TEMPORAL PATTERNS OF SETTLEMENT OF 
THREE SPECIES OF DAMSELFISH OF 
THE GENUS DASCYLUS (POMACENTRIDAE) 
IN THE CORAL REEFS OF FRENCH POLYNESIA 

by 

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ABSTRACT. - Patterns of settlement from the plankton of three damselfish species in the genus Dascyllus were estimated at the island of Moorea, French Polynesia, for three temporal scales: among seasons of the year, within a lunar month, and among days. The three species (D. trimaculatus, D. flavicaudus, and D. aruanus) displayed qualitatively similar settlement patterns at all scales examined. There was distinct seasonality with the greatest settlement occurring in the Austral winter months of June-August. Within a lunar month, fish primarily settled around the two quarter moon phases, with substantially lower settlement occurring near periods of full and new moon. Daily estimates of larval settlement revealed distinct peaks, typically lasting 3-5 days, with little settlement during intervening days. The mean interval between settlement peaks was 14 days, resulting in an average of two pulses of settlement each lunar month. The timing of peak settlement during a colonization cycle was quite similar among the damselfishes, but was not constant with respect to the actual date of the quarter moon. For all three species, the intensity of settlement (density of new colonists) varied among cycles by about 1.5 orders of magnitude. D. trimaculatus and D. flavicaudus showed high temporal concordance in the intensity of settlement among cycles, whereas variation among cycles in the settlement strength of D. aruanus was uncorrelated with either D. trimaculatus or D. flavicaudus.

RÉSUMÉ. - Chronologie de l’installation de trois espèces de poissons-demoiselles du genre Dascyllus (Pomacentridae) sur les récifs coralliens de Polynésie française.

Nous avons étudié l’installation, à partir des larves planctoniques, de trois espèces de poissons-demoiselles du genre Dascyllus sur l’île de Moorea, en Polynésie Française et selon trois échelles de temps: la saison, le cycle lunaire et d’un jour à l’autre. Qualitativement les trois espèces (D. trimaculatus, D. flavicaudus et D. aruanus) présentent des modèles semblables d’installation à tous les niveaux et à toutes les échelles. En ce qui concerne la saisonnalité, l’installation est la plus importante de juin à août, durant l’hiver austral. Pour le cycle lunaire, l’installation est la plus importante lors des quarts de lune, avec les diminutions d’intensité lors des pleines et nouvelles lunes. Les estimations quotidiennes des intensités d’installation montrent tous les 14 jours un pic d’une durée de 3 à 5 jours environ, soit deux pics d’installation chaque cycle lunaire. Durant un cycle de colonisation, ces pics semblent relativement constants chez ces poissons-demoiselles et ne semblent pas être directement corrélés aux cycles des quarts de lune. Pour les trois espèces étudiées, l’intensité de l’installation (densité des nouveaux arrivants) varie d’un facteur 1.5 entre les différents cycles. Les espèces D. trimaculatus et D. flavicaudus montrent une grande concordance temporelle dans l’intensité de leur installation au cours des différents cycles étudiés; il n’en est pas de même entre chacune d’entre-elles et D. aruanus.

