

Temporal patterns in the post-larval supply of two crustacean taxa in Rangiroa Atoll, French Polynesia

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Abstract The post-larval supply of two crustacean taxa (Brachyura and Stomatopoda) was monitored using one crest net over three lunar months at Rangiroa Atoll, French Polynesia. We captured a total of 37,068 brachyuran and 12,697 stomatopod post-larvae during the study. Post-larval supply was higher during the warm season (February–April) than during the cold season (June–July) for both Brachyura (warm season: 85% of total post-larval supply) and Stomatopoda (warm season: 92%). Moreover, the pulse of the brachyuran post-larval supply occurred predominantly around the last quarter, while the pulse of stomatopods occurred predominantly around the new moon. However, for both taxa, the post-larval supply was lowest around the full moon and the first quarter. Overall, our monitoring highlighted that the post-larval supply of Brachyura and Stomatopoda was modulated by seasons and lunar phases at Rangiroa.

Keywords Brachyura · Stomatopoda · Reef colonization · Lunar cycle · Crest net

Introduction

Most marine species (molluscs, crustaceans, and fish) have a life cycle that includes a dispersive planktonic larval phase (in the open ocean), which usually lasts from a few days to six weeks, followed by a sedentary site-associated juvenile and adult reef phase [1]. A potentially “critical” period in the development of these marine larvae is the migration from continental shelf waters back to shore (i.e., usually more than 80% of the larval population dies during this period) [2, 3]. Thus, one of the first steps in building predictive models of population dynamics that will aid in the future management of marine systems under climatic or human changes is identifying the environmental attributes that influence the patterns of larval supply [4].

In coral reefs, marine larvae at the end of their pelagic phase have to return to a reef habitat to continue their ontogenetic development [5]. It has been shown that fish larval supply in French Polynesia [6, 7] and in the Solomon Islands [8] occurs in the highest densities over the reef crest during the new moon. However, little information is available on the spatio-temporal variations in larval supply of other coral reef taxa [9–11]. Indeed, the majority of studies on the patterns and processes of connectivity of reef-dwelling populations have concentrated on coral reef fish [5]. The present study is one of the first to explore the temporal variation of Stomatopoda larval supply to coral reefs and to enhance previous studies concerning Brachyuran species in tropical areas [12].

Among the different methods that can be utilized to study marine larval supply (e.g., light traps and nets either

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towed or dropped in the water column), crest nets have a number of advantages over other methods [13]: (1) marine larvae are caught just before settlement, which would give a suitable measure of larval supply; (2) the high energy and turbulence of the reef crest minimizes net avoidance by larvae; and (3) since the net is deployed at night, the net is cryptic, and thus it is passive gear for easy larval capture. Crest nets sample late-stage larvae of marine species in the process of, or immediately prior to, settlement in the reef. For this reason, they provide an accurate estimate of larval supply to reef habitats [14, 15].

Specifically, our aims were to assess the arrival of post-larval crustaceans at the reef (with crest net sampling) and to monitor how post-larval supply varied over the lunar phases (new moon, first quarter, full moon vs. last quarter) and seasons (warm vs. cold season). The term “post-larvae” was used in the study, as crustaceans captured with the crest net were ready for settlement in the coral lagoon, but they colonized at different developmental stages (e.g., megalopa, alima, erichtus) [11, 12, 15].

Materials and methods

Crustacean post-larval supply was monitored daily on the north coast of Rangiroa Atoll, French Polynesia (14°57'48S; 147°38'79W) during three lunar months (warm season: 29 February to 28 March 2008 and 29 March to 26 April 2008; cold season: 29 June to 27 July 2008) using a crest net. At Rangiroa Atoll, seawater temperature ranges from 26 to 28°C during the warm season (September–May) and from 23 to 25°C during the cold season (June to August—data from Meteo-France: <http://www.meteo-france.fr>). There is a prevailing wind that changes direction with the season: east/northeast direction during the warm season, and east/southeast direction during the cold season (data from the Service Hydrographique et Oceanographique de la Marine; <http://www.shom.fr>).

The crest net used was similar to the one used by Lo-Yat at Rangiroa [4]. The net (5.0 m long) had a rectangular mouth (2.0 m wide, 1.5 m high), and was made of a 1 mm mesh, which was fine enough to retain most of the incoming crustacean post-larvae before settlement and the subsequent molting process. The mouth of the net was open to the offshore. Four hinged panels (2.0 m long, 1.5 m high) of 0.7 mm mesh enlarged the mouth area of the net to 6 m. Thus, the crest net was divided into two chambers: the mouth where post-larvae entered, and the cod end where the post-larvae were captured. The whole structure was fastened and secured by steel cables that were bolted firmly onto the reef rock to prevent the net from being swept away during periods of strong current. The cod

end was attached to the net at dusk (6 pm) to minimize the accumulation of debris in the net during the day, when few marine post-larvae are usually captured [6, 11, 12], and was cleared of catches at dawn (6 am). Catches were transported into laboratory tanks (60 × 50 × 50 cm) supplied with air pumps.

