer western PLD difference (two days) between *S. partitus* collected at each reef area, and the average current speed in the Lagoon of Chinchorro Bank (about 0.045 m/s in summer; (Ezer *et al.* 2005, Navarrete 2006); thus, the larvae would be transported by the current through 7.8 km during those two days. Considering that the distance between the reef sample sites was about 6 to 7 km from each other, we suggest this small time difference in mean

PLDs is influenced by the current regimes and availability to find a suitable settlement habitat. Thus, the variable nature of PLD in *Stegastes partitus* is probably a response to a range of food and habitat availability. A fast growth may be coupled with a strategy of remaining in high food areas promptly (Leis 1991). In Chinchorro, as the larvae are transported by currents throughout the reef they may have fewer options to settle following optimum environmental cues; however, the Windward may represent the best settlement reef area due its well developed and defined reef structures (Jordan and Martin 1987). In *Stegastes partitus*, fish in better condition at settlement have higher chances of survival after settlement (Booth and Hixon 1999). Vigliola and Meekan (2002) found that fish that survived size-selective mortality one month after settlement were individuals showing faster growing during planktonic life, suggesting that fast growth may not only provide a survival advantage at settlement but may also have the potential to influence post-settlement survivorship in reef fishes.

#### Otolith Shape Analysis

In Chinchorro Bank, otolith shape of *S. partitus* did not show a linear trend “along the reef gradient (South-North)”; however, “across the reef gradient (East-West)” there were differences (Table 1) demonstrating the consistency in otolith shape among locations within each reef area. While the immediate environmental characteristics where *S. partitus* were collected (Windward, Lagoon and Leeward) are not known in detail, the characteristics may vary due to the location in relation to energy wave exposure and depth. This suggests that the influence of the environment on otolith shape is relatively uniform among reef areas but not among cays. The apparent uniformity may be facilitated by relatively homogeneous postsettlement processes within each reef area. In general, it is assumed that fish that encounter the same kind of environmental conditions produce otoliths having a similar pattern in growth and, consequently, in shape. Campana and Casselman (1993) suggested that environmental effects are generally more influential on otolith shape as these changes in response to differences in growth rate. This could be the case for *S. partitus* in Chinchorro Bank; individuals from similar reef areas may be affected by similar local environmental conditions which in turns influence otolith shape. Using the Fourier analysis, Gagliano and McCormick (2004) analyzed the influence of feeding history on otolith shape from a variety of experimental feeding treatments. They found that differences in otolith shape are influenced by recent feeding history just before, during, and after recruitment. Our data indicate that the environmental conditions of settlement areas of *S. partitus* are not homogeneous throughout the Chinchorro Bank, and these conditions may have a profound effect on aspects of the juvenile and adult ecology of *Stegastes partitus*.



## CONCLUSIONS

Our findings suggest that differences in the settlement patterns of *Stegastes partitus* at Windward, Lagoon, and Leeward from the Chinchorro Bank are consistent with a passively northwest transport of larvae promoted by the Caribbean current. On the other hand, longer PLDs for *S. partitus* settling at Leeward are not due to differences in larval growth rates but more likely to a lack of access to suitable settlement habitat by the time the larvae is passing throughout the reef system. The overall results are consistent with the fact that larvae settle, no matter the size they have, as soon as they reach the successive suitable settlement reef habitat; otherwise, the larvae will continue growing and simply dying if they fail to encounter a reef. Relatively uniform local environmental conditions among reef areas influencing growth, such as temperature and food availability, may be the basis for the observed differences in otolith shape. While other studies have emphasized the utility of the otolith shape analysis in differentiating populations, stocks, and species, the present study suggests that otolith shape can be used to discriminate much finer scale events, such as differential settlement on a reef system. Further studies, combining age and growth with studies related with otolith microchemistry, genetic markers (microsatellites), and larval transport models are needed to gain a better understanding on the settlement dynamics and population connectivity of *Stegastes partitus*.

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