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The replenishment of populations of most coral reef fishes is via a planktonic larval stage that disperses from the parental population before settling to the reef environment. Despite the centrally important role of such replenishment to the population dynamics of coral reef fishes, major gaps exist in our basic understanding of temporal patterns in larval settlement. While it is clear that variation in settlement of coral reef fishes has been found at every temporal scale examined (Williams, 1983), relatively few generalities have emerged. Among the few, seemingly universal features are that settlement of coral reef fishes almost always occurs during the night rather than during daylight hours (Doherty and Williams, 1988; Booth, 1991), and that settlement typically is lower during the full moon period than at other times of the lunar month (Sale, 1985; Doherty and Williams, 1988; Dufour et al., 1996). Presumably these patterns reflect evolved adaptations that reduce mortality of highly vulnerable young fishes from visual predators (e.g., Sale, 1985; Doherty and Williams, 1988; Doherty, 1990; Dufour and Galzin, 1993). However, there appears to be considerable variation among species and/or locations in the existence or extent of seasonality, in the existence or type of lunar periodicity, and in the pattern of variation in the magnitude of settlement of a species among different colonization episodes. For example, MacFarland et al. (1985) found that the French grunt Haemulon flavolineatum in the Caribbean settled monthly near the new moon in discrete peaks that were of similar magnitude throughout the year, whereas Booth (1992) reported that the damselfish Dascyllus albisella settled in Hawaii in two episodes, each spread over several weeks, only during summer months without any clear indication of lunar periodicity. Until more systematic studies are conducted, it is not possible to determine how much of the observed variation in such temporal patterns of settlement can be attributed to different locations (e.g., the Caribbean vs. Hawaii), differences among taxonomic groups of species (e.g., grunts vs. damselfishes) and/or differences among similar species (e.g., among damselfishes).

Among the most comprehensive studies of temporal patterns in the colonization of an assemblage of coral reef fishes are those of Dufour and Galzin (1993), Dufour et al. (1996) and Planes et al. (1993) for the island of Moorea, French Polynesia. Dufour and co-workers used stationary nets at the crest of the barrier reef to estimate nightly the flux of late stage larvae that entered lagoons; at all sites and times sampled, the highest fluxes occurred near periods of new moon. The larvae of some taxa, however, appeared to enter the lagoon most abundantly near quarter moon phases (Dufour et al., 1996). This stationary crest net approach, which subsequently has been used to estimate larval flux rates to coral reefs in eastern and western Australia (Doherty and Mellwain, 1996), has several advantages and drawbacks. It provides a means to compare concurrent patterns of larval colonization across many species and taxa of fishes. However, the approach is highly labor intensive, potential sampling biases (among species or taxa) are difficult to assess, and analysis of patterns at the species level is limited to the relatively few species that are caught in sufficiently high abundance. For example, only one species of damselfish (Stegastes nigricans) was trapped in sufficient numbers by Dufour et al. (1996) to allow analyses of temporal patterns, despite the fact that damselfishes are among the most
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numerous (by species and abundance) reef fishes in the lagoons of Moorea (Galzin, 1987a, 1987b).

We take a complementary approach to that used by Dufour and Galzin (1993), Dufour et al. (1996) and Doherty and McIlwain (1996) to examine temporal patterns of settlement of three closely related species of damselfishes. Our approach was to census daily the number of new settlers that colonized a standard amount of settlement microhabitat, and to use that technique to examine temporal patterns and coherence among the species at a series of scales (i.e., seasonal, lunar, daily) in the same location (the north shore of Moorea, French Polynesia). Other workers have estimated settlement from daily counts of new colonists (Booth, 1991; Robertson, 1992), although more typically the interval between successive samples has been considerably longer than a day (e.g., Milichich et al., 1992; Meekan et al., 1993; Planes et al., 1993; Sponaugle and Cowen, 1994, 1996, 1997). Further, the time frame over which observations are made typically has been relatively short (e.g., ~2 lunar months) and the number of species examined concurrently usually has been quite low (for an exception, see Planes et al., 1993). This general approach, however, has the advantage of providing a more accurate estimation of actual settlement patterns, especially when estimates are made daily, microhabitat associations are known and care is taken to reduce the influence of older conspecifics and other species (Booth, 1991; Robertson, 1992).

