

Flexibility in size and age at settlement of coral reef fish: spatial and temporal variations in Wallis Islands (South Central Pacific)

Matthieu Juncker¹, Laurent Wantiez^{1,a} and Dominique Ponton²

¹ LERVEM, Université de la Nouvelle-Calédonie, BP R4, 98851 Nouméa Cedex, New Caledonia

² IRD, UR128, BP A5, 98848 Nouméa Cedex, New Caledonia

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Abstract – Competent larvae of 4 tropical reef fish species, i.e. two pelagic spawners (*Parupeneus barberinus* and *Acanthurus triostegus*) and two benthic spawners (*Abudefduf sexfasciatus* and *Dascyllus aruanus*) were collected over two years in Wallis Islands, in order to compare 1) their size and age at settlement, 2) the variability of these parameters and 3) their spatial and temporal variations. The larvae were collected in three sites approximately 10 km apart in September 2002, December 2002, March 2003 and June 2003. The otoliths were examined to obtain early life history information: pelagic larval duration and timing of settlement. Size at settlement varied from 3 mm for *A. sexfasciatus*, *D. aruanus* and *A. triostegus* to 10 mm for *P. barberinus*. For the benthic spawners, settlement occurred after 17 and 19 days within a narrow age interval (7 to 9 days) and mainly in the middle of the interval. For the pelagic spawners, settlement occurred later (after 35 and 42 days), within a larger age interval (13 days). These estimates are lower than those from other locations in the Pacific but their range is larger. Size at settlement differed significantly between sampling sites only for *D. aruanus* and between surveys only for *A. sexfasciatus*. Age at settlement differed significantly between sampling sites only for *A. sexfasciatus* and between surveys only for *D. aruanus*. For the pelagic spawners the variability of size and age within site and survey was up to ten times greater than for the benthic spawners. This flexibility would be an advantage for larvae of the pelagic spawners that have to travel greater distances to settle.

Key words: Tropical fish larvae / Settlement / Size distribution / Pelagic larval duration / otoliths

Résumé – **Flexibilité de la taille et de l'âge à la colonisation des poissons coralliens : variations spatiales et temporelles à Wallis (sud Pacifique Central).** Les larves compétentes de quatre espèces de poissons coralliens, deux espèces à ponte pélagique (*Parupeneus barberinus* et *Acanthurus triostegus*) et deux autres à ponte benthique (*Abudefduf sexfasciatus* et *Dascyllus aruanus*), ont été collectées sur deux années à Wallis afin de comparer 1) leur taille et leur âge à la colonisation, 2) la variabilité de ces estimations et 3) leur évolution spatio-temporelle. Les larves ont été collectées sur trois sites séparés d'environ 10 km et durant quatre périodes d'échantillonnage, en septembre et décembre 2002, puis en mars et juin 2003. Les variations de la taille moyenne à la colonisation sont respectivement de 3 mm pour *A. sexfasciatus*, *D. aruanus* et *A. triostegus* et 10 mm pour *P. barberinus*. Pour les pondeurs benthiques, la colonisation est intervenue après 17 et 19 jours en moyenne – durée de vie larvaire – et principalement centrée dans un intervalle étroit (7 à 9 jours). Pour les pondeurs pélagiques, la colonisation intervient plus tardivement (après 35 et 42 jours en moyenne), dans un large intervalle (13 jours) et avec une plus grande variabilité. Ces estimations sont inférieures à celles d'autres zones du Pacifique mais présentent de plus grandes variabilités. La taille à la colonisation varie significativement entre les sites échantillonnés pour *D. aruanus* uniquement, et entre les échantillonnages pour *A. sexfasciatus*. Tandis que l'âge à la colonisation varie significativement entre les sites uniquement pour *A. sexfasciatus*, et entre les échantillonnages pour *D. aruanus*. Pour les poissons à ponte pélagique, la variabilité de la taille et de l'âge à la colonisation, au sein d'un site et d'un échantillonnage, a été jusqu'à dix fois plus importante que celle des poissons pondeurs benthiques. Cette flexibilité serait un avantage pour les larves des pondeurs pélagiques qui doivent franchir de plus grandes distances avant de pouvoir s'installer.

1 Introduction

Settlement, i.e. when larvae leave the pelagic environment to settle onto the reef is one of the major transition phases

in coral fish life history (Searcy and Sponaugle 2001). The number of larvae that colonize the reef and their survival influence the dynamics of juvenile (Cowen 1985; Doherty and Fowler 1994) and adult populations (Cushing 1975; Caley et al. 1996). During this transition phase, larval phenotype may be predictive of its survival in its new habitat (McCormick

^a Corresponding author: wantiez@univ-nc.nc

1998a; Hoey and McCormick 2004). Size and age of larvae at settlement are thus parameters that can play an important role on the recruitment variability and the subsequent dynamics of coral reef fish populations (McCormick 1994; Leis and McCormick 2002).

Size at settlement varies under the influence of environmental factors, such as temperature, food availability and oceanographic processes (Benoit et al. 2000; Rissik and Suthers 2000; Bergenius et al. 2005), and intrinsic components, such as maternal predispositions, egg size, endocrinology, metabolism and nutrition processes (McCormick 1998b, 1999a; McCormick and Nechaev 2002). Age at settlement, expressed as the pelagic larval duration (PLD), is the sum of the duration of the pre-competent and competent periods of the larvae, i.e. the moment they are able to settle on a reef (Victor 1986a; Jenkins and May 1994). For a given species, increased PLD is largely due to an extended competent period and characterized by reduced growth rates at the end of the larval stage (Victor 1986b; Cowen 1991; McCormick 1999b; Zapata and Herrón 2002). An important protraction of the competent period, which increases predation risk and thus decreases post-settlement success, has been observed for only few species (Leis and McCormick 2002). Generally, differences in PLD have been found to vary, depending on species, between 2 and more than 15 days among areas separated by ten kilometers to thousand kilometers (Victor 1986a; Thresher et al. 1989; Thorrold and Milicich 1990; Wellington and Victor 1992; McCormick 1994; Philibotte 2002; Bay et al. 2006) and between less than 1 day and more than 15 days between seasons and years (McCormick 1994; Wilson and Meekan 2002; Sponaugle et al. 2006).

