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Nocturnal and lunar input patterns of pre-settlement coral reef fish in Wallis lagoon (Central South Pacific): Implications for sampling strategies

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Received 27 March 2007; Accepted 11 June 2007

Abstract – Diel, nocturnal and lunar input patterns of pre-settlement coral reef fish were described in Wallis, a typical high-island in the south-central Pacific, with a mid-size lagoon and a 2-m spring tidal range. Crest nets were set on the barrier reef to collect incoming pre-settlement fish. A diel input pattern was observed, with 82 to 99% of the larvae arriving at night. Nocturnal input of pre-settlement fish occurred throughout the night, at different times depending on the lunar phases. In contrast to studies done in other locations, the input was not higher during the first part of the night. The input level was related to moonlight and water level, but independent of tide direction. High input levels were recorded during all lunar phases, except the full moon. This lunar pattern differed from maximum settlement observed during the new moon in other locations. Consequently, a sampling strategy for studying temporal patterns of coral reef fish settlement in typical west Pacific high-islands should include new and quarter of the moon phases and should be extended to the entire night.

Key words: Tropical fish larvae / Recruitment pattern / Pacific island / Sampling design

1 Introduction

Almost all coral reef fish are characterized by massive spawning, a pelagic dispersal phase and a return to the reef (Leis 1991). When the competent larvae find a suitable habitat they metamorphose into demersal juveniles, which corresponds to the settlement phase (Dufour 1992). The role of settlement in structuring coral reef fish assemblages is a complex issue and no consensus has been reached about its importance (Caley et al. 1996; Hixon 1998). In order to clarify the apparent controversial recruitment limitation concept (Doherty 1981; Doherty and Williams 1988; Durville et al. 2002) and the density-dependent post-settlement mortality concept (Caley et al. 1996; Hixon 1998), settlement patterns must be well described.

In the Pacific, most studies of settlement patterns have been conducted in French Polynesia (atolls and high-islands with small lagoons), the Great Barrier Reef and Western Australia (Dufour and Galzin 1993; Dufour et al. 1996; Doherty and Carleton 1997; Kingsford and Finn 1997; McIlwain 1997, 2003; among others). The settlement patterns described in these studies are widely applied to all Pacific coral reef environments and used to design sampling protocols in modern studies of recruitment processes. Most of these patterns

indicate peaks of settlement in the first part of the night during the new moon phase.

To our knowledge, no data have been published on typical high-islands of the West and Central Pacific, with medium to large lagoons and a significant tidal range, such as Wallis. The purpose of the present work was to study 1) the diel variations, 2) the nocturnal variations and 3) the lunar variations of the input of pre-settlement fish in Wallis, in order to verify whether the settlement patterns described in other locations could be applied to environments similar to Wallis.

2 Materials and methods

Wallis (76 km²) is an isolated archipelago located in the south-central Pacific. The island is surrounded by a medium-sized lagoon (200 km²) which is limited by a continuous barrier reef interrupted by 4 passages. The moon is present all night during the full moon phase (FM), until 11:30 pm during the first quarter of the moon phase (FQ), from 2:45 am during the last quarter of the moon phase (LQ), and absent during the new moon phase (NM). The tidal range is 2 m during spring tide. The tide is high at 6 am and 6 pm and low at 12 am and 12 pm during NM and FM. During these lunar phases the water level is too low to pass over the barrier reef from one hour before until one hour after low tide. The tide is high at 12 am and

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12 pm and low at 6 am and 6 pm during FQ and LQ. During these lunar phases the water level is sufficient to assure a continuous flow of oceanic water over the barrier reef during low tide.

The input of pre-settlement larvae over the barrier reef was studied using crest nets. Larvae were fished during their transfer from an oceanic environment to a coral reef and lagoon environment (Dufour 1992). The use of crest nets is appropriate to characterize the end of the pelagic larval phase and entry into the lagoon, just before the settlement. The net was similar to the one used by Juncker et al. (2006).

The sampling site was located on the northern part of the Wallis barrier reef. Two nets were set side-by-side. Diel input of pre-settlement fish was studied by comparing diurnal (from 6 am until 6 pm) and nocturnal catches (from 6 pm until 6 am), over 4 days in March 2001 (2 FQ and 2 LQ) and over 12 days in June 2002 (3 days for each moon phase). Nocturnal input of pre-settlement fish was studied by catches every two hours from nightfall (6 pm) until sunrise (6 am), over 2 nights at NM, FQ, FM and LQ in March-April 2001. Lunar input of pre-settlement fish was studied by nocturnal fishing (from 6 pm until 6 am) during one lunar cycle in March-April 2001 and one in June 2002.

