Abstract

Replenishment of local populations of reef fishes typically occurs via settlement of planktonic larvae, a process that is variable in space and time. We examined spatial variation in settlement of three species of damselfishes (genus *Dascyllus*) in relation to variation in average near-field current speed. Although the larvae of these species colonized at the same times, they repeatedly exhibited qualitatively different spatial patterns of settlement in the lagoons of Moorea, French Polynesia. Each damselfish had a unique, temporally consistent pattern of variation in settlement relative to among-site variation in near-field flow speed. At the speeds encountered, settlement was related linearly to increasing average current flow for yellow-tail dascyllus (*D. flavicaudus*), was a positive but decelerating function for humbug dascyllus (*D. aruanus*) and was a hump-shaped function for three-spot dascyllus (*D. trimaculatus*). Such qualitatively different relationships could arise if variation in current speed affected an individual’s probability of settling differently among the species. The generalized relationships between flow speed and settlement of these species predicted well the pattern of covariation in settlement of these species among new sites where the availability of suitable habitat was standardized. These findings imply that differences in larval abilities in the near-field can result in distinctly different patterns of larval colonization among species, even in the absence of any other source of variation.

Keywords

Settlement · Recruitment · Coral reef fishes · *Dascyllus* · Larval supply

Introduction

Numerous species have complex life cycles in which different stages inhabit different environments. While it is recognized widely that the movement of individuals as they make transitions from one life stage to another has important population and community consequences, our understanding of the processes involved is often incomplete. This is the case for marine reef invertebrates and fishes in which early developmental stages disperse in the plankton before transitioning to the reef habitats occupied by older stages. The input of young to the reef environment can be extremely variable in space and time, and ecologists have focused considerable attention on the underlying causes of this variation. Despite a plethora of studies, we still lack a comprehensive answer to the general question of why larval colonization to marine reefs is so variable (Gaines and Bertness 1993). Further, even closely related species that settle at the same time often exhibit substantially different patterns of colonization (e.g., Wellington 1992; Milicich and Doherty 1994; Sponaugle and Cowen 1996a; Schmitt and Holbrook 1999a; Booth et al. 2000). This raises the important issue of what produces variation in larval colonization among species that settle concurrently (Wellington 1992; Booth et al. 2000; Schmitt and Holbrook 2002).

The general mechanisms that give rise to variation in settlement are well known (Underwood and Keough 2001) and include the production of larvae (Meekan et al. 1993), death during the planktonic stage (Houde 1987), oceanographic features that mix, retain and transport larvae (Roughgarden et al. 1987; Kingsford 1990; Jones et al. 1999; Swearer et al. 1999; Cowen et al. 2000), and larval behavior during dispersal and at settlement (Raimondi 1991; Kcough and Raimondi 1995; Leis et al. 1996; Leis and Carson-Ewart 1998; Raimondi and Morse 2000; Schultz et al. 2000). Butman (1987) postulated that the importance of behavior increases relative to oceanographic features as larvae approach settlement. Settlement in response to cues is thought to be wide-
spread (Zimmer-Faust and Tamburri 1994; Morse and Morse 1996), small-scale (millimeters to meters scale) hydrodynamic forces are known to influence rates of larval transition to the benthos (Butman 1987; Butman et al. 1988; Mullineaux and Butman 1990, 1991; Pawlik et al. 1991; Snellgrove et al. 1993), and late-stage larvae of reef fishes do not act like passive particles (Elliott et al. 1995; Holbrook and Schmitt 1997; Leis and Carson-Ewart 1998). At the scale of meters to several kilometers, physical processes that influence the concentration or advection of larvae can have a dominant role (Kingsford 1990; Gaines and Bertness 1992; Bertness et al. 1996). At the scale of tens to hundreds of kilometers, such oceanographic features as current systems and large eddies can influence spatial patterns of larval abundance and/or long-distance dispersal (Scheltema 1971; Cowen 1985; Farrell et al. 1991; Hare and Cowen 1996).