Here we present data on concurrent patterns of settlement of the damselfishes at three temporal scales: among seasons of the year, within a lunar month, and among days. The species of damselfishes we examined were the Three-spot dascyllus (*Dascyllus trimaculatus*), the Yellow-tailed dascyllus (*D. flavicaudus*), and the Humbug dascyllus (*D. aruanus*). Like all damselfishes, these species lay benthic eggs that are fertilized externally. Larvae hatch and enter the plankton after ~3 days (Garnaud, 1957; Thresher, 1984), and settle back to the reef environment after a planktonic duration that averages 22-24 days (Brothers et al., 1983; Wellington and Victor, 1989). *D. trimaculatus* settle to sea anemones (Dunn, 1981; Fautin, 1985; Fautin and Allen, 1992) where they remain throughout the juvenile phase; adults are free-living and do not associate closely with anemones for shelter. By contrast, *D. aruanus* settle to corals and remain associated with them throughout their lives (Sale, 1971; Forrester, 1990; Allen, 1991). *D. flavicaudus* tend to retain some degree of microhabitat association as they age. In Moorea, the most common species of anemone (*Heteractis magnifica*) is occupied by *D. trimaculatus*, whereas young *D. aruanus* and *D. flavicaudus* primarily settle to heads of live *Pocillopora* (primarily *P. meandrina* and *P. eydouxi*; hereafter *Pocillopora*); *D. flavicaudus* also settle to plating Acropora and certain species of Montipora.

**MATERIALS AND METHODS**

All field work reported here was conducted in lagoons on the north shore of Moorea (17°30'S, 149°50'W) in French Polynesia. A barrier reef encircles the triangular-shaped island, forming a system of lagoons that average ~1 km in width and ~5 m in water depth (for more details, see Galzin and Pointier, 1985). The bottom within the lagoons is composed of patch reefs that are interspersed with unconsolidated sediments. On the north shore, the barrier reef is cut by two deep bays (Cooks and Oponohu) and three smaller passes. Water primarily enters the lagoons over the crest of the barrier reef and exits through the passes. It should be noted that the tidal amplitude at Moorea is quite
small (~50 cm) with little direct influence of the moon as the island is close to an amphidromic point (Bongers and Wyrski, 1987). As a consequence, water flow within the lagoon appears to be influenced principally by offshore swell conditions.

To estimate settlement, we transplanted settlement microhabitat (anemones and corals) to areas that previously lacked such habitat. Forty anemones (*Heteractis magnifica*) were transplanted at depths of 4-6 m to a fringing reef on the eastern flank of the Vaipahu Lagoon adjacent to the Gump South Pacific Biological Station, and forty live heads of *Pocillopora* at 3 m depth on an expanse of sand approximately 0.5 km north-west of the anemone transplant site (for more complete description of the study sites, see Schmitt and Holbrook, 1996). Corals were affixed individually to cinder blocks using Z-Spar Splash Zone Compound®, while anemones were allowed to attach naturally on the fringing reef or a cinder block. Each settlement microhabitat was approximately 5 m from its nearest neighbor, and a minimum of 25 m from naturally occurring anemones or live heads of coral.

Unless noted otherwise, estimates of settlement were obtained from daily counts of fish in all settlement microhabitats (i.e., transplanted anemones and corals). New settlers, which arrived at night, are distinguished from individuals that settled on previous days by the lack of pigmentation of the tail and peduncle (Schmitt and Holbrook, 1996; Holbrook and Schmitt, 1997). At the initiation of observations, resident fish were removed from the microhabitats as resident conspecifics can influence the settlement of *Dascyllus* (e.g., Sweatman, 1983, 1985; Sweatman and St. John, 1990; Schmitt and Holbrook, 1996). Fish that accumulated were removed at least every two weeks during extended periods of observation. As settlement tended to occur in 14-day cycles (see Results), we estimated the number of new settlers over periods of two weeks, each of which encompassed the period of maximum settlement. The location and total area of microhabitat sampled each date remained constant; data on *D. trimaculatus* settlers are expressed as the number per 40 anemones (each with a diameter of ~30 cm), whereas those for the other two species are given as the number per 40 heads of *Pocillopora* (each was ~30 cm in diameter and 20 cm tall).

