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**COLONIZATION OF FISH LARVAE IN LAGOONS OF RANGIROA
(TUAMOTU ARCHIPELAGO) AND MOOREA (SOCIETY ARCHIPELAGO)**

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COLONIZATION OF FISH LARVAE IN LAGOONS OF RANGIROA (TUAMOTU ARCHIPELAGO) AND MOOREA (SOCIETY ARCHIPELAGO)

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ABSTRACT

The colonization of the lagoon by coral reef fish larvae was compared between two islands of French Polynesia, the atoll of Rangiroa and the high volcanic island of Moorea. In both cases the larval flux coming into the lagoon followed a daily cycle. Larvae were mainly caught at dusk and during the night, and on both islands the colonization was higher during moonless than moonlit periods. The larval flux did not appear to be dependent on the waterflow in the lagoons. A comparison of larval abundance and taxonomic lists indicates that Scarids and Labrids were dominant in Rangiroa while Gobiidae was the major family on Moorea. This difference could be in part related to the different sampling periods, but other environmental and biological factors could also be important.

INTRODUCTION

Most reef fishes have a pelagic larval phase, ending with the colonization of the reef (Leis, 1991). This recruitment of fish larvae on coral reefs is now studied in detail since it has been assumed that events occurring during this period determine the characteristics of reef-fish stocks (Sale, 1980; Richards and Lindeman, 1987; Doherty and Williams, 1988). Although some studies emphasized the importance of the processes during the settlement of fish larvae among coral reefs (Sweatman, 1985, 1988; Victor, 1986), this phenomenon is not clearly understood. For fifteen years, scientists have studied mechanisms of this return to the parental habitat. These studies have been limited mainly to continental reefs (e. g.: reefs of Central America), or patch reefs along continental platforms (e.g.: Great Barrier Reef of Australia) with very little data available on recruitment of reef fish species in oceanic islands and in atolls. This is a first attempt to compare some features of fish colonization of the lagoons of two geomorphologically different islands located in French Polynesia.

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Although the data were not obtained simultaneously in both islands, it is still useful to compare these two sets of data. It is also worth considering whether or not the observed differences are due to the location, the geomorphological features of the islands, or the time lag between sample collecting on the two islands.

MATERIAL AND METHODS

STUDY AREA

Rangiroa Atoll (figure 1) is one of the largest atolls in the world and the most important of the Tuamotu Archipelago (Ricard, 1985). It is 70 km long, 30 km wide and the peripheral rim is 225 km long. One third of the rim is above the sea surface and consists of small cays separated by channels. The rim flat is generally wider in the northern than in the southern part (800 m vs 500 m). The lagoon is biologically very rich compared to the other atolls of Tuamotu and is one of the most important reef fisheries centers of this Archipelago. The maximum estimated depth is 35 m and a lot of pinnacles are evenly distributed on its surface. Two passes, 450 to 550 m wide and 14 to 35 m deep are located in the North coast and lagoon waters are flushed out through these passes during ebb tides (35 cm to 60 cm tide range). Oceanic waters flow into the lagoon through channels over the atoll rim and the two passes during flood tides and also when trade winds blow. The fish larvae were collected in a channel, midway between the two passes.

Moorea Island (figure 1) is located 25 km north-west of Tahiti (Galzin and Pointier, 1985). This volcanic island has a triangular shape with a 61 km coastline and a relief of 1200 m. The island is surrounded by a barrier reef, which encloses a lagoon, 800 to 1600 m wide. The reef is intersected by several passes. Two bays are located on the northern part of the island. The lagoon is generally shallow (1 to 5 m), but deeper near the passes. The oceanic water enters the lagoon by waves breaking over the outer reef crest, and return to the ocean through the passes. The very weak tides on Moorea (average range 15 cm) do not reverse the current in the passes. Sampling was carried out on the outer reef crest, 600 m away from the pass.

METHODS

Samples were collected off the northern coasts of both islands. Fish larvae were collected with an anchored net that filtered the waterflow coming into the lagoon. The net with rectangular mouth (1 x 0.25 m) was of mesh size 0.5 mm. A General Oceanics flowmeter was fixed in the mouth of the net.