Once at the laboratory, catches were sorted in a large aquarium (100 × 50 × 10 cm), and crustaceans (alive or dead larvae) were identified and counted. Post-larval identification was undertaken under a dissecting microscope (Wild M3B, Wild Heerbrugg, Heerbrugg, Switzerland) using meristic and morphologic characters of crustaceans [16]. Some post-larvae were kept alive in aquaria for several weeks (fed with nauplii of *Artemia salina*) to confirm their identification (allowing metamorphosis into the juvenile phase). Thus, all brachyuran and stomatopod post-larvae were counted, and six species were identified: two species of Brachyura (*Pachygrapsus planifrons* de Man, 1888; *Calappa calappa* Linnaeus, 1758) and four species of Stomatopoda (*Lysiosquilla maculata* Fabricius, 1793; *Lysiosquilla sulcata* Manning, 1978; *Raoulserenea* sp., *Pseudosquilla* sp.). The other unidentifiable brachyuran and stomatopod post-larvae were placed into another category (Brachyura spp. or Stomatopoda spp.).

To highlight a potential seasonal effect on larval supply, a Kruskal–Wallis test was conducted with month as the variable (29 February–28 March 2008, 29 March–26 April 2008, and 29 June–27 July 2008; days were repeat observations). To highlight a potential lunar effect on larval supply, a Kruskal–Wallis test was conducted with lunar quarters as the variable (new moon quarter: week centered on new moon, first quarter, full moon quarter, and last quarter; days were repeat observations). This last analysis was conducted separately for each month. Lastly, the correlation of catches with tide height was investigated separately for each month using a Spearman test. Tidal data were provided daily by the Service Hydrographique et Oceanographique de la Marine.