To examine seasonality, the calendar year was divided into four seasons representing the Austral winter (June-August), spring (September-November), summer (December-February) and fall (March-May). For each season, the cumulative number of *Dascyllus* that settled on the transplanted settlement microhabitats in 'replicate' two-week cycles was counted on the focal anemones and corals. For each season, cycles were counted in two (fall) or three (all other seasons) different years (1995-1997), with the 'replicate' number of cycles being 12 (winter), 5 (spring and summer) and 3 (fall). For each species and season, the mean density of settlers (cumulative total in two weeks per 40 settlement microhabitats) was calculated and difference among seasons tested by ANOVA.

Possible lunar patterns in settlement were examined for 9 (*D. trimaculatus*) or 6 (remaining 2 species) lunar months during periods of heavy settlement in 1995-1997. For four of the lunar months used in this analysis, estimates of settlement for *D. flavicaudus* and *D. aruanus* to corals were made approximately every other day (rather than daily) on the 40 transplanted corals; settlement of *D. trimaculatus* was estimated daily to the transplanted anemones for all lunar months. The lunar month was divided into four equal periods (weeks), with a week centered on the time of new moon, the first quarter, full moon or the third quarter. Since the absolute number of settlers varied considerably among the species and among the lunar months, we standardized the data to facilitate comparisons. This was done by dividing the number of settlers of a given species that arrived during
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![Graphs of *D. trimaculatus*, *D. flavicaudus*, and *D. aruanus*]

Fig. 1. - Seasonality in settlement of the 3 species of *Dascyllus* at Moorea, French Polynesia. Data are the mean (1 SE) number of settlers that colonized 40 initially empty settlement microhabitats (anemones or coral heads) in replicate 14-day periods, each of which encompassed a quarter moon and a new or full moon period. Seasons correspond to the months of March-May (fall; n = 3 replicate periods), June-August (winter; n = 12), September-November (spring; n = 5), and December-February (summer; n = 5).

Each of the four weeks by the total number that colonized during that lunar month. For each species, the mean proportion (and standard error) of settlers that arrived was calculated for each of the four moon phases.

We had a sufficiently long record of daily settlement estimates of *D. trimaculatus* to perform time-series analyses. To determine whether cycles existed and estimate the periodicity in settlement, autocorrelations among different lag (day) intervals were calculated using an ARIMA (autoregressive integrated moving-average) model. Lag lengths up to 60 days were calculated using log$_{10}$(settler density + 1) transformed data. (Using log transformed data not only resolved the inherent problem that variance scales positively with the mean for density estimates, in the present application it also facilitated detection of cycle periodicities by reducing the influence of especially large settlement peaks.)
Concordance among the three damselfish species in the timing of colonization was examined for five two-week periods when daily counts of all species were made concurrently and when species settled in relatively high numbers. To facilitate comparisons in timing among species and settlement episodes, data for each species and 14-day settlement event were standardized by dividing the number of settlers each day by the total that arrived over that 14-day period.

Temporal concordance among the species in the intensity of settlement (i.e., total density of colonists) was examined using 15 two-week long periods when we had estimates for all three species. Data for 9 of these periods were obtained from counts of the forty anemones and corals used for the analyses described above. Data for the remaining six two-week periods were obtained from counts of settlers to thirty additional anemones and corals that were transplanted to other lagoon locations on the north shore of Moorea using techniques described previously. These additional sites were located halfway between the barrier reef and shore off the villages of Maharepa and Papetoai. For two of the
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six periods, counts of the thirty additional microhabitats were made daily; for the remaining four periods, settlement intensities were estimated from counts made bi-weekly (3-4 days after peak settlement). Correlations in the total density of settlers (number per standardized area of microhabitat) were calculated for the three pairwise combinations of damselfish species.

**RESULTS**

Although all three species of *Dascyllus* settled throughout the year at Moorea, there was a marked pattern of seasonality (Fig. 1). For all species, the average density of new colonists that arrived in a standardized settlement episode (i.e., a 14-day period that encompassed peak colonization) differed statistically among the seasons (p < 0.05 for all ANOVAs). The period of greatest settlement for each species of *Dascyllus* occurred during the Austral winter months of June-August when the average density of colonists per settlement event was 2-4 times greater than the season with the next highest settlement rate (Fig. 1). Within a species, levels of settlement were generally similar among the three non-winter seasons, although *D. aruanus* appeared to have especially low settlement during the Austral fall period of September-December. It should be noted, however, that our estimates for the Austral fall were based on substantially fewer measurements than for other periods of the year (see Materials and Methods). Nonetheless, the data do support the conclusion that settlement of these *Dascyllus* at Moorea was seasonal and that all three species showed the same qualitative pattern at this temporal scale.