On Rangiroa Atoll, the net filtered the water coming from the seaward reef flat to the lagoon. It was located 500 m from the outer reef front. The channel was made of gravel in a shallow area (0.5 m).

On Moorea Island, the fish larvae were collected on the outer reef crest. The net was fixed on the reef substrate and filtered the water coming over the crest with the

breaking waves. Thus, the water flow was not constant but it was estimated over the time period of each sample (10 minutes).

The time lag between two samples was 1h or 2h. Two diel cycles were made in February 1989 on Rangiroa. At Moorea, two diel cycles were made in April 1989 and a third one was made in October 1989. At Rangiroa, the first cycle was 3 days before the new moon and the second was around the first quarter. The diel cycles were made during same lunar phases on Moorea.

The collected larvae were then fixed with 5% formalin seawater and identified under a dissecting microscope at the lowest taxonomic level following the recommendations of Leis and Rennis (1983) and Leis and Trnski (1989). This correspond to a family-level identification for all the larvae but the Goboids. In several cases, genus-level identification was accomplished. Most of the larvae caught were in the postflexion stage or in metamorphosis and were identified. Abundances of unidentified prefixion larvae and juveniles were very low and were simply pooled into prefixion and juveniles types. Results are expressed in larval abundance per sample which represents the larval flux, i. e. the number of larvae for 1m of reef section and for 10 minutes (Dufour, 1993).

RESULTS

DIEL CYCLES

The diel cycles from Rangiroa (figure 2) represent changes in larval composition over a two night period. Although the samples do not cover 24 hours, they take into account the two consecutive daily changes at dusk and dawn. Our data clearly indicate that fish larvae were present only at night and during twilight. Because the waterflow may influence the larval flux, the volume filtered by the net was also presented. The Kendall coefficient correlation rank calculated with Statiew software (Abacus Concepts, Inc, Berkeley, 1992) was significant for the comparison between the two larval fluxes of the two cycles and also between the two water flows (Table I). But it was positive between the larval fluxes (+0.524) while it was negative between the water flows (-0.486). This result indicates that the change of the larval flux was somewhat similar during the two sampling periods. But the water flow was negatively correlated between the two cycles. The Kendall coefficient correlation rank calculated between the water flow and the larval flux for the two diel cycles made on Rangiroa was very small and not significant (table II). However, the second cycle shows a strong decrease of the water flow in the middle of the night and this decrease was also observed for the larval abundance. These results indicate that there was no clear link between water flow and larval flux, except for low water flow, which could hinder larval colonization in the lagoon.

The diel cycles made on Moorea also show that most fish larvae were taken at night and dusk (figure 2). The Kendall's tau calculated between the larval flux and the water flow (Table II) was not significant. The absence of significant correlation in the

four studied cycles confirms that larval flux did not seem to be quantitatively dependent of the water flow.

The study of larval flux on the two islands reveals that the larval flux on Rangiroa reached 3 times the value of 500 larvae per sample, which was obtained only once on Moorea, despite a larger sampling effort. On both islands these larval peaks occurred in the early evening. A second peak was found just before dawn on the second cycle on Rangiroa. The water flow during these larval peaks on Rangiroa was not very high and similar to that found during larval peaks of Moorea. As a result, these high peaks of larval colonization on Rangiroa and Moorea do not appear to be created by variation in water flow over the reef of these islands. The comparison of the average larval flux recorded on the two islands at different times indicates that this flux appears to be more significant on Rangiroa than on Moorea (Table III). It was obvious that a high larval flux from these islands was never recorded during full moon. However, during moonlight periods of the first lunar quarter, the larval abundance on Rangiroa was higher than the abundance on Moorea.

TAXONOMIC ANALYSIS OF THE SAMPLES

The number of larvae and the number of larval types were different between the two islands (Table IV). The total number of larvae from Rangiroa was almost half the number of those collected from Moorea during eleven months, although the number of samples was higher. Based on the two studied periods, the average larval flux on Rangiroa reached three times the average larval flux on Moorea. The number of larval types on Moorea was 56 for the three cycles. The number of larval types on Rangiroa during only two nights was 43. Several larval types from Moorea were not found on Rangiroa, while only one larval type from Rangiroa was missing from Moorea. Some of these types were represented by more than 50 larvae. The comparison between Rangiroa and all the samples of Moorea indicates that the number of types was twice as less as that found in all the samples of Moorea despite the fact that the number of samples collected was eight times higher and the sample period was much longer in Moorea. Therefore, the number of larval types caught in two nights on Rangiroa was significantly higher than those caught off Moorea.