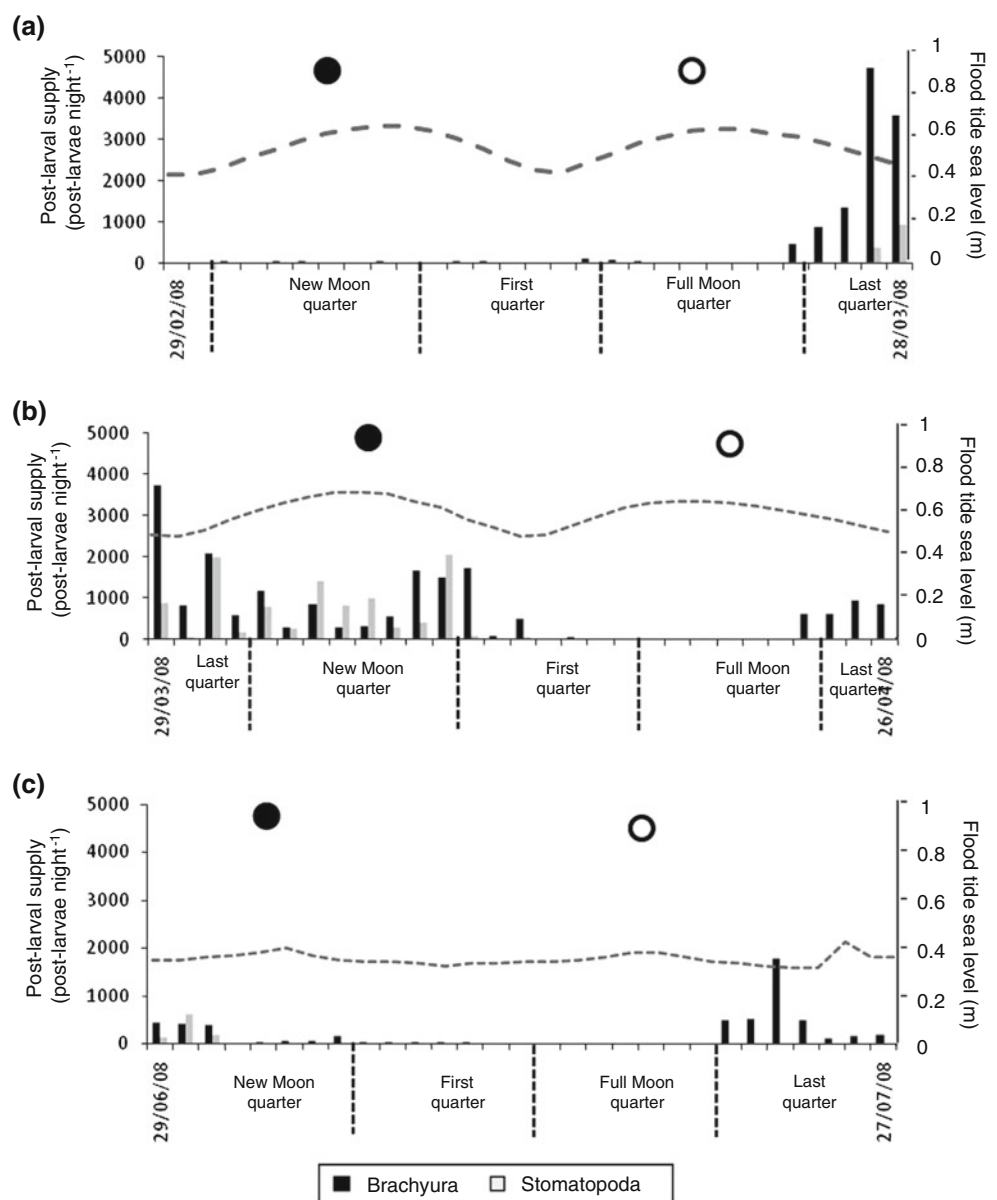
Results

A total of 37,068 brachyuran post-larvae and 12,697 stomatopod post-larvae were collected during the three months of the study (Fig. 1). A significant temporal variation in post-larval supply with lunar month was found (Kruskal–Wallis test: $df = 2$, $F = 2.34$, $P = 0.012$ for Brachyura, $df = 2$, $F = 6.92$, $P = 0.001$ for Stomatopoda). The highest post-larval supply occurred in March/April (54 and 81% of the total post-larval supply for Brachyura and Stomatopoda, respectively) during the warm season. The lowest post-larval supply occurred in June/July (15 and 8% of the

total post-larval supply for Brachyura and Stomatopoda, respectively) during the cold season. No significant relationship was observed between the post-larval supply of Brachyura or Stomatopoda and tidal height for any month (Spearman correlation: for Brachyura: $n = 30$, $r < 0.21$, $P > 0.19$ for each month; for Stomatopoda, $n = 30$, $r < 0.08$, $P > 0.71$ for each month). Lastly, a significant temporal variation in post-larval supply with lunar phase was noted (Kruskal–Wallis test: $df = 3$, $P < 0.05$ for both Brachyura and Stomatopoda). For both Brachyura and Stomatopoda, the post-larval supply was highest in the last quarter in February/March (Fig. 1). In March/April and June/July, the post-larval supply was highest in the last quarter for Brachyura and around the new moon for Stomatopoda (Fig. 1).

At the species level, the same temporal patterns were observed with the lunar month and phase (Fig. 2a, b). Among the post-larvae of Brachyura, *Calappa calappa* arrived mainly during the last quarter of March (27–29 March), while *Pachygrapsus planifrons* post-larvae arrived daily from the last quarter of March (23 March) to a few days after the new moon (12 April). For Stomatopoda, *Lysiosquillina maculata* and *L. sulcata* post-larvae arrived on one night only (both on 30 March, last quarter). For *Raoulserenea* sp., post-larval supply occurred mainly in the last quarter (27 March–02 April), while *Pseudosquilla* sp. post-larvae arrived around the new moon (3–9 April). Lastly, the post-larval supply of these six species was weak in June/July (less than 5% of the total post-larval supply), except for *P. planifrons* (1,612 larvae on 23 July, last

Fig. 1 Temporal variations in the post-larval abundances of Brachyura and Stomatopoda per night during three lunar months: **a** 29 February–28 March, **b** 29 March–26 April, **c** 29 June–27 July 2008. Each month was separated into four lunar quarters: new moon quarter, first quarter, full moon quarter, and last quarter. The dashed line represents the flood tide sea level (m) in Rangiroa. Black and white circles represent the new moon and full moon, respectively