With respect to settlement at the scale of a lunar month, colonization from the plankton of each *Dascyllus* species was non-random among the four lunar weeks. While larvae of each species settled during all phases of the lunar month, most colonized during the weeks of the two quarter moon phases (Fig. 2). *D. trimaculatus* showed the greatest disparity between quarter moon and full and new moon periods, whereas *D. aruanus* showed the smallest difference. On average, 80% of the *D. trimaculatus* colonizers that arrived during a lunar month settled during the quarter moon periods, compared with 76% for *D. flavicaudus* and 66% for *D. aruanus* (Fig. 2; p < 0.05 for each test of uniform settlement). With the possible exception of *D. trimaculatus*, there was little difference in the proportion of new colonists that arrived during new and full moon periods (Fig. 2). The average proportion of *D. trimaculatus* that settled during the week of full moon (6.6%) was half that during the new moon period (13.1%), although the difference was not statistically significant (p = 0.12).

We had the longest time series of daily settlement for *Dascyllus trimaculatus*, which revealed that the temporal pattern of colonization was more complex than was suggested by the analyses above. In general, daily settlement of *D. trimaculatus* over the course of several lunar months was episodic, showing distinct peaks with relatively little or no settlement during intervening days (Fig. 3). The cyclic nature of settlement was indicated by positive autocorrelation in the density of *D. trimaculatus* settlers at about 14-day intervals (i.e., lags of -14, -28, -42, -56 days; Fig. 4), a periodicity that generally resulted in two pulses of settlers per lunar month. The highest positive autocorrelations after lags of 1-3 days suggested that settlement was not stochastic, but the values were only between 0.2 and 0.4, which might be attributed to a number of causes. First, there was tremendous variation in the density of settlers among the different settlement peaks, which ranged upwards of two orders of magnitude (Fig. 3). Second, while many settlement
Fig. 3. - Daily pattern of colonization of *Dasyxylus trimaculatus* during the winter settlement seasons of 1995-1997. Data are the number of new settlers counted each day on 40 anemones from which residents and settlers were regularly removed.
pulses were brief in duration (3-5 days), some pulses occurred over 7-10 days (Fig. 3). Pulses that were longer tended to be those with greater densities of settlers during the peak days of the event (Fig. 3). Third, it was not uncommon for there to be just a single pulse in a lunar month instead of two (Fig. 3). Fourth, the exact timing of settlement in relation to the quarter moon phases of the lunar month was not constant; peak settlement could occur well before, relatively near or well after the actual date of the quarter moon. Finally, several settlement events appeared to be bi-modal, consisting of two distinct closely-timed peaks instead of a single sharp peak (Figs 3, 5). Nonetheless, the temporal pattern of daily settlement of *D. trimaculatus* generally was regular and predictable with a ~14 day periodicity. However, the amplitude of the cycles (i.e., the total density of settlers that arrived during a settlement cycle) was far less predictable.

Our estimates of daily settlement of all three species of *Dascyllus* for 5 different two-week long cycles of settlement revealed relatively high concordance in the timing of peak settlement among the species (Fig. 5). Except in one case where peak settlement of *D. flavicaudus* occurred 4 days earlier than the others (Fig. 5c), maximum settlement of all species was within a day of one another (Fig. 5). One of the five two-week periods was notable for the multiple, concurrent peaks in settlement of all three *Dascyllus* species (Fig. 5d). Rather than the typical single, relatively sharp peak, settlement of each species during this period was characterized by 2-3 peaks separated by 1-2 days of much lower settlement (Fig. 5d). Since all three species showed the same qualitative pattern, the cause likely was related to some unusual external driving force such as the strong south wind that developed during this settlement period but not the others.