Spatial and temporal variations in size and age of larvae at settlement have been rarely studied altogether for a given species. Variability in size and age of larvae at settlement may also increase with increasing duration of PLD as larvae are exposed during a greater period of time to variable oceanographic processes (Cowen 1991). As larvae from pelagic spawners tend to be small at hatching, they usually require a longer time to reach competency than larvae from benthic spawners that are better provisioned (Leis and Miller 1976; Leis 1991). It can thus be predicted that variability of size and age at settlement should be greater for larvae of pelagic spawners than benthic spawners.

In this context, the aim of the present study was 1) to compare the size and age at settlement of the larvae of two pelagic spawners and two benthic spawners, 2) to confirm that variability in size and age at settlement are greater for larvae of pelagic spawners than those of benthic spawners and 3) to test the hypothesis that temporal variations in size and age at settlement are greater than spatial variations. In order to increase the probability that all the studied larvae were of the same origin, this study was undertaken on larvae settlement in the lagoon of Wallis Islands, Central Pacific. These islands are isolated as the Tonga Archipelago is 130 km to the south, Futuna and Alofi Islands are 240 km to the south-west, and Savaii Island of Occidental Samoa is 350 km to the east.

2 Material and methods

2.1 Studied species

The benthic spawners, *Abudefduf sexfasciatus* (Lacepède, 1801) (maximum adult size 19 cm; Randall 2005) and *Dacyllus aruanus* (Linné, 1758) (maximum adult size 7.8 cm; Randall 2005), both Pomacentridae and the pelagic spawners, *Parupeneus barberinus* (Lacepède, 1801) (maximum adult size 53 cm; Randall 2005), Mullidae and *Acanthurus triostegus* (Linné, 1758) (maximum adult size 27cm; Randall 2005), Acanthuridae, were selected for this study. These four species were selected because they are common as adults in the lagoon of Wallis Islands (Wantiez and Chauvet 2004), their larvae are easily identifiable at settlement and are frequent in the catches (Juncker 2005).

2.2 Sampling strategy and study area

Larvae were collected using crest nets similar to those used by Dufour et al. (1996). Each crest net consisted of a 1.5 × 2 m steel frame secured on the barrier reef on which a 4 m long 2 mm mesh size conical net was attached. The net passively filtered the water passing over the reef crest. A 2 mm mesh size funnel kept the larvae in a 0.8 m removable cylindrical codend equipped with 1 mm mesh size filtration windows.

Three nets were set on the northern, eastern and southern sides of the barrier reef of Wallis Islands (Fig. 1). General water circulation and barrier reef configuration prevent sampling on the west side. Sampling was carried out in September and December 2002, and in March and June 2003. Each survey consisted in 5 successive nights centered on the first quarter-moon and 5 successive nights centered on the last quarter-moon, as Wantiez and Juncker (unpublished data) observed that settlement in Wallis Islands is maximal in terms of numbers of individuals and taxa caught per night during these lunar phases. These periods would gather the optimal environmental conditions to colonize the lagoon of Wallis Islands. Each night, the codend was set on the net at 18:00 and removed at 07:00 the following day. Upon retrieval, fish were preserved in 95% ethanol.

2.3 Fish sub-sampling and age estimation

Young fish were identified to the species level. The standard lengths (SL) of the four species were measured to the nearest mm. Taking into account the small number of individuals of *A. sexfasciatus*, *P. barberinus* and *A. triostegus* captured during the surveys (Table 1), all individuals of these species were selected without subsampling. As *D. aruanus* were more abundant (Table 1), up to 10 individuals were randomly selected in proportion to their abundance in 0.5 mm size classes of SL for each group of five nights.

Then, the sagittae of each selected individual were extracted, cleaned of adhering tissues and kept dry in labeled vials. One of the pair was later processed following Wilson and McCormick (1997). Briefly, each otolith was mounted over the edge of a glass slide using thermoplastic glue and then oriented