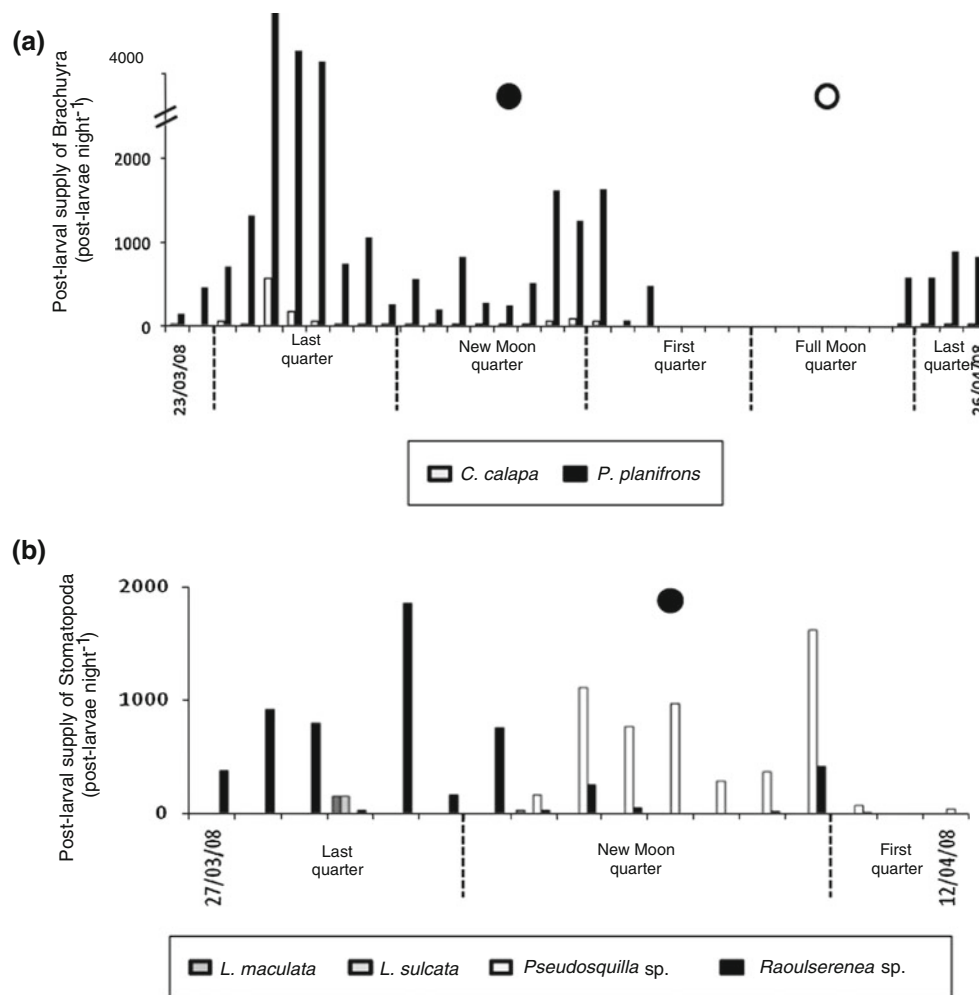


Fig. 2 **a** Temporal variation in post-larval abundance per night for two species of Brachyura from 23 March to 26 April 2008: *Calappa calappa* (3% of total post-larval supply) and *Pachygrapsus planifrons* (69%); **b** temporal variation in post-larval abundance per night for four species of Stomatopoda from 27 March to 12 April 2008: *Lysiosquillina maculata* (2% of total post-larval supply), *L. sulcata*

(1%), *Raoulserenea* sp. (44%) and *Pseudosquilla* sp. (45%). Outside of these periods, the post-larval supply of the six species was weak (less than 5% of the total post-larval supply), except for *P. planifrons* (1,612 post-larvae on 23 July) and *Pseudosquilla* sp. (415 post-larvae on 30 June)

quarter) and *Pseudosquilla* sp. (415 post-larvae on 30 June, around the new moon).

Discussion

The recruitment of marine invertebrates is highly variable, causing temporal and spatial fluctuations in adult populations and community dynamics, but the processes creating this variability are poorly understood, especially for Brachyura and Stomatopoda taxa in coral reefs [11, 12]. Our monitoring highlighted that the post-larval supply of Brachyura and Stomatopoda was modulated by seasons and lunar phases at Rangiroa.