The list of the larval types and their abundance is presented for both Rangiroa and Moorea (Fig. 3). The pie diagrams show the percentages of the main larval types for each island. The abundance of the larvae from Moorea is presented for all the 358 samples made between March 1989 and November 1989 (grey bars) and for the three diel cycles previously studied (black bars). The most abundant larval type on Rangiroa was the Scaridae forming 52% of the total catch. The two most abundant larval types on Moorea were Gobiidae (Gobiidae type 1 and Gobiidae type 56). The abundance of Gobioid types on Moorea represents 63% of the total catch. Scaridae were the second most abundant family on Moorea but they represented half the number of Scaridae collected from Rangiroa. On Rangiroa Gobioid types were the second most important group but their number were far below those of the Scaridae. The other significant larval types were found in similar numbers on both islands although periods of sampling were

different. This was the case for the Labridae, the Callionymidae and the Schindleriidae. It is apparent that the number of larvae of these families would have been much higher on Rangiroa if the extent of sampling was similar to that carried out off Moorea. The Apogonidae type 2 were more abundant on Rangiroa but the total number of Apogonidae from both areas was not very different. Juvenile fishes were caught in both islands in relatively high number. Different families were gathered in this type (Mullidae, Holocentridae...). It is interesting to note that these juveniles were collected at dusk despite the fact that daylight was supposed to assist in a higher avoidance of the net. The Gobiidae type 8 was only collected at Rangiroa.

DISCUSSION

The daily patterns of the reef colonization by reef fish larvae have been demonstrated only recently on coral reefs (Dufour, 1991, 1993). The fish larvae that enter the lagoon were caught only at night and dusk. Their abundance was also found to be higher during moonless periods. This pattern has been confirmed by samples over a two years period. The data from Rangiroa in this study confirm this finding. Each cycle made at Rangiroa demonstrated that fish larvae were abundant during the moonless nights in the channel of the atoll. The larval abundance could reflect higher larval activity above the reef at night (Hobson et Chess, 1978). However, the fixed nets could not catch larvae that do not move into the lagoon. Hobson and Chess (1978, 1986) have demonstrated that planktonic organisms drifted at night over the reef of Enewetak atoll to enter the lagoon. Their appearance over the reef was related to a vertical migration at night, followed by a passive drift in a current flow induced by breaking waves. However, colonization by fish larvae at Rangiroa and at Moorea was only accomplished by individuals ready to settle. The larval flux observations do not include preflexion larvae because these larvae were scarce in samples, although they could have drifted more easily than postflexion larvae. It is known that postflexion larvae are able to swim (Blaxter, 1986; Webb and Weihs, 1986). Moreover, reef fish larvae can avoid the reef area until they are competent for metamorphosis (Kingsford and Choat, 1989). These phenomena imply other mechanisms of colonization in addition to passive drift. The larval flux in the lagoon could thus be viewed as an active process made nightly by competent fish larvae. Night activity correlated to the darker phases of the moon cycle has also been demonstrated for other planktonic organisms over reefs (Aldredge and King, 1980, Tranter *and al.*, 1981). These authors found that this moonless activity was an adaptative advantage against predation. In a similar way, the colonization of fish larvae occurs at night when predation is lower (Hobson, 1973, 1975). Therefore, larval colonization of the lagoons at night could be viewed as an adaptative process against predation, as predation plays a major role during the recruitment of reef fishes (Shulman and Ogden, 1987, Victor, 1986, Hixton, 1991). Both the geomorphology of the reef and hydrodynamic characteristics of the waters flushing into the lagoons appear to have no significant control on larval colonization.