Like *Dascyllus trimaculatus* (Fig. 3), the total density of settlers of *D. flavicaudus* and *D. aruanus* that arrived in a pulse varied among the two-week settlement periods by about 1.5 orders of magnitude (Fig. 6). There was high temporal concordance in the strength of settlement events between *D. trimaculatus* and *D. flavicaudus* (Fig. 6): when
Fig. 5. - Temporal coherence in the timing of settlement of three species of *Dascyllus* at Moorea, French Polynesia, for five different two-week long settlement cycles (labeled A through E, followed by year of observation). Data are the proportion of settlers of a species in a cycle that colonized each day for a given settlement cycle. *D. trimaculatus* is represented by triangles and dotted line, *D. flavicaudus* by squares and dashed line, and *D. aruanus* by circles and solid line.

one of these species settled in large or small numbers, so did the other. However, there was no correlation among settlement events in the density of *D. aruanus* settlers and that of either *D. flavicaudus* or *D. trimaculatus* (Fig. 6).

**DISCUSSION**

Damsel fishes in the genus *Dascyllus* at Moorea, French Polynesia showed considerable temporal variation in the settlement of larvae from the plankton to the reef environment. All three species examined displayed qualitatively similar temporal patterns, and, for the most part, fluctuations were reasonably predictable with respect to periodicity
Temporal patterns of settlement of three *Dascyllus* spp.

![Graphs showing settlement of *Dascyllus* species](image)

Fig. 6 - Temporal concordance among the *Dascyllus* species in the magnitude of settlement. For each pairwise combination of the damselfish species, the joint densities of settlers (number per 40 microhabitats) that arrived in each of 15 two-week long settlement cycles are plotted together; correlation coefficients also are given.

or timing of settlement events. While *Dascyllus* larvae settled throughout the year, there was strong seasonality with the greatest colonization occurring during Austral winter months. Seasonality in larval settlement of coral reef fishes has been reported for many other locations, including the Great Barrier Reef (Williams and Sale, 1981; Williams, 1985; Williams *et al.*, 1994), Hawaii (Booth, 1992), the Caribbean (Munro *et al.*, 1973; Luckhurst and Luckhurst, 1977; Booth and Beretta, 1994), the eastern Indian Ocean (Doherty and MacIwain, 1996), southern Japan (Ochi, 1985), Guam (Kami and Ikehara, 1976) and the northern Red Sea (Fishelson *et al.*, 1974). However, even where considerable seasonality has been documented, such as in the Caribbean, some species of reef fishes can show relatively little variation in colonization rates among the seasons (e.g., MacFarland *et al.*, 1985).

Lunar periodicity in settlement of coral reef fishes has been detected for many different species. When a lunar cycle has been found, settlement typically peaks near the new moon period (Sale, 1985; Doherty and Williams, 1988; Robertson, 1992; Dufour *et al.*, ...
1996; Sponaugle and Cowen, 1997). As settlement to coral reefs appears to occur mainly at night, the typical lunar pattern of settlement during the darkest phase of the lunar month has been suggested to be an evolved response that reduces mortality from visual predators during the period of transition from the plankton to the reef (Sale, 1985; Doherty and Williams, 1988; Doherty, 1990). However, many species of tropical pomacentrids and some labrids with a lunar settlement cycle primarily colonize the reef during one or both quarter moon phases rather than the darker new moon period (Nakazono et al., 1979; Pressley, 1980; Schmale, 1981; Williams, 1983; Robertson et al., 1988; Millicich et al., 1992; Robertson, 1992; Meekan et al., 1993; Millicich and Doherty, 1994; Sponaugle and Cowen, 1996; Sponaugle and Cowen, 1997). The three species of Dascyllus we examined showed this pattern of highest settlement near quarter moon periods and considerably lower colonization during both full and new moon phases. Like most other species, settlement peaks for these Dascyllus tended to be brief in duration (~3-5 days), although the exact timing of the peaks with respect to quarter moon periods was not constant among settlement events. However, the underlying periodicity of the settlement cycle for these Dascyllus was ~14 days, which generally resulted in two pulses of settlement each lunar month.