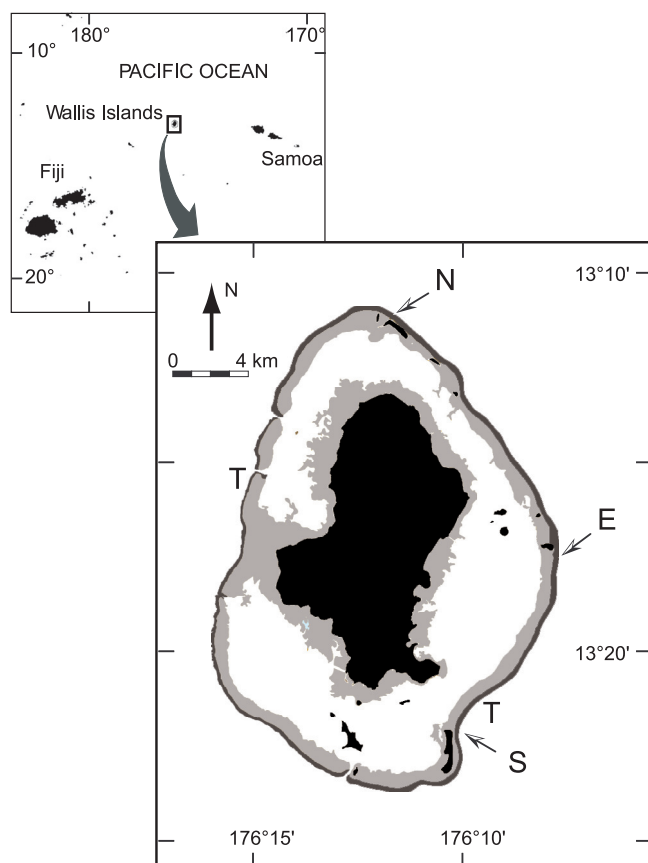


Fig. 1. Sampling sites on the northern (N), eastern (E) and southern (S) sides of the barrier reef of Wallis Islands. Light grey areas correspond to reefs and white areas to open waters. With T: locations of the temperature recorders.

internal face up, rostrum outside the glass and the core inside the edge of the glass. The protruding portion was ground off using 9, 3 and 1 μm lapping film. The otolith was then mounted on a new glass slide so that it sat upright on its cut edge, in the center of the slide. The upright portion was then ground on the same series of lapping films to produce a thin transverse section that contained the core. The number of increments on each preparation was counted by the first author along the dorso-ventral axis from the core to the edge (two counts) and from the periphery to the core (two counts) at $\times 400$ or $\times 1000$ depending on microstructure clarity. When the increments were difficult to count, i.e. miscount was more than two between the four counts, the sample was rejected. In the other cases, the mean of these four counts, rounded to the nearest integer, was subsequently used as an estimate of the pelagic larval duration (Wellington and Victor 1989). The discarded otoliths (19%) were mainly due to badly preserved otoliths (77%) because of an excessive delay between the larvae death and its transfer into alcohol (i.e. larvae that were caught in the net at the beginning of the night). The processing of some otoliths was not successful (6%) and some otoliths were difficult to read (miscounts; 17%). Daily microstructure deposition has been validated for numerous reef fish species and is now supposed to be observable in nearly all fish larvae (McCormick 1999b). Consequently, we assumed that one increment corresponded

to one day and that the first increment closest to the core of the otolith was formed at the time of hatching (Campana and Neilson 1985; Wellington and Victor 1989).

2.4 Data analysis

In order to assess differences in the size and PLD distributions between species, data were first standardized and then compared using a Kolmogorov-Smirnov test. The relationships between size and PLD were estimated using Pearson correlation coefficients.

The settlement was discontinuous in space and time for species that settled in low numbers (Table 1). As a consequence, for some species, only a small number of individuals could figure in a given treatment (at a given site over a given survey) and sometimes for one of the species no fish was analyzed during a treatment. Therefore, the data set was unbalanced and we analyzed the spatial and the temporal factors independently, precluding analyses of potential interactions. Selecting a subset of data to obtain a balanced data set and perform a two-way analysis was not possible (Table 1). Consequently, the spatial variations of size and PLD were studied using 1-way ANOVA for unequal sample sizes (Sokal and Rohlf 1995). The temporal variations were studied using the same technique. The homogeneity of variance was checked before each test, using Bartlett test. The variances were not significantly different (all Bartlett tests, $p > 0.050$) when the data were Log transformed. Tukey-Kramer post hoc tests were carried out when ANOVAs on Log transformed data were significant.

3 Results

In all, 100 *A. sexfasciatus*, 335 *D. aruanus*, 66 *P. barberinus* and 36 *A. triostegus* were caught during the four surveys (Table 1). Larval settlement was discontinuous in space and time. The smallest (SL = 6.5 mm) and the youngest (PLD = 14 days) larvae were *D. aruanus*, whereas the largest larvae was a *P. barberinus* (SL = 43 mm) and the oldest an *A. triostegus* (PLD = 50 days). Settlement was higher in December 2002 for the four species and lower in September 2002 and June 2003, particularly for the pelagic spawners. Size at settlement and PLD were studied for 85 *A. sexfasciatus*, 122 *D. aruanus*, 45 *P. barberinus* and 33 *A. triostegus* (Table 1).

3.1 Size at settlement

Size (standard length) at settlement differed significantly between species (1-way ANOVA, $F_{3,281} = 11449.5$, $p < 0.001$, all Tukey-Kramer tests, $p < 0.001$). Larvae of *A. sexfasciatus* (mean SL \pm SE = 10.1 ± 0.1 mm) and *D. aruanus* (7.1 ± 0.1 mm) colonized the reef at a smaller size than larvae of *P. barberinus* (37.4 ± 0.3 mm) and *A. triostegus* (21.2 ± 0.2 mm) (Fig. 2).

All the larvae presented a narrow size range (3 mm) at settlement, except *P. barberinus* which settled at variable sizes (range = 10 mm) (Fig. 2). However, the range observed for

Table 1. Number of *A. sexfasciatus*, *D. aruanus*, *P. barberinus*, and *A. triostegus* caught (Nc), measured (Nm) and aged (Na) for each survey, period and site.