Diel, nocturnal and lunar differences in the input of pre-settlement fish were tested using parametric tests (*t*-paired test and 1-way ANOVA) in the case of homoscedasticity (Bartlett test, $p > 0.05$), and non-parametric tests (Wilcoxon-Mann-Whitney and Kruskal-Wallis) in the case of heteroscedasticity (Bartlett test, $p \leq 0.05$).

3 Results

3.1 Diel variations

The input of pre-settlement fish was significantly higher during the night (mean = 232.8 larvae in 2001 and mean = 186.7 larvae in 2002) than during daytime (mean = 51.8 larvae in 2001 and mean = 0.9 larvae in 2002) (one-sided *t*-paired test; $p < 0.01$ in 2001 and $p < 0.001$ in 2002). 81.8% and 99.5% of the larvae were captured at night in 2001 and 2002 respectively.

3.2 Nocturnal variations

During the FQ, the input patterns of pre-settlement fish were not significantly different between the two nights sampled (*t*-paired test, $p > 0.05$) (Fig. 1). The input of pre-settlement fish occurred between 11 pm and 5 am. The input was higher between 1 and 3 am both nights, and a second maximum was observed at 6 pm on the first sampling night (Fig. 1). The input of pre-settlement fish was significantly lower when the moon was present (mean = 8.7) than after moonset during ebb tide (mean = 181.8) (Mann-Whitney test, $p < 0.05$) (Fig. 1).

During the LQ, the input patterns of pre-settlement fish were not significantly different between the two nights sampled (*t*-paired test, $p > 0.05$) (Fig. 1). The input of pre-settlement fish occurred between 9 and 11 pm, and was very