The difference of the abundance of fish larvae between the two islands can be explained by the difference of the sampling periods. Although it has not been established that fish larvae were more abundant in French Polynesia during February than during

April, the summer season was considered to be the recruitment season in other coral reef areas (Williams, 1983, Victor, 1987). Thus, the lower abundance in samples from Moorea could be explained by variations related to seasonal recruitment. The difference in abundance and diversity of fishes during colonization between these two islands could also be related to the size of the lagoon. The quotient of reef periphery to surface of the lagoon is also much lower for Rangiroa than for Moorea. This is because the lagoon of Moorea encloses the volcanic island and does not cover all the surface delimited by the outer reef like an atoll. On Moorea, the quotient of the lagoon surface to the reef length is around 0.86 km^{-1} ($60 \text{ km}/70 \text{ km}^2$), on Rangiroa it is 0.11 km^{-1} ($230 \text{ km}/2100 \text{ km}^2$), but the sand cays over one third of the reef lower this coefficient to 0.074. This last value is more than 10 times smaller than on Moorea. If we could assume that the density of the larval flux per unit of lagoon surface over the crest was related to this coefficient, the number of fish colonizing the lagoon should be proportionally higher. This assumption could explain the higher rate of colonization for Rangiroa. This hypothesis cannot be verified, however, because the larval flux over all the reef rim has not been determined.

The difference between the major larval types from the two islands could also be explained by other hypothesis. The composition and diversity of adult fishes in both lagoons was probably not the same. It is possible that the number of fish species in the lagoons of atoll is related to the surface area of these atolls (Galzin et al., 1994). Scaridae and Labridae are among the most abundant fishes in atoll lagoons (Bouchon-Navarro, 1983, Morize *et al.*, 1990), while Pomacentridae and Acanthuridae are more abundant in Moorea lagoon (Galzin, 1987). Although we have no information about their density in Rangiroa atoll, the higher abundance of Scaridae larvae on Rangiroa was not surprising. But this higher abundance could be related to the low number of samples collected in Rangiroa, and the period when they were collected. It is possible, however, that the pattern of settlement of fish larvae on reefs could be relatively unpredictable and chaotic and peaks of larvae have been described as randomly distributed at different time scales (Doherty and Williams, 1988). Another explanation could be the reproduction period of Scaridae, which could occur earlier. Larvae of Scaridae, however, were caught on Moorea until the end of June and Scaridae and Labridae were also the most abundant families in samples made in May and June 1988 on Moorea.

CONCLUSIONS

The study of the larval flux over the reef on Rangiroa and Moorea was useful to the understanding of some aspects of the settlement processes of fish larvae in lagoons. This study has confirmed some trends in the diel and lunar cycles of reef colonization by fish larvae. The difference of larval abundance between samples on both islands can be related to the time lag between the sampling periods of each island. The sizes of the two lagoons could also play a role in this difference. It was more difficult to understand the taxonomic difference. It could be explained by the difference in size of the two lagoons, or by the period of fish reproduction or even by the density of the different families, but few data were available to confirm these hypotheses.

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Table I: Values of the Kendall coefficient correlation rank for the larval flux and the water flow between the two diel cycles from Rangiroa (n.s: not significant at 5%, s: significant at 5%).

Rangiroa	Kendall coefficient
Comparison of the larval fluxes	0.524 s
Comparison of the Water flows	-0.486 s

Table II: Values of the Kendall coefficient correlation rank between the water flow and the larval flux (n.s: not significant at 5%).

	Rangiroa 1	Rangiroa 2	Moorea 1	Moorea 2	Moorea 3
Kendall coefficient	0.206 n.s	-0.176 n.s	-0.109 n.s	-0.036 n.s	0.345 n.s

Tableau III : Average values of the water flow and the larval flux for the cycles from Rangiroa (R) and Moorea (M), standard deviation are in brackets.

sampling dates	water flow : $-m^3 \cdot sample^{-1}$	abundance : larves $\cdot sample^{-1}$
R 03.02	109.9 (54.01)	72.4 (118.4)
R 10.02	71.41 (47.53)	122.5 (156.4)
M 05.04	41.3 (6.47)	74.5 (130)
M 12.04	48.6 (12.1)	8.45 (8.47)
M 23.10	35.9 (11.1)	38.1 (25.9)

Tableau IV : Abundance of larvae and larval types from Rangiroa and Moorea

	Rangiroa	Moorea (3 cycles)	Moorea (all samples)
number of samples	44	34	358
number of larvae	4165	1369	10050
larvae / sample	94.66	40.26	28.1
number of types	43	56	71