Survey	Period	Moon	Site	<i>A. sexfasciatus</i>			<i>D. aruanus</i>			<i>P. barberinus</i>			<i>A. triostegus</i>			
				Nc	Nm	Na	Nc	Nm	Na	Nc	Nm	Na	Nc	Nm	Na	
1	12–16 Sep. 2002	FQ	N	1	1	1	7	7	5	5	5	5	9	9	9	
			E	6	6	3	2	1	-	-	-	-	1	1	1	
			S	2	2	1	17	17	12	-	-	-	1	1	1	
	29 Sep.- 3 Oct. 2002	LQ	N	-	-	-	3	3	-	-	-	-	-	-	-	
			E	-	-	-	-	-	-	-	-	-	-	-	-	
			S	-	-	-	16	16	-	-	-	-	-	-	-	
2	11–16 Dec. 2002	FQ	N	4	4	4	4	4	2	2	1	1	-	-	-	
			E	8	8	3	1	1	1	2	2	2	2	2	2	
			S	10	10	10	43	41	3	22	22	19	6	5	5	
	26–30 Dec. 2002	LQ	N	1	1	1	5	4	3	1	1	1	1	1	1	
			E	8	8	8	3	3	3	1	-	-	2	2	2	
			S	41	41	38	12	12	12	4	4	3	7	6	6	
	3	10–14 Mar. 2003	FQ	N	5	5	5	14	14	10	4	4	4	1	1	-
				E	5	5	4	86	81	11	4	4	4	-	-	-
				S	1	1	1	10	10	8	7	6	6	2	2	2
24–29 Mar. 2003		LQ	N	-	-	-	-	-	-	-	-	-	-	-	-	
			E	-	-	-	2	2	2	-	-	-	-	-	-	
			S	-	-	-	-	-	-	-	-	-	3	3	3	
4	7–12 Jun. 2003	FQ	N	-	-	-	8	8	7	6	6	-	-	-	-	
			E	4	4	3	63	60	13	-	-	-	-	-	-	
			S	-	-	-	8	8	8	2	2	-	-	-	-	
	21–25 Jun. 2003	LQ	N	-	-	-	-	-	-	-	-	-	-	-	-	
			E	2	2	1	12	12	11	-	-	-	-	-	-	
			S	2	2	2	19	19	11	6	6	-	1	1	1	
Total				100	100	85	335	323	122	66	63	45	36	34	33	

FQ: first quarter-moon; LQ: last quarter-moon; N: north; E: east; S: south (see Fig. 1 for exact position of the sites). Because of bad conservation of few samples, some fish caught could not be measured or aged.

this last species corresponds to 27% of the mean size, which is within the range of the other species studied (from 14% of the mean size for *A. triostegus* to 43% for *D. aruanus*).

The size distributions at settlement differed significantly in their shape between *A. sexfasciatus* and *P. barberinus*, and between *P. barberinus* and *A. triostegus* (Kolmogorov-Smirnov tests, $p < 0.05$) (Fig. 2). However, the relative variations (expressed as the coefficient of variation, CV) in the size at settlement were small for the four species ($CV = 4.1$ to 6.0%). For all species, except *A. triostegus*, size at settlement increased significantly with PLD (all Pearson correlations, $p < 0.050$) (Fig. 3).

3.2 Pelagic larval duration (PLD)

Pelagic larval duration also differed significantly between species (1-way ANOVA, $F_{3,281} = 1377.27$, $p < 0.001$, all Tukey-Kramer tests, $p < 0.001$). *A. sexfasciatus* (mean $PLD \pm SE = 18.9 \pm 0.2$ days) and *D. aruanus* (18.1 ± 0.2 d) were the youngest at settlement with a range of 7 and 9 days respectively. Not surprisingly pelagic larval duration was longer for *P. barberinus* (34.9 ± 0.5 d) and *A. triostegus* (42.4 ± 0.5 d), and more variable as the range reached 13 days for both species (Fig. 2). However, the variations of PLD were proportionally higher for *D. aruanus* (51% of the mean PLD) than for the other species (from 31% of the mean PLD for *A. triostegus* to 37% for *P. barberinus*).

PLD distributions differed significantly between *A. sexfasciatus* and *A. triostegus*, and between *D. aruanus* and the two pelagic spawners (Kolmogorov-Smirnov tests, $p < 0.05$). The two benthic spawners have unimodal distributions when those of the pelagic spawners were clearly multimodal (Fig. 2). Relative variations in the age at settlement were higher than in the size at settlement for all the species ($CV = 6.6$ to 9.4%), with a small difference between species.

3.3 Spatial and temporal variations

3.3.1 Size at settlement

Size at settlement differed significantly between sampling sites only for *D. aruanus* (Fig. 4, 1-way ANOVA, $F_{2,119} = 5.17$, $p = 0.007$). Larvae of this species colonized the North site at a significantly smaller size (mean $SL \pm SE$, 6.9 ± 0.4 mm) than the East (7.2 ± 0.2 mm) (Tukey-Kramer test, $p = 0.010$) or the South sites (7.1 ± 0.2 mm) (Tukey-Kramer test, $p = 0.015$).

Size at settlement differed significantly between surveys only for *A. sexfasciatus* (Fig. 5, 1-way ANOVA, $F_{3,81} = 5.30$, $p = 0.002$). Individuals of this species captured in September 2002 were significantly smaller (9.2 ± 0.8 mm) than those captured during the rest of the year (from 10.1 ± 0.2 mm in December 2002 to 10.4 ± 0.3 mm in March 2003) (Tukey-Kramer test, $p < 0.001$).