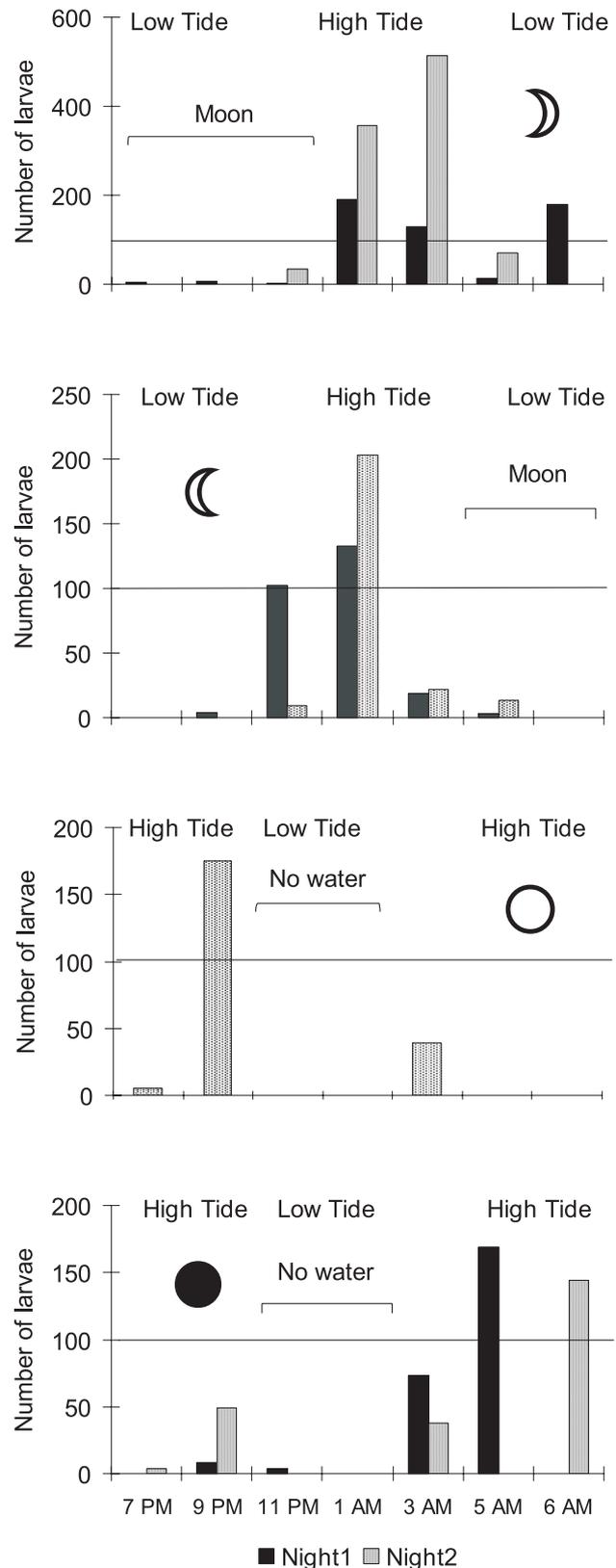


Fig. 1. Nocturnal variations of the input of pre-settlement fish during the FQ (☽), the LQ (☾), the FM (○) and the NM (●). Night1 and Night2 represent the two nights sampled during each of the lunar phase in April 2001. The presence of the moon (Moon) and low water level (No water) over the barrier reef are indicated.

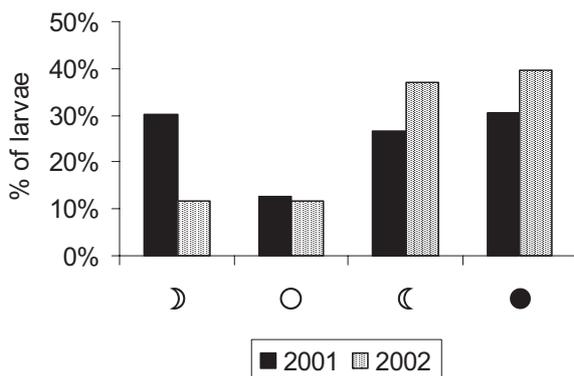


Fig. 2. Percentage of the pre-settlement fish caught during the FQ (☽), the FM (○), the LQ (☾) and the NM (●) during the lunar cycles studied in 2001 and 2002.

low after 3 am (Fig. 1). The input of pre-settlement fish was higher (mean = 49.2 larvae) before moonrise during flowing tide, than when the moon was present (mean = 4.0 larvae). However, the differences were not significant (Mann-Whitney test, $p > 0.05$) because of the high variability of the catches (CV > 140%).

Unfortunately, no replicate was made during the FM (bad weather conditions). Two input pulses of pre-settlement fish were recorded, one between 7 and 9 pm during ebb tide and one between 1 and 3 am during flowing tide (Fig. 1). During the NM, the input patterns were not different between the two nights sampled (Fig. 1) (t -paired test, $p > 0.05$). Two input pulses of pre-settlement fish were observed, a minor one at 9 pm (ebb tide) and a major one between 3 and 6 am (flowing tide) (Fig. 1). During NM and FM the input of pre-settlement fish was interrupted at low tide. The mean number of incoming larvae was significantly lower when the water level was too low (mean = 0.5), than when water flow over the reef was continuous (mean = 46.2) (Mann-Whitney test, $p < 0.05$).

3.3 Lunar variations

The input of pre-settlement fish was significantly different between years (t -paired test, $p < 0.05$), but the daily catches were significantly correlated ($R = 0.50$, $p < 0.01$). Consequently, the input levels were different but their patterns were consistent between years. However, input differences between lunar phases were not significant in 2001 (Kruskal-Wallis test, $p > 0.05$) and significant in 2002 (Kruskal-Wallis test, $p = 0.05$) (Fig. 2). The input of pre-settlement fish was lower during FM both years. They were of similar levels during the other moon phases in 2001, whereas input was higher during the LQ and the NM in 2002.

4 Discussion

4.1 Diel variations

The input of pre-settlement fish was significantly higher during the night, which is consistent with numerous studies

(Victor 1991; Dufour and Galzin 1992, 1993; Kingsford and Finn 1997; McIlwain 1997; Kingsford 2001; among others). This confirmation validates the choice of night fishing to study fish settlement on coral reefs of high-islands in the Pacific. Settlement is a response to a lowering of light intensity (Dufour and Galzin 1993), which was confirmed by the effect of moonlight observed during this study.