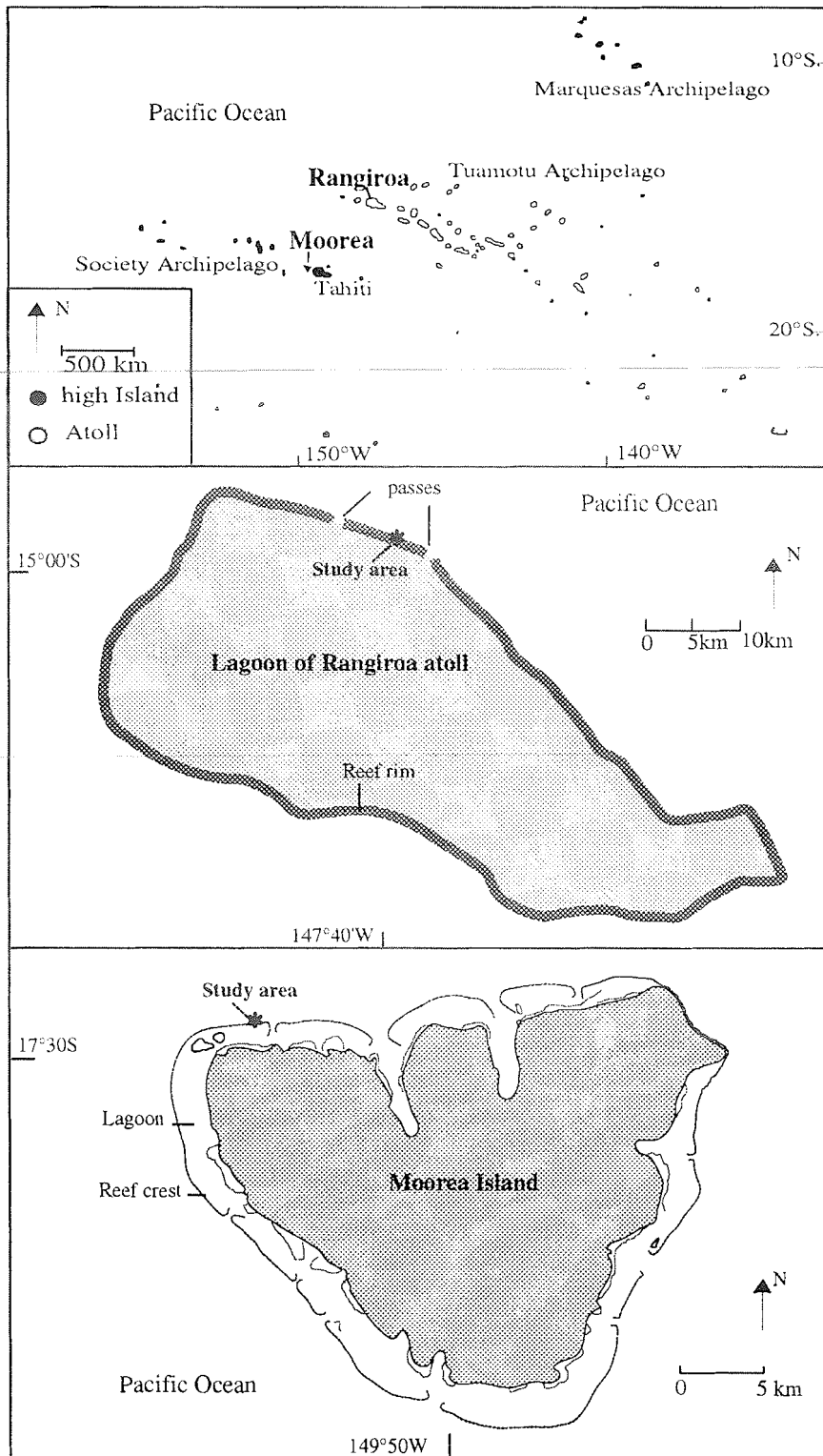


Figure 1. French Polynesia (above) with the atoll of Rangiroa, Tuamotu archipelago (middle), and the high Island of Moorea, Society archipelago (below).

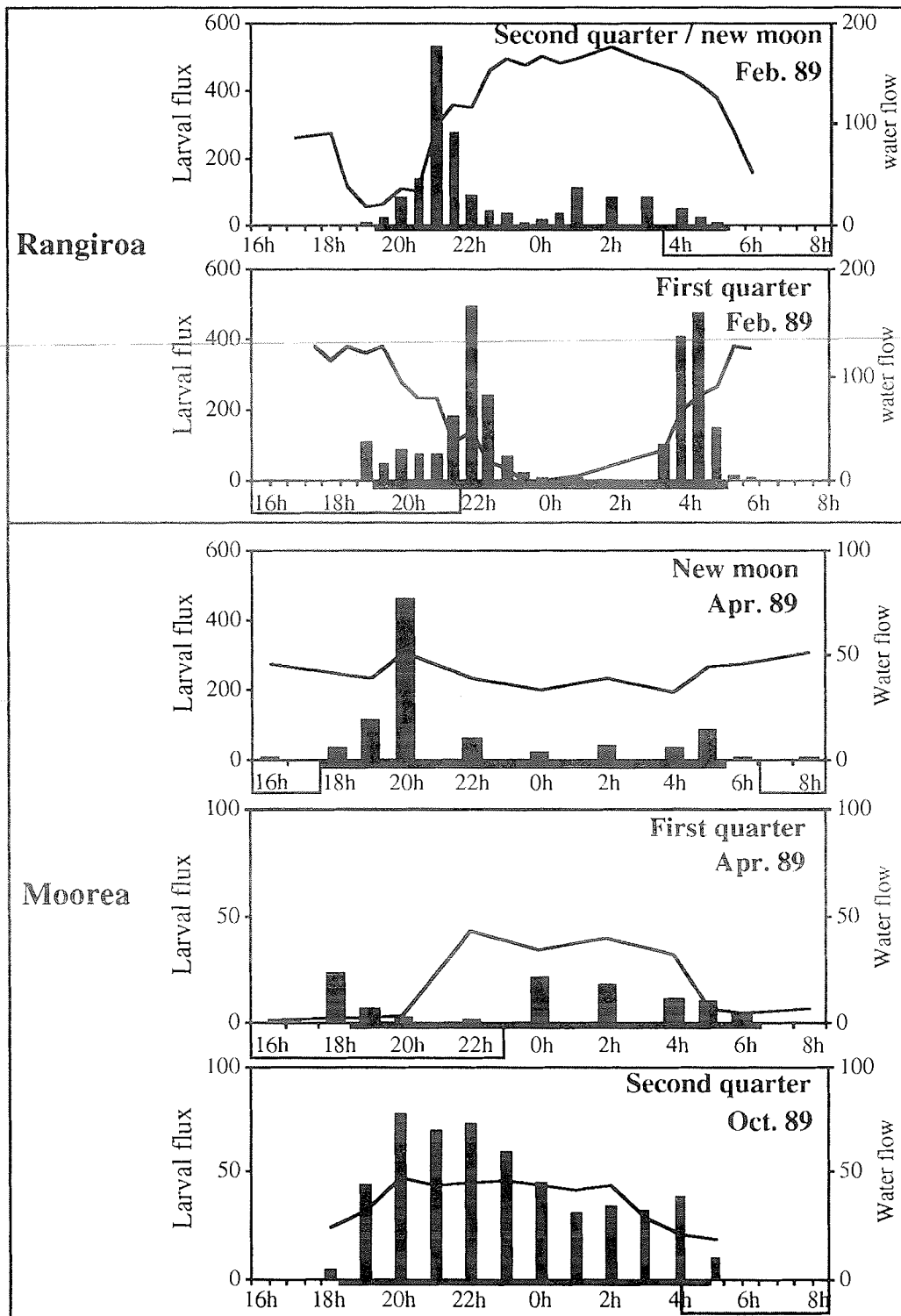


Figure 2. Evolution of the larval flux expressed in number of larvae. sample⁻¹ (bars) and the water flow in m⁻³. sample⁻¹ (line) during nycthemeral cycles made on Rangiroa and on Moorea. The black thickness on the categories axis represents the night hours, the white frame on the same axis represents moonlit hours.