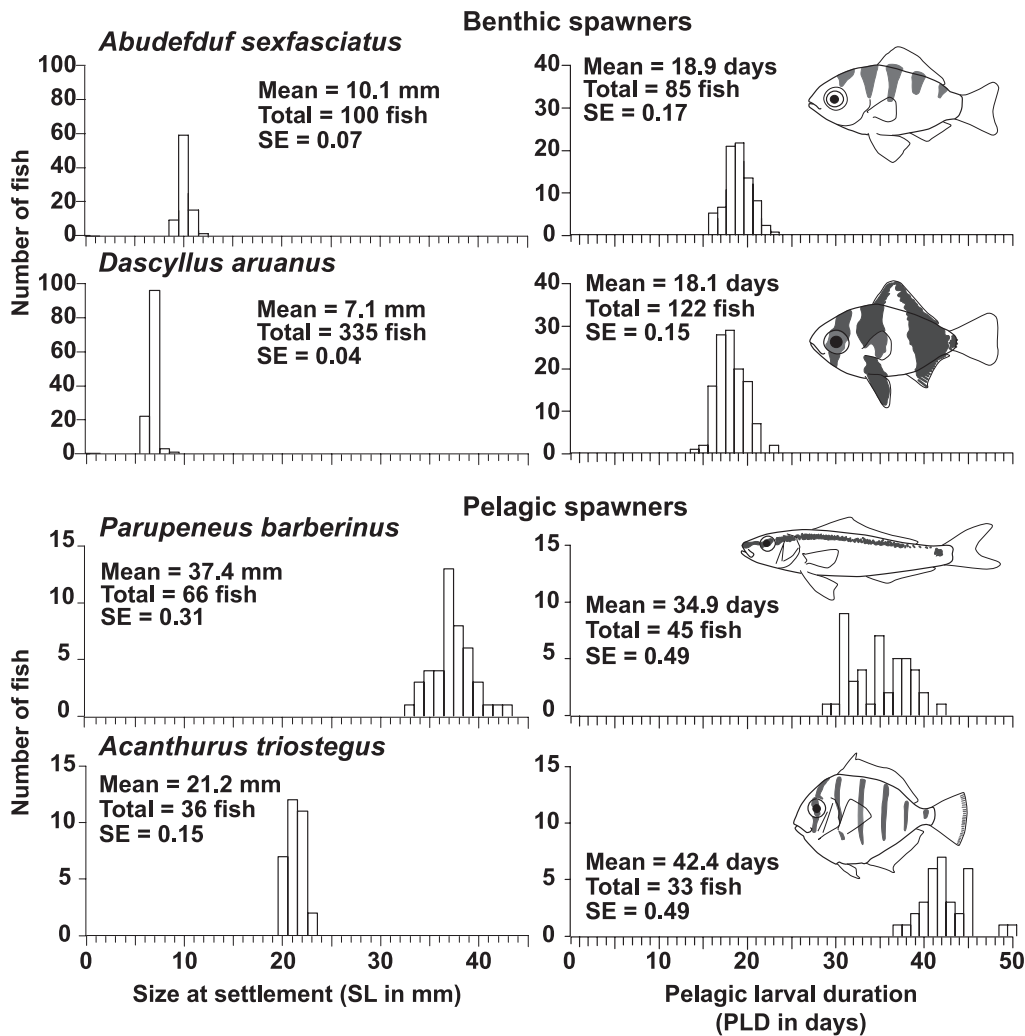


Fig. 2. Larval size (standard length, SL in mm) at settlement and estimated pelagic larval duration (PLD in days) of reef fish: *Abudefduf sexfasciatus*, *Dascyllus aruanus*, *Parupeneus barberinus* and *Acanthurus triostegus*. SE = standard error.

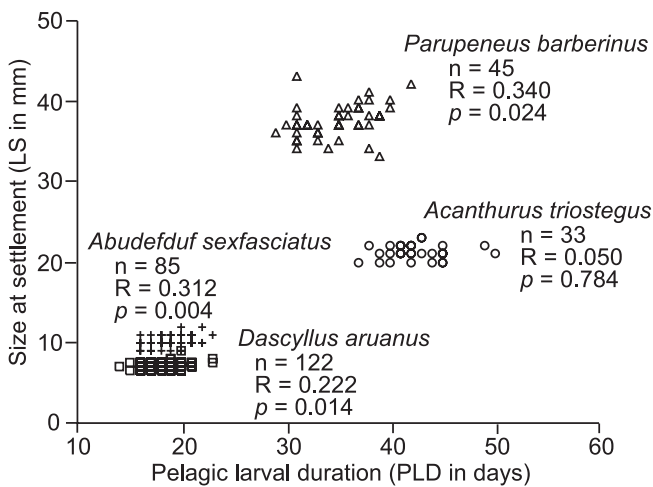


Fig. 3. Relationships between larval size at settlement (SL, mm) and estimated pelagic larval duration (PLD, days) of *Abudefduf sexfasciatus*, *Dascyllus aruanus*, *Parupeneus barberinus* and *Acanthurus triostegus*; n = number of individuals, R = Pearson coefficient of correlation, p = associated probability.

No significant difference was found for *P. barberinus* and *A. triostegus* because of the high variability of size at settlement.

3.3.2 Pelagic larval duration

Pelagic larval duration differed significantly between sampling sites only for *A. sexfasciatus* (Fig. 4, 1-way ANOVA, $F_{2,82} = 4.06$, $p = 0.021$). The individuals captured at the North site were significantly younger (mean PLD \pm SE = 17.9 ± 0.4 days) than those captured at the East site (19.4 ± 0.4 d) (Tukey-Kramer test, $p = 0.016$).

Temporal variations of pelagic larval duration were not significant except for *D. aruanus* (1-way ANOVA, $F_{3,118} = 4.55$, $p = 0.005$). For this species, individuals caught in March 2003 were significantly younger (mean PLD \pm SE = 17.4 ± 0.3 d) than those caught in June 2003 (18.7 ± 0.3 d) (Tukey-Kramer test, $p = 0.003$).

As for size at settlement, no significant difference of pelagic larval duration was found for *P. barberinus* and *A. triostegus* because of the high variability of age at settlement.

Table 2. Mean estimated pelagic larval duration, PLD and range in days of benthic spawners (*D. aruanus*, *A. sexfasciatus*) and pelagic spawners (*P. barberinus*, and *A. triostegus*) for different locations and reef systems; *n*: number of fish.

Mean PLD (range) in days	<i>n</i>	Locations	Reef Systems	Authors
<i>D. aruanus</i>				
23.8 (2)	4	French Polynesia	Archipelago	Lo-Yat (2002)
22.4 (6)	5	Great Barrier Reef	Contiguous reefs	Thresher et al. (1989)
20.0 (5)	12	Palau	Archipelago	Wellington and Victor (1989)
18.1 (9)	122	Wallis	Isolated island	Present study
<i>A. sexfasciatus</i>				
21.4 (5)	8	Great Barrier Reef and Papua New Guinea	Continuous reefs and Archipelago	Thresher et al. (1989)
17.3 (2)	6	Palau	Archipelago	Wellington and Victor (1989)
18.9 (7)	85	Wallis	Isolated island	Present study
<i>P. barberinus</i>				
50.0	1	Great Barrier Reef	Contiguous reefs	Wilson and McCormick (1999)
39.4 (13)	45	Wallis	Isolated island	Present study
<i>A. triostegus</i>				
53.0 (16)	90	French Polynesia	Archipelago	McCormick (1999b)
44.0 (8)	5	French Polynesia	Archipelago	Lo-Yat (2002)
42.4 (13)	33	Wallis	Isolated island	Present study

The range (difference between the maximum and the minimum) is given in parentheses.

4 Discussion

4.1 Pelagic larval duration

The mean PLD of *D. aruanus*, *P. barberinus* and *A. triostegus* caught in Wallis were shorter compared with other locations in Pacific Ocean (Table 2). Competent larvae are less likely to find a suitable habitat in a small isolated island such as Wallis than in an archipelago or contiguous reef. A short PLD reduces dispersion and thus increases the probability for the larvae to return to its original reef (Leis 1991). However, geographic isolation usually confers a long PLD (Victor and Wellington 2000). Consequently, a lower PLD is more probably due to local effects of the environment on larval growth. The range of PLD observed in Wallis were larger than those found in the literature, with the exception of *A. triostegus* (Table 2). The reason might be that most of these studies were based on samples obtained from a single locality (Thresher et al. 1989), over a short period of time (less than one month in Wellington and Victor 1989) or from a small number of individuals (more than 82% of the ranges were estimated with less than 10 individuals). Consequently, the greater range of PLD observed in our study may be the result of an increased variability due to sampling at three different locations over four periods of time.

4.2 Sources of variations in size at settlement and pelagic larval duration

4.2.1 Spatial variations

Size variations at settlement were small between sites, and significant for *D. aruanus* only. Differences in size at settlement have already been observed for the Mullidae *Upeneus tragula* for similar spatial scales (approx. 20 km) (McCormick 1994). For larger spatial scales (>100 km) differences in size at settlement reached 4 mm for the Pomacentridae *Pomacentrus coelestis* but were not significant for another Pomacentridae *Chromis atripectoralis* (Thorrold and Milicich 1990). These discrepancies point out the complexity of these patterns and the need for dedicated studies to identify the sources of these variations.

Age variations at settlement between sites were also small, and significant for *A. sexfasciatus* only. However, PLD range was lower for benthic spawners (7 days) than for pelagic spawners (13 days). These differences may be explained by variations in growth rate during the pelagic stage and/or delayed metamorphosis and/or state of development at hatching. Larvae growth rate, which depends on environmental parameters such as temperature and food supply, is known to influence PLD (Wellington and Victor 1992; Sponaugle et al. 2006). Variations in PLD observed by Thresher et al. (1989)

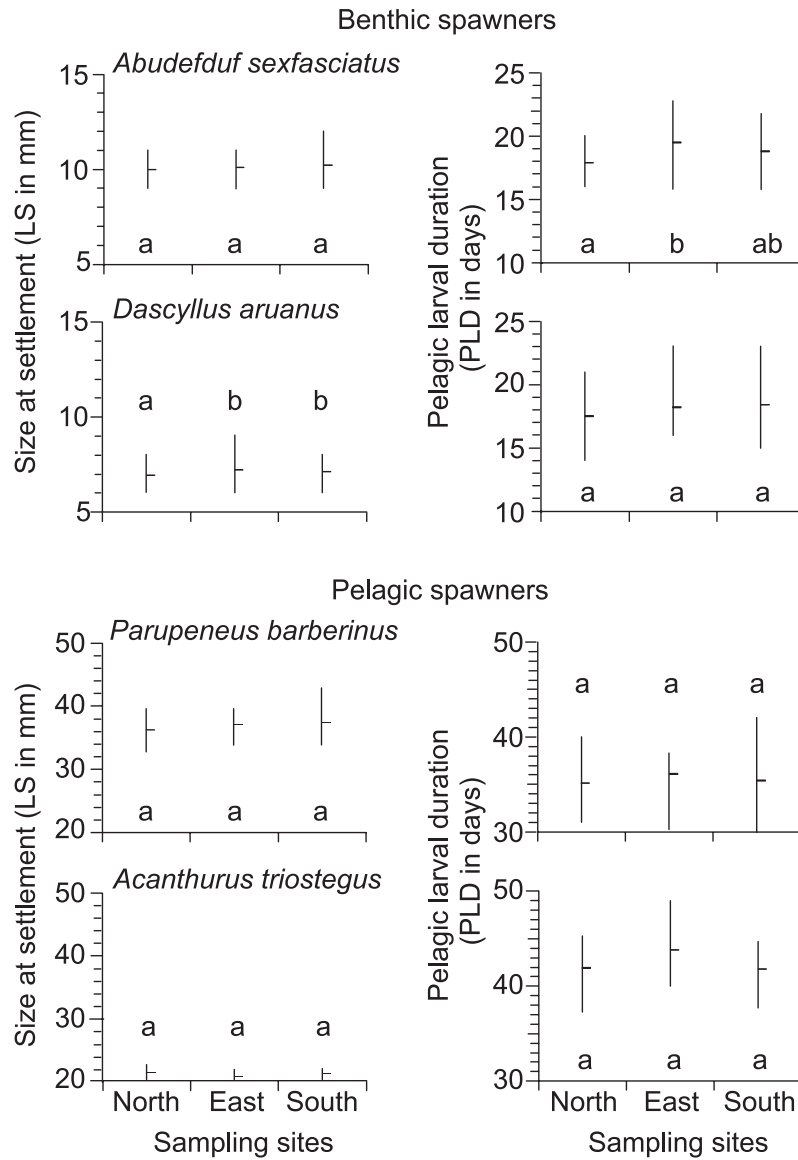


Fig. 4. Mean larval size at settlement (SL, mm) and estimated pelagic larval duration (PLD, days) of *Abudefduf sexfasciatus*, *Dascyllus aruanus*, *Parupeneus barberinus* and *Acanthurus triostegus* caught on the northern, eastern and southern sides of the barrier reef of Wallis Islands. The vertical bar corresponds to the maximum and minimum. Identical letters indicate no significant difference between sampling sites (all tests performed using 1-way ANOVAs followed by Tukey-Kramer tests in the case of significant results).

and Thorrold and Milicich (1990) for *Pomacentrus coelestis* caught on sites hundreds of kilometers apart may come from the different environmental conditions experienced by the larvae. On the opposite, a delayed metamorphosis may increase PLD by several days in similar oceanic environments (McCormick 1999b), on coastal islands in Panama (Victor 1986b,c) and in the Caribbean (Sponaugle and Cowen 1994, 1997). The assumption of small variations of the environmental parameters between sites during each survey in Wallis can explain the small spatial variations during this study. The range of PLD were likely due to a delayed metamorphosis, or may be influenced by a different timing of spawning across the island, or influenced by the delivery of the larval pool around the island through the action of complex local oceanographic factors.

4.2.2 Temporal variations

PLD of *D. aruanus* varied significantly between surveys, larvae being collected at a younger age in December 2002 and March 2003 than in September 2002 and June 2003. *Abudefduf sexfasciatus* followed the same trend and all species had a shorter PLD in March than in June and September, albeit variations of PLD were small and not significant. Such temporal variations in PLD have been observed for the Pomacentridae *Stegastes partitus* on San Blas reefs where colonizing larvae were on average younger during the wet season than during the dry season (Wilson and Meekan 2002), for the Gobiidae *Lentipes concolor* and for the Labridae *Thalassoma bifasciatum* with shorter PLD during months with warmer sea surface temperatures (Radtke et al. 2001; Sponaugle et al. 2006).