4.2 Nocturnal variations

Different nocturnal input patterns of pre-settlement fish were identified in Wallis. These patterns were linked to two environmental factors: tidal range and moonlight. When tidal range was important (NM and FM) settlement was impossible for two hours at low tide because the water level was too low. This characteristic limits settlement during these nights. The second factor affecting the input of pre-settlement fish was moonlight. The input was higher when the moon was absent during FQ and LQ. Dufour and Galzin (1992, 1993) identified moonlight as a significant factor influencing larvae settlement in Moorea (French Polynesia), the input of larvae being 3.5 times higher when the moon was absent, during FQ and LQ. This ratio was even higher in Wallis ranging from 10.5 (LQ) to 21.8 (FQ). However, unlike Dufour and Galzin (1992) we did not observe a higher larval input at dusk. Dufour and Galzin (1993) also indicated that the larval flux was generally higher when moonless periods immediately followed dusk. During our study the input of larvae was higher during the second part of the night (FQ), which could indicate a different pattern.

In the present study, the input of pre-settlement fish was not linked to tidal direction. It was higher during ebb tide in the FQ, during flowing tide in the LQ, and during flowing tide in the NM. Most studies using crest nets were carried out in locations where tidal range was not significant (French Polynesia). On the Great Barrier Reef, Kingsford (2001) reported that the greatest input of pre-settlement fish was on flowing tide at night. Doherty and McIlwain (1996) also indicated that a large proportion of the catch was taken early at night on flowing tide, with the catch in the first hour being higher than during the rest of the sampling. However, they could not attribute the decrease of the catches to an attenuated water flow. Shenker et al. (1993) collected 97% of reef fish on flowing tide at night in the Bahamas, and McIlwain (1997) showed that larval flux started soon after dusk and continued throughout the flowing tide on West Australian coast (Indian ocean). Active pre-settlement fish during their final approach to shallow habitats could explain these results (Doherty and Carleton 1997; McIlwain 1997; Kingsford 2001). Consequently, if a pool of pelagic juveniles does assemble in front of the reef in the evening to settle on the reef, the decline of larval flux during the night may be explained by the depletion of this pool if not replenished (McIlwain 1997). However, McIlwain (1997) did not sample after midnight and was not able to record any late larvae pulses. The pattern was apparently different in Wallis where the input of larvae could be significant all night long, even during ebb tide when there was no moonlight and water level was sufficient to ensure a continuous flow over the reef. Sponaugle and Cowen (1996) reported pulses in the supply of

larvae associated with flowing tide during the LQ but not during the FQ, in Barbados. These authors concluded that larval supply was influenced, not only by tidal amplitude, but also by lunar phase and relative brightness at night, which were also significant factors in our study.

4.3 Lunar variations

Numerous studies report lunar variations of the input of pre-settlement fish. The most common pattern is a high input during NM and a low input during FM (Dufour and Galzin 1992, 1993; Dufour et al. 1996; among others). However, these studies were conducted in locations where the tidal range is low (French Polynesia). Moreover, no sampling was done after midnight, which prevents the recording of possible late-night input pulses, such as those observed in Wallis. The pattern could be different in regions where tidal range is high or with all-night sampling. Different factors can limit the input of pre-settlement fish despite favorable no-light conditions. In Wallis, the water level over the reef crest was too low to ensure an input of pre-settlement fish at low tide during NM. If low larval input is probably a common characteristic to FM everywhere, high larval inputs were observed around the FQ and the LQ in Wallis. To our knowledge, only Sponaule and Cowen (1996) and D'Alessandro et al. (2007) have observed a greater larval abundance in light traps during the second half of the lunar cycle, with a peak during the LQ (Barbados) or the NM and the LQ (Florida Keys), because of the interaction of tidal currents and lunar phase. McIlwain (2003) reported dichotomous patterns in arrival from semi-lunar (near the quarter moons) to stochastic for selected families in Ningaloo reef (Western Australia).

5 Conclusion

The nocturnal and lunar input patterns of pre-settlement fish observed in Wallis are different than those generally described for coral reefs. However, the patterns described in Wallis could be representative of numerous high-islands in the Pacific, with a medium-sized lagoon and a significant tidal range. Consequently, significant processes could be omitted when sampling is only scheduled during the new moon phase (NM) and/or the first part of the night, as is the case in numerous studies. Because a significant number of larvae can settle during the first quarter (FQ) or the last quarter (LQ) of the moon phase, and during the second part of the night, sampling must include these lunar phases and must be extended to cover the entire night.

Acknowledgements. We are grateful to the *Service Territorial de l'Environnement de Wallis et Futuna* for funding and technical support.

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