The processes above that create variation in settlement can be grouped into two broad categories: those that cause heterogeneity in larval concentrations and those that would produce variation even if larval pools were completely mixed. Many studies of variation in settlement of reef fishes have focused on the former, and several have examined the relationship between spatial variation in larval abundance and in subsequent colonization. In some cases, there was at least crude agreement between the distribution of larvae near shore (frequently estimated by net or light trap captures) and spatial patterns of settlement (e.g., Milicich et al. 1992; Sponaugle and Cowan 1996a, b). Frequently, however, there was little congruence between patterns of larval abundance and of subsequent recruits in the reef environment (Milicich et al. 1992; Sponaugle and Cowan 1996a). This has prompted some workers to invoke habitat selection by settling larvae as a possible explanation for the observed decoupling (Milicich et al. 1992; Wellington 1992; Doherty et al. 1996; Booth et al. 2000). An unexplored alternative is premised on the fact that the local flux of larvae is a function of both the concentration of larvae and the speed at which they move past a habitat (Bertness et al. 1992; Gaines and Bertness 1993). At this scale, larval behavior or physical capabilities can affect the probability of settling; these attributes might vary as a function of the speed at which they move past a reef (i.e., current speed in the near-field), and the interplay between abilities and flow may differ even among closely related species. Thus, even if local pools of larvae were well mixed, differences among species in response to current flow could produce dissimilar patterns of settlement. Larval pools of reef fishes, of course, can be highly heterogeneous even over relatively small spatial scales (Milicich et al. 1992; Cowen and Castro 1994; Dufour et al. 1996; Sponaugle and Cowen 1996b), but there has been little attention given to the interplay between larval abilities and flow speeds near suitable habitat in shaping spatial patterns of covariation in settlement of reef fishes.

Here we explore the relationship between near-field current speed and spatial patterns of concurrent settlement of three closely related species of tropical damselfishes of the genus *Dascyllus*. Settlement was estimated using standard amounts of suitable microhabitat that initially were unoccupied, which removed the influence of two important features – variation in appropriate settlement space and possible interactions with residents (Schmitt and Holbrook 1996, 2000). Our aims were to (1) characterize the relationships between average current speed and density of settlers and (2) determine the degree to which these relationships predicted spatial variation in larval colonization within a species and covariation among the species. Our findings have important implications for Chesson’s lottery model of coexistence (Chesson and Warner 1981; Chesson 1994, 2000a, b).

**Materials and methods**

The field location and study species

Fieldwork was done in the lagoons of Moorea (17°30’S 149°50’W), French Polynesia. This triangular island, which has a coastline perimeter of ~60 km, is encircled by a barrier reef that forms a system of shallow lagoons (~5 to 7 m mean depth) that are 0.8 to 1.3 km wide (Galzin and Pointier 1985). Water bearing larvae of reef fishes enters lagoons over the crest of the barrier reef and exits through three to five passes per side of the island. The lagoon bottom is a mosaic of patch reefs and sand.

We examined concurrent settlement of three abundant species of planktivorous damselfishes: yellow-tail dascyllus (*Dascyllus flavicaudus*), humberg dascyllus (*D. aruanus*) and three-spot dascyllus (*D. trimaculatus*) (Galzin 1987a, b). These species lay benthic eggs that hatch after ~3 days (Thresher 1984). Larvae develop in the plankton for 22 to 24 days before settling back to the reef environment (Brothers et al. 1983; Wellington and Victor 1989). The species display similar temporal patterns of settlement at Moorea (Schmitt and Holbrook 1999b). There is strong lunar periodicity in settlement, and most settlement occurs over 3- to 5-day-long pulses around the first and third quarter phases of the moon (Holbrook and Schmitt 1997; Schmitt and Holbrook 1999b). While the timing of settlement is virtually identical for these damselfish at Moorea, the overall magnitude of settlement can vary considerably among the species for a given settlement event (Schmitt and Holbrook 1999b).

Yellow-tail dascyllus and humberg dascyllus settle onto and remain on branching corals throughout adulthood (Forrester 1990; Allen 1991); in Moorea they are commonly found on *Pocillopora eydouxi* and *P. meandrina*. By contrast, three-spot dascyllus only settle onto sea anemones (*Heteractis magnifica* in Moorea), where they remain until sexual maturity (Fautin and Allen 1992). Adult three-spot dascyllus are free-ranging and shelter opportunistically on the reefs.

Settlement of all three species occurs at night (Holbrook and Schmitt 1997; Schmitt and Holbrook 1999b). We previously examined the process of settlement of three-spot dascyllus, using infrared-illuminated video systems mounted ~2 m above focal anemones (Holbrook and Schmitt 1997). Larvae were observed drifting about 1 m above the bottom at the ambient current speed. After drifting ~1 m past an anemone, the larva actively dropped to a few centimeters off the bottom and rapidly swam up current toward the anemone. Actively searching larvae frequently made course corrections and occasionally circled the anemone in a manner that suggested the use of an odor plume as a guide to the anemone. Once a larva made contact with the anemone, it abruptly stopped swimming and nestled within the tentacles on the oral surface of the anemone.