Two factors have been identified as possible determinants of observed lunar patterns in settlement of reef fishes. One is periodicity in production of eggs of species with relatively fixed durations of the planktonic stage (Robertson et al., 1988). For example, Meekan et al. (1993) found that the cyclic nature of settlement of the damselfish Pomacentrus amboinensis on the Great Barrier Reef likely was driven by the temporal pattern of spawning. Adult P. amboinensis tended to spawn benthic eggs near times of new and full moon, and the timing of subsequent peaks in settlement matched well the incubation period of benthic eggs plus the duration of the planktonic phase (Meekan et al., 1993; also see Millicich and Doherty, 1994). Robertson et al. (1988) reached a similar conclusion for lunar periodicity in settlement of the Caribbean damselfish Stegastes partitus. In addition, variation in tidal amplitude associated with lunar cycles also has been identified as having a role in shaping temporal patterns of settlement. Sponaugle and Cowen (1997) found that the timing of settlement of many Caribbean labrids was well predicted by the maximum tidal amplitude during a lunar month, and suggested that monthly patterns may be due to variable transport of late-stage larvae to reefs by onshore flood tides. However, since maximum tidal amplitudes typically are associated with new and full moon phases, it is difficult for this mechanism to explain consistent patterns of peak settlement during quarter moon periods, as has been observed for many species of coral reef fishes including the species of Dascyllus we studied.

The observation that many species have much lower settlement during the darkest moon phase than the quarter moon periods suggests that the “avoidance of visual predators while settling” hypothesis is not a complete explanation for the lunar timing of larval colonization. Morgan and Christy (1995) proposed that the mortality of newly-hatched larvae from visual predators would be minimized if they were released at night during the greatest amplitude tides of a lunar month. Tidally-driven current flow is predictably the greatest during spring tides (new and full moon phases), which may enhance the transport of newly-hatched young away from reef environments that contain abundant predators of larvae. Since the larvae of many damselfishes appear to have relatively fixed durations of around three weeks (Brothers et al., 1983; Wellington and Victor, 1989), synchronous spawning during periods of maximum tidal amplitude would result in settlement peaks around the quarter moon phases of the lunar month. When examined, damselfishes have
shown maximum spawning around the new moon with some having a second maximum near the full moon phase (Robertson et al., 1988; Meekan et al., 1993; Milicich and Doherty, 1994). This possibility remains to be explored as a contributor to the temporal patterns of settlement of Dascyllus at Moorea, particularly since tidal flux may have less influence than the offshore swell climate on current conditions at this location (see Bongers and Wyrtki, 1987).

In addition to the timing of settlement, most species of coral reef fishes examined have displayed considerable variation in the intensity of settlement (i.e., total density of colonists) among different pulses. The Dascyllus species were no exception. However, the two most common species (D. trimaculatus and D. flavicaudus) showed high temporal correlation in the magnitude of settlement among pulses, suggesting that some common processes influenced variation in peak densities of colonists. While temporal pattern in spawning is a plausible mechanism for the general seasonal and lunar cycles of settlement displayed by the Dascyllus species, it is less likely that this explains much of the variation in the intensity of settlement among different pulses within a season. Meekan et al. (1993) made a similar judgement for the damselfish Pomacentrus amboinensis, as did Robertson et al. (1988) for Siganus partitus. Reproductive patterns may only have influenced the timing of settlement events rather than their magnitude. Like others (Milicich and Doherty, 1994), these workers presumed that variability in settler densities not explained by reproduction was caused by planktonic processes. A promising area of future inquiry is to relate variation in production and subsequent fate of early life stages with variation in physical transport processes (e.g., Gaines and Bertness, 1992).

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