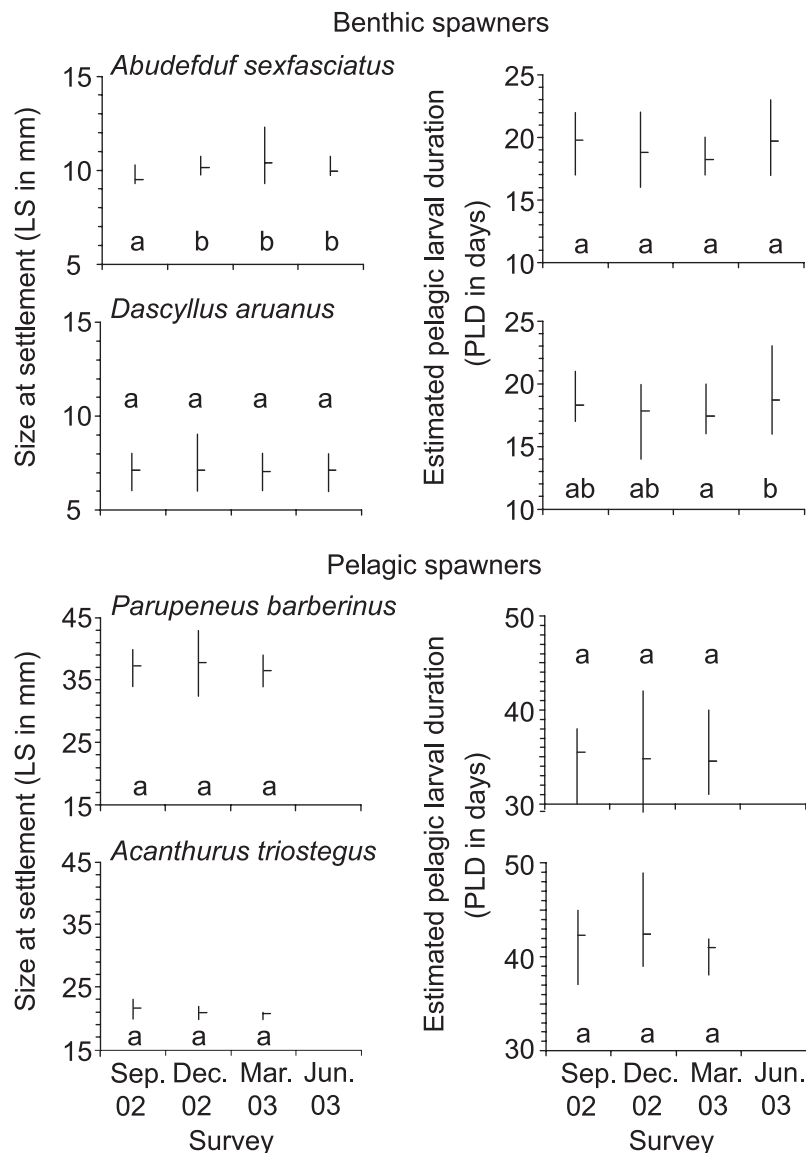


Fig. 5. Mean larval size at settlement (SL, mm) and mean estimated pelagic larval duration (PLD, days) of *Abudefduf sexfasciatus*, *Dascyllus aruanus*, *Parupeneus barberinus* and *Acanthurus triostegus* caught in September 2002, December 2002, March 2003 and June 2003. The vertical bar corresponds to the maximum and minimum. Identical letters indicate no significant difference between surveys (all tests performed using 1-way ANOVAs for unequal sample size followed by Tukey-Kramer tests in the case of significant results).

Many studies have stressed the influence of water temperature on larval growth and development rate for both temperate and tropical fishes (Blaxter 1992; Osse and Boogaart 1995; Benoit et al. 2000; Shima and Findlay 2002; Hutchinson and Hawkins 2004; Sponaugle and Pinkard 2004). Higher water temperatures speed up development and lead to shorter PLD (Leis and McCormick 2002; Sponaugle et al. 2006).

Temperature recorders set on the outer slope of Wallis Islands indicated that the average summer water temperature ranged from 29.4 °C in December 2002 to 30.6 °C in March 2003, whereas the average winter water temperature ranged from 28.1 °C in September 2002 to 29.2 °C in June 2003. As relatively small differences in water temperature can greatly influence size and age at settlement of tropical reef fishes (McCormick and Molony 1995; Green and Fisher 2004), the

small seasonal differences in water temperature around Wallis Islands may explain the seasonal variations in PLD observed for *D. aruanus*. However, temperature is one, but not the only important factor that may influence size and age at settlement. Other factors such as phytoplankton productivity, salinity, solar radiation, rainfall and wind may significantly influence the life traits of larvae until settlement (McCormick 1994; McCormick and Molony 1995; Sponaugle and Pinkard 2004; Bergenius et al. 2005; Sponaugle and Grorud-Colvert 2006).

4.3 Size at settlement and pelagic larval duration vs. reproductive strategy of adults

Size at settlement differed between the four studied species. The difference in size between the smaller and the

larger larvae at settlement were at least 3 mm. Such a size range at settlement has already been observed for the Labridae *Thalassoma bifasciatum* (Victor 1986b) and *Semicossyphus pulcher* (Cowen 1991) and for the Acanthuridae *A. triostegus* (McCormick 1999b). The size range at settlement for *P. barberinus* was wider (10 mm) because of the larger size of the competent larvae. However, this range was proportionally within the range (26.7% of the mean size) of the other species studied (14.2% for *A. triostegus* to 42.8% for *D. aruanus*). Moreover, the variability in size at settlement (CV) does not really differ between species (from 4.1% to 9.4%). Important transitions during ontogeny generally occur over a narrow range of sizes (Zwiefel and Lasker 1976; Fuiman and Webb 1988). The competent period can be considered as the beginning of an important step in reef fish ontogeny. Reduction in growth rates characterizing this period would explain the low variations of size (Radtke et al. 2001).

Age at settlement, expressed as PLD, varied also between and within species. The mean PLD was only 17.6 and 18.9 days for benthic spawners and reached 34.9 and 42.4 days for pelagic spawners. Pomacentridae are known to have the shortest PLD among coral reef fish families (Wellington and Victor 1989; Lo-Yat 2002). For most Pomacentridae, PLD varies from 10 to 35 days (Brothers et al. 1983; Thresher et al. 1989; Wellington and Victor 1989; Thorrold and Milicich 1990; Kerrigan 1996; Wellington and Robertson 2001) when that of pelagic spawners, such as Mullidae or Acanthuridae, have PLD ranging from 30 to 60 days (Doherty et al. 1995; McCormick 1994 and 1999b; Lo-Yat 2002).

Low relative variations in size at settlement and high relative variations in PLD are a general pattern observed for most coral reef fish species (Victor 1986b; Wellington and Victor 1989; McCormick 1994; McCormick 1999b; Wilson and Meekan 2002). These studies suggest that fish larvae may have the ability to delay the time of settlement but do not settle at a larger size (Tupper and Boutilier 1995; Shima and Findlay 2002; Hutchinson and Hawkins 2004). Some marine reef fish species seem to have the ability to slow down their growth at the pelagic larval stages before, or at the beginning of, the competent period (Victor 1986b; Thorrold and Milicich 1990; Cowen 1991; McCormick 1999b; Zapata and Herrón 2002). Such decrease in daily growth rate may explain why no significant correlation was observed between size at settlement and PLD for *A. triostegus* in this study. Another hypothesis is that slow growers took longer to reach the size at which they were competent to settle. If the size of competency is fixed than the relationship between size and age will be weaker. Wellington and Victor (1989) noticed an identical lack of correlation for eight out of ten species of Pomacentridae they examined, concluding that size of larvae at settlement is not directly related to the time spent in the plankton.

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