The post-larval supply of Brachyura and Stomatopoda in the present study was higher during the warm season than

the cold season for both Brachyura (February/March 31% of total larval supply, March/April 54%, and June/July 15%) and Stomatopoda (February/March 11%, March/April 81%, and June/July 8%). The same temporal variation was highlighted for coral reef fish post-larvae, with the highest post-larval supply during the warm season [4, 6]. Three main factors might explain these differences in post-larval supply between warm and cold seasons: (1) spawning periodicity, (2) seawater temperature, and (3) prevailing wind [9]. (1) Although there are no data on the seasonal reproduction of brachyurans and stomatopods in French Polynesia, Eggleston [17] showed that differences in spawning periodicity explained the temporal variation of spiny lobster post-larval supply in the central Bahamas. (2) Shanks [3] highlighted that the temporal variation of crab post-larvae with season was correlated with oceanographic

processes that can transport post-larvae to shore, as well as with seawater temperature (lowest post-larval supply in the cold season). At Rangiroa Atoll, seawater temperature was higher during the warm season (27.5°C from 29 February to 28 March 2008 and 27.4°C from 29 March to 26 April 2008) than during the cold season (24.3°C from 29 June to 27 July 2008—data from Meteo-France). (3) Robertson [18] showed that strong prevailing winds have major effects on the temporal variation of post-larval supply by reducing the survivorship of eggs and larvae in ocean, whereas weak winds may enable post-larvae to more actively determine their settlement destination compared with when water currents are stronger. In agreement, the wind at Rangiroa was very strong during the cold season (“Maraamuu”—east/southeast direction, intensity range: 15–25 knots). In contrast, the wind was relatively weak during the warm season (east/northeast direction, intensity range: 5–15 knots—data from Service Hydrographique et Oceanographique de la Marine). Thus, the strong prevailing wind (Maraamuu) during the cold season might have reduced post-larval survival at Rangiroa Atoll [4]. Nevertheless, the crest net was only located on the north coast (lack of spatial replication in our study). For coral reef fish, the spatial variation is characterized by a post-larval distribution that occurred simultaneously at sites separated by 200 m (on the same coast) [7, 19] or by 10 km (on different coasts) [20]. As crustacean post-larvae had reduced swimming abilities compared to fish post-larvae [1], a stronger spatial variability in the post-larval supply of crustaceans could be expected, based on prevailing wind direction. Overall, even though additional data should be recorded for a whole year and several crest nets should be set up on the different coasts of Rangiroa, our monitoring highlighted significant differences in post-larval supply for both *Brachyura* and *Stomatopoda* with the season (warm vs. cold season) that could be explained by seasonal reproduction, seawater temperature, and/or the prevailing wind.

Our monitoring highlighted some temporal variation with lunar phase (Figs. 1, 2). For each sampling month, the pulse of the brachyuran post-larval supply occurred predominantly around the last quarter. In contrast, the pulse of stomatopod post-larvae occurred predominantly around the new moon in March/April and June/July, and around the last quarter in February/March. However, for both taxa, the post-larval supply was lowest around the full moon and the first quarter. Reyns [12] analyzed the temporal patterns of megalopal brachyuran crab in the Caribbean with respect to daily wind and ambient current regime. The results showed that Xanthidae and Grapsidae post-larvae colonized predominately during the last quarter moon and intermediate to minimum amplitude tides. The same lunar variation was highlighted for coral

reef fish post-larvae, with the highest post-larval supply occurring from the last quarter to the new moon period [6, 7]. To explain the pulse of crustaceans around the last quarter, we suggest an effect of tide (as in Reyns’ study [12]), even though no significant relationship was found between post-larval supply and tidal height. Indeed, the third quarter period at Rangiroa was often associated with high tides during the middle of the night (data from Service Hydrographique et Oceanographique de la Marine). This could potentially result in crest nets being exposed to greater quantities of water-containing nocturnal animals than during other lunar phases (in comparison with the first quarter) when the high tides are closer to dawn and dusk. Yet, post-larval supply is often low at dawn and dusk [4, 6]. To explain the pulse of crustaceans around the new moon, we suggest an effect of light intensity. This temporal pattern might take advantage of these incoming darker nighttime tides for predator avoidance [10]. Indeed, the new moon period is a lunar phase when visual predation is likely reduced due to low light levels [17, 21]. Predation is so intense that all marine post-larvae arriving on reefs have been said to make “a suicide drop onto the reef” and to face a “wall of mouths” [2].

In conclusion, even over a short sampling period, our monitoring of *Brachyura* and *Stomatopoda* highlighted some temporal variations in post-larval supply according to season (higher post-larval supply in the warm than the cold season) and lunar phase (higher post-larval supply from the last quarter to the new moon period than around the full moon and the first quarter). These temporal variations in post-larval supply significantly influence on the dynamics of marine populations [2], and have therefore been the subject of much scientific scrutiny [4, 5, 14]. Examining how biological and physical factors contribute to fluctuations in post-larval supply is important when attempting to understand how populations are maintained over time